

prepared from CO₂ from the three chemical fractions of the Sunnyvale bone sample are listed in Table 2. Preliminary values for ¹⁴C determinations obtained by direct counting were previously reported (22) and were expressed with respect to 5050 B.C. wood. The values cited here represent a large number of subsequent measurements and have been expressed in ¹⁴C years B.P.

The oldest radiocarbon value of approximately 5000 ¹⁴C years B.P. is exhibited on the total NaOH-soluble organic fraction (UCR-1437B/AA-52). We would suggest that the most probable age of the Sunnyvale skeleton is between 3500 and 5000 ¹⁴C years B.P. However, we recognize that the organic separation and purification techniques employed are not necessarily completely effective for all bone samples (23). Nevertheless, we are not aware of any instance where undetected contamination in carefully prepared, known-age bone samples has documented anomalies of the magnitude required to bring the indicated ¹⁴C ages of the organic fractions of the Sunnyvale bone into agreement with its racemization-deduced age.

The ¹⁴C values obtained on the Sunnyvale skeleton clearly assign it to the middle Holocene. This age assignment is fully consistent with the geologic, archeological, and anthropometric evidence and with associated ¹⁴C determinations. The age of the Sunnyvale hominid deduced from its aspartic acid D/L ratio differs by more than an order of magnitude from that indicated by the ¹⁴C values. The uranium series-derived age estimate also appears to be somewhat discordant when compared with the ¹⁴C determinations, although there is certainly a possibility that modern carbon contamination in the bone was not totally excluded by the purification techniques employed in the ¹⁴C analysis.

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Winteraceous Pollen in the Lower Cretaceous of Israel: Early Evidence of a Magnolialean Angiosperm Family

Abstract. *Pollen of the primitive angiosperm family Winteraceae has been discovered in the Aptian-Albian of Israel, extending the fossil record of this phylogenetically important family of flowering plants from the uppermost Upper Cretaceous back some 40 million years to the upper Lower Cretaceous. This appears to represent the earliest known record of a magnolialean angiosperm family and is convincing evidence for the existence in the Early Cretaceous of an extant family of angiosperms.*

The early fossil record of the angiosperms or flowering plants consists almost entirely of isolated parts of various organs that only rarely can be related to the same plant. The paleobotany of early angiosperms has therefore mostly been concerned with the separate study of diverse kinds of angiosperm megafossils (leaves, wood, flowers, fruits, and seeds) and microfossils (pollen grains, cuticle, and wood fragments). This fact, coupled with the strong bias of most early paleobotanical investigations toward the study of angiosperm leaves, helped contribute to a situation that puzzled botanists for many years—namely the apparent rapidity with which the angiosperms seemed to appear approximately 115 million years ago late in the Early Cretaceous. It has become clear that the seeming sudden appearance of angiosperms in the fossil record was an erroneous impression resulting from the misidentification

of early fossil angiosperm leaves as the leaves of relatively advanced living angiosperms (1).

Although spectacular finds of early fossil angiosperm floral parts occasionally occur (2), most of the new insight into the early history of the flowering plants has been gained from study of early fossil angiosperm pollen grains along with the critical reexamination of early fossil angiosperm leaves (1). Although some Early Cretaceous leaves show systematic affinities with extant angiosperms, and in particular with the order Magnoliales, which is widely considered to be the most primitive group of living flowering plants (3), none apparently is referable to any extant angiosperm family (4). This is not the case with the fossil angiosperm pollen from the Early Cretaceous that we describe.

In his review of the fossil pollen records of extant angiosperms, Muller (5)

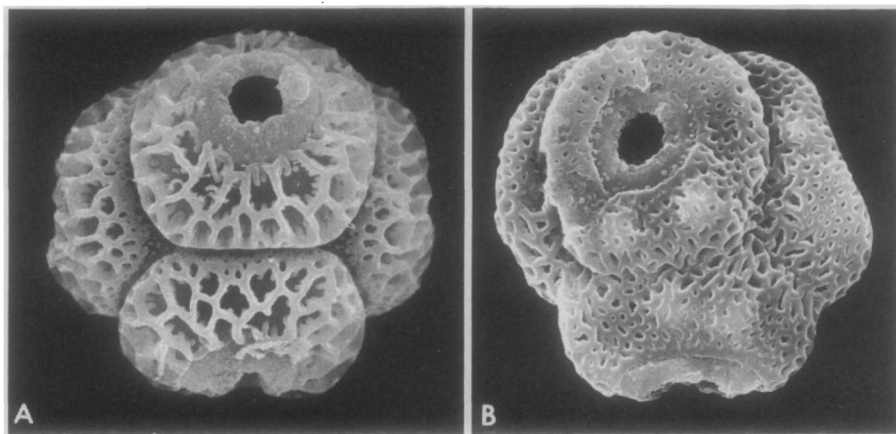


Fig. 1. Scanning electron micrographs of pollen of the angiosperm family Winteraceae. (A) Pollen tetrad of the extant winteraceous species *Drimys granadensis* L.f. from Costa Rica ($\times 1250$). (B) Fossil winteraceous pollen tetrad (Walker & Walker fossil palynomorph 393) from the Lower Cretaceous (Upper Aptian–Lower Albian) of Israel ($\times 1450$).

accepts as reliable the published fossil pollen records for 139 angiosperm families and recognizes 31 angiosperm families as having a pre-Tertiary pollen record more than 65 million years old. Of these 31 angiosperm families, only the Chloranthaceae is considered by Muller to date back to the Early Cretaceous, appearing more than 100 million years ago in the Aptian (109 to 114 million years ago). Muller's acceptance of the Early Cretaceous angiosperm pollen *Clavatipollenites* as chloranthaceous was based on light microscope comparisons with modern chloranthaceous pollen; ultrastructural studies of *Clavatipollenites* and modern chloranthaceous pollen (6) support this, at least for some of the *Clavatipollenites* pollen. Even though the Chloranthaceae are generally recognized as primitive angiosperms in the wide sense, most taxonomists consider them to be a relatively specialized primitive family (3). Our discovery is of pollen of the primitive magnolialean angiosperm family Winteraceae, found in the Upper Aptian–Lower Albian of Israel (Figs. 1B and 2).

The family Winteraceae has attracted the interest of systematists since the early 1940's (7). One of only five living angiosperm families with primitively vessel-less wood, the Winteraceae is also known for the unsealed carpels of the genus *Tasmannia*, which rival those of the angiosperm family Degeneriaceae in primitiveness. According to Muller (5), the oldest pollen record of the Winteraceae is *Pseudowinterapollis wahooensis* from the uppermost Cretaceous (~ 65 to 70 million years old) of southern Australia and New Zealand. Thus the discovery of winteraceous pollen in the Upper Aptian–Lower Albian of Israel (~ 105 to 110 million years old) extends the known fossil record of this family

from near the Upper Cretaceous–Tertiary boundary back some 40 million years to the upper Lower Cretaceous. This fossil winteraceous pollen appears to represent the earliest known record of a magnolialean angiosperm family, placing an extant family of flowering plants in the Early Cretaceous.

Winteraceous pollen, including that shown in Figs. 1B and 2, was found in Geological Survey of Israel core sample 5, box 6 (Brenner sample 45), of the Zohar 1 well from the Northern Negev of Israel. This core is in the Lower Cretaceous Kurnub Group, which is divided into the Zewaira (basal), Dragot, Malhata, and Uza (top) formations. Core sample 5 comes from the Dragot Formation at 910 m, which has been correlated with the iron-oxide oolite horizon exposed in the Makhtesh HaGadol (8). This horizon represents the first marine intercalation in the Makhtesh HaGadol,

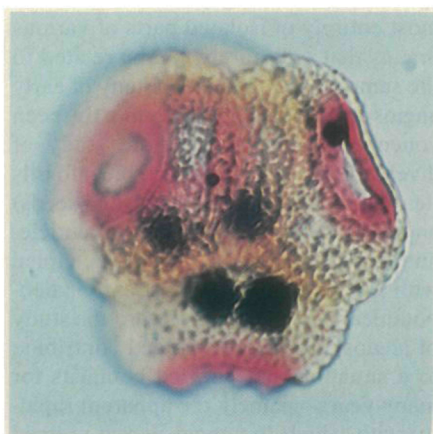


Fig. 2. Photomicrograph of the same fossil winteraceous pollen tetrad shown in Fig. 1B stained with safranin, showing a chemically distinct inner wall layer or endexine (red-stained areas) that forms a prominent ring around the inside of the porelike aperture of each pollen grain in the tetrad ($\times 1450$).

which has been dated as Late Aptian–Early Albian (9) or Early Albian (10). So far we have recovered three winteraceous pollen tetrads from this sample, and two others from the Uza Formation at 665 m in Geological Survey of Israel core sample 3, box 2 (Brenner sample 55), of the Zohar 1 well. On the basis of the spore and pollen assemblage this latter sample appears to be Early to early Middle Albian in age. Angiosperm pollen as a whole is rare in these core samples and constitutes no more than 5 to 10 percent of their total palynoflora and is represented mostly by small tricolpate pollen grains (tricolpate pollen is lacking and monosulcate angiosperm pollen grains are rare). Although fossil winteraceous pollen is rare in these samples, it is unlikely a contaminant because the family Winteraceae does not occur now in either the Middle East or the United States. Moreover, this fossil pollen is not referable to that of any extant Winteraceae.

The Winteraceae have some of the most distinctive angiosperm pollen known (11). Features of pollen of extant Winteraceae (Fig. 1A) that occur in this fossil pollen (Fig. 1B) include (i) pollen grains in permanent, tetrahedral tetrads; (ii) each pollen grain with a single, large, porelike aperture on the side facing away from the center of the tetrad; and (iii) a distinct, ringlike annulus around each porelike aperture. In addition, a chemically distinct inner wall layer, the endexine, is present in this fossil pollen, forming a prominent ring around the inside of the porelike aperture of each pollen grain in the tetrad (Fig. 2). This combination of pollen features is not known in any other family of flowering plants (11, 12).

Basic fuchsin is widely used to identify endexine in fossil (as well as modern) pollen (13), but it is somewhat unusual for the nonspecific stain safranin to produce strong differential staining of the endexine (Fig. 2), although this is not unknown in fossil pollen (14). The fossil pollen is definitely winteraceous, but it cannot be referred to any genus of extant Winteraceae described by Pragowski (11). Moreover, this Early Cretaceous pollen is decidedly more primitive than any extant winteraceous pollen in that it has only small holes or tectal perforations in its outermost, rooflike wall layer or tectum (Fig. 1B), instead of the large spaces or lumina that are characteristic of the coarsely reticulate pollen of most extant Winteraceae (Fig. 1A). This lends additional support to the proposal that the path of the evolutionary trend was from tectate-imperforate pollen (without tectal perforations) to tectate-perforate

pollen (with tectal perforations) to semitectate pollen (with a prominent reticulum formed by enlarged tectal perforations) (15).

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When Is an Island Community in Equilibrium?

Abstract. *To determine whether the number of species in a biota is in equilibrium requires a colonization model. In a simple Markov model, each species' extinction and immigration probabilities are estimated independently from available data. For one inland and two island avifaunas, a simulation with these probabilities shows that the trajectories of species richness through time do not manifest the regulatory tendencies expected if species interactions cause species richness to be continuously redressed toward an equilibrium.*

The equilibrium model of island biogeography (1) received instant approbation and was quickly applied to many taxa of oceanic and habitat islands (2). Early objections were dismissed (3), but reconsideration of assumptions and predictions of the model has led to a more tempered judgment of its applicability (4, 5).

A persistent problem with the model is subjective assessment of its most fundamental contention—that species number tends toward an equilibrium. The avifauna of the Farne Islands (Fig. 1) seems equilibrial to some (6), though number of species varies more than 100 percent. By contrast, the passerine birds of Skokholm Island (Fig. 1) are judged nonequilibrial (5), though to me the trajectory of species number does not seem qualitatively different from that of the Farne Islands. How much variation in species number is permitted in an equilibrium biota appears to be arbitrary (5). A coefficient of variation less than .20 (6) or less than .05 (7) may be demanded. Although variation in species number of 16 percent or less may be classed as equilibrial (8), the Farne Islands variation far exceeds this percentage.

A colonization model is required before equilibrium can be assessed, just as a null model is needed generally to interpret ecological data (9). The model may predict a specific equilibrium and a certain amount of temporal variation about it; the trajectory of species numbers may then be compared to predictions. Or the model may simply state certain characteristics that an equilibrated process should have that an unequilibrated process should lack. In either event, criteria for judging whether given data are equilibrial must be clearly stated; the hypothesis of equilibration must be falsifiable or the entire equilibrium concept will degenerate into a truism.

The original equilibrium model (1) connotes a regulation of species number by interactions among species, such that the presence of species A modifies the probability that species B will suffer extinction (10). Though for mutualistic or commensal species pairs this extinction probability may be lowered, advocates of the model argue that on average for all species pairs, one species' presence raises the extinction probability of the other (11). Consequently, high species numbers will, on average, increase ex-

tingtion probabilities for all species, and species numbers will fall. Low species numbers will lower extinction probabilities, and species number will be redressed upward. Higher order interactions such as diffuse competition can modify the details of any particular scheme, but not the general expectation of regulation: high species numbers are followed by increased extinctions per species, and low species numbers by low extinctions per species.

One cannot simply correlate the extinction rates per species with number of species present, since a positive correlation would be expected as an artifact (10). In a bounded sequence of random, independent numbers, S_i , one would expect a positive correlation between S_i and $(S_i - S_{i+1})/S_i$. One might, however, be able to perceive regulation (as opposed to a null hypothesis of no regulation) by a version of a runs test (12) that allows for the event of "no change."

One appropriate model to test against the regulatory equilibrium model is a Markov model, recently termed the "molecular theory of island biogeography" (13). If every species in a pool of size p has constant immigration and extinction probabilities (i_k and e_k), an equilibrium number of species ultimately obtains (14):

$$S_{eq} = \sum_{k=1}^p \frac{i_k}{i_k + e_k} \quad (1)$$

The colonization curve is a sum of independent Markov processes, where each species has constant transition probabilities of absent to present (i_k), present to absent (e_k), absent to absent ($1 - i_k$), and present to present ($1 - e_k$). To take this model further one must know the distributions of i_k and e_k (15), but the only species pool for which these distributions are available is Florida Keys mangrove insects (16). Since the data on birds of Skokholm and the Farne Islands were tabulated species by species (17), they can be used to estimate Markov transition probabilities. For any species k , the fraction of presences followed by absences is an estimate of e_k , and the fraction of absences followed by presences is an estimate of i_k . For example, if species k were absent during 20 censuses, and for 10 of these it was present at the next census, one would estimate i_k as $10/20 = 0.5$. In addition to the two insular avifaunas, I also tabulated transition probabilities for birds of Eastern Wood (18), a 16-ha wood in 112-ha Bookham Common, an inland "habitat island" in Surrey, England (19).

For each avifauna, I simulated colonization. Each simulation began with the