[AMERICAN JOURNAL OF SCIENCE, VOL. 276, JANUARY, 1976, P. 56-76]

FOSSIL DATA AND THE PRECAMBRIAN-CAMBRIAN EVOLUTIONARY TRANSITION

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ABSTRACT. Undoubted trace fossils first appear in the stratigraphic record in rocks slightly older than those containing the earliest skeletal faunas and diversify upward into the Cambrian System. Their record apparently documents the initial proliferation of multicellular life, and it is possible that none are appreciably older than 700 m.y. The early part of the pre-skeletal record represents a time when metazoan communities consisted largely of medusoid coelenterates, flatworms, annelid worms, and comparably simple creatures to which skeletonization would have had little potential value. Even when viewed at the crude level of resolution provided by stratigraphic correlation, skeletonized taxa appear sequentially rather than simultaneously. Their origins require no special explanation but were simply part of the overall adaptive radiation. The earliest abundant skeletal faunas, those of the Tommotian Stage, lack many important Cambro-Ordovician groups and contain certain problematical forms not found in younger strata. Skeletonization represented an adaptive breakthrough in many groups and accelerated rates of diversification. Even so, documented rates of evolution in the Precambrian- Cambrian transition were not extraordinarily high in comparison to those documented by the later Phanerozoic record. The high rates can easily be accounted for by rapid speciation, and their polyphyletic nature offers evidence that the rectangular model of evolution is generally valid, as opposed to the traditional gradualistic model, which holds that most evolutionary change is of a phyletic nature.

INTRODUCTION

Since the time of Darwin, one of the most perplexing questions of geology has been why a diverse fossil record appears near the base of the Cambrian, leading us to separate Earth history into its two primary divisions, the Cryptozoic and Phanerozoic Eons. Over the years a varied array of hypotheses has accumulated in the search for an explanation. These will not be reviewed in detail here. Many have been summarized elsewhere (Seilacher, 1956; Axelrod, 1958; Simpson, 1960; Shevyrev, 1962; Rudwick, 1964; Nicol, 1966). The purpose of this paper will be to assess important new fossil evidence that will require us to channel our analysis of the problem in more restricted directions than have been followed in the past.

A brief history.—Until recently the view prevailed that a long history of multicellular evolution must have preceded the beginning of the Cambrian Period in order that a fauna as rich as that of the Cambrian appear abruptly in the stratigraphic column. Various explanations were offered for the absence of a fossil record representing the imagined early period of diversification. Darwin (1859), the first worker seriously confronted with the problem, postulated that rocks in which Precambrian life had been entombed might be largely metamorphosed or lie sunken beneath present-day ocean basins. Others have suggested that Precambrian organisms were small or planktonic or confined to marginal marine environments (Brooks, 1894; Walcott, 1910; Schindewolf, 1956; Axelrod, 1958; Nursall, 1959; Nicol, 1966). Walcott (1910) coined the phrase Lipalian Interval for an alleged gap in the stratigraphic succession representing the proposed period of diversification. More recently it became

popular to assume that Precambrian metazoans (multicellular animals) existed for a considerable time without hard parts and that the appearance of a well-displayed record in the Cambrian represented the advent of skeletonziation. The general weakness of these hypotheses is that, while each might account for a sparse metazoan fossil record in the Precambrian, none can realistically explain why no unequivocal record is known for the long interval of evolution that is envisioned. It is a general rule of Phanerozoic evolution that animal groups tend to diversify rapidly when they first appear, and it is difficult to imagine how higher life, once established, could for hundreds of millions of years have been suppressed to the extent of leaving no certain record.

In 1948 Cloud opposed the idea of a long Precambrian interval of diversification with the alternative idea that the Cambrian record documents the rapid initial adaptive radiation of higher life. This newer idea is now supported by a wealth of fossil evidence that will be reviewed here. It is also consistent with our modern concept of phylogeny. The evolutionary episode in question would, after all, have represented the adaptive divergence of most animal phyla. The Phanerozoic record shows that within these phyla peak rates of appearance of classes precede peak rates of apearance of orders, which precede peak rates for families, and so on down the taxonomic scale (Simpson, 1953). Extrapolating backward, we should expect to find very high rates of appearance of the phyla themselves when animals first arose. Schindewolf (1950) also judged that the fossil record documented rapid diversification in the Early Cambrian, but to provide an explanation he unfortunately fell back upon the discredited early twentieth-century concept of macromutation.

As recently as 1964 Rudwick wrote, "The known contrast between the almost unfossiliferous Precambrian and the highly fossiliferous Cambrian, far from being less striking than in Darwin's time . . . , has been accentuated by the progress of geology". This statement was a fair assessment of our situation in the early 1960's. Discoveries of the last decade, however, have dramatically reversed the trend. Although most American geologists may still believe that trilobites are the first shelled creatures to appear in the fossil record, several other groups are now considered by experts to precede them. Furthermore, new discoveries of body fossils, including skeletal remains, as well as trace fossils (behavioral markings formed chiefly by soft-bodied creatures), demonstrate that higher life began to diversify over a period of time preceding the interval traditionally recognized as Cambrian, but representing only a brief, final segment of what has traditionally been called the Precambrian. As often happens in science, what seemed a simple picture has become complex with the addition of data, and, although some major gaps will forever remain, paleontologists are now beginning to piece together the sequence by which higher organisms first proliferated on Earth.

There is also another side to the coin. In the past few years, nearly all the alleged finds of metazoan remains in rocks appreciably older than Cambrian have been rejected through re-examination (Schindewolf, 1956;

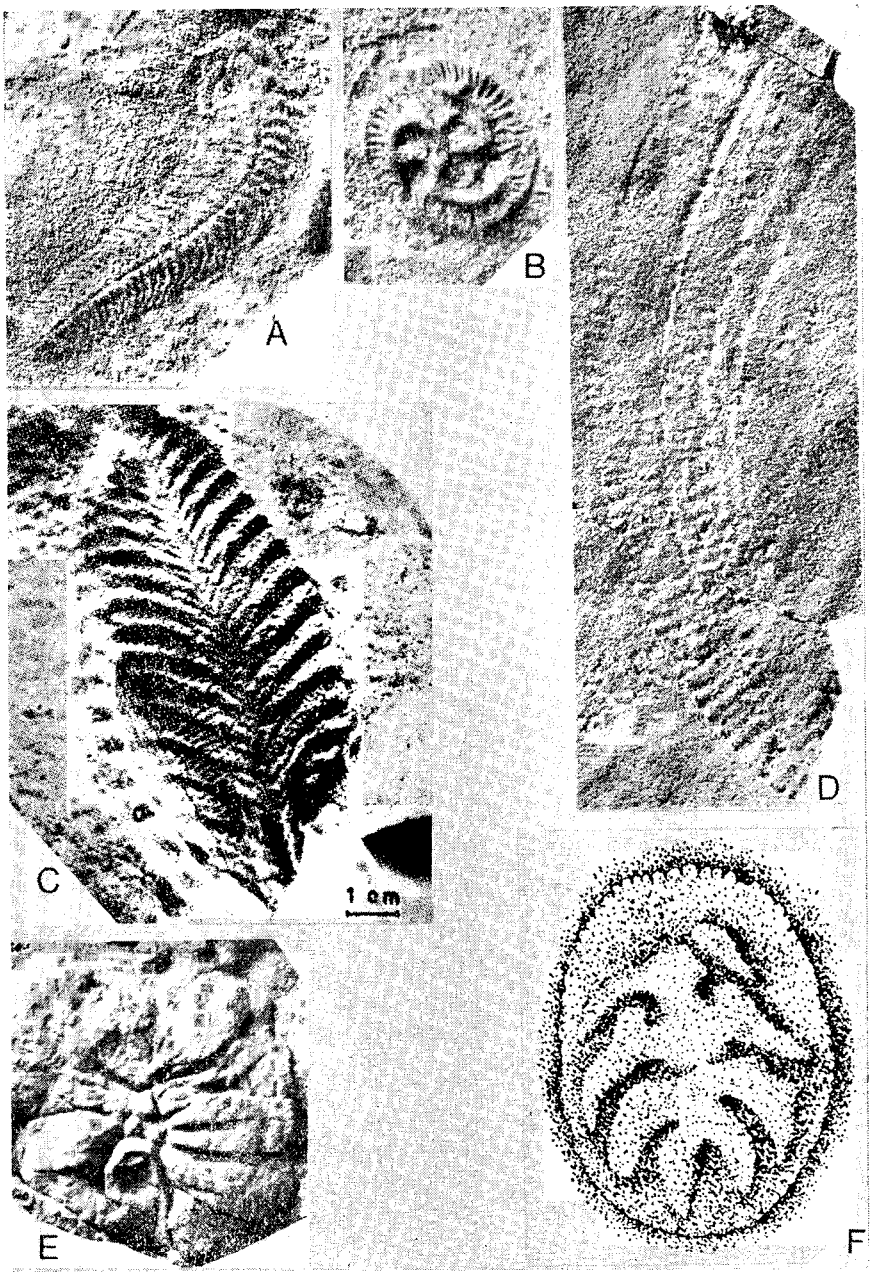
Seilacher, 1956; Glaessner, 1962). In a most recent, thorough analysis, Cloud (1968) would appear to have administered the final death blow to claims of early metazoan fossils. One or two possibly viable claims will be mentioned in subsequent discussions, but if, as seems justified, one takes a skeptical view of all evidence, no case can be made for the presence of metazoans before quite late in the Proterozoic.

Recent discoveries of unquestioned soft-bodied macrofossils slightly below what has traditionally been considered the Lower Cambrian boundary in various regions have led some to suggest that a formal system of rocks be recognized within the Phanerozoic (and Paleozoic) but below the Cambrian (Termier and Termier, 1960). Others have also suggested that the lower boundaries for the Cambrian, Paleozoic, and Phanerozoic need not coincide (Cloud and Nelson, 1966). As of now, however, most workers tend to regard the oldest abundant shelly faunas as approximately marking the coincident lower boundaries of the Cambrian, Paleozoic, and Phanerozoic, and this tradition will be followed here, with the understanding that it is a crude convention in need of refinement, if not revision.

Soft-bodied faunas.—As recently as 1956, Schindewolf judged that only fossils of algae and primitive worm-like organisms were reliably recognizable in the Precambrian. Other alleged Precambrian fossils seemed either to be questionably identified or questionably dated.

For many years purported fossils of Precambrian jellyfish attracted little attention, because it was known that inorganic processes could produce jellyfish-like markings and because some of the supposed Precambrian finds were considered to be of possible Cambrian age. Included in the second category were specimens from the Nama Group of South West Africa (Gürich, 1930, 1933; Richter, 1955) and from the Pound Quartzite of South Australia (Sprigg, 1947, 1949). It was only with the discovery of a wider variety of soft-bodied taxa in the Pound Quartzite (Glaessner, 1958, 1959a, 1959b) that this unit became widely regarded as Precambrian in age. Now comprising this so-called Ediacara Fauna are about 19 species of coelenterates, consisting mostly of jellyfish-like forms but including four species of bottom-dwelling sea pens (see pl. 1-C); five species of annelid worms, two of which may represent a transitional stage between the Annelida and Arthropoda (see pl. 1-A); a species assigned to the genus *Praecambridium* (pl. 1-F) that Glaessner and Wade (1971) believe to be a primitive arthropod, possibly bearing an ancestral relationship to the trilobites or chelicerates; and two bizarre species of uncertain affinities, including *Tribrachidium* (pl. 1-B), which may have affinities with the Echinodermata (Glaessner and Wade, 1966; Glaessner, 1971). It is indeed remarkable that such a large number of soft-bodied species occur, as they do, about 200 m below the oldest known shelly fossils of the area and separated from them by an unconformity. These facts of occurrence by themselves suggest that the Ediacara Fauna may also predate skeletal faunas traditionally used to define the Lower Cambrian boundary on other continents.

PLATE 1



A. *Spriggina foundersi* Glaessner (x1.3) from the Pound Quartzite, Ediacara, South Australia (from Raup and Stanley, 1971, courtesy of M. F. Glaessner).

B. *Tribrachidium heraldicum* Glaessner (x0.9) from the Pound Quartzite, Ediacara, South Australia (from Glaessner, 1962).

C. *Rangia schneiderhoehni* Gurich from the Upper Clastic Member of the Kuibis Formation, Vrede, South West Africa (from Germs, 1973).

D. *Bunyerichnus dalgarnoi* Glaessner (x0.7) from the Brachina Formation, South Australia (from Glaessner, 1969).

E. Plaster cast of "*Brooksella*" *canyonensis* Bassler (x0.7) from the Nankoweap Group of the Grand Canyon (from Glaessner, 1962).

F. Reconstruction of *Praecambridium sigillum* Glaessner and Wade (x10) from the Pound Quartzite, Ediacara, South Australia (from Glaessner and Wade, 1966).

Since the discovery of the more diverse Ediacara Fauna, similar assemblages containing fewer taxa have been recognized in comparable stratigraphic positions throughout the world. Most contain only coelenterates. The jellyfish and sea pen fauna of the Nama Group of South West Africa (see pl. 1-C) had been discovered earlier, but its age and taxonomic placement remained in doubt. The Charnwood Forest fauna of jellyfishes and sea pens from Leicestershire, England was described more-or-less concurrently with the announcement of the new Ediacara discoveries but was at first considered possibly to represent fossil algae (Ford, 1958, 1963). More recently, the known geographic range within Australia of certain Ediacara forms has been extended (Glaessner, 1971); an assemblage of jellyfishes and sea pens of comparable age has been discovered in southeastern Newfoundland (Anderson and Misra, 1968; Misra, 1969); and a jellyfish resembling the Ediacara genus *Cyclomedusa* has been reported from the Ukraine (Novatskiy, Velikanov, and Koval, 1968). Glaessner (1971) has also cited other recently discovered Russian fossils of the same general age seeming to show affinities with the Ediacara Fauna. One of these, the genus *Vendia* of the latest Precambrian, is very similar to the primitive Ediacara arthropod *Praecambriduim* reconstructed in plate 1-F (Glaessner and Wade, 1971).

Trace fossil faunas.—More recently discovered and less widely known evidence in the form of trace fossils (tracks, trails, and burrows) confirms the idea that soft-bodied creatures arose and diversified in what has traditionally been considered the latest Precambrian.

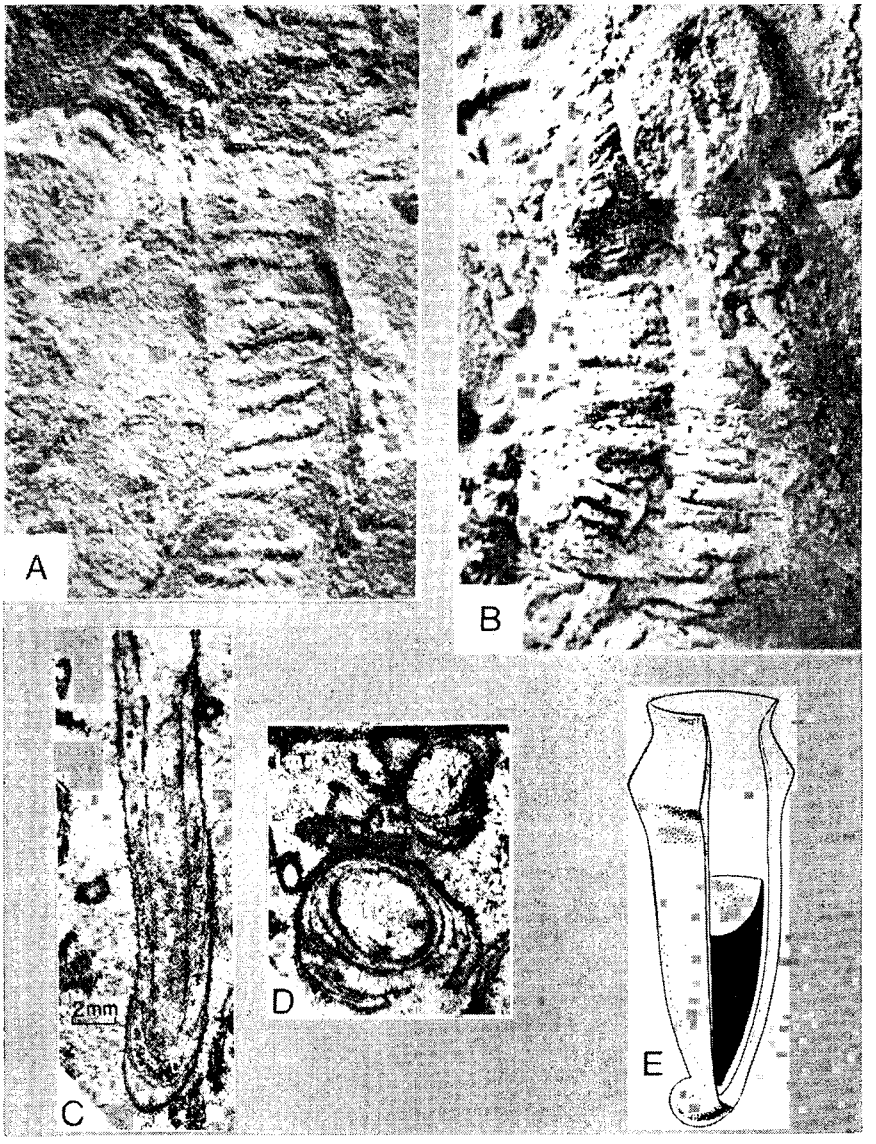
In 1956 Seilacher reached the important conclusion that the record of trace fossils is very meager in the Precambrian but demonstrates explosive diversification at the base of the Cambrian. This represented the strongest piece of evidence yet introduced that the Cambrian record reflects the initial proliferation of higher life in general and not simply the sudden advent of skeletonization. Discoveries of the past few years have confirmed Seilacher's assertion, with the qualification that both shelly and trace-fossil faunas show an initial sequence of expansion, rather than displaying high degrees of diversity abruptly in the Lower Cambrian. It must be borne in mind, however, that the exact placement of the Cambrian boundary is everywhere in question.

Glaessner (1962) appears to have been the first to mention evidence of the more gradual diversification of trace fossils in the vicinity of the Precambrian-Cambrian boundary. He later documented this idea in a discussion of the Arumbera Formation of Central Australia, which is thought to straddle the Lower Cambrian boundary (Glaessner, 1969). The lower part of this unit has also yielded an imprint of a sea pen assigned to the genus *Rangea* that resembles an Ediacaran species of the same genus (see pl. 1-C for another species of this genus). Otherwise it contains only simple worm tubes, whereas the upper part of the formation has yielded a diverse assemblage of trace fossils resembling those known to be of Cambrian age in other regions. Among these are some specimens that resemble *Rusophycus* and others that are assigned to *Plagiogmus*,

both of which are described in the next paragraph. Webby (1970) reviewed other discoveries of Australian trace fossils in the vicinity of the Lower Cambrian boundary and discussed in detail those of the Torrowangee Group of New South Wales. The oldest trace fossils of this unit are simple trails (of 3 to 7 varieties, depending on interpretation). These were apparently formed by deposit feeders and occur in the Fowler's Gap Beds, nearly 3000 m above the "Upper Tillite" of the Late Precambrian. About 2000 m higher in the section the Lintess Vale Beds contain a much greater variety of behavioral markings (10 to 21, depending on interpretation). These include what appear to be a few types of resting marks and crawling trails in addition to numerous feeding burrows. The Torrowangee faunas appear to predate skeletal faunas, and all are considered to be of Precambrian age.

In Finmark, Norway, lying less than 200 m above the uppermost Proterozoic tillite, a sequence of trace fossil faunas was reported by Banks (1970). This sequence begins with simple vertical burrows and reveals diversification upward in a stratigraphic interval of less than 400 m. Banks regarded the earliest faunas as Precambrian. The upper turbidite beds of the sequence, however, have yielded a diverse assemblage of markings, including *Rusophycus* (pl. 2-B), a type of resting track apparently produced by trilobites, and *Plagiogmus* (pl. 2-A), a burrow that Glaessner (1971) suggested may have been produced by a primitive mollusk. This upper assemblage closely resembles faunas recognized elsewhere as Cambrian and can probably be correlated with them. Most significantly, in a second paper Banks (1973) described a parallel sequence of diversification in the laterally equivalent, but thinner Dividal Group. This finding represents evidence that the trend of diversification is an evolutionary phenomenon rather than the product of chance occurrence or facies change. Young (1972) simultaneously reported a similar example of parallel diversification in North America. Working in the Southern Cordillera of Canada, he compared trace fossils of the Miette and Gog Groups with those of the neighboring Cariboo Group. Both packages of rocks straddle the traditionally recognized Lower Cambrian boundary, harboring early trilobites and archaeocyathids only in their upper portions, and both reveal a marked increase in the abundance and diversity of trace fossils just below the appearance of these shelled fossils. Below the zone of diverse trace fossils in each package there occur only simple deposit-feeding burrows like those found in other late Precambrian trace fossil sequences, along with less common, double-furrowed trails. Of special importance, Young noted that the general sequence of diversification, culminating with the appearance of shelled faunas, is found in both packages of rock despite the fact that the two packages reflect quite different environments of deposition: the diverse trace fossil assemblage of the Cariboo Group appears in muddy units of deep-water origin, while the comparable assemblage of the Gog Group appears in sandy, shallow-water deposits.

PLATE 2



A. *Plagiogmus* sp. (x0.9) from the Lower Duolbasgaissa Member, Duolbasgaissa Formation, Finmark, Norway (from Banks, 1970).

B. *Rusophycus* sp. (x0.9) from the same unit as *Plagiomus* sp. of (A) (from Banks, 1970).

C. and D. Longitudinal and cross sections of *Cloudina hartmannae* Germs from the Nama Group, South West Africa (from Germs, 1972).

E. Interpretive reconstruction of *Wyattia reedensis* Taylor (x11) from the Reed Dolomite, California (from Taylor, 1966).

Germs (1972) reported numerous trace fossils from the Nama Group of South West Africa, which, as discussed above, also contains imprints of soft-bodied coelenterates related to members of the Ediacara Fauna and problematical skeletal fossils (cribricyathids), which will be discussed below. The oldest fossils of this unit lie near its base, which rests unconformably on a group of rocks containing the youngest Precambrian tillite, and perhaps for this reason no record of diversification of trace fossils is shown. Cowie and Spencer (1970) have also reported trace fossils occurring less than 300 m above the latest Precambrian tillite of East Greenland. Diversification across the Precambrian boundary may also be demonstrated here, depending on whether some questionable structures are worm burrows and casts or inorganic features.

It is quite striking that at several widespread localities among those just discussed the earliest trace fossils appear above what has been taken as a stratigraphic marker, the tillite of what was probably a nearly worldwide "Infra-Cambrian Glaciation" (Harland, 1964). Schermerhorn (1974) has expressed skepticism of the glacial interpretation for late Precambrian mixtites, but his is a minority point of view. Glaessner (1969) considers the crawling trail named *Bunyerichnus* (pl. 1-D) to be one of the oldest known trace fossils. It has been found in South Australia about 2000 m below the traditional Lower Cambrian boundary, but it too occurs above the local Infra-Cambrian tillite. Glaessner has argued that one apparently older structure, the famous "*Brooksella*" of the Nankoweap Group of the Grand Canyon Series (pl. 1-E), may be a trace fossil more than 1000 m.y. old. It was originally considered a jellyfish, however, and Cloud (1968, 1973) has judged it to be inorganic ("a deformed sedimentary blister whose petallate margin is the product of small-scale jointing"). Certainly no strong argument can be made that it is indeed a trace fossil of extraordinary age. The exact age of the alleged Infra-Cambrian glacial interval is uncertain but probably does not exceed 700 m.y. (Banks, 1970), and a strong case is now being developed that trace fossils were first formed only very late in the Precambrian. To quote Banks, "It is unlikely that any true trace fossils exist in rocks which are significantly older than about 700 m.y." It is difficult to imagine that the equivalence of this approximate date and the approximate date for the earliest Ediacara-like faunas (Glaessner, 1971) is sheer coincidence.

Skeletal faunas.—In recent years Soviet workers have come to recognize skeletal faunas that predate the oldest known trilobites (Spizharskiy, 1963; Rozanov, 1967; Zhuravleva, 1970). These faunas are assigned to a new basal stage of the Cambrian known as the Tommotian. Below it lies the latest stage of the Precambrian, commonly termed the Vendian. The Tommotian skeletal faunas consist chiefly of archaeogastropods, brachiopods, and sponges, along with groups of uncertain affinities including archaeocyathids, hyolithids, and worm-like taxa (Zhuravleva, 1970). Tommotian shelled faunas are especially well known from many localities in Europe and Asia but have also been discovered in Australia, southeastern Newfoundland, Morocco (Rozanov, 1967), and Scandinavia (Bengston,

1970). Germs (1972) has recently described calcareous tubes from South West Africa (pl. 2-C,D) that predate other local skeletal faunas and may have affinities with tubiculous annelids. Various workers are now studying Tommotian faunas throughout the world, and we will soon have much new information about them. Even when better understood morphologically, many Tommotian fossils will remain problematical in terms of affinities with previously recognized phyla and classes. Some skeletal taxa precede the Tommotian and will probably be regarded as Precambrian in age even when experts agree upon a more specific Precambrian-Cambrian boundary than is now in use. For example, the problematical Hyolithelminthes, which are preserved as small, operculate conical tubes composed of calcium phosphate (Fisher, 1962), occur just below the Tommotian faunas, in the upper Vendian of Russia, as do problematical chitinoid tubes assigned to the Sabellitida (Zhuravleva, 1970). There is some sentiment among specialists that the Precambrian-Cambrian boundary should be placed above the first known occurrences of skeletonized taxa, in order to facilitate correlation (Cowie and Rozanov, 1974).

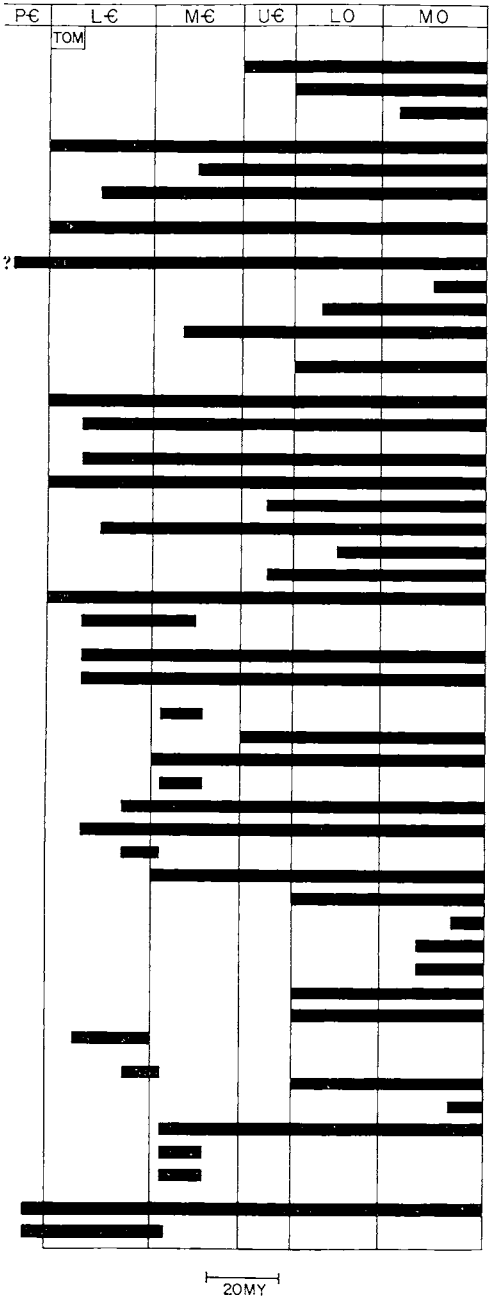
The rarity of pre-trilobite skeletal fossils in the United States has introduced a profound bias to American views on the origin of higher animal groups. For years we have clung to the "trilobites first" idea, while unfortunately lacking the raw material to attempt to reconstruct the true sequence of appearance of Early Cambrian taxa. An exceptional occurrence is that of the genus *Wyattia* in the White-Inyo Mountain area of southeastern California (pl. 2-E). This mollusk-like form, characterized by a conical calcareous shell about 0.5 cm long, occurs at least 900 m below the lowest regional occurrence of olenellid trilobites (Taylor, 1966).

Zhuravleva (1970) has estimated that the Early Cambrian lasted 30 to 40 m.y., of which the Tommotian comprised the first 10 m.y. or so. In addition to the trilobites, many other Cambrian taxa are known only from post-Tommotian deposits. Among these is another arthropod group, the Ostracoda, which arose later in the Early Cambrian. Within the Mollusca, first appearances of classes are blurred by convergence backward in time and by the difficulty of interpreting certain primitive forms, but it appears that cephalopods, bivalves, stenothecoids, and monoplacophorans all arose in post-Tommotian times. The Echinodermata are apparently unknown from the Tommotian, and many echinoderm classes did not appear until at least the Ordovician. The Ediacara genus *Tribrachidium* (pl. 1-B), which has three-fold symmetry, has been likened to members of the Echinodermata (Glaessner and Wade, 1966). This idea seems strengthened by the discovery of a trimerous mutant of the Mississippian blastoid genus Pentremites (Macurda, 1964). Possibly the structure of *Tribrachidium* is but a single mutation away from the five-fold brachidial arrangement of normal echinoderms.

Figure 1 is a range diagram of first appearances of major skeletonized taxa of the Lower Paleozoic. It must be regarded as a current summary that will need amending with future discoveries and reinterpretations. It does not include several problematical Tommotian groups. First appear-

ances of known Tommotian taxa seem to be controlled to a large degree by facies relationships (Cowie and Rozanov, 1974). The sequence of appearance of taxa of the Tommotian Stage is unknown and may never be documented in detail, but the presence of several shelled groups clearly predating the oldest known trilobites places in fresh perspective the sudden appearance of the trilobites, which were represented by a total of about 30 families during the Early Cambrian. Clearly, ancestors lacking calcareous skeletons but closely resembling trilobites must have existed in the Tommotian, and perhaps even earlier, but the advent of calcification in this group did not coincide with the advent of skeletonization in many other taxa. It is possible that calcification arose polyphyletically among trilobites at the family level, but it is also possible that what we see in the record is simply rapid diversification following calcification in a single family. For comparison, it is worth noting that in the Scythian, the first stage of the Triassic, the ammonites produced about 25 new families. Although Wiedemann (1973) has questioned this view, it has conventionally been accepted that all these families arose from a small group of closely related species that survived the Permo-Triassic faunal crisis. At any rate, skeletonization of diverse classes and phyla in the Cambrian was by no means instantaneous. Even in the generally soft-bodied and probably Precambrian Ediacara Fauna, Glaessner and Wade (1966) report what appear to be impressions of spicules in specimens of the sea pen *Arborea*. The presence of spicules in modern sea pens lends credence to this interpretation. The pre-Tommotian occurrence in Russia of skeletal representatives of the Hyolithelminthes and Sabellitida was mentioned earlier.

Assuming that skeletonization was merely one aspect of the initial adaptive radiation of higher life, two basic factors can account for its rapid, polyphyletic origin. One is that skeletons served the important functions of thwarting predators, which must have been diversifying as part of the initial adaptive radiation of animals. This reason for widespread skeletonization was independently proposed by Hutchinson and Brooks (see Hutchinson, 1961), but the idea seems first to have been advanced by Evans (1912). In addition, skeletons perform fundamental mechanical functions of support and muscle attachment for many groups. Most higher taxa that possess skeletons could not exist without them. Thus, as many workers have suggested, the advent of skeletonization must have been an adaptive breakthrough within primitive taxa leading to preferential survival and adaptive radiation. For example, Cisne (1974) has made a case that skeletonization in the Arthropoda improved energetic efficiency. Certainly calcification may have represented an adaptive breakthrough in the early evolution of the trilobites, perhaps accounting for their rapid initial diversification. Stasek (1972) argued that the phylum Mollusca "could have arisen in direct relation to a single evolutionary accomplishment — the secretion of a cuticle over the dorsal body surface, together with trends toward increase in size." As Stasek also makes clear, the basic body plans of the various classes of mollusks could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(SUBGROUP)
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AGGLUTINATED FORAM.
CALCAREOUS FORAM.
RADIOLARIA
PROTOZOA
HEXACTINELLIDA
DEMOSPONGIA
STROMATOPOROIDEA
PORIFERA
ARCHAEOCYATHA
PENNATULACEA
RUGOSA
TABULATA
CONULARIIDA
COELENTERATA
BRYOZOA
INARTICULATA
ARTICULATA
BRACHIOPODA
MONOPLACOPHORA
GASTROPODA
CEPHALOPODA
BIVALVIA
ROSTROCONCHIA
AMPHINEURA
CALYPTOPTOMATIDA
STENOTHECOIDA
MOLLUSCA
TRILOBITA
OSTRACODA
ARTHROPODA
HOMOSTELEA
HOMOIOSTELEA
STYLOPHORA
CTENOCYSTOIDEA
EDRIOASTEROIDEA
EOCRINOIDEA
LEPIDOCYSTOIDEA
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STELLEROIDEA
HELICOPLACOIDEA
CAMPTOSTROMATOIDEA
OPHIOCISTOIDEA
ECHINOIDEA
HOLOTHUROIDEA
CYCLOIDEA
CYAMOIDEA
ECHINODERMATA
HYOLITHELMINTHES
SABELLITIDA
PROBLEMATICA

only then have arisen through calcification of this cuticle. The origin of the Porifera is also relevant here. The sponge body plan includes a hollow shape that requires support, and the most primitive sponges, the Hexactinellida, lack a mesoglea. They rely upon their siliceous skeleton for rigidity. According to Finks (1970) all known Early Cambrian hexactinellid spicules are two-dimensional stauractins. Hexactins, which would have supported a thicker body wall, appear in the Middle Cambrian. We can concluded that the origin of spicules represented an adaptive breakthrough in the origin of the phylum Porifera, and the most primitive Cambrian forms must occupy a position very close to the ancestry of the phylum. Even if they represent an evolutionary cul-de-sac, sponges are not far removed from the protozoans in level of organization, and had protozoans been in existence long before the Cambrian, the sponges or some comparable group should have arisen from them and left an earlier record. Even more striking is the lack of concrete evidence of skeletonized protozoans in rocks of Precambrian age. The oldest unquestioned foraminifera that formed tests of agglutinated sedimentary particles are found in the Late Cambrian. Calcareous tests are not recognized in pre-Ordovician strata.

Clearly the Cambrian record documents the unfolding of skeletonized body plans in numerous taxa, and yet the variety of skeletal components that appeared renders improbable any of the classical explanations of this coincidence in time based on changes in the chemistry of the world's oceans. Even in Tommotian rocks there are inarticulate brachiopods and other phosphatic taxa, siliceous sponges, and several calcareous groups.

THE SEQUENCE OF DIVERSIFICATION

Many workers seem to favor recognizing as lowest Cambrian all deposits younger than those containing the very first skeletal faunas, in order that reasonably abundant and widespread taxa be used for correlation of the lowest Cambrian (Cowie and Rozanov, 1974). It therefore seems certain that some trace fossils and likely that some soft-bodied im-

Fig. 1. Currently recognized stratigraphic ranges of major skeletonized taxa of the lower Paleozoic. Minor groups of questionable taxonomic validity are excluded. Only Tommotian groups with significant records in post-Tommotian strata are included; most others are of uncertain taxonomic affinity. Where sources have specified only the series during which a group appeared, the origin of the group is shown in the middle of the series. Tom—Tommotian stage of Lower Cambrian. Time scale from Harland, Smith, and Wilcock (1964). Echinoderm data from Durham (1969). Other sources as follows (*Treatise* refers to appropriate volue of the *Treatise on Invertebrate Paleontology*, R. C. Moore, ed.): Foraminifera—*Treatise*, Harland and others (1967); Radiolaria—Harland and others (1967); Hexactinellida—Zhuravleva (1970); Demospongia—Harland and others (1967); Stromatoporoidea—Harland and others (1967); Archaeocyatha—Zhuravleva (1970); Pennatulacea—Glaessner and Wade (1966); Rugosa—*Treatise*; Tabulata—*Treatise*; Conulariida—Harland and others (1967); Bryozoa—Harland and others (1967); Inarticulata—Zhuravleva (1970); Articulata—*Treatise*; Monoplacophora—Harland and others (1967); Gastropoda—Zhuravleva (1970); Cephalopoda—Yochelson, Flower, and Webbers (1973); Bivalva—Pojeta, Runnegar, and Kriz (1973); Rostroconchia—Pojeta and others (1972); Amphineura—Harland and others (1967); Calyptoptomatida—Harland and others (1967); Stenothecoida—Yochelson (1969); Trilobita—Zhuravleva (1970); Ostracoda—*Treatise;* Hyolithelminthes—Zhuravleva (1970); Sabellitida—Zhuravleva (1970).

prints will continue to be regarded as Precambrian. Unfortunately, radiometric dating yields rather crude age estimates for rocks of Cambrian age, at least in comparison to the resolution obtained using index fossils (Harland, Smith, and Wilcox, 1964), and even correlation by fossils is at a primitive stage for the Lower Cambrian and latest Precambrian. Nonetheless, useful new data for correlation and reconstruction of phylogenies are now accumulating more rapidly than ever before.

Correlation of faunas.—Trace fossil faunas seem often to precede the oldest shelled faunas in particular regions. Unfortunately, no one has yet provided stratigraphic studies correlating trace fossil faunas with the Tommotian shelled faunas. A major barrier here has been the typical occurrence of shelled faunas of the Lower Cambrian in carbonate rocks, while recognizable trace fossils are preserved chiefly in clastic rocks. The sequence of appearance of faunas in a given region may be controlled largely by facies relationships rather than by phylogeny. The dominance of clastic deposits in Lower Cambrian sequences of the Eastern United States, for example, is undoubtedly in part responsible for the general absence here of shelled faunas of Tommotian age.

The soft-bodied Ediacara Fauna and its equivalents outside Australia are also preserved in clastic sediments. It has become customary to think of these faunas as predating any skeletal faunas despite possible facies control of their occurrence because they predate local shelled faunas. The stratigraphic evidence favoring this view is supported by the logic of phylogeny: skeletons of most Early Cambrian Metazoa were obviously not derived directly from skeletonized single-celled ancestors, and many of the metazoan skeletons are so distinctive that it is also unlikely that they were inherited from other multicellular groups. For these reasons we should not be surprised to find rather diverse pre-skeletal metazoan faunas. Nonetheless, evidence has recently surfaced suggesting that at least some faunas of the Ediacara type may be younger than conventionally believed. Germs (1972) described small calcareous tubes from the Nama Group of South West Africa for which he erected the genus *Cloudina* (pl. 2-C,D). These appear to represent crybricyathids like those of the Soviet Tommotian, and while they occur in limestone facies of the Kuibis and Schwarzrand Formations, detrital sediments of these units have yielded soft-bodied coelenterates assigned to three genera of the Ediacara Fauna of Australia (*Rangea, Pteridinium,* and *Cyclomedusa*). It is therefore possible that faunas of the Ediacara type may eventually be considered to be of Tommotian age. Nonetheless, Glaessner (1971) believes that the Ediacara-like faunas may span as much as 100 m.y. of geologic time, in which case some may predate the oldest skeletal fossils while others turn out to be contemporaneous with them.

Geographic control of early metazoan fossil occurrences represents another hurdle to the correlation of soft-bodied, trace fossil, and shelled faunas. Because of their excellent preservation, trilobites can be used as good indices of provinciality in post-Tommotian Early Cambrian seas. While also stressing facies control of occurrences, Palmer (1973) concluded

that Early Cambrian trilobites "show many contrasts that could be attributed to 'provincial' differences". For example, he pointed out (1973, p. 6):

> The southern part of the Siberian Platform was an area of restricted environments characterized by limestone– . . . dolomite–evaporite sequences and an endemic trilobite complex. This area was flanked to the east and south by an area of archaeocyathid bioherms and a different, largely endemic, trilobite complex. Still farther to the east . . . and southward . . . a third trilobite complex has been recognized.

It is on the Siberian Platform that the Tommotian skeletal faunas are best developed, and in light of the provinciality displayed by Lower Cambrian trilobite faunas of this region, the difficulty of tracing many Tommotian elements to other regions is not surprising. More widespread occurrences may, of course, be documented through the increased efforts now being made.

In summary, despite present uncertainties, it seems evident that soft-bodied animals arose before shelled animals, leaving a record of trace fossils that may predate the first shelled creatures by a few tens of millions of years. The Ediacara-like faunas may entirely predate the earliest unquestioned (Tommotian) shelled faunas or overlap with them fully or in part.

The pattern and rate of divergence.—For much of the interval of diversification preceding the Tommotian, it would seem that only a few phyla and classes of animals were in existence. Annelid worms and unknown (and perhaps mostly extinct) taxa of equivalent or lower anatomical complexity can account potentially for most types of pre-skeletal trace fossils. Coelenterates, which are among the least advanced modern Metazoa, comprise roughly 70 percent of the described species of the Ediacara Fauna of Australia and constitute an even greater percentage of the similar faunas of other continents. It is probably no accident that taxa like medusoid coelenterates, flatworms, and annelid worms, which account for a large fraction of the earliest metazoan record, lie near the base of metazoan phylogenies constructed from purely zoologcial evidence. Exoskeletons, which are not easily accommodated within the body plans of these groups, have always been lacking or rather uncommon among them. It is chiefly other taxa, descended from these early groups, that became skeletonized, which partly explains why exoskeletons do not appear earlier in the initial radiation of the Metazoa.

Banks (1970) and Valentine (1973) directed attention to the origin of the coelom (cavity between body wall and digestive tract) as a late Precambrian adaptive innovation of great importance. The idea of Clark (1964) that the coelom functioned originally as a hydrostatic skeleton for burrowing is now widely accepted, and its origin and development among annelid worms played a major role in producing the early diversification of trace fossils.

It is almost universally agreed that the arthropods evolved from annelid worms. In the process, or soon after, they became largely epifaunal in habit. As would be expected, none of the earliest Precambrian trace fossils — only some of those approaching Cambrian age — have been interpreted as markings of arthropods. The arthropods also represented a group in which mineralized skeletons could arise with great usefulness and did, after the Tommotian, in the origin of the calcareous trilobites and ostracods. Clearly, other groups in which hard skeletons were potentially useful or even essential for adaptive radiation must also have been arising shortly before the beginning of the Cambrian, as were other characteristically soft-bodied taxa.

The proliferation of skeletons was both a result and a cause of adaptive radiation. Most early Paleozoic shelled taxa belonged to epifaunal groups that only secondarily evolved burrowing modes of life by the acquisition of special adaptations (Stanley, 1968; Valentine, 1973). These shelled groups necessarily evolved burrowing mechanisms quite distinct from those of soft-bodied worm-like groups of pre-Tommotian times. Many skeletonized groups of the Early Cambrian also appeared at small body sizes. It has been suggested that many arose from ancestral groups that could not attain large size because of their very lack of skeletal support (Nicol, 1966). In addition, scaling problems at large size generally tend to restrict major morphologic transitions to taxa of small relative body size (Stanley, 1973b). As shown in figure 1, the origin of most major skeletonized taxa was spread over several tens of millions of years. Most of the important early Paleozoic phyla that had skeletons developed them in the Early Cambrian. About four persistent phyla are known to have done so before the end of the Tommotian.

It is reasonable to invoke a kind of threshold effect in analyzing the origin of skeletonization. A certain minimum period of time should be required for any soft-bodied taxon to evolve the capacity for skeletal secretion. The weight of evidence suggests that, following an interval of dominance by simple groups that had little potential use for skeletons, most major skeletonized phyla of the Early Paleozoic arose without skeletons during an interval of the latest Precambrian not exceeding 50 m.y. Most of these newer phyla became skeletonized during the Early Cambrian, which lasted perhaps 30 to 40 m.y. Thus the origin of skeletons within the newer phyla was probably not appreciably more simultaneous than the origin of the phyla themselves.

During the last 50 to 100 m.y. of the Precambrian and the first 30 m.y. or so of the Cambrian (the Early Cambrian), basic body plans that were later to become more highly specialized were diverging from anatomically simple ancestral groups, most of which are now undoubtedly extinct. Was the implied rate of divergence extraordinarily rapid? An illuminating comparison can be made with the early Cenozoic adaptive radiation of the mammals. Following the extinction of major reptile groups, representatives of nearly all mammal orders, ranging in morphology from the bats to the whale, arose from primitive ancestors during an

interval of only about 15 m.y. (Romer, 1966). The major invertebrate phyla may have taken an order of magnitude longer to appear, but their degree of morphologic divergence would not seem to have been any more than an order of magnitude greater. The initial divergence of the animal phyla was by no means inordinately rapid.

Durham (1969) claimed that a very long period of metazoan evolution must have transpired in the Precambrian to account for the high levels of organic complexity that we see in the Lower Cambrian. His argument was based on the combination of two ideas: first, that typical durations of marine invertebrate species are approximately 6 m.y.; and, second, that many species would have to be stacked end to end to produce a new phylum or class from a preexisting one. Clearly the Precambrian interval postulated here seems unlikely on the basis of evidence offered above. Furthermore, no early (Mesozoic) period of diversification is even conceivable for the Mammalia, and yet this group poses the same kind of problem. Cenozoic mammal species have lasted an average of more than 1 m.y., so that the 15 m.y. interval during which nearly all orders are known to have arisen cannot represent more than about 10 average species durations stacked end to end. Clearly gradual change at rates typical for established species cannot account for the observed rate of divergence. This line of reasoning has led to testing of the gradualistic model of phylogeny. This model holds that rate of evolution is largely independent of the multiplication of species, with most change occurring phyletically, within established species. The alternative view, that most change is concentrated in speciation events, has been denoted the punctuated equilibrium model (Eldredge and Gould, 1972) or simply the rectangular model (Stanley, 1975).

Eldredge and Gould (1972) noted that the presence of many classes of Ordovician echinoderms containing few genera was difficult to account for by the "stately unfolding" of body plans required by the gradualistic model. The idea here is that stately unfolding would require the passage of more geologic time and the attainment of greater diversity within classes than we find documented by the geological record. The arguments in the preceding paragraph support this view. It must be recognized, however, that as viewed by Simpson (1953), adaptive breakthroughs of the sort that yield new classes occur rapidly in small taxonomic groups by dramatic acceleration of phyletic evolution. The phyletic process invoked here is not one of stately unfolding, as envisioned by Durham (1969), and is quite compatible with the low diversity observed for certain early echinoderm groups. Furthermore, generic diversity is generally poorly known for taxa from which adaptive breakthroughs proceeded in the Precambrian-Cambrian transition and should perhaps be excluded from our analysis of the problem. Taking a somewhat different tack, I have viewed the crux of the matter as being the failure of gradualism reasonably to account for dramatic adaptive radiations like the one under consideration here. The problematic phenomenon is the approximately simultaneous acceleration of evolution to extraordinary rates in numerous

diverging taxa. Validity of the gradualistic model would require that selection pressure be intensified markedly for a substantial interval of time within a variety of groups occupying quite unrelated adaptive zones. It is difficult to conceive of a reason why phyletic change should behave in such a way. The rectangular model, on the other hand, offers a ready explanation for the phenomenon. All that is required is for either rate of speciation or degree of change per speciation event (Stanley, 1973c) to be exceptionally high. These conditions are to be expected as vacant adaptive zones are invaded during unrestrained adaptive radiation. Such conditions arose for primitive mammals with the sudden demise of Mesozoic Reptilia and also obtained in the late Precambrian when the Metazoa first arose.

At the start of adaptive radiation of a phylum or class, the great ancestral potential of generalized early members commonly permits the divergence of a wide variety of subtaxa. Commonly, however, many of the subtaxa suffer rapid extinction. This fate befalls them for one of several reasons: they turn out to be inferior competitors or unsuccessful avoiders of newly arising predators; their body plans offer limited potential for diversification; they fail to adapt to changes in the physical environment; or they simply happen to decline by chance before attaining high enough diversity for stochastic fluctuations to pose no threat. Subtaxa that persist tend to become specialized and to lose the potential for readily spawning a variety of different subtaxa. In groups characterized by severe interspecific competition, successful subtaxa may also oppose the appearance of new subtaxa by monopolizing adaptive zones (Stanley, 1973c). The general pattern of initial adaptive radiation just described is sometimes described as evolutionary "experimentation". It is exhibited especially well by the Echinodermata (fig. 1) the Mollusca, in which diverse early taxa are lumped in the Calyptoptomatida (Harland, Smith, and Wilcock, 1967) and the Mammalia. It must also account for the variety of problematical forms now being reported from the Tommotian Stage. These would seem to document "experimentation" in animal evolution not merely at the level of order or class but, for the only time in geological history, at the level of phylum.

If the foregoing assessment is generally correct, we can abandon the traditional view that the origins of major fossil taxa near the start of the Cambrian were so sudden and simultaneous as to represent a major enigma. What remains as the "Cambrian Problem" is the delay of the origin of multicellularity until the Earth was nearly 4 b.y. old. Possible explanations, including one based on ecological theory (Stanley, 1973) and another based on the origin of sexuality (Schopf, 1968), will be reviewed in a separate contribution (Stanley, in preparation).

SUMMARY AND CONCLUSIONS

1. New fossil discoveries have greatly reduced the apparent abruptness with which early multicellular taxa appear in the fossil record.

2. All unequivocally recognized metazoan trace fossils are restricted to an interval of geologic time not appreciably older than 700 m.y.

3. Trace fossil faunas found in separate geographic regions and in differing lithologies diversify upward toward and into the Cambrian, offering evidence that their record forms a part of the initial adaptive radiation of the Metazoa.

4. The Ediacara Fauna of Australia and equivalent soft-bodied faunas of other continents may represent a considerable span of geologic time. Some may predate the oldest skeletal faunas, and some may not.

5. Major skeletal taxa appeared sequentially, not simultaneously, as one aspect of the initial divergence of the Metazoa. The appearance of a skeletal record in the Cambrian was simply part of the general diversification and requires no special explanation.

6. The earliest (Tommotian) skeletal faunas contain certain unique and problematical taxa, as well as many important Cambro-Ordovician groups. Much of the pre-Tommotian record was produced by groups of coelenterates and worm-like creatures that had little use for skeletons. This condition and the metabolic difficulty of skeletal secretion account for what delay there was in the polyphyletic origin of skeletonization.

7. Stratigraphic correlation between trace fossil faunas and skeletal faunas is difficult because the former are found largely in clastic sedimentary rocks and the latter, in carbonate rocks. In most regions where early faunas of both types are found, however, trace fossils appear lower in the record. This fact supports the conclusion from zoological evidence and from the occurrence of the Ediacara Fauna and its equivalents that various early metazoan taxa originated without skeletons.

8. Skeletonization represented an important adaptive breakthrough for many groups, which in part accounts for the rapid diversification observed.

9. Rates of evolution documented by fossil data for the Precambrian-Cambrian transition are not extraordinrily rapid compared to rates of evolution observed in later adaptive radiations of the Phanerozoic.

10. The rectangular model of evolution, which holds that most evolution occurs in association with speciation, can easily account for polyphyletic high rates of evolution during the interval in question. The gradualistic model, which holds that most evolution is phyletic, or occurs within established species, offers no reasonable explanation.

ACKNOWLEDGMENTS

I thank Drs. P. E. Cloud, A. R. Palmer, and J. W. Schopf for their useful comments on the initial draft of this paper. Acknowledgement is made to the Donors of the Petroleum Research Fund, administered by the American Chemical Society, for partial support of this research, and to the National Science Foundation, for partial support (GA-40515).

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