



A Systematic Revision of *Adansonia* (Bombacaceae)

David A. Baum

Annals of the Missouri Botanical Garden, Vol. 82, No. 3 (1995), 440-471.

Stable URL:

<http://links.jstor.org/sici?sici=0026-6493%281995%2982%3A3%3C440%3AASROA%28%3E2.0.CO%3B2-U>

Annals of the Missouri Botanical Garden is currently published by Missouri Botanical Garden Press.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/mobot.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

A SYSTEMATIC REVISION OF *ADANSONIA* (BOMBACACEAE)¹

David A. Baum²

ABSTRACT

The baobabs (Bombacaceae: *Adansonia*) are tropical trees native to Africa, Australia, and Madagascar but dispersed widely by humans. The members of the genus are united by several derived characters that serve to distinguish them from other Bombacaceae, including a characteristic, indehiscent fruit with reniform seeds and a powdery pulp. The systematics of *Adansonia* is revised, with three sections and eight species being recognized. The support for each species is discussed in the context of the "Genealogical Species Concept." Several nomenclatural problems are resolved, and a new combination, *A. gibbosa* (A. Cunn.) Guymer ex D. Baum, is made. In addition, the ecology, ethnobotany, and conservation status of *Adansonia* is summarized, focusing especially on the poorly known Malagasy and Australian species.

The earliest references to the African baobab, *Adansonia digitata* L., are descriptions of the tree and its water-storage capacity in the travelogue of the 14th-century Arab traveler Ibn Batuta (e.g., 1922, vol. 4: 381; 1929: 322). Occasional mentions of the tree can also be found in the reports of European explorers who visited Africa from the 15th century onwards. For example, Aloysius Cadamosto (1507 in 1937: 70) described a tree of huge girth that was almost certainly a baobab. Likewise, André Thevet (1558 in 1878: 47) described an edible fruit from Cape Verde with kidney-shaped seeds. However, these sources were overlooked and European botanists came to know of *A. digitata* through fruits carried by traders to Egypt. Alpino (1592) described these fruits and their reputed medicinal properties using the name *Bahobab*, probably derived from the Arabic "bu hibab," meaning "many-seeded fruit" (Nicolas, 1955; Wickens, 1983). The description and accompanying illustrations published by Alpino (1592) constituted the main information about the plant for over 150 years (e.g., Clusius, 1605; Veslingius, 1638; Ray, 1693; Lippi, 1704).

In the mid 18th century Michel Adanson visited Senegal and provided the first detailed botanical

description and illustrations of *A. digitata* (Adanson, 1757, 1771). He realized the connection to the fruit described by Alpino (1592) and named the plant *Baobab*. Although Linnaeus (1753, 1759) did not retain this name for the genus, preferring instead an honorific for Adanson, the name baobab has persisted as the common name for *A. digitata* and other species of *Adansonia*.

In the early 18th century Allan Cunningham, the naturalist on the HMS Mermaid under Captain King, discovered the "Gouty-stem Tree" in north-western Australia. He believed it to be a *Capparis* (*C. gibbosa* A. Cunn.), but mentioned that it had a superficial resemblance to the baobabs of Africa (Cunningham, 1827; Heward, 1842). Later voyages to the area (Grey, 1841; Stokes, 1846) added further information, but it was left to Ferdinand von Mueller on the Gregory Expedition to the Victoria River basin to recognize formally its taxonomic affinity with the African baobab and to describe it in the genus *Adansonia* as *Adansonia gregorii* (Mueller, 1857, 1858).

The first record of a baobab in Madagascar appears to be the plates in de Bry's *Indiae Orientalis Icones Quarta*, published in 1605 (plates 62 and 63 in Teil, 1979). These plates illustrate cu-

¹ I thank the following herbaria for loaning material and/or providing access to their collections: A, AD, BM, BR, BRI, CANB, E, ECON, F, G, GH, K, MEL, MO, NSW, P, PERTH, TAN, TEF, US. The fieldwork was supported by grants from the National Geographic Society (grants 4178-89 and 4615-91), the Roger Tory Peterson Institute, and the Madagascar Research and Conservation Program of the Missouri Botanical Garden. I thank the many governmental and non-governmental institutions and individuals that helped me in Madagascar and Australia. Field assistance was provided by: Sylvain Razafimandimbison, Roland Ranaivojoana, Jeanine Raharilala, and especially Tricia Handasyde and Ruth Litovsky. I was advised on nomenclature by: P. Hoch, C. Jarvis, R. Kowal, A. Leeuwenberg, and D. Nicolson. I am also grateful for the help and advice provided by numerous individuals including: William Alverson, Patrick Armstrong, Michael Donoghue, Kevin Kenneally, Laurie Godfrey, Peter Hoch, Porter P. Lowry, John Martin, Martin Nicoll, Nat Quansah, James Ross, George Schatz, Ken Sytsma, and Tim Willing.

² Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. Current Address: Harvard University Herbaria, 22 Divinity Ave., Cambridge, Massachusetts 02138, U.S.A.

rious, swollen, bottle-shaped trees that clearly correspond to *Adansonia rubrostipa* Jum. & H. Perrier (Keraudren, 1963). Nonetheless, it was not until the late 19th century that the presence of *Adansonia* in Madagascar was recognized (Baillon, 1876). In the late 19th and early 20th centuries several Malagasy species were described (Baillon, 1889, 1890b; Jumelle & Perrier de la Bâthie, 1909a, 1910), but these were based on poor specimens and inaccurate field observations and resulted in much nomenclatural confusion (see, e.g., Hochreutiner, 1908; Jumelle & Perrier de la Bâthie, 1910). Perrier de la Bâthie (1952a, 1955) resolved many of these problems, but a few have persisted until the present.

Apart from *Adansonia digitata*, the genus is poorly known. Within the last 30 years the only scientific work on the Malagasy and Australian species (apart from descriptions in floras) has been a single article by Keraudren (1963), a series of papers by Miège and coworkers (Miège & Burdet, 1968; Cretton, 1972; Miège & Lambert, 1973; Miège, 1974, 1975), and four papers by Armstrong (1977a, b, 1982, 1983). These papers were based largely upon previous taxonomic literature and incorporated few new field observations.

I spent over 14 months in Madagascar and Australia working on the genus *Adansonia*. In the course of this fieldwork, it became clear that significant inaccuracies have been perpetuated in the literature and that a taxonomic revision of the genus was needed. Elsewhere I have documented the pollination and floral biology of all the species (Baum, 1995), and reported new chromosome counts for all members of the genus (Baum & Oginuma, 1994).

GENERIC AFFINITIES

Adansonia was assigned to Malvaceae by de Jussieu (1789) when he named that family. It was one of the ten genera segregated by Kunth (1822) as the family Bombacaceae, and has remained there ever since. Within Bombacaceae, *Adansonia* is usually united with *Bombax* L. and its allies in the tribe Adansonieae (Schumann, 1890; Bakhuizen van der Brink, 1924; Hutchinson, 1967) or Bombaceae (Edlin, 1935). The tribe comprises *Adansonia*, *Bombax* L. and segregates (Robyns, 1963; Alverson, 1994), and, according to some authors (e.g., Bakhuizen van der Brink, 1924), *Ceiba* Miller and segregates (Gibbs et al., 1988). Members of Bombaceae are usually trees, often with swollen trunks, having palmately compound (rarely unifoliate), stipulate leaves, 3-bracteolate pedicels,

and a distinct androphore (staminal tube). These characters all occur elsewhere in the family, hence the monophyletic status of the tribe is uncertain.

Adansonia occupies an isolated position in tribe Bombaceae (Hutchinson, 1967) and is almost certainly monophyletic. The fruit is unique in the family, consisting of a woody, indehiscent pericarp surrounding numerous, reniform seeds embedded in a chalky or spongy matrix. Similarly, *Adansonia* is unique in the family in that the calyx encloses the floral buds completely, in contrast to the truncate calyx occurring in other genera.

VEGETATIVE MORPHOLOGY

Baobabs are long-lived (Swart, 1963), small to large trees with broad, sometimes bottle-shaped trunks and relatively compact crowns. Juvenile plants usually have slender, tapering trunks that are often swollen at ground level. Trunks comprise soft, fibrous wood arranged in concentric layers. The wood appears to store water, with a tree's diameter fluctuating depending on rainfall (Guy, 1970, 1971). Surrounding the wood is a thick sheath of longitudinal fibers, and outside that a thin photosynthetic layer beneath a skin of outer bark.

The vegetative and reproductive shoots of baobabs are, to varying degrees, dimorphic. The vegetative axes are usually relatively slender, often green and with long internodes, whereas reproductive axes tend to be stouter, generally woody, and with short internodes. Vegetative and reproductive shoots may also differ in indumentum, petiole length, leaflet shape, and the presence or absence of marginal teeth. However, the degree of shoot dimorphism in the different species and the particular differences between vegetative and reproductive shoots is not sufficiently well characterized to be of systematic use.

Baobab leaves have caducous stipules (persistent in *Adansonia perrieri* Capuron) and are palmately compound. However, seedlings and in some cases regenerating shoots, may have simple (not unifoliate) leaves. The number of simple leaves produced prior to the switch to compound leaves varies and is a useful character for identifying seedlings. In particular, *A. digitata* (and to some extent *A. madagascariensis* Baill.) seedlings produce simple leaves much longer than the other species. The transition to compound leaves can be gradual, with a variety of intermediate morphologies produced. Leaflets may be entire or toothed and may be glabrous or have simple or clumped trichomes.

Germination is hypogeal, but there is great variation in the length of the hypocotyl. In section

Brevitubae the hypocotyl is very short, with the cotyledons remaining at soil level, usually still encased in the remains of the testa ("cryptocotylar"). In other species, the hypocotyl is longer (though there is much variation between species), and the cotyledons usually break free of the testa ("phanerocotylar").

REPRODUCTIVE MORPHOLOGY

Inflorescences of baobabs are borne in the axils of leaves close to the tips of reproductive branches. The inflorescence almost always comprises a single flower whose flower stalk is made up of a proximal peduncle and a distal pedicel demarcated by a distinct joint. This implies reduction from an ancestral multiple-flowered inflorescence, which gains support from the occasional occurrence of pairs of flowers having distinct pedicels but a shared peduncle.

The flowers are large, showy, and odoriferous and in all cases open just before or soon after dusk. Anthesis occurs rapidly in all species, generally taking less than 30 minutes. Some species of section *Longitubae* have flowers that open in as little as 30 seconds (Baum, 1995). The movements of the flower parts are sufficiently rapid to be detected with the naked eye. Although in some species flowers may remain attached to trees for several days, all the pollen is released during the first night and the stigmas become shriveled on the first morning. Thus the flowers are in their reproductive phase for at most 15 hours.

The calyx in *Adansonia* spp. is usually green (brown in *A. grandidieri* Baill.). The lobes are valvate and fused almost to their tips in bud. At anthesis the five lobes tear apart and become either reflexed or coiled at the base of the flower. The separation of the lobes is not precise, and frequently two or more adjacent lobes remain fused to each other. When adjacent lobes are fused they reflex, but usually less completely than single lobes, and often distort the shape of the flower.

The unsplit portion of the calyx, the "tube," varies in shape from flat to cup-shaped to tubular and is one of the key characters for separating the sections. The calyx has a ring of nectar-producing tissue near its base, which may be localized in an annular swelling of the calyx tube in some members of section *Longitubae*.

A useful systematic character is calyx persistence. In section *Longitubae* (except *Adansonia gibbosa* (A. Cunn.) Guymer ex D. Baum) the calyx drops with the other flower parts, whereas in *A. gibbosa*, section *Brevitubae*, and section *Adansonia* the calyx is persistent.

The petals are inserted on the staminal tube a few millimeters above its base. The variation in the shape of the petals provides useful diagnostic characters. Petal length is useful for distinguishing *Adansonia rubrostipa*, with petals significantly shorter than the androecium, from *A. za* Baill. and *A. madagascariensis*, with which it can otherwise be confused. Petal color varies from white, through cream to bright yellow and dark red. However, due to the fact that most collections of *Adansonia* are of fallen rather than fresh flowers, petal color has proved to be a source of confusion. Even flowers that are pure white at anthesis appear cream or yellow after they have sat on the ground for a few days. Furthermore, once flowers have completely dried out they turn a reddish brown, which may have led Perrier de la Bâthie (1952a, 1953, 1955) to the false conclusion that *A. suarezensis* H. Perrier has red rather than white petals.

The androecium comprises a sturdy staminal tube below, with numerous free filaments above. The length of both the tube and the free filaments varies greatly and is important for delimiting the sections and species. In addition, the fusion of a central bundle of filaments above the top of the staminal tube is a diagnostic character in *Adansonia rubrostipa* (though this is usually not easy to see on pressed flowers).

The gynoecium consists of a densely pubescent ovary enclosed in the staminal tube, a long style emerging from the middle of the free filaments, and a terminal stigma. In several species, especially *Adansonia digitata*, the style becomes bent over or kinked in the floral bud. However, this may be a developmental phenomenon and it is not a fixed character in any one species. In contrast, stylar abscission is useful in identifying fallen flowers. Whereas most species have styles that persist after floral abscission, *A. madagascariensis*, *A. rubrostipa*, and *A. perrieri* have styles that fall as a unit with the androecium and other flower parts.

The fruit of *Adansonia* is best described as a large, dry berry with an indehiscent woody pericarp, a spongy or chalky "pulp," and numerous reniform seeds. The fruit of *A. gibbosa* is unique in the genus in that it is functionally dehiscent, tending to crack irregularly while still on the tree and usually breaking open upon falling to the ground. Fruit shape and pericarp thickness vary among species but are also highly variable within *A. digitata*, *A. gibbosa*, and *A. za*. These and other characters of fruit morphology (e.g., pericarp anatomy) seem to have great potential in the systematics of *Adansonia*, but have yet to be fully exploited.

For much of its range, *Adansonia za* Baill. is

characterized by fruit with a markedly swollen peduncle. This character is, however, absent from some northern populations of *A. za*, and thus, though useful for identification, is not diagnostic. Likewise, *A. za* fruits often, but not always, have longitudinal ridges which serve to distinguish it from other members of the genus.

Seeds, though always more or less reniform, vary in size and shape. The two species of section *Brevitubae* are distinguished from the others by having larger seeds that have a relatively shallow sinus and are not laterally flattened. Among the other species there is variation in seed size and sinus depth, but much is intraspecific and thus seed characters are difficult to use for identification or diagnosis at the species level. In the species descriptions seed dimensions are given in a standard format: length \times width (dorso-ventral) \times width (lateral), where the seed's ventral surface is defined as the sinus.

ANATOMY AND PALYNOLOGY

While the anatomy of the African species, *Adansonia digitata*, is fairly well known (e.g., Gerber, 1895; Braun, 1900; Metcalfe & Chalk, 1950; Rao, 1952, 1954; Van Heel, 1966, 1974; Inamdar & Chohan, 1969; Davis & Ghosh, 1976), little work has been carried out on the Malagasy or Australian species (but see Gerber, 1895). Clearly, further comparative work is needed.

The palynological work has also been restricted primarily to *Adansonia digitata* (Fuchs, 1967; Sharma, 1969; Vaishampayan & Sharma, 1981), but data are available for the Australian species, *A. gibbosa*, and the Malagasy species *A. grandidieri*, *A. rubrostipa* and *A. madagascariensis* (Presting et al., 1983; Nilsson & Robyns, 1986). The pollen grains (ca. 60 μm diam.) are 3-porate/pororate, suboblate to prolate spheroidal. The pores are 3–8 μm , rounded to oval, and the exine is microreticulate to tectate-perforate and is adorned with blunt processes (ca. 0.5–2.0 μm). The studies to date have not suggested any palynological characters that have any use in infrageneric classification.

PHYTOGEOGRAPHY

Adansonia is almost exclusively tropical, extending only a few degrees south of the tropic of Capricorn in Madagascar and Africa (cultivated populations of *A. digitata* occur in the northern subtropics, e.g., Florida, U.S.A.). Section *Brevitubae* (two spp.) is restricted to Madagascar; sec-

tion *Longitubae* (five spp.) has one species in northwestern Australia and four in Madagascar; and section *Adansonia* comprises one species that is native to continental Africa but has been widely dispersed by humans.

The African/Australian disjunction was formerly explained as being the result of continental drift (e.g., Maheshwari, 1971; Raven & Axelrod, 1972; Aubréville, 1975). With improvements in our knowledge of the history of the southern continents (e.g., Rabinowitz et al., 1983), this scenario now seems improbable. Instead, it is now thought that *Adansonia* arrived in Australia via long-distance dispersal (Raven & Axelrod, 1974; Armstrong, 1983). Circumstantial support comes from the occurrence of water dispersal in the genus (see below) and the arrival of drifting fruits of *A. digitata* on Aldabra (Wickens, 1983; but note the reference given, Wickens (1979), makes no mention of fruit arriving on Aldabra). Dispersal to Australia probably occurred within the last 30 million years, after Australia entered the tropics.

POLLINATION BIOLOGY

Full details of the pollination biology of the Malagasy and Australian species of *Adansonia* are given in Baum (1995), but a brief summary follows.

The African baobab, *A. digitata*, has long been known to be bat-pollinated (e.g., van der Pijl, 1934; Porsch, 1935; Jaeger, 1945, 1950, 1954; Start, 1972), though other visitors, including bushbabies, do visit the flowers and may occasionally bring about pollination (Coe & Isaac, 1965; Wickens, 1983). By extrapolation, it was argued that the remaining baobabs would also be bat-pollinated (van der Pijl, 1956; J. Armstrong, 1979), although P. Armstrong (1977a, 1983) suspected bird-pollination. My work in both Madagascar and Australia found that the situation is more complex.

Both species in section *Brevitubae* receive visits from moths, bees, and sunbirds but are pollinated only by mammals. I have observed fruit bats visiting and pollinating *A. suarezensis*, whereas the only pollinatory visits to *A. grandidieri* were those of the nocturnal lemur *Phaner furcifer*. Further observations would be useful, however, to rule out bat-pollination of the latter species and to determine if any nocturnal lemurs visit the former.

All species of section *Longitubae* studied to date are pollinated by long-tongued hawkmoths. The Australian species, *Adansonia gibbosa*, is visited by the hawkmoth *Agrius convolvuli*. *Adansonia perrieri*, *A. za*, and *A. rubrostipa* are pollinated by *Coelonia solanii*, with additional pollination by

Xanthopan morgani (*A. perrieri*), *Coelonia brevis* (*A. za*), and *Coelonia mauritii* (*A. za*). Nocturnal lemurs in Madagascar and honeyeaters in Australia were important floral visitors that may contribute somewhat to pollination. In contrast, other animals visiting *Longitubae* flowers (bees, flies, ants, settling moths, and sunbirds) seemed to function exclusively as nectar or pollen thieves.

DISPERSAL BIOLOGY

The pulp of baobab fruit is tasty and nutritious, being a particularly rich source of potassium tartrate, tartaric acid, and vitamin C (Greene, 1932; French, 1944; Carr, 1955; Nicol, 1957; Nour et al., 1980). The seeds, while having a high lipid content (de Wildeman, 1903; Rey, 1912), are surrounded by a very tough, thick testa.

In Africa the main dispersal agents of *Adansonia digitata* are terrestrial mammals, particularly elephants and baboons (Wickens, 1983). Enhanced germination rates have been reported for seeds that have passed through an animal's digestive system (Baker, in Rick & Bowman, 1961), suggesting that the African baobab is primarily endozoochorous.

It has recently been determined that the Australian baobab, *Adansonia gibbosa*, is also dispersed by terrestrial mammals, in this case kangaroos and wallabies (Done, 1987; Baum & Handasyde, unpublished data). Fallen fruits are eaten and the seeds pass intact. However, unlike *A. digitata*, there was no significant difference in the germination percentage of seeds collected from droppings (2%) versus seeds taken directly from fruit (5%) (Baum & Handasyde, unpublished data). In view of the viability of seeds that have been eaten by mammals and the large number of seeds that are eaten (shown by the frequency of droppings containing seeds), we may conclude that *A. gibbosa* is primarily endozoochorous. However, the suggestion of bat-dispersal in *A. gibbosa* (Froggatt, 1934) seems unlikely.

In Madagascar, animal dispersal of *Adansonia* has not been documented. In view of the intensive ecological and behavioral work conducted on lemurs, the only extant animals potentially capable of acting as seed dispersers, it appears that the baobabs of Madagascar are not currently endozoochorous. However, among the many animals that have become extinct since humans colonized Madagascar (ca. 1500–2000 years ago; Mack, 1986) are some that could have been seed-dispersers of the Malagasy baobabs. The most likely candidates for this role are two species of the

subfossil genus *Archaeolemur* (L. Godfrey, pers. comm.). They were abundant throughout much of Madagascar until human colonization and persisted until at least 1000 years ago (D. Burney, pers. comm.). They are thought to have been similar in size, habits, and locomotion to baboons (*Papio* spp.) and were "primarily frugivorous, or at least dietarily generalized, consuming large food items, such as hard-skinned fruits" (Tattersall, 1982: 220). Another candidate worth considering is the elephant bird, *Aepyornis* spp. (P. Armstrong, pers. comm.), a large terrestrial ratite (the heaviest bird that ever lived) that occurred primarily in the south and west of the country as recently as the 17th century. They were potentially important seed-dispersers, as their "very powerful beak would enable [them] to dig up tubers and open large fruit" (Mahé, 1972: 344).

In the absence of animals as seed-dispersers, it seems that water offers the only means of dispersal available to the extant Malagasy baobabs. The buoyant fruit and tough waterproof pericarp of *Adansonia digitata* means that dispersal along rivers, on floodwaters, and along strandlines is probably frequent (Wickens, 1983). In contrast, water dispersal may be ruled out for the Australian species on account of its fragile, usually dehiscent pericarp. In Madagascar, water dispersal occurs in *A. perrieri* growing alongside rivers. For example, in Montagne d'Ambre numerous fruit may be found in the Rivière de Makis floating as much as 1/2 km below the nearest tree (pers. obs.). Similarly, *A. za* and *A. madagascariensis* fruit, which have tough, indehiscent pericarps and are frequently found along watercourses, are likely to be water dispersed. However, hydrochory is unlikely in *A. grandidieri* and *A. suarezensis* because of their fragile pericarps and in *A. rubrostipa* because it rarely occurs near rivers or streams.

TAXONOMIC TREATMENT

GENEALOGICAL SPECIES CONCEPT EMPLOYED

In view of the current lack of consensus as to how species are to be defined, it is necessary to specify the criteria I have employed in the following taxonomic treatment. In evaluating whether a group of organisms constitutes a species, I have evaluated whether there is evidence that they show "exclusivity of descent," wherein each member of the group is genealogically more closely related to all other members of the group than to any individuals outside the group (de Queiroz & Donoghue, 1990). The concept of genealogical relatedness I have in mind is, however, not the conventional notion of

recency of descent from a common ancestor, but rather the recency of common ancestry of all their genes when considered simultaneously. Under this view of relatedness (and hence exclusivity), species are composed of organisms that constitute a clade on every gene tree (although the arrangement within the clade will vary from gene to gene). The practical and theoretical implications of this perspective on species are discussed in more detail elsewhere (Baum & Shaw, 1995). The important point to note here is that in order to become a species a group must be genetically isolated from other groups for many generations. The actual number of generations varies, depending especially on the population size. The recently developed branch of population genetics called *coalescent theory* (e.g., Hudson, 1990; Maddison, 1995) shows that smaller populations (or those that have passed through bottlenecks) take less time to become exclusive than larger ones.

Because the criterion of exclusivity applies not just to species but also to higher taxa, species are defined as "basal" exclusive groups, i.e., groups that contain within them no nested, exclusive groups (Baum & Shaw, 1995). In this treatment of *Adansonia*, I have hypothesized that groups of organisms are species when they share a number of fixed differences from their nearest relatives and contain no subgroups that could be exclusive. This follows because groups that have diagnostic characters (especially if they are apomorphic characters), are likely to have been isolated from other such groups, and thus have a high probability of being exclusive. Nonetheless it should be stressed that, unlike the "Phylogenetic Species Concept" (Cracraft 1983, 1989; Nixon & Wheeler, 1990; Davis & Nixon, 1992), the possession of diagnostic characters is *evidence* of species status but does not in itself *confer* species status. Ultimately, the species hypothesized in this paper could be tested using, for example, genealogical analysis of molecular variation (discussed in Baum & Shaw, 1995; Baum & Donoghue, in press). In the meantime, however, the species proposed here should be seen as the best estimates of the genealogical units existing within *Adansonia*.

In the case of *Adansonia*, I believe that the genealogical species I have described are coextensive (i.e., have similar boundaries) with the species that would be recognized by applying other widely held species concepts, for example: the "Biological Species Concept" (Mayr, 1942), the "Phylogenetic Species Concept" (Cracraft, 1983; Nixon & Wheeler, 1990), the "Cohesion Species Concept" (Templeton, 1989), or the traditional phenetic ap-

proach. Thus, even if my perspective on the definition of "species" is rejected, the taxonomy I propose may be seen as having some general validity.

METHODS

This treatment is based upon herbarium studies and fieldwork conducted during a total of a year in Madagascar (four visits) and two and a half months in Australia (one visit).

The measurements given in the species descriptions below are based primarily on fresh material. Depending on the way they were dried and whether collections comprise freshly picked material or fallen and already desiccated flowers, flowers may have shrunk by as much as 50%. Well-pressed specimens have measurements that approximately match those made on fresh material.

Adansonia L., Syst. Nat. ed. 10, 2: 1144. 1759.
Baobab Adans. Fam. ii 399. 1763. *Ophelus* Lour., Fl. Coch. 412. 1790. *Baobabus* Kuntze, Rev. Gen. 1: 66. 1891. TYPE: *Adansonia digitata* L.

Deciduous trees 5–30 m tall, with unarmed trunks and usually compact crowns. Trunks massive, cylindrical, tapering from bottom to top or bottle-shaped. Primary branches massive, unarmed (rarely with conical spines in *A. rubrostipa*), horizontal or ascending. Bark smooth or foliaceous, reddish brown to gray, often with a yellow or green photosynthetic layer close to the surface. Inner bark layers with tough, longitudinal fibers. Wood fibrous and soft, arranged in concentric sheets with an odorless, mucilaginous gum often exuding from damaged wood. Leaves palmately compound, membranaceous to coriaceous, arranged spirally with very short internodes at the tips of reproductive branches, but with longer internodes on juvenile shoots; deciduous during dry season. Stipules up to 2 mm long, caducous, rarely 1.0–1.5 cm and persistent. Petiole bipulvinate. Leaflets 5–11, elliptic, lanceolate or oblanceolate, lateral leaflets smaller than medial, sessile or petiolulate; apex acute (rarely obtuse) to apiculate; margins entire or toothed; lamina glabrous to tomentose with simple or clumped hairs. Flowers perfect and hypogynous, in single-flowered, axillary inflorescences (very rarely 2 flowers to an inflorescence), up to 5 per branch apex. Peduncle and pedicel \pm distinct, the latter with usually 3 caducous bracteoles. Buds subglobose, ovoid or cylindrical. Calyx synsepalous, enclosing flower until at least 6 hours before anthesis; calyx lobes 5 (but lobes may fail

to separate completely), reflexed or contorted at base of flower; scabrous and green or brown outside; sericeous and cream, pink, or red within; nectariferous tissue in a narrow strip at the base, sometimes within an annular cavity formed by the base of the calyx tube. *Corolla* actinomorphic or slightly zygomorphic; petals 5, free, convolute, inserted on the lowermost portion of the staminal tube, creamy white, yellow, or red. *Androecium* comprising a distinct tube surmounted by numerous free filaments; tube cylindrical or slightly tapering, usually glabrous, white or yellowish; anthers monothecate with the thecae long and sinuous around the margin of the connective, longitudinally dehiscent. *Ovary* superior, conical to oblong, densely brown or yellowish tomentose, with cylindrical or flattened, long, simple, upward-pointing hairs; ovules numerous, anatropous, borne on long, dichotomizing funicles arising from the edges of 7–9 deeply intruded placentae. Style simple, filiform, densely tomentose near base, white or dark red; stigma

usually with 5–10 short lobes, yellowish or dark red, browning with cessation of receptivity. *Fruit* a dry, large, many-seeded berry; globose, ovoid, or oblong-cylindrical; pericarp reddish or blackish brown, tomentose, hard and woody (5–15 mm thick) with longitudinal fibers on the inner surface; usually indehiscent. Seeds enveloped in a white or cream, dry, powdery or spongy pulp. Seeds 10–15(–20) mm long, reniform; cotyledons 2 (rarely polycotylous), \pm equal, folded and achlorophyllous. Seedlings cryptocotylar or phanerocotylar. Juvenile leaves initially simple, later lobed, trifoliate or irregularly digitate.

Nomenclature. Although the type species, *A. digitata*, appears in *Species Plantarum* (Linnaeus, 1753), the generic name was omitted from *Genera Plantarum*. Hence, the correct date of publication is 1759, when Linnaeus validly published the generic name in *Systema Naturae* (Jarvis et al., 1993).

KEY TO THE SECTIONS AND SPECIES OF *ADANSONIA*

- 1a. Flower buds ovoid to oblong (approximately twice as long as broad), on short, \pm erect pedicels; staminal tubes ca. 1 cm long, approximately one-fifth as long as free filaments; seeds 12–20 mm long and not laterally flattened; trees with flat-topped crowns; Madagascar. I. sect. *Brevitubae*
- 2a. Leaflets (6–)9–11, bluish green, densely tomentose, narrowly elliptic to lanceolate; fruit subglobose to ovoid, usually less than 2 times as long as wide; outer surface of calyx reddish brown; restricted distribution in southwestern Madagascar. 1. *A. grandidieri*
- 2b. Leaflets 6–9, yellowish green, subglabrous to scabrous, broadly elliptic to broadly oblanceolate; fruit elongated ovoid to oblong-cylindrical, usually more than 2 times as long as wide; outer surface of calyx green; restricted distribution in northern Madagascar. 2. *A. suarezensis*
- 1b. Flower buds very elongated (at least 5 times as long as broad) or globose (equally long and broad), pedicels erect, horizontal or pendent; staminal tubes 3–20 cm, at least one-third the length of the free filaments; seeds 10–14 mm long, laterally flattened; trees with usually rounded crowns; tropics.
- 3a. Flowers and fruit borne on long, pendulous flower stalks; buds globose; petals white, as broad as long; semiarid continental Africa; cultivated and naturalized in other tropical regions. II. sect. *Adansonia*; 3. *Adansonia digitata*
- 3b. Flowers and fruit borne on short, erect or horizontal flower stalks; buds elongated-cylindrical; petals white, red or yellow, at least 5 times as long as broad; Madagascar and Australia. III. sect. *Longitubae*
- 4a. Flower buds usually 10–15 cm; petals white or cream, erect for lower $\frac{3}{4}$ of length, reflexed above; fruit usually cracked when mature; rocky outcrops, creek beds and floodplains in northwestern Australia. 4. *Adansonia gibbosa*
- 4b. Flower buds usually 15–28 cm; petals yellow or red, curled outward evenly throughout length; fruit indehiscent; Madagascar only.
- 5a. Leaflets with serrate margins, sessile, medial leaflets less than 2 cm wide; petals shorter than androecium; central 10–20 filaments fused into a bundle above the top of the staminal tube; style caducous with other flower parts; fruit \pm globose; deciduous forest on sand or limestone, dry “spiny” forest or sublittoral scrub in western and southern Madagascar. 5. *Adansonia rubrostipa*
- 5b. Leaflets with entire margins, petiolulate or subsessile, medial leaflets greater than 2 cm wide; petals longer than androecium; filaments free from top of staminal tube; style persistent or caducous; fruit spherical, ovoid or oblong.
- 6a. Staminal tube at least 8 times longer than the free filaments; leaflets obovate to obovate-elliptic, 15–24 pairs of secondary veins on reproductive shoots; stipules persistent; fruit broadly ovoid to oblong, peduncle not swollen; northern Madagascar. 8. *Adansonia perrieri*
- 6b. Staminal tube equaling or shorter than the free filaments; leaflets broadly lanceolate or elliptic with usually 8–20 pairs of secondary veins on reproductive shoots; stipules caducous; fruit oblong or globose, but if oblong then the peduncle is usually markedly swollen.

- 7a. Leaflets long-petiolulate (up to 3 cm) to sessile, 10–20 pairs of secondary veins; style persists after floral abscission; fruit usually ovoid with a markedly thickened peduncle, or broadly oblong to subglobose with normal pedicel/peduncle; longer than wide; flowering November to February; widespread and variable species from extreme southern to northwestern Madagascar. 7. *Adansonia za*
- 7b. Leaflets subsessile with winged petiolules, 8–16 pairs of secondary veins; style caducous; fruit globose to subglobose, usually wider than long; flowering February to April; northwestern to northern Madagascar. 6. *Adansonia madagascariensis*

I. *Adansonia* section *Brevitubae* Hochreutiner, Ann. Conserv. Jard. Bot. Genève 1907/1908: 136. 1908. TYPE: *Adansonia grandidieri* Baill. (lectotype, here designated).

Large trees with massive cylindrical or tapering trunks and flat-topped crowns. Flowering during dry season (May–August). Flower buds brown or green, ovoid, approximately 2 to 3 times as long as broad; borne on short, erect peduncles/pedicels. Petals white, oblanceolate, approximately 5 times as long as broad. Androecium white; staminal tube ca. 1 cm × 1.5 cm diam., free filaments 600–1100, 3–7 cm long. Fruit oblong, ovoid, or subglobose with persistent calyx bases and a dense, reddish brown indumentum; pericarp thin and fragile. Seeds large (12–20 mm long), reniform, not flattened (i.e., lateral width approximately equal to dorso-ventral width). Germination cryptocotylar.

Nomenclature. In his description of this section, Hochreutiner (1908) listed two species: *Adansonia grandidieri* and *A. za*. In the latter case, Hochreutiner was referring to *A. za* sensu Drake (= *A. suarezensis* Perr.) rather than *A. za* Baill. Thus, to avoid possible confusion, *A. grandidieri* is selected as lectotype.

1. *Adansonia grandidieri* Baillon, Hist. Nat. Pl. Plates 79Bbis/2, 79E/1. 1893. TYPE: Madagascar. Morondava, *Grevé* 275 (lectotype, here designated, P).

Large deciduous trees up to 25 m tall and 3 m diam., with usually single, cylindrical trunks (tapering from bottom to top when young) and flat-topped crowns; primary branches regularly distributed, mainly horizontal. Bark reddish gray and smooth. Leaves (6–)9–11-foliolate; petiole 5–13 cm, 1–3 mm diam., pubescent; stipules caducous; leaflets shortly petiolulate (1–5 mm), medial leaflets 6–12 × 1.3–3 cm, lanceolate to narrowly elliptic, bluish green when fresh; densely tomentose with short, clumped, yellowish hairs; margins entire. Flowers emerging when leafless; buds erect, ovoid; flower stalk ca. 1 cm diam., dark brown tomentose; peduncle 3–5 mm long; pedicel 6–8 mm long. Calyx lobes (3–)5, reflexed and twisted at the base

of the flower, 7.5–8.5 cm long, 1.5–2 cm wide; reddish brown tomentose outside, cream villous within. Calyx tube forming an open cup ca. 1 cm deep within. Petals white (yellowing with age), twisted, narrowly lanceolate or oblanceolate, approximately 5 times as long as broad, ca. 9–10 cm × 17–20 mm. Androecium white, comprising a staminal tube, ca. 8–10 × 14–16 mm, surmounted by 600–700 free, spreading filaments, 3.5–6.5 cm long. Ovary broadly rounded-conical, 1.1 cm high, with dense, upward-pointing, lemon-yellow hairs; containing ca. 300 ovules. Style white, straight or rarely slightly kinked; usually 2–3 cm longer than the central filaments, densely villous below, glabrous above, fitting loosely into the staminal tube and persisting after floral abscission. Stigma white or pinkish, with very short irregular lobes. Fruit subglobose to broadly ovoid with persistent calyx bases and a dense reddish brown indumentum; pericarp 2.5–4 mm thick, fragile, with few longitudinal fibers. Seeds reniform, not markedly laterally flattened, 12–14 × 10–12 × 9–10 mm. Germination cryptocotylar.

Specimens examined. MADAGASCAR. **Toliara Province:** Marofandelina, ca. 40 km NW of Morondava on road to Belo-sur-Tsiribihina, 44°33'E, 20°08'S, alt. 20 m, 20 July 1989 (fl), *Baum* 321 (MO, TAN); Morondava, center of the town by the hotel Menabe, 44°16'40"E, 20°17'30"S, alt. 3 m, 25 Dec. 1991 (l), *Baum* 345 (MO, P, TAN); Morombe, May 1963 (fl), *Chabonis s.n.* (TAN); Taolampia, Morondava (l, fr), *Grevé* 20 (BM, G, K, P); Morondava, 1891 (fl, fr), *Grevé* 275 (P); Morondava (fl), *Grevé s.n.* (a) (P); Taolampia (Morondava), Apr. 1894 (fl), *Grevé s.n.* (b) (P); Marosalaza forest, 50 km N of Morondava, alt. 0 m, 13 Dec. 1973 (fl), *Hladik* 27 (P); near Morondava (l, fl, fr), *Keraudren-Aymonin & Keraudren* 25860 (P); Morondava (fr), *Keraudren-Aymonin & Keraudren* 25918 (P); Marofandelina, Morondava, Nov. 1914 (l), *Perrier de la Bâthie* 4805 (P); Morondava, May 1910 (l, fl), *Perrier de la Bâthie* 8172 (P); N of Tulear, Lac Ihotry near village of Andreketa, 21°55'S, 43°37'E, alt. 50 m, 1 Jan. 1989 (l), *P. B. Phillipson* 3063 (MO, P); District of Morondava, Canton of Analaiava, Marofototra, 44°24'E, 20°17'S, 8 Jan. 1954 (l), *SF (Collector #76)* 45 (P, TEF). **Without Further Locality:** Sep. 1956 (l), *J. Bossier* 9907 (TAN), 1895 (fr), *Grandidier s.n.* (P), 1897 (fr), *Grandidier s.n.* (P), Without date (fr), *Grevé* F6771 (P).

Distribution (Fig. 1). Southwestern Madagascar between Lac Ihotry (near Morombe) and Ber-

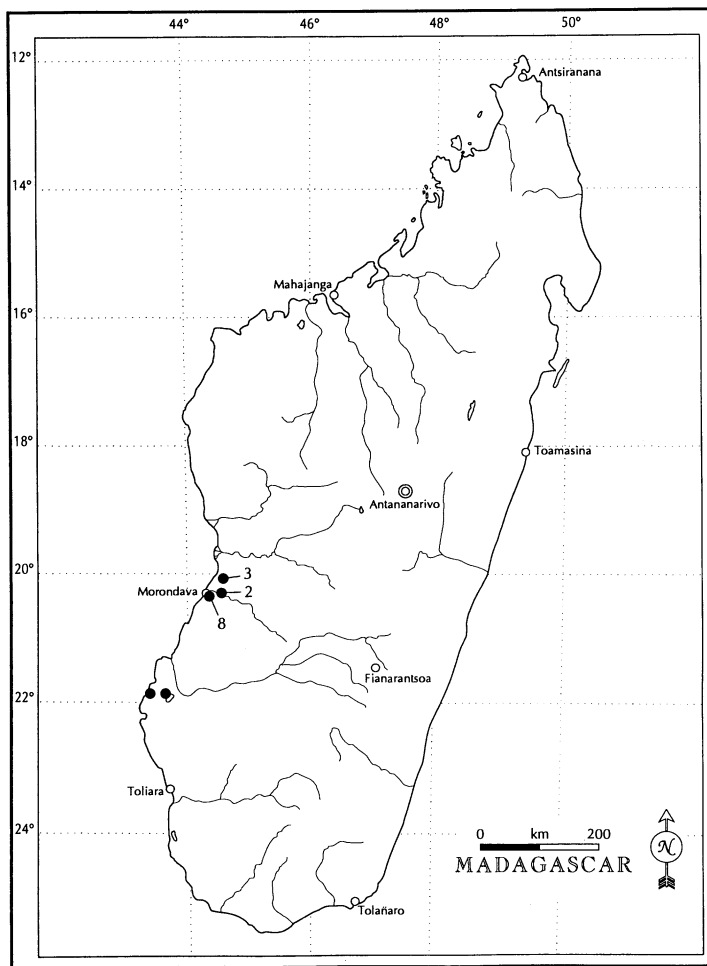


Figure 1. The distribution of *Adansonia grandidieri* in Madagascar. Collection sites are marked with a circle. When more than one collection is made from the same locality the number of separate collections is indicated.

eboka (ca. 50 km north of Morondava). Dry deciduous forest, especially close to seasonal rivers, lakes, and waterholes. Now mainly found in degraded agricultural lands.

Phenology. In leaf from October to May. Flowering May to August. Fruit ripe in November and December.

Cytology. Miège (1974) reported a chromosome count of $2n = 60-64$. Mangenot & Mangenot (1962) and Baum & Oginuma (1994) found $2n = 88$.

Taxonomy and nomenclature. *Adansonia grandidieri* is diagnosed by a combination of characters (see the key) including at least two that are unique in the genus and probably autapomorphic: bluish green and densely stellate-pubescent leaves,

and a dark brown floral bud. It is geographically and phenetically isolated from its nearest relative (*A. suarezensis*), manifests no significant internal variation, and is, thus, recognized as a species.

According to Article 44.1 of the *Code* (Greuter et al., 1988), a name of a species is validly published before 1908 by "an illustration with analysis showing essential characters." As noted by Cheek (1989), many taxa of Malagasy plants were published as analytical drawings in the *Histoire Naturelle des Plantes* that accompanied the *Histoire Physique, Naturelle et Politique de Madagascar* edited by Alfred (and later Guillaume) Grandidier. Baillon was responsible for most of the botanical names associated with the plates, including those illustrating species of *Adansonia* (Stafleu & Cowan, 1976: 979–981). Thus, the correct author of

A. grandidieri is Baillon, and the date of publication is 1893, when plates 79Bbis/2 and 79E/1 were issued.

The question of typification is problematic. Cheek (1989) argued that there is less ambiguity if the plate itself is treated as the holotype rather than attaching the name to one of the specimens from which the plate was drawn. However, a specimen has the advantage that it has not been “filtered” through an artist’s eyes and, thus, future systematists have the ability to score the type for characters absent from the illustration (e.g., trichomes, stomata, DNA). Additionally, in typifying an illustration there is some ambiguity as to whether specific elements of plates, whole plates or sets of plates issued simultaneously should be typified. Thus, the decision must be made on a case by case basis. If a good quality specimen used by the author is available it should be typified. Failing that, it is preferable to typify the plate rather than select a poor quality specimen or a neotype.

The main element of plate 79E/1 is a longitudinal section of a flower showing several important features of *Adansonia grandidieri*. This illustration was, I believe, based on *Grevé* 275, as this specimen includes a sectioned flower that closely resembles the drawing. However, although *Grevé* 275 may be designated the type, it cannot be considered the holotype because it is not the only specimen that contributed to the species description. Specifically, the fruit illustrated on plate 79Bbis/1 resembles that of *Grevé* 20. Thus, I designate *Grevé* 275 as lectotype of *A. grandidieri*.

Ethnobotany. *Adansonia grandidieri* is known locally as “renala” or “reniala” (meaning “mother of the forest”) and is the most widely exploited of all the Malagasy baobabs (Baillon, 1890a; Perrier de la Bâthie, 1952b). The fruit pulp and seeds are eaten fresh, and cooking oil is extracted from the seeds. The fruit are collected from the ground or with the aid of wooden pegs that are hammered into the trunks and used to climb the trees. In some villages near Morondava, the fruits are fed to goats, who digest the pulp but pass the seeds intact. These are then collected and used for oil-extraction (T. Willing, pers. comm.). The oil extracted from *A. grandidieri* seeds is of good quality, and economic exploitation has been considered (Rey, 1912). Perrier de la Bâthie (1952b) reported that from 1874 until the early 20th century, the seeds of *A. grandidieri* were exported to Marseilles for the extraction of cooking oil. However, according to Perrier de la Bâthie

(1952b) the supply of fruit was insufficient to sustain the market.

Keraudren (1963) reported that around the turn of the century the fruit of *Adansonia grandidieri* was exported to England and used to make small, dry tea cakes. However, it is unclear whether Keraudren was referring to the use of the pulp or seeds, and she does not give her historical sources.

In a full-grown tree, the bark is 10–15 cm thick, and composed of tough longitudinal fibers that are used to make ropes, particularly for use on outrigger sailing canoes (Perrier de la Bâthie, 1952b). A majority of *Adansonia grandidieri* show signs of having been used as a source of fiber for rope-making. The bark is cut off a living tree from ground level to about 2 m. Although the scar persists, bark regenerates over the damaged tissue.

The wood is spongy and moisture-rich, comprising concentric sheets of fiber that probably correspond to annual growth rings. The Malagasy collect these fibrous sheets from either dead or living trees, dry them in the sun, and sell them in local markets for use as thatch. In addition, the undried wood is sometimes fed to cattle in periods of drought.

On account of its spectacular appearance it is not surprising that *Adansonia grandidieri* is the focus of superstitions and folklore. Individual trees are often considered the dwelling places of spirits. Offerings are made at the foot of these trees: grains or other food items for a good harvest, money for fortune, and rum for general prayers and fertility. Giant land snail shells arranged at the foot of a tree (repositories for rum offerings) indicate its sacred status.

Conservation. Most mature *Adansonia grandidieri* now grow in open, agricultural land or degraded scrub rather than in forests. There is a noticeable lack of young trees in these disturbed ecosystems, suggesting that recruitment is low. Of course, it is difficult to be sure that the skewed population structure is caused by disturbance without knowledge of the demography of undisturbed populations. Nonetheless, there are several factors acting in disturbed habitats that might adversely affect recruitment (e.g., fire, seed predation, competition from weeds, and an altered physical environment). Without the ability to perpetuate themselves, the conservational outlook for *A. grandidieri* is far from hopeful. However, Perrier de la Bâthie may have been overly pessimistic when he noted: “Actuellement l’espèce n’est plus représentée que par quelques pieds dont il ne restera rien dans quelques années” (Perrier de la Bâthie, 1952b:

287) [At present this species is only represented by a few individuals of which there will be none remaining within a few years].

- 2. *Adansonia suarezensis* H. Perrier, Notul. Syst. 14: 300–304. 1952. TYPES:** Madagascar. Diégo-Suarez (= Antsiranana), 1893, *Allaud s.n. (a)* (lectotype, here designated, P); *Coridou F6769* (syntype, P).

Large deciduous trees up to 25 m tall and 2 m diam. Trunks single, cylindrical or tapering from bottom to top. Crowns flat-topped; primary branches regularly distributed, mainly horizontal, sometimes with irregular protuberances on their upper surfaces. *Bark* grayish brown and smooth with a yellowish green layer beneath the surface. *Leaves* 6–9-foliolate; petioles 12–18 cm × 2–4 mm, ridged, glabrous; stipules caducous; petiolules 3–5 mm; medial leaflets 11–17 cm × 3.5–5.5 cm, broadly elliptic-oblongate, lateral leaflets 6–10 cm × 3.0–3.5 cm; yellowish green, subglabrous to scabrous; margins entire. *Flowers* produced when leafless; buds erect, ovoid; flower stalk ca. 1 cm diam., peduncle 3–5 mm long, pedicel 8–10 mm long. *Calyx* lobes 5, succulent, reflexed and twisted at the base of the flower; green scabrous outside, cream villous within; calyx tube forming a nectar-containing cup ca. 1.5 cm deep. *Petals* white, yellowing with age, oblongate, flat or somewhat twisted, approximately 5 times as long as wide, ca. 8–10 × 1.5–2 cm. *Androecium* white comprising a staminal tube ca. 1 cm long × 1.5 cm wide, surmounted by 800–1100 5–7-cm-long, free, spreading filaments. *Ovary* cylindrical to somewhat conical with dense, upward-pointing, golden hairs. *Style* white, straight, densely villous below, glabrous above, fitting loosely into staminal tube and usually persisting after floral abscission. *Stigma* white, club-shaped, entire. *Fruit* irregularly oblong-cylindrical to elongated ovoid, 20–40 cm long and 8–14 cm wide, with persistent calyx bases and a dense brown indumentum; pericarp 3–4 mm thick, fragile, with few longitudinal fibers. *Seeds* reniform, not markedly laterally flattened, ca. 17–20 × 13–15 × 13–14 mm. Germination cryptocotylar, but sometimes forming an unusual resting stage in which the swollen radicle projects 4–5 cm above the soil while the cotyledons and epicotyl remain at ground level.

Specimens examined. MADAGASCAR. **Antsiranana Province:** Antsiranana District: Diégo-Suarez, 1893 (fl, seeds), *Allaud s.n. (a)* (P); S side of Antsiranana to Ramena road where it passes close to the Montagnes des Français, 49°20'E, 12°19'S, alt. 10 m, 15 June 1989

(fl), *Baum 319A* (MO, P, TAN); Beantely forest on W side of the Antsiranana to Cap d'Ambre road, ca. 10 km N of Antsahampano, 49°10'E, 12°16'S, alt. 100–150 m, 21 June 1989 (fl), *Baum 320A* (MO, P, TAN); Diégo-Suarez, 1896 (l, fr), *Coridou F6769* (P); Diégo-Suarez, 1933 (fl), *Goudot s.n. (b)* (G); Ihotrofratry (fr), *Keraudren-Aymonin & Keraudren 25612* (P); near Diégo-Suarez on Basalt, Sep. 1926 (fl, fr), *Perrier de la Bâthie 17686* (G, K, P); Montagnes des Français near Betahitra on Karst, 25 May 1955 (fl), *SF 14225* (P, TEF); limestone mound on road from Diégo-Suarez to Orangea, 8 June 1970 (fl), *SF (Capuron) 29223* (TEF).

Distribution (Fig. 2). *Adansonia suarezensis* is restricted to the very northern tip of Madagascar around the Baie d'Antsiranana. Its precise distribution around the bay is poorly known, but most of the sites known are in deciduous forest, especially on limestone. Whereas small individuals can be found close to the sea in heavily disturbed sublittoral scrub (e.g., 2–5 km south of Cap Diégo or along the Ramena Road, close to the Montagnes des Français), populations of larger trees are found as emergents in less disturbed deciduous forest on steep slopes (e.g., in the southwestern Montagnes des Français, Windsor Castle, and Beantely).

Phenology. Flowering late May to early July. Fruit ripe in November. In leaf, December to April.

Cytology. Miège (1974) reported two conflicting chromosome counts for this species, $2n = 48$ or 72 . Baum & Oginuma (1994) found $2n = 88$.

Taxonomy and nomenclature. *Adansonia suarezensis* is diagnosed by a unique combination of characters (see the key), but none of these characters is clearly apomorphic. Nonetheless, *A. suarezensis* is most likely an exclusive group in view of its small population size and presumably long period of genetic isolation, as indicated by its geographic isolation and the fixation of several characters in its probable sister group, *A. grandidieri*. Thus, in the absence of any significant variation within *A. suarezensis*, I consider it a valid species.

In the *Histoire Naturelle des Plantes* (Baillon, 1893: plates 79C, 79I), *Adansonia suarezensis* is illustrated but is incorrectly labeled "*A. za.*" Drake (1902) and Hochreutiner (1908) continued to misapply the name "*A. za.*" until corrected by Jumelle & Perrier de la Bâthie (1910). However, Jumelle and Perrier de la Bâthie assumed that the taxon illustrated by Baillon (1893) was *A. grandidieri*, whose flowers closely resemble *A. suarezensis*.

Perrier de la Bâthie (1952a) recognized that the baobabs occurring near Diégo-Suarez (recently ren-



Figure 2. The distribution of *Adansonia suarezensis* in northern Madagascar. Collection sites are marked with a circle. When more than one collection is made from the same locality the number of separate collections is indicated. Some additional localities known by the author are marked with a triangle.

amed Antsiranana) were distinct from the south-western *Adansonia grandidieri* and described them under the name *A. suarezensis*. However, the descriptions in Perrier de la Bâthie (1952a, 1955) are mistaken in one regard. Probably due to confusion with the sympatric *A. madagascariensis*, or perhaps through observations of dried flowers, the inner calyx and petals are incorrectly described as red.

The type of *Adansonia suarezensis* must be selected from the two specimens listed as "type de l'espèce" by Perrier de la Bâthie (1952a). Perrier de la Bâthie (1955) was therefore incorrect in

selecting *Perrier de la Bâthie* 17686 as lectotype, because this specimen was labeled "co-type" rather than "type de l'espèce" in the original species description. Of the two syntypes, I have selected *Allaud s.n. (a)* as lectotype because it includes flowers, whereas *Coridou F6769* includes only leaves and fruit.

Ethnobotany. The common name of *Adansonia suarezensis* is "bozy" (pronounced "boojy"), the name used for all the northern Malagasy baobabs. Fruit and seeds are eaten. An infusion of bark is said to cure diabetes. Perrier de la Bâthie

(1953) suggested that *A. suarezensis* seeds, like *A. grandidieri*, might be a valuable source of oil.

Conservation. Although *Adansonia suarezensis* is not quite as rare as suggested by Perrier de la Bâthie (1953), it has a very restricted distribution and is nowhere abundant. The deciduous forests close to Antsiranana are being rapidly devastated, primarily for charcoal and timber. Although the baobabs are usually left standing so they can be exploited for fruit, there is no evidence of any regeneration in these disturbed ecosystems. Already there are very few remnant forest patches left intact and, thus, at the current rate of destruction *A. suarezensis* is likely to be ecologically extinct (i.e., unable to regenerate *in situ*) within the next decade or two. In view of this poor outlook, *A. suarezensis* is certainly an endangered species.

II. *Adansonia* section *Adansonia*

Adansonia section *Pendentes* Hochreutiner, Ann. Conserv. Jard. Bot. Genève 1907/1908: 136. 1908.

Trees with irregular, often very broad trunks and irregular crowns. Flowering during the wet or dry season. Flower buds globose, approximately as long as broad; borne on long pendulous peduncle/pedicels. Petals white, broadly obcordate, equally long and broad. Androecium white; staminal tube ca. 3–6 cm long, free filaments 720–1600, ca. 3–5 cm long. Fruit varying in shape, persistence of the calyx, and indumentum; pericarp thick and woody. Seeds usually less than 12 mm long, reniform, and laterally flattened. Germination phanerocotylar.

- 3. *Adansonia digitata* L.**, Syst. Nat. ed. 10, 2: 1144. 1759. *Adansonia bahobab* L., Sp. Pl. 2: 960. 1763. *Adansonia baobab* Gaertn., Fruct. 2: 253, t. 135. 1791. *Boababus digitata* (L.) Kuntze, Rev. Gen. 1: 66. 1891. TYPE: 862.1 LINN (lectotype, designated by Robyns, 1980).

Ophelus sitularius Lour., Fl. Coch. 412. 1790. *Adansonia situla* (Lour.) Spreng., Syst. 3: 124. 1826. *Adansonia scutula* Steud., Nom. Bot., ed. 2: 24. 1840. *Adansonia integrifolia* Raf., Sylva Tell., 149. 1838. TYPE: Not seen, probably destroyed.

Adansonia sphaerocarpa A. Chev., Végét. Rég. Tombouctou. In Actes Congrès Int. Bot. 1900: 271. 1901. TYPE: Mali. Tombouctou, Fouta-Djalou, Chevalier 12424 (holotype, P).

Adansonia digitata var. *congolensis* A. Chev., Bull. Soc. Bot. Fr. 53: 493. 1906. TYPE: San-Thomé Island. Near the town of San-Thomé, Chevalier s.n. (holotype, P not located).

Adansonia sulcata A. Chev., Bull. Soc. Bot. Fr. 53: 494.

1906. TYPE: Congo. Brazzaville, Chevalier 4230 (holotype, P).

Adansonia somaliensis Chiov. Fl. Somalia, 8: 30. 1932. Provisional name and therefore invalidly published.

Usually massive deciduous trees reaching 25 m in height and up to 10 m diam., with single or multiple, cylindrical or fluted, often buttressed trunks and spreading, rounded crowns. Branches irregularly distributed, massive. *Bark* gray, smooth to irregularly tuberculate. *Leaves* 5–7(–9)-foliolate; petioles pubescent or glabrous; stipules caducous; leaflets sessile to subsessile, varying greatly in size, medial leaflet 5–15 × 3–7 cm, usually elliptic-obovate, with acuminate apices and decurrent bases; glabrous or with simple or clumped hairs; margins entire. *Flowers* produced during dry or wet season; buds globose with an acute-conical apex, solitary, rarely paired; flower stalk pendulous, 15–90 cm long. *Calyx* lobes (3–)5, triangular, green and tomentose to scabrous outside, cream and villous within, reflexed, 5–9 × 3–5 cm, fused into a broad (5 cm diam.) disc below. *Petals* white, crumpled in bud, broadly obovate, approximately equal in length to breadth, 4–8 × 4–8 cm, narrowing to a thickened base. *Androecium* white, comprising a 3–6-cm cylindrical or tapering staminal tube, surmounted by 720–1600 (Davis & Ghosh, 1976) free filaments, ± equal in length to the staminal tube. *Ovary* conical-ovoid or globose with a thick indumentum of upward-pointing hairs; 7–9 deeply intruded placentae. *Style* white, bent over at right angles or rarely straight; densely villous below, glabrous above, fitting loosely into staminal tube and persisting after floral abscission. *Stigma* white with irregular lobes. *Fruit* variable; globose to ovoid to oblong-cylindrical, calyx lobes persistent or caducous; pericarp up to 8–10 mm thick, woody, with few embedded longitudinal fibers, covered in a velvety indumentum of yellow-brown or greenish hairs. Seeds reniform, laterally flattened, 10–13 × 8–10 × 4–5 mm. Germination phanerocotylar.

Representative specimens examined. WEST AFRICA. BURKINA FASO: Ouagadougou to Sapone, km 15–16, Bassayam, 12°12'N, 1°33'W, 18 Nov. 1980 (l, fr), *J. Lejoly* 80/217 (BR). CAPE VERDE ISLANDS: near Porto Prago, St. Iago, 7 May 1861 (l), *A. Anon* s.n. (E). CAMEROON: Marona, Aug. 1945 (fl, l), *A. Vaillant* 100 (P). DAHOMEY: Mid Dahomey, Bassas country, Bassas-Zoumé and vicinity, 9–10 May 1910 (l, fl), Chevalier 23641 (P). GHANA: Amansare, 2 July 1913 (fl, l), *N. P. Ashanti* 513 (K). GUINEA: banks of the Niger, 19 Jan. 1909 (fl, l), Chevalier 20453 (K, P). IVORY COAST: Ferkessedougou to Ouango Fitini, 13 Mar. 1969 (l), *P. Bamps* 2227 (BR). MALI: Ian (?), around village, 24 June 1899 (l, fl), *A. Chevalier* 1104 (P). NIGER: without further locality, 1857–1859 (fl, l), *Barter* 1528 (GH).

SENEGAL: Kaslack distr., Menirah Village, 5 May 1940 (l, fl), *J.-G. Adam 27199* (MO). TOGO: NE Agouenyivé (Agouévé), 17 Apr. 1978 (fl, l), *Zepernik 124* (K). SIERRA LEONE: Jigaya, 28 Sep. 1914 (l, fl), *N. W. Thomas 2799* (K). CENTRAL AFRICA. ZAIRE: M'vuazi, 28 Dec. 1949 (l, fl), *R. Devred 648* (BR, K). NORTH/EAST AFRICA. CHAD: Bogor Siéké near Logone, 26 Aug. 1969 (l), *Fotius 1689* (P). EGYPT: Cairo, *Schweinfurth 1605* (US). ETHIOPIA: road from Gondar to Axum, 265 km from Gondar near Takazza River, 5 June 1968 (fl, l), *G. J. H. Amshoff 4973* (BR, MO). KENYA: Meru National Park, just S of Rojewero main bridge, 18 Dec. 1972 (l, imm. fr), *J. Ament 444* (K); Mombassa near Lineoni Ferry, Feb. 1970 (fl), *Tweadie 3782* (K). SOMALIA: S Somalia, Bur Akaba, E foot of Mountain, 20 June 1983 (fl, l), *J. B. Gillett & C. F. Hemming 24910* (K). OMAN: Wadi Ghazir, 2 July 1982 (l, buds), *Macconochie 3523* (E, K). SUDAN: Djerme (l), *Chevalier 3055* (BR). TANZANIA: Iringa distr., Ruaha National Park, 2km NNW of Msembe at Mbagi track, 22 Oct. 1970 (fl), *A. Bjornstadt 657* (K). Zanzibar, Massazine, 25 Nov. 1960 (l, fl), *H. G. Faulkner 2735* (BR, K). YEMEN: Taiz Prov., Samsarah, 35 km S of Taiz on road to Turbah, 23 May 1984 (l, fl), *K. J. Gordon 3300* (E). SOUTHERN AFRICA. ANGOLA: near Andongo, Feb. 1857 (l, fl), *Welwitsch 5415* (BM). BOTSWANA: Umtali distr., Hot Springs, 22 Oct. 1948 (fl, l), *N. C. Chase 3728* (BM). MALAWI: Northern prov., Nkhata Bay distr., Nkata Bay, Chikale Beach, 5 Dec. 1976 (fl), *J. Pawek 12000* (K). MOZAMBIQUE: Mulanye distr., Nambwale village near Tunitulu hill, Lake Chilwa, 27 Nov. 1980 (fl, l), *J. D. Chapman 5188* (BR). NAMIBIA: Ombalantu, 1 Apr. 1973 (l, fl, fr), *R. J. Rodin 9201* (ECON, MO). SOUTH AFRICA: Zoutspansberg, Transvaal, 12 Nov. 1932 (fl, l), *Obermeyer et al 69* (K). ZAMBIA: 2 mi. N of Sinazezi, Gwerabe valley, *White 2627* (K). ZIMBABWE: Victoria Falls, 13 Nov. 1919 (fl, l), *L. Shantz 416* (K). INDIAN OCEAN. COMORES: Mayotte, Chissioi Caroni (islet off SW coast), 27 July 1979 (fl, l), *D. Lorence 2800* (MO). MADAGASCAR: Mahajanga, large tree in center of town near the sea, 20 Oct. 1991 (l, fl), *Baum 329* (MO, P, TAN); around villages near Lac Gnamby, near Mt. Tsitondroina, Dec. 1905 (l, fl), *Perrier de la Bâthie 1019bis* (P); around village of Anaboringy near Soalala (Ambongo), Mar. 1903 (l), *Perrier de la Bâthie 5734* (P). FRANCE. RÉUNION: St. Denis, Nov. 1973 (l, fl), *F. Friedman 2461* (P). MAURITIUS: Port Louis, 17 Dec. 1975 (l, fl), *D. Lorence & J. Guého 17639* (P). ASIA. INDIA: Banda, NWP, Aug. 1901 (l, fl), *A. Bell 712* (K); Madras, St. Thomas Mount, 1856 (fl, l), *Drew s.n.* (E). SRI LANKA: Mannar district, Tirukketisvaram, 11 Dec. 1970 (fl, fr), *F. R. Fosberg 53631* (US); Jaffna district, Delft Island, *A. Robyns 6966* (BR, E, K). TAIWAN: Pingtung City, *Chang 10168* (A). PACIFIC. HAWAII. Oahu: Honolulu, Queen's Hospital, 14 Sep. 1950 (fl, l), *O. Degener 20716* (NY). CARIBBEAN. ANTIGUA: Donovans Estate, 26 Sep. 1938 (fl, l), *H. E. Box 1550* (BM). GRENADA: St. Georges, July 1905 (l, fl), *W. E. Broadway s.n.* (F). CUBA: vicinity of Soledad, Santa Clara Prov., Aug. 1940 (fl, l), *R. A. Howard 4188* (A). HAITI: Plaine Centrale, Michel de l'Adalaye, 18 Feb. 1925 (l, fl), *E. L. Ekman 3258* (US). MARTINIQUE: without further locality (fl), *P. Duss 2032* (NY). PUERTO RICO: Mita, Mayaguez, 1 Oct. 1981 (l, fl), *A. H. & P. Liogier 32387* (NY). ST. CROIX: Ham's Bay, 16 July 1897 (l, fl), *J. J. Ricksecker 451* (E, F). ST. KITTS: Bassterre, the park, Aug. 1967 (fl, l), *R. K. Wadsworth*

579 (A). U.S.A. **Florida:** Fairchild Botanical Garden, 15 May 1970 (l, fl), *W. T. Gillis 9418* (A).

Distribution. The distribution of *Adansonia digitata* was previously described by Miège (1974), Lucas (1971), and Wickens (1983). It is indigenous in semiarid sub-Saharan Africa, extending from Angola, through Southern Africa to East Africa, as far north as southern Sudan and Ethiopia. The extensive populations in West Africa are isolated from those in East Africa by a major, and not fully explained, gap which includes the whole of the Central African Republic (Miège, 1974; Wickens, 1983). It should be noted that the current distribution of *A. digitata* in Africa is partly anthropogenic with naturalized populations, e.g., in Zaire (Miège, 1974; Wickens, 1983). It has been introduced by humans throughout the tropics (see specimen localities above).

Wickens (1983) reported that in Africa *Adansonia digitata* is mainly found in drier lowland areas (up to 1250 m in Sudan) having 200–800 mm annual rainfall (extremes of 90 mm and 1400 mm). Well-drained sandy soils seem to be preferred, although the plants are also found on lateritic soils around the margins of seasonal pools and along rivers.

The populations in Madagascar have been the subject of some controversy. Miège (1974) suggested that the Malagasy *Adansonia digitata* could be relics of the populations that colonized continental Africa. However, since most *A. digitata* in Madagascar are associated with villages, it is more likely that they were recently introduced by Arab traders (Jumelle & Perrier de la Bâthie, 1910; Perrier de la Bâthie, 1952b; Wickens, 1983). This latter explanation is supported by the documented transport of *A. digitata* to Zanzibar, India, and Sri Lanka (see Burton-Page, 1969; Vaid, 1978; Wickens, 1983).

Phenology. Varies greatly between localities. Leaves are shed during the dry season. Flowering can occur in the presence or absence of leaves.

Cytology. Chromosome counts from East and West Africa are $2n = 144$ (Baker & Baker, 1968, Miège & Burdet, 1968) and $2n = 160$ (Baum & Oginuma, 1994), with $2n = 96$ and 128 reported for Southern Africa (Riley, 1960; Schröder in Wickens, 1983).

Taxonomy and nomenclature. *Adansonia digitata* has many diagnostic characters, including several that are unique in the genus and likely to be apomorphic, e.g., a pendulous flower, globose buds, and broad petals. I thus have no doubt that

A. digitata is an exclusive group. However, the question of whether *A. digitata* is a basal, exclusive group is harder to answer. Chevalier (1906) argued for the subdivision of *A. digitata* into at least three species diagnosed by differences in fruit shape. However, I see no evidence that fruit shape diagnoses discrete groups and hence reject Chevalier's taxonomy. Without further studies of variation within *A. digitata* I cannot rule out the existence of exclusive subgroups, but in the absence of evidence for such subgroups, (e.g., fixed differences between West Africa, East Africa, and Southern Africa), I advocate that *A. digitata* be treated at the species rank.

Ethnobotany. A substantial body of literature documents the multitudinous uses of the roots, hollow trunks, bark, wood, leaves, flowers, and fruit of *Adansonia digitata*. Reviews and access to the ethnobotanical, anthropological, and economic literature are provided by: Chevalier (1906), Dalziel (1948), Adam (1962), Watt & Breyer-Brandwijk (1962), Owen (1970, 1974), Guy (1971), Wickens (1979, 1983), Armstrong (1983), Burkill (1985), and von Maydell (1986).

Conservation. Despite ongoing ecosystem destruction in Africa, *Adansonia digitata* is conservationally secure because of its wide ecological tolerance. Nonetheless, as pointed out by Wickens (1983), some management may be useful in ensuring that the species survives in areas where it is threatened by tree-clearance or destruction by elephants.

III. *Adansonia* section *Longitubae* Hochreutiner, Ann. Conserv. Jard. Bot. Genève 1907/1908: 136. 1908. TYPE: *Adansonia madagascariensis* Baill. (lectotype, here designated).

Small to large trees with cylindrical, tapering or bottle-shaped trunks and rounded or irregular crowns. Flowering during the wet season. Flower buds green, elongated-cylindrical, at least 5 times as long as broad; borne on short erect flower stalks. Petals white, yellow, or red; narrowly oblanceolate to narrowly lanceolate, at least 5 times as long as wide. Androecium white or pale yellow; staminal tube 10–25 × 1–1.5 cm; filaments 100–350, 2–12 cm long; usually free, rarely a central bundle of 10–20 filaments fused for about half their length. Fruit globose to ovoid with persistent or caducous calyx bases and a sparse to dense, reddish brown or greenish indumentum; pericarp varying in thickness. Seeds at most 14 mm long, reniform, laterally flattened. Germination phanerocotylar.

Nomenclature. Hochreutiner (1908) described this section and listed three species, *A. madagascariensis*, *A. gregorii* (= *A. gibbosa*), and *A. stanburyana* (= *A. gibbosa*). Of these, the latter two are now considered synonyms, and I select the remaining one, *A. madagascariensis*, as lectotype of the section.

4. *Adansonia gibbosa* (A. Cunn.) Guymer ex D. Baum, comb. nov. Basionym: *Capparis gibbosa* A. Cunn. in Heward, J. Bot. British and Foreign 4: 261. 1842. TYPE: Australia. Western Australia: South Grailbourne Island, Careening Cove, *Cunningham 308* (holotype, BM).

Adansonia gregorii Mueller, Hooker's J. Bot. 9: 14. 1857. *Baobabus gregorii* (Mueller) Kuntze, Rev. Gen. Pl. 1: 67. 1891. TYPE: Australia. Northern Territory: Victoria River, *Mueller s.n.* (lectotype, here designated, MEL 229658).

Adansonia rupestris W. Saville-Kent, The Naturalist in Australia, 266–271. 1897. TYPE: Plate V, The Naturalist in Australia (holotype).

Adansonia stanburyana Hochreutiner, Ann. Conserv. Jard. Bot. Genève, 1907/1908: 136. 1908. TYPE: Australia. Western Australia: in the town of Broome outside the police station, *Hochreutiner 2849* (holotype, G).

Small, irregularly shaped, deciduous trees (rarely over 10 m) often with multiple trunks, sometimes having a marked constriction beneath the branches (particularly in the east of its range); crown irregular, primary branches ascending, horizontal or descending. *Bark* smooth, gray. *Leaves* 5–9-foliolate; stipules caducous; leaflets sessile, elliptic or lanceolate with acute apices and decurrent bases, medial leaflet 8–13(–16) × 2–3(–4) cm, glabrous to pubescent, often pubescent below subglabrous above (especially in east); margins entire. *Flowers* emerging just before or just after leaves; buds erect to horizontal, cylindrical or somewhat wider at the apex than at the base, 10–15 cm long; peduncle 0–2.5 cm; pedicel 2–4(–5.5) cm, longer than the peduncle. *Calyx* lobes (2–)5, 6–9 × 1–1.5 cm, reflexed and twisted at the base of the flower, separating at apex in the morning prior to anthesis; pale green, scabrous to subglabrous outside, cream and villous within; tube 6–10 mm, lacking a well-defined annular swelling. *Petals* white to cream, reflexed for upper 2–4 cm, erect for lower ¾ of length; oblanceolate, approximately 5 times as long as wide (10–15 × 2–3 cm). *Androecium* white to pale yellow, comprising a ± cylindrical staminal tube 3–5 cm × 7–9 mm, surmounted by 170–350 ± erect, free filaments 3–7 cm long. *Ovary* rounded-conical with a thick

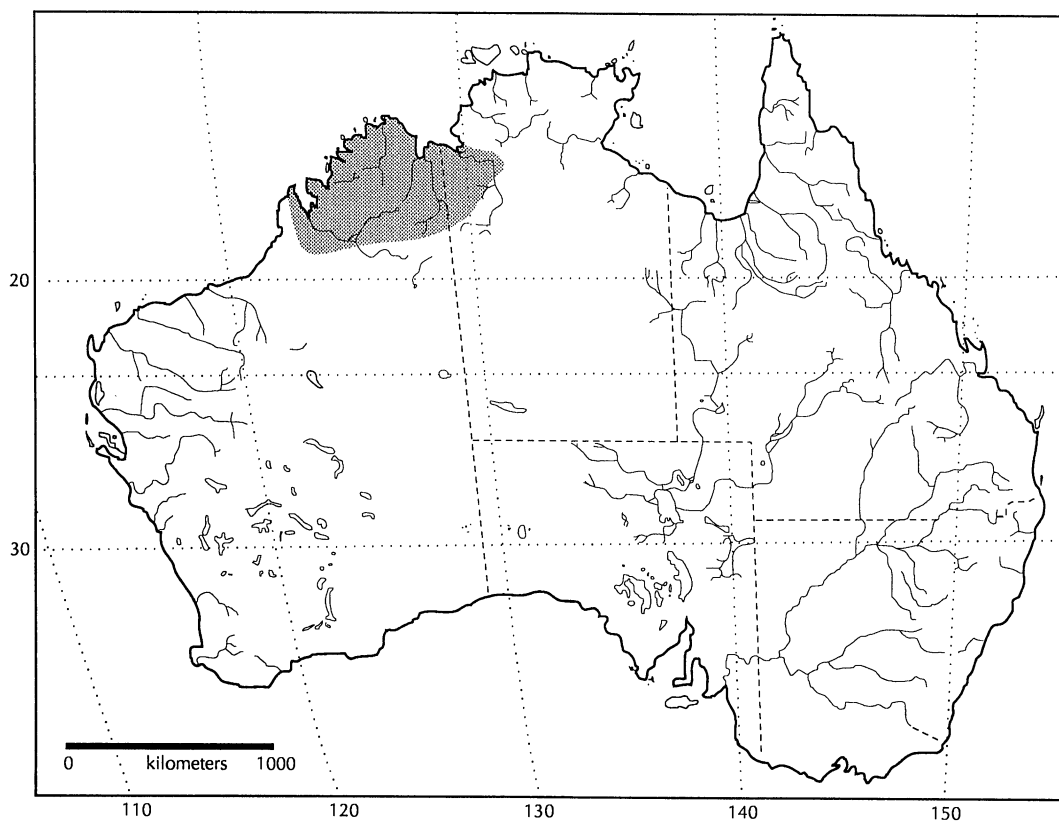


Figure 3. The range of *Adansonia gibbosa* in Australia.

indumentum of brownish upward-pointing hairs. Ovules 300–600. Style white, straight, 8–10 cm, not significantly longer than the longest filaments; densely tomentose below, glabrous above, fitting loosely into staminal tube and usually persisting after floral abscission. Stigma lobes spreading, white, browning at tips during the night. Fruit globose to ovoid, calyx caducous. Pericarp 3–4 mm thick, brittle, usually cracking while the fruit is still attached to the tree, with few longitudinal fibers and a sparse or dense, brownish or greenish indumentum. Seeds 10–13 × 7–9 × 5–6 mm, reniform, laterally flattened. Germination phanerocotylar.

Representative specimens examined. AUSTRALIA. **Western Australia. West Kimberley:** Oscar Range, close to the Windjana-Tunnel Creek road, 125°17'E, 17°54'S, alt. 200–250 m, 29 Nov. 1989 (l, fl), *Baum* 322 & 323 (MO, PERTH); Walcott Inlet, Dec. 1931 (l, fl), *J. R. B. Love* s.n. (PERTH). **North Kimberley:** King Edward River Banks, 24 Nov. 1952 (l, fl), *Broadbent* 428 (BM); Port Warrender, Admiralty Gulf, NW Kimberley, 125°50'E, 14°34'S, 22 June 1976 (l), *K. F. Kenneally* 5255 (PERTH). **East Kimberley:** alluvial plain between Pentecost and King Rivers, 6.3 km E of Pentecost River on Gibb River road, 125°55'E, 15°51'S,

alt. ca. 20 m, 5 Dec. 1989 (l, fl), *Baum* 324 (MO, PERTH); 48 mi. NE of Hall's Creek Township, 16 July 1949 (l), *Perry* 2501 (CANB, K, NSW, US). **Northern Territory:** banks of Sullivan Creek where it crosses the Victoria highway, 32 km E of Victoria River Crossing, 131°24'E, 15°28'S, alt. ca. 220 m, 8 Dec. 1989 (l, fl), *Baum* 325 (MO, PERTH); 2 mi. W of Victoria River, Timber-chalk road, 15 Dec. 1971 (l, fl, fr), *J. Must* 904 (BRI, CANB, K, PERTH).

Specimens from naturalized or cultivated plants. AUSTRALIA. **Western Australia:** Broome, in front of police station, 4 Feb. 1905 (l, fl), *Hochreutiner* 2849 (G); Broome, outside library, 21 May 1986 (l, fl), *K. F. Kenneally* 9733 (PERTH). **Northern Territory:** Darwin (Palmerston), (l, fl), *Mueller* s.n. (G 27).

Distribution (Fig. 3). *Adansonia gibbosa* is restricted to the Kimberley region of north Western Australia and the Victoria River area of northwest Northern Territory. The westernmost limit is roughly at the boundary between the shires of Broome and Derby, 100 km east of Broome (the trees in Broome 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.). These trees may have been dispersed by humans, as they are often located close to aboriginal middens (T. Willing, pers. comm.; Armstrong, 1983). The southernmost 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, approximately 32 km east of Victoria River Inn. The northern limit is unclear, but it is likely that throughout most of its range, *A. gibbosa* reaches as far as the coast.

Adansonia gibbosa trees are concentrated around the fringes of rocky ranges, along seasonal creeks, and on the floodplains of the larger rivers. They are absent from the gallery forest along permanent rivers but persist in open areas subject to frequent burning.

Phenology. Leaves November to March. Flowers mid November to mid January, progressing east to west. Fruit ripe May to December.

Cytology. Baker & Baker (1968) reported three separate counts of $2n = 72$, Miège & Burdet (1968) reported $2n = 96$, whereas Baum & Ogina (1994) found $2n = 88$ from both east and west Kimberley.

Taxonomy and nomenclature. *Adansonia gibbosa* probably arrived in Australia via long-distance dispersal (see above) and, hence, it most likely experienced a severe bottleneck at some point after it separated from the rest of the genus. This suggests that exclusivity has been attained by *A. gibbosa*, as supported by the possession of several diagnostic characters (see key), of which at least one is apomorphic (fruit dehiscence). Furthermore, the current distribution of *A. gibbosa* in north-western Australia gives no grounds for suspecting long-term genetic isolation of any parts of the species. Thus, I believe that *A. gibbosa* is both exclusive and basal, and hence I recognize it as a species.

The "boab" tree was first discovered by Allan Cunningham, who thought it was a *Capparis*. He left it unnamed in the report of his exploration (Cunningham, 1827), but referred to it as *C. gibbosa* on the specimen and in his diary. Extracts from his diary were published posthumously by Heward (1842), including the description of *C. gibbosa*, constituting a valid publication for that name. The connection between *C. gibbosa* and the Australian baobab (generally referred to as *Adansonia gregorii* Muell.) has been overlooked until recently. However, G. Guymer recognized Cunningham's nomenclatural priority ten years ago and annotated several specimens at Kew and the British Museum "*A. gibbosa* (Cunn.) Guymer." None-

theless, the new combination had not been published.

The type selected for *Adansonia gregorii* Muell. was annotated with the collection locality "Victoria River," one of the three localities mentioned by Mueller (1857). Other specimens from the same locality are housed at BM and GH; these may or may not constitute isotypes (J. H. Ross, pers. comm.).

Hochreutiner (1908), during a very brief visit to Broome, named a second Australian species, *Adansonia stanburyana*, which was said to differ from *A. gibbosa* in having 5–6 leaflets each about 16 cm long, glabrous below (vs. *A. gibbosa* having 7–9 leaflets of less than 13 cm, tomentose below), a calyx glabrous outside (vs. tomentose in *A. gibbosa*), and a more slender trunk. These traits vary within *A. gibbosa*, but the pattern of variation in no way supports the recognition of more than one species (Ostenfeld, 1918; Wickens, 1983; pers. obs.).

The tree on which Hochreutiner based his description of *Adansonia stanburyana* is located outside the old police station in Broome. Neither its leaves, flowers, nor trunk suggest any deviation from that typical of *A. gibbosa*. The tree bears a plaque indicating that it was planted in 1897, which would have made it about eight years old when Hochreutiner visited Broome in 1905. Thus many of the "distinguishing features" of *A. stanburyana* could, in fact, be juvenile traits.

In a travelogue, the naturalist Saville-Kent (1897) referred to the boab tree by the name *Adansonia rupestris*, thereby validly publishing this epithet. He stated that the species is "well exemplified" by plate V; in the absence of any specimens collected by Saville-Kent, or any indications that he consulted any other specimens, this plate is designated holotype.

Ethnobotany. Reported uses of *Adansonia gibbosa* include: fruit eaten as food and anti-scorbutic (e.g., Bennett, 1860; Jackson, 1868; Armstrong, 1983); hollow, water-filled trees and moisture-rich wood used as emergency water supplies (Bennett, 1860; Jackson, 1868; Froggatt, 1934); leaves and the gum exuding from damaged wood eaten (Armstrong, 1983; Boland et al., 1984; Saville-Kent, 1897); bark used to make rope (Armstrong, 1983); and pollen used to make glue (Armstrong, 1983). Furthermore, *A. gibbosa* plays a significant role in aboriginal culture, as illustrated by the large number of trees with carvings and paintings (Crawford, 1968). A bibliography for the Australian baobab (Willis, 1955) gives further references of ethnobotanical interest.

5. *Adansonia rubrostipa* Jum. & H. Perrier, Mat. Grass. Jan 1909: 8. *Adansonia fony* var. *rubrostipa* (Jum. & H. Perrier) H. Perrier, Notul. Syst., 14: 300. 1952. TYPE: Madagascar. Tsingy de Namoroka (Ambongo), May 1904, *Perrier de la Bâthie* 1447 (lectotype, here designated, P).

Adansonia fony Baill. ex H. Perrier, Notul. Syst., 14: 304. 1952 (nom. superfl. based on Baillon's provisional and hence invalid publication, Bull. Mens. Soc. Linn. Paris, 2: 845–846. 1890.). TYPE: Madagascar. Morondava, Apr. 1869, *Grandidier* 39 (lectotype, here designated, P).

Small to large deciduous trees (5–20 m) with cylindrical, bottle-shaped, or, rarely, tapering trunks, usually with a distinct constriction beneath the branches. Crown irregular, major branches most often horizontal becoming erect distally, rarely conical spines on upper surfaces of branches. *Bark* usually reddish brown and exfoliating. *Leaves* (3–) 5-foliate; petioles thin and tapering, 3–7 cm × 0.5–1 mm, glabrous; stipules caducous; leaflets sessile, medial leaflet 4–6(–8) × 1–2 cm, elliptic with acute apices; margin distinctly serrate (teeth ca. 1 mm). *Flowers* emerging when in leaf; buds ± horizontal, elongated-cylindrical, 16–28 cm; flower stalk 1–2.5 cm, green. *Calyx* lobes (3–)5, linear, 15–25 cm × 7–12 mm, reflexed and twisted tightly at the base of the flower, subglabrous, yellowish green with faint, reddish stripes outside, bright red and sparsely villous within. Calyx tube fitting tightly around the petal bases and lacking a distinct annular swelling. *Petals* bright yellow to orange-yellow, spreading, linear with expanded overlapping bases, significantly shorter than the androecium, 12–16 cm × 1.5–2.5 cm. *Androecium* pale yellow, comprising a long, ± cylindrical staminal tube, (3–) 6–10 cm long, 1–1.2 cm diam., surmounted by 100–150 filaments 10–12 cm long, the outer free and spreading, the inner 10–20 erect and united into a central bundle ca. 6 cm beyond the top of the tube. *Ovary* broadly rounded-conical, 7.5 × 9.5 mm, with dense upward-pointing golden hairs. *Style* bright pink, straight, 20–25 cm long, tapering gradually toward stigma; dense upward pointing hairs at base, glabrous above, fitting tightly in staminal tube and falling with it. Stigma red, blackening with age, 5–8 irregular spreading lobes. *Fruit* ± globose, calyx caducous; pericarp 4–5 mm thick with few longitudinal fibers and a dense reddish brown indumentum. Seeds reniform and laterally flattened, size variable, up to 16 × 12 × 8 mm. Germination phanerocotylar.

Representative specimens examined. MADAGASCAR. **Mahajanga Province:** Soalala District: Village

of Baly, 4 June 1930 (l, fl), *Decary* 7842 (P). Besalamy District: Besalamy, Sep. 1914 (fr), *Perrier de la Bâthie* s.n. (P). Antsalova District: basalt slabs SW of Cap Kimby, Antsalova, 1 Apr. 1966 (l, fl), *SF (Capuron)* 24622 (P, TEF). **Toliara Province:** Morondava District: 0.1 km E of Swiss Summer Camp, Kirindy forest, 5 km E of Morondava to Belo-sur-Tsiribihina road, 42 km from Morondava, 44°39'E, 20°02'S, alt. ca. 15 m, 27 Feb. 1989 (l, fl), *Baum* 313 (MO, P, TAN). Morombe District: Ambohibitika (Mangoky), Sep. 1911 (l, fl), *Perrier de la Bâthie* 8175 (P). Toliara District: 36.6 km N of Toliara, 22 Mar. 1985 (l, fl, imm. fr), *Dorr* 4113 (BR, K, MO, P, US); 3 km from La Table towards Toliara, N of road, 21 Mar. 1988 (l, fl), *T. Willing* 72 (P). Betioky District: near Lac Tsimanampetsotsa, 14 Feb. 1947 (l, fl), *Humbert* 20224 (P); R.N. 10, Soalary, Betioky, 21 Mar. 1953 (fl), *Ravelonahary* 4992 (K, P, TEF). District of Ampahy: 13 km N of Itampolo on road to Beheloka, 24°34'S, 43°56'E, alt. 100 m, 8 Feb. 1990 (l, fl), *P. B. Philippson* 3468 (P).

Distribution (Fig. 4). *Adansonia rubrostipa* extends along the west coast of Madagascar from near Itampolo in the southwest to Soalala in the northwest. It mainly occurs in spiny forest and dry deciduous forest on well-drained calcareous soils and on karstic limestone.

Phenology. Leaves November to April. Flowers February to April (rarely as late as June). Fruit ripe October–November.

Cytology. Miège (1974) reported a chromosome count for *A. rubrostipa* as $2n = 72$, whereas Mangenot & Mangenot (1962) and Baum & Oginkuma (1994) found $2n = 88$.

Taxonomy and nomenclature. *Adansonia rubrostipa* is a well-supported exclusive group with a unique combination of characters, including two strong autapomorphies: serrate leaflets and a central bundle of filaments fused beyond the top of the staminal tube. Perrier de la Bâthie (1952a, 1955) recognized two varieties of *A. rubrostipa* (under the name *A. fony*): the northern variety *rubrostipa* and the southern variety *fony*. However, the single feature distinguishing the two varieties, staminal tube length, shows much variation and does not support the recognition of subspecific taxa. In view of the exclusivity of *A. rubrostipa* and the absence of any subdivision, I believe its specific status to be well supported.

The earliest description of *Adansonia rubrostipa* was by Baillon (1890b), who gave it the name *A. fony*: “On le croit bien distinct de l’*A. mada-gascariensis*, et nous le nommerons, provisoirement, *A. fony*.” However, according to the *Code* (Greuter et al., 1988: Art. 34.1b) names suggested provisionally are invalid and, hence, this epithet must be rejected. By the time *A. fony* was validly published (Perrier de la Bâthie, 1952a), Jumelle

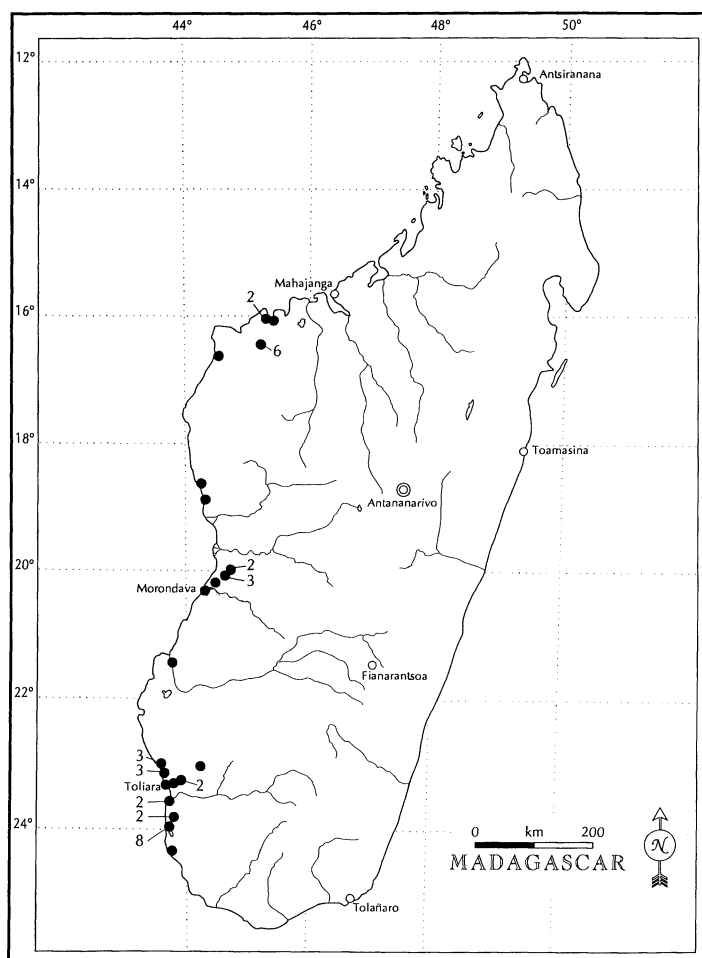


Figure 4. The distribution of *Adansonia rubrostipa* in Madagascar. Collection sites are marked with a circle. When more than one collection is made from the same locality the number of separate collections is indicated.

& Perrier de la Bâthie (1909a) had already published the name *A. rubrostipa*, giving the latter name nomenclatural priority.

Of the two "types" of *Adansonia fony* var. *rubrostipa* mentioned by Perrier de la Bâthie (1955), only Perrier de la Bâthie 1447 was collected prior to the original 1909 description of *A. rubrostipa*, and this is here designated the lectotype of *A. rubrostipa*. Two other specimens collected by Perrier de la Bâthie prior to 1909 (1047, 1447bis), and almost certainly used for the species description, should be considered syntypes.

Perrier de la Bâthie (1952a) did not indicate types of *Adansonia fony* Baill. ex H. Perrier at the time of publication. Perrier de la Bâthie (1955) designated two "types," *Grevé 38* and *Grandidieri 39*. Of these, the latter is the more complete spec-

imen and is here designated lectotype of *A. fony*, with *Grevé 38* being a syntype.

Ethnobotany. *Adansonia rubrostipa* has edible fruits, seeds, and roots (Perrier de la Bâthie, 1952b, 1953), but there is no documentation of them being utilized extensively in Madagascar. In Toliara, *A. rubrostipa* fruits are sometimes sold in the market. They are collected by climbing the small trees, often with the aid of wooden pegs hammered into the trunks. In the vicinity of Morondava, the wood of fire-killed trees is used as thatching (in the same manner as *A. grandidieri*). A species of fungus, with an edible and much sought after fruiting body, is said to grow only on dead *A. rubrostipa* and *A. grandidieri* trunks (Cabanis et al., 1970; pers. obs.). De Bry (in Teil, 1979) mentioned, in the annotation to a drawing that

clearly corresponds to *A. rubrostipa*, that it was used to make canoes. The wood of baobabs is not suited for this use and, hence, this comment is mistaken.

Conservation. In view of its extensive geographical distribution *Adansonia rubrostipa* is conservationally secure, although some populations, such as those 30 km north of Toliara, are threatened by forest destruction for charcoal extraction. In western deciduous forests close to Morondava, *A. rubrostipa* is the dominant tree species and provides an important resource for lemurs (nectar, gum, insects) and insects (sap, nectar, leaves, seeds, and pollen) and probably other animals as well.

- 6. *Adansonia madagascariensis* Baillon,** *Adansonia*, 11: 251. 1876. *Baobabus madagascariensis* (Baill.) Kuntze, *Rev. Gen. Pl.* 1: 67. 1891. *Adansonia bernieri* Baill. ex Poisson, *Rech. Fl. Merid. Madag.*, 20. 1912. **TYPE:** North Madagascar, *Bernier 2e envoi* 364 (lectotype, designated by Perrier de la Bâthie (1955), P; islectotype, G).

Small to large deciduous trees (5–20 m) with bottle-shaped to cylindrical or tapering trunks and irregular crowns. Primary branches erect, horizontal, or descending. *Bark* smooth, pale gray. *Leaves* 5–7-foliolate; petiole 6–12 cm × 1–2 mm, tapering; stipules caducous; leaflets subsessile with winged petioles, elliptic to oblanceolate with a prominent midrib (markedly raised below when dry), medial leaflet 7–12 × 2–3 cm with 8–16 pairs of irregularly spaced secondary veins, glabrous, apex obtuse to acute; margins entire. *Flowers* produced when in leaf; buds erect to horizontal, elongated-cylindrical, 15–20 cm; flower stalk 2–3 cm, green above, brownish below. *Calyx* lobes linear, up to 18 cm, reflexed and twisted at the base of the flower, green and scabrous outside, dark red and villous within. *Calyx* tube ca. 2 cm long, fitting tightly around petal bases with a pronounced annular swelling (2–4 mm wide). *Petals* dark red (rarely yellow), linear, approximately 10 times as long as broad, longer than the androecium but usually shorter than the style, ca. 15–20 × 0.8–1.5 cm. *Androecium* pale yellow comprising a cylindrical or tapering tube, 5–6 cm long, 0.6–1 cm diam., surmounted by 90–100 free filaments 7–13 cm long. *Ovary* globose to ovoid, densely covered in brownish upward-pointing hairs. *Style* straight or kinked, dark red, glabrous above with dense upward-pointing hairs below, fitting tightly in the staminal tube and falling with it. *Stigma* red,

lobes irregular, spreading. *Fruit* globose to subglobose, often broader than long (rarely almost ovoid), small (usually less than 10 cm in length), with a sparse indumentum of short brown hairs; pericarp thick (7–9 mm), very tough and woody, with many longitudinal fibers. Seeds distinctly reniform and laterally flattened (10–11 × 7–9 × 4.5–6 mm). Germination phanerocotylar.

Representative specimens examined. MADAGASCAR. **Antsiranana Province:** Antsiranana District: Mahory forest NE of Ankarana, 5 km E of Anivorano to Ambondromifehy road, 49°15'E, 12°52'S, alt. ca. 100 m, 19 Mar. 1989 (l, fl), *Baum* 319 (MO, P, TAN); on S side of Antsiranana to Ramena road where it passes the Montagnes des Français, 49°20'E, 12°19'S, alt. 10 m, 23 Mar. 1989 (l, fl), *Baum* 320 (MO, P, TAN); Ankarana W of Ambondromifehy, 5 Mar. 1951 (l, fl), *SF (Capuron)* 3029 (A, BR, G, K, P, TEF). Vohemar District: Ankarafa (= Ankorefo?), Canton Daraina, 13 May 1955 (l), *SF* 14042 (b) (P, TEF). Ambanja District: Zangoa (= Djangoa) River (l, fl, fr), *Perrier de la Bâthie* 5368 (P). **Mahajanga Province:** Maromandia District: Maromandia (Marovato), 23 Mar. 1923 (l, fl, fr), *Decary* 1593 (P); near Andranosamonta, May 1909 (l), *Perrier de la Bâthie* 8179 (P). Mahajanga District: NE of Mahajanga, 11 June 1940 (fr), *Decary* 15343 (P). Ambato-Boeny District: Iabohazo River (of the Bemarivo), Oct. 1907 (fallen fl, fr) *Perrier de la Bâthie* 5356 (P).

Cultivated. FRANCE. Paris: seed from Madagascar, 1893 (seedling), *Museum Series* F26 (P). MADAGASCAR. **Mahajanga Province:** Marovoay: seeds from Loky, Apr. 1929 (fl, fr), *Perrier* 14671 (P).

Material with Uncertain Determination: MADAGASCAR. **Mahajanga Province:** Soalala District: near Soalala, (l), *Decary* 7814 (P).

Distribution (Fig. 5). The range of *Adansonia madagascariensis* has been a source of some confusion. Perrier de la Bâthie (1955) suggested that it extends from the very north of Madagascar right down to Ambovombé in the southeast, and his data formed the basis for the maps found in Miège (1974). However, a reassessment of these southern specimens shows that they actually correspond to *A. za. Adansonia madagascariensis* thus extends from Antsiranana to the Sambirano region as far as Ankara (Boina region) and perhaps Soalala (Ambongo region) in the northwest.

Adansonia madagascariensis is found in dry or moist deciduous forest on limestone, sandstone, and gneiss. In the vicinity of Antsiranana it often grows within meters of the sea.

Phenology. Leaves present November to April. Flowering February to April. Fruit ripening by November.

Cytology. Miège (1974) reported a chromosome count of $2n = 80-84$; however, this is suspect because the seed came from Morondava, which is

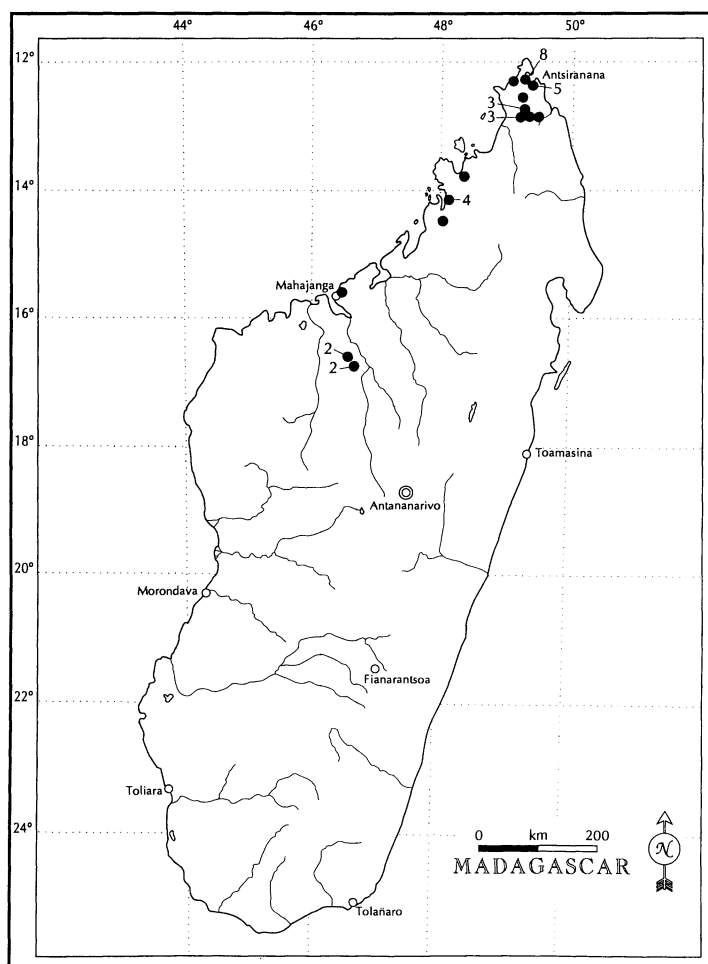


Figure 5. The distribution of *Adansonia madagascariensis* in Madagascar. Collection sites are marked with a circle. When more than one collection is made from the same locality the number of separate collections is indicated.

outside the range of *A. madagascariensis*. Baum & Oginuma (1994) found $2n = 88$.

Taxonomy and nomenclature. *Adansonia madagascariensis* and *A. za* are very similar but are easily distinguished, especially in areas of sympatry (for example, in and around Maromandia), by: petals usually red in *A. madagascariensis* vs. yellow in *A. za*; flowering from February to April vs. November to February; style usually detaching from the ovary during floral abscission vs. usually persistent; fruit globose to subglobose, generally broader than long without a thickened peduncle vs. subglobose to ovoid, usually longer than broad, with a thickened peduncle in the south of its range (see photographs in Jumelle & Perrier de la Bâthie, 1913). Less reliable characters include: ovary globose to ovoid in *A. madagascariensis* vs. conical

to ovoid in *A. za*; first 10 or more leaves in seedling simple vs. usually just 1–5 simple leaves; and leaflets with 8–16 secondary veins vs. 10–20.

None of the above characters separating *Adansonia madagascariensis* and *A. za* are diagnostic, i.e., fixed within one taxon and entirely absent from the other (with the possible exception of flowering season). Nonetheless, there are grounds for believing that *A. madagascariensis* is exclusive. The fact that despite the occurrence of sympatry the two species have remained distinct with no evidence of hybridization implies that there is sufficient genetic isolation for barriers to interbreeding (“isolating mechanisms”) to have become fixed in the two taxa. Thus, I believe that the best supported hypothesis at this time is that *A. madagascariensis* is exclusive, and in the absence of any indication of genetic subdivision, I treat it as a valid species.

Adansonia madagascariensis was the first Malagasy baobab to be named (Baillon, 1876). The name was misapplied to the fruit of *A. grandidieri* in Baillon (1889), but this error was corrected by Baillon (1893). Poisson (1912) validly published the superfluous name *A. bernieri* based on an annotation by Baillon on the lectotype sheet.

Ethnobotany. The hard dry fruits of *Adansonia madagascariensis* are the least palatable in the genus and, hence, are rarely exploited for food. The swollen roots of young seedlings are edible and reportedly make an excellent vegetable (Perrier de la Bâthie, 1952b). No other uses are reported, although Perrier de la Bâthie (1953) suggested that, in view of its prodigious growth rate (12–15 m and 40–60 cm diam. after 12 years), it could be exploited for cellulose. However, his claim that at 24 years the trees had attained 40 m is probably a typographical error.

Conservation. The conservational status of *Adansonia madagascariensis* is unknown, although it is clearly less threatened than the other northern species, *A. perrieri* and *A. suarezensis*.

7. *Adansonia* za Baill., Bull. Mens. Soc. Linn. Paris, 2: 844. 1890. TYPE: Madagascar. Mahafaly plateau, *Grevé 37* (lectotype, designated by Perrier de la Bâthie (1952a), P).

Adansonia za var. *boinensis* H. Perrier, Notul. Syst., 14: 304. 1952. TYPE: Madagascar. Ankara, Kamakama, Oct. 1902, *Perrier de la Bâthie 960A* (lectotype, here designated, P).

Adansonia bozy Jum. & H. Perrier, Ann. Mus. Colon. Marseille, 18: 447–451. 1910. *Adansonia* za Baill. var. *bozy* (Jum. & H. Perrier) H. Perrier, Notul. Syst., 14: 304. 1952 (= *Adansonia* za var. *bozo*). TYPE: Madagascar. Andranomandevao, Sambirano valley, Jan. 1909, *Perrier de la Bâthie 8159* (holotype, P).

Adansonia alba Jum. & H. Perrier, Matières Grasses, 1909: 1511. 1909. TYPE: Madagascar. Upper basin of the Andranomalaza to the N of Bezofa (Bejofo), in dense forest by a waterfall close to 500 m, on rocks (syenite), Oct. 1908, *Perrier de la Bâthie 8166* (holotype, P).

Usually tall (up to 30 m), rarely stunted (less than 5 m when mature), deciduous trees with usually single, cylindrical or slightly tapering trunks, often with irregular swellings; crowns rounded; primary branches usually ascending and tapering. *Bark* gray and \pm smooth. *Leaves* 5–8-foliolate; petiole 5–15 cm \times 1–4 mm; stipules caducous; leaflets sessile to long-petiolulate (up to 3 cm), broadly elliptic to lanceolate, apex usually apiculate, rarely mucronate; medial leaflets up to 20 \times 8 cm in the north, usually less than 10 \times 4 cm

in the south, with 10–20 pairs of regularly spaced secondary veins (more in north), usually alternating with prominent intersecondaries, glabrous or somewhat scabrous; margins entire. *Flowers* emerging simultaneously or soon after the leaves; buds erect to horizontal, elongated-cylindrical, 15–24 cm \times 1.5–2.5 cm; flower stalk 2–3 cm, green. *Calyx* lobes (3–)5, reflexed and twisted at the base of the flower, 15–22 cm \times 10–12 mm, green and scabrous outside, dark red villous within. *Calyx* tube fitting tightly around the petal bases, with a marked annular swelling (ca. 2 mm wide). *Petals* yellow, sometimes with a diffuse reddish medial streak on the adaxial surface, linear, at least 10 times as long as wide, 14–24 cm \times 10–16 mm, exceeding the style and androecium. *Androecium* pale yellow, comprising a long cylindrical or tapering staminal tube, 4–6.5 cm, surmounted by 100–120 free filaments, up to 12 cm long. *Ovary* conical to ovoid, covered in dense, upward-pointed hairs. *Style* dark red, straight, 16–22 cm glabrous above, dense, upward-pointing hairs below, usually fitting loosely in the staminal tube and persisting after floral abscission (rarely to fruit). *Stigma* red, 3–5 mm diam. with irregular lobes. *Fruit* subglobose, oblong or ovoid, 10–30 cm long, 6–15 cm wide, rarely curved; usually with longitudinal ridges and, except in the north, a distinctly swollen peduncle. *Pericarp* thick and tough with many longitudinal fibers, usually blackish with a sparse indumentum. *Seeds* reniform, laterally flattened, variable in size, up to 12 \times 11 \times 8 mm. Germination phanerocotylar.

Representative specimens examined. MADAGASCAR. **Antsiranana Province:** Ambanja District: Ambodibo near Ambanja, alt. ca. 5 m, Mar. 1951 (l, fr), *Humbert & Capuron 25500* (K, P). **Mahajanga Province:** Maromandia District: Antanandava I village, ca. 11 km E of Maromandia, isolated tree ca. 1.5 km W of village, 14°16'S, 48°08'E, 1 Nov. 1991 (l, fl), *Baum 332* (MO, P, TAN); Ambondrona village (ca. 2 km E of Ambaibo), 500 m E of village near the Andranomalaza river, 14°13'30"S, 48°22'30"E, alt. ca. 100 m, 4 Nov. 1991 (l, fl), *Baum 336* (MO, P, TAN). Marovoay District: Ankaboka near Marovoay, Dec. 1909 (l, fl), *Perrier de la Bâthie 8189* (BR, G, P). Ambato-Boeny District: Ankara, Kamakama, Oct. 1902 (l, fl, fr), *Perrier de la Bâthie 960A & 960C* (P). Kandrehio District: Kariza forest on Kelifely tablelands, Nov. 1904 (fl), *Perrier de la Bâthie 960E* (P). Maevatanana District: Andriba, isolated trees at foot of Mount Andriba on Gneiss, 17 Jan. 1942 (l, fl), *Decary 17088* (P). **Toliara Province:** Morondava District: Kirindy forest, 4.5 km E of Morondava to Belo-sur-Tsiribihina road 42 km from Morondava, 50 m from the Kirindy river bed, 20°02'S, 44°39'E, alt. 25 m, 24 Dec. 1991 (l, fl), *Baum 344* (MO, P, TAN); near Analaiava, E of Morondava, 28 Dec. 1962 (l, fl), *SF (Capuron) 22141* (A, BR, G, K, MO, P, TEF). Mahabo District: 21 km E of Mahabo, 4 Dec. 1920 (fl), *Keraudren-Aymonin & Aymonin 25917* (P). Miandrivazo Dis-

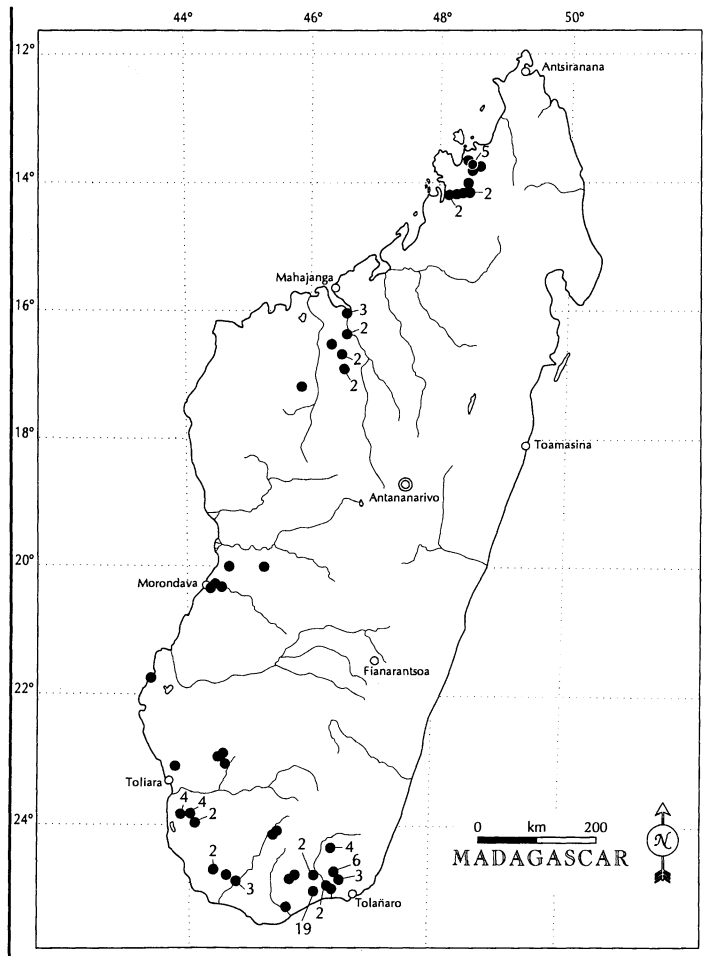


Figure 6. The distribution of *Adansonia za* in Madagascar. Collection sites are marked with a circle. When more than one collection is made from the same locality the number of separate collections is indicated.

trict: Sakeny River, Aug. 1910 (l, fl), *Perrier de la Bâthie* 8180 (P). Morombe District: Morombe, Oct. 1940 (fr), *Decary* 16426 (P). Sakaraha District: Analamarina, SE of Sakaraha, alt. 500 m, 28 Dec. 1961 (l, fl), *SF (Capuron)* 20595 (BR, G, MO, P, TEF). Toliara District: limestone plane of the basin of the Fiherana, Jan. 1910 (l), *Perrier de la Bâthie* 8182 (P). Betioky District: near Beza Mahafaly reserve, near Betioky, valley of the Eha-zoara river, E of Sakamena, 23°40'S, 44°39'E, alt. 170 m, 29 Nov. 1987 (l, fl), *P. B. Philippson* 2638 (MO, P). Ampanihy District: between Beloha and Ampanihy, 19 Feb. 1949 (l, fl), *SF* 455 (P, TEF). Bekily District: Ambatofotsy, 15 Jan. 1957 (l, fl), *SF* 3376 (P, TEF). Ambovombe District: Ambovombe, 24 Jan 1925 (fl, l), *Decary* 3554 (BR, G, P, TAN). Amboasary District: Fangidraty NE Androy, 21 Nov. 1931 (l, fl), *Decary* 9319 (K, P); Andohahela parcelle 2, NE of Amboasary near Hazafotsy, 24°50'S, 46°32'E, 100 m, 12 Dec. 1991 (l, fl), *S. T. Malcomber* 1141 (MO, P).

s.n. (P). MADAGASCAR. Jardin Tsimbazaza, 7 May 1941 (l), *Jardin Tsimbazaza* 4896 (TAN).

Immature or incomplete material with uncertain determinations. Near Radama [= Sahamalaza], Maromandia, 11 Oct. 1922 (imm. l), *Decary* 1146 (P); N of Fiherana, dry forest of Fandrare, 40 km N of Tulear, Mar. 1934 (juv. shoot), *Humbert* 14348bis (P); Besevo, Oct. 1899 (l), *Perrier de la Bâthie* 960 (P); Ambolibozo, Sambirano May 1924 (seedlings), *Perrier de la Bâthie* 16340a (P).

Distribution (Fig. 6). *Adansonia za* occurs in dry deciduous forest, spiny forest, savannas, and scrubland from Andohahela and the Mandrare River in the southwest through southern and western Madagascar to the Boina region and the Sambirano River basin. In some deciduous forests in the south it constitutes the dominant tree species (e.g., Analava west of Betioky and to a lesser extent Sakaraha and the forests east of Ankilizato). In the

Cultivated. FRANCE. Paris, 1893 (seedling) *Baillon*

northwest it is less abundant, concentrated near rivers.

Phenology. In leaf throughout the wet season. Flowering November to February, earlier in the north, later in the south. Ripe fruit from end of dry season.

Cytology. Miège (1974) reported $2n = 48$ for specimens collected in the southwest of Madagascar. Baum & Oginuma (1994) found $2n = 88$ from both south and north Madagascar.

Taxonomy and nomenclature. As discussed above, there are few fixed differences between *Adansonia za* and *A. madagascariensis*. The case for exclusivity is weaker in *A. za* than it was in *A. madagascariensis* in view of its wide geographical range and the fact that some individuals in the north share features with *A. madagascariensis* that are absent from southern individuals assigned to *A. za*. One possibility is that *A. za* is a "metaspecies" (Donoghue, 1985), i.e., that the organisms constituting *A. za* are not members of any exclusive species. This situation could have arisen, for example, under the following scenario, which assumes for the sake of illustration that *A. madagascariensis* and *A. za* are sister groups. (1) A small subset of the common ancestral taxon became genetically isolated. (2) This subset continued to have a small population size and/or went through a severe bottleneck, becoming the exclusive species *A. madagascariensis*. (3) The remainder of the common ancestor, constituting the putative taxon "*A. za*," retained a large population size and did not become exclusive. If this scenario were correct, the organisms in "*A. za*" would not be in any basal, exclusive group, because the smallest exclusive group that they are members of is *A. madagascariensis* + *A. za*, which contains the exclusive group *A. madagascariensis*. We do not know if such a series of events occurred, and thus we cannot determine if *A. za* is a species or a metaspecies. Given this uncertainty, what is the prudent course? In the absence of guidelines for dealing with metaspecies in a taxonomy, and in order to avoid unnecessarily destabilizing the taxonomy of *Adansonia*, I here advocate recognition of *A. za* as a species, while flagging it as a taxon worthy of more detailed analysis.

Perrier de la Bâthie (1955) proposed an infra-specific classification of *Adansonia za*, recognizing three varieties. Although there is significant variation from the north to the south of the range of *A. za*, this variation is gradual and I see no value in recognizing subspecific taxa. The southern pop-

ulations of *A. za* are the most distinctive because of their long-petiolulate leaflets and ovoid-cylindrical fruit with swollen peduncles. These characters are only gradually replaced by sessile leaflets and normal peduncles as one goes north. Some other characters also vary clinally, such as leaflet size (larger in north) and flowering season (earlier in north), but again I see no use in forcing a continuum of variation into discrete taxa.

There is some nomenclatural confusion as to the taxon to which the name *Adansonia za* should apply. Hochreutiner (1908) pointed out that the description given by Baillon (1890b) contradicts the illustration labeled "*A. za*" (79C) in *Histoire Naturelle des Plantes* (Baillon, 1893) and the description given by Drake del Castillo (1902). Hochreutiner concluded that the plate predated Baillon's description and hence had priority. However, Jumelle & Perrier de la Bâthie (1910) pointed out that although plates 79A and 79B predate Baillon (1890b), the others, 79C to 79I, were not issued until 1893, and hence the written description has priority. Of the three plates (79C, D, and I) labeled *A. za*, two (79C and I) appear to be *A. suarezensis*, whereas plate 79D is an accurate representation of the fruit of *A. za* Baill. Thus, the original description of *A. za* is Baillon (1890b). The lectotype (Grevé 37) was selected by Perrier de la Bâthie (1952a), but he incorrectly gave the collection locality as Morondava.

The first mention of *Adansonia bozy* is in Jumelle & Perrier de la Bâthie (1909b), but the taxon was only recognized provisionally and hence this name was not validly published until 1910 (Jumelle & Perrier de la Bâthie, 1910). Perrier de la Bâthie (1952a) subsumed this taxon as a variety of *A. za*. However, in this publication Perrier de la Bâthie used the spelling *bozo*, an error which was corrected by Perrier de la Bâthie (1955). Only one specimen of *A. za* var. *bozy* was collected early enough to have been consulted by Jumelle & Perrier de la Bâthie (1910), and this is, therefore, assumed to be the holotype.

In selecting a lectotype for *Adansonia za* var. *boinensis* I chose Perrier de la Bâthie 960A, the most complete specimen from one of the localities mentioned by Jumelle & Perrier de la Bâthie (1909a, 1910) that predates these articles.

The putative species *Adansonia alba* was named by Jumelle & Perrier de la Bâthie (1909a) to accommodate a specimen Perrier de la Bâthie collected along the Andranomalaza River. This species was said to be diagnosed by its white flowers and short staminal tube. In the course of my observations and collections along the Andranomalaza

River, all the baobabs I encountered could be assigned to *A. za*. Furthermore, the type specimen, though of poor quality, shows no features that distinguish it from *A. za*. Thus, I believe that *A. alba* is synonymous with *A. za*. The characters that supposedly separate the species, white petals and short staminal tube, were probably incorrectly scored by Perrier de la Bâthie, being based upon fallen flowers.

Ethnobotany. *Adansonia za* has several common names, for example, “za” or “zabe” in the south and “bozy” or “bozybe” in the north, and “ringy” or “boringy” in the Ambongo region (Perrier de la Bâthie, 1955).

Little is known about the human exploitation of *Adansonia za*, but Jumelle & Perrier de la Bâthie (1912) reported that the seeds are eaten and the trunk is sometimes hollowed out as a cistern for storing water. Perrier de la Bâthie (1952b) mentioned that the seedling roots are an edible vegetable, and Miège (1974) reported that *A. za* is destroyed by ranchers so that their cattle can feed on the moist wood.

Conservation. In view of the extensive geographical range, *Adansonia za* is conservationally secure, despite the fact that several local populations are endangered by forest clearance. *Adansonia za* has diverse interactions with animals: it provides nesting sites for birds, holes for carnivores and lemurs (M. Nicoll, pers. comm.); perches for territorial surveillance and display by birds and the sportive lemur (*Lepilemur* sp.); many insects feed on the leaves, sap, nectar, and pollen; sunbirds (*Nectarinia souimanga*) feed on nectar; sifaka (*Propithecus verreauxi verreauxi*) feed on flower buds; and fork-marked lemurs (*Phaner furcifer*) feed on exuded gum (Petter et al., 1975).

- 8. *Adansonia perrieri*** Capuron, Notul. Syst. (Paris) 16: 66. 1960. TYPE: North Madagascar. Ankarana Plateau E of Ambondromifehy, valley on clay and limestone, 13 Nov. 1958, *SF* (Capuron) 19000 (holotype, P; isotype, TEF).

Medium to tall deciduous trees (up to 30 m) with \pm cylindrical trunks and irregular crowns. Major branches horizontal or ascending at about 45°. Bark smooth, pale gray. Leaves 5–11-foliate (usually over 9 on reproductive shoots); petioles sturdy, usually pubescent; stipules triangular or linear, up to 15 mm, persistent; leaflets sessile or subsessile (petiolule up to 5 mm long on vegetative

shoots), medial leaflet 8–12 \times 3–4.5 cm, elliptic-obovate, with 15–24 pairs of secondary veins on reproductive shoots; apex acute to apiculate, pubescent (subglabrous on vegetative shoots). Flowers emerging at or just before leaf emergence; buds erect to horizontal, elongated-cylindrical; flower stalk ca. 2 cm long, yellowish green, pubescent. Calyx lobes (3–)5, 13–18 cm \times 8–11 mm, reflexed and twisted at the base of the flower; green scabrous outside, cream or pinkish and villous within. Calyx tube fitting tightly around the petal bases and lacking a marked annular swelling. Petals pale yellow, becoming darker with age, oblong, 15–23 cm \times 35–45 mm, approximately 5 times as long as broad. Androecium pale yellow, comprising a very long and narrow tube tapering from bottom to top, 13–20 cm long, 3–13 mm diam., surmounted by 180–220 spreading, free filaments, 1.0–2.2 cm. Ovary conical to ovoid, with dense upward-pointing hairs. Style red, at least distally, 16–22 cm, exceeding staminal tube by 2–4 cm, glabrous, fitting tightly into the staminal tube and falling with it at anthesis. Stigma red or pink, 4–8 mm diam., irregularly lobed. Fruit broadly ovoid to oblong, up to 25 cm long, 1.5–2.5 times as long as broad. Pericarp 8–9 mm thick and tough with many longitudinal fibers, indumentum of short, brown, clumped hairs. Seeds reniform, laterally flattened, 9–11 \times 8–9 \times 5–6 mm. Germination phanerocotylar.

Specimens examined. NORTH MADAGASCAR. **Antsiranana Province:** Antsiranana District: 7 km N of Station Roussette where the trail to Andranonaomby crosses the Makis River, Parc National de Montagne d'Ambre, 49°10'E, 12°29'S, alt. 650 m, 18 Nov. 1988 (fl), *Baum* 308 (MO); 1 km W of Beanamalao on the banks of the Andranofanjava River where it is crossed by the trail from Station Roussette to Andranofanjava village, 49°05'E, 12°31.5'S, alt. 475 m, 11 Mar. 1989 (l), *Baum* 314 (MO); 7 km N of Station Roussette where the trail to Ankorefo crosses the Makis River, Parc National de Montagne d'Ambre, 49°10'30"E, 12°29'S, alt. 650 m, 4 Dec. 1991 (l, fl), *Baum* 340 & 341 (MO, P, TAN); Montagne d'Ambre, left bank of Makis River by the path from Joffreville to Andranofanjava, 21 Nov. 1958 (l, fl), *SF* (Capuron) 20076 (G, P, TEF); Camp d'Ambre, Jan. 1926 (fr), *Humbert* 17560 (P); S of Antsiranana on main highway, streamside, 12°40'S, 49°15'E, 400 m, 24 Nov. 1989 (fl, l), *McPherson* 14538 (MO, P); near Montagne d'Ambre, *Perrier de la Bâthie* 17560 (P). Ambilobe District: limestone plateau of Ankarana to the NE of Ambondromifehy, 13 Nov. 1958 (l, fl), *SF* (Capuron) 19000 (K, MO, P, TEF); Ankarana, 200–350 m, 4–9 Mar. 1951 (l, fr), *Humbert* & *Capuron* 25680 (P); Ankarana Plateau, dry valley E of Ambondromifehy on limestone and basalt outcrops, 6 Mar. 1951 (l, fr), *SF* 3038 (P, TEF). **Toamasina Province:** Ambatondrazaka District: Lac Alaotra (cultivated?), 1000 m, 1945 (l), *Perrier de la Bâthie* 17560bis (P).

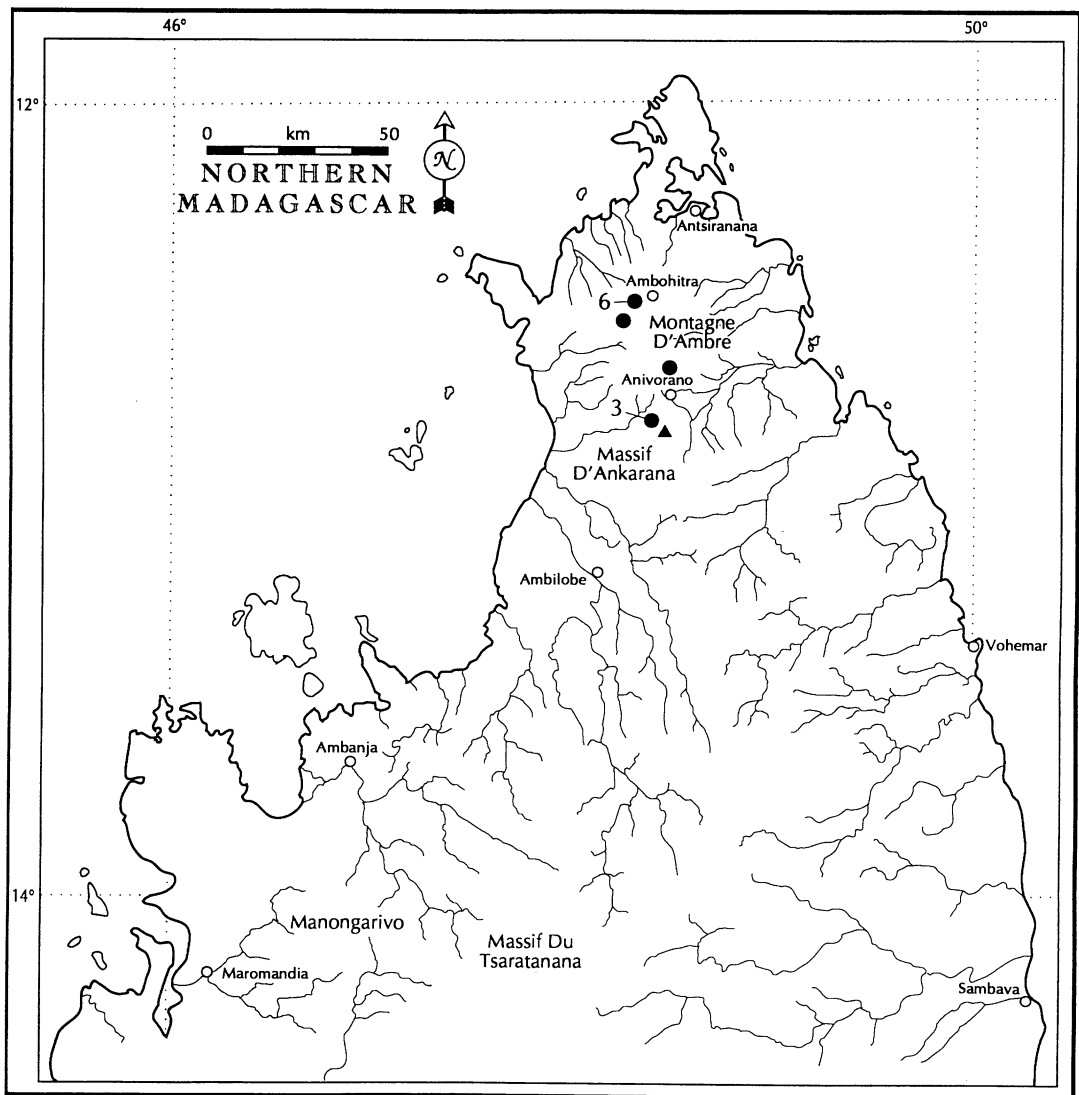


Figure 7. The distribution of *Adansonia perrieri* in northern Madagascar. Collection sites are marked with a circle. When more than one collection is made from the same locality the number of separate collections is indicated. Some additional localities known by the author are marked with a triangle.

Distribution (Fig. 7). *Adansonia perrieri* is known from only five sites. The population at Montagne d'Ambre is at about 650 m in evergreen rainforest on the banks of the Rivière des Makis and comprises about 12 individuals. The Ambondromifely population is made up of many individuals (even hundreds; Capuron, 1960) scattered in dry deciduous forest. The remaining three localities comprise three or fewer individuals (one of them, Mahory forest, eastern Ankarana, is not represented by a collection). Other populations certainly remain to be discovered in the region of Ankarana and Montagne d'Ambre.

Phenology. Leaves throughout wet season (November to April). Flowering November to December. Fruit ripe in October and November.

Cytology. Miège (1974) reported $2n = 96$. Baum & Oginuma (1994) found $2n = 88$.

Taxonomy and nomenclature. In view of its limited geographic range, the possession of several unique characters, some of which are apomorphic (e.g., persistent stipules, extremely long, narrow staminal tube), and in the absence of intraspecific variation, *Adansonia perrieri* is a well-supported species.

Ethnobotany. *Adansonia perrieri* shares its common name, "bozy," with other species of *Adansonia* occurring in northern Madagascar. Fruit is collected for the edible pulp, but no other uses are reported.

Conservation. Although it is quite likely that *Adansonia perrieri* is more widespread than now thought, only one of four sites is populated by more than a handful of individuals. All the populations except at Montagne d'Ambre are significantly disturbed by humans, especially through fire and the extraction of wood for charcoal and timber. Even in Montagne d'Ambre the long-term survival of *A. perrieri* is threatened due to seed predation by introduced rats. Despite the extensive production of fruit, very few remain intact, and only those that fall directly into the river have a good chance of escaping predation. In view of its rarity and the various threats it faces, *A. perrieri* is perhaps the most endangered Malagasy baobab.

Literature Cited

- Adam, J. G. 1962. Le Baobab. Notes Africaines 94: 33-44.
- Adanson, M. 1757. Histoire Naturelle du Sénégal. C.-J.-B. Bauche, Paris.
- . 1771. Description d'un arbre nouveau genre appelé Baobab, observé au Sénégal. Hist. Acad. Roy. Sci. (Paris) 1791: 218-243.
- Alpino, P. 1592. De Plantis Aegypti Liber. Franciscum de Francis Senensem, Venice.
- Alverson, W. S. 1994. New species and combinations of *Catostemma* and *Pachira* (Bombacaceae) from the Venezuelan Guayana. Novon 4: 3-8.
- Armstrong, J. A. 1979. Biotic pollination mechanisms in the Australian flora: A review. New Zealand J. Bot. 17: 467-508.
- Armstrong, P. 1977a. Baobabs—Remnant of Gondwanaland? New Sci. 73: 212-213.
- . 1977b. The baobab tree. Austral. Pl. 9: 226-229.
- . 1982. The wandering baobab. Hemisphere 26: 84-87.
- . 1983. The disjunct distribution of the genus *Adansonia*. Natl. Geog. J. India 29: 142-163.
- Aubréville, A. 1975. Essais de géophylétique de Bombacacées. Adansonia n.s. 15: 57-64.
- Baillon, H. E. 1876. *Adansonia madagascariensis*. Adansonia 11: 251.
- . 1889. Histoire Naturelle des Plantes, vol. 28 (fasc. 20). In: A. Grandidier, Histoire Physique, Naturelle et Politique de Madagascar. Paris.
- . 1890a. Sur le Reine-ala et ses usages. Bull. Mens. Soc. Linn. Paris 1: 539-540.
- . 1890b. Sur les Baobabs de Madagascar. Bull. Mens. Soc. Linn. Paris 1: 844-846.
- . 1893. Histoire Naturelle des Plantes, vol. 34 (fasc. 34). In: A. Grandidier, Histoire Physique, Naturelle et Politique de Madagascar. Paris.
- Baker, H. G. & I. Baker. 1968. Chromosome numbers in the Bombacaceae. Bot. Gaz. 129: 294-296.
- Bakhuizen van der Brink, R. C. 1924. Revisio Bombacearum. Bull. Jard. Bot. Buitenzorg Ser. 3, 6: 161-240.
- Baum, D. A. 1995. The comparative pollination and floral biology of baobabs (*Adansonia*-Bombacaceae). Ann. Missouri Bot. Gard. 82: 322-348.
- & M. J. Donoghue. In press. Choosing among alternative phylogenetic species concepts. Syst. Bot.
- & K. Oginuma. 1994. A review of chromosome numbers in Bombacaceae with new counts for *Adansonia* (Bombacaceae). Taxon 43: 11-20.
- & K. L. Shaw. 1995. Genealogical perspectives on the species problem. In: P. C. Hoch & A. G. Stephenson (editors), Experimental and Molecular Approaches to Plant Biosystematics. Monogr. Syst. Bot. Missouri Bot. Gard. 53.
- Bennett, G. 1860. Gatherings of a Naturalist in Australia. John Van Voorst, London.
- Boland, D. J., M. Brooker, G. M. Chippendale, N. Hall, B. P. M. Hyland, R. D. Johnston, A. Kleinig & J. D. Turner. 1984. Forest Trees of Australia. Nelson-CSIRO, Melbourne.
- Braun, K. 1900. Beiträge zur Anatomie de *Adansonia digitata*. Inaugural-Dissertation, Universität Basel, Basel.
- Burkill, H. M. 1985. The Useful Plants of West Tropical Africa, 2nd ed. Royal Botanic Gardens, Kew.
- Burton-Page, J. 1969. The problem of the introduction of *Adansonia digitata* into Africa. Pp. 331-335 in P. J. Ucko & G. W. Dimbleday (editors), Domestication and Exploitation of Plants and Animals. Duckworth, Chicago.
- Cabanis, Y., L. Chabouis & F. Chabouis. 1970. Végétaux et groupements végétaux de Madagascar et de Mascareignes. Bureau pour le Développement de la Production Agricole. Tananarive.
- Cadamosto, A. 1937. The Voyages of Cadamosto [Translated by G. R. Crone]. Hakluyt Society, London.
- Capuron, R. 1960. Contributions à l'étude de la flore forestière de Madagascar. Notul. Syst. (Paris) 16: 60-80.
- Carr, W. R. 1955. Ascorbic acid content of baobab fruit. Nature 176: 1273.
- Cheek, M. 1989. On typifying names validated by plates unaccompanied by text. Taxon 38: 636-638.
- Chevalier, A. 1906. Les Baobabs (*Adansonia*) de l'Afrique continentale. Bull. Soc. Bot. France 53: 480-496.
- Clusius, J. C. 1605. Exoticum libri decem. Ex Officina Plantiniana Raphalengii, Leiden.
- Coe, M. J. & F. M. Isaac. 1965. Pollination of the baobab, *Adansonia digitata*, by the Lesser Bushbaby, *Galago crassicaudatus*. E. African Wildlife J. 3: 123-124.
- Cracraft, J. 1983. Species concepts and speciation analysis. Curr. Ornithology 1: 159-187.
- . 1989. Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. Pp. 28-59 in D. Otte & J. A. Endler (editors), Speciation and Its Consequences. Sinauer Press, Sunderland, Massachusetts.
- Crawford, I. M. 1968. The Art of the Wandjina: Aboriginal Cave-paintings in the Kimberley, Western Australia. Oxford Univ. Press, Melbourne.
- Cretton, N. 1972. Contribution à l'étude morphologique

- et anatomique des premiers stades de développement d'*Adansonia* (Bombacacées). Thesis, University of Geneva.
- Cunningham, A. 1827. Natural history appendix. Pp. 408–629 in P. P. King, Narrative of a Survey of the Intertropical and Western Coasts of Australia Performed Between the Years 1818 and 1822. John Murray, London.
- Dalziel, J. M. 1948. The Useful Plants of West Tropical Africa. Crown Agents for the Colonies, London.
- Davis, J. I. & K. C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Syst. Biol.* 41: 421–435.
- Davis, T. A. & S. S. Ghosh. 1976. Morphology of *Adansonia digitata*. *Adansonia* n.s. 15: 471–479.
- Done, C. 1987. Wallaby scats solve mystery. *Conservation and Land Management News* 3(23): 1.
- Donoghue, M. J. 1985. A critique of the biological species concept and recommendations for a phylogenetic alternative. *Bryologist* 88: 172–181.
- Drake del Castillo, E. 1902. Madagascar au début de XXe Siècle. F. R. de Rudeval, Paris.
- Edlin, H. L. 1935. A critical revision of certain taxonomic groups of Malvales. *New Phytol.* 34: 1–20, 122–143.
- French, M. H. 1944. Composition and nutritive value of pulp and seeds in the fruit of the baobab. *E. African Agric. J. Kenya* 9: 144–145.
- Froggatt, W. W. 1934. A naturalist in Kimberley in 1887. *Austral. Naturalist* 9: 69–82.
- Fuchs, H. P. 1967. Pollen morphology of the family Bombacaceae. *Rev. Palaeobot. Palynol.* 3: 119–132.
- Gerber, C. 1895. Contribution à l'histoire botanique thérapeutique et chimique de genre *Adansonia*. *Ann. Inst. Bot.-Géol. Colon. Marseille* 2, 2: 1–78.
- Gibbs, P. E., J. Semir & N. D. da Cruz. 1988. A proposal to unite the genera *Chorisia* Kunth and *Ceiba* Miller (Bombacaceae). *Notes Roy. Bot. Gard. Edinburgh* 45: 125–136.
- Greene, R. A. 1932. Composition of the pulp and seeds of *Adansonia digitata*. *Bot. Gaz.* 94: 215–220.
- Greuter, W., H. M. Burdet, W. G. Chaloner, V. Demoulin, R. Grolle, D. L. Hawksworth, D. H. Nicolson, P. C. Silva, F. A. Stafleu, E. G. Voss & J. McNeill. Editors. 1988. International Code of Botanical Nomenclature. *Regnum Veg.* 118: 1–328.
- Grey, G. 1841. Journals of Two Expeditions of Discovery in North-west and Western Australia During the Years 1837–1839. T. & W. Boone, London.
- Guy, G. L. 1970. *Adansonia digitata* and its rate of growth in relation to rainfall in south central Africa. *Proc. Trans. Rhodesian Sci. Assoc.* 54: 68–84.
- . 1971. The Baobabs: *Adansonia* spp. (Bombacaceae). *J. Bot. Soc. South Africa* 57: 30–37.
- Heel, W. A. van. 1966. Morphology of the androecium in Malvales. *Blumea* 13: 182–394.
- . 1974. On dichotomy with special reference to the funicles of the ovules of *Adansonia*. *Proc. Kon. Ned. Akad. Wetensch.* C. 77: 321–337.
- Heward, R. 1842. Biographical sketch of the late Allan Cunningham. *J. Bot. British and Foreign* 4: 231–320.
- Hochreutiner, B. P. G. 1908. Un Nouveau Baobab et Revision du Genre *Adansonia*. *Ann. Conserv. Jard. Bot. Genève* 1908: 136–143.
- Hudson, R. R. 1990. Gene genealogies and the coalescent process. *Oxford Surveys in Evolutionary Biology* 7: 1–44.
- Hutchinson, J. 1967. The Genera of Flowering Plants. Oxford Univ. Press, Oxford.
- Ibn Batuta. 1922. Voyages d'Ibn Batoutah: Texte Arabe, Accompagné d'une Traduction par C. Defrémery & B. R. Sanguinetti. Vol. 4. Société Asiatique, Paris.
- . 1929. Ibn Battuta: Travels in Asia and Africa [Translated by H. A. R. Gibb]. Routledge & Kegan Paul, London.
- Inamdar, J. A. & A. J. Chohan. 1969. Epidermal structure and stomatal development in some Malvaceae and Bombacaceae. *Ann. Bot.* 33: 865–878.
- Jackson, J. R. 1868. The gouty stem tree. *The Student and Intellectual Observer* 1: 401–406.
- Jaeger, P. 1945. Évanouissement et pollinisation de la fleur du Baobab. *Compt. Rend. Acad. Sci. Paris* 220: 369–371.
- . 1950. La vie nocturne de la fleur du Baobab. *Nature (Paris)* 3177: 28–29.
- . 1954. Les aspects actuel de problème de la chéiroptérogamie. *Bull. Inst. Franç. Afrique Noire* 16: 796–821.
- Jarvis, C. E., F. R. Barrie, D. M. Allan & J. L. Reveal. 1993. A List of Linnaean Generic Names and Their Types. International Association for Plant Taxonomy, Koeltz Scientific Books, Königstein.
- Jumelle, H. & H. Perrier de la Bâthie. 1909a. Les baobabs du nord-ouest de Madagascar. *Les Matières Grasses Jan.* 1909: 1306–1308.
- & ———. 1909b. Nouvelles observations sur les baobabs de Madagascar. *Les Matières Grasses Aug.* 1909: 1509–1512.
- & ———. 1910. Fragments biologique de la flore de Madagascar. *Ann. Inst. Bot.-Géol. Colon. Marseille* 2^e sér. 8: 373–468.
- & ———. 1912. Les baobabs du sud-ouest de Madagascar. *Rev. Gen. Bot. (Paris)* 24: 372–381.
- & ———. 1913. Les baobabs de Madagascar. *Agric. Prat. Pays Chauds* 125: 61–74.
- Jussieu, A. L. de. 1789. *Genera Plantarum*. Apud Vindiam Herrissant, Typographum, & Theophilum Barrois, Paris.
- Keraudren, M. 1963. Pachypodes et baobabs à Madagascar. *Sci. & Nat.* 55: 2–11.
- Kunth, C. S. 1822. Nova genera et species plantarum. In: F. Humboldt, A. Bonpland & C. S. Kunth, Voyage aux Régions Equinoctiales du Nouveau Continent. Paris.
- Linnaeus, C. 1753. *Species Plantarum*. Impensis Laurentii Salvii, Stockholm.
- . 1759. *Systema Naturae*, ed. 10. Impensis Direct Laurentii Salvii, Stockholm.
- Lippi, A. 1704. Description des Plantes Observées en Egypte. Unpublished Manuscript.
- Lucas, G. L. 1971. The baobab map project. *Mitt. Bot. Staatssamml. München* 10: 162–164.
- Mack, J. 1986. Madagascar: Island of Ancestors. British Museum, London.
- Maddison, W. 1995. Phylogenetic histories within and among species. In: P. C. Hoch & A. G. Stephenson (editors), *Experimental and Molecular Approaches to Plant Biosystematics*. Monogr. Syst. Bot. Missouri Bot. Gard. 53.
- Mahé, J. 1972. The Malagasy subfossils. Pp. 311–

- 338 in R. Battistini & G. Richard-Vindard (editors), Biogeography and Ecology in Madagascar. W. Junk B. V., The Hague.
- Maheshawari, J. K. 1971. The baobab tree: Disjunctive distribution and conservation. *Biol. Conservation* 4: 57-60.
- Mangenot, S. & G. Mangenot. 1962. Enquête sur les nombres chromosomiques dans une collection d'espèces tropicales. *Rev. Cytol. Biol. Vég.* 25: 411-447.
- Maydell, H.-J. von. 1986. Trees and Shrubs of the Sahel. Their Characteristics and Uses. Deutsche Gesellschaft für Technische Zusammenarbeit, Eschborn.
- Mayr, E. 1942. Systematics and the Origin of Species from the Viewpoint of a Zoologist. Columbia Univ. Press, New York.
- Metcalf, C. R. & L. Chalk. 1950. Anatomy of Dicotyledons. Oxford Univ. Press, Oxford.
- Miège, J. 1974. Étude du genre *Adansonia* II. Caryologie et Blastogénèse. *Candollea* 29: 457-475.
- . 1975. Contribution à l'étude de genre *Adansonia* III. Intérêt taxonomique de l'examen électrophorétique des protéines des graines. *Boissiera* 24: 345-352.
- & H. Burdet. 1968. Étude du genre *Adansonia* I. Caryologie. *Candollea* 23: 59-66.
- & J. Lambert. 1973. Réalisation d'hétérogreffes dans la famille de Bombacacées. *Saussurea* 3: 27-34.
- Mueller, F. von. 1857. New genera and species. Hooker's J. Bot. Kew Gard. Misc. 9: 14.
- . 1858. Botanical report on the North Australian exploring expedition. *Proc. Linn. Soc. Lond. (Bot.)* 2: 140.
- Nicol, B. M. 1957. Ascorbic acid content of Baobab fruit. *Nature* 180: 287.
- Nicolas, R.-P. F.-J. 1955. Recherches sur la valeur sémantique du mot "Baobab." *Notes Africaines* 67: 77-78.
- Nilsson, S. & A. Robyns. 1986. Bombacaceae Kunth. *World Pollen Spore Fl.* 14: 1-59.
- Nixon, K. C. & Q. D. Wheeler. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211-223.
- Nour, A. A., B. I. Magboul & N. H. Kheiri. 1980. Chemical composition of Baobab fruit (*Adansonia digitata*). *Trop. Sci.* 22: 383-388.
- Ostenfeld, C. H. 1918. Contributions to West Australian Botany II. *Dansk. Bot. Ark.* 2: 22-24.
- Owen, J. 1970. The medico-cultural significance of *Adansonia digitata* (baobab) in African communities. *African Notes* 6: 26-36.
- . 1974. A contribution to the ecology of the African baobab. *Savanna* 3: 1-12.
- Perrier de la Bâthie, H. 1952a. *Adansonia* de Madagascar. Clef et diagnoses. *Notul. Syst. (Paris)* 14: 300-304.
- . 1952b. Sur les utilités de l'*Adansonia grandidieri* et les possibilités de culture. *Rev. Int. Bot. Appl. Agric. Trop.* 32: 286-288.
- . 1953. Les *Adansonia* de Madagascar et leur utilisation. *Rev. Int. Bot. Appl. Agric. Trop.* 33: 241-244.
- . 1955. Bombacacées. Pp. 1-17 in H. Humbert (editor), Flore de Madagascar et des Comores. Botanical Society of France, Paris.
- Petter, J.-J., A. Schilling & G. Pariente. 1975. Observations on the behavior and ecology of *Phaner furcifer*. Pp. 209-218 in I. Tattersall & R. W. Sussman (editors), *Lemur Biology*. Plenum, New York.
- Pijl, L. van der. 1934. The relations between flowers and higher mammals. *Hong Kong Naturalist* 5: 176-181.
- . 1956. Remarks on pollination by bats in the genera *Freycinetia*, *Duabanga* and *Haplophragma*, and on chiropterophily in general. *Acta Bot. Neerl.* 5: 135-144.
- Poisson, H. 1912. Recherches sur la Flore Méridionale de Madagascar. Librairie Maritime et Coloniale, Paris.
- Porsch, O. 1935. Zur Blütenbiologie des Affenbrotbaumes. *Oesterr. Bot. Z.* 84: 219-224.
- Presting, D., H. Straka & B. Friedrich. 1983. Paly-nologia Madagassica et Mascarenica. *Trop. Subtrop. Pflanzenwelt* 44: 139-225.
- Queiroz, K. de & M. J. Donoghue. 1990. Phylogenetic systematics or Nelson's version of cladistics? *Cladistics* 6: 61-75.
- Rabinowitz, P. D., M. F. Coffin & D. Falvey. 1983. The separation of Madagascar and Africa. *Science* 220: 67-69.
- Rao, C. V. 1952. Floral anatomy of some Malvales and its bearing on the affinities of families included in the order. *J. Indian Bot.* 31: 171-203.
- . 1954. A contribution to the embryology of Bombacaceae. *Proc. Indian Acad. Sci., Sect. B* 39: 51-75.
- Raven, P. H. & D. I. Axelrod. 1972. Plate tectonics and Australasian Paleobiogeography. *Science* 176: 1379-1386.
- & ———. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539-673.
- Ray, J. 1693. *Historia Plantarum*. Samuel Smith and Benjamin Walford, London.
- Rey, H. 1912. Notice sur l'huile de baobab. *Bull. Econ. Madagascar* 12: 135-140.
- Rick, C. M. & R. I. Bowman. 1961. Galapagos tomatoes and tortoises. *Evolution* 15: 407-417.
- Riley, H. P. 1960. Chromosomes of some plants from the Kruger national park. *J. S. African Bot.* 26: 37-44.
- Robyns, A. 1963. Essai de Monographie du genre *Bombax*. *Bull. Jard. Bot. État.* 33: 1-316.
- . 1980. Bombacaceae. Pp. 58-91 in M. D. Dassanayake & F. R. Fosberg, *A Revised Handbook of the Flora of Ceylon*, Vol. 1. Amerind Publishing, New Delhi.
- Saville-Kent, W. 1897. *The Naturalist in Australia*. Chapman and Hall, London.
- Schumann, K. 1890. Bombacaceae. Pp. 53-68 in A. Engler & K. Prantl (editors), *Die Natürlichen Pflanzenfamilien*, III. Teil, 6 Abteilung. W. Engelmann, Leipzig.
- Sharma, B. D. 1969. Contribution to the pollen morphology and plant taxonomy of the family Bombacaceae. *Proc. Indian Acad. Sci.* 36B: 174-191.
- Stafleu, F. A. & R. S. Cowan. 1976. *TL-2 Taxonomic Literature*, Vol. 1: A-G. Regnura Veg. 94.
- Start, A. N. 1972. Pollination of the Baobab (*Adansonia digitata*) by the fruit bat, *Rousettus aegyptiacus*. *E. African Wildlife J.* 10: 71-72.

- Stokes, J. 1846. Discoveries in Australia. Voyages of HMS Beagle. T. & W. Boone, London.
- Swart, E. R. 1963. Age of the baobab tree. *Nature* 198: 708–709.
- Tattersall, I. 1982. The Primates of Madagascar. Columbia Univ. Press, New York.
- Teil, E. 1979. De Bry: India Orientalis. Gustav Kiepenheuer, Leipzig and Weimar.
- Templeton, A. R. 1989. The meaning of species and speciation: A genetic perspective. Pp. 3–27 in D. Otte & J. A. Endler (editors), *Speciation and Its Consequences*. Sinauer Press, Sunderland, Massachusetts.
- Thevet, A. 1878. Les Singularitez de la France Antarctique. Maisonneuve, Paris.
- Vaid, K. M. 1978. Where is the mythical “wishing tree”? *Science Today*, April 1978: 35–44.
- Vaishampayan, N. & Y. N. Sharma. 1981. On the pollen morphology of the genus *Adansonia*. *Curr. Sci.* 50: 919.
- Veslingius, J. 1638. De Plantis Aegyptiis Observationes et Notae ad Prosp. Alpinum. In: P. Alpino, De Plantis Aegypti Liber, 2nd Ed. Franciscum de Franciscis Senensem, Venice.
- Verdoorn, I. C. 1933. The Baobab. *S. African J. Sci.* 30: 255–257.
- Watt, J. M. & M. G. Breyer-Brandwijk. 1962. The Medicinal and Poisonous Plants of Southern and Eastern Africa. Ed. 2. E. & S. Livingstone, Edinburgh.
- Wickens, G. E. 1979. The use of the baobab (*Adansonia digitata*) in Africa. Pp. 27–34 in G. Kunkel, *Taxonomic Aspects of African Economic Botany*, Proceedings of the IX Plenary Meeting of AETFAT. Excmo. Ayuntamiento, Las Palmas de Gran Canaria, Canary Islands.
- . 1983. The baobab: Africa's upside-down tree. *Kew Bull.* 37: 173–209.
- Wildeman, E. de. 1903. Notices sur des Plantes Utiles ou Intéressantes de la Flore du Congo, Vol. 1. Veuve Monnom, Brussels.
- Willis, J. H. 1955. A bibliography of the Australian baobab. *Muelleria* 1: 61–63.
- List of Species**
1. *Adansonia grandidieri* Baill.
 2. *Adansonia suarezensis* H. Perrier
 3. *Adansonia digitata* L.
 4. *Adansonia gibbosa* (A. Cunn.) Guymer ex D. Baum
 5. *Adansonia rubrostipa* Jum. & H. Perrier
 6. *Adansonia madagascariensis* Baill.
 7. *Adansonia za* Baill.
 8. *Adansonia perrieri* Capuron
- Collections of *Adansonia* Examined**
- Specimens are listed alphabetically by collector. The numbers in parentheses correspond to the number of the species in the text.
- Abraham, J.-P. 48 (5). Adam, J.-G. 27199 (3). Allan, K. M. 610 (4). Allaud s.n.(a) (2); s.n.(b) (6). Ament, J. 444 (3). Ament, J. & F. Magogo 281 (3). Amshoff, G. J. H. 4973 (3). Angus, A. 1768 (3). Anonymous E s.n. (5); P F6375 (5). Ashanti 513 (3). Baillon s.n. (7). Balakrishnan, N. 605 (3). Balsinhas, A. 22 (3). Bamps, P. 2227 (3). Baron 35a (3); 516 (7). Barter 1528 (3). Baum, D. A. 305 (7); 307 (7); 308 (8); 311 (7); 313 (5); 314 (8); 315 (6); 316 (6); 317 (6); 318 (6); 319 (6); 319A (2); 320 (6); 320A (2); 321 (1); 322 (4); 323 (4); 324 (4); 325 (4); 326 (4); 327 (7); 329 (3); 330 (7); 331 (7); 332 (7); 334 (7); 335 (7); 336 (7); 337 (7); 338 (6); 339 (7); 340 (8); 341 (8); 344 (7); 345 (1). Beaglehole, A. C. 11099 (4); 47638 (4); 48114 (4); 52476 (4); 53798 (4); 54043 (4); s.n. (4). Bell, A. S. 712 (3). Bellamy 657 (3). Bellemy, M. s.n. (7). Bennet, E. M. 1895 (4). Berhaut, R. P. 103 (3). Bernardi 11802 (3). Bernier 2/364 (6). Bjornstadt, A. 657 (3); 1965 (3). Blackburn s.n. (3). Boivin M. 2592 (6); 2593 (6); s.n. 1847–1852 (3). Bosser, J. 4343 (7); 9907 (1); 13860 (7); 14228 (5); 15743 (5); 15865 (7); 19286 (7). Box, H. E. 1550 (3). Breniere s.n. (7). Breyne, H. 241 (3). Britton, N. L. & E. G. Britton 9387 (3). Broadbent 428 (4). Broadway, W. E. s.n. (3). Bruce, E. M. 210 (3). Bullock, A. A. 3462 (3). Burnett, G. F. 48/40 (3). Burtt, B. D. 5510 (3). Burtt Davy, J. L. 22555 (3). Bynoe s.n. (4).
- Calvert Expedition s.n. (4). Campbell, W. S. 92 (4). Carr, G. W. 3860 (4); 4336 (4). Cassaigne, V. s.n. (3). Chabonis s.n. (1). Chang 10168 (3). Chapman, J. D. 5188 (3). Chase, N. C. 3728 (3). Chevalier, A. 1104 (3); 3055 (3); 3066 (3); 4230 (3); 11371 (3); 12541 (3); 20145 (3); 20453 (3); 23017 (3); 23641 (3); 24451 (3); 25691 (3); 44992 (3). Chinnock, R. J. 6911 (4). Chipp, T. T. 513 (3). Closel s.n. (7). Cook, O. F. 7 (3). Corbisier-Baland, A. 1507 (3). Coridou F6769 (2). Cramer, L. H. 4092 (3). Croat, T. B. 31006 (5); 31469 (7). Cunningham, A. 308 (4). Curran, H. M. 139 (3).
- Dacremont 366 (3). de Winter 3643 (3). Decary 17 (6); 1146 (7?); 1212 (7); 1464 (6); 1593 (6); 1604 (6); 3552 (7); 3553 (7); 3554 (7); 3555 (7); 3556 (7); 3557 (7); 3558 (7); 3559 (7); 3560 (7); 3561 (7); 3562 (7); 3563 (7); 3564 (7); 3570 (7); 3571 (7); 3572 (7); 7814 (6?); 7842 (5); 8348 (7); 8350 (7); 9319 (7); 9622 (7); 9623 (7); 15343 (6); 15346 (3); 15506 (5); 15789 (5); 16413 (5); 16426 (7); 16431 (7); 16433 (7); 16434 (7); 16435 (7); 17088 (7); 18824 (5); s.n. (7). Degener, O. 20716 (3). Devred, R. 648 (3). Dorr 4113 (5). Drew s.n. (3). Drummond & Seagriff 5244 (3). Dupus, P. s.n. (3). Duss, P. 2032 (3).
- Edward 491a (4). Ekman, E. L. 3258 (3).
- Farnar, L. 515 (3). Faulkner, H. G. 2735 (3). Fidalgo de Carvalho, M. 868 (3). Fitzgerald, W. s.n. (4). Flamigni 10488 (3). Fosberg, F. R. 53631 (3). Fotius 1689 (3). Freney, R. s.n. (4). Friedman, F. 2461 (3). Fryxell & Craven 4210 (4).
- Gardner, C. A. 1128 (4); 9772 (4); s.n. (4). Gentry 11935 (6). Gereau, R. et al. 2814 (3). Gillett, J. B. 1657 (3). Gillett, J. B. & C. F. Hemming 24910 (3). Gillis, W. T. 9418 (3). Gomes & Sousa 4276 (3). Gordon, K. J. 545 (3); 3300 (3). Goudot s.n.(a) (6); s.n.(b) (2). Grandier 39 (5); s.n., 1895 (1); s.n., 1897 (1). Greenway, P. J. 6416 (3). Greenway, P. J. & Kanuri 14614 (3). Greenway & Kirrika 10953 (3). Grévé 20 (1); 37, F6376 (7); 38 (5); 275 (1); F6771 (1); s.n. (a) (1); s.n. (b) (1); s.n. (c) (7). Guillaumet 2286 (5).
- Hakki, M. B. et al. 124 (3); 727 (3). Hamilton, F. 1527 (3). Hardwicke s.n. (3). Hartley 14411 (4). Hazlewood s.n. (4). Hildebrandt, J. M. 1930 (3). Hladik 27 (1); s.n. (5). Hochreutiner, B. P. C. 2849 (4). Homolle 1563 (5). Howard, R. A. 4188 (3). Humbert, H. 6738 (7); 11523 (5); 12326 (7); 12441 (7); 12800 (7); 14348bis (7?); 17560 (8); 18756 (7); 20224 (5). Humbert & Capuron 25500 (7); 25680 (8); 25720 (6). Humblot, L. 379 (3). Hyland 8546 (4).

- Jardin Tsimbazaza 4492 (5); 4896 (7).
 Kenneally, K. F. 5255 (4); 8997 (4); 9733 (4). Keraudren, M. 871 (7); 1385 (7); 1412 (5). Keraudren-Aymonin, M. & G. G. Aymonin 24738C (7); 25612 (2); 25613 (6); 25700 (7); 25840 (7); 25860 (1); 25917 (7); 25918 (1); 25920 (7); 25924 (7). Koechlin, J. 1033 (3); 5531 (3).
 Latz, P. K. 1003 (4). Lazarides 8484 (4). Leandri, J. 3999 (5); 4017 (5); 4231 (7); 4232 (7); 4233 (7). LeBrun 709 (3); 2603 (3); 5726 (3). Lejoly, J. 80/217 (3). Letouzey 7314 (3); Leutert 11 (4). Liogier, A. H. & P. Liogier 32387 (3). Long, D. G. 12389 (3). Lorence, D. 1550 (3); 1906 (7); 2800 (3). Lorence, D. & J. Guého 17639 (3). Lørsen 13741 (4). Love, J. R. B. s.n. (4).
 Maconochie, J. R. 3523 (3). Maheshawari, J. K. 82773 (3). Malcomber, S. T. 1141 (7). Mavi, S. 1480 (3). McPherson, G. 14538 (8). McPherson, G. & M. Pigeon 14932 (7). McVicar, D. 1802 (4). Mendonca, F. A. 3179 (3). Menyharth 189 (3); 772 (3). Migeod, F. W. 617 (3). Miller, A. G. 7039. Miller, G. S. 315 (3). Miller, J. & A. Randrianasolo 6118 (5). Mission Cirtat s.n. (7). Morat 210 (3); 704 (7); 3065 (6). Mosnier, M. 2133 (3). Mueller, F. BM 14381 (4); G 27 (4); GH s.n. (4); MEL 229657. Mulilo, K. et al. 178 (3). Museum Series F26 (6). Must, J. 904 (4).
 Newton, L. E. 727 (3).
 Obermeyer et al. 69 (3). Ostenfeld, C. H. 1175 (4).
 Pawek, J. 12000 (3). Peltier & Peltier 2854 (7). Perrier de la Bâthie 960 (7?); 960A (7); 960B (7); ex960B (7); 960C (7); 960D (7); 960E (7); 1019 (a) (6); 1019 (b) (6); 1019bis (3); 1047 (5); 1447 (5); 1447bis (5); 4805 (1); 5356 (6); 5368 (6); 5396 (7); 5734 (3); 5735 (5); 8159 (7); 8160 (6); 8162 (5); 8165 (7); 8166 (7); 8167 (3); 8168 (3); 8168bis (3); 8169 (3); 8171 (3); 8172 (1); 8174 (5); 8175 (5); 8176 (5); 8177 (5); 8178 (7); 8179 (6); 8180 (7); 8181 (7); 8182 (7); 8183 (7); 8184 (7); 8187 (7); 8188 (7); 8189 (7); 8189bis (7); 8190 (7); 13447 (7); 13448 (6); 13449 (6); 13478bis (7); 14671 (6); 15910 (7); 16194 (6); 16340a (7?); 16340b (7); 16429 (6); 16737 (7); 17560 (8); 17560bis (8); 17686 (2); 17834 (5); 18849 (6); 19113 (5); s.n. (5); s.n. (7). Perry 2501 (4). Phillipson, P. B. 2638 (7); 3063 (1); 3468 (5). Poisson 109 (6); 647 (7); 1001 (7).
 Portere, R. 1803 (3). Puff 781 (7); 784 (7); 1103 (5). Pullen 10664 (4).
 Radcliffe-Smith 5548 (3). Rakotozafy 793 (5); 1227 (3). Ravelonahary 4992 (5). Raynal, J. & A. R. Raynal 5987 (3). Read, R. W. 1262 (3). Reb Deb 8702 (3). Reserve Naturelle (RN) (Randrianasolo) 3306 (5); (Randriamiera) 7343 (5). Richards, H. M. 11521 (3); Richards, M. 26329 (3). Ricksecker, J. J. 451 (3). Robyns, A. G. 6966 (3); 6969 (3); 6970 (3); 7339 (3). Rock, J. F. s.n. (3). Rodin, R. J. 2637 (3); 4237 (3); 9042 (3); 9201 (3). Rose, M. 614 (3). Rose et al. 3511 (3). Royce, R. D. 6884 (4). Ruffo 1471 (3).
 Sacleux, R. P. 666 (3); 1751 (3). Salubeni, A. 886 (3). Schatz, G. E. 1751 (5); 1780 (7). Schimper s.n. (3). Schleiben, H. J. 5406 (3). Schweinfurth 1605 (3). Seligson, D. 359 (3). Service Forestière (SF) (Collector #76) 45 (1); 455 (7); 3022 (7); (Capuron) 3029 (6); 3038 (8); 3376 (7); (Capuron) 6938; (5) (Belin) 9733 (6); 12439 (5); 13209 (6); 14042 (a) (6); 14042 (b) (6); 14225 (2); (Champsoloix) 17924 (5); (Capuron) 19000 (8); (Capuron) 20076 (8); (Capuron) 20252 (7); (Capuron) 20595 (7); (Capuron) 22141 (7); (Capuron) 24283 (3); (Capuron) 24622 (5); (Capuron) 29223 (2); 30877 (5). Seyrig 91 (7). Shantz, L. 416 (3). Shaw, E. A. 790 (4). Smith, G. G. s.n. (4). Staer s.n. (4). Stewart, J. L. s.n. (3). Stocks, J. 72 (3). Sussman, L. 179 (7). Swabrick 2451 (3). Swynnerton, C. F. M. s.n. (3).
 Tanner, R. E. S. 1104 (3); 2833 (3). Thomas, N. W. 2626 (3); 2799 (3). Tracey 13922 (4). Tweadie 3782 (3).
 Ugor, E. 21948 (3).
 Vaillant A. 100 (3). Vanderyst 1447 (3); 27201 (3); 28763 (3); s.n. (3). Vasse, G. 330 (3). Verdcourt 1602 (3). Vermoesen, F. 1109 (3); 1300 (3).
 Wadsworth, R. K. 579 (3). Wagemans, J. 1821 (3); 2255 (3); 2261 (3). Wallace, G. B. 514 (3). Wallich s.n. (3). Waterhouse, J. T. & P. G. Wilson 4650 (4). Welwitsch 5415 (3); 5416 (3); 5418 (3); 5418b (3); 5419b (3); 5420 (3). White, F. 2627 (3). Whiting, M. 4842-105 (3). Wickens, G. E. 3050B (3); 3087 (3); 3093 (3). Wight 227 (3). Willing, T. 72 (5). Wilson, P. G. 292 (4). Wirawan et al. 954 (3). Wood, J. R. 8 (3).
 Zarucchi, J. L. 7468 (7). Zepernik 124 (3); 727 (3).

STATISTICAL SUMMARY OF SOME OF THE ACTIVITIES IN THE MISSOURI BOTANICAL GARDEN HERBARIUM, 1994

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections (includes bryophytes)	27,518	—	27,518
Purchase	211	10,000	10,211
Exchange	42,688	2,150	44,838
Gifts	<u>8,103</u>	<u>55</u>	<u>8,158</u>
Total acquisitions	78,520	12,205	90,725
Mountings			
Newly mounted	79,736	21,304	101,040
Mounted when received	<u>84,000*</u>	<u>0</u>	<u>84,000</u>
Total specimens filed	163,736	21,304	185,040
Repairs			
Specimens repaired	30,556	n/a	30,556
Specimens stamped	<u>5,784</u>	<u>n/a</u>	<u>5,784</u>
Total repairs	36,340	0	36,340
Specimens sent			
On exchange	29,828	4,824	34,652
As gifts	<u>28,892</u>	<u>1,539</u>	<u>30,431</u>
Total	58,720	6,363	65,083
Loans sent			
Total transactions	680	33	713
Total specimens	29,307	2,551	31,858
To U.S. institutions			
Transactions	407	27	434
Specimens	16,084	2,368	18,452
To foreign institutions			
Transactions	273	6	279
Specimens	13,223	183	13,406
To student investigators			
Transactions	66	7	73
Specimens	6,633	822	7,455
To professional investigators			
Transactions	614	26	640
Specimens	22,674	1,729	24,403
Loans received			
Transactions	321	22	343
Specimens	16,697	1,818	18,515

* The 84,000 vascular plants "mounted when received" are all specimens of Chinese plants purchased directly from China.

	From U.S.	From abroad	Total
Visitors	427	123	550

On 31 December 1994 the total number of mounted, accessioned specimens in the herbarium was 4,488,028 (4,225,255 vascular plants and 262,773 bryophytes). Corrected total figures for 1993 are: 4,297,204 total mounted, accessioned specimens in the herbarium (4,055,735 vascular plants and 241,469 bryophytes).—David Brunner, *Curator of the Herbarium*.