ABSOLUTE DIVERSIFICATION RATES IN ANGIOSPERM CLADES

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Susana Magallón[1] and Michael J. Sanderson[2]

Section of Evolution and Ecology, University of California, One Shields Avenue, Davis, California 95616
[1]*E-mail: magallon@ucdavis.edu*
[2]*E-mail: mjsanderson@ucdavis.edu*

Abstract.—The extraordinary contemporary species richness and ecological predominance of flowering plants (angiosperms) are even more remarkable when considering the relatively recent onset of their evolutionary diversification. We examine the evolutionary diversification of angiosperms and the observed differential distribution of species in angiosperm clades by estimating the rate of diversification for angiosperms as a whole and for a large set of angiosperm clades. We also identify angiosperm clades with a standing diversity that is either much higher or lower than expected, given the estimated background diversification rate. Recognition of angiosperm clades, the phylogenetic relationships among them, and their taxonomic composition are based on an empirical compilation of primary phylogenetic studies. By making an integrative and critical use of the paleobotanical record, we obtain reasonably secure approximations for the age of a large set of angiosperm clades. Diversification was modeled as a stochastic, time-homogeneous birth-and-death process that depends on the diversification rate (r) and the relative extinction rate (ϵ). A statistical analysis of the birth and death process was then used to obtain 95% confidence intervals for the expected number of species through time in a clade that diversifies at a rate equal to that of angiosperms as a whole. Confidence intervals were obtained for stem group and for crown group ages in the absence of extinction ($\epsilon = 0.0$) and under a high relative extinction rate ($\epsilon = 0.9$). The standing diversity of angiosperm clades was then compared to expected species diversity according to the background rate of diversification, and, depending on their placement with respect to the calculated confidence intervals, exceedingly species-rich or exceedingly species-poor clades were identified. The rate of diversification for angiosperms as a whole ranges from 0.077 ($\epsilon = 0.9$) to 0.089 ($\epsilon = 0.0$) net speciation events per million years. Ten clades fall above the confidence intervals of expected species diversity, and 13 clades were found to be unexpectedly species poor. The phylogenetic distribution of clades with an exceedingly high number of species suggests that traits that confer high rates of diversification evolved independently in different instances and do not characterize the angiosperms as a whole.

Key words.—Birth-and-death process, crown group, extinction, fossil record, phylogeny, speciation, stem group.

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The flowering plants, which include more than 260,000 species, are often singled out as an example of unusually rich taxonomic diversity (Heywood 1993) emerging in a relatively brief period of time. With an initial radiation in the Early Cretaceous, which is recent when compared to the time of origin of other groups of seed plants or land plants as a whole, angiosperms have dominated terrestrial plant communities since at least the beginning of the Tertiary (Lidgard and Crane 1988; Lupia et al. 1999). Species richness within angiosperms is not distributed evenly, at least according to taxonomic treatments. For example, Takhtajan (1997) recognized approximately 72 families that include only a single species, while circumscribing five other families (Asteraceae, Orchidaceae, Fabaceae, Rubiaceae, and Poaceae) to include more than 10,000 species each. However, a study of species richness in angiosperms begins with a simple question: Does the perceived impression that groups of angiosperms contain dramatically different numbers of species reflect real differences in evolutionary processes, measurable as differences in speciation and extinction rates? This question must be answered prior to asking what the correlates and causes of taxonomic diversity differences might be.

Previous workers have addressed this fundamental question. Statistically robust comparisons of phylogenetic sister groups (Slowinski and Guyer 1993) have identified many pairs of sister clades in flowering plants that differ significantly in their species richness, and possible correlates of these differences have been considered, such as antiherbivory secondary chemicals (Farrell et al. 1991), pollination syndrome and growth form (Dodd et al. 1999), breeding system

(Heilbuth 2000), as well as rate of substitution at the molecular level (Barraclough et al. 1996). However, as useful as sister group comparisons are for identification of diversity correlates, they can only provide a relative assessment of rate variation between sister clades in any given tree (Sanderson and Donoghue 1994, 1996). A relative comparison in one part of a tree cannot itself be judged in relationship to a comparison elsewhere in the tree because the ages of the most recent common ancestors of the pairs may be very different (e.g., Warheit et al. 1999). This problem is shared by all relative-rates type tests, and the weakness of these in other applications is well known (Bromham et al. 2000). In this study, we therefore assess the extent of variation in *absolute* rates of diversification in angiosperm clades by combining paleobotanical evidence on clade ages, recent advances in phylogenetic understanding of angiosperm relationships, and new statistical results on models of the diversification process.

Previous studies have considered the fossil record as a possible source of ages in estimating the variability in absolute rates of diversification across angiosperms (e.g., Levin and Wilson 1976; Niklas et al. 1985; Eriksson and Bremer 1992; Ricklefs and Renner 1994; Tiffney and Mazer 1995). Following the approach of Stanley (1979), Eriksson and Bremer (1992) and Ricklefs and Renner (1994) used ages from the fossil record and counts of extant species diversity to estimate net diversification rate for several angiosperm taxa. Their perspectives on the record were quite different, however. Eriksson and Bremer (1992) included many angiosperm families with extremely poor records and unreliable ages of

origin (e.g., Geraniaceae) and based conclusions about the correlates of diversity on rates estimated from such data. Ricklefs and Renner (1994), noting the poor correspondence between the assumed age of origin of families and their present-day species diversity, concluded that the ages of origin were too unreliable to be used. However, they recognized that the existence of dramatically different rates of diversification is an alternative explanation for the observed discrepancy. Consequently, they analyzed species richness by making sister-group comparisons without reference to absolute time or rates.

In this study, we provide an intermediate approach. To provide a more comprehensive survey of absolute rate variation within angiosperms, we have taken account of the improved resolution of clades within the angiosperms obtained from recent phylogenetic analyses. Additionally, in analyzing the angiosperm fossil record, we have incorporated numerous significant recent findings, and have taken care to distinguish between the age of a stem group and the age of a crown group. Lastly, we have incorporated new results on statistical estimation and hypothesis tests for diversification models.

Identification of the major clades within the angiosperms and understanding of their phylogenetic relationships has advanced substantially in the last few years. Studies of a broad taxonomic scope, which sample the angiosperms as a whole (e.g., Soltis et al. 1997, 1999; Qiu et al. 1999; Savolainen et al. 2000) or large subclades within the angiosperms (e.g., the monocots; Duvall et al. 1995), provide information about phylogenetic relations among major clades. Studies of a narrower scope provide information about the taxonomic circumscription of major clades (e.g., Laurales-Calycanthales, Renner 1999; orchids and Asparagales, Cameron et al. 1999; basal eudicots, Hoot et al. 1999). The comprehensive sampling found in many of these recent analyses allows greater overlap and compatibility among results of independent studies. The combined use of two or more molecular datasets has lent greater support to many previously detected clades (e.g., an analysis based on five genes, Qiu et al. 1999), while the increasing number of phylogenetic studies based on new sources of molecular data, such as duplicate genes (e.g., Mathews and Donoghue 1999), have, in some cases, revealed the branching pattern of previously uncertain parts of the tree.

The quality of the angiosperm fossil record has been substantially improved by a number of recent paleobotanical findings (e.g., Drinnan et al. 1990; Crane et al. 1993, 1994; Friis et al. 1994a,b, 2001; Frumin and Friis 1999). Worldwide reports of critically evaluated vegetative and reproductive remains are a valuable source of information about the time of origin and early history of angiosperm taxa. Explicit information about minimum ages for particular nodes can be obtained by placing these confidently identified fossil remains in the available angiosperm phylogenetic framework.

Our analysis involves estimating rates of diversification for the angiosperms as a whole and for a large set of angiosperm clades for which reliable information on stem group age or crown group age is available. We then perform a statistical analysis of stochastic birth-and-death processes to obtain a confidence interval of the expected number of species through time in a clade that diversifies at a background rate
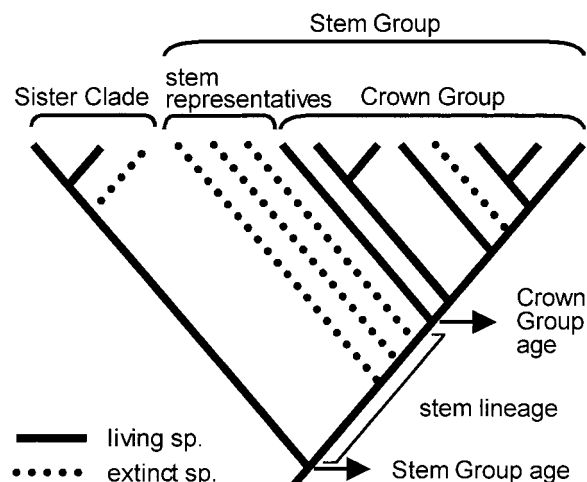

FIG. 1. Stem group and crown group age. The age of the stem group is the time of divergence of the clade from its sister taxon. The age of the crown group is the time of the deepest bifurcation within the crown group. Solid lines represent living species; dotted lines represent extinct species.

equal to the estimated rate for angiosperms as a whole. Finally, we compare the standing diversity of angiosperm clades with the expected number of species for a clade of equivalent age and identify clades whose standing diversity differs significantly, either by being too high or too low, relative to expectation.

METHODS

A Clade's Stem Group and Crown Group

The distinction between the age of a clade's stem lineage and the age of its crown group is crucially important when estimating rates of diversification. Although it is relatively straightforward to define these terms in the absence of fossils, fossils introduce some complications (Smith 1994). Here we define a crown group as the *least* inclusive monophyletic group that includes all the *extant* members of a clade (Fig. 1). The crown group may include some lineages that are extinct in the present day, but which diverged *after* the origin of the most recent common ancestor of all extant representatives. The stem group is the *most* inclusive monophyletic group containing the extant members of a clade, but no other extant taxa. It also includes the *extinct* lineages that diverged from the lineage leading to the crown group. These must all be more closely related to the crown group than to any other extant group, specifically the crown group's extant sister group. The age of the crown group corresponds to the time of the first phylogenetic split within the crown group (Fig. 1). The age of the stem group, which may be considerably older, corresponds to the time of divergence between the crown group in question and its extant sister group (Fig. 1; Doyle and Donoghue 1993).

Diversification Model

Speciation and extinction of lineages in clades is modeled as a stochastic birth-and-death process (Bailey 1964). Specifically, speciation is assumed to occur at a constant rate,

λ, and extinction at a constant rate, μ, making the process homogeneous through time and leading to either exponentially increasing or decreasing diversity. The dynamics of lineage diversification are characterized by two parameters that are simple transformations of λ and μ. Diversification rate is defined as $r = \lambda - \mu$, and relative extinction rate is defined as $\epsilon = \mu/\lambda$. The former can range from negative to positive infinity, the latter from zero to positive infinity. If extinction is lower than speciation, then $\epsilon < 1$. It is well known that as long as the extinction rate in the process is greater than zero ($\epsilon > 0$), there is a finite probability that the entire clade will go extinct (see below). If the extinction rate is greater than or equal to the speciation rate ($\epsilon \geq 1$), the extinction probability is one (although it may take a long time). In the results presented below, we ignore this special case, because estimation of parameters is highly problematic, given the loss of information about phylogenetic history in this case. In either case, a possible outcome of diversification is ultimate extinction of the clade. In the absence of a good fossil record, this might well mean failure to observe that the process ever existed.

The properties of birth and death models have been studied extensively both by mathematicians (Kendall 1948; Moran 1953; Harris 1964) and biologists (Strathmann and Slatkin 1983; Raup 1985; Sanderson and Bharathan 1993; Nee et al. 1994; Kubo and Iwasa 1995). Although results for pure birth models have been widely applied in phylogenetic studies of diversity based on sister-group comparisons (Slowinski and Guyer 1989), relatively few statistical results are available for more general birth and death processes (Nee et al. 1994). Some results involving estimation of diversification rates and hypothesis testing in a historical (retrospective) framework have not been widely applied, and a few new, necessary, but relatively technical results are presented here.

Let the number of lineages present at the start of the birth-and-death process be denoted a. Bailey (1964, eq. 8.47; see also Raup 1985, eq. 18A) showed that the probability distribution for the number of lineages, $N(t)$, observed at some time, t, given a lineages at $t = 0$ is:

$$\text{Prob}[N(t) = 0] = \alpha_t^a, \quad \text{and} \tag{1a}$$

$$\text{Prob}[N(t) = i] = \sum_{j=0}^{\min(i,a)} \binom{a}{j}\binom{a+i-j-1}{1}$$
$$\times \alpha^{a-j}\beta^{i-j}(1-\alpha-\beta)^j,$$
$$(i \geq 1), \tag{1b}$$

which involves two new parameters, α_t and β_t, that depend on time,

$$\alpha_t = \epsilon\beta_t \quad \text{and} \tag{2a}$$

$$\beta_t = \frac{e^{rt}-1}{e^{rt}-\epsilon}. \tag{2b}$$

Note that Foote et al. (1999) provided a different equation, which they suggested was a correction to Bailey's (1964) equation (8.47) and Raup's (1985) identical equation (A18). However, in fact, Foote et al.'s equation is equal to Bailey's, following algebraic reduction, at least for the cases relevant here, which are $a = 1$ and $a = 2$.

Two complications arise when the birth-and-death process is applied to real data. The first one involves the distinction between the age of the stem group and the age of the crown group (Fig. 1). In the case of a stem group, the initiation of the birth-and-death process (i.e., $t = 0$) corresponds to the instant immediately after the bifurcation between the clade in question and its sister clade. At that instant, the lineage consists of only a single species, and thus $a = 1$. In the case of a crown group, the initiation of the birth and death process corresponds to the instant immediately after the deepest bifurcation within the crown group, and thus $a = 2$.

The second complicating factor, which was highlighted by Strathmann and Slatkin (1983), Raup (1985), and more recently by Nee et al. (1994), is the conditional nature of retrospective inferences of rates of diversification based on the standing diversity of surviving clades. With nonzero extinction, there is always a chance that a clade does not survive to be noticed by an observer at time t. Thus, relevant probability distributions for the standing diversity of a clade must be conditioned on the survival of the clade to time t, which occurs with probability $1 - \alpha_t^a$.

Estimation of Diversification Rates

Obtaining the rate of diversification of a clade, $r = \lambda - \mu$, requires explicit information about the number of lineages that originate and become extinct during an interval of time. Niklas et al. (1985), for example, obtained r for a number of land plant taxa, based on counts of number of species through stratigraphic intervals. In the absence of explicit information about a clade's diversity through time, the rate of diversification of a given clade can be estimated by considering its present day species diversity and its age. In the context of a birth-and-death model of diversification and if extinction is negligible, the maximum-likelihood estimate of diversification rate is easily obtained as

$$\hat{r} = \hat{\lambda} = \log(n)/t \tag{3}$$

for a stem group age and

$$\hat{r} = \hat{\lambda} = [\log(n) - \log 2]/t \tag{4}$$

for a crown group age. A substantial literature has developed around the use of equation (3) to estimate r even in cases in which extinction is presumably not negligible (Stanley 1979; Wilson 1983; Eriksson and Bremer 1992). However, in the presence of extinction, unbiased estimation of r and ϵ based on standing diversity alone is problematic. Although the estimates above are reasonable for deterministic models in which extinction never occurs (as long as $\lambda > \mu$), stochastic extinction in a birth-and-death model causes these estimators to be biased by failure to sample extinct, unobserved clades. A sense of this can be obtained by noticing the form of the mean clade size over time, conditional on survival of the clade, which is (cf. Raup 1985)

$$\bar{N}(t) = \frac{ae^{rt}}{1 - \alpha_t^a}. \tag{5}$$

The mean is much larger than ae^{rt}, which is the mean without extinction, when relative extinction is high. This seemingly paradoxical result stems from the fact that the pool of clades

that survive to be observed has higher diversity, on average, than the pool of clades that includes the extinct ones. The mean clade size obtained by counting the species diversity of extant clades is higher than what it would be if species diversity of all clades, including extinct ones, were counted (for extensive discussion of this problem, see Nee et al. 1994). Consequently, the application of the simple formula $\log(n)/t$ (or its crown group age analog) will tend to overestimate the true diversification rate if extinction is present.

As an alternative to the maximum-likelihood estimators, we can estimate r by using a method-of-moments estimator (Rohatgi 1976). Here we equate the mean given by equation (5) with an observation on diversity, n. Then

$$\hat{r}_\epsilon = \frac{1}{t}\log[n(1 - \epsilon) + \epsilon] \qquad (6)$$

for stem group age, and

$$\hat{r}_\epsilon = \frac{1}{t}\left\{\log\left[\frac{1}{2}n(1 - \epsilon^2) + 2\epsilon \right.\right.$$
$$\left.\left. + \frac{1}{2}(1 - \epsilon)\sqrt{n(n\epsilon^2 - 8\epsilon + 2n\epsilon + n)}\right] - \log 2\right\}$$
$$(7)$$

for crown group age. A maximum-likelihood estimator provides the same result, at least for the stem group age (unpubl. data; we have not tried to construct the corresponding crown group maximum-likelihood estimator).

We estimate rates of diversification for the angiosperms as a whole, and for selected clades within the angiosperms, by using equation (6) or equation (7), depending respectively on whether the earliest appearance in the fossil record for the clade provides a stem group or crown group age. The value of ϵ, the relative extinction rate, is unknown. However, we can construct estimators of r if we assume that ϵ varies between reasonable bounds. What are the reasonable bounds of the relative extinction rate? Obviously, zero, which implies no extinction, is a lower bound. We chose somewhat arbitrarily a value of 0.9 as an upper bound for the relative extinction rate for two reasons. First, for large clades, the probability of survival to the present is very closely approximated by $1 - \epsilon$ (cf. eq. 2, in which $\alpha_t \to \epsilon$, as $rt \to \infty$), which means that values of ϵ greater than 0.9 correspond to clades having less than a 10% chance of surviving to the present. For angiosperms as a whole, with a standing diversity of more than 260,000 species, retrospectively, it seems improbable that ϵ could have been much higher than 0.9 on average. Second, as $\epsilon \to 1$, the magnitude of speciation and extinction rates, λ and μ, increases rapidly to maintain the same net diversification rate, r. At values above $\epsilon = 0.9$, estimated values of λ and μ begin to exceed 1.0 events per million years, which is approximately the upper limit estimated from real data from a variety of taxa (Stanley 1979; Hulbert 1993). When relative extinction has higher values than this, diversification quickly becomes a highly chaotic process dominated by stochastic extinction and extremely rapid turnover. Thus, we provide two estimates of r for each clade, one corresponding to zero extinction ($r_{0.0}$) and the other corresponding to what we believe to be an exceptionally high relative extinction rate ($r_{0.9}$). Strathmann and Slatkin (1983) adopted a similar approach.

Hypothesis Tests on Diversity

We conduct a statistical test on one of the most basic questions in studies of taxon diversification rate (Strathmann and Slatkin 1983). Given a specific background diversification rate (r) and a relative extinction rate (ϵ), what levels of species diversity are unexpectedly high or low at a given time after the origin of a clade? Specifically, we ask which angiosperm clades are excessively species rich or species poor, given their age and the estimated diversification rate for angiosperms as a whole. To address this question, first we estimate a 95% confidence interval for the expected number of species in a hypothetical clade that diversifies with a rate equal to that obtained for the angiosperms as a whole, for each interval of time since its origin ($t = 0$), until 132 million years after its origin ($t = 132$ million years, i.e., the age of the angiosperm crown group). Then, we compare the standing diversity of real angiosperm clades with the 95% confidence interval for expected species diversity for a clade of similar age.

To obtain a confidence interval of the expected number of species at a given time, we started by considering the probability of finding exactly a number of species i in a clade, at a time t after its origin. This probability is given by equation (1). The general result for the conditional probability of finding exactly i species in a clade at a time t after its origin, given the probability that the clade survives to time t, is

$$P[N(t) = i \,|\, N(t) > 0] = \frac{P[N(t) = i]}{P[N(t) > 0]} = \frac{P[N(t) = i]}{1 - \alpha_t^a}. \qquad (8)$$

Because we are not interested in calculating the probability of a clade having exactly i species at a given time, but rather a confidence interval around an expected value, it is possible to use the tail probabilities of equation (8) to obtain the combined probability of having k or more species and the combined probability of having fewer than k species. The combined probability of having k or more species at t is obtained by adding the probability of having exactly each number of species from k to infinity, considering in each case that the clade survives to t. Likewise, the combined probability of having a number of species $<k$ at t is obtained by adding the probability of having exactly each number of species from one to $(k - 1)$, also considering that the clade survives to t. The sum of these two combined probabilities is one. The general results are:

$$P[N(t) \geq k \,|\, N(t) > 0] = \frac{P[N(t) \geq k]}{P[N(t) > 0]} = \frac{\sum_{i=k}^{\infty} P[N(t) = i]}{1 - \alpha_t^a} \qquad (9a)$$

and

$$P[N(t) < k \,|\, N(t) > 0] = \frac{P[N(t) < k]}{P[N(t) > 0]} = \frac{\sum_{i=1}^{k-1} P[N(t) = i]}{1 - \alpha_t^a}. \qquad (9b)$$

The results for the stem group age were shown by Strathmann and Slatkin (1983) to be

$$P[N(t) \geq k] = \beta_t^{k-1} \quad \text{and} \tag{10a}$$

$$P[N(t) < k] = 1 - \beta_t^{k-1}. \tag{10b}$$

The results for the crown group age (after considerable algebra) are:

$$P[N(t) \geq k] = \frac{\beta_t^{k-2}}{1 + \alpha_t}[r(1 - \alpha_t - \beta_t + \alpha_t\beta_t) + \alpha_t$$

$$+ 2\beta_t - 1] \quad \text{and} \tag{11a}$$

$$P[N(t) < k] = 1 - P(i \geq k). \tag{11b}$$

Either pair of equations can be used to obtain critical values of k above or below which the results of a certain percentage of replicates of the stochastic process are expected to fall. To obtain a 95% confidence interval on a clade at time t with diversity $N(t)$, given a diversification rate, r, and relative extinction rate, ϵ, it is necessary to calculate an upper boundary value, k_u, at or below which 97.5% of the results of the replicates of the stochastic process will fall, and a lower boundary value, k_l, above which 97.5% of the results of replicates of the stochastic process will fall. The range of values between k_u and k_l is the 95% confidence interval of the expected number of species at a time t after the origin of a clade, under a given r and ϵ. In the case of a stem group, for example, a value for k_u for every t from $t = 0$ to $t = 130$ million years is obtained by fixing the upper part of equation (10) to be equal to 0.025. Values for r (estimated $r_{0.0}$ or $r_{0.9}$ for angiosperms as a whole), ϵ ($\epsilon = 0.0$ and $\epsilon = 0.9$) and t ($t = 0$ to $t = 130$ million years in intervals of 5 million years) are given, and the equation can then be solved analytically for k_u. The sequence of obtained values for k_u represents the upper boundary of the 95% confidence interval of expected species diversity, given the background diversification rate, and the corresponding relative extinction rate. The lower boundary of the 95% confidence interval is obtained in the same way, by solving the lower part of equation (10) for k_l. To obtain k_u and k_l in the case of crown groups, equation (11) was solved numerically.

The standing diversity of selected angiosperm clades can then be assessed in relation to the 95% confidence interval of the expected number of species of a clade of similar age that diversifies under the estimated background rate. We make this comparison by placing the calculated confidence intervals in plots for stem group ages and for crown group ages of (log) species diversity versus age and by mapping in them datapoints corresponding to each angiosperm clade, according to their present-day species diversity and their stem group or crown group age, respectively. Those clades that fall outside the confidence intervals are then provisionally regarded as being excessively species rich or poor. Of course, if the datapoints were a random sample from the assumed distribution, 5% of them should fall outside the confidence interval just by chance. Therefore, we must be careful inferring that any particular datapoint is an outlier.

DATA

Angiosperm Clades

Clades of angiosperms were delimited on the basis of recent primary phylogenetic studies. In view of the amount of phylogenetic information available since the publication of the Angiosperm Phylogeny Group (1998) summary (e.g., Qiu et al. 1999; Soltis et al. 1999, 2000), we readdressed the taxonomic content and phylogenetic relationships among major angiosperm clades. Many of the taxonomic delimitation of clades used here are narrower than in the Angiosperm Phylogeny Group system, and changes in relationships involve areas in which our reconstructed trees have greater resolution, thanks to recent phylogenetic analyses (e.g., the first-diverging branches within the angiosperms). Figure 2 shows the reconstructed angiosperm phylogeny used in this study. Detailed information about the taxonomic content of each clade is available from the authors.

Species Diversity

Species diversity for angiosperm clades was estimated from the number of species in included families, and isolated genera where relevant, on the basis of the taxonomic circumscription for each clade (see above). Number of species in families of eudicots and magnoliids was obtained from Takhtajan (1997); number of species for monocot families was obtained from Dahlgren et al. (1985). When the number of species included in a family is available as a range (e.g., from 80 to 100 species), we used the midpoint value between the extremes. Species diversity for Laurales was modified according to information kindly provided by S. Renner (pers. comm.). Species diversity in each angiosperm clade is shown in Table 1.

Stem Lineage Representative or Crown Group Member?

Any given fossil taxon is either an extinct member of a clade's crown group or a member of its associated stem group (see above). Distinguishing in practice between these alternatives is not trivial, however. The relationship of a fossil to the extant members of a given clade can be explicitly known only through phylogenetic analysis. But, at least in the case of angiosperms, phylogenetic analyses in which fossil and extant taxa are simultaneously included have so far only seldomly been performed (e.g., Keller et al. 1996; Magallón et al. 1996; Gandolfo et al. 1998a; Magallón 1999, 2000).

In the absence of explicit phylogenetic analyses, we use two empirical criteria to determine whether any given fossil is a crown group member or a stem lineage representative. The existence of synapomorphies is the first criterion. If a fossil presents the synapomorphies that characterize the extant members of a particular subclade within a larger clade, then this fossil can be assigned unambiguously to the crown group of the larger clade (e.g., *Androdecidua* displays synapomorphies of Loropetalinae [Hamamelidoideae; Magallón et al. 2001], a sublcade within the Saxifragales, and thus, it can be identified as a crown group member of Saxifragales). Whether this particular fossil belongs to the crown group of the subclade is ambiguous, because, although it displays all the synapomorphies of the subclade, the fossil could still represent a branch that diverged after all the syanpomorphies had evolved, but before any of the extant members diverged. If a fossil displays some, but not all the synapomorphies shared by extant members of a clade, then it is considered
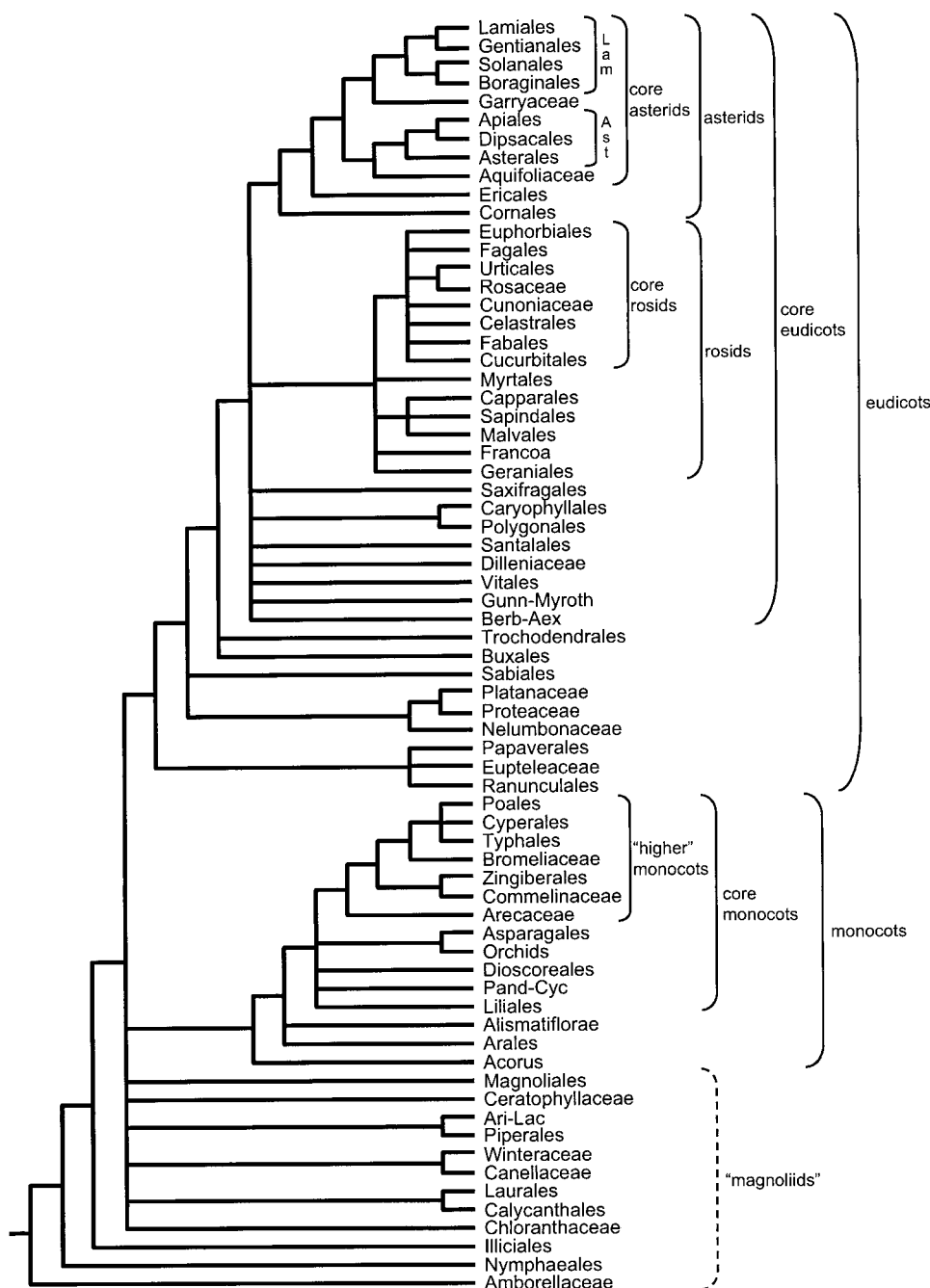
FIG. 2. Angiosperm phylogeny based on empirical compilation of primary phylogenetic studies. Taxonomic composition of clades and equivalencies with Angiosperm Phylogeny Group (1998) system is available from the authors. Abbreviations: Ari-Lac, Aristolochiaceae-Lactoridaceae; Ast, Asteridae s.l.; Berb-Aex, Berberidaceae-Aextoxicaceae; Gunn-Myroth, Gunneraceae-Myrothamnaceae; Lam, Lamiidae s.l.; Pand-Cyc, Pandanaceae-Cyclanthaceae.

to be a stem lineage representative (e.g., *Spanomera* in Buxaceae; Drinnan et al. 1991). Taxonomic assignment is the second criterion. If a fossil has been assigned to any distinct taxon within an angiosperm clade, we considered it as a member of the crown group of that clade (e.g., *Archaeanthus,* related to Magnoliaceae [Dilcher and Crane 1984], is considered a member of crown group Magnoliales). If a fossil displays a general similarity with members of a particular clade, but lacks features that allow assignment of it into any

of the subgroups within that clade, then it is considered to be a stem lineage representative (e.g., ''magnolialean gynoecium'' [Crane et al. 1994] is considered a stem lineage representative of Magnoliales).

All the assignments to crown group or to stem group presented here may be subject to revision. Whereas recognition of stem lineage representatives appears to be secure, our assignments to crown groups may be less so. The reason for this is that fossil remains, especially in the case of plants,

TABLE 1. Species diversity and age of angiosperms and angiosperm clades. Angiosperm clades are listed alphabetically under three categories: "magnoliids," monocots, and eudicots. Species diversity is based on taxonomic composition of each clade (available from the authors) and familial and generic diversity obtained from Takhtajan (1997) for "magnoliids" and eudicots and from Dahlgren et al. (1985) for monocots. Species diversity for eudicots and core eudicots are also provided. The sum of total angiosperm species diversity is larger than the sum of the clades included here because the former includes several clades of unknown phylogenetic position, which are not included in this table. Age of clades is based on their first appearance in the fossil record, considering whether their oldest fossil represents a stem representative (SG) or a crown group member (CG). Supporting references for fossil occurrences are included. Stratigraphic occurrences of fossils were transformed into absolute ages (in millions of years) based on time scales of Gradstein et al. (1995) and Palmer and Geissman (1999; see text). Triuridales are included, although their exact phylogenetic placement within the monocots is unknown. Abbreviations for clade names, used in Figures 3–5, are listed in the second column. Twelve clades with an unreliable or nonexistent fossil record, as well as eight clades that are much younger than their sister clade and display biological traits that hinder preservation (see text), were excluded from analyses and are marked with an x in the abbreviations column.

Clade	No. of species		Abbr.	Age	Fossil record	Reference
Angiosperms						
Angiosperm pollen grains (Incertae sedis angiosperms)	262,196	CG	Angios	132	late Valanginian–early Hauterivian	Brenner 1996
"magnoliids"						
Amborellaceae	1	—	x		no known fossil record	—
Aristolochiaceae-Lactoridaceae	601	CG	Ari-Lac	91.2	Turonian	Zavada and Benson 1987; MacPhail et al. 1999
Calycanthales	10	SG	Cal	108.8	early Albian	Friis et al. 1994a
Canellaceae	16	—	x		no reliable fossil record	—
Ceratophyllaceae	11	CG	Cer	59.9	Paleocene	Herendeen et al. 1990
Chloranthaceae	75	CG	Chl	121.0	Barremian–Aptian	Friis et al. 1994b, 1999
Illiciales	98	CG	Ill	93.5	Cenomanian–Turonian	Frumin and Friis 1999
Laurales	3094	CG	Lau	108.8	early Albian	Crane et al. 1994
Magnoliales	3016	SG	Mag	108.8	early Albian	Crane et al. 1994
Magnoliales	3016	CG	Mag	97.5	early Cenomanian	Dilcher and Crane 1984
Nymphaeales	85	CG	Nym	121.0	Barremian–Aptian	Friis et al. 2001
Piperales	2107	—	x		no reliable fossil record	—
Winteraceae	80	SG	Win	122.5	late Barremian	Doyle et al. 1990a,b; Doyle 2000
Monocots						
Acorus	1	—	x		no known fossil record	—
Alismatiflorae	454	CG	Ali	68.1	Maastrichtian	Voight 1981
Arales	2480	CG	Ara	105.5	Albian	Herendeen and Crane 1995
Arecaceae	2780	SG	Are	84.0	Upper Santonian	Daghlain 1981
Arecaceae	2780	CG	Are	77.4	Campanian	Crabtree 1987
Asparagales[1]	6635	CG	x	37.5	Late Eocene	Couper 1960; Muller 1981; Herendeen and Crane 1995
Bromeliaceae[2]	1600	CG	x	37.5	Late Eocene	Graham 1987; Herendeen and Crane 1995
Commelinaceae[3]	700	CG	x	13.8	Middle Miocene	Jacobs and Kabuye 1989; Herendeen and Crane 1995
Cyperales	11,022	CG	Cyp	45.15	Middle Eocene	Erwin and Stockey 1992; Herendeen and Crane 1995
Dioscoreales	771	—	x		no known fossil record	—
Liliales[4]	1229	CG	x	45.15	Middle Eocene	Sun and Dilcher 1988; Wilde 1989; Herendeen and Crane 1995
Orchids	20,115	—	x		no reliable fossil record	—
Pandanaceae-Cyclanthaceae	1420	—	x		no reliable fossil record	—
Poales	10,447	CG	Poa	68.1	Maastrichtian	Jarzen 1978; Muller 1981; Linder 1987
Triuridaceae	75	SG	Tri	91.2	Turonian	Gandolfo et al. 1998a
Typhales	35	CG	Type	77.4	Campanian	Médus 1987; Herendeen and Crane 1995
Zingiberales	1560	CG	Zin	83.5	Santonian–Campanian	Friis 1988
Eudicots						
Tricolpate pollen grains (eudicots)	191,480	CG	Eudi	121.0	late Barremian–early Aptian	Doyle and Hotton 1991

TABLE 1. Continued.

Clade	Abbr.	No. of species	Fossil record	Age	Reference
Normapolles pollen grains (core eudicots)	C-Eudi	185,809	CG	middle Cenomanian	96.2	Pacltová 1966, 1981
Apiales	Api	4898	CG	Middle Eocene	45.15	Manchester 1994
Aquifoliaceae	x	416	—	no known fossil record	—	—
Asterales	Ast	25,996	CG	Oligocene	28.75	Muller 1981; Collinson et al. 1993
Berberidopsidaceae-Aextoxicaceae	x	4	—	no known fossil record	—	—
Boraginales	Bor	2757	CG	Eocene	44.25	Chandler 1964
Buxales	Bux	72	SG	late Albian	102.2	Drinnan et al. 1991
Capparales	Cap	4366	SG	Turonian	91.2	Gandolfo et al. 1998b
Caryophyllales	Car	10,003	CG	Santonian–Campanian	83.5	Collinson et al. 1993
Celastrales[5]	x	944	CG	Oligocene	28.75	Muller 1981
Cornales	Cor	670	CG	Coniacian–Santonian	85.8	Magallón 1997
Cucurbitales	Cuc	1852	CG	Paleocene	59.9	Collinson et al. 1993
Cunoniaceae	Cun	1407	CG	Paleocene	59.9	Hill 1991
Dilleniaceae	Dil	400	CG	Early Eocene	51.9	Chandler 1964; Collinson et al. 1993
Dipsacales	Dip	1216	CG	Eocene	44.25	Manchester and Donoghue 1995
Ericales	Eri	10,620	CG	Turonian	91.2	Nixon and Crepet 1993
Euphorbiales	Euph	15,402	CG	Turonian	91.2	Crepet and Nixon 1998
Eupteleaceae	Eupt	2	CG	Late Eocene	37.5	Wolfe 1977
Fabales	Fab	19,054	CG	Paleocene	59.9	Herendeen and Crane 1992
Fagales	Fag	1385	CG	middle Cenomanian	96.2	Pacltová 1966, 1981
Francoa clade	x	25	—	no known fossil record	—	—
Garryaceae	Gar	25	CG	Eocene	4.425	Call and Dilcher 1997
Gentianales	Gen	17,730	CG	Eocene	4.425	Chandler 1964; Mai and Walther 1985; Manchester 1999
Geraniales	x	724	—	no reliable fossil record	—	—
Gunneraceae-Myrothamnaceae	x	42	—	no reliable fossil record	—	—
Lamiales	Lam	23,379	CG	Eocene	44.25	Chandler 1964; Mai and Walther 1985; Call and Dilcher 1992
Malvales	Mal	5607	CG	early Maastrichtian	69.7	Wolfe 1976
Myrtales	Myr	10,782	CG	early Coniacian	88.2	Takahashi et al. 1999
Nelumbonaceae	Nel	2	SG	late Albian	102.2	Upchurch et al. 1994
Papaverales[6]	x	799	CG	Miocene	14.55	Dorofeev 1964
Platanaceae	Pla	10	SG	early Albian	108.8	Crane and Herendeen 1996
Polygonales[7]	x	2147	CG	Eocene	44.25	Chandler 1964; Mai 1985
Proteaceae	Pro	1050	SG	Cenomanian	96.2	Dettmann and Jarzen 1998
Ranunculales[8]	x	3652	CG	Maastrichtian	68.1	Collinson et al. 1993
Rosaceae	Ros	3251	CG	Eocene	44.25	Basinger 1976; Cevallos-Ferriz et al. 1993
Sabiales	Sab	80	CG	Maastrichtian	68.1	Knobloch and Mai 1986
Santalales	San	2120	CG	Early Eocene	51.9	Chandler 1964; Collinson et al. 1993
Sapindales	Sap	5773	CG	Maastrichtian–Paleocene	65.0	Knobloch and Mai 1986
Saxifragales	Sax	2558	CG	Turonian	91.2	Gandolfo et al. 1998c
Solanales	Sol	4188	CG	Eocene	44.25	Collinson et al. 1993
Trochodendrales	Tro	2	SG	Albian	105.5	Crane 1989; Doyle and Hickey 1976
Urticales	Urt	3531	CG	Maastrichtian	68.1	Manchester 1989
Vitales	Vit	784	CG	Late Paleocene	57.9	Mai and Walther 1978, 1985; Collinson et al. 1993

[1] Asparagales: age of single reliably dated clade in polytomy: Santonian–Campanian.
[2] Bromeliaceae: age of sister clade: at least Campanian.
[3] Commelinaceae: age of sister clade: Santonian–Campanian.
[4] Liliales: age of single reliably dated clade in polytomy: Santonian–Campanian.
[5] Celastrales: age of sister clade: minimum: Eocene; maximum: middle Cenomanian.
[6] Papaverales: age of possible sister clade to ranunculid clade: at least lower Albian.
[7] Polygonales: age of sister clade: Santonian–Campanian.
[8] Ranunculales: age of sister taxon to ranunculid clade: at least lower Albian.

represent only a part of the whole organism. Even if the characters of the preserved organ display all the crown group synapomorphies, the possibility that other parts of the organism, which did not enter the fossil record, lacked some of the synapomorphies of extant taxa, cannot be excluded. Therefore, because of the unavailability of the complete set of characters of extinct organisms, we may have unknowingly interpreted a stem representative as a crown group member.

Age

The age for each angiosperm clade was obtained from the first reliable appearance in the fossil record of any member of its constituent taxa. We considered first appearances based on worldwide reports of reliably identified remains of pollen grains (microfossils), vegetative and reproductive organs (macrofossils), as well as reports based on three-dimensional, charcoalified remains of flowers, fruits, seeds, and in situ pollen grains (mesofossils). In most cases a fossil provides a minimum age, regardless of whether it refers to a crown or stem group. Only in those rare instances in which the fossil record is so dense that some confidence is associated with the absence of fossils can an absolute age be assigned to a node. We report results based on the assumption that a minimum age is a good approximation of the real age of the clade, but discuss the robustness of results with this issue in mind. First appearances of monocot and eudicot taxa were obtained mostly from previous compilations (e.g., Herendeen and Crane 1995; Magallón et al. 1999), supplemented with more recent primary reports.

Stratigraphic occurrences of fossil taxa were transformed into absolute ages (millions of years) by assigning an age value to each geological interval corresponding to the midpoint between the ages of its inferior and superior boundaries. Ages for informal intervals (e.g., early Campanian) were derived from the midpoint between the obtained midpoint of the interval and the age of the inferior or superior boundary, as relevant. Absolute ages for stratigraphic boundaries were obtained from Gradstein et al. (1995) for Cretaceous intervals and from the geologic time scale of the Geological Society of America (Palmer and Geissman 1999) for Tertiary and Cretaceous intervals. Earliest reliable fossil reports for each angiosperm clade, together with its stratigraphic occurrence, estimated age in millions of years, and the assignment to stem lineage or crown group are shown in Table 1.

Sample of Angiosperm Clades

We take a conservative approach to selecting angiosperm clades for estimating their rate of diversification and assessing their standing species diversity. From an initial pool of 70 clades, a total of 20 clades were excluded from our analyses. Ages for 12 clades cannot be obtained, because they have an unreliable or entirely missing fossil history (Table 1). The available fossil record of the remaining clades was nevertheless considered critically. Although we support the view that currently known first appearances in the fossil record represent appropriate approximations to the ages of most angiosperm clades, it is entirely possible that, for some clades, their oldest known fossil is substantially younger than the clade itself. In an attempt to identify these clades, we relied in the combined presence of two factors. First, we looked for a much later first appearance in the fossil record than its sister clade (or closely related clades, in the case of polytomies). By definition, the stem group age of sister taxa is the same. If one of the members of a sister pair first appears in the fossil record in strata that are substantially younger than those that bear the oldest remains of its sister taxon, then a segment of the early history of the former must be missing from the fossil record. Second, we looked for the presence of biological traits that reduce their potential to enter the fossil record. Herendeen and Crane (1995) note that the fact that the angiosperm fossil record is dominated by leaves and pollen of arborescent deciduous, wind-pollinated taxa is probably the result of the low preservation potential of herbaceous plants, because their leaves are usually not shed, and of the relatively low pollen output of animal-pollinated taxa. Therefore, herbaceous, animal-pollinated taxa have the lowest probability to enter the fossil record. Neither of these two condition by itself is improbable, but together they raise the specter of underestimating a clade's true age. Eight angiosperm clades displaying these two conditions were identified and excluded from our analyses (Table 1).

RESULTS

Angiosperm Diversification Rate

On the basis of the earliest-known occurrence of angiosperm pollen in the fossil record, in late Valanginian to early Hauterivian strata of Israel (Brenner 1996), corresponding to approximately 132 million years before the present, and on an estimated standing diversity of 262,196 species, we obtained possible values of the net diversification rate for angiosperms as a whole, as a function of postulated relative extinction rate (ϵ). We estimate a maximum diversification rate of 0.0893 net speciation events per million years in the absence of extinction ($r_{0.0} = 0.0893$; Table 2) and a minimum of 0.0767 net speciation events per million years under a high relative extinction rate ($r_{0.9} = 0.0767$; Table 2). The obtained values for the rate of diversification of angiosperms in absence of extinction ($r_{0.0}$) and under a high relative extinction rate ($r_{0.9}$) are used as estimates of the background diversification rate for angiosperms as a whole.

Diversification Rates of Angiosperm Clades

Absolute diversification rates for selected angiosperm clades are shown in Table 2. Rates estimated in the absence of extinction ($\epsilon = 0.0$) are higher than rates estimated under a high relative extinction rate ($\epsilon = 0.9$). This is the expected behavior of the rate of diversification in the face of an increasing relative extinction: As the relative extinction rate increases, the impact of the bias due to the conditioning of the estimator on survival of the clade becomes more important and the estimate of diversification rate drops accordingly.

For two clades, Magnoliales and Arecaceae, both stem group and crown group ages are available. A comparison between the diversification rates estimated for each clade under stem group and crown group age allows to verify if the rates estimated under the two conditions are similar. Diversification rates obtained by using stem group age and

TABLE 2. Absolute rate of diversification for angiosperms and angiosperm clades. Rates of diversification were estimated in absence of extinction (ϵ = 0.0, left) and under a high relative extinction rate (ϵ = 0.9, right). Use of a stem group (SG) or crown group (CG) age for each clade is indicated. Rates of diversification are presented in ascending order. Rates for inclusive clades (angiosperms, ''higher'' monocots, eudicots, core eudicots, core rosids, and core asterids) are in bold. Ari-Lac, Aristolochiaceae-Lactoridaceae.

Clade		ϵ = 00	Clade		ϵ = 0.9
Eupteleaceae	CG	0.0000	Eupteleaceae	CG	0.0000
Trochodendrales	SG	0.0066	Nelumbonaceae	SG	0.0009
Nelumbonaceae	SG	0.0068	Trochodendrales	SG	0.0009
Calycanthales	SG	0.0212	Calycanthales	SG	0.0059
Platanaceae	SG	0.0212	Platanaceae	SG	0.0059
Ceratophyllaceae	CG	0.0285	Ceratophyllaceae	CG	0.0107
Chloranthaceae	CG	0.0300	Chloranthaceae	CG	0.0172
Nymphaeales	CG	0.0310	Winteraceae	SG	0.0178
Winteraceae	SG	0.0358	Nyphaeales	CG	0.0181
Typhales	CG	0.0370	Typhales	CG	0.0185
Illiciales	CG	0.0416	Buxales	SG	0.0205
Buxales	SG	0.0418	Triuridaceae	SG	0.0233
Triuridaceae	SG	0.0473	Illiciales	CG	0.0248
Sabiales	CG	0.0542	Garryaceae	CG	0.0265
Nymphaeales	CG	0.0551	Sabiales	CG	0.0313
Garryaceae	CG	0.0571	Nymphaeales	CG	0.0321
Ari-Lac	CG	0.0626	Ari-Lac	CG	0.0445
Laurales	CG	0.0675	Proteaceae	SG	0.0485
Arales	CG	0.0675	Cornales	CG	0.0486
Cornales	CG	0.0678	Fagales	CG	0.0508
Fagales	CG	0.0680	Arales	CG	0.0518
Proteaceae	SG	0.0723	Laurales	CG	0.0523
Magnoliales	SG	0.0736	Magnoliales	SG	0.0525
Magnoliales	CG	0.0751	Alismatiflorae	CG	0.0556
Saxifragales	CG	0.0784	Magnoliales	CG	0.0581
Alismatiflorae	CG	0.0797	Zingiberales	CG	0.0599
Zingiberales	CG	0.0798	Saxifragales	CG	0.0603
Angiosperms	**CG**	**0.0893**	Capparales	SG	0.0667
Capparales	SG	0.0919	Arecaceae	SG	0.0670
Arecaceae	CG	0.0935	Dilleniaceae	CG	0.0705
Ericales	CG	0.0940	Arecaceae	CG	0.0721
Arecaceae	SG	0.0944	Vitales	CG	0.0746
Eudicots	**CG**	**0.0948**	Ericales	CG	0.0758
Myrtales	CG	0.0974	**Angiosperms**	**CG**	**0.0767**
Euphorbiales	CG	0.0981	Myrtales	CG	0.0786
Caryophyllales	CG	0.1020	Euphorbiales	CG	0.0799
Dilleniaceae	CG	0.1021	**Eudicots**	**CG**	**0.0811**
Vitales	CG	0.1031	Cunoniaceae	CG	0.0818
Core Rosids	**CG**	**0.1046**	Caryphyllales	CG	0.0821
Cunoniaceae	CG	0.1095	Urticales	CG	0.0854
Urticales	CG	0.1098	Cucurbitales	CG	0.0864
Malvales	CG	0.1139	**Core Rosids**	**CG**	**0.0873**
Cucurbitales	CG	0.1140	Malvales	CG	0.0901
''Higher'' Monocots	**CG**	**0.1144**	**''Higher'' Monocots**	**CG**	**0.0945**
Core Eudicots	**CG**	**0.1189**	Sapindales	CG	0.0971
Sapindales	CG	0.1226	Poales	CG	0.1013
Poales	CG	0.1257	**Core Eudicots**	**CG**	**0.1016**
Santalales	CG	0.1342	Santalales	CG	0.1023
Dipsacales	CG	0.1449	Dipsacales	CG	0.1075
Fabales	CG	0.1530	Fabales	CG	0.1252
Boraginales	CG	0.1634	Boraginales	CG	0.1259
Rosaceae	CG	0.1671	Rosaceae	CG	0.1296
Apiales	CG	0.1728	Solanales	CG	0.1353
Solanales	CG	0.1728	Apiales	CG	0.1361
Cyperales	CG	0.1908	Cyperales	CG	0.1540
Gentianales	CG	0.2054	Gentianales	CG	0.1679
Lamiales	CG	0.2117	Lamiales	CG	0.1741
Core Asterids	**CG**	**0.2349**	**Core Asterids**	**CG**	**0.1981**
Asterales	CG	0.3295	Asterales	CG	0.2717

crown group age are close in the two cases (Table 2), although the difference between rates obtained in absence of extinction is always smaller (i.e., 0.0015 and 0.0009, respectively) than the difference between rates obtained using a high relative extinction (i.e., 0.0056 and 0.0051, respectively). In the four possible comparisons, rates estimated using a crown group age are higher than those using a stem group age.

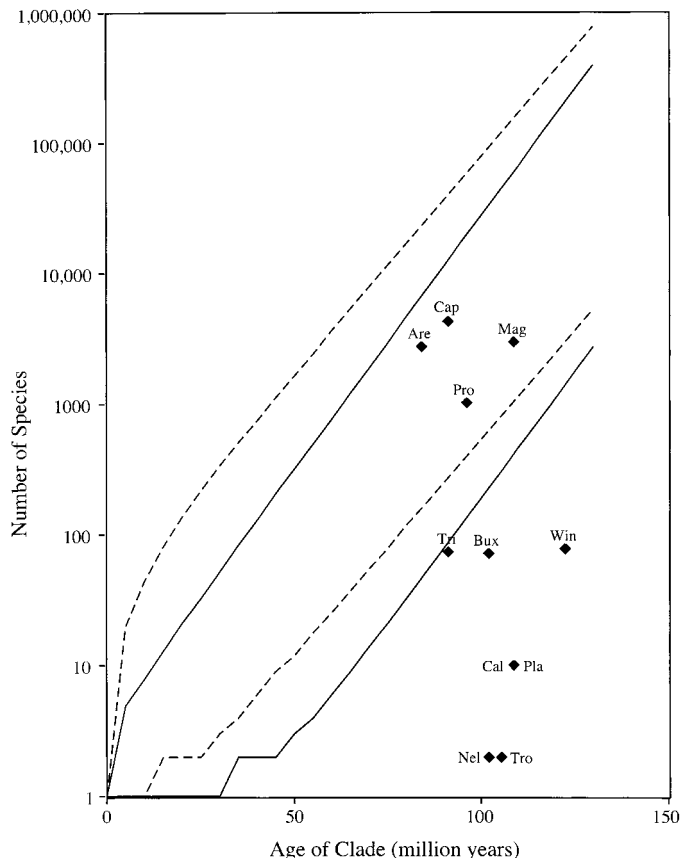In the absence of extinction (ϵ = 0.0), the number of clades

FIG. 3. Confidence intervals of expected species diversity according to age of stem group. The 95% confidence interval of expected species diversity through time of a clade that diversifies with a rate equal to that of angiosperms as a whole in the absence of extinction ($\epsilon = 0.0$; $r_{0.0} = 0.0893$; solid lines) and under a high relative extinction rate ($\epsilon = 0.9$; $r_{0.9} = 0.0767$; dashed lines), according to a starting stem group age is shown. Angiosperm clades are mapped according to stem group age and standing species diversity. Clades that fall above the upper limit of the highest confidence interval (i.e., under $\epsilon = 0.9$) are considered extremely species rich. Clades that fall below the lower limit of lowest confidence interval (i.e., under $\epsilon = 0.0$) are considered extremely species poor. Abbreviations for clade names as in Table 1.
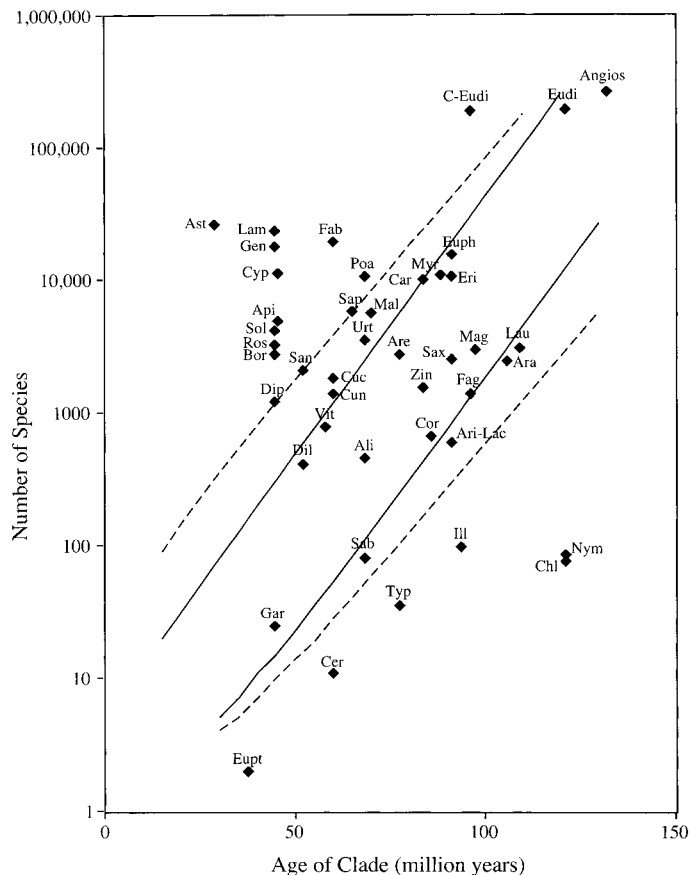
FIG. 4. Confidence intervals of expected species diversity according to age of crown group. The 95% confidence interval of expected species diversity through time of a clade that diversifies with a rate equal to that of angiosperms as a whole in the absence of extinction ($\epsilon = 0.0$; $r_{0.0} = 0.0893$; solid lines) and under a high relative extinction rate ($\epsilon = 0.9$; $r_{0.9} = 0.0767$; dashed lines), according to a starting crown group age is shown. Angiosperm clades are mapped according to crown group age and standing species diversity. Clades that fall above the upper limit of the highest confidence interval (i.e., under $\epsilon = 0.9$) are considered extremely species rich. Clades that fall below the lower limit of lowest confidence interval (i.e., under $\epsilon = 0.9$) are considered extremely species poor. Abbreviations for clade names as in Table 1.

with a rate lower than the background is approximately the same as the number of clades with a rate higher than the background (i.e., 27 vs. 26, respectively; Table 2). However, under a high relative extinction rate ($\epsilon = 0.9$), many more than half of the clades have an absolute rate lower than the background (i.e., 33 vs. 20, respectively; Table 2). The clades with highest overall rates are Asterales ($r_{0.0} = 0.33$, $r_{0.9} = 0.27$), Lamiales ($r_{0.0} = 0.21$, $r_{0.9} = 0.17$), Gentianales ($r_{0.0} = 0.21$, $r_{0.9} = 0.17$), Cyperales ($r_{0.0} = 0.19$, $r_{0.9} = 0.15$), Solanales ($r_{0.0} = 0.17$, $r_{0.9} = 0.14$), and Apiales ($r_{0.0} = 0.17$, $r_{0.9} = 0.14$). The estimated rates of diversification for Poales and Fabales, both extraordinarily species-rich clades, are lower than for the clades above. The reason for this is that Poales and Fabales are comparatively ancient (see Discussion). Nevertheless, the estimated rates of diversification for Fabales ($r_{0.0} = 0.15$, $r_{0.9} = 0.13$) and Poales ($r_{0.0} = 0.13$, $r_{0.9} = 0.10$) are still high among angiosperm clades overall.

The five clades with lowest rates of diversification are Eup-

teleaceae ($r_{0.0} = 0$, $r_{0.9} = 0$), Trochodendrales ($r_{0.0} = 0.007$, $r_{0.9} = 0.001$), Nelumbonaceae ($r_{0.0} = 0.007$, $r_{0.9} = 0.001$), Calycanthales ($r_{0.0} = 0.021$, $r_{0.9} = 0.006$), and Platanaceae ($r_{0.0} = 0.021$, $r_{0.9} = 0.006$). Except for Eupteleaceae, these clades are more than 100 million years old and each has a standing diversity of 10 or fewer species. The exception, Eupteleaceae, with two living species, first appears in the fossil record in relatively young strata (~37.5 million years), however, there has been no net increase in number of species since the origin of the Eupteleaceae crown group.

Hypothesis Tests on Diversity

Confidence intervals for the expected number of species through time under background rates of diversification are shown in Figure 3 for stem groups and in Figure 4 for crown groups. The slope of the confidence band is shallower at high extinction, reflecting the bias due to conditioning on surviv-

ing clades. For crown group ages, the confidence interval for expected number of species in the absence of extinction is narrower than and falls within the interval under high relative extinction. For stem group ages, the confidence interval under high relative extinction is slightly broader than the interval obtained in the absence of extinction, largely because the lower confidence boundary for stem group age is significantly lower than for crown group ages. The position of this boundary is heavily influenced by the fact that the number of species at the onset of the diversification process is one, rather than two.

Angiosperm clades are plotted in Figures 3 and 4, as a function of their standing species diversity and their age. Clades for which a stem group age is available are fewer (i.e., 11) than clades with a known crown group age (i.e., 41). The two clades for which both stem group age and crown group age are available (i.e., Magnoliales and Arecaceae), are included in the two plots. We regard only clades that fall outside the widest confidence band at any point in time as being extraordinarily species rich or species poor.

Ten angiosperm clades fall above the highest limit of confidence intervals for expected diversity, given a background diversification rate (corresponding to $\epsilon = 0.9$ for crown group ages; Fig. 4). These extraordinarily species-rich clades are the Cyperales, Poales, Fabales, Rosaceae, Apiales, Asterales, Boraginales, Solanales, Gentianales, and Lamiales. The Santalales, Sapindales, and Dipsacales are also very species rich, and fall on the borderline of the broadest 95% confidence interval of expected diversity. If the 95% confidence interval estimated in the absence of extinction ($\epsilon = 0.0$) is considered, the number of extraordinarily species-rich clades is greater (Fig. 4).

A total of 13 clades, seven dated with stem group ages (Fig. 3) and six with crown group ages (Fig. 4), fall below the lowest limit of the expected number of species given a background diversification rate (corresponding to $\epsilon = 0.0$ for stem group ages, and $\epsilon = 0.9$ for crown group ages). These surprisingly species-poor clades are Calycanthales, Winteraceae, Triuridaceae, Nelumbonaceae, Platanaceae, Buxales, and Trochodendrales (derived from stem group ages) and Nymphaeales, Illiciales, Ceratophyllaceae, Chloranthaceae, Typhales, and Eupteleaceae (derived from crown group ages).

DISCUSSION

The analyses provide estimates of the absolute rate of diversification for angiosperms as a whole and a large set of angiosperm clades, for a range of reasonable values of relative extinction. This identifies extraordinarily species-rich or species-poor clades, relative to an estimated background diversification rate. These results rely on stochastic diversification models (Bailey 1964; Raup 1985), the utility of which has been addressed previously (e.g., Stanley 1979; Strathmann and Slatkin 1983; Foote et al. 1999). Models based on constant diversification rates, such as ours, lead to exponential growth. If a clade's rate of diversification decreases through time, estimates of average rates, based on the assumption of a constant rate, will underestimate the rate of diversification during the early evolution of the clade, but will overestimate the rate during its old age.

Of greater concern is the accuracy of the values used for ages of clades. Although the angiosperm fossil record likely provides adequate approximations to the ages of most clades, some of the available earliest appearances may substantially postdate the origin of the stem group or crown group of a particular clade. The use of a falsely young age for any given clade has an asymmetric effect on tests on diversity, depending on whether the clade is above or below the sloping confidence bands in Figures 3 and 4. Correcting the age of a clade that is apparently species rich (above the band) will move it into regions where its species diversity is unremarkable. Correcting the age of a species-poor clade (below the band) will move its position further away from the confidence band, and it will become more significantly species poor.

Relationship between Diversification and Age

Species-rich clades do not necessarily have extremely high diversification rates, if they are sufficiently old. This is the reason why the rates estimated for Poales (grasses) and Fabales (legumes), two clades usually perceived as being extraordinarily diverse, are not among the very highest within angiosperms. The Fabales, including more than 19,000 species, is only smaller than Lamiales, Asterales, and the orchids. However, because the Fabales are substantially older than Lamiales and Asterales (the age of the orchids is not reliably known), their diversification rate is comparatively low (cf. Tables 1, 2). The Poales, with more than 10,000 species, has a species diversity roughly similar to that of Cyperales. Nevertheless, the older crown group age of Poales indicates a comparatively lower rate (cf. Tables 1, 2).

A clade with a low diversification rate, however, may only be detected when it is old, simply because both slowly diversifying and rapidly diversifying clades have few species when they are very young. Whereas a clade with a high rate of diversification will rapidly accumulate species as time proceeds, a clade with a low rate of diversification will retain a small diversity as it ages.

Extraordinary Species Richness under Extreme Diversification Rates

Ten angiosperm clades fall above the confidence intervals for expected species diversity (Fig. 4) and thus were identified as being extraordinarily species rich. Because clades do not diversify in a time-homogeneous manner and early rates of diversification of any given clade may be higher than those that occur later (see especially Hulbert 1993), the mean diversification rate of a clade through all its history may be inappropriately low to calculate the expected species diversity of a clade during its early radiation. This leads us to ask whether modern clades of angiosperms are unusually rich even with respect to earlier and higher rates of diversification at the origin of the clade.

To address this question, we estimated the rate of angiosperm diversification during their initial radiation from counts of number of species during Cretaceous geological intervals. Estimates for the number of angiosperm species in Cretaceous intervals were obtained from datapoints in figure 2 of Lidgard and Crane (1988), which depicts the change in

diversity of angiosperms and other land plant taxa through time, obtained from occurrence of species and genera in macrofossil floras extending from the Late Jurassic to the Paleocene. If the proportion of the total floristic diversity represented in fossil assemblages is approximately constant and the effect of loss of older rocks is not significant among temporally close intervals, then the difference in diversity between floristic assemblages is a proportional representation of the net increase (or decrease) in diversity between different geological intervals.

Absolute values of angiosperm species diversity for each Cretaceous geological interval (from Lidgard and Crane 1988) were placed in a (log) diversity versus age plot. Species diversity shows a rapid rise from the Barremian-Aptian to the mid-Cenomanian (Lidgard and Crane 1988), documenting a phase of rapid early radiation. By calculating the slope among the datapoints from the Barremian-Aptian to the Cenomanian through linear regression, we estimated a rate of diversification during the early phase of angiosperm radiation of $r = 0.123$ net speciation events per million years. Two 95% confidence intervals of expected species diversity through time, corresponding to the absence of extinction ($\epsilon = 0.0$) and to a high relative extinction rate ($\epsilon = 0.9$), were obtained using the rate of diversification during the early angiosperm radiation ($r = 0.123$). The resulting extreme confidence intervals are presented in diversity/age plots, in which datapoints for each angiosperm clade are included. Confidence intervals were produced for crown groups only; previous results show that none of the clades for which stem group age is available fall above the upper limit of expected species diversity, given a background rate of diversification (Fig. 3). Clades that fall above the upper limit of the confidence intervals can be identified as being unexpectedly species rich, even under extremely high rates of diversification (Fig. 5).

Only three clades, Asterales, Lamiales, and Gentianales, fall above the limit of the highest confidence interval (corresponding to $\epsilon = 0.9$) obtained using the extreme rate of diversification, and the Cyperales are on the border line. However, in the absence of extinction ($\epsilon = 0.0$), the Apiales, Solanales, Rosaceae, Boraginales, and Fabales are also unexpectedly species rich. Therefore, even if rates of diversification corresponding to the early radiation of angiosperms are considered, some angiosperm clades are more diverse than expected.

Phylogenetic Component

Are clades with unusually high or low diversification rates phylogenetically scattered, or is there a nonrandom pattern to their phylogenetic distribution? Clades with rates higher than background are found only within the monocot and eudicot clades. None of the independent ''magnoliid'' lineages exhibit rates that are higher than background. Within the monocots, Arecaceae, Poales, and Cyperales have rates higher than background. These three clades are members of a larger, distinct, and well-supported clade, the higher monocots (Fig. 2), that includes, among others, the Zingiberales and Bromeliaceae (Figs. 2, 6). Rates of diversification estimated for the higher monocots as a whole are $r_{0.0} = 0.11$
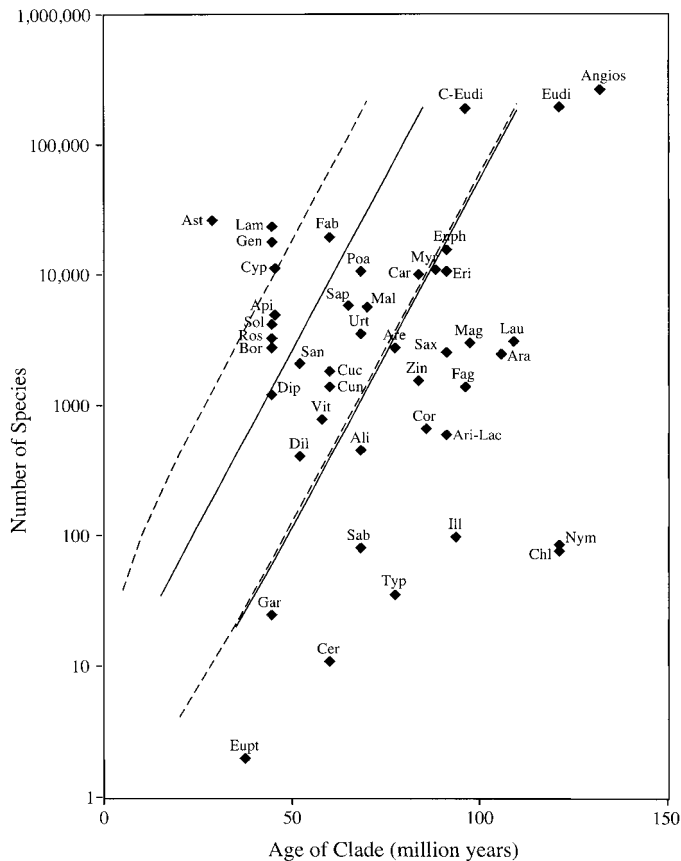

FIG. 5. Confidence intervals of expected species diversity under an extremely high diversification rate. The 95% confidence interval of expected species diversity through time of a clade that diversifies with a rate of diversification corresponding to that of the earliest radiation within the angiosperms ($r = 0.123$), under no extinction ($\varepsilon = 0.0$; solid lines) and under a high relative extinction rate ($\varepsilon = 0.9$; dashed lines), according to a starting crown group age is shown. Angiosperm clades are mapped according to crown group age and standing species diversity. Clades that fall above the upper limit of the highest confidence interval (i.e., under $\varepsilon = 0.9$) are considered as extraordinarily species rich, even under an extremely high rate of diversification. Abbreviations for clade names as in Table 1.

and $r_{0.9} = 0.09$, which are slightly higher than the rates of eudicots as a whole ($r_{0.0} = 0.09$, $r_{0.9} = 0.08$) and slightly lower than those of the core eudicots as a whole ($r_{0.0} = 0.12$, $r_{0.9} = 0.10$). Within the eudicots, clades with high diversification rates are found within the core eudicot clade (Figs. 2, 6). Two of these clades are the Santalales, which is a distinct lineage of unresolved phylogenetic placement among the major core eudicot clades, and the Caryophyllales, which includes the bulk of diversity within the Caryophyllid clade. All other core eudicot clades with high diversification rates are found within the rosids and the core asterids (Figs. 2, 6). Within the rosids (Figs. 2, 6), nine clades have rates that are higher than background, both under $\epsilon = 0.0$ and $\epsilon = 0.9$. Three of these are Sapindales, Malvales, and Myrtales, and the six remaining clades are members of the core rosid clade (Figs. 2, 6). In fact, except for the Fagales, all the clades within the core rosid clade have rates of diversification higher than background (Celastrales were excluded from consider-
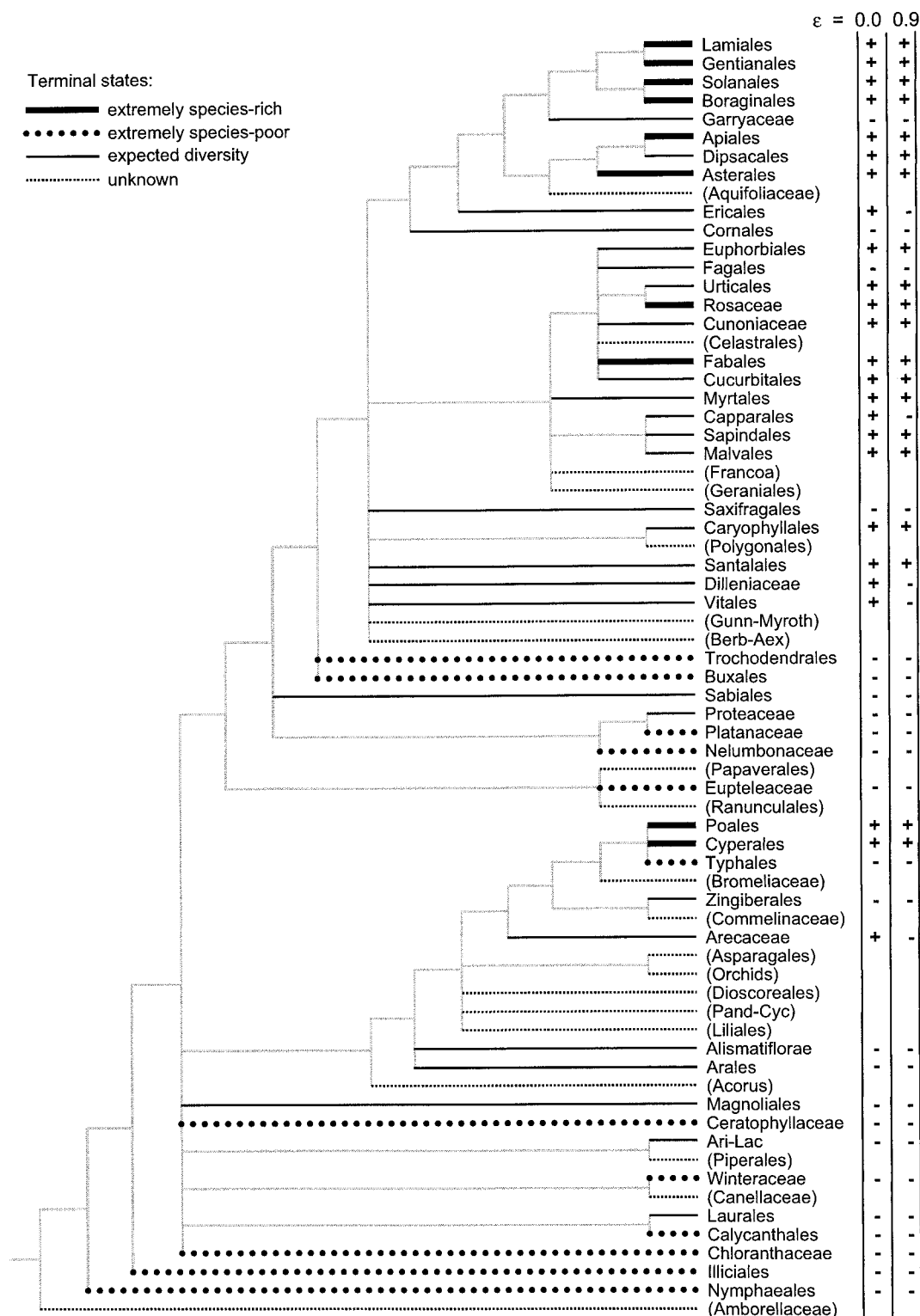
FIG. 6. Phylogenetic distribution of species diversity. Extremely species-rich and species-poor clades (cf. Figs. 3, 4) are indicated on the reconstructed angiosperm phylogeny. Only terminal states are indicated. Species-poor clades (dotted lines) mostly occur close to the root of the angiosperms (i.e., Nymphaeales, Illiciales, Calycanthales, Winteraceae, Ceratophyllaceae, and Chloranthaceae) and close to the root of eudicots (i.e., Eupteleaceae, Nelumbonaceae, Platanaceae, Buxales, and Trochodendrales). Typhales, which is nested highly within the monocots, is also extremely species poor. Species-rich clades (bold black lines) are highly nested (i.e., Poales and Cyperales within the "higher" monocots; Fabales and Rosaceae within the core rosids; Asterales and Apiales within Asteridae s.l.; and Boraginales, Solanales, Gentianales, and Lamiales within Lamiidae s.l.). Columns on the right indicate if the diversification rate of each clade is higher (+) or lower (−) than that of angiosperms as a whole, according to $\varepsilon = 0.0$ and $\varepsilon = 0.9$. Names of clades that were not included in analyses (see text) are shown in parentheses and marked in the phylogeny with a thin dotted line. Abbreviations: Ari-Lac, Aristolochiaceae-Lactoridaceae; Berb-Aex, Berberidaceae-Aextoxicaceae; Gunn-Myroth, Gunneraceae-Myrothamnaceae; Pand-Cyc, Pandanaceae-Cyclanthaceae.

ation; see Data section). Diversification rates for the core rosids as a whole are $r_{0.0} = 0.10$ and $r_{0.9} = 0.09$. Seven asterid clades (Figs. 2, 6) have diversification rates higher than background. These seven clades belong within the core asterid clade (Figs. 2, 6): three of them, the Apiales, Dipsacales, and Asterales, constitute Asteridae s.l., and the remaining four, Lamiales, Gentianales, Solanales, and Boraginales, constitute Lamiidae s.l. (Figs. 2, 6). Core asterids as a whole have extremely high rates, estimated as $r_{0.0} = 0.23$ and $r_{0.9} = 0.20$.

Extraordinarily species-rich clades

Unexpectedly species-rich and species-poor clades are indicated on a phylogeny for angiosperms (Fig. 6). Clades with the highest rates of diversification, and thus with an exceedingly high number of species, occur within the ''higher'' monocots (Poales and Cyperales), core rosids (Fabales and Rosaceae), and core asterids (Apiales and Asterales [in Asteridae s.l.], and Boraginales, Solanales, Gentianales, and Lamiales [in Lamiidae s.l.]; Figs. 2, 6).

Poales and Cyperales are members of a clade that also includes Typhales, within the monocots (Fig. 6). Phylogenetic relationships among these three clades are not fully resolved, but according to several analyses (e.g., Duvall et al. 1995; Soltis et al. 2000), Poales and Cyperales are sister taxa. If this is true, then the high rates of diversification that produced these extremely species-rich clades most likely do not characterize Poales and Cyperales independently, but rather, characterize the lineage that gave rise to both.

The same is probably true for the four clades of Lamiidae s.l. and the three that constitute Asteridae s.l., all of which are exceedingly species rich. A more interesting possibility is that the elevated diversification appeared in the lineage that gave rise to all core asterids (Fig. 6). Estimated rates of diversification for Garryaceae, the sister group of Lamiidae s.l., are substantially lower than background (Table 2). Absolute rates were not estimated for Aquifoliaceae, the sister group of Asteridae s.l., due to the absence of fossils for this clade. If the elevated rates of diversification of Asteridae s.l. and Lamiidae s.l. resulted from a single shift toward higher rates in the lineage that gave rise to both clades, then the low rate of Garryaceae (and perhaps also of Aquifoliaceae) represents an independent loss of high diversification rates. Nevertheless, it is simplest to interpret the elevated rates that characterize Lamiidae s.l. and Asteridae s.l. as independent acquisitions. Interestingly, as several botanists have remarked, Garryaceae and Aquifoliaceae comprise dioecious plants, whereas all other asterid clades are dominated by monoecious species.

The two remaining unexpectedly species-rich clades are Fabales and Rosaceae, both members of the core rosid clade. Although phylogenetic relationships within the core rosids are not fully resolved, it appears that Fabales and Rosaceae are not particularly closely related (Figs. 2, 6; e.g., Savolainen et al. 2000; Soltis et al. 2000), and thus, their high rates of diversification were derived independently. Furthermore, at least within Fabales, it is clear that species richness is unevenly distributed. Not only are the legumes (Fabaceae s.l.) overwhelmingly more species rich than all other members of

the Fabales clade (i.e., Polygalaceae, Surianaceae, and *Quillaja*), but also within Fabaceae, Mimosoideae, and especially Papilionoideae, are substantially more diverse than the caesalpinioid legumes. This uneven distribution of species diversity suggests that elevated rates of diversification evolved within distinct clades of Fabaceae (cf. Sanderson and Wojciechowski 1996). More detailed analyses of distribution of species diversity within other species-rich clades are likely to reveal similar uneven patterns.

Extraordinarily species-poor clades

Because the angiosperms as a whole are extraordinarily diverse and ecologically predominant, it is easy to overlook the fact that some angiosperm clades have diversified at an extremely low rate. Angiosperm clades with extremely low rates of diversification, that include unexpectedly few species, occur among the magnoliid lineages, that is, Nymphaeales, Illiciales, Chloranthaceae, Calycanthales, Winteraceae, and Ceratophyllaceae (Fig. 6); within the eudicot clade, that is, Eupteleaceae, Nelumbonaceae, Platanaceae, Buxales, and Trochodendrales (Fig. 6); and within the higher monocots, that is, Typhales. The mere existence of ancient, species-poor clades is remarkable because, as demonstrated by Strathmann and Slatkin (1983) under a variety of assumptions, clades should either become diverse or become extinct.

Strathmann and Slatkin (1983) identified the conditions that, under several different models of diversification, are most likely to produce ancient, species-poor clades. Their first model is time homogeneous, with equal rates of speciation and extinction ($\lambda = \mu$; $r = 0$). Under these conditions, the long-term survival of species-poor clades is best explained by very low rates of speciation and extinction and a large number of lineages at the onset of the diversification process (table 2 in Strathmann and Slatkin 1983).

Their second model is also time homogeneous, but the rates of speciation and extinction are unequal ($\lambda \neq \mu$). If the extinction rate is higher than speciation ($\lambda < \mu$; $r < 0$) the extended survival of a clade is unlikely, but if it does survive, it will probably have very few species. The number of initial lineages necessary to produce at least a few ancient and species-poor clades is very high (table 3 in Strathmann and Slatkin 1983). If the speciation rate is higher than extinction ($\lambda > \mu$; $r > 0$), the possibility of extended survival is obviously greater, as is the chance of producing large clades. Ancient and species-poor clades can still result, but only if rates of speciation and extinction are both very low. A clade resulting from this diversification model has always been species poor and its standing diversity has accumulated very slowly through time.

Strathmann and Slatkin's (1983) third model is time-heterogeneous, with a very short initial period in which the speciation rate is much higher than the extinction rate ($\lambda \gg \mu$), followed by a long period during which speciation and extinction are approximately equal ($\lambda \approx \mu$). This model corresponds to a radiation in which the diversity of a clade is controlled by the diversity of other clades or the availability of environmental resources (Sepkoski 1979). In this case, there is a significant chance that a clade persists for an ex-

tended period of time, after which it will have a low species diversity. An ancient and species-poor clade that results from this model must have been formerly diverse, but is depauperate in the present day. Among angiosperms, a prime example of this is the family Platanaceae, with a high diversity and abundance during the Cretaceous and early Tertiary (e.g., Kvaček 1970; Manchester 1986; Friis et al. 1988; Pigg and Stockey 1991; Crane et al. 1993; Pedersen et al. 1994; Magallón et al. 1997), but a present-day diversity of only 10 species.

Comparison with Other Taxa

Available estimated diversification rates for other taxa generally do not compensate for extinction in diversity counts and are therefore likely to overestimate the true diversification rates. However, comparisons may still be useful. Angiosperms as a whole diversify with rates equivalent to or slightly higher than those of the fastest-diversifying bivalves (i.e., Petricolidae, $r = 0.072$; Mesodesmatidae, $r = 0.078$; Semelidae, $r = 0.087$; Stanley 1979). Angiosperm clades with the lowest rates of diversification (e.g., Chloranthaceae, Trochodendrales, and Platanaceae) diversify even more slowly than the slowest bivalves. The opposite extreme is represented by angiosperm clades with the highest rates (e.g., Cyperales, Gentianales, and Lamiales), which diversify at rates equivalent to those of slowly diversifying mammals (i.e., Bovidae, $r = 0.15$; Cebidae, $r = 0.19$; Cricetidae, $r = 0.19$; Stanley 1979) and comparable to several species-rich clades of insects (i.e., Coleoptera, $r \leq 0.20$; Diptera, $r \leq 0.23$; Hymenoptera, $r \leq 0.25$; Wilson 1983). However, the highest estimated rate for an angiosperm clade, the Asterales ($r = 0.33$), is close to that of the fastest-diversifying major clade of mammals, the murid rodents ($r = 0.35$; Stanley 1979).

Nevertheless, all these values are far below the rates estimated for the early phase of adaptive radiation in Neogene horses ($r = 0.5–1.4$; Hulbert 1993) or the radiation of colubrid snakes ($r = 0.56$; Stanley 1979). Estimates for comparable plant taxa are rare. Hawaiian silverswords, a textbook case of an island adaptive radiation in plants, may have a net diversification rate of about $r = 0.57$ (Baldwin and Sanderson 1998), which is also far above the values estimated for major angiosperm clades in this paper.

Concluding Remarks

The differential phylogenetic distribution of angiosperm clades with low and high rates of diversification provides at least two insights regarding angiosperm evolution. Diversification models that best explain the existence of ancient and species-poor clades (see above) predict that these clades are the survivors of an initially large pool of lineages, most of which became extinct. If at least some of these ancient and species-poor angiosperm clades evolved according to the processes depicted in the models, then there should be numerous extinct angiosperm lineages at least in phylogenetic proximity to ancient and species-poor clades. Although so far these have not been recognized formally, their likely existence is supported by empirical observations regarding the composition of ancient paleofloras. Friis et al. (2001), for example, mention the existence of more than 100 different

angiosperm taxa that cannot be assigned to extant families, in early Cretaceous (Barremian-Aptian) fossiliferous localities of Portugal. These localities have yielded the oldest remains of some presently species-poor angiosperm clades: Chloranthaceae and Nymphaeales.

In this study, we deliberately make no attempt to identify the proximal causes for high diversification rates or to test the existence of a correlation between putative diversity-enhancing traits and high rates of diversification. The phylogenetically localized distribution of clades with high rates of diversification, and particularly of clades with an exceedingly high standing species diversity, strongly suggest that traits that promote diversification, whichever they are, are not distributed homogeneously among angiosperms (Doyle and Donoghue 1993; Sanderson and Donoghue 1994). It seems likely that these traits are not prevalent among early diverging angiosperm lineages and that they probably evolved within particular angiosperm clades (i.e., within core rosids, core asterids, and some ''higher'' monocots). Consequently, high rates of diversification are not derived from the presence of a single character, but rather from sets of traits, including morphological, anatomical, vegetative, and reproductive characters, habits, and syndromes, that, in combination, result in high rates of diversification for particular clades or closely related group of clades. These sets of diversity-promoting features may be entirely different among independent species-rich clades.

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ERRATUM

Equation (11a) in Magallón and Sanderson (2001, Evolution 55:1762–1780), on page 1766, contains an error. The term on the right should have a factor of k, rather than r, as originally published. This is also a conditional probability, as implied by equation (9) and shown below on the left side of the equality.

$$P[N(t) \geq k \mid k > 0] = \frac{\beta_t^{k-2}}{1 + \alpha_t}\{k(1 - \alpha_t - \beta_t + \alpha_t\beta_t) + \alpha_t + 2\beta_t - 1\} \qquad (11a)$$

The paper's results, shown in Figure 4, were based on the correct version of this equation and are not affected by this error.