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The Ediacarian Period and System: Metazoa Inherit the Earth

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Ever since Darwin, the geologically abrupt appearance and rapid diversification of early animal life have fascinated biologists and students of Earth history alike. Yet, until recently, convention and lack of data limited serious discussion of planetary evolution to its last eighth, with emphasis on details of metazoan and tracheophyte evolution, sedimentology, and paleogeography, and with but passing reference to earlier Earth history.

Summary. The Ediacarian, here defined as the initial period and system of the Phanerozoic Eon, is characterized by the oldest known multicellular animal life. The distinctive biotal assemblage comprises naked Metazoa, represented in the type region by 26 species in 18 genera and 4 or more phyla, plus simple metazoan surface tracks. Elements of this unique biota appeared worldwide at low paleolatitudes, following terminal Proterozoic glaciation. Ediacarian history lasted from about 670 million to 550 million years ago. This interval, plus Early Cambrian, was the time during which metazoan life diversified into nearly all of the major phyla and most of the invertebrate classes and orders subsequently known.

This constraint loosened with the growing perception that some seven-eighths of geologic time had already elapsed before the Cambrian Period began. Increased knowledge, both of the extent of time and of the older rocks, stimulated reconsideration of the nature of biological processes during those long eons that preceded the Cambrian and accelerated the search for evidence concerning them. Well-preserved sequences of sedimentary rocks, at places extending far beneath the Cambrian without apparent major interruption, showed that there was neither a great historical discontinuity nor a universally high degree of metamorphism beneath the Cambrian, as once supposed. The common presence in these rocks of glauconite and other sedimentary peculiarities indicative of a marine origin bolstered the expectation that, if there were antecedents to the Cambrian biotas, they would be found here.

That prognosis was confirmed with the discovery by Sprigg in 1947 (*1*) of what has come to be called the Ediacara fauna, together with its description by Glaessner and others (*2–5*), and with the recognition that Ediacara fossils are older than and different from those of the conventional Cambrian (*4*, *6*). Further support came with the discovery of similar faunas in ancient rocks of southwestern Africa (*7*) and new finds in the English Midlands (*8*). It is the gist of this article that this Ediacara fauna characterizes a distinctive episode of pre-Cambrian history but of Phanerozoic age and that, among names available, it is most appropriately called the Ediacarian Period. Rocks formed within this period of history then constitute the Ediacarian System, and the appearance of this fauna marks the geological transition from the preceding Proterozoic Eon to the following Phanerozoic Eon, comprising the rest of geologic time.

Semantic impediments have made unambiguous discussion difficult. Until 1930 no term existed for all of Earth history characterized by metazoan faunas and evolution, while pre-Cambrian was the only inclusive term available for the long preceding interval which, heretofore, had yielded no convincing records of visible animal life. Chadwick (*9*) then proposed a solution: the geological record characterized by conspicuous animal life would become the Phanerozoic (Greek for visible plus animal life), whereas antecedent history and rocks would be called Cryptozoic.

Phanerozoic is now widely accepted, but Cryptozoic has had only limited use. By definition, the term Phanerozoic must be extended downward to include older discoveries of manifest animal life. In the opinion of one of us (P.C.) this should take the Paleozoic with it, adding a basal extension to previous additions at the younger end of the original Paleozoic Era. Chadwick's definition, geologic consistency, and etymological congruity all equate the base of the Phanerozoic Eon with that of the Paleozoic Era. Inasmuch as the initial Phanerozoic rocks and history are also pre-Cambrian, still older divisions of rocks and history can no longer be unambiguously designated as simply pre-Cambrian. Clarity demands that the term Cryptozoic be accepted or pre-Phanerozoic employed where the intent is to designate by one word the long sequence of rocks and history that preceded the appearance of metazoan body fossils, imprints, and tracks as conspicuous components of the geologic record of life. The other writer (M.F.G.) considers it unlikely that the great majority of geologists will refrain from using the entrenched formal term Precambrian.

Discussion relevant to the base of the Cambrian (and, by implication, the Paleozoic) became active from the late 1940's through the 1960's (*10–12*). It grew in scale and scope with research and discussion within the framework of

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the International Geological Correlation Program (IGCP), established by the International Union of Geological Sciences and UNESCO in 1971 (*13–16*). As a result, the conventional base of the Cambrian has moved stepwise downward from being defined by the first appearance of the trilobite *Olenellus* to nearly coinciding with the massive incoming of shelly fauna—mainly small primitive mollusks and tubular to conical fossils of uncertain systematic position.

A broad consensus has also emerged concerning the grounds on which useful historical-stratigraphic subdivisions are best made (*11, 14, 17*). The agreed upon criteria are biological, with emphasis on the ranges in time of marine invertebrate animals where dealing with the Phanerozoic. More attention has focused on boundaries than on the modal characteristics or distinctive contents of the divisions bounded, perhaps because the regional variations are so great. Whether for boundaries or for modal characterization, however, it is clear that paleobotanical, paleomicrobiological, and other criteria must also become important as we undertake to define the lower limits of Phanerozoic and Paleozoic rocks and history and to delineate older divisions of the historical and sedimentary record.

Granted that the purpose of nomenclature is to facilitate unambiguous discussion, we must somehow specify the semantic content of terms utilized and seek to eliminate or clarify words that now mean different things to different people.

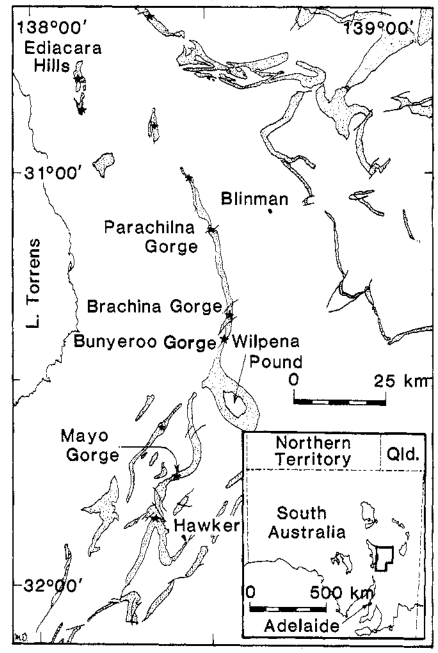

Fig. 1. Index map for key localities in Flinders Ranges. Stippling indicates outcrop of Pound Subgroup. Stars mark Ediacarian fossil localities. [Adapted from Wade (*19*) and Jenkins and Gehling (*48*)]

Ediacarian Period and System

In this spirit, we turn to the matter of how best to treat the historical episode represented by the Ediacara fauna and its equivalents. It turns out that this fauna not only has a circumglobal distribution, but it is clearly antecedent to conventional Cambrian. In fact, the term Ediacarian has already been applied to this part of Earth history—as the Ediacarian Stage of Termier and Termier (*12*) and the Ediacarian Period of Cloud (*16*). In the present article we seek more clearly to define and document the historical episode, to consider its appropriate position in the geologic time scale, and to review alternative nomenclatures. Other names that have included some or all of the rocks and history we here call Ediacarian either have not been clearly defined, have meant something different from the type Ediacarian, or have fluctuated too much in meaning to be useful (*18*).

In brief, the Ediacarian Period and System—named from and characterized by fossil evidence now known from some dozen South Australian localities along almost continuously exposed lines of outcrop 140-kilometers long (Fig. 1), and with equivalent strata worldwide—is not synonymous either with the officially defined Vendian of the Soviet Union or the Vend of general usage. The Ediacarian System is the oldest unit definable by metazoan fossil content. In its stratotype area it follows conformably above tillite-containing late Proterozoic sequences, but it is succeeded disconformably or unconformably by fossiliferous Lower Cambrian deposits.

We then define the Ediacarian Period as that interval of geologic history characterized by the soft-bodied, macroscopic, marine invertebrates of the Ediacara fauna and allied forms. Rocks of the Ediacarian System range from immediately above the last preceding episode of glacial sedimentation in South Australia and, with important exceptions, the last of the fossil stromatolite *Conophyton* beneath equivalents elsewhere, to the massive onset of shelly fauna and distinctive trace fossils (for instance, *Skolithos*, *Rusophycus*, *Plagiogmus*, and *Phycodes pedum*) that marks the initial Cambrian at many places.

In the stratotype area of the Ediacarian System, described below, these rocks are represented by the fossiliferous strata of the Wilpena Group. The distinctive fauna is one of soft-bodied arthropods (*Praecambridium* and *Parvancorina*), segmented worms (*Spriggina* and *Dickinsonia*, Fig. 2, C and D), primitive colonial cnidarian coelenterates (*Charniodiscus*, Fig. 2A; *Glaessnerina*, *Pteridinium*, and *Phyllozoon*), a possible proechinoderm (*Tribrachidium*, Fig. 2E), and some dozen genera of early medusoids (Fig. 2B) and other simple coelenterates. It is widely distributed through an interval that reaches a thickness of 112 meters near the middle of the Pound Subgroup at Mayo Gorge 15 km north of Hawker (*19*) (Fig. 1). The fossiliferous portion of the Pound has been called the Ediacara Member (*20*).

On fossil evidence from the type sequence the base of the Ediacarian is at least as low in the Wilpena Group as the middle of its upper clastic division, the Pound Subgroup. A new discovery of simple metazoan tracks in the Elkera Formation of north central Australia implies a still lower position—at or beneath the base of Bunyeroo Formation (*21*). Combining paleontology with paleoclimatology, operational convenience, and the probability that the metazoan record will be extended downward to some extent, we find it more appropriate, at this time, to equate the base of the Ediacarian with the base of the first stratigraphic unit above the highest tillite-containing deposits beneath known Ediacarian fossils. In South Australia that is the conformable lower surface of the Nuccaleena Dolomite and equivalent rocks at the base of the local Wilpena Group, overlying the tillitic Elatina Formation of the Umberatana Group. From data now available, this could be of roughly the same age as the terminal surfaces of other ice-related deposits that occur shortly below faunas of Ediacarian aspect in other parts of the world (*22, 23*).

Biological support for placing the boundary so low is the structure called *Bunyerichnus* (Fig. 2F), found near the middle of the Brachina Formation some 1800 m below the main Ediacarian fossil zone (*3*). Although we agree with Jenkins (*24*) that this surface marking is not a true crawling track, we do not agree that it is "unlikely to be of metazoan origin" (*25*).

Thus the basal Ediacarian approximately coincides with the oldest record of manifest animal life. For those who may still harbor reservations about that conclusion, it should be noted that most (P.C. thinks all) so far reported pre-Ediacarian Metazoa are pseudofossils, are misdated, or are not Metazoa. Some are even modern organisms or their traces intruded into older rocks (*16, 26*). Among recently proposed examples, the structure called *Rugoinfractus*, suggested as evidence for a metazoan presence 1100 million years ago, appears to be the fillings of shrinkage cracks in underlying strata (*27*), a common form of pseudofossil. Other supposed ancient Metazoa cited by Durham (*27*) from the Huronian Ajibik Quartzite of Michigan and the early Proterozoic Medicine Peak Quartzite of Wyoming are also of inorganic origin, as at least one of their authors has now recognized (*27a*).

Concerning prior usage, Termier and Termier (*12*) proposed "L'Ediacarien, premier étage paléontologique . . . caracterise par ces fossiles et qui s'insère au sein du sous-système Eocambrien." Despite their assignment of Ediacarian tc Eocambrian and some erroneous correlations (for instance, with the much older Belt Supergroup of Montana), there is no doubt that the Termiers intended the Ediacarian to comprise the initial Phanerozoic strata, characterized paleontologically. Here, moreover, although we follow Cloud (*16*) in elevating this term from stage to period rank, we also comply with standard Phanerozoic nomenclature in adopting Ediacarian for both geohistory (period) and rocks (system). Although biostratigraphically defined, it is not a biostratigraphic unit (a zone) in terms of the current International Stratigraphic Guide (*28*). In those terms it is a chronostratigraphic (system) and geochronologic (period) unit.

Division of the Ediacarian into formal epochs of history and series of rocks is not proposed here, although it may be suggested by faunal variation. Cribricyathids of Early Cambrian aspect (*Cloudina*) occur with Ediacarian forms through much of the lower Nama Group in the southwest Africa, whereas typical Early Cambrian trace fossils (such as *Phycodes pedum*) mark the overlying Nomtsas Formation and the Fish River Subgroup (*29*). By contrast, strata of the Wilpena Group have so far revealed neither shelly fauna nor such advanced trace fossils. This, with its unconformable base, suggests (to P.C.) that the Kuibis fauna of the lower Nama Group may be younger than the Ediacara fauna proper and that, if this should be substantiated, subdivision of Ediacarian on faunal grounds into epochs and series may become possible. Until then, the divisions shown as Early (Lower) and Late (Upper) Ediacarian on our global correlation chart are provisional.

Type Site and Global Reference Section

The discovery site for the Ediacara fauna is at the southern end of the Ediacara [also Idracourza, Idyakra, or Etikaura (*29a*)] Hills near Randell Lookout, southwest corner of the 1/250,000 Copley map sheet (~ 30°50'S, 138°8'E). Most Ediacarian fossils so far described from Australia have come from this area, but only a small part of the sequence of interest is exposed there.

The thickest fossiliferous sequence, 112 m, is in Mayo Gorge at the southwest corner of the 1/250,000 Parachilna map sheet, whereas the type sections for the Wilpena Group itself and all its named subdivisions are in the middle third of the Parachilna sheet between Mayo Gorge and Brachina Gorge, along the western flank of the central Flinders Ranges (Fig. 1). The general stratigraphy, paleogeography, and correlation of the rocks of the Wilpena Group and related strata in this and adjacent areas are summarized by Preiss *et al.* (*30*). Descriptions of the individual units appear in papers by others (*19, 31*).

We designate the steeply northwest dipping (55° to 60°) sequence in Bunyeroo Gorge (~ 31°25'S, 138°32'–35'E), 380 km north of Adelaide, as the standard reference section for the Ediacarian System (Fig. 3) (*32*), with the sections in

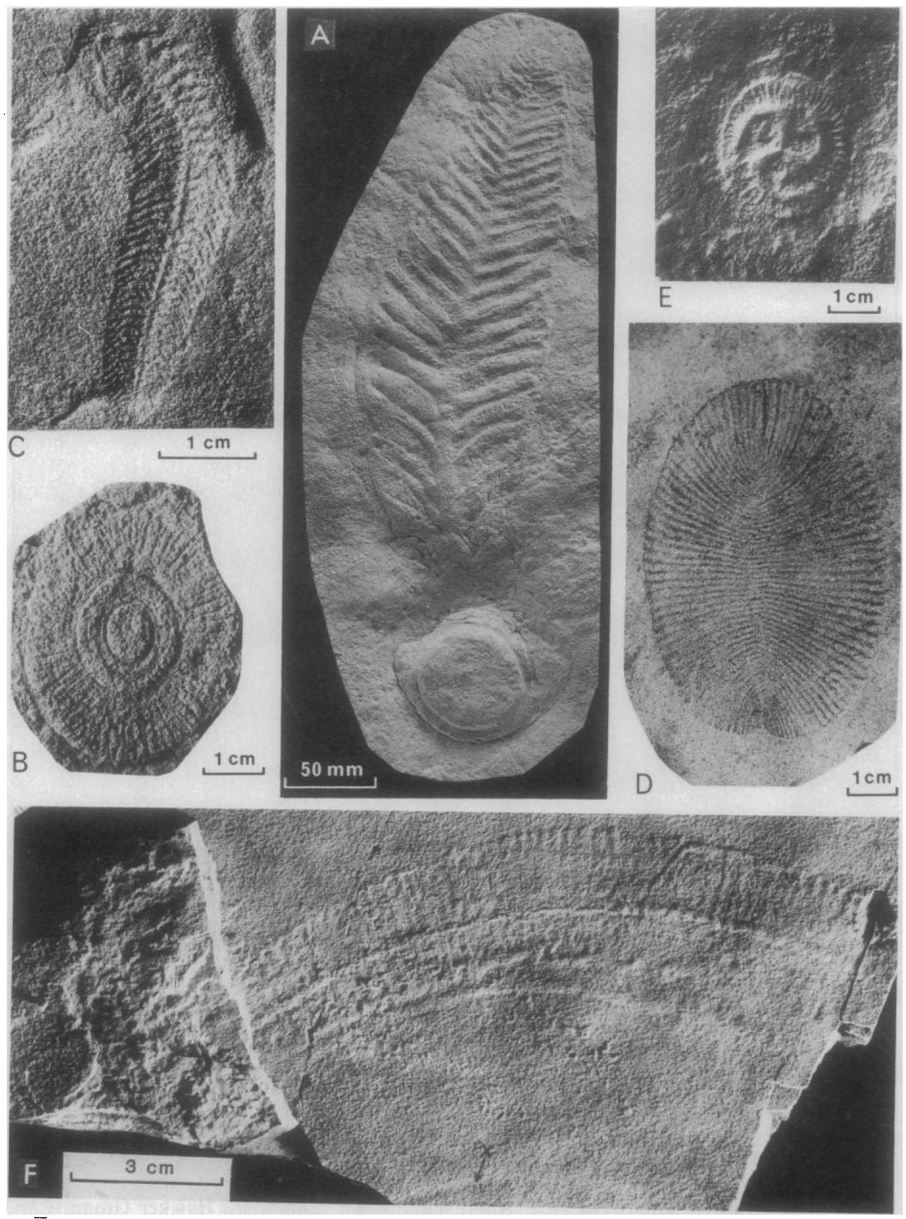

Fig. 2. Some distinctive Ediacarian Metazoa (A) to (E) are from Ediacara Hills. (A) *Charniodiscus arboreus* (Glaessner), plaster mold, photography by R. J. F. Jenkins; (B) *Cyclomedusa radiata* Sprigg; (C) *Spriggina*; (D) *Dickinsonia costata* Sprigg; (E) *Tribrachidium heraldicum* Glaessner. (F) *Bunyerichnus dalgarnoi* Glaessner, from near middle of Brachina Formation in Bunyeroo Gorge; compare with (B).

the Brachina Gorge and Mayo Gorge as supplementary reference sections. We choose Bunyeroo Gorge as the stratotype (*32*) because (i) an uninterrupted sequence of some 3000 m of Ediacarian strata is here compactly exposed in almost continuous outcrop within a horizontal distance of less than 5 km, (ii) the usual fossiliferous interval is well displayed, and (iii) the oldest known record of likely metazoan life (*Bunyerichnus*) occurs in this sequence. The Brachina Gorge section is more accessible by car, and the incomplete Mayo Gorge section adds information on the stratigraphic range of the most distinctive Ediacarian fossils.

Geochronology

The available geochronologic data for rocks of the Ediacarian System have limited usefulness. Some papers in which ages are cited do not state the method employed, the kind of rock or mineral dated, or the decay constant utilized. Where such data are available, the method used was often potassium-argon dating, which is susceptible to error in both directions. Argon loss with time and metamorphism results in minimal ages for materials dated. Other K-Ar numbers may be too old because of absorption of argon by thermally altered pyroxenes or because the mineral dated was glauconite, which may be detrital or formed by alteration of old biotite, giving exaggerated ages for enclosing sediments. Such a number, for example, led to the erroneous report of a Proterozoic age for the Cambrian trace fossil *Skolithos* in the Wessel Group of Northern Australia (*33*). Finally, international agreement on decay constants was only reached in 1976. Before then potassium-argon, rubidium-strontium, and even uranium-lead ages included a computational variance among laboratories of several percent.

Cowie and Cribb (*34*) sought to ameliorate such problems for the Cambrian by choosing 40 selected radiometric ages and recalculating them to the new decay constants. These were plotted on a calibrated chart to ascertain average numbers for Cambrian, Ediacarian, and related rock boundaries. The number so obtained for the base of the Cambrian was 560 million years if defined as the top of the Tommotian Stage, or 590 million years if placed at its base, a placing that we favor. We have reservations, however, about the validity of dating statistics that depend so heavily on K-Ar ages of glauconite.

A more credible age for the Ediacarian-Cambrian transition comes from assessment of recent data for the English Midlands: Nuneaton, Warwickshire; Charnwood Forest, Leicestershire; and the Wrekin area of Shropshire.

The Nuneaton ages are on distinctive diorites ("markfieldites") that intrude (and are thus younger than) the Caldecote Volcanics of supposed latest pre-Cambrian age. At Cliffe Hill in Charnwood Forest these "southern diorites" also intrude strata containing an Ediacarian type of medusoid fossil (*35*). This locality provided most of the samples from which a Rb-Sr isochron age of 552 ± 58 million years was obtained for the southern diorites by Cribb (*36*), recalculated to 540 ± 57 million years with the 1976 decay constant. That is close to the 546 ± 22 million years found for similar South Leicestershire diorites some 10 km distant. In the Nuneaton area the Caldecote Volcanics are unconformably overlain by the Hartshill Formation, containing fossils of the Baltic Lower Cambrian *Mobergella* zone 250 m above the volcanics (*37*). These Lower Cambrian fossils are thus younger than the age of 540 million to 546 million years found for the diorites that intrude rocks with Ediacarian fossils.

In the Wrekin area, about 100 km west of Charnwood Forest, Patchett *et al.* (*38*) obtained a good Rb-Sr whole-rock iso-

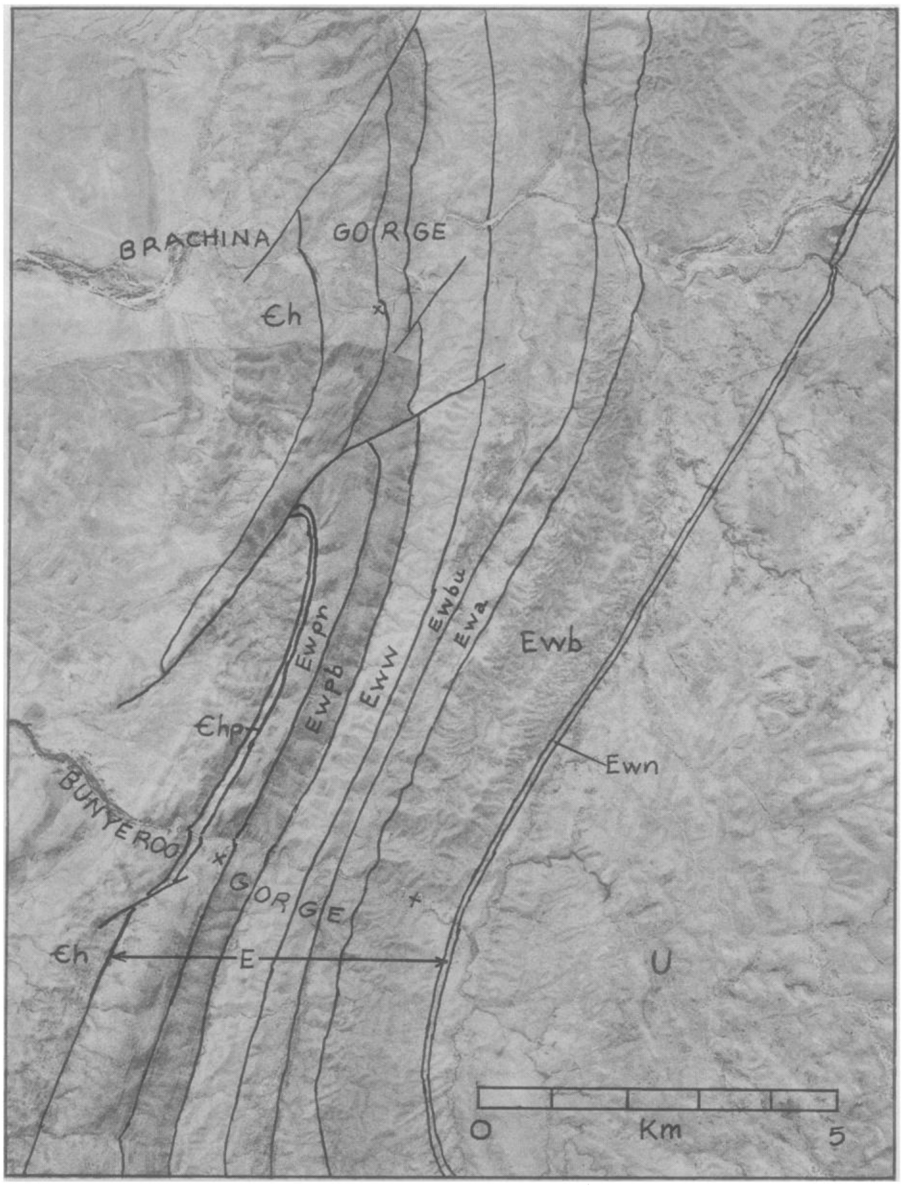

Fig. 3. Aerial view of stratotype area. Abbreviations: *Ꞓh*, Cambrian, Hawker Group; *Ꞓhp*, Parachilna Formation (basal Hawker Group); *E*, Ediacarian System; *Ewpr*, Ediacarian, Wilpena Group, Pound Subgroup, Rawnsley Quartzite; *Ewpb*, Pound Subgroup, Bonney Sandstone; *Eww*, Wonoka Formation; *Ewbu*, Bunyeroo Formation; *Ewa*, ABC Range Quartzite; *Ewb*, Brachina Formation; *Ewn*, Nuccaleena Dolomite; *U*, Umberatana Group (Proterozoic). North is at the top. [Courtesy of the Department of Lands of South Australia]

chron age of 533 ± 13 million years on the Ercall granophyre, unconformably overlain by fossiliferous Lower Cambrian of uppermost Tommotian to Atdabanian age.

The numbers and stratigraphic relations in these three Midlands areas thus reveal an episode of igneous activity around 533 million to 546 million years ago, following deposition of most of the Charnian strata of Ediacarian age. Much but not all of the Lower Cambrian, however, is younger than that. In order to find a realistic age for the base of the Cambrian we must add some years to these numbers to compensate for missing Tommotian sediments. Estimating that missing time as 10 million to 20 million years and averaging, we find 550 million to 560 million years as a likely age for basal Tommotian and hence the Ediacarian-Cambrian boundary.

That number is not far from earlier accepted estimates of around 570 million years. It differs significantly from the estimate of 590 million years given by Cowie and Cribb (*34*), for basal Tommotian, based mainly on K-Ar ages for glauconite from the Soviet Union. These ages, however, are increasingly being questioned by Soviet authors.

Concerning numbers relevant to the base of the Ediacarian, Coates and Preiss (*39*) reviewed Rb-Sr data for the ages of glacial and overlying sedimentary rocks in Western Australia, converting them to the new decay constant $\lambda^{87}Rb = 1.42 \times 10^{-11}$ year^{-1}. They concluded that three shales of lower to middle Ediacarian age above the uppermost glacials gave reasonably good Rb-Sr whole rock isochrons. Two of the three, correlated with the lower Brachina Formation of the stratotype Ediacarian, give ages of 672 ± 70 million and 670 ± 84 million years, respectively, compared with a less well constrained date of 676 ± 204 million years on the Brachina itself. A younger shale equivalent to the Bunyeroo Formation midway of the stratotype sequence gives an age of 639 ± 47 million years.

Other dates of interest include those related to fossils of Ediacarian aspect in Scandinavia, Newfoundland, and North Carolina. Kulling (*40*) illustrated simple trace fossils and a medusoid (*Kullingia concentrica* Glaessner) from beds correlated with strata above the uppermost Varangerian tillites and below Early Cambrian fossils (*Volborthella*) in northeast Sweden. The age is younger than an adjusted Rb-Sr isochron age of 654 million years reported (*41*) for the Nyborg Formation below the uppermost tillites of nearby Finmark in northern Norway, a number close to those reported for Soviet diamictites of presumed Varangerian age and glacial origin (*42*). Ages around 650 million years are commonly suggested for the Varangerian elsewhere. Thus it is possible either that these mainly K-Ar ages are too young (because of Ar loss), that they date metamorphism rather than sedimentation, or that the north European tillites are in fact younger than the ones that give older Rb-Sr dates in Australia. In any event, the top of the terminal Proterozoic tillites cannot at present be dated more closely than between ~ 670 million and 650 million years.

Table 1. Taxonomic affiliations of metazoan fossils from the Ediacarian of South Australia. Numbers of additional taxa from central Australia are added in parentheses. Percentages refer to specimens collected at Ediacara.

Phylum and class	Genera	Species
Cnidaria (67 percent)		
Hydrozoa, Chondrophorina	3	3
Scyphozoa	4 (+2)	4 (+2)
Conulata	1	1
Others (medusoids)	3 (+1)	6 (+1)
Colonial Cnidaria	4	5
Annelida (25 percent)		
Polychaeta	3	7
Arthropoda (5 percent)	2	2
Phylum uncertain (3 percent)	1	1
	21	29
Trace fossils	6	7
	27	36

In Newfoundland, Hughes and Brückner (*43*) suggested that the intrusive Holyrood Granite, with an adjusted Rb-Sr age of 594 million years (*44*), is also of about the same age as the Harbour Main volcanics and the Conception Group of marine volcanogenic sediments. The latter contains in its upper part the Mistaken Point fauna of Ediacarian affinity (*45*), found well above tillites but below the Random Formation and equivalent or older rocks with Tommotian fossils (*46*). Similarities between the Mistaken Point fauna and the Ediacarian of Charnwood Forest combine with lithological resemblances to imply equivalence and predrift proximity.

The firmest number available for rocks that probably represent part of the Ediacarian System is a U-Pb concordia age of 620 ± 20 million years on zircons from little metamorphosed pyroclastic rocks in conformable stratigraphic sequence with fossiliferous volcanogenic sediments in North Carolina (*47*). No distinctive Ediacarian elements are present at this place, but ages and local succession strongly imply an Ediacarian equivalence, and imprints of soft-bodied wormlike metazoans occur in these sediments.

The numbers given above are believed to be the best so far available for Ediacarian rocks. They imply a range in time from perhaps 670 million years at the base to around 550 million years at the top.

Metazoa

The distinctive fauna of the Pound Quartzite at Ediacara (Fig. 2 and Table 1) has already been described (*1–5*, *48*) and tabulated (*49*). It consists entirely of remains and imprints of soft-bodied Metazoa and trace fossils. Some show indications of chitinous or minor spicular strengthening elements such as are found in similar living soft-bodied invertebrates, but none had mineralized shells or solid skeletons. About two-thirds of the specimens known are cnidarian coelenterates. Such a dominance is rare at younger pre-Cenozoic fossiliferous localities and unknown in the Cenozoic. Unique though they be, however, fossils of the Ediacarian assemblage are clearly related to younger fossil and even living forms.

Hydrozoa are represented by the distinctive floats of the Chondrophorina. Among them is *Eoporpita*, belonging to the same family as the living *Porpita*, colonies of differentiated polyps that drift at the surface of the sea. The only other living genus, *Velella*, resembles the Ediacarian genera *Ovatoscutum* and *Chondroplon*, although these have bilaterally symmetrical floats. A number of other genera of similar colonial hydrozoans occur in the Paleozoic, but only two still live. It seems that either competition among planktotrophic Metazoa or predation on them increased with time.

The Scyphozoa are apparently represented by such genera as *Brachina*, *Ediacaria*, *Rugoconites*, and *Kimberella*, considered to be a possible ancestor of the Cubomedusae. The Conulata, an important group of Paleozoic fossils, are represented by *Conomedusites*, strikingly like the Ordovician *Conchopeltis*. A number of medusoid fossils, particularly the common *Cyclomedusa* and *Medusinites*, are not sufficiently distinctive to be placed in classes and orders of the Cnidaria. There is, however, little doubt that most of them lived like common modern jellyfish.

Sessile colonial Cnidaria have left

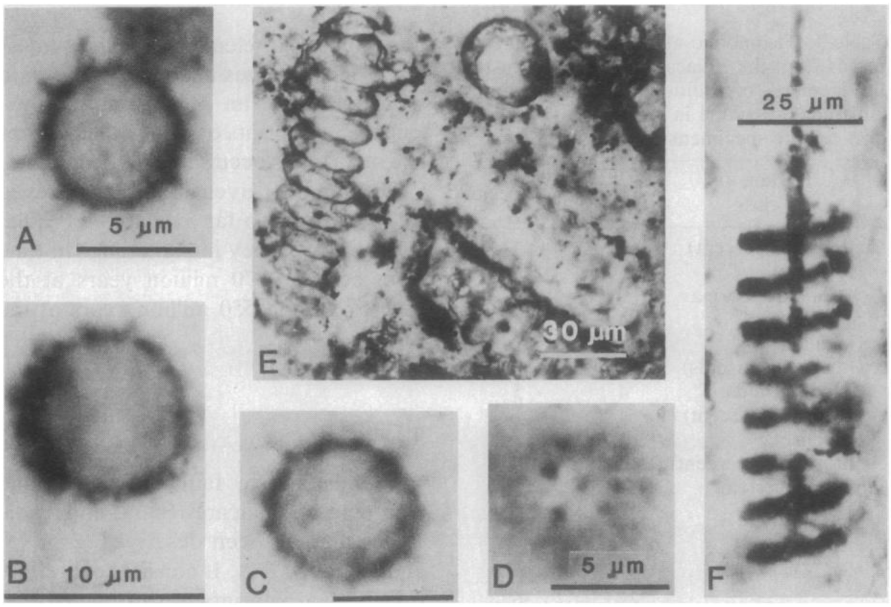

Fig. 4. Distinctive microbial fossils. (A) to (D) *Micrhystridium* sp. from lower Yudoma Group (Ediacarian), right bank Aldan River, upstream from Belaya (or Xanda) River, East Siberia. (E) and (F) *Obruchevella parva* Reitlinger from Muraykhah Formation, Jubaylah Group (Ediacarian or Cambrian), Jabal Umm al'Aisah, northeastern Saudi Arabia (*59*).

strikingly leaf-like fossils, up to 1 m long. Some of them (*Charniodiscus*, Fig. 2A) show distinctive characters of the living Pennatulacea (Anthozoa, Octocorallia), while others (*Pteridinium*, *Phyllozoon*), although pennatulacean in some respects, are more difficult to interpret. New specimens of *Rangea* (*50*) have shown it to be an endemic Namibian genus to which the first finds of this group of fossils from Ediacara were mistakenly assigned. The term "Petalonamae," proposed by Pflug (*50*) for these and other Namibian leaf- or cup-shaped fossils and for similar Ediacarian genera, has proved confusing and unnecessary. The significance of these fossils is the wide geographic distribution and the great age of ancient colonial cnidarians, some of which closely resemble living seapens (for instance, *Pennatula*), organisms that are rare or missing in most of the Phanerozoic fossil record.

About 25 percent of the specimens collected at Ediacara are annelids. The most common genus, *Dickinsonia*, may have survived into Paleozoic time (*51*). A similar form, *Spinther*, is still living as an ectoparasite on sponges. *Spriggina* is a very different kind of free-living, probably nectobenthic, polychaete worm. These fossils are still under study in connection with problems of annelid-arthropod relations. Two primitive arthropods, *Praecambridium* and *Parvancorina*, are rare. Together with the enigmatic triradiate *Tribrachidium* (resembling edrioasteroid echinoderms without calcareous plates) they amount to but a few percent of the fauna (Table 1).

The status of the Ediacarian as a valid Phanerozoic chronostratigraphic unit of system rank in the standard global stratigraphic scale is reflected in this fauna and reinforced by its position in the geochronologic scale. It is characterized by the global distribution of distinctive metazoan assemblages resembling those found at Ediacara and differing from those of the succeeding Cambrian System. The recognition of their potentiality for long-range correlation began with the discovery of Charniidae and medusoids comparable with those from Ediacara in the Charnian of the English Midlands (*2–5, 8, 48, 49*) and related forms in southwestern Africa (*7, 29*). Charnian types of fossils were later found, together with others, in the Mistaken Point fauna of Newfoundland (*45*) and in Siberia (*52*). A remarkable display of this fauna is that in the Valdai sediments of the White Sea Coast of the Soviet Union (*53*). It includes about ten species and ten genera (not all represented by previously known species) also found at Ediacara. A similar assemblage occurs on the southwestern margin of the East European platform. The Soviet faunas include numerous *Dickinsonia costata*, *Tribrachidium*, and the primitive arthropod *Vendia*, similar to *Praecambridium* from Ediacara. These assemblages, irrespective of sedimentary facies, share the numerical dominance of the phylum Cnidaria, reflecting evolutionary level at Ediacarian time. From some regions (central Australia, China, Scandinavia, and North Carolina), however, finds reported are limited or unique.

The wide distribution of Ediacarian faunas and even species supports paleogeographic reconstructions that place fossiliferous localities of the Proterozoic-Phanerozoic transition interval in low latitudes (*54*). Equatorial currents favored by such reconstructions would have facilitated the observed spread of marine faunas.

The Proterozoic to Early Cambrian sedimentary succession has been intensively studied in recent years in search of data on which a stratigraphic definition of the base of the Cambrian might be based. It is clear from this work (*15*) that the Ediacarian fauna of soft-bodied animals disappeared from or became very scarce in the preserved record after Ediacarian time. In its place appeared a fauna of small shelly fossils, many difficult to place in the zoological system of classification (*5*). They are not descended from members of the Ediacarian assemblage. Their ancestors may have been too small to be fossilized or may not have developed mineralized tissues. That this post-Ediacarian fauna with abundant and diverse small shelly fossils should be considered Cambrian, despite its lack of trilobites, is supported by the occurrence in Siberia of small, primitive archaeocyathids at the base of the Tommotian Stage. They soon developed complex calcareous skeletons which built reef-like structures in post-Ediacarian time. Their evolution through the Early Cambrian to their extinction in early Middle Cambrian time illustrates the successes of minor groups during the initial Phanerozoic adaptive radiation of the emerging Metazoa.

Like other transitions in the geologic record, however, the replacement of Ediacarian soft-bodied by younger skeletal Cambrian faunas was neither complete nor geologically instantaneous. The evolution of chitinous cuticles and of tubes formed from discrete grains cemented with mucus started during Ediacarian times, and we note reports of Sabelliditidae with organic tubes, possibly representing Pogonophora, of putative Riphean to Early Cambrian age. The characteristically Lower Cambrian cribricyathids are represented by the genus *Cloudina* in calcareous strata of the Ediacarian Nama Group of Namibia, mentioned above as implying a young Ediacarian age.

The poor showing in the Phanerozoic fossil record of soft-bodied Metazoa, abundant in the present marine fauna, is probably due to preservational or collecting bias, the evolution of macrophagous predators, an increase in saprophagous macro- and microbiota, or some combination of such factors. Biostratigraphic studies have shown that the "sudden" appearance of abundant small shells of the Tommotian Stage (basal Cambrian) was preceded in the latest Ediacarian (latest Yudomian of Siberia and probably the Sinian of the Yangtze Platform) by the occurrence of three or four genera of minute tubular and spicular fossils (*Anabarites trisulcatus*, probably a worm tube; *Protohertzina*, similar to chaetognath grasping spicules; and *Cambrotubulus* and/or *Hyolithellus*). The seemingly abrupt appearance of small shelly fossils in many places is enhanced by the common transgression of Early Cambrian on older sediments, leaving gaps in the record. Ecological effects of this transgression are well displayed in England (*55*). The onset of biomineralization was part of the rapid early Phanerozoic diversification of the Metazoa. No universally causal extrinsic environmental factor has been credibly invoked for it.

Metazoan diversification during the Ediacarian-Cambrian transition was paralleled by an increase in diversity of trace fossils (*3, 53, 56*). These are indicators of mainly metazoan life activities on and in sediments, made by live animals at the places where their markings are found. They may reveal much about the nature of these activities (feeding, locomotion, and so on), but only exceptionally do they indicate the place of the originator in the zoological classification. Different kinds of traces can be made by different activities of the same animal and similar traces by different animals. Thus the number of named form genera does not indicate taxonomic diversity but ethological differentiation.

Known Ediacarian trace fossils, probably of detritus feeders, are simple shallow burrows and relatively poorly oriented search trails on bedding surfaces. By contrast, early Cambrian assemblages include deep, vertical burrows (*Skolithos*), complex burrows (*Phycodes pedum, Diplocraterion, Chondrites, Treptichnus*, and *Plagiogmus*), excavations made by trilobite-like arthropodan appendages (*Rusophycus*), and a variety of trackways. Fedonkin (*53*) recognized Ediacarian trace fossils as dominantly two-dimensional and horizontal, in contrast to three-dimensional Early Cambrian forms. Some relatively complex locomotion trails that occur only rarely in the Ediacarian become common in the Cambrian, for instance, *Didymaulichnus*, which suggests the actions of a mollusk-like gliding foot rather than the peristaltic movement of a wormlike animal. Much more analytical work remains to be done in paleoichnology, but what has been observed confirms the rapid morphological and ethological diversification of the Metazoa during the transition from Ediacarian to Cambrian, a product of their increasing exploitation of the trophic resources of the sea floor and its sediments in the littoral and neritic zones.

Plant Microfossils and Stromatolites

Paleobotanical evidence related to the age, paleoecology, and correlation of Ediacarian rocks comes from microscopic filamentous algae, acritarchs (small, spheroidal, organic bodies of unknown but probably plant origin), stromatolites (accretionary buildups, mainly of $CaCO_3$ and thought to be generally of blue-green algal origin), and perhaps some ambiguous structures called microphytolites.

The microbial flora of the pre-Phanerozoic and early Phanerozoic sediments is only beginning to receive the attention it warrants. Available evidence, however, implies that such a flora has existed from Archean times to the present and that forms preserved increased markedly in size, abundance, and diversity during later Proterozoic and early Phanerozoic time. Although such material has not yet been systematically studied in the Ediacarian and immediately underlying strata of Australia, it is known to be biostratigraphically useful in correlative beds elsewhere and will become more so as our now limited knowledge of it increases (*57*).

The ranges of four distinctive, stratigraphically limited, organic-walled, microbial forms known to us are shown on the left of the correlation chart. Spiny planktonic acritarchs of the sort called *Micrhystridium* (*58*) and the spiral filaments of the microalga *Obruchevella* (*59*), illustrated in Fig. 4, apparently first appear in strata of Ediacarian age and range upward through the Cambrian. The spheroidal, multicomponent form genus *Bavlinella*, representing the endosporangia or clonal colonies of *Sphaerocongregus* (*57, 60*), ranges from upper Proterozoic through Ediacarian equivalents into the Cambrian of the Northern Hemisphere. Vidal (*57*) describes it as a characteristically Vendian form, but records it in the Cambrian and in and beneath the Varangerian tillites, as well as in other truly upper Proterozoic rocks such as those of the upper Sinian "Suberathem" of northern China. Bushlike colonies of the bifid branching microalga *Epiphyton* (commonly commensal on archaeocyathids or a bioherm builder) are unknown below the Nemakit-Daldyn and lower Baltic beds of the Soviet Union, widely considered to be upper Yudomian (Ediacarian) in Siberia but post-Vend (post-Ediacarian) in European Russia. Elsewhere we have not seen it below the basal Cambrian (Tommotian), which leads us to regard the *Epiphyton*-bearing beds of the Nemakit-Daldyn as Cambrian. A fifth algal type, the large, usually compressed, algal spheroids that comprise the form genus *Chuaria*, ranges through the uppermost Proterozoic, from strata perhaps as old as 1200 million years or more to its very top. Here it overlaps the lower range of *Bavlinella* and may extend into the Paleozoic under other names.

Vidal (*57*) is more explicit with reference to Eurasian acritarchs. Among 22 previously known acritarch taxa he studied, he finds that 18 percent first appear in the Vend, 10 percent are limited to the Vend, and 6 percent are limited to the upper Riphean (uppermost Proterozoic). We are not sufficiently confident about either the identification of acritarch species or the ages of the stratigraphic units discussed (for instance, the upper Sinian Suberathem of northern China) to accept these estimates as a basis for the definition of systemic boundaries. We are hopeful, however, that continued acritarch research will eventually lead to a better Proterozoic biostratigraphy and contribute to a more cogent definition than we can presently give for the base of the Ediacarian.

Stromatolites undergo a decline in abundance and diversity with the transition from Proterozoic to Phanerozoic, and with the appearance of metazoan browsers, eukaryotic precipitation and secretion of $CaCO_3$, and competitive exclusion. They are, however, still relatively abundant during Ediacarian time. Although few are uniquely Ediacarian, an association of certain distinctive columnar forms with strongly enveloping laminae or lateral wall-like structures would suggest a late Proterozoic to Ediacarian age (*61*). The simple peripherally enveloped columns of *Boxonia grumulosa*, combined with branching columnar "walled" forms like *Gymnosolen* and the lumpy *Linella ukka* and *Paniscollenia*, would be such an association. Where found above a sequence containing evidence of extensive late Proterozoic glaciation an Ediacarian age would seem likely.

Finally, in the Soviet Union and to some extent in China, subdivision and correlation of late Proterozoic and early Phanerozoic strata has, in some in-

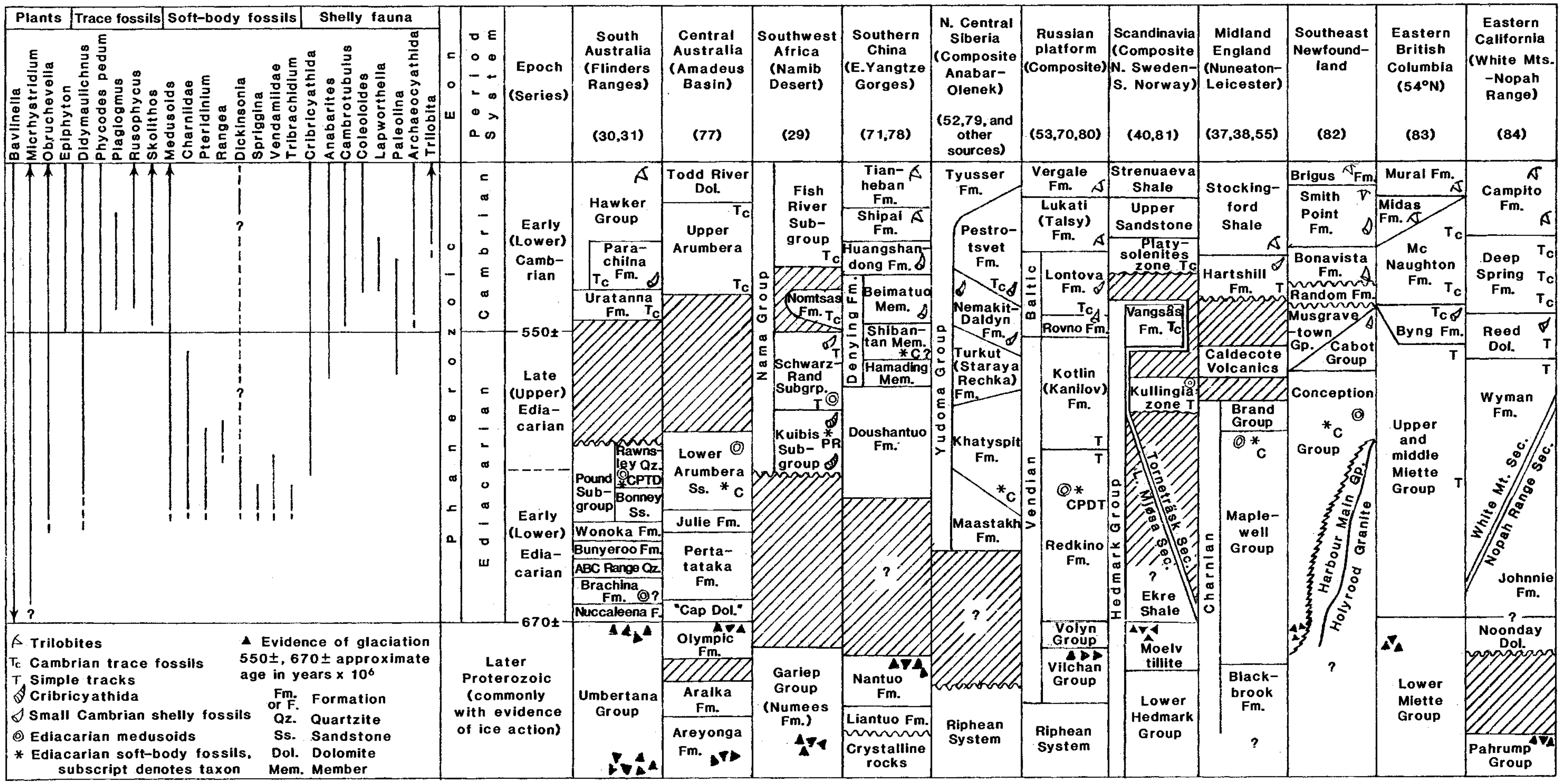

Fig. 5. Provisional global correlation of Ediacarian System. (Not to scale; omits many details and some whole regions.)

stances, been based on a heterogeneous group of microstructures referred to as microphytolites. Although we have doubts about the biological nature of most of these structures and the validity of subdivision and correlation based on them, several named entities have been reported from Ediacarian and adjacent strata in South Australia, and it is claimed that partial success in correlation was attained in tests based on samples of provenance unknown to the identifier (*62*).

Global Distribution

Beyond South Australia, Ediacarian fossils are known from the Amadeus Basin of central Australia and from some dozen other regions on four other continents (Africa, Asia, Europe, and North America). Figure 5 summarizes the main features of nine of these fossiliferous sequences plus two western North American sequences that are expected eventually to yield Ediacarian fossils. Space, regrettably, does not permit further discussion of these areas in this article. Their stratigraphy, biotas, and paleoecology, however, are detailed in references cited at the top of each regional column.

It should be stressed that Fig. 5 shows only relative positions in geologic sequence and does not conform to any scale of thickness or time, other than as ages are indicated for the top and base of the Ediacarian. The underlying upper Proterozoic is simply whatever occurs beneath the Ediacarian, with no special reference to age other than the supposed approximate time equivalence of the probably glacial rocks. The overlying Lower Cambrian here includes only the Tommotian and Atdabanian Stages of earliest Cambrian age.

In addition to sequences shown in Fig. 5, evidence available is *consistent* with an Ediacarian presence in North Carolina in the United States (*47*); the upper Brioverian of Brittany, Normandy, and the Channel Islands (*63*); Antarctica (*64*); South America (*65*); and the northern Arabian Shield (*59*). Also possible is an Ediacarian presence somewhere beneath or in the basal part of the Cándana Quartzite of northern Spain (*66*). In India, Svalbard, and Alaska also, well-preserved sedimentary rocks of the right age range and facies to yield an Ediacarian biota may be present. Indeed, there is reason to believe that future discovery will show the Ediacarian to have an areal extent worthy of its rich historical and evolutionary interest (*85*).

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18. The terms "Eocambrian" (*67, 68*) and "Infracambrian" (*68, 69*) are ambiguous. They are not based on biological criteria, no type sequences have been designated, and they have been used loosely to include widely varying parts of the Precambrian sequence and locally, though unintentionally, rocks now known to be Cambrian (for instance, the Ringsaker Quartzite of Norway, upper member of the Vangsås Formation). They have been generally abandoned. Sinian, although once officially adopted in the Soviet Union for rocks of Vendian and Riphean age (*70*), suffers similar disadvantages. It is still widely used in China, but in two very different senses. The thin Sinian System of the Yangtze Gorges and neighboring parts of southern China, younger than about 680 to 720 million years (*71*) and with glacial sediments at its base, is apparently not even represented in the standard northern China reference section for the Sinian Suberathem. Only if the glacial sediments were excluded from its base and the local basal Cambrian (Tommotian) from its top would it approximately coincide in time with our Ediacarian System.
    The term most deserving consideration and comparison with the Ediacarian is Vend or Vendian. This name was proposed by Sokolov (*72*), who later (*73*) referred to the Ediacarian as "the Australian equivalent of the Vendian." This equivalence is less straightforward than it may appear. A new stratigraphic scale for the Proterozoic of the Soviet Union was accepted by a large number of specialists at a conference in Ufa in 1977 (*74*). This makes the Vend the uppermost division of the Proterozoic, including (from base upward) the Vilchan, Volyn, and Valdai Groups. Its stratotype is in the western part of the Moscow basin, where it was studied from numerous bore holes. It is inaccessible to direct observation.
    The Vend was originally equated with the Valdai only (*72*). It was later extended downward to include the Volyn, partly volcanogenic (*70*), and then the Vilchan, partly glaciogenic (together comprising the Drevlyany "series" of some). The Ediacarian fauna of soft-bodied Metazoa is found only in the Valdai, and, for this and other reasons, Keller (*74*), Yakobson and Krylov (*75*), and other Soviet geologists have deplored the acceptance of the "greater Vendian." If, as many believe, the late Proterozoic glaciogenic deposits of the East European Platform and the margins of the Baltic Shield are of approximately the same age as those of Australia, only the Valdai (including Redkino and Kotlin strata) would correspond to the Ediacarian as here defined, not the official Vendian *sensu lato* which Sokolov accepts at least since 1973 (*52*). Vendian has also been used in this broad sense by Harland and Herod (*76*) and by Cowie and Cribb (*34*), among others, to include both fossiliferous rocks of Ediacarian age and the Varangerian tillites beneath.
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25. The enigmatic structure called *Bunyerichnus* is so far known only from the fragment shown in Fig. 2F, its counterpart, and one smaller fragment. The view illustrated is of an upper bedding surface. The arcuate grooves and ridges of this specimen, from the scalloped outer margin to the faint groove at the lower edge (*x* in Fig. 2F) deviate only slightly from a set of concentric circles that would close on themselves, if continued, with a maximum diameter of 24 cm. They clearly represent either (i) the tracing of a longish (12 cm) stalklike, flexible structure of some complexity that swung by currents about a point of attachment or (ii) the imprint of a large (24 cm in diameter) discoidal structure, having enough plasticity to account for asymmetries observed. These characteristics imply that it was the product of a once living organism, very likely a metazoan. Although such a marking might be produced by the swinging about a central point of an elongate wormlike form [for instance, *Vermiforma* Cloud (in *47*)] or a pennatulacean (*53*), the positive epi-relief displayed is more consistent with it being an imprint than a drag mark; for example, compare Fig. 2F with Fig. 2B. The counterpart imprint also shows features resembling gonadal imprints of some recent medusae. We conclude that *Bunyerichnus* is certainly biologic, very probably metazoan, and most likely medusoid.
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32. Briefly, the divisions of the Wilpena Group, comprising the type Ediacarian System in Bunyeroo Gorge, are (from bottom upward) as follows:
    1) Nuccaleena Formation; basal Wilpena Group, conformable on the underlying locally tillitic rocks of the Umberatana Group. Pinkish, laminated, flaggy dolomite going upward to purple shale with dolomite lenses. These were the initial shallow marine sediments of the postglacial warming and marine innundation that introduced the Ediacarian System. Thickness, 10 m.
    2) Brachina Formation; reddish-brown to olive-green, thin-bedded, micaceous siltites with shale and fine-grained sandstone. *Bunyerichnus* near the middle. Current marks, flute marks, local coarsening and grading, and ripple marks imply submarine conditions of varying depth,

with flat-topped ripples indicating local subaerial exposure. Thickness, ~ 1200 m.

3) ABC Range Quartzite; light colored, flaggy to massive, cross-bedded and ripple-marked, ridge-forming, locally feldspathic sandstone and quartzite. Flat-topped ripple marks and desiccation polygons indicate episodes of subaerial exposure within a shoaling marine environment. Thickness in Bunyeroo Gorge is 80 to 120 m, thickening westward.

4) Bunyeroo Formation; monotonous, reddish-brown and green, silty shales with thin cupriferous dolomite bands, local carbonaceous shale, and dolomitic sandstones showing local ball-and-pillow structure and sole markings indicative of a western source and gravity mass transport. Basally equivalent Elkera Formation of central Australia contains metazoan trace fossils (*21*). Thickness in Bunyeroo Gorge is ~ 400 m (reaching 700 m elsewhere).

5) Wonoka Formation; greenish-gray calcareous siltstones and fine-grained channel sandstones in the lower part, going upward to mainly cross-bedded, silty, commonly sole-marked, detrital limestones, locally stromatolitic. Thickness is 460 m in Bunyeroo Gorge, but the formation thickens dramatically, changes facies, and cuts downward across underlying sequences in a series of submarine canyon deposits dispersed south to north across the center of the Copley map sheet, next north of the Parachilna sheet [C. C. von der Borch, R. Smit, A. E. Grady, *Flinders Univ. Inst. Aust. Geodyn. 81/3* (1981), pp. 1–44].

6) Pound Subgroup; massive ridge- and bluff-forming sandstone and quartzite, including the lower Bonney Sandstone and upper Rawnsley Quartzite:

6A) Bonney Sandstone; mostly arkosic and micaceous lenticular siltstones showing ripple marks, desiccation polygons, local ball-and-pillow structure, and cross-bedding, including trough cross-beds indicative of fluviatile processes. A periodically emerged coastal environment is indicated. Thickness, ~ 300 m.

6B) Rawnsley Quartzite; whitish quartzite and sandstone with local siltite layers, locally ripple-marked and cross-bedded, gradational from Bonney Sandstone beneath. Contains t[illegible]cal Ediacarian body fossils and imprints [illegible] a massive, basal, bluff-forming unit. Represents final overfilling of Adelaide Geosyncline prior to late Ediacarian and Cambrian truncation and onlap of initial Cambrian seas. Thickness, ~ 500 m. Unconformably overlain by argillaceous sandstones of Parachilna Formation, Hawker Group (lower Cambrian), with vertical trace fossils *Skolithos* and *Diplocraterion*.

Total thickness, ~ 2970 m.

The description above applies to the stratotype section and nearby outcrops. The sequence is broadly similar over other parts of the Flinders Ranges but with the variations in thickness and facies to be expected in an evolving mobile shelf environment (*30*).

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85. While this article was in press a parallel endorsement of a new basal Phanerozoic System and Period was published by R. J. F. Jenkins [*Trans. R. Soc. South Aust.* **105** (No. 4), 179 (1981)].
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