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International Journal of Paleobiology & Paleontology
ISSN: 2642-1283

Palynostratigraphy of Upper Mesozoic Outcrops near Anjiajia (Mahajanga Basin), and Manamana (Morondava Basin), and It's Bearing on the Development of Cretaceous Angiosperm Floras in Madagascar

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Review Article

Volume 3 Issue 1

Received Date: November 21, 2020

Published Date: December 24, 2020

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Abstract

The two outcrops were investigated palynologically. One outcrop is approximately a 17meter section near Anjiajia in the Mahajanga Basin and the second outcrop is approximately a 5meter section located in the Manamana massif-South Ankazoabo in the Morondava Basin. The section from Anjiajia was dominated by Cryptogrames (56%), Gymnosperms (29.5%) and a minor component of angiosperms (19%). Based on the sedimentology, composition of the palynoflora, the low percentage of angiosperms, and the occurrence of the dinoflagellate *Litosphaeridium arundum* at the Anjiajia sample is estimated to be Albian to Cenomanian in age. The section from Manamana is dominated by Cryptogrames (47%), Angiosperm (30.5%) and Gymnosperms (17.5 %). Based on the sedimentology, floral composition, the higher percentage of angiosperms relative to the Anjiajia sample, the occurrence of the Dinoflagellates *Leberidocysta chlamydata* and *Odontochitina operculata* and the location of the section beneath the Coniacian basalts in the Morondava basin, these data suggest a Turonian-Coniacian age for this sample. Based on these two Cretaceous palynofloras and a megafossil fossil flora from the Maevarano Formation (Santonian to Maastrichtian), which has only a few species of gymnosperms and is dominated by the Lower Cretaceous angiosperm *Sapindopsis*, it appears the southern hemisphere floras are lagging behind the northern hemisphere angiosperm floras in diversity and abundance.

Keywords: Angiosperm floras; Palynology; Cretaceous; Mahajanga Basin; Morondava Basin

Introduction

Madagascar separated from the African Continent about 160 million years ago and subsequently from India about 88 mya [1-6]. The isolation of Madagascar in the mid Cretaceous and through the Late Cretaceous and Tertiary has been implicated in the high rate of extant endemism in the fauna and flora of Madagascar. Madagascar is one of the seven biodiversity hotspots in the world [7]. The primate fauna has attracted worldwide interest of scholars and conservationist) [7]. The Late Tertiary fauna and flora has been of particular interest to track and reconstruct the development of

Madagascar's unique biota through the Tertiary and the Holocene [8-11]. Palynological investigations may be used to detect the effects of climatic changes on terrestrial plant vegetation and as additional tool to envisage the past climatic changes [12].

The Mesozoic dinosaurian fauna has been equally significant and has attracted attention [13,14]. Madagascar's flora has also attracted interest because of its diversity and the high number of endemic taxa [15-17], especially the occurrence of basal angiosperms, e.g. the genus Takhtajania perrieri of the Winteraceae [18]. However, interest and recovery of the megafossil flora from the Mesozoic and Tertiary are confined to reports of various species of microfossils [19-26] and just a few reports of megafossil floras [27-29]. Otherwise, the Mesozoic and Tertiary megafossil floras have remain largely unknown.

In the 1980s and in subsequent field seasons our field team began surveys to assess the abundance and distribution of plant fossils in the Mesozoic sediments of the Morondova and Mahajanga Basins. The Mesozoic sequences within these two basins preserve a number of high- energy environments. Environments more conducive to vertebrate preservation than the preservation of plants [13,14]. There have been reports of petrified wood in Madagascar, but few have been studied [30]. During our field surveys, palynological samples were collected from both basins, however, few of these samples produced palynofloras that could provide insight into the floristic composition and abundance of various taxonomic groups. One location in the Mahajanga Basin (Maevarano Formation) produced various species of leaf impressions including angiosperms. This Upper Cretaceous (Campanian –Maastrichtian) age locality is dominated by the primarily early Cretaceous taxon *Sapindopsis* presumed to be closely related to members of the Platanaceae (see below), however this locality was disturbed by subsequent road work and was unable to be relocated to extract more extensive collections.

This study is to characterize the palynofloras from the Anjiajia site, Mahajanga basin, and the Manamana site, Morondava basin and to assess the age of the sediments based on the microfossil assemblages. This study is to expand our understanding of the fossil flora of Madagascar during the Mesozoic, particularly during the first major diversification of the angiosperms in the world.

Collection Localities and Sedimentology

Anjiajia

Anjiajia is located in the Mahajanga Basin (S 16°22'15'', E 46°55'02''). Geographically, the area studied is in the southwest part of the Mahajanga Basin, 35 km east of the District of Ambato- Boeny on National Route 4. Between the Isalian sandstone reliefs and the northwest coast lay the alluvial plains of Anjiajia, Madirovalo and Marovoay, which were the focus of this field survey [31-33] (Figure 1).

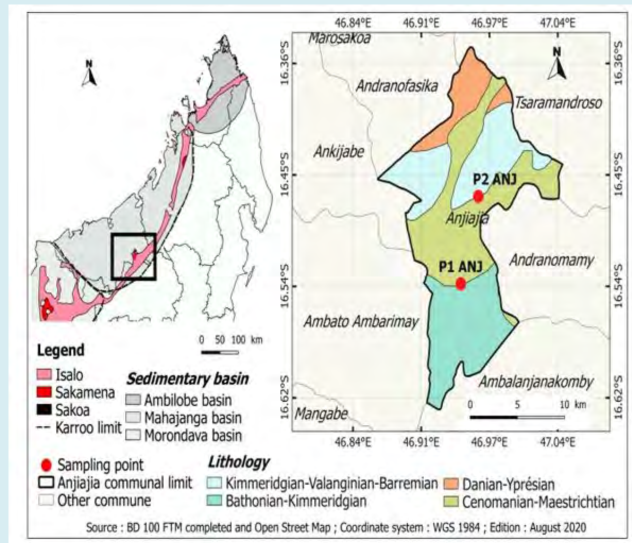

Figure 1: Location of the Anjiajia site, Mahajanga Basin. P1_ANJ is located at S 160 31' 59.9" E 460 56' 42.6", and P2_ANJ is located at S 160 27' 48.7" E 460 57' 42.6".

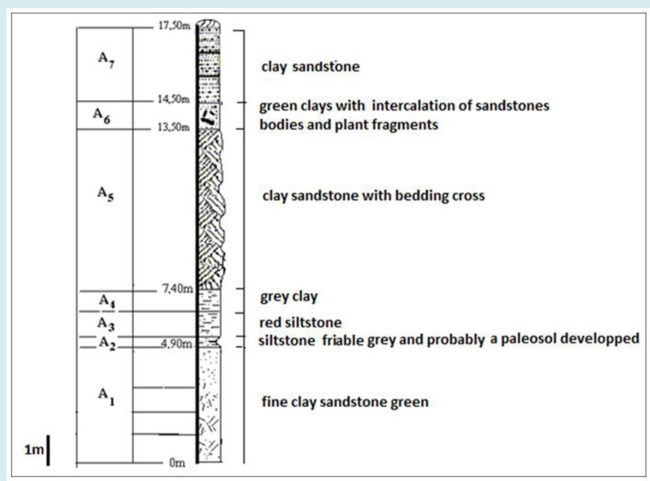

Figure 2: The section sampled near Anjiajia, Mahajanga Basin.

The 17.5-meter section near Anjiajia is comprised of seven (7) lithological units (Figure 2). The base of the section consists primarily of a fine-grained green clay interbedded occasionally with a cross bedded sandstone (A1) with traces of iron-stained clay and concretions. A2 is weathered grey sandy clay to siltstone, probably a paleosol. A3 is a sandy silt to claystone becoming variegated grey to red at the top, and grading into the A4 grey clay. The upper portion of this section A5 is characterized by the succession of green interbedded clays with cross-bedded sandstones. A6 is a sandy siltstone to clay and is the unit that produced the playnoflora. A6 grades into a fine-grained sandy silt and sandstone clay (A7) about 3 meters thick (Figure 2).

The entire outcropping section was sampled and processed for microfossil. The A6 level was the only lithological unit to produce a palynoflora.

Manamana

The 5-meter Cretaceous portion of the section at Manamana is located in the Morondava basin southwest of the District of Ankazoabo, and located 3 km from the fokontany of Ambatomainty whose geographical coordinates are: S 22°30'00", E 44° 27' 00". This site has been characterized as Upper Jurassic sediments (Callovien-Oxfordian) grading into Cretaceous sediments [34] (Figure 3).

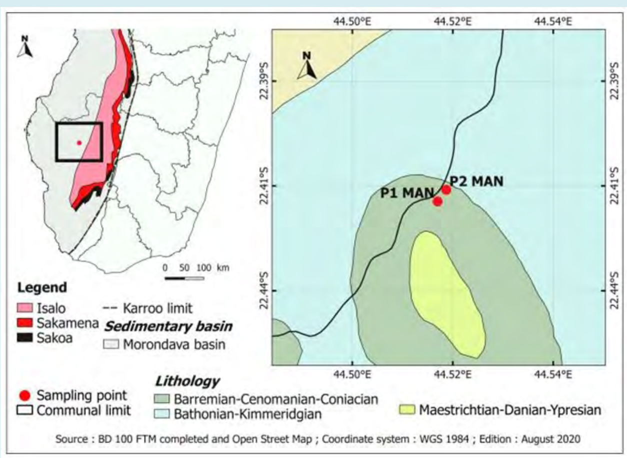

Figure 3: Location of the Manamana site, Morondava Basin. P1_MAN is located at S 220 24' 46.9" E 440 31' 04.8", and P2_MAN is located at S 220 24' 56.5" E 440 30' 57.6".

This section at Manamana has seven (7) distinctive levels (Figure 4). The Cretaceous part of the section has a thickness of about 5 m. The basal bed (M1) is a fine grained, friable white sandstone overlain by a fine to medium grained brown cross-bedded sandstone (M2). The M1 – M2 levels comprise the Jurassic portion of the section. The Cretaceous M3 is a medium to course grained greenish-grey sandstone and is overlain by the M4 consolidated sandstone. M5 is cross-bedded fine-grained sandstone interbedded with silt to claystone with invertebrate fossils and is the lithological unit that produced the palynoflora. M5 is capped off by consolidated blocky sandstone (M6). The overall section is overlain by a basalt (Figure 4).

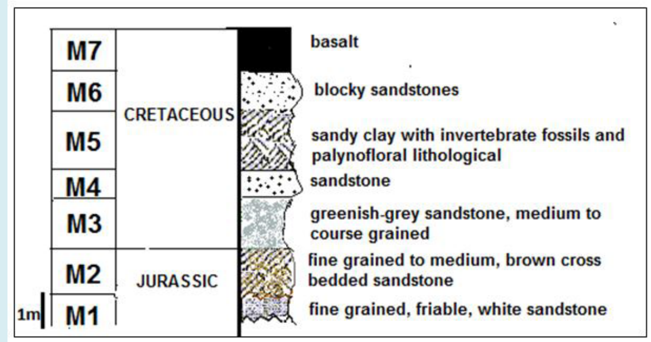

Figure 4: Stratigraphic section that was sampled near Manamana. Note the section is just below the basalts of Coniacian Age [35-40].

Sample Processing Methods

All of the samples were processed according to the method of Barss and Williams [41] modified by Zavada [42] for palynological analysis. Slides were examined to determine the taxonomic affinities of the palynomorphs and the relative abundance of each taxon in the samples. These data along with an analysis of the sedimentological data were used for the elucidating the paleoenvironments of the two localities (after Chateauneuf [43] and Reyre; Demchuk, et al. [44].

The Pollen and Spore Flora, Age and Depositional Environment

The palynoflora from Anjiajia has approximately 29 taxa and the flora from Manamana has approximately 32 taxa and both are considered to be Cretaceous. Another feature of these palynoforas is that the two localities share 80 percent of the same taxa suggesting that the two palynofloras may be close in age (Table 1).

The major difference between the two localities is the abundance of angiosperms. Anjiajia is comprised of 19% angiosperms and the Manamana has 30.5% angiosperms (Table 1).

The difference in the percentage of angiosperm pollen indicates that the Anjiajia palynoflora is of Lower Cretaceous age and the Manamana percentage is more indicative of floras from the Lower-Upper Cretaceous [45]. The increase in the percentage of angiosperms may represent the Lower and Upper Cretaceous angiosperm diversification that was occurring in many regions of the world [45,46]. Fifteen of the twenty-one taxa of spore and pollen in the Anjiajia sample are common Lower Cretaceous palynofloras, but not necessarily restricted to Lower Cretaceous palynofloras [47-50].

Taxon	Anjiajia (A6)	Manamana (M5)
Aequitriradites spp.	4	1
Appendicisporites baconicus	2	6
Appendicisporites tricomitus	6	7
Appendicisporites dorogensis	2	2.5
Appendicisporites potomaensis	5	1.5
Cicatricosporites australiensis	4	10
Cicatricosporites ludbrookiae	6	4
Cingulatisporites sp.	4	1
Concavisporites sp.	5	1
Cyathidites spp.	NP	2.5
Gleicheniidites spp.	2	NP
Matonia pectinata	2	2.5
Marattiopsis	1	1
Osmundacidites	3	NP
Paxillitrilites dakotaensis	NP	1
Polypodiasporites sp.	4	2
Retitriletes sp.	4	NP
Verrucosisporites rarus	2	2
TOTAL CRYPTOGAMS	56	45
Alisporites grandis	1	1.5
Araucariacites australis	3	2
Balmeiopsis imbatus	4	NP
Callialasporites segmentatus	NP	1.5
Callialasporites trilobatus	1.5	NP
Classopollis classoides	NP	2
Cycadopites spp.	NP	2
Microcachrydites antarcticus	12	2
Podocarpidites spp.	3	4
Trichotomonosulcites subgranulosus complex	5	2
TOTAL GYMNOSPERMS	29.5	17
Clavatipollenites Figure 5A	NP	5
Ericipites spp.	5	2.5
Liliacidites giganteus	NP	4
Monocolpopollenites sp.	4	2
Monosulcites Figure 5C	4	4
Proteacidites polymorphus	2	2
Retimonocolpites Figure 5B	2	7
Tricolpites spp. Figures D,E,F	2	4
TOTAL ANGIOSPERMS	19	30.5
UNDETERMINED	5.5	5
REWORKED POLLEN	0	2.5

Table 1: The percentages of the taxa observed from Level A6 (Anjiajia) and M5 (Manamana). NP = Not Present.

All of the angiosperm taxa recovered from the Anjiajia locality occur frequently in lower Cretaceous palynofloras in other regions of the world [51]. The common occurrence and abundance of Lower Cretaceous spores and pollen, coupled with the low percentage of angiosperms indicates a Lower Cretaceous to Lower - Upper Cretaceous age for the Anjiajia and suggest this locality belongs to the Ankazomihaboka Beds Rogers, et al. [33] or the Serie d'Ankazomihaboka of Besairie [31] (Table 1). The presence of the dinoflagellate cyst *Litosphaeridium arundum*, further refines the age to Albian [52-56] (Table 2).

Dinoflagellate / Location	Anjiajia (A6)	Manamana (M5)	Age range
Litosphaeridium arundum	X	NP	Albian
Leberidocysta chlamydata	NP	X	Albian-Cenomanian
Odontochitina operculata	NP	X	Senonian

Table 2: Distribution and age range of identifiable dinoflagellates. NP = Not Present.

Although the rock units from these two sites indicate similar depositional environments, they two localities may be of two different ages. The sediments at Manamana are considered to be Upper Cretaceous possibly Coniacian. This palynoflora does have some common Upper cretaceous taxa that are not found in the Anjiajia palynoflora, e.g. *Liliacidites giganteus, Paxillitriletes dakotaensis, Cyathidites*, and *Cycadopites* (Table1). The occurrence of the dinoflagellates *Leberidocysta chlamydata* and *Odontochitina operculata* suggest a Turonian-Coniacian (Senonian) age for the beds, but no older than the Cenomanian [57] (Table 2). A basalt overlays the entire section (Figure 4). During the Cretaceous, Madagascar and India underwent a southward lateral displacement, which resulted in the initial separation of Madagascar and India causing magmatism during and after the rifting, these basalts in the Morondava Basin are a result of this rifting. The basalts have been dated Coniacian [35-40] and support the interpretation that the Cretaceous section, which lies beneath these basalts is of Senonian age (Turonian- Coniacian).

Discussion

Rifting between east and west Gondwanaland began about 176 million years ago [58]. This initiated a breakup of Africa (west Gondwanaland) and Madagascar which occurred about 165 million years ago [5,6,58]. Madagascar drifted southeast along the trend of the Davie Ridge. Spreading ceased approximately 130 my ago. Since that time Madagascar has not changed its position significantly [59]. This event first isolated Madagascar from the African continent (western Gondwanaland), and subsequently in the Coniacian, India separated from Madagascar and began to drift northward, reducing the land area that can act as a target for migrating organisms to Madagascar and further isolated the island through the remainder of the Cretaceous and Tertiary. The high rate of extant endemism in Madagascar is attributed to this early isolation. Concurrent with these tectonic events during the Upper Jurassic to Coniacian, is the Lower Cretaceous and Upper Cretaceous worldwide distribution and diversification of angiosperms.

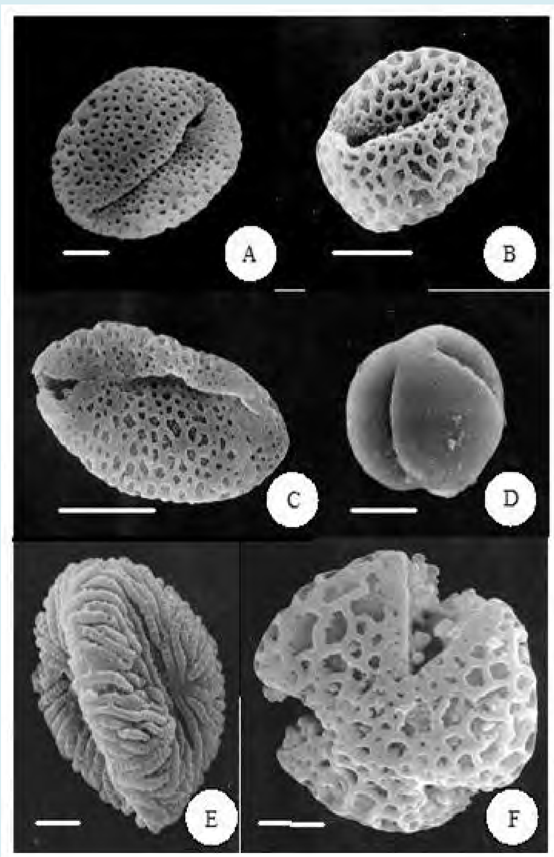

Figure 5: Representative Palynomorphs from the Manamana Locality in the Morondova Basin, similar taxa also occur at Anjiajia. A) *Clavatipollenites* sp., Scale Bar = 5 um. B) *Retimonocolpites* sp. Scale Bar = 10 um C) Monosulcites Scale Bar = 8 um D) *Tricolpites* sp. Scale Bar = 8 um. E) Striate – Tricolpate, Scale Bar = 3 um F) *Tricolpites* sp. cf. Rousea, a tricoplate type. Scale Bar = 8 um

Angiosperms comprised a relatively small percent of palynofloras during the Lower Cretaceous (no more than 15-20% of a flora, Lidgard and Crane,) [45]. During the Upper Cretaceous, however, palynofloras steadily increased in diversity and increased as a percent of the palynoflora reaching about 55% in the Northern Hemisphere palynofloras in the Maastrichtian [45,60]. The two palynofloras in this study share about 80 % of the same or similar taxa (Figure 5), however angiosperm taxa through this time interval in Madagascar continue to be a relatively minor component of the palynofloras, approximately 19% in the lower Cretaceous and 30% by the Coniacian. This lags behind the increase in diversity and dominance observed in other parts of the world, notably in the Northern Hemisphere.

Megafossil floras also track the increase in angiosperm diversity and dominance that the palynofloras exhibit during this time interval. In addition to the two palynofloras in Madagascar our team also found a megafossil locality 25 km north of the turn off to Marovoay in the Maevarano Formation just off of the RN4 [33]. The Maevarano Formation is primarily Upper Cretaceous (Santonian to Maastrichtian) in age, and has produced a rich dinosaurian fauna. The megafossil flora produce an assemblage of leaves, seeds and insect remains (mostly Beetle elytra). An unusual feature of this flora is it is dominated by *Sapindopsis* leaves with only 2-3 other gymnosperm species present. *Sapindopsis* is a taxon more indicative of Lower Cretaceous and Lower Upper Cretaceous floras than the more diverse Late Cretaceous megafossil floras. *Sapindopsis* leaves are simple, margins are entire, leaves are alternate, linear to elliptic in outline. The terminal portion of the leaf is acute, and basal portion is cuneate (Figure 6, A, B,C). The leaf has a prominent midrib and the secondary venation appears to be alternate to sub-opposite. The leaves are net veined (Figure 6 C).

Beetle elytra are common at this Upper Cretaceous megafossil locality (Figure 6, D,E), in addition to seed and fruit- like structures (Figure 6, F). The flora is dominated by a single species of *Sapindopsis*, i.e. a monculture of this early angiosperm. Beetles may be predators or pollinatiors of this species of angiosperm. The pattern visible on the elytra is found in the Curculionidae, Tenebrionidae, and in Boganiidae, Oedemeridae. The latter two families are known from the Cretaceous and have been implicated as angiosperm pollinators [61].

Much like the palynofloras, the megafossil flora was not as diverse as fossil floras found elsewhere in the world in the same time interval. This suggest that the initial angiosperm diversitfication and migration may have been dampened by the isloation of Madagascar due to tectonic events in the southern hemisphere.

The paleoenvironmental setting of the two localities based on the palynomorph assemblages and the sedimentology represent near shore environments, i.e., lower delta plain [43,44].

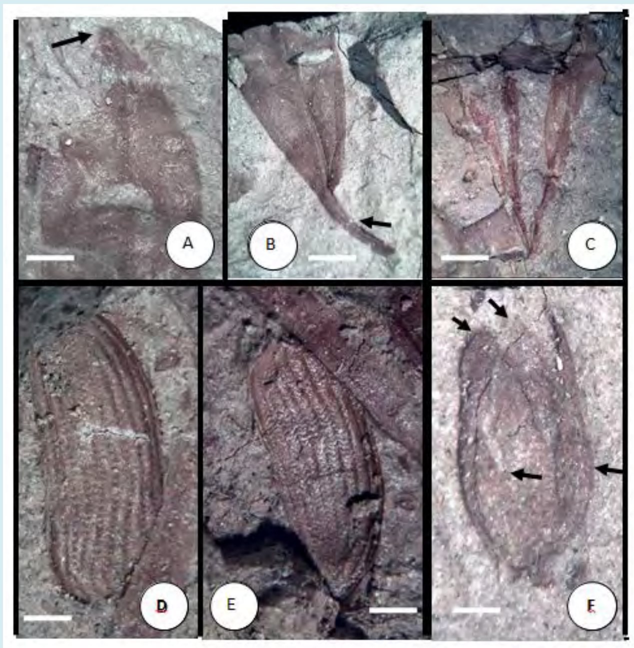

Figure 6: Examples of the megafosssil flora recovered from the Maevarano Formation (Campanian – Maastrictian) 25 km north of the turn off to Maroavay on the NR 4. A) The terminal portion of a *Sapindopsis* leaf showing the acut apex (arrow). Note the prominent midrib. Scale Bar = 4 mm. B) A portion of a *Sapindopsis* leaf showing the cuneate basal portion of the leaf and the petiole (arrow). Note that the leaf venation appears to be alternate to sub-opposite. Scale Bar= 4 mm C) Terminal branch of *Sapindopsis* showing the alterate arrangement of the leaves. Scale Bar = 4 mm D-E) Beetle elytron, possibly of the families Curculionidae (e.g. *Hylastinus* sp), Tenebrionidae (e.g. *Tribolium*), Boganiidae, or Oedemeridae. Scale Bar = 1 mm F) Possibly a four-loculate capsule (arrows) Scale Bar= 1 mm.

Conclusion

The timing of the breakup of Madagascar from the African Continent in the Upper Jurassic and the subsequent separation of Madagascar from India in the coniacian severed Madagascar's connection to continuous land masses during the initial diversification and migration of the angiosperms throughout the world [6]. It is also interesting that angiosperm diversification in southern Africa [62] and Australia [63] exhibit a similar pattern, i.e., a lag in the diversification and dominance of angiosperms through the Lower and Upper Cretaceous of these continents. The timing of these tectonic events may have prevented the spread of angiosperms not only to Madagascar, but to other areas in the southern hemisphere. The approximately 90 million years of isolation have significantly contributed to the high rate of endemism in the fauna and flora of Madagascar.

Acknowledgment

We would like to thank the Faculty of Sciences, from the Department of Paleontology and Biological Anthropology (DPAB) at the University of Antananarivo, Madagascar. Our appreciation is to all the Faculty and staff of the Biology Department at Providence College for welcoming VR during her 2005 internship in the USA. The authors wish to thank the National Geographic Society who provided funding for this field work related to this research project.

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