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GEOGRAPHIC RELATIONSHIPS OF MALAGASY ANNONACEAE

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ABSTRACT.- The pantropical family Annonaceae (130 genera) is relatively poorly represented in Madagascar, with only nine genera. A cladistic analysis of the principal genera or groups of Annonaceae, using 78 macro- and micro-morphological characters, allows the Malagasy taxa to be placed in major lines of the family. It confirms the primitive character of the one endemic genus, *Ambavia*, which is near the base of the family and belongs to a small clade with other members in South America, Africa, and Asia, suggesting an early origin when exchanges between Laurasia and Gondwana were still easy (Early Cretaceous?). *Isolona* (Africa, Madagascar) and *Annona* (Africa, America), which are nested among other African-American groups, may be derived from a radiation in Africa and South America when the South Atlantic was narrower (Late Cretaceous?). The Asian-Malagasy *Polyalthia* group is nested among American « malmeoids, » suggesting an African-South American origin followed by dispersal to Madagascar and then Asia, perhaps by way of India (Early Tertiary?). *Artabotrys*, *Uvaria*, and *Monanthotaxis*, African-Asian genera related to African-South American taxa, and the only pantropical genus, *Xylopia*, linked with *Cananga* (Asia) and *Neostenanthera* (Africa), may have had a similar history.

KEY-WORDS.- Annonaceae, angiosperms, phylogeny, biogeography, Madagascar

RESUME.- La représentation de la famille pantropicale des Annonaceae (130 genres) est relativement faible à Madagascar, avec seulement 9 genres. Une analyse cladistique des principaux genres ou groupes d'Annonaceae, utilisant 78 caractères macro et micromorphologiques, permet de situer les taxons malgaches dans les grandes lignées de la famille. Elle confirme le caractère primitif du seul genre endémique, *Ambavia*, qui est proche de la base de la famille et appartient à un petit clade dont les autres membres se trouvent en Amérique, en Afrique et en Asie, suggérant une origine ancienne quand les échanges entre la Laurasie et le Gondwana étaient encore faciles (Crétacé inférieur?). *Isolona* (afro-malgache) et *Annona* (afro-américain), qui sont entourés d'autres groupes afro-américains, seraient dérivés d'une radiation en Afrique et en Amérique du Sud lorsque l'Atlantique Sud était plus étroit (Crétacé supérieur?). Le groupe asiatico-malgache du genre *Polyalthia* se situe parmi les « Malmeoïdes » américains, impliquant une origine afro-américaine suivie d'une dispersion de l'Afrique en Asie, peut-être par l'intermédiaire de l'Inde (Tertiaire inférieur?). *Artabotrys*, *Uvaria* et *Monanthotaxis*, genres afro-asiatiques apparentés à des taxons afro-américains, et le seul genre pantropical, *Xylopia*, lié à *Cananga* (Asie) et à *Neostenanthera* (Afrique), pourraient avoir une histoire comparable.

MOTS-CLES.- Annonaceae, Angiospermes, phylogénie, biogéographie, Madagascar

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INTRODUCTION

Annonaceae are the most diverse family of primitive angiosperms, with about 130 genera and 2500 species. Except for two related North American genera (*Asimina* and *Deeringothamnus*), the family is entirely tropical and characterized by a high level of continental generic endemism. Most of the nine genera recognized in Madagascar also occur in Africa and/or Asia, such as *Polyalthia*, *Artabotrys*, *Isolona*, *Uvaria*, and *Monanthotaxis*, which are widely distributed in the various forest types of the island, and the introduced Asian genus *Cananga* (ylang-ylang). *Xylopia*, represented by about 25 species, is the only pantropical genus in the family, whereas the one species of *Annona* establishes an African-American connection. The only endemic genus is *Ambavia*, which includes two species of trees or shrubs in the eastern forest (LE THOMAS, 1972).

There has long been little agreement on classification of the Annonaceae, especially at higher taxonomic levels. Since the 1970s, palynological studies have led to important progress. Based on a study of the entire family, using light and scanning electron microscopy, WALKER (1971) proposed an informal classification, in which he postulated that the *Malmea* tribe, which has monosulcate pollen with columellar exine structure, is most primitive. From this group he derived several evolutionary trends, particularly two independent lines making up the *Fusaea* and *Annona* subfamilies, both of which have pollen in tetrads, but which differ in exine structure. Despite the diversity of the family in Asia, he placed its origin in tropical America because of the greater number of lines in that region, including the putatively primitive *Malmea* tribe.

Subsequent ultrastructural studies by LE THOMAS and LUGARDON (1974), emphasizing the African genera, revealed that the many pollen types described by WALKER (1971) as « microtectate » actually have granular exine structure. Based on comparisons with other Magnoliidae and with gymnosperms, they interpreted monosulcate pollen with granular structure as most primitive. The concentration of granular monosulcates in Africa led LE THOMAS (1980/81) to propose that the family originated in the African-South American region, which constituted one province (Northern Gondwana) in the Cretaceous.

To test these hypotheses, we undertook a cladistic (parsimony) analysis of the Annonaceae, using 11 pollen characters and 68 other macro- and micro-morphological characters, and including other Magnoliales as outgroups. Our first analysis (DOYLE & LE THOMAS, 1994) emphasized the importance of pollen characters for phylogeny of the family and confirmed the main conclusions of WALKER (1971) and LE THOMAS (1980/81) on pollen evolution, especially the view that the primitive pollen type is granular and monosulcate, as in the basal genus *Anaxagorea*, and tetrads are derived. A more recent study, in which we added the African genera *Mkilua* and *Afroguatteria*, led to similar results, but with some changes in the relationships among major clades (DOYLE & LE THOMAS, 1995), most notably that the main tetrad groups represent one line rather than two.

In LE THOMAS and DOYLE (1995), we presented a scenario for the geographic history of Annonaceae, based on a comparison of the results of our first analysis with the geographic distributions of the genera studied. We hypothesized that the basal split into *Anaxagorea* and the rest of the family occurred at a time when exchanges between Laurasia and Gondwana were still easy (Early Cretaceous). *Anaxagorea*, as the only genus found in both Asia and the American tropics, would the sole descendant of a Laurasian line, which more recently migrated from Central America into South America.

Since the basal lineages in the rest of the family are African and/or South American, they would be derived from a Gondwanan line. This line radiated in Africa and South America during the Late Cretaceous, when the South Atlantic was still narrow enough to permit exchange of taxa. In the Early Tertiary, as the Tethys became narrower, several Gondwanan groups dispersed into Asia and Australia.

In the present study, we evaluate the phytogeographic relationships of Malagasy Annonaceae by concentrating on those characters that determine their position in the general phylogenetic scheme and the geographic distributions of related groups.

MATERIALS AND METHODS

This analysis is based on our most recent data set (DOYLE & LE THOMAS, 1995). It includes 42 taxa of Annonaceae, which represent a global sampling of groups for which exine structure is known, and 79 characters, 51 binary and 28 multistate. Character definitions and the data matrix were published in DOYLE and LE THOMAS (1994, 1995). Trees were constructed using the program PAUP (SWOFFORD, 1990). Characters supporting the various clades were studied with MacClade (MADDISON & MADDISON, 1992), which allows one to visualize the evolution of characters on a previously defined tree and to assess their importance in the recognition of groups.

RESULTS

Our analysis yielded 60 most parsimonious trees of 418 steps. These represent two « islands » of 36 and 24 trees each, which differ primarily in whether the groups between *Polyalthia stuhlmannii* and *Annickia* (including most of the « malmeoids » with columellar monosulcate pollen) constitute a monophyletic group (island 1) or a paraphyletic series of lines (island 2) (DOYLE & LE THOMAS, 1995). For simplicity, our discussion of the Malagasy genera will concentrate on island 2, illustrated in figure 1. Phytogeographic implications of the other island are essentially identical.

The three basal lines consist of *Anaxagorea*, three genera called the ambavioids, and *Greenwayodendron*. In contrast to our first analysis (DOYLE & LE THOMAS, 1994), *Artabotrys* and the groups with columellar tetrads no longer split off near the base of the tree, just above the ambavioids, but are directly associated with the columellar-sulcate « malmeoids, » with the African genus *Annickia* acting as a link. The xylopioids (with granular tetrads) and the uvarioids no longer constitute a separate line but rather a derived group within the annonoid clade in a new, extended sense. This implies that, in this case, granular structure is derived (a reversal), as are the single pollen grains of most uvarioids. The groups with columellar tetrads now consist of two lines, one being the *Annona* group, the other including all the other genera, which we call the asiminoids.

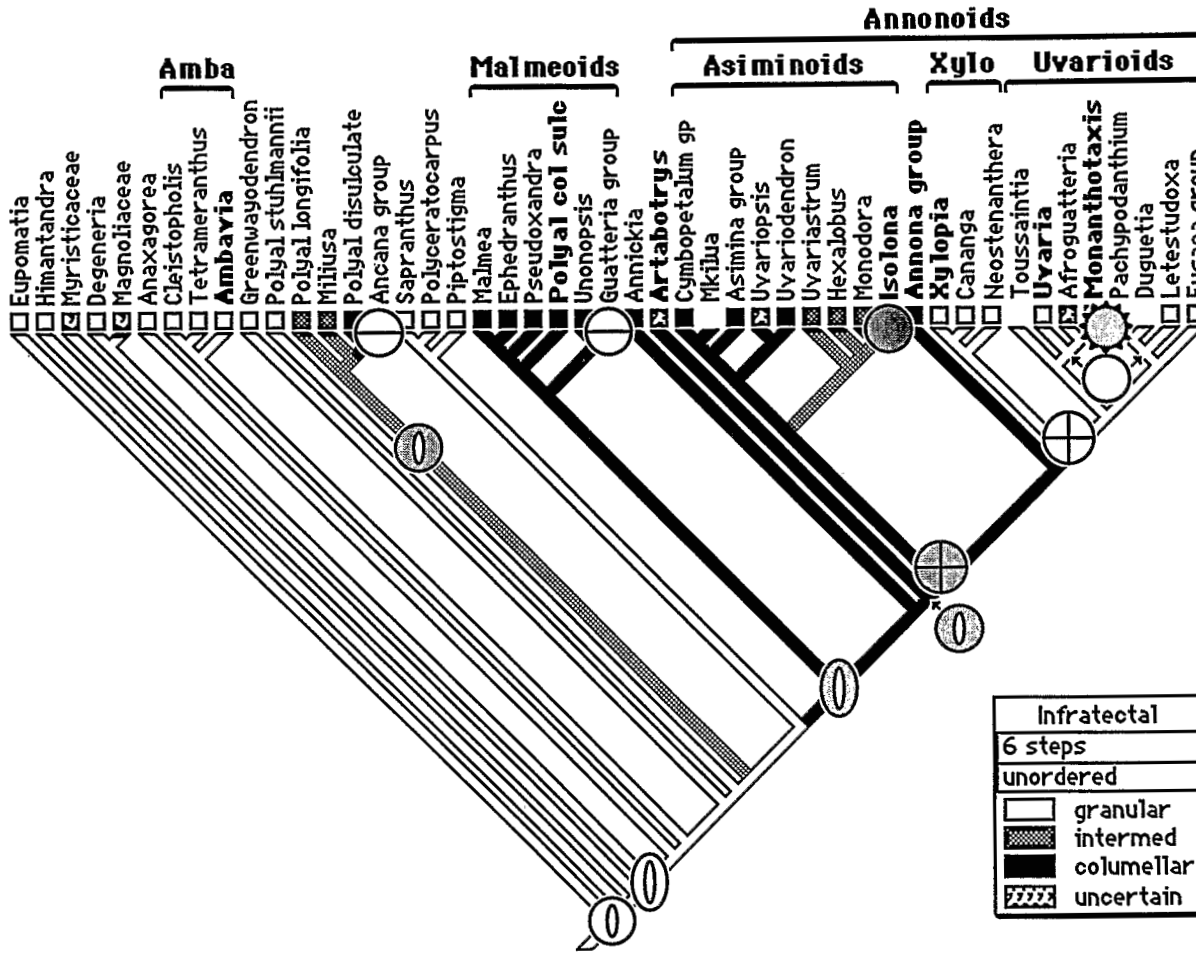

Fig. 1. Representative most parsimonious cladogram of Annonaceae and related Magnoliales (island 2), showing the distribution of the infratectal structure character, with sketches of the principal pollen types.

DISCUSSION

Ambavia

The near-basal position of this endemic Malagasy genus (LE THOMAS, 1972) is supported both by pollen characters - monosulcate with granular exine structure, nexine consisting of one or two lamellar foliations, as in *Anaxagorea* - and by several primitive macro-morphological features. The stamens are not laminar, as they are in *Anaxagorea* and other Magnoliales, but the connective is still prolonged, rather than peltate as in most other Annonaceae. The endosperm ruminations are thick and irregular, also like

those of *Anaxagorea* and other families of Magnoliales, whereas above the ambavioids they become spiniform. Another primitive character state is the sessile stigma, although this reappears as a reversal in the annonoids.

In the ambavioid clade, *Ambavia* is linked with *Cleistopholis* (Africa) and *Tetrameranthus* (South America), which share the same unusual chromosome number of n = 7 (MORAWETZ & LE THOMAS, 1988), as does the Asian genus *Mezzettia*. *Mezzettia* was not included in our analysis because of lack of pollen ultrastructural data, but it has several non-palynological features that suggest it also belongs here (two ovules, three integuments, thick ruminations). Each of these small genera has specializations that are rare or unknown elsewhere in the family (monosulcate pollen with reduced proximal exine in *Ambavia*, tetramerous flowers and spiral phyllotaxy in *Tetrameranthus*, reduced inner petals in *Cleistopholis*, one carpel in *Mezzettia*). The highly disjunct distribution of the four ambavioid genera, each endemic to one tropical region, suggests a very ancient origin, a view expressed for *Ambavia* by DEROIN and LE THOMAS (1989). It is possible that their disjunction dates from the same period as the split into *Anaxagorea* (Asia, America) and the rest of the family (Early Cretaceous?) (LE THOMAS & DOYLE, 1995), and that *Mezzettia* is an ancient Laurasian line, like *Anaxagorea*. However, because of the presence of ambavioids in Africa and Madagascar, we cannot rule out an African-South American radiation followed by dispersal of the ancestors of *Mezzettia* to Asia, as postulated for the following groups.

Polyalthia

This genus, which is particularly diverse in Asia, includes about 150 species, 18 of which occur in Madagascar (SCHATZ & LE THOMAS, 1990). Our results imply that *Polyalthia* is highly polyphyletic. Most of the Malagasy species, which are clearly related to the Malesian *Polyalthia hypoleuca* complex (ROGSTAD & LE THOMAS, 1989), have columellar monosulcate pollen grains that distinguish them from the other groups of *Polyalthia* (including *Greenwayodendron*) and associate them with the main group of « malmeoids, » which are basically American. They also resemble related « malmeoids » and differ from most or all other *Polyalthia* groups in their leaf venation (straight secondary veins, reticulate tertiaries), concave receptacle apex, and glass-like endosperm (VAN SETTEN & KOEK-NOORMAN, 1992).

The relationship of the columellar-sulcate *Polyalthia* group with the « malmeoids » suggests that it originated in Africa-South America during the inferred Late Cretaceous radiation of the bulk of the family (LE THOMAS & DOYLE, 1995) and dispersed first to Madagascar, then to Asia, perhaps carried by the northward movement of India. This hypothesis implies that ancestors of the Malagasy *Polyalthia* group formerly existed in Africa but went extinct, like several taxa known from the Tertiary of South Africa but now restricted to Madagascar (COETZEE & MULLER, 1984).

Artabotrys

This large African-Asian genus, with about 100 species, is remarkable for its lianescent habit and leaf-opposed inflorescences, with the axis modified into a flattened hook for climbing. In Madagascar, *Artabotrys* is represented by only six species

(CAVACO & KERAUDREN, 1958). According to our analysis, it serves as a link between the « malmeoid » groups with columellar-sulcate pollen and the huge annonoid clade (*Annona* group, asiminoids, xylopioids, uvarioids), which has round, inaperturate pollen, originally in tetrads. It is more primitive than the annonoids in having single (monad) pollen, with a vestigial sulcus and no reduction of the proximal exine, but it is linked with them in having round rather than boat-shaped monads. This connection is strengthened by multiple foliations in the basal exine layer and lamelliform endosperm ruminations, both synapomorphies that appear at this point on the cladogram.

Isolona

This genus, represented by some 20 species in Africa and five species endemic to Madagascar (CAVACO & KERAUDREN, 1958), is remarkable for its unilocular, parasyncarpous gynoecium, a synapomorphy with the African genus *Monodora*. Fused petals associate these two genera with *Hexalobus*, and the three are linked with *Uvariastrum* by intermediate infratectal structure (LE THOMAS, 1980/81) and a rib-like raphe (VAN SETTEN & KOEK-NOORMAN, 1992). *Hexalobus* and *Uvariastrum* are also African. Spreading petals, numerous ovules, and a thick fruit wall place the whole group in the asiminoids. Unlike other asiminoids, *Isolona* has single pollen grains rather than tetrads. Its position among the asiminoids implies that this feature is a reversal; interestingly, its monads resemble the grains making up the tetrads in having a reduced proximal exine. Based on the distribution of its relatives, *Isolona* is most likely of African origin.

Annona

This genus, which is particularly rich in America, where it is represented by about 100 species, includes a single species in Madagascar, *Annona senegalensis*, also found in Africa (LE THOMAS, 1969). In our present analysis, the *Annona* group (including segregate genera that may be derived subgroups of *Annona*: SCHATZ & LE THOMAS, 1993) forms an separate line within the annonoids, associated with this clade based primarily on its inaperturate tetrads with reduced proximal exine. Like the asiminoids, *Annona* retains the basic reticulate exine of the annonoids, with columellar infratectal structure and a thickened outer nexine foliation.

Xylopia

Xylopia, the only pantropical genus of Annonaceae, includes about 150 species, of which about 25 occur in Madagascar (CAVACO & KERAUDREN, 1958). The xylopioid clade is united by elongate petals, peltate-apiculate stamen connective, and pollen characters - loose tetrads with a continuous tectum, granular infratectal structure, and a thick but non-foliated basal layer. Other xylopioids include *Neostenanthera* (Africa) and *Cananga* (Asia, introduced in Madagascar). *Xylopia* is linked with *Cananga* by its low vessel density, inflorescences of axillary cymes, concave receptacle apex, numerous ovules, and loss of idioblasts in the nucellus. With its pantropical distribution and the

distributions of its relatives, *Xylopia* shows equally strong links with both Africa and Asia.

Uvaria

This large African-Asian lianescent genus is well represented in Madagascar, with about 15 species (CAVACO & KERAUDREN, 1958). It belongs to one of the two subgroups of the uvarioid clade, which are united by imbricate, spreading petals and a rudimentary aril. Synapomorphies of the primarily African line that includes *Uvaria* are lianescent habit, sessile stigma, and numerous ovules (secondarily reduced in *Afroguatteria*). *Uvaria* is linked with *Afroguatteria* and *Monanthotaxis* by pollen characters, namely monads with granular infratectal structure and no proximal exine reduction, plus presence of oil cells in the endosperm. *Uvaria* appears to be another member of an originally African group that extended into Asia.

FRIES (1959) used the character of imbricate vs. valvate petal estivation to divide most of the Annonaceae into two tribes, Uvarieae and Unoneae, and he considered the former more primitive. In contrast, our results indicate that valvate petals are primitive in Annonaceae, and imbricate petals are not homologous in all the groups where they occur, but rather originate independently in six lines. The largest of these lines is the uvarioid clade recognized here, but other « Uvarieae » belong among the « malmeoids » (*Malmea*, *Pseudoxandra*, *Ephedranthus*, *Guatteria*) and in other clades (*Sapranthus*, *Asimina*).

Monanthotaxis

As circumscribed by VERDCOURT (1971), this genus of African-Malagasy lianas includes *Enneastemon* and plants previously confused with the Asian genus *Popowia*. We treated *Monanthotaxis* as part of the *Monanthotaxis* group, together with *Exellia* and *Gilbertiella* (Africa) and *Friesodielsia* (Africa, Asia). This is a highly specialized group that our analysis places in the same uvarioid liana group as *Uvaria*, despite the fact that it lacks many basic uvarioid features (including imbricate petals), apparently as a result of reversal. It is linked with other uvarioids by the African genus *Afroguatteria*, with which it shares small, round, inaperturate monad pollen and exarillate seeds, but its exine is more advanced in that the tectum is reduced to small spines rooted in the granular layer (a convergence with the uvarioid pseudosyncarp *Pachypodanthium*: LE THOMAS *et al.*, 1994). With relatives in both Africa and Asia, the phytogeographic relationships of *Monanthotaxis* are comparable to those of *Uvaria*, suggesting that it had a similar history.

CONCLUSIONS

These observations suggest that the Annonaceae of Madagascar include examples of all three main stages in the geographic history of the family hypothesized by LE THOMAS and DOYLE (1995). This may be illustrated by reference to figure 2 (modified

from LE THOMAS & DOYLE, 1995), in which geographic distribution is treated as an unordered multistate character and plotted *a posteriori* on the tree obtained from analysis of morphological characters.

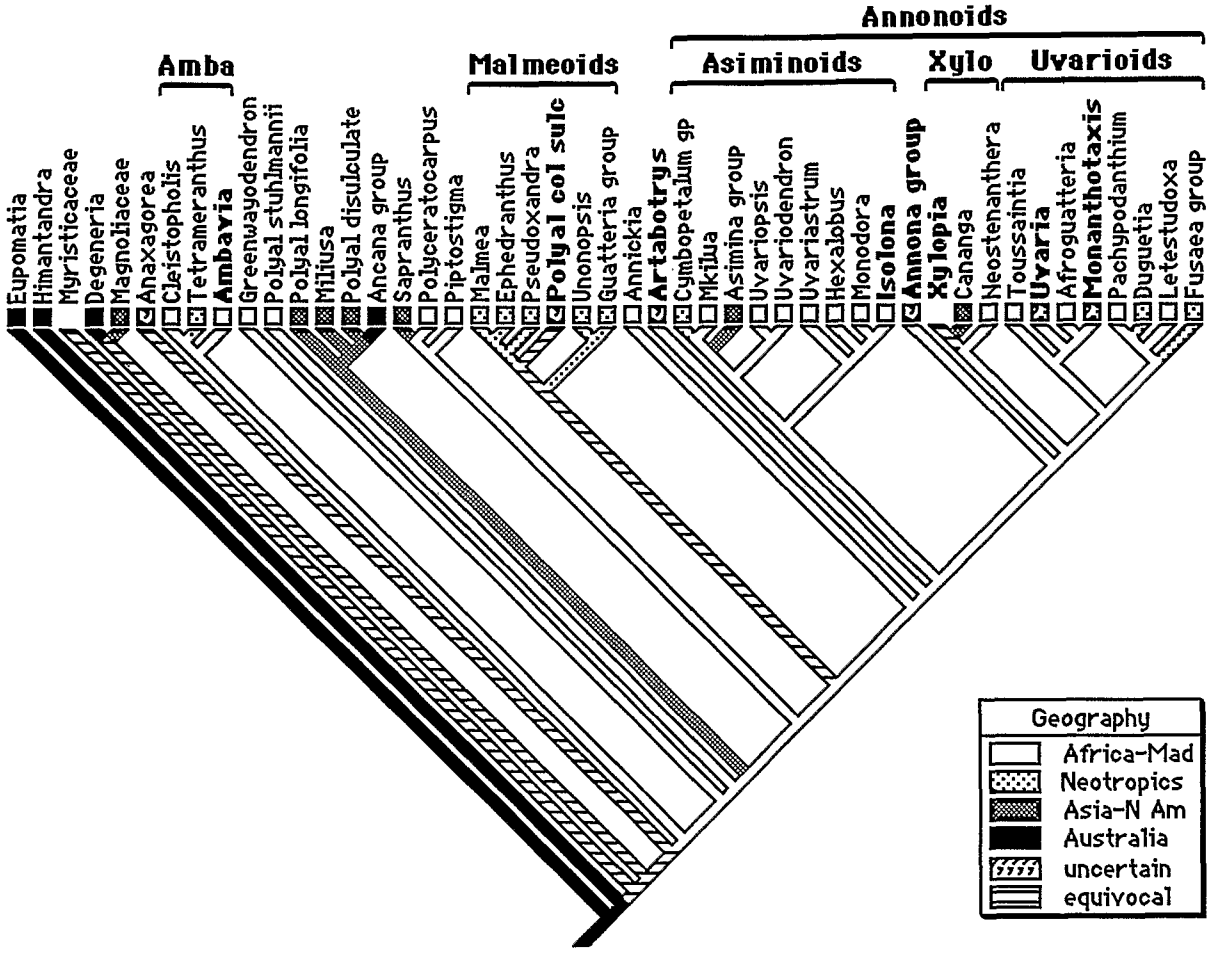

Fig. 2. Geographic distribution of Annonaceae and other Magnoliales treated as an unordered multistate character and plotted on the cladogram shown in Fig. 1, derived from morphological characters. Taxa found in more than one region are scored as having either of two states (*Anaxagorea*: 1/2; *Annona* group: 0/1; *Artabotrys*, *Monanthotaxis* group, columellar-sulcate *Polyalthia* group, *Uvaria*: 0/2) or unknown (pantropical genus *Xylopia*).

Ambavia, one of four highly disjunct genera that make up the near-basal ambavioid clade, represents the earliest stage in radiation of the family, possibly at a time (Early Cretaceous?) when Laurasia and Gondwana were still close enough together for exchange of taxa, as proposed for the basal split into *Anaxagorea* and the rest of the family.

Annona senegalensis and *Isolona* belong to otherwise African and/or South American groups that may have originated during a subsequent phase (Late Cretaceous?) when Africa and South America were separated from other continents but the South Atlantic was still relatively narrow.

Finally, the columellar-sulcate *Polyalthia* group, which also occurs in tropical Asia but belongs to a predominantly South American clade, may represent a phase (Early Tertiary?) when groups that originated in Africa-South America dispersed to Eurasia as the Tethys began to close, perhaps in some cases as « passengers » on India during its northward movement. The pantropical genus *Xylopia* may have had a similar history. Relationships of the African-Asian genera *Artabotrys*, *Uvaria*, and *Monanthotaxis* also suggest dispersal from Africa to Asia, but there is no indication that they ever occurred in South America. It is notable that all the groups found in both Africa and Asia also occur in Madagascar, which may support the hypothesis that Madagascar formed part of their dispersal route to Asia, although it could also reflect simply a higher capacity for long distance dispersal.

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