Article

"Phylogeny and Geographic History of Annonaceae"

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PHYLOGENY AND GEOGRAPHIC HISTORY OF ANNONACEAE

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ABSTRACT Whereas Takhtajan and Smith situated the origin of angiosperms between Southeast Asia and Australia, Walker and Le Thomas emphasized the concentration of primitive pollen types of Annonaceae in South America and Africa, suggesting instead a Northern Gondwanan origin for this family of primitive angiosperms. A cladistic analysis of Annonaceae shows a basal split of the family into *Anaxagorea*, the only genus with an Asian and Neotropical distribution, and a basically African and Neotropical line that includes the rest of the family. Several advanced lines occur in both Africa and Asia, one of which reaches Australia. This pattern may reflect the following history: (a) disjunction of Laurasian (*Anaxagorea*) and Northern Gondwanan lines in the Early Cretaceous, when interchanges across the Tethys were still easy and the major lines of Magnoliidae are documented by paleobotany; (b) radiation of the Northern Gondwanan line during the Late Cretaceous, while oceanic barriers were widening; (c) dispersal of African lines into Laurasia due to northward movement of Africa and India in the Early Tertiary, attested by the presence of fossil seeds of Annonaceae in Europe, and interchanges between North and South America at the end of the Tertiary.

RÉSUMÉ *Phylogénie et histoire géographique des Annonaceae*. Alors que Takhtajan et Smith situaient l'origine des Angiospermes entre le Sud-Est asiatique et l'Australie, Walker et Le Thomas ont souligné la concentration des types polliniques primitifs d'Annonaceae en Amérique du Sud et en Afrique, laissant plutôt supposer une origine nord-gondwanienne pour cette famille d'Angiospermes primitives. Une analyse cladistique des Annonaceae révèle une division basale de la famille en *Anaxagorea*, seul genre de répartition asiatique et néotropicale, et une lignée fondamentalement africaine et néotropicale qui comprend le reste de la famille. Plusieurs lignées évoluées sont partagées entre l'Afrique et l'Asie, dont une atteint l'Australie. Ce schéma pourrait traduire l'histoire suivante : (a) la disjonction des lignées laurasienne (*Anaxagorea*) et nord-gondwanienne au Crétacé inférieur, alors que les échanges à travers la Téthys étaient encore faciles et que les grandes lignées de Magnoliidae sont établies par la paléobotanique ; (b) la radiation de la lignée nord-gondwanienne pendant le Crétacé supérieur, lorsque les barrières océaniques s'élargissaient ; (c) la dispersion de lignées africaines en Laurasie due au mouvement de l'Afrique et de l'Inde vers le nord au début du Tertiaire, attestée par la présence de graines fossiles d'Annonaceae en Europe, et des échanges entre l'Amérique du Nord et l'Amérique du Sud à la fin du Tertiaire.

ZUSAMMENFASSUNG *Phylogenie und geographische Geschichte der Annonaceae*. Während Takhtajan und Smith den Ursprung der Angiospermen zwischen Südostasien und Australien ansiedelten, haben Walker und Le Thomas die Konzentration primitiver Pollen-Typen von Annonaceae in Südamerika und Afrika hervorgehoben und so stattdessen einen Ursprung in Nord-Gondwanaland für diese Familie primitiver Angiospermen vorgeschlagen. Eine kladistische Analyse der Annonaceae zeigt eine Basis-Aufspaltung der Familie in *Anaxagorea*, die einzige Gattung mit asiatischer und neotropischer Verteilung und in eine grundsätzlich afrikanische und neotropische Linie, welche den Rest der Familie einschliesst. Mehrere entwickelte Linien treten sowohl in Afrika wie Asien auf und eine davon erreicht Australien. Dies Schema könnte die folgende Geschichte spiegeln: (a) Trennung der laurasischen (*Anaxagorea*) und der Nord-Godwanaland-Linien in der frühen Kreidezeit, zu einer Zeit als der Austausch über das Tethys noch einfach war und die Hauptlinien von Magnoliidae durch die Paleobotanik dokumentiert sind; (b) Radiation der Nord-Gondwanaland-Linie während der späten Kreidezeit, als die Ozeanbarrieren sich verbreiterten; (c) Verbreitung der afrikanischen Linie über Laurasia aufgrund der Nordwärts-Verschiebung von Afrika und Indien im frühen Tertiär, welche durch das Vorkommen fossiler Samen von Annonaceae in Europa bezeugt wird, und Austausch zwischen Nord- und Südamerika am Ende des Tertiärs.

INTRODUCTION

With about 200 genera and 2500 species, Annonaceae are the most diverse family of primitive angiosperms. They have therefore played an important role in discussions of the origin, evolution, and dispersal of angiosperms as a whole. In this paper, we first review previous ideas on the geographic history of Annonaceae, then compare present geographic distributions in the family with phylogenetic analyses of morphological characters, the geologic history of the continents on which Annonaceae are found, and the fossil record. It is our hope that this discussion will illustrate the value of a phylogenetic framework in constructing biogeographic scenarios in general. Most of these considerations have been presented in another article (Le Thomas and Doyle, 1996b), but here we take into account the results of a more recent phylogenetic analysis (Doyle and Le Thomas, 1996) and additional insights gained in an examination of the Annonaceae of Madagascar (Le Thomas and Doyle, 1996a).

PREVIOUS CONCEPTS

Annonaceae are an almost entirely tropical family, except for the closely related North American genera *Asimina* and *Deeringothamnus*. Geographically, Annonaceae show a high level of continental generic endemism: *e.g., Guatteria, Malmea, Cymbopetalum* and related genera in tropical America; *Piptostigma, Toussaintia, Hexalobus,* and *Monodora* in Africa; *Cananga* and *Miliusa* in Asia. Only one genus (*Xylopia*) is pantropical. Among the Neotropical genera, only *Annona* has a few species in Africa, of which one (*A. senegalensis*) reaches Madagascar. In contrast, there are more genera in common between Africa and Asia (*Polyalthia, Artabotrys, Uvaria*). *Anaxagorea* is notable as the one genus that is disjunct between tropical America and Asia, while being totally absent in Africa.

Several hypotheses have been put forth to explain these distributions and to locate the origin of the family. For primitive angiosperms in general, the dominant hypothesis for many years was that of Takhtajan (1969) and Smith (1973), who placed the "cradle" of the angiosperms "between Assam and Fiji." This view was based on the fact that the number of families of primitive angiosperms (*i.e.,* Magnoliidae in the broad sense of Cronquist, 1981) is much higher in the region encompassing tropical Asia and Australasia than in either the American or the African tropics. Sinclair (1955) supported the same hypothesis for Annonaceae, because of their high species diversity in Asia.

However, at almost the same time, acceptance of the theory of plate tectonics began to raise doubts about this hypothesis (Schuster, 1972, 1976; Raven and Axelrod, 1974). Plate tectonic reconstructions showed that Takhtajan's and Smith's cradle of the angiosperms was actually two widely separated areas at the time of appearance of angiosperms in the Early Cretaceous: Southeast Asia was part of Laurasia, whereas Australasia was part of Gondwana. Schuster (1976) in particular argued that even today some primitive angiosperm families, such as Magnoliaceae, are almost exclusively Asian and North American (and thus Laurasian),

whereas others, such as Winteraceae, are instead Australasian, South American, and African-Madagascan (thus Gondwanan). The high number of primitive angiosperm families between Assam and Fiji can thus be explained as a result of later juxtaposition of two floras, each containing different primitive angiosperms. This suggests that there is no reason to assume that either of these areas was the cradle of the angiosperms; they could have originated in some quite different intermediate region, for which Raven and Axelrod (1974) favored "West Gondwana" - *i.e.,* Africa plus South America.

Palynological studies of Annonaceae provided important support for this general hypothesis. Based on a survey of pollen morphology in the family, Walker (1971) noted that the monosulcate pollen types that he considered most primitive (in his "*Malmea* tribe") are concentrated in South America, where almost all the other main lines of pollen evolution are also present, whereas most Asian taxa have highly derived echinate or inaperturate pollen (some actually disulculate, based on more recent data). From this he inferred that the family probably originated in South America, or possibly Africa plus South America before the two continents were separated. The ultrastructural studies of Le Thomas (1980-1981) refined the concept of the primitive pollen type as monosulcate with granular exine structure, rather than columellar, as in the *Malmea* tribe. Le Thomas argued that the concentration of this type in Africa (with the exception of *Anaxagorea*) tends to support an origin of the family not in South America but rather in Africa, or the combined African-South American landmass. Walker (1971) and Raven and Axelrod (1974) also suggested an African-South American or West Gondwanan origin for the magnoliid families Canellaceae and Myristicaceae.

Similar conclusions have been drawn from paleopalynology. Near the beginning of the definite record of angiosperms (Early Cretaceous, Barremian and Aptian stages), it is in Africa and South America, the Northern Gondwana province of Brenner (1976), that one finds the highest diversity of angiosperm pollen (Brenner, 1976; Doyle *et al.,* 1977, 1982; Doyle, 1984), although the differences between regions now appear to be less absolute than they did previously (Doyle, 1992).

RESULTS OF CLADISTIC ANALYSES

Cladistic studies have helped clarify phylogenetic relationships among primitive angiosperms. Cladistic methods attempt to find the phylogenetic scheme most consistent with all available characters by searching for the most parsimonious tree(s); *i.e.,* involving the fewest total character state changes (steps). In an analysis of morphological data by Donoghue and Doyle (1989), the basal group (*i.e.,* the sister group of all other angiosperms) consisted of four to seven families of Magnoliales that retain the primitive granular monosulcate pollen type, including Annonaceae. One family, Canellaceae, was associated with Magnoliales in some most parsimonious trees, with Winteraceae in others. Analyses of ribosomal DNA sequences (Hamby and Zimmer, 1992; Doyle *et al.,* 1994) "rooted" the angiosperms among herbaceous

magnoliids (Nymphaeales, Piperales, Aristolochiaceae) and monocots, or "paleoherbs" of Donoghue and Doyle (1989), rather than among woody magnoliids, but they also showed a close relationship between Annonaceae and Magnoliaceae (the two Magnoliales included). Studies of *rbc*L sequences (Qiu *et al.*, 1993) rooted angiosperms next to the aquatic genus *Ceratophyllum* but revealed many of the same clades in magnoliids, including the same six families of Magnoliales (excluding Canellaceae, associated with Winteraceae).

In Doyle and Le Thomas (1994), we used these results as a basis for an analysis of Annonaceae, including other Magnoliales (except Canellaceae) as outgroups, which was especially intended to test ideas on pollen evolution. Among the 79 macro- and micromorphological characters used, the 11 pollen characters were found to be among the most informative. The results generally confirmed the pollen trends proposed by Walker (1971) and Le Thomas (1980-1981): the ancestral type was monosulcate with granular exine structure, as in *Anaxagorea*, which was located at the base of the family, and this gave rise to columellar monosulcate pollen (malmeoids), granular and columellar tetrads (xylopioids, annonoids), inaperturate monads (uvarioids), echinates (*Monanthotaxis* group, *Pachypodanthium*), and disulculates (*Guatteria* group, *Sapranthus*, *Miliusa*, *Ancana* group, and one group of *Polyalthia* species). Other important characters were stamen morphology, which shows a series from laminar in *Anaxagorea* and the outgroups to the peltate type typical of most Annonaceae, and seed anatomy, including a trend in endosperm ruminations from irregular (*Anaxagorea*, ambavioids) to spiniform and lamelliform. The large genus

Polyalthia, which we split into four groups because of its great diversity of pollen types, appears to be polyphyletic, with each group associated with different outgroups having similar pollen.

In Doyle and Le Thomas (1995), we expanded this analysis by adding the African genera *Mkilua* and *Afroguatteria*. The resulting trees differed in that the xylopioids and uvarioids, which previously formed a separate clade, were nested within the "annonoids," implying that the granular inaperturate tetrads of the xylopioids and single grains of the uvarioids were *secondarily derived from annonoid columellar tetrads*. This whole clade was linked with the columellar monosulcate malmeoids by *Artabotrys*, which has single grains with a reduced aperture, and the African malmeoid genus *Annickia*. The echinate *Monanthotaxis* group moved from below the xylopioids into the uvarioids.

The present discussion is based on a still more recent analysis (Doyle and Le Thomas, 1996), which included more substantial changes in definition and interpretation of taxa (*e.g.*, reducing the *Ancana* group to *Ancana*, rescoring the *Cymbopetalum* group based on the cladistic results of Johnson and Murray, 1995) and characters (*e.g.*, floral type, carpel number), incorporating observations of van Heusden (1992) and others. A representative most parsimonious tree is shown in Figure 1, with the pollen exine character plotted on the branches and sketches of major pollen types placed where they originate.

As in Doyle and Le Thomas (1995), the groups with tetrad pollen and inaperturate single grains form a clade, called the

FIGURE 1. Representative most parsimonious tree of Doyle and Le Thomas (1996), showing evolution of the infratectal structure character and major pollen types. Outgps: outgroups; Amb: ambavioids; Pip: piptostigmoids; Milu: miliusoids; Uva: uvarioids; Psyn: pseudo-syncarps; Xyl: xylopioids.

Un des arbres les plus parcimonieux de Doyle et Le Thomas (1996), montrant l'évolution du caractère de la structure infratectale et les types polliniques principaux. Outgps : extra-groupes ; Amb : Ambavioïdes ; Pip : Piptostigmoïdes ; Milu : Miliusoïdes ; Uva : Uvarioïdes ; Psyn : Pseudosyncarpes ; Xyl : Xylopioïdes.
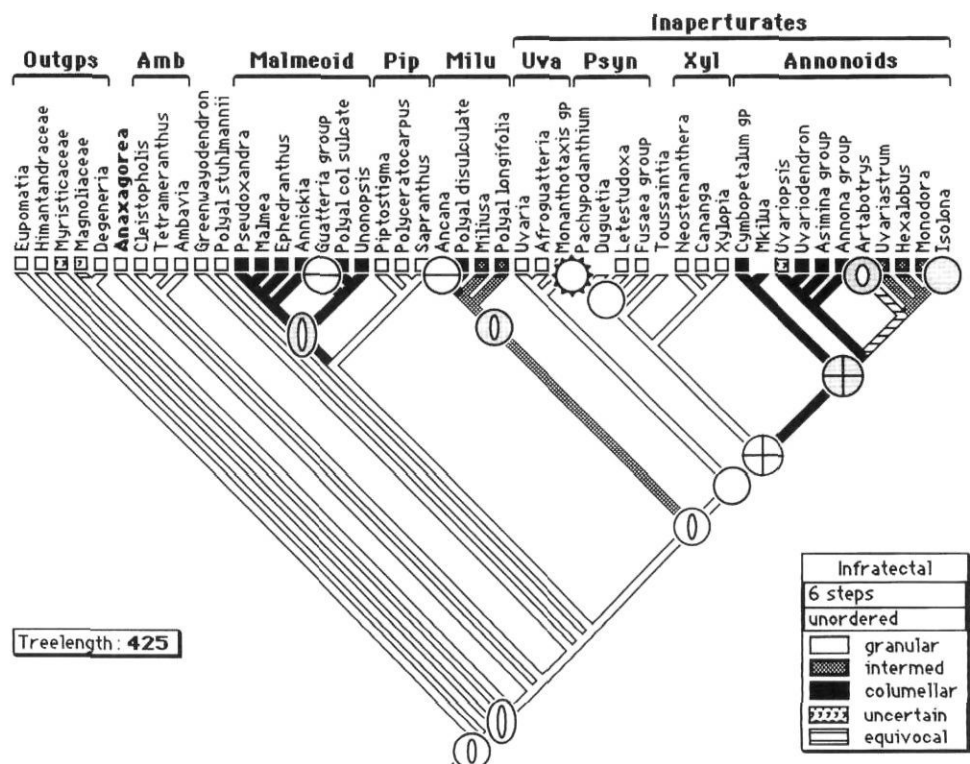
inaperturates. However, the former uvarioids are broken into two clades, one including *Toussaintia* and four pseudosyncarpous taxa, originally with tetrad pollen, the other lianas with monads, to which we restrict the term uvarioids. The uvarioids, pseudosyncarps, and xylopioids are located *below the annonoids rather than nested within them.* The inaperturate clade is linked with the miliusoids (three disulculate taxa and the monosulcate species *Polyalthia longifolia*) rather than *Artabotrys* and *Annickia. Artabotrys* is nested within the annonoids, implying that its single grains are derived from tetrads. The small ambavioid clade, *Greenwayodendron*, and *Polyalthia stuhlmannii*, with granular monosulcate pollen, and a clade made up of the granular monosulcate piptostigmoids and columellar monosulcate malmeoids (including one *Polyalthia* group) form a series of lines between *Anaxagorea* and the miliusoids. The basal position of *Anaxagorea* and the unity of the inaperturate clade have been confirmed by molecular phylogenetic analyses of van Zuilen (1996) and Paul Bygrave and Mark Chase (pers. comm.).

The biogeographic implications of these results can be examined by treating geographic distribution as an unordered multistate character and plotting this character *a posteriori* on the independently obtained cladogram, using the program MacClade (Maddison and Maddison, 1992) (Fig. 2). A similar approach was used by Maddison (1991) to evaluate molecular data on the center of origin of modern humans. The squares at the tips of the branches represent the present-day distributions of taxa in the analysis. In defining areas, we combined North and Central America with Asia (a change from Le Thomas and Doyle, 1996b, where we associated

Central with South America). Only two American taxa are assigned to this area: the *Asimina* group, which is associated with other plants that show a classic disjunction between North America and temperate East Asia; and *Sapranthus*, which occurs in Central but not South America, unlike other Neotropical Annonaceae. When taxa occur in two or more regions, they are scored as uncertain. For example, *Anaxagorea* is scored as either Asian-North American or South American (1/2), since it occurs in Asia, Central America, and South America. The only taxon scored as Australasian is *Ancana*, which is endemic to Australia; a few other Annonaceae occur in Australasia (Morawetz, 1988), but they belong to groups that are more diverse in Malesia (*Cananga, Desmos, Miliusa, Polyalthia, Xylopia*, etc.).

Given a tree, MacClade determines the most parsimonious state in the common ancestor of any two groups. When MacClade indicates that the ancestral area is "equivocal" (*i.e.*, either of two regions), this suggests that the common ancestor of the two groups may have existed in either of the two areas, or in a combined area that later split into two (a vicariance event). When two groups occur in different regions but the ancestral area is unequivocal (as when taxa located lower on the tree occur in only one of the two regions), this suggests a dispersal event from the ancestral area to the other.

The two outgroups located nearest the base of the Magnoliales (*Eupomatia*, Himantandraceae) are Australasian. The sister group of Annonaceae varies in different most parsimonious trees: Magnoliaceae, Myristicaceae, Magnoliaceae plus Myristicaceae, Magnoliaceae plus *Degeneria*, or all three groups together. *Degeneria* is Australasian (Fiji), whereas
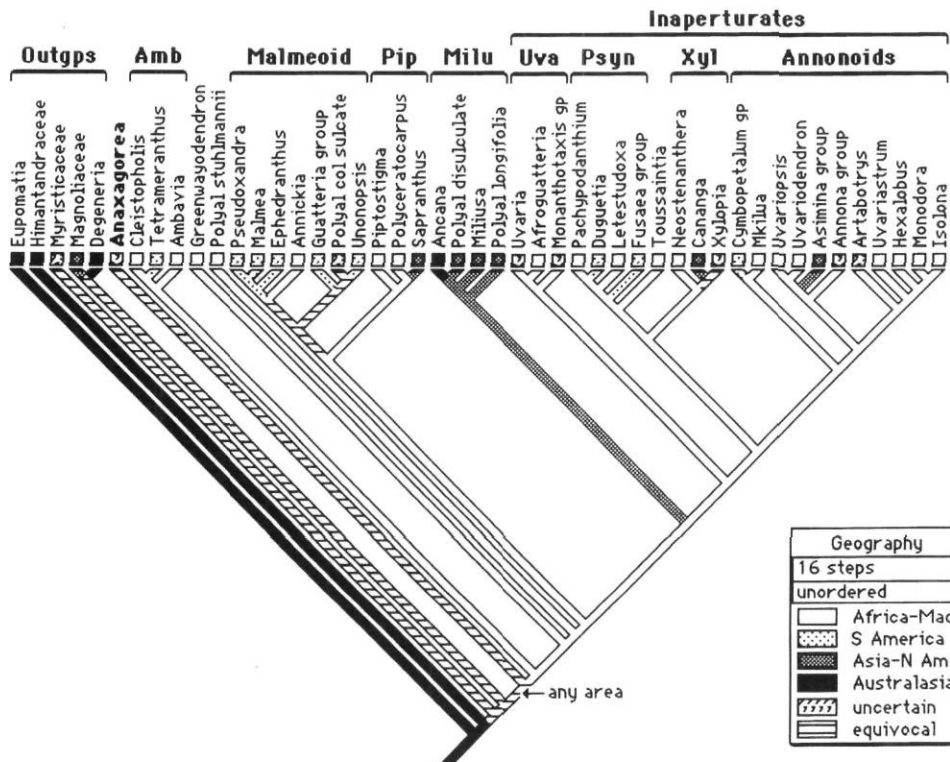

FIGURE 2. Geographic distribution treated as an unordered multistate character and plotted *a posteriori* on the tree shown in Figure 1. Distributions of taxa found in more than one region are scored as uncertain (Myristicaceae, *Annona* group: 0/1; *Anaxagorea*: 1/2; *Artabotrys, Monanthotaxis* group, columellar-sulcate *Polyalthia* group, *Uvaria*: 0/2; *Xylopia*: 0/1/2).

La répartition géographique traitée comme un caractère à états multiples non ordonnés et tracée a posteriori sur l'arbre montré à la figure 1. Les répartitions des taxons trouvés dans plus d'une région ont été codées comme incertaines (Myristicaceae, groupe Annona : *0/1 ;* Anaxagorea : *1/2 ;* Artabotrys, *groupe* Monanthotaxis, Polyalthia *sulqués-columellaires,* Uvaria : *0/2 ;* Xylopia : *0/1/2).*

Magnoliaceae are mostly Asian and North American (and therefore Laurasian), although a few extend into South America (cf. Schuster, 1976). Myristicaceae occur in South America, Africa, Madagascar, and Asia, but their highest generic diversity is in South America and Africa, and the most primitive taxa occur in Madagascar (*Brochoneura*, *Mauloutchia*), suggesting a Northern Gondwanan origin (Walker, 1971; Walker and Walker, 1981). Because of the scattered distribution of other Magnoliales, the ancestral area for Annonaceae as a whole is ambiguous. If Myristicaceae are scored as South American or African-Madagascan, MacClade reconstructs the "geography" state for the common ancestor of Annonaceae as (1) any of the four areas (when the sister group of Annonaceae is Magnoliaceae plus *Degeneria*, as in Fig. 2, or all three taxa); (2) Africa, South America, or Laurasia (when the sister group is Magnoliaceae, or Magnoliaceae plus Myristicaceae); or (3) Africa or South America (when the sister group is Myristicaceae).

Annonaceae then split into two lines: (1) the Asian and tropical American genus *Anaxagorea*; and (2) a clade that includes all the other genera of the family, which is basically African-Madagascan but contains many prominent Neotropical lines. Only two clades are Asian, *Cananga* (in the xylopioids) and the miliusoids (*Miliusa*, two *Polyalthia* groups); other Asian Annonaceae belong to taxa that occur in both Africa and Asia (columellar-sulcate *Polyalthia* group, *Xylopia*, *Uvaria*, *Monanthotaxis* group, *Artabotrys*). The one Australasian line, *Ancana*, is nested within the primarily Asian miliusoid clade.

INTERPRETATION

To explain these results, we propose the following scenario, which may be divided into three main phases (Fig. 3).

(a) The Annonaceae originated at a time when interchange of taxa between Laurasia and Northern Gondwana was still relatively easy. This was followed by a split into a Laurasian line ancestral to *Anaxagorea* and a Northern Gondwanan line that gave rise to the rest of the family. This split may date from the late Early Cretaceous, when the distance between Laurasia (Europe) and Gondwana (Africa) was still small. At this time, although there were important latitudinal gradients in the percentages of dominant elements, fossil floras show a near-continuity between the two continents (Doyle *et al.*, 1982; Doyle, 1984, 1992).

A mid-Cretaceous age for the line leading to Annonaceae is plausible in the light of evidence on the systematic differentiation of angiosperms at this time (Doyle and Hotton, 1991; Doyle and Donoghue, 1993; Crane *et al.*, 1995). Around the Barremian-Aptian boundary, all five major lines of angiosperms recognized by Donoghue and Doyle (1989) are already recognizable, namely Magnoliales, Laurales (relatives of Chloranthaceae), winteroids (winteraceous pollen tetrads), paleoherbs (monocot-like pollen and leaves, reniform dicot leaves), and eudicots (tricolpate pollen). Magnoliales may be represented by *Lethomasites*, a large monosulcate pollen type with granular exine structure from the lower Potomac Group (Aptian) (Ward *et al.*, 1989). The same sediments also contain

leaves that may represent either Magnoliales or winteroids (*Ficophyllum*, *Rogersia*, *Proteaephyllum p.p.*: Wolfe *et al.*, 1975; Hickey and Doyle, 1977).

From two stages later, in the Cenomanian, Dilcher and Crane (1984) described fossil fructifications (*Archaeanthus*) that can be confidently related to Magnoliaceae. Fossils related to families of the Laurales are also known from the Cenomanian or the preceding Albian stage (Lauraceae: Drinnan *et al.*, 1990; Chloranthaceae: Pedersen *et al.*, 1991; Calycanthaceae: Friis *et al.*, 1994), while relatives of *Eupomatia* and/or Calycanthaceae are reported from the following Turonian stage (Crepet and Nixon, 1994). If Magnoliaceae (with or without *Degeneria* and/or Myristicaceae) constitute the sister group of the Annonaceae, the presence of Magnoliaceae in the Cenomanian implies that the line leading to Annonaceae existed at the same time.

(b) After splitting of the Annonaceae into two lines, the line leading to most of the modern genera diversified during the Late Cretaceous in Northern Gondwana (now separating into Africa and South America), which had become more isolated from Laurasia by continued widening of the Tethys and marine transgressions that flooded much of the continents. Our results imply that this diversification may have been more active in Africa, since African Annonaceae consist of many lines (often monotypic) distributed along the branches of the tree, so that the reconstructed ancestral state is African-Madagascan, whereas most South American Annonaceae belong to a few large clades (*Malmea* and related genera, *Guatteria* group, *Annona* group, *Cymbopetalum* group, *Xylopia*, *Duguetia*) nested among African taxa. The only large group for which the ancestral area may be either Africa or South America is the malmeoid clade. In general, the African tropical flora is depauperate relative to that of South America, presumably as a result of extinction caused by increasing aridity during the Tertiary. If the original diversity of Annonaceae was equal in Africa and South America, we would expect fewer lines to have survived in Africa, not more.

The existence of Annonaceae in Northern Gondwana near the end of the Cretaceous is confirmed by the fossil record. The oldest remains definitely assignable to the Annonaceae are seeds with the perichalazal ring and ruminate endosperm characteristic of the family from the Maastrichtian of Nigeria (Chesters, 1955). Reticulate monosulcate pollen similar to that of the malmeoids has also been described from the Maastrichtian of Colombia (Sole de Porta, 1971; Muller, 1981). In contrast, except for leaves without diagnostic characters from North America (Hollick, 1906), no remains of Annonaceae have been reported from Cretaceous floras of Laurasia, despite a growing number of fossil flowers and fruits (Friis and Crepet, 1987; Nixon and Crepet, 1994; Crane *et al.*, 1995).

(c) The next stage in the history of the Annonaceae involved renewed exchanges between the fragments of Gondwana and Laurasia, which were coming back together toward the end of the Cretaceous and the beginning of the Tertiary. The Tethys between Africa and Europe was narrowing and India was approaching Asia, while North America was separating from Eurasia as a result of opening of the North
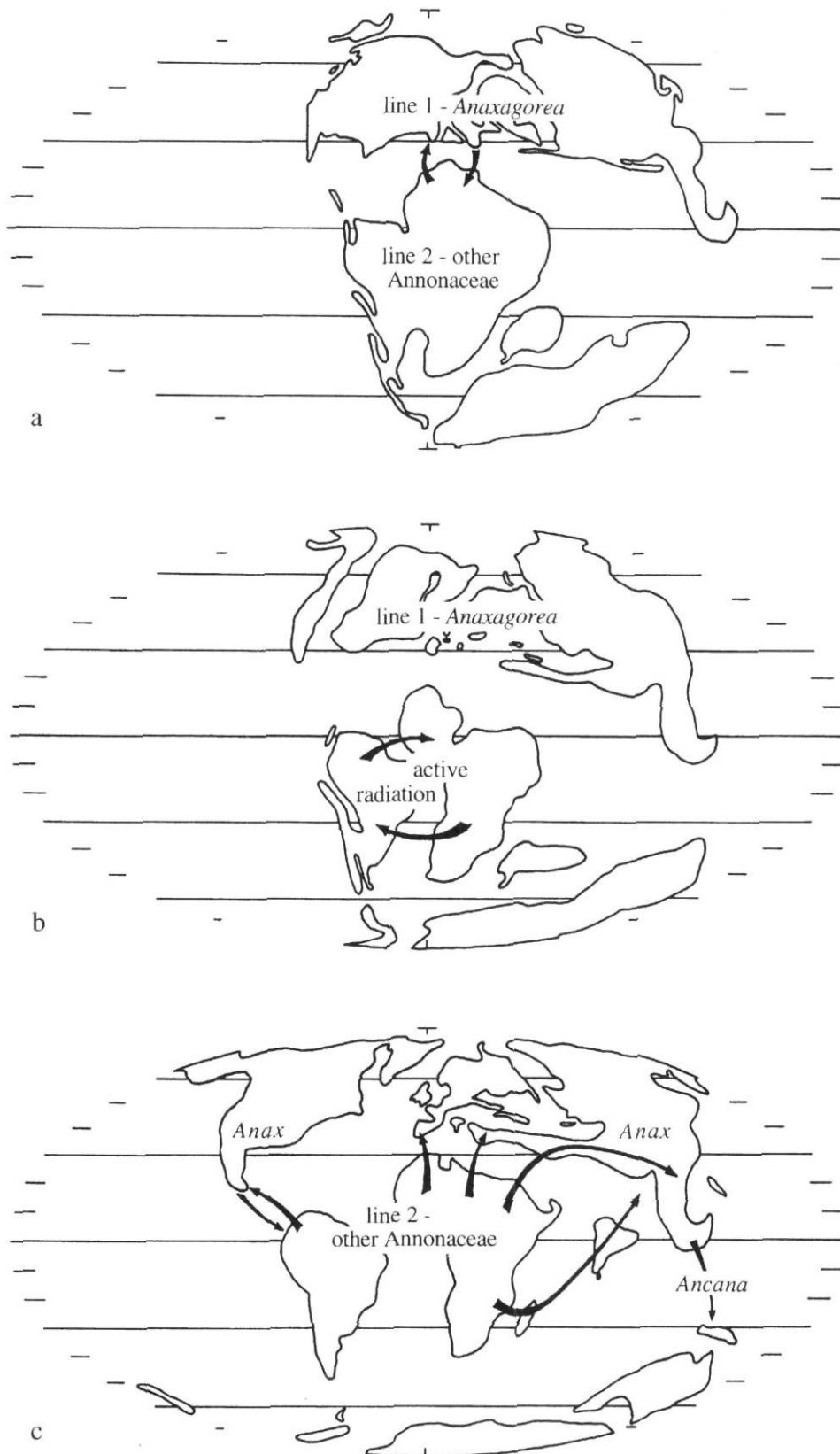
FIGURE 3. Three proposed phases in the geographic history of Annonaceae: (a) Early Cretaceous, (b) Late Cretaceous, (c) Tertiary. Paleogeographic maps after Parrish (1987) (Barremian, Cenomanian, Eocene).

Trois étapes proposées dans l'histoire géographique des Annonaceae : (a) Crétacé inférieur, (b) Crétacé supérieur, (c) Tertiaire. Cartes paléogéographiques d'après Parrish (1987) (Barrémien, Cénomanien, Eocène).

Atlantic. At this time lines that had originated in Northern Gondwana could have crossed the Tethys and become established along the southern coast of Eurasia, which then had a tropical climate. After the Eocene, global cooling and contraction of tropical vegetation into Southeast Asia would result in disjunct distributions of taxa between Africa and Asia.

The North American *Asimina* group, being the only non-African member of the annonoid clade other than the predominantly or exclusively Neotropical *Annona* and *Cymbopetalum* groups, may also represent this pattern (Lars Chatrou, pers. comm.), assuming that it either became extinct in Asia or spread west rather than east after crossing the Tethys.

This hypothesis is supported by the presence of diverse seeds of Annonaceae in the Early Eocene London Clay flora (Reid and Chandler, 1933; Collinson, 1983), which shows many affinities with present-day Southeast Asia. Besides the perichalazal ring, these seeds show almost all the types of endosperm rumination observed in the family, including the spiniform type that is mainly associated with the malmeoids and piptostigmoids (*Anonaspermum punctatum*). More detailed anatomical study might indicate whether or not some of these seeds represent lines that are now restricted to Southeast Asia, as predicted by our hypothesis.

In Le Thomas and Doyle (1996a), we expanded this concept to acknowledge the possible role of Madagascar and India as a dispersal route from Africa to Asia (*cf.* Schuster, 1976). This idea is supported by the fact that all groups with an African-Asian distribution also occur in Madagascar (*Artabotrys*, *Uvaria*, *Monanthotaxis* group). The columellar-sulcate *Polyalthia* group of Madagascar and Southeast Asia (*P. hypoleuca* complex: Rogstad and Le Thomas, 1989), which belongs to the predominantly Neotropical malmeoid clade, also suggests dispersal from Gondwana to Asia, although this assumes that it once had relatives in Africa that have died out. A similar scenario could explain the pantropical distribution of *Xylopia*. However, it should be recognized that the presence of these groups in both Madagascar and Asia might reflect a high capacity for long-distance dispersal, rather than passage across Madagascar.

The concept that the Asian members of African-Asian groups are Tertiary immigrants from Gondwana might be tested by better data on phylogenetic relationships: whether the Asian members are nested among the African-South American members, or instead have a sister-group relationship with them.

During the Tertiary, northward plate movement also brought Australasia into proximity with Southeast Asia. This is the time when we would envision that a line belonging to the Asian miliusoid group gave rise to the only exclusively Australasian taxon in our analysis, *Ancana*. Two other Australian genera, *Fitzalania* and *Haplostichanthus*, may also belong to this line (Morawetz, 1988). This relationship was questioned by van Heusden (1992), but the disulculate pollen of the two genera suggests that they belong somewhere in the miliusoid clade.

South America was also approaching North America in the Tertiary, and the two continents became connected by the Panama isthmus in the Pliocene. This would have facilitated migration of South American taxa (*Guatteria*, *Malmea*, *Unonopsis*, *Annona*, etc.) into Central America and of *Anaxagorea* (which we interpret as Laurasian) into South America. According to this hypothesis, Neotropical Annonaceae are a very unequal mixture of Gondwanan and Laurasian elements. The preponderance of Gondwanan elements in the modern rainforests of Central America, despite the presence of tropical floras of more Asian character in North America at the beginning of the Tertiary, is a general phenomenon explained by Wolfe (1975) as a result of drying and cooling of tropical North and Central America after the Early Eocene. Chatrou (1997) has proposed a more detailed scenario: that some Central American groups such as *Annona* represent older dispersals from South America, but others (such as *Malmea*) are post-Pliocene invaders through Panama.

ANOMALIES, ALTERNATIVES, AND PROSPECTS

One challenge to this scheme is the fact that *Anaxagorea* is a common element in the Amazonian lowland rainforest and has its greatest species diversity there (Maas and Westra, 1984). This appears to conflict with its proposed Laurasian origin. Furthermore, *Anaxagorea* would be an exception to the general rule that most recent invaders from Laurasia are upland temperate rather than lowland tropical elements (*e.g.*, Juglandaceae: Wolfe, 1975). Better data on the phylogenetic relationships of the Central American and Amazonian species might help resolve this problem.

Another problem is the case of *Sapranthus*, which is endemic to Central America, along with the presumably related genera *Desmopsis*, *Stenanona*, and *Tridimeris* (Schatz and Le Thomas, 1993). According to our analysis, *Sapranthus* is related to the African genera *Piptostigma* and *Polyceratocarpus*. If *Sapranthus* originated in the Late Cretaceous radiation in Gondwana and moved into Central America at the end of the Tertiary, as we infer for other Neotropical elements, its absence in South America today is anomalous. It thus seems more likely that its history paralleled that of *Asimina* and the Asian genera, which we suggest entered Laurasia from Africa without passing through South America. However, the systematic position of *Sapranthus* is insecure. Emphasizing its disulculate pollen, Morawetz (1988) proposed that *Sapranthus* is related to *Ancana*, the other Australian endemic genera, and the Asian disulculate *Polyalthia* group - *i.e.*, our miliusoid clade. As Morawetz noted, the resulting disjunction would parallel that of *Anaxagorea*. Our data do not strongly contradict this alternative, since we have found only one step less parsimonious trees in which *Sapranthus* is linked with the miliusoids. This would suggest that *Sapranthus* and the miliusoids are disjunct members of a group that was widespread in southern Laurasia, whether this group was derived from immigrants from Africa in the Early Tertiary or a more ancient Laurasian lineage, as we propose for *Anaxagorea*.

The ambavioids, which form the next branch above *Anaxagorea* and show many primitive states (prolonged stamen connective, sessile stigma, irregular endosperm ruminations), also deserve closer examination. Based on the genera included in our analysis, the ambavioids seem clearly Gondwanan (*Ambavia* in Madagascar, *Tetrameranthus* in South America, *Cleistopholis* in Africa). However, this clade may also include the Asian genus *Mezzettia*, which resembles

the ambavioids included here in having two lateral ovules, three integuments, thick ruminations, and a chromosome number of n = 7 (Le Thomas and Doyle, 1996a). Several considerations suggest that the ambavioids are very ancient (proposed for *Ambavia* by Deroin and Le Thomas, 1989), as their position on our trees would allow. Besides having highly disjunct geographic distributions, each genus is morphologically specialized in its own way, with rare or unique advances (autapomorphies) such as reduced proximal exine in *Ambavia*, spiral leaves and tetramerous flowers in *Tetrameranthus*, reduced inner petals in *Cleistopholis*, and a single carpel in *Mezzettia*. The Asian distribution of *Mezzettia* raises the possibility that the ambavioids, like *Anaxagorea*, originated before the maximum (Late Cretaceous) isolation of Gondwana and Laurasia. However, it is more difficult to rule out the alternative hypothesis that *Mezzettia* dispersed more recently from Africa into Asia, as proposed for *Artabotrys*, *Uvaria*, and the *Monanthotaxis* group, than it is for *Anaxagorea*, which is absent in Africa and Madagascar.

Two general kinds of evidence might help decide among these hypotheses. First is better evidence on relationships within groups that are found in more than one area: whether their members in the two areas form sister groups, suggesting a more ancient disjunction, or those in one area are nested among those in the other area, suggesting a more recent dispersal. Second is recognition of fossils representing particular clades in the family, such as precursors of *Anaxagorea* in the Late Cretaceous of Europe or North America, particularly in the pollen and seed records. This search may be facilitated by the fact that cladistic analyses now provide better indications of which pollen and seed characters are diagnostic for particular clades in Annonaceae.

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