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18. Data for the radiosonde stations listed in Table 1 and gridded monthly mean surface temperature data over Antarctica are available starting from 1958. However, because the temporal coverage of these data improved markedly in the late 1960s, our analysis is restricted to the period after 1969. Results based on the NCEP/NCAR reanalysis were found to be in excellent agreement with those derived from the radiosonde data after ~1979, which corresponds to the introduction of satellite data into the reanalysis assimilation scheme. For example, the monthly mean time series of 500-hPa geopotential height averaged over the radiosonde stations listed in Table 1 is correlated with 500-hPa geopotential height anomalies from the reanalysis averaged over the SH polar cap (poleward of 60°S) at a level of $r = 0.89$ for the period 1979–1998, and the amplitude and seasonality of trends calculated from these two time series are virtually identical. Results based on the NCEP/NCAR reanalysis were found to diverge from those derived from the radiosonde data before 1979, particularly in the lower stratosphere. For a thorough comparison of the NCEP/NCAR reanalysis and radiosonde data over Antarctica, see (*51*).
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31. The significance of the correlations in Table 3 was estimated from the t statistic, assuming only one degree of freedom for every 2 years. The significance of the linkages in Fig. 3 was estimated assuming one degree of freedom for every year (the time series used in Fig. 3 consist of 6 months per year).
32. Because the trend in the SAM accounts for a relatively small fraction (9%) of the total month-to-month variance during December-May from 1969–1998, the fractions of the trends that are linearly congruent with the SAM index in Fig. 3 are not strongly sensitive to shared trends in the time series. For the shortest period of record considered (December-May monthly means from 1979–2000), the total fraction was found to vary by ~5% when the indices were detrended before the calculation of the regression coefficients.
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21 December 2001; accepted 26 March 2002

Archaefructaceae, a New Basal Angiosperm Family

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Archaefructaceae is proposed as a new basal angiosperm family of herbaceous aquatic plants. This family consists of the fossils *Archaefructus liaoningensis* and *A. sinensis* sp. nov. Complete plants from roots to fertile shoots are known. Their age is a minimum of 124.6 million years from the Yixian Formation, Liaoning, China. They are a sister clade to all angiosperms when their characters are included in a combined three-gene molecular and morphological analysis. Their reproductive axes lack petals and sepals and bear stamens in pairs below conduplicate carpels.

The fossil record provides information about the evolution of major groups of organisms living on Earth today as well as those that have become extinct. The earliest history of flowering plants is poorly documented. Some of the sparse data from fossils have been accommodated into current phylogenetic models. Current phylogenetic studies (*1*, *2*) and recent paleobotanic finds (*3*) support the nature of the basal angiosperms (*Amborella* and Nymphaeales) consistent with combined multiple gene and morphologic analyses (*4*–*6*). Newly discovered fossils reveal a combination of unique characters. These fossils consist of new material of *Archaefructus liaoningensis* (*7*) and *A. sinensis* sp. nov. (*8*), a new species preserved as nearly whole plants in various stages of reproductive maturity. The fossils were recovered from the lower part of the Upper Jurassic/Lower Cretaceous Yixian Formation (*9*) in Beipiao and Lingyuan of western Liaoning, China (41°12′N, 119°22′E). The formation is at least 124.6 million years old (*10*) and may be as old as uppermost Upper Jurassic (*11*). All aspects of these plants are known, including their roots, leaves, and reproductive organs, as complete plants with all organs attached. When all characters of *A. liaoningensis* (*7*) and *A. sinensis* (*8*) are evaluated in a phylogenetic context, they require a new extinct family of flowering plants, Archaefructaceae (*12*). An analysis of the characters of this family demonstrates that it is best considered a sister taxon to extant angiosperms (Fig. 1).

Morphologic characters, especially those of the reproductive (flower) organs, have been the traditional basis for organizing the phylogeny of the angiosperms (*13*). We need to integrate a detailed morphologic character database with the molecular database in order to place fossils into the whole record of angiosperm phylogeny. The early angiosperm fossils have various levels of preservation of morphologic characters but lack any molecular characters. With sufficient data, some fossils can be intercalated into existing taxa in the current molecular-based angiosperm phylogenies (*3*). However, when novel character combinations are present that do not clearly align a fossil with particular extant angiosperm families, and when no molecular data are available, it becomes necessary to use methods that combine morphologic and molecular characters in a "total evidence" cladistic analysis. In this context, we performed numerous phylogenetic analyses of *Archaefructus* with modern angiosperms, using a combined matrix of morphology and molecular data. Figure 1 presents the results of one such analysis, in which we reduced the number of morphologic characters to only those relevant to the fossil. In all analyses, *Archaefructus* was maintained in a position as a sister taxon to the extant angiosperms.

The "flower" of *Archaefructus* is a unique collection of female and male reproductive organs (Fig. 2, A to C, E to G, J, and K). The carpels mature last, after the pollen has been dispersed and the anthers have been lost on the same axis. The shoot apex terminates in the carpel production. The immature carpels are clustered close together and then become spaced out as the axis elongates and they mature; most are arranged helically. Each carpel is attached to the axis by a pedicle that has no visible bract scars or evidence that other organs were ever attached near them. The same is the case for the stalks upon which the pairs of stamens are borne. In Archaefructaceae, the carpels are terminal, pseudo-whorled in threes or subopposite to helical in arrangement, and subtended by helical stamen-bearing stalks.

The stamens were produced in pairs and remained attached to the stalks only while the carpels were young (Fig. 2, A to C, E, J, and K), as suggested by their small size and close spacing. As the carpels matured, the stamens abscised, leaving the short stalks that remain on the mature shoots. Two stamens commonly arise from the terminus of each stalk. The stamens consist of short slender filaments and long anthers. The anthers are basifixed and consist of two distinct parallel thecae, each probably containing two longitudinal pollen sacs. This is the typical organization of modern angiosperm anthers (*14–17*). Each theca opened by a longitudinal slit extending the full length of the anther. Once opened, the anthers probably remained open.

The anthers often show apical extensions (Fig. 2, B, C, and E) that may have served as pollinator attractants (*14–17*). These stamens demonstrate a distinct differentiation between the short filament and the nonlaminar anthers. This finding supports the hypothesis that there is no homologous relationship between the stamen and the carpel (*18*). The pre-Cenomanian record of stamens is sparse, but new discoveries in Lower Cretaceous sediments hold promise that more will be found (*3, 19, 20*). Each stamen record provides useful information for the phylogenetic analysis of angiosperm characters (*21–25*). For example, the presence of nonlaminar stamens early in angiosperm history supports the view that stalked anthers are primitive.

Stamen bundles are formed in a variety of living angiosperms when there is a secondary subdivision of the androecial primordium (*26*). As a result of this secondary primordial activity, a single primordium may produce several stamens. The stamens produced this way are basally fused. The stalks found in *Archaefructus* may represent the remains of stamen filaments that are fused together. The paired stamens of *Archaefructus* may be collateral pairs of stamens that result in doubling of organs, as has been observed in the Magnoliidae and in the Alismatidae (*26*). Such stamen pairs resulting from paired initial primordia might reflect an ancient history of this character found in the stamen bundles of *Archaefructus*. This type of primordia in the androecium has been presented as a possible primitive character (*27, 28*). An alternative hypothesis is that the two stamens attached to the stalks are the last remnant of larger branching systems that contained male flowers or terminal isolated stamens. In support of this hypothesis, the paired stamens attached to the stalks might represent the last remnants of stamens attached to a reduced branching system. We think the paired stamens are best construed as dichotomous remnants of an earlier, more extensive dichotomous branching system.

Pollen has been obtained in situ from the anthers. The pollen is monosulcate (Fig. 2, F and G). It is of moderate size (17 to 36 μm long) with an exine pattern that is vermiform (Fig. 2F) or fossulate, similar to large monosulcate pollen described from the Lower Cretaceous (*29*). A granular texture is evident in high magnification on a scanning electron microscope (SEM) (Fig. 2G). Under epifluo-

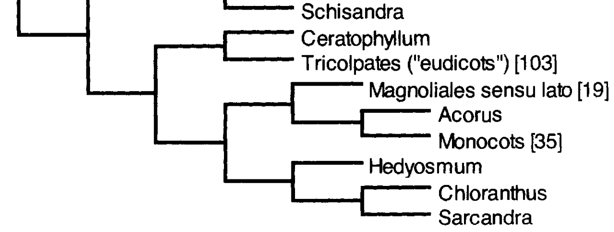

Fig. 1. Consensus cladogram of most parsimonious trees for analysis of 173 living taxa of seed plants, plus the fossil *Archaefructus*. Various analyses included 1628 molecular characters and 17 to 108 morphological characters (*47*). Taxa with numbers in brackets after some names indicate the number of species in that clade that were analyzed as separate terminals and monophyletic in all trees but are not shown here to save space. The Bremer support (or "decay index") for the branches subtending the angiosperms and *Archaefructus* is indicated above the branches. For taxa and character matrix, see (*48*).

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rescent microscopy, we observed some isolated pollen on the stigmatic crests of the carpels, particularly on the extended tips of the young carpels (*7*).

Relatively long pedicles and apical extensions characterize the young carpels associated with the shoots bearing stamens (Fig. 2J). The apical extension may be an elongation of the adaxial stigmatic crest that, in combination with the elongated pedicle, could help accommodate wind or insect pollination. As the carpels matured, they probably bent outward, forming a wider angle with the shoot. At the same time, the relative proportions of the parts of the carpel changed, so that the extension of the carpel tip and the pedicle are not as obvious in the fossils of mature fruits.

Even though the stamens matured while the carpels were young, it is impossible to know whether *Archaefructus* was protandrous. The functional nature of the pollen and stigmas cannot be determined from the fossils, but it is possible for pollen to mature and be dispersed before the carpels associated on the same axis were receptive. This type of dichogamy would increase the fitness of *Archaefructus* by establishing a self-isolating mechanism to ensure outbreeding (*16*). It is possible that *Archaefructus* possessed the po-

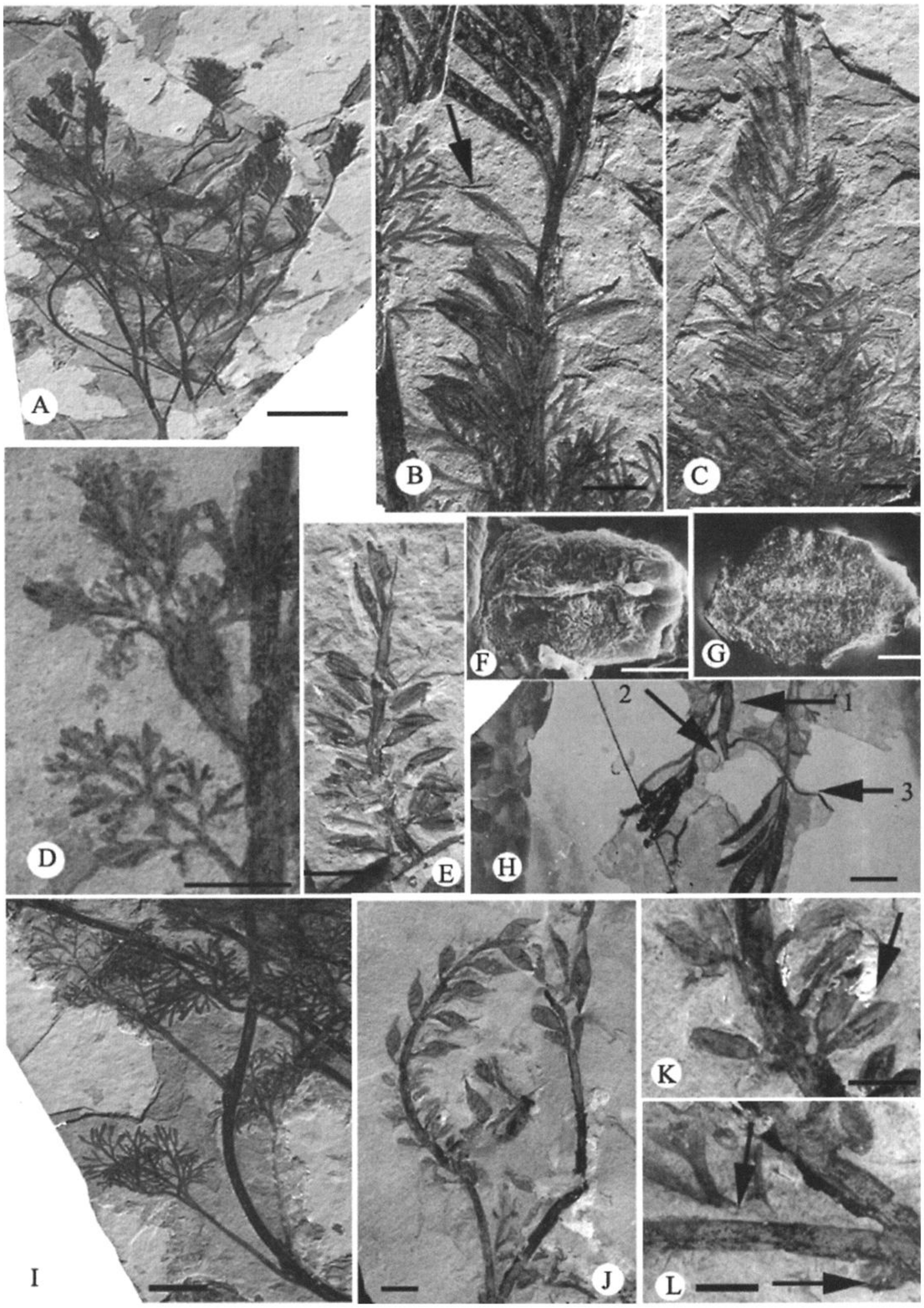

Fig. 2. (**A** to **D**, **H**, and **I**) *Archaefructus sinensis* Sun, Dilcher, Ji et Nixon: samples J-0721 (A, B, C, I), NMD-001 (D), and NMD-002 (H). (**E** to **G**, **J** to **L**) *Archaefructus liaoningensis* Sun, Dilcher, Zheng et Zhou: samples B-2000 (J to L), PB18943 (E to G). (A) Whole specimen (holotype). Scale bar, 5 cm. (B and C) Multiseeded stalked carpels and paired stamens (indicated by arrow). Scale bars, 5 mm. (D) Swollen leaf base of upper dissected leaf. Scale bar, 5 mm. (E) Two young fruits with stamens below, from specimen PB18943. Scale bar, 3 mm. (F and G) SEM images of pollen from specimen PB18943. Pollen grains show monosulcate aperture (F) and rugulate exine (G). Scale bars, 10 μm. (H) Base of stem (1) of a fruiting plant folded in half upon itself; root (2) bears a few simple lateral roots (3). Scale bar, 1 cm. (I) Lower dissected leaf. Scale bar, 5 mm. (J) Paratype showing mature fruits and peg-like projections on the main shoot; to the left side is a lateral shoot with stamens and young fruits. Scale bar, 5 mm. (K) Enlargement of portion of (J). Shoot shows paired stamens (indicated by arrow). Scale bar, 2 mm. (L) Same as (J). A leaf base with missing petiole that extended across the lateral shoot with the distal portion of the dissected leaf preserved. Arrows indicate leaf base and leaf blade. Scale bar, 2 mm.

tential in its reproductive biology to avoid self-pollination. The small size of the immature carpels and the ovules contained in them suggests that unless pollination and fertilization occurred, they would never have developed into mature fruits and seeds. Early in angiosperm history, fruit development was probably tied to successful pollination. In this way, angiosperms avoided investing energy in the production of sterile fruit and seed tissue.

The carpels and stamens are borne together on the same flowering shoots. The carpels are terminal and the stamens subtend them. There are no petals, sepals, or other organs associated with the carpels and stamens. The fertile shoots are produced in a leaf axis or a leaf may subtend terminal fertile shoots. The leaf petioles remain attached to these fertile shoots. The leaf blades are seldom preserved in specimens of *A. liaoningensis*, whereas they are more often preserved attached in *A. sinensis* (Fig. 2, A, D, and I). In one specimen of *A. liaoningensis*, the partial remains of a preserved leaf are attached (Fig. 2, J and L). More complete isolated dispersed leaves, three to four times pinnately compound, are found associated from the same sediments.

The Archaefructaceae probably were aquatic plants. The herbaceous nature of the plants is obvious by the thin stems that extend for some distance, which would require water for support. The finely dissected compound leaves suggest an aquatic habitat. The basal leaves have long petioles and are larger than the more distal leaves. The basal leaves are more dissected than the distal leaves. All leaves have a swollen petiole base. It is especially enlarged in those leaves that are most distal from the base but nearest to the reproductive organs and probably the surface of the water. These may have given some buoyancy to the plant. The roots are poorly developed in *A. sinensis* (Fig. 2H). Numerous fish (*Lycoptera*) are preserved and mixed in with the fossil plants or found in association with both species. The reproductive organs of *Archaefructus* probably were exposed above the water during pollination and may have remained so for seed dispersal.

A Lower Cretaceous (125 to 115 million years old) fossil with affinities to the Nymphaeales (*3*) is more specialized in its floral morphology and much smaller than *Archaefructus*. Although *Archaefructus* has some features similar to Cabombaceae in the Nymphaeales, it does not fit the characters of that order or any extant order. We consider *Archaefructus* distinct from the Nymphaeales and *Amborella*. Figure 1 suggests that *Archaefructus* is a sister taxon to all known angiosperms. The characters that are unique to the Archaefructaceae are illustrated in the reconstruction of *A. sinensis* (Fig. 3).

Although the reproductive structures of *Archaefructus* superficially resemble those of *Caytonia* and other seed ferns of similar or older age, they are different when examined closely. *Archaefructus* has female structures clearly interpretable as angiospermous carpels that are closed along an adaxial stigmatic crest, the stamens are angiospermous with bilateral symmetry, and pollen is nonsaccate and monosulcate. In contrast, the outer seed-enclosing structure of *Caytonia* is not conduplicate, and in recent phylogenetic analyses is usually interpreted as homologous with the outer seed integument (*25*). In the male structures usually reconstructed as belonging with *Caytonia* (*Caytonanthus*), the stamen symmetry is radial and the pollen is bisaccate, as in various modern conifers (*30*). All these features place *Caytonia* (and other seed ferns) outside of the clade formed by *Archaefructus* + extant angiosperms. Because of the fragmentary nature of Mesozoic seed ferns such as *Caytonia*, and the markedly different and complex interpretations of their reproductive structures, it was not possible or advisable to include these in our cladistic analyses. For example, in addition to uncertainty in interpretation of homology of the female structures in *Caytonia*, the female and male structures are not organically connected and were likely borne on separate axes. In the current analysis, these taxa would be unstable but would clearly not be closer to angiosperms than *Archaefructus*, which possesses strictly angiospermous features of carpels borne above stamens on bisexual axes. It can be confidently stated that *Archaefructus* is the closest phylogenetically to angiosperms of any available fossil, but has features that exclude placing it within the angiosperm "crown group" or extant clade.

The lack of similarity between *Archaefructus* and other known fossil plants during the Upper Jurassic/Lower Cretaceous (*31*) provides us with more information about the primitive angiosperm (as defined by the characteristic of seeds enclosed in carpels) than it does about related pre-angiospermous seed plants. However, it should be noted that, like other angiosperms (both fossil and living), *Archaefructus* does not represent the original angiosperm and likely had its own derived features. The complex of features seen in *Archaefructus* provides an important point of extrapolation to the original angiosperm, suggesting the possibility that it lacked petals and sepals (previous phylogenies without *Archaefructus* favor an ancestor with a perianth) and may have been a submerged aquatic (like some Nymphaeales). *Archaefructus* is, rather, part of a complex basal group in angiosperm evolution.

Detailed examination of the reproductive shoots in *Archaefructus* by epifluorescence microscopy reveals a continuous covering of epidermal cells preserved on these shoots extending between the attached organs.

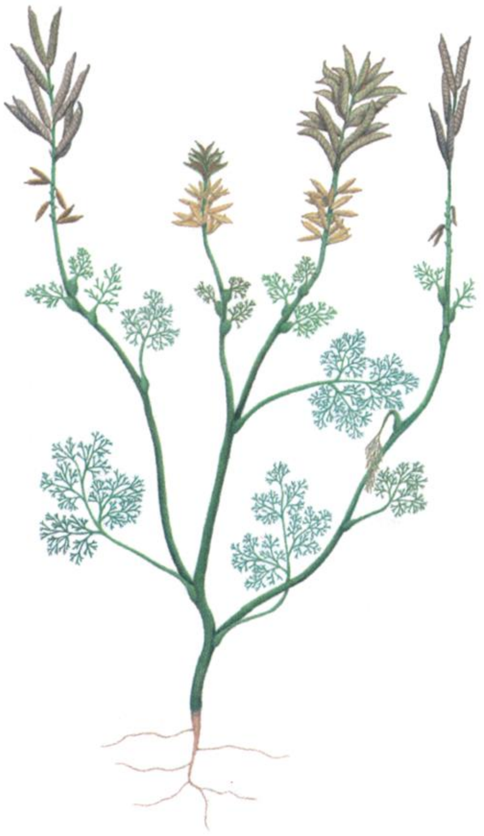

Fig. 3. Reconstruction of *A. sinensis*. These are terminal shoots. The main shoot is more mature so the stamens are deciduous, leaving short pegs. The latter shoot is younger, the carpels are smaller, and the stamens are borne in pairs on short pegs. For interpretation and reconstruction, see (*48*). [Diagram by K. Simons and D. Dilcher]

When examined cell by cell, no interruptions in the cell pattern were found that would indicate the presence of scars left by deciduous bracts or other organs, so each entire shoot represents a flower, not an inflorescence. In *Archaefructus* the leaves help to define the morphologic floral units, beginning at the point of its origin in a leaf axis and extending to the reproductive tip of the shoot (*11*). Thus, the *Archaefructus* flower terminates a lateral branch system. Paired stamens arise from the short stalks on these lateral axillary shoots. Each of these stamen units could be considered reduced complex male branches existing in *Archaefructus* as small individual male flowers. In that case, the *Archaefructus* flower would be an inflorescence derived from a complex branched ancestor. On the other hand, the stalk with the stamen pairs could be viewed as a normal androecium in a single flower.

If we consider that the term "flower" is related to an organizational plan (*26*), then it is reasonable to consider that each set of multiple carpels and stamens helically arranged along individual elongated shoots and subtended by leaves could be considered a flower. However, *Archaefructus* does not lend itself to such easy interpretation. The "flower" of *Archaefructus* may represent a stage in evolution in which its reproduction was angiospermous (ovules enclosed in carpels) while the organization of the traditional floral unit(s) was still poorly defined. Perhaps, just as the evolutionary history of the modern ovulate pine cone can be understood only by knowing its complex branching ancestors, the evolutionary history of the flower may also involve complex branched ancestral axes.

The origin of the organization of reproductive organs seen in *Archaefructus* has a bearing on how we view the potential ancestor of flowering plants. Many theories and hypotheses of angiosperm origin have been proposed; among these are the euanthium (euthial) (*32*) and the pseudanthium (*33–35*) theories. The euanthium theory indicates that the angiosperm flower organization evolved from a bisexual strobilus with numerous, helically arranged ovules and pollen-bearing organs, as found in *Cycadoidea* or other Mesozoic bennettialean fossil plants. The ovule and pollen-bearing organs were already differentiated and associated with perianth organs that were suggested to be conspicuous and attractive to insect pollinators (*36, 37*). The pseudanthium theory proposed that the ancestral plants of angiosperms had separate branching systems containing ovules and pollen organs. As the hypothetical floral units that formed these branching systems were clustered together, they eventually condensed and modified into a shoot with terminal carpels subtended by stamens. Petals and sepals probably evolved from subtending modified leaves and became part of the whole unit subtending these newly organized reproductive shoots. Ancestors with male and female organs on separate branches are found in the Mesozoic seed ferns. *Archaefructus* appears to support the pseudanthium theory, with the stalks bearing paired stamens perhaps being remnants of an earlier branching system while the petals and sepals have not yet evolved from associated subtending leaves.

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7. *Archaefructus liaoningensis* Sun, Dilcher, Zheng et Zhou (Fig. 2, E to G, J to L). Emended description: Main fertile shoots with lateral fertile shoots common (Fig. 2, J and L). Lateral shoots borne in the axes of leaves, and leaves often subtending the main fertile shoot. Main shoots up to 85 mm long and 3 mm wide basally, tapering to 1 mm distally. Lateral fertile shoots up to 86 mm long, tapering from 1 mm wide basally to 0.5 mm distally. Fruits attached by pedicles (0.75 to 1.5 mm long, 0.25 to 0.6 mm wide). Fruits larger basally (7 to 10 mm long, 2 to 3 mm wide), each containing two to four seeds. Finger-like prominences extend about 1 mm past the apex of the fruits (Fig. 2, E and J). Young fruits positioned at acute angles to the shoot while mature fruits spread out at wider angles (Fig. 2, E and J). The fruits are follicles derived from conduplicate carpels. The main shoot has numerous fruits (up to 18 were observed on one specimen) and the lateral shoots also terminate in numerous fruits (up to 30 were observed). The fruits are crowded at the shoot apex and decrease in size distally. Fruits near the apex are about 3 mm long by 2 mm wide, each with two seeds. The seeds fill the fruits and have an oblique orientation. They appear to be attached to the adaxial side of the fruits. Seeds may overlap within the fruits or may be distinctly separated by oblique bands of tissue. Cuticle of the seed coats are thin. Epidermal cells are rectangular-polygonal, about 25 to 45 μm by 12 to 20 μm. Anticlinal cell walls are sinuous and cutinized, about 2.5 to 3.5 μm thick. Periclinal cell walls are somewhat unevenly cutinized. Often 10 to 12 short (0.3 to 0.5 mm long) stalks are located about 2.5 to 5 mm below the fruits in a zone that extends for about 15 mm along the shoot. These stalks may commonly have two or rarely one (perhaps very rarely three) stamens (Fig. 2, E, J, and K). Between 15 and 26 stamens have been observed. Stamens are deciduous as the shoot matures. Stamens consist of a short filament (0.25 to 0.5 mm long) basifixed to an anther (2 to 3 mm long by 1 to 1.2 mm wide) and may have an extended tip (0.5 to 1 mm long) (Fig. 2E). The narrow tip of the anther extends past the thecae and may be a narrow attenuate connective tip or an extension of the filament. The anthers appear to have two distinct thecae parallel in arrangement and perhaps each containing two longitudinal pollen sacs. The pollen isolated from the anthers is more or less elliptic (17 to 36 μm long, 15 to 20 μm wide). The pollen appear monosulcate and have a verriform or fossulate/rugulate exine pattern. Exine appears granular under the SEM (Fig. 2, F and G). The leaves, attached (Fig. 2L) and associated, are small, pinnately dissected three or four times. The petiole base may be slightly swollen. Multiple vascular strands (up to five) are observed in the petiole. Leaves frequently subtend a central fertile shoot or bear a lateral fertile shoot in their axis. The presence of nearly complete isolated leaves suggests that they were deciduous. Petiole about 10 mm, pinnate leaflet branches opposite to alternate, further dissected ending in rounded lobes, 0.5 to 1 mm wide.
8. *Archaefructus sinensis* Sun, Dilcher, Ji et Nixon sp. nov. (Fig. 2, A to D, H, and I). Description: Plants herbaceous, reproductive axes subtended by vegetative shoots 30.1 cm long by 17 cm wide (Fig. 2A). Main axes basally 3 mm wide, narrowing gradually upward, apically 1 mm wide. Roots poorly developed, consisting of a primary and few short secondary axes (Fig. 2H). Leaves dissected, leaf blade dissected two to five times, petiole length variable (0.5 to 4.0 cm). Basal leaves with long petioles with slightly swollen bases (Fig. 2I). Leaves near reproductive organs have short petioles and swollen bases (Fig. 2D). Ultimate leaf segments are about 2 mm long by 0.3 mm wide with rounded tips. Freely forming lateral branches (1 to 1.5 mm wide) in leaf axils diverge from the main stem at 30° to 35°. Each lateral branch terminates in a fertile shoot. Fertile axes terminate with numerous (12 to 20) small (10 to 18 mm long, 1.5 to 2.0 mm wide) carpels. These are subtended by several (8 to 18) short, blunt, helical stalks, each bearing two stamens. Carpels small when anthers mature; carpels helical, whorled, or opposite. Carpels matured into elongate follicles containing multiple seeds (8 to 12). Stamens consist of short fine filaments (about 1 mm long) attached to broad long anthers (4 to 5 mm long, 0.5 to 0.8 mm wide) ending with a prominent tip (0.5 mm long). Petals, sepals, or bracts absent. Holotype: J-0721. Specimen deposited in Geological Institute of Chinese Academy of Geoscience, Beijing, China. Etymology: The specific name refers to where the fossil was found. Number of specimens examined: 5 (two have 6 each, one has 12 reproductive axes attached together in each plant or in various stages of maturity) (Fig. 2A).
9. The age of the Yixian Formation of western Liaoning, China, is uncertain. We allow for a range from 145 to 125 million years, which corresponds with the Upper Jurassic to Lower Cretaceous (*12, 31, 38–45*).
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12. Family Archaefructaceae Dilcher, Sun et Nixon fam. nov. Description: Herbaceous, aquatic plants with branching stems. Branches originate as axillary shoots terminating in reproductive organs. Poorly developed sparsely branched roots. Leaves alternate, petiole bases enlarged, petioles of various lengths. Blades pinnately dissected two to five times, stipules absent. Flowers medium size (5 cm long) and terminal on axillary branches, hypogynous. Carpels numerous, helical to whorled, stalked, conduplicate. Stamens borne in pairs on short helically arranged stalks, filaments short, large basifixed anthers with terminal apical extensions. Pollen monosulcate, exine reticulate to verriform. Fruits multiseeded folicules, persistent stamens deciduous with stalks persisted on floral axis. The family Archaefructaceae consists of a single genus, *Archaefructus*, with two species known, *A. liaoningensis* and *A. sinensis*. These species are currently known to occur in western Liaoning, northeastern China, from Upper Jurassic/Lower Cretaceous sediments (9). *Archaefructus liaoningensis* and *A. sinensis* are the current species recognized in the family.
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47. Consensus cladogram of most parsimonious trees for analysis of 173 living taxa of seed plants, plus the fossil *Archaefructus*. Various analyses included 1628 molecular characters and 17 to 108 morphological characters. The molecular characters are based on the three-gene matrix (*rbcL*, *atpB*, *18s*) that was recently published for 567 species (*2*). Taxa were selected to provide a good representation of variation throughout the angiosperms, including a dense sampling of the so-called basal angiosperms. The tree shown was generated with a matrix of 1645 characters (17 morphological characters, including only those relevant characters that could be scored for the fossil). Parsimony analysis was undertaken using the parsimony ratchet of Nixon (*46*), with numerous runs of 200 replications for each analysis. In all analyses, *Archaefructus* is a sister taxon to the angiosperms as shown in this tree. Depending on the data set used, the overall length of the tree varied, with an overall consistency index of ~0.18 (consistent with the original three-gene analysis). The taxa *Cycas*, *Bowenia*, *Zamia*, *Ginkgo*, *Ephedra*, and *Pinus* represent the modern gymnosperms; the other taxa in the analysis are angiosperms (flowering plants). Note that this data set does not address the question of whether the gymnosperms are monophyletic, because no taxa outside of the seed plants were included. The tree has been drawn to be neutral on this point, and it supports either hypothesis equally. The tree differs from the original three-gene analysis only in the position of *Ephedra*, which in these trees is more consistent with analyses of other genes that place gnetopsids with Pinaceae, suggesting that the morphology may play a positive role in resolving discrepancies.
48. See supplemental material on *Science* Online (www.sciencemag.org/cgi/content/full/296/5569/899/DC1).
49. Supported by the National Natural Science Foundation of China (projects 39970050 and 39770059), Key Project of Ministry of Land and Resources, China, Special Project Stz. 98-1-02 (Chinese Academy of Sciences), and by NSF grants INT-0074295 and DEB 0090283 and the Becker/Dilcher Endowment for Paleobotany of the University of Florida Foundation. We thank T. A. Lott for assistance with photography, illustration, and manuscript preparation; K. Simons for diagramming the reconstruction of *Archaefructus*; and J. Y. Liu and C. L. Gao of the Natural Museum of Dalian for their help in observation of some specimens of *Archaefructus*. This paper is University of Florida Contribution to Paleobiology publication number 525.

28 December 2001; accepted 20 March 2002

Mammal Population Losses and the Extinction Crisis

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The disappearance of populations is a prelude to species extinction. No geographically explicit estimates have been made of current population losses of major indicator taxa. Here we compare historic and present distributions of 173 declining mammal species from six continents. These species have collectively lost over 50% of their historic range area, mostly where human activities are intensive. This implies a serious loss of ecosystem services and goods. It also signals a substantial threat to species diversity.

Population extinctions are a more sensitive indicator of the loss of biological capital than species extinctions. This is because many of the species that have lost a substantial portion of their populations [thus altering ecosystems and perhaps reducing the ability of those systems to deliver services (*1*)] are unlikely to go globally extinct and enter the species extinction statistics in the foreseeable future (*2*). Most analyses of the current loss of biodiversity emphasize species extinctions (*3–5*) and patterns of species decline (*6–8*) and do not convey the true extent of the depletion of humanity's natural capital. To measure that depletion, we need to analyze extinctions of both populations and species. Here we give a rough minimum estimate of the global loss of continental mammal populations. We believe that mammals, because of their great taxonomic diversity and the wide range of ecological niches they exploit, can serve as an indicator of what is occurring in the rest of Earth's biota.

Our data consist of historic (i.e., mostly 19th century) and present-day distributional ranges of all of the terrestrial mammals of Australia and subsets of the terrestrial mammal faunas of Africa, South East Asia, Europe, and North and South America (Table 1 and table S1). These subsets consist of all mammal species whose ranges are known to be shrinking for which we had access to data. They comprise roughly 4% of the ~4650 known species. We assume that loss of range area is due to the extinction of populations, but we do not attempt to equate a given areal loss with a precise number of population extinctions due to the complexities of defining and delimiting populations (*9*). Data were gathered from the specialized literature (Web references). In general, because they are better known, most of our range data are from medium- and large-sized species. Whether globally these are more or less liable to population extinction than medium to small species is a matter of conjecture (*10–12*), but at present there is little reason to assume an important directional bias in our samples. There was no correlation between body mass and range shrinkage in our data ($P > 0.05$, $r^2 = 0.22$). There does remain a possible source of bias in the relative lack of very small species in the total sample (*12*).

The ranges were digitized and the historic and present range areas were calculated. For each species, we estimated both total area occupied historically and percent historic range area now occupied. Using ArcView 3.1, the ranges were superimposed to produce synthetic maps summarizing the losses of species populations in 2 degree by 2 degree quadrats (i.e., the number of species that have disappeared from each quadrat because all of their populations previously located in that quadrat have disappeared). The area of these quadrats, of course, varies with latitude, but the average of such quadrats over land is about 30,000 km^2.

Declining species of mammals in our sample had lost from 3 to 100% of their

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