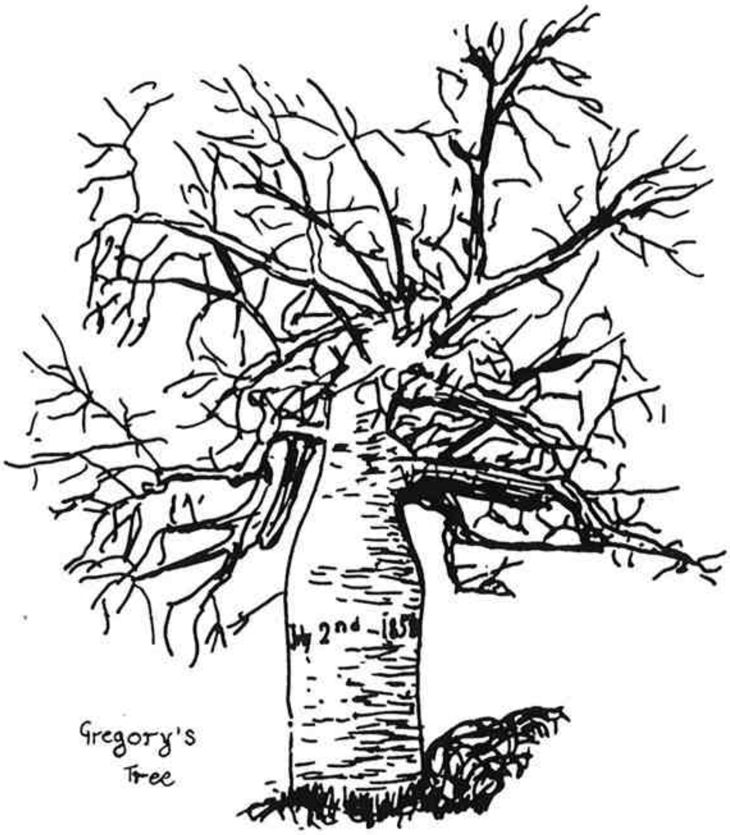
The Boab Tree (*Adansonia gregorii*)

In North-west Australia



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Introduction

There are nine species of Baobab (genus *Adansonia*) in all, of which the Boab Tree is the only representative found in Australia. Seven species are endemic to Madagascar and one, originally restricted to semi-arid Africa, has been dispersed by humans throughout the tropics. The African Baobab (*A.digitata*) is one of the best known tropical trees. In contrast, the seven Malagasy species were poorly known until two years ago and the Australian species had hardly been studied at all. Willis (1955) gives a bibliography of the early literature on the Australian Boab Tree, little of which is based upon direct field observations. Later studies have mainly been flora treatments (such as Boland et al., 1984), though recent research has looked at anatomy (D.A.Wilkins) and ethnobotany (B.Stidham).

We undertook field research in the Kimberley region of Western Australia and adjacent Northern Territory from November 1989 to early January 1990. The main focus of the field-work was to undertake the first detailed study of the pollination and dispersal biology of the Australian Boab. However, we also made general observations of distribution, ecology and systematics of this species. The results of this work will eventually be published in scientific and popular articles. However, since it will be some time before these will be available, we present here a summary of our most interesting conclusions.

Nomenclatural Note

The earliest scientific name given to the Australian Boab tree was *Capparis gibbosa* Cunningham. Under the rules of Botanical nomenclature the correct name is therefore, *Adansonia gibbosa*. However, this combination has not yet been published so we will use the established name, *A.gregorii* F.V.Muell., in this report.

"Boab Tree", the name for *A.gregorii* used in Australia, is derived from "Baobab" which is used in Africa. However, a review of the literature shows that, at least until the late fifties, *A.gregorii* was referred to as "Gouty-stem tree", "Baobab" or rarely "Gregory's tree", and thus the current name appears to be recently acquired.

Distribution and Ecology

In so short a time it was impossible to survey even a small proportion of the range of *A.gregorii*. Nonetheless, we made a habit of recording the presence or absence of trees on each 5 km stretch of road we traversed. These results combined with collection localities and reliable reports permit us to summarise the approximate limits of Boab distribution as currently ascertained (see Figure 1).

The western-most limit is roughly at the boundary between the shires of Broome and Derby, 100 km east of Broome (the trees in Broome itself are all planted). A few individual trees are known from the western shore of King Sound, but only close to the sea (J.Martin Pers. Comm.). The southern-most individuals are reportedly along Gee Gully (J.Martin Pers. Comm.). In the east, the limit appears to coincide with the extent of the Victoria River basin. The eastern-most tree we found was 32 km east of the Victoria River Inn. The northern limit is unclear, but it is likely that throughout most of its range, *A.gregorii* reaches as far as the coast. During our road survey we noted a gap between Gibb River Station and the Pentecost River valley along the Gibb River Beef Road. This apparent hole in the range is worthy of additional study, and may prove to relate to the geology of that area (L.Rosenberg Pers.Comm.).

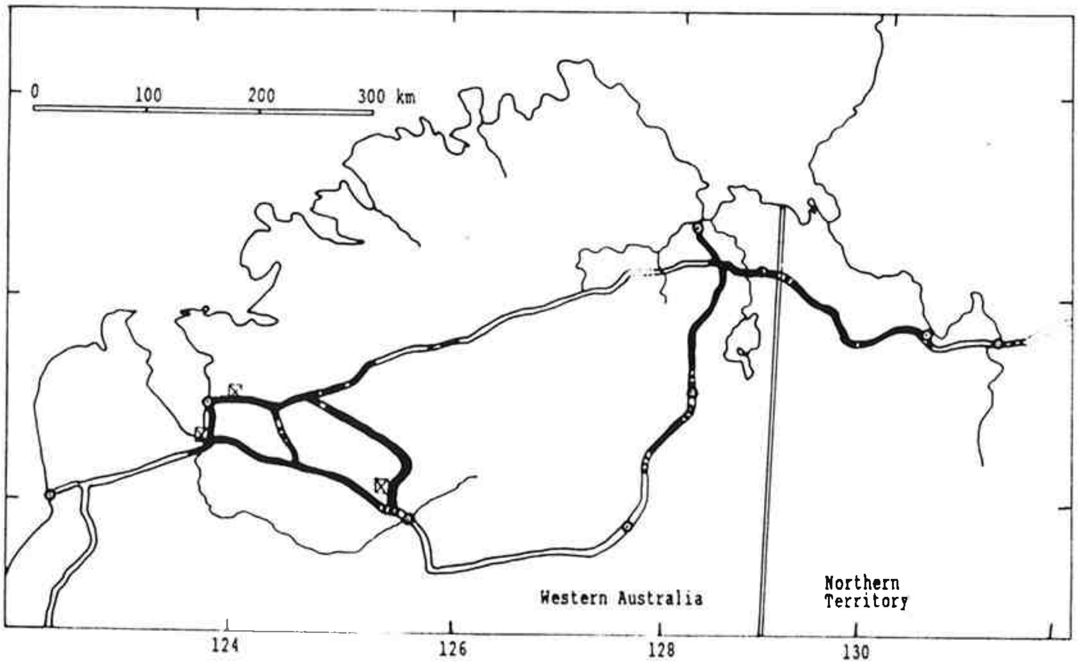

Figure 1. The results of a road survey for the presence or absence of A.gibbosa. The map shows roads that were censused and found to have at least one tree visible within a 5km stretch (═══════) and stretches of road with no trees visible (═══════). Some uncensused roads are also shown (··········). Study sites are shown, ⊠ . The map is not perfectly to scale and should be taken as a rough guide to areas of A.gibbosa abundance rather than a precise documentation of specific populations. Precise localities are available from the authors.

Ecologically the most important factor controlling the distribution of *A.gregorii* appears to be the availability of ground-water. This would explain why trees were concentrated around the fringes of rocky ranges, along seasonal creeks and on the flood-plains of the larger rivers. Nonetheless, boabs are probably poor competitors, explaining their absence from the gallery forest along permanent rivers. They show remarkable powers of regeneration after fire and hence they persist even in areas that are frequently burned.

Although there is a lot of variation between individual Boabs, the level and pattern of variation does not support the subdivision of *A.gregorii* into more than one species. Thus *A.stanburyana* (Hochreutiner 1908) is not a valid species as suggested by Ostenfeld (1918). A few minor differences between the populations in east and west Kimberley were noted (e.g. many trees in the east have a silvery underside to their leaves) but these do not seem sufficient to warrant subspecific or varietal status. Nonetheless, more collections are needed particularly from poorly known areas such as the north-west and the King Leopold and Durrack Ranges.

Pollination Biology

In order to place our results in perspective it is necessary to review the pollination biology of the other baobabs.

The African baobab has long been known to be bat-pollinated (Van der Pijl 1934). Its pollination biology has been studied several times (e.g. Jaeger 1945, Harris and Baker 1959, Coe and Isaac 1965, Start 1972). It has large white flowers which hang down on long stalks. They open after dark and emit an unpleasant musky smell which fruit-bats find attractive. The bats land upside-down, envelop the flower, and lap-up the sticky nectar. In the process, they are dusted with pollen which may be deposited on the stigma of another flower, thereby causing fertilization. Although animals other than bats collect nectar or pollen, none of these are as effective as bats at bringing about pollination.

In Madagascar, six of the seven species have had their pollination studied, and it has been found that they fall into two groups. Two species have ovoid buds and broad, cup-like, white flowers. They produce copious amounts of musky nectar and, like *A.digitata*, are probably bat-pollinated. The other four species have long, narrow buds and elongated, brush-like yellow or red flowers. They are sweetly fragrant, produce little nectar and are primarily pollinated by long-tongued hawkmoths.

Although *A.gregorii* was thought to be bat-pollinated (Van de Pijl 1956; Armstrong 1979), no field studies are reported in the literature. The study reported here had two aspects. Firstly, the floral biology of *A.gregorii*, concentrating on those features that might influence animal behaviour, was documented. Secondly, observations and experiments aimed at determining which flower visitors contribute to pollination were carried-out.

1) Floral Biology

Flowering progresses across the range of *A.gregorii* from east to west. The first flowers in the east appear in late October, and most trees finish flowering by mid-December. In the west flowering starts in early November and lasts until early January. This pattern reflects the fact that the rains start earlier in the east. Nonetheless, in the current climatic conditions most flowering precedes the onset of the rainy season.

The buds of *A.gregorii* are usually about 12cm long. In the morning or afternoon prior to anthesis (flower-opening) the white petals push through the tip of the calyx (the "fused" sepals). The Australian Boab has flowers that open relatively slowly compared to other baobabs; anthesis lasts about 20 or 30 minutes as compared to 2 minutes for *A.fony.* Like other baobabs anthesis takes place around dusk, by which time some nectar (as much as 0.07ml) and pollen have already been released. The stigma, though, is not yet fully expanded (this takes 1-2hrs) and is unreceptive (according to the peroxidase test). Nonetheless, timed pollination experiments showed that pollen placed on the stigma at, or even just before anthesis, can result in seed set. The flowers have a pleasant, sweet fragrance (somewhat reminiscent of vanilla). This is emitted throughout the night but fades in the morning.

In total, anywhere from 0.06 to 0.24 ml is produced per flower, with production concentrated soon after opening. At dawn, unvisited flowers have receptive stigmas, free pollen and contain some nectar.

In order to understand the pollination biology of *A.gregorii* it is important to know whether self-pollination can lead to seed-set. This was determined by emasculating and bagging buds on the morning before anthesis and then either cross- or self-pollinating the flowers during the night. As a control some flowers were left unpollinated. The results are summarised in table 1, and show that *A.gregorii* is functionally self-incompatible; that is to say, pollen from another tree is required for seeds to be set. One selfed and one unpollinated flower remained on the trees at the end of the experiment (the latter looked close to aborting). One possible explanation of this could be pollen transferred accidentally to the stigma on the bags used to isolate the flowers.

TABLE 1 - Breeding Experiment on *A.gregorii*. The four subject trees were located at the Oscar Range site. Each was pollinated with a different pollen donor situated at various distances from the subject trees. The flowers were tagged and emasculated prior to anthesis and kept in a fine-mesh nylon bag. Pollinations were carried-out between 2030 and 2130. The bags were not removed until at least 1200 the next day. The number of fruit still attached to the tree on 1/1/1990 were recorded, and compared to the number originally bagged.

Tree	# Days fruit allowed to develop	Distance to Pollen Donor	# remaining (# at start)		
			Unpoll.	Self	Cross
1	36	4.5km	0(10)	0(10)	10(10)
2	38	350m	-	1(10)	6(10)
3	34	115m	0(5)	0(4)	2(5)
	32		0(5)	0(6)	4(5)
4	34	8m	0(5)	0(4)	4(5)
	32		1(5)	0(6)	4(5)
TOTALS			1(30)	1(40)	30(40)

In order to determine the mechanism underlying this self-incompatibility, styles and ovaries of selfed and crossed flowers were fixed in 2:1 Ethanol:Acetic Acid and pollen tubes viewed using the technique of Martin (1959). It was found that pollen of self-pollinated and cross-pollinated both successfully germinate, grow down the style and penetrate the ovules within less than 48hrs. Thus *A.gregorii* appears to show late-acting self-incompatibility in which either fertilization fails or the selfed ovules fail to develop normally (Seavey and Bawa 1986). It is possible that the genetic mechanism might be similar to the complex self-incompatibility found in Cocoa (Cope 1962), which is quite closely related to *Adansonia*.

The floral biology of *A.gregorii* is summarised in table 2, and compared to that found in *A.digitata*, and the six Malagasy species studied to date.

Table 2. A comparison of the floral features of **A.gregorii** and **A.digitata** with the bat-pollinated Malagasy species (**A.grandidieri** and **A.suarezensis**) and hawkmoth-pollinated malagasy species (**A.fony**, **A.madagascariensis**, **A.perrieri** and **A.za**). The poorly known **A.alba** is excluded. The numerical ranges given are the maximum observed extent of the trait, where the column includes more than one species the range is inclusive. Standard deviations are given where possible (1).

Floral Trait			Malagasy Species	
	A.gregorii	A.digitata	Bat-species	Hawkmoth Species
Flowering season	Early Wet	All Year	Dry season	Wet season
Crown form	Irregular	Irregular	"Pagoda" form	Varies
Bud shape	Elongated	Round	Ovoid	Elongated
Flower orientation	±Erect	Pendulous	±Erect	±Erect
Time of anthesis	2030-2130	1930-2030	1630-1820	1730-2130
Time to open	20-30min	15-30mins	30-80mins	1-10mins
Flowers functional	1 night	1 night	1 night	1 night
Stigma receptivity	c2200-0600	-	all night	all night
Nectar volume at anthesis	40.5µl±23.1[1]	>200µl	10-200µl	0-70µl
Total nectar vol.	100.5µl±54.5[1]	-	1.4-1.91ml	59-620µl
Nectar concentration at anthesis	20.2%±1.81[1]	-	11.75-17%	13-18%
Scent	Sweet	Sour/Musky	Sour/Musky	Sweet
Calyx colour-inside	Creamy white	Creamy white	Creamy white	Red (or white)
Petals exceed calyx	Yes	No	No	No
Petal colour	White	White	White	Yellow or red
Androecium colour	White	White	White	White
Staminal tube length	2.5-5.0cm	c4cm	c0.9cm	5.5-12cm
Filament length	5-8cm	c4cm	3.5-6.5cm	7-12cm(1.5[2])
Anther distribution	Concave	Sphere	Hemisphere	Variable
Stigma colour	White	White	White or pink	Red
Style persistant	Yes	Yes	Yes	Yes or no
Self pollen tubes equal crosses	Yes	-	Yes	Yes
Self pollen enters ovules	Yes	-	-	-
Self-incompatible	Yes	-	-	-

2) Flower Visitors

When considering flower visitors it is important to distinguish animals that could bring about pollination from those that are merely nectar/pollen thieves. Native bees were very occasionally seen collecting pollen in the early morning and settling moths sometimes collected boab nectar at night. Besides these non-pollinating thieves, the only floral visitors were birds and hawkmoths. We did not observe any bat-visits though the blossom bat, *Glossophaga*, has been seen visiting flowers (K.Kenneally Pers. Comm.).

Yellow-throated Miners (*Manorina flavigula*), Little Friarbirds (*Philemon citreogularis*) and Brown Honeyeaters (*Lichmera indistincta*) were the most important bird visitors. They are all members of the very diverse australasian family Meliphagidae which specialize in nectar-feeding. Other Meliphagid species were observed to visit flowers less frequently, (Singing Honeyeaters, *Lichenostomus versicolor*; Grey-fronted Honeyeaters, *Lichenostomus plumulus,* and; Banded Honeyeaters, *Certhyonix pectoralis*), as were Yellow White-eyes (*Zosterops citrinella*) and Rainbow Lorikeets (*Trichoglossus haematodus*). All these species were primarily nectar feeders except the White-eyes, which searched for insects. The peak visitation period was 0430-0530h but infrequently visits were observed later in the morning.

All the nectar-feeding birds usually foraged in a similar way. They perched on the peduncle or calyx and inserted their beaks into the base of the flower (were the nectar accumulates). This behaviour, while efficient for collecting nectar, does not cause the bird to make contact with the anthers or stigma and hence cannot result in pollination. However, every so often birds will perch on a branch above the flower and from this position pollination is a possibility. We estimate that, at most, 5% of bird visits are of the latter sort.

In order to determine whether birds could potentially bring about pollination we emasculated and bagged flowers and then pollinated them in the early morning (0400, 0500 or 0600). The sample sizes were insufficient to say whether these times differed from each other and from flowers pollinated during the night, but it was clear that some of each category set fruit. This indicates that the stigmata are still receptive and, hence, that birds could, potentially contribute to pollination.

Tropical hawkmoths often show a well-defined seasonal peak coinciding with the onset of the wet season (Owen, 1969, Nilsson et al., 1985). This pattern probably applies to hawkmoths in the Kimberley and, hence, in the current climatic conditions most boabs have finished flowering before the hawkmoths appear. However, this fact does not rule-out hawkmoth-pollination - the timing of the first rains varies from year to year and, probably, from century to century as well. Hence, trees as long-lived as boabs might be "synchronised" for a past climatic conditions and it might take centuries before adjustment to current conditions could occur (by which time the climate may have changed once again).

In the western Kimberley, very few hawkmoth visited flowers before January 2nd. However, at this time many visits were observed (concentrated in the first half-hour after anthesis). The moths (*Agrius convolvuli*) hovered in front of the flowers, inserting their proboscides (c9cm) through the filaments, down to the base of the flower. In the process they clearly came into contact with both the anthers and stigma and hence a majority of visits were pollinatory. Hawkmoths are known to travel long-distances, and hence they are likely to transfer pollen between trees (which is necessary in self-incompatible species). Thus, we infer that hawkmoths are major pollinators of the boab, *A.gregorii*.

As well as *A.convolvuli* there are at least four other hawkmoths which could contribute to pollination: *Daphnis placida, Gnatholibus erotus, Nephele subvaria* and *Psilogramma menephron* (E.D.Edwards, Pers. Comm.).

Considering the probable importance of hawkmoths in the pollination of *A.gregorii*, it is possible to pick out some features from table 2 which would be expected to enhance pollination efficiency (see Faegri and Van der Pijl 1979). It should be noted that we are not claiming that these floral characteristics evolved for the "purpose" of enhancing hawkmoth pollination, just that they are currently "useful". The factors responsible for the evolution of each floral trait will become clearer once the relationships among the African, Malagasy and Australian Baobabs are worked-out. Such an analysis is already underway (D.Baum).

1) Nocturnal anthesis (hawkmoths forage at night).
2) Wet-season flowering (hawkmoths emerge in the wet season).
3) White/light coloured flowers (more visible at night).
4) Elongated staminal tubes and/or filaments (hawkmoths have long proboscides).
5) Sweet fragrance (hawkmoths have a very acute sense of smell, and favour what, to humans, are pleasant fragrances).
6) Well-protected nectar (accessible to hawkmoths, but harder for other animals to steal nectar)
7) Little nectar (excess nectar might attract destructive animals).

Although these data represents an advance over what was previously known about Boab pollination biology, several important questions remain unresolved. Foremost among these, we do not know which hawkmoth species are the main pollinators, and whether they are the same in the East and West Kimberley. There are, no doubt, many intricacies of the pollination system of *A.gregorii* which remain to be discovered. For example; How often do hawkmoths move between trees ? What is the contribution of nectar feeding birds ? Do bats play a role ? etc. We hope that this preliminary study will encourage others to pursue these fascinating evolutionary and ecological issues.

Dispersal Biology

One of the most distinctive features of baobabs are their fruit. While most of the close relatives of the baobabs (e.g. Kapok, *Bombax*, *Sterculia*, *Brachychiton*, *Hibiscus*) possess fruit which split-open (dehisce) along predetermined lines of weakness, baobabs have indehiscent fruits comprising a tough outer layer (pericarp) and a dry, powdery pulp in which the hard seeds are embedded. This pulp is tasty and nutritious, being rich in protein, carbohydrate and potassium (Anon. 1984).

The dispersal biology of the Baobabs of Africa and Madagascar have been poorly studied. It is known that the fruit of *A.digitata* are eaten and probably dispersed by mammals such as elephants and baboons (Wickens 1983). Furthermore, it has been shown that the germination of *A.digitata* seeds is enhanced after passing through an animals digestive system (Baker in Rick and Bowman 1961). There are no references to water dispersal of the African baobab but this cannot be ruled-out in view of the ability of the fruit to float in fresh or salt-water.

No studies of baobab dispersal in Madagascar have been published. Despite the extensive work on the nutrition of lemurs (the only living mammals on Madagascar which could be dispersers), we know of no reports of *Adansonia* fruit being eaten. One possibility that should certainly be considered is that extinct animals were formerly important. In Madagascar, giant lemurs (some of which were as large as gorillas) and Elephant-Birds (related to ostriches - but over 3m tall) only disappeared within the last few thousand years. Prior to their extinction these large creatures may have eaten baobab fruit and thereby dispersed their seed (as suggested by P.Armstrong, pers.comm.). In the absence of animal dispersers, water dispersal seems to be important in several species, particularly in riverine populations of *A.perrieri*, *A.grandidieri* and *A.madagascariensis*.

Adansonia gregorii is unique in the genus in having re-evolved fruit-dehiscence. However, instead of splitting along regular lines of weakness, irregular cracks usually appear in the brittle pericarp as the fruit ripen. When the fragile fruit hit the ground they generally break-open, exposing the pulp and seeds to dispersers and predators alike. In view of the fact that the origin of *A.gregorii* almost certainly involved oceanic flotation from Africa or Asia, we conclude that fruit dehiscence could only have evolved after the Boab became established in Australia. This raises the difficult question: Did this evolutionary switch relate to seed dispersal agents on the new continent ?

The only previous work on the dispersal of *A.gregorii* was by Done (1987) who observed that Rock Wallaby scat frequently contained boab seeds. We found a similar phenomenon, but with Euro Wallaroos. A significant proportion (over 5%) of the Euro scat found in the vicinity of boabs in the Oscar Range were found to contain intact boab seeds. A germination experiment was conducted with the help of R. O'Donnell (CALM Nursery, Broome), as summarised below.

One hundred seeds were extracted from euro scat in the Oscar Range. These were planted (without scarification) in 5 flats, with twenty seeds per flat. One hundred seeds taken straight from a fresh fruit (still embedded in pulp) and a hundred taken from an old fruit in which insects had eaten-away the pulp, were planted out in a similar arrangement, as controls. After 6 weeks the number of seedlings which had germinated per flat was recorded and the three classes were statistically compared (treating each flat as a replicate) using t-tests. Although the germination percentage of the seeds from scat (2%) was lower than that of seeds still embedded in pulp (5%) this difference was not statistically significant (df=8, p=0.273). Interestingly the naturally depulped seeds (29%) had a significantly higher germination percentage than seeds embedded in pulp (df=8, p=0.003). It is unlikely that this difference is due to the pulped seeds being inviable. The naturally depulped seeds have effectively been scarified by insect mandibles, and this may enable them to germinate more rapidly. Although the seeds derived from scat did not show enhanced germination the fact that any germination was possible supports the possibility that Euros, and other macropods, disperse *A.gregorii* seed.

These data all suggest the following evolutionary hypothesis. Sometime after *Adansonia* arrived in Australia, fruit dehiscence evolved, enhancing the efficiency of seed dispersal by macropods but diminishing the importance of water dispersal. This feature would probably also be advantageous for dispersal in Africa and Madagascar were it not for the many seed-boring insects which would destroy the exposed seeds. Our observations suggest that Boab seeds are not attacked in Australia, though we cannot say whether this is because the requisite seed predators are absent, or because *A.gregorii* has some additional defence mechanism not present in other species. Whatever, the reason for the low seed-predation, we would argue that this was critical in order for fruit dehiscence to re-evolve.

Phytogeography

With the development of the theory of continental drift and the realisation that Australia, Madagascar and Africa (along with South America, Antarctica and India) were formerly all parts of the super-continent, Gondwanaland, the distribution of *Adansonia* took on special significance. Several authors suggested that *A.gregorii* was isolated from its relatives during the Gondwanan break-up (Maheshawari 1971, Raven and Axelrod 1972, Aubréville 1975). However, as information on the timing of the break-up of the continents developed this point of view rapidly lost favour. Instead, it was suggested that *Adansonia* arrived in Australia as a result of long-distance dispersal from Africa/Madagascar, or from extinct populations of Baobabs in Asia (Raven and Axelrod 1974, Armstrong 1977a, 1977b, 1983).

This model for the origin of *A.gregorii* on Australia can be refined by taking into account some of the observations reported here. The only dispersal-agent by which seed can cross an oceanic barrier are wind, water, birds and bats. Wind can be rejected out of hand, and neither bird nor bat dispersal is reported for *Adansonia*. Water is known to be a major dispersal mechanisms in Malagasy Baobabs, and we therefore suggest that it is the most likely explanation of the presence in Australia. It is known that intact *Adansonia* fruit, float well but additional data is still needed. For example, we do not know how long buoyancy is maintained or how long seeds remain viable (we are planning to determine these parameters by experiment) and the oceanic currents at various periods of the past are poorly understood. Nonetheless, in the absence of any more convincing explanation we will assume that oceanic flotation is responsible for the presence of *A.gregorii* in Australia.

The closest relatives of *A. gregorii* (see Perrier de la Bâthie, 1955) are hawkmoth pollinated. Unless hawkmoth pollination was lost and regained (which seems unlikely) hawkmoths must have been present when *Adansonia* reached Australia. The distribution of hawkmoths suggests that they only arrived on Australia after collision with the Asian plate (E.Edwards, Pers.Comm.), which occurred during the Miocene. This lower limit is confirmed by climatic considerations. The climate in the Kimberley so closely resembles that in Madagascar that it seems simplest to assume that, when *A.gregorii* arrived, climatic conditions were already like those at present. Little is known about the palaeoclimates of northern Australia but we will assume that such a climate could not have existed in Australia until the continent crossed into the tropics. This event occurred a little before collision with the Asian plate, probably at the start of the Miocene, about 27 million years ago (Barlow, 1981). Thus two pieces of information concur in indicating that *A.gregorii* arrived in Australia no earlier than the Miocene.

Conclusions

Despite its conspicuousness, the natural history of *A.gregorii* had hardly been studied prior to the field-work reported here. Several undescribed aspects of their reproductive ecology were noted and comparisons made to other the other Baobab species. Hawkmoths were found to be major pollinators of *A.gregorii* whose flowers are well suited to attracting the animals. Likewise, we confirmed that the Boab is Kangaroo dispersed, and inferred that fruit dehiscence facilitates this process. Finally, we were able to utilize ecological observations to support and refine the hypothesis that *A.gregorii* arrived in Australia as a result of long-distance dispersal from African or Asian populations during the Tertiary.

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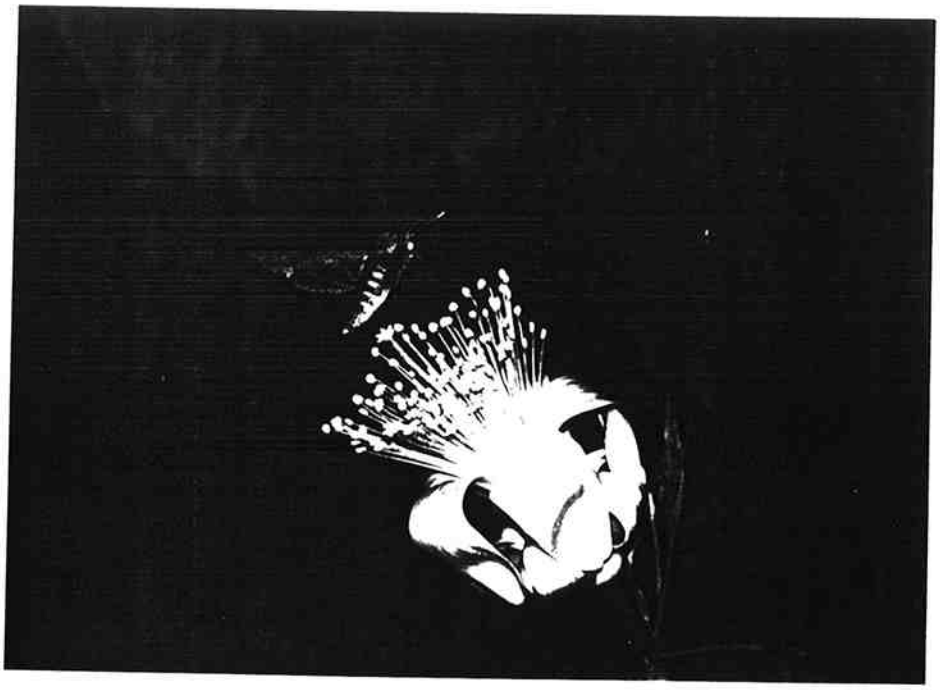

Plate 1. The photograph shows a hawkmoth (*Agrius convolvuli*) visiting a flower of *A. gregorii* at about 2100h, soon after anthesis. The hawkmoths hover in front of the flower and insert their proboscides (c 10cm long) through the filaments, down to the nectar at the flower base. In doing so their wings and body come into contact with both anthers and stigma, and hence they can bring about pollination.