Book Reviews

The Angiosperm Question

Origin and Early Evolution of Angiosperms. Boulder, Colo., Aug. 1973. CHARLES B. BECK, Ed. Columbia University Press, New York, 1976. x, 342 pp., illus. $17.50.

This book includes most of the papers presented at a symposium of the First International Congress of Systematic and Evolutionary Biology. None of the contributing authors suggests that he has answered the question of the origin of angiosperms, but it is easier now to see why the answer has been elusive, and the authors present views of remarkable general consistency.

Papers on similar themes treated in a different context by some of the same authors have recently been published in another symposium volume (*The Bases of Angiosperm Phylogeny*, 1975) by the Missouri Botanical Garden. I do not think either volume detracts from the other, and both should be read if one is to keep abreast of current thinking about the related topics of angiosperm paleobotany and phylogeny. All the contributions to the present volume have to do with origin and evolution and contribute data that serve to narrow the range for speculation. Excellent references accompany each of the chapters, and the book has an adequate index.

A perspective is provided for the book by an introductory chapter by Charles B. Beck, organizer of the symposium and editor of the volume, who mentions the many contrasting theories concerning the origin of angiosperms. We still do not know when or where angiosperms originated but, like Beck, I feel we may be getting closer to an answer.

N. F. Hughes presents a brief review of evidence that suggests to him that many problems of angiosperm origin and early evolution will be fully elucidated by study of pollen and other small-fragment fossils of early Cretaceous age. A much more extended account of this evidence has been presented by Hughes recently in book form (*Paleobiology of Angiosperm Origins*, Cambridge University Press, 1976). Hughes indicates that part of the difficulty in recognizing angiosperm origins may result from imperfect knowledge of ancestral Mesozoic gymnosperms.

One of the more significant papers is that of Gilbert J. Brenner, who discusses early records of angiospermous pollen from all over the world. The first tricolpate pollen noted occurs in Barremian–Early Aptian deposits in Israel and in Aptian beds in Brazil. In middle latitudes similar pollen appears during the middle Albian. By Cenomanian time similar fossil pollen occurs in deposits in the Arctic. Tricolpate pollen appears in middle-latitude Australian deposits during the middle Albian at about the same time as in middle latitudes of the Northern Hemisphere. The taxonomic affinity of the early tricolpate pollen is not clear, but Brenner thinks the pollen might have originated by an abrupt change in tetrad configuration from the magnolioid, monosulcate type. Although the amounts of information available from Barremian-to-Cenomanian beds in different parts of the world are unequal, Brenner has been able to distinguish low-, middle-, and high-latitude paleogeographic areas and to suggest a migration of angiosperms northward from tropical areas. A northern and southern Laurasian and a northern and southern Gondwana provinciality are indicated. Perhaps this use of the term "Gondwana" is questionable, since it refers to a period of time following break-up of Gondwanaland and to an area somewhat outside of those characterized by an earlier *Glossopteris* flora. Thirteen important localities for pollen of early angiosperms are listed and microfossil assemblages from five of them are illustrated.

The long paper on angiosperm dispersal by Rudolf M. Schuster makes use of the concept of centers of survival (relict centers) and plate tectonic history, rather than centers of origin and migration with continents stationary, to explain present angiosperm distribution. This explanation involves transfer of plant assemblages from a deglaciated Antarctica and India following the breakup of Gondwanaland. It predicts and explains the mixed character of the floras of Malesia and, to a lesser extent, of the Himalayan region, on the grounds that fewer descendants of angiosperm assemblages survived the equatorial transit of India. The Mesozoic and Tertiary sequence of tectonic displacement of India and Australia receives critical consideration. Schuster has been aided materially by his earlier studies of Asian bryophytes, which were better adapted to survive the long period of plate movement across the equator. Although the "drift" of Atlantic continents is best documented geologically, it is somewhat older than the displacement attributed to India and Australia and, for this reason and because it does not involve collision of continental areas, the Atlantic "rift" may not have materially influenced angiosperm distribution. Schuster does not bring it into the discussion, but he is aware that long-distance dispersal by other means can account for many distributional anomalies, particularly those of incidental floristic elements that probably have a diverse origin. It is easy to accept the idea that angiosperm dispersal patterns are much more complicated and the relicts more fragmented than they are often conceived to be even though this also leads to the conclusion that the distribution of extant taxa is inadequate to provide any indication of their ancestral origin. Many new and modified distributional maps are included in this chapter.

The study of James A. Doyle and Leo J. Hickey is based on pollen-stratigraphic control provided by detailed palynologic sampling of two deep cores that penetrate the Potomac Group in New Jersey. Pollen from the matrix of specimens of fossil leaves in the classical collections deposited at the U.S. National Museum (Smithsonian) provided a reliable basis for age determination entirely independent of assignments based upon the leaves. A morphologic basis for treatment has been used, which avoids entrapment by nomenclatural problems that are not yet resolved. The age sequence of results from both pollen and leaves turned out to be fully compatible with the arbitrary ranks of foliar organization that had been proposed earlier by Hickey and by Hickey and Doyle in 1971 and 1972. The demonstrated consistency of evolutionary progression in two separate organ systems of the early angiosperms thus provides a much better basis for phyletic interpretation than was previously available. Similar records elsewhere in the world suggest additional problems for distributional study. It is

not likely that angiosperms arose directly within the eastern United States.

On the basis of the new information, Doyle and Hickey present a speculative model for the origin of angiosperms. The angiosperm ancestor may have been a xeromorphous derivative from the cycadopsid gymnosperms, which developed "weedy" tendencies in a variable, probably xeric-temperate, environment. In a riparian setting the weedy early angiosperms may have diversified rapidly into nymphaeoid (monocot) and magnolioid (dicot) alliances, with subsequent facile development of different habits of growth and environmental preferences. The period for these important developments is almost entirely Albian. It appears from this that a critical time for the rapid diversification of angiosperms extended over about 8 million years at the end of the Early Cretaceous.

"Neoteny" is the process whereby essentially juvenile, developmental phases are prolonged and projected in ontogeny into mature stages of a life cycle. Armen Takhtajan discusses many such occurrences that may have been involved in the origin of angiosperms. Neoteny may be induced by stress of environmental conditions, like the seasonal arid regime and disturbed habitats postulated by Doyle and Hickey.

Although many have supposed that chromosome records can contribute little to solving general problems in evolution, F. Ehrendorfer has been able to draw general conclusions about angiosperm evolution from the patterns of chromosomal differentiation in gymnosperms and angiosperms. Karyological patterns favor a common origin for all angiosperms, as well as a common origin of Coniferophytina and Cycadophytina. The association of smaller chromosomes in angiosperms has facilitated polyploidy and was conducive to their greater evolutionary versatility.

The pollen morphology of 230 genera assigned to 35 families of plants in nine modern orders of angiosperms, treated informally as a "ranalean complex," has been examined by James W. Walker. He gives a concise, thorough review of the principal pollen characters that are phyletically useful, followed by data systematically presented on geographic distribution and pollen morphology, remarks, and assembled references for each of the 35 families. About 65 beautiful scanning electron micrographs of pollen, magnification various, but chiefly ranging from 300 to 5000, illustrate variation for each family. All data are vouchered for possible future reference. This extensive survey provides a basis for discussion of evolutionary trends and conclusions about the ancestral type determinable from modern angiosperm pollen.

Walker believes pollen evolution progressed from large grains to small; the primitive pollen coat may have resembled neither the alveolate exine of gymnosperms nor the tectate structure of modern angiosperms but might be better described as "atectate." The fossil pollen of *Clavatipollenites*, cited as the oldest tricolpate angiosperm pollen (Barremian) by Doyle and Hickey, probably is not close to the ancestral type (its closest alliance may be with the Chloranthaceae). Walker insists the most primitive angiospermous pollen grains were boat-shaped and large, anasulcate with a long sulcus, atectate, and more or less psilate. This agrees with the suggestion made by Brenner, and also conforms with the Albian evolutionary sequence proposed by Doyle and Hickey. Walker's most interesting suggestion is that the earliest primitive angiospermous pollen may have been confused as fossil "cycadophyte pollen" by palynologists. If this should be the case, the most primitive angiosperm pollen might be somewhat older than the Barremian.

G. Ledyard Stebbins has contributed an article "Seeds, seedlings, and the origin of angiosperms" that also reflects the consensus, although he does not preclude much earlier origin. Paraphrasing Stebbins only slightly, one may say that, from about the end of the Paleozoic until the early part of the Cretaceous, the evolutionary line leading to the angiosperms passes through a dark tunnel of ignorance. The important characters of angiosperms, such as the pollen tube, stigma and style, carpel or ovary, double-integumented anatropous ovule, reduced gametophyte, double fertilization, triploid endosperm, intercalary vegetative growth, and overall physiologic versatility, seem designed to provide for rapid response to selective environmental pressures such as drought, seasonal variation, and growth in disturbed habitats like talus slopes and eroded stream banks. Thus far, fossil evidence has shed little light within the tunnel, although caytonian fruiting structures may suggest an origin for the second integument. Stebbins thinks, however, that no really significant fossils have been found that can be related to the origin of angiosperms.

Character correlation designed to indicate general evolutionary status (degree of primitiveness or advancement) within the angiosperms is treated by Kenneth R. Sporne. Although the concept is simple, the statistical proof of it is not clear to me—one can appreciate the difficulty in avoiding circular argument. Twenty-four carefully chosen characters have been utilized for evaluation in dicots, and 12 in monocots. One objective has been calculation of an "advancement index" which would provide a numerical basis for relative evaluation for taxonomic groups. The data lend themselves to excellent diagrammatic representation, but it is difficult to evaluate the degree of generalization that is required for mathematical treatment. Sporne appreciates the importance of the fossil record, particularly fossil pollen, but it is difficult to incorporate the available fossil information for comparison with selected characters determinable in the extant flora.

The collection of papers in this volume must be of interest to anyone concerned with the derivation of our angiospermous flora. There is now a great revival of interest in this subject, which I can attribute only to the greatly enhanced fossil record that has recently become available through the serious botanical study of palynomorphs. Explanation of why modern plant distribution provides few answers that bear directly on angiosperm origin is provided by Schuster, but I am just as sanguine as Hughes is that fossil studies will eventually fully elucidate the origin and early evolution of angiosperms.

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Glacial Geomorphology

Glaciers and Landscape. A Geomorphological Approach. DAVID E. SUGDEN and BRIAN S. JOHN. Arnold, London, 1976 (U.S. distributor, Halsted [Wiley], New York). viii, 376 pp., illus. Cloth, £12; paper, £5.95; U.S. prices, $30 and $12.50.

Sugden and John, geographers from the Universities of Aberdeen and Durham, have produced an unusual and striking textbook about glaciers and their effects on the landscape beneath them. The book is divided into five almost equal parts, with three chapters in each. It treats glaciers and glacier dynamics, glacier distribution in space and time, glacial erosion and deposition and their effects on landforms and landscapes, and the meltwater system within, but not beyond, the confines of the glaciers.