16. The stated condition appears to be consistent with the sketchy observational data that is available. We expect that the precise necessary condition is more subtle, even within the model.
17. D. S. Luther, D. E. Harrison, R. A. Knox, *Science* **222**, 327 (1983). The model does not produce these westerly bursts; more generally, it understates the variability of the atmosphere over the western Pacific. However, the model does exhibit high-frequency variability in the central Pacific, which can have the same triggering effect.
18. A calculation without the mean annual cycle (perpetual May condition) also gives long-period oscillations, but its evolution and amplitude decays in a completely different way than real events and the full model.
19. Ocean dynamics determine a tendency toward a positive heat anomaly along the equator in response to equatorially confined easterly wind anomalies. [See M. A. Cane and E. S. Sarachik, *J. Mar. Res.* **39**, 651 (1981), figures 2 and 3.]
20. Supported by NASA grants NAGW 463 and NAGW-582 and grant OCE 84-44718 from the National Science Foundation. Contribution 3803 of the Lamont-Doherty Geological Observatory.

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The Diversification of the Leguminosae: First Fossil Evidence of the Mimosoideae and Papilionoideae

Abstract. *The legumes are an important group of flowering plants with a poorly documented evolutionary history. New fossil evidence provides data on the timing of the origin of the two derived subfamilies of legumes (the Mimosoideae and Papilionoideae). These data strongly suggest the importance of bee pollinators during a major period of angiosperm diversification.*

The legume family of flowering plants is large (14,000 species) and economically and ecologically important. Because the fossil record has not provided enough information to allow an assessment of their putative evolutionary history, it has been necessary to reconstruct their evolutionary history from contemporary biogeography or to infer it from the comparative morphology of modern taxa (*1, 2*). The legumes are generally thought to have originated during the Upper Cretaceous in west Gondwanaland and to have subsequently diversified into three subfamilies, Mimosoideae, Caesalpinioideae, and Papilionoideae, which were well defined by the Middle Eocene (*1, 2*). Evolution within the legumes is regarded as having proceeded from taxa with generally open flowers and vulnerable nectar and pollen, mostly in the subfamily Caesalpinioideae, toward taxa with flowers modified to protect these resources, the Mimosoideae and Papilionoideae, in conjunction with increasing pollinator specificity, in particular the bee pollinators that are fundamental to the family today (*3*).

The fossil record of the legumes is tantalizing; leaflets and fruits are fairly well known from the Middle Eocene on, but the reports are rarely accompanied by data that support the suggested affinities. As interpreted on the basis of unequivocal fossil evidence (*2*), the history of the legumes begins with Upper Cretaceous pollen of the Caesalpinioideae. The Mimosoideae appeared by the Middle Eocene on the basis of pollen and varied megafossil evidence (*2*), and the Papilionoideae with highly derived zygomorphic flowers have no fossil record until the appearance of Pliocene pollen (*4*). New fossil floral evidence, discovered at a single locality in western Tennessee, reveals that the two derived subfamilies, the Mimosoideae and Papilionoideae, were well developed by the Paleocene-Eocene boundary.

The fossil mimosoid inflorescences are racemose. Floral envelopes consist of a deeply lobed calyx and five valvate petals. There are ten stamens of uneven length with versatile, sagittate anthers (Fig. 1a). Pollen is shed in monads of tricolporate grains, and exine is smooth perforate with tectate-columellate ultrastructure (Fig. 1, d through f). The pollen wall is distinctive because the columellae are relatively long (Fig. 1e). Ovaries are superior and stipitate and are sometimes preserved in an expanding condition (Fig. 1a). The stigmatic region is occasionally well preserved. Stigmas are tubular (a mimosoid character) and tiny (0.10 mm in diameter). In one fossil the stigma is packed with the same type of pollen that has been isolated from its anthers and those of similar specimens (Fig. 1, c and d). The presence of pollen in the stigma of this flower is consistent with the expanding ovary and suggests that it had been fertilized as well as pollinated at the time of preservation. The extremely small size of the stigma and the fact that it was filled with one kind of pollen are evidence consistent with insect pollination.

We verified the affinities of these fossil flowers by entering 23 discernible characters into an open access key (*5*) and then by considering pollen micromorphology, ultrastructure, stigma type, and ovary position. Only the subfamily Mimosoideae of the Leguminosae circumscribes all these characters. The fossils do not, however, share their entire complement of characters with the flowers of any single modern genus and represent an extinct taxon.

Character state polarities in the Mimosoideae were recently suggested on the assumption that the *Dimorphandra* group of the subfamily Caesalpiniodeae, tribe Caesalpineae, are the closest related nonmimosoid legumes (*6*). By this standard, most of the characters of these fossil flowers are primitive in the subfamily [that is, the morphocline and chronocline are congruent (*7*)]. Moreover, the fossils are consistent with the possibility that mimosoid ancestors were *Dimorphandra*-like because they share several characters with the taxa composing that subfamily (*8*). One of these characters, pollen micromorphology, appears to be a synapomorphy linking the Mimosoideae and the *Dimorphandra* group of the Caesalpinieae (Fig. 1f) (*8*).

Unequivocal evidence of the most derived of legume subfamilies, the Papilionoideae, is missing from the pre-Pliocene fossil record (*4*), but papilionoid flowers have been discovered in Paleocene-Eocene sediments (Fig. 1, b and g). Flowers are often preserved with an expanding ovary (Fig. 1b). Floral and fruit characters limit the affinities to the legumes (*5*), and floral envelope features are typical of the papilionoid legumes in particular. The calyx is unevenly lobed, and the corolla consists of a standard, two wing petals, and a partially fused keel (Fig. 1, b and g). In the Leguminosae, zygomorphic flowers are not restricted to the Papilionoideae. Although uncommon, they are also found in the subfamily Caesalpinioideae. Two floral envelope characters differentiate flowers of the two subfamilies. First, there is a significant difference in aestivation. In the true papilionoid flower the standard is inserted outside the wing petals, whereas in the caesalpinioids the wing petals include the standard (*9*). In the fossils it has been possible to determine the relative positions of the standard and wing petals, because in one specimen floral envelope preservation is three-dimensional and illustrates that the base of the standard is outside the wing petals.

Another floral envelope feature that separates the papilionaceous caesalpinioids from the true Papilionoideae is wing petal sculpturing (*10*). Wing petals serve three functions in the papilionoid legumes: they are attractants, they provide a landing platform, and they serve as levers to move the wing-keel complex downward to facilitate pollination and pollen pickup (*10*). In order to accomplish the latter two functions, the wing petals must provide a good foothold for pollinators. In many papilionoid blossoms, but in no caesalpinioids, the wings are sculptured, a morphological character that is assumed to provide better traction for the pollinator. Wing sculpturing was recently reviewed with respect to its distribution, variation, and taxonomic significance (*10*). Sculpturing may be found on any location on the wing or on the whole wing but is usually (68 percent of the time) found in the upper proximal region (*10*). Sculpturing also varies in form from deeply grooved in a lunate fashion in rows (Fig. 1h) to a more undulating pattern. Examination of the proximal area of the wing petals of the fossil flowers reveals typical papilionoid sculpturing patterns (Fig. 1i). Floral envelope characters, then, are strongly suggestive of affinities with the modern Papilionoideae.

These are the first zygomorphic flowers in the fossil record (*11*). Zygomorphic flowers are generally associated with bee pollinators (*12*), and bee pollinators are specifically associated with papilionoid legumes (*3*). These fossils are thus the earliest and perhaps strongest indirect evidence of bee pollination.

The presence of flowers of both of the derived subfamilies of legumes at the Paleocene-Eocene boundary reveals that these taxa had diversified by that time and implies that the process of diversification began earlier. The assumption that bee pollination was important in the divergence of papilionoid and mimosoid legumes from caesalpinioid ancestors further suggests that bee pollination was an important factor earlier in the Paleocene. This fossil evidence is consistent with other evidence (*11, 13, 14*) in suggesting that pollination by bees, and therefore pollinator fidelity, were significant elements in a major Late Cretaceous–Early Tertiary radiation of the flowering plants.

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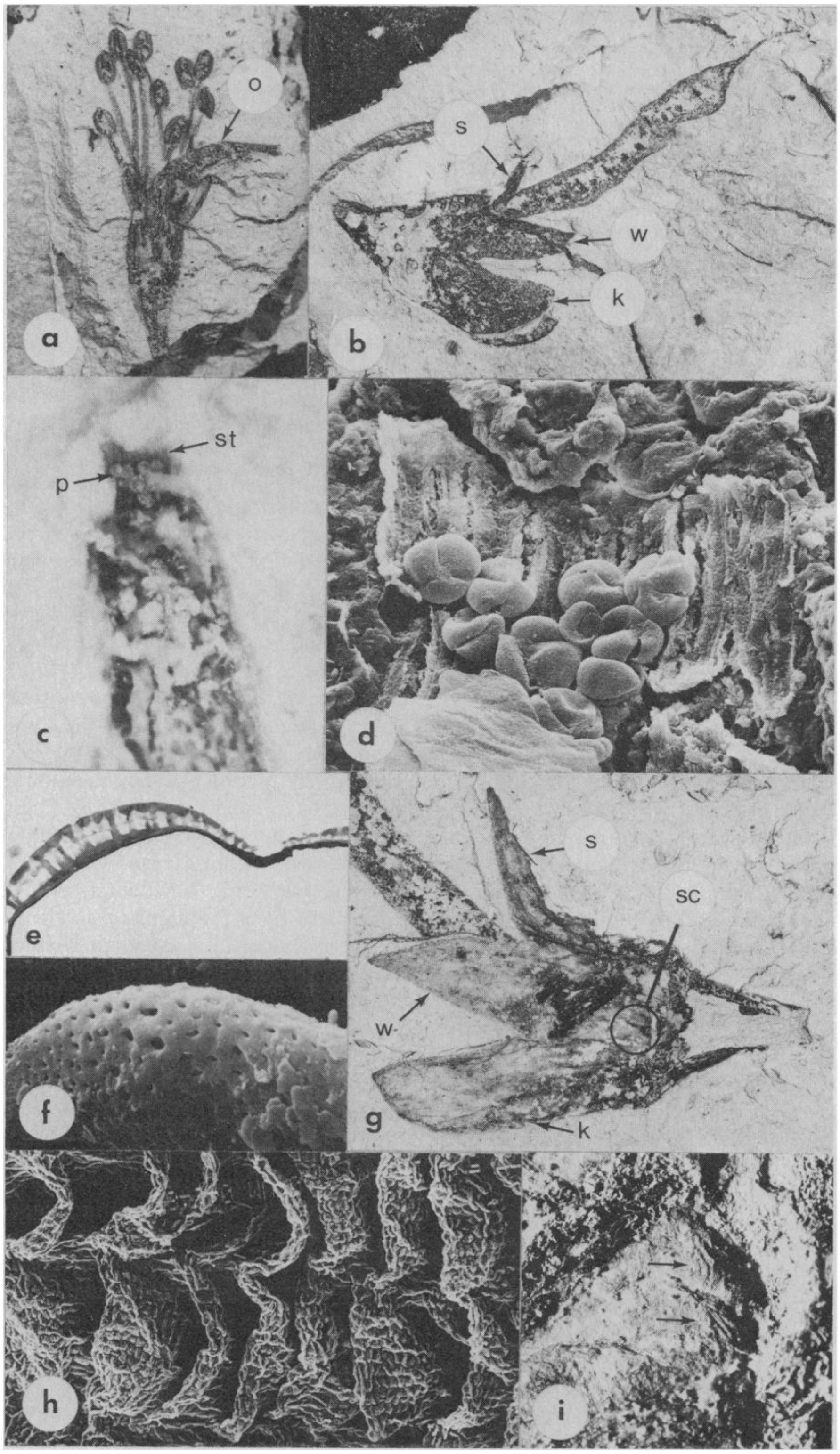

Fig. 1. Illustrations of fossil (a through g and i) and extant (h) material. (a) Mimosoid blossom showing the basic floral features and an expanding ovary (o) (×4). (b) Papilionoid blossom with an expanding ovary; standard (s), wing petals (w), keel petals (k) (×2.5). (c) Enlargement of the tip of the expanding ovary of the counterpart of the specimen illustrated in (a) showing the wall of the tubular stigma (st) and the pollen grains (p) within. (×120). (d) Scanning electron micrograph (SEM) of the stigmatic region illustrated in (c). There are striations in the stigma wall and tricolporate pollen grains (×711). (e) Transmission electron micrograph view of the mimosoid pollen wall (×4150). (f) SEM close-up of mimosoid pollen illustrating the micromorphology (×3660). (g) Another papilionoid blossom illustrating the standard (s), wing petals (w), and keel petals (k). The proximal part of the wing petal (enclosed by the circle labeled sc) is sculptured. The sculptured part of the wing petal is illustrated at higher magnification in (i) (×5). (h) SEM view of the abaxial proximal part of the wing petal of extant *Sophora augustifolia* showing two rows of lunate sculpturing (×77). (i) Obliquely illuminated view of the abaxial proximal wing petal of the specimen shown in (g) (sc), illustrating at least two rows of lunate sculpturing (arrows) (×13).

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Chronic Herbivory: Impacts on Architecture and Sex Expression of Pinyon Pine

Abstract. *Pinyon pine,* Pinus edulis *(Engelm.), in Northern Arizona is exposed to recurring high levels of herbivory by the moth* Dioryctria albovitella *(Hust.). During a 3-year period, infested trees experienced on average a 30 percent reduction in annual shoot production. This herbivory affects tree architecture, growth rate, reproductive output, and sexual expression. Less infested trees produce 47 percent more trunk wood, 43 percent more branch wood, and are monoecious. Architectural changes in infested trees can result in functionally male plants due to a complete loss of normal female cone-bearing ability. When herbivores are experimentally removed, normal growth and reproduction patterns resume. These strong herbivore impacts should represent a potent selection pressure in the evolution of host traits.*

The demonstration of significant herbivore impacts on ecologically and evolutionarily important plant traits is often lacking data on native plant-herbivore systems (*1, 2*). In the absence of such data, purported plant defenses and adaptationist's arguments in general have been questioned (*3–5*). Furthermore, with herbivores generally consuming less than 3 to 8 percent of the annual foliage production (*6*), examples of herbivory by native pests that is both acute and chronic (that is, repeated high levels of attack) are few (*7*). We examined the impacts of the stem- and cone-boring moth *Dioryctria albovitella* on architecture, growth rates, reproduction, and sex expression of the monoecious conifer *Pinus edulis*. Herbivore-mediated sex expression in plants has been little studied (*8*) because sex expression is thought to be governed by other factors such as plant stress, age, or density (*9–15*).

Studies were conducted from 1982 to 1984 near Sunset Crater National Monument, Flagstaff, Arizona. From a study site of approximately five hectares, 40 trees were selected on the basis of growth form; 20 had a prostrate shrublike crown and 20 an upright treelike crown. Because tree age may be correlated with resistance to herbivore attack (*16, 17*) and sexual expression (*12–14*), trees were matched for age. Mean counts of tree rings (± standard error of the mean) showed both groups to be nearly identical in age (prostrate, 147 ± 8.5 years; upright, 144 ± 7.9 years). All trees were fitted with dendrometers to measure current year's growth and censused for insect-caused shoot mortality as well as female cone and male strobili production. An average of 205 shoots was collected from all sides and heights of each tree.

Tree architecture is highly correlated with shoot mortality caused by *D. albovitella*. In trees with the prostrate growth form, 28.1 ± 2.52 percent of the current year's shoots were destroyed in 1983, whereas only 7.8 ± 1.28 percent of the shoots of upright trees were destroyed ($t = 7.180$, d.f. = 38, $P < 0.001$). This represents a 3.6-fold difference in shoot loss due to herbivory.

The complex branching architecture of heavily infested trees results from the selective destruction of terminal shoots by the stem-boring larvae of *D. albovitella*. In an examination of 360 shoots from a single tree, 82 percent of the terminal shoots and 10.4 percent of the lateral shoots were killed ($\chi^2 = 175.461$, d.f. = 1, $P < 0.001$). Thus, the probability that a terminal shoot will be destroyed is nearly eight times that for a lateral shoot. Such selective shoot mortality eliminates the normal patterns of apical dominance that are so important in determining tree architecture (*18, 19*).

The selective destruction of terminal shoots stimulates the production and growth of lateral buds, and the plant becomes a dense shrub. Figures 1A and 1B show that as the shoot mortality increases, the production of new terminal buds declines ($r^2 = 68.4$ percent, $n = 40$, $P < 0.01$), and the production of new lateral buds increases ($r^2 = 35.7$ percent, $n = 40$, $P < 0.01$).

When *D. albovitella* is experimentally removed from heavily infested pinyons, tree architecture is affected by an increase and decrease, respectively, in the production of new terminal and lateral buds. Three trees were sprayed with a systemic insecticide (Cygon) to kill stem-boring insects. Shoot mortality and bud production before and 1 year after treatment was compared with that on 20 nearby heavily infested control trees (Table 1). Although control trees showed no statistically significant changes from year to year ($P >> 0.05$), experimental

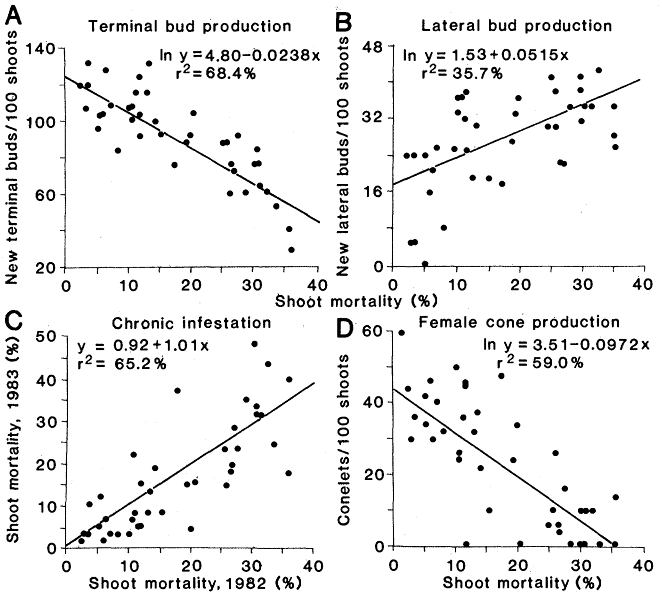

Fig. 1. Herbivory affects the production of terminal and lateral buds, which determines tree architecture and sexual expression. (A) As shoot mortality increases, the production of terminal buds declines, whereas (B) lateral bud production increases. This alters the pattern of apical dominance, and trees eventually become shrubs. Pinyons suffer chronic and acute herbivory (C). Trees with the highest shoot mortality in 1982 also suffered the highest shoot mortality in 1983. With increasing shoot mortality trees change in their sexual expression from monoecious to functionally male plants (D). The production of female cones declines to 0. Mortality percentages are based on average samples of 205 shoots from each of 40 study trees. Variables in Figures A, B, and D are transformed with a natural logarithm. The standard errors of the slopes in A, B, C, and D are 0.00257, 0.0108, 0.01176, and 0.0129, respectively.