SOLANACEAE OF MADAGASCAR: FORM AND GEOGRAPHY[1]

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ABSTRACT

About half of the small representation of Solanaceae on Madagascar is introduced. The largely endemic representation of native species displays unusual features in hair type, floral egress, anthers, and fruits, which may relate to unusual pollinators and dispersal agents present on the island. Affinities are noted with plants in Africa, South America, and Australia, suggesting that various ancestral stocks probably arrived at different times and have undergone different degrees and kinds of specialization. The Mozambique Channel is a barrier crossed by only one species that can germinate after marine flotation.

Madagascar has a long history of isolation, and its biota has evolved many unusual adaptations that are of general evolutionary interest. This paper results from studies made for a recent floristic treatment of the Solanaceae for Madagascar and the Comoro Islands. Some unusual features of the Solanaceae of Madagascar are discussed, and speculations are offered on relationships and biogeography of these plants.

Solanaceae are not well represented on Madagascar. Fourteen genera and about 60 species are present, of which only two genera and about 30 species are clearly native (Table 1). Of the species native to the flora area, all except six shared with Africa are endemic. Although few in number, the Solanaceae of Madagascar display interesting diversity in both form and presumed source area.

In the present century, the Solanaceae of Madagascar were studied by Bitter (1913, 1917, 1921, 1923), Whalen (1984), Jaeger (1985), and Jaeger & Hepper (1986), each of whom considered the elements from Madagascar in the context of an African or larger sphere. The new treatment (D'Arcy & Rakotozafy, in press) covers Madagascar and the Comoro Islands.

THE FLORISTIC STUDY

My study of the Solanaceae for the flora spanned more than a decade and included examination of specimens at several European institutions, borrowed specimens, and two trips to Madagascar. During the first trip, in 1983, I visited the south of the country, the wet forest and coast east of Tananarive, and Nosi Be and Anivorano Nord at the north end of the island.

In 1987, I went to the Comoro Islands of Grande Comore, Anjouan, and Moheli and revisited places east of Tananarive and in the north of Madagascar. I also studied the wet northeast coast near Mt. Marojejy. A valuable part of the study was observation in the Missouri Botanical Garden research greenhouses of living plants, which were grown from seed obtained personally in Madagascar or

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[1] Grateful acknowledgment is made to the National Geographic Society for help with the underlying floristic treatment (D'Arcy & Rakotozafy, in press), and to the following, not only for specific assistance, but also for generally helpful dialogue: Richard C. Keating, Southern Illinois University at Edwardsville; Alwyn H. Gentry and George Schatz, Missouri Botanical Garden, David E. Symon, State Herbarium of South Australia, Botanic Garden, Adelaide, South Australia; Sandra D. Knapp, Mississippi State University; and Joan Nowicke, Smithsonian Institution. Laboratory, technical, and photographic assistance was provided by Richard C. Keating and his technician, Sue Eder, and photographic assistance was also provided by Michael Vieth, Washington University. K. Kathleen Pickett, Missouri Botanical Garden, helped in cultivation of plants and observations of their characters. Photos that were helpful in assessing characteristics of plants from Madagascar were provided by George Schatz and James Miller, and seeds were provided by these two and by Peter Phillipson and Sigrid Liede, all associated with the Missouri Botanical Garden. Seeds, pickled plant material, and microscope slides were provided by Joseph E. Armstrong, Illinois State University. Information on bees was provided by: L. Anders Nilsson, Department of Systematic Botany, Uppsala University; Steven L. Buchmann, Carl Hayden Bee Research Center, Tucson, Arizona; and Charles D. Michener and Robert W. Brooks, Department of Entomology, University of Kansas. Information relating to the new genus *Tsoala* was provided by J. Bosser, Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris.

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ANN. MISSOURI BOT. GARD. 79: 29–45. 1992.

TABLE 1. Numbers of species of Solanaceae on Madagascar.

Genera	Total species	Native species		Introduced species		Doubtful species[b]
		Endemics	Also Africa	Total	Cultivated/ Naturalized[a]	
Brugmansia	2			2	2/0	
Brunfelsia	3			3	3/0	
Capsicum	1			1	1/0	
Cestrum	3			3	3/0	
Cyphomandra	1			1	1/0	
Datura	3			3	3/0	1
Lycium	1		1			
Lycopersicon	1			1	1/0	
Nicandra	1			1	?/1	
Nicotiana	1			1	1/0	
Petunia	1			1	1/0	
Physalis	4			4	0/4	
Tsoala	1	1				
Solanum	39	23	5	11	8/7	2
Totals	62	24	6	32	21/12	3

[a] Includes species that are cultivated, naturalized, or both.

[b] *Datura metel, Solanum aphananthum, Solanum virginianum.*

provided by helpful coworkers. In the notes that follow, observations and speculations are my own unless identified otherwise.

THE SOLANACEAE

Worldwide, the Solanaceae include about 2,300 species arranged in about 95 genera (D'Arcy, 1991). The family comprises two major subfamilies, the Solanoideae, which are cosmopolitan, and the Cestroideae, which have more restricted distribution, occurring mainly in the Americas and Australia.

The greatest diversity of Solanaceae, at both generic and species levels, occurs in western South America, and the extension of this solanaceous flora across Central America into southern Mexico has an elaboration of species but little development at higher taxonomic levels. Other centers of solanaceous diversity are northern Mexico, where a group of endemic genera and infrageneric taxa ranges into the southwestern United States. Southwestern Australia hosts a group of isolated genera, and a group of distinctive but species-poor temperate genera ranges from Japan westward to Gibraltar. The large genera, *Lycianthes* and *Solanum*, have secondary centers in New Guinea with species ranging westward into China and India.

The genus *Solanum* comprises about half the species in the family and is currently (D'Arcy, 1972) arranged in five subgenera and about 55 sections, many of which are more distinctive than genera in other families. *Solanum* is best developed in the New World, but two subgenera, *Leptostemonum* and *Solanum*, are native in the Old World. Subgenus *Leptostemonum*, one of the few large groups of Solanaceae with adaptations to hot and xeric conditions, is well elaborated in Africa and Australia. Subgenus *Solanum* is more widely distributed but has fewer species in the Old World.

Although there is significant development of Solanaceae in Africa, with many species and some development at higher taxonomic levels, there is a notable decrease in the diversity to the east of Africa and Madagascar. Peninsular India and southeast Asia have notably low representation of Solanaceae.

THE ISLAND SETTING

Madagascar is an island continent some 1,000 miles (1,600 km) long with a central uplands, a wet eastern escarpment and lowlands, and drier shelving on the west. The southern part (about as far from the equator as southern Florida) has vegetation distinct from the northern part of the island. Along the island's central core there are several peaks and massifs between 2,000 and almost 3,000 m elevation.

Madagascar was once part of the ancient, southern Gondwanaland continent. It separated from Africa 180–170 mya and reached its present position, somewhat south of its place of origin, about 120 mya (Rabinowitz et al., 1983; Philip Rabinowitz, pers. comm.). Madagascar is now separated from Africa by the Mozambique Channel, which is about 250 mi. (400 km) wide at its narrowest point. The separation occurred before flowering plants are known in the fossil record and long before the South American and African continents separated and began to move apart ca. 130 mya (Pitman, in press). Most texts assume that Madagascar has been at least partly emergent since its separation from Africa. Barron (1987) has suggested that a strike-slip motion between India and Madagascar prior to 120 mya resulted in the linear nature of the continental eastern margin of Madagascar. Although Madagascar drifted away from Africa too early to have carried along any flowering plants, land has been present for colonization by flowering plants since an early date in their evolutionary development.

Introductions of plants and animals across the incipient and actual Mozambique Channel are believed to have led to a more or less continuous flora in the past, but extinction episodes in Africa that were not shared by Madagascar have extirpated African ranges of many taxa (Coetzee, in press). During past aeons, Africa received taxa from Asia or Europe to the north that apparently did not disperse across the Mozambique Channel to Madagascar. Today, Madagascar has a different suite of animal and plant taxa from those of Africa and other regions. For example, there are few mammals—no marsupials, no lagomorphs, one ungulate (extinct), few rodents, and few carnivores—except for a conspicuous elaboration of insectivores and lemurs (Eisenberg, 1981). Bees are apparently not numerous, either in numbers or species, and they relate mostly to African bees (Brooks & Michener, 1988). The bird fauna is unexpectedly small (Jenkins, 1987). Nevertheless, reptiles (Duellman, in press) and hawkmoths (George Schatz, pers. comm.) are well represented.

Human settlement began 1,500–1,000 years ago, with immigrants coming mostly from Indonesia and Africa (Verin, 1986). There was also early contact with Arabia via the Comoro Islands, and Portuguese ships reached Madagascar in 1500. Most of the interior uplands were deforested before 1950. With economic improvement that began about 1983, deforestation has accelerated, as supplies and machinery associated with removal of natural growth have become more plentiful. Today the original vegetation is mainly represented by remnants that are being rapidly replaced by fire-maintained grasslands.

The Comoro Islands are a four-island group about halfway between northern Madagascar and the African mainland. The recent volcanic nature and succession of island ages from east to west is striking. The surface of Grande Comore, the youngest and westernmost, consists of lava rock and boulders and contains little soil. Anjouan and Mayotte, older islands, have well-developed agriculture. Moheli, the smallest island, has less relief, soil, agriculture, and rainfall. The main affinity of the native flora is with Madagascar, although this is now almost entirely replaced by introduced, pantropical species. The Comoro Islands have long been part of the African–Arabic coastal trading province.

THE INTRODUCED SOLANACEAE

On Madagascar, 12 of the 14 Solanaceae genera and more than half the species are introduced, some of them known only in cultivation. Most of the cultivated/introduced flora is now cosmopolitan in tropical cultivation or disturbance. More will be said below of Solanaceae of uncertain origin.

Two introduced species, *Solandra grandiflora* Sw. and *Solanum seaforthianum* Andrews, are known in the Comoro Islands but have not been collected on Madagascar. The first is cultivated in Moroni, Grande Comore, and there are sight records (George Schatz, pers. comm.) from Tananarive, Madagascar. The second is naturalized in woodlands of Grande Comore and Anjouan. Both are widely used as tropical ornamentals.

LYCIUM

Lycium acutifolium is common in southeastern Madagascar, especially near the south coast, but it ranges at least as far north as Betroka and to within 25 km of Tulear on the west. This species displays remarkable variation in growth form, occurring as a free-standing or near-prostrate shrub, and also as a vinelike plant hanging from coastal cliffs. It also occurs in the east Cape region of southern Africa (Fig. 1), according to Prof. H. J. T. Venter, who is revising the South African species of *Lycium*. Because there are other species of *Lycium* in southern Africa, *Lycium acutifolium* is assumed to have been brought, perhaps by natural vectors, to Madagascar from Africa.

TSOALA TUBIFLORA

Tsoala is a new genus discovered among undetermined collections at the Laboratoire de Phanérogamie (Paris) by Jean Bosser. It was collected at several sites in western Madagascar, where most of the forest has been turned into grassland.

The flower has a long tube (8–15 cm), indicative

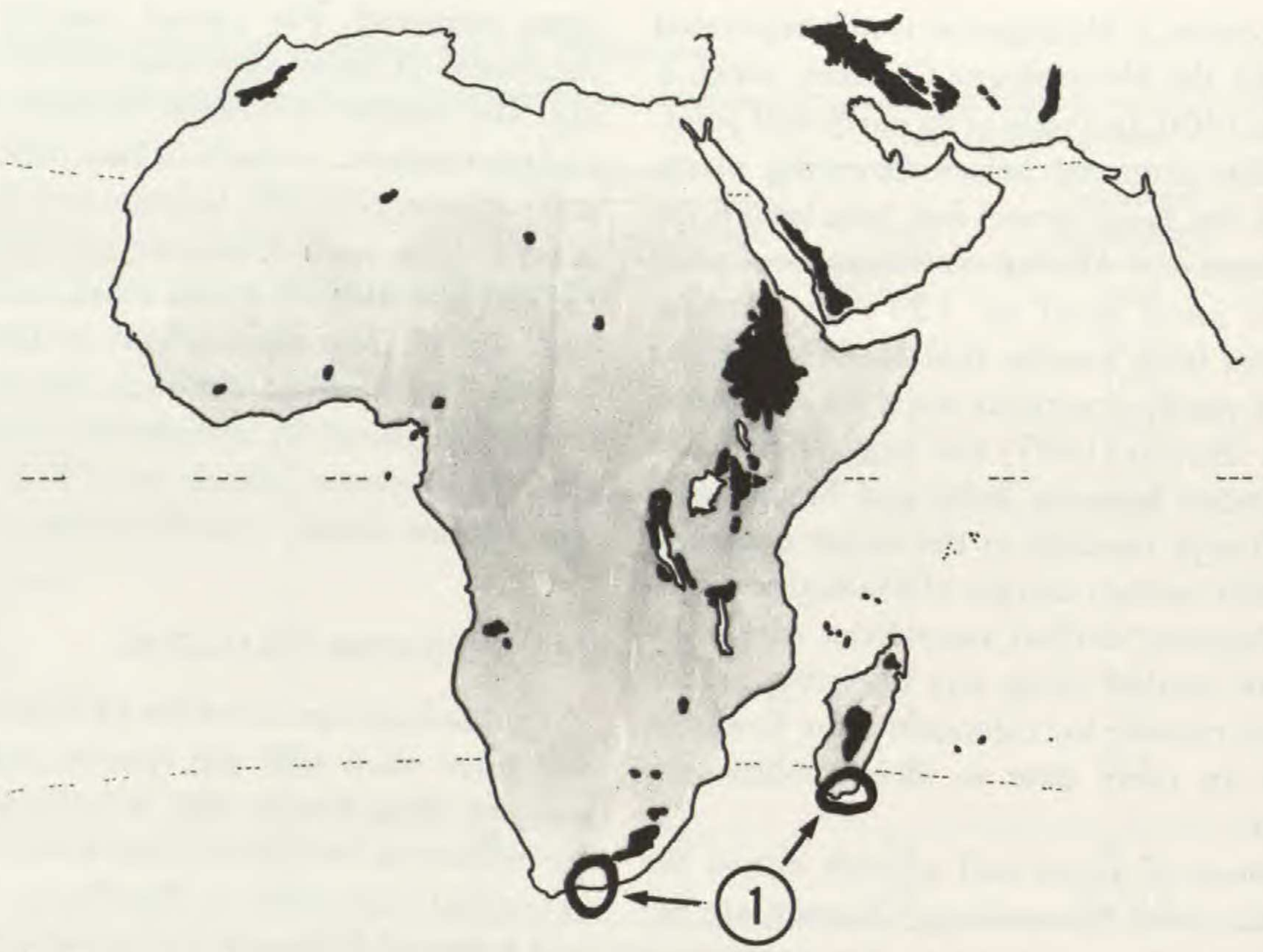

FIGURE 1. Distribution of *Lycium acutifolium* (at 1). Elevations above 2,700–3,000 m are darkened. Data from collections at P and MO.

of hawkmoth pollination, which is especially well developed on Madagascar (George Schatz, pers. comm.). This remarkable species is a shrub with simple leaves and pubescence of simple hairs. The fruit is a woody capsule with large seeds that have nearly straight embryos. We have been unable to detect included phloem, which is diagnostic for Solanaceae, in our material, but this tissue is difficult to detect in dried leaves. The ovary is one-locular except at the base, and there is no sign of an expanded placenta as is common in Solanaceae. All other characters argue for placement in the Solanaceae. A nuclear magnetic resonance spectrum analysis (Soren Jensen, pers. comm.) revealed

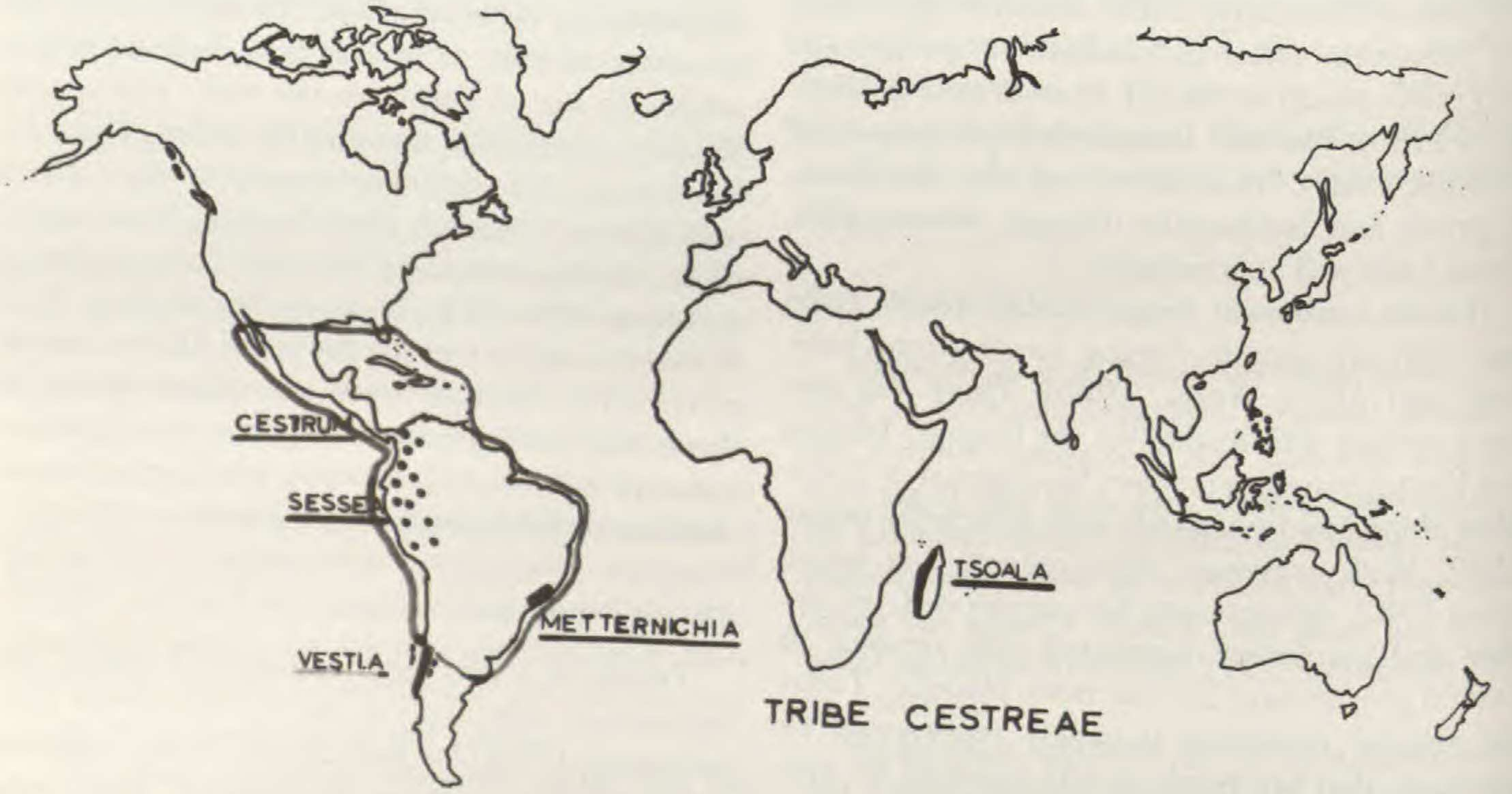

FIGURE 2. Distribution of genera comprising Solanaceae tribe Cestreae. Data from collections at MO and from various literature references.

no iridoid alkaloids. The Solanaceae lack such compounds, while similar-appearing families in the Scrophulariales/Lamiales often have them.

These features place *Tsoala* in tribe Cestreae of subfamily Cestroideae, neither of which was hitherto known from the Africa/Asia region. Tribe Cestreae (Fig. 2) includes four other poorly known genera: *Cestrum* (widespread, tropical America), *Vestia* (Chile), *Sessea* (Andes), and *Metternichia* (Rio de Janeiro). The last two have woody capsules not unlike those of *Tsoala*, but the corollas are of quite different shapes. The occurrence of a member of the Cestreae on Madagascar supports the views that the Solanaceae have a southern or Gondwanaland origin (Raven & Axelrod, 1974; D'Arcy, 1975, 1991).

SOLANUM: THE INTRODUCED SPECIES

About half the species of *Solanum* occurring on Madagascar and the Comoro Islands today are introduced species, including species that occur only in cultivation. Some of the introduced species are so well established and integrated into the present environment of Madagascar that they are commonly considered to be part of the flora. The presumed status of species and groups of *Solanum* is indicated in Table 2.

Solanum americanum Miller, the tropical black nightshade, is one of the most common table vegetables in Madagascar: its aboveground parts are served boiled on rice in most country restaurants and homes throughout the land. The species occurs widely in warm countries, and plants on Madagascar are indistinguishable from those of the Caribbean region. The similar *Solanum scabrum* Miller is cultivated for its berries, and it is sparingly naturalized. This species is commonly cultivated in upland areas of west Africa. Most species of this section, *Solanum*, are found in South America, which is its presumed region of origin, but some Old World elements (*S. nigrum* L., *S. villosum* Miller, *S. scabrum*) seem to have no counterparts in South America, and their presence in the Old World is presumed to be of long standing.

Two other New World species have become pervasive, shrubby weeds in the tropical Africa/Asia region and are common in Madagascar except in the south. These are *Solanum mauritianum* Scop. and *S. torvum* Sw. The fruits of *S. torvum* are commonly eaten in India but perhaps not in Madagascar.

Solanum incanum L., the presumed ancestor of *S. melongena* L., the eggplant, is widespread around the island near villages and along roads, and populations were found whose individuals (in flower) could not be distinguished from *S. melongena*. *Solanum incanum* is widespread in Africa, India, and China. Fruits of both *Solanum incanum* and *S. melongena* float, and seeds of the first can survive a period in sea water of at least five weeks (D'Arcy & Pickett, 1991). Because of its uniform appearance on Madagascar and the great variety of related species in Africa, this group is assumed to have arrived on the island in relatively recent times.

TABLE 2. Taxonomic arrangement of solanums on Madagascar.

- Subgenus *Solanum*
  - Section *Lemurisolanum* (8 species, all endemic) *S. antalaha*[a], *S. apocynifolium*, *S. ivohibe*[a], *S. madagascariense*, *S. macrothrysum*, *S. marojejy*[a], *S. myrsinoides*[a], *S. trichopetiolum*[a]
  - Section *Macronesiotes* (5 species, all endemic) *S. ankazobe*[a], *S. betroka*[a], *S. humblotii*, *S. imamense*, *S. sambiranense*[a]
  - Section *Afrosolanum* (1 Comoros and Africa) *S. terminale*
- Other groups (introduced: cultivated and/or naturalized) *S. americanum*, *S. pseudocapsicum*, *S. scabrum*, *S. seaforthianum*
- Subgenus *Leptostemonum*
  - Section *Melongena* (*Andromonoecum*) (3 species, 1 Madagascar and Africa, 2 introduced, cultivated) *S. incanum*, *S. macrocarpon*, *S. melongena*
  - Section *Croatianum* (3 species, all endemic) *S. bumeliaeifolium*, *S. croatii*, *S. heinianum*
  - Section *Oliganthes* (plentiful in Africa)
    - Series *Afroindica* (3 species, also in Asia, 1 perhaps native) *S. aethiopicum*, *S. anguivi*, *S. violaceum*
    - Series *Eoafra* (3 species, all endemic) *S. batoides*[a], *S. erythracanthum*, *S. myoxotrichum*
    - Series *Acanthocalyx* (1 species, Africa, Comoros, Madagascar, Mauritius) *S. richardii*
    - Series *Pyracanthum* (1 species, endemic) *S. pyracanthos*
  - Section *Cryptocarpum* (1, endemic) *S. mahoriensis*
- Isolated species (1, endemic) *S. toliaraea*
- Other groups (introduced: cultivated and/or naturalized) *S. torvum*
- Other subgenera (introduced: cultivated and/or naturalized) *S. mauritianum*, *S. tuberosum*

[a] Species to be described in the *Flore de Madagascar et des Comores* (D'Arcy & Rakotozafy, in press).

Solanum anguivi Lam. (*S. indicum*) is common around homes in many parts of the island, and it seems to intergrade and perhaps to be interfertile with *S. aethiopicum* L. (*S. integrifolium*). Fruits of *Solanum aethiopicum* will float in sea water (not in fresh water), but those of *S. anguivi* do not. These plants were domesticated in west Africa (Lester & Niakan, 1986), and many forms and related wild "species" exist across the African continent, including the ribbed-fruited forms seen on Madagascar. As there appears to be no series of wild associates in Madagascar, these species are presumed to have been introduced from Africa, where many similar forms are found. Both species are used medicinally and sometimes as food. In Africa, fruits and leaves are eaten, and many wild stocks are used for medicines.

The earliest name for what was formerly called *S. indicum* L. is *S. anguivi*, described from a Commerson collection from Madagascar. The common name for this species in Madagascar is "angivi." Several explanations are available for the presence of a presumed ancestor for a west African cultigen in Madagascar. That the species was introduced to Madagascar well before 1769 when the species was collected by Commerson seems most likely. The species need not have been taken by sea travelers from west Africa to Madagascar. It may occur or have occurred in this form widely across Africa and been present in the wild on the east coast for transport to Madagascar or further east. Or it may have been carried by Islamic pilgrims into their Ethiopian villages on the several-year journey from west Africa to Mecca (Bunting, 1990). From there, it would have been a candidate for transport to the Comoro Islands by coastal traders and thence to Madagascar.

Solanum aethiopicum may have entered Madagascar in the same way as *S. anguivi*, but as the fruit and plants seem identical to some forms cultivated in the United States, it may have been introduced more recently, perhaps by French agriculturists.

To the east of Madagascar, in India and southeast Asia, *S. anguivi* appears to be replaced by *S. violaceum* Ortega. Both species occur on Madagascar, but *S. violaceum* is known by only a few records. As differences between these two extremely similar species have only recently been elucidated, investigation will be necessary to determine more precisely the range of *S. violaceum* and its likely region of origin.

SOLANUM: THE NATIVE SPECIES

Except for the newly discovered endemic genus *Tsoala* noted above, all native Solanaceae on Madagascar are of genus *Solanum*. There are about 25 species of *Solanum* in the flora area, all but two of these endemic. The two largest subgenera, *Solanum* and *Leoptostemonum*, are well represented. Subgenus *Leptostemonum* includes species often having slender anthers with small pores, spines, and stellate pubescence. Subgenus *Solanum* includes species with stout anthers, no spines, and simple or dendritic rather than stellate hairs. The taxonomic arrangement of native species is presented in Table 2. This generally follows the arrangements of Bitter (1913, 1917, 1921, 1923) and Jaeger (1985), and for *Leptostemonum*, Whalen (1984), with a few adjustments made in the current study. Infrageneric names and their authors are as presented in D'Arcy (1972).

UNARMED *SOLANUM* GROUPS (SUBGENUS *SOLANUM*)

SECTION *AFROSOLANUM*

Section *Afrosolanum*, which, unlike the other species treated below, is not strictly native to the flora area, includes many named species, but recent works recognize three (Jaeger, 1985), or only one (Heine, 1960) species, *Solanum terminale* Forsskal. *Solanum terminale* ranges across tropical Africa and the Arabian Peninsula (Fig. 3), mostly at elevations above 2,500 m. It occurs in moist forests as a shrub, scrambler, or climber. The inflorescences are purplish or white flowers in terminal paniculate clusters, the base of the rachis often bearing a series of leaves or bracts that diminish in size upwards.

A noteworthy feature in section *Afrosolanum* and some other African sections is the type of anther dehiscence. The terminal pores, which occur in all species of *Solanum*, soon elongate into longitudinal slits that run to the base of the anther and open to expose the pollen (Fig. 4A).

In contrast, spiny solanums and most New World groups of spineless solanums either lack longitudinal dehiscence, or they develop longitudinal slits from separate sites below the anther apex, and the slits are not continuous with the terminal pore, at least before late anthesis. They seldom or never open below the pore wide enough to expose much pollen. The type of anther dehiscence in section *Afrosolanum* is also found in section *Quadrangulare* and in subgenus *Lyciosolanum*, both groups of southern Africa and in section *Archaeosolanum* of Australia. Bitter (1917) considered subgenus *Lyciosolanum* (*Solanum quineense* L. = *S. aggregatum* Jacq.) to be intermediate between *Lycium* and *Solanum* and "another primitive species among the numerous other ancient types in the Cape Flora." He may also, to judge from the appellation chosen for it, have considered section

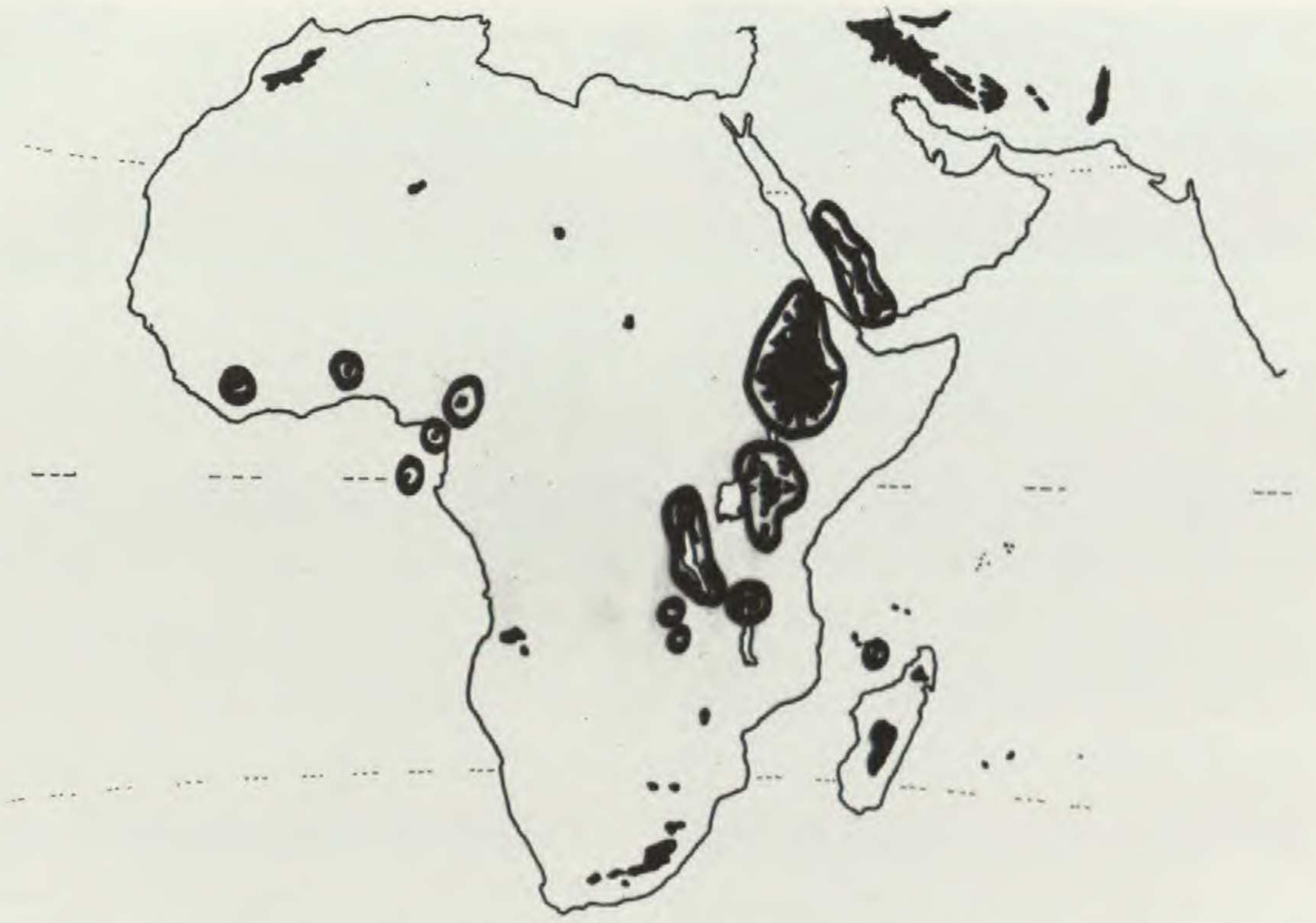

FIGURE 3. Distribution of *Solanum terminale* Forsskal in circled areas. Elevations above 2,700–3,000 m are darkened. Data from Bitter (1913, 1923) and from collections at MO.

Archaeosolanum to be archetypal in the genus. The rapid longitudinal dehiscence may be considered a primitive feature in the genus, if one assumes that *Solanum* evolved from taxa having longitudinally dehiscent anthers as in most other genera of Solanaceae.

The perhaps monotypic section *Afrosolanum* has been collected only once in the flora area, on Mayotte in the Comoro Islands, in 1884. This collection of *S. terminale* became the type collection of *S. comorense* Dammer, a name now relegated to synonymy. Because the species is found on widely isolated mountains, including sites on land masses (Africa and Arabia) that have not been united for many millions of years, it seems to be capable of dispersal over considerable distances. However, it has not been found on Madagascar; this enigma will be discussed later.

SECTIONS *LEMURISOLANUM* AND *MACRONESIOTES*

Two other nonspiny *Solanum* groups, sections *Lemurisolanum* and *Macronesiotes*, occur in the flora area, each represented by several species on Madagascar and the Comoros. Both are similar in many respects and also similar to section *Afrosolanum*, often developing dendritic hairs, sarmentose to epiphytic growth habits, plurifoliate inflorescences, leafing and flowering on short shoots, purplish or bluish flowers, and often conical ovaries. However, they differ from section *Afrosolanum* in their anthers, calyces, and other features. The anthers are sometimes laterally connate, and the presence and degree of this connation seems to vary considerably within species. Dehiscence is by distinctly margined terminal pores with no tendency to longitudinal dehiscence (Fig. 5A). Both groups occur widely in the flora area in all original forests except in southern Madagascar, and both are endemic to the flora area.

FLORAL EGRESS

In species in section *Lemurisolanum*, calyx prefloration is nearly perfect (fused to the top), the only signs of lobes being minute apical tufts of trichomes where the primary veins terminate (Fig. 4B), and floral egress is by stretching (Fig. 4C) with no sign of splitting. See D'Arcy (1986) for an explanation of egress modes in solanaceous calyces. This mode of egress is almost unknown in *Solanum*, which typically opens the calyx by splitting at the sinuses, sometimes with some stretching before splitting. One such case is known in *Solanum* sect. *Geminata*, *S. leucocarpon* Dunal (*S. surinamense* Steudel) in South America, and other examples may be found in this section. Egress by stretching occurs in several other genera of Solanaceae, e.g., *Lycianthes*, *Capsicum*, *Witheringia*. See D'Arcy (1991) for a more complete list. This also occurs in other families, e.g., Melastomataceae (*Medinilla*, Madagascar). Such groups are characteristic of

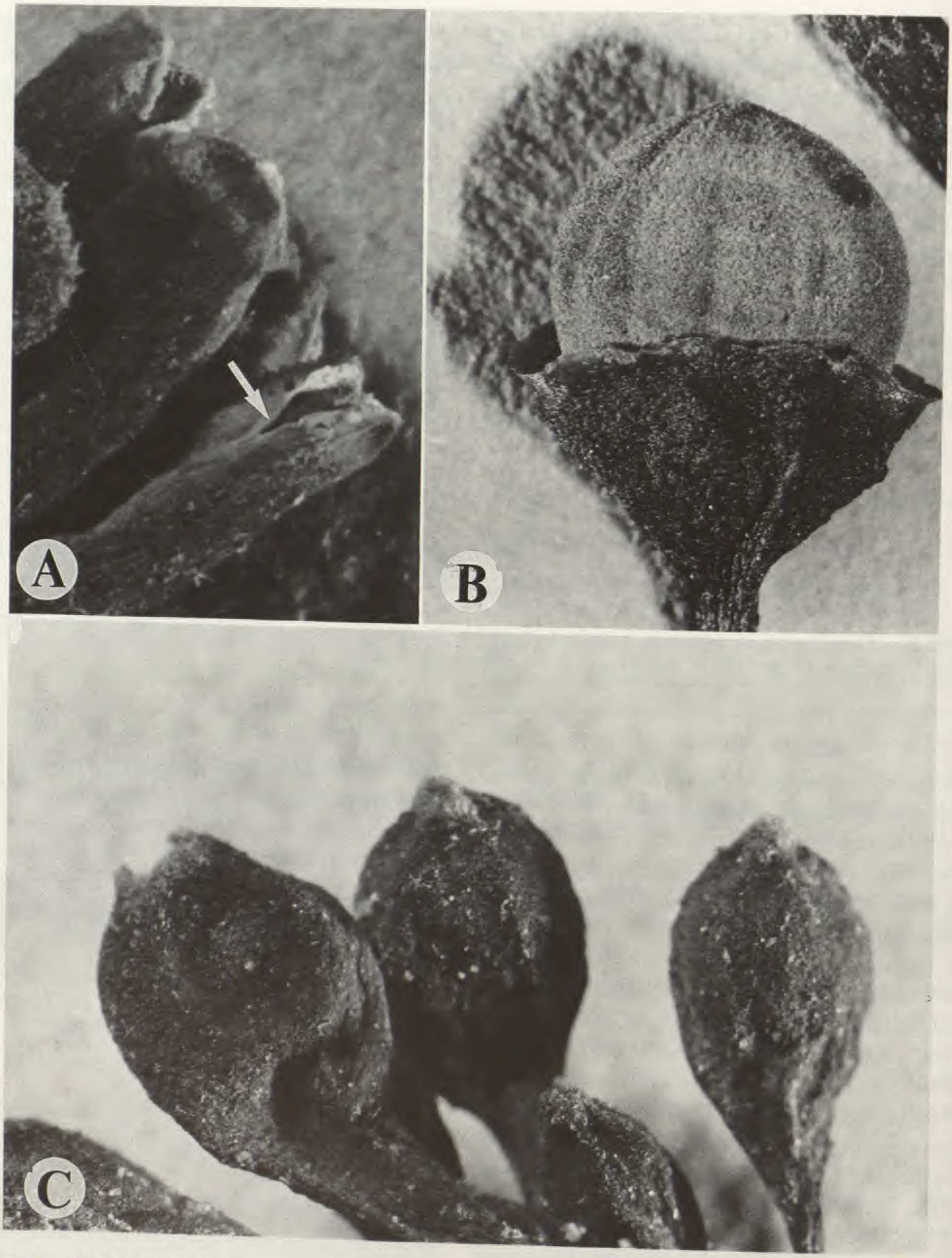

FIGURE 4. Features of *Solanum* species.—A. *Solanum terminale* showing extention of terminal pores into longitudinal slits (at arrow). (After *Humblot 284* (P), type collection of *Solanum comorense* Dammer.)—B. Floral egress of *Solanum madagascariense.* Bud with emerging corolla and fertile parts. The calyx has stretched thin at the apex to permit egress, and there is no sign of splitting or of calyx teeth. (After *Cours 2807* (P).)—C. Floral egress of *Solanum madagascariense* Dunal. Early buds with the calyx fused to the top and minute tufts of trichomes marking the five rudimentary teeth. (After *Cours 2807* (P).)

wet tropical forests, so it is speculated that this mode of egress has evolved independently in several groups under selection by unknown features of wet forests. It is postulated that this feature is one of high specialization, which took considerable time to develop.

ANTHER EMERGENCES

Another interesting feature of section *Lemurisolanum* is the unusual emergences or sculpturing on the anthers (Fig. 5), which Dunal (1852) referred to as hirsute. These are most striking on

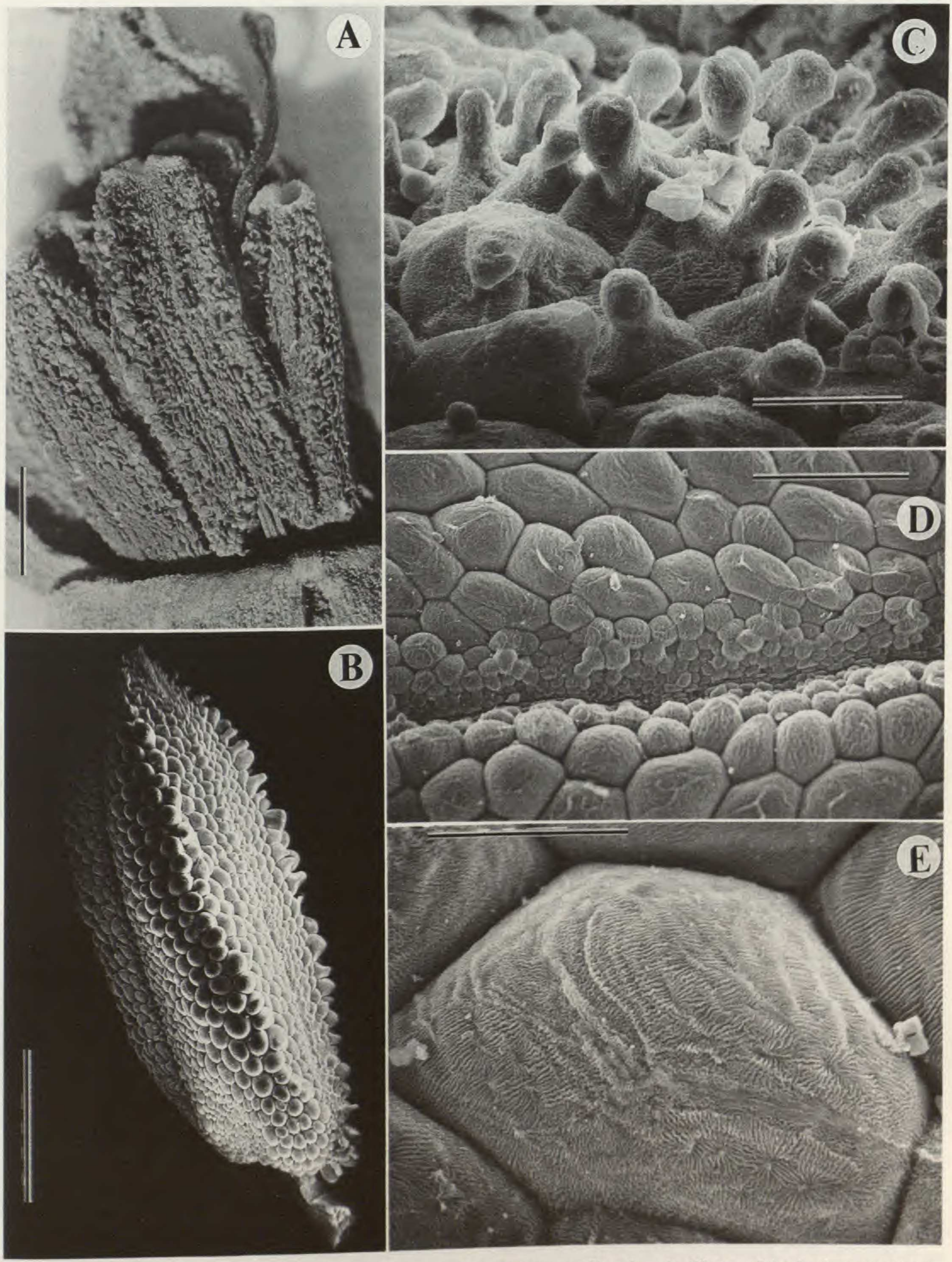

FIGURE 5. Emergences on anthers of *Solanum madagascariense* Dunal.—A. Photo of herbarium specimen. Scale = 1 mm.—B. SEM of material preserved in 50% FAA. Material rinsed in a graded ethanol series and critical point dried from liquid CO_2. Specimen was sputter-coated with 200 Å of gold, then photographed with I.S.I. Super IIIA scanning electron microscope. Scale = 1 mm.—C. SEM of restored material. Dried herbarium material treated overnight in concentrated ammonium hydroxide at 60°C in a sealed container under pressure. Preparation as in B. Scale 50 = μm.—D. SEM of liquid preserved material. Preparation as in B. Scale = 200 μm.—E. SEM of liquid preserved material. Preparation as in B. Scale = 50 μm. (All after *Miller 3413* (MO).)

specimens of the north and east coast of Madagascar, but they are also seen in material from other areas of the country and to a slight degree on anthers of the similar sections *Afrosolanum* and *Quadrangulare* on the African continent. I have not seen anything like these in plants from other parts of the world. Such emergences are not to be confused with the trichomes that Bitter (1917: 437–438) noted near the pores of *S. apocynifolium* Baker, which are minute, granular material localized on the contrasting yellow rim of the pores of a few specimens.

The anther emergences are probably pollinator related, and at least three suggestions come to mind on the nature of this relationship. Flowers of *Solanum* and other plants with anther dehiscence by terminal pores are usually pollinated by bees that buzz the anthers to extract the pollen (Buchmann, 1983a, b). One possibility is that the emergences restrict access to pollen by nonpollinating visitors. As noted above, sections *Lemurisolanum* and *Macronesiotes* differ notably from the African *Afrosolanum, Quadrangulare,* and *Lyciosolanum* species in their lack of longitudinal dehiscence, presenting pollen to only those visitors able to access it via the pores or by chewing their way to it. In the Americas, trigonid bees are known to rob pollen regularly from anthers without affecting pollination (Renner, 1983), and they may actually restrict some taxa of flowering plants to sites where these bees are not numerous. If these emergences act as deterrents to chewing through the anther to obtain pollen, they may, in addition to completing closure of the anther wall, help to restrict pollen dispersal to those visitors that can buzz the flowers, the means by which pollinators avail themselves of pollen from terminal-pored anthers. A second possibility is that the emergences provide grasping holds for pollinating bees, enabling them to hold the anther while they "buzz" the stamens. The third possibility is that the emergences are ultraviolet absorptive and provide an orientation cue to pollinating insects. Similar papillate emergences on patches of corolla tissue in some species of the scrophulariaceous genus *Diascia* were illustrated by Steiner (1990) and were demonstrated to affect orientation behavior of at least one pollinator.

It has not been possible to test these hypotheses either by observing bees in their visits to flowers or by testing the nature or contents of the emergences for a chewing-deterrent role or by testing the light reflectance of the anthers and the surrounding corolla tissue. Because these features are restricted to, or best displayed on, plants of Madagascar, they may relate to organisms restricted to this faunal area. Anders Nilsson (pers. comm.) relates that on Madagascar several genera of anthophorid bees hover and grasp anthers of *Solanum* to buzz them and obtain pollen, and at least two genera of halictid bees, and endemic genus *Spegocephala*, with about six species, and *Thrinchostoma*, which is restricted to Madagascar and Africa, also buzz anthers but must land on the anthers to do so. Possibly one or more of these halictids benefits from the availability of the emergences as holdfasts, and perhaps all classes of pollinators are attracted by light contrast between the anthers and corollas.

The contrast between the pollen presentation of otherwise similar plants in Africa and Madagascar is striking. In the African groups the pollen is exposed through an open longitudinal slit and is readily available for any pollen predators. In contrast, in the groups on Madagascar, the pollen is hidden beneath an intact anther wall and elaborate emergences, and the area presented to the outside is reduced by the frequent connation of adjacent anthers, seemingly offering a complicated system of deterrents to pollen predation. The African taxa are distributed across the continent and in the Arabian Peninsula, but they are restricted mainly to cool areas: above 2,500–3,000 m in the tropics or to the south at lower elevations, while the species of Madagascar occur at all elevations below 3,000 m in the tropics. Trigonid and apid bees, both pollen-scavenging groups, are present in Africa and Madagascar and seem likely to be pollen predators in both places. Further findings are needed to suggest how possible differences in pollinator capabilities or pollen predation levels may justify the contrasting pollen presentation systems. The differences in pollen-predation environments may explain why the Mozambique Channel has been such a formidable barrier to migration and establishment of these *Solanum* groups on neighboring continents, especially of the African groups that have well-demonstrated capability for long-distance range extension.

The occurrence of emergences on anthers and of anther connation in section *Lemurisolanum* does not appear to be entirely species specific, varying from completely absent to well developed on similar-looking specimens from neighboring sites. The biological interaction leading to development of these phenomena appears to have acted on a spectrum of taxa and populations in varying degrees, so that anther connation and emergences are of limited value as taxonomic markers. Similar anther emergences, somewhat different in detail, occur on species of *Exacum* (Gentianaceae), which are numer-

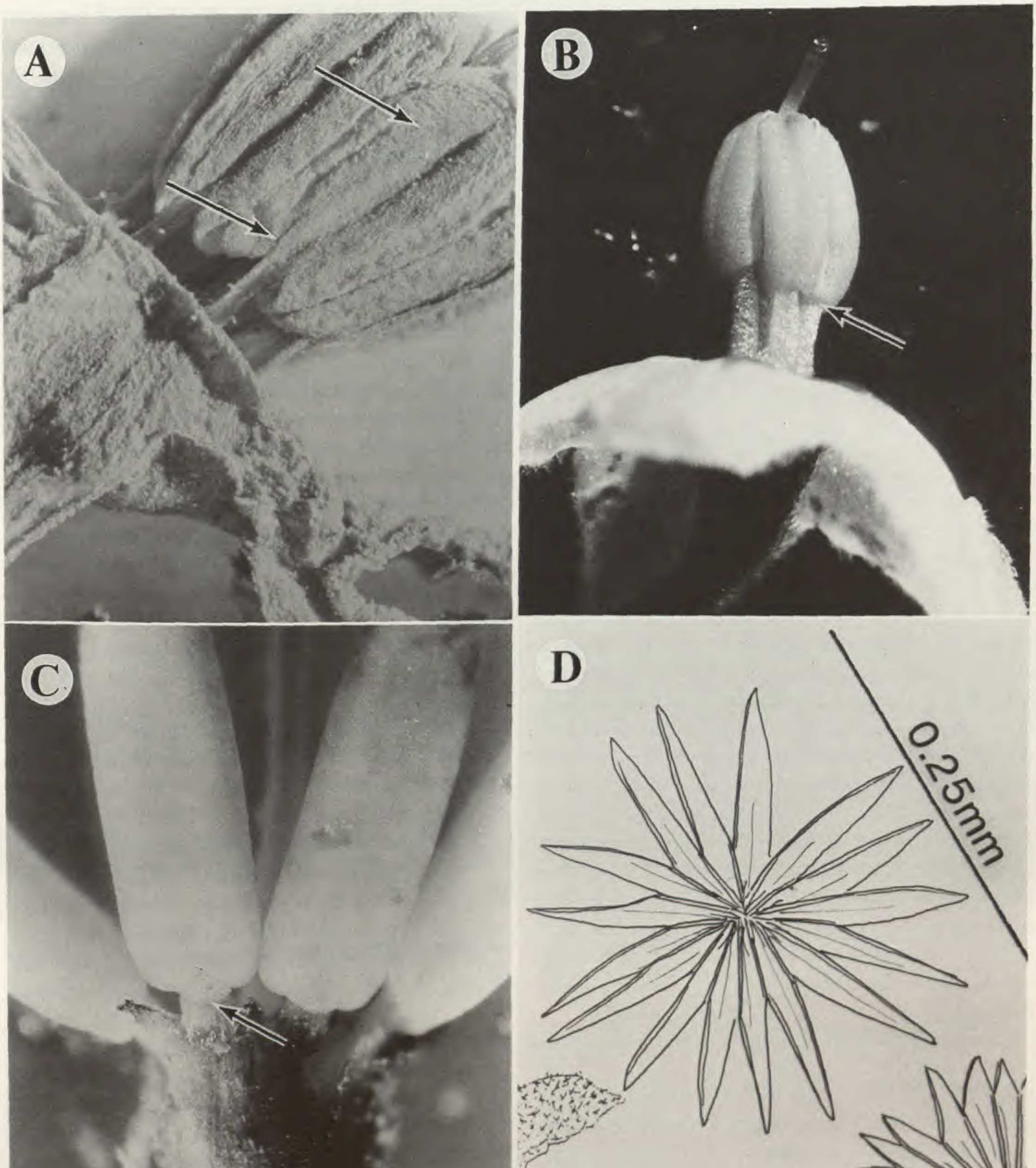

FIGURE 6. Features of some *Solanum* species. A–D Views of abaxial (dorsal) sides of anthers illustrating anther insertion.—A. *Solanum madagascariense* Dunal. Arrows show continuous dorsal position of filament/connective up the length of the anther.—B. *Solanum americanum* Miller. The basal, dorsal overhanging tissue is shown at arrow. In this species, this tissue recedes greatly on drying but still shields the point of anther insertion on the filament from view.—C. *Solanum pyracanthos* Jacq. The basal, dorsal overhanging tissue is shown at arrow.—D. Scutellate hair of *S. croatii*. (After *D'Arcy & Rakotozafy 15341* (MO).)

ous in the same forests on Madagascar (pers. obs.; Klackenberg, 1985). Collections from near Marojejy, the high (2,137 m) mountain near the wet-forested northeast coast of the island, seem to have the best development of emergences, but there are also species in this area with none at all. This is the part of Madagascar where the greatest development of wet forest solanums occurs. To judge from collection dates, blooming or occurrence of at least some of these *Solanum* species is restricted seasonally and in elevation range, which suggests that varied means of reproductive isolation are affecting similar plants within this relatively small area.

ANTHER INSERTION

In most species of *Solanum*, anthers are basifixed, and the filament enters a kind of socket in the anther where a flange of dorsal anther tissue shields the top of the filament and the point of insertion from abaxial view (Fig. 6A, B). When dried, this flange sometimes recedes up the back of the anther, but the point where the filament joins the anther is still within an anther socket. However, in *Solanum madagascariense* Dunal, the insertion of the anther is dorsal, the filament running up the abaxial side to the apex without interruption (Fig. 6C). Sometimes (Fig. 5A) the dorsal sides of the locule walls converge over the back of the filament, but these are not connate or coherent, and the filament can be viewed at least partly exposed all along the dorsal side. The type of anther insertion was verified as *Solanum madagascariense* and a range of other species by histological preparations (floral cross sections).

Similar dorsifixed anthers were not seen in African *S. terminale* or the related section *Quadrangulare* (*S. africanum* Miller). In the Australian section *Archaesolanum*, which is suggested by Bitter's name for it as a primitive group in the genus, anthers sometimes appear be dorsifixed, but histological sections have not yet been made to verify this. However, truly dorsal fixation occurs in solanums belonging to at least two other groups: *Solanum dulcamara* L. (sect. *Dulcamara*) from northern Asia and Europe and *Solanum pensile* Ruíz Lopez & Pavón (sect. *Andropedas*), widespread in tropical lowland South America. Each of these and section *Lemurisolanum* are woody vines or climbers with purple or violet flowers, often with a contrasting eye, borne in lax, many-flowered paniculate inflorescences. In both sections *Dulcamara* and *Lemurisolanum* there may be connation of the anthers. Specimens of *Solanum pensile* look very much like those of *S. madagascariense* in section *Lemurisolanum*, but the androecia differ: one stamen has a longer filament that places its anther well in advance of the others; and the anther dehiscence is by terminal pores and tardily forming longitudinal slits. Each of these groups has been divided into numerous species by various taxonomists, attesting to a considerable variability that has evolved in each group on its respective continent. Because dorsifixed anthers occur in many related genera and basifixed anthers are hardly found, and because these other genera have longitudinal anther dehiscence, which is generally considered to be less specialized than dehiscence by terminal pores as in *Solanum*, dorsifixed anthers are presumed, a priori, to be a character state primitive to basifixed anthers. The widespread taxa of *Solanum* with this feature would appear to represent isolated relict elements in the genus. Michael Nee (pers. comm.) may be correct that these vines are a distinct phylad within *Solanum*.

FRUIT SHAPE

Several species of section *Lemurisolanum* have conical ovaries and fruits, in contrast to the usual rounded ovaries and globose fruits in *Solanum*. One species from Marojejy has fusiform fruits to 4 cm long, which may indicate a shift from bird dispersal to mammal dispersal on an island where bird diversity is low.

SECTION *MACRONESIOTES*

The second group of forest climbers and epiphytes is section *Macronesiotes*. These have many of the features of section *Lemurisolanum*, but the calyx lobes, instead of being nearly obsolete, are well defined, and there is sometimes splitting at the sutures. Plants in this section are of two kinds. The group including the typical *S. imamense* Dunal comprises plants with membranaceous, pubescent leaves, lanceolate or deltoid calyx lobes, which sometimes elongate by splitting at the sinuses, and terrestrial habit. Species in this group closely resemble the American section *Pseudocapsicum*, from which they differ mainly in the small anther pores and lack of longitudinal dehiscence. Also placed in section *Macronesiotes*, as *S. humblotii* Dammer, are some specimens with coriaceous, glabrate leaves, linear calyx lobes, and epiphytic tendencies. In *S. humblotii*, the lobes and pedicels are recorded as red or violet, perhaps acting as part of pollinator attractant. In this section, ovaries are rounded or conical, and at least one large, turbinoid fruit is known resembling the unusual one referred to above in section *Lemurisolanum*.

SPINY *SOLANUM* GROUPS (SUBGENUS *LEPTOSTEMONUM*)

Whalen (1984) estimated that there are about 450 species of subgenus *Leptostemonum*, the spiny solanums, worldwide. He recognized them as forming 33 groups, of which only nine occur in the Africa/Asia sphere of distribution. Only three sections and two isolated species occur on Madagascar (Table 2).

Section *Croatianum* displays a distinctive, scutellate hair type (Fig. 6D). The section was described with three species from southern Madagascar. These are trees or large shrubs bearing sturdy, mostly straight spines as juveniles but usually lacking armature as mature plants. Morphological changes across the group seem to follow a gradient of diminishing rainfall from east to west. *Solanum croatii* D'Arcy & Keating has many-flowered branched inflorescences, ovaries that are basally 4-locular and apically 2-locular, and hairs that are mostly slightly stipitate. *Solanum heinianum* D'Arcy & Keating has leaves and flowers in fascicles or on short shoots (brachyblasts), the hairs resemble those of *S. croatii*, and the ovaries are 4-locular to the top. *Solanum bumeliaefolium* Dunal, apparently the most advanced species in the group, has leaves and flowers in fascicles, the flowers are in short, unbranched racemes, the ovaries are 4-locular, and the trichomes are sessile, scutellate hairs that form lepidote scales that give the leaves a somewhat silvery appearance. Occasional intermediates are found between *S. croatii* and *S. bumeliaefolium*.

The scutellate hair type of section *Croatianum* is highly distinctive in *Solanum*. It is otherwise known in this form only in section *Lepidotum* of South America (Carvalho et al., 1991). Although their hairs are apparently identical, the two sections are not thought to be closely related, so this unusual hair is assumed to have arisen independently in each group. However, in dry parts of western and interior Australia, several species, e.g., *S. sturtianum* F. Muell., *S. nummularium* S. Moore, *S. tumulicolum* Symon, have stellate hairs, the rays of which are fused basally, suggesting an incipient development of the scutellate hair. Use of this hair type as a taxonomic marker may have been overdone in section *Croatianum*; *S. heinianum* differs from the other two species in the section in its brachyblastic growth and other features, and its relationship may actually be elsewhere.

Solanum croatii seems to have no African relationship, but it resembles and seems closely related to *S. sturtianum* from arid western and interior Australia (Symon, 1982). That species has similar leaves, pubescence, flowers, fruits, and overall appearance but has smaller stature (0.5–3 m), smaller leaves, acicular rather than broad-based spines, larger corolla (3–4 cm diam.), dark-colored seeds, and rays of the stellate trichomes are fused only at the bases or not at all. Symon (1981: 206) stated: "*S. sturtianum* does not appear to have close relatives amongst the Australian species of *Solanum*." Both species occur at similar latitudes. In spite of the differences noted, there are enough similarities (synapomorphies?) to suggest that they are sister species.

Section *Oliganthes* is represented on Madagascar by two series and by isolated species (Whalen, 1984; Jaeger, 1985). Series *Afroindica* includes *S. anguivi* and *S. aethiopicum*, which were discussed above under introduced solanums. In this group, flowers are all perfect, and fruits are moist and mostly reddish.

Series *Eoafra*, which was divided into subseries by Bitter (1923), is well represented in eastern Africa with several xeric-tolerant species. The group is well developed and troublesome on Madagascar, both taxonomically and ecologically. Members of the group are found everywhere on the island, and at least one species, *S. erythracanthum* Bojer, is highly resistant to human disturbance. Plants on Madagascar have sessile inflorescences and frequently 4-parted flowers, as do some of the African species. The group appears to be an intergrading series of plants with strikingly different morphologies at the extremes.

One noteworthy species is *S. myoxotrichum* Baker. This appears to intergrade with *S. erythracanthum*, from which it differs in few details other than the echinoid appearance of its setose stems, vining habit, and copious, reddish pubescence. *Solanum myoxotrichum* seems to occupy regions of greater moisture than *S. erythracanthum*.

Similar echinoid stems appear on species of subgenus *Leptostemonum* on other continents. These are generally wetter habitat members of species pairs in which the other member, occupying drier but still mesophytic sites, lacks the density of spines or bristles that gives an echinoid appearance. Such wet/mesophytic species pairs are *S. aturense* Dunal/*S. lanceifolium* Jacq. (sect. *Micracantha*, tropical America); *S. sessilistellatum* Bitter/*S. incanum* (sect. *Melongena*, Africa), *S. densiaculeatum* Symon/*S. turraeafolium* S. Moore (sect. *Graciliflora*, New Guinea); *S. semiarmatum* F. Muell./*S. stelligerum* Smith (sect. *Graciliflora*, Australia).

FIGURE 7. Distribution of three *Solanum* species that are isolated taxonomically. 1. *Solanum mahoriense* D'Arcy & Rakotozafy. 2. *Solanum tolearaea* D'Arcy & Rakotozafy. 3. *Solanum pyracanthos* Jacq. Elevations above 2,700–3,000 m are darkened. Data from collections at P and MO.

One extreme in development of this group on Madagascar is an unnamed, small-leaved species from the south that forms bramblelike thickets in the south of the island. Similar-appearing herbarium specimens with slightly larger leaves from eastern Africa, the Arabian Peninsula, Sri Lanka, tropical Asia, Australia, and the Antilles are usually determined as different species, e.g., *S. procumbens* Lour., *S. trilobatum* L. If these are not a result of recent dispersals, there has been convergence on this gross morphology in diverse regions.

Section *Andromonoecum* on Madagascar includes both native species and the two introduced species, *S. incanum* and *S. melongena*. The group is characterized by having andromonoecious sexual expression, felty leaves, calyces slightly accrescent in flower and just after (not in fruit), and mostly yellow fruits with seeds that can germinate after lengthy flotation in sea water (D'Arcy & Pickett, 1991).

TABLE 3. Postulated affinities of *Solanum* groups of Madagascar.

Subgenus *Solanum*	
Section *Afrosolanum*	High African mountains
Section *Lemurisolanum*	Endemic—relictual climbers
Section *Macronesiotes*	Endemic—South America
Subgenus *Leptostemonum*	
Section *Croatianum*	*Solanum sturtianum*, Australia
Section Oliganthes	Widespread, Africa, Tropical Asia
Series *Afroindica*	Widespread, Africa, Tropical Asia
Series *Eoafra*	Eastern Africa and eastern Asia
Section *Andromonoecum*	Widespread, Old World
Series *Pyracanthum*	Madagascar, reentered Africa?
Isolated species	
Solanum mahoriense	*Solanum sisymbriifolium*? South America
Solanum tolearaea	Australian groups?

Andromonoecy in *Solanum* subg. *Leptostemonum* was discussed by Whalen (1984) and Whalen & Costich (1986), who considered plants with this character to be a monophyletic group. In these plants, usually the first flowers in an inflorescence are perfect, while others are staminate. The perfect, or pistillate, flowers tend to have spinier calyces, while the staminate flowers have reduced gynoecia, the styles often not exceeding the filaments. Andromonoecy is sometimes difficult to determine from herbarium material. On Madagascar, it occurs in section *Andromonoecum* and also in all three species of section *Croatianum*.

Solanum pyracanthos Jacq. and *S. richardii* Lam., formerly considered to be isolates and placed in different sections, may actually have a closer relationship. Greenhouse plants of these species were both found to be andromonoecious. A cross (two successful tries) of *S. richardii* pollen onto the stigma of an emasculated flower of *S. pyracanthos* produced a fruit that contained a few developed but sterile seeds. Further testing is needed for verification of the cross. Juvenile leaves of the two species are similar, but mature plants and especially the fruits are quite different. In the golf-ball-sized fruits of *S. richardii* the mesocarp is

FIGURE 8. Distribution of *Solanum richardii* Dunal (at 1). Elevations above 2,700–3,000 m are darkened. Data from Bitter (1923) and from collections at MO.

thick, spongy, and white, typical of section *Andromonoecum*, and the exocarp is bright orange and opaque. Fruits of *S. pyracanthos* are grape-sized, the mesocarp is thick, hard, and juicy, and the exocarp is green or pale yellow and translucent.

Solanum pyracanthos, which has been grown as an ornamental in European gardens, is endemic to southeastern Madagascar (Fig. 7). *Solanum richardii* occurs in northern coastal Madagascar and the Comoros and has been reported from the island of Mauritius and from coastal Africa (Fig. 8). The ability of seeds to germinate after more than a month in the sea (D'Arcy & Pickett, 1991) may account for this distribution. Because all recent workers have considered these to be isolated species, and no similar plants have been noted by workers studying African relatives (Richard Lester, pers. comm.), they are perhaps an autochthonous group on Madagascar that has dispersed by sea to eastern Africa.

In addition to the groups discussed above, two isolated species are noteworthy in having quite narrow ranges, berries enclosed by accrescent, spiny, bladdery calyces, and andromonoecious sexual expression, but few other similarities. The fruiting calyces are quite different in size but are otherwise alike. *Solanum mahoriense* D'Arcy & Rakotozafy (Fig. 7) occurs in the tropical north of the island, a low sprawling shrub with dissected leaves, purple flowers, and sticky green berries. Some of these features are shared with *S. sisymbriifolium* Lam. of Argentina, which, however, is herbaceous and has white flowers and red fruits. *Solanum toliaraea* D'Arcy & Rakotozafy (Fig. 7) occurs in the temperate southwest of the island and is a small, erect tree. Its relatives are unknown within subgenus *Leptostemonum*.

RELATIONSHIPS OF SOLANACEAE OF MADAGASCAR

The Solanace on Madagascar display interesting features suggestive of both recent and ancient relationships. *Tsoala tubiflora* Bosser & D'Arcy appears to be related to South American genera, suggesting a southern or Gondwanan history for tribe Cestreae, which would reflect an ancient, probably pre-Tertiary distribution.

Postulated affinities of the *Solanum* taxa found on Madagascar are indicated in Table 3. Section *Afrosolanum* clearly relates to the African continent where there is a diverse array of relatives and plants with similar morphology (sects. *Quadrangulare* and *Lyciosolanum*). Its sole record on the Comoro Islands does not suggest antiquity in the flora area. Section *Lemurisolanum*, which displays unusual features, both primitive and advanced, may have evolved from stocks that are represented today by similar, relict groups in temperate Asia and South America. Differing mainly in its elongated calyces, section *Macronesiotes* may have originated from ancestors similar to those of section *Lemurisolanum*.

Section *Croatianum* appears to have its closest relative in Australia, and because of the differentiation in the group on Madagascar, its presence there may be quite old. Species of series *Eoafra* are much like those on adjacent African land areas, and they may have come from Africa more recently, but long enough ago to have evolved a number of distinctive elements. It likely that ancestral stocks arrived more than once, and it is also possible that taxa differentiated on Madagascar migrated back to Africa, although this cannot be determined from present information.

The Mozambique Channel has been a limit for most groups and for most species in the Solanaceae until the arrival of humans. Only one clearly indigenous species, *S. richardii*, which has sea-dispersal capability, is known to straddle this water barrier, occurring in Africa and also the Mascarene Islands.

Those groups that appear to share affinities with Africa and Madagascar, both spiny and spineless, have anthers with small pores. African species with longitudinally dehiscent, relatively open anthers are not found among the *Solanum* groups native to Madagascar. Nonpollinating pollen feeders may prevent colonization by these species on Madagascar. To counter this speculation, three New World species are naturalized and abundant on parts or all of Madagascar. *Solanum mauritianum* has large pores and tardily appearing longitudinal slits, and *S. torvum* and *S. americanum* have small (in absolute size) pores and longtitudinal slits. These species occur mainly in disturbed sites and might not be subject to elimination by pollen predators that are perhaps restricted to natural areas. However, this explanation seems unlikely.

Thus, the Solanaceae of Madagascar display a variety of patterns that may be postulated as both primitive and advanced, and the different stocks may have arrived in Madagascar at different times and from different places. The history of their geography and evolution in relation to their closest relatives is conjectural but must be viewed in light of the observations outlined above.

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