BIOGEOGRAPHY AND BIOSTRATIGRAPHY

PRECAMBRIAN[1]

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CONTENTS

NAMES GIVEN TO PRECAMBRIAN NONMETAZOAN AND TRACE FOSSILS

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INTRODUCTION

Precambrian time comprises about seven-eighths of the time since the planet Earth came into being, or about five-sixths of the time represented by actually or potentially fossiliferous rocks. The ratio of fossil taxa of Precambrian age to younger ones can only be a minute fraction. The main reasons for this disproportionality have now become clearer. Although it is true that most Precambrian rocks have been so much altered that organic remains are not preserved in them, intensive exploration of less altered Precambrian sediments has indicated that during the greater part of Precambrian time organic evolution advanced only slowly. One-half of the entire time span of evolution for which there is fossil evidence produced only Procaryota, non-nucleated cells without organelles. The oldest "fossils" are microscopic bodies of simple structure and mostly spheroidal shape from rocks 3.1 to 3.4 billion years old. Their biogenic origin is at present controversial. Permineralized, cellular remains of Procaryota, the blue-green algae (Cyanophyta) and bacteria, have been found in many cherts of Proterozoic age. Stromatolites, large, layered, biogenic sedimentary structures in carbonates and siliceous sediments, are known from rocks about 3 billion years old. They are abundantly represented in Proterozoic sediments, commencing with some that are about 2.3 billion years old. "Stromatolitic, microbial biocoenoses of this time and the later Precambrian were based on filamentous photoautotrophs" (SCHOPF, 1975). They became markedly less abundant during the Paleozoic, but are still being formed today in restricted environmental conditions that are unfavorable for Metazoa. In some stromatolitic rocks the fossilized cells of blue-green algae and bacteria that caused their deposition have been observed. Some 20 different Proterozoic fossil microbiota are known, mostly from cherts associated with algal-laminated (stromatolitic) carbonate rocks. The best known are those described by BARGHOORN and TYLER (1965) and J. W. SCHOPF (1968). Eucaryotic cells, with traces of nuclei and evidence of cell division, appeared in middle to late Proterozoic time. SCHOPF (1972) claimed that spore-like cells about one billion years old may represent an early stage in the establishment of meiotic cell division, documenting the origin of sexuality that tended to spread variability, enhance selection and accelerate evolution, but this interpretation has been challenged (KNOLL & BARGHOORN, 1975). His later assessment (SCHOPF, 1975) "that the development of the megascopic, multicellular, eukaryotic level of organization was a relatively recent innovation, possibly occurring about 800-700 m.y. ago" is more likely. Sporomorphs or acritarchs of simple morphology are widespread and common in some Upper Precambrian shale and limestone, particularly those known to be less than 800 my[1] old.

Many biologists consider it as likely that the first "animal" Protista developed aerobic respiration and "cell-eating," herbivorous, and "carnivorous" habits almost as soon as eukaryotic cells evolved. STANLEY (1973) has drawn attention to the increase in organic diversity, which according to ecological theory would have followed the advent of heterotrophy and the development of new trophic levels after the long, purely resource-limited reign of relatively undiffer-

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[1] In conformity with current *Treatise* style, abbreviations of units of measure are written without periods, including "my" and "by" for "million years" and "billion years"; however, the author of this chapter disapproves of this style and prefers "m.y." and "b.y."

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entiated autotrophic prokaryotes; however, the chances of preservation of amoeboid or ciliate cells that lack resistant cell walls are infinitely less than those of fossilization of plant Protista. The long evolutionary pathways to the first animal Protista and from them to the first fossilizable Metazoa are unlikely to be documented in the rocks. At the present state of our knowledge all known Precambrian microfossils must be considered as plants in the widest sense of the term and therefore as outside the scope of this *Treatise*. No skeleton-forming Protista (Radiolaria, Foraminiferida) of Precambrian age are known. There are reports (DUNN, 1964; VOLOGDIN & DROZDOVA, 1970) of Proterozoic sponge spicules, which, if confirmed, would make the Parazoa the earliest animals with fossil representatives. There are also reports of bioturbation traces and burrows filled with fecal matter in Precambrian rocks from southern Norway and from the Soviet Union (SINGH, 1969; SABRODIN, 1971), which are more than 900 my old, and of "feeding burrows" in rocks about 750 my old (SQUIRE, 1973). Their interpretation as traces of ancient Metazoa requires confirmation.

From a practical, pragmatic viewpoint the known diversity of Precambrian fossils can be divided into the following categories: 1) filamentous and coccoid algal (and possibly fungal) cells, 2) sporomorphs and acritarchs, 3) megascopic algae, 4) stromatolites (and oncolites), 5) trace fossils, 6) problematic fossils (including microphytoliths), 7) metazoan body fossils.

Fossils in these categories are, in general, prepared and investigated according to different technical methods. Those in the first category are studied in thin sections by microscopy. Those in the second category have organic walls and are revealed and studied by palynological methods involving acid treatment of the rock matrix and concentration. Megascopic algae are investigated by other paleobotanic methods. Stromatolites are studied by and reconstructed from serial sections, in addition to studies of the microstructure of their layers. These categories of fossils are outside the scope of invertebrate paleontology. Trace fossils have been reviewed in a recently published volume of this *Treatise* (HÄNTZSCHEL, 1975) and the few names proposed for Precambrian genera are listed below (p. *A*112). A number of names, also listed below (p. *A*111), have been applied to fossils whose biogenic origin is here considered as problematic. Their substance may be partly organic but they do not necessarily represent formerly living organisms. Also included in this category are "microphytoliths" that were formed probably under the influence of some ill-defined organic activity on sedimentary processes, grading into the formation of oolites and spherulites. A few of these structures resemble fecal pellets; if they are that, their originators must be Metazoa.

The following discussion concerns mainly the last category, the body fossils of metazoan origin and their taxonomy. It is followed by lists of generic names that have been proposed for objects in the other categories and finally by a list of rejected and unrecognizable taxa. Many names have been given to configurations in Precambrian rocks that resemble metazoan or other organic remains, but which are now known or at least generally believed to be of chemical (concretionary) or mechanical origin. It will be noted that few of these names are of recent date. This hopefully indicates a significant advance in the approach to Precambrian paleontology since it was reviewed a decade ago (GLAESSNER, 1966) and a welcome clarification of the fossil record of Precambrian time.

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STRATIGRAPHIC DISTRIBUTION

The first definite metazoan body fossils appear in uppermost Precambrian strata (Upper Proterozoic; Vendian, upper Vendomian, or Terminal Riphean in the Russian literature; see Fig. 1). None of them is demonstrably older than the youngest Precambrian glacigene rocks ("tillites"). These fossils constitute a distinctive assemblage of marine animals that are characterized by the absence of mineralized skeletons or shells and by the prevalence of coelenterates, the presence of diversified polychaete annelids, and the rare occurrence of arthropods that are markedly more primitive than those occurring in Cambrian faunas. These assemblages document a definite pre-Cambrian level of metazoan evolution. They are collectively referred to as the Ediacaran faunas, after the locality where the first abundant finds were made by R. C. Sprigg in 1947. At the present time it is not possible to divide the occurrences of Precambrian bodily preserved Metazoa into a number of zonal assemblages defining a sequence of stratigraphic intervals preceding the Cambrian, but with the rapid increase in discoveries of Late Precambrian Metazoa and the advance in dating of sedimentary rocks containing them, this may become possible. The first discoverer of the fossils at Ediacara in South Australia considered their age to be Early Cambrian because this was the age conventionally and conveniently assigned to the rocks containing them, the Pound Quartzite, which had been placed at the base of the Cambrian in the regional stratigraphic scheme. There are now three basic reasons for placing these fossiliferous rocks below the Cambrian. Firstly, they do not contain any fossils that are found together with Cambrian faunas. Secondly, the Pound Quartzite is separated from rocks containing the first Lower Cambrian fossils by profound regional unconformities. Thirdly, similar fossils are found elsewhere, also not in synchronous association with, but below strata containing Lower Cambrian fossils. Most of these fossiliferous rocks cannot be dated precisely by geochronological methods, but all available evidence places them in the latest Precambrian (Vendian).

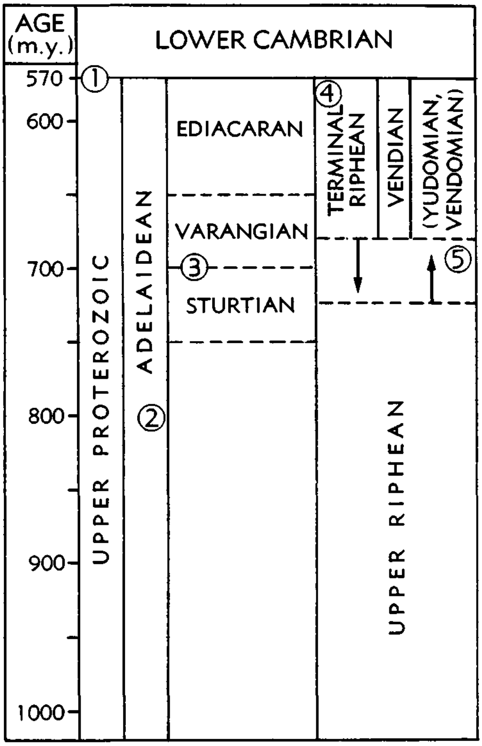

Fig. 1. Proposed subdivisions of the upper Proterozoic (Glaessner, n). (Numbers correspond to numbered statements below.)

1. Agreement on the definition of the Precambrian-Cambrian boundary is being sought by the International Commission on Stratigraphy through the efforts of a Working Group. Pending completion and adoption of its final report, position and dating of this boundary remain uncertain. There is substantial agreement that the Ediacaran faunas pre-date it and that the first appearance of trilobite body fossils is in the Lower Cambrian. A boundary stratotype is being sought between these two biohorizons.

2.The dating of the lower boundary of the Adelaidean is being investigated.

3. The general use of the three divisions in this column (as Periods) was proposed by W. B. Harland and K. N. Herod (Geol. Jour., Spec. Issue 6, Liverpool 1975, p.205). Their acceptance is conditional on agreement on boundary stratotypes and their dating relies on long-range correlations. Use of the terms Eocambrian or Infracambrian for their combined time span is not recommended. Both carry the undesirable implication of being subdivisions of the Cambrian. The term Infracambrian is said to have been applied originally to significantly older rocks.

4. The stratotype of the Riphean is in Bashkiria, on the western slope of the Ural Mountains. Paleontological studies have led to a four-fold division and to adoption by a number of Russian authors of "Terminal Riphean" for its uppermost part. This is correlated with the Vendian of the Russian platform and the Yudomian of Siberia. Some Russian stratigraphers (Keller, Semikhatov, and others) believe that adoption of the combined term Vendomian based on a combination of stratotypes will avoid existing difficulties

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GEOGRAPHIC DISTRIBUTION

Australia. The fossiliferous layers in the Pound Quartzite at Ediacara in South Australia (Fig. 2, Loc. 1) have yielded over 1,500 specimens. Two-thirds of them are coelenterates, most of them medusoids; not less than one-quarter are annelid worms and five percent are arthropods. Similar but poorer faunas are now known throughout the Flinders Ranges of South Australia, an area of approximately 100 × 200 km (Fig. 2, Loc. 2). All fossils come from one stratigraphic horizon of varying thickness, up to a maximum thickness of 112 m. An isolated locality in northwest South Australia, Punkerri Hills (130°25′ E, 27°40′ S, Fig. 2 Loc. 3), has yielded a large external mold of a remotely *Pteridinium*-like petaloid, probably representing the genus *Charniodiscus*; a single, smaller, similar specimen was found at the base of the Arumbera Sandstone south of Alice Springs in central Australia (Fig. 2, Loc. 4). At other localities in the same formation or its equivalents, the medusoids *Hallidaya* and *Skinnera* and abundant molds of *Arumberia* occur.

Southwest Africa. A rich fauna is preserved locally in the Upper Clastic Member of the Kuibis Formation at the base of the Nama Group (Fig. 2, Loc. 5) where *Rangea*, *Pteridinium*, *Namalia*, possibly a sprigginid worm and, in the uppermost part, Erniettidae occur in considerable numbers. The first two of these fossils are also recorded from the basal clastic member of the next higher Schwarzrand Formation. Above them, but in the same formation, a medusoid was found that was first recorded as *Cyclomedusa* but later as *Eoporpita*. Limestone members intercalated in both formations contain abundant worm tubes of the genus *Cloudina*. In the Nasep Quartzite Member of the Schwarzrand Formation a medusoid and the genus *Nasepia* were found. The upper part of the Nama Group contains only trace fossils. The fossiliferous outcrops of the Lower Nama Group extend over an area that is approximately equal to that of the fossiliferous Pound Quartzite in South Australia.

England. In the Precambrian of Charnwood Forest near Leicester (Fig. 2, Loc. 6), about 20 fossils were found on bedding planes of slaty tuffaceous siltstones (Woodhouse Beds) and described as *Charnia* and *Charniodiscus*. Both resemble fossils from Ediacara. Concentrically ribbed medusoid casts also occur.

Scandinavia. In northern Sweden, north and south of Lake Torneträsk (Strand & Kulling, 1972), two medusoid specimens with strong and regular concentric ribs were found in sandy shale, in what appear to be the youngest Precambrian strata, below Lower Cambrian with *Platysolenites, Volborthella*, and hyolithids (Fig. 2, Loc. 7).

Northern Russia. In a core taken at 1,552 m from a bore at Yarensk, some 750 km northeast of Moscow (Fig. 2, Loc. 9), a specimen of *Vendia* was found in siltstone of the Valdai "Series" (upper Vendian). A rich fauna of about the same age was found on the coast of the White Sea near Arkhangelsk (Fig. 2, Loc. 13). It includes *Pteridinium, Dickinsonia*, and several new genera, one of which resembles *Vendia.* These beds, which contain also acritarchs of the genus *Leiospheridia*, are considered as upper Vendian (Keller *et al.*, 1974). Another locality is farther east, on the river Pesha (Fig. 2, Loc. 12), where *Glaessnerina* was found.

Southwestern U.S.S.R. In outcrops along the river Dniestr, on the southwestern border of the Ukrainian massif (Fig. 2, Loc. 8), *Cyclomedusa* occurs together with other medusoid remains and trace fossils in siltstones and sandstones that are equivalents of the Valdai "Series" of the Vendian (Zaika-Novatskiy *et al.*, 1968; Paliy, 1969).

Northern Siberia. A specimen of *Glaessnerina* was found in the sandy dolomites

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(Continued from facing page.)

about defining the base of the Vendian.

5. The boundary between Upper and Terminal Riphean is stratigraphically and geochronologically uncertain. Absence of glacigene deposits in some and presence of one or of two glaciations in other areas cause problems as they have been used in boundary definitions. Long-range correlations used in assigning dates to boundaries and intervals lead to other problems.

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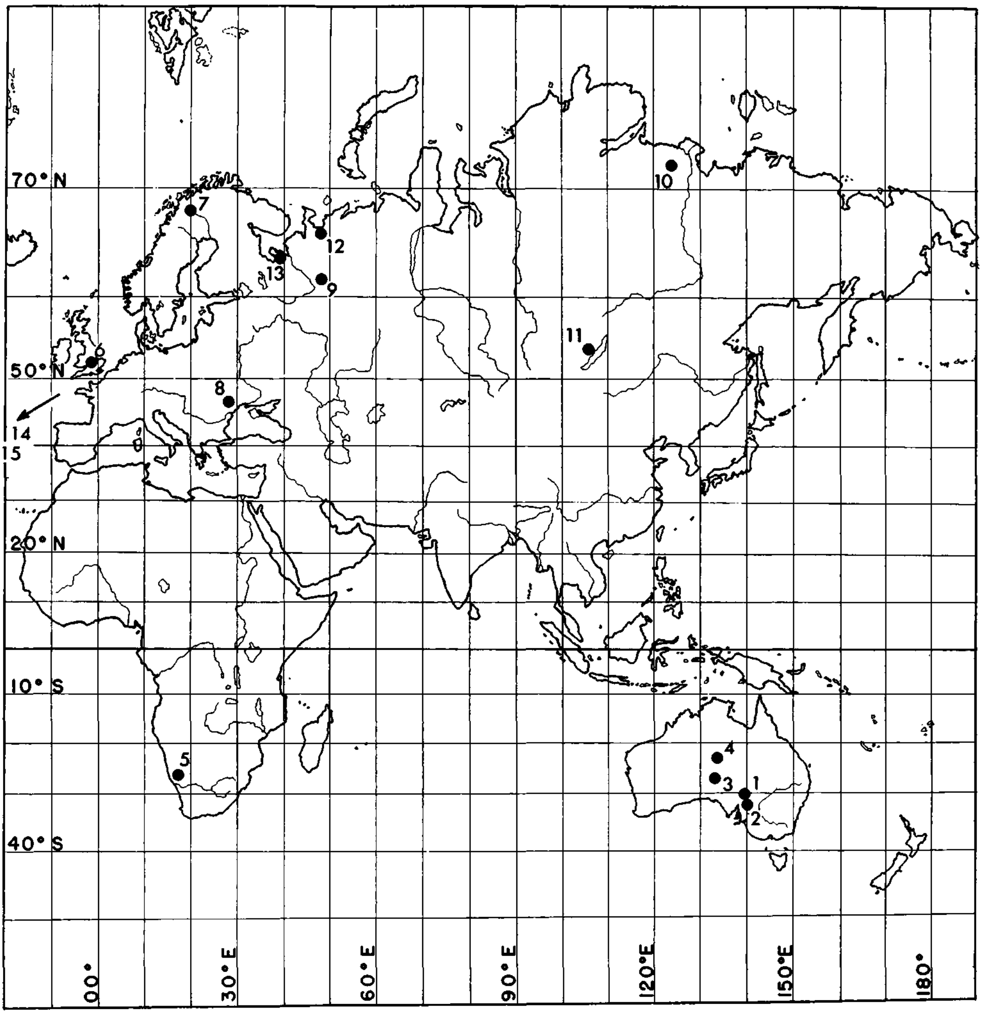

FIG. 2. Geographic distribution of Upper Precambrian fossil localities. The position of the North American localities (14, Newfoundland; 15, North Carolina) relative to Europe in Late Precambrian time is not precisely known but believed to have been at no great distance in the direction of the arrow (Glaessner, n). [For explanation of numbers see text, p. *A*83.]

of the Khatyspit Formation, in the uppermost Precambrian of the Olenek uplift (Fig. 2, Loc. 10) (SOKOLOV, 1973).

Lake Baikal region. Several fragmentary fossils were found west of Lake Baikal (Fig. 2, Loc. 11) in the Irkutsk "Series" at the top of the Precambrian sequence (SOKOLOV, 1973).

North America. Fossils occur abundantly in tuffaceous shales of the Conception Group near Mistaken Point, Avalon Peninsula, southeastern Newfoundland (Fig. 3). This fauna has yet to be described (MISRA, 1969). Large fossil worms were recently found in tuffaceous sediments of Late Precambrian age near Durham, North Carolina, and have been described by CLOUD *et al.* (1976).

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FIG. 3. Cast of impression of undescribed fossil (?hydrozoan colony) from the Upper Precambrian of Newfoundland (Misra, 1969), ×0.85.

CHRONOSTRATIGRAPHIC DATA

The ages of few of the known assemblages of Late Precambrian fossils have been fixed directly by radiometric methods. By the use of combined data from known ages of tillitic rocks occurring in some sequences below the fossiliferous sediments, and from their relations to overlying Lower Cambrian strata, a probable age range of the known occurrences of Precambrian metazoan body fossils can be deduced. These approximate datings confirm a rough correlation of these fossiliferous rocks but they do not support any biostratigraphic subdivision at the present state of our knowledge.

The oldest occurrence of metazoans in Australia is significantly younger than the youngest tillitic rocks. Such rocks have been dated directly only in northwestern Australia where no Precambrian metazoan fossils are known. The minimum age of the youngest glaciation in this area is 660 to 670 my. This is compatible with the dating of other upper Proterozoic rocks in central and South Australia. A correlation of the glacigene strata in these areas is widely accepted. A claim for alternation of tillitic and fossiliferous rocks in the Nama Group in southwest Africa was made by GERMS (1972a). The Nama Group has not yet been dated directly but it is known to be older than 510 and significantly younger than 720 my. The fossiliferous lower part may correspond, in part, to the interval from 600 to 650 my. This is in agreement with the polar wandering curve based on the latest paleomagnetic data (MCELHINNY *et al.*, 1974) and the pre-Nama age of the Numees Tillite. The widespread glacigene rocks ("Varangian") found around the Baltic and Ukrainian shields in northeastern Europe occur below the fossiliferous strata in the Vendian sequence wherever the stratigraphic relations between them can be observed. The K-Ar dating of glauconites from the fossiliferous Upper Precambrian strata of the Soviet Union (northern Russia and Baikal area) gave ages near or slightly younger than 600 my. If corrected for the use of the generally accepted decay constant ($\lambda_e = 0.585 \times 10^{-10}$), these ages would be approximately 575 to 580 my. The fossiliferous strata in the Ukraine are considered to be of about the same, middle to late Vendian, age. The northern Siberian occurrence is in a rock series that was dated on glauconite at 670 my. This should be similarly corrected to about 640 my. The age of the fossiliferous strata of the Conception Group of southeastern Newfoundland has not been determined directly. It is believed by ANDERSON (1972) to be 610 to 630 my. The use of a slightly different decay constant for Rb^{87} (1.42×10^{-11}), which is now recommended, may reduce these numbers to about 590 to 610 my. The latest find of fossils in North Carolina (CLOUD *et al.*, 1976) was made in rocks that are

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known to be 620 my old. There is reason to doubt the previously accepted date of 680 my for the age of the fossiliferous Charnian rocks in England (Dunning, 1975). Except for this doubtful instance, the stratigraphic positions of rocks with Ediacaran assemblages of fossil Metazoa tend to fall in the age range from 575 to 640 my. This equals the length of the Tertiary Period. Only a few trace fossils may be older, but none is likely to be older than 1,000 my, except the as yet unconfirmed finds of sponge spicules in the Middle Proterozoic rocks of eastern Siberia and Australia, which are about 1,500 my old.

PALEOECOLOGY AND TAPHONOMY

With a few localized exceptions, metazoan fossils of Precambrian age are rare. This is only partly due to peculiarities of the Precambrian environment. Prior to the acquisition of mineralized skeletons, relatively few fossils would have been preserved in the sediments. Shells and skeletons were an evolutionary novelty essentially of Cambrian and later age. The total number of Metazoa able to leave traces of their locomotion or feeding on the surface of sediments or within them (bioturbation) must have been smaller in Late Precambrian time than in the Early Cambrian. In many sequences of unaltered clastic rocks extending across the Precambrian-Cambrian boundary, for example in the United States, in Scandinavia, and in Australia, there are few and relatively undifferentiated trace fossils in the Precambrian, contrasting with their abundance and diversity in the Lower Cambrian. A lower level of evolutionary differentiation compared with that in the early Paleozoic undoubtedly contributed to the poverty of the Precambrian fossil record. Nonenvironmental factors make it difficult to deduce the nature of environmental changes at the beginning of the Cambrian directly from the results of comparative paleoecological studies. Almost any conceivable change in the environment claimed to be unique in character or magnitude has been held responsible for the poverty of the Precambrian fossil record: absence of sedimentation during the supposed "Lipalian interval"; dominance of shallow or of deep water; change in salinity or in temperature, or in the distribution of continents and oceans; and changes in the composition of the atmosphere. With the exception of the now disproved "Lipalian interval," all other factors could have contributed but they were not uniquely active during the Precambrian-Cambrian transition.

The assumption that the amount of oxygen in the atmosphere reached a significant threshold value (one percent of the present level) at the beginning of the Cambrian was based originally on the then current belief that prior to that point in time there was no animal life and no oxydative respiration, and that the absence of the ozone shield permitted ultraviolet radiation to penetrate most of the photic zone, excluding from it phytoplankton and thus reducing primary nutrient supply from the ocean and its floor. This view is no longer tenable.

A distinctive phase in the history of the Metazoa, older than the earliest Cambrian, is now known. It is characterized by the following ecologically significant features: 1) exclusively microphagous feeding and absence of large predators; 2) presence of numerous surface- and bottom-feeding coelenterates; of benthonic, probably detritus-feeding worms; of the first few arthropods; 3) occupation of a variety of marine habitats such as near-shore areas with sandy and silty bottom (Australia, southwest Africa), shallow-water muddy areas (eastern Europe), deeper water with turbidity current activity (Newfoundland), and occasionally areas of carbonate deposition (southwest Africa, possibly northern Siberia). The biogenic reef environment is notably absent. Algal mats and columnar stromatolitic structures could flourish in normal marine littoral to sublittoral environments without being affected by grazing. No clear environmental grounds for the absence of tissue mineralization can be deduced from present observations and the lack of basic differences between Precambrian and younger sediments (apart from the absence of skeletal carbonate rocks) makes their existence unlikely. It is probable that the complex

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biochemical basis for the formation of mineralized shells and skeletons had not evolved by the time of the first appearance in the record of megascopic Metazoa. This evolutionary novelty was heralded by the appearance of the first agglutinated, calcareous worm tubes (*Cloudina*).

It must be remembered that large numbers of marine invertebrates without mineralized tissues still flourish in the present oceans (Siphonophora, Actiniaria, Ctenophora, Chaetognatha, Aschelminthes, Platyhelminthes, Sipunculida, Nudibranchia, Aplacophora, Annelida, Euphausiacea, Tunicata, etc.). Most of them, although almost certainly quite ancient, have left no fossil record or only an insignificant one, except the annelids that acquired in Late Precambrian time the ability to build calcareous tubes. Collagen fibers and probably chitinous deposits accounted for the stiffness of many of the "soft-bodied" organisms in the Ediacara fauna, such as medusae, chondrophoran hydrozoans, and a conulariid. In "Petalonamae," silicified fibrous tissues have been observed but other microscopic structures described in this group could well be the result of alteration by silicification and weathering. Where the fossils are preserved as casts and molds, the mechanical deformability of soft bodies in more or less compressible sediments makes interpretation difficult. Partly decomposed bodies are preserved, and in others shrinkage or contraction of muscles occurred after the first contact between body and sediment. Even the escape of organic decomposition products to the sediment surface can produce trace fossils (in the sense of "*Spurenfossilien*" or signs of former presence of life, not of "*Lebensspuren*" or traces of life activities), for example, *Pseudorhizostomites* (Wade, 1968). The amazing variability of many of the Ediacara and most of the Nama fossils may be largely due to taphonomic factors; however, it is possible that the characters of medusae from Ediacara, and of "Petalonamae" from both regions, may not have been as stable as had been expected by the first observers who named them. It is not yet possible to assess the relative significance of phenotypic and genetic varibility in these ancient fossil organisms or to state unequivocally that variability was uncommonly great compared with that of the present fauna.

Much work remains to be done before the composition of these assemblages is sufficiently well known to be analyzed in terms of community structure and ecological factors. Though they are thanatocoenoses, the fact that they consist of more or less easily decomposable soft-bodied animals means that at each locality they are strictly contemporaneous and that most of them must have lived within short distances of their place of burial. The "Petalonamae" are almost certainly sessile coelenterates and many of them were embedded where they lived. Medusae and chondrophores drifted inshore from the sea in swarms, as they still do today. Worms and small arthropods fed on the organic detritus and may have provided food for the large medusae. Meander traces of feeding on sedimentary surfaces prove that the detritus was abundant and that it was exploited, as was the organic content of the sediments, though apparently to a limited extent. This limited picture will be augmented by an analysis of other biofacies when the faunas from Newfoundland and other newer localities are described. It is not likely to be changed fundamentally. (For imaginative, comprehensive views on Precambrian evolution and environments see Cloud, 1968, 1974, 1976a,b; Fischer, 1972).

EVOLUTIONARY SIGNIFICANCE

The Ediacaran faunas are the earliest known assemblages of Metazoa. They differ fundamentally in their composition from Cambrian and younger assemblages; they appear to have been preceded by a long, undocumented phase of metazoan evolution. The most advanced members are relatively undifferentiated arthropods. They include *Parvancorina,* possibly ancestors of notostracan Crustacea, and *Praecambridium* and *Vendia,* which resemble either primitive Trilobitomorpha or Merostomata. The level of differentiation indicated by the first Cambrian Crustacea, trilobites, and Merostomata

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had obviously not yet been reached but the distinction of the first from the other two lines is already indicated. In this context it is significant to recall MANTON's (1969, p. R53) remark: "The head shields and limbs of the Merostomata and Trilobita have more in common than either had with the heads and limbs of Crustacea." Pending the discovery of the limbs of *Praecambridium* it can be said that there is now some paleontological evidence for MANTON's view of the early relations and differences between arthropod lineages (MANTON, 1969, p. R8, Fig. C).

In contrast with the arthropods, the annelids are represented by four very different orders. Two of them are still extant and may be considered as relatively primitive polychaetes. The other two are represented only by simple or complexly structured tubes that are so different from younger ones that these orders must be considered as extinct after the Early Cambrian.

It has long been known that the Ediacaran faunas are dominated by coelenterates, in number of taxa as well as of individuals. At first it seemed easy to distinguish between hydrozoan and scyphozoan medusae and to place most of the fossils in extant orders (see this *Treatise*, Part F, 1956). This is no longer considered as justifiable, for two reasons. Firstly, the preservation of these soft-bodied organisms is such that diagnostic characters are not usually ascertainable, and secondly, the taxonomic characters by which orders are defined in the living fauna may not have existed in Precambrian time. It is now obvious that as much evolutionary change has occurred at lower grades of metazoan organization, such as the coelenterate grade, as at some higher ones. Notwithstanding these difficulties, some answers to phylogenetic problems posed by living coelenterates can now be based on the results of studies of Ediacaran fossils. Chondrophoran hydrozoans have been recognized because of the preservability of their distinctive chitinous pneumatophores. The genera *Ovatoscutum* and *Chondroplon* had many Paleozoic successors. Among them was probably the late Early or early Middle Cambrian *Velumbrella* with its stiffly radiating ribs indicating floating rather than medusoid contractile swimming locomotion. Other chondrophorans are *Archaeonectris* (Ord.-L.Sil.), *Discophyllum* (Ord.), *Palaeonectris* (Dev.), *Plectodiscus* and *Paropsonema* (Sil.-U.Dev.). Compared with this relative abundance, the sole living genera *Velella* and *Porpita* are seen as survivors of an ancient and formerly diverse group of hydrozoans that early discovered the surface of the sea as a feeding area and adapted to it. Diversity was strikingly reduced in late Paleozoic time by competition or predation. The resemblance of the floats of *Ovatoscutum* and *Chondroplon* to those of the surviving Porpitidae is so specific that we can be sure of the hydrozoan affinities of these Precambrian fossils, without confirmation from polyp morphology. *Conomedusites* is now considered as related to the Conulariida, a subclass of the Scyphozoa. This placement was confirmed by comparison of Paleozoic conulariids with living chitinous *Stephanoscyphus*, a coronatan polyp form (WERNER, 1966). Though this comparison was disputed by KOZŁOWSKI (1968), early growth stages of conulariids found by him are identical with hydrozoan hydrorhizae (GLAESSNER, 1971). This establishes an early link between the Hydrozoa and the Scyphozoa to which several Ediacaran medusae are assigned. Whether other medusae, including the great majority of specimens in the Ediacaran assemblages, have hydrozoan or scyphozoan affinities cannot be established.

In the absence of polyps the precise zoological affinities of a large number of Precambrian, sessile benthonic, colonial forms with strong resemblances to some living Pennatulacea cannot be established. There are no reasons why they should be placed in a higher than coelenterate structural grade and there is no justification for speculation about the possibility of evolutionary links between these Metazoa and unspecified Metaphyta as suggested repeatedly by PFLUG (1974a) following the now generally discounted views of HARDY (1953). PFLUG proposed the name "Petalonamae" for this group of intergrading but highly diversified fossil organisms. Some of them have striking and specific structural resemblances to living Pennatulacea, but in the absence of traces of fossil polyps, the possibility of convergence between Precam-

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brian Hydrozoa and later octocorallian Anthozoa cannot be excluded. The silicified and calcified cellular tissues described by PFLUG in some "Petalonamae" are here considered as the effects of fossilization. No spicules are preserved and fractureless folding-over or bending of many of these leaf-shaped fossils proves the absence of biogenic mineralization of their tissues. If the "Petalonamae" include ancestral Pennatulacea, the Anthozoa must have separated early from the Hydrozoa, before these evolved a medusoid stage as a locomotive and reproductive stage in their life cycle. The Scyphozoa appear to have evolved from Hydrozoa not long before the time of the Ediacaran faunas, and to have elaborated the medusoid at the expense of the polyp stage.

The early Metazoa were almost certainly planula-like and very small. Their chances of preservation were minimal, also because of the absence of resistant integuments or cell walls, or of readily mineralized mucous sheaths that enabled Precambrian plant microfossils to be preserved in large numbers. The undetected and probably undetectable evolution from amoeboid or ciliate cells to cell colonies and to tissue grade could well have taken as much time as the entire Phanerozoic phase of metazoan evolution. Between the attainment of tissue grade and the level of the Ediacaran faunas lies the evolution of the mesoderm and the coelom, which must have preceded the observed diversification of the annelids and arthropods. These processes could have occurred in late Proterozoic (late Riphean) time, within a time span of some 300 my, preceding the oldest Ediacaran fauna. It is possible that further discoveries or reinterpretations will extend through this time interval the range of either such body fossils as have been found at Ediacara, or definite trace fossils, or bioturbation, or microcoprolites. Such finds have been announced, but not yet convincingly described or stratigraphically documented.

The scarcity of Precambrian traces of animal life compared with Cambrian and later ones may be indicative of an abrupt increase in total metazoan abundance (biomass) about the beginning of Cambrian time. It was probably related to changing oceanographic conditions. About that time, but not simultaneously, many (but by no means all) invertebrates acquired mineralized tissues (shells or skeletons). Some polychaete worms (*Cloudina, Anabarites*) appear to have been the first to take this step in evolution by building calcareous tubes. At the beginning of Cambrian time they were followed by archaeocyathans, brachiopods, gastropods, Hyolithelminthes, Tommotiidae, and Hyolithida (of uncertain affinities), later by trilobites, crustaceans, and echinoderms. It should be noted that the unique *Xenusion* (see this *Treatise*, p. O19-O20), formerly considered as a Precambrian fossil, has now been convincingly traced to a basal Cambrian source bed (JAEGER & MARTINSSON, 1967), and that the hyolithid *Wyattia* (TAYLOR, 1966) is probably also of earliest Cambrian age. Some groups of invertebrates are so highly differentiated at the time of their first appearance in the Early Cambrian that the existence of unknown ancestors in Late Precambrian time has been assumed. Mollusca, small brachiopods, and various small arthropods could have been present in Ediacaran time without possessing mineralized shells and without leaving fossil evidence. Some Precambrian tracks show a degree of complexity that suggests mollusks as their originators. The earliest trilobites were markedly thin-shelled. The fact that numerous marine arthropods with unmineralized, thin, chitinous exoskeletons still exist in large numbers, whereas their fossil representatives are unknown, suggests why the Precambrian ancestors of the trilobites have not been fossilized. In contrast to this group, the earliest Cambrian Archaeocyatha (ROZANOV, 1973) are rare and structurally primitive and may not have had a long history. The early stages in the evolution of the echinoderms (UBAGHS, 1971) are problematic. They are highly differentiated in early Cambrian time and yet it is difficult to postulate their existence in the Precambrian as unmineralized, minute, and unfossilizable creatures, without their distinctive calcite skeleton. One genus in the Ediacara fauna, *Tribrachidium*, has no trace of calcareous plates, yet resembles nothing as much as some Edrioasteroidea; however, they are not considered as primitive echinoderms. The problem remains unsolved. So does the question

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of the origin of the deuterostomatous phyla Hemichordata and Chordata. It has been claimed that the organic-walled tubes of the Sabelliditida that are found in the Riphean and Vendian represent the Pogonophora (Sokolov, 1967, 1972). They have been considered as aberrant "Deuterostomata" but zoologists are no longer unanimous about the placing of the Pogonophora in the system of the Metazoa (Nørrevang, 1975).

Although Precambrian fossils are rarely mentioned in current discussions on problems of metazoan evolution and relationships, the Late Precambrian faunas can contribute important data. Their effective use will depend on speedy and comprehensive description of the collected specimens and also on a deeper understanding of the chemical and mechanical alteration of their soft, organic material in the course of fossilization.

SUPRAGENERIC TAXA OF PRECAMBRIAN METAZOA

Figures in parentheses indicate numbers of included genera.

- ?Phylum Porifera
  - Class, order, family uncertain (1)
- Phylum Coelenterata
  - Subphylum Cnidaria
    - Class Hydrozoa
      - Order Hydroida
        - Suborder Chondrophorina
          - Family Chondroplidae (2)
          - Family Porpitidae (1)
    - Class Scyphozoa
      - Family uncertain (5)
    - Class Conulata
      - Order Conulariida
        - Suborder Conchopeltina
          - Family Conchopeltidae (1)
    - Medusae of uncertain affinities (8)
    - Problematical Coelenterata
      - Family Pteridiniidae (1)
      - Family Rangeidae (1)
      - Family Charniidae (3)
      - Family Erniettidae (5)
      - Family uncertain (4)
- Phylum Annelida
  - Class Polychaeta
    - Order Cribricyathea
      - ?Family Vologdinophyllidae (1)
    - Order uncertain
      - Family Dickinsoniidae (1)
      - Family Sprigginidae (2)
      - Family Anabaritidae (1)
- Phylum Arthropoda
  - Superclass Trilobitomorpha (or Chelicerata)
    - Class and order uncertain
      - Family Vendomiidae (4)
  - Superclass Crustacea
    - Class Branchiopoda
      - Order unknown
        - Family Parvancorinidae (1)
- Doubtful Arthropoda (1)
- ?Phylum Pogonophora
  - Order Sabelliditida
    - Family Saarinidae (1)
    - Family Sabelliditidae (1)
- Phylum uncertain (3)
- Doubtful invertebrates
  - Family Suvorovellidae (2)
  - Family uncertain (1)

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SYSTEMATIC DESCRIPTIONS[1]

?Phylum PORIFERA Grant, 1872

Class, Order, and Family UNCERTAIN

Tyrkanispongia VOLOGDIN & DROZDOVA, 1970, p. 197 [**T. tenua*; OD]. Siliceous, straight or curved, fragmentary spicules, hollow, with pointed, rounded or narrowed ends, diameter 40-110 μm, occurring together with hook-shaped and globular siliceous bodies of similar size. [The fragmentary preservation and the unusual shape of spicules with narrowed or hooked tips does not support unequivocal assignment of the *"Tyrkanispongia"* assemblage to the Porifera. The rocks containing it are 1,500-1,550 my old. The only other documented Precambrian occurrence of apparent sponge spicules are triact-like shapes observed in thin sections of cherts from the Carpentarian of northern Australia, about 1,500 my old (DUNN, 1964). In the absence of clear axial canals it is difficult to distinguish supposed sponge spicules from glass shards of volcanic origin where only thin sections are available.] *U.Precam.(Gonam "Ser."),* E.Sib. (Uchur R.).

Phylum COELENTERATA Frey & Leuckart, 1847

[See this *Treatise*, 1956, p. *F*9]

Class HYDROZOA Owen, 1843

[See this *Treatise*, 1956, p. *F*67]

Order HYDROIDA Johnston, 1836

[See this *Treatise*, 1956, p. *F*83]

Suborder CHONDROPHORINA Chamisso & Eysenhardt, 1821

[See this *Treatise*, 1956, p. *F*148]

The status of this suborder is uncertain. It is widely accepted that it does not belong to the order Siphonophorida to which it had been subordinated in earlier zoological classifications, but to the order Hydroida. Within it, relations to the suborder Athecata are so close that some authors included the chondrophorans in the athecate hydrozoans. One or two living monotypic families are recognized and several Paleozoic genera are included in them; for *Palaeoscia* CASTER, 1942, see also HÄNTZSCHEL, 1975, p. *W*147.

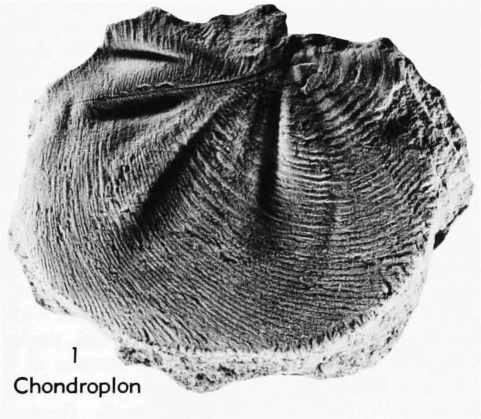

FIG. 4. Chondroplidae (p. *A*91-*A*92).

Family CHONDROPLIDAE Wade, 1971

[Chondroplidae WADE, 1971, p. 188]

Float chambered, bilaterally symmetrical, axis narrow, chambers narrowing from one end of the axis to the other, leaving a notch between them either at the narrow or at both ends. *U.Precam.(Vend.).*

Chondroplon WADE, 1971, p. 184 [**C. bilobatum*; OD]. Float large, bilobed, with rounded outline, axis strongly marked as ventral groove and probably as blunt dorsal keel, initial chamber large and elongate, early chambers annular, later chambers leaving peripheral notch where they are wide, last-formed chambers leaving notch also at opposite end where they are narrow and disposed transversely; their outer ends form a scalloped margin; chambers higher than wide, separated by depressed sutures. [Conspicuous, large, radial folds on the surface of the only known specimen were considered as fortuitous by WADE.] *U.Precam.,* S.Australia.——FIG. 4,*1*. **C. bilobatum,* Ediacara; holotype, ×0.32 (Wade, 1971).

Ovatoscutum GLAESSNER & WADE, 1966, p. 612 [**O. concentricum*; OD]. Float shieldlike, with weakly marked axis, initial chamber small, oval,

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[1] After completion of the typescript for this chapter, the discovery of a Precambrian microscopic flatworm (*Brabbinithes churkini* ALLISON, Class Turbellaria) was announced (ALLISON, 1975). It is 0.45 mm long, apparently known only from one thin section, and comes from the Tindir Group of eastern Alaska, which is correlated with the Rapitan Formation in northwestern Canada; its age is less than 850 my. Regrettably, the available morphological data are not sufficiently well defined to support the author's far-reaching evolutionary conclusions. CLOUD, WRIGHT, & GLOVER (1976) now prefer an interpretation of this fossil as an hexactinellid sponge spicule.

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surrounded concentrically by narrow, elongate, sinuous chambers, leaving a somewhat ill-defined triangular notch in peripheral margin where they are narrowest; notch is situated axially but does not reach center; chambers separated by deep, narrow grooves. *U.Precam.*, S.Australia.——FIG. 5,*1*. **O. concentricum*, Ediacara; holotype, ×0.8 (Glaessner & Wade, 1966).

Family PORPITIDAE Brandt, 1835

[See this *Treatise*, 1956, *p.* F150]

Eoporpita WADE, 1972, p. 198 [**E. medusa*; OD]. Circular or elliptical in outline, two groups of club-shaped polypides, outer ones of nearly constant lengths and in several series, inner series with inwardly reducing size, grouped around single, large, central cone; above them, the remains of a delicate float with numerous narrow, concentric, annular, chambers surrounding small, circular, central chamber; aboral side of disc showing faint radial striae. [It seems reasonable to consider the outer series as dactylozooids, the inner series as gonozooids, and the larger central cone as the gastrozooid, when comparing these fossils with the living *Porpita* LINNÉ.] *U.Precam.*, S.Australia. ——FIG. 6,*1*. **E. medusa*, Ediacara; paratype, ×0.6 (Wade, 1972a).

FIG. 6. Porpitidae (p. A92).

Class SCYPHOZOA Götte, 1887

[For diagnosis see this *Treatise*, 1956, p. F27]

The following genera are assigned to the Scyphozoa with varying degrees of uncertainty because of incomplete preservation and morphological and evolutionary remoteness from other fossil and living genera. They are not at present placed in orders or families. Among the Precambrian "Medusae of uncertain affinities" (p. A94), *Rugoconites* has been provisionally restored as a scyphozoan (WADE, 1972).

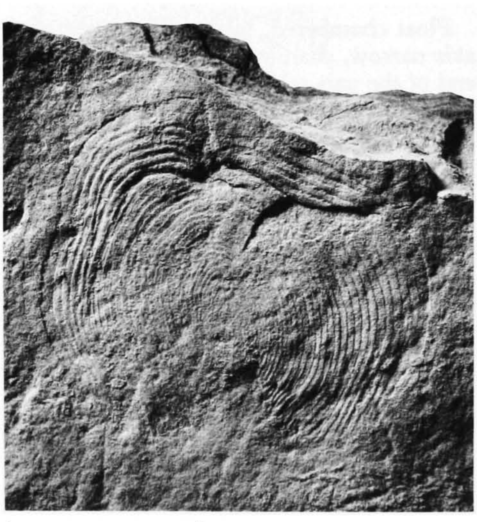

FIG. 5. Chondroplidae (p. A91-A92).

Family UNCERTAIN

Albumares FEDONKIN in KELLER & FEDONKIN, 1976, p. 38 [**A. brunsae*; OD]. Disc shield-like, lobate, with 3 circumoral ridges narrowing radially; delicate gastrovascular canals, 3 on each lobe, dividing dichotomously 4 times each toward the periphery; over 100 short, very thin, marginal tentacles. Resembling *Skinnera* which differs in absence of fine, dichotomously branching canals, lobes and tentacles. *U.Precam.(U.Vend.)*, N.Russia.

Brachina WADE, 1972, p. 207 [**B. delicata*; OD]. Discoid medusa with numerous small marginal lappets attached to an outer ring; on exumbrellar side two concentric outer grooves, an inner groove and a central peak; on subumbrellar side probably with a small, conical manubrium, outwardly branching and inwardly anastomosing gastrovascular canals, and apparently an annular gonad. *U. Precam.*, S.Australia.——FIG. 7,*3*. **B. delicata*, Brachina Gorge; *3a*, reconstr., ×0.5; *3b*, holotype, int. mold, ×1.5 (Wade, 1972a).

Hallidaya WADE, 1969, p. 356 [**H. brueri*; OD]. Discoid medusa with truncated margin, low-domed or flat, with scattered "nuclei" (3-13) near center;

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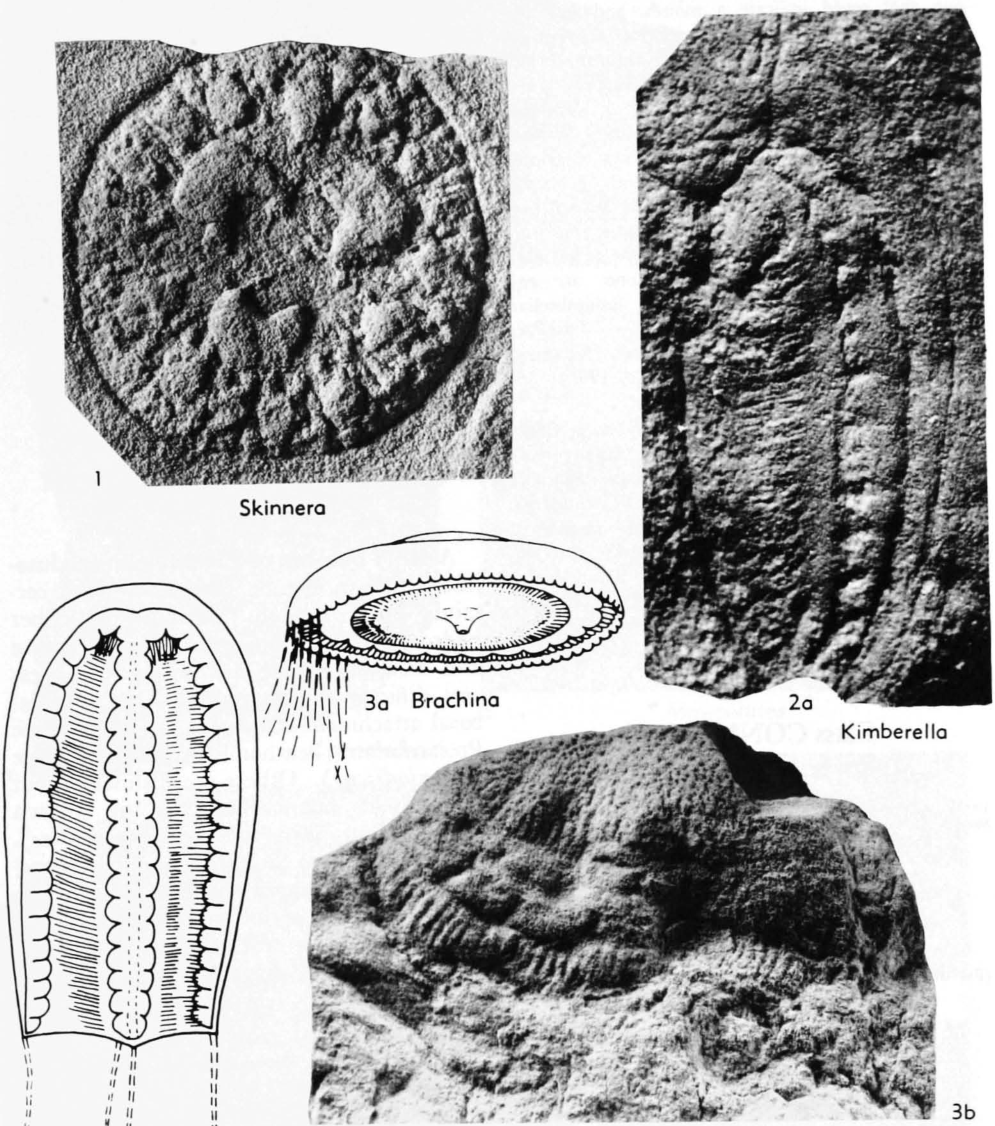

FIG. 7. Family uncertain (p. *A*92-*A*94).

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some specimens with a rayed subcentral impression that could indicate a mouth, and dichotomous, radial furrows near periphery. *Uppermost Precam.,* C.Australia.——FIG. 7,*4*. **H. brueri,* Mt. Skinner; paratype, ×1 (Wade, 1969).

Kimberella WADE, 1972, p. 215 [*pro Kimberia* GLAESSNER & WADE, 1966 (*non* COTTON & WOODS, 1935)] [**Kimberia quadrata* GLAESSNER & WADE, 1966; OD]. Elongate, slender bell, probably squarish in transverse section, with 4 pouched gonads attached to radial canals projecting into cavity of bell; gastric filaments present adapically; conspicuous transversely striated zones are explained as representing contracted subumbrellar muscle bands. *U.Precam.,* S.Australia.——FIG. 7,*2*. **K. quadrata* (GLAESSNER & WADE), Ediacara; *2a,* holotype, ×1 (Glaessner & Wade, 1966); *2b,* reconstr. (Wade, 1972a).

Skinnera WADE, 1969, p. 361 [**S. brooksi*; OD]. Disc-shaped, probably originally plano-convex, with 3 large inner "pouches" and, connected with them by paired canals, 15 outer (secondary) "pouches" symmetrically placed near periphery. [According to WADE, "the shape of the internal system of spaces and canals closely parallels the gastrovascular system of a medusa of the scyphozoan grade of complexity."] *Uppermost Precam.,* C.Australia.——FIG. 7,*1*. **S. brooksi,* Mt. Skinner; holotype, ×2 (Wade, 1969).

Class CONULATA
Moore & Harrington, 1956

[*nom. transl.* GLAESSNER, 1971, p. 15 (*ex* Subclass Conulata MOORE & HARRINGTON, 1956, p. *F*28)] [For diagnosis see Subclass Conulata, this *Treatise,* 1956, p. *F*28]

Order CONULARIIDA
Miller & Gurley, 1896

[For diagnosis see Suborder Conulariina, this *Treatise,* 1956, p. *F*58]

Suborder CONCHOPELTINA
Moore & Harrington, 1956

[For diagnosis see this *Treatise,* 1956, p. *F*57]

Family CONCHOPELTIDAE
Moore & Harrington, 1956

[For diagnosis see this *Treatise,* 1956, p. *F*57]

Conomedusites GLAESSNER & WADE, 1966, p. 608 [**C. lobatus*; OD]. Theca forming low cone with concentric rugosities, divided by 4 deep radial grooves; peripheral margin correspondingly with 4 lobes, each of which may be further subdivided by a shallow indentation; fringe of rather thick tentacles may be preserved around peripheral margin. *U.Precam.,* S.Australia.——FIG. 8,*1*. **C. lobatus,* Ediacara; ×0.7 (Glaessner, 1971).

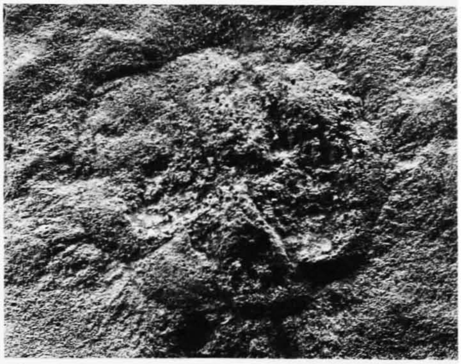

FIG. 8. Conchopeltidae (p. *A*94).

MEDUSAE OF UNCERTAIN AFFINITIES

A large number of Precambrian medusa-like fossils cannot be recognized with certainty or even high probability as either hydrozoan or scyphozoan in their structure and affinities. Some are rather featureless and difficult to distinguish from discoidal basal attachment structures known in some Precambrian benthonic cnidarians (see *Charniodiscus*). Others are distinctive, but only their exumbrellar side is known (*Mawsonites, Planomedusites, Rugoconites*). Others again are so variable, either inherently (*Ediacaria*) or because of varying degrees of decomposition (*Pseudorhizostomites*), that their true morphology cannot be discerned and diagnosed.

Cyclomedusa SPRIGG, 1947, p. 220 [**C. davidi;* OD] [=*Madigania* SPRIGG, 1949, p. 93 (*non* WHITLEY, 1945); *Tateana* SPRIGG, 1949, p. 86; *Spriggia* SOUTHCOTT, 1958, p. 59]. Outline subcircular, surface of disc with several to many concentric grooves separating slightly elevated areas (rugae); their arrangement indicates an originally conical shape of the center or, in some species, of most of the body. Many specimens show fine, straight, radial grooves interpreted as gastrodermal canals showing on surface because of partial composite molding. [The oral surfaces of these commonly occurring medusae are unknown. They may have been attached by their aboral cones. WADE (1972a, p. 204) placed *Cyclomedusa* under "Class Hydrozoa?" A very similar genus, *Tirasiana,* was named by PALIY in a dissertation abstract dated 1975 but it remained unpublished until BEKKER (1977) published *T. concentralis* n. sp. from the Vendian of the W. Ural.]

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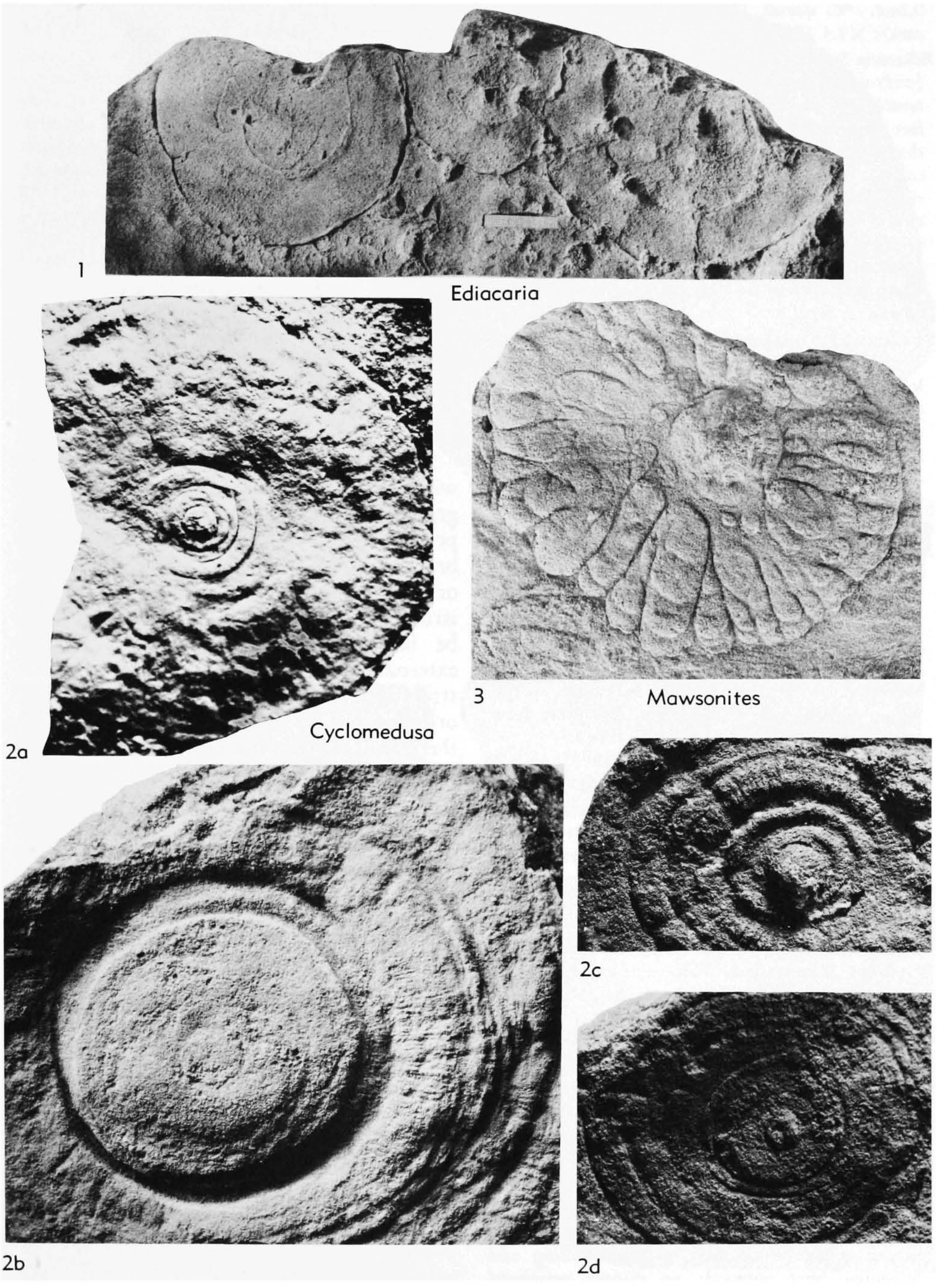

Fig. 9. Medusae of uncertain affinities (p. *A*94-*A*96).

U.Precam., S.Australia-SW.Afr.-S.USSR-N.Swed.-E.Sib.——Fig. 9,2*a*. *C. plana* Glaessner & Wade, U.Precam., SW.USSR (Dnjestr R., Ukraine); ×0.67 (Zaika-Novatskii *et al.*, 1968).——Fig. 9,2*b*. *C. gigantea* Sprigg, U.Precam., Australia (Ediacara); holotype, ×1 (Sprigg, 1949).——Fig.

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9,2*c,d*. **C. davidi*, U.Precam., S.Australia (Ediacara); ×1.4 (Sprigg, 1949).

Ediacaria Sprigg, 1947, p. 215 [**E. flindersi*; OD] [=*Protodipleurosoma* Sprigg, 1949, p. 79; ?*Beltanella* Sprigg, 1947, p. 218]. Exumbrellar surface showing central disc and an outer ring; sharp circular furrow may mark edge of gastric cavity; radial furrows mostly confined to outer ring; on subumbrellar surface a rounded central mouth without appendages; one specimen appears to show numerous, long, fine, peripheral tentacles. *U.Precam.*, S.Australia.——Fig. 9,*1*. *E.* sp., Ediacara; 3 specimens on slab, ×0.3 (fig. by Wade, Glaessner, n).

Lorenzinites Glaessner & Wade, 1966, p. 608 [**L. rarus*; OD]. Small central disc from which lobes radiate to length equal to or exceeding that of radius of disc, broadening and flattening at outer ends. [As only one specimen is known, the status of this taxon is doubtful. For a discussion of similar Phanerozoic fossils, which may be trace fossils, see Häntzschel, 1975, p. *W*144.] *U.Precam.*, S.Australia.

Mawsonites Glaessner & Wade, 1966, p. 607 [**M. spriggi*; OD]. Large, with smooth conical center; greater part of surface strongly sculptured with large, irregular bosses that increase in size outward to form radially elongate lobes separated by furrows leading to the lobate peripheral margin. Subumbrellar surface unknown. *U.Precam.*, S.Australia.——Fig. 9,*3*. **M. spriggi*, Ediacara; paratype, ×0.67 (Glaessner & Wade, 1966).

Medusinites Glaessner & Wade, 1966, p. 605 [**Medusina asteroides* Sprigg, 1949; OD]. Small, subcircular, discoidal bodies with central disc separated by deep circular groove from large outer ring with radius greater than that of central disc and with radial grooves irregularly preserved on it; there is a very narrow marginal flange; faint concentric markings occur more commonly on central disc; subumbrellar surface unknown. *U. Precam.*, S.Australia-S.USSR.——Fig. 10,*1*. **M. asteroides*, S.Australia (Ediacara); *1a,b*, ×1 (Glaessner & Wade, 1966).

Planomedusites Sokolov, 1972 [**P. grandis*; M]. Large, saucer shaped, surface smooth, edge raised as a narrow rim, apparently surrounded by narrow, thin flange. *U.Precam.(Vend.)*, S.USSR.——Fig. 10,*3*. **P. grandis*; Dnjestr R., Ukraine; holotype, ×0.77 (Sokolov, 1972).

Pseudorhizostomites Sprigg, 1949, p. 87 [**P. howchini*; OD] [=*Pseudorhopilema* Sprigg, 1949, p. 88]. Furrows radiating outward from variably shaped center; bifurcating or anastomosing and becoming finer outward; no distinct peripheral margin; fluted passage extending vertically upward from center through overlying sediment suggests that shape of fossils was influenced by decay and escape of decay products of a medusoid which is probably not yet known in better preservation. *U.Precam.*, S.Australia.——Fig. 10,2. **P. howchini*, Ediacara; *2a,b*, ×1.3 (Sprigg, 1949).

Rugoconites Glaessner & Wade, 1966, p. 610 [**R. enigmaticus*; OD]. Low conical body with circular to oval peripheral margin; a few furrows diverge from small polygonal center, repeatedly branching dichotomously and anastomosing; furrows either few and coarse or numerous and fine; peripheral margin with narrow flange and numerous fine tentacles. *U.Precam.*, S.Australia.——Fig. 10,*4*. **R. enigmaticus*, Ediacara; holotype, ×1 (Glaessner & Wade, 1966).

PROBLEMATICAL COELENTERATA

"PETALONAMAE" Pflug, 1970

[Petalonamidae Pflug 1970a, p. 258; Phylum Petalonamae Pflug, 1972b, p. 158]

Leaflike structures ("petaloids"), often with a median line or zone and lateral grooves and ribs on each leaf, disposed as primary, secondary and occasionally tertiary branches; petaloids may occur in clusters or be joined to form fanlike composite structures ("flabella" and "petalodia"), or be bent into bun or bag shapes; their external layer may show fibrous microstructure; they appear to represent colonial organisms. [According to Pflug (1970a,b), the petaloids are typically linked in groups but the evidence for dendroid branching, and for the assumed extensive structural homologies between the groupings of petaloids in flabella composing the petalodia in different genera is inconclusive. Pflug has built up an elaborate and complex terminology that is not intended to be purely descriptive, but which tends to explain conceptual "structural plans." A discussion of these theoretical views is considered to be outside the scope of this *Treatise* (see Pflug, 1970a-1974b, for details); however, it is convenient to group the interconnected taxa listed below provisionally under the name proposed by Pflug (which was accepted by Germs, 1972a, and Glaessner & Walter, 1975), without defining its status in classification and nomenclature, until clear distinctions between observable and hypothetically postulated characters can be drawn.] *U. Precam.*

Family PTERIDINIIDAE Richter, 1955

[=Class Pteridiniomorpha Pflug, 1972b, p. 158]

Leaflike, elongate structures ("petal-

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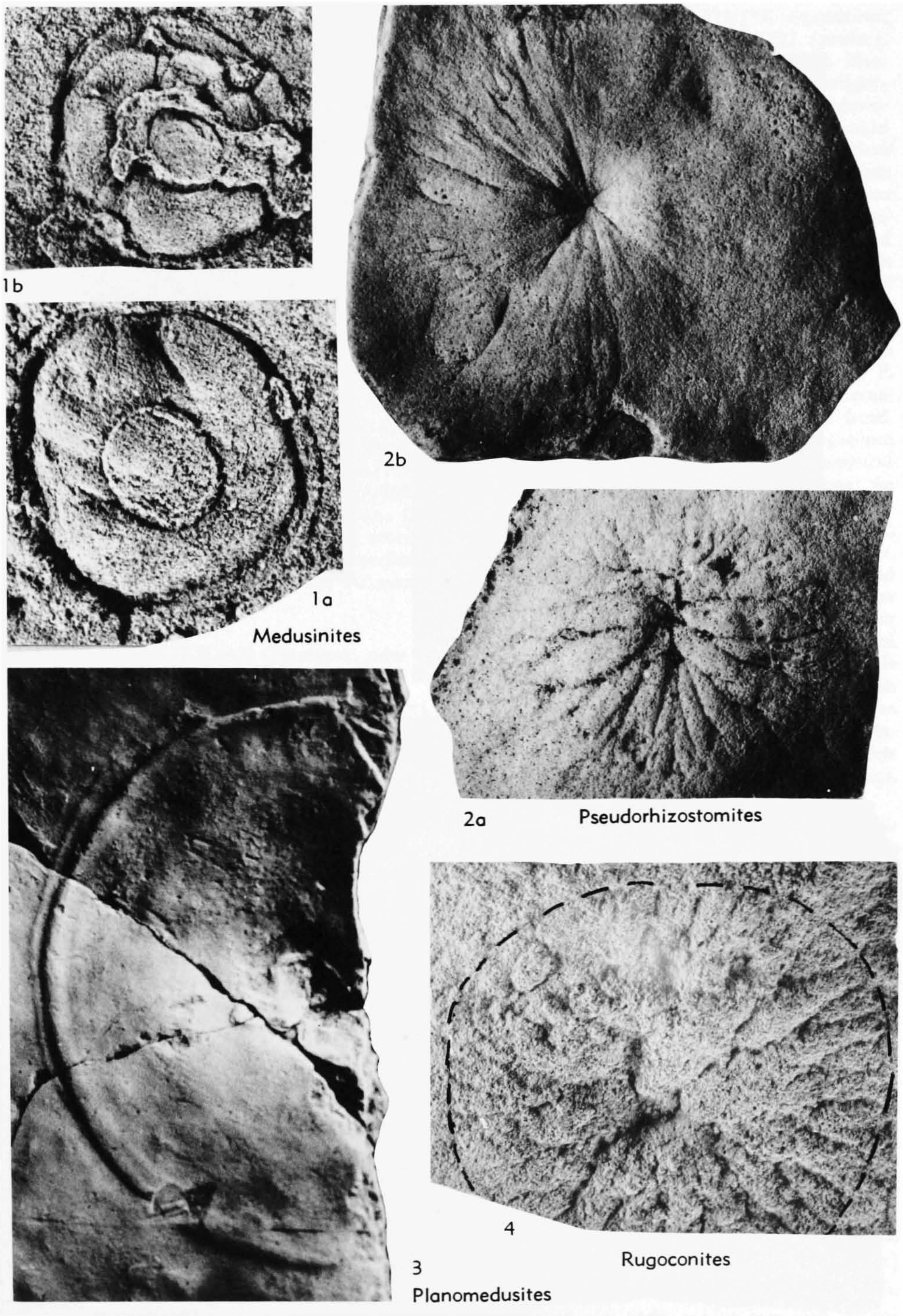

Fig. 10. Medusae of uncertain affinities (p. *A94-A96*).

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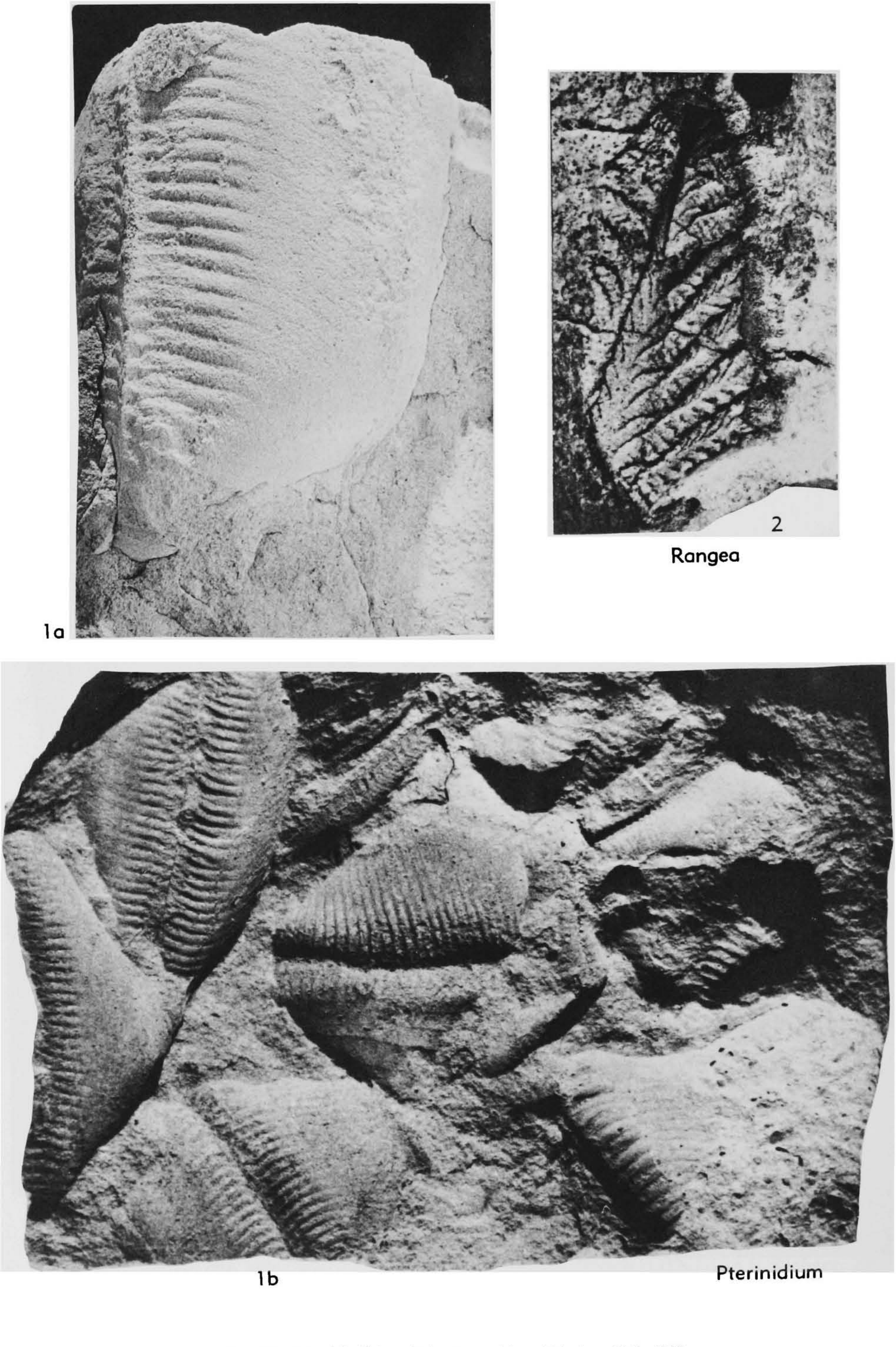

Fig. 11. Pteridiniidae *(1)*; Rangeidae *(2)* (p. *A96-A99*).

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oids"), roughly bilaterally symmetrical, probably composite, elastically deformed during embedding, with distinct median groove often showing a series of small rhombical elements ("commissurae"); more conspicuous are transverse, sharply incised, primary furrows and convex branches; a marginal zone, which is almost smooth, may be present. [The evidence for strictly defined dendroid branching modes proposed by PFLUG is unconvincing. These fossils, together with *Rangea*, were considered by RICHTER (1955) as Gorgonaria and by GLAESSNER (in GLAESSNER & DAILY, 1959) as Pennatulacea.] *U.Precam.(Vend.).*

Pteridinium GÜRICH, 1933, p. 144 [**P. simplex*; OD] [=*Pteridium* GÜRICH, 1930, p. 637 *(nom. nud.)* (*non* SCOPOLI, 1777); *?Onegia* SOKOLOV, 1976]. Characters of family. *U.Precam.(Nama Gr.),* SW.Afr.; *U.Precam.(up. Vend.),* N.USSR-S. Australia.——FIG. 11,*1*. **P. simplex,* Nama Gr., SW.Afr.; *1a,* specimen closely resembling neotype, ×0.8 (Glaessner, 1963); *1b,* group of specimens on slab in State Museum, Windhook) (Glaessner, n).

Family RANGEIDAE Glaessner, new

[=Class Rangeomorpha PFLUG, 1972b, p. 158]

Leaflike rounded structures ("petaloids"), roughly bilaterally symmetrical, probably composite; with median groove or track and lateral primary branches that are divided into small, chevron-shaped secondary branches. *U.Precam.*

Rangea GÜRICH, 1930, p. 680 [**R. schneiderhöhni*; OD]. Characters of family. *U.Precam.(Nama Gr.),* SW.Afr.——FIG. 11,*2*. **R. schneiderhöhni,* ×1.6 (Pflug, 1970b).

Family CHARNIIDAE Glaessner, new

Leaflike bodies ("petaloids") single, elongate, often with narrow stem and expanded discoidal base, with median groove or track; secondary branches disposed as convex, parallel structures between primary branches. *U.Precam.*

Charnia FORD, 1958, p. 212 [**C. masoni*; OD]. Narrow petaloids with sinuous median line and sharply defined primary grooves forming acute angles with corresponding secondary grooves and branches; these are therefore in almost transverse position on the petaloids. *U.Precam.(Charn.),* Eng.——FIG. 12,*3*. **C. masoni*; plaster cast of holotype, ×0.45 (Glaessner, n; Leicester City Museum no. 279,1958).

Charniodiscus FORD, 1958, p. 213 [**C. concentricus*; OD] [=*Charnia* FORD, 1958, p. 212 *(partim)*; *Arborea* GLAESSNER & WADE, 1966, p. 618]. Elongate petaloids with broad "dorsal" and slightly narrower "ventral" median track, extending downward into a stalk ending in an expanded discoidal base; secondary branches on flangelike expansions on the "ventral" faces of primary branches. [FORD (1958) distinguished *Charniodiscus concentricus* from *Charnia masoni* because only in one specimen (the holotype of the former) were "frond and disc apparently associated" and there "it could be interpreted as a distinct type of frond. . . ." Hence he diagnosed *Charniodiscus* as a "disc-like organism." In 1963 he figured this entire specimen as *C. concentricus* "with *Charnia masoni* frond attached." Dr. R. J. F. JENKINS (pers. commun.) agrees with the alternative view that this is a distinct type of frond. He considers that therefore the entire specimen becomes the holotype of *Charniodiscus concentricus* and concludes also that this frond shows the characters of *Arborea,* which consequently becomes a synonym of *Charniodiscus*.] *U.Precam.,* Eng.-S.Australia.——FIG. 12,*2a*. **C. concentricus,* Charn., Eng.; plaster cast of holotype with frond attached, approx. ×0.3 (Glaessner, n; Leicester Univ. no. 2383/1-2).——FIG. 12,*2b,c*. *C. arboreus* (GLAESSNER); *2b,* S.Australia (Ediacara), discoidal base and stalk, ×0.3 (Glaessner, n; Adelaide Univ., unnumbered specimen); *2c,* S.Australia (Bunyeroo Gorge), plaster cast of impression on lower bedding plane showing discoidal base inferred to have been attached to adjacent complete petaloid, about ×0.2 (fig. by R. J. F. Jenkins, Glaessner, n; Adelaide Univ.).

Glaessnerina GERMS, 1973, p. 5 [**Rangea grandis* GLAESSNER & WADE, 1966; OD]. Resembling *Charnia* but secondary grooves and ribs form large angles with primary grooves and hence are in markedly oblique to almost longitudinal position on the petaloids. *U.Precam.,* S.Australia-N. USSR-N.Sib.——FIG. 12,*1*. *G. sibirica* (SOKOLOV), N.Sib.; ×0.67 (Sokolov, 1972).

Family ERNIETTIDAE Pflug, 1972

[Erniettidae PFLUG, 1972b, p. 163] [=Class Erniettomorpha PFLUG, 1972b, p. 158; Family Ernionormidae PFLUG, 1972b, p. 158]

Rounded, bun- or bag-shaped, ellipsoidal or cylindrical bodies with external ribs generally divided by a median groove disposed so as to suggest derivation from or interpretation as folded petaloids similar to those of *Pteridinium*. *U. Precam.* [PFLUG (1972b) has studied these fossils in great detail. He considered not only major but also minor differences in shape as taxonomic characters, distinguishing 13 genera (with 28 species)

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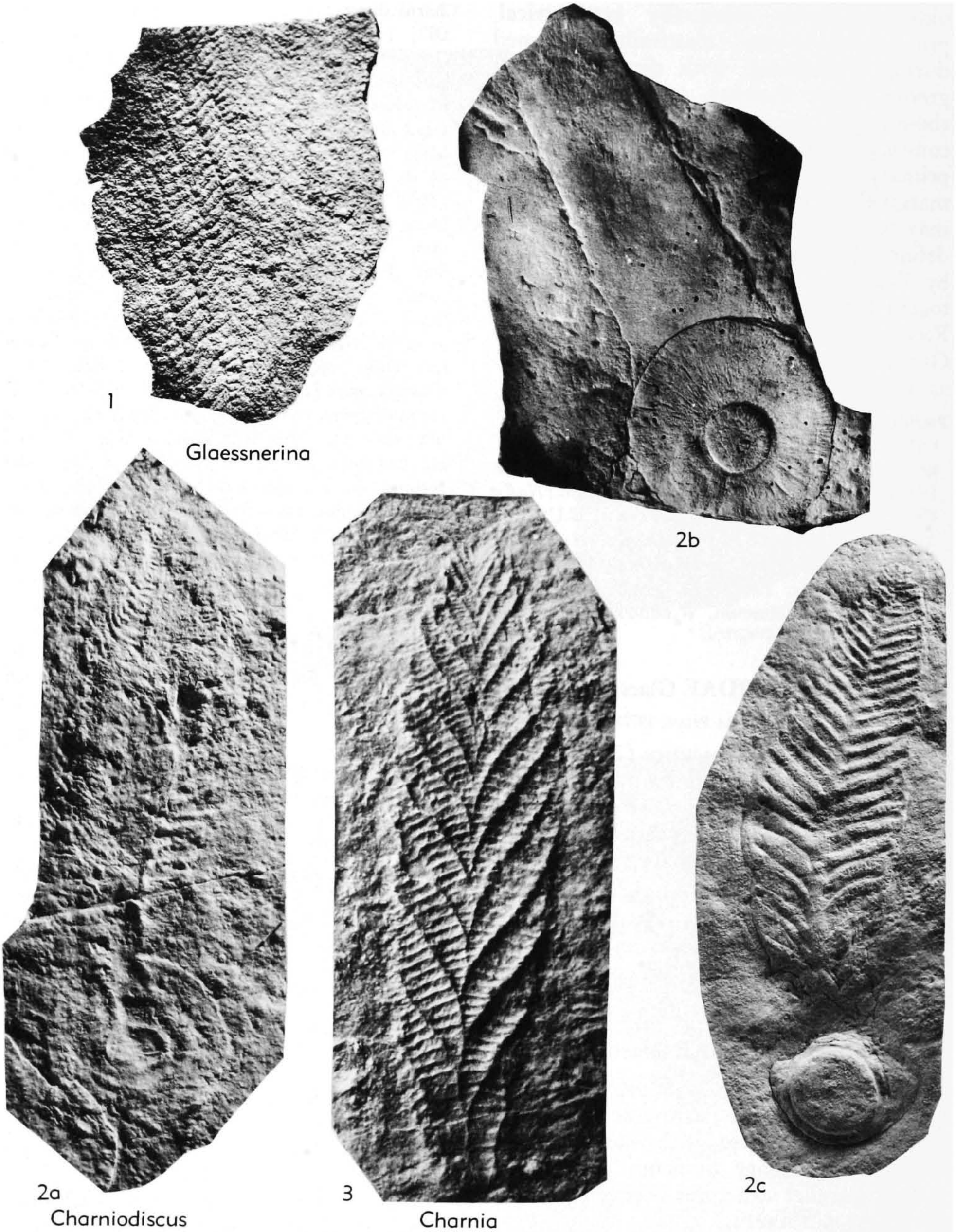

FIG. 12. Charniidae (p. *A*99).

in five subfamilies, four families and two orders of a class Erniettomorpha; however, many apparent differences could be the results of postmortal deformation whereas others appear to be due to variability of growth and preservation. Some genera have type specimens that are so poorly preserved as to be unrecognizable (see list on p. *A*112). It seems appropriate to separate the tall, complexly sutured forms at subfamily level from those more or less close to *Ernietta*.]

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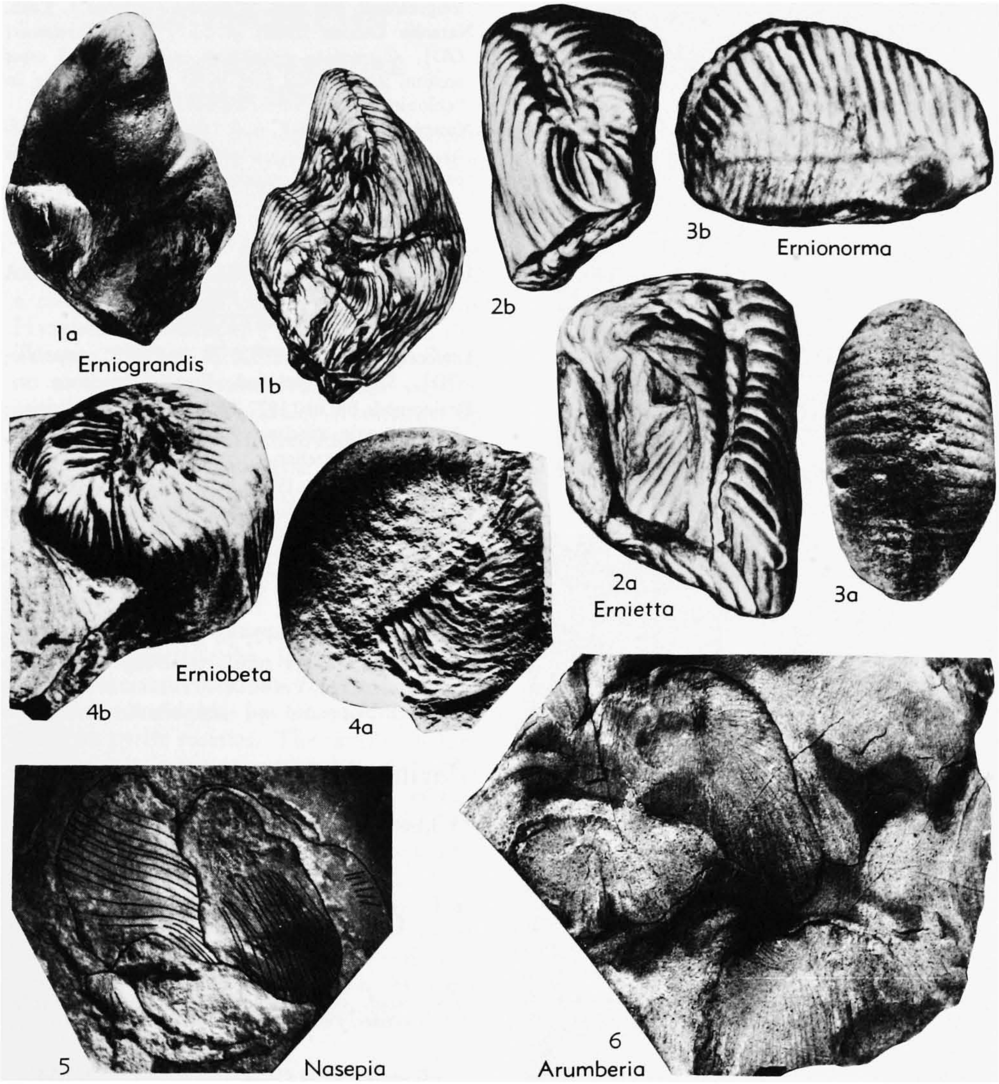

Fig. 13. Erniettidae *(1-4)*; Family uncertain *(5,6)* (p. *A*99-*A*102).

Subfamily ERNIETTINAE Pflug, 1972

[Erniettinae Pflug, 1972b, p. 163] [=Ernionorminae Pflug, 1972b, p. 160; Erniodiscinae Pflug, 1972b, p. 158]

Body flattened, round to subcylindrical, with ribs more or less clearly divided by median zigzag line. *U.Precam.*

Ernietta Pflug, 1966, p. 19 [**E. plateauensis*; OD]. Body compressed or bent into U-shape; ribs strongly developed, separated by zigzag median line; resembling a folded petaloid of *Pteridinium*. *U.Precam.*, SW.Afr.——Fig. 13,*2*. **E. plateauensis; 2a,b,* ×1 (Pflug, 1972b).

Erniofossa Pflug, 1972, p. 159 [**E. prognatha*; OD] [=*?Erniodiscus* Pflug, 1972b, p. 158; *?Erniaster* Pflug, 1972b, p. 159]. Body with rounded to elliptic basal outline, upper surface convex, with central depression or flattened; general shape varying from discoidal to cylindrical, median groove short or indistinct. *U.Precam. (Nama Gr.),* SW.Afr.

Ernionorma Pflug, 1972, p. 160 [**E. abyssoides*; OD] [=*Erniobaris* Pflug, 1972b, p. 161]. Body with elliptic basal outline, highly convex, with median groove between distinct lateral ribs. *U. Precam.(Nama Gr.),* SW.Afr.——Fig. 13,*3*. *E.*

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FIG. 14. Vologdinophyllidae (p. *A*102).

corrector PFLUG; *3a,* ×1; *3b,* ×1 (Pflug, 1972b).

Subfamily ERNIOBETINAE Pflug, 1972

[Erniobetinae PFLUG, 1972b, p. 165]

Body columnar, tall, ribbed, with median line near apex and with transverse, incised sutures. *U.Precam.*

Erniobeta PFLUG, 1972, p. 166 [**E. scapulosa*; OD]. Body columnar, ribbed, top surface convex, with median groove, sutures more or less distinct; occurring in "colonies." *U.Precam.(Nama Gr.),* SW. Afr.——FIG. 13,*4*. *E. forensis* PFLUG; *4a,b,* ×1 (Pflug, 1972b).

Erniograndis PFLUG, 1972, p. 165 [**E. sandalix*; OD]. Body tall, ribbed, bulbous, transversely sutured, open end narrowed, median line subapical. *U.Precam.(Nama Gr.),* SW.Afr.——FIG. 13,*1*. **E. sandalix; 1a,b,* ×0.3 (Pflug, 1972b).

Family UNCERTAIN

Arumberia GLAESSNER & WALTER, 1975, p. 61 [**A. banksi*; OD]. Hollow, compressible, ribbed, conical to cylindrical bodies, attached by blunt apex; ribs may bifurcate. *Uppermost Precam.,* C.Australia.——FIG. 13,*6*. **A. banksi,* Laura Creek (nr. Alice Springs); casts of several specimens on lower bedding surface; ×0.2 (Glaessner & Walter, 1975).

Baikalina SOKOLOV, 1972 [**B. sessilis*; M]. Bag-shaped body, narrow at base, with mm-sized, longitudinal, flat ribs. *U.Precam.(U.Vend.),* S.Sib.

Namalia GERMS, 1968, p. 53 [**N. villiersiensis*; OD]. Conical to cylindrical, with rounded cross section, longitudinal ribs, blunt apex; occurring in "colonies." *U.Precam.(Nama Gr.),* SW.Afr.

Nasepia GERMS, 1972, p. 7 [**N. altae*; OD]. Leaf-like bodies with fine ribs subparallel to long axis and with clearly marked margins. *U.Precam. (Nama Gr.),* SW.Afr.——FIG. 13,*5*. **N. altae*; ×0.6 (Germs, 1973a).

UNRECOGNIZABLE AND REJECTED GENERA ASSIGNED BY PFLUG (1972b) TO "ERNIETTOMORPHA"

Erniocarpus PFLUG, 1972, p. 164 [**E. carpoides*; OD]. Single, weathered, discoidal specimen.

Erniocentris PFLUG, 1972, p. 159 [**E. centriformis*; OD]. Single specimen with concentric ribbing. Possibly a concretion.

Erniocoris PFLUG, 1972, p. 164 [**E. orbiformis*; OD]. Single weathered specimen superficially resembling mold of bivalve shell.

Erniopelta PFLUG, 1972, p. 162 [**E. scrupula*; OD]. Convex bodies with obscure and irregular sculpture.

Erniotaxis PFLUG, 1972, p. 165 [**E. segmentrix*; OD]. Fragmentary molds consisting of few ribs only, placed by PFLUG (1972b) in a monotypic family Erniotaxidae and subfamily Erniotaxinae.

Phylum ANNELIDA Lamarck, 1809

Class POLYCHAETA Grube, 1850

[see this *Treatise*, 1962, p. *W*148]

Order CRIBRICYATHEA Vologdin, 1961

[*nom. transl.* GLAESSNER, 1976a (*ex* Class Cribricyathea VOLOGDIN, 1961, p. 177); see HILL, 1972, p. *E*134]

?Family VOLOGDINOPHYLLIDAE Radugin, 1964

[see HILL, 1972, p. *E*138]

Cloudina GERMS, 1972b, p. 752 [**C. hartmannae* (=*C. hartmanae* GLAESSNER, 1976a, *emend.*); OD]. Tubes sinuous, conical to almost cylindrical, walls with outer layer covered with close-set transverse annular ridges and grooves; the main layer consisting of stacked, inverted cones sloping inward toward the apex, incomplete in transverse section (forming half-rings); inner surface of tube elliptical, smooth. [For a discussion of the relations of *Cloudina* to the Cribricyathea and of this order to the Polychaeta, see GLAESSNER, 1976a.] *U.Precam.,* SW.Afr.; *?L.Cam.,* S.Am.(Arg.).——FIG. 14,*1*. **C. hartmanae*; U.Precam., SW.Afr.; ×0.3 (Germs, 1972b).

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Order UNCERTAIN

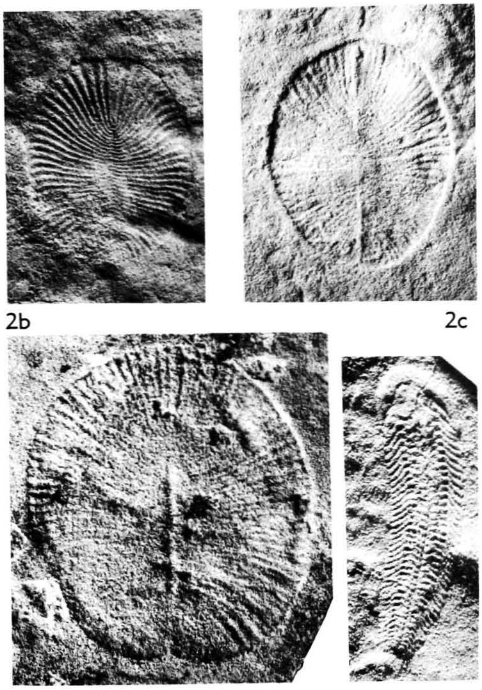
Family DICKINSONIIDAE Harrington & Moore, 1955

Body elliptical to elongate, segments numerous, generally widening outwardly, anterior segments fused medially. *U. Precam.*

[The monotypic family Dickinsoniidae was placed in an order Dickinsoniida and a class Dipleurozoa of the Coelenterata by Harrington & Moore (1955) (see also this *Treatise,* 1956, p. *F*24-*F*25). This was based on a series of misunderstandings starting with Sprigg's (1947) faulty reconstruction of *Dickinsonia* as "symmetrical across both longitudinal and transverse planes." Since the close relationship between *Dickinsonia* and the living polychaete *Spinther* has been established by the study of much additional material, there is no need for higher taxa above family rank for the former genus. The supposed Silurian "Dipleurozoa" named *Rutgersella* by Johnson and Fox (1968) are unrelated to *Dickinsonia* and are now considered by Cloud (1973) as based on pyrite rosettes. The family Dickinsoniidae can be accommodated in the order Amphinomorpha in Clark's (1969) system of the Polychaeta, in view of its proximity to the Spintheridae. Wade (1972b) suggested the use of the order Dickinsoniida for both Dickinsoniidae and Spintheridae. The classification of the Polychaeta above family level is in a state of flux and (with one exception) higher taxa will not be used here for the known Precambrian polychaetes.]

Dickinsonia Sprigg, 1947, p. 221 [**D. costata*; OD] [=*Papilionata* Sprigg, 1947, p. 223]. Broad, flat, with numerous, short segments; anterior body segments fused pre-orally along median line; segmental furrows depressed dorsally and ventrally; neuropodia reduced, notopodial-elytral ridges well developed; filled intestine with intestinal caeca may be preserved. *U.Precam.,* S.Australia-N.USSR.——Fig. 15,*2*. **D. costata,* S.Australia(Ediacara); *2a,* ×0.64; *2b,c,* ×0.8 (Sprigg, 1949).

Marywadea



Dickinsonia Spriggina

Fig. 15. Dickinsoniidae *(2)*; Sprigginidae *(1,3)* (p. *A*103-*A*104).

Family SPRIGGINIDAE Glaessner, 1958

[See Howell, 1962, *Treatise,* p. *W*154]

Spriggina Glaessner, 1958, p. 158 [**S. floundersi*; OD]. Prostomium horseshoe-shaped, strongly sclerotized, with a sharp medio-posterior semicircular impression on its margin, without external segmentation. Body flexible, rather flat, consisting of up to 40 segments, tapering gently to a rounded, minutely segmented posterior end; neuropodia with acicular setae, a double series of mediodorsal paired convexities separated by a sagittal groove probably represent dorsal longitudinal mus-

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FIG. 16. Anabaritidae (p. *A*104).

cles; convexity variably placed near the first trunk segments suggests a well-developed pharynx. *U. Precam.,* S.Australia.——FIG. 15,*3*. **S. floundersi,* Ediacara; ×1 (Glaessner, n; Univ. Adelaide coll. no. F17354).

Marywadea GLAESSNER, 1976, p. 169 [**Spriggina ? ovata* GLAESSNER & WADE, 1966, p. 622; OD]. Prostomium half-moon shaped, not wider than the body with appendages, integument thin; up to 50 short, broad segments bearing long, curved setae; behind the prostomium a pair of elongate impressions suggesting teeth; posterior end of body broadly rounded. *U.Precam.,* S.Australia-?SW.Afr.——FIG. 15,*1*. **M. ovata* (GLAESSNER & WADE), Australia (Ediacara); holotype, ×3.2 (Glaessner & Wade, 1966).

Family ANABARITIDAE Glaessner, new

[=Angustiochreidae VALKOV & SYSOIEV, 1970, p. 96 (*invalid name*)]

Small, straight or curved, conical tubes of calcareous composition, with rounded to triangular or stellate cross section; three or more evenly spaced straight or curved longitudinal grooves and corresponding internal ribs or rows of spines. [VALKOV & SYSOIEV (1970, p. 97) erected a new genus *Angustiochrea* for Lower Cambrian tubular fossils and placed it together with (among others) the closely similar *Anabarites* MISSARZHEVSKY in a new family Augustiochreidae (p. 96), expressly based on *Anabarites* as "type genus," in violation of the International Code of Zoological Nomenclature. They also erected a new order Angustiochreida.] *U.Precam., ?L.Cam.*

Anabarites MISSARZHEVSKY in VORONOVA & MISSARZHEVSKY, 1969, p. 209 [**A. trisulcatus*; OD] [=*Angustiochrea* VALKOV & SYSOIEV, 1970, p. 97 (type, *A. lata*; OD)]. Small, thin-walled, elongate-conical tubes, trilobed to triangular or triradiate in transverse section. [The synonymy of *Angustiochrea* and *Anabarites* was suggested to me by V. V. MISSARZHEVSKY (pers. commun., May, 1975) and appears justified.] *Uppermost Precam.* and *basal Cam.,* N.&E.Sib.——FIG. 16,*1*. **A. trisulcatus,* U.Precam.(Vend.), Anabar reg.; ×25 (Matthews & Missharzhevsky, 1975).

Phylum ARTHROPODA
Siebold & Stannius, 1845

[see this *Treatise*, 1959, p. *O*4]

Superclass TRILOBITOMORPHA Størmer, 1944 (or CHELICERATA Heymons, 1901)

[See this *Treatise*, 1959, p. *O*22; 1955, p. *P*1, and 1969, p. *R*13]

Class and Order UNCERTAIN

Family VENDOMIIDAE
Keller in Keller & Fedonkin, 1976

Small, elongate, discoidal body with broadly arcuate anterior margin; head shield large, followed by up to five chevron-shaped segments and a small telson. [In the absence of any traces of appendages it cannot be decided whether this family should be placed in the Trilobitomorpha or Chelicerata; the general morphology of the body resembles both.] *U.Precam.*

Vendomia KELLER in KELLER & FEDONKIN, 1976, p. 43 [**V. menneri*; OD]. Horseshoe-shaped cephalic area occupying ⅔ of length, separated from trunk area consisting of 5 somites, decreasing in size posteriorly, with median groove; telson not clearly observable. *U.Precam.(U.Vend.),* N.USSR.

Onega FEDONKIN in KELLER & FEDONKIN, 1976, p. 42 [**O. stepanovi*; OD]. Elliptic flat body with sharp outline; wide, smooth, marginal area, wider at anterior (?) end which is crescent-shaped; behind it an axially segmented series of 5 paired lobes, transversely elongate, slightly curved towards anterior (?) end, with deep, wide axial groove, length of segments decreases posteriorly. *U.Precam.(U.Vend.),* N.USSR.

Praecambridium GLAESSNER & WADE, 1966, p. 623 [**P. sigillum*; OD]. Body small, dorsal side with horseshoe-shaped head region bearing a heart-shaped glabellar area surrounded by surface crenulations (?digestive caeca) and followed by 3 to 5 chevron-shaped segmental ridges and a triangular terminal somite. *U.Precam.,* S.Australia.——FIG.

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17,*1*. **P. sigillum;* diagramm. reconstr., ×7.5 (Glaessner & Wade, 1971).

Vendia Keller in Rozanov *et al.,* 1969, p. 175 [**V. sokolovi*; OD]. Body elongate, disc shaped; horseshoe-shaped cephalic area followed by 5 narrow, inverted V-shaped segments diverging outward and backward, weak and uneven median ridge. *U.Precam.(Vend.),* N.USSR.——Fig. 17,*2*. **V. sokolovi,* Yarensk; ×5 (Sokolov, 1972).

Superclass CRUSTACEA Pennant, 1777

Class BRANCHIOPODA Latreille, 1817

(see this *Treatise*, 1969, p. *R*131)

Order UNCERTAIN

Family PARVANCORINIDAE Glaessner, new

Shieldlike carapace elongate, with faint marginal raised rim and distinctly elevated, anterolateral and median, smooth, dorsal ridges; about five pairs of stout anterior appendages are followed by up to 20 pairs of posterior, undifferentiated, filiform appendages. [Some resemblance with *Vachonisia* Lehmann, but also with *Marrella* Walcott and *Mimetaster* Gürich, should be noted. The observation of trilobitomorph legs in the Devonian genus *Vachonisia* appears to require its transfer to the Marellomorpha from the Crustacea Branchiopoda (see Stürmer & Bergström, 1976). Similarity of *Parvancorina* with Marellomorpha may suggest that it is close to the ancestors of the Crustacea, the derivation of which from Trilobitomorpha was suggested by Hessler and Neuman (1975). Delle Cave and Simonetta (1975) indicated similarities with *Skania fragilis* Walcott, 1931. If confirmed, this could extend the range of the family to *M.Cam.*] *U.Precam.*

Parvancorina Glaessner in Glaessner & Daily, 1959, p. 187 [**P. minchami*; OD]. Characters of family (see Fig. 18). *U.Precam.,* S.Australia.

DOUBTFUL ARTHROPODA

Velancorina Pflug, 1966, p. 17 [**V. martina*; OD]. Outline arcuate anteriorly, converging posteriorly, several marginal ridges and furrows, two stronger central ridges separated by a pronounced median furrow, not extending to margins; some fine longitudinal striae, no pronounced transverse sculpture except short grooves near axis. *U.Precam.,* SW.Afr.; *L.Cam.,* W.Can. [Young (1972) described a "*Rusophycus* sp." from the Lower Cambrian. It lacks the characteristic transverse sculpture. It does not show the transverse grooves described by Pflug that are shown in his drawing of *Velancorina* but not discernible in his photographs; the Canadian fossil is otherwise indistinguishable from *Velancorina.* Although not a trilobite "resting trail," this fossil with its bilaterally symmetrical shieldlike outline and median groove may represent the ventral impression of a primitive arthropod.]

1

Praecambridium

2 Vendia

Fig. 17. Vendomiidae (p. *A*104-*A*105).

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FIG. 18. Growth series of *Parvancorina minchami* GLAESSNER from S. Australia (Ediacara) plotted on expanded scale (×5) of length and width, with illustrations of specimens (×1) placed in approximate coordinate positions. Strictly nonallometric growth is not implied; the carapace seems to be more elongate in early growth stages and as wide as long in late growth stages when the entire material is considered. Biometric tests tend to be invalidated by distortion of the flexible carapaces; the specimens

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?Phylum POGONOPHORA
Johannson, 1938

Order SABELLIDITIDA
Sokolov, 1965

Elastic, thin, very long, slender, cylindrical tubes; walls often fibrous with smooth terminal portions, or irregularly wrinkled transversely; not branching; black, brown, or translucent yellow, organic (combustible). *U.Precam.-L.Cam.*

[This order is considered by Sokolov as representing Pogonophora. It should be noted that zoologists tend to disagree as to whether the Pogonophora is a separate phylum or where it should be placed in the classification of the Metazoa, since significant similarities between them and polychaete annelids have been discovered (see Nørrevang, 1975).]

Family SAARINIDAE Sokolov, 1965

Tubes very thin, translucent, consisting of funnel-shaped narrow rings. *U.Precam. (Vend.)-L.Cam.*

Calyptrina Sokolov, 1965, p. 91 [**C. partita*; OD]. Tubes light yellow or colorless, consisting of narrow, transverse rings with rounded, projecting edges. *U.Precam.(Vend.),* Sib.; *L.Cam.,* N.USSR.

Family SABELLIDITIDAE Sokolov, 1965

Tubes long and thin, black, brown or light yellow, elastic and collapsible, transversely wrinkled, or smooth at one end. *U.Precam.(up.Vend.)-basal Cam.*

Paleolina Sokolov, 1965, p. 90 [**P. evenkiana*; OD]. Tubes very thin, narrow, semi-transparent to transparent, yellow; walls smooth or sharply and irregularly transversely wrinkled; diameter 1.0-1.2 mm, length to 120 mm. *U.Precam.(up. Vend.)-basal Cam.,* Sib.-N.USSR.——Fig. 19,*1*. **P. cf. P. evenkiana,* int. molds, up.Vend., S.Sib.; ×5 (Sokolov, 1975).

Fig. 19. Sabelliditidae (p. *A*107).

Phylum UNCERTAIN

Class, Order, and Family UNCERTAIN

Redkinia Sokolov, 1976, p. 141 [**R. spinosa*; OD]. Brown to black, chitinoid, blade-like fossils with 13-15 curved spines about 0.5 mm long along one edge, which is up to 3.5 mm long. Possibly annelid jaws. Considered by Sokolov as possibly legs of Protonychophora. *U.Precam.(Vend.,* Redkino Ser.), Nepeitsino bore, central Russia.

Tribrachidium Glaessner in Glaessner & Daily, 1959, p. 389 [**T. heraldicum*; OD]. Disc shaped, slightly convex, with steeply sloping peripheral margin; one side (oral?) has three raised arms (brachia) radiating at equal angles, curving clockwise (in artificial casts representing bodies as deposited) to join periphery of disc where they taper.

(Continued from facing page.)

above the line are shortened by overfolding, that below the line is lengthened by lateral compression. Reconstruction (below, right) shows appendages on left only (*M*, hypothetical position of mouth, flanked by proximal parts of anterior appendages). The adaxial and abaxial ends of appendages are not preserved, probably mainly because of the greater rigidity of the ridges (specimens selected, cast in latex and photographed by Dr. M. Wade) (Glaessner, n; specimen numbers, from left to right, 806/2, P 14245/2, P 12774, P 13815, P 14252/1, P 14245/1, P 14251, P 14206, P 14204, 943, 543, P 14190, P 12901/1; specimens prefixed "P" are in collections of S. Austral. Mus., others are in collections of Dept. Geol., Univ. Adelaide).

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FIG. 20. Family uncertain (p. *A*107-*A*108).

Small, Y-shaped groove (?mouth) is rarely seen in center between arms; attached to each arm on its convexly curved side is a small, raised area ("bulla"). Distal 0.7 of each arm bears short, stout tentacles on outer side and tip. Fine, long, straight or gently curved bristlelike structures may extend from crest and concave side of each arm across tips of adjoining arms. Opposite (?aboral) side of disc shows only a few concentric grooves. *U.Precam.*, S.Australia.——FIG. 20,*1*. **T. heraldicum*, Ediacara; ×1 (Glaessner & Daily, 1959).

Vermiforma CLOUD, in CLOUD *et al.*, 1976, p. 405 [**V. antiqua*; OD]. Wormlike, coiled and looped impressions, 1.5-2 cm wide, up to 1-1.1 m long, with scalloped or scaly surface texture; on bedding surfaces of meta-tuffaceous sediments. *U.Precam.*, USA(N.Car.). [This genus was classified by its authors as Annelida, class, order, and family unknown.]

TAXA WITH DOUBTFUL INVERTEBRATE AFFINITIES

Family SUVOROVELLIDAE Vologdin & Maslov, 1960

Calcareous, non-porous, double-walled discoidal or flatly conical skeletons; no structural elements between the walls; external wall may be sculptured with raised rhomboidal areas. *Uppermost Precam.(low. Yudom.)*.

Suvorovella VOLOGDIN & MASLOV, 1960, p. 691 [**S. aldanica*; OD]. Skeleton saucer shaped, diameter to 30 mm, surface with small raised rhombs in intersecting curved rows. *Uppermost Precam. (low.Yudom.)*, E.Sib.

Majella VOLOGDIN & MASLOV, 1960, p. 692 [**M. verkhojanica*; OD]. Skeleton irregularly discoidal or saucer shaped, consisting of two flat walls, often with irregular concentric wrinkles. *Uppermost Precam.(low.Yudom.)*, E.Sib.

Family UNCERTAIN

Petalostroma PFLUG, 1973, p. 192 [**P. kuibis*; OD]. Saucer-shaped bodies up to tens of cm in size, without internal cavities; surface irregularly wrinkled radially and concentrically, with fibrous and cellular external tissues; skeleton said to consist of organic and carbonate material. [PFLUG (1973) claims to have observed petaloids consisting of microscopic tubular structures. His proposed homologies and transitions between Petalonamae and Petalostromae are unconvincing.] *U.Precam.* (Nama Gr.), SW.Afr.

NAMES GIVEN TO PRECAMBRIAN NONMETAZOAN AND TRACE FOSSILS

Only taxa of generic rank are included, generally without reference to synonymy. Genera based on Cambrian or younger species are generally excluded.

FILAMENTOUS, COCCOID, AND OTHER MICROSCOPIC ALGAE

(This list possibly also includes fungal or bacterial remains.)

Anabaenidium SCHOPF, 1968 [**A. johnsonii*]
Animikiea BARGHOORN, 1965 [**A. septata*]
Antigus BUTIN, 1959 [**A. cusarandicus*]
Archaeogloeocapsa REITLINGER, 1956 [**A. povarovkensis*]
Archaeonema SCHOPF, 1968 [**A. longicellularis*]
Archaeorestis BARGHOORN, 1965 [**A. schreiberensis*]
?**Archaeosphaeroides** SCHOPF & BARGHOORN, 1967 [**A. barbertonensis*]
Archaeotrichion SCHOPF, 1968 [**A. contortum*]
Bigeminococcus SCHOPF & BLACIC, 1971 [**B. lamellosus*]
Biocatenoides SCHOPF, 1968 [**B. sphaerula*]
Calyptothrix SCHOPF, 1968 [**C. annulata*]
Caryosphaeroides SCHOPF, 1968 [**C. pristina*]
?**Catinella** PFLUG, 1966a [**C. polymorpha*]
Caudiculophycus SCHOPF, 1968 [**C. rivularioides*]
Cephalophytarion SCHOPF, 1968 [**C. grande*]

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Chlamydomonopsis Edhorn, 1973 [*_C. primordialis_]
Contortothrix Schopf, 1968 [*_C. vermiformis_]
Cumulosphaera Edhorn, 1973 [*_C. lamellosa_]
Cyanonema Schopf, 1968 [*_C. attenuata_]
Entosphaeroides Barghoorn, 1965 [*_E. amplus_]
Eoastrion Barghoorn, 1965 [*_E. simplex_]
Eobacterium Barghoorn & Schopf, 1966 [*_E. isolatum_]
Eoepiphyton Butin, 1959 [*_E. jalgamicum_]
Eomycetopsis Schopf, 1968 [*_E. robusta_]
Eosphaera Barghoorn, 1965 [*_E. tyleri_]
Eotetrahedrion Schopf & Blacic, 1971 [*_E. princeps_]
Eozygion Schopf & Blacic, 1971 [*_E. grande_]
?**Fibularix** Pflug, 1965 [*_F. funicula_]
Filamentella Pflug, 1965 [*_F. plurima_]
Filiconstrictosus Schopf & Blacic, 1971 [*_F. majusculus_]
Glenobotrydion Schopf, 1968 [*_G. aenigmatis_]
Globophycus Schopf, 1968 [*_G. rugosus_]
Gloeodiniopsis Schopf, 1968 [*_G. lamellosa_]
Gunflintia Barghoorn, 1965 [*_G. minuta_]
Halythrix Schopf, 1968 [*_H. nodosa_]
Heliconema Schopf, 1968 [*_H. australiensis_]
Huroniospora Barghoorn, 1965 [*_H. microreticulata_]
Kakabekia Barghoorn, 1965 [*_K. umbellata_]
Millaria Pflug, 1966a [*_M. implexa_]
Montanella Pflug, 1965 [*_M. beltensis_]
Myxococcoides Schopf, 1968 [*_M. minor_]
Obconiphycus Schopf & Blacic, 1971 [*_O. amadeus_]
Oscillatoriopsis Schopf, 1968 [*_O. obtusa_]
Palaeoanacystis Schopf, 1968 [*_P. vulgaris_]
Palaeolyngbya Schopf, 1968 [*_P. barghoorniana_]
Palaeomicrocoleus Korde in Vologdin & Korde, 1965 [*_P. gruneri_]
Palaeopleurocapsa Knoll, Barghoorn, & Golubić, 1975 [*_P. wopfnerii_]
Palaeorivularia Korde, 1965 [*_P. ontarica_]
Palaeoscytonema Edhorn, 1973 [*_P. moorhousei_]
Palaeospiralis Edhorn, 1973 [*_P. canadensis_]
Palaeospirulina Edhorn, 1973 [*_P. arcuata_]
Partitiofilum Schopf & Blacic, 1971 [*_P. gongyloides_]
Petraphera L. Nagy, 1974 [*_P. vivescenticula_]
Phanerosphaerops Schopf & Blacic, 1971 [*_P. capitaneus_]
Polycellaria Pflug, 1965 [*_P. bonnerensis_]
Primorivularia Edhorn, 1973 [*_P. thunderbayensis_]
?**Protorivularia** Butin, 1959 [*_P. onega_]
Ramsaysphaera Pflug, 1976 [*_R. ramses_] [The systematic placement of this 3.4 by old fossil is uncertain]
Scintilla Pflug, 1966 [*_S. perforata_]
Siphonophycus Schopf, 1968 [*_S. kestron_]
Sphaerocongregus Moorman, 1974 [*_S. variabilis_] [According to Vidal (1976), an acritarch, and a synonym of _Bavlinella_ Shepeleva, 1962]
Sphaerophycus Schopf, 1968 [*_S. parvum_]
Tenuofilum Schopf, 1968 [*_T. septatum_]
Tormentella Pflug, 1966a [*_T. tubiformis_]
Tricellaria Pflug, 1965 [*_T. deylensis_]
Veteronostocale Schopf & Blacic, 1971 [*_V. amoenum_]
Zosterosphaera Schopf, 1968 [*_Z. tripunctata_]

SPOROMORPHS AND ACRITARCHS

It is not possible to give a complete list of taxa established for Precambrian sporomorphs and acritarchs because their nomenclature is exceedingly confused. The most common acritarchs from the Upper Precambrian are Sphaeromorphitae. Many of them have been placed in the Paleozoic genus _Leiosphaeridia_ Eisenack, 1958, with the following tentative synonymy (after Volkova _et al._, 1968, with additions): [=_Botholigotriletum_ Timofeev, 1958, _Ocridoligotriletum_ Timofeev, 1958; _Stenozonoligotriletum_ Timofeev, 1958; _Trachyoligotriletum_ Timofeev, 1958; _Protoleiosphaeridium_ Timofeev, 1959; _Leiosphaeridium_ Timofeev, 1959; _Lopholigotriletum_ Timofeev, 1959; _Leiopsophosphaera_ Naumova, 1960, _Wendiella_ Timofeev, 1960 _(nom. nud.); Kildinella_ Shepeleva & Timofeev, 1963; _Turuchania_ Rudavskaya, 1964; _Protosphaeridium_ Timofeev, 1966; _?Menneria_ Lopukhin, 1971]. Others, mostly larger, are placed in the genus _Chuaria_ Walcott, 1899 [*_C. circularis_] [=_Fermoria_ Chapman, 1935; _Protobolella_ Chapman, 1935; _Vindhyanella_ Sahni, 1936; _Krishnania_ Sahni & Srivastava, 1954; _Kildinella_ Shepeleva & Timofeev, 1963 _(partim)_]. (Synonymy from Ford & Breed, 1973.) A similar form, ranging up to 44 mm in diameter, is _Beltanelloides_ Sokolov, 1965 [*_B. sorichevae_] [=_Beltanelliformis_ Menner, 1963 (_nom. nud.,_ figured but not described until 1968) (type, *_B. brunsae_)]. Some of these Upper Precambrian fossils have been mistakenly considered as Metazoa or Protozoa.

STROMATOLITES

A comprehensive bibliography, together with other information on stromatolites, is included in a monographic work by Walter (1976).

Acaciella Walter, 1972 [*_Cryptozoon australicum_ Howchin, 1914]

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Alcheringa Walter, 1972 [**A. narrina*]
Aldania Krylov, 1969 [**Gymnosolen sibericus* Yakovlev, 1934]
Alternella Raaben, 1972 [**A. hyperboreica*]
Anabaria Komar, 1964 [**A. radialis*]
Archaeozoon Mathews, 1890 [**A. acadiense*]
Baicalia Krylov, 1963 [**Collenia baicalica* Maslov, 1937]
Basisphaera Walter, 1972 [**B. irregularis*]
Boxonia Koroljuk, 1960 [**B. gracilis*]
Calevia Butin, 1959 [**C. olenica*]
Carelozoon Metzger, 1924 [**C. jatulicum*] [=*Carelosoon* Butin, 1966 *(nom. van.)*] [See Häntzschel, 1975, p. *W*182. Recent work has made it clear that material from Karelia, identical with the original material from Finland, represents stromatolites]
Collenella Komar, 1964 [**C. cormosa*]
Collenia Walcott, 1914 [**C. undosa*]
Colleniella Koroljuk, 1960 [**C. idensis*]
Columnacollenia Koroljuk, 1960 [No type species designated]
Columnaefacta Koroljuk, 1960 [**C. elongata*]
Columnaria Vologdin, 1962 [No type species designated]
Compactocollenia Koroljuk, 1960 [No type species designated]
Conophyton Maslov, 1937 [**C. lituum*]
Conusella Golovanov, 1970 [**C. regularis*]
Dabania Shenfil, 1972 [**D. chopichica*]
Dgerbia Dolnik, 1974 [**D. grumulosa*] [=*Djerbia* auctt. *(nom. van.)*]
Eucapsiphora Cloud & Semikhatov, 1969 [**E. paradisa*]
Gaia Krylov, 1975 [**G. irkuskanica*]
Georginia Walter, 1972 [**G. howchini*]
Gongylina Komar, 1964 [**G. differenciata*]
Gruneria Cloud & Semikhatov, 1969 [**G. biwabikia*]
Gymnosolen Steinmann, 1911 [**G. ramsayi*]
Iliella Krylov, 1975 [**I. kotuikanica*]
Inzeria Krylov, 1963 [**I. tjomusi*]
Irregularia Koroljuk, 1960 [No species mentioned]
Jacutophyton Shapovalova, 1968 [**J. ramosum*]
Jurusania Krylov, 1963 [**J. cylindrica*]
Kasaia Bertrand-Safati, 1972 [**K. convexa*]
Katavia Krylov, 1963 [**K. karatavica*]
Katernia Cloud & Semikhatov, 1969 [**K. africana*]
Kotuikania Komar, 1964 [**K. torulosa*]
Kulparia Preiss & Walter, in Walter, 1972 [**K. kulparensis* Preiss, 1973]
Kurtunia Shenfil, 1972 [**K. uluntuica*]
Kussiella Krylov, 1963 [**Collenia kussiensis*; (=C. *kussiensis* Maslov MS., *nom. nud.*)]
Lenia Dolnik, 1971 [**L. jacutica*]
Linella Krylov, 1967 [**L. ukka*]
Malginella Komar & Semikhatov, 1970 [?]
Microstylus Komar, 1966 [**M. perplexus*]
Minjaria Krylov, 1963 [**M. uralica*]
Nouatila Bertrand-Sarfati, 1972 [**N. frutectosa*]
Nucleella Komar, 1966 [**N. figurata*]
Olenia Butin, 1960 [**O. rasus*]
Omachtenia Nuzhnov, 1967 [**O. omachtensis*]
?**Palia** Butin, 1966 [**P. septentrionalis*]
Paniscollenia Koroljuk, 1960 [**P. vulgaris*]
Parmites Raaben, 1964 [**P. concrescens*]
Patomia Krylov, 1967 [**P. ossica*]
Pilbaria Walter, 1972 [**P. perplexa*]
Pitella Semikhatov, 1962 [**P. lanceolata*]
Planocollina Koroljuk, 1960 [**P. serrata*]
Platella Koroljuk, 1963 [No species mentioned]
Poludia Raaben, 1964 [**P. polymorpha*]
Pseudokussiella Krylov, 1963 [**P. aii*]
Ramulus Raaben, 1972 [**R. sociabilis*]
Sacculia Koroljuk, 1960 [**S. ovata*]
Segosia Butin, 1966 [**S. columnaris*]
Serizia Bertrand-Sarfati, 1972 [**S. radians*]
Stratifera Koroljuk, 1963 [**S. rara*]
Sundia Butin, 1966 [**S. ramosa*]
Svetliella Shapovalova, 1968 [**S. svetlica*]
Tarioufetia Bertrand-Sarfati, 1972 [**T. hemispherica*]
Tenupalusella Golovanov, 1970 [**T. bracteata*]
Tifounkeia Bertrand-Sarfati, 1972 [**T. ramificata*]
Tilemsina Bertrand-Sarfati, 1970 [**T. divergens*]
Tinnia Dolnik, 1971 [**T. patomica*]
Tungussia Semikhatov, 1962 [**T. nodosa*]

DOUBTFUL TAXA

Most investigators consider that genera established on the basis of microstructures from stromatolites in carbonate preservation are of questionable value because these structures are affected by diagenetic processes. A reexamination of this material may lead to a reassessment as there is now growing interest in algal assemblages that form stromatolites. Vologdin (1962) considered these taxa as Cyanophyta except *Pustularia, Rubellophyton* (possibly Rhodophyta), and *Tubulistroma* (possibly Chlorophyta).

Abruptophycus Vologdin, 1962 [**A. compositus*]
Amplectostroma Vologdin, 1966b [**A. ramificata*]
Angarophycus Vologdin, 1962 [**A. depictus*]
Antiquophytolithus Vologdin, 1962 [**A. filamentaris*]
Azyrtalia Vologdin, 1969b [**A. zonulata*]
Borlogella Vologdin, 1962 [**B. multifaria*]
Bulbistroma Vologdin, 1962 [**B. curtothallum*]
Bursiphycus Vologdin, 1962 [**B. bullatus*]
Cirriphycus Vologdin, 1962 [**C. ordinatus*]
Columnaria Vologdin, 1962 [**C. turuchanica*]
Crispophycus Vologdin, 1962 [**C. sibiricus*]
Crustophycus Vologdin, 1962 [**C. angaricus*]
Cyanostroma Vologdin, 1962 [**C. turuchanicum*]
Cystostroma Vologdin, 1962 [**C. varians*]

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Echaninia Vologdin, 1969a [**E. mucosa*]
Fibrostroma Vologdin, 1962 [**F. fibrillatum*]
Fillostroma Vologdin, 1962 [**F. moticum*]
Grabauella Vologdin, 1964 [**G. dependitis*]
Granifer Vologdin, 1955 [**G. conicus*]
Jatuliana Korde in Vologdin & Korde, 1965 [**J. furcata*]
Lamellophycus Vologdin, 1962 [**L. aculeatus*]
Lamellostroma Vologdin, 1962 [**L. vesiculare*]
Leiostroma Vologdin, 1966b [**L. eleganta*]
Leptotrichomaria Vologdin, 1962 [**L. intermissa*]
Lermontovaephycus Vologdin, 1962 [**L. lamellosus*]
Lopatinella Vologdin, 1962 [**L. bipartita*]
Mucostroma Vologdin, 1966b [**M. carelica*]
Murandavia Vologdin, 1965b [**M. amurica*] [=?*Kareliana* Korde in Vologdin & Korde, 1965]
Nerusiandella Vologdin, 1962 [**N. faveolata*]
Papulophycus Vologdin, 1962 [**P. pennatus*]
Perennaria Vologdin, 1962 [**P. ambigua*]
Pilostroma Vologdin, 1962 [**P. grumosum*]
Plexostroma Vologdin, 1962 [**P. pleurotropum*]
Praechroococcus Vologdin, 1962 [**P. catervatus*]
Protoepiphyton Vologdin, 1962 [**P. curtofiligerum*]
Pustularia Vologdin, 1955 [**P. taeniata*]
Ramulostroma Vologdin, 1962 [**R. ramulosum*]
Rubellophyton Vologdin, 1966b [**R. rameus*]
Sarmaella Vologdin, 1962 [**S. vesiculosa*]
Scandophycus Vologdin, 1962 [**S. crispobilis*]
Sphaerothallus Vologdin, 1962 [**S. spissus*]
Telastroma Vologdin, 1962 [**T. tenuirimulatum*]
Thysanoplanta Vologdin & Titorenko, 1966 [**T. filamentosa*]
Trichostroma Vologdin, 1962 [**T. capilliforme*]
Tschichatschevia Vologdin, 1955 [**Conophyton lituus* Maslov] [obj. syn. of *Conophyton*]
Tubulistroma Vologdin, 1962 [**T. scrofulosum*]
Vesicularia Vologdin, 1962 [**V. nidifica*]
Vittophyton Vologdin, 1962 [**V. parvum*]

PROBLEMATIC FOSSILS (INCLUDING MICROPHYTOLITHS)

Mostly microscopic structures, often associated with stromatolites, occasionally grading into sedimentary structures resembling oolites or coprolites, of more or less questionable organic origin. Some are associated with volcanic rocks and may be droplets of abiogenic organic compounds.

Agamus Vologdin, 1970 [**A. shungiticus*]
Ambigolamellatus Zhuravleva, 1968 [**A. horridus*]
Antholithina Choubert & H. & G. Termier, 1951 [**A. rosacea*] [*see* Häntzschel, 1975, p. *W*169]
Aseptalia Vologdin in Vologdin & Strygin, 1969 [**A. ukrainika*] [2 billion years old; certainly not metazoan as claimed]
Asterosphaeroides Reitlinger, 1959 [No type species designated]
Birrimarnoldia Hovasse & Couture, 1961 [**Arnoldia antiqua* Hovasse] [*see* Häntzschel, 1975, p. *W*155]
Cayeuxipora Graindor, 1957 [No type species designated] [*see* Häntzschel, 1975, p. *W*155]
Cayeuxistylus Graindor, 1957 [No species designated] [*see* Häntzschel, 1975, p. *W*155]
Conferta Klinger, 1968 [**C. rara*]
Crenulata Bertrand-Sarfati, 1972 [**C. gigantea*]
Foninia Korde, 1973 [**F. fasciculata*]
Globoidella Milstein, 1970 [**G. jusmastachica*]
Gonamophyton Vologdin & Drozdova, 1964b [**G. ovale*]
Gorlovella Vologdin, 1970 [**G. obvoluta*]
?**Ladogaella** Vologdin, 1967 [**L. variabilis*]
Marenita Korde, 1973 [**M. kundatica*]
Medullarites Narozhnykh in Narozhnykh & Rabotnov, 1965 [No type species designated]
Nelcanella Vologdin & Drozdova, 1964a [**N. stellata*]
Protospira Vologdin in Vologdin & Strygin, 1969 [**P. strygini*]
Ptilophyton Vologdin, 1967 [**P. makarovae*]
Radiosus Zhuravleva, 1964 [**R. limpidus*]
Tazenakhtia Choubert & H. & G. Termier, 1951 [**T. aenigmatica*] [*see* Häntzschel, 1975, p. *W*179]
Tubiphyton Choubert & H. & G. Termier, 1951 [**T. taghdoutensis*] [*see* Häntzschel, 1975, p. *W*179]
Vallenia Raunsgaard Pedersen, 1967 [**V. erlingi*] [*see* Häntzschel, 1975, p. *W*167]
Vermiculites Reitlinger, 1959 [*non Vermiculites* Rouault, 1850, *nec* Bronn, 1848]
Vermiculus Bertrand-Sarfati, 1972 [**V. contortus*]
Vesicophyton Vologdin in Vologdin & Drozdova, 1969 [**V. punctatum*]
Vesicularites Reitlinger, 1959 [**V. flexuosus*]
Volvatella Narozhnykh, 1967 [**V. obsoleta*]

MEGASCOPIC ALGAE

Aataenia Gnilovskaya, 1976 [**A. reticularis*]
Eoholynia Gnilovskaya, 1975 [**E. mosquensis*]
Grypania Walter, Oehler, & Oehler, 1976 [**Helminthoidichnites? spiralis* Walcott, 1899 (*non H.* Fitch, 1850)]
Laminarites Brongniart, 1828 [*see* Häntzschel, 1975, p. *W*186] [The name *L. antiquissimus* Eichwald, 1856, is often used for megascopic plant remains, probably algae, from the uppermost Precambrian of eastern Europe; they are unlikely to represent this genus and are specifically unidentifiable].
Lanceoforma Walter, Oehler, & Oehler, 1976 [**L. striata*]

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Papillomembrana Spjeldnaes, 1963 [**P. compta*] [This fossil, though not strictly megascopic, with a diameter of 0.5 mm, is included here because it is thought to represent a dasycladacean alga from the Upper Precambrian, Norway].

Proterotainia Walter, Oehler, & Oehler, 1976 [**P. montana*]

Timanella Vologdin in Vologdin & Kochetkov, 1966 [**T. gigas*] [Described as Chlorophyta Dasycladacea, 10-20 cm long, from Lower Cambrian-Proterozoic of N.USSR].

Tyrasotaenia Gnilovskaya, 1971 [**T. podolica*] [? Phaeophyta]

Vendotaenia Gnilovskaya, 1971 [**V. antiqua*] [? Phaeophyta]

TRACE FOSSILS

Archaeichnium Glaessner, 1963 [**A. haughtoni*] [*see* Häntzschel, 1975, p. *W*37]

Buchholzbrunnichnus Germs, 1973 [**B. kroeneri*]

Bunyerichnus Glaessner, 1969 [**B. dalgarnoi*] [*see* Häntzschel, 1975, p. *W*49]

Harlaniella Sokolov, 1973 [**H. podolica*]

Nenoxites Fedonkin, 1976 [**N. curvus*]

Suzmites Fedonkin, 1976 [**S. volutatus*]

Torrowangea Webby, 1970 [**T. rosei*] [*see* Häntzschel, 1975, p. *W*117] [The Precambrian age of the Lintiss Vale Formation (W. New South Wales, Australia) was disputed by Daily (1973) but insisted on by Webby (1973), who accepted correlation of the Lintiss Vale with the Uratanna Formation, generally considered to be post-Ediacaran].

REJECTED AND UNRECOGNIZABLE TAXA

[With few exceptions, these taxa are included in *Treatise* Part W, Supplement 1 (Häntzschel, 1975), to which page references are given and where relevant bibliographic references can be found.]

Amanlisia Lebesconte, 1891 [**A. simplex*] [p. *W*180]

Archaeophyton Britton, 1888 [**A. newberryanum*] [p. *W*169]

Archaeosphaerina Dawson, 1875 [No species named] [p. *W*169]

Aristophycus Miller & Dyer, 1878 [**A. ramosum*] [p. *W*169]

Armelia Lebesconte, 1891 [**A. barrandei*] [p. *W*180]

Aspidella Billings, 1872 [**A. terranovica*] [p. *W*171]

Atikokania Walcott, 1912 [**A. lawsoni*] [p. *W*171]

Beaumontia David, 1928 [**B. eckersleyi*] [p. *W*180] [=*Beaumontella* David, 1928 *(nom. null.)*]

Beltina Walcott, 1899 [**B. danai*] [p.*W*182]

Botswanella Pflug & Strübel, 1969 [Considered by the authors as postsedimentary products of iron bacteria; the name is not meant as biological nomenclature]

Camasia Walcott, 1914 [**C. spongiosa*] [p. *W*171]

Caragassia Vologdin, 1965a [**C. krassevi*] [Casts of mud flakes]

Collinsia Bain, 1927 [**C. mississagiense*] [p.*W*173]

Copperia Walcott, 1914 [**C. tubiformis*] [p. *W*173] [=*Cooperia* Choubert & H. & G. Termier *(nom. null.)*]

Corycium Sederholm, 1911 [**C. enigmaticum*] [p. *W*184] [Accumulation of organic carbon in a distinctive form; not a biosystematic taxon]

Ctenichnites Matthew in Selwyn, 1890 [No species mentioned] [p. *W*173]

Eospicula de Laubenfels, 1955 [**E. cayeuxi*] [p. *E*33]

Eozoon Dawson, 1865 [**E. canadense*] [p. *W*173]

Gakarusia Haughton, 1964 [**G. addisoni*] [p. *W*147]

Gallatinia Walcott, 1914 [**G. pertexta*] [p. *W*175]

Greysonia Walcott, 1914 [**G. basaltica*] [p. *W*175]

Ikeya Vologdin, 1965a [**I. tumida*] [Casts of mud flakes]

Iyaia Vologdin, 1965a [**I. sayanica*] [Casts of mud flakes]

Kempia Bain, 1927 [**K. huronense*] [p. *W*175]

Kinneya Walcott, 1914 [**K. simulans*] [p. *W*176]

Manchuriophycus Endo, 1933 [**M. yamamotoi*] [p. *W*176]

Mawsonella Chapman, 1927 [**M. wooltanensis*] [Described as green alga, now considered as intraformational carbonate breccia]

Medusichnites Matthew, 1891 [No species] [p. *W*175]

Montfortia Lebesconte, 1887 [p. *W*190]

Neantia Lebesconte, 1887 [p. *W*176]

Newlandia Walcott, 1914 [**N. frondosa*] [p. *W*176]

Orthogonium Gürich, 1933 [**O. parallelum*] [p. *W*186]

Palaeotrochis Emmons, 1856 [No type species designated] [p. *W*177]

Protadelaidea Tillyard, 1936 [**P. howchini*] [p. *W*177]

Protoniobia Sprigg, 1949 [**P. wadea*] [*see* Har-

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rington & Moore, 1956, p. *F*159]

Reynella David, 1928 [**R. howchini*] [p. *W*178]

Rhysonetron Hofmann, 1967 [**R. lahtii*] [p. *W*178]

Sayanella Vologdin, 1966a [**S. akshanica*] [Bedding plane features of mechanical origin]

Telemarkites Dons, 1959 [**T. enigmaticus*] [p. *W*179] [Concretions which according to some authors may have been formed under the influence of syngenetic organic activity]

REFERENCES

Allison, C. W., 1975, *Primitive fossil flatworm from Alaska: New evidence bearing on ancestry of the Metazoa:* Geology, v. 3, p. 649-652, text-fig. 1.

Anderson, M. M., 1972, *A possible time span for the Late Precambrian of the Avalon Peninsula, southeastern Newfoundland in the light of worldwide correlation of fossils, tillites, and rock units within the succession:* Canadian Jour. Earth Sci., v. 9, p. 1710-1726.

Barghoorn, E. S., & **Schopf, J. W.**, 1966, *Microorganisms three billion years old from the Precambrian of South Africa:* Science, v. 152, p. 758-763.

———, & **Tyler, S. A.**, 1965, *Microorganisms from the Gunflint Chert:* Science, v. 147, p. 563-577, text-fig. 1-10.

Bekker, Yu. K., 1977, *Pervye paleontologicheskie nakhodki v rifee Urala:* Akad. Nauk SSSR, Izvestiya, Ser. Geol., No. 3, p. 90-100. [*The first paleontological finds in the Riphean of the Ural.*]

Bertrand-Sarfati, J., 1972, *Stromatolites columnaires du Précambrien supérieur:* Centre Rech. Zones Arides, sér. géol. no. 14, CNRS Paris, 235 p., 30 pl.

Bondesen, E., **Raunsgaard Pedersen, K. T.**, & **Jørgensen, O.**, 1967, *Precambrian organisms and the isotopic composition of organic remains in the Ketilidian of south-west Greenland:* Medd. Grønland, v. 164, p. 5-41, pl. 1-13.

Butin, R. V., 1966, *Iskopaemye vodorosli proterozoya karelii:* in Ostatki organismov i problematika proterozoiskykh obrazovanii Karelii: Geol. Inst. Petrozavodsk, p. 34-63. [*Fossil algae from the Proterozoic of Karelia,* in Remains of organisms and problematica from Proterozoic formations of Karelia.]

Choubert, Georges, & **Termier, Henri**, & **Geneviéve**, 1951, *Les calcaires précambriens de Taghdout et leurs organismes problématiques:* Serv. Géol. Maroc, Notes Mém., v. 85, p. 9-34.

Clark, R. B., 1969, *Systematics and phylogeny: Annelida, Echiura, Sipuncula:* in Chemical zoology, M. Florkin, & B. T. Scheer (eds.), v. 4, p. 1-68, Academic Press (New York & London).

Cloud, P. E., Jr., 1968, *Pre-Metazoan evolution and the origins of the Metazoa:* in Evolution and environment, T. Drake (ed.), 72 p., 11 text-fig., Yale Univ. Press (New Haven and London). ——1973, *Pseudofossils: a plea for caution:* Geology, v. 1, p. 123-127, text-fig. 1-7.——1974, *Evolution of ecosystems:* Am. Scientist, v. 62, p. 54-66.——1976a, *Beginnings of biospheric evolution and their biogeochemical consequences:* Paleobiology, v. 2, p. 351-387, 5 pl., 2 fig.——1976b, *Major features of crustal evolution:* Geol. Soc. S. Afr., Annex to v. 79 (Alex L. du Toit Memorial Lecture No. 14), 33 p.

———, **Wright, James**, & **Glover, Lynn**, 1976, *Traces of animal life from 620-million-year-old rocks in North Carolina:* Am. Scientist, v. 64, p. 396-406, 11 text-fig.

Daily, Brian, 1973, *Discovery and significance of basal Cambrian Uratanna Formation, Mt. Scott Range, Flinders Ranges, South Australia:* Search, v. 4, p. 202-205.

Delle Cave, L., & **Simonetta, A. M.**, 1975, *Notes on the morphology and taxonomic position of Aysheaia (Onycophora?) and of Skania (undetermined phylum):* Monitore Zool. Ital. (n. ser.) v. 9, p. 67-81.

Downie, Charles, 1974, *Acritarchs near the Precambrian-Cambrian boundary. A preliminary report:* Rev. Palaeobotony, Palynology, v. 18, p. 57-60.

Dunn, P. R., 1964, *Triact spicules in Proterozoic rocks of the Northern Territory of Australia:* Geol. Soc. Australia, Jour., v. 11, pt. 2, p. 195-197, pl. 1.

Dunning, F. W., 1975, *Precambrian craton of central England and Welsh Borders; in Precambrian. A correlation of Precambrian rocks in the British Isles:* Geol. Soc. London, Spec. Rept. no. 6, p. 83-95.

Edhorn, A. -S., 1973, *Further investigations of fossils from the Animikie, Thunder Bay, Ontario:* Geol. Assoc. Canada, Proc., v. 25, p. 37-66, pl. 1-10.

Eichwald, Edouard d', 1856, *Beitrag zur geographischen Verbreitung der fossilen Thiere Russlands. Alte Periode:* Soc. Impér. Naturalistes Moscou, Bull., v. 29, p. 406-453.

Fedonkin, M. A., 1976, *Sledy mnogokletochnykh iz valdayskoy serii:* Akad. Nauk SSSR, Izvestiya, Ser. Geol. 4, p. 129-132, text-fig. 1-5. [*Tracks of multicellular organisms from the Valday Series.*]

Fischer, A. G., 1972, *Atmosphere and the evolution of life:* Main currents in modern thought, v. 28, no. 5, 9 p., 1 text-fig.

Ford, T. D., 1958, *Pre-Cambrian fossils from*

© 2009 University of Kansas Paleontological Institute

Charnwood Forest: Yorkshire Geol. Soc., Proc., v. 31, p. 211-217, text-fig. 1-3.——1963, *The Pre-Cambrian fossils of Charnwood Forest:* Leicester Lit. Philos. Soc., Trans., v. 57, p. 57-62, pl. 1.

———, & **Breed, W. J.**, 1973, *The problematical fossil Chuaria:* Palaeontology, v. 16, no. 3, p. 535-550, pl. 61-63.

Germs, G. J. B., 1968, *Discovery of a new fossil in the Nama System, South West Africa:* Nature, v. 219, p. 53-54, fig. 1, 2.——1972a, *The stratigraphy and paleontology of the Lower Nama Group, South West Africa:* Univ. Cape Town Dept. Geology, Chamber of Mines Precambrian Research Unit, Bull. 12, 250 p.——1972b, *New shelly fossils from the Nama Group, South West Africa:* Am. Jour. Sci., v. 272, p. 752-761, text-fig. 1-4.——1973a, *A reinterpretation of Rangea schneiderhoehni and the discovery of a related new fossil from the Nama Group, South West Africa:* Lethaia, v. 6, p. 1-10, text-fig. 1, 2.——1973b, *Possible sprigginid worms and a new trace fossil from the Nama Group, South West Africa:* Geology, v. 1, p. 69-70.

Glaessner, M. F., 1958, *New fossils from the base of the Cambrian in South Australia:* Royal Soc. S. Australia, Trans., v. 81, p. 185-188, 1 pl.——1963, *Zur Kenntnis der Nama-Fossilien Südwest-Afrikas:* Naturhist. Mus. Wien, Ann., v. 66, p. 113-120, 3 pl. (pl. 1, fig. 1).——1966, *Precambrian palaeontology:* Earth Sci. Rev., v. 1, p. 29-50, text-fig. 1, 2.——1969, *Trace fossils from the Precambrian and basal Cambrian:* Lethaia, v. 2, p. 369-393.——1971, *The genus Conomedusites Glaessner & Wade and the diversification of the Cnidaria:* Paläont. Zeitschr., v. 45, no. 1/2, p. 7-17, 1 pl.——1976a, *Early Phanerozoic annelid worms and their geological and biological significance:* Geol. Soc. London, Jour., v. 132, no. 3, p. 259-275, 2 pl.——1976b, *A new genus of Late Precambrian polychaete worms from South Australia:* Royal Soc. S. Australia, Trans., v. 100, p. 169-170.

———, & **Daily, Brian**, 1959, *The geology and Late Precambrian fauna of the Ediacara Fossil Reserve:* S. Australian Museum, Rec., v. 13, no. 3, p. 369-401, pl. 42-47.

———, & **Wade, Mary**, 1966, *The late Precambrian fossils from Ediacara, South Australia:* Palaeontology, v. 9, pt. 4, p. 599-628, pl. 97-103.——1971, *Praecambridium—a primitive arthropod:* Lethaia, v. 4, p. 71-77, text-fig. 1-4.

———, & **Walter, M. R.**, 1975, *New Precambrian fossils from the Arumbera Sandstone, Northern Territory, Australia:* Alcheringa, v. 1, p. 11-28, text-fig. 1-4.

Gnilovskaya, M. B., 1971, *Drevneyshie vodnye rasteniya venda Russkoy Platformy (Pozdniy dokembriy):* Paleont. Zhurnal, 1971, no. 3, p. 101-107, pl. 11. [*The most ancient Vendian water plants of the Russian platform (Late Precambrian).*]——1975, *Novye dannye o prirode vendotenid:* Akad. Nauk SSSR, Doklady, Ser. Geol., v. 221, no. 4, p. 953-955, pl. 1. [*New data on the nature of vendotaenids.*]——1976, *Drevneyshie Metaphyta:* Internatl. Geol. Congr., 25th Sess., Rept. Soviet Geologists, Paleont. Marine Geol. "Nauka," Moscow, p. 10-14, pl. 1. [*The oldest Metaphyta.*]

Graindor, M. J., 1957, *Cayeuxidae nov. fam., organismes à squelette du briovérien:* Acad. Sci. Paris, Comptes Rendus, v. 244, p. 2075-2077.

Gürich, Georg, 1930, *Die bislang ältesten Spuren von Organismen in Südafrika:* 15th Internatl. Geol. Congr. South Africa 1929, Comptes Rendus, p. 670-680, text-fig. 1-5.

———, 1933, *Die Kuibis-Fossilien der Nama-Formation von Südwestafrika:* Paläont. Zeitschr., v. 15, p. 137-154.

Häntzschel, Walter, 1975, *Trace fossils and problematica:* in Treatise on invertebrate paleontology, Part W, suppl. 1, Curt Teichert (ed.), 269 p., 912 fig., Geol. Soc. America, Univ. Kansas (Boulder, Colo.; Lawrence, Kans.).

Hardy, A. C., 1953, *On the origin of the Metazoa:* Quart. Jour. Micros. Sci., v. 94, p. 441-443.

Harrington, H. J., & **Moore, R. C.**, 1955, *Fossil jellyfishes from Kansas Pennsylvanian rocks and elsewhere:* Kansas Geol. Survey, Bull. 114, pt. 5, p. 153-163, pl. 1, 2.

———, & ———, 1956, *Medusae incertae sedis and unrecognizable forms:* in Treatise on invertebrate paleontology, R. C. Moore (ed.), Part F, p. *F*153-*F*161, text-fig. 122-131, Geological Soc. America & Univ. Kansas Press (New York; Lawrence, Kans.).

Hessler, R. R., & **Newman, W. A.**, 1975, *A trilobitomorph origin for the Crustacea:* Fossils & Strata, No. 4, p. 437-459, text-fig. 1-12.

Hill, Dorothy, 1972, *Archaeocyatha:* in Treatise on invertebrate paleontology, Part E (revised), Curt Teichert (ed.), 158 p., 871 text-fig., Geol. Soc. America, Univ. Kansas (Boulder, Colo.; Lawrence, Kans.).

Hovasse, R., & **Couture, R.**, 1961, *Nouvelle découverte dans l'Antécambrien de la Côte d'Ivoire, de Birrimarnoldia antiqua (gen. nov.) = Arnoldia antiqua:* Acad. Sci. Paris, Comptes Rendus, v. 252, p. 1054-1056.

Howell, B. F., 1962, *Worms:* in Treatise on invertebrate paleontology, R. C. Moore (ed.), Part W, p. *W*144-*W*177, text-fig. 85-108, Geol. Soc. America, & Univ. Kansas Press (New York; Lawrence, Kans.).

Jaeger, H., & **Martinsson, Anders**, 1967, *Remarks on the problematic fossil Xenusion auerswaldae:* Geol. Foren. Förhandl., v. 88, p. 435-452, text-fig. 1-5.

Johnson, H., & **Fox, S. K., Jr.**, 1968, *Dipleurozoa from Lower Silurian of North America:* Science, v. 162, p. 119-120, fig. 1-3.

Keller, B. M., **Menner, V. V.**, **Stepanov, V. A.**, &

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Chumakov, N. M., 1974, *Novye nakhodki Metazoa v Vendomii Russkoy platformy:* Akad. Nauk SSSR, Izvestiya, Ser. Geol., no. 12, p. 130-134, 1 pl. [*New finds of Metazoa in the Vendomian of the Russian platform.*]

———, & **Fedonkin, M. A.,** 1976, *Novye nakhodki okamenelostey v valdayskoy serii dokembriya po r. Syuzme:* Akad. Nauk SSSR, Izvestiya, Ser. Geol. 3, p. 38-44, 2 pl. [*New finds of fossils in the Precambrian Valday Series on the R. Syuzma.*]

Knoll, A. H., & **Barghoorn, E. S.,** 1975, *Precambrian eucaryote organisms: a reassessment of the evidence:* Science, v. 190, no. 4209, p. 52-54.

———, ———, & **Golubic, S.,** 1975, *Palaeopleurocapsa wopfnerii gen. et sp. nov.: a Late Precambrian alga and its modern counterpart:* Natl. Acad. Sci. USA, Proc., v. 72, p. 2488-2492.

Kozłowski, Roman, 1968, *Nouvelles observations sur les Conulaires:* Acta Palaeont. Polonica, v. 8, p. 497-529.

McElhinny, M. W., Giddings, J. W., & **Embleton, B. J. J.,** 1974, *Palaeomagnetic results and late Precambrian glaciations:* Nature, v. 248, p. 557-561.

Manton, S. M., 1969, *(a) Classification of Arthropoda, (b) Evolution and affinities of Oncychophora, Myriapoda, Hexapoda, and Crustacea:* in Treatise on invertebrate paleontology, Part R, Arthropoda 4, R. C. Moore (ed.), (a) p. *R*3-*R*15, (b) p. *R*15-*R*57, Geol. Soc. America, Univ. Kansas (Boulder, Colo.; Lawrence, Kans.).

Matthews, S. C., & **Missarzhevsky, V. V.,** 1975, *Small shelly fossils of Late Precambrian and Early Cambrian age: a review of recent work:* Geol. Soc. London, Quart. Jour., v. 131, p. 289-304.

Misra, S. B., 1969, *Late Precambrian (?) fossils from southeastern Newfoundland:* Geol. Soc. America, Bull., v. 80, p. 2133-2140, text-fig. 1, 2, pl. 1-8.

Moorman, Mary, 1974, *Microbiota of the late Proterozoic Hector Formation, southeastern Alberta, Canada:* Jour. Paleontology, v. 48, no. 3, p. 524-539, text-fig. 1-3, pl. 1-3.

Nagy, L. A., 1974, *Transvaal stromatolite: first evidence for the diversification of cells about* 2.2×10^9 *years ago:* Science, v. 183, p. 514-516.

Narozhnykh, L. I., 1967, *Onkolity i katagrafii Yudomskoy svity Uchuro-Mayskogo rayona:* Akad. Nauk SSSR, Doklady, v. 173, p. 887-890. [*Oncolites and catagraphites of the Yudoma Suite in the Uchur-Maya area.*]

———, & **Rabotnov, V. T.,** 1965, *Stratigrafiya i novyye formy organicheskykh ostatkov Rifeya (Siniya) i Yudomskogo kompleksa severnogo sklona Aldanskogo shchita:* Akad. Nauk SSSR, Doklady, v. 160, p. 910-913. [*Stratigraphy and new fossil remains from the Riphean (Sinian) and the Yudoma Complex on the northern slope of the Aldan Shield.*]

Nørrevang, Axel, 1975, *The phylogeny and systematic position of the Pogonophora:* Zeitschr. Zool. Syst. Evolutionsforsch, Sonderheft, 143 p., 104 text-fig.

Oehler, J. H., 1976, *Experimental studies in Precambrian paleontology: Structural and chemical changes in blue-green algae during simulated fossilization in synthetic chert:* Geol. Soc. America, Bull., v. 87, p. 117-129, text-fig. 1-14.

Paliy, V. M., 1969, *O novom vide tsiklomedus iz venda Podolii:* Lvov Univ., Paleont. Sbornik, v. 1, no. 6, p. 110-113, 1 fig. [*On a new species of Cyclomedusa from the Vendian of Podolia.*]

Pflug, H. D., 1964, *Niedere Algen und ähnliche Kleinformen aus dem Algonkium der Belt-Serie:* Oberhess. Ges. Natur- und Heilkunde, Bericht, n. ser., Naturwiss., Abt., v. 33, no. 4, p. 403-411, 1 pl.——1965, *Organische Reste aus der Belt Serie (Algonkium) von Nordamerika:* Paläont. Zeitschr., v. 39, no. 1-2, p. 10-25.——1966a, *Einige Reste niederer Pflanzen aus dem Algonkium:* Palaeontographica, v. 117, Abt. B, p. 59-74.——1966b, *Neue Fossilreste aus den Nama-Schichten in Südwest-Afrika:* Paläont. Zeitschr., v. 40, no. 1-2, p. 14-25, pl. 1, 2.——1968, *Gesteinsbildende Organismen aus dem Molar Tooth Limestone der Beltserie (Präkambrium):* Palaeontographica, v. 121, Abt. B, Lief 4-6, p. 134-141, pl. 1, 2.——1970a, *Zur Fauna der Nama-Schichten in Südwest-Afrika. I. Pteridinia, Bau und systematische Zugehörigkeit:* Palaeontographica, v. 134, Abt. A, no. 4-6, p. 153-262, text-fig. 1-14, pl. 21-23.——1970b, *Zur fauna der Nama-Schichten in Südwest-Afrika. II. Rangeidae, Bau und systematische Zugehörigkeit:* Palaeontographica, v. 135, Abt. A, no. 3-6, p. 198-231, text-fig. 1-12, pl. 33-35.——1972a, *Systematik der jung-präkambrischen Petalonamae Pflug 1970:* Paläont. Zeitschr., v. 46, no. 1-2, p. 56-67.——1972b, *Zur Fauna der Nama-Schichten in Südwest-Afrika. III. Erniettomorpha, Bau und Systematik:* Palaeontographica, v. 139, Abt. A, p. 134-170, text-fig. 1-9, pl. 27-39.——1973, *Zur Fauna der Nama-Schichten in Südwest-Afrika. IV. Mikroskopische Anatomie der Petalo-Organismen:* Palaeontographica, v. 144, Abt. A, p. 166-202, text-fig. 1-10, pl. 35-43.——1974a, *Vor- und Frühgeschichte der Metazoen:* Neues Jahrb. Geologie, Paläontologie, Abt., v. 145, no. 3, p. 328-347.——1974b, *Feinstruktur und Ontogenie der jung-präkambrischen Petalo-Organismen:* Paläont. Zeitschr., v. 48, no. 1/2, p. 77-109.——1976, *Ramsaysphaera ramses n. gen. n. sp. aus den Onverwacht-Schichten (Archaikum) von Süd-Afrika:* Palaeontographica, v. 158, Abt. B (Lfg. 5,6), p. 130-168.

———, & **Strübel, G.,** 1969, *Algen und Bakterien in Präkambrischen Konkretionen:* Palaeontographica, v. 127, Abt. B, Lief. 1-6, p. 143-158.

© 2009 University of Kansas Paleontological Institute

Reitlinger, E. A., 1956, *Mikroskopicheskie organicheskiye (?) ostatki serdobskoy serii:* Akad. Nauk SSSR, Doklady, v. 111, p. 1098-1100. [*Microscopic organic (?) remains from the Serdobsk Series.*]——1959, *Atlas mikroskopicheskikh organicheskikh ostatkov i problematiki drevnikh tolshch Sibiri:* Akad. Nauk SSSR, Trudy, Geol. Inst., v. 25, 59 p., pl. 1-22. [*Atlas of microscopic organic remains and problematica from ancient rocks of Siberia.*]

Richter, Rudolf, 1955, *Die ältesten Fossilien Süd-Afrikas:* Senckenberg. Lethaea, v. 36, p. 243-289, pl.

Rozanov, A. Yu., 1973, *Zakonomernosti morfologicheskoy evolyutsii arkheotsiat i voprosy yarusnogo raschleneniya nizhnego kembriya:* Akad. Nauk USSR, Trudy, Geol. Inst., v. 241, 164 p. [*Regularities in the morphological evolution of regular Archaeocyatha and the problems of the Lower Cambrian Stage division.*]

———, **Missarzhevsky, V. V., Volkova, N. A., Voronova, L. G., Krylov, I. N., Keller, B. M., Korolyuk, I. K., Lendzion, K., Michniak, R., Pychova, N. G., & Sidorov, A. D.**, 1969, *Tommotskii yarus i problema nizhnei granitsy kembriya:* Akad. Nauk USSR, Trudy, Geol. Inst., v. 206, 380 p., 79 text-fig., 15 tables. [*Tommotian stage and the Cambrian lower boundary problem.*]

Sabrodin [Zabrodin], Wladimir, 1971, *Leben im Präkambrium:* Ideen d. exakten Wissens 12/71, p. 835-842.

Schopf, J. M., 1970, *Precambrian microfossils:* in Aspects of palynology, R. H. Tschudy, & R. A. Scott (eds.), p. 145-161, 8 text-fig., Wiley Interscience (London, New York).

Schopf, J. W., 1968, *Microflora of the Bitter Springs Formation, Late Precambrian, Central Australia:* Jour. Paleontology, v. 42, no. 3, p. 651-688, pl. 77-86.——1972, *Evolutionary significance of the Bitter Springs (Late Precambrian) microflora:* Internatl. Geol. Congress 24th Sess., sec. 1, p. 68-77, 53 text-fig.——1975, *Precambrian paleobiology: problems and perspectives:* Annual Rev. Earth & Planetary Sci., v. 3, p. 213-249.

———, & **Barghoorn, E. S.**, 1967, *Alga-like fossils from the Early Precambrian of South Africa:* Science, v. 156, p. 508-512.

———, & **Blacic, J. M.**, 1971, *New microorganisms from the Bitter Springs Formation (Late Precambrian) of the north-central Amadeus Basin, Australia:* Jour. Paleontology, v. 45, no. 6, p. 925-960, pl. 105-113.

———, **Haugh, B. N., Molnar, R. E., & Satterthwait, D. F.**, 1973, *On the development of metaphytes and metazoans:* Jour. Paleontology, v. 47, no. 1, p. 1-9.

Singh, I. B., 1969, *Primary sedimentary structures in Precambrian quartzites of Telemark, southern Norway, and their environmental significance:* Norsk Geol. Tidsskr., v. 49, no. 1, p. 1-31.

Sokolov, B. S., 1965, *Drevneyshie otlozheniya rannego kembriya i Sabelliditidy:* in Vses. simpozium po paleontologii dokembriya (Tesizy dokladov), p. 78-91, Akad. Nauk SSSR, Sibir. Otdel., Inst. Geol. Geofiz. (Novosibirsk). [*The oldest deposits of the early Cambrian and the sabelliditids,* in All-Union symposium on the paleontology of the Precambrian. Abstracts.]——1967, *Drevneyshiye pogonofory:* Akad. Nauk SSSR, Doklady, v. 177, p. 201-204. [*The oldest Pogonophora.*]——1972, *Vendskii etap v istorii zemli:* Akad. Nauk SSSR, M.G.K. 24 Sess., Doklady, Sov. Geol., Probl. 7, p. 114-123, 5 pl. [*Vendian Stage in the earth history.*]——1973, *Vendian of northern Eurasia:* Am. Assoc. Petrol. Geologists, Mem. 19, p. 204-218, 6 text-fig.——1975, *O paleontologicheskikh nakhodkakh v dousolskikh otlozheniyakh Irkutskogo Amfiteatra:* in Analogi Vendskogo kompleksa v Sibiri, Akad. Nauk SSSR, Sibir. Otdel., Inst. Geol. Geofiz., Trudy, v. 232, p. 112-117, pl. 1-3. [*On paleontological discoveries in pre-Usolje deposits of Irkutsk Amphitheatre,* in Analogues of Vendian complex in Siberia.]——1976, *Organicheskiy mir zenli na puti k fanerozoiskoy differentsiatsii:* Akad. Nauk SSSR, Vestnik, no. 1, p. 126-143. [*The organic world on the path of Phanerozoic differentiation.*]

Southcott, R. V., 1958, *South Australian jellyfish:* South Australian Naturalist, v. 32, p. 53-81.

Spjeldnaes, Nils., 1963, *A new fossil (Papillomembrana sp.) from the Upper Precambrian of Norway*: Nature, v. 200, p. 63-64.

Sprigg, R. C., 1947, *Early Cambrian (?) jellyfishes from the Flinders Ranges, S. Australia:* Royal Soc. S. Australia, Trans., v. 71, p. 212-224, pl. 5-8.——1949, *Early Cambrian "jellyfishes" of Ediacara, South Australia, and Mount John, Kimberley District, Western Australia:* Royal Soc. S. Australia, Trans., v. 73, p. 72-99, pl. 9-21.

Squire, A. D., 1973, *Discovery of Late Precambrian trace fossils in Jersey, Channel Islands:* Geol. Mag., v. 110, no. 3, p. 223-226.

Stanley, S. M., 1973, *An ecological theory for the sudden origin of multicellular life in the Late Precambrian:* Natl. Acad. Sci. USA, Proc., v. 70, no. 5, p. 1486-1489.

Strand, Trygve, & Kulling, Oscar, 1972, *The Scandinavian Caledonides:* 302 p., Wiley-Interscience Publishers (London-New York).

Stürmer, Wilhelm, & Bergström, Jan, 1976, *The arthropods Mimetaster and Vachonisia from the Devonian Hunsruck Shale:* Paläont. Zeitschr., v. 50, p. 78-111, pl. 9-18.

Taylor, M. E., 1966, *Precambrian mollusc-like fossils from Inyo County, California:* Science, v. 153, p. 198-201.

Ubaghs, Georges, 1971, *Diversité et spécialisation des plus anciens échinodermes que l'on connaisse:* Biol. Rev., v. 46, no. 1, p. 157-200.

Valkov, A. K., & Sysoiev, B. A., 1970, *Angustio-*

© 2009 University of Kansas Paleontological Institute

kreidy kembriya sibiri: in Stratigrafiya Proterozoya i kembriya vostoka Sibirskoy Plaformy, Akad. Nauk SSSR, Yakut. Branch Sib. Div. Int. Geol., p. 94-100. [*The Angustiochreida of the Siberian Cambrian,* in Stratigraphy and paleontology of the Proterozoic and Cambrian of the eastern part of the Siberian platform.]

Vidal, Gonzalo, 1976, *Late Precambrian microfossils from the Visingsö beds in southern Sweden:* Fossils & Strata No. 9, p. 1-57, text-fig. 1-23.

Volkova, N. A., Zhuravleva, Z. A., Zabrodin, V. E., & **Klinger, B. S.**, 1968, *Problematika pogranichnykh sloyev rifeya i kembriya Russkoy platformy, Urala i Kazakhstana:* Akad. Nauk SSSR, Trudy, v. 188, p. 5-106. [*Problematica of the boundary strata of the Riphean and Cambrian of the Russian platform, the Urals and Kazakhstan.*]

Vologdin, A. G., 1961, *Arkheotsiaty i ikh stratigraficheskoe znachenie:* Mezhdunar. geol. Kongr. 20th sess., Simpoziuma po kembriyu, v. 3, p. 173-177. [*Archaeocyatha and their stratigraphical significance.*]——1962, *Drevneyshiye vodorosli SSSR:* 656 p., 80 pl., Akad. Nauk (Moskva), [*The oldest algae of the USSR.*]——1965a, *Otkrytiye ostatkov ogromnykh pantsirnykh zhivotnykh v karagasskoy svite Vostochnogo Sayana:* Akad. Nauk SSSR, Doklady, v. 161, p. 216-220. [*Discovery of the remains of large carapacial animals in the Karagas Suite of the Eastern Sayan.*]——1965b, *K otkrytiyu ostatkov vodorosley v murandavskoy svite proterozoya Malogo Khingana (DVK):* Akad. Nauk SSSR, Doklady, v. 164, p. 677-680. [*Toward discovery of algal remains in the Proterozoic Murandav Suite of the Lesser Khingan (Far Eastern Region).*].——1966a, *Ostatki protomedus iz nizov karagaskoy svity Vostochnogo Sayana:* Akad. Nauk SSSR, Doklady, v. 167, p. 434-436. [*Remains of protomedusae from the base of the East Sayan Karagas Suite.*]——1966b, *Ostatki mikrovodorosley is proterozoya Karelii:* in Ostatki organismov i problematika proterozoiskykh obrazovanii Karelii: Geol. Inst. Petrozavodsk, p. 65-95. [*Remains of microscopic algae from the Proterozoic of Karelia,* in Remains of organisms and problematica from Proterozoic formations of Karelia.]——1967, *Ostatki organizmov iz ladozhskoy serii proterozoya Karelii:* Akad. Nauk SSSR, Doklady, v. 175, p. 217-220. [*Remains of organisms from the Proterozoic Ladoga Series of Karelia.*]——1969a, *Novye sinezelenyye vodorosli dokembryskogo vozrasta iz Batenevskogo kryazha:* Akad. Nauk SSSR, Doklady, v. 187, p. 440-442. [*New Precambrian cyanophyceans from Batenev Ridge.*]—— 1969b, *K otkrytiyu vodorosley semeystva Rivulariaceae v pozdnem dokembrii:* Akad. Nauk SSSR, Doklady, v. 187, p. 1162-1163. [*A discovery of algae of the Family Rivulariaceae in the Upper Precambrian.*]——1970, *Ostatki organizmov iz shungitov dokembriya Karelii:* Akad. Nauk SSSR, Doklady, v. 193, p. 258-261. [*Organic remains from shungites of the Precambrian of Karelia.*]

———, & **Drozdov, N. A.**, 1964a, *Neskolko vidov vodorosley iz gonamskoy svity uchurskoy serii proterozoya Ayano-Mayskogo rayona Dalnego Vostoka:* Akad. Nauk SSSR, Doklady, v. 159, p. 114-116. [*Several species of algae from the Gonam Suite of the Proterozoic Uchur Series, Ayan-Maya District, Far East.*]——1964b, *Iskopayemaya sinezelenaya vodorosl v pozdnedokembriyskykh otlozheniyakh Dalnego Vostoka:* Akad. Nauk SSSR, Doklady, v. 159, p. 576-578. [*Cyanophycean algae in Upper Precambrian sediments of the Far East.*]——1969, *Vodorosli sem. Gloeocapsaceae v osadkakh dokembriya Batenevskogo Kryazha:* Akad. Nauk SSSR, Doklady, v. 186, p. 1419-1421. [*Algae of the Family Gloeocapsaceae in the Precambrian of the Batenev Ridge.*]——1970, *Novaya nakhodka drevneyshey fauny:* Akad. Nauk SSSR, Doklady, v. 190, p. 195-197. [*A new find of the oldest fauna.*]

———, & **Kochetkov, O. S.**, 1966, *Ob otkrytii ostatkov gigantícheskikh sifoney v drevnikh sloyakh Timanskogo kryazha:* Akad. Nauk SSSR, Doklady, v. 169, p. 672-675. [*Discovery of the remains of gigantic siphonean algae in the ancient strata of Timan Ridge.*]

———, & **Korde, K. B.**, 1965, *Neskolko vidov drevnikh Cyanophyta i ikh tsenosy:* Akad. Nauk SSSR, Doklady, v. 164, p. 207-210. [*Several species of ancient Cyanophyta and their coenoses.*]

———, & **Maslov, A. B.**, 1960, *O novoy gruppe iskopayemykh organizmov iz nizov yudomskoy svity sibirskoy platformy:* Akad. Nauk SSSR, Doklady, v. 134, p. 691-693. [*A new group of fossil organisms from the base of the Yudoma series of the Siberian platform.*]

———, & **Strygin, A. I.**, 1969, *Otkrytie ostatkov organismov v verkhney svite krivorozhskoy serii dokembriya Ukrainy:* Akad. Nauk SSSR, Doklady, v. 188, p. 446-449. [*A discovery of organic remains in the Upper Suite of the Krivoy Rog Series in the Precambrian of the Ukraine.*]

———, & **Titorenko, T. N.**, 1966, *Proterozoyskiye vodorosli s reki Kurtun, yugo-zapadnoye Pribaykalye:* Akad. Nauk SSSR, Doklady, v. 166, p. 193-196. [*Proterozoic algae from the Kurtun River, southwest Baikal region.*]

Voronova, L. G., & **Missarzhevsky, V. V.**, 1969, *Nakhodki vodoroslei i trubok chervei v pogranichnykh sloyakh kembriya i dokembriya na severe sibirskoy platformy:* Akad. Nauk SSSR, Doklady, v. 184, p. 207-210. [*Finds of algae and worm tubes in boundary layers of Cambrian and Precambrian in the north of the Siberian platform.*]

Wade, Mary, 1968, *Preservation of soft-bodied animals in Precambrian sandstones at Ediacara,*

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South Australia: Lethaia, v. 1, 1968, p. 238-267, 29 text-fig.—— 1969, *Medusae from uppermost Precambrian or Cambrian sandstones, central Australia:* Palaeontology, v. 12, no. 3, p. 351-365, pl. 68,69.——1971, *Bilateral Precambrian chondrophores from the Ediacara fauna, South Australia:* Royal Soc. Victoria, Proc., v. 84, pt. 1, p. 183-188, pl. 6.——1972a, *Hydrozoa and Scyphozoa and other medusoids from the Precambrian Ediacara fauna, South Australia:* Palaeontology, v. 15, no. 2, p. 197-225, pl. 40-43.—— 1972b, *Dickinsonia: polychaete worms from the Late Precambrian Ediacara fauna, South Australia*: Queensland Museum, Mem., v. 16, no. 2, p. 171-190.

Walter, M. R. (ed.), 1976, *Stromatolites:* in Developments in sedimentology, v. 20, xii + 790 p., Elsevier (Amsterdam, New York).

———, Oehler, J. H., & Oehler, D. Z., 1976, *Megascopic algae 1300 million years old from the Belt Supergroup, Montana: A reinterpretation of Walcott's Helminthoidichnites:* Jour. Paleontology, v. 50, p. 872-881, pl. 1, 2.

Webby, B. D., 1970, *Late Precambrian trace fossils from New South Wales:* Lethaia, v. 3, p. 79-109. ——1973, *Trace fossils from the Lintiss Vale Formation of New South Wales: a late Precambrian fauna:* Search, v. 4, p. 494-496.

Werner, Bernhard, 1966, *Stephanoscyphus (Scyphozoa, Coronatae) and seine direkte Abstammung von den fossilen Conulata:* Helgoländer Wiss. Meeresunters., v. 13, p. 317-347.

Young, F. G., 1972, *Early Cambrian and older trace fossils from the southern Cordillera of Canada:* Canadian Jour. Earth Sci., v. 9, p. 1-17, 10 text-fig.

Zaika-Novatskiy, V. S., Velikanov, V. A., & Koval, A. P., 1968, *Pervyy predstavitel ediakarskoy fauny v vende Russkoy platformy (Verkhniy Dokembriy):* Paleont. Zhurnal, 1968, no. 2, p. 132-134, text-fig. 1. [*The first representative of the Ediacara fauna in the Vendian of the Russian platform (Upper Precambrian).*]

Zhuravleva, Z. A., 1964, *Onkolity i katagrafii rifeya i nizhnego kembriya Sibiri i ikh stratigraficheskoye znacheniye:* Akad. Nauk SSSR, Trudy, Geol. Inst., v. 114, p. 1-73, pl. 1-24. [*Riphean and Lower Cambrian oncolites and catagraphites of Siberia and their stratigraphic importance.*]

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CAMBRIAN[1]

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CONTENTS

INTRODUCTION

Cambrian rocks of marine origin are widely distributed in Europe, Asia, Australia, and North America, and they are found in parts of North Africa, the Cordilleran region of South America, New Zealand, and Antarctica, indicating that much of the present land area of the world was inundated during at least part of Cambrian time. Because strong evidence now indicates that the present distribution and composition of the continents is related to Mesozoic and younger movements of continental blocks, the present distribution of Cambrian rocks and faunas does not accurately reflect global Cambrian biogeography and paleogeography. Nevertheless, observations that can be made about Cambrian faunal and stratigraphic relations on the present continental blocks must be considered in any attempt to construct early Paleozoic global geography and environmental distributions. In the following pages the general characteristics of Cambrian biota are outlined and the present distribution of Cambrian outcrops and major faunal elements are presented. Finally, a global synthesis is suggested and the current state of Cambrian biostratigraphy is reviewed.

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CAMBRIAN BIOTA

At the beginning of Cambrian time, the seas of the world were already populated by a diverse biota that included representatives of one or more classes of most of the major invertebrate phyla. With the exception of the Archaeocyatha, which flourished in the Early Cambrian but almost completely disappeared from younger rocks, all of the phyla present at the beginning of the Cambrian have survived to the present time. Among these, the principal phyla, in order of stratigraphic importance, are the Arthropoda, Brachiopoda, Mollusca, Echinodermata, and Porifera. Lesser phyla are the Coelenterata, Annelida, Hemichordata, and Protista. The Bryozoa have no unequivocal Cambrian record.

The Arthropoda of the Cambrian include, first and foremost, the Trilobita. This was the largest and most diverse group of Cambrian organisms and apparently occupied most normal marine environments. It included open-ocean planktonic representatives, as well as probably restricted vagile benthos. Trilobites are the most commonly encountered Cambrian fossils and are the group from which almost all biogeographic data have been derived (Sdzuy, 1958; Lochman-Balk & Wilson, 1958; Kobayashi, 1967; Repina, 1968; Palmer, 1969, 1972, 1973; Cowie, 1971). All other Arthropoda are rare and insignificant elements of the Cambrian faunas.

The Brachiopoda are represented by both inarticulate and articulate forms. Inarticulate brachiopods are numerous and the phosphatic shells of lingulides, paterinides, and acrotretides are found in many Cambrian rocks. The Acrotretida, particularly those obtained from insoluble residues of limestones, have considerable potential for future biostratigraphic and biogeographic studies. Articulate brachiopods, although locally abundant, are not common.

Among the Mollusca, the subphylum Cyrtosoma is well represented from the earliest Cambrian onward; however, several distinctive subgroups (e.g., Stenothecoididae, Helcionellidae, Pelagiellida) became extinct before the Ordovician. Cephalopoda appeared only as rare forms in the latest Cambrian. The subphylum Diasoma is comparatively poorly represented in Cambrian rocks by rare ribeirioids and by the Early Cambrian supposed bivalve, *Fordilla.* The next younger record of the Bivalvia is in rocks of Ordovician age.

Hyolitha, regarded by some as a small phylum separate from the Mollusca and related to the Sipunculoidea, are common in many parts of the Cambrian where they often are found in high concentrations.

Echinodermata were abundant in the Cambrian seas and contributed significant quantities of skeletal debris to Cambrian sediments, but only rarely are articulated skeletons preserved. Echinozoans, crinozoans (?), blastozoans, and homalozoans all have records from the Early or Middle Cambrian.

Porifera, represented by rare individuals, and moderately abundant siliceous or calcareous spicules, are present in most Cambrian areas.

Coelenterata are represented by rare Scyphozoa and Hydrozoa. No Cambrian record for the Anthozoa is given.

Many Cambrian sediments show signs of active burrowing inhabitants. Some of the burrows have been attributed to the Annelida, and a few tube-forming annelids have been recognized in some Early Cambrian deposits.

Conodonts, the biologic affinities of which are uncertain, are known from rocks as old as Early Cambrian and Hemichordata represented by the dendroid graptolites have been found in rocks as old as Middle Cambrian.

Typical Cambrian assemblages, particularly in carbonate rocks, yield several species of trilobites, lingulide, paterinide and acrotretide brachiopods, hexactinellid or chancelloriid sponge spicules, or both kinds, hyolithids or small coiled mollusks, and disarticulated echinoderms.

CAMBRIAN OF NORTH AMERICA

Cambrian rocks are sufficiently widespread in North America to permit a reasonably accurate evaluation of the broader aspects of Cambrian biogeography for this

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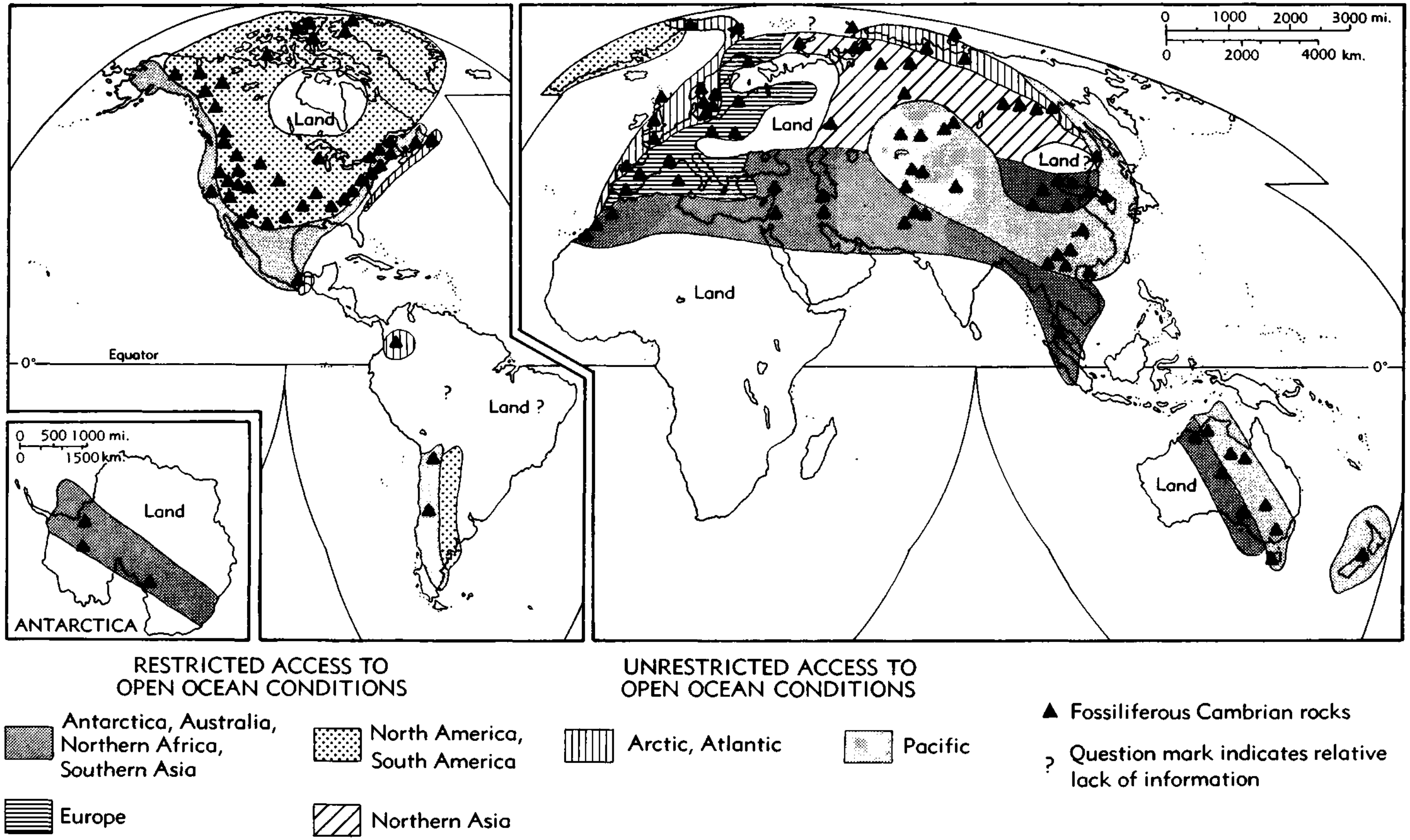

FIG. 1. Distribution of fossiliferous Cambrian outcrop areas and general distribution of the principal paleogeographic and biogeographic regions during the Cambrian Period ("Cambrian Period," Encyclopaedia Britannica, published with permission; modified figure).

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continent. Their outcrops reflect a generally concentric distribution of Cambrian biotas about the continental center in north-central Canada.

Outcrops are found in the Cordilleran region from Alaska and northwestern Canada to northern Mexico, Appalachian region of eastern United States, maritime provinces of Canada, eastern and northern coasts of Greenland, several Arctic islands, several isolated regions in central United States, and one small area of southern Mexico (see Fig. 1). Some subsurface information is available for many parts of the United States and the plains of western Canada. A major land area extended southwestward from the Hudson Bay region of Canada to south-central United States throughout the Early and Middle Cambrian. Its extension in the United States was gradually submerged during the Late Cambrian and by the beginning of the Ordovician most of the United States was submerged beneath a shallow sea.

Lochman-Balk and Wilson (1958) in their pioneering synthesis of North American Cambrian biogeography recognized three apparently concentric biofacies realms characterized by both tectonic and environmental criteria: a cratonic realm characteristic of the shallow shelves; an extracratonic-intermediate realm characteristic of the miogeosynclines; and an extracratonic-euxinic realm characteristic of the eugeosynclines. The faunas of the first two realms have been traditionally representative of the Pacific province of North America. The faunas of the extracratonic-euxinic realm have been traditionally representative of the Atlantic province. Subsequent work in western United States and Alaska, however, has led to an alternative interpretation of concentric faunal relationships around North America.

In western North America, a broad belt of carbonate sediments, largely reflecting extremely shallow-water conditions across a broad carbonate bank, paralleled the western cratonic margin during most of Middle and Late Cambrian time. The carbonate belt separated an inner region of light-colored terrigenous sediments ("inner detrital belt") generally reflecting shallow-water conditions, from an outer region of dark-gray or black silty and shaly sediments ("outer detrital belt"), commonly associated with dark-colored thin-bedded limestone, that reflects deeper water conditions. A similar tripartite facies pattern is present in eastern United States, and this pattern may have existed around much of North America. The shallow carbonate banks served as an effective barrier separating two major faunal regions: an inner region, including the inner bank margins and the inner detrital belt; and an outer region, including the outer bank margin and the outer detrital belt. The inner region corresponds approximately to the cratonic realm of Lochman-Balk and Wilson, and the outer region corresponds to their extracratonic-intermediate realm. Their extracratonic-euxinic realm, which has been documented only in extreme eastern North America, seems to be unrelated to the remainder of the continent (see p. A124).

Throughout Cambrian time, wherever faunal documentation is adequate, the trilobite faunas became increasingly varied and cosmopolitan toward the most peripheral regions. The faunas toward the continental interior consist largely of endemic species and genera of polymerid trilobites. The faunas in the peripheral regions include, in addition to endemic American families, significant numbers of Eodiscidae, Oryctocephalidae, and Pagetiidae in parts of the Early Cambrian and early Middle Cambrian, and a variety of common agnostids from the middle Middle Cambrian through the Late Cambrian. Many of these, both genera and species, are found on other continents. Where carbonate banks existed as significant barriers to easy migration in the seas bordering the continent, the differences between the peripheral and inner faunas were accentuated. During the late Middle Cambrian and through much of the Late Cambrian, the contrast is so striking that precise correlation of faunal sequences between the areas is difficult.

In the Early Cambrian, the oldest beds are fossiliferous shale and sandstone units and no areal differentiation in the faunas has been noted. The most fossiliferous beds are in western North America and contain species of *Fallotaspis, Daguinaspis,* and *Holmia*, typical of similar facies in North Africa and northwestern Europe, as well as species of *Nevadia* that are restricted

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to North America. Slightly later, areas of carbonate sedimentation developed in the peripheral regions, in some cases forming substantial carbonate banks locally rich in archaeocyathids. With the appearance of these areas of carbonate sedimentation, a subtle gradation in character of the Early Cambrian faunas from the shaly and sandy inner regions extended onto and across the carbonate areas, and the Early Cambrian biota increased seaward in richness and variety. The inner regions had small trilobite faunas composed almost wholly of olenellids, including species of *Olenellus, Nevadella,* and *Bristolia.* In the carbonate areas and at their outer margins, several groups of simple ptychopariids, oryctocephalids, corynexochids, and eodiscids, as well as many nontrilobite organisms, and the olenellid *Wanneria,* appeared with *Olenellus* or *Nevadella.* Among the more peripheral trilobite faunas, eodiscid genera (e.g., *Calodiscus, Serrodiscus*) were also widely distributed in Eurasia. Other indications of intercontinental exchange of faunas in the peripheral regions are shown by the occurrence of the same or related genera of unusual spinose eodiscids in both the Taconic region of eastern United States and the Nuneaton area of central England, and the strong affinity of some of the Early Cambrian trilobites of Alaska and northern Canada with the faunas of Siberia.

In the early Middle Cambrian, the pattern of increasingly varied and cosmopolitan faunas in the peripheral regions was well established. The shales of the inner regions typically contained a small selection of corynexochid genera, including *Albertella* and the slightly younger *Glossopleura.* In the areas of carbonate sedimentation, these genera were associated with a variety of other corynexochid genera and a rich assortment of ptychopariid trilobites, all of which were endemic to North America. Toward the outer margins of the carbonate areas and in the deeper water areas beyond, Pagetiidae, Oryctocephalidae, Agnostidae, and Dorypygidae appeared and genera of these families were also widespread on other continents. The deeper water sediments beyond the outer edge of the banks at this time were the repository for the rich and varied Burgess Shale fauna. In eastern North America early Middle Cambrian faunas are lacking in all areas of deeper water sediments. Throughout this region, very little stratigraphic distance separates beds bearing late Middle Cambrian faunas from underlying Lower Cambrian beds.

During late Middle Cambrian and early Late Cambrian time the faunas of the inner region, including the inner margins of the banks, were strikingly different from those of the outer margin of the banks and the deeper waters beyond. The carbonate banks had by then become extensive around much of North America and seem to have been very effective barriers to free exchange of trilobites. The inner trilobite faunas during the late Middle Cambrian are dominated by simple ptychopariid trilobites, together with a few species of *Bathyuriscus* and *Kootenia,* all of which are endemic forms. The outer trilobite faunas include largely different genera and species of ptychopariid trilobites, together with some Dorypygidae and abundant agnostids. Most of the agnostid genera and species and the ubiquitous paradoxidid, *Centropleura,* are found on other continents and provide important means for intercontinental correlation of the upper Middle Cambrian (Robison, 1964).

An extensive transgression into the continental interior near the end of the Middle Cambrian established the general facies patterns that persisted to the end of the period. The trilobite genera that are dominant in the faunas of the broad inner detrital belt during the early Late Cambrian, such as *Crepicephalus, Lonchocephalus*, and *Menomonia*, became minor elements in the faunas of the carbonate banks and almost completely disappeared in the faunas of the outer detrital belt. In contrast, *Tricrepicephalus* and species of the Kingstoniidae, Llanoaspidae, and Blountiidae, which are rare in the sandy facies of the inner detrital belt, are common in the carbonate belt, and true *Cedaria*, which is probably not congeneric with the *"Cedaria"* species of the inner detrital belt, is found only in the faunas of the outer detrital belt associated with early species of *Glyptagnostus* and other widespread agnostids.

During late Dresbachian and early Franconian time, the only extensive Cambrian marine regression in North America took place. This did not significantly influence the faunal patterns but did affect the record

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of this time in the inner regions. A hiatus in the continental interior separates the early representatives of the principal families of this time, the Elviniidae and Pterocephaliidae, from their descendants and the resultant "faunal break" has been the traditional boundary between the Dresbachian and Franconian stages. In the peripheral regions the Elviniidae and Pterocephaliidae are well represented by complete evolutionary sequences and they are associated with species of *Glyptagnostus, Pseudagnostus, Aspidagnostus*, and the ubiquitous genus *Irvingella*, which are found on most other continents.

During the later part of the Cambrian, facies conditions similar to those preceding the late Dresbachian regression were restored. With them came a contrast in trilobite faunas between the major facies belts that is comparable to the earlier Late Cambrian contrasts. In the inner detrital belt, species of *Conaspis, Ptychaspis, Dikelocephalus*, and Saukiidae are common. In the carbonate belt, these are not significant faunal elements and the Parabolinoididae, Idahoiidae, and Eurekiidae are characteristic. The outer detrital belt faunas of both the east and the west during this time contain a strikingly different suite of trilobites, many of which are representative of the *Hungaia magnifica* fauna and such cosmopolitan agnostids as *Lotagnostus, Pseudagnostus,* and *Geragnostus*. In Alaska and western Nevada these are associated with species of the Ceratopygidae and *Hedinaspis*, which are widespread in Asia. In western Newfoundland, they are associated with rare species of olenids that are abundant in eastern Newfoundland and western Europe. This indicates some degree of access between adjacent major faunal regions, but the foreign trilobites seem to have been "tourists" and they never established a serious base in North America. With only a few exceptions, the principal cosmopolitan trilobite genera represent the Agnostida and it is largely through this group that intercontinental correlation and evaluation of Cambrian events is possible.

CAMBRIAN OF EURASIA AND AFRICA

Unlike North America, Eurasia is a complex and perhaps composite continent that includes three major regions distinct both faunally and in the character of their stratigraphy. Europe, together with the Mediterranean region and North Africa, but exclusive of northwestern Scotland, constitutes one region; the Soviet Union east of the Urals constitutes a second region; and southeastern Asia, including China and Korea, constitutes a third region.

EUROPE-MEDITERRANEAN-NORTH AFRICA

In this region (see Fig. 1), outcrops of Cambrian rocks are known along the eastern margin of the Caledonian mountains in Norway and Sweden, the lowlands of southern Sweden and the islands of Bornholm and Öland in the Baltic Sea, the southern coast of the Gulf of Finland, southern Poland, western Czechoslovakia and adjacent parts of East and West Germany to the north, central England and the coastal regions of north and south Wales, northwestern Scotland, the Normandy region of western France, the Montagne Noire in southern France, northern and southern Spain and a small area in southern Portugal, southern Sardinia, northwestern Africa, eastern Turkey, and the mountains east of the Dead Sea. Subsurface information is available for southern Sweden, Poland, and western Soviet Union. Except for southern Sweden and North Africa, outcrops showing continuous successions through significant parts of the Cambrian System are rare. In most regions the exposures are poor, or strongly disturbed by later tectonic movements, or both.

As a result of these deficiencies, as well as significant local variations in stratigraphic detail and considerable distances between major outcrop areas, only the most general aspects of European Cambrian paleogeography can be defined. To the northeast, a large positive area variously called the Baltic or Balto-Samartian shield persisted throughout the Cambrian Period. Similarly, most of North Africa and southern Arabia constituted positive areas flanking the Cambrian marine regions on the south. Smaller positive areas have been postulated south of the Cambrian outcrop areas of Czechoslovakia and Poland, west of Normandy, and in northern and southern Spain.

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From late Early Cambrian through the Late Cambrian, the region shares many common polymerid trilobite genera that are rare or absent in other parts of Eurasia. Some differentiation into northern and southern regions has been suggested (Sdzuy, 1958), but the similarities of the faunas of this region far outweigh the differences, and the scattered nature of the fossiliferous areas makes differentiation into meaningful subregions difficult.

During the Early Cambrian, an extensive development of limestone took place in southern Europe and North Africa, clearly distinguishing this region from northern Europe, which lacked carbonate sedimentation. Most of the Early Cambrian limestone sequences have varying quantities of associated archaeocyathids. After the Early Cambrian, all of the European-Mediterranean-North African region is characterized by the absence or poor development of carbonate sediment. The Early Cambrian trilobite faunas are characterized by species of the Protolenidae and Ellipsocephalidae, and by olenellids that are largely different from those of North America. However, some of the olenellids (*e.g., Fallotaspis, Daguinaspis, Holmia*) have been reported from western North America, and *Fallotaspis* is also found in Siberia. *Redlichia,* which is common in the Lower Cambrian of China, is a rare element of the southern European faunas. The Early Cambrian Eodiscidae, which are particularly well developed in central England and in Spain, are also found in parts of North America and Siberia.

The Middle Cambrian faunas are particularly characterized by the Paradoxididae and Conocoryphidae. In southern and central Europe, various ptychopariid genera representing the Saoinae are also characteristic. In Sweden, which has the only rich development of Middle Cambrian faunas in northern Europe, black shales and thin associated limestones have abundant agnostids that are found on most other continents, and associated Anomocaridae, Solenopleuridae, and Agraulidae, some of which are also found outside of the European region.

Late Cambrian faunas are known only in northern and central Europe, where they are dominated by the Olenidae. In Scandinavia and Great Britain, where the Late Cambrian faunas are found in black shale or black limestone, the olenids are associated with agnostid genera and species found on most other continents, and a few other forms, such as *Irvingella*, that have wide geographic distribution. In contrast, trilobites other than olenids are almost completely absent from the sandy facies of Poland.

The Cambrian faunas of Europe provide important data that cannot be ignored in discussions of plate tectonics. Almost all of the common genera of northwestern Europe are found in eastern Newfoundland, Nova Scotia, and New Brunswick in eastern Canada, and the Early Cambrian genera are also found in eastern Massachusetts in northeastern United States. These genera occur in the same faunal assemblages as in Europe, and have no admixture of North American forms. The North American rocks in which they are found include most of the typical lithologies described from the Cambrian of Great Britain in approximately the same stratigraphic succession. With little doubt these rocks and their faunas are "un-American." Despite the occurrence of the ubiquitous paradoxidid *Centropleura* in western North America, the easternmost North American faunas as a whole are not found in the west and do not constitute a peripheral North American facies as suggested by Lochman-Balk and Wilson (1958). The seaway that separated these "Atlantic Province" areas from the rest of North America was probably the same seaway that separated the Cambrian of England and Wales from that of northwest Scotland where the Lower Cambrian terrigenous rocks and overlying thick succession of carbonates are entirely of North American aspect (Palmer, 1969).

In contrast, the close faunal and stratigraphic affinities of Spain to North Africa, as well as to central Europe and the eastern Mediterranean, raise some real problems concerning significant separation of Gondwanaland from Laurasia through the present Mediterranean region.

EASTERN SOVIET UNION

In the Soviet Union east of the Urals (Fig. 1), outcrops are known in the Arctic

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islands of Novaya Zemlya, Severnaya Zemlya, and Bennett Island of the New Siberian Islands; the Taymyr Peninsula; the northeastern part of the central Siberian Plateau between the Kotuy and Lena rivers; the western part of the plateau region near the lower reaches of the Yenesei River; a broad belt extending from the Aldan River basin on the east to the vicinity of the junction of the Angara and Yenesei rivers; the complexly folded areas of southern Siberia; and Kazakhstan, Kirgizstan, and Tadzhikstan.

In contrast to Europe, carbonate sediments and volcanic activity played important roles in the development of Cambrian facies and their related faunas. These may be responsible for many of the faunal contrasts between the two regions.

In a very general way, the Soviet Union east of the Urals can be divided into three large facies regions with contrasting marine sedimentary sequences. Details of tectonically positive areas related to these sedimentary sequences are not yet clear.

A southern region includes the complexly folded and faulted areas of southern Siberia, Kazakhstan, Kirgizstan, and Tadzhikstan. This was a region of active volcanism throughout most of the Cambrian Period. It projects westward to the southern Urals where Cambrian volcanics are also known. Toward the southern part of this region, in Kirgizstan and Tadzhikstan (referred to by Russians as Middle Asia), volcanism seems to have been less intense than in Kazakhstan.

The central region includes most of the rest of the mainland outcrops of the Soviet Union except for some eastern tributaries of the Aldan River, the Olenek uplift, and the Kharaulak Mountains near the mouth of the Lena River, and the eastern part of Taymyr Peninsula. All Cambrian sections of this region are dominated by limestone and dolomite or evaporites.

The northern and northeastern regions include the areas excluded from the central region described in the preceding paragraph, and the Arctic islands. This region is characterized by predominantly shaly or sandy sedimentary sequences, with or without associated thin-bedded cherty or pyritic limestones.

In the Early Cambrian, the southern part of the central region was an area of restricted environments characterized by limestone-dolomite-evaporite sequences and an endemic trilobite complex. This area was flanked on the east and south by an area of archaeocyathid bioherms and a different, also largely endemic, trilobite complex. Still farther east, in sequences of limestone and terrigenous rocks, and southward in the volcanic regions, a third trilobite complex has been recognized (Repina, 1968). Eodiscina, including both endemic genera and the widespread *Serrodiscus, Calodiscus, Triangulaspis*, and *Hebediscus* are characteristic of the third complex. Relatively rare olenellids and *Redlichia* are found also in this complex, and in association with the archaeocyathid bioherms, in areas interpreted as normal marine environments.

During the Middle and Late Cambrian, the central carbonate region continued to support a varied trilobite fauna composed largely of endemic genera and species of ptychopariid trilobites. In the volcanic region to the south, and particularly in black-shale and thin-bedded limestone areas to the east and north, ubiquitous agnostid genera and species became increasingly abundant, associated in the Middle Cambrian with Paradoxididae and Oryctocephalidae, and, in the Late Cambrian, with Olenidae and Pterocephaliidae. These faunas have many almost cosmopolitan elements and can be related easily to the faunas in similar facies elsewhere in the world. Intercalations of the sediments and faunas of this facies into the principal carbonate sequences along the margins of the central carbonate region provide some slight help in relating the largely endemic carbonate facies faunas to those in other parts of the world.

SOUTHEASTERN ASIA

In southeastern Asia (Fig. 1), Cambrian outcrops are known in South and North Korea and adjacent parts of southeastern Siberia, many parts of eastern China, the mountains of northern and northwestern China, South China and the boundary region between China and North Viet Nam, and the small island of Turatao off the west coast of Thailand. Early Cambrian seas transgressed northward toward a major

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land area located in eastern Mongolia and perhaps also northeast of Korea. Other major land areas are not well documented.

Two principal facies regions have been described by KOBAYASHI (1967): the Hwang-ho facies, principally distributed in north China and also recognized in the China-North Viet Nam border region; and the Yangtze or Machari facies of east-central and western China and South Korea.

During the Early Cambrian, the region of the Hwang-ho facies was the site of shale deposition and is characterized by the presence of species of *Redlichia.* The region of the Yangtze facies included significant areas of carbonate sedimentation with locally flourishing archaeocyathids in east-central China, and the associated trilobites included a few Eodiscidae, in addition to *Redlichia* and some Protolenidae. No Olenellidae have been reported from the Early Cambrian of China.

During the Middle Cambrian, the Hwang-ho facies reflects shallow-water carbonate sedimentation, grading northward in north China and Korea into increasingly terrigenous sediments. The trilobite faunas are largely endemic and include such typical genera as *Amphoton, Solenoparia,* and *Anomocarella.* The contrasting Yangtze and Machari facies are characterized by shaly and silty sequences with associated thin-bedded pyritic limestone indicative of deeper water conditions. In northwestern China, volcanic rocks are associated with this facies, and the trilobite faunas are characterized by cosmopolitan agnostid genera.

Toward the end of the Middle Cambrian and in the early Late Cambrian, the Yangtze facies spread into parts of the northern region where it is represented by a variety of genera of the Damesellidae.

During the remainder of the Late Cambrian, the regions of the Hwang-ho facies were again dominated by endemic trilobites, including Chuangiidae and, later, genera such as *Asioptychaspis* and *Quadraticephalus,* which are related to North American Ptychaspididae and Saukiidae. The area of the Yangtze facies continued to have a cosmopolitan agnostid fauna, including such genera as *Glyptagnostus* and *Lotagnostus,* associated with Ceratopygidae.

CAMBRIAN OF AUSTRALIA

The only other major area of the world for which regional data are available is Australia. Cambrian outcrops are known (Fig. 1) in northwestern Queensland, broad areas of the Northern Territory, the northeastern part of Western Australia, south-central South Australia, small outcrops in western New South Wales, Victoria, and Tasmania. ÖPIK (1957) postulated a narrow north-south seaway through the middle of Australia in Early Cambrian time, and a complex marine region covering most of eastern Australia in Middle and Late Cambrian times. Western Australia was a land area throughout most of the Cambrian.

During Early Cambrian time, South Australia was a region of carbonate sedimentation with locally rich archaeocyathid faunas. The few trilobites in the sequence include species of *Redlichia* and Protolenidae.

During Middle Cambrian time, Queensland and the northern part of the Northern Territory was a region of limestone and shale sedimentation that supported a rich and varied fauna of trilobites including many agnostids and oryctocephalids and the distinctive paradoxidid *Xystridura.* To the south, in Victoria and Tasmania, thick sequences of shales and interbedded volcanics are known. These contain a few fossiliferous intervals characterized by cosmopolitan agnostids in Tasmania and by agnostids and polymerid genera (*e.g., Fouchouia, Amphoton, Dinesus*) typical of eastern Asia, in Victoria.

In the early part of the Late Cambrian, the faunas of western Queensland contained a rich association of endemic genera together with Damesellidae and other trilobites typical of eastern Asia, many cosmopolitan agnostid genera, and a few widespread polymerids such as *Irvingella* and *Erixanium.* Younger Late Cambrian faunas recorded from sandstones in the Northern Territory include Ptychaspididae and Saukiidae similar to forms from China. To the east, contemporaneous faunas include abundant agnostids and genera with both Chinese and western American affinites.

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MISCELLANEOUS CAMBRIAN AREAS

Cambrian rocks are known without much regional context (Fig. 1) in western Argentina, southern Bolivia, and eastern Colombia, New Zealand, Antarctica, the Himalayan region of India and Pakistan, northern and southern Iran, and the island of Spitsbergen in the North Atlantic.

In New Zealand, a Middle Cambrian trilobite fauna has its affinities entirely with faunas of Queensland in Australia. In the Antarctic, Early, Middle, and Late Cambrian trilobites and Early Cambrian archaeocyathids have their affinities with the faunas of Australia and Asia. In contrast, the Early, Middle, and Late Cambrian faunas of northwestern Argentina are essentially the same as those of western United States. The latest Cambrian trilobite faunas of Bolivia have their closest affinities with the faunas of southern Mexico which, in turn, have strong affinities to both North America and northwestern Europe. In Colombia, a small collection with *Paradoxides* suggests affinities to northwestern Europe. The faunas of the Himalayan region and Iran include Early and Late Cambrian trilobites closely related to those of eastern Asia and, in the Middle Cambrian, ubiquitous representatives of the Oryctocephalidae. The Early Cambrian fauna of Spitzbergen includes Olenellidae related to those of North America.

BIOGEOGRAPHIC "PROVINCES"

The basic clue to understanding the biogeographic framework of the Cambrian on a global scale lies in an appreciation of the distribution of trilobites at various taxonomic levels. At the specific level, the only group with wide geographic distribution is the Agnostida. At the generic level, the most widely distributed trilobites are the Agnostida and polymerid forms commonly associated with them. Regions poor in Agnostida commonly have geographically restricted genera. Many trilobite families have worldwide distribution but are restricted to particular environmental areas.

Further important data are provided by the faunal distribution patterns around North America. These show that the regions rich in Agnostida and their associates, particularly in the Middle and Late Cambrian, are in the peripheral marine areas on the outer side of the carbonate banks—the regions with unrestricted access to the open ocean. In the protected marine areas on or behind the carbonate banks, the Agnostida are not abundant and most trilobite genera are typically North American.

The open ocean also served as a genetic reservoir. Several times during the Cambrian, the polymerid trilobite faunas of the carbonate banks and the protected areas behind the banks in North America were virtually annihilated by abrupt changes in environmental conditions—perhaps temperature—that left no record in the sediments beyond an abrupt nonevolutionary change in the trilobite faunas. The changes took place first in the peripheral regions beyond the carbonate banks, thus indicating that the source for the new faunas was the oceanic region. Furthermore, the incoming elements of each new fauna had their greatest affinities with the incoming elements of the fauna that followed the previous annihilation. This similarity was not superficial, and supports the idea that the source of genetic continuity was in the oceanic region. Additional support comes from the fact that long-ranging genera, such as *Ogygopsis* and *Zacanthoides*, and long-ranging families, such as the Oryctocephalidae and Pagetiidae, are typical of the unrestricted environments beyond the carbonate banks.

Neither the geotectonic criteria of geosyncline versus craton (Lochman-Balk & Wilson, 1958) nor the lithofacies pattern of carbonate banks and inner and outer detrital belts (Palmer, 1969) described above for North America, are applicable on a worldwide basis to explain the general trilobite distribution. The major faunal contrasts on the largest scale are between those areas that had unrestricted access to

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the open ocean, and those areas where such access was restricted either by a carbonate barrier, or by undefined modifications of environmental parameters such as temperature and salinity that were related to broad expanses of shallow sea over either carbonate or terrigenous substrates. Areas of the first type are the agnostid-rich areas that share many common faunal characteristics on a global scale. Areas of the second type are those where endemic polymerid genera dominate. If trilobite distributions are viewed in this context of contrasting marine environments—restricted versus unrestricted access to open ocean conditions—then a reasonable explanation for both the intracontinental diversity and intercontinental similarity of the trilobite faunas can be found. Taylor (1973) has suggested that an additional strong factor in the geographic control of the trilobite faunas here referred to as open-ocean may be temperature. This suggestion should be given serious consideration in future compilations of Cambrian biogeography.

Figure 1 shows the general distribution of persistent areas of open-ocean and restricted conditions during Cambrian time. The margins between these areas fluctuated throughout the Cambrian and in addition were not sharply defined. Thus, boundaries on the maps indicate only an approximate average position on a shifting spectrum of conditions.

Within this broad framework, both the open-ocean regions and the restricted regions supported biotas of limited extent that define "provinces." Because very little is known about the precise habitat requirements of almost all trilobites, the "provinces" are, again, only crude generalizations that outline regions sharing certain distinctive taxa.

EARLY CAMBRIAN BIOGEOGRAPHY

The described trilobite faunas of the Early Cambrian show many contrasts that could be attributed to "provincial" differences (Cowie, 1971); however, many of these reflect differences in the environments available for sampling and the inadequacy of the Early Cambrian record on a global scale. The rich and varied invertebrate faunas of the Asiatic Soviet Union are associated with broad areas of carbonate banks where margins were exposed to open ocean conditions. Most western North American and Arctic Early Cambrian faunas are in restricted regions associated with terrigenous sequences of the inner detrital belt or the inner margins of the carbonate belt; however, sequences representing the outer detrital belt and outer margin of the carbonate belt have recently been described from northwestern Canada. The faunas of southwestern Europe and North Africa are associated with terrigenous sequences but they seem to have had better access to open-ocean conditions than most of the North American faunas.

Two "provinces"—an "olenellid province" and a "redlichiid province"—characterized by trilobite families typical for the restricted regions can be recognized. In regions with better access to the open ocean, representatives of both families are known. The "olenellid province" includes North America, South America, and northwestern Europe. The "redlichiid province" includes China, southern Asia eastward from the Mediterranean region, Australia, and Antarctica. In southwestern Europe and adjacent parts of Africa, and in the Asiatic Soviet Union, elements of both "provinces" are found.

The only other Early Cambrian group for which biogeography has been evaluated on a global scale is the Archaeocyatha (Zhuravleva, 1968; Hill, 1972). These are almost completely confined to regions interpreted here as open ocean. During much of this time, many families and genera were common to all areas. During the middle Early Cambrian, when the Archaeocyatha reached their evolutionary peak, the complexes of Australia and Antarctica included a significant number of forms not known in the Northern Hemisphere. Within the eastern Soviet Union consistent differences existed during the early and middle Early Cambrian between the archaeocyathid complexes of the volcanic regions in the south and the nonvolcanic limestone regions to the north.

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MIDDLE AND LATE CAMBRIAN BIOGEOGRAPHY

During the Middle and Late Cambrian, "provincial" differences are shown in both the restricted and the open-ocean regions. In the restricted regions, four provincial areas typified by many endemic genera and species can be recognized: 1) the inner detrital belt and adjacent margins of the carbonate belt of North America; 2) the sandy facies of central Europe; 3) the carbonate banks of the Siberian platform; and 4) the Hwang-ho facies of China. The Late Cambrian sandy facies of central Australia seems to have a close relationship to the Hwang-ho facies.

In the regions with unrestricted access to the open ocean, the number of provincial areas is less and they are much less well defined. Three provincial regions focused on western Europe, North America, and southeast Asia-Australia can be recognized. The western European "province" is characterized by the Olenidae, Conocoryphidae, and Paradoxididae. Significant elements of the faunas of this province are found in the open-ocean regions of the Asiatic Soviet Union. The North American "province" is characterized by Oryctocephalidae, certain Corynexochida (*Bathyuriscus, Ogygopsis, Zacanthoides*), Marjumiidae, Pterocephaliidae, Richardsonellidae, and Catillicephalidae. However, some of the typical elements of this province are found in the open-ocean regions of the Asiatic Soviet Union and Australia. The southeast Asia-Australia "province" is characterized by Damesellidae, certain Corynexochida (*Amphoton*), Anomocarellidae, Ceratopygidae, and Xystridurinae. Some elements of these faunas are found in the open-ocean regions of Asiatic Soviet Union and northwestern North America.

CAMBRIAN BIOSTRATIGRAPHY

For almost a century, attempts have been made to divide rocks of Cambrian age into ever smaller chronostratigraphic units using primarily stratigraphic ranges of trilobites. In some areas, and for different times within the Cambrian Period, fossils other than trilobites have also been used. Lower Cambrian sequences on the Baltic shield include zones based on characteristic and common occurrences of *Mobergella* and *Volborthella*—fossils whose biologic affinities are still being debated. The lowermost Cambrian beds of the Siberian platform, which include faunas assigned to several zones of the Tommotian Stage, are characterized by abundant nontrilobite fossils. Some of these fossils are now being found in Lower Cambrian beds of the Baltic region, England, and Australia. In the eastern part of the Soviet Union, archaeocyathids have been effectively used to characterize divisions of the Lower Cambrian. Recently, conodonts have been found in sufficient abundance in Upper Cambrian beds to characterize zones that will be important in discussions of intercontinental correlation of the Cambrian-Ordovician boundary. Acrotretide brachiopods have the potential to be useful biostratigraphic tools in Middle and Upper Cambrian carbonate sequences in many areas; however, at the present time, effective interregional biostratigraphic synthesis for the Cambrian System must be based on trilobites.

In each region where reasonably detailed work has been done, successions of assemblage zones have been established. In some regions, these have been grouped into stages. Neither zones nor stages have consistent interregional utility now. Even the Lower, Middle, and Upper Cambrian series, which have received different local names in some areas, can only be approximately correlated on a global scale. The basal boundary of the Cambrian is a special philosophical problem and is hotly debated. The Lower-Middle Cambrian boundary and the Cambrian-Ordovician boundary are both subject to international disagreement about correlation involving possible discrepancies of the order of a stage. The Middle-Upper Cambrian boundary seems to be the least disputed, but even there possible intercontinental discrepancies exist.

The reason for the difficulty in correlation of Cambrian faunal sequences is the fact that trilobite distribution is strongly facies controlled. This is well demonstrated by

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stratigraphic analyses of Cambrian faunal differences in the Cordilleran region of western North America, in eastern China, and along the southern boundary of the Siberian platform. Polymerid trilobite faunas in the Cordilleran region of North America, for example, represent three or four distinct depositional environments: the restricted shelf, with subtle contrasts between regions of clastic and carbonate sedimentation; the ocean-facing shelf margin; the shelf slope; and the deep shelf or open ocean. Due to shifting sites of these environments the often distinctly different faunas representing them may be stacked in different orders, in different stratigraphic sections. Alternatively, different biofacies dominated the same time intervals in different geographic areas. Thus, in order to work out a meaningful biostratigraphy, the biofacies and lithofacies relationships of the Cambrian faunas must be more clearly established. This work is still in progress.

The "classical" North American trilobite zonation reviewed by LOCHMAN-BALK and WILSON (1958) is a typical example of the problems introduced by nonrecognition of trilobite biofacies. The Lower Cambrian zonation and the Middle Cambrian zonation up through the *Glossopleura* Zone is representative only of the restricted-shelf biofacies; the remainder of the Middle Cambrian zones represent the shelf-margin and shelf-slope biofacies. There is no quarrel with the faunal sequence, which has been adequately tested and is generally reliable; however, the biostratigraphy of the restricted shelf region must be separated from the biostratigraphies of the ocean-facing and oceanic regions. Subsequent integration of the different biostratigraphies will then permit maximum utilization of faunal information for correlation purposes.

Empirical observations indicate that a useful global biostratigraphy will probably have to be based on the faunas of the oceanic regions, which are dominated by Agnostida, and that precise interregional correlation between faunas of the restricted-shelf regions will have to be based on fortuitous interlayering of these faunas with distinctive elements of the oceanic faunas.

One additional factor that may be important for problems of intercontinental correlation is that of extinction events referred to earlier (p. *A*128). In the North American Cambrian sequences at least three, perhaps as many as six, major continent-wide extinctions affected the trilobite faunas of the shelf regions. The extinction events mark the boundaries of biostratigraphic units called biomeres, which may include several trilobite zones. The causes of the extinctions are postulated to be abrupt cooling events, but conclusive evidence of this hypothesis must still be obtained. Similar and apparently synchronous events have been reported at several levels in Australia, but are seemingly absent from the Siberian and Baltic regions. Further work on the significance of extinctions at biomere boundaries may provide a basis for global biostratigraphic units of stage magnitude. For the moment, local zonal and stage schemes will have to remain as the only available, although inadequate, descriptions of Cambrian biostratigraphy. These schemes, for each of the principal Cambrian regions of the world, are discussed below.

NORTH AMERICA

The sequence of zones given in Table 1 has wide applicability in North America, but it cannot be applied uniformly to all Cambrian regions.

The Lower Cambrian subdivisions are recognizable only in the Cordilleran region. Early Cambrian localities in the Appalachian region, the Canadian Arctic islands, and Greenland have faunas that can be related only in a general way to the Cordilleran zonal scheme. Most of the faunas from those regions can be included in the *Bonnia-Olenellus* Zone but exact positioning within this rather broad zone is not yet possible.

The Middle Cambrian subdivisions are also primarily recognizable in the Cordilleran region. Early Middle Cambrian faunas assignable to the *Plagiura-Poliella* and *Albertella* Zones have not been recognized in eastern North America. In the deeper water facies, there seems to be an anomalous hiatus at this time. The *Glossopleura* Zone is known in the restricted-shelf facies in the Appalachian region and in Greenland, but is also absent from the deeper water facies adjacent to the shelf. Faunas repre-

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TABLE 1. *Cambrian Biostratigraphy of North America.*

- Upper Cambrian Series
  - Trempealeauan Stage
    - *Saukia* Zone
  - Franconian Stage
    - *Saratogia* Zone
    - *Taenicephalus* Zone
    - *Elvinia* Zone
  - Dresbachian Stage
    - *Dunderbergia* Zone
    - *Prehousia* Zone
    - *Dicanthopyge* Zone
    - *Aphelaspis* Zone
    - *Crepicephalus* Zone
    - *Cedaria* Zone
- Middle Cambrian Series
    - *Bolaspidella* Zone
    - *Bathyuriscus-Elrathina* Zone
    - *Glossopleura* Zone
    - *Albertella* Zone
    - *Plagiura-Poliella* Zone
- Lower Cambrian Series
    - *Bonnia-Olenellus* Zone
    - *Nevadella* Zone
    - *Fallotaspis* Zone

senting most of the younger zones are known from the restricted-shelf and deeper water facies of the Appalachian region and have recently been discovered in the Canadian Arctic islands and Greenland.

Precise intercontinental correlation is only possible for parts of the upper Middle Cambrian and Upper Cambrian, where agnostid trilobites are particularly abundant and varied and for the uppermost Cambrian where conodont biostratigraphy is beginning to produce useful results.

NORTHERN EUROPE

The zonal succession shown in Table 2 can be used effectively from Poland across northern Europe to Great Britain. In addition, many of the elements of this succession are found in the coastal Cambrian exposures of eastern North America from Newfoundland to New England, in the Middle and Upper Cambrian of northeastern Siberia, and in the Middle Cambrian of southern Europe and North Africa so that reasonably precise correlations can be effected among parts of these regions. The nearly cosmopolitan agnostid trilobites permit correlation with several parts of the North American, Australian, and Chinese sequences. Throughout this region, Lower and Middle Cambrian beds are separated by a hiatus.

TABLE 2. *Cambrian Biostratigraphy of Northern Europe (Martinsson, 1974).*

- Upper Cambrian Series
    - *Acerocare* Zone
    - *Peltura scarabaeoides* Zone
    - *Peltura minor* Zone
    - *Protopeltura praecursor* Zone
    - *Leptoplastus* Zone
    - *Parabolina spinulosa* Zone
    - *Homagnostus obesus* Zone
    - *Agnostus pisiformis* Zone
- Middle Cambrian Series
  - *Paradoxides forchhammeri* Stage
    - *Lejopyge laevigata* Zone
    - *Jincella brachymetopa* Zone
  - *Paradoxides paradoxissimus* Stage
    - *Ptychagnostus lundgreni-Goniagnostus nathorsti* Zone
    - *Ptychagnostus punctuosus* Zone
    - *Hypagnostus parvifrons* Zone
    - *Tomagnostus fissus-Ptychagnostus atavus* Zone
    - *Ptychagnostus gibbus* Zone
  - *Eccaparadoxides oelandicus* Stage
    - *Eccaparadoxides pinus* Zone
    - *Eccaparadoxides insularis* Zone
  - Hiatus
- Lower Cambrian Series
    - *Strenuaeva linnarssoni* Zone
    - *Holmia kjerulfi* Zone
    - *Volborthella-Schmidtiellus mickwitzi* Zone
    - *Mobergella holsti* Zone

CENTRAL AND SOUTHERN EUROPE

Within this region, the only biostratigraphic zonation of more than local value is that of the Middle Cambrian (Table 3). The sequence established by SDZUY (1972) for Spain is applicable in the Montagne Noire of southern France, Sardinia, and North Africa. Upper Cambrian beds are poorly fossiliferous or absent. Lower Cambrian beds are variably fossiliferous but only in North Africa has a zonal sequence been established (HUPÉ, 1952) and its regional applicability has not yet been demonstrated.

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TABLE 3. *Cambrian Biostratigraphy of Spain, France, Sardinia, and North Africa (Sdzuy, 1972).*

- Upper Cambrian Series (not described, poorly represented)
- Middle Cambrian Series
  - *Solenopleuropsis* Zone
  - *Pardailhania* Zone
  - *Badulesia* Zone
  - *Acadolenus* Zone
  - *Conocoryphe ovata* Zone
  - *Paradoxides (Acadoparadoxides) mureroensis* Zone
- Lower Cambrian Series (various local sequences)

SOVIET UNION

Because of the vast area of eastern Soviet Union that contains Cambrian rocks, no single scheme has yet been established at any level in the intrasystemic biostratigraphic hierachy. Each major outcrop area has its own local zonation. Table 4 shows the stages that are most commonly used, but critiques of the Lower and Middle Cambrian stage structure by ROZANOV (1973) and SAVITSKIY (1969) have pointed out many difficulties with this scheme.

TABLE 4. *Commonly Used Cambrian Stages of the Soviet Union.*

- Upper Cambrian Series
  - Shidertinian Stage
  - Tuorian Stage
- Middle Cambrian Series
  - Amgan Stage
  - Mayan Stage
- Lower Cambrian Series
  - Lenian Stage
  - Botomian Stage
  - Atdabanian Stage
  - Tommotian Stage

On the northeastern and southeastern margins of the Siberian platform, and in the orogenic belts of Kazakhstan, the Middle and Upper Cambrian faunas contain agnostids and other trilobites that permit some precise correlation with other major world Cambrian areas. The area of the Kharaulakh Mountains near the mouth of the Lena River has a particularly significant interrelationship between western American and western Europe Cambrian faunal elements.

CHINA

The biostratigraphy of China has been summarized by LU and others (1974). Three trilobite biofacies, designated the Northern Type, Transitional Type, and Southeastern Type have been recognized. The formal stage and zone nomenclature encountered in many publications about the Cambrian of China (Table 5) applies pri-

TABLE 5. *Cambrian Stages and Zones of the Northern Type Biofacies Region of China.*

- Upper Cambrian Series
  - Fengshan Stage
    - *Tellerina-Calvinella* Zone
    - *Ellesmeroceras-Dictyella* Zone
    - *Quadraticephalus* Zone
    - *Ptychaspis-Tsinania* Zone
  - Changshan Stage
    - *Kaolishania* Zone
    - *Changshania* Zone
    - *Chuangia* Zone
  - Kushan Stage
    - *Drepanura* Zone
    - *Blackwelderia* Zone
- Middle Cambrian Series
  - Changhia Stage
    - *Damesella* Zone
    - *Taitzuia* Zone
    - *Amphoton* Zone
    - *Crepicephalina* Zone
    - *Liaoyangaspis* Zone
  - Hsuchuan Stage
    - *Bailiella* Zone
    - *Poriagraulos* Zone
    - *Sunaspis* Zone
    - *Kochaspis hsuchuangensis* Zone
- Lower Cambrian Series
  - Maochuan Stage
    - *Shantungaspis* Zone
  - Manto Stage
    - *Redlichia chinensis* Zone
  - Tsangpin Stage
    - **Megapaleolenus* Zone
    - **Paleolenus* Zone
    - **Drepanuroides* Zone
    - **Malungia* Zone
    - *Unnamed zones—including interval with pre-trilobite shelly fossils.

* Recognized only in the Yangtze area.

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marily to the shallow-water, normal marine faunas of Northern Type. Faunas of Southeastern Type, which include beds rich in agnostids and eodiscids, have not been formally subdivided biostratigraphically. These faunas contain many elements permitting precise correlation of parts of the enclosing formations with those of other parts of the world that have comparable facies. The faunas of Northern Type have many elements also found in the Australian Cambrian and some precise correlations are possible between similar facies of these two areas. Localities with Transitional Type faunas contain interbedding or admixtures of the Northern and Southeastern type faunas that greatly facilitate intercontinental correlation of many parts of the Chinese Cambrian.

AUSTRALIA

Most of the published detailed biostratigraphy of the Australian Cambrian is concentrated in the late Middle Cambrian and lower Upper Cambrian where an elaborate sequence of zones has been proposed by Öpik (1957, 1961, 1967). Lower and Upper Cambrian beds have been assigned to Australian stages (Öpik, 1968; Jones *et al.*, 1971), but details of the zonations have not yet been published. The present biostratigraphic breakdown of the Australian Cambrian is shown in Table 6. The rich Middle and Upper Cambrian agnostid sequences of Queensland provide many opportunities for intercontinental correlation. Associated polymerid trilobites, many of Chinese aspect, provide a key for correlation of some of the Chinese faunas with the restricted-shelf faunas of Siberia and North America.

Pending resolution of problems of detailed intercontinental correlation in the vicinity of the upper boundary of the Middle Cambrian, some parts of the Mindyallan Stage may be reassignable to the Middle Cambrian (Jago & Daily, 1975).

Table 6. *Cambrian Biostratigraphy of Australia.*

- Upper Cambrian Series
  - Payntonian Stage
    - Zones not established
  - Unnamed pre-Payntonian and post-Idamean stages
  - Idamean Stage
    - *Irvingella tropica-Agnostotes inconstans* Zone
    - *Erixanium sentum* Zone
    - *Corynexochus plumula* Zone
    - *Glyptagnostus reticulatus* Zone
  - Mindyallan Stage
    - *Glyptagnostus stolidotus* Zone
    - *Cyclagnostus quasivespa* Zone
    - *Erediaspis eretes* Zone
    - *Damesella torosa-Ascionepea janitrix* Zone
- Middle Cambrian Series
  - Stage(s) undesignated
    - *Holteria arepo* Zone
    - *Proampyx agra* Zone
    - *Ptychagnostus cassis* Zone
    - *Ptychagnostus nathorsti* Zone
    - *Ptychagnostus punctuosus* Zone
    - *Euagnostus opimus* Zone
    - *Ptychagnostus atavus* Zone
  - Templetonian Stage
    - *Ptychagnostus gibbus* Zone
    - *"Dinesus-Xystridura"* Zone
  - Ordian Stage
    - Zones not designated
- Lower Cambrian Series
  - Stages not designated
    - Zones not designated (Faunal assemblages 1 to 9 of Daily, in Öpik *et al.*, 1957).

REFERENCES

Cowie, J. W., 1971, *Lower Cambrian faunal provinces:* in Faunal provinces in space and time, F. A. Middlemiss *et al.*, p. 31-46, Seel House Press (Liverpool).

Daily, Brian, 1957, *The Cambrian in South Australia:* in The Cambrian geology of Australia, A. A. Öpik *et al.*, Austral. Bur. Min. Res. Bull. 49, p. 91-147.

Hill, Dorothy, 1972, *Archaeocyatha:* in Treatise on invertebrate paleontology, Part E, vol. 1, 2nd edit. (revised), Curt Teichert (ed.), xxx + 158 p., 871 fig., Geol. Soc. America & Univ. Kansas Press (Boulder, Colo.; Lawrence, Kans.).

Hupé, Pierre, 1952, *Contribution a l'étude du Cambrien inférieur et du Précambrien III de l'Anti-Atlas Marocain:* Serv. Mines Carte Géol. Maroc, Notes Mém., v. 103, p. 1-402.

Jago, J. A., & Daily, Brian, 1975, *The trilobite*

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Lejopyge Hawle and Corda and the Middle-Upper Cambrian boundary: Palaeontology, v. 18, p. 527-550, pl. 62-63.

Jones, P. J., et al., 1971, *Late Cambrian and Early Ordovician stages in western Queensland:* Geol. Soc. Australia, Jour., v. 18, p. 1-32.

Kobayashi, Teiichi, 1967, *The Cambrian of eastern Asia and other parts of the continent:* Univ. Tokyo, Jour. Fac. Sci., sec. II, v. 16, pt. 3, p. 381-534.

Lochman-Balk, Christina, & Wilson, J. L., 1958, *Cambrian biostratigraphy in North America:* Jour. Paleontology, v. 32, no. 2, p. 321-350.

Lu Yen-hao, et al., 1974, *Sheng wuh hwan jing kong jyh lun jyi chyi tzai harn wu jih sheng wuh ti jseng shyue shang her ku donq wuh ti li shang de ing yonq:* Nan king ti chi ku sheng wuh yan jiou shoo jyi kan (Nanking Inst. Geology and Paleontology), Mem., no. 5, p. 27-116. [*Bio-environmental control hypothesis and its application to Cambrian biostratigraphy and paleozoogeography.*]

Martinsson, Anders, 1974, *The Cambrian of Norden:* in Cambrian of the British Isles, Norden and Spitzbergen, p. 185-284, John Wiley & Sons (New York).

Öpik, A. A., 1957, *Cambrian geology of Queensland:* in The Cambrian geology of Australia, A. A. Öpik *et al.*, Austral. Bur. Min. Res. Bull. 49, p. 1-24.——1961, *The geology and paleontology of the headwaters of the Burke River, Queensland:* Austral. Bur. Min. Res. Bull. 53, 249 p., 24 pl.——1967, *The Mindyallan fauna of northwestern Queensland:* Austral. Bur. Min. Res. Bull. 74, v. 1, 404 p.; v. 2, 166 p., 67 pl.——1968, *The Ordian Stage of the Cambrian and its Australian Metadoxidae:* Austral. Bur. Min. Res. Bull. 92, p. 133-169.

Palmer, A. R., 1969, *Cambrian trilobite distributions in North America and their bearing on the Cambrian paleogeography of Newfoundland:* Am. Assoc. Petroleum Geologists, Mem. 12, p. 139-144.——1972, *Problems in Cambrian biogeography:* 24th Internatl. Geol. Congress, Proc., sec. 7, p. 310-315 (Montreal).——1973, *Cambrian trilobites:* in Atlas of paleobiogeography, A. Hallam (ed.), p. 3-11, Elsevier Sci. Publ. Co. (London).

Repina, L. N., 1968, *Biogeografiya rannego kembriya Sibiri po trilobitam:* 23rd Internatl. Geol. Congress (Prague), Doklady Sovetskikh Geologov, p. 46-56, Izadatelstvo "Nauka" (Moskva) (English abstract). [*Biogeography of Early Cambrian Siberian trilobites.*]

Robison, R. A., 1964, *Middle-Upper Cambrian boundary in North America:* Geol. Soc. America, Bull., v. 75, p. 987-994, text-fig. 1, 2.

Rozanov, A. Yu., 1973, *Zakonomernosti morfologicheskoy evolyutsii Arkheotsiat i voprosy yarusnogo raschleneniya Nizhnego Kembriya:* Akad. Nauk SSSR, Geol. Inst., Trudy, v. 241, 164 p. [*Principles of morphological evolution of the Archaeocyatha and questions of the stage subdivision of the Lower Cambrian.*]

Savitskiy, V. E., 1969, *O yarusnom raschlenenii srednego kembriya Sibiri i nekotorykh obshchikh voprosakh razrabotki etalonnoy shkaly yarusnykh podrazdeleniy:* Sibir. Nauchno-Issledov. Inst. Geologii Geofiziki Mineral. Syrya (SNIIGGIMS) Trudy, v. 94, p. 140-149. [*Subdivision of the Middle Cambrian of Siberia into stages and problems of establishing a standard scale for stage divisions.*]

Sdzuy, Klaus, 1958, *Tiergeographie und Paläogeographie im europäischen Mittelkambrium:* Geol. Rundschau, v. 47, p. 450-462.——1972, *Das Kambrium der acadobaltischen Faunenprovinz:* Zentralbl. Geologie Paläontologie, Teil II, Jahrg. 1972, no. 1/2, p. 1-91 (July).

Taylor, M. E., 1973, *Late Cambrian biofacies in the western United States:* Geol. Soc. America, Abstr. with Programs, v. 5, no. 7, p. 836-837.

Zhuravleva, I. T., 1968, *Biogeografiya i geokhronologiya rannego Kembriya po Arkheotsiatam:* 23rd Internatl. Geol. Congress, Prague, 1968, Doklady Sovetskikh Geologov, p. 33-45, Izdatelstvo "Nauka" (Moskva) (English abstract). [*Biogeography and geochronology of the Early Cambrian based on Archaeocyatha.*]

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ORDOVICIAN[1]

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CONTENTS

INTRODUCTION

Ordovician time, with a duration of approximately 60 million years, had a considerable biogeographic differentiation. This can be traced in the distribution of most groups of organisms, although many are comparatively rare or have not yet been intensely studied. In this contribution, distributional data of shelly groups (mainly trilobites and articulate brachiopods), planktonic graptolites, and conodonts are treated separately. Owing to limited space available, documentation is restricted to a minimum.

Distribution of various faunas is illustrated by the known occurrence of selected taxa plotted on maps rather than by showing the distribution of inferred biogeographic units or faunas. After considerable experimenting, the map of the modern world was chosen for illustrating Ordovician distribution patterns, although during Ordovician time the location of oceans and continental lithospheric plates obviously was completely different. Not only is the former geographic position of many individual Ordovician lithospheric plates uncertain, but in several cases it is not known what constituted an individual plate. For this reason the use of any of the proposed geographical models for the Ordovician would introduce considerable speculation. The situation will not improve until more paleomagnetic data are available from Ordovician rocks in various parts of the world. The maps (Fig. 2, 4, 6-13) show the distribution

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of land and sea, roughly reconstructed, based on available paleogeographic maps (Keller & Predtechensky in Vinogradov, 1968; Liu, 1958, complemented with Jen, 1964, and Hu *et al.*, 1965; Wolfart, 1967; Cuerda, 1973; Legrand, 1974; and others).

According to all recent reconstructions of Ordovician geography, Africa, Arabian Peninsula, peninsular India, South America, Antarctica, and Australia formed a single huge continental plate, Gondwanaland. The Ordovician South Pole was located somewhere in northwestern Africa (Smith *et al.*, 1973) and thus much of the plate was situated in a cold climatic zone. Much of Ordovician Gondwanaland was dry land and it may have been the main source of terrigenous sediments to southern Europe, where the Ordovician sequence consists of clastic rocks; however, in some reconstructions (Whittington & Hughes, 1972, 1973) southern Europe is considered to have constituted a separate lithospheric plate, separated from Gondwanaland by a wide proto-Tethyan ocean and from northeastern Europe by a mid-European ocean.

In the rest of the Ordovician world, land areas were scattered and formed archipelagos rather than continents. At least three individual continental lithospheric plates are distinguished: 1) North America and Arctic islands, 2) Russian platform and adjoining areas to the west, and 3) Asia. On these plates the Ordovician epicontinental deposits consist mostly of carbonates. On most reconstructions of Ordovician geography much of all three plates is in tropical and subtropical latitudes. The boundary between the north European and south European plates is variously drawn along the Alpine chain (Smith *et al.*, 1973; Williams, 1973), the southwestern margin of the Russian platform (Whittington & Hughes, 1972, 1973), or roughly along the northern limit of the Variscan Mountains (Burrett, 1973). This part of Europe has widely distributed fossiliferous Ordovician rocks, and differences in position of the plate boundary have a profound effect on biogeographic interpretations. North America and northern Europe were separated by the Iapetus Ocean (Harland & Gayer, 1972; Proto-Atlantic Ocean, Wilson, 1966; Whittington & Hughes, 1972) that is generally considered to have decreased in width during the Ordovician. Asia, with the western plate margin along the present Ural Mountains, is tentatively treated as a single lithospheric plate, or up to five separate plates, variously situated relative to the other plates. Paleomagnetic data are available only for Siberia.

ACKNOWLEDGMENTS

During the completion of various versions of this contribution since 1968, many colleagues generously helped by providing unpublished information as well as inaccessible publications. For this I am particularly indebted to M. K. Apollonov (Alma-Ata), S. M. Bergström (Columbus), W. T. Dean (Ottawa), R. Männil (Tallinn), R. B. Neuman (Washington, D.C.), Zoya E. Petrunina (Novokuznetsk), R. J. Ross (Denver), and A. D. Wright (Belfast).

LOWER BOUNDARY OF THE ORDOVICIAN

In accordance with general practice (except among British geologists), the Tremadoc Series is here treated as the lowermost Ordovician. The intercontinental correlation of the lower boundary of the Tremadocian presents problems and must be briefly discussed because of its biogeographic implications. More exactly, on account of differences in correlation, the biogeographic conclusions presented in this chapter differ in several respects from those given for the Tremadocian by Whittington and Hughes (1974).

The lower boundary of the Tremadocian is traditionally drawn at the level of appearance in northern Europe of the first dendroid graptolites with a "free" sicula indicating a change from sedentary to planktonic mode of life (Fig. 1). The correlation of this horizon in regions without graptolites is difficult. The particular problem is whether and how much of the

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British series		Atlantic graptolite zones, Oslo region, Norway		North Atlantic conodont zones	North American midcontinent conodont zones	North American series	Trilobite zones, western North America
TREMADOCIAN	UPPER	Ceratopyge beds	Poorly graptolitiferous, zonal classification not yet well established	Paltodus deltifer	Chosonodina herfurthi	CANADIAN	D Leiostegium-Kainella
							C Paraplethopeltis
	LOWER	Dictyonema Shale	Anisograptus	Cordylodus angulatus	Cordylodus angulatus		
			Dictyonema norvegicum	------?------	------------		B Symphysurina
			Dictyonema flabelliforme		Cordylodus proavus		
			Dictyonema sociale	?			A Missisquoia
			Dictyonema parabola			U.€.	Corbinia apopsis

Fig. 1. Correlation of the Tremadocian Series (Jaanusson, n).

North American Trempealeauan Stage and comparable beds elsewhere containing saukiid trilobites, generally referred to the Upper Cambrian, are equivalent to the Lower Tremadocian. Records of saukiids and *Richardsonella* associated with early Tremadocian trilobites in Oaxaca, Mexico (Robison & Pantoja-Alor, 1968), initially seemed to indicate that a substantial part of the Trempealeauan is equivalent to the early Tremadocian; however, recent studies on conodonts do not confirm such a correlation. In the conodont fauna, the entry of *Cordylodus* forms a clearly recognizable level and has been suggested for use as a tentative additional criterion of the base of the Ordovician (Miller, 1969). The earliest Ordovician conodont faunas are largely cosmopolitan and closely similar successions of species have been reported from widely separated regions (Miller, 1969, 1970; Druce & Jones, 1971; Jones, 1971, etc.). It is now known (Miller, 1970) that *Cordylodus* enters at the base of the *Corbinia apopsis* Subzone which, by tradition, is regarded as the top of the Upper Cambrian Trempealeauan Stage but could as well be included in the Ordovician.

The exact level of the entry of *Cordylodus* in the North European sequence is not known because *Dictyonema* shales and associated rocks are mostly devoid of identifiable conodonts. There the earliest known Ordovician conodont fauna is from the upper Maardu (*"Obolus"*) Sandstone of northwestern Estonia (Viira, 1966), below the local lithostratigraphic *Dictyonema* Shale, and associated with *Dictyonema flabelliforme flabelliforme.* The level is probably fairly high within a complete *Dictyonema* Shale sequence. The assemblage is comparable to that from the upper part of the North American *Symphysurina* Zone that is thus obviously of Lower and not Upper Tremadocian age. The overlap between the Tremadocian and the Trempealeauan, if present at all, seems to be inconsiderable (cf. also Miller *et al.*, 1974). For these reasons the Tsinaniid and *Rasettia* provinces distinguished by Whittington & Hughes (1974) are here regarded as Upper Cambrian and not Tremadocian (see also Shergold, 1975).

The Ordovician Period began with a transgression that was one of the most extensive in the Paleozoic. Over almost the whole of Europe and northern Africa there is a conspicuous break at the base of the

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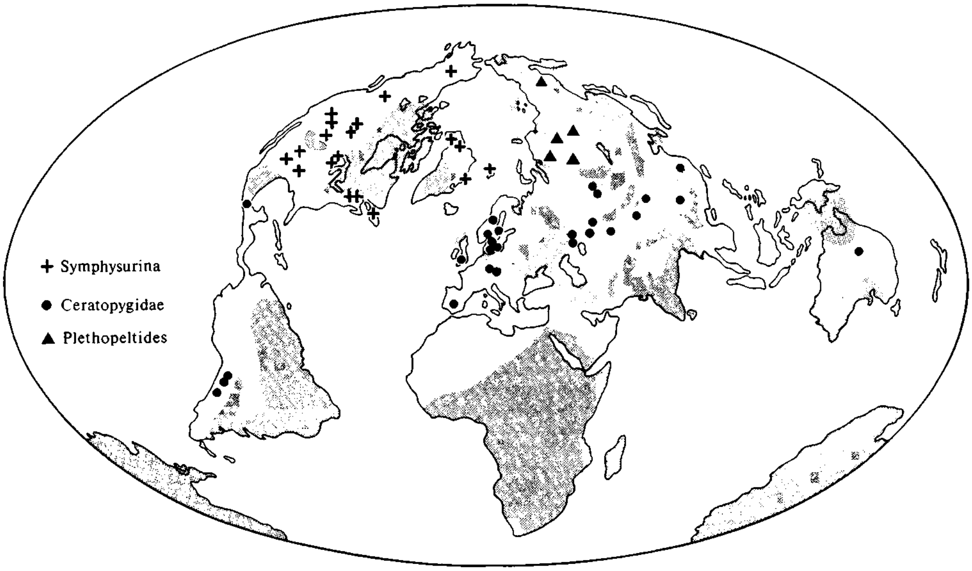

FIG. 2. Distribution of selected Tremadocian trilobite taxa. The asaphid *Symphysurina* characterizes the North American fauna, the plethopeltid *Plethopeltides* the possibly separate Tungusian fauna, and ceratopygids the Southern fauna (Jaanusson, n). [Shaded area in this as well as in other maps indicates probable land areas. For probable boundaries between the main lithospheric plates, see Figure 13.]

Lower Tremadocian, and what appear to be continuous sequences from the Cambrian to Ordovician are known only in some areas of southern Scandinavia and along a belt to central Poland. In most of continental Europe and northern Africa the break comprises the entire Upper Cambrian and on the Russian platform east of the Baltic also the Middle Cambrian. In extensive Arctic areas, such as the Canadian Arctic Archipelago, Greenland, with the exception of Washington Land in western North Greenland, and Spitzbergen, Lower Tremadocian rests on Middle Cambrian, in southern Mexico on Precambrian, and in the allochthonous Taconic sequence of New York on Lower Cambrian. The widespread occurrence of the break suggests an eustatic control of the transgression. The early Tremadocian transgression opened new communications between shelf areas. The most important of these was along the "Paleotethys" from northwestern Africa over southern Europe, which may have been a prerequisite for the development of WHITTINGTON's (1966) "Southern Fauna."

SHELLY FAUNAS

TREMADOCIAN

Among Tremadocian shelly fossils, only trilobites are widely distributed and reasonably well studied. Among trilobites two main faunas can be distinguished, here provisionally termed the North American (*Hystricurus* fauna, WHITTINGTON, 1966; *Highgatella* Province, WHITTINGTON & HUGHES, 1974) and Southern Faunas (Ceratopygid Province, WHITTINGTON & HUGHES, 1974). The distribution of the faunas largely follows that of *Symphysurina* and Ceratopygidae (Fig. 2). Compared with the distribution of Upper Cambrian trilobites the degree of biogeographic differentiation seems to have decreased. Moreover, biogeographic affinities have changed in several areas. Most notably, the fauna in western Argentina is now related to European-southwestern Siberian faunas whereas in the Upper Cambrian it has close North American affinities.

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The North American Fauna occupied North America, Greenland, and Spitzbergen and is characterized by *Symphysurina* (Fig. 2) and its allies, *Clelandia* and its allies, *Missisquoia, Highgatella,* and other genera. In comparison with many southern faunas the taxonomic diversity is small. The earliest undoubted leperditiacean ostracodes have been described from the post-*Symphysurina* Tremadocian beds of Vermont (Creath & Shaw, 1968), and throughout the Ordovician Period this group remained one of the distinctive elements of North American and related faunas.

The Southern Fauna extended over a vast area (see the distribution of the Ceratopygidae, Fig. 2), from the present South America and southern Mexico in the west over Morocco, Wales, and Scandinavia to southeastern China in the east. The fauna is characterized by ceratopygids, dikelokephalinids, nileids, orometopids, *Macropyge,* and other trilobites. Some areas have a high taxonomic diversity (some 75 trilobite genera in the Sayan-Altai mountain region; Petrunina, 1966).

The known Tremadocian shelly fauna from the Siberian platform and northeastern Siberia indicates that a separate Lower Tremadocian Tungusian fauna may be distinguishable (cf. the distribution of *Plethopeltides,* Fig. 2; other distinctive genera include *Diceratocephalina, Pseudoacrocephalites,* and *Dolgeuloma*). The known Tremadocian trilobite faunas from these regions and from northern Korea, northern China, and Australia, however, are small and are at present difficult to evaluate biogeographically.

In eastern North America a belt in eastern New Brunswick, Nova Scotia, and Newfoundland has yielded a Cambrian fauna with close affinities to that in northern Europe. On eastern Nova Scotia the sequence includes Tremadocian strata and the small shelly fauna encountered there is astonishingly similar to that of Wales. The current explanation of the faunal and lithological similarity is that the areas in eastern North America mentioned above belonged to the North European plate. During closing of the Iapetus Ocean, the North American and North European plates collided, and the areas became welded to the North American plate. When the present Atlantic Ocean was initiated, this part of the original North European plate followed North America.

ARENIGIAN (POST-TREMADOCIAN CANADIAN)

At the base of the Arenigian the biogeographic diversity increased. The region with the North American Fauna retained its biogeographic identity and boundaries. In the post-Tremadocian Canadian carbonate sequence of North America, Greenland, and Spitzbergen, the trilobite fauna is characterized by various bathyurids and hystricurids (Bathyurid Fanua; Whittington, 1963) (Fig. 3). Further distinctive forms include the gastropod *Ceratopea* as well as leperditiacean ostracodes. The Durness Limestone in northern Scotland has yielded distinctive trilobites and cephalopods of the North American Fauna (very little faunal information is available on the probable Tremadocian portion of the limestone) suggesting that this part of Scotland, and probably also northern Ireland, may originally have been a part of the North American lithospheric plate.

The known Upper Canadian shelly fauna of the Siberian platform, Taymyr Peninsula, and northeastern Siberia is in several respects close to that of North America (Whittington & Hughes, 1972; included in American-Siberian Biogeographic Region, Chugaeva, 1968, 1973) but with endemic elements such as the bathyurid trilobite *Biolgina* (Fig. 4), *Prodalmanitina,* and the widespread brachiopod *Angarella.* Many characteristic North American forms, including leperditiacean ostracodes, have not been found.

In the Balto-Scandian region a fauna developed that includes numerous endemic elements (Asaphid Fauna, Whittington, 1963, 1973, and Whittington & Hughes, 1972; Baltic Province, Williams, 1973; Baltic Biogeographic Region, Chugaeva, 1968, 1973; Balto-Scandian fauna, Jaanusson, 1973a). During the Arenigian the fauna extended from the Vaygach Island and the Pay Khoy Peninsula in the north to central Poland in the south and from the Oslo

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British series	Atlantic graptolite zones, Oslo region, Norway		Balto-Scandian series and stages		North Atlantic conodont zones	Pacific graptolite zones, North America	Trilobite zones, western North America	
ARENIGIAN		Didymograptus hirundo	ONTIKAN	VOLKHOVIAN	Microzarkodina parva – Prioniodus triangularis	Isograptus caduceus	CHAMP.	WHITEROCKIAN
	Didymograptus extensus	Phyllograptus angustifolius elongatus		BILLINGENIAN	Prioniodus evae	Didymograptus bifidus	CANADIAN SERIES	J Pseudocybele nasuta
		Phyllograptus densus				Didymograptus protobifidus		I Presbynileus ibexensis
		Didymograptus balticus			Prioniodus elegans	Tetragraptus fruticosus		H Trigonocerca typica
		Tetrograptus approximatus		HUNNEBERGIAN	Paroistodus proteus	Tetragraptus approximatus		G2 Protopliomerella contracta G1 Hintzeia celsaora
		Poorly graptolitiferous, zonal classification not yet well established				Clonograptus		F Rossaspis superciliosa E Tesselecauda

Fig. 3. Correlation of the Arenigian Series and equivalent strata (Jaanusson, n).

region in the west to the Moscow basin in the east. Information on the Arenigian fauna from the Ural Mountains is scanty but the brachiopods from the southern Ural Mountains include Balto-Scandian elements together with endemic forms (Andreeva, 1972). Characteristic elements of the Balto-Scandian fauna include a number of asaphid genera, and the illaenid *Panderia. Agerina* is a possible bathyurid, but hystricurids, calymenaceans, and trinucleids are lacking. The porambonitacean brachiopods that frequently dominate Arenigian faunas elsewhere are represented only by porambonitids and angusticardiniids; characteristic North American-Siberian taxa, such as polytoechiids and finkelnburgiids, are absent. The brachiopod fauna is in places dominated by a variety of gonambonitids, *Productorthis,* and *Paurorthis.*

The Arenigian "southern" fauna (Calymenid-Trinucleid Province, Whittington, 1963; Southern Region, Whittington, 1966; Sino-European Biogeographic Region, Chugaeva, 1968; Paleotethyan Region, Chugaeva, 1973) is less homogeneous than the Tremadocian "southern" fauna. What is here provisionally termed as the Mediterranean fauna (Tethyan fauna, Dean, 1967; *Selenopeltis* fauna, Whittington, 1966; Whittington & Hughes, 1972; Mediterranean Province, Havlíček, 1974) extended from Wales in the north to Morocco in the south and from the Iberian Peninsula in the west over Bohemia possibly as far as the Pamir in the east. The fauna is characterized by a variety of calymenaceans, trinucleids, taihungshaniids, and cyclopygids. Even within the region, the fauna is not particularly homogeneous (Dean, 1967; Havlíček, 1976). The known Arenigian fauna from central and southern China is small and difficult to evaluate biogeographically but occurrences of *Taihungshania* (Fig. 4), *Hanchunglithus,* and *Neseuretus* links it with the Mediterranean fauna.

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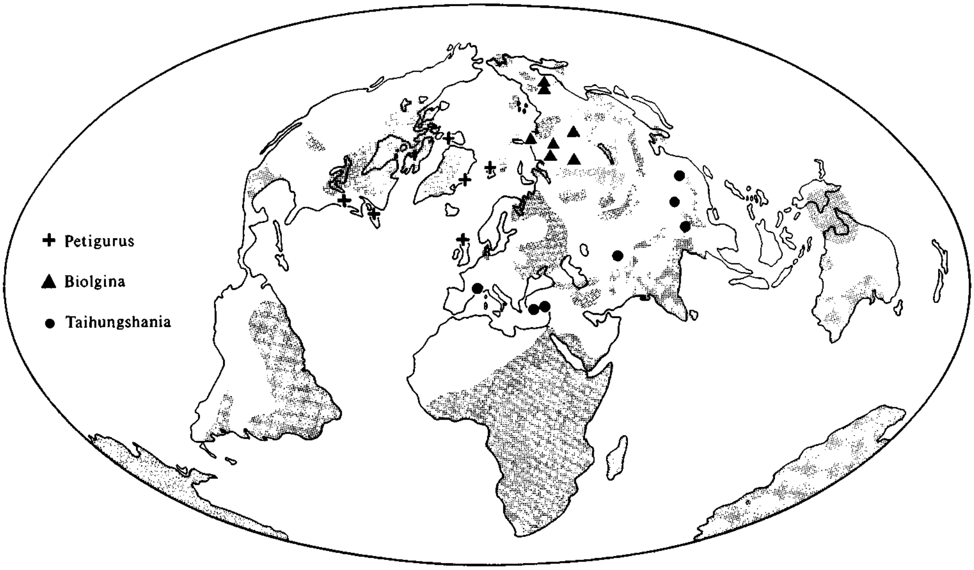

FIG. 4. Distribution of selected Arenigian (post-Tremadocian Canadian) trilobite genera. Occurrence of the bathyurid *Petigurus* is restricted to the North American fauna, the bathyurid *Biolgina* characterizes the Tungusian fauna, and the taihungshaniid *Taihungshania* is one of the southern elements with a trans-Eurasian distribution (Jaanusson, n).

These are examples of distribution of various taxa from Europe to China or, in terms of present-day geography, of the Ordovician "transeurasiatic migration route" for which there are numerous examples from different Ordovician epochs (KOBAYASHI, 1971; BURRETT, 1973).

Within the Mediterranean fauna WILLIAMS (1973) distinguished Celtic (Anglesey and southeastern Ireland) and Anglo-Welsh (Shropshire and Montagne Noire) Arenigian provinces, based on cluster analysis of brachiopod genera. The evaluation of this classification is difficult because the taxonomic diversity is mostly low and only four assemblages are available for analysis.

The Arenigian trilobite fauna of South America includes endemic elements (the asaphid subfamily Thysanopyginae). WHITTINGTON and HUGHES (1972) included it together with Australian faunas in a separate *Asaphopsis* Province. The Australian faunas of this age have not been described in detail and may turn out to include a stronger endemic component than known at present. BURRETT (1973) doubted that close affinities exist between the Australian and South American Arenigian and Llanvirnian faunas.

Information on Arenigian shelly faunas in central Asia, Kazakhstan, and southwestern Siberia is at present very limited.

LLANVIRNIAN (INCLUDING WHITEROCK AND KUNDA STAGES)

At the end of the Canadian Epoch much of the North American craton and Appalachian miogeosyncline emerged, causing a break in deposition. Carbonate sedimentation was more continuous along the western margin of the craton from southern Nevada to Yukon, in the south (Oklahoma), and in the northeast (western Newfoundland). There the gap is filled by beds with the so-called Whiterockian fauna (COOPER, 1956) (Fig. 5). During the Whiterockian Age a number of trilobites of possible "southern" and Balto-Scandian origin entered North America *(Cybelurus, Raymondaspis, Nileus)*. Other new forms include *Illaenus, Endymionia*, and *Ectenonotus* among trilobites, and *Orthidiella, Rhysostrophia,* and earliest triplesiaceans among articulate brachiopods. Except for the possible upper

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Canadian *Polydesmia* from Manchuria, the Whiterockian beds contain the earliest actinoceroid cephalopods and the latest cyrtoconic ellesmerocerids. Close equivalents to the Whiterockian faunas are known in Spitzbergen (FORTEY & BRUTON, 1973), western Ireland (WILLIAMS, 1972), and northeastern Siberia (CHUGAEVA, 1973; ORADOVSKAYA, 1973). On the Siberian platform this fauna has not been recognized and SIDYARENKO and KANYGIN (1965) have suggested that there is a break in the sequence, roughly corresponding to the beds with the Whiterockian fauna in northeastern Siberia. If this is true, then the Siberian platform behaved during this time much the same as did the North American craton.

Kazakhstan has a southern Tremadocian fauna, but in beds roughly comparable to the Llanvirnian the general affinities of the fauna are with North America (NIKITIN, 1972; WHITTINGTON & HUGHES, 1972). The fauna has a strong endemic component however, that may increase in importance when more material has been studied. The same applies also to Gornyi Altay in southwestern Siberia.

In the Balto-Scandian region the Kunda Stage is the equivalent of the lower, main part of the Whiterockian. There the fauna retained its provincial character with numerous endemic taxa (*Asaphus, Megistaspidella, Cyrtometopus,* and others among trilobites, gonambonitids and *Lycophoria* [Fig. 6] among brachiopods). In the west, the trilobite fauna of the Otta Conglomerate in the Caledonidian eugeosynclinal belt of southcentral Norway is decidely of the Balto-Scandian type (e.g., *Neoasaphus, Megistaspidella)* and the postulated strong North American affinities of its gastropod fauna (YOCHELSON, 1963) are questionable. On the other hand, the Trondheim region of the Scandinavian Caledonides has a fauna related to the North American Whiterockian fauna (NEUMAN & BRUTON, 1974). WILSON (1966) suggested that this part of Scandinavia was originally part of the North American lithospheric plate (see also WHITTINGTON & HUGHES, 1972).

Based on cluster analysis of brachiopods, WILLIAMS (1973) concluded that the Llanvirnian Baltic Province extended westward to Anglesey and Maine. Brachiopod assemblages on Anglesey (BATES, 1968) and in the Magog belt of the northern Appalachians from Maine to Newfoundland (NEUMAN, 1970) are unusual in that taxa otherwise characteristic for different faunas and ages are associated in the same beds. In beds of roughly Whiterockian age Balto-Scandian taxa (e.g., gonambonitids, *Ahtiella*) occur together with polytoechiids (elsewhere in North America not known above Canadian), taxa that characterize the middle Ordovician Scoto-Appalachian fauna (e.g., *Christiania, Eoplectodonta*), and genera that have not yet been found elsewhere (NEUMAN, 1972). Biogeographic classification of these exotic assemblages is difficult at present. NEUMAN (1972) suggested that these faunas originally inhabited the ocean floor around dominantly volcanic islands and that this environment was the site of evolution of many stocks that later spread to continental platforms. On Anglesey the Arenigian and Llanvirnian brachiopod assemblages are associated with a trilobite fauna of Mediterranean type (WHITTINGTON & HUGHES, 1972), which further complicates the matter.

The distribution of the Llanvirnian Mediterranean (cf. that of *Placoparia,* Fig. 6) and other southern faunas agrees in the main with those of the Arenigian.

MIDDLE ORDOVICIAN

For the purpose of this contribution the middle part of the Ordovician, comprising the interval from about the upper *Didymograptus murchisoni* Zone to the base of the *Pleurograptus linearis* Zone, is informally termed the middle Ordovician. It should be emphasized that this term is here not used as designating a formal series or epoch and that at present there does not exist any international agreement as to the definition of a middle Ordovician series.

During the middle Ordovician, sea invaded successively the southern and central Appalachian miogeosyncline and extensive cratonic areas of North America. This was associated with a differentiation of the fauna in which the element in the main miogeosynclinal belt came to differ in several respects from that of the cratonic region. Roughly comparable differentiation existed

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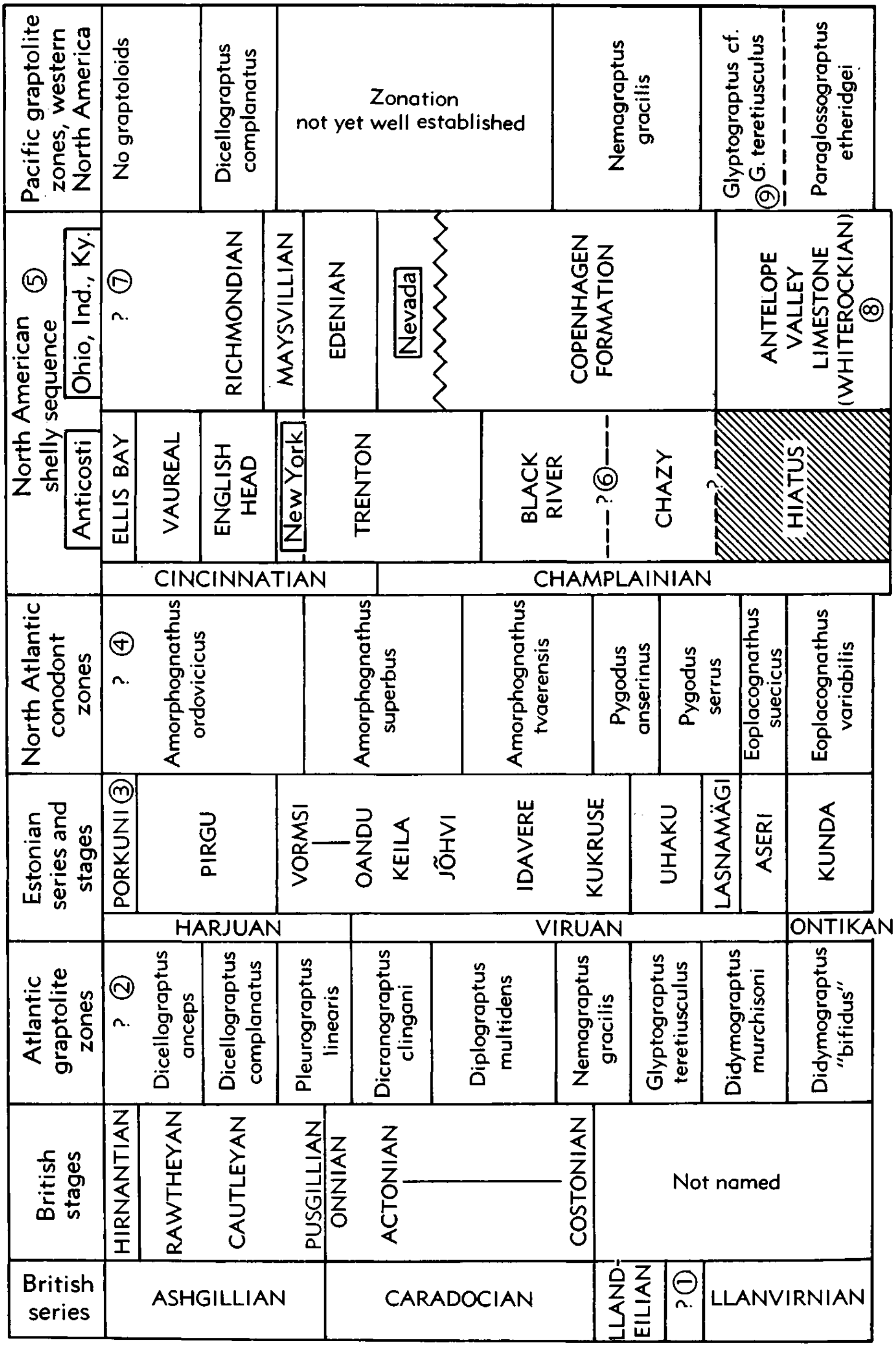

FIG. 5. Correlation of the middle and Upper Ordovician (Jaanusson, n). [Numbers in circles refer to notes at foot of facing page.]

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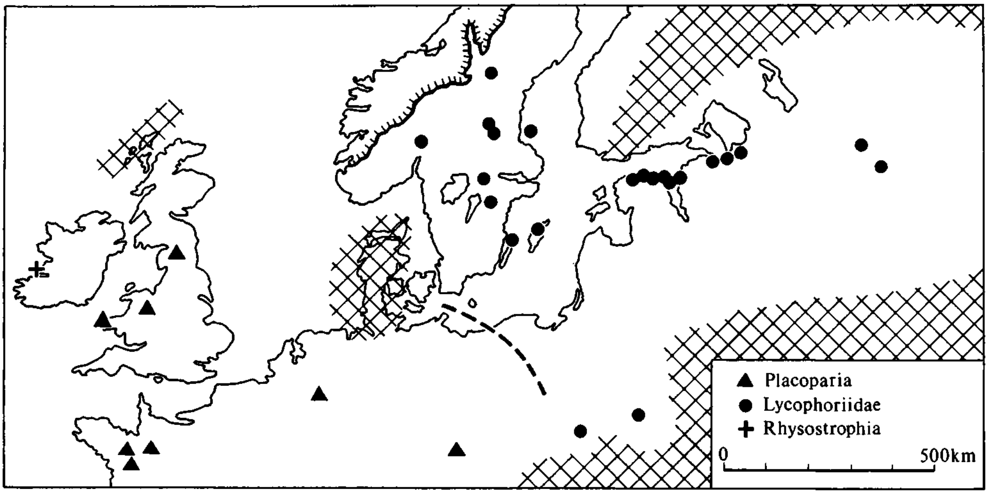

FIG. 6. Distribution of selected Llanvirnian taxa in northern Europe. Occurrence of the brachiopod family Lycophoriidae is restricted to the Balto-Scandian fauna and the trilobite subfamily Placopariinae is a member of the Mediterranean fauna (Llanvirnian representatives of *Placoparia* are known also from Spain, Portugal, Morocco, and Kazakhstan; finds in southwestern Turkey came from a somewhat uncertain horizon). The porambonitacean brachiopod *Rhysostrophia* in Ireland indicates Whiterockian affinities (Jaanusson, n). [Dashed line indicates the western boundary of the Russian platform (so-called Tornquist's Line); cross-hatched pattern represents probable land areas.]

also in earlier Ordovician deposits along the Cordilleran geosyncline (Ross, 1975) and in parts of the northern Appalachians.

In the southern Appalachians many genera do not reach westward beyond the Helena-Saltville thrust (McLAUGHLIN, 1973), which also is an important biogeographic boundary in the conodont faunas (BERGSTRÖM, 1971). Such genera are *Christiania, Bimuria, Bilobia, Ptychoglyptus, Glyptambonites, Titanambonites, Cyphomena, Productorthis, Taphrorthis, Laticrura*, and *Kul-*

FIG. 5. *(Continued from facing page.)*

1. The lower boundary of the type Llandeilian is within the *Glyptograptus teretiusculus* Zone as distinguished in Sweden (BERGSTRÖM, 1971). The upper boundary of Llanvirnian is defined as that of the Zone of *Didymograptus murchisoni.* Thus, a portion of the British sequence, corresponding to the basal *Glyptograptus teretiusculus* Zone, is at present not included in the British serial classification.
2. In Europe no distinctive graptolite fauna has been found in beds of Hirnantian age. In Kazakhstan, beds with a comparable macrofauna have yielded *Glyptograptus persculptus,* the index fossil of the lowermost Silurian graptolite zone; however, whether this species has a longer range than previously believed or at least the upper part of the Hirnantian belongs to the *Glyptograptus persculptus* Assemblage-zone is at present not known.
3. Equivalent beds in the central Balto-Scandian confacies belt contain a *Dalmanitina-Hirnantia* fauna and are known as *Dalmanitina* beds or Tommarpian Stage (a junior synonym of Hirnantian Stage).
4. In beds of undoubted Hirnantian age no representative conodont fauna has yet been described in detail.
5. Increasing bulk of evidence indicates that COOPER's (1956) stages Ashbyan, Porterfieldian, and Wildernessian, each defined in a separate belt in the southern Appalachians, are largely contemporaneous (BERGSTRÖM, 1971). They reflect spatial faunal differentiation rather than faunal changes in time.
6. Exact position of the boundary between Chazyan and Blackriveran stages with respect to North Atlantic conodont zones is not known at present.
7. No undoubted Hirnantian equivalents at present can be distinguished in Ohio, Indiana, and Kentucky. Whether this depends upon a break in the sequence, poorly fossiliferous condition of the uppermost Richmondian beds, or biogeographic differentiation is not known. Beds of Hirnantian age are developed in western Illinois and eastern Missouri (Edgewood Limestone and its equivalents).
8. According to the evidence from conodonts, the top of the Antelope Valley Formation is comparable to the lower Lasnamägian of Balto-Scandia (BERGSTRÖM, ETHINGTON, & JAANUSSON, 1973); however, it is not clear whether the Whiterockian Stage of COOPER (1956) should be considered to coincide with the extent of the Antelope Valley Limestone or defined in the Ikes Canyon section of the Toquima Range based on the succession of faunal zones listed by COOPER. In the latter case, the upper boundary of the Whiterockian is probably below the base of the Lasnamägian Stage.
9. Graptolite faunas strongly indicate that the uppermost Darriwilian Zone of *Glyptograptus teretiusculus* of Australia is equivalent to the Zone of *Didymograptus murchisoni* (JAANUSSON, 1960). The correlation of the North American Zone of *Glyptograptus* cf. *G. teretiusculus* is more difficult to determine because the known fauna comprises few species; however, it may be largely of a comparable age. The Scandinavian equivalent to the Zone of *Glyptograptus teretiusculus* is characterized by the appearance of *Dicellograptus, Dicranograptus,* and *Nemagraptus.* The equivalent beds of North America probably have been included in the Zone of *Nemagraptus gracilis.*

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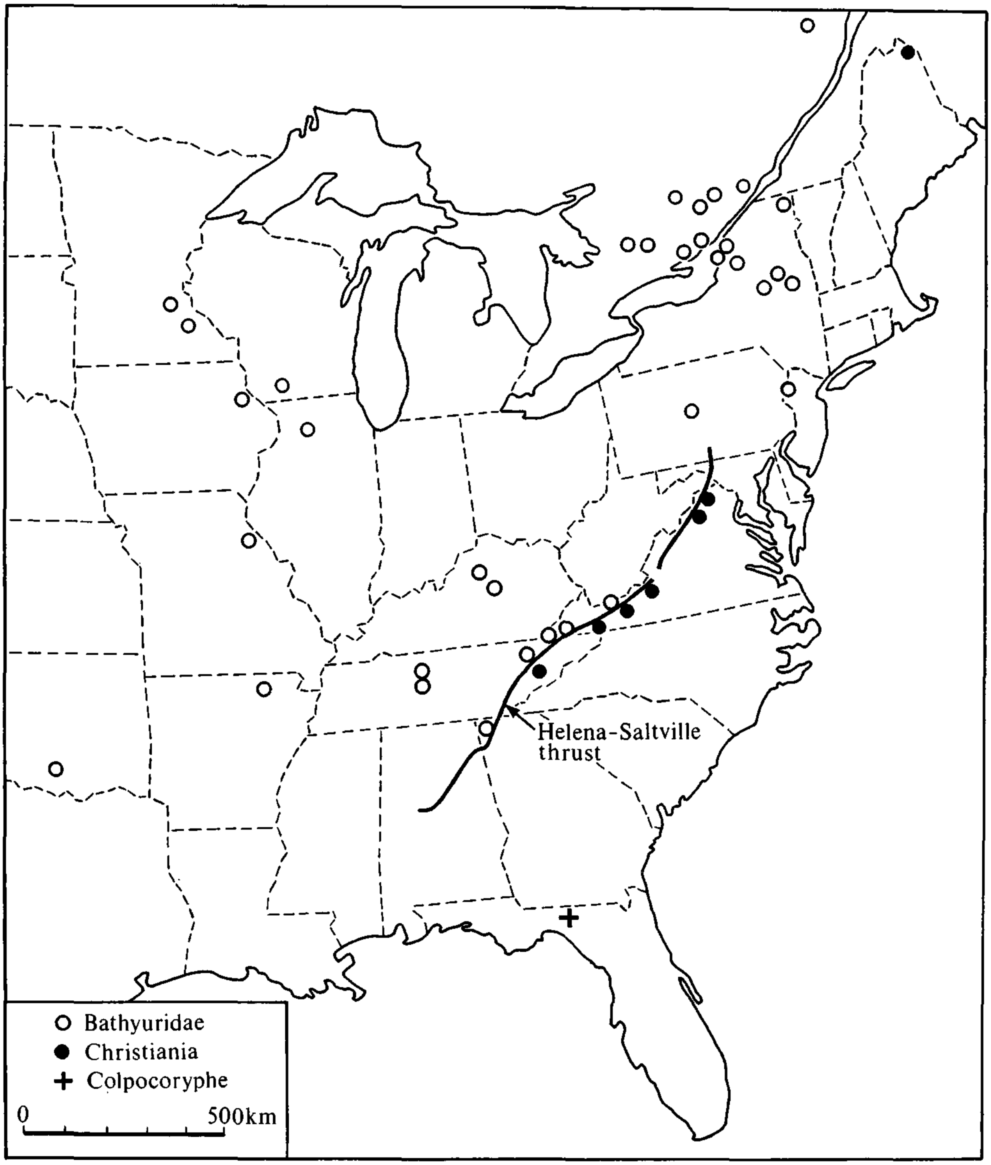

Fig. 7. Distribution of bathyurid trilobites and the strophomenacean brachiopod family Christianiidae in eastern North America in beds equivalent to the Zone of *Nemagraptus gracilis* and the lower part of the Zone of *Diplograptus multidens.* The bathyurids characterize the North American Midcontinent fauna and the christianiids the Scoto-Appalachian fauna. The subsurface occurrence of the calymenacean *Colpocoryphe* in northern Florida is also indicated although it probably comes from somewhat lower beds (Jaanusson, n).

lervo. Other taxa reach farther to the west, but not beyond the St. Paul-St. Clair thrusts (e.g., *Palaeostrophomena, Isophragma, Leptellina, Cyrtonotella,* styginid trilobites). On the other hand, several taxa that are widely distributed on the midcontinent have not been found east of the Helena-Saltville thrust. Such taxa are bathyurid trilobites (Fig. 7), the articulate brachiopods *Strophomena* and *Ancistrorhynchia,* and *Gonioceras*

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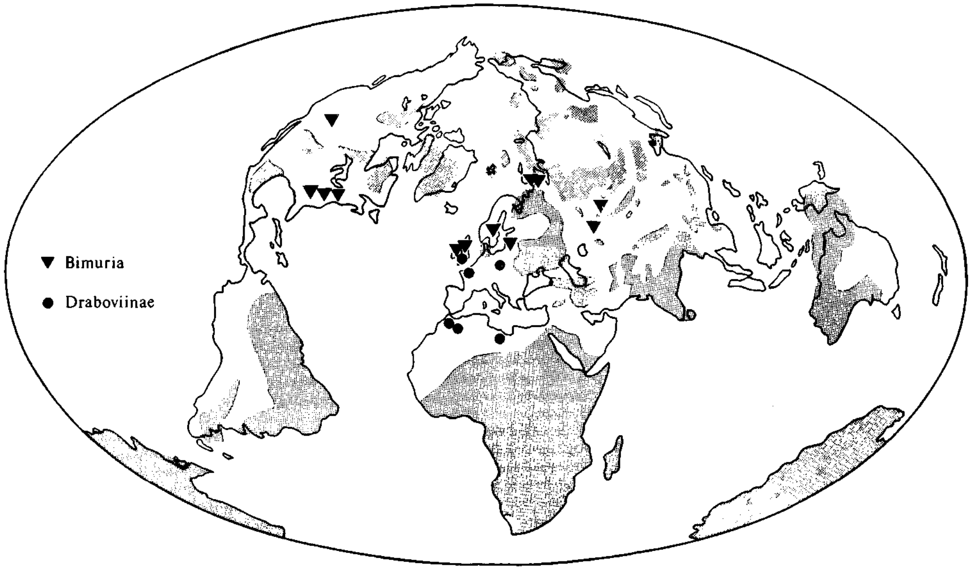

FIG. 8. Distribution of the plectambonitacean brachiopod family Bimuriidae (indicative of the Scoto-Appalachian and related faunas) and the enteletacean brachiopod subfamily Draboviinae (a member of the Mediterranean fauna) in beds equivalent to the Zone of *Nemagraptus gracilis* and the lower part of the Zone of *Diplograptus multidens*. In the Balto-Scandian region *Bimuria* is known only from the central confacies belt (Jaanusson, n).

among cephalopods.

A fauna very similar to the Appalachian fauna east of the Helena-Saltville thrust is known from the Girvan district of southern Scotland (WILLIAMS, 1962, 1969; TRIPP, 1962, 1965, 1967), and the term Scoto-Appalachian fauna (WHITTINGTON & WILLIAMS, 1955) can be used as a designation of middle Ordovician faunas of similar type elsewhere (JAANUSSON, 1973a; not in the wide sense applied to this term by WILLIAMS, 1973). The middle Ordovician fauna of Scoto-Appalachian type, better defined in brachiopod than trilobite assemblages, has a wide distribution. In North America a fauna of this type has an amphicratonic distribution in that several distinctive genera are known also from the western side of the craton (for example, in the Copenhagen Formation in Nevada). A related fauna occurs also in the Novaya Zemlya-Pay Khoy region (BONDAREV, 1968) and it can be followed as far as to Gornyi Altay in southwestern Siberia (LEVITSKIY, 1963; cf. distribution of *Bimuria*, Fig. 8). Also in parts of Kazakhstan the brachiopod fauna has Scoto-Appalachian affinities.

Cratonic North America, the Canadian Arctic Archipelago, and Greenland were inhabited by a fauna (North American Midcontinent fauna) with mostly smaller taxonomic diversity than in the Scoto-Appalachian area. Middle Ordovician bathyurid trilobites (Fig. 9) are not known elsewhere in the world.

The middle Ordovician fauna of the Siberian platform and the southern "structural-facial zone" of the Taymyr Peninsula is similar to the North American Midcontinent fauna, but has monorakid trilobites as a distinctive element (Fig. 9) and lacks enteletacean brachiopods. For convenience this fauna can be termed the Tungusian fauna or, combined with the fauna in the North American continental interior, the North American Midcontinent-Tungusian fauna (JAANUSSON, 1973a). Monorakids are known also from northeastern Siberia, Chukot Peninsula (ORADOVSKAYA, 1970), and Novosibirskoe Ostrova. All these regions have yielded middle Ordovician faunas similar to that of the Siberian platform. Monorakids have also been reported from the Sayan Mountains and Tuva, but the known

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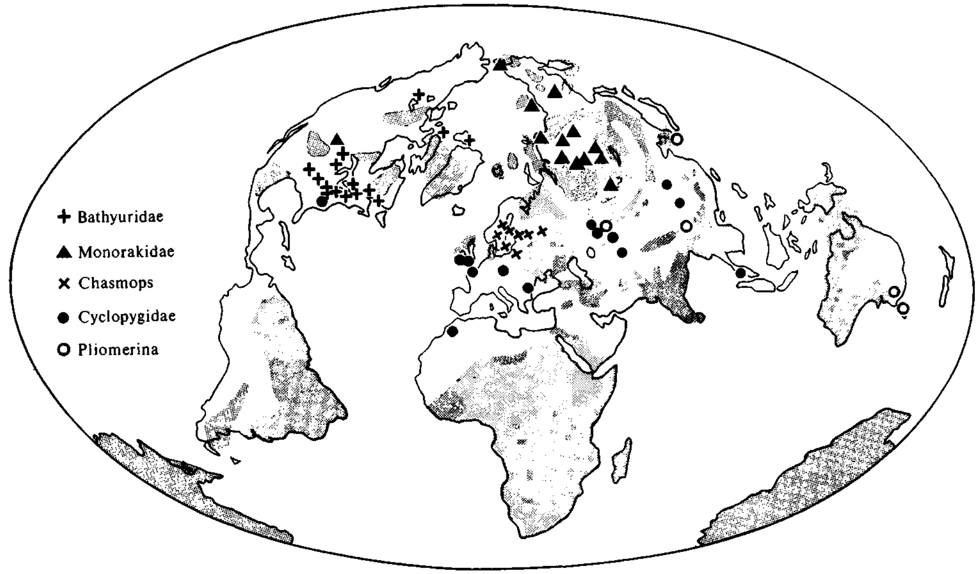

FIG. 9. Distribution of selected trilobite taxa in beds equivalent to the Zone of *Nemagraptus gracilis* and the lower part of the Zone of *Diplograptus multidens*. Bathyurids characterize the North American Midcontinent fauna and monorakids the Tungusian fauna. In this interval *Chasmops* is restricted to the Balto-Scandian region, but attains a somewhat wider distribution in the upper part of the middle Ordovician. Cyclopygids are a southern element with a trans-Eurasian distribution and *Pliomerina* characterizes the southeastern Asian-Australian fauna (Jaanusson, n).

middle Ordovician faunas from these areas are far too small for biogeographic conclusions. A possibly related genus *(Isalaux)* occurs on the Siberian platform and in Colorado.

Based mainly on cephalopods, the North American affinities of the fauna in northern China and northern Korea have repeatedly been pointed out; however, very little information on trilobites and brachiopods is available from these regions.

During the middle Ordovician the provincial character of the Balto-Scandian fauna became progressively less pronounced. The region still possessed a number of taxa that are not known elsewhere (*Asaphus* and six additional asaphid genera; some other genera, such as *Chasmops,* Fig. 9, and *Estoniops,* were endemic for Balto-Scandia during the early part of the middle Ordovician, but then spread to the southern part of British Isles). Within the region, faunal differentiation increased considerably (JAANUSSON, 1976). In the central Balto-Scandian confacies belt[1] a successively increasing Scoto-Appalachian influence is apparent in the brachiopod faunas, whereas the North Estonian belt retained some of the provincial character (gonambonitid brachiopods such as *Estlandia, Clitambonites,* apatorthids). The Balto-Scandian fauna can be followed to the central Ural Mountains (ANZYGIN in VARGANOV, 1973) in the east and to Moldavia in the south.

During late middle Ordovician time a notable exchange took place between some faunas: several Mediterranean trilobite genera (WHITTINGTON, 1966) and *Platystrophia* entered the North American midcontinent; Balto-Scandian and Scoto-Appalachian genera appeared in England and Wales; and close to the end of the epoch, the Balto-Scandian *Asaphus (Neoasaphus)* reached as far as southwestern China. A remarkable invasion of new faunal elements took place at the end of the epoch in northwestern Estonia, as well as in the Mjøsa and

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[1] A *confacies belt* differs from adjacent contemporaneous belts in lithology and fauna, and although lithology, as well as fauna, changes with time within the belt, the geographic position and individuality of the belt remains roughly the same during appreciable time. For further discussion and examples, see JAANUSSON, 1976.

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Langesund-Skien districts of the Oslo region, Norway. The invading taxa include leperditiacean ostracodes (Mjøsa district), telotremate brachiopods *(Rhynchotrema, Rostricellula, Zygospira), Bumastoides* and *Encrinuroides* among trilobites, and the earliest stromatoporoids for the region. These elements are mainly North American and the associated conodont fauna is of North American Midcontinent type (SWEET & BERGSTRÖM, 1974). The new fauna is mostly associated with bahamitic carbonate sediments, previously unknown from the Balto-Scandian region (JAANUSSON, 1973b). This fauna is poorly represented in contemporaneous beds elsewhere in the Balto-Scandian region and most of it soon disappeared. The invasion and associated sediments suggest a shift to subtropical or tropical temperatures in shallow-water areas of northern Balto-Scandia during a relatively short time.

The middle Ordovician trilobite fauna of Australia, Southeast Asia, and Kazakhstan has general northern ("remopleuridid," WHITTINGTON & HUGHES, 1972) affinities, but it includes endemic elements (see distribution of *Pliomerina,* Fig. 9) and has been distinguished as the *Heptabronteus-Pliomerina* Province (WEBBY, 1974; *Encrinurella* fauna, WHITTINGTON, 1966). Further endemic genera are the blind cheirurid *Prosopiscus,* the raphiophorid *Ampyxinella,* and others (see also LU, 1975). Brachiopods from these regions are still very poorly described.

Lower Ordovician trilobite faunas, up to the base of the *Nemagraptus gracilis* Zone of western England, Wales, and southern Ireland, have strong Mediterranean affinities (WHITTINGTON & HUGHES, 1972). The middle and upper middle Ordovician faunas, on the other hand, are linked to the Scoto-Appalachian fauna (WHITTINGTON & HUGHES, 1972), although there still is a considerable Mediterranean component. Otherwise, the Mediterranean fauna *(Selenopeltis* fauna, WHITTINGTON, 1966, WHITTINGTON & HUGHES, 1972; Anglo-French and Bohemian Provinces, WILLIAMS, 1973; Mediterranean Province, HAVLIČEK, 1976) occupies the same area as earlier, from Morocco in the west over Bohemia to Turkey in the east. The fauna is characterized by cyclopygid (Fig. 9) and homalonotid trilobites, several endemic dalmanitids, and a variety of enteletacean brachiopods such as *Svobodaina* (SPJELDNAES, 1967) and Draboviinae (Fig. 8). The distribution of several taxa follows the "trans-Eurasian migration route" from northwestern Africa and southern Europe to central and southern China. Examples are cyclopygids (Fig. 9) among trilobites, porambonitids among brachiopods, and *Aristocystites* and *Sinocystis* among cystoids.

The few middle Ordovician trilobites known from South America have uncertain biogeographic affinity.

UPPER ORDOVICIAN (EXCLUDING THE HIRNANTIAN)

Over wide areas, Upper Ordovician (from the zone of *Pleurograptus linearis,* inclusively, to the top of the system) deposits are either missing (northern China, northern Korea, the Tarim platform) or with a break at the top (e.g., the Siberian platform, western continental Europe, Greenland, and parts of North America). In South America undoubted Upper Ordovician is known only from the Precordillera of western Argentina.

Most authors have concluded that faunal provinciality decreased progressively during the middle and Late Ordovician (WHITTINGTON & HUGHES, 1972; WILLIAMS, 1973) so that during the Ashgillian a cosmopolitan fauna began to emerge (WILLIAMS, 1973), culminating with the latest Ordovician *Dalmanitina (Mucronaspis)-Hirnantia* fauna that is regarded by some as worldwide. The general trend during this time toward reduced provinciality is fairly evident but there still is a considerable biogeographic differentiation up to the end of the period.

Based on statistical analysis of 14 lists of genera, WHITTINGTON and HUGHES (1972) suggested that in Ashgillian trilobite faunas two provinces can be distinguished, one (*Selenopeltis* Province) restricted to Morocco and Bohemia and the other (Remopleuridid Province) comprising the rest of the samples analyzed (North America, northern Europe, Kazakhstan, and China). Their interpretation of the statistical results may be questioned. The only sample from the

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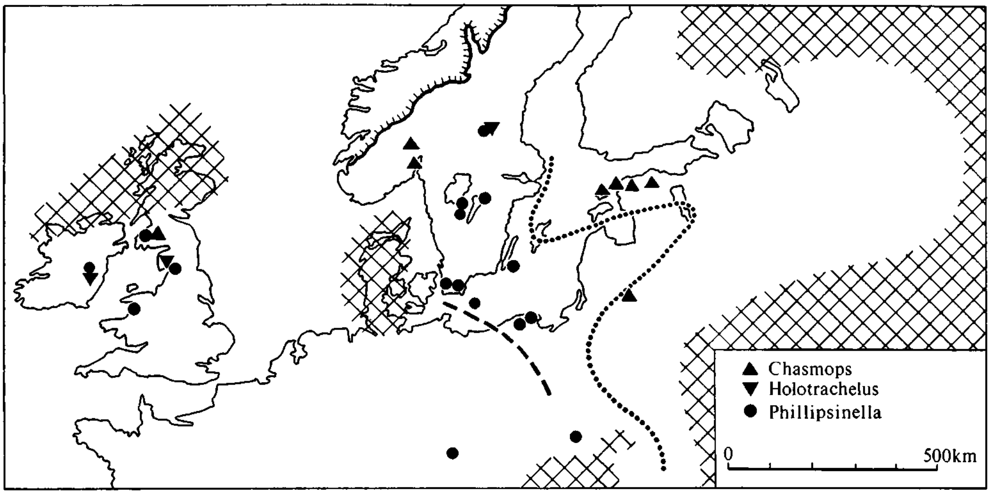

Fig. 10. Distribution of selected lower and middle Ashgillian trilobites in northern Europe. *Phillipsinella* characterizes faunas with Mediterranean affinities, whereas *Holotrachelus* is mostly confined to limestones with a Hiberno-Salairian fauna. The main occurrence of *Chasmops* in northern Europe is in limestones of the North Estonian and Lithuanian belts and the Oslo region. Ashgillian *Phillipsinella* is known also from Carnic Alps, Kazakhstan, and Uzbekistan. [Western boundary of the Russian platform indicated by dashed line and eastern boundary of the central Balto-Scandian confacies indicated by dotted line (Jaanusson, n).]

North American Midcontinent (Iowa) was found to be linked at low dissimilarity indices over Anticosti, and several other samples, to Poland and several other North European samples; however, none of the 16 genera in the Maquoketa Shale of Iowa (Walter, 1926; generic names updated herein) is known from the lower and middle Ashgillian of Poland (about 37 genera; Kielan, 1959), close to the other end of the chain of samples linked at low dissimilarity indices. In this case two completely different faunas are included in the same province because they have come to be linked over a chain of samples that happen to include transitional ("mingled") faunas.

The trilobite fauna of the Maquoketa Shale contains a distinctive assemblage of genera (*Anataphrus, Ectenaspis, Thaleops, Bumastoides, Ceraurus, Remipyga,* etc.) that, in the Upper Ordovician, is not known outside North America except for occasional occurrences in the Taymyr Peninsula and northeastern Siberia. Most of the genera continue from the middle Ordovician within the same regions. Indeed, in the carbonate deposits of North America and the Arctic Islands, the North American Midcontinent fauna continues into the Upper Ordovician with few modifications. Distinctive taxa include, in addition to several trilobite genera (for *Isotelus,* see Fig. 11), *Zygospira* among brachiopods (Jaanusson, 1973a, fig. 3; known also from the Altay region and other places), leperditiacean ostracodes (known also from northeastern Siberia), and aulacerid stromatoporoids (also on Siberian platform). Rhynchotrematid brachiopods are common in many areas.

On the Siberian platform and Taymyr Peninsula a related fauna ranges from middle to Upper Ordovician without great change. Monorakid trilobites continue to be characteristic. They occur also in northeastern Siberia (see Fig. 11) but the fauna there includes also *Eospirigerina, Ptychoglyptus,* and large pentameraceans (*Tcherķidium;* Nikolaev *et al.,* 1974).

In northern Europe, where Upper Ordovician rocks are widespread, three spatially different lower and middle Ashgillian faunas can be distinguished (Fig. 10):

1) Sequences that consist predominantly of mudstone, have a high taxonomic diversity of trilobites, a limited brachiopod fauna, and few other fossils. The important, in

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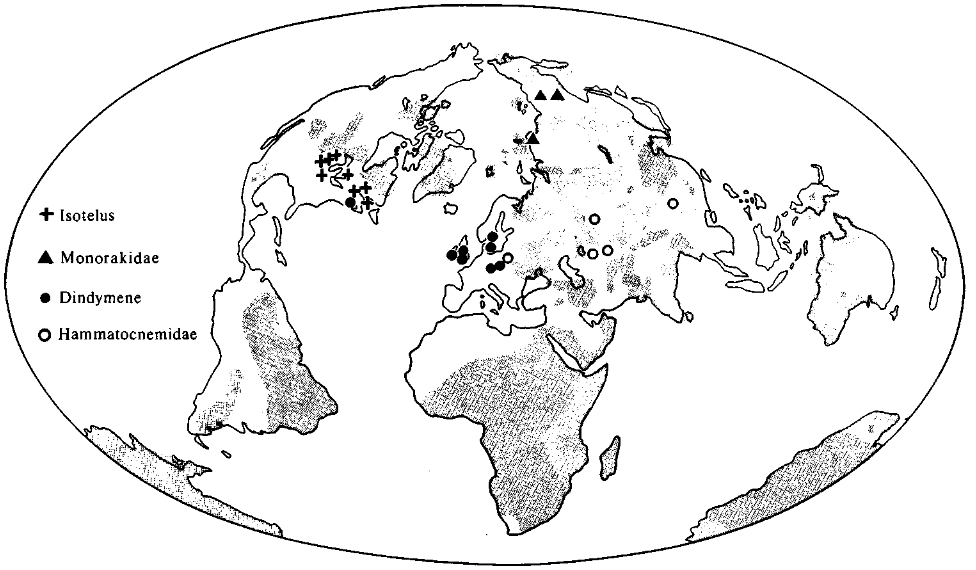

FIG. 11. Distribution of selected trilobite taxa in beds equivalent to the lower and middle Ashgillian. The asaphid *Isotelus* is widely distributed in the North American Midcontinent fauna and monorakids are confined to the Tungusian fauna. The encrinurid subfamily Dindymeninae is restricted to the Mediterranean fauna and hammatocnemids extend from central Poland to central China. Ashgillian *Isotelus* has been recorded also from some additional areas but figured specimens indicate that other genera are probably involved. Middle Ordovician dindymenines are known from Bohemia, Kazakhstan, and western Pamir (Jaanusson, n).

places main, component of the fauna consists of taxa that in the middle Ordovician occurred in the Mediterranean (Bohemian) region (KIELAN, 1959), such as Dindymeninae, Cyclopygidae, Ectillaeninae, Dionidae, and *Dalmanitina (Mucronaspis),* and continued to be characteristic for the Mediterranean region also during the Late Ordovician. Trinucleids were common. That during this time Bohemia and central Poland should belong to different provinces (WHITTINGTON & HUGHES, 1972) is questionable, and may depend upon which index values are selected in the statistical analysis. The contemporaneous brachiopod fauna in Scania, Sweden, is of Bohemian type (SHEEHAN, 1973). Thus, in Europe a fauna of Mediterranean type spread northward to the British Isles (as far as western Ireland and Scotland) and to the central Balto-Scandian confacies belt (cf. the distribution of *Phillipsinella,* Fig. 10, and of *Dindymene,* Fig. 11). Similar faunas are known in the Percé district, Quebec (*Stenopareia* fauna; LESPÉRANCE, 1968), and particularly in the Magog belt of Maine (NEUMAN, 1970).

2) Limestones that are associated with mudstone have mostly a patchy distribution and a varied fauna. Both trilobites and brachiopods have a high taxonomic diversity. The trilobite fauna has little in common with that of contemporaneous mudstone facies close-by. In fact, in statistical analysis the magnitude of the difference may be that between different faunal provinces (WHITTINGTON & HUGHES, 1972, with regard to the Boda Limestone in the Siljan district, Sweden). The Boda Limestone (carbonate mounds with stromatactis) lacks all the taxa mentioned as characteristic for the Mediterranean mudstone fauna as well as *Chasmops.* The brachiopod fauna, too, is very different from that of Mediterranean mudstones. It has much in common with the middle Ordovician Scoto-Appalachian fauna *(Christiania, Bimuria, Ptychoglyptus, Dolerorthis, Kullervo),* but includes new elements such as dicoelosiids, *Eospirigerina,* and meristellids. Limestone facies with a similar fauna (see also the distribution

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of *Holotrachelus,* Fig. 10) are known in Ireland (Portane and Chair of Kildare limestones), northern England (Keisley Limestone), and Salair Mountains in southwestern Siberia (so-called Weberian Limestone). Jaanusson (1973a) termed this type of Ordovician fauna the Hiberno-Salairian fauna. In several limestone facies the fauna of Hiberno-Salairian type is mingled with Mediterranean elements and, conversely, Hiberno-Salairian elements are in places found associated with a preponderantly Mediterranean fauna. This may, in part at least, be a consequence of the occurrence of transitional lithologies, reflecting transitional environments; however, a biogeographic gradient may also be involved because limestone with the Hiberno-Salairian fauna, as well as mingled assemblages, occurs only in a belt along the northern boundary of the distribution of the Mediterranean fauna (Fig. 10). Geographic proximity of the different faunas may be a factor contributing to mingling.

3) The North Estonian carbonate confacies belt still retains its provincial character. No Mediterranean element had entered the area. The fauna is rich, particularly in corals, but the trilobite fauna has a low diversity with *Chasmops* as one of the commonest elements (Fig. 10). The brachiopod fauna is varied, in several respects close to the Hiberno-Salairian fauna *(Dicoelosia, Eospirigerina),* but it lacks the Scoto-Appalachian imprint. Endemic forms include *Equirostra, Ilmarinia,* and *Apatorthis,* all descendents of the middle Ordovician fauna of the belt. The trilobite fauna in the 5a-limestone belt in the Oslo region, Norway, is in many respects similar to that of the North Estonian belt, as is much of the rest of the fauna, but it lacks the North Estonian endemics.

The Balto-Scandian coral fauna in the Upper Ordovician limestone facies has been considered to belong to a separate Baltic province (Leleshus, 1970; European Province, Kaljo *et al.,* 1970) or form together with the central Asiatic and Chinese faunas the Eurasiatic province (Kaljo & Klaamann, 1973). It is interesting to note that although the Ural Mountains show Balto-Scandian affinities in the trilobite and brachiopod faunas (Varganov *et al.,* 1973), its coral faunas are regarded as intermediate between the Arctic (North America, northeastern Siberia, Soviet Arctic) and the Siberian (Siberian platform, southwestern Siberia) provinces (Leleshus, 1970) or they are included in the Americo-Siberian province (Kaljo *et al.,* 1970). Also, the trilobite and brachiopod faunas of the Ural Mountains include, in each Ordovician epoch, some genera that are not known in the East Baltic or Scandinavia, but occur either in North America *(Hypodicranotus)* or the Siberian platform *(Dolgeuloma, Angarella, Xenelasmella, Cyrtophyllum),* or both.

In the southern and central Appalachians the Scoto-Appalachian fauna disappeared close to the end of the middle Ordovician and all Upper Ordovician faunas from the region are of the Midcontinent type; however, an Upper Ordovician brachiopod fauna resembling the Scoto-Appalachian fauna occurs in some areas in the periphery of the continent: east-central Alaska, Klamath Mountains in northern California, and Percé district in Quebec. Rozman (1968, 1970) suggested that the Alaskan and northeast Siberian Upper Ordovician brachiopod faunas belong to a separate Kolyma-Alaskan biogeographic belt but the evidence is inconclusive. All these peripheral North American Upper Ordovician brachiopod faunas have close affinities with the Hiberno-Salairian fauna.

The Late Ordovician trilobite fauna of Bukantau (Abdullaev, 1972), central Tien Shan (Abdullaev in Abdullaev & Khaletskaya, 1970), parts of Kazakhstan (Apollonov, 1974), and southwestern China (Szechuan-Kueichou border; Sheng, 1964) show affinities with the Mediterranean fauna. Several taxa have a "trans-Eurasian" distribution (cyclopygids, *Nankinolithus*). A characteristic early and middle Ashgillian element in Kazakhstan, Uzbekistan, and southwestern China is the family Hammatocnemidae (Fig. 11), endemic in some of the regions also in the late middle Ordovician. It reached central Poland in the middle Ashgillian (Kielan, 1959), but has not been found in the rest of Europe. From Australia and South America no contemporaneous shelly fauna is known.

In parts of Kazakhstan and Uzbekistan

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FIG. 12. Distribution of the trilobites *Dalmanitina (Dalmanitina)* and *Dalmanitina (Mucronaspis)* in the Hirnantian (Jaanusson, n).

the fauna in middle Ashgillian limestones shows some Hiberno-Salairian affinities (e.g., *Holotrachelus, Eospirigerina),* but the brachiopod fauna has not yet been described in detail. The coral faunas seem to indicate that Kazakhstan, Soviet Central Asia, and parts of China formed during the Late Ordovician either a separate province (the central Asian Province; KALJO *et al.*, 1970; LELESHUS, 1970) or a part of the Euroasiatic province (KALJO & KLAAMANN, 1973).

UPPERMOST UPPER ORDOVICIAN (HIRNANTIAN)

The distribution of the so-called *Dalmanitina-Hirnantia* fauna in the uppermost Ordovician has recently been the subject of much discussion in connection with the Ordovician glaciation. Distribution of the fauna coincides largely with that of the earlier mudstone fauna of Mediterranean type, from Percé in Quebec over British Isles to the Central Balto-Scandian confacies belt in the north and over central Poland and Bohemia to Morocco in the south (see *Dalmanitina (Mucronaspis);* Fig. 12). The trilobite assemblage has been claimed to extend eastward to Kazakhstan (APOLLONOV, 1974), southern China (SHENG, 1964), and Australia (WHITTINGTON & HUGHES, 1972, fig. 12). The dominating elements in the European assemblage, however, are *Dalmanitina (Mucronaspis) mucronata* and *Brongniartella* whereas in Kazakhstan and China they are replaced by *Dalmanitina (Dalmanitina)* and *Platycoryphe,* and it is *Dalmanitina (Dalmanitina)* that reached Australia (CAMPBELL, 1973) and the Precordillera of western Argentina (BALDIS & BLASCO, 1975). The *Hirnantia* assemblage of brachiopods is characterized by *Hirnantia sagittifera, Kinnella, Eostropheodonta, Plectothyrella,* and some other genera. Evidence of this fauna east of Europe, or possibly Kazakhstan, is at present tenuous. The appearance of the *Dalmanitina-Hirnantia* assemblage does not denote any major change in the fauna because most genera and several species are known in earlier beds (LESPÉRANCE, 1974) with the Mediterranean fauna. In many areas the taxonomic diversity of trilobites decreased considerably (LESPÉRANCE, 1974).

In limestone facies with a Hiberno-Salairian and related fauna, beds equivalent to the Hirnantian, such as the upper part of the Boda carbonate mounds in Sweden and the 5b-calcareous sandstone of the Oslo region, Norway, do not differ faunally very much

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from the underlying beds and have almost nothing in common with the *Dalmanitina-Hirnantia* assemblage. New elements include large pentameracean brachiopods *(Holorhynchus, Proconchidium)*. Uppermost Ordovician beds characterized by these pentamerids have a wide distribution, from the eugeosynclinal Caledonian deposits in Västerbotten, northern Sweden, and western and parts of the central Balto-Scandian belts over Ural Mountains to southern Tien Shan (NIKIFOROVA & SAPELNIKOV, 1973) and Kazakhstan. In Kazakhstan the uppermost Upper Ordovician limestone facies have yielded at least seven different pentameracean genera (SAPELNIKOV & RUKAVISHNIKOVA, 1975), but it is not always clear whether they all have come from beds equivalent to the Hirnantian. A comparable uppermost Ordovician limestone with large pentameraceans *(Eoconchidium)* is known also from northeastern Siberia. Many of the uppermost Ordovician limestone beds with pentameraceans are poor in trilobites but have in places a rich coral fauna.

Differences between the fauna of the North Estonian belt, equivalent to the Hirnantian (Porkuni Stage), and the other faunas are the same as in underlying beds. Endemic relicts still occur *(Chasmops, Conolichas, Ilmarinia, Vellamo)*, and the fauna has no Mediterranean elements.

The Edgewood Limestone and its equivalents in southwestern Illinois, eastern Missouri, and southern Oklahoma contain a varied brachiopod fauna showing some affinities to the *Hirnantia* fauna (AMSDEN, 1974). The Ordovician age of this fauna has been in doubt, but in Illinois these beds have yielded also an asaphid trilobite (SAVAGE, 1917; most probably *Anataphrus*), and other indications suggesting a Hirnantian age. The fauna includes *Eospirigerina, Cryptothyrella, Dicoelosia,* and a pentameracean, all belonging to subfamilies or families not known in the Upper Ordovician Midcontinent fauna of North America, but in part widely distributed in earlier beds with the Hiberno-Salairian and related faunas. Associated forms include *Hirnantia* and *Dalmanitina (Mucronaspis)* known in earlier beds of the Mediterranean region. The Ellis Bay Formation of Anticosti (roughly of Hirnantian age) still has a strong Midcontinent component (e.g., *"Brachyaspis," Remipyga, Vellamo, Dinorthis*), but mingled with genera having a wide distribution in Hiberno-Salairian and related faunas (*Eospirigerina,* meristellids), or of unknown origin (*Protatrypa*).

No contemporaneous fauna is known from the Siberian platform where uppermost Ordovician deposits may be missing. Thus, it seems that the North American Midcontinent and Tungusian faunas virtually ceased to exist as biogeographic units before the end of the Ordovician, although some of their elements (such as *Anataphrus* and *Strophomena* in the Edgewood fauna) still lingered as relicts into the Hirnantian. The biogeographic situation of Anticosti during the Hirnantian may be comparable to that of the North Estonian belt in Balto-Scandia: a marginal platform area with numerous relicts.

PLANKTONIC GRAPTOLITES

Rich and varied planktonic graptolite faunas are confined to dark shale, and these sediments have a sporadic distribution. Thus, our main knowledge of graptolite faunas is restricted to limited geographical regions, mostly outside cratonic platforms.

As in the shelly faunas, the degree of biogeographic differentiation varies with time. In the Tremadocian and lowermost Arenigian, provincialism is relatively weak although not yet well understood. The differentiation is greatest in the middle and upper Arenigian and Llanvirnian. From the *Nemagraptus gracilis* Zone (as defined in Scania) to the top of the Ordovician the graptolite faunas are almost cosmopolitan and, although provincial trends do occur (RIVA, 1969), they are almost exclusively at the species level and at present difficult to define.

Biogeography of the Ordovician graptolites has recently been treated in several papers (BULMAN, 1964, 1971; SKEVINGTON, 1969, 1973, 1974; BOUČEK, 1972; MU, 1974). Generally two Arenigian and Llanvirnian provinces are distinguished.

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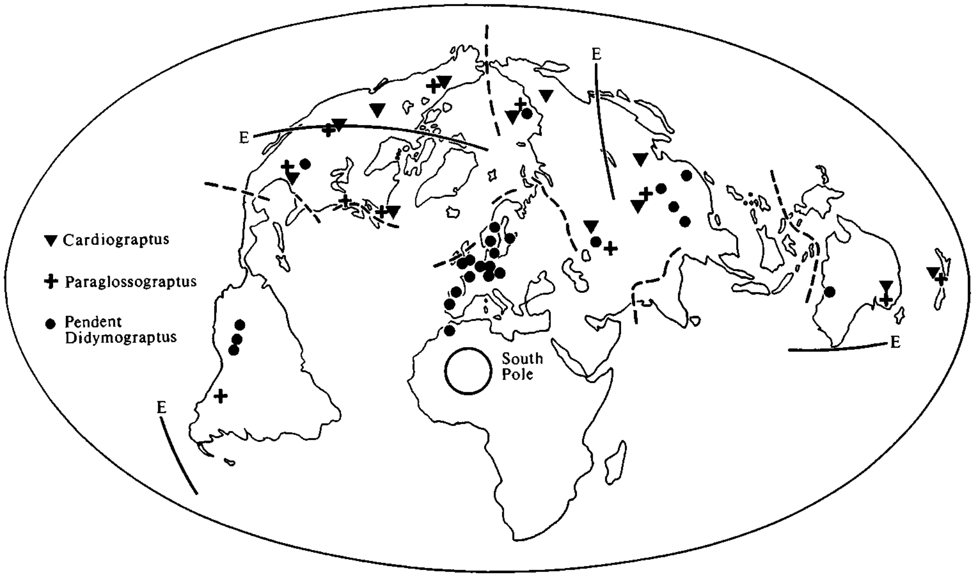

FIG. 13. Distribution of some graptoloids in the Llanvirnian and its equivalents. *Paraglossograptus* and *Cardiograptus* characterize the Pacific fauna and the main distribution of pendent species of *Didymograptus* is in the Atlantic fauna. [Dashed lines indicate probable boundaries between main lithospheric plates (according to several writers the number of separate Ordovician cratonic lithospheric plates is far greater but in these cases the position of plate boundaries is uncertain). Lines marked with *E* indicate the approximate positions of the Ordovician equators for North America, South America, Siberia, and Australia, based on paleomagnetic data (SMITH *et al.*, 1973). Probable Ordovician position of the South ("Gondwana") Pole indicated by a circle (Jaanusson, n).]

The fauna of the Pacific province is developed in southeastern Australia (Victoria and New South Wales), New Zealand, Texas (Marathon region), Cordilleran North America (from Nevada to Yukon), the Canadian Arctic Archipelago, Appalachians (Georgia, New York, Quebec, Newfoundland), western Ireland (Galway and Mayo), northern Taymyr Peninsula, Bennett Island, northeastern Siberia, northwestern (Chilianshan, Ordos) and north-central China (Honan), Kirgizistan, and Kazakhstan (Chu-Ili Mountains).

The graptolite fauna of the Atlantic (or European; BULMAN, 1971) province occurs in Scandinavia (e.g., Scania, Oslo region in Norway, Västergötland and Jämtland in Sweden), subsurface eastern Latvia and eastern Moscow basin, Wales, England (Lake district and subsurface London platform), southern and eastern Ireland, in limited areas on continental Europe (e.g., Belgium, central Poland, Bohemia), and northern Africa.

The distribution of graptolite faunas in South America is particularly interesting. The Llanvirnian fauna in Peru and Bolivia is decidedly Atlantic whereas farther southward, in the Precordillera of western Argentina, the affinities of the fauna (CUERDA, 1973) are Pacific. The situation is somewhat similar also in China with the Pacific fauna in northern China but an Atlantic fauna in southwestern China (MU, 1974; Szechuan, northern Kueichou, Yunnan). In southeastern China (Anhui, Chekian) the fauna is preponderantly Pacific (MU, 1974) but mingled with Atlantic elements.

The middle and late Arenigian Pacific fauna is characterized by *Goniograptus, Sigmagraptus, Skiagraptus, Apiograptus, Oncograptus,* and *Cardiograptus.* A profusion of various forms of *Isograptus* is characteristic for the upper part of the sequence. The Atlantic fauna differs by lack of Pacific elements rather than by endemics, and by the order of appearance and disappearance of various taxa in relation to other taxa.

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Azygograptus and some multiramous dichograptids may be endemic.

The Llanvirnian Pacific fauna contains a number of genera restricted to the province, such as *Paraglossograptus* (Fig. 13), *Pseudobryograptus, Cardiograptus* (Fig. 13), and *Brachiograptus.* The Llanvirnian Atlantic fauna is distinguished by the abundance of pendent *Didymograptus* (Fig. 13) that is rare or missing in the contemporaneous Pacific fauna.

The Balto-Scandian Arenigian and Llanvirnian graptolite assemblages are not quite like those of Wales and northern England. Berry (1960) suggested that Scandinavia belonged to a separate faunal region, but differences are mostly in quantitative composition of the assemblages and may characterize one of several subprovinces that at present are difficult to define; however, during the time corresponding to the zone of *Glyptograptus teretiusculus* in Scania, provincial features increased in importance in Balto-Scandia and a separate province may have come into existence. The fauna is characterized by *Gymnograptus* associated with a complex of species not known outside Balto-Scandia. *Gymnograptus* has been found also in central China (Szechuan-Kueichou border) in a contemporaneous assemblage poor in species. The correlation of this Balto-Scandian fauna with those of the other areas is otherwise notoriously difficult. It is probable that contemporaneous beds elsewhere form the lower part of the undifferentiated zone of *Nemagraptus gracilis* (Jaanusson, 1960).

CONODONT FAUNAS

Our knowledge of conodont faunas comes almost exclusively from carbonate rocks. As a consequence, little information on conodonts is available from wide areas without carbonate deposits (in the Ordovician, for example, from much of the region with a Mediterranean shelly fauna). Information on the distribution of Ordovician conodonts is also incomplete because in many areas with suitable rocks systematic work on conodonts has barely started (e.g., southwestern Siberia, Kazakhstan, eastern Asia, Ural Mountains).

Available evidence on the biogeography of Ordovician condonts has been summarized by Bergström (1971, 1973), Sweet *et al.* (1971), Barnes *et al.* (1973), Sweet & Bergström (1974), and Barnes & Fåhraeus (1975). The lower Tremadocian conodont fauna has a low taxonomic diversity and seems to have an almost cosmopolitan distribution. A well-defined biogeographic differentiation begins with the Arenigian and can be followed throughout the middle and Upper Ordovician. In most papers two provinces or faunas have been distinguished.

The North American Midcontinent province (Sweet *et al.,* 1959) is developed in North American cratonic and inner miogeosynclinal areas from Chihuahua in Mexico in the south to Ellesmereland on the north and from inner miogeosynclinal belts of the Appalachians in the east to eastern Nevada in the west. Faunas of the same type are known from northern Scotland (Durness Limestone), eugeosynclinal sequence of Norway (Hølonda Limestone in the Trondheim region, Bergström, 1971), Korea, Siberian platform, and northeastern Siberia. In the latest middle Ordovician the fauna temporarily invaded parts of Balto-Scandia (Bergström, 1971; Sweet & Bergström, 1974).

Conodont faunas of the North Atlantic province (Bergström, 1971; Anglo-Scandinavian-Appalachian Province, Sweet *et al.,* 1959; European Province, Bergström & Sweet, 1966) have been reported from Balto-Scandia, British Isles, and scattered areas in continental Europe. In North America this type of fauna has an amphicratonic distribution, occurring along the Appalachians as well as the Cordillera. In the Lower Ordovician of the Appalachians the North Atlantic conodonts are known only in limited eastern areas with "exotic" rocks (Newfoundland, Pennsylvania; Bergström *et al.,* 1973). In the middle Ordovician the North Atlantic fauna spread westward to the Helena-Saltville thrust of the southern Appalachians (Bergström, 1971) and into corresponding belts farther to the north as far as Newfoundland. The fauna is also known from Texas (Marathon

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region) and in the Cordillera from Nevada to Yukon and Alaska. A Lower Ordovician conodont fauna with North Atlantic affinities has been described from Precordilleran Argentina (Serpagli, 1974).

In Australia, collections from New South Wales and Queensland show North American Midcontinent affinities (Sweet & Bergström, 1974), whereas Lower Ordovician conodonts from the Canning basin (McTavish, 1973) are mostly related to those from the North Atlantic province. Undescribed collections from the middle Ordovician of central Australia and Tasmania are characterized by species largely unknown in either the Midcontinent or North Atlantic provinces, which led Bergström (1971) to postulate that a separate Australian province may be recognizable.

In the Early Ordovician simple-cone species apparently dominate Midcontinent faunas to the virtual exclusion of other types, whereas in the North Atlantic province taxa with ramiform-element apparatuses form an important component in the conodont faunas. Middle and Upper Ordovician faunas of Midcontinent type are composed largely of "fibrous" conodonts and "nonfibrous" ramiform-element genera (e.g., *Phragmodus, Plectodina*). Genera with platform-type skeletal elements are rare. North Atlantic fauna mostly lacks the ramiform-element "fibrous" conodonts and includes a far greater variety of taxa with platform-type skeletal elements (e.g., *Eoplacognathus, Pygodus*).

The well-defined provinciality of the conodont faunas ended with the Ordovician, and the succeeding Silurian fauna is described as cosmopolitan.

BIOGEOGRAPHIC EVALUATION OF FAUNAL DIFFERENTIATION

North America has one of the simplest geological structures of all continental lithospheric plates and provides valuable clues for interpretation of faunal differentiation. The amphicratonic distribution of the shelly faunas of the Scoto-Appalachian and Hiberno-Salairian types (peripheral faunas) relative to the Midcontinent fauna is analogous to the apparently concentric arrangement of Middle and Late Cambrian biofacies realms (for summaries, see Palmer, 1969, 1972, 1973, 1974; Cook & Taylor, 1975) and is probably controlled by the same main factors. The same spatial distribution shows also the North Atlantic conodont fauna relative to the North American Midcontinent fauna. The Midcontinent faunas inhabited a wide carbonate platform in the continental interior, whereas the peripheral faunas occupied the outer, oceanward margin of the carbonate platform and extended in places in what has been termed the eugeosynclinal zone (Magog belt, etc.). An outer Ordovician biofacies realm, corresponding to that occupying much of the Cambrian "outer detrital belt," is characterized by planktonic graptolite fauna that has no exact counterpart in the Cambrian.

The similarity to the concentric arrangement of Cambrian biofacies realms was greatest during the Early Ordovician. The extensive Ordovician carbonate deposits of the continental interior and much of the Appalachians reflect shallow-water conditions over wide areas and the fauna that inhabited the region includes numerous endemic supraspecific taxa. The peripheral shelly fauna is best preserved in the west (Ross, 1975). In the middle and Late Ordovician the conditions were somewhat different. The depositional environment of the Midcontinent region was more varied and not so markedly associated with shallow water as during the Late Cambrian and Early Ordovician. The Midcontinent shelly fauna is far less specialized than in earlier epochs and differs from the faunas of the Scoto-Appalachian and Hiberno-Salairian type by lack of taxa widely distributed in the peripheral faunas rather than by endemic elements.

The bulk of evidence indicates that the difference between the peripheral and Midcontinent shelly faunas was primarily due to ecological factors; however, those environmental factors that caused the differentiation are not always clear. With respect to the Cambrian peripheral faunas it has been stressed that they are found in former shelf-margin to open-sea areas with "unrestricted access to open ocean conditions" (Palmer, 1973) where widespread to cosmopolitan

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forms either lived or were transported. According to Whittington and Hughes (1972), comparable Ordovician faunas have occupied shelf slopes, which probably implies that they lived in deeper water than contemporaneous faunas on the continental platform; however, water depth was not always the main ecological factor that controlled the distribution of Ordovician peripheral shelly faunas because in places these faunas are associated with sediment indicating shallow-water environment or at least deposition within the photic zone. Also, in parts of the Girvan district, Scotland, the Scoto-Appalachian fauna is associated with sediment of very shallow water (Williams, 1962). The difference in water temperature between open ocean and relatively shallow water upon a platform may constitute a possibly important ecologic factor. On several platform areas, such as the North American continental interior, Canadian Arctic Archipelago, northwestern Greenland, Severnaya Zemlya, Siberian platform, and northern China (Shensi), presence of Ordovician evaporites indicates that in some areas evaporation was temporarily greater than precipitation. This, in turn, indicates that water salinity on the platforms was higher than in the oceans, at least temporarily (Ross, 1976). This may have influenced faunal differentiation.

In North America, distribution of the North Atlantic conodont fauna follows closely that of the peripheral shelly faunas, indicating that the same factors may have controlled both faunal differentiations. Sweet and Bergström (1974) and Serpagli (1974) suggested that distribution of the conodont faunas was controlled by water temperature, the North Atlantic fauna forming a warm-temperate fauna on both sides of a continental platform inhabited by a tropical-subtropical fauna. According to these authors, most, if not all, conodonts were planktonic or nektonic. Barnes *et al.*, (1973) and Barnes and Fahraeus (1975) suggested that the majority of Ordovician conodonts were benthonic or nektobenthonic. The Midcontinent province was largely restricted to equatorial regions characterized by raised salinity and temperature, whereas the North Atlantic faunas represented a normal marine, virtually cosmopolitan province (Barnes & Fåhraeus, 1975).

If the peripheral Ordovician faunas of North America were ecologically controlled, it follows that a similar ecological control has affected faunas of the same type elsewhere in the world, complicating the biogeographical evaluation of the distributional data in the same way as some Cambrian faunas do. A further complication arises from ecologic zonation (in paleontological literature often inappropriately termed "communities") within a region. Examples are described from shelly faunas (for trilobites, see Webby, 1974; Fortey, 1975; Apollonov, 1975) and conodont faunas (Seddon & Sweet, 1971; Barnes *et al.,* 1973; Barnes & Fåhraeus, 1975), and there exists clear evidence for a roughly similar zonation in graptolite faunas. Much of the ecological differentiation in shelly faunas is usually attributed to depth zonation, but it is often not clear whether the main ecological factor responsible for differentiation was depth or physical properties of the substrate, or an intricate combination of both these and possibly some additional factors. In the Upper Ordovician of northern Europe the distribution of various shelly faunas tends to be patchy (Fig. 10). In the Siljan district, Sweden, for example, carbonate mounds with a rich Hiberno-Salairian fauna form patches surrounded by contemporaneous mudstones and calcareous mudstones with a completely different fauna of the same Mediterranean type as further southward (cf. distribution of *Phillipsinella*, Fig. 10). A similar patchy distribution of Upper Ordovician limestone facies and associated fauna seems to prevail in Ireland and parts of northern England, although there the limestones have not yet proved to represent stromatactis carbonate mounds and some mingling of the faunas took place. In these cases the main ecological factor controlling faunal distribution may be physical properties of the substrate (whereby major ecologically important differences in the substrate do not necessarily follow the petrographic classification of rocks). Faunas of the Mediterranean type are commonly associated with terrigenous sediments, mostly former mud bottoms, and the type of substrate may have controlled the distribution of many elements in these faunas.

Much further work on Ordovician faunas is needed in order to understand what is

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ecologically and what is distributionally controlled. For this reason the neutral term "fauna" or "type of fauna" is used in this paper rather than formal categories, such as "faunal region" or "province," applied in biogeographic classification.

Evidence accumulated during the last 10 years demonstrates that the present position of cratonic lithospheric plates has very little relationship to geographies in the past. Although reconstructions of the geography back to the Permian have been shown to be possible by reversing the data of sea-floor spreading, reconstructions of the conditions before Pangaea are difficult and no satisfactory model has been presented. For the Ordovician reliable paleomagnetic data are still too few for presenting a coherent picture of latitudinal positions of various lithospheric plates (for a recent discussion, see BRIDEN *et al.*, 1973). During the last few years much attention has been focused on biogeographic data as a tool for determining the longitudinal geographic position of the cratonic lithospheric plates during Ordovician time (WHITTINGTON & HUGHES, 1972, 1973, 1975; BURRETT, 1973; WILLIAMS, 1973; ROSS, 1975). The reconstructions are based on the assumption that oceans were the major barriers to migrations of shallow-water faunas and that the degree of faunal resemblance is proportional to the width of the ocean. The classical examples from the Ordovician faunas pertaining to continental drift in the northern Atlantic region have been referred to in appropriate places of the text. In other parts of the world interpretation of available data on faunal similarities or dissimilarities is difficult at present. Oceanic barriers are not the only cause of dissimilarity between faunas. For example, in shelf areas where major cold and warm oceanic currents meet, the effect on faunas may be of comparable magnitude.

In modern seas the primary factor regulating the distribution of faunal provinces is temperature. Within a temperature zone, further biogeographic differentiation is due to the lack or restriction of communications between seas, in modern time as well as in the immediate past. According to paleomagnetic data, the Ordovician north ("Pacific") pole was situated somewhere in the present southwestern Pacific ocean, far away from any continental plates. This implies that no northern ice cap existed because water in the polar region had free exchange with the water of a vast ocean. This, in turn, suggests that climatic zones of the Ordovician northern hemisphere were probably poorly defined. The Ordovician south ("Gondwana") pole on the other hand, was very likely situated on a continent, more exactly somewhere in northwestern Africa (SMITH *et al.*, 1973). An ice cap was probably present, and the reported widespread occurrence of the middle and Late Ordovician glaciation phenomena in northwestern Africa (BEUF *et al.*, 1971) may have been in part associated with this ice cap. Glacial deposits (Pakhuis Tillite) that may be roughly contemporaneous have been reported from western South Africa. The Ordovician southern hemisphere presumably had well-defined climate zones. BURRETT (1973) suggested that climate was not the major control of faunal distribution in the Ordovician, chiefly because most plates do not appear to show any obvious latitudinal zonation. Several regions in the Ordovician southern hemisphere (Balto-Scandia, England, China) do show some spatial faunal zonation, although it is not easy to prove that the cause was climatic.

Paleomagnetic data indicate that the Ordovician equator passed across North America and the Siberian platform (Fig. 13). Thus, the shelly faunas of North American Midcontinent-Tungusian type inhabited warm to tropical seas. According to paleomagnetic evidence, Australia was situated just north of the Ordovician equator in the range of warm to tropical temperatures. No paleomagnetic data are available from east Asia.

In northern Africa fauna of the Mediterranean type occurs close to the probable Ordovician south ("Gondwana") pole and in part within the region of Ordovician glaciation. A brachiopod assemblage, probably of latest Ordovician age and comparable to the *Hirnantia* fauna, has been recorded also from western Cape Province in South Africa (COCKS *et al.*, 1970) above the Pakhuis Tillite. Upper Ordovician glacigene deposits have been recorded as far to the north as Normandy, and even from Scotland (for a general review, see HARLAND, 1972b). This

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indicates that the Mediterranean fauna lived mainly in cold water (Spjeldnaes, 1961; Havliček, 1974; Ross, 1975).

Distribution of the Pacific graptolite fauna is associated with lithospheric plates, which, according to paleomagnetic or other evidence, were situated in the region of warm to tropical climate (e.g., North America, Siberia, Australia-New Zealand). Thus, this fauna probably represents a warm-water planktonic fauna (Skevington, 1974). Graptolites in areas with the Mediterranean shelly fauna belong to the Atlantic province that obviously extended into cold water.

Skevington (1974) suggested that the cosmopolitan distribution of Ordovician graptoloids from the *Nemagraptus gracilis* Zone onward is due to disappearance of graptolites from regions with cold water (northern Africa, southern Europe) so that from then on all Ordovician graptoloid faunas, with rare exceptions, were confined to the tropical zone. Based on current models of Ordovician geography, this conclusion is possible only if the boundary between the South and North European lithospheric plates is drawn along the Alpine chain (as done by Skevington, following Smith *et al.*, 1973), and Bohemia is included in the North European plate. Evidence from shelly faunas does not support this plate boundary. The rarity of middle and Late Ordovician graptolites in northern Africa and southern Europe is more likely due to the lack of suitable sediments for preservation.

Distribution of graptolite faunas in South America suggests the presence of latitudinal faunal zonation. In all recent reconstructions of Ordovician geography, this continent forms part of Gondwanaland and is oriented with Patagonia toward the equator so that the Precordillera of Argentina with a Pacific fauna reaches low latitudes. Peru and Bolivia with an Atlantic fauna are situated at temperate latitudes. Thus, the faunas with Pacific affinities may have inhabited warm water and the Atlantic fauna a temperate water. A similar suggestion with respect to climate was put forth by Serpagli (1973, 1974), who showed that the Lower Ordovician limestones of the Precordillera are in part bahamitic, indicating deposition in warm water. The middle Ordovician marine glacigene deposits in northernmost Argentina and Bolivia may be an indicator of temporary cool water in areas with an Atlantic graptolite fauna.

The position of the Russian platform and Scandinavia close to the equator in almost all recent reconstructions of Ordovician geography does not fit into this model at all. The Balto-Scandian region has an Atlantic graptolite fauna and its shelly fauna differs from that of other presumed warm-water faunas. Based on faunal (Troedsson, 1928; Spjeldnaes, 1961; Skevington, 1974) and lithological (Lindström, 1972; Jaanusson, 1973b) evidence, it has been suggested that the Balto-Scandian region was during at least most of Ordovician time within the temperate or unspecified cold-climate zone. If this was the case, the zone possibly embraced also southwestern China (and the Tarim platform?). Northern China, with a Pacific graptolite fauna, evaporites, extensive carbonate sequence, and shelly faunas showing some North American affinities, probably was within the zone of warm to tropical water.

BIOGEOGRAPHIC CHANGES LEADING TO THE COSMOPOLITAN SILURIAN FAUNA

The Ordovician biogeographic differentiation was greatest during the Arenigian-Llanvirnian and their equivalents. During the middle and Late Ordovician the provinciality decreased successively in the shelly faunas (Whittington, 1966; Whittington & Hughes, 1972) ultimately followed by a cosmopolitan fauna in the Early Silurian. In this process of successively decreasing provinciality the greatest single step was at the boundary between the Ordovician and Silurian (at the top of the Hirnantian).

Diversity of the Ordovician trilobite fauna of Mediterranean type decreased at about the base of the Hirnantian by extinction of many taxa (Cyclopygidae, Dionidae, Remopleurididae, Hammatocnemidae, Dindymeninae, Ectillaeninae, and others). A further wave of extinction at the top of the Hirnantian (Trinucleidae, Agnostida, Phillipsinellidae) virtually eliminated the Mediterranean fauna. In the region with the

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Ordovician Mediterranean fauna the Lower Silurian deposits consist almost exclusively of graptolitic shale that is practically devoid of shelly fossils. This makes one wonder whether or not elimination of habitats was a contributing factor in the extinction of the Mediterranean shelly fauna. In areas with Ordovician cold-water fauna no Llandoverian shelly fauna is known (except the *Clarkeia* fauna, the appearance of which is difficult to date, Cocks, 1972; Cocks & McKerrow, 1973). The rarity of preserved remains of a cold-water benthic fauna undoubtedly exaggerates the cosmopolitan nature of the known Early Silurian shelly fauna.

The North American Midcontinent-Tungusian faunas began to lose their biogeographic identity before the Hirnantian. In the equivalents to the Hirnantian the importance of some of its distinctive elements (e.g., *Anataphrus, "Brachyaspis"*) seems to have been reduced to the status of relicts. Large areas of epicontinental seas previously occupied by these faunas emerged and this may have contributed to extinction by elimination of habitats.

Extinction during the middle and late Ashgillian and their equivalents affected all groups of organisms and all faunas. Of some 38 trilobite families known in the Ashgillian, only 14 continued into the Silurian (and only one added). Of about 70 Upper Ordovician genera of tabulate and heliolitid corals about 50 became extinct before the Silurian (Kaljo & Klaamann, 1973). Extinction affected also brachiopods (Clitambonitacea and Porambonitacea, as well as many families), cephalopods (Endoceratoidea, with the possible exception of the enigmatic *Humeoceras*), stromatoporoids (Aulaceridae) and other groups. Thus, the physical event or combination of events that triggered the extinction had a profound effect. The change to the cosmopolitan Silurian shelly fauna was associated with a considerable loss of overall taxonomic diversity.

The Hirnantian and Llandoverian trilobite faunas have a low taxonomic diversity and the center of origin of the Silurian fauna is not obvious. The Silurian brachiopod fauna is largely based on the peripheral Ordovician faunas of Hiberno-Salairian type (see p. *A*157) where many of the taxa that became worldwide in the Silurian have a wide distribution (e.g., Atrypidae, Dicoelosiidae, Pentameracea, Meristellidae, *Dolerorthis*). During the Hirnantian elements of this fauna invaded parts of the North American Midcontinent and Anticosti. The relation of these peripheral faunas to temperature or ecologic zonation is not clear. Balto-Scandia and possibly also the Kazakhstan-Tien Shan region may have occupied the temperate climatic zone. If this was the case, the cosmopolitan spread of many of its elements during the Silurian might indicate that the Silurian climate became more uniformly temperate. On the other hand, the Silurian conodont fauna developed mainly from the presumably tropical-subtropical North American Midcontinent fauna (Sweet & Bergström, 1974).

It has been suggested that the major event causing the faunal change from Ordovician to Silurian was the Late Ordovician glaciation (Sheehan, 1973; Berry & Boucot, 1973). It may have affected the faunas in two ways. Firstly, accumulation of precipitation in glaciers caused eustatic lowering of sea level and widespread regression of shelf seas resulting in elimination of habitats of shallow marine faunas. Secondly, the glaciation caused cooling of the oceans and extinction of stenothermal organisms; however, Pleistocene glaciations have not produced effects of a comparable magnitude on marine faunas, indicating that at the transition from Ordovician to Silurian other factors were involved. Another explanation of the change to a cosmopolitan fauna is that because of continental drift oceans between cratonic lithospheric plates decreased in width so much that they did not act any more as distributional barriers (Whittington & Hughes, 1972); however, in this case biogeographic changes are expected to have been more gradual than they appear to have been and also not so contemporaneously worldwide. It is probable that the faunal changes from Ordovician to Silurian were caused by a combined effect of several factors whereby the relative importance of individual factors is at present difficult to determine.

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REFERENCES

Abdullaev, R. N., 1972, *Trilobity verkhnego ordovika Bukantau:* in Novye dannye po faune paleozoya i mezozoya Uzbekistana, p. 103-126, pl. 44-49, Akad. Nauk Uzbek. SSR, Inst. Geol. Geofiz. (Tashkent). [*Upper Ordovician trilobites of Bukantau.*]

———, **& Khaletskaya, O. N.**, 1970, *Nizhniy paleozoy Chatkalskogo khrebta, trilobity i graptolity ordovika Pskemskogo khrebta:* Akad. Nauk Uzbek. SSR, Inst. Geol. Geofiz., 104 p., 8 pl. [*Lower Paleozoic of the Chatkal Range, Ordovician trilobites and graptolites of the Pskem Range.*]

Amsden, T. W., 1974, *Late Ordovician and Early Silurian articulate brachiopods from Oklahoma, southwestern Illinois, and eastern Missouri:* Oklahoma Geol. Survey, Bull. 119, 154 p., pl. 1-28.

Andreeva, O. N., 1972, *Brakhiopody kuraganskoy svity ordovika Yuzhnogo Urala:* Paleont. Zhurnal 1972, p. 45-56, pl. 7, 8. [*Brachiopods of the Ordovician Kuragan Formation in southern Urals.*]

Apollonov, M. K., 1974, *Ashgillskie trilobity Kazakhstana:* Akad. Nauk Kazakh. SSR, Inst. Geol. Nauk, 136 p., 21 pl. [*Ashgillian trilobites of Kazakhstan.*]——1975, *Ordovician trilobite assemblages of Kazakhstan:* Fossils and Strata, no. 4, p. 375-380.

Baldis, B. A., & Blasco, Graciela, 1975, *Primeros trilobites ashgillianos del Ordovicico Sudamericano:* Actas I Congr. Argent. Paleont. Bioestr., v. 1, p. 33-48.

Barnes, C. R., & Fåhraeus, L. E., 1975, *Provinces, communities, and the proposed nektobenthic habit of Ordovician conodontophorids:* Lethaia, v. 8, p. 133-149.

———, **Rexroad, C. B., & Miller, J. F.**, 1973, *Lower Paleozoic provincialism:* in Conodont paleozoology, F. H. T. Rhodes (ed.), Geol. Soc. America, Spec. Paper 141, p. 157-190.

Bates, D. E. B., 1968, *The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey:* Brit. Museum (Nat. History), Bull., Geol., v. 16, p. 127-199, pl. 1-14.

Bergström, S. M., 1971, *Conodont biostratigraphy of the Middle and Upper Ordovician of Europe and eastern North America:* in Symposium on conodont biostratigraphy, W. C. Sweet & S. M. Bergström (eds.), Geol. Soc. America, Mem. 127, p. 83-157.——1973, *Ordovician conodonts:* in Atlas of palaeobiogeography, Anthony Hallam (ed.), p. 47-58, Elsevier (Amsterdam).

———, **Epstein, Anita G., & Epstein, J. B.**, 1973, *Early Ordovician North Atlantic Province conodonts in eastern Pennsylvania:* U.S. Geol. Survey, Prof. Paper 800-D, p. D37-D44.

———, **Ethington, R. L., & Jaanusson, Valdar**, 1973, *On the stage subdivision of the North American lower Middle Ordovician: Age of strata at the top of Whiterock reference sequences in Nevada:* Geol. Soc. America, Abstracts with Programs, North-Central Section Ann. Mtg. 1973, p. 299.

———, **& Sweet, W. C.**, 1966, *Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana:* Bull. Am. Paleontology, v. 50, p. 271-441.

Berry, W. B. N., 1960, *Correlation of Ordovician graptolite-bearing sequences:* Internatl. Geol. Congress, 21st Sess., Proc. Sec. 7, p. 97-108 (Copenhagen).

———, **& Boucot, A. J.**, 1973, *Glacio-eustatic control of Late Ordovician-Early Silurian platform sedimentation and faunal changes:* Geol. Soc. America, Bull., v. 84, p. 275-284.

Beuf, Serge, Biju-Duval, Bernard, de Charpal, Olivier, Rognon, Pierre, Gariel, Olivier, & Bennacef, Abdelkrim, 1971, *Les grès du Paléozoique inférieur au Sahara (Sedimentation et discontinuités; évolution structurale d'un craton):* Inst. Français Pétrole, Publ. Coll. Sci. et Techn. Pétrole no. 18, iv + 464 p.

Bondarev, V. I., 1968, *Stratigrafiya i kharakternye brakhiopody ordovikskikh otlozheniy yuga Novoy Zemli, ostrova Vaygasch i severnogo Pay-Khoya:* Nauchno-Issledov. Inst. Geol. Arktiki, Trudy, v. 157, p. 3-144, pl. 1-13. [*Stratigraphy and characteristic brachiopods of the Ordovician deposits of southern Novaya Zemlya, the Island of Vaygach, and northern Pay-Khoy.*]

Bouček, Bedřich, 1972, *The palaeogeography of Lower Ordovician graptolite faunas: a possible evidence of continental drift:* Internatl. Geol. Congress, 24th Sess., Proc. Sec. 7, p. 266-272 (Montreal).

Briden, J. C., Morris, W. A., & Piper, J. D. A., 1973, *Palaeomagnetic studies in the British Caledonides—VI. Regional and global implications:* Geophys. Jour. Res., abstr. Soc. 34, p. 107-134.

Bulman, O. M. B., 1964, *Lower Palaeozoic plankton:* Geol. Soc. London, Quart. Jour., v. 120, p. 455-476.——1971, *Graptolite faunal distribution:* in Faunal provinces in space and time, F. A. Rawson, P. F. Middlemiss, & G. Newall (eds.), Geol. Jour., Spec. Issue 4, p. 47-60.

Burrett, Clive, 1973, *Ordovician biogeography and continental drift:* Palaeogeography, Palaeoclimatology, Palaeoecology, v. 13, p. 161-201.

Campbell, K. S. W., 1973, *A species of the trilobite Dalmanitina (Dalmanitina) from Australia:* Geol. Fören. Stockholm, Förhandl., v. 95, p. 69-77.

Chugaeva, M. N., 1968, *Biogeograficheskie oblasti kontsa rannego ordovika (Areniga) po trilobitam:* Internatl. Geol. Congress, 23rd Sess., Rept. Soviet Geologists, Probl. 9, p. 63-68 (Mos-

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cow). [*Biogeographical areas at the end of Early Ordovician (Arenig) on the basis of trilobites.*] (In Russian with English summary.)——1973, *Biogeografiya ḳontsa rannego ordoviḳa:* in Biostratigrafiya nizhney chasti ordovika severo-vostoka SSSR i biogeografiya kontsa rannego ordovika, Akad. Nauk Geol. Inst., Trudy, v. 213, p. 238-280. [*Biogeography of the uppermost Lower Ordovician,* in Biostratigraphy of the lower part of the Ordovician in the northeast of the USSR and biogeography of the uppermost Lower Ordovician.]

Cocks, L. R. M., 1972, *The origin of the Silurian Clarḳeia shelly fauna of South America, and its extension to West Africa:* Palaeontology, v. 15, p. 623-630.

———, **Brunton, C. H. C., Rowell, A. J., & Rust, I. C.,** 1970, *The first Lower Palaeozoic fauna proved from South Africa:* Geol. Soc. London, Quart. Jour., v. 125, p. 583-603.

———, **& McKerrow, W. S.,** 1973, *Brachiopod distributions and faunal provinces in the Silurian and Lower Devonian:* Spec. Papers in Palaeontology, no. 12, p. 291-304.

Cook, H. E., & Taylor, M. E., 1975, *Early Paleozoic continental margin sedimentation, trilobite biofacies, and the thermocline, western United States:* Geology, v. 3, p. 559-562.

Cooper, G. A., 1956, *Chazyan and related brachiopods:* Smithson. Misc. Coll., v. 127, pt. 1, p. 1-1024; pt. 2, p. 1025-1245, pl. 1-209.

Creath, W. G., & Shaw, A. B., 1966, *Paleontology of northwestern Vermont. XIII. Isochilina from the Ordovician Highgate Formation:* Jour. Paleontology, v. 40, p. 1312-1330, pl. 161-163.

Cuerda, A. J., 1973, *Resena del ordovicio Argentina:* Ameghiniana, v. 10, 272-312.

Dean, W. T., 1967, *The distribution of Ordovician shelly faunas in the Tethyan region:* in Aspects of Tethyan biogeography, C. G. Adams, & D. V. Ager (eds.), Systematics Assoc. Publ. 7, p. 11-44.

Druce, E. C., & Jones, P. J., 1971, *Cambro-Ordovician conodonts from the Burḳe River structural belt:* Australia Bur. Min. Resources, Bull. 110, 167 p., pl. 1-20.

Fortey, R. A., 1975, *Early Ordovician trilobite communities:* Fossils and Strata, no. 4, p. 339-360.

———, **& Bruton, D. L.,** 1973, *Cambrian-Ordovician rocḳs adjacent to Hinlopenstretet, North Ny Friesland, Spitsbergen:* Geol. Soc. America, Bull., v. 84, p. 2227-2242.

Harland, W. B., 1972, *The Ordovician ice age:* Geol. Mag., v. 109, p. 451-456.

———, **& Gayer, R. A.,** 1972, *The Arctic Caledonides and earlier oceans:* Geol. Mag., v. 109, p. 289-314.

Havliček, Vladimír, 1974, *Some problems of the Ordovician in the Mediterranean region:* Ustřed. Ustav. Geol., Věstnik, no. 49, p. 343-348.——1976, *Evolution of Ordovician brachiopod communities in the Mediterranean Province:* in The Ordovician System: Proceedings of a Palaeontological Association symposium, M. G. Bassett (ed.), p. 349-358, Palaeont. Assoc., Univ. Wales Press (Cardiff).

Hu Bing, Wang Jing-bin, Gao Zhen-jia, & Fang Xiao-di, 1965, [*Problems of the Paleozoics of Tarim platform*]*:* Ti Chih Hsüeh Pao (Acta Geol. Sinica), v. 45, p. 131-142. [In Chinese.]

Jaanusson, Valdar, 1960, *Graptoloids from the Ontiḳan and Viruan (Ordov.) limestones of Estonia and Sweden:* Geol. Inst. Univ. Uppsala, Bull., v. 37, p. 289-366.——1973a, *Ordovician articulate brachiopods:* in Atlas of Palaeobiogeography, A. Hallam (ed.), p. 19-25, Elsevier (Amsterdam).——1973b, *Aspects of carbonate sedimentation in the Ordovician of Baltoscandia:* Lethaia, v. 6, p. 11-34.——1976, *Faunal dynamics in the Middle Ordovician (Viruan) of Balto-Scandia:* in Ordovician System: Proceedings of a Palaeontological Association symposium, M. G. Bassett (ed.), p. 301-326, Palaeont. Assoc. (Cardiff).

Jen Chi-shun, 1964, [*Certain geotectonic formations occurring before the Devonian in southeastern China*]: Ti Chih Hsüeh Pao (Acta Geol. Sinica), v. 44, p. 418-431. [In Chinese.]

Jones, P. J., 1971, *Lower Ordovician conodonts from the Bonaparte Gulf Basin and the Daly River Basin, northwestern Australia:* Bur. Min. Resources Australia, Bull. 117, 80 p.

Kaljo, Dimitri, & Klaamann, Einar, 1973, *Ordovician and Silurian corals:* in Atlas of Palaeobiogeography, A. Hallam (ed.), p. 37-45, Elsevier (Amsterdam).

———, ———, **& Nestor, Heldur,** 1970, *Paleobiogeografichesḳiy obzor ordoviḳsḳiḳh i siluriysḳiḳh ḳorallov i stromatoporoidey:* in Distribution and sequence of Paleozoic corals of the USSR, Papers of II All-union Symposium on fossil corals of the USSR, v. 3, p. 6-15. [*Paleobiogeographic survey of Ordovician and Silurian corals and stromatoporoids.*]

Kielan, Zofia, 1959, *Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia:* Palaeont. Polonica, v. 11, p. 1-198, pl. 1-35.

Kobayashi, Teiichi, 1971, *The Eurasiatic faunal connection in the Ordovician Period:* Bur. Rech. Geol. Min., Mém., no. 73, p. 281-290.

Legrand, Philippe, 1974, *Essai sur la paléogéographie de l'Ordovicien au Sahara Algérien:* Compagnie Francaise des Pétroles, Notes & Mém. 11, p. 121-138, 8 pl.

Leleshus, V. L., 1970, *Paleozoogeografiya ordoviḳa, silura i rannego devona po tabulyatomorfnym ḳorallam i granitsy siluriysḳoy sistemy:* Akad. Nauk SSSR, Izvestiya, ser. geol., 1970, p. 184-192. [*Ordovician, Silurian, and Early Devonian paleozoogeography based on tabulatomorph cor-*

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als, and boundaries of the Silurian System.]

Lespérance, P. J., 1968, *Faunal affinities of the trilobite faunas, White Head Formation, Percé region, Quebec, Canada:* Internatl. Geol. Congress, 23rd Sess., Proc. Sec. 9, p. 145-159 (Prague).——1974, *The Hirnantian fauna of the Percé area (Quebec) and the Ordovician-Silurian boundary:* Am. Jour. Sci., v. 274, p. 10-30.

Levitskiy, E. S., 1963, *Trilobity srednego ordovika severo-zapada Gornogo Altaya i ikh stratigraficheskoe znachenie:* Avtoreferat dissertatsii, p. 1-23 (Moskva). [*Middle Ordovician trilobites of northwestern Gornyi Altay, and their stratigraphic significance.*]

Lindström, Maurits, 1972, *Ice-marked sand grains in the Lower Ordovician of Sweden:* Geologica et Palaeontologica, v. 6, p. 25-32.

Lu Yen-hao, 1975, *Ordovician trilobite faunas of central and southwestern China:* Chung-kuo ku shêng wu chih (Palaeontologia Sinica), no. 152, p. 1-463, 50 pl. [In Chinese and English.]

Lui Hung-yun, 1958, [*Paleogeographic map of China*]: Science Press (?Peking). [In Chinese.]

McLaughlin, R. E., 1973, *Observations on the biostratigraphy and stratigraphy of Knox County, Tennessee, and vicinity:* Tennessee Div. Geol., Bull. 70, p. 25-62.

McTavish, R. A., 1973, *Prioniodontacean conodonts from the Emanuel Formation (Lower Ordovician) of western Australia:* Geologica et Palaeontologica, v. 7, p. 27-58, 3 pl.

Miller, J. F., 1969, *Conodont fauna of the Notch Peak Limestone (Cambro-Ordovician), House Range, Utah:* Jour. Paleontology, v. 43, p. 413-439, pl. 63-66.——1970, *Conodont zonation of the uppermost Cambrian and lowest Ordovician:* Geol. Soc. America, Abstracts with Programs, Ann. Mtg. 1970, p. 624.

———, **Robison, R. A.**, & **Clark, D. L.**, 1974, *Correlation of Tremadocian conodont and trilobite faunas, Europe and North America:* Geol. Soc. America, Abstracts with Programs, Ann. Mtg. 1974, p. 1048-1049.

Mu, A. T., 1974, *Evolution, classification and distribution of Graptoloidea and graptodendroids:* Scientia Sinica, v. 17, p. 227-238.

Neuman, R. B., 1970, *Paleogeographic implications of Ordovician shelly fossils in the Magog belt of the northern Appalachian region:* in Studies of Appalachian geology; northern and maritime, E. A. Zen *et al.* (eds.), p. 35-48, Intersci. Publ. (New York).——1972, *Brachiopods of Early Ordovician volcanic islands:* Internatl. Geol. Congress, 24th Sess., Sec. 7, p. 297-302 (Montreal).

———, & **Bruton, D. L.**, 1974, *Early Middle Ordovician fossils from the Hølanda area, Trondheim region, Norway:* Norsk Geol. Tidsskr., v. 54, p. 69-115.

Nikiforova, O. I., & **Sapelnikov, V. P.**, 1973, *Nekotorye drevnie pentameridy Zeravshanskogo khrebta:* Akad. Nauk SSSR, Uralskiy Nauchnyy Tsentr, Trudy, Inst. Geol. Geokhim., v. 99, p. 64-82, pl. 1-6. [*Some ancient pentamerids from the Zeravshan Range.*]

Nikitin, I. F., 1972, *Ordovik Kazakhstana, I, Stratigrafiya:* Akad. Nauk Kazakh. SSR, Inst. Geol. Nauk, 242 p. (with English summary). [*The Ordovician of Kazakhstan, I. Stratigraphy.*]

Nikolaev, A. A., **Oradovskaya, M. M.**, **Preobrazhenskiy, B. V.**, **Obut, A. M.**, **Sobolevskaya, R. F.**, & **Kabankov, V. Ya.**, 1974, *Opornye razrezy paleozoya severo-vostoka SSSR:* Akad. Nauk SSSR, Dalnevostochnyy Nauchnyy Tsentr, 161 p., pl. 1-43 (Magadan). [*Key sections of the Upper Ordovician in the north-east of the USSR.*]

Oradovskaya, M. M., 1970, *Stratigrafiya ordovika i silura Chukotskogo poluostrova:* Akad. Nauk SSSR, Doklady, v. 191, p. 190-193. [*Ordovician and Silurian stratigraphy of the Chukot Peninsula.*]——1973, *Brakhiopody:* in Biostratigrafiya nizhney ordovika severo-vostoka SSSR, i biogeografiya kontsa rannego ordovika, Akad. Nauk SSSR, Trudy, Geol. Inst., v. 213, p. 141-209. [*Brachiopods, in Biostratigraphy of the lower part of the Ordovician in the northeast of the USSR and biogeography of the uppermost Early Ordovician.*]

Palmer, A. R., 1969, *Cambrian trilobite distributions in North America and their bearing on the Cambrian paleogeography of Newfoundland:* in North Atlantic geology and continental drift, G. M. Kay (ed.), Am. Assoc. Petrol. Geologists, Mem. 12, p. 139-144.——1972, *Problems of Cambrian biogeography:* Internatl. Geol. Congress, 24th Sess., Proc. Sec. 7, p. 310-315 (Montreal).——1973, *Cambrian trilobites:* in Atlas of palaeobiogeography, A. Hallam (ed.), p. 3-11, Elsevier (Amsterdam).——1974, *Search for the Cambrian world:* Am. Scientist, v. 62, p. 216-224.

Petrunina, Z. E., 1966, *Trilobity i biostratigrafiya tremadoka zapadnoy chasti Sayano-Altayskoy gornoy oblasti:* Avtoreferat dissertatsii, p. 1-30 (Alma-Ata). [*Tremadocian trilobites and biostratigraphy in the western part of the Sayan-Altai Mountain Region.*]

Riva, John, 1969, *Middle and Upper Ordovician graptolite faunas of St. Lawrence Lowlands of Quebec, and of Anticosti Island:* Am. Assoc. Petrol. Geologists, Mem. 12, p. 513-556.

Robison, R. A., & **Pantoja-Alor, Jeres**, 1968, *Tremadocian trilobites from the Nochixtlán region, Oaxaca, Mexico:* Jour. Paleontology, v. 42, p. 767-800.

Ross, R. J., Jr., 1975, *Early Paleozoic trilobites, sedimentary facies, lithospheric plates, and ocean currents:* Fossils and Strata, no. 4, p. 307-329. ——1976, *Ordovician sedimentation in the western United States:* in The Ordovician System: Proceedings of a Palaeontological Association

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symposium, M. G. Bassett (ed.), p. 73-105, Palaeont. Assoc. (Cardiff).

Rozman, K. S., 1968, *Yarusnoe raschlenenie verkhnego ordovika i biogeograficheskie osobennosti razvitia pozdneordovikskoy fauny:* Internatl. Geol. Congress, 23rd Sess., Repts. Soviet Geologists, Prob. 9, p. 95-103 (Moskva). (In Russian with English summary.) [*Stage subdivision of the Upper Ordovician and biogeographical peculiarities in the development of Late Ordovician fossils.*]——1970, *Biostratigrafiya i paleobiogeografiya verkhnego ordovika Severo-Vostoka SSSR:* in Biostratigrafiya verkhnego ordovika Severo-Vostoka SSSR, Kh. S. Rozman, V. A. Ivanova, I. N. Krasilova, & E. A. Modzalevskaya (eds.), Akad. Nauk SSSR, Trudy, Geol. Inst., v. 205, p. 212-270. [*Upper Ordovician biostratigraphy and paleobiogeography of the northeast USSR.*]

Sapelnikov, V. P., & **Rukavishnikova, T. B.**, 1975, *Verkhneordovikskie, siluriyskie i nizhnedevonskie pentameridy Kazakhstana:* Akad. Nauk SSSR, Uralskiy Nauchnyy Tsentr, 227 p., pl. 1-43. [*Upper Ordovician, Silurian and Lower Devonian pentamerids of Kazakhstan.*]

Savage, T. E., 1917, *Stratigraphy and paleontology of the Alexandrian Series in Illinois and Missouri:* Illinois Geol. Survey, Bull., v. 23, p. 67-160, pl. 3-9.

Seddon, George, & **Sweet, W. C.**, 1971, *An ecological model for conodonts:* Jour. Paleontology, v. 45, p. 869-880.

Serpagli, Enrico, 1973, *Carbonati di tipo bahamitico nell'Ordoviciano inferiore della Precordillera Argentina e relative osservazioni paleoclimatologiche:* Soc. Nat. Mat. Modena, Atti, v. 104, p. 239-245.——1974, *Lower Ordovician conodonts from Precordilleran Argentina (Province of San Juan):* Soc. Paleont. Italiana, Boll., v. 13, p. 17-98, pl. 7-31.

Sheehan, P. M., 1973, *Brachiopods from the Jerrestad Mudstone (Early Ashgillian, Ordovician) from a boring in southern Sweden:* Geologica et Palaeontologica, v. 7, p. 59-76.——1973, *The relation of Late Ordovician glaciation to the Ordovician-Silurian changeover in North American brachiopod faunas:* Lethaia, v. 6, p. 147-154.

Sheng, Shin-fu, 1964, *Chuan chyan woan au taur shyh san yeh chorng de yan jiow ping tao lun shang aw taur toong de shang shiah jieh shiann wenn ti:* Ku Sheng Wu Hsüeh Pao (Acta Palaeont. Sinica), v. 12, p. 537-552, pl. 1-4. [*Upper Ordovician trilobites of Szechuan-Kweichow with special discussion on the classification and boundaries of the Upper Ordovician.*] (In Chinese with English summary.)

Shergold, J. H., 1975, *Late Cambrian and Early Ordovician trilobites from the Burke River structural belt, western Queensland, Australia:* Bur. Min. Resources, Australia, Bull. 153, v. 1 (text), 251 p., v. 2 (plates), pl. 1-58.

Sidyarenko, A. I., & **Kanygin, A. V.**, 1965, *O stratigraficheskom polozhenii krivolutskogo yarusa Sibirskoy platformy:* Akad. Nauk SSSR, Doklady, v. 161, p. 187-189. [*On the stratigraphical position of the Krivoi Luk Stage of the Siberian platform.*]

Skevington, David, 1969, *Graptolite faunal provinces in the Ordovician of north-west Europe:* in North Atlantic geology and continental drift, G. M. Kay (ed.), Am. Assoc. Petrol. Geologists, Mem. 12, p. 557-562.——1973, *Ordovician graptolites:* in Atlas of palaeobiogeography, A. Hallam (ed.), p. 27-35, Elsevier (Amsterdam). ——1974, *Controls influencing the composition and distribution of Ordovician graptolite faunal provinces:* Spec. Papers in Palaeontology, no. 13, p. 59-73.

Smith, A. G., **Briden, J. C.**, & **Drewry, G. E.**, 1973, *Phanerozoic world maps:* Spec. Papers in Palaeontology, no. 12, p. 1-42.

Spjeldnaes, Nils, 1961, *Ordovician climatic zones:* Norsk Geol. Tidsskr. v. 41, p. 45-77.——1967, *The palaeogeography of the Tethyan region during the Ordovician:* in Aspects of Tethyan biogeography, C. G. Adams & D. V. Ager (eds.), Systematics Assoc. Publ. 7, p. 45-57.

Sweet, W. C., & **Bergström, S. M.**, 1974, *Provincialism exhibited by Ordovician conodont faunas:* in Paleogeographic provinces and provinciality, C. A. Ross (ed.), Soc. Econ. Paleontologists & Mineralogists, Spec. Publ. 21, p. 189-202.

———, **Ethington, R. L.**, & **Barnes, C. R.**, 1971, *North American Middle and Upper Ordovician conodont faunas:* in Symposium on conodont biostratigraphy, W. C. Sweet & S. M. Bergström (eds.), Geol. Soc. America, Mem. 127, p. 163-193.

———, **Turco, C. A.**, **Warner, Earl**, & **Wilkie, L. C.**, 1959, *The American Upper Ordovician standard. I. Eden conodonts from the Cincinnati region of Ohio and Kentucky:* Jour. Paleontology, v. 33, p. 1029-1068.

Tripp, R. P., 1962, *Trilobites from the "Confinis" Flags (Ordovician) of the Girvan district, Ayrshire:* Royal Soc. Edinburgh, Trans., v. 65, p. 1-40, pl. 1-4.——1965, *Trilobites from the Albany division (Ordovician) of the Girvan district, Ayrshire:* Palaeontology, v. 8, p. 577-603, pl. 80-83.——1967, *Trilobites from the Upper Stinchar Limestone (Ordovician) of the Girvan district, Ayrshire:* Royal Soc. Edinburgh, Trans., v. 67, p. 43-93, pl. 1-6.

Troedsson, G. T., 1928, *On the Middle and Upper Ordovician faunas of northern Greenland. II:* Meddel. Grønland, v. 72, p. 1-197, pl. 1-56.

Varganov, V. G., **Antsygin, N. Ya.**, **Nasedkina, V. A.**, **Shurygina, M. V.**, & **Militsina, V. S.**, 1973, *Stratigrafiya i fauna ordovika srednego Urala:* Ural. Terr. Geol. Uprav., 228 p., pl. 1-30, Nedra (Moskva). [*Ordovician stratigraphy and fauna in central Urals.*]

Viira, Viive, 1966, *Rasprostranenie konodontov v*

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nizhneordovikskikh otlozheniyakh razreza Suhkrumägi (g. Tallinn): Eesti Teaduste Akad. Toimetised, v. 15, Füüs.-Mat. Tehn. Seeria, no. 1, p. 150-155 (with English summary). [*Distribution of conodonts in the Lower Ordovician sequence of Suhkrumägi* (Tallinn district).]

Vinogradov, A. P. (ed.), 1968, *Atlas litologo-paleogeograficheskikh kart SSSR:* v. 1, 52 maps, Vses. Aerogeol. Trest Minist. Geologii SSSR (Moskva). [*Atlas of the lithological-paleogeographical maps of the USSR* (Precambrian, Cambrian, Ordovician and Silurian).]

Walter, O. T., 1926, *Trilobites of Iowa and some related Paleozoic forms:* Iowa Geol. Survey, v. 31, p. 169-388, pl. 10-27.

Webby, B. D., 1974, *Upper Ordovician trilobites from central New South Wales:* Palaeontology, v. 17, p. 203-252.

Whittington, H. B., 1963, *Middle Ordovician trilobites from Lower Head, western Newfoundland:* Harvard Univ., Museum Comp. Zoology, Bull., v. 129, p. 1-119.——1966, *Phylogeny and distribution of Ordovician trilobites:* Jour. Paleontology, v. 40, p. 696-737.——1973, *Ordovician trilobites:* in Atlas of palaeobiogeography, A. Hallam (ed.), p. 13-18, Elsevier (Amsterdam).

———, & **Hughes, C. P.**, 1972, *Ordovician geography and faunal provinces deduced from trilobite distribution:* Royal Soc. London, Philos. Trans., ser. B, v. 263, p. 235-278.——1973, *Ordovician trilobite distribution and geography:* Spec. Papers Palaeontology, no. 12, p. 235-240.——1974, *Geography and faunal provinces in the Tremadoc Epoch:* in Paleogeographic provinces and provinciality, C. A. Ross (ed.), Soc. Econ. Paleontologists & Mineralogists, Spec. Publ. 21, p. 203-218.

———, & **Williams, Alwyn**, 1955, *The fauna of the Derfel Limestone of the Arenig district, North Wales:* Royal Soc. London, Philos. Trans., ser. B, v. 238, p. 397-430.

Williams, Alwyn, 1962, *The Barr and Lower Ardmillan Series (Caradoc) of the Girvan district, southwest Ayrshire, with descriptions of the Brachiopoda:* Geol. Soc. London, Mem. 3, p. 1-267, pl. 1-25.——1969, *Ordovician faunal provinces with reference to brachiopod distribution:* in The Pre-Cambrian and Lower Palaeozoic rocks of Wales, A. Wood (ed.), p. 117-150, Univ. Wales Press (Cardiff).——1972, *An Ordovician Whiterock fauna in western Ireland:* Royal Irish Acad., Proc., v. 72, sec. B, p. 209-219, pl. 10,11.——1973, *Distribution of brachiopod assemblages in relation to Ordovician palaeogeography:* Spec. Papers in Palaeontology, no. 12, p. 241-269.

Wilson, J. T., 1966, *Did the Atlantic close and then re-open?:* Nature, London, v. 211, p. 676-681.

Wolfart, Reinhard, 1967, *Zur Entwicklung der paläozoischen Tethys in Vorderasien:* Erdöl u. Kohle, v. 20, p. 168-180.

Yochelson, E. L., 1963, *Gastropods from the Otta Conglomerate:* Norsk Geol. Tidsskr., v. 43, p. 75-81.

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SILURIAN

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GENERAL TRENDS

During Silurian time, a period with a duration of about 30 million years (Boucot, 1975), the stratigraphic, paleontologic, and paleogeographic entities developed during the Cambrian-Ordovician were further extended without major changes. The relative time duration of the following major subdivisions of the Silurian have been estimated from considerations of "average" evolutionary rates: early and middle Llandoverian 0.9, late Llandoverian 1.0, Wenlockian 0.9, Ludlovian 1.0, and Pridolian 0.5 (Boucot, 1975).

The Silurian was a time of little or no orogeny, except for the later phases of Taconic age orogenies that may have persisted in some areas from the Late Ordovician into the Early Silurian; however, on a worldwide basis the areas affected by Taconic orogeny appear to be very restricted.

Major regression accompanying the continental glaciation affecting much of Africa and South America during the Ashgillian and possibly parts of the earlier Llandoverian occurred in the earlier part of the Silurian. Major transgression on a worldwide scale occurred later in the period (see Boucot, 1975, and references therein for details); however, regression occurred in areas subject to isostatic rebound, particularly in Africa.

Volcanism of Silurian age was very limited in distribution, only portions of a few geosynclines exhibiting any significant developments.

The climate of the Silurian is poorly known; however, available evidence (see Boucot, 1975, for summary) indicates that the North Silurian realm (North America, Europe except for part of the Mediterranean region, Asia, Australia, and northern and westermost South America) was the site of a "warm" climate contrasting markedly with a "cold" climate present in the Malvinokaffric realm (Africa, Mediterranean Europe, southern two-thirds of South America).

Reefs composed of calcareous algae, stromatoporoids, tabulate corals, and other taxa were prominent in the later Silurian, but virtually absent during the Llandoverian and early Wenlockian (the bulk of the Ordovician reef biota disappeared during the Ashgillian extinction event that coincided with major continental regression and glaciation in parts of Africa and South America). The Late Silurian reefs reached a maximum during the late Wenlockian-Ludlovian and then appear to have declined in importance during the Pridolian. Limestone and secondary dolomite are abundant in the North Silurian realm, but are essentially absent in the Malvinokaffric realm.

Marine evaporites are unknown in the Lower Silurian, possibly as a result of a pluvial regime in the North Silurian realm that corresponded with a glacial or very cold regime in the Malvinokaffric realm, followed by the deposition of widespread evaporites on the North American, Siberian, Australian platforms, and possibly on the Russian platform during the Late Silurian.

Red beds, including material probably weathered out of warm, humid land areas, are characteristic of the North Silurian realm but absent in the Malvinokaffric realm.

Taxonomic diversity in level-bottom communities is very low in the Malvinokaffric realm as contrasted with the North Silurian realm. Overall taxonomic diversity is far higher at species through superfamily levels in the North Silurian realm as compared with the Malvinokaffric realm, although the Late Silurian presence of reef communities in the North Silurian realm serves to exaggerate this effect (Boucot, 1975).

Biogeography of the marine shelf and platform biota of the Silurian is characterized by a southern Malvinokaffric realm and a northern North Silurian realm (Fig. 1). The North Silurian realm during the Late Silurian may be divided into the North Atlantic, Uralian-Cordilleran, and Mongolo-Okhotsk regions, followed by the appearance during the Pridolian of faunas presaging those of the Devonian in the Eastern Americas realm and Rhenish-Bohemian region of the Old World realm (see Boucot, 1975, for extensive treatment).

The initial Silurian faunas of the lower Llandoverian are essentially relict continu-

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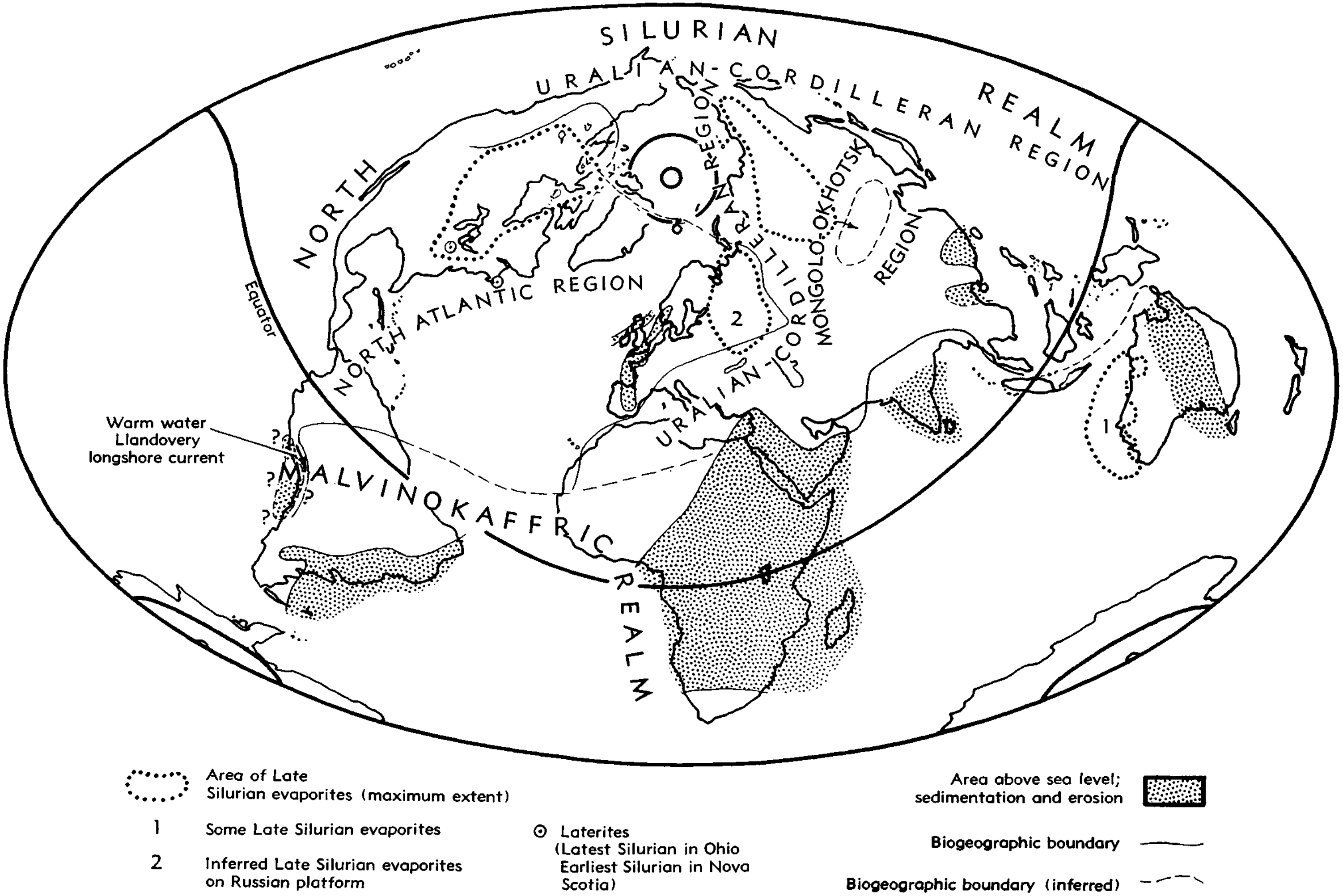

Fig. 1. Silurian biogeographic units and shorelines (modified from Boucot, 1975).

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ations of the Ashgillian Old World realm faunas (those of the North American realm became extinct by the end of the Ashgillian). Near the beginning of the late Llandoverian new taxa, some at the superfamily level, migrated from southeastern Kazakhstan and replaced many preexisting Ordovician types (Boucot, 1975). A marked enrichment of the Silurian marine fauna during the later Wenlockian was coincident with rapid spread and diversification of reef biotas. At the end of the Ludlovian, marked extinction coincided with the diminution of the reef environment.

The fossil record provides no positive evidence for the existence of either plants or animals on the land or in freshwater during the Silurian, despite an abundance of such evidence for the earliest Devonian. Cutinized trilete spores, spore tetrads, cuticle-like and tracheid-like microfossils are abundant in nearshore facies of the entire Silurian (see work of Gray cited in Boucot, 1975), but it is uncertain whether or not these materials of land-plant types represent plants deposited in the nearshore region after transportation from the land, or whether they represent materials of land-plant type that first developed in nearshore marine and brackish regions.

Silurian graptolites, acritarchs, chitinozoans, and possibly conodonts were depth stratified (see Boucot, 1975, for discussion). The benthos of the shelves and platforms was organized into a large number of communities belonging to level-bottom and reef, as well as rocky bottom associations (see Boucot, 1975, for an analysis of the changing communities in the level-bottom environment). In general, the intertidal benthic communities have lower diversity than do subtidal communities. Also, a general trend toward smaller shell size from the intertidal to the shelf-margin region is evident in the Silurian (see Boucot, 1975, for discussion). The Silurian marine benthos is highly correlated with bottom-sediment type; taxa of rough-water type commonly occur with sand- and granule-size materials, whereas taxa of quiet-water type occur with clay- and silt-size sediment. The photic zone biota differs significantly from that of the subphotic (Boucot, 1975).

Much is known about marine filter feeders, suspension feeders, and deposit feeders of the Silurian, but little is known about the carnivores of higher trophic levels and parasites.

We have no solid information about the nature, or even existence, of oceanic benthos, plankton, or nekton during the Silurian, although good evidence is known for a rich neritic planktonic fauna as well as rich shelf-depth benthos. It is logical to deduce that an oceanic fauna was present, however, as there is no rational mechanism for preventing nutrients from having been distributed into the oceanic environment nor for the development of a fauna capable of utilizing those nutrients.

The Silurian benthic faunas are widespread over the vast continental platforms, as are similar Cambrian and Ordovician faunas, in contrast to those of the later Phanerozoic during breakup of the vast pre-Devonian platforms, which were inherited from the worldwide peneplanation of the late Precambrian.

Rates of evolution during the Silurian are easily interpreted in terms of worldwide size of interbreeding populations (see Boucot, 1975, for discussion). Extraterrestrial or cataclysmic events are unnecessary to explain the known facts of the fossil record. Major extinction events were absent during the Silurian, although the rate of terminal extinction did fluctuate for one reason or another, as did the rates of phyletic and cladogenetic evolution.

CORRELATION AND BIOSTRATIGRAPHY

Worldwide correlation of Silurian marine beds is presently based almost entirely on brachiopods, graptolites, and conodonts (Fig. 2). These are supplemented locally by chitinozoans, tetracorals, tabulate corals, stromatoporoids, and ostracodes. Little use is currently made of acritarchs, foraminifers, radiolarians, sponges, bryozoans, bivalves, gastropods, nautiloids, trilobites, echinoderms, vertebrates, cutinized spores of land-plant type, as well as many additional groups, although many of them have the

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STANDARD SERIES		CZECHO-SLOVAKIA STANDARD	Graptolite Zones of the British Isles (Elles & Wood, 1901-1918) Modified by Berry		German Sequence (after Jaeger) Thuringia, Saxony, North Bavaria	German Sequence (after Jaeger) Graptolite Zones	Graptolite Zones of the Cape Phillips Formation Bothurst Island Modified from Thorsteinsson (1958)	Conodont Zones Modified from Walliser (1962 & 1964)
PRIDOLIAN (=SKALA) (Post-Ludlow pre-Gedinnian)	eβ2	PRIDOLI (SHELLY AND GRAPTOLITIC)			Upper Graptolitic Slates Ocherous Limestone	*M. transgrediens*	 *Monograptus n sp. T* *Monograptus n sp. P* *Monograptus ultimus*	Zone VII *eosteinhornensis*
LUDLOVIAN	eβ1	KOPANINA (SHELLY AND GRAPTOLITIC)	* 36	*Monograptus bohemicus* group	Lower Graptolite Slates	*M dubius thuringicus*	*Monograptus tumescens minor*	Zone VI *latialatus* and *crispus*
			35	*Monograptus leintwardinensis*		*M fritschi linearis* *M leintwardinensis*		Zone V *siluricus*
			34	*Monograptus scanicus*		*M chimaera* & *M scanicus*	*Monograptus n sp. O* *Monograptus n sp. N.*	*crassa* and *ploeckensis*
			33	*Monograptus nilssoni*		*M nilssoni* & *M colonus*	*Monograptus bohemicus* *Monograptus nilssoni*	*sagitta*
WENLOCKIAN	ea	LITEN (Shelly & Graptolitic)	32	*Monograptus ludensis*		*M ludensis* *M deubeli*	*Monograptus testis*	
		LITEN (GRAPTOLITIC ONLY)	31	*Cyrtograptus lundgreni*		*Monog dubius/G nassa* *M testis*	*Cyrtograptus lundgreni*	
			30	*Cyrtograptus ellesi* (=*C rigidus* E&W)		*Cyrtogr radians*	*Cyrtograptus perneri* *Cyrtograptus n sp G* *Cyrtograptus n sp F* *Cyrtograptus n sp C* *Cyrtograptus rigidus*	Zone IV *patula*
			29	*Cyrtograptus linnarssoni*		*Monograptus flexilis*		
			28	*Cyrtograptus rigidus* (=*C. symmetricus*-E&W)				
			27	*Monograptus riccartonensis*		*Cyrtograptus murchisoni*	*Monograptus riccartonensis*	
			26	*Cyrtograptus murchisoni*			*Cyrtograptus murchisoni* *Stomatograptus grandis*	
LLANDOVERIAN C UPPER			25	*Monograptus crenulatus*		(*Monog spiralis*) *Monograptus crenulatus*	*Monograptus spiralis*	Zone III *Amorphognathoides*
			24	*Monograptus griestoniensis*		*Monograptus griestoniensis*		
			23	*Monograptus crispus*		*Monograptus crispus*		Zone II *celloni*
			22	*Monograptus turriculatus*		*Monograptus turriculatus*	*Monograptus turriculatus*	
			21	*Monograptus sedgwicki*		*Monograptus sedgwicki* (*Cephalograptus cometa*)		
B MIDDLE			20	*Monograptus convolutus*		*Monograptus convolutus*	*Monograptus millepeda*	Zone I *Icriodina* bearing
A LOWER			19	*Monograptus gregarius*		*Monograptus gregarius*		
			18	*Monograptus cyphus*		*Monograptus cyphus*	*Monograptus cyphus*	
			17	*Orthograptus vesiculosus*		*Orthograptus vesiculosus*		
			16	*Akidograptus acuminatus*		*Akidograptus acuminatus*		pre-*Icriodina*

FIG. 2. Zonal schemes for Silurian graptolites and conodonts (modified from Berry & Boucot, 1970, pl. 2).

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potential for making important contributions.

Enough work has been done in the Silurian to make it clear that the precision of correlation is, of course, controlled by rates of evolution. *But,* rates of evolution vary from one biologic group to another. Also, biologic groups are not evenly distributed, either locally or worldwide. Thus, we find that the correlation of certain evolving community groups containing taxa characterized by rapid phyletic evolution or rapid cladogenetic evolution (controlled in both cases by sizes of interbreeding populations as the first order control) is excellent, whereas that in slowly evolving groups is correspondingly poor (BOUCOT, 1975). For example, worldwide correlation in the confines of the evolving *Eocoelia* community (*sensu* BOUCOT, 1975, not ZIEGLER, 1965) is very precise as compared with the *Pentamerus* community (*sensu* BOUCOT, 1975, not ZIEGLER, 1965). In the same way correlation employing planktonic communities is most precise for deeper water aggregations, as they sum up the evolution of everything from the surface down, as opposed to shallow-water communities. In other words, a separate correlation scheme must be devised for each evolving community and also for each evolving biogeographic unit that includes its own distinctive communities, with a firm understanding that each of these entities will have its own level of correlation precision; this is the kernel of ecostratigraphic correlation precision.

At the present time, biostratigraphic subdivision of the Silurian is based upon the modified ELLES and WOOD graptolite zones as used by BERRY for those regions yielding graptolites in reasonable abundance (in BERRY & BOUCOT, 1970; BERRY & BOUCOT, eds., 1974; see also BULMAN, 1970). The widespread Silurian shelly faunas commonly lack graptolites in sufficient numbers to make them useful for zonal purposes. In shelly beds recourse at the present time is had to brachiopods as discussed in BERRY and BOUCOT (1970). For the Llandoverian and Wenlockian, the latter only in North America above the lower Wenlockian, the various stricklandiid lineages are employed (see BERRY & BOUCOT, 1970). The stricklandiids are supplemented in the upper Llandoverian-lower Wenlockian by species of *Eocoelia.* Brachiopods useful for the bulk of the Upper Silurian are at present used on a first or last appearance basis as we currently do not have enough information about their evolution. Corals and stromatoporoids are of some use for zonal purposes, although the extensive potential of tabulate corals, stromatoporoids and pelmatozoan columnals has not as yet been taken advantage of outside the Soviet Union. Conodonts have recently become of great use in zoning the Silurian in the shelly carbonate lithofacies. Other groups of marine organisms, including the various arthropods (except for the ostracodes that are of considerable local value in a few regions), and the molluscan classes, are presently of little value for biostratigraphic work within the Silurian, a situation that undoubtedly reflects lack of work upon them rather than any intrinsic biologic characteristic. Chitinozoa are presently beginning to be of value for interregional correlation. The bulk of bivalve taxa appears to have been so environmentally restricted to very shallow waters that it is doubtful if they will ever loom very large for purposes of zonation and correlation within the Silurian.

DISTRIBUTION OF SILURIAN STRATA

Beginning in 1960, W. B. N. BERRY and I made an intensive effort to compile the available data concerning Silurian correlation, paleogeography, and lithofacies on maps at the scale of 1:5,000,000. In this work we have received the aid and encouragement of some hundreds of interested geologists and paleontologists from all over the world. The work is far enough advanced now to enable certain generalizations to be made (see Fig. 1).

1) During most of Silurian time the present-day continental areas of the Northern Hemisphere were subject to relatively shallow-water marine sedimentation. Known Silurian land areas were relatively

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minor as contrasted with the vast reaches subjected to marine sedimentation. These land areas included the "Appalachia" of eastern North America; a relatively small island or islands involving portions of southeastern Britain, western Scandinavia, Brittany, and adjacent portions of northwestern Spain; plus a portion of the Siberian platform during post-Wenlockian time; much of the Angaran shield; Africa southeast of the central Sahara, as well as much of Arabia and adjacent Egypt.

2) On the contrary, much of the present-day Southern Hemisphere continental area may have been above sea level including the bulk of Africa, Australia west of the Tasman geosynclinal region (except for the western and northwestern fringe), Antarctica, and eastern South America including the Falkland Islands.

3) The area occupied by Silurian geosynclines is relatively minor (see Berry & Boucot, 1967) as contrasted with the broad platform expanses. The stratified geosynclinal rocks of the Silurian are predominantly of terrigenous, nonvolcanic nature except for the Ural-Kazakhstan geosyncline, which includes a very large proportion of dark-colored volcanic and volcanogenic rocks.

4) Silurian platform rocks may be divided into Platform Carbonates (including a dolomitic suite and a limestone suite) and Platform Mudstones (Berry & Boucot, 1967, 1970).

5) The present-day continental distribution of Silurian strata indicates that during the Silurian significant areas of land and platform, which were subject to shallow-water marine sedimentation, extended out beyond the present-day continental strandlines. Our knowledge of the distribution of Silurian shallow-water animal communities upon the present-day continents helps to reinforce the conclusions based upon lithofacies distributions.

6) All of this information indicates that the present-day Northern Hemisphere continental areas were regions upon which marine faunas faced few obstacles to distribution insofar as land is concerned in breaking up current or temperature patterns. Boucot (1974) discussed most of the possible Silurian continental relations.

NORTH AMERICA

North America during the Silurian was characterized by the presence of a vast continental platform, the continuation of that present during the Cambrian-Ordovician, extending from central Nevada and eastern British Columbia to Anticosti Island and Davis Strait in the east, and from El Paso, Texas, north to Cornwallis Island. This vast platform is covered with a veneer of marine strata consisting chiefly of limestone and dolomite, including two restricted areas (Michigan basin and Hudson Bay basin) containing Upper Silurian evaporitic suite rocks. It is doubtful if any extensive land areas were situated upon this platform.

Geosynclinal belts are located around the periphery of the North American platform. The Appalachian geosyncline on the southeast was characterized by a linear land mass twice the length of Cuba separating it from the platform. This land mass, the Appalachia of the literature, steadily diminished in size throughout the period until it was completely, or almost totally, submerged by the end of the period. Within the Appalachian geosyncline a complex Silurian paleogeography changed continually throughout the period (see Berry & Boucot, 1970). A narrow coastal volcanic belt was present from southeastern New Brunswick southwest to the Boston region.

The Ouachita geosyncline to the south is very poorly known, and extends from the subsurface of the Mississippi embayment west-southwest into at least central Chihuahua. Insofar as we have knowledge of the sedimentary rocks, it contains pelitic and arenaceous Silurian strata.

The Cordilleran geosyncline on the west is poorly known as contrasted with the Appalachian, but several linear lithofacies belts can be recognized (Berry & Boucot, 1970). The presence in western North America of extensive transverse faulting of San Andreas type makes the restoration of the original paleogeography of the Cordilleran geosyncline away from the platform margin very difficult. In any case, a variety of rock types is present.

The Franklinian geosyncline to the north can be subdivided into several belts (Berry & Boucot, 1970). The Cape Phillips belt

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next to the platform margin is relatively similar to the Western Assemblage belt in the same position in the Cordilleran geosyncline.

Off most of East Greenland we lack evidence about Silurian rocks. It is remarkable that during the Silurian the margins of the North American platform remained relatively fixed.

EUROPE

The Silurian of Europe consists of the western, Eurafrican portion of the vast Old World platform, which covers most of Eurafrica and Asia, including the Caledonian geosyncline to the northwest, and the Novaya Zemlya-Ural-southeast Kazakhstan geosyncline to the east, which terminated against the land mass of the Angaran shield in the south.

The Eurafrican portion of the Old World platform may be divided into an eastern Dolomite and Limestone region (the so-called Russian platform) that continues to the southeast into southwestern Asia; a northern and central Platform Mudstone region that extends from Sweden in the north, southward into the central Sahara, as well as from Morocco in the west to Jordan in the east; and a central and southern nonmarine region that extends from the central Sahara to Capetown, and includes much of Arabia (BERRY & BOUCOT, 1972, 1973). The presence of a single shallow-water *Heterorthella* community occurrence in the Capetown region serves to substantiate the African picture. The Eurafrican portion of the Old World platform has commonly in the past had those portions occurring on the sites of younger geosynclinal areas (e.g., the Pyrenees, Alps, Hercynian chains) assigned a geosynclinal character themselves, but no significant difference in lithologic character, thickness, or fauna between these rocks and the Platform Mudstone appears to exist on either side in tectonically nongeosynclinal areas (for example, the Barrandian basin, the Carnic Alps, the Polish subsurface, and Scania as contrasted to the previously cited locales).

The extant portions of the Caledonian geosyncline contain a variety of clastic strata, together with rare, localized volcanics. This geosyncline is relatively narrow. It is bounded to the northwest in Britain by an extensive land area (BERRY & BOUCOT, 1974), and to the southeast by another land area. This southeastern British land area separated the Platform Mudstone to the east from the geosyncline proper. This southeastern land area can be linked with similar areas in western France, northern Spain, and southwestern Norway to make a relatively linear island or belt of islands.

The Uralian geosyncline (BOUCOT, 1969) is characterized by a tremendous accumulation of greenstone derived from basic volcanics, and bounded to the west and east by banded argillites that further grade laterally into platform carbonate rocks. The width of the Uralian geosyncline diminished by about 50 percent near the end of the Wenlockian.

During the early and middle Llandoverian much of the Russian platform was probably above sea level; late Llandoverian time saw extensive submergence; and Pridolian time, at least in the north and northwest, saw the initiation again of nonmarine conditions.

AFRICA

As noted earlier, the African portion of the Old World platform can be subdivided into a southern nonmarine region extending north into the central Sahara, and a northern half of platform mudstone extending from the central Sahara into the Mediterranean region. African Silurian stratigraphy appears to be very monotonous (BERRY & BOUCOT, 1973).

ASIA

The Silurian of Asia is less well known than that of either North America or Eurafrica. The Asian Silurian can be divided, for convenience, into a northern, Siberian platform separated by the Angaran shield land area (also of platform nature) from the southern Chinese-Southeast Asian platform, which grades farther west through the Himalayan region to join the Eurafrican portion of the Old World platform.

The Siberian platform is characterized by a thin veneer of platform carbonates of Llandoverian-Wenlockian age, overlain by a red-bed and evaporite sequence of later

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Silurian age. The southern margin of the Siberian platform (interpreted by Berry & Boucot, 1967, as extending from the Yenissei River east into the Chegitun region of Chukotka, i.e., including the Verkhoyansk Range, Kolyma, and the Chegitun region) onlapped the northern margins of the Angaran shield during the early half of the Silurian and offlapped it during the latter half.

The Angaran shield area is characterized by fringing nonmarine deposits extending from southeastern Kazakhstan easterly through the southern margins of the Siberian platform into the Amur River region. To the south, the Angaran shield is poorly known from a Silurian point of view, but can be inferred to have shown an offlap relationship relative to China from the beginning to the end of the period. The western margins of the land area are situated in the southeastern Kazakhstan region.

The Chinese-Southeast Asian platform was characterized by extensive platform mudstone development during the early half of the period, and was succeeded by clastic shallow-water and limestone strata during the late half. Small land areas were present in southeastern China and Yunnan during the period. From the Shan States south through the Isthmus of Kra as far as Kuala Lumpur there is a western gradation in platform carbonate rocks of Silurian age (Berry & Boucot, 1972).

Geosynclinal rocks may be present in the eastern portions of the Japanese Islands, but are absent elsewhere except along the geosynclinal boundary with the Russian platform from southeast Kazakhstan to Novaya Zemlya.

AUSTRALIA, NEW ZEALAND, OCEANIA, INDONESIA, AND THE PHILIPPINES

The Silurian of the Tasman geosyncline extends north from Tasmania through Victoria, New South Wales, and Queensland, and may be inferred to swing westerly through the mountainous spine of New Guinea into the Vogelkop region. A variety of geosynclinal rocks are present, but are not too well studied on a regional scale. The mainland of Australia is devoid of marine Silurian rocks west of the Tasman geosyncline, although relatively unfossiliferous nonmarine strata may be present. A borehole on Australia's westernmost island, Dirk Hartog, penetrated Silurian fossiliferous carbonate rocks unrelated to those elsewhere (Talent, Berry, & Boucot, 1975).

Northwestern South Island, New Zealand, contains Silurian clastic rocks in sequence with other geosynclinal early Paleozoic strata; whether or not these rocks are part of the Tasman geosyncline remains to be determined.

Silurian rocks have not been recognized in Oceania, Indonesia, or the Philippines, although their absence may be ascribed to lack of adequate field work rather than other causes.

CENTRAL AND SOUTH AMERICA

The Silurian of South America consists of platform mudstone to the west and north, and is inferred to grade easterly into nonmarine platform beds. Fossiliferous Silurian rocks are presently known from the Merida Andes of Venezuela, the Lake Titicaca region of Peru, much of Bolivia, from northern Argentina south to about Latitude 40, in Paraguay, and in the Amazon and Parnaiba-Maranhao basins of central and eastern Brazil. It is of interest that the Parana basin of southern Brazil and adjacent Uruguay has not yielded Silurian fossils nor have the Paleozoic strata of the Falkland Islands; these two regions may have been nonmarine during the Silurian. Marine Silurian rocks have not been found along the little known coast of southern Chile, but are predicted to occur there. Berry and Boucot (1972), have further summarized the Silurian of South America.

Silurian strata have not been recognized in Central America.

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SILURIAN PALEOECOLOGY

Silurian marine paleoecology, both benthic and planktonic, has been recently compiled and reviewed (Boucot, 1975). A variety of shelly benthic communities may be encountered on various transects from the shoreline to the continental margin. The precise communities encountered depend on local conditions determined by such factors as turbulent- or quiet-water conditions, hypersaline or normal salinity, or brackish water, light penetration (as deduced from the presence of organisms dependent on light such as calcareous algae), oxygen tenor as it affects either infaunal or epifaunal organisms, and others. The number of such communities encountered on a particular transect depends in part on the uniformity or nonuniformity of the environmental conditions encountered. This refers to level-bottom communities dominated in large part by brachiopods. Additional are level-bottom communities dominated by organisms such as stromatoporoids and tabulate corals. The complex of reef communities is important in the Upper Silurian. Silurian reefs are dominated by calcareous algae, stromatoporoids, and tabulate corals, but include a variety of communities dominated by both attached and vagrant organisms occupying a great variety of niches. Planktonic communities, including such organisms as graptolites and conodonts, and possibly acritarchs, are in large part depth stratified. Global temperature and other biogeographic barriers resulted in a variety of communities developing in isolation from each other although reflecting similar physical conditions in part. Communities of the Malvinokaffric realm probably existed in a relatively low-temperature regime characterized by low taxonomic diversity for the level-bottom benthic organisms. The communities concluded to represent the intertidal region (Benthic Assemblages 1 and 2 of Boucot, 1975) are characteristically of low diversity, whereas the photic-zone communities (Benthic Assemblage 3) range from high to low taxonomic diversity, depending on the restrictiveness of the environment, and the subphotic to continental-margin communities may also be either low or high in taxonomic diversity. Beyond the position of the continental margin (Benthic Assemblages 5 and 6) there is little evidence for the presence of shelly organisms, although trace fossils are present. Trace fossils occur from the intertidal Benthic Assemblage 1 position seaward to well beyond Benthic Assemblage 6 in a taxonomically systematic manner. Among closely related taxa, shells in the intertidal zone tend to be significantly larger than those of the subtidal, and in general, shells decrease in size from the shallow-intertidal to the shelf-margin region.

Little is known of trophic relations in the Silurian owing, naturally, to our ignorance of much of the fauna and flora. It is uncertain as to what organisms played the role of phytoplankton, although the acritarchs may possibly have fulfilled this role. The bulk of the benthic marine invertebrates were low-level filter and suspension feeders as well as deposit feeders. We know little about the various higher trophic levels, although it is reasonable to infer that there were a variety of carnivores including such animals as eurypterids and nautiloid cephalopods.

The shelly biomass decreased significantly from the intertidal and shallow-subtidal region through the shelf-margin region where it finally failed.

SILURIAN FLORA AND FAUNA

It is presently uncertain whether there was a nonmarine flora and fauna during the Silurian. By contrast, the marine fauna of the Silurian is rich, and has been subjected to intensive study since interest in fossils first arose over two hundred years ago. In general, Silurian invertebrates form a relatively perfect continuum with those of the Ordovician and the Devonian with no major breaks of the type encountered adjacent to the Permian-Triassic boundary. This situation manifests itself by the difficulty that specialists have in assigning many boundary faunas to the Silurian or

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adjacent systems. The only break of any consequence, and this is relatively minor when compared with some other parts of the Phanerozoic, is that between the middle and upper Llandoverian. A number of new families first appear in the interval C_1-C_3 of JONES (1925) in the upper Llandoverian. The geologically almost instantaneous appearance of these families is perplexing, but at least in the case of the brachiopods (which see), those of southeastern Kazakhstan provide a satisfactory pre-late Llandoverian source. The Devonian boundary is recognized by the appearance of taxa belonging to several families previously unrecognized in the record insofar as brachiopods are concerned, but most groups, including the brachiopods, manifest a relatively continuous record across this boundary. The early and middle Llandoverian faunas have, as would be expected, a very late Ordovician aspect (they are essentially relict holdovers). To a lesser extent, those of the Pridolian begin to show a Devonian aspect.

Biogeographically the marine fauna of the Silurian is relatively cosmopolitan, especially as contrasted with the immediately preceding and succeeding faunas, which are highly provincial. The bulk of the widespread Silurian invertebrates are concluded to have had their origins in the northwestern part of the Old World during the Late Ordovician (see section on brachiopods), although some taxa belong to widespread Late Ordovician groups. As detailed in the section on the brachiopods, the only regions of strong Silurian provincialism are a restricted area in central Asia and another which includes southern South America and central and southern Africa. During the late half of the Silurian (Wenlockian through Pridolian) a degree of provincialism developed which heralded the high endemism of the succeeding Early Devonian.

When studied on a worldwide basis, the strongly developed faunal differentiation characterizing the Silurian can best be ascribed to the effects of environment. Many characteristic associations of Silurian invertebrate taxa have such an irregular, disjunct worldwide distribution, related in part, however, to geographic factors such as proximity to ancient shorelines or to reef masses, that an environmental control appears to be the only logical conclusion at the present time.

CHITINOZOANS AND ACRITARCHS

Chitinozoa have been little studied except in Europe and North Africa, and minor work has been done in the New World, Asia, and Australia. It is obvious that their distribution will be found to be worldwide, but at present too little information is available with which to make biogeographic conclusions although they are beginning to be of great value. Silurian zonation based on information from acritarchs is at present very crude as contrasted with that derived from brachiopods, ostracodes, graptolites, and conodonts.

ARENACEOUS FORAMINIFERS

Arenaceous foraminifers have been recovered from acid residues in many regions of the world, but knowledge concerning their detailed stratigraphic and geographic distribution is still too fragmentary to form the basis for conclusions of worldwide utility.

PORIFERA

Porifera are widely distributed in marine strata of Silurian age, but are too seldom recognized, collected, and studied to be of much stratigraphic, ecologic, or biogeographic value at the present time.

COELENTERATES

Tetracorals, tabulate corals, and stromatoporoids are among the most abundant fossils in the Silurian fauna (jellyfish are so rarely preserved as to be little more than curiosities). The stromatoporoids appear to be one of the major, if not the major, agents in the formation of Silurian bioherms and biostromes. Algae have not been considered extensively in this facies. Isolated occurrences of stromatoporoids in shallow-water environments are not uncommon.

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Stromatoporoidal masses are abundant in platform carbonate environments, and also much of the limestone (admittedly small in volume) found in the geosynclinal terrigenous and volcanic terrains is rich in stromatoporoids. The platform mudstones do not yield a stromatoporoid fauna, except in those rare instances (Prague region, Carnic Alps) where the bottom was shallowed enough by volcanism or other agencies for a shelly fauna to flourish locally. The worldwide distribution of Silurian stromatoporoid taxa is too little known to provide significant biogeographic data. The situation regarding tabulate corals and tetracorals differs little from that for Silurian stromatoporoids except that the former are also very widely distributed in nonbioherm, nonbiostrome platform carbonate and geosynclinal shallow-water beds, and are not major contributors in making up the volume of bioherms and biostromes. It should be noted, however, that within the Soviet Union, where tabulate corals and stromatoporoids have been intensively studied, they have proved to be of great stratigraphic value. Studies elsewhere in Europe are in agreement with the Soviet experience. These groups will be of great worldwide value when studied more fully.

BRYOZOANS

Stony and fenestellid bryozoans are widely distributed within the platform carbonates, but their stratigraphic, ecologic, and biogeographic value is at present poorly known on a worldwide basis. Their abundance, however, augurs well for the future.

BRACHIOPODS

Brachiopods are widely distributed in relatively shallow-water platform and geosynclinal marine Silurian rocks of the world. Origins of the Silurian brachiopod fauna are twofold, including an early Llandoverian complement (Boucot, 1968) transitional from the Late Ordovician of northern Europe as far east as the Urals and Kazakhstan, and a late Llandoverian complement transitional from Late Ordovician to middle Llandoverian taxa restricted during this earlier time interval to southeastern Kazakhstan. Ecologically the brachiopods were strongly controlled in their distribution by a variety of factors. For the late Llandoverian in Britain, Ziegler (1965) has demonstrated a correlation of brachiopod distribution with depth; Ziegler and Boucot (in Berry & Boucot, 1970) have shown the same for North America; and Berry and Boucot (1967) have suggested that in Britain and North America, though not always elsewhere, temperature varying with depth is the primary factor in their distribution. Certain taxa appear to have been ecologically restricted to reef environments during the Silurian. Boucot (1975) has provided more detail on the Silurian brachiopod-dominated communities.

At the generic level, the Silurian brachiopod fauna is relatively cosmopolitan, contrasting strongly in this regard with the preceding Late Ordovician and succeeding Early Devonian faunas. The only areas of strong provincialism during the Silurian are in South America south of Lake Titicaca and in South Africa where the *Clarkeia* community (a shallow-water entity) is found, and in the narrow belt extending from the Amur River in the east, westward through the southeastern Sayan and Altay, Tuva, and Mongolia to a few parts of southeastern Kazakhstan where the *Tuvaella* community (another shallow-water entity) is found. At the regional level, brachiopods of Wenlockian through Pridolian age in the vast region from the east slope of the Urals and Kazakhstan, Australia to southeastern Alaska, the Yukon, Cornwallis Island, North Greenland, and Nevada display increasing endemism when compared with faunas known from the west slope of the Urals, Europe, the bulk of North America, northern and westermost South America, and southern Asia. It must be emphasized, however, that this growing endemism is of much smaller magnitude than the succeeding provincialism of the Early Devonian (Boucot, 1975).

A simple observation whose significance is hard to assess is the fact that most Silurian brachiopod taxa are represented by smaller specimens than are found in the Lower Devonian, in accord with Cope's Rule.

Brachiopods are now of great service in zoning and correlating the Silurian of the world as well as in making ecologic analy-

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ses of community distributions on a worldwide scale.

GASTROPODS

Gastropods are widespread, but low in frequency, in marine Silurian rocks of the world. In an average collection of Silurian invertebrates, it is seldom that more than one or two gastropods occur with a thousand other shells. Poleumitid gastropods and euomphalopterids are the most characteristic Silurian gastropods, persisting as Silurian relicts in the Early Devonian Old World realm. Poleumitids are widespread in platform carbonates, with relatively high abundance in reef and calcareous shale associations, and also occur in many shallow-water terrigenous and carbonate geosynclinal areas. Platyceratids are relatively ubiquitous. Bellerophontids are widespread, but most abundant in Benthic Assemblages 1 and 2 (Boucot, 1975). The platform mudstones are very poor in gastropods. Plectonotid gastropods are largely restricted to Benthic Assemblages 1 and 2. Presently known anomalies in the distribution patterns of Silurian gastropods may be most easily ascribed to either environmental factors or lack of information. General lack of interest in Silurian gastropods is not conducive to correcting this situation.

CEPHALOPODS

Nautiloid cephalopods are among the most widely distributed Silurian invertebrates in all marine rock types. They are particularly abundant in the *"Orthoceras"* limestones forming a characteristic, although volumetrically small, part of the Eurafrican platform mudstones, and in the biohermal and biostromal structures of the platform carbonates. An average collection of Silurian invertebrates almost invariably contains a few percent of nautiloid fragments. Unfortunately, the nautiloids have not received the intensive worldwide treatment that they need in order to be of prime importance for ecologic, biostratigraphic, and biogeographic purposes.

BIVALVES

Bivalves are widespread in the marine Silurian of the world. Their most common occurrences are in the bivalve-graptolite-rich platform mudstones of the Eurafrican platform (see Berry & Boucot, 1967), where the so-called "Bohemian forms" occur in relative abundance, in reef environments where the genus *Megalomus* is commonly cited, and in the Benthic Assemblage 1 and 2. Elsewhere, bivalves are relatively rare in Silurian rocks, seldom making up more than one percent of the number of specimens in a collection. In the bivalve-graptolite faunas, as well as in Benthic Assemblages 1 and 2, bivalves may commonly form the most abundant element in the fauna, both in number of species and specimens. Worldwide distribution patterns of Silurian bivalves have been too little investigated to provide any current information of biogeographic importance. Presently known anomalies in distribution pattern can rationally be ascribed to environmental factors rather than to isolating mechanisms.

TRILOBITES

Trilobites are widely distributed in Silurian rocks in almost every marine environment. At present, their stratigraphic and geographic distribution is poorly known in comparison with other major invertebrate groups. Trilobites form on the average about five percent or less of the invertebrate fauna in terms of specimens. It is notable that Silurian, as well as Early and Middle Devonian, homolanotids are almost completely restricted to the relatively shallow-water regions of Benthic Assemblages 1 and 2. The ecologic distribution and zonation of trilobites will undoubtedly prove very valuable, although up to the present no systematic efforts have been made in this direction. Biogeographically, no systematic attempt has been made to synthesize available information regarding trilobites, although scattered comments are consistent with the more extensive data for brachiopods.

EURYPTERIDS

Eurypterids are relatively uncommon in Silurian strata, except in a few specialized facies. Ecologically they are of great po-

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tential use in discriminating between certain marine, brackish, and hypersaline environments. Particular assemblages are characteristic of brackish and hypersaline environments (see information in Boucot, 1975). Their occurrences are so few as to make them of little value for biogeographic considerations, but they are of some biostratigraphic value.

OSTRACODES

Ostracodes are widely distributed in marine Silurian rocks of the world. In those regions and parts of the column subjected to intensive study they have proved to have great stratigraphic and biogeographic value. Upper Llandoverian through Pridolian ostracodes of the Appalachians appear to represent a series of relatively endemic faunas known from Anticosti Island southwest through the central Appalachians, including occurrences in the northern Appalachians of Quebec and northern Maine. Ludlovian and Pridolian ostracodes of the Baltic region, Great Britain, Nova Scotia, southeastern New Brunswick, coastal Maine, and eastern Massachusetts, as well as Podolia, form another apparently endemic fauna, which has been zoned stratigraphically in some detail. The lowest upper Llandoverian of the North American platform contains some forms that may be endemic and stratigraphically restricted. Isolated Silurian faunas elsewhere are too little known and unique to afford information for stratigraphic or biogeographic generalizations. In summary, it can be stated that the ostracodes may possibly provide important biogeographic insights within the Silurian (see Berdan & Martinsson, in Berry & Boucot, 1970).

OTHER ARTHROPODS

At present, other groups of Silurian arthropods are too little known to be of stratigraphic or biogeographic value.

ECHINODERMS

Pelmatozoan debris is widespread and volumetrically important in marine Silurian rocks of the world, particularly platform carbonates; however, such material is present in very low abundance in platform mudstones. Silurian crinoids are widespread, particularly in platform carbonates, but are too uncommon on a worldwide basis to contribute much to our knowledge of Silurian biogeography. The same situation obtains with the cystoids and blastoids. Other groups of echinoderms are relatively rare in the Silurian.

Except in certain quiet-water, marly facies (both reef and level-bottom), articulated echinoderms are relatively rare. Twenty years of collecting have provided the writer with less than a dozen specimens from outside these facies, despite the abundance of pelmatozoan debris in many places, which suggests that our knowledge of Silurian echinoderms may be very distorted.

Of biogeographic interest are the European, African, eastern North American, and Oklahoma occurrences of *Camarocrinus* in strata of Pridolian age (except for Tennessee and Missouri where an early Gedinnian age is indicated as well), and its occurrence in southern China and Burma in strata of early Llandoverian age.

Disarticulated pelmatozoan debris has been extensively employed within the Soviet Union for purposes of zonation and correlation, but specialists in other countries have not yet employed or tested this work.

GRAPTOLITES

Together with the conodonts, the graptolites are the most ubiquitous of the well-studied Silurian invertebrates. They are known from every marine environment; presumably owing to their depth-stratified, planktonic mode of life. Graptolites are abundant in platform mudstones (Berry & Boucot, 1967), and every other marine facies, except for the hypersaline, has yielded at least a few graptolites. The popular notion ascribing the graptolites only to the "black shale" and "basin" facies is grossly in error, although statistically it is true that these rocks have yielded the great majority of specimens. They display a certain level of biogeographic differentiation in the Silurian (see Boucot, 1975, for summary).

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CONODONTS

Silurian conodonts are worldwide in their distribution, having been recovered in abundance by acid treatment from carbonate rocks of the platform carbonate, platform mudstone, and geosynclinal facies (carbonate interbeds with terrigenous and volcanic strata). They have proved of prime importance in the zonation of upper Llandoverian through Pridolian beds (see Klapper, Berry, & Boucot, in Berry & Boucot, 1970). Conodonts have been recovered in abundance from strata reflecting so many environments in the Silurian, from the intertidal to shelf margin and regions beyond, that it is tempting to conclude that like the graptolites they probably are the remains of primarily pelagic organisms. Their ubiquitous worldwide occurrence and zonation indicates that like brachiopods and graptolites they were a relatively cosmopolitan group during the Silurian.

VERTEBRATES

Vertebrates obtained from brackish beds are too rare and poorly known at present to be of widespread stratigraphic or biogeographic value; however, where studied, particularly in northern Europe, isolated microscopic denticles, plates, and spines obtained from acid residues are beginning to have stratigraphic value in beds of Ludlovian and Pridolian age. Vertebrates are widespread in North Silurian realm marine beds, although normally they are rare as individuals.

CALCAREOUS ALGAE

Although calcareous algae are widespread and abundant in marine Silurian beds deposited in the photic zone, they have been little studied. Therefore, they are not used for either biostratigraphic or biogeographic purposes, although they have been used to to a limited extent in paleoecologic considerations, chiefly in determining the lower limits of the photic zone, and relative degrees of turbulence as indicated by different types of oncolites.

REMAINS OF LAND PLANT TYPE

Acid-resistant spores, tracheid-like and cuticle-like microfossils, are abundant in shallow-water and nearshore Silurian facies (see Gray, Laufeld, & Boucot, 1974, for a typical example), but it is highly uncertain as to whether or not the parent organisms lived on land, in the intertidal environment, or in the shallow subtidal region, although the desiccation-resistant structure of the fossils indicates an affinity for at least in part a life style involving the nonaqueous. Macrofossils of land plant type are known from the Wenlockian onward, but their growth site is fully as uncertain as is that of plant microfossils of land type.

REFERENCES

Berry, W. B. N., & Boucot, A. J., 1967, *Pelecypod-graptolite association in the Old World Silurian:* Geol. Soc. America, Bull., v. 78, p. 1515-1522. ——1970, *Correlation of the North American Silurian rocks:* Geol. Soc. America, Spec. Paper 102, 189 p.——(eds.), 1972, *Correlation of the South American Silurian rocks:* Geol. Soc. America, Spec. Paper 133, 59 p.——1972, *Correlation of the southeast Asian and near eastern Silurian rocks:* Geol. Soc. America, Spec. Paper 137, 65 p.——1973, *Correlation of the African Silurian rocks:* Geol. Soc. America, Spec. Paper 147, 83 p.——(eds.), 1974, *Correlation of the Silurian rocks of the British Isles:* Geol. Soc. America, Spec. Paper 154, 154 p.

Boucot, A. J., 1968, *Origins of the Silurian fauna:* Geol. Soc. America, Spec. Pap. 121, p. 33-34. ——1969, *The Soviet Silurian: recent impressions:* Geol. Soc. America, Bull., v. 80, p. 1155-1162.——1974, *Early Paleozoic evidence of continental drift: pro and con:* in Plate tectonics—assessments and reassessments, C. F. Kahle (ed.), Am. Assoc. Petrol. Geologists, Mem. 23, p. 273-294.——1975, *Evolution and extinction rate controls:* 427 p., Elsevier (Amsterdam).

Bulman, O. M. B., 1970, *Graptolithina:* in Treatise on invertebrate paleontology, Part V (Revised), Curt Teichert (ed.), 163 p., Geol. Soc. America and Univ. Kansas (Boulder, Colo.; Lawrence, Kans.).

Gray, Jane, Laufeld, Sven, & Boucot, A. J., 1974, *Silurian trilete spores and spore tetrads from Gotland: their implications for land plant evolution:* Science, v. 185, p. 260-263.

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Jones, O. T., 1925, *On the geology of the Llandovery district, pt. 1:* Geol. Soc. London, Quart. Jour., v. 81, p. 344-388.

Talent, J. A., Berry, W. B. N., & Boucot, A. J., 1975, *Correlation of the Silurian rocks of Australia, New Zealand, and New Guinea:* Geol. Soc. America, Spec. Paper 150, 108 p.

Ziegler, A. M., 1965, *Silurian marine communities and their environmental significance:* Nature, v. 207, no. 4994, p. 270-272.

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