

REVOLUTIONS IN THE PLANT WORLD

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ABSTRACT

The abrupt appearance of new land floras that represent fundamentally new adaptive types has corresponded largely with times of major transgressions. The taxa spread widely ("cosmopolitan") under broadly-zoned climates, undergoing adaptive radiation as environments (adaptive zones) diversify. However, as major marine regressions bring more narrowly-zoned climates with greater extremes, older taxa are restricted or exterminated as their adaptive zones shrink and/or disappear. These conditions also favour the origination in local areas of environmental diversity of new adaptive types which may then spread with the next transgression.

Thus the appearance of new forms and the disappearance of old forms . . . are bound together.

Darwin (1909, p. 279).

INTRODUCTION

The notion that changing global climate resulting from major changes in land-sea relations has had a guiding role in the history of life is scarcely new. It is either explicit or implicit in the works of DARWIN (1909, p. 256), LYELL (1867, Ch. 12, 14), and WALLACE (1880, pp. 68 & 220) and was considered by CHAMBERLIN (1898, pp. 457-8), CHAMBERLIN AND SALISBURY (1905, vol. 1, p. 671-2), and MATTHEW (1939, pp. 4-8). More recently, SIMPSON (1952) has discussed changing environments in terms of adaptive zones and the manner in which their changes have affected life. These and more recent studies have been concerned chiefly with the history of animal life, both marine and non-marine. To my knowledge, the major changes in vascular land floras since Silurian time have not previously been related to global climatic modifications that have resulted from shifting land-sea relations; hence they are outlined here.

The times of major change in global floras were relatively brief. They were marked by the rapid appearance of taxa previously unknown or at least very rare in the record, and by the restriction or extinction of groups previously dominant. These changes, which have been recognized for over a century (SAPORTA, 1881; WARD, 1885; CLEMENTS, 1916; SCOTT, 1924; SEWARD, 1936; SAHNI, 1937), are recalled briefly.

The initial appearance of simply constructed, undoubted vascular land plant is in the late Silurian to early Devonian, as exemplified by *Bucheria*, *Cooksonia*, *Gosslingia*, *Hedeia*, *Taeniocrada*, *Zosterophyllum*, and others. Some of them persisted into the middle Devonian, during which time other simply constructed plants (e.g. *Asteroxylon*, *Horneophyton*, *Rhynia*) are recorded, as well as those of more complex structure (e.g. *Gladoxylon*, *Pseudosporochnus*, *Protolepidodendron*).

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This early land flora was replaced late in the Middle Devonian by larger, more robust plants typical of the late Devonian that may be captioned the "first forests". Most were small trees or large shrubs that included early lycopods (*Zimmermannia*, *Archaeosigillaria*, *Cyclostigma*), arthrophytes (*Archaeocalamites*), early ferns (*Zygopteris*, *Cladoxyton*) and progymnosperms (*Archaeopteris*—*Gallixylon*, *Svalbardia*, *Paleopitys*, *Tetraxylopteris*).

These alliances gave way gradually to more advanced taxa during the Mississippian, and by the later part of the period the typical "Coal Measures" forests had become established over the lowlands. Among the commoner plants were dendroid lycopods (*Lepidodendron*, *Sigillaria*) and arthrophytes (*Annularia*, *Calamites*), seed ferns (*Mariopteris*, *Lyginopteris*, *Cyclopteris*), ancient conifers (*Calamopitys*, *Gordaites*), and new primitive ferns (*Botryopteris*, *Asterotheca*, *Anachoropteris*).

Near the close of the Carboniferous, (ELIAS, 1933; FREDERIKSEN, 1972), and gathering momentum in the early Permian, the lowlands were invaded by an entirely new flora characterized by ancient representatives of modern fern families (Osmundaceae, Gleicheniaceae, Marattiaceae), advanced seed ferns (*Taeniopteris*, *Gallipteris*), transitional conifers (*Voltzia*, *Walchia*), ginkgophytes (*Trichopitys*) and probably some early cycadophytes. Derivatives of this Permian flora dominated the Triassic and Jurassic landscapes. Those times are marked by the appearance of numerous new cycadophyte, conifer, and fern genera largely unrelated to those previously represented in the record.

The typical fern-cycadophyte-coniferophyte flora was supplanted rapidly by flowering plants late in the early Cretaceous, with the latter assuming dominance over the lowlands across middle latitudes during the late Albian-Cenomanian, and thence migrating polewards to dominate at high latitudes in post-Cenomanian time (AXELROD, 1959; SMILEY, 1969, 1972; STANLEY, 1967; BRENNER, 1974).

Inasmuch as these changes were global in scope, and included diverse lines of descent, such terms as Palaeophytic, Mesophytic, and Cenophytic have been used to denote the Eras of time in which vegetation composed of ancient, intermediate, and modern life-types lived (CLEMENS, 1916, esp. p. 283 *et seq.*). The principal vascular floras have been captioned Psilophyte, Pterophyte, Gymnophyte, and Angiophyte Palaeofloras, the names alluding to representative taxa of the four major levels or grades of organization (AXELROD, 1952, p. 50).

The origin of the successive new plant alliances commenced long before they appeared in the record. The problem of (a) where and when they evolved, and (b) the factors that account for the replacement of the older by the newer taxa, are clarified by Fig. 1. The upper graph depicts the fluctuations of seas on the continents. The data used by EYGED (1956) to construct it are the 34 palaeogeographic maps compiled by TERMIER AND TERMIER (1952), the numbers referring to their figures. The graph shows that the area of the continents covered by seas has decreased since the early Palaeozoic. The oscillations reflect variations in the volume of the oceans due chiefly to the building up and extension, or to the subsidence, of oceanic ridge systems (HALLUM, 1963; RUSSELL, 1968; HAYS & PITMAN, 1973). These are correlated with increased or decreased spreading rates and hence with lithospheric plate motions that appear to be controlled chiefly by variations in heat flow within the upper mantle. The lower graph (Fig. 1) represents Fig. 19 from *The Fossil Record* and was prepared by CUTBILL AND FUNNELL (1967) from data assembled by several palaeobotanists. It depicts the time of appearance of new and the extinction of older alliances of vascular plants, as based on the number of families in each major category (psilophyta, lepidophyta, arthrophyta, coniferophyta,

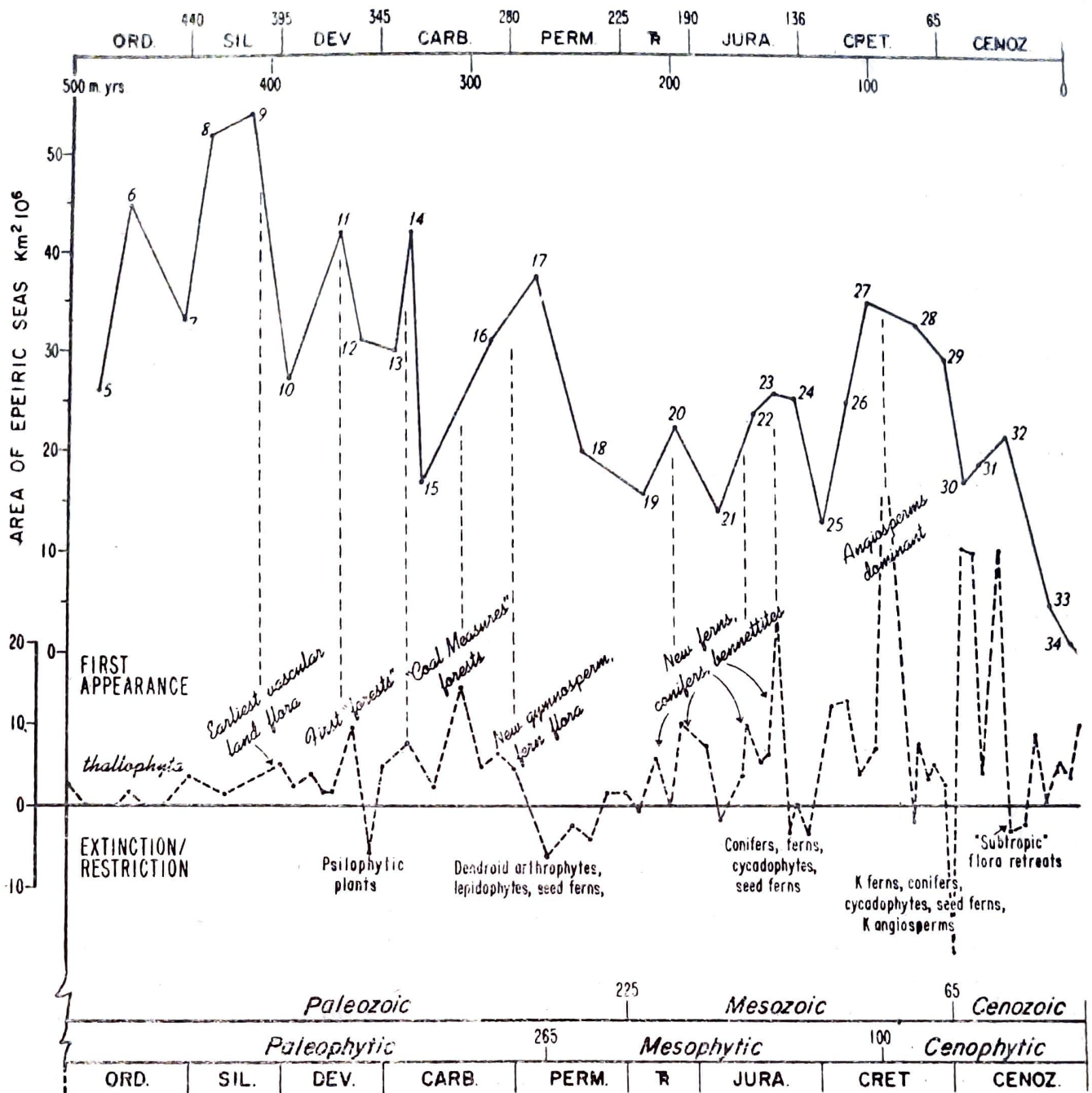


Fig. 1. The graphs show a relation between (above) the area of fluctuating seas on the continents (Eyged, 1956) calculated from data provided by TERMIER'S AND TERMIER (1952), and (below) the times of appearance of new and elimination of old taxa, based on data for 300-odd families summarized by CUTBILL AND FUNNELL (1967, fig. 19).

etc.). It is amply clear that both graphs have a similar tempo of change, and they are presumed to be causally related.

It is at times of major transgression plants representing new adaptive types appear and replace older ones (Fig. 1). There often is little affinity with taxa in slightly older strata in the same sequence. As emphasized by HARRIS (1931), the earlier Liassic flora of Europe has very few species from the previous Rhaetic flora: "...most of its species could not possibly have been derived from the known European Rhaetic species—they belong to different genera or families. Even when a Liassic species replacing a Rhaetic one belongs to the same genus... there is no sign of evolution from one species to the other."... (HARRIS, 1931, p. 159). He notes that this is also true of the differences

between the Bunter and Keuper, the Keuper and Rhaetic, and the Lias and Oolite floras. Comparable relations are also shown by taxa in the successive floral zones of the Carboniferous and Permian in eastern North America-Europe (DIX, 1939; READ & MAMAY, 1964).

The evidence supports the inference that transgressing seas bring conditions favourable for the invasion into the lowlands of plants that earlier had evolved in distant areas (see ELIAS, 1933), probably under local environments not then common near sites where the fossil record accumulated (AXELROD, 1952, p. 35; 1970, pp. 284-287; FREDERICKSON, 1972). The plants that originated in these sites often were under drought-stress provided by climates with a dry season or by local rainshadows (STEBBINS, 1952; AXELROD, 1967), and also by semibarren to barren monoliths, ridges, and stripped Precambrian basement terrains of subcontinental extent (AXELROD, 1972*a*). As discussed by STEBBINS (1952), conditions suitable for rapid and divergent evolution would be present in such areas. However, as seas encroached and thermal conditions moderated, many ancestral taxa would become extinct as their narrow adaptive zones diminished in size and disappeared (AXELROD, 1952, p. 47; 1970, p. 313). Nonetheless, some might readapt to more mesic conditions and spread widely over the region as new taxa. In this regard, STEBBINS (1952), following a suggestion by MATTHEW (1939, p. 8), has shown that some plants that apparently were adapted to drought have readapted to moister tropical and extra-tropical environments. The probable environmental basis for at least some of this readaptation is now apparent: climatic moderation on a global scale brought on by major transgressions resulting from the building up of mid-ocean ridges associated with active sea-floor spreading which rafts continents to new positions.

As epeiric seas retreat in response to ridge subsidence following active spreading, areas previously moist and relatively isothermal develop more continental climates. Numerous local new environments now appear and hence novel opportunities may arise for the origin of new adaptive types. There is some direct and much circumstantial evidence to indicate that major new groups have originated as small populations scattered in regions of diverse relief and climate remote from lowland basins where the bulk of the record accumulated (SIMPSON, 1952, Ch. 11). Since they occupied distant, often restricted areas, they entered the record only rarely, and chiefly when suitable conditions arose. In the case of plants, their appearance over the lowlands has corresponded with times of climatic moderation (Fig. 1). Such conditions result from the rifting of a continent and rafting its segments away by ocean-floor spreading, which brings transgressing seas that reduce environmental diversity over the lowlands. At the same time, it results in the restriction and extinction of older taxa as their narrow, specialized adaptive zones shrink and disappear (AXELROD, 1952, p. 47; 1960, p. 236).

These relations appear to explain the nature of the record in terms of plant taxa that have no forerunners in the underlying sequence. The data also support current views concerning factors that may account for some of the major crises in the history of life (SIMPSON, 1952; NEWELL, 1967). The principal selective factor in both extinction and replacement is certainly environmental—a new ecologic relation that is unfavourable for some, but not others: the adaptive zones of which they are a part have ceased to exist. The present data also reveal a relationship emphasized by SIMPSON (1952, p. 243) and by NEWELL (1967, p. 86). The major episodes of mass extinction among lowland and neritic animals that make up the bulk of the record have corresponded with times of widespread emergence, that is, at times of restricted seas as (*a*) in the late Devonian (high extinction among brachiopods, corals, trilobites, ammonoids, ostracods, fish, amphibia),

(b) in the late Permian (crinoids, brachiopods, corals, trilobites, ammonoids, ostracods, bryozoans, foraminifera, fish, amphibians, reptiles), (c) in the late Triassic (brachiopods, conodonts, reptiles, amphibia), and (d) at the end of the Cretaceous (crinoids, ammonoids, echinoids, sponges, bryozoans, fish, reptiles-dinosaurs).

The principal episodes of extinction were marked by a gradual geographic restriction in range and the variety of taxa in each alliance gradually diminished, though some lingered on into the next period. Extinctions owe to the multiple interactions of the numerous physical and biological factors that are always operating. As SIMPSON (1952, pp. 294-303), has emphasized a single cause of extinction of many groups at a particular time (e.g. late Permian) is likely only if it includes the concept that their adaptive zones have ceased to exist. This is because any environmental change will affect different taxa in diverse ways simply because each taxon is a unique biological system that responds in its own particular way to varied environmental stimuli. It is for this reason that we can never really know the exact cause of extinction of any fossil group, the exact factors are unknowable. Since each taxon responds differently to environmental stimuli it becomes understandable that advancing and retreating seas, by affecting the organism-environmental relationship (adaptation), have triggered major episodes of proliferation and extinction in different ways which have had different rates and different results in different groups—which is precisely what the record shows.

In this connection, it is recalled that the Era boundaries based on animals (Palaeozoic-Mesozoic, Mesozoic-Cenozoic) and on plants (Palaeophytic-Mesophytic, Mesophytic-Cenophytic) are offset (Fig. 1). The fundamental changes in the plant world occurred fully 30 million years earlier. This may be explicable on the basis that plants are rooted to their environment, whereas most animals can and do wander. That floras are more sensitive to climatic change is apparent from the much narrower (zonal) distribution of plant as compared with animal communities, both today and in the past. Thus, it seems expectable that climatic moderation due to broadly transgressing seas that produced rapid changes in the composition of global floras in the early Permian and the middle Cretaceous would have preceded those that affected animals later, in transitional Permian-Triassic and Cretaceous-Tertiary times. Numerous vascular plants of older alliances also disappeared at the end of the Palaeozoic and the Mesozoic, but the major changes in the flora of the world had *already* taken place. By the early Permian, the dominant lepidophytes, arthropytes and early seed ferns that typified the Carboniferous were being replaced rapidly by advanced ferns, gymnosperms and seed ferns whose derivatives were to typify the flora of the world into the middle Cretaceous. Then, as the major transgression commenced with the active breakup of Gondwanaland, angiosperms surged into the lowlands, fully 30 million years prior to the end of the Mesozoic.

Summarizing, there appears to be a correlation between the appearance of new global floras and major transgressing seas. These bring into the lowlands broadly-zoned, more uniform climates that promote adaptive radiation of major new groups that had originated earlier in local areas of environmental diversity. However, adaptation to relatively stable, broadly zoned climates is jeopardized by climatic change. Hence, times of major regression that bring increased thermal gradients, greater seasonal contrasts, and restriction of moist climates, not only result in widespread restriction and/or extinction, but favour the origination of new adaptive types. It is possible that the major changes at the plant Era boundaries preceded those in the animal world by some 30 million years chiefly because plants are more responsive to climatic zonation, and to climatic change.

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