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SYSTEMATICS AND EVOLUTION OF THE TROPICAL-SUBTROPICAL TILLANDSIA SUBGENUS DIAPHORANTHEMA (BROMELIACEAE)

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ABSTRACT. All currently known taxa of *Tillandsia* subgenus *Diaphoranthema* have been studied and treated in a taxonomic revision and other papers. Six groups of species ("aggregates"), distinguished by floral morphology and certain vegetative features, are recognized. These groups contain a series of taxa that display morphological reduction accompanied by shortening of life cycles (neoteny). Polyploidy is frequent within *Diaphoranthema*. Compared with subgenus *Phytarrhiza*, the closest related subunit of the genus *Tillandsia*, neotenic species of *Diaphoranthema* have migrated into more isolated and climatically extreme areas than have any other *Tillandsia* species. Abbreviated life cycles and strong tendencies of autogamy and cleistogamy, in connection with increasing polyploidy, are proposed to be responsible for the high stress tolerance and dispersibility of the species of *Diaphoranthema*.

Sistemática y evolución en *Tillandsia* subgenero *Diaphoranthema* (Bromeliaceae).

RESUMEN. Todos los taxa que actualmente son conocidos fueron estudiados y fueron tratados en una revisión taxonómica y otras publicaciones. Seis grupos de especies ("aggregates"), que demuestran neotenia progresiva son aceptados según sus morfologías florales y vegetativas. Poliploidía existe con frecuencia en el subgénero *Diaphoranthema*. Comparado con el subgénero *Phytarrhiza*, que es el pariente próximo, las especies neotenas de *Diaphoranthema* se han propagado hacia áreas más aisladas y hacia zonas climáticas más extremas que otras especies del género *Tillandsia*. Ciclos biológicos abreviados y tendencias pronunciadas de autogamia y de cleistogamia son propuestos como responsables de la tolerancia pronunciada contra "stress" y de la propagación de las especies de *Diaphoranthema*.

INTRODUCTION

The large neotropical genus *Tillandsia* L., which currently comprises about 550 species, is distributed from southern United States to Central Argentina and Chile. It has been divided several times into subunits at various taxonomic levels and even into separate genera (Smith & Downs, 1977). In the most modern monographic treatment (Smith & Downs, 1977), seven subgenera are accepted. They only represent natural alliances in part, as this work was based mainly on herbarium studies. Recent investigations (Till, 1984; Gilmartin & Brown, 1986a) have revealed that the circumscriptions of the subgenera should be revised in some cases. Classifications will be altered in the light of discoveries from research on flower morphology, pollen and stigma structures, cytology, isozymes, and cp-DNA. Very little is known about pollination types, breeding systems, and ecology.

MATERIALS AND METHODS

This paper deals with the highly specialized subgenus *Diaphoranthema* (Beer) Baker, a xeric group with Bolivian-Argentinian centers of distribution. The following research has been done (Till, 1984, 1989a, 1989b, 1991): thorough morphological analysis of inflorescences, flowers, and

vegetative traits of living plants; study of anthesis in cultivation and in the field; germination tests; and extensive herbarium studies, including examination of all types. The herbarium vouchers and the type specimens allowed the interpretation of the taxa accepted within this subgenus and provided distribution maps. After a taxonomic revision of *Diaphoranthema* (Till, 1984, 1989a, 1989b, 1991), six species groups have been recognized, and several new taxa have been described (Till & Hromadnik, 1983, 1984; Hromadnik & Till, 1991; Till, 1992). Caryological examination (Till, 1984) revealed a high degree of polyploidy upon the currently accepted base number of $x = 25$ (Marchant, 1967; Till, 1984; Brown & Gilmartin, 1989a). The distributions of individual species have been compared with the species group concept and the ploidy levels, but only a selected example is represented here.

The distributions of the species of *Diaphoranthema* cannot be interpreted correctly without also considering the xeric members of subgenus *Phytarrhiza* (Visiani) Baker (e.g., *T. streptocarpa* Baker, *T. kurt-horstii* Rauh, *T. reichenbachii* Baker, *T. duratii* Visiani, *T. arhiza* Mez in C. DC., *T. paleacea* Presl, *T. marconae* W. Till & E. Vittek, *T. kirschnekii* Rauh & W. Till, *T. cacticola* L. B. Smith, *T. purpurea* Ruiz Lopez & Pavón y Jiménez, *T. humilis* Presl, *T. aurea* Mez, *T.*

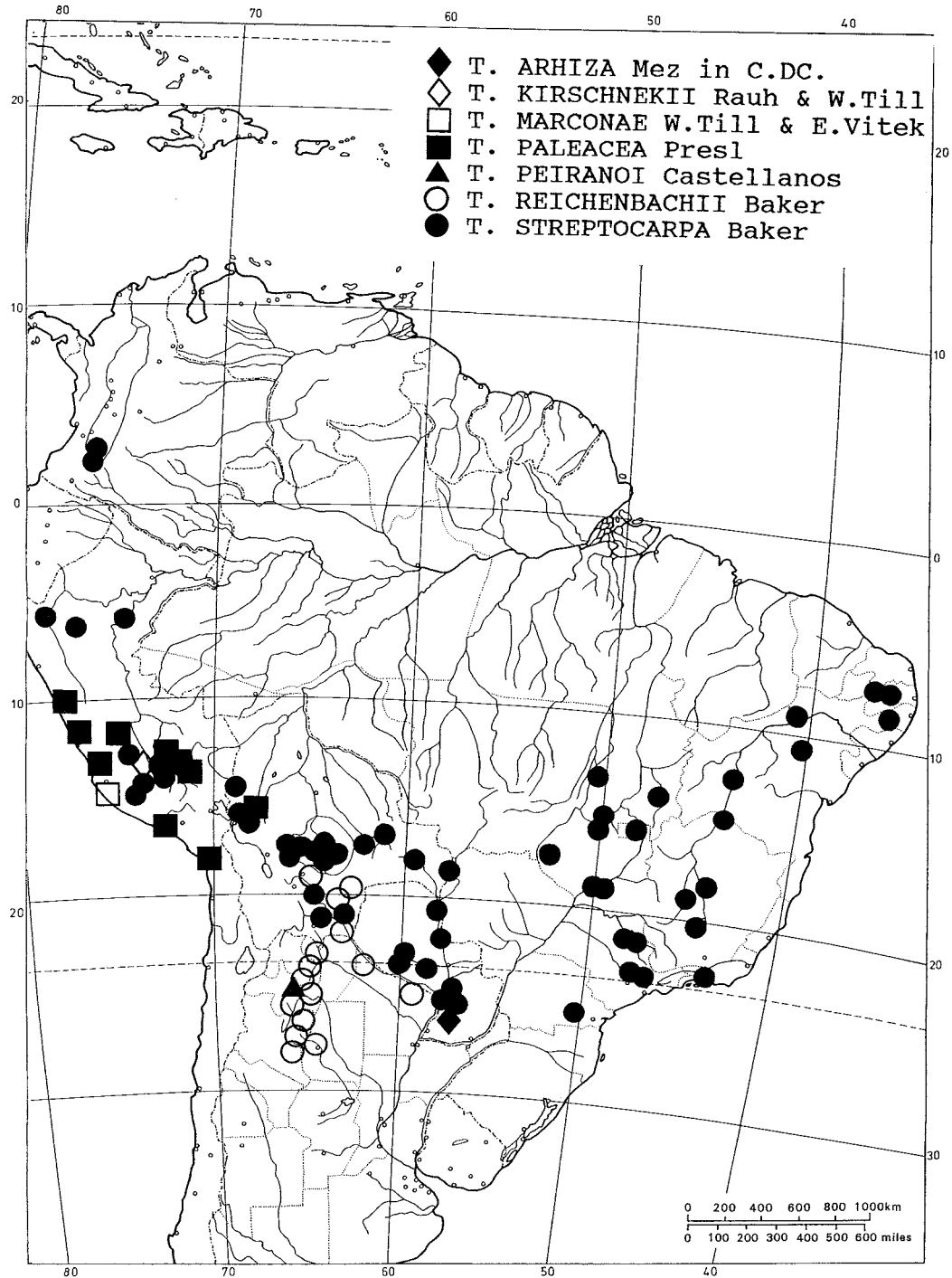


FIGURE 1. Selected xeric species of subgenus *Phytarrhiza*; *T. reichenbachii* is distributed much further south than *T. streptocarpa*; local endemics, like *T. arhiza*, *T. kirschnekii*, *T. marconae*, and *T. peiranoi*, are always peripheral.

TABLE 1. Species groups ("aggregates") of *Tillandsia* subgenus *Diaphoranthema*.

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1. CALIGINOSA group (leaves distichous, floral bracts lepidote, petals brown to violet-brown)
 - T. caliginosa* W. Till
 - T. cotagaitensis* L. Hromadnik in Till & Hromadnik
 - T. porongoensis* L. Hromadnik & P. Schneider
 - T. tenebra* L. Hromadnik & W. Till
 2. MYOSURA group (leaves distichous, rarely polystichous, floral bracts lepidote, petals yellowish to brownish, rarely dark violet)
 - T. andicola* Gillies ex Baker
 - T. angulosa* Mez in C. DC.
 - T. gilliesii* Baker subsp. *gilliesii*
 - T. gilliesii* subsp. *polysticha* W. Till & L. Hromadnik
 - T. hirta* W. Till & L. Hromadnik
 - T. mandonii* Mez in C. DC.
 - T. myosura* Grisebach ex Baker
 - T. retorta* Grisebach ex Baker
 3. LOLIACEA group (leaves polystichous, floral bracts mostly lepidote, petals yellow, rarely dark brown)
 - T. bryoides* auct. non Grisebach
 - T. copynii* Gouda
 - T. loliacea* Martius ex Schultes & Schultes fil. in Roemer & Schultes
 - T. spiralipectala* Gouda
 - T. tricholepis* Baker
 4. RECTANGULA group (leaves polystichous, floral bracts mostly glabrous, petals brownish to dark violet, rarely yellowish or light violet)
 - T. aizoides* Mez in C. DC.
 - T. brealitoensis* L. Hromadnik in Till & Hromadnik
 - T. erecta* Gillies ex Baker
 - T. funebris* Castellanos
 - T. pedicellata* (Mez in C. DC.) Castellanos
 - T. rectangula* Baker
 5. CAPILLARIS group (leaves distichous, floral bracts glabrous to lepidote, petals yellow to brown, rarely light to dark violet)
 - T. capillaris* Ruiz Lopez & Pavón y Jiménez
 - T. castellanii* L. B. Smith
 - T. virescens* Ruiz Lopez & Pavón y Jiménez
 6. RECURVATA group (leaves distichous, rarely polystichous, floral bracts lepidote, rarely glabrous, flowers with a scape bract \pm beyond the floral bract, petals violet, white, brownish, green or yellow)
 - T. landbeckii* Philippi subsp. *landbeckii*
 - T. landbeckii* subsp. *andina* W. Till var. *andina*
 - T. landbeckii* subsp. *andina* var. *rigidor* W. Till
 - T. mollis* H. Hromadnik & W. Till
 - T. recurvata* (Linné) Linné
 - T. usneoides* (Linné) Linné
-

peiranoi Castellanos, *T. caerulea* Humboldt, Bonpland & Kunth, *T. bandensis* Baker, *T. mallemontii* Glaziou ex Mez in Martius, and *T. crocata* (E. Morren) Baker). Therefore several species of this subgenus are included (FIGURE 1).

RESULTS

Smith and Downs (1977) separated *Phytarrhiza* and *Diaphoranthema* on the basis of two characteristics: "petal-blades conspicuous" versus "inconspicuous," and "leaf-blades flat or terete" versus "terete and cinereous-lepidote." Both subgenera share the following characteristics: stamens and pistils are deeply included within the corolla; the anthers are short and contain orange sticky pollen; the pollen grains are subglobular and have a coarse and deep reticulum with copious pollenkitt, and have more or less compact exine fragments upon the sulcus which has an irregular margin (Halbritter, 1988); the styles are short and stout; and the stigma lobes are erect and papillose (Gortan, 1991) (simple erect according to Brown & Gilmartin, 1989b). At first glance, close relationships of both groups and the weakness of these artificial distinctions are apparent. The traits of reproductive organs are shared in large part only with a third subgenus of *Tillandsia*: *Pseudo-Catopsis* Baker. Gilmartin and Brown (1986a) are correct to consider the latter as a cladistic sister group of *Phytarrhiza*. The anatomical features of the septal nectaries are the same in *Phytarrhiza*, *Diaphoranthema*, and *Pseudo-Catopsis*; Böhme (1988) classified them under the "pectinata"-type. Morphological studies of Bromeliaceae (Gross, 1988) revealed that the seeds of the xeric species of *Phytarrhiza* and *Diaphoranthema* are very similar. The "cotagaitensis-Typus" and the "bryoides-Typus" comprise the xeric species from both subgenera (but no species of *Pseudo-Catopsis*), and are considered the most derived ones among all types of her classification.

Comparison of *Phytarrhiza* with *Diaphoranthema* reveals a trend in the vegetative body. Xeric species of *Phytarrhiza* are polystichously leaved with rather conspicuous foliage in most cases; distichously leaved species are few (ca. 14%). About 50% of all species of *Diaphoranthema* exhibit distichous phyllotaxis. Distichous foliage is a seedling characteristic; its occurrence in adult plants is a clear expression of neoteny. This latter phenomenon is further corroborated by characteristics of reproductive parts; the morphological changes from xerix *Phytarrhiza* towards *Diaphoranthema* are the reduction of inflorescence branching, reduction of the number of flowers per spike, and the reduction of the size

TABLE 2. Progressions of characteristics in *Tillandsia* subgenera *Phytarrhiza* and *Diaphoranthema*.

Ancestral	Derived
Roots well developed	Roots strongly reduced or absent
Leaves in a rosette	Leaves distributed along a distinct stem
Leaves wide and flat, not succulent	Leaves narrow and terete, succulent
Leaves polystichous	Leaves distichous
Scape of inflorescence well-developed	Scape of inflorescence abbreviated or lacking
Inflorescence compound, many-flowered	Inflorescence simple, few- to 1-flowered
Floral bracts glabrous outside	Floral bracts densely lepidote outside
Sepals glabrous, free, obtuse	Sepals lepidote, especially posteriorly (=adaxially) connate, acute
Petals conspicuous, blades enlarged	Petals inconspicuous, blades narrowed
Style and filaments rather long, stigma and anthers reaching the throat of the corolla or exerted	Style and filaments strongly abbreviated, stigma and anthers deeply included in the corolla
Flowers without fragrance	Flowers fragrant

of the flowers (Smith & Downs, 1977; Till, 1984). One-flowered inflorescences are lacking in *Phytarrhiza* (rare exceptions in *T. caerulea*) but common in *Diaphoranthema*.

According to leaf arrangement and floral morphology (including the floral bracts), six species groups are proposed (TABLE 1). In each of these groups or "aggregates," the morphological progressions listed in TABLE 2 can be found. This arrangement of species groups suggests two ideas: 1) the six aggregates have evolved in a parallel matter at least in part and must have their phylogenetic roots within the xeric species of *Phytarrhiza*, and 2) the xeric species of *Phytarrhiza* and *Diaphoranthema* are directly related and should not be segregated in different subgenera.

Within the genus *Tillandsia*, *Diaphoranthema* displays an unusually high degree of polyploidy (TABLE 3). Eight taxa were found to be diploid, while 12 taxa are tetraploid. One can assume that more than 50% of all taxa are tetraploid and a few even hexaploid (e.g., *T. capillaris*; TABLE 3; Gilmartin & Brown, 1986b). The species groups containing tetraploids comprise the most polymorphic taxa.

The corollas of xeric species of *Phytarrhiza* are usually conspicuous, violet, and fragrant. Autogamy and cleistogamy have not been noted. In *Diaphoranthema*, the petals are reduced in size, the blade is strongly narrowed, and the prevailing color is yellowish and brown. Flower fragrance occurs in some species.

In several species of *Diaphoranthema* (e.g., *T. aizoides*, *T. capillaris*, *T. funebris*, *T. rectangula*, *T. usneoides* and *T. virescens*), a diurnal fragrance rhythm was observed: the flowers emitted fragrance beginning at dawn, maintained strong fragrance during the night, and were without scent between about 1000 hr and 1700 hr under European greenhouse conditions. Many species that

TABLE 3. Ploidy levels in *Tillandsia* subgenus *Diaphoranthema*. The haploid base number is assumed to be $x = 25$ (Marchant, 1967; Till, 1984; Brown & Gilmartin, 1989a), but the likelihood of dysploidy should be kept in mind. ♦ means that the level concerned has been determined by Till (1984).

Taxon	2x	4x	6x
<i>T. caliginosa</i>	—	—	—
<i>T. cotagaitensis</i>	♦	—	—
<i>T. porongoensis</i>	—	—	—
<i>T. tenebra</i>	—	—	—
<i>T. andicola</i>	—	♦	—
<i>T. angulosa</i>	—	♦	—
<i>T. gilliesii</i> subsp. <i>gilliesii</i>	—	—	—
<i>T. gilliesii</i> subsp. <i>polysticha</i>	—	♦	—
<i>T. hirta</i>	—	♦	—
<i>T. mandonii</i>	—	—	—
<i>T. myosura</i>	—	—	—
<i>T. retorta</i>	—	♦	—
<i>T. bryoides</i> auct.	—	♦	—
<i>T. copynii</i>	—	—	—
<i>T. loliacea</i>	♦	♦	—
<i>T. spiralipetala</i>	♦	—	—
<i>T. tricholepis</i>	—	♦	—
<i>T. aizoides</i>	♦	?	—
<i>T. brealitoensis</i>	—	—	—
<i>T. erecta</i>	—	♦	—
<i>T. funebris</i>	♦	—	—
<i>T. pedicellata</i>	—	—	—
<i>T. rectangula</i>	♦	—	—
<i>T. capillaris</i>	—	♦	?*
<i>T. castellanii</i>	—	♦	—
<i>T. virescens</i>	—	♦	—
<i>T. landbeckii</i>	?	—	—
<i>T. mollis</i>	—	—	—
<i>T. recurvata</i>	♦	—	—
<i>T. usneoides</i>	♦	—	—

* From Gilmartin and Brown (1986b).



FIGURE 2. Geographic distributions of the species of the RECTANGULA group; *T. rectangula* reaches further south than *T. funebris*, the latter having the less neotenic gross morphology within this group; *T. pedicellata*, the most neotenic species of this group, is able to settle both in high altitudes (Lake Titicaca region) and temperate Argentina.

tended to be autogamous produced scentless flowers; cleistogamous taxa always lacked floral odors. Fertile seeds were produced in the greenhouse during the European winter without any pollinators, so the ability for germination has been demonstrated.

DISCUSSION

The flowers of the xeric species of *Phytarrhiza* appear to be attractive to insects but have a very narrow throat. These species sometimes emit a distinct flower fragrance and are considered to be entomophilous. The usually violet petals are fitting for insect visits during the day (as has been observed in *T. purpurea* in the coastal desert of Peru); autogamy and cleistogamy have not been noted. The enclosed anthers are located above the stigma and are not in contact with it. The sticky pollen rarely seems to drop onto the receptive surface of the stigma in the same flower. It is unknown, however, whether germination onto its own style is prevented by chemical agents produced by its own stigma. In species of *Diaphoranthema*, the attractive function of the petals is of minor importance. The petals are often inconspicuous in size and usually yellowish-brownish. Pollinator attraction is effected by flower fragrance in several allogamous species. Some species of *Diaphoranthema* develop fragrant flowers with open corollas (spreading petal tips) which contrary to all expectation are autogamous (e.g., *T. capillaris*, *T. myosura*, and *T. virescens*, which should be considered as facultative autogamous species). Several species are autogamous (e.g., *T. bryoides* auct., *T. capillaris*, *T. myosura*, *T. pedicellata*, *T. retorta*, and *T. virescens*) or even cleistogamous (e.g., *T. angulosa*, *T. castellanii*, and *T. landbeckii* subsp. *landbeckii*). The anthers are often in close contact with the stigma and form a hood above it which prevents cross-pollination. Pollen grains have been found to germinate into its own style (H. Halbritter, G. Gortan, unpubl. data). These autogamous and cleistogamous species produce fertile seeds that are easily cultivated.

If the distributions of xeric *Phytarrhiza* species are compared, the association of reduced plant size and incipient neoteny of *T. reichenbachii* versus *T. streptocarpa* with the occurrence in drier and more extreme habitats is obvious: annual precipitation of 800–2,000 mm, mean temperature of 20°–27°C in the areas for *T. streptocarpa*; annual precipitation of 100–800 mm, mean temperature of 14°–20°C in regions for *T. reichenbachii* (Hueck & Seibert, 1972). Depending on cross-pollination and insect (butterfly) visits, the areas of the xeric species of *Phytarrhiza* are lim-

ited in southward extensions and in altitudinal ranges. Although well-adapted against water stress by voluminous water storage tissue, species of *Phytarrhiza* need too much time to reach the age of reproduction to survive in extreme habitats. In contrast, the species of *Diaphoranthema*, with distinct neotenic growth forms and the ability for autogamy and cleistogamy, are more successful and have been able to migrate into temperate Argentina (provinces of Río Negro and Chubut, FIGURE 2). The ability of settlement in extreme habitats (in the Andes of Peru, *T. virescens* grows at 4,000 m) is likewise associated with the increasing independence from pollinators.

The highly neotenic species within *Diaphoranthema* are characterized by reduced size of the vegetative body and depauperate inflorescences which are often one-flowered. They rapidly reach reproductive age. These species behave like island plants, as they establish populations that are often remote from each other. As with island floras, the degree of polyploidy is high. Independence from pollinators by the way of facultative autogamy and/or cleistogamy promotes founder success in extreme habitats, but encourages inbreeding. The combination of both outbreeding and inbreeding as demonstrated by the species groups of *T. capillaris* and *T. myosura* seems to be the "superior" evolutionary strategy. Outbreeding requires visitors for flowers and it seems that the fragrance during the night compensates in part for the missing attractiveness of the petals. Pollinators are expected to be active during the night or the dawn.

It is evident, however, that in spite of new biological information about xeric members of *Phytarrhiza* and *Diaphoranthema*, the taxonomy of both groups is still unsatisfactory. Under the heading "Results," I explained that a segregation of *Phytarrhiza* and *Diaphoranthema* in two subgenera is not reasonable, as many more characteristics unite than separate them. At the species level, however, the situation is reversed. In *Diaphoranthema*, the species exhibit strong neoteny, are frequently polyploid, and in several cases, facultatively autogamous and cleistogamous. A narrow species concept, recognizing microspecies within groups (aggregates), seems to be more appropriate than working with collective species. Microevolution, which also occurs within *Phytarrhiza* (xeric members only, e.g., *T. streptocarpa* with several distinctive local races), is somewhat obscured by frequent outbreeding. The reasons for the evolution of the neotenic forms of *Diaphoranthema* could be the climatic changes during the Pleistocene, which caused the creation of new features to survive in the drastically altered environment. Later, exactly these

new features were an advantage for occupying new ecological niches.

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