

Biogeography and Evolution in Neo- and Paleotropical Rhipsalinae (Cactaceae)

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With 4 figures

Summary: The Cactaceae comprise about 2 200 species in North and South America. They are dispersed by animals; some anemochorous and hydrochorous exceptions are mentioned. The distribution of most species is rather limited, apart from a few widespread *Opuntia* spp. and *Rhipsalis* spp. According to a revised concept, the Rhipsalinae (published are 12 genera with some 300 species) consist of 5 genera with about 60 species: *Rhipsalis* (ca. 42 spp., incl. *Lepismium* and *Erythrorhipsalis*), *Pfeiffera* (5 spp., incl. *Acanthorhipsalis*), *Hattiora* (2 spp.), *Rhipsalidopsis* (3 spp., incl. *Epiphyllopsis* and *Pseudozygocactus*) and *Schlumbergera* (5 spp., incl. *Zygocactus* and *Epiphyllanthus*). The distribution of Rhipsalinae in the neotropics is illustrated by a map. It shows two evolutionary centers: a minor center in eastern Bolivia and adjacent regions (with about 10 spp.) and the main center of diversity in south eastern Brazil (with about 50 spp.). Only three species of *Rhipsalis* are widely distributed in tropical America, of which *R. baccifera* (= *R. cassutha*) occurs from Paraguay in the south to Florida in the north. For the first time a detailed distribution map of *Rhipsalis* in the paleotropics is provided: *R. baccifera* occurs throughout tropical Africa (from Sierra Leone and Ethiopia in the north to Angola and South Africa in the south), Madagascar and adjacent islands, and Ceylon. The Old World evolutionary center is Madagascar with two additional endemic species (*R. fasciculata* and *R. horrida*). All paleotropic taxa differ in several characters from the neotropical plants; they are all tetra- to octoploid. Neoteny plays an important role as evolutionary mechanisms of the dwarf terrestrial forms in Madagascar. *Rhipsalis* was not introduced by man into the Old World. A clear correlation between distribution and dispersal is demonstrated: the widespread species show an enormous production of bird-dispersed fruits and seeds embedded into an extremely viscid pulpa. These taxa show the extremest adaptation to epi-ornithochory within the Cactaceae and also have the widest distribution within the family.

The Cactaceae comprise about 2 200 species in North and South America. Their fruits and seeds are dispersed by animals, probably predominantly endo-ornithochorous. Several dwarf globular genera (e. g. *Ariocarpus*, *Mammillaria* spp., *Aztekium*, *Strombocactus*, *Blossfeldia*) are probably hydrochorous (the latter three genera

possibly also myrmecochorous). The opuntioid genus *Pterocactus* with large winged seeds and probably also certain South American cereoid genera with dry fruits (e. g. *Thrixanthocereus blossfeldiorum*) are anemochorous. The distribution of single species is rather limited, with the exception of some *Opuntia* spp. (dispersal by burr-like fruits and stem segments) and the genus *Rhipsalis*.

Most of the stem succulent cacti inhabit arid and semi-arid regions. But about 10 % of all species of the family are adapted to the life as epiphytes in more humid regions; some of them have secondarily lost their succulency. These about 220 epiphytic species belong into the subfamily Cactoideae and form two natural groups: the Hylocereinae with the evolutionary center in southern Mexico and the Central American land bridge (important genera: *Hylocereus*, *Selenicereus*, *Weberocereus*, *Heliocereus*, *Epiphyllum*, and *Disocactus*) and the Rhipsalinae with the evolutionary center in southern South America (fig. 1). It is not yet clear, if Rhipsalinae and Hylocereinae are closely related or if they have developed conver-

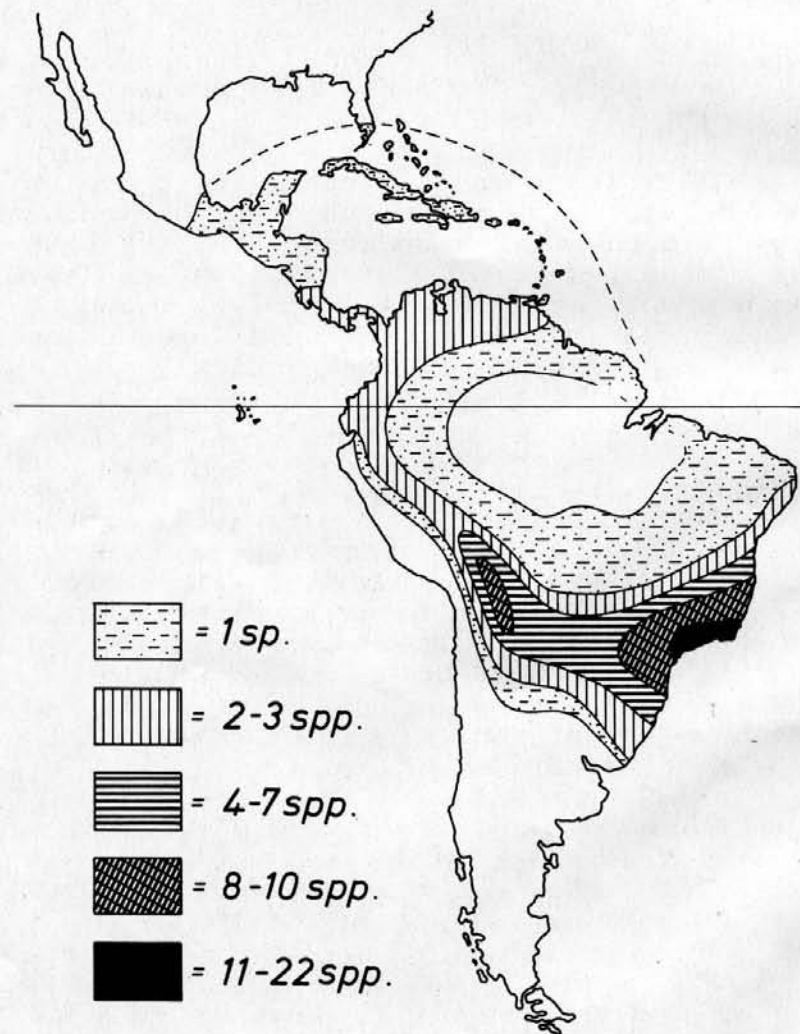


Fig. 1: Distribution of the Rhipsalinae in the New World. — The different patterns indicate the number of species occurring with the area. The two evolutionary centers are eastern Bolivia and mainly southeastern Brazil.

gently from different groups within the Cactoideae (further data in BARTHLOTT 1979).

Rhipsalis and allied genera are here treated in the rank of a subtribe. Described are 12 genera with some 300 species. In the process of a revision and monograph of the subtribe, the number of taxa had to be reduced drastically. In the following concept 5 genera with some 60 species are accepted: *Rhipsalis* (ca. 42 spp., incl. *Lepismium* and *Erythrorhipsalis*), *Pfeiffera* (5 spp., incl. *Acanthorhipsalis*), *Hattiora* (2 spp.), *Rhipsalidopsis* (3 spp., incl. *Epiphyllopsis* and *Pseudozygocactus*) and *Schlumbergera* (5 spp., incl. *Zygocactus* and *Epiphyllanthus*).

Like the Hyllocereinae, the Rhipsalinae show a great plasticity in their vegetative morphology. The repent or mostly pendent plants show within closely allied species three- to six-angular, or terete, or leaf-like flattened stems. Their floral morphology is - like in all Cactaceae - less diverse. The flowers are amongst the smallest in the family (diameter usually less than 2 cm), they have a ring-like disk, they are actinomorphic with mostly pale colored or white free tepals (*Hattiora* and *Rhipsalidopsis* have bright yellow, pink, or red flowers). The genus *Schlumbergera* has large red zygomorphic flowers with a petaloid receptacular tube; this genus also differs in its pollen morphology (LEUENBERGER 1976).

Fig. 1 shows distribution and centers of diversity of the Rhipsalinae in tropical America (the numbers of species indicated are already based on the concept of a reduced number of taxa). With the exception of some *Rhipsalis* spp. all genera are restricted to the two evolutionary centers in eastern Bolivia and south eastern Brazil with adjacent regions. Characteristic for the Bolivian center is the succulent spiny genus *Pfeiffera* (incl. *Acanthorhipsalis*), plus a few rather ancestral spiniferous repent species of *Rhipsalis*, such as *R. lumbricoides* (LEM.) LEM. and *R. acculeata* WEBER.

The genera *Hattiora*, *Rhipsalidopsis* and *Schlumbergera* are restricted to the Brazilian evolutionary center, which comprises approximately the States of São Paulo, Minas Gerais, and Paraná. The ornithogamous genus *Schlumbergera* must be considered as rather advanced; but this genus also comprises some succulent spiny species (e. g. *Schl. opuntiioides*), which have evolved secondarily by neotenic mechanisms (BARTHLOTT & RAUH 1975). Southeastern Brazil is also the evolutionary center for *Rhipsalis* itself with more than a dozen species out of several sub-genera.

Only three species of *Rhipsalis* have a wide distribution in tropical America. *Rhipsalis micrantha* H.B.K. occurs from Peru to Colombia (BARTHLOTT 1974), reaches the western part of Venezuela and has its northern limit in Costa Rica (described from there as *R. tonduzii* WEBER and *R. wercklei* BERGER). Another species, *Rhipsalis floccosa* SALM-DYCK, occurs with slightly differing geographical forms (described as species under different names) from Paraguay in the south to Venezuela in the north (from there described as *R. pittieri* BRITTON & ROSE). Finally, *Rhipsalis baccifera* (MILLER) W.T. STEARN (= *R. cassutha* GAERTNER) occurs throughout the whole range of the subtribe from Argentina and Uruguay in the south throughout South America - with the exception of inner Ama-

zonia* - up to the humid parts of Mexico, the Caribbean Islands and reaches its northern limits in the Everglades in Florida, U.S.A. (fig. 1).

The fruits of the Rhipsalinae are fleshy white, yellow, or red juicy berries. Each berry contains about 10 to 100 blackish seeds, which are only about 1,5 millimeter long. These seeds (survey in BARTHOLOTT & VOIT 1979) possess in their hilum-micropyle region a gelatinous sticky appendix. The fruit pulpa of most species is watery to gelatinous; but in the genera *Rhipsalidopsis* and *Schlumbergera* (both with very restricted distribution), this pulpa is more or less absent. The diaspores of the Rhipsalinae are obviously adapted to endo- and epi-ornithochorous dispersal: Ornithochory and anemochory are the characteristic dispersal mechanisms for epiphytes (e. g. MADISON 1977).

Some species of *Rhipsalis* are self-fertile and show a high production of diaspores; in these species an extremely viscid pulpa is also developed. All the three wide-spread species (*R. micrantha*, *R. floccosa*, and *R. baccifera*) belong to this group; the latter is characterized by an enormous production of viscid berries which resemble the fruits of *Viscum album* (the common name of *R. baccifera* is "mistletoe-cactus"). This highly sticky pulpa must be considered as an extreme adaptation to epi-ornithochory; this is also the extremest case within the family Cactaceae.

Rhipsalis baccifera has not only the widest distribution in the Neotropics (fig. 1), but also occurs in wide parts of the Palearctica. Fig. 2 shows for the first time a detailed distribution map of *Rhipsalis* in the Old World, based on herbarium specimens (mainly K, BM, and P). The area comprises all parts of humid tropical Africa: in the west from Sierra Leone into northern Angola; throughout Central Africa; in the east from Ethiopia to South Africa (southwards actually reaching the Cape Province). Eastwards the distribution extends via the Comores, Madagascar, the Seychelles, Mauritius and Réunion to Ceylon, but does not reach the Indian subcontinent.

Since the publication of the description of "*Rhipsalis aethiopica*" by F. WELWITSCH in the year 1859, it has been violently disputed whether these cacti are indigenous to the Old World or introduced by man. Altogether about a dozen species of *Rhipsalis* have been described from the palearctica. Most authors have considered them identical with neotropical taxa and therefore introduced by man in rather recent times (e. g. ROLAND-GOSSELIN 1912, BRITTON & ROSE 1919-1923, ANTHONY 1949, BUXBAUM 1970). Others expected them to be indigenous (SCHUMANN 1891, SCHUMANN 1903, WEBER 1892, CROIZAT 1952, BACKEBERG 1942, BACKEBERG 1958-1962). Most of the arguments used on both sides were more or less speculative: comparative studies of neo- and palearctical material could only be done in the past few years, beginning with extensive collections of living material in Madagascar by Werner RAUH.

*) During the symposium Dr. G.T. PRANCE (New York) has drawn my attention to the possible occurrence of *Rhipsalis* in Amazonia, which needs further investigations

The neotropical Rhipsalinae have the characteristic cactoid chromosome number of $2n = 22$ (excepted are tetraploid forms of *R. micrantha*). This is also true for the *R. baccifera* of the South American subcontinent, but this species becomes tetraploid towards

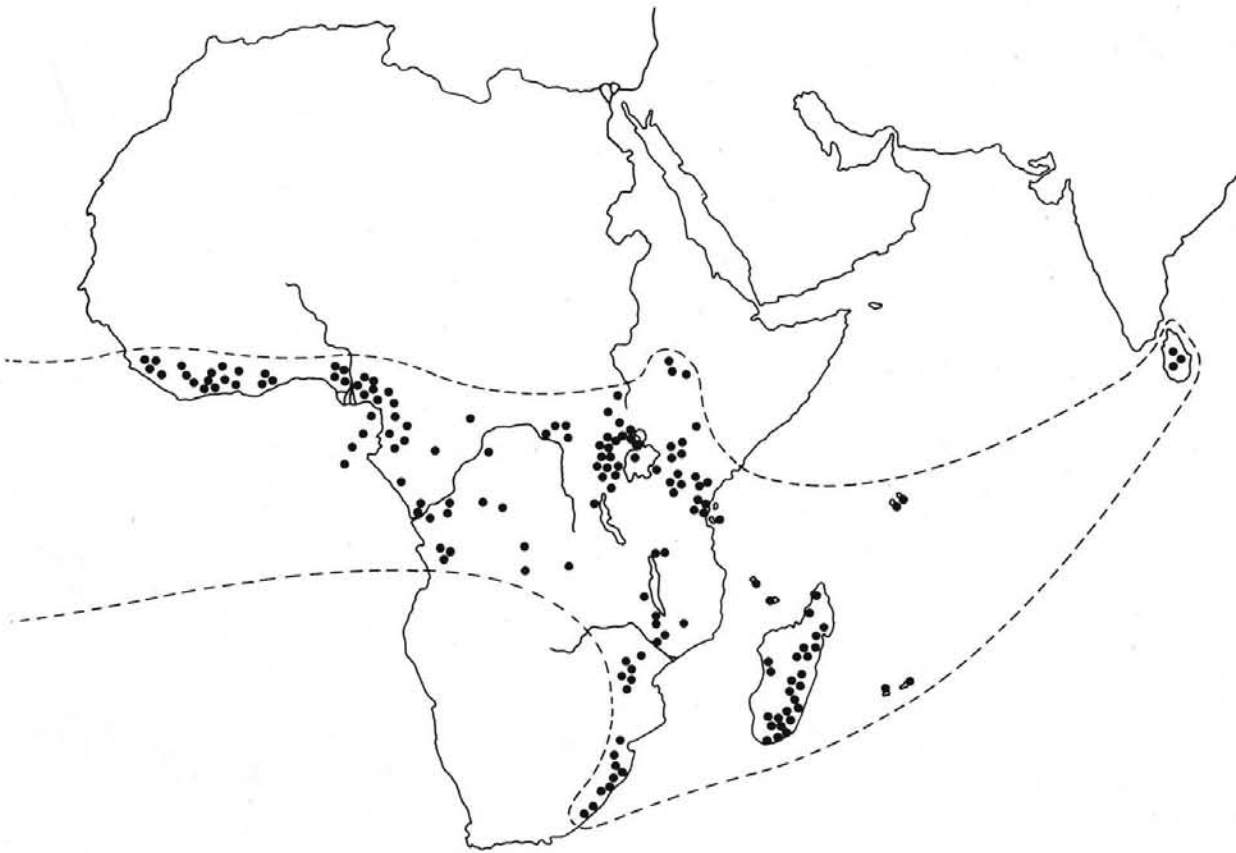


Fig. 2: The paleotropical distribution of *Rhipsalis*. — The map is based on herbarium specimens (mainly K, BM, P). The species concerned are *R. baccifera* and the two species endemic to Madagascar: *R. horrida* and *R. fasciculata*.

the northern boarder of its distribution (e. g. Florida; further data in BARTHLOTT 1976). In contrast to the South American populations, all paleotropical populations of *Rhipsalis baccifera* are tetraploid ($2n = 44$). These tetraploid paleotropical forms also differ from the neotropical taxa by having larger and a higher number of fruits. During field work in the Ivory Coast, we observed plants of *R. baccifera* (fig. 3) consisting of more than 50 % of their total weight of diaspores — a ratio which reminds one of the productivity of zooparasites. The West African taxa differ only slightly (e. g. pollen morphology) from the neotropical populations. But one encounters an increase of differences and variability in East Africa. As an example, the red-fruited varieties of *Rhipsalis baccifera* in the mountains of Kenya and Tanzania could be mentioned; these have already been described by K. SCHUMANN as "*Rhipsalis erythrocarpa*".

But the paleotropical evolutionary center of the genus *Rhipsalis* is Madagascar. There occur pendent terete forms of *R. baccifera* with globular or elliptic, white, greenish, or pink fruits; also

hanging bristly epiphytes, which can be considered as an own species *R. fasciculata* (WILLD.) HAWORTH. Finally, in the dry southwest of Madagascar occur very bristly dwarf terrestrial forms of *Rhipsalis*, forming cushions only a few centimeters high. These forms are tetra- to octoploid ($2n = 88$); their oldest valid name is *Rhipsalis horrida* BAKER (incl. *R. madagascariensis* WEBER, *R. suareziana* WEBER, *R. corallioides* RAUH; compare also GUILLAUMET 1972). These taxa look very cactoid "primitive", but they are de-

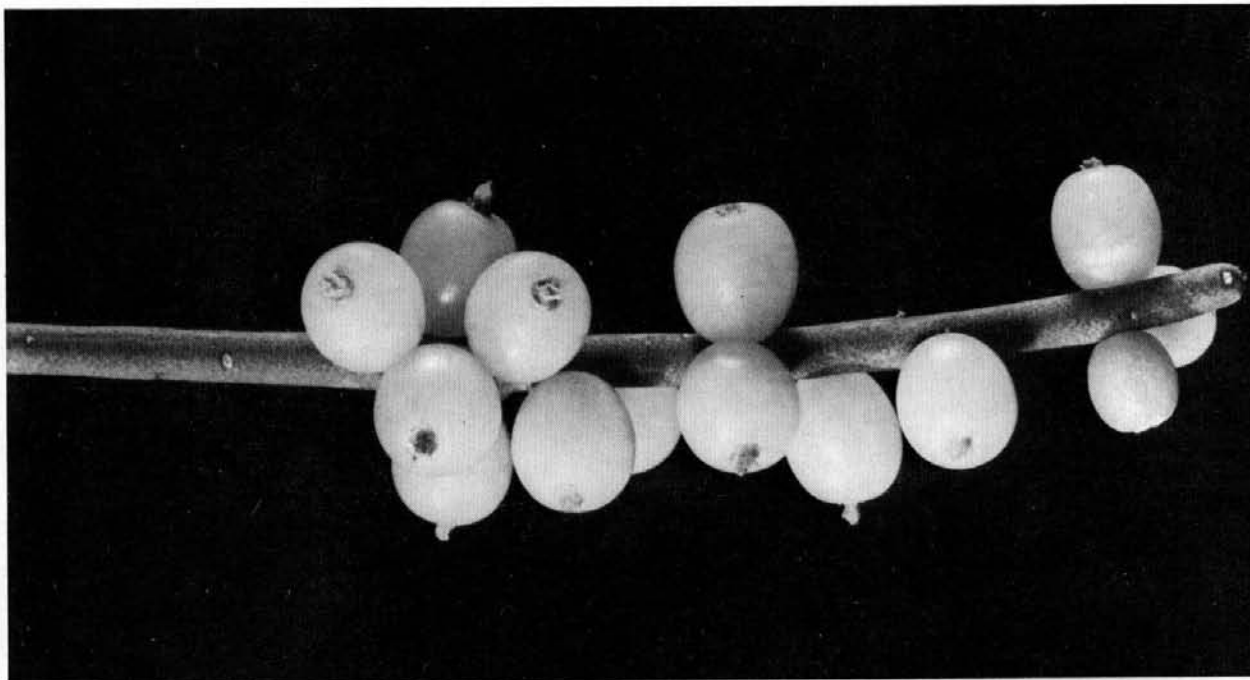


Fig. 3: *Rhipsalis baccifera* (MILLER) STEARN (= *R. cassutha* GAERTNER), a fruiting tetraploid ($2n = 44$) plant from southwestern Ivory Coast. — More than 50 % of the total weight of these West African plants can consist of fruits. Each berry contains about 50 minute viscid seeds.

rived from epiphytic ancestors and have secondarily adapted to terrestrial life. They are "de-specialized" by neotenic evolutionary mechanisms ("escape from specialization" by ontogenetic abbreviation in the sense of HARDY 1954). There exist series of all intermediate stages: taxa, which flower as spiny dwarf cushion-plants and remain under dry environmental conditions all their life in this juvenile stage. Some of these forms - but not all populations - can develop in greenhouse culture under humid conditions into the terete hanging epiphyte without any spines. In their pollen morphology the polyploid paleotropical *Rhipsalis* show a high diversity: they usually have more than 12 colpi (up to 26-colpate in the octoploid forms of *R. horrida*); the tectum is often not completely developed. This does not occur in the neotropical taxa, which also have usually 3- to 9-colpate pollen grains.

These paleotropic taxa of *Rhipsalis* do not occur in the neotropics; contradictory statements by BRITTON & ROSE and others have proved to be erroneous. On the other hand, it is definitely difficult to accept for example the opinion of CROIZAT (1952) that a

very derived angiosperm like *Rhipsalis* should be an old Gondwana relict. But all the data suggest (presented here are only some results of the more comprehensive investigations) that *Rhipsalis* cannot have been introduced by man into the paleotropics in recent times. Based on old herbarium material, fig. 4 shows that *Rhipsalis* has been known from the whole range of its paleotropic occurrence since the middle of the 19th century (e. g. collected in the most remote parts by STUHLMANN on the occasion of the first attempt to cross tropical Africa by Emin PASCHA). The comparison between fig. 2 and fig. 4 also shows that the paleotropical area of *Rhipsalis* is very stable and has not undergone any changes in the last 130 years.

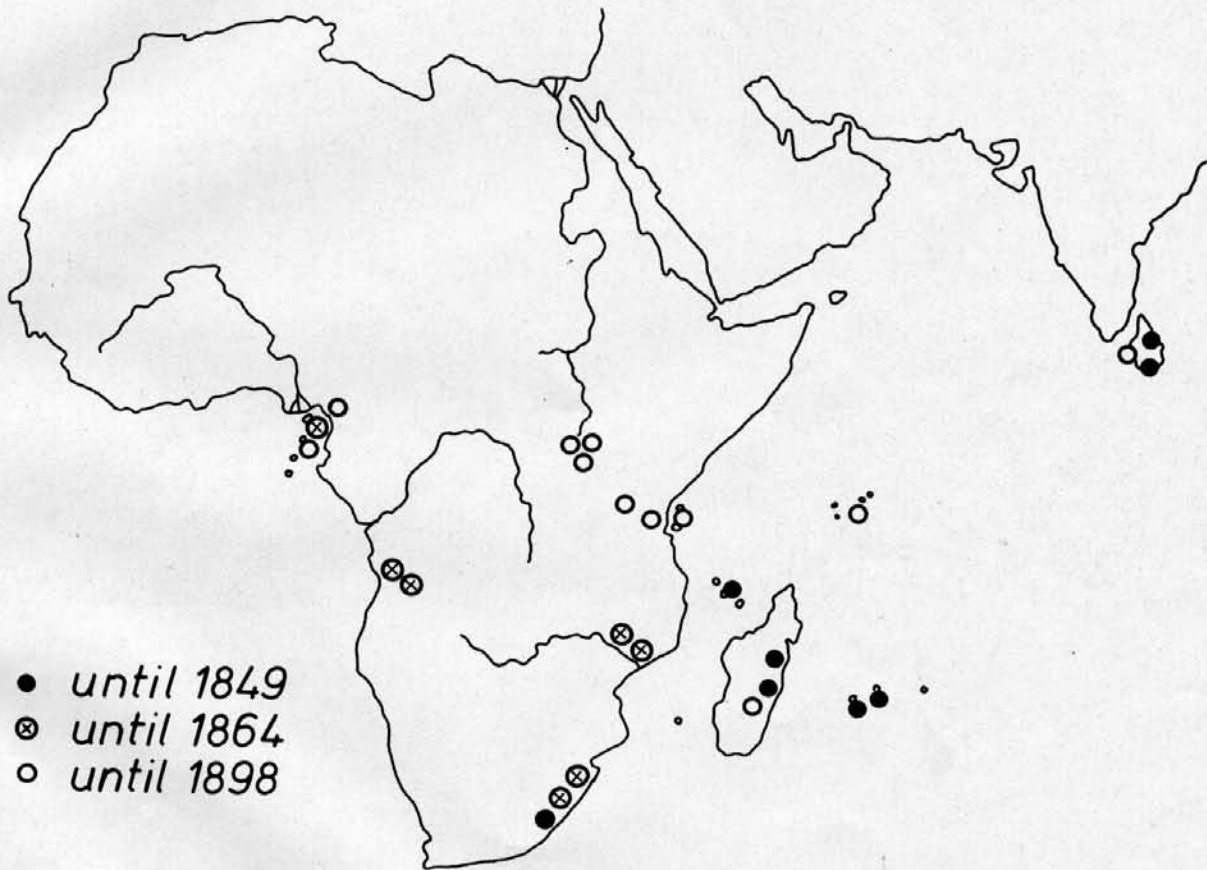


Fig. 4: Map illustrating the history of discovery of *Rhipsalis* in the paleotropics. — The different symbols indicate the known locations up to the years 1849, 1864, and 1898.

The systematic status of the paleotropic *Rhipsalis* excludes the possibility that their occurrence may be related in any form to plate tectonic events. All data suggest that *Rhipsalis baccifera* must have crossed the Atlantic by means of ornithochory, spread from West Africa eastwards, and developed a secondary evolutionary center in Madagascar. In the very particular case of *Rhipsalis*, a clear interrelationship between dispersal and distribution can be recognized: within the Cactaceae, these species show the extremest adaptation to epi-ornithochorous dispersal by producing high numbers of fruits with highly viscid seeds. At the same time, these taxa have the widest distribution within the Cactaceae and occur as the only members of the family outside the Americas.

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