PRINCIPAL FLORAS OF PALAEOZOIC MARINE CALCAREOUS ALGAE

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ABSTRACT. The stratigraphic distribution of eighteen groups of fossils commonly assigned to the calcareous algae reveals three major floras in shallow marine carbonate deposits of Palaeozoic age: (1) Cambrian flora, (2) Ordovician flora, (3) Carboniferous flora. The Cambrian flora appears abruptly near the Precambrian–Cambrian boundary and is dominated by cyanophytes. The Ordovician flora appears quickly during the lower and middle Ordovician and is dominated by chlorophytes, ?rhodophytes, and problematic groups. The Carboniferous flora appears gradually, mainly during the Carboniferous, and is dominated by rhodophytes, chlorophytes, and problematic groups. Important extinctions occurred near the ends of the Devonian, Carboniferous, and Permian.

The succession of floras is reflected in the changing sedimentological roles of Palaeozoic calcareous algae. Cambrian reefs are dominated by *Epiphyton–Renalcis* assemblages which reappear briefly in the Devonian. During most of the middle Palaeozoic algae are subordinate to metazoan reef-builders, but Solenoporaceae, *Rothpletzella*, and *Wetheredella* are nevertheless important locally. Following a hiatus during the lower Carboniferous, *Donezella*, *Ungdarella*, phylloid algae, and *Tubiphytes* were important reef-builders. Skeletal oncoids built by *Girvanella*, *Hedstroemia*, *Ortonella*, and *Rothpletzella*, together with *Solenopora* rhodoliths, are common at many levels in the Palaeozoic, but skeletal stromatolites are generally rare. Nodules formed by *Archaeolithophyllum* and *Cuneiphycus* occur in the upper Palaeozoic. Sand- and gravel-size fragments, mainly of chlorophytes and rhodophytes, increase in abundance from the Ordovician onwards.

По особенностям стратиграфического распространения восемнадцати групп окаменелостей, обычно относимых к известковым водорослям, различаются три основных комплекса в мелководных морских карбонатных отложениях палеозоя: (1) кембрийский комплекс; (2) ордовикский комплекс; (3) каменноугольный комплекс.

Кембрийский комплекс водорослей появляется видимо вблизи нижней границы кембрия; в его составе доминируют цианофиты. Ордовикский комплекс появился быстро в среднем ордовике и представлен преимущественно хлорофитами, родофитами (?) и проблематичными группами. Каменноугольная флора формируется постепенно, главным образом, в течении карбона. В ее составе доминировали родофиты, хлорофиты и проблематичные группы. Важные изменения происходили в конце девона, карбона и перми.

Установленная последовательность в развитии водорослей отражается в изменении седиментологического значения палеозойских известковых водорослей.

Среди кембрийских рифов доминировало сообщество родов *Epiphyton–Renalcis*, которое затем на короткое время появляется вновь в девоне. В течение среднего палеозоя водоросли, как рифообразователи, были подчинены метазоа, но Solenoporaceae, *Rothpletzella* и *Wetheredella* играли местами важную роль в создании осадков.

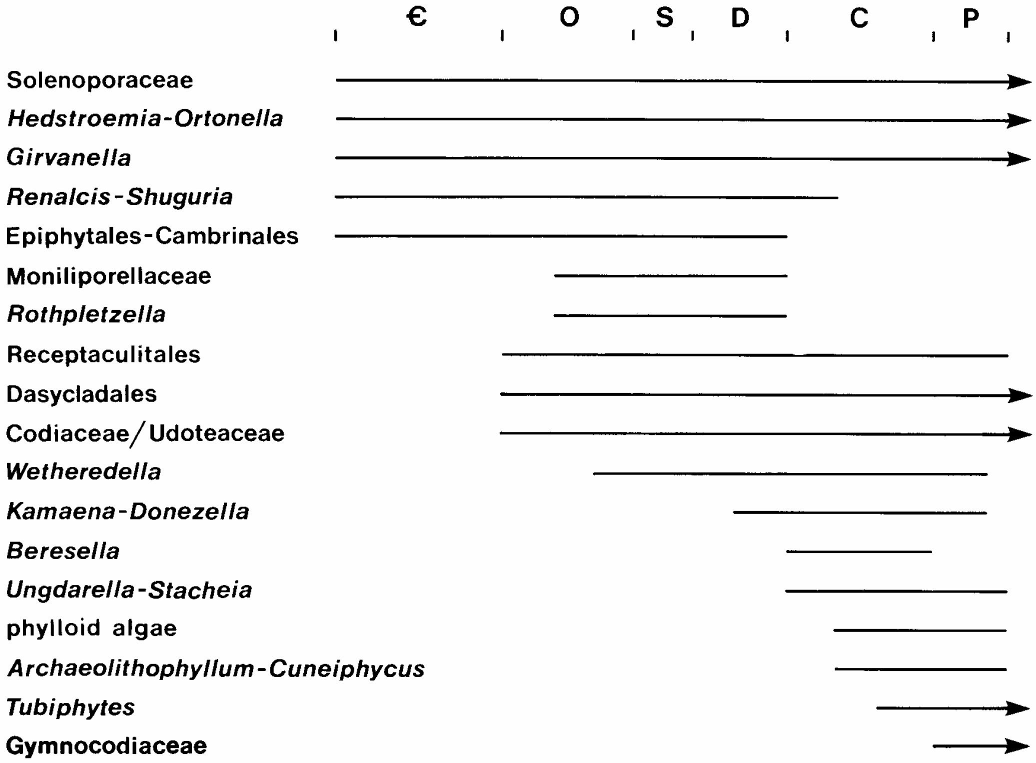
После нижнего карбона, в течение которого породообразующее значение известковых водорослей заметно падает, *Donezella*, *Ungdarella*, филлоидные водоросли, а также *Tubiphytes* были важными рифообразователями.

Скелетные онкоиды, построенные *Girvanella*, *Hedstroemia*, *Ortonella* и *Rothpletzella* совместно с *Solenopora*-родолитами являются обычными на многих уровнях палеозоя, но скелетные строматолиты обычно редки. Желваки, образованные с участием *Archaeolithophyllum* и *Cuneiphycus* встречаются в верхнем палеозое. Зерна песчаной и гравийной размерности образованы, главным образом, за счет зеленых и красных водорослей, увеличиваются количественно в осадках с позднего ордовика.

WE present a general overview of the stratigraphic distribution of calcareous algae during the Palaeozoic. Our aims are to discern broad patterns of calcareous algal evolution and to evaluate briefly how these are reflected in the sedimentological importance of these fossils. We have

[Palaeontology, Vol. 27, Part 3, 1984, pp. 487–500.]

incorporated available data from North America and one or two other areas, but most of our information is derived from work in Europe and the USSR. In order to present this we have divided the many genera involved into a number of groups which have a broad base within current systematic schemes. The problems of affinity in Palaeozoic calcareous algae are well known (Riding 1977*a*), but remain largely unresolved. They are mainly responsible for uncertainty concerning the systematics of these fossils. We have selected groups which have some degree of morphological similarity. In some cases their affinities are clear, in others doubtful. Some groups include members which are possibly not algae. In this paper we attempt to encompass all groups which are commonly regarded as algae, even if we personally have doubts concerning such an attribution. However, we have neglected some small groups represented by only a few genera. It would be a major undertaking to plot accurately and comprehensively the distribution of the large number of genera involved, and such a compilation would necessitate substantial taxonomic revision. Our aim here is to review the changing composition of these floras during the Palaeozoic in a very broad way in order to assess general patterns. Thus, these results are preliminary and doubtless imperfect with respect both to the groups selected and their ranges. In particular we have recognized the fewest possible number of major groups, and this has involved a degree of 'lumping' which will be open to criticism. Nevertheless, we believe that this procedure enhances, rather than detracts from, the validity of the patterns elucidated here.



TEXT-FIG. 1. Stratigraphic ranges of eighteen major calcareous algal groups during the Palaeozoic. Generic names indicate groups, not individual genera (see Table 1), except in the case of *Tubiphytes*. Ranges are drawn from the base of the sub-period (early, middle, late) in which the first member of a group appears, to the top of the sub-period in which the last member occurs. Arrow indicates that group continues into the Mesozoic. Length of periods is based upon Harland *et al.* (1982).

TABLE 1. Eighteen major groups of Palaeozoic calcareous algae and possible calcareous algae, showing their main characters and the affinities confidently or currently attributed to them. The references give sources of further information but in many cases do not cite the authors of the groups or of the named genera themselves.

Group	Contents	Characters	Affinities	References
1. Solenoporaceae	*Solenopora* Dybowski, *Parachaetetes* Deninger, etc.	Massive, tabular, hemispherical or nodular skeleton composed of closely packed cellular filaments, sometimes possibly containing sporangia	Probable rhodophytes; possibly related to the Corallinaceae	Johnson (1960); Maslov (1962)
2. *Hedstroemia*-*Ortonella* group	*Botomaella* Korde, *Bevocastria*, Garwood, *Garwoodia* Wood, *Hestroemia* Rothpletz, *Ortonella* Garwood, etc.	Fan-like bundles of branched tubes of varying cross-sectional shape. In some genera the tubes are closely packed and share walls, in others the tubes are separate. Branching ranges from dichothomous, to irregular and multiple	Several of the genera resemble extant calcareous cyanophytes	Wray (1977, pp. 38–39)
3. *Girvanella* group	*Batenevia* Korde, *Botominella* Reitlinger, *Cladogirvanella* Ott, *Girvanella* Nicholson and Etheridge, *Obruchevella* Reitlinger, etc.	Narrow simple tubes of constant diameter and without cross-partitions. Tubes may be straight, sinuous, irregularly tangled, or spiral, and may be arranged in tightly woven, cable-like bundles or loose masses	Probably filamentous cyanophytes	Wray (1977, pp. 36–37)
4. *Renalcis*-*Shugaria* group	*Gemma* Luchina, *Izhella* Antropov, *Renalcis* Vologdin, *Shuguria* Antropov, *Tarthinia* Drosdova, etc.	Cloud-like forms consisting of clusters of a few or many hollow, bubble-like compartments, sometimes arranged in short branched series	Possibly cyanophytes	Drosdova (1980, pp. 14–19); Wray (1977, p. 40)
5. Epiphytales-Cambrinales	*Cambrina* Korde, *Epiphyton* Bornemann, *Gordonophyton* Korde, *Potentillina* Korde, *Tubomorphophyton* Korde, etc.	Dendritic solid micritic, tubiform or chambered thalli. Branches narrow; branching dichothomous or irregular	Possibly cyanophytes or rhodophytes	Korde (1973, pp. 125–212); Luchinina (1975)
6. Codiaceae/ Udoteaceae	*Dimorphosiphon* Høeg *Lancicula Maslov*, *Litanaia* Maslov, *Palaeoporella* Stolley, etc.	Entire or segmented thallus, may be branched, internally divided into cortex and medulla consisting of numerous branched tubes	Chlorophytes	Gnilovskaya (1972, pp. 79–100); Shuysky (1973, pp. 61–80)
7. *Rothpletzella* group	*Flabellia* Shuysky, *Halysis* Høeg, *Rothpletzella* Wood	Flat, curved, or encrusting sheets of juxtaposed tubes which branch dichothomously in one plane	Microproblematica, often regarded as cyanophytes or chlorophytes	Flügel and Wolf (1969)

Group	Contents	Characters	Affinities	References
8. *Wetheredella* group	*Aphralysia* Garwood, *Asphaltina* Mamet, *Sphaeroporella* Antropov, *Wetheredella* Wood, etc.	Short tubes, possibly branched, with blister-like or rounded cross-sections; fibrous wall structure sometimes with additional micritic layer	Microproblematica sometimes regarded as chlorophytes, foraminifers, or worms	Ischenko and Radionova (1981); Mamet and Roux (1975, pp. 156-166)
9. Receptaculitales	*Calathium* Billings, *Ischadites* Murchison, *Receptaculites* Deshayes, etc.	Large, hollow, pear- or sack-like bodies, usually open at one end, with double-walls and faceted outer surfaces	Problematica, often referred to the Chlorophyta	Nitecki (1972); Rietschel (1969); Zhuravleva and Myagkova (1981)
10. Dasycladales	I. *Dasyporella* Stolley, *Rhabdoporella* Stolley, *Vermiporella* Stolley, etc. in middle Palaeozoic; II. *Diplopora* Schafhaütl, *Epimastopora* Pia, *Globiferoporella* Tchuvashov, *Macroporella* Pia, *Mizzia* Schubert, etc. in upper Palaeozoic	Hollow sack- or stick-like algae, usually large and erect, sometimes segmented; relatively thick walls pierced by simple or branched pores Palaeozoic forms show clear separation into middle Palaeozoic and upper Palaeozoic assemblages (I and II)	Chlorophyta	Pia (1920); Elliott (1972); Shuysky (1973, pp. 80-87), Chuvashov (1974)
11. *Kamaena–Donezella* group	*Donezella* Maslov, *Jansaella* Mamet and Roux, *Kamaena* Antropov, *Palaeoberesella* Mamet and Roux, etc.	Branched, mainly dichotomously, septate tubes with finely porous or fibrous wall-structure. Septa may be entire or incomplete	Microproblematica, often regarded as chlorophytes or rhodophytes, sometimes as foraminifers	Maslov (1956); Antropov (1967); Mamet and Roux (1974)
12. *Beresella* group	*Beresella* Machaev, *Dvinella* Khvorova, *Uraloporella* Korde, etc.	Moderately large, straight to sinuous, branched tubes; sometimes septate; wall relatively thick with pores which may be simple or branched	Microproblematica, but commonly regarded as dasycladaleans	Korde *et al.* (1963, p. 211, p. 217)
13. Phylloid algae	*Anchicodium* Johnson, *Eugonophyllum* Konishi and Wray, *Ivanovia* Khvorova, *Neoanchicodium* Endo, etc.	Large, thin, wavy, leaf-like thallus; cortex thick, usually porous, sometimes containing 'sporangia'; medulla filamentous, usually poorly preserved	Commonly regarded as codiaceans/udoteaceans; some genera are comparable with Squamariaceae (Peyssoneliaceae, Rhodophyta)	Wray (1968; 1977, pp. 52-54)
14. *Archaeolithophyllum–Cuneiphycus* group	*Archaeolithophyllum* Johnson, *Cuneiphycus* Johnson, *Eflugelia*.	Encrusting or hemispherical masses; coarse cellular construction, occasionally bearing conceptacles	Rhodophyta (*Archaeolithophyllum*) and Microproblematica	Wray (1977, pp. 71-72)

Group	Contents	Characters	Affinities	References
15. *Ungdarella–Stacheia* group	*Aoujgalia* Termier and Termier, *Epistacheoides* Petryk and Mamet, *Fourstonella* Cummings, *Komia* Korde, *Stacheia* Brady, *Stacheoides* Cummings, *Ungdarella* Maslov, etc.	Encrusting or erect, rod-like, branched fossils with cellular construction; cells sometimes aligned in coarse rope-like strands	Microproblematica, often regarded as rhodophytes	Maslov (1962); Petryk and Mamet (1972); Massa and Vachard (1979)
16. Gymnocodiaceae	*Gymnocodium* Pia, *Permocalculus* Elliott, etc.	Cylindrical or sack-like fossils, sometimes segmented; cortex thin, with external pores; medulla filamentous. Sporangia may be present	Chlorophytes or rhodophytes	Elliott (1955); Korde (1965)
17. *Tubiphytes* group	*Tubiphytes* Maslov	Large erect, irregular, or encrusting skeletons with a dense, dark, pseudo-cellular construction showing concentric bands; irregular internal tubes often present	Microproblematicum, sometimes regarded as a cyanophyte; possibly a sponge (E. Ott, pers. comm. 1982)	Maslov (1956); Flügel (1977, pp. 324–325, p. 339)
18. Moniliporellaceae	*Ansoporella* Gnilovskaya, *Contexta* Gnilovskaya, *Moniliporella* Gnilovskaya, etc.	Cylindrical, nodular, or irregular fossils with hollow interior; sometimes segmented; thick wall consisting of cellular filaments	Rhodophytes or chlorophytes	Gnilovskaya (1972, pp. 100–126)

GROUPS OF CALCAREOUS ALGAE

In Table 1 we list the certain and the equivocal algal groups whose stratigraphic distribution we have plotted in text-fig. 1. Each group is distinguished by either a supra-generic name or by one or two genera representing typical or well-known elements of the group. We list a few additional generic examples which normally represent only a small fraction of the total for each group. In addition we indicate the likely affinities (or doubts concerning affinities) for each group. Pertinent references are also given.

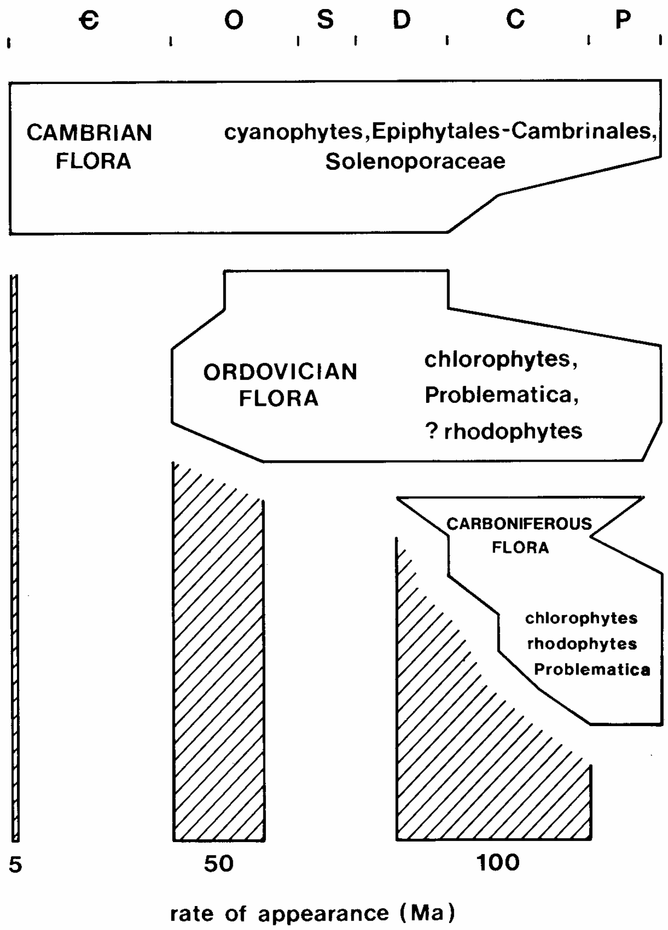
STRATIGRAPHIC DISTRIBUTION

The distribution chart of major calcareous algal groups (text-fig. 1) has been compiled from the literature cited in the table and from our personal experience of working with these fossils. It shows the first and last occurrences of each group as a whole, and not of the named genera alone. For example, *Hedstroemia* and *Ortonella* are principally Silurian and Carboniferous fossils respectively, but other members of the *Hedstroemia–Ortonella* group, as it is defined here, such as *Botomaella*, occur in the Cambrian and related types like *Cayeuxia* Frollo occur in the Mesozoic.

The pattern of stratigraphic distribution of the major groups (text-fig. 1) allows three distinct floras to be recognized (table 1; text-fig. 2): (1) Cambrian flora, (2) Ordovician flora, (3) Carboniferous flora.

The Cambrian flora is dominated by cyanophytes (*Hedstroemia-Ortonella* group, *Girvanella* group) and possible cyanophytes (Epiphytales-Cambrinales, *Renalcis-Shuguria* group); the possible rhodophyte group, Solenoporaceae, is present but rare. This flora ranges intact into the upper Devonian but then loses the Epiphytales-Cambrinales and *Renalcis-Shuguria* groups. The remaining elements continue beyond the Permian-Triassic boundary.

The Ordovician flora is dominated by Codiaceae/Udoteaceae, Dasycladales, the possible rhodophyte Monilioporellaceae, the possible chlorophyte Receptaculitales, the problematic *Rothpletzella* and



TEXT-FIG. 2. Three principal floras of Palaeozoic marine calcareous algae (from text-fig. 1) showing ranges, general composition, and rates of appearance. The Cambrian, Ordovician, and Carboniferous floras appeared over periods of 5, 50, and 100 Ma respectively. Length of periods is based upon Harland *et al.* (1982).

Wetheredella groups, together with the major elements of the Cambrian flora. Its new, characteristic, elements originated mainly in the lower and middle Ordovician and persist to the upper Devonian or beyond.

The Carboniferous flora is dominated by the problematic *Kamaena-Donezella* group, the possible chlorophyte *Beresella* group, a new assemblage of dasycladaleans, the possible rhodophyte *Ungdarella-Stacheia* group, the chlorophyte or rhodophyte phylloid algae and Gymnocodiaceae, the partly rhodophyte *Archaeolithophyllum-Cuneiphycus* group, and the doubtfully algal *Tubiphytes* group, together with elements of the Cambrian and Ordovician-Devonian floras which survived an important phase of extinction near the Devonian-Carboniferous boundary. The Carboniferous flora was introduced episodically, mainly during the lower and middle Carboniferous, with the *Kamaena-Donezella* group appearing earlier (in the middle Devonian) and the *Tubiphytes* group and Gymnocodiaceae later (in the upper Carboniferous and early Permian respectively). Most of these new upper Palaeozoic groups did not survive into the Mesozoic.

SEDIMENTOLOGICAL ROLES

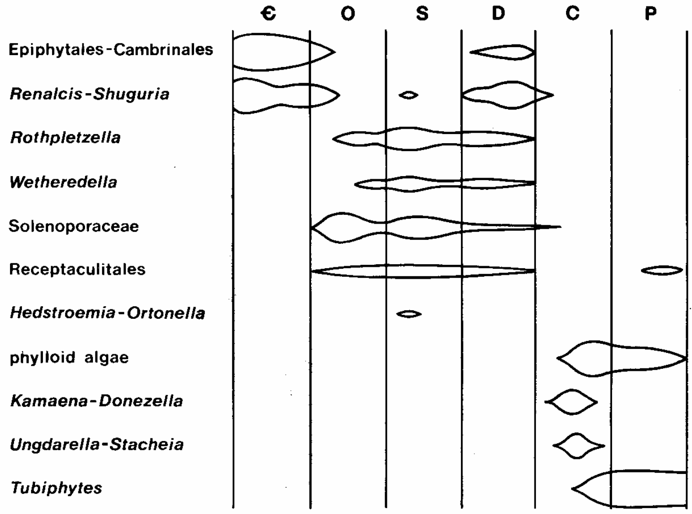
The importance of calcareous algae as producers of loose and *in situ* sediment is clear in Recent carbonate environments. It is equally recognizable in its effects upon limestone deposition from the first appearance of calcareous algae near the base of the Cambrian. The sedimentological roles of particular algal groups depend essentially upon the morphology and mode of growth of the algae, and the succession of algal floras has in turn imprinted a stratigraphic pattern upon their sedimentary products. The reef-building algae of the Cambrian differ in size, shape, and effects from those of the Carboniferous, the abundance of algal skeletal fragments changes through time, and the types of nodule-forming algae also change. The broad patterns of these variations are controlled by evolution and extinctions more than by sedimentary processes and palaeogeography.

In order to show these changes we have plotted qualitative assessments of the relative importance of Palaeozoic algal groups in the following roles: reef-building; stromatolite, oncoid, and rhodolith formation; and the production of recognizable, usually sand- to gravel-size, fragmentary (broken or disaggregated) material (text-figs. 3-7).

Reef-building

The three floras recognized here are clearly reflected in Palaeozoic reef-building (text-fig. 3). The Cambrian algal reef-builders belong mainly to two groups: the Epiphytales-Cambrinales and *Renalcis-Shuguria*. *Angulocellularia* Vologdin, omitted from these distribution charts because it constitutes a taxonomically small group, is also locally an important reef-builder (see Riding and Voronova 1982). These are all small but abundant fossils and commonly exceed archaeocyathans in volumetric importance in the early lower Cambrian (James and Debrenne 1980).

Ordovician-Devonian algal reef-builders are more diverse and, in general, none has the individual importance of those in the Cambrian. Receptaculitaleans are rather rare fossils, and *Hedstroemia* is at present only known to be important in reefs in the Silurian (Riding and Watts 1981). *Rothpletzella* and *Wetheredella* form thick crusts (Copper 1976), but usually on large metazoan reef builders such as stromatoporoids, corals, and bryozoans. Solenoporaceans form the largest individual skeletons but are, nevertheless, usually subordinate to metazoans (Harland 1981). On the whole, a variety of algal groups is locally conspicuous in middle Palaeozoic reefs, but they are usually only accessory to larger and more abundant metazoans. A curious feature of middle Palaeozoic algal history is the reappearance of 'Cambrian' reef-building genera in the Devonian, especially the upper Devonian. These are members of the Epiphytales and *Renalcis-Shuguria* groups and their return to prominance at this level, after insignificance from the middle Ordovician to early Devonian, has so far defied satisfactory explanation.

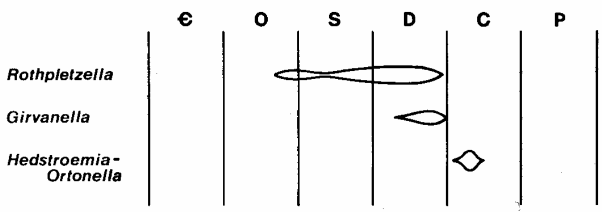


TEXT-FIG. 3. Reef-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.

There is a hiatus in the early Carboniferous with few algal reef-builders following the demise of some of the Cambrian–Devonian groups. Only members of the *Renalcis–Shuguria* group have been reported as common reef constituents at this level. However, the phase of algal evolution which took place in the lower to middle Carboniferous yielded several important groups which filled this gap. In particular *Donezella* (Rich 1967, Riding 1979) and *Ungdarella–Komia* (Freeman 1964) are important mound-builders or, at least, mound-associates in the middle Carboniferous and Pennsylvanian. Phylloid algae also created bioherms from the middle Carboniferous to early Permian (Wilson 1975) and *Tubiphytes* is important from the upper Carboniferous until the Triassic (Flügel 1977).

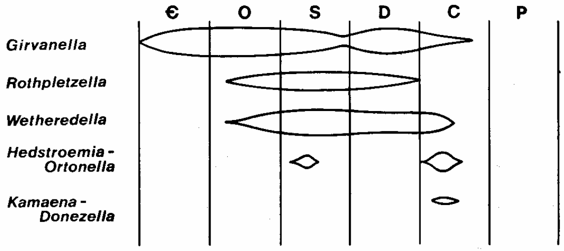
Stromatolites

Skeletal stromatolites, i.e. stromatolites formed by calcareous algae rather than by algae which merely trap and bind sediment (Riding 1977*b*) are, so far, only known to be common in parts of the Ordovician, Devonian, and Carboniferous (text-fig. 4). *Rothpletzella* and *Wetheredella* form stromatolitic crusts on metazoan skeletons in upper Ordovician reefs (Copper 1976). *Rothpletzella* forms stromatolitic caps on stabilized oncoids on the fore-reef slope of the upper Devonian Canning Basin reefs in Western Australia (Playford, Cockburn, Druce and Wray 1976). *Girvanella* builds stromatolites in the Devonian of the Ural Mountains, USSR, and *Ortonella* and *Bevocastria* build stromatolites in the lower Carboniferous of the Scottish border country, Great Britain (Garwood 1931).



TEXT-FIG. 4. Stromatolite-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.

TEXT-FIG. 5. Oncoid-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.



Oncoids

Skeletal oncoids are much more widespread than skeletal stromatolites in the Palaeozoic (text-fig. 5). *Girvanella* forms oncoids from the Cambrian to Carboniferous, and in association with *Nubecularia* it was responsible for *Osagia* nodules in the Pennsylvanian (Johnson 1946). *Rothpletzella* and *Wetheredella* are often mutually associated in oncoids from the Ordovician to Devonian. *Hedstroemia* forms oncoids in the Silurian of Gotland and *Bevocastria*, *Ortonella* and *Garwoodia* are involved in oncoid formation, as well as stromatolite formation in the Lower Carboniferous of Britain. In addition, *Donezella* forms encrusted nodules in the middle Carboniferous.

Rhodoliths

Solenoporacean nodules are common during the Ordovician and Silurian (Johnson 1960) and are also locally abundant in the Upper Palaeozoic (Belka 1979). *Archaeolithophyllum* and *Cuneiphycus* form nodules in the upper Carboniferous (text-fig. 6).

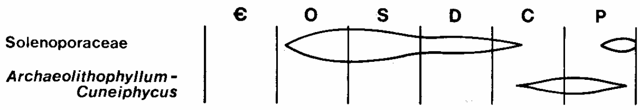
Fragments

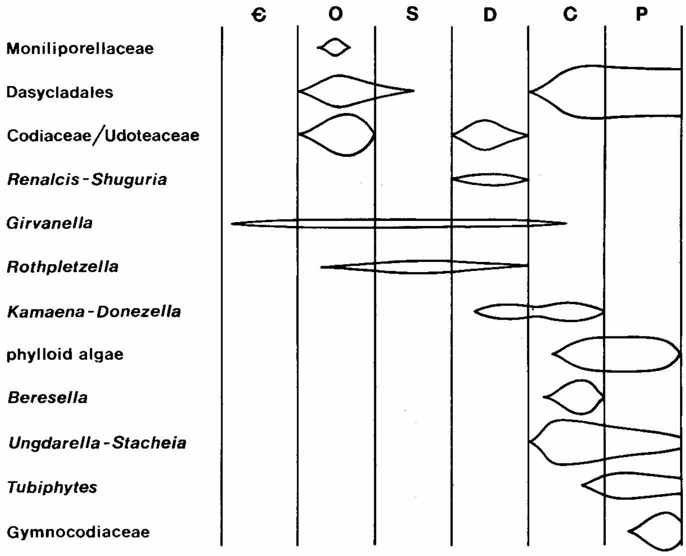
The presence of algal skeletal debris in shallow marine Palaeozoic limestones reflects the history of fragile or jointed specimens which were readily broken or disaggregated into sand- or gravel-size pieces (text-fig. 7). Algae, like the modern codiacean/udoteacean *Penicillus*, which may have disaggregated after death into mud- and silt-size particles leave no readily recognizable trace because the resulting particles are too small for their origin to be recognized.

At times during the Palaeozoic, as in subsequent geological eras, chlorophytes produced large quantities of calcareous debris. This sedimentological role commenced in the Ordovician when codiaceans/udoteaceans and dasycladalean fragments are also associated with those of moniliporellaceans. Codiacean/udoteacean debris is also locally common in the Devonian, but is more rare in the Carboniferous when this role was mainly occupied by dasycladaleans.

In the Cambrian, algal fragments are rare. This is a result both of the absence of calcareous chlorophytes and the fact that the common cyanophytes were generally firmly attached reef-builders. If the latter were broken from their substrates they produced small, micritic fragments difficult to distinguish from peloids. Nevertheless, in the Devonian, members of the *Renalcis–Shugaria* group are locally common as transported grains, as are *Girvanella* and *Rothpletzella*. The latter are also minor components of near-reef sediments in the Ordovician and Silurian. *Kamaena–Donezella* group fragments are common at various levels from middle Devonian to upper Carboniferous, but the

TEXT-FIG. 6. Rhodolith-forming calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.





TEXT-FIG. 7. Debris-producing calcareous algae during the Palaeozoic: estimated relative importance. Groups with minor roles are omitted.

principal increase in algal debris in the upper Palaeozoic took place in the middle Carboniferous when fragments of phylloid algae, plus the *Beresella*, *Ungdarella-Stacheia*, and *Tubiphytes* groups, combined with those of the new assemblage of dasycladaleans to produce loose material which often dominated shallow marine carbonate microfacies. The Gymnocodiaceae added to this, especially in the upper Permian.

DISCUSSION

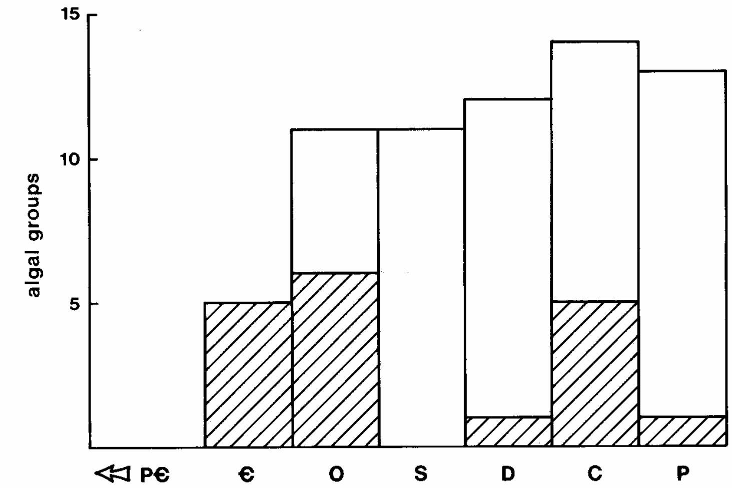
Floras

The Cambrian calcareous algal flora was dominated by cyanophytes and possible cyanophytes: Solenoporaceae were relatively rare. The Ordovician and Carboniferous floras are both more mixed. If groups whose affinities are unclear are not considered, then the resulting picture of algal evolution is that calcareous cyanophytes appeared in the Cambrian, chlorophytes (codiaceans/udoteaceans and dasycladaleans) in the Ordovician, and rhodophytes (*Archaeolithophyllum*) in the Carboniferous. If we take *possible* affinity into consideration, this time-distribution does not change for cyanophytes and chlorophytes but calcareous rhodophytes may be present from the early Cambrian (Solenoporaceae, Epiphytales). It is clearly a matter of current importance for research to attempt to clarify the affinities of these and other possible algal groups in the Palaeozoic.

Diversity of major algal groups increases from the Cambrian (five groups) to the Ordovician (eleven groups). Subsequent increase is slight, rising to twelve groups in the Devonian, fourteen in the Carboniferous, and falling slightly to thirteen in the Permian (text-fig. 8). The resulting sigmoidal curve resembles the pattern of exponential diversification followed by equilibrium derived for marine metazoan orders during the Phanerozoic (Sepkoski 1978, fig. 9).

Evolutionary events, extinctions, ranges

The three principal algal floras recognized here were introduced in the earliest Cambrian, Ordovician, and Devonian-Carboniferous respectively. Of these, the first event near the Precambrian-Cambrian boundary was abrupt, the Ordovician event more gradual, and that in the Devonian–Carboniferous slow (text-fig. 2). In the Nemakit Daldyn Formation of late Precambrian or early Cambrian age in northern Siberia members of the *Hedstroemia–Ortonella*, *Girvanella*, Epiphytales-Cambrinales, and *Renalcis–Shuguria* groups appear together virtually synchronously (Riding and Voronova, in prep.) and are joined, probably within 5 Ma, by solenoporaceans. The Ordovician event spanned approximately 50 Ma from early to late Ordovician, and the third phase of evolution was a slow episodic appearance of groups over a period approaching 100 Ma between the middle Devonian and early Permian (text-fig. 2). Nevertheless, both the last two events show some concentration, first in the lower-middle Ordovician and secondly in the lower-middle Carboniferous.

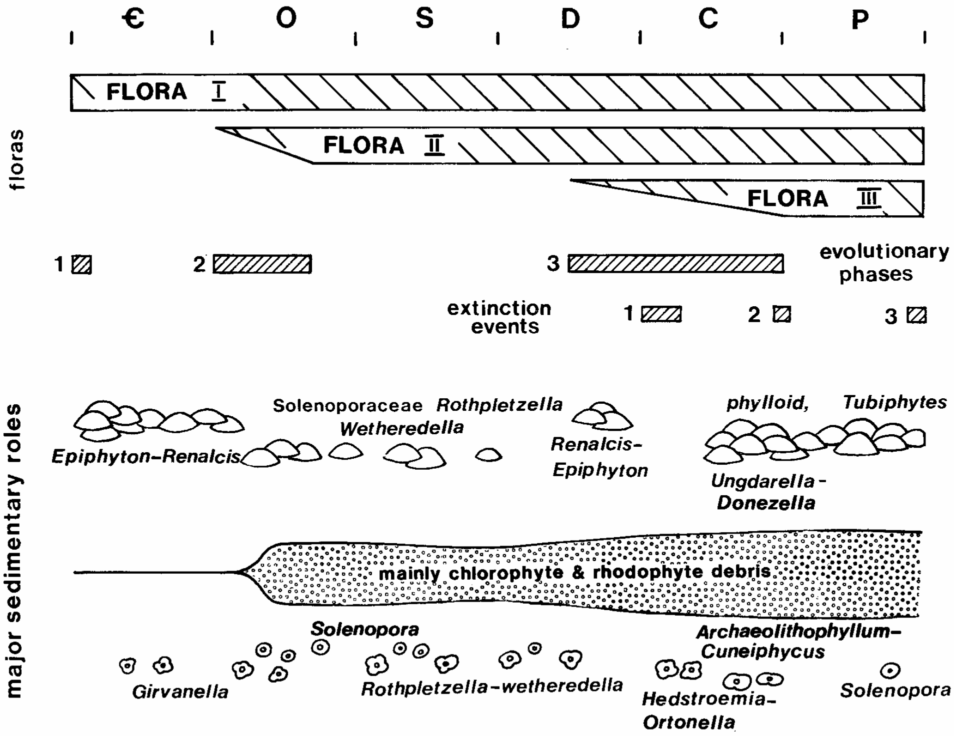


TEXT-FIG. 8. Number of major algal groups present in each Palaeozoic period. Data from text-fig. 1. Shading indicates first appearances.

Extinctions, at group-level, were concentrated near the Devonian–Carboniferous boundary, in the early Permian, and at the Permian–Triassic boundary (text-fig. 9). It is noteworthy that each flora has nearly similar numbers of groups persisting into the Mesozoic: three in the case of the Cambrian flora, two each for the other two floras (text-fig. 1). In fact, most of the groups appearing during the Cambrian and Ordovician are very long-ranging, five out of the eleven continuing not only into the Mesozoic but also into the Cenozoic. The groups appearing during the Devonian to Permian are relatively short-ranging, only *Tubiphytes* (which is also of doubtfully algal affinity) surviving into the Triassic.

Sedimentology

Cyanophytes locally dominated Cambrian reefs. In comparison Ordovician–Devonian algae were nearly always subordinate to metazoan reef-builders, although *Solenopora*, *Rothpletzella*, and *Wetheredella* can be important in the Ordovician and Silurian, and the 'Cambrian' *Epiphyton–Renalcis* association reappears in upper Devonian bioherms. However, nodules, including oncoids and *Solenopora* rhodoliths, are more common in the middle Palaeozoic than in either the Cambrian or Permian. The poor algal contribution to reef-building in the lower Carboniferous could be due to the scarcity of bioherms generally at this level, other than waulsortian mounds. It was middle Carboniferous expansion of the groups containing *Donezella*, *Ungdarella-Komia*, phylloid algae, and *Tubiphytes* which provided the new algal reef-builders for the upper Palaeozoic. Stromatolites built by calcareous algae are generally uncommon in the Palaeozoic.



TEXT-FIG. 9. Summary of calcareous algal floras during the Palaeozoic, showing phases of development and extinction, and sedimentological roles.

Although the patterns of reef-, nodule-, and stromatolite-formation by calcareous algae show sharp variations during the Palaeozoic, that of debris production is a relatively simple trend of increase throughout the era (text-fig. 9). Essentially this reflects the history of various fragile chlorophyte and rhodophyte groups.

Acknowledgements. This work is an outcome of discussion facilitated by the USSR Academy of Sciences at the Palaeontological Institute, Moscow, in September 1982, during a visit by Riding sponsored by the Academy and the Royal Society. We are grateful to Eleonora Radionova for advice on several algal groups. Larisa Voronova provided working space. Graham Elliott and Donald Toomey read the manuscript and made valuable suggestions for its improvement.

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Manuscript received 7 May 1983
Revised manuscript received 21 November 1983