

The Genus *Thrinax*
(Palmae: Coryphoideae)

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ABSTRACT

Read, Robert W. The Genus *Thrinax* (Palmae: Coryphoideae). *Smithsonian Contributions to Botany*, number 19, 98 pages, frontispiece, 57 figures, 1975.—The history, distribution, ecology, morphology, cytology, anatomy, and taxonomy of the four species of *Thrinax* are presented. The objective is to demonstrate that quantitative characters, formerly believed to be important in distinguishing species, merely represent random selections from clinal patterns and are therefore of little value in distinguishing taxa. Certain characters described for the first time—leaf sheath, blade, color and puberulence of the inflorescence—have proved to be of great taxonomic value. Particular attention is given to the variability of *Thrinax parviflora* Sw. over a wide range of climatic conditions and to its unusual phenotypic behavior, in special situations, in the Cockpit Country and on the slopes of Mt. Diablo in Jamaica. The haploid chromosome number (determined at pollen-tube mitosis) of all four species is 18. Little difference in size or morphology of the chromosomes exists among these taxa. Anatomically all four species can be distinguished by comparison of leaf segment sections.

The taxonomic portion is a thorough revision of the genus. It includes literature references, synonymy, complete descriptions, and specimens examined. *Thrinax parviflora* Sw. and *T. excelsa* Lodd. ex Griseb. are endemic to Jamaica while *T. radiata* Lodd. ex J. A. & J. H. Schult. occurs in the littoral of the Greater Antilles (except Puerto Rico), the Bahamas, Florida, and Mexico. *Thrinax morrisii* H. Wendl. occurs on most of the islands from Anegada (east of the Virgin Islands) to the islands off the coast of British Honduras, and Florida, but not in Jamaica.

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Thrinax morrisii H. Wendl. recently photographed on Anguilla. This population, at Long Bay Hill, is very near the site of its original discovery in 1890, where its leaves are still used for making brooms.

The Genus *Thrinax* (Palmae: Coryphoideae)

Robert W. Read

Introduction

Thrinax is a genus of true palmate-leaved palms in the subfamily Coryphoideae. The genus occurs only on the islands of the northern Caribbean and the nearby continental coastal areas bordering on the Gulf Stream. Its nearest allies are *Hemithrinax* and *Coccothrinax*, which share the same general range of distribution.

The genus *Thrinax* may be recognized by the unarmed split leaf-petioles, flowers with a single whorl of perianth, and nonruminant seeds which have the center partially or completely intruded by the testa. Stamen number varies from 5 to 15 (rarely more) and the abaxial surface of the leaf may or may not be white or silvery. Fully mature fruits are always white or ivory colored.

At the beginning of this study five species of *Thrinax* were attributed to Jamaica with an additional seven or eight distributed throughout the Caribbean region apart from Jamaica. With the exception of a few quantitative characters of dubious value, no convincing differences could be found between Beccari's *T. parviflora*, *T. tessellata*, and *T. harrisiana*. This was also true concerning *T. morrisii* of Wendland, *T. ponceana* and *T. praecipua* of Cook, *T. drudei* and *T. punctulata* of Beccari, and *T. microcarpa* of Sargent. Similarly, Bailey's *T. parviflora* and *T. excelsa* were separated in a key based solely on the size of the fruit and leaf segments. During the present study it has been found that, with the exception of Beccari's *T. parviflora* (in part), none of the names in common use

have been applied correctly, and all of the names of the species not occurring in Jamaica are to be relegated to synonymy or to subspecific status of the least commonly used specific epithet. The reasons for the previous confusion are inadequate herbarium material and a lack of understanding of the variability of *Thrinax* species in natural populations.

My interest in *Thrinax* developed as a result of an attempt to understand the palms of southern Florida, and the necessity of clearing up nomenclatural problems of the plants used in my cytological studies. After several trips to the islands of the Caribbean, and to Jamaica in particular, it was soon obvious that the same taxon known in Florida as *T. parviflora* was known under a different specific epithet on each of the various islands. In Jamaica, the type locality of *T. parviflora* Sw., the Florida taxon was known as *T. excelsa* and the epithet *T. parviflora* was applied to an entirely distinct but very poorly understood local taxon. It was clear that a study of the Jamaican taxa of *Thrinax* was essential before an understanding of the taxa elsewhere was possible.

Before revisionary work in palms could be accomplished at the species level, it was essential to understand the range and type of variation possible within each taxon and to have some understanding of the effects of environment on the variation. It was also important to determine the kinds of characters (key characters) which unquestionably distinguish taxa and which remain recognizable regardless of environment. Far too often descriptions of palms drawn from incomplete and inadequate collections have been relied upon

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for identification. The situation clearly stated by Joseph D. Hooker and Thomas Thomson (1855) has been found true today in the study of palms. They wrote that "the more specimens we examined, and especially if taken from different individuals, the greater the difficulty in framing diagnosis. . . . We are firmly convinced that no species can be properly defined, until it has been examined in all the variations induced by those differences in climate, locality, and soil." It seems superfluous to restate these well-known facts, but this basic information has yet to be acquired in most tropical families, particularly those with large cumbersome plants such as the *Palmae*.

No amount of statistical analysis, numerical taxonomy, or classical taxonomy for that matter, will solve the problems of species definition when based on inadequate collections, incomplete herbarium specimens, and insufficient knowledge of ecological tolerances. A study of the scope undertaken here is too laborious and time-consuming to be applied within the foreseeable future to more than a fraction of the palm species described. Proof of conclusions regarding genetic differences is not possible without transplant experiments; but the obstacles to long-term experiments with such slowly developing plants as palms preclude this approach.

Proper study of palms has until recently also been hampered because of their size, complexity, general unwieldiness, and inaccessibility in tropical regions. In addition, portions of the plants which did not conform to the limits set by the standard herbarium sheet or "pigeonholes" were often disregarded by collectors. The opportunity was taken during this study to make intensive observations of *Thrinax* in the field and to analyze and present the data in a comparative way for taxonomic purposes. This has led to detailed examination of the development and mature condition of all organs whose nature could in any way assist the accurate and complete definition of the genus *Thrinax* and its species in Jamaica.

The result is a statement of the natural variability of *Thrinax* against the background of the physical factors of the environment, leading to a complete taxonomic revision of the genus.

ACKNOWLEDGMENTS.—The basis of the present monograph is a thesis for the Ph.D. degree. The author wishes to express his sincere appreciation to

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Additional research was made possible for me as a National Research Council Visiting Research Associate in the Department of Botany, Smithsonian Institution, later as a Research Associate of the Department, and now as an Associate Curator in the same Institution. This has made it possible to change "A Study of the Genus *Thrinax* in Jamaica" into a monograph of the genus as a whole.

History of the Genus

Although Linnaeus did not include any palms of the Caribbean islands in his *Species Plantarum*, their existence had been recorded by various authors during the century prior to 1753. In fact Sir Hans Sloane (1696) described ten true palms in his *Catalogus Plantarum*, of which one has been determined to be a member of the genus *Thrinax*. It is important to understand that while Sloane was writing specifically of palms he observed in Jamaica, he also attempted to identify them with descriptions already in the literature. This association of earlier accounts with the Jamaican palms was often incorrect; therefore in order to understand the application of Sloane's descriptions, it is essential to ignore these misleading synonymies. Nor did that practice end with Sloane for it has continued to plague the study of palms to the present.

The palm to be discussed most fully in the present paper appeared for the first time in the literature as the last true palm mentioned by Sloane (1696:178, 179). Sloane unfortunately associated the Jamaican "thatch" with Ray's "4. *Palma Brasiliensis prunifera*" (1688:1368) because of the similarity of the leaf form. Ray's palm, however, is Brazilian and has been determined to belong to the genus *Copernicia* (Moore, 1963). Since no *Copernicia* has been found in Jamaica, the plicate-leaved palm growing "In sylvis saxosis & collibus sterilioribus Jamaicae Insulae ubique reperitur" (Sloane 1696:179) can only be one of those presently known as *Thrinax* or *Coccothrinax*. In 1725, Sloane again cited "*Palma Brasiliensis*" as the "thatch" (p. 121) of Jamaica and again the sole indication of its identity, in the text, is that, "This grows on all the Honey-comb Rocks of this island" (p. 122). Sloane's pl. 213: fig. 2 of the same work, however, unquestionably illustrates a *Thrinax*-like palm leaf. The lack of teeth on the petiole, the nonacuminate hastula, and the irregular fusion of the segments, if this was intended to be diagnostic, clearly indicate that this illustration depicts the plant now determined to be *Thrinax parviflora* Sw.

The first complete account of a palm readily identifiable as *Thrinax parviflora* Sw. in the literature appeared in Patrick Browne's *Civil and Natural History of Jamaica*, published in 1756. The

Latin diagnosis of "*Corypha* I. *Palmacea*"¹ is accurate, but the association of Ray's Brazilian palm again apparently contributed to Grisebach's (1864) belief that a *Copernicia* was to be found in Jamaica.

In 1784, Olof Swartz left Sweden at the age of 24 and spent the next two years traveling through the West Indies and Jamaica. Following his trip through the Caribbean, Swartz went to England to study the Hans Sloane Jamaican collection and the herbarium of Sir Joseph Banks at the British Museum. Within two years of his return to Sweden he published (1788) the first of his major works on West Indian plants, *Nova Genera et Species Plantarum seu Prodrromus*. In the *Prodrromus*, as it is known, appeared the first published description of the palm *Thrinax parviflora*. A diagnosis of the genus appeared on page 4, number 29, and the single species was described on page 57.

It is possible that Swartz went to Jamaica with some foreknowledge of the palm he later described as *Thrinax parviflora*. Although he gave no indication in the *Prodrromus* of the source of the name or its meaning, he attempted to rectify his debt to Linnaeus the younger by inserting a note of acknowledgment in his *Flora* (1797). That the younger Linnaeus was preparing to publish the binomial, before his death in 1783, is now an established fact. A complete and accurate description of *Thrinax*, under the binomial *T. parviflora*, has been found in an unpublished manuscript belonging to the younger Linnaeus. The manuscript² reproduced in part in Figure 2 is clearly the source of the binomial, and whether Swartz saw the manuscript before he went to Jamaica or upon his return is not known. Linnaeus' description is a composite of Browne's *Corypha* I., Sloane's illustration (pl. 213) and a specimen of an inflorescence preserved in the Banksian herbarium at the British Museum. Since the Linnaean manuscript was never published, we must consider only Swartz's speci-

¹ Correspondence between Dr. Bailey and the Linnean Society of London in 1937, in a letter signed by S. Savage, Assistant Secretary, revealed that "no specimen of the species of *Corypha* described by Patrick Browne in *Hist. Jam.* p. 190 exists in the Linnean Herbarium. In Linnaeus' copy of Browne's book there is no annotation by Linnaeus to show that a specimen of this plant was received by him with Browne's herbarium."

² Provided by the courtesy of the Linnean Society, London, through Dr. H. E. Moore of Cornell University (List no. 40, "*Linn. fil. Palmarum Descriptiones*").



FIGURE 1.—*Thrinax parviflora*, cut and removed from the forest for photographing, being examined by Dr. Ivor Cornman.

men and his descriptions based on personal experience in Jamaica in typifying *Thrinax parviflora*. The finding of the Linnaean manuscript is, however, of historical significance and provides answers concerning the source of the binomial and its meaning. *Thrinax* according to the manuscript is derived from the Greek θριναξ, which can be translated as "trident" or as indicated by Linnaeus "ventilabrum" meaning, "winnowing fork."

Thrinax was the tenth genus described in the Palmae after the publication of Linnaeus' *Species Plantarum* in 1753. It should not then be sur-

prising that a number of dissimilar and unrelated palms have been included in the genus (see Appendix I). The original description by Swartz in the *Prodrum* (1788) clearly sets down characters that are still diagnostic for the genus. The six-lobed perianth cupule, unilocular ovary, and infundibuliform stigma apply exclusively to the *Thrinax* alliance.

Early in 1789, W. Aiton reported in his *Hortus Kewensis* that there was a palm growing at Kew under the name of *Thrinax parviflora*, which was introduced by Dr. William Wright upon his return

Thrinax ⊕ (⊕ θριναξ) ventilabrum.
parviflora

Brown jam. n: 190 Palmis Royal or Palmata Thales
Sloan jam f. 213

Inflorescentia Flores racemosa

Cal: Perianthium ^{monophyllum} ~~monophyllum~~ campanulatum pro sex dentatum, dentes
in minimi interdum bifidi

Cor: nulla.

Stamina filam: sex, longiorae calcei, basi gemini / orientis / adaxi
tubulata
anthera oblonga utrinque emarginata, angulata. fascium
bento

Styl: grem: superum, parvum, ^{ovatum, angulata} glaberrimum. Stylus brevissimus prople.
stigma oblique truncatum, concavum saepe angulatum usque
ne uncinata

Macropodites



Sto



Sto & Pist.
bento calyx



Stigma

Habitat in India occidentali: Jamaica
medicam reportatum a di in mases Banksii spiritibus vino conser.

FIGURE 2.—Facsimile of a portion of Linnaeus the younger's unpublished manuscript on *Thrinax parviflora*.

from Jamaica in 1777. The palm at Kew was mentioned again by W. T. Aiton in 1811, and again seventy-one years later by Hooker in the Kew Report for 1882. *Thrinax* was treated in the eighth edition of Linnaeus' *Genera Plantarum* (edited by C. D. Schreber, 1791), and *T. parviflora* was treated later in the fourth edition of the *Species Plantarum*, edited by C. L. Willdenow (1799).

In his magnum opus on West Indian plants, Swartz (1797:613-615) published a much amplified account of the genus and species in the *Flora Indiae Occidentalis*; flowers and fruit were illustrated on plate 13.

The first mention of additional species in the genus *Thrinax* appeared in 1829 in Desfontaines' *Catalogus Plantarum* (3rd ed.) where *T. radiata* and *T. argentea* appeared in a list without descriptions. The father and son team of J. A. and J. H. Schultes (1830) took up the Desfontaines names for which, with the addition of *T. pumilio*, they published diagnoses based on specimens sent by Loddiges, a nurseryman, to the botanical garden at Munich. Martius (1838) elaborated on the descriptions of *T. parviflora*, *T. radiata*, and *T. argentea* and added two new species, *T. multiflora* and *T. barbadosis*. In 1845, nurseryman Loddiges, from whom Martius also obtained several specific epithets, published a catalog of palms; there are no descriptions, thus the names that were not already provided with diagnoses are nomina nuda. During the one hundred years between treatments by Martius and Bailey (1838 and 1938 respectively) forty additional epithets were attributed to the genus *Thrinax*.

In 1866, A. H. Grisebach attempted to erect a new genus, *Porothrinax*, based on *Thrinax pumilio* of J. A. & J. H. Schultes. The lack of a separate diagnosis or description for a monotypic genus based on an old species does not satisfy the requirements of the present International Code of Botanical Nomenclature (see Appendix II), so I am treating the genus as a nomen nudum.

Charles S. Sargent (1899:88) made the first clear division of the genus when he recognized that specimens collected in Florida, and attributed to *Thrinax*, could be separated from that genus on the basis of the seeds being "vertically sulcate by the infolding of the testa into the ruminant albumin." Thus he described *Coccothrinax*, a new genus based on *C. jucunda* Sargent. He also transferred

Thrinax garberi Chapman into the genus to make a second species, *C. garberi* (Chap.) Sarg. He further suggested that *Thrinax radiata* and *T. argentea* both of Lodd. ex. J. A. & J. H. Schultes might also belong in the newly described genus, but it remained for K. Schumann to make the formal transfers in 1901. Sargent (1899) divided the species remaining in *Thrinax* into two sections, the *Pedunculatae* and *Sessiliflorae*, and described two new species, *T. floridana* and *T. keyensis*.

In 1883, Bentham and Hooker included *Thrinax* along with their newly founded *Hemithrinax* in the tribe Corypheeae, but Drude (1887) reduced *Hemithrinax* and *Porothrinax* along with *Euthrinax* as subgenera of *Thrinax*. Thus it remained until Beccari (1907) produced his work on American Corypheid palms. Beccari raised *Hemithrinax* to full generic status again and divided the Corypheeae into two subtribes: *Eucorypheeae*, characterized by the perianth having two whorls and the ovary being three-locular or with three carpels; and *Thrinaceae*, with a perianth of a single six-lobed whorl and the ovary consisting of a single uniovulate carpel. He divided the genus *Thrinax* into two subgenera based on the degree of intrusion of the testa into the seed: *Euthrinax*, including the earlier *Porothrinax* of uncertain identity, and *Typhlothrinax*. No mention was made of Sargent's earlier division of the genus based on pedicels. The genus as outlined by Beccari (1907) contained ten species that he considered good, including four new names, plus three names of dubious application. Beccari (1912) published a series of articles on the palms of Cuba in which he treated three species of *Thrinax*. A supplement to his earlier work, in English, was included in a larger posthumously published work in 1933 ["1931"].

A new genus, *Simpsonia*, based on *Thrinax microcarpa* Sarg., was published by Cook (1937); however, the requirements of Article 36 of the *International Code of Botanical Nomenclature*, 1966, were not satisfied and the genus was not validly published.

Bailey (1938), in an attempt to clear up some identification problems among palms in horticulture, produced a comprehensive study on the genus *Thrinax*. He accepted ten species, which he arranged in two subgenera as suggested earlier by Sargent. In a review of Beccari's work Britton wrote (1908:240) that, "This is probably the most

difficult of the American palm genera to understand," to which Bailey (1938:133) replied thirty years later:

Any subsequent student of the genus will be sympathetic with this estimate; but many of the difficulties vanish if one knows the plants in the field, has really good herbarium material, and does not assume he must necessarily recognize all the species that have been described. Differences one draws diligently from poor herbarium sheets may disappear in the living plant.

The present author must agree with this, and with Bailey's earlier statement (1938:133) concerning *Thrinax parviflora* Sw. and *T. microcarpa* Sarg. that, "If the student understands these two, all the other species fall readily into place." Unfortunately Bailey did not have an adequate understanding of *T. parviflora* in Jamaica, hence the species there did not fall so readily into their proper places.

Distribution and Ecology

Palms of the genus *Thrinax* occur only on alkaline substrate, specifically coralline sands or limestone outcrops, from sea level to about 1200 meters elevation. They are distributed from areas of strong seasonal drought with rainfall averaging 100–112 cm per year (with no more than 6 months having rainfall less than 8 cm per month) to regions where the rainfall may reach 762 cm per year. Two species endemic to Jamaica—*Thrinax parviflora* and *T. excelsa*—are restricted entirely to exceedingly well-drained sites far from the influence of salt spray. *Thrinax radiata*, in addition to Jamaica, is widely distributed in the littoral throughout the northern Caribbean and nearby shores of the Gulf Stream, and tolerates considerable exposure to salt-laden winds. The fourth species, *T. morrisii*, not found in Jamaica, is fairly tolerant of salt and, although usually at sites similar to the aforementioned, is commonly found farther inland beyond the worst effects of salt spray.

Each of the three species in Jamaica is confined to one of three major environmental situations (see Asprey, 1959): e.g., Dry Evergreen Woodland or Thicket, Lower Montane Rain Forest, and Littoral Woodland or Thicket. Species of *Thrinax* have not been found naturally in areas lacking limestone or alkaline sand, they are strict calciphils.

THRINAX RADIATA.—One of the two most widely distributed species in the genus, *T. radiata*, is found only in coastal areas on limestone and alkaline sand, under the influence of salt-laden breezes, throughout the Greater Antilles (excluding Puerto Rico). It is also found on many of the smaller islands to the north and west such as the Cayman Islands and the cays off the coast of Cuba and British Honduras, the Yucatan Peninsula of Mexico, the Bahama Islands, and southern Florida. In nature this palm is confined to saline conditions of the littoral but where there is adequate rainfall (127–254 cm per year) throughout the year. This is also the most commonly cultivated species and is grown under various conditions of soil and moisture far from the influence of salt.

In Jamaica, *Thrinax radiata* may occur in dense stands but is more common in small scattered populations along most of the coastline from extreme eastern Morant Point along the north coast west to Negril lighthouse and south to Little Bay. A small population also occurs at Long Acre Point, near Black River, and another is believed to be on Big Pelican Cay some distance off the southern coast of Jamaica.

In 1958, G. F. Asprey and A. R. Loveless described a new addition to their list of Littoral Dry Evergreen formations in Jamaica based on a population of *Thrinax radiata*³ situated at Galina Point on the north-central coast in the parish of St. Mary. This formation, which they called "Littoral Palm thicket," occurs on a raised coralline limestone shelf, 3.05 to 7.62 m (10 to 25 ft) above sea level. The shelf is relatively flat, devoid of soil, and is exposed to the full force of strong salt-laden trade winds. The sea is frequently rough and breaks over the low cliffs to produce a splash zone up to 12 meters broad. The species forms a characteristic feature of the littoral hedge, becoming increasingly plentiful on the landward side, "where it would appear to take the place of Littoral Evergreen bushland, but no explanation as to why this occurs can be offered" (p. 560). The authors further pointed out (p. 560) that

³ Asprey and Loveless (1958) failed to distinguish between *T. parviflora* Sw., a conspicuous element in their studies on the Dry Evergreen thicket of Portland Ridge on the south coast, and the very different *T. radiata* at Galina Point.

The raised limestone beach is dominated by *Thrinax parviflora* [sic] to the exclusion of other plants. The trees grow out of fissures in the bare soilless rock and vary in height from 7.5–12 m (25–40 ft). They are spaced, on the average, about 1.2 m (4 ft) apart and form a closed canopy. The palm reproduces actively since seedlings abound and the plant is evidently in a most favourable environment.

A somewhat similar situation occurs at Morant Point near the lighthouse where the palms form small stands in the thicket along the windward coast. Throughout the rest of its range in Jamaica, *T. radiata* occurs as scattered individuals in coastal

thickets within the range of salt spray. The dense stand at Galina Point is not unique, for of Florida's upper Keys, J. K. Small (1925:53) wrote: "There the growth is phenomenal, or at least it was, before the lust for destroying every living thing reached these islands with the advent of civilized man. Thatch hammocks clothed large and small areas." In some small low areas and on outlying keys the palms still dominate the landscape.

In the paper by Asprey and Loveless, a site at Fort Point on the eastern edge of Discovery Bay



FIGURE 3.—The Cockpit County of western Jamaica, in the vicinity of Barbecue Bottom.

(Dry Harbour) was also described. Fort Point is approximately 36 miles west from Galina Point. Meteorological data used for both localities were based on records for Richmond Llandovery Sugar Estate, which is nearer to Fort Point than to Galina Point. The rainfall figures quoted were 55 to 70 inches (139.7–177.8 cm) per year which, when compared with evaporation figures over the same period of seventy years, presents a condition where there are only 5 months in an average year when precipitation exceeds evaporation. It must be realized,

however, that the utilization of such figures is indeed tenuous in a region where abrupt changes can occur in very short distances depending on the exposure and topography. According to the most recent rainfall figures, Galina Point, at the western edge of one of the wettest regions of the Island, has between 60 and 80 inches (152.4 and 203.2 cm) of rain per year, while Fort Point is in a region of considerably lower rainfall not exceeding 50 inches (127 cm) per year.

The preceding observations are brought out be-



FIGURE 4.—*Thrinax radiata*, base of the caudex and low mound of surface roots, growing on exposed and eroded limestone in the Florida Keys.

cause even as Asprey and Loveless noted (1958: 561): "The only major anomaly in the data is brought about by the megaphyllous palm *Thrinax parviflora* Sw. [sic]." Had they recognized that the palm from Galina Point was distinct from the palm in their Portland Ridge studies, a very important fact would have been realized and quite different conclusions might have been reached. Characters for separating the two species are in the key to the species in the taxonomic section; however, a very important characteristic, not in the key, is the fact that *T. radiata* is a true halophyte and *T. parviflora* is not. Further, *T. radiata* occurs only where regular deposition of salt is accompanied by regular high rainfall. *Thrinax parviflora* on the other hand occurs not at all where saline conditions prevail but can survive very dry environments. The present author agrees with the observation made by Asprey and Loveless (1958:562) "that the vegetation reflects the climate far more accurately than any meteorological data."

It seems appropriate here to point out a few very

important differences between the two localities studied by Asprey and Loveless on the north coast of Jamaica, which bear on the ecology of *Thrinax radiata*. Galina Point is exposed directly to the full impact of strong trade winds and heavy seas. Ample rainfall is indicated by its proximity to the high-rainfall zone of Portland and by the character of the vegetation in the immediate vicinity beyond the reach of the salt spray where herbaceous ground cover is plentiful. Asprey and Loveless noted (1958: 561) that, "The presence of *Philodendron* sp. [lacerum] among the fringing woodland plants indicates a moist habitat," from which they concluded that "the relationship of Palm thicket to rainfall distribution might repay further investigation." A further observation by the authors (1958: 562):

In view of the fact that the rainfall along the stretch of coastline in which Fort Point and Galena Point are situated is more than twice as much as at Port Henderson, although the monthly distribution patterns are similar, it might at first sight seem surprising that Evergreen bushland is found at both centres.



FIGURE 5.—*Thrinax radiata* in Jamaica: A, near the lighthouse at Morant Point; B, plants exposed along the limestone shelf at Galina Point.

This is not surprising, for they did not in fact find bushland at Galina Point, it was displaced by palm thicket, and the bushland described at Fort Point is in a much drier area than Richmond Llandoverly, where the rainfall records were made. The authors relied too much on interpolation of rainfall data and included too extensive a stretch of north coast in their data. Furthermore the additional effects of strong constant winds in conjunction with salt would produce drought conditions in the spray zone more intense than might be indicated by rainfall figures, no matter how accurate.

A short distance away, to the west of Discovery Bay in the vicinity of the Queen's Highway, *Thrinax radiata* occurs under what appear to be pessimum conditions for the species. Several widely spaced individuals are growing on the seaward side of the highway on a flat limestone terrace where there is an accumulation of sand and decaying vegetation. Evidence of low rainfall can be seen in the abundant xerophytic vegetation containing plants such as *Agave harrisii*, *Euphorbia punicea*, and *Plumeria jamaicensis*, which become increasingly abundant on bare rock toward the east in a thicket of semideciduous trees and shrubs. *Coccothrinax jamaicensis*, a palm otherwise limited to the drier thicket vegetation along the south coast (Read, 1966), occurs in abundance along the eastern portion of the Queen's Highway. Toward the western end of the Highway, halfway between Discovery Bay and Bengal Bridge, the climate changes rapidly to a more moist environment containing none of the species mentioned as characterizing the dry thicket toward the east. A single plant of *T. parviflora* stands out conspicuously in the ecotone on the inland side of the highway. On the seaward side of the highway *Coccothrinax* persists farther west among the plants of *T. radiata*, where it appears to tolerate increased moisture under saline conditions. It has been the author's experience with palms in cultivation that many species which occur naturally in a very dry climate also have a high tolerance for saline conditions; e.g., species of *Washingtonia*, *Erythea*, *Hyphaene*, *Phoenix*. That is not to say that the converse is also true, for it is not.

At the westernmost end of Jamaica between Orange Bay and Negril there occurs a variety of habitats in a region of fairly regular, often high rainfall. On Orange Point, *Thrinax radiata* thrives

on a limestone ridge a few feet removed from the weatherworn, absolutely soilless, clinker-type dog-tooth limestone. Farther south along the shores of Bloody Bay and inland from Negril Beach the land is low, almost flat but slopes imperceptibly into the nearby Great Morass. The substrate is white sand, with a very high water table, and *Thrinax radiata* occurs as scattered individuals along the better drained rise, only a few feet above sea level. The species is fairly common along the high cliffs near the Negril lighthouse and occurs as scattered individuals southeastward to Little Bay and Long Acre Point.

THRINAX EXCELSA.—This is a Jamaican endemic which is very restricted in its distribution, occurring only in the region of the John Crow Mountains of the easternmost parishes of Portland and St. Thomas, and on Uncommon Hill, a limestone outcrop on the lower slopes of the Blue Mountains above Fruitful Vale in Portland. Its environmental requirements are rather unusual in that it is limited to the driest, best drained, most exposed situations in the wettest part of Jamaica. According to Asprey and Robbins (1953), the John Crow Mountains are clothed with lower montane rain forest on the lower slopes, where the rainfall may be as much as 762 cm per year.

That the vegetation is very characteristic of the substrate and drainage is strikingly illustrated by the situation in the John Crow Mountains. In the vicinity of Winchester Peak at the southern end of the range, the deep heavy soil on the lower slopes supports a tall forest with a dense canopy. In the relatively low illumination, epiphytes are rare and the undergrowth consists mainly of seedlings, some ferns, and a few herbaceous plants. Higher on the steep slopes below the peak, the well-drained substrate consists of a mixture of soil, decaying matter, and loose broken rock. The forest here is lower and more open with smaller more slender trees but with occasional large emergent trees. Ferns and herbaceous plants are more common in the increased illumination and abundant moisture. At elevations between 304 and 762 m on the slopes and ridges throughout the range the foundation rock is frequently exposed, particularly along water courses. It is peculiar that in such a wet environment the exposed rock is usually devoid of vegetation other than the palm *Thrinax excelsa*, which dominates the forest on nearly all exposed

solid rock. Winchester Peak, at the southern end of the John Crows, receives less rain than elsewhere in the range. The southeast face of this peak is dominated by a palm brake of *T. excelsa* at between 457.2 and 533.4 m elevation.

Throughout the rest of the range of the John Crow Mountains the forest is considerably more

dense and more typical of lower montane rain forest, than that just described, because of the greater rainfall. On Uncommon Hill in the northeastern foothills of the Blue Mountains and in the John Crows, where the rainfall is consistently high, *T. excelsa* occurs only on rock outcrops at the higher elevations. An exception was more recently



FIGURE 6.—*Thrinax morrisii* in the pinelands of New Providence in the Bahamas. This species is found in almost identical associations on Big Pine Key in Florida.

found on a rocky hill near the mouth of the Rio Grande.

THRINAX MORRISII.—With much the same range as *Thrinax radiata*, this species extends farther east to the Virgin Islands and Anguilla, but it is conspicuous by its absence on both Hispaniola and Jamaica; however, the tiny island of Navassa, situated immediately between the two much larger islands, supports a small population of *T. morrisii*. In Puerto Rico and Cuba the species is common on limestone hills of the interior where it occupies habitats apparently paralleling those of *T. parviflora* in Jamaica. Occupying a niche which seems to be intermediate between *T. parviflora* and *T. radiata*, the Morris palm apparently cannot compete with either. Although somewhat tolerant of saline conditions, *T. morrisii* does not readily compete with *T. radiata* except on the smaller islands where annual rainfall probably falls below the minimum necessary for survival of the latter. Intermittent periods of rigorous drought may also restrict competition from *T. radiata*. *Thrinax morrisii* exhibits a very wide range of tolerance for extremes of climatic conditions.

As might be expected from a species that has two synonyms in Puerto Rico, two in Cuba, and two more in the Florida Keys, *Thrinax morrisii* is morphologically very variable; however, there does appear to be a pattern suggestive of more than a single genotype. Considerably more research is needed before anything more definite can be written concerning the delimitation of subspecies.

One of the earliest reports of ecological consideration and competition between palms and other plants appeared in a discussion of *T. ponceana* by Cook (1901:536):

Many of the palms are scattered among the taller shrubs and trees wherever there is sufficient soil and water to permit these to grow and yet not enough to give them exclusive possession, but on many of the drier and more sterile higher slopes the advantage is with the palms.

THRINAX PARVIFLORA.—In the broadest sense this species occurs on nearly all exposed and eroded "Jamaican Hard White Limestone" throughout the western two-thirds of Jamaica. Along the southern part of its range *Thrinax parviflora* is a conspicuous element of the formation described by Loveless and Asprey (1957:813) as "Dry Evergreen Thicket," typified by the vegetation of Portland Ridge in the parish of Clarendon. *Thrinax parviflora* was

described as "The commonest member," of the shrub layer, ". . . which although capable of growing much taller, does not do so in this community except where there is a gap in the canopy." These authors included the species as the principal representative of the Palmae among the five most important families of arborescent species in the Dry Evergreen Thicket. Apart from the presence of the "thatch," the formation is characterized by the absence of herbaceous ground cover and terrestrial ferns. The substrate is generally deeply eroded bare rock with occasional pockets of shallow soil and very little humus. "Epiphytes are not well developed but are represented by two xerophytic species, the bromeliad *Tillandsia fasciculata* and the orchid *Broughtonia sanguinea*." Dry Evergreen Thicket is a widespread formation on most of the hills and ridges of low to middle elevations from sea level to about 457.2 m (1500 ft) where the limestone is naturally exposed. Local variations in floristic composition result from local changes in topography and edaphic conditions.

Areas of dry evergreen thickets on Dallas Mountain, Long Mountain, lower Molynees Mountain, and Ferry Hill in St. Andrew represent the easternmost part of the range of *T. parviflora*. The Hellshire Hills of St. Catherine; Portland Ridge, Brazillito Mountain, and Round Hill in Clarendon; and the low irregular hills which rise along the northern edge of the St. Catherine and Clarendon plains, all support a dry evergreen thicket formation which continues northward past Juan de Bolas and Mocho Mountains, Mendez and Point Hills to the slopes of Mt. Diablo. This same formation containing *T. parviflora* continues along the base of the May Day Mountains in Manchester from the vicinity of Clarendon Park south past Round Hill and west toward Alligator Pond, then north along the southwestern escarpment of the Don Figuero Mountains in the vicinity of Gutters and Spur Tree. In St. Elizabeth a small area near Bull Savanna in the Santa Cruz Mountains represents the only significant population in that parish.

In a few places at low elevation such as Cane River Gorge, where cool moist air flows down from the Blue Mountains, the physical environment is modified by the lower temperatures and increased atmospheric moisture causing the formation of dew and fogs or increased rainfall. Somewhat similar conditions seem to exist along the Rio Cobre

in the gorge between Bogwalk and Spanish Town and on the eastern slopes of the mountains near Clarendon Park. In the extreme southwest of Jamaica lies Negril Hill, a long low ridge running parallel to the south coast in a region of moderate precipitation 127–190.5 cm (50–75 inches) per year. *Thrinax parviflora* occurs here at the westernmost limit of its range as scattered individuals between New Hope Estate and Rivival. Similar populations occur to the north along the eastern edge of the Great Morass near Silver Spring, Hanover.

Areas of frequent drought, described as Dry Evergreen Bushland by Loveless and Asprey (1957), support only the more drought resistant palm *Coccothrinax jamaicensis* in the ecotone between the two vegetation formations where it replaces



FIGURE 7.—*Thrinax parviflora* growing in a sisal field near Palmer's Cross, Clarendon, Jamaica. Note the heavy texture and corrugated appearance of the leaves.

T. parviflora. This is the situation east of Cane River in St. Andrew; south of May Pen, Clarendon; the western end of Portland Ridge; and between Gut River and Alligator Pond in Manchester. Between Black River and Savanna-la-mar, an area with less than 88.9 cm (35 inches) of rain per year and subject to long drought, *T. parviflora* is absent and *Coccothrinax jamaicensis* occurs only near the parish boundary shared by St. Elizabeth and Westmoreland.

At Lances Bay in Hanover, an area of high rainfall with over 190.5 cm (75 inches) per year, a few individuals of *T. parviflora* have been found growing on the low rocky slopes overlooking the sea only a short distance from a population of *T. radiata*. While the cliffs supporting the latter face northeast and are exposed to frequent salt-laden winds, however, *T. parviflora* occurs only on the lee side of the ridge facing west. Along the north coast, *T. parviflora* has been found at only two localities near the sea: at White Bay, Trelawny, and along the Queen's Highway near Bengal Bridge in St. Ann. The region around White Bay apparently experiences occasional drought since the vegetation consists mainly of logwood and thorn scrub. Rainfall is normally under 127 cm (50 inches) per year. The solitary robust plant of *T. parviflora* growing along the Queen's Highway stands among *T. radiata* and *Coccothrinax jamaicensis*.

Dolphin Head, south of Lucea in Hanover, is a somewhat isolated mass of limestone rising to about 548.64 m (1800 ft). Although dry evergreen thicket occurs on the lower cliffs, the upper ridge and peak are swept by clouds and support a dense woodland. *Thrinax parviflora* is a conspicuous element of the more exposed and higher levels of the mountain. A short distance to the east in the parish of St. James, *T. parviflora* has been collected at Bubby Hill under conditions similar to those on Dolphin Head. A single plant was seen near Hastings along the road to Maroon Town. It is curious that although conditions appear to be favorable for *Thrinax*, over the western Cockpit Country the species, with one exception, has not been collected or recorded anywhere between Deeside and Cata-dupa. The species no doubt occurs as widely scattered individuals, but the fairly evenly distributed and high rainfall of 190.5 to 508.0 cm (75 to 200 inches) per year seems to be the limiting factor determining its exclusion.

In the vicinity of Windsor Cave, Trelawny, sharply eroded limestone hills form both the northern edge of the Cockpit Country and the headwaters of the Martha Brae River. The annual rainfall in the area averages between 127 and 190.5 cm (50 to 75 inches) and appears to be fairly evenly distributed throughout the year. The ridges are heavily wooded and *T. parviflora* occurs as widely spaced individuals; however, the palm reaches its best development on exposed cliffs. A short distance to the north where the rainfall is much less, about 127 cm (50 inches) per year, the hills and ridges support larger populations of the species near Mt. Pantrepant and Sherwood Content where typical dry evergreen thicket again prevails.

The eastern portion of the Cockpit Country is characterized by a region of jagged limestone pinnacles and interconnecting ridges 457.2 to 548.6 m (1500 to 1800 ft) in elevation which set off huge pits or "bottoms" often having vertical walls 60.96 to 152.4 m (200 to 500 ft) high. *Thrinax parviflora* again assumes a conspicuous place on the top of each pinnacle, ridge, and cliff as at Mango Tree Hill.⁴ Frequent rains permit a rather dense woodland at all places where soil or humus can collect in the "bottoms" and on the slopes between the pinnacles. A peculiar and most interesting situation exists in the huge cockpit extending from Barbecue Bottom along the road to Burnt Hill. This is fully described elsewhere.

East of the Cockpit Country is a region called the Dry Harbour Mountains which closely resembles the Cockpit Country but differs principally in the more extensive scrubby to thicket vegetation and higher elevations. This somewhat drier, rather inaccessible region supports a large population of *Thrinax* on the numerous ridges and pinnacles, particularly in the neighborhood of Albion Mountain. The lower elevation in the vicinity of Pedro and Grierfield supports a heavily wooded vegetation and relatively fewer *Thrinax*. Scattered plants occur in the vicinity of Browns Town where limestone is exposed, but along the northern escarpment the annual rainfall increases steadily toward the east where 190.5 to 254 cm (75 to 100 inches) of rain per year may prevail. *Thrinax parviflora* is

⁴When questioned concerning a name for Mango Tree Hill, the local farmers gave the name "Carambi Hill"; however, "Mango Tree Hill" is the name coined by G. R. Proctor of the Institute of Jamaica.

found only occasionally near Bamboo and is rare on the cliffs of Fern Gully. North and east of a line from Bamboo through Claremont, Moneague, Guys Hill, Glengoffe to Stony Hill, *Thrinax* does not occur except as individual outliers such as that at Fern Gully, no doubt because of a lack of proper substrate and the effects of increased rainfall. It is now clear, after comparing the distribution of *T. parviflora* with a rainfall distribution map, that the greatest concentration of plants of the species is to be found in the region classified as having 127 to 190.5 cm (50 to 75 inches) of rainfall per year with numbers decreasing rapidly as rainfall increases above 215.9 cm (85 inches) per year or decreases below 101.6 cm (40 inches) per year. Optimum rainfall for *T. parviflora* must then be 101.6 to 203.2 cm (40 to 80 inches) per year.

In the center of the Island between the fertile rolling cattle country of Claremont and the rich valley of St. Thomas in the Vale (Ewarton-Linstead) lies Mt. Diablo, a mass of limestone rising gradually from the north to over 914 m (3000 ft) near the parish boundaries of St. Ann and St. Catherine. An extension running to the northeast forms a range of irregular limestone pinnacles (herein referred to as the Devils Backbone) about 762 m (2500 ft) in elevation along the parish boundary. The principal mass of Mt. Diablo terminates in a very steep escarpment about 609 m (2000 ft) high along the southeast and west, overlooking Ewarton and Worthy Park respectively. A spur projects to the south and connects with a system of hills, of which Point Hill and Mendez Hill are a part, and encircles the valley of St. Thomas in the Vale to the gorge of the Rio Cobre. *Thrinax parviflora* occurs on almost all exposed limestone and great numbers cling to the walls of the gorge.

The vegetation above 548.64 m (1800 ft) elevation on Mt. Diablo and associated slopes, which are frequently bathed throughout the year in morning clouds and mists, most closely conforms to the formation described by J. S. Beard (1955) as "Dry Evergreen Woodland." Perhaps a new formation to be called Montane Dry Evergreen Woodland would be preferred, since Beard's formation applies primarily to the lower elevations and not to those influenced by clouds and mists. *Thrinax parviflora* occurs on the more exposed cliffs and nearly all of the higher peaks, e.g., Hollymount, Grier Mount, Blue Mountain, Devils Backbone. The environ-

ment is perpetually moist and temperatures are normally in the 20s (°C) or often lower. Soft-leaved epiphytes are quite numerous on the tree trunks and rocks where a lush growth of moss, miniature orchids (*Pleurothallis*, *Lepanthes*), and delicate ferns often obscure the substrate. *Hohenbergia polycephala* and *Vriesea platynema*, bromeliads requiring a somewhat drier environment, are

restricted to the upper level of the canopy. *Guzmania erythrolepis*, *G. lingulata*, and *Vriesea ringens* require cool moist conditions and are common on the rocks and lower parts of the tree trunks.

The limestone outcrop upon which mature plants of *T. parviflora* are localized, occurs as ridges and small peaks with intervening valleys of deep heavy soil or scree slopes. Although *Thrinax*



FIGURE 8.—*Thrinax parviflora* growing at about 914 m elevation on Mt. Diablo. Note the open crown and peculiar form of the leaves. These plants and those in Figure 7 probably represent the two greatest extremes of phenotypic variability of the species.

seedlings are plentiful on all types of soil, they are not known to reach maturity except on the stable rock outcrop where similar lithophilus species such as *Euphorbia punicea* and *Plumeria marchii* grow. Similar environmental conditions are met with on nearly all high limestone peaks and ridges such as Albion Mountain, Top Hill, Somerset, and Dolphin Head.

The foregoing is a general account of the distribution and ecology of *Thrinax parviflora* in Jamaica. Further details of the behavior of this species in two series of habitats where special ecological features can be recognized are described elsewhere.

Morphology

The genus *Thrinax*, in common with *Hemithrinax*, *Coccothrinax*, *Zombia*, and *Haitiella* of the *Thrinax* alliance, is distinguished from all other palms by having bisexual flowers in which the perianth consists of a single irregularly lobed cupule. The genus is further distinguished from *Coccothrinax*, *Zombia*, and *Haitiella* by the splitting of the base of the petiole in the region of the sheath (Figure 9c). From *Hemithrinax* it is apparently separated solely on the character of the stamens. *Hemithrinax* with subsessile anthers, a broad connective, and extrorse dehiscence is in need of additional intensive study, but adequate material of the different species is lacking at present.

During this study certain characters, mainly of a quantitative nature and formerly believed to be of diagnostic importance, were given particular emphasis in order to test their usefulness as diagnostic characters. The literature is full of descriptions in which the size of the various organs (usually from a single incomplete specimen) is all one has for comparison of taxa. Good qualitative characters were all but lacking.

SELECTION OF SAMPLES FOR MEASUREMENT.—Only mature flowering size plants were considered in the data presented. Whenever possible, specimens were taken from all accessible plants in a particular locality (measurements and specimens were collected from every plant exhibiting an inflorescence at some stage from anthesis onward even if the fruit had fallen already). Local populations consisted of all the plants in a particular niche or environment, e.g., a rocky pinnacle, gully, cliff, or hillside. These are usually of limited size; how-

ever, if the population was extensive the collections consisted of all the material that could possibly be collected during the time available in one or more trips to the area.

In order to study the species in every conceivable environmental situation at all elevations in Jamaica, a great deal of time was devoted to exploring the island in search of new localities. This was necessary in order to describe the range of distribution and the range of tolerance of each species. It was also necessary to collect representative specimens from as many different localities as possible in order to eliminate the bias caused by information from classical collecting areas.

As much information as possible was obtained from herbarium specimens early in the study, but a concerted effort was made to re-collect in the localities represented by existing specimens in addition to the numerous new localities. It should be noted that herbarium specimens rarely if ever contain complete leaves or inflorescences. The most commonly occurring materials on herbarium sheets usually comprise one or more of the lower primary branches of the inflorescence at some stage between anthesis and maturation of the fruit but rarely at either of these stages, and fragments of a single leaf, most commonly juvenile, without petiole or sheath. Most frequently if a petiole is present it and the hastula, and the blade, are split in two rendering them fairly useless for measurements.

Measurements of the length and diameter of the caudex were made at the time and on the plant from which leaf and inflorescence specimens were taken. The specimens consisted of one complete inflorescence (usually cut at the sheath level, if the plant was not cut down), two fully expanded leaves with full petiole, two fully mature sheaths, and one unexpanded bud leaf. The leaves comprised the most recently expanded leaf blade and one of the older but still whole leaves. About half of the segments were removed from the blade and discarded by cutting them several inches above the hastula and slightly to the side of the central group of segments.

In order to achieve as much uniformity as possible in the data from both field and herbarium collection, where the apical portion of the inflorescence was usually either badly damaged or missing, it was necessary to restrict the collection of data to the five lowermost primary branches on

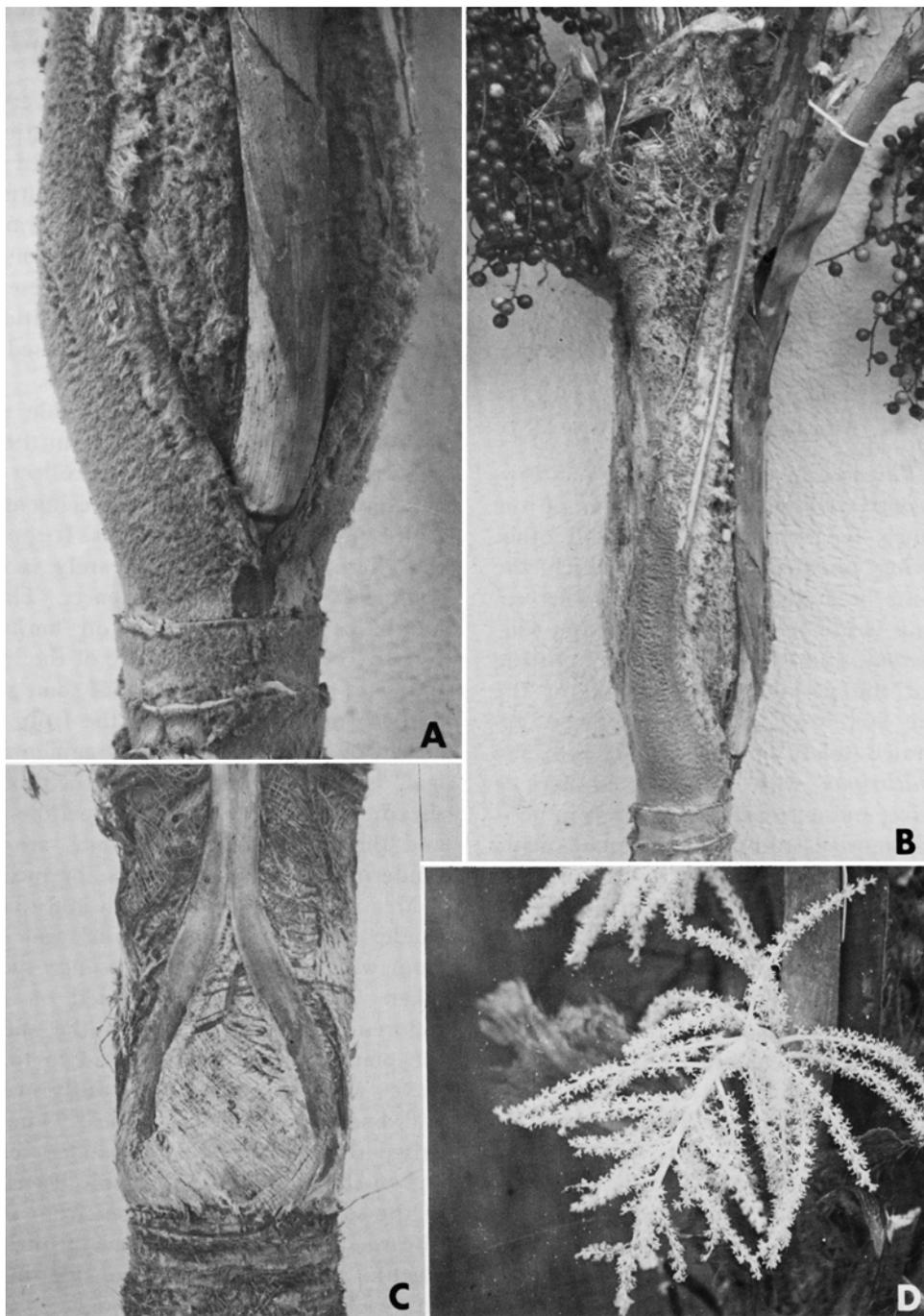


FIGURE 9.—*Thrinax parviflora*: A, bud region showing indumentum on the leaf sheaths and internodes; B, the same as A but demonstrating how the inflorescence emerges from the split sheath and arches out beneath the subtending leaf petiole; C, the same as in A but a heavier caudex showing more clearly the broad split which distinguishes the genus from *Coccothrinax*; D, a single primary branch with its numerous flowers at anthesis.

each inflorescence. In the calculation of inflorescence length (length of exposure above the sheath apex), number of primary branches per inflorescence, primary branch rachis length, number of ultimate branches per primary branch, and the length and diameter (at the point of insertion on the rachis) of the ultimate branches, all parts of the five primary branches were measured; however, since the number of flower or fruit pedicels per primary branch is excessively large a random sample was necessary. This was achieved by randomly selecting five ultimate branches from each of the five lowermost primary branches per inflorescence.

The ultimate branches on each primary branch were numbered from the base to the apex along the rachis. These branches were randomly selected by placing a pointer on some digit in the table (I.2) of Snedecor's (1948) table of random digits. That digit and the one following it, be it "01" or "25," indicated the branch to be sampled. If the number was greater than the number of branches present, a second combination of digits was necessary. Once the branches were chosen all pedicels on each branch were measured.

CAUDEX.—The caudex of *Thrinax* is columnar and nearly uniform in diameter throughout its length but tapers almost imperceptibly toward the apex, while the base is often noticeably expanded 2 to 5 dm above the substrate by the production of masses of tough wiry roots. It is not uncommon to see plants with large mounds of exposed roots. The caudex may be gray or tan and is roughened by alternating smooth internodes and slightly raised leaf scars. As the palm ages the length of the internodes being produced is much reduced, eventually becoming a mere line encircling the apical portion of the caudex in tall plants. The leaf bases are persistent for some time following the death of the leaf and are always conspicuous below the crown. Within the tightly congested overlapping leaf bases the internodes are velvety tomentose (Figure 9A).

A striking feature of plants of *T. parviflora* when growing at the higher elevations is the very tall slender caudex; however, measurements from a number of populations throughout the range of the species show that there is great variability in caudex height and diameter even within local populations. The range of variation in caudex height of 86 individuals of *Thrinax parviflora* from among

19 different localities⁵ is 1.0 to 10.0 (–13.0) m. The mean heights for each locality varied from 1.5 to 10.0 m. These figures are to be compared to (1.0–)1.5 to 7.5 (–12.0) (\bar{x} =4.0) m for *T. radiata* (51 samples) and 3.5 to 9.0 (–11.0) (\bar{x} =6.5) m for *T. excelsa* (25 samples).⁶ The range of variation in caudex diameter of the same individuals of *T. parviflora* mentioned above is 5.0 to 14.0 (–15.0) cm. The mean diameters for each locality varied from 6.0 to 12.5 cm. These figures are also to be compared to (7.5–)8.0 to 11.0 cm (\bar{x} =9.0 cm) for *T. radiata* and 12.0 to 16.0 cm (\bar{x} =14.5 cm) for *T. excelsa*.

LEAF.—*Sheath*: The fully expanded leaf of *Thrinax* is composed of four principal parts: blade, hastula, petiole, and sheath. The mature sheath is at first tubular and encloses the younger developing organs. The sheath has no doubt been the most neglected portion of the palm in the making of herbarium specimens and in studies of palm morphology. Although it has not been fully exploited as a diagnostic character, the form of the leaf sheath is of utmost importance in distinguishing *Thrinax* and *Hemithrinax* from their closest allies *Coccothrinax* and *Zombia*. Even very young seedlings can be recognized by examination of the leaf sheath. *Coccothrinax* and *Zombia* have leaf sheaths which at maturity are still completely tubular with the solid petiolar base continuing unchanged to the point of insertion on the caudex. The netlike tubular portion of the sheath retains its appearance long after the blade has died and broken off.

The mature leaf sheath of *Thrinax* and *Hemithrinax* is, however, quite different from that described for *Coccothrinax* and *Zombia*. The petiole on entering the sheath portion is divided basally in the form of an inverted wedge or λ (Figure 9c). The fibrous portion is netlike at first as in *Coccothrinax* but soon breaks down and becomes ragged or loosely fibrous. The conspicuously split

⁵ The localities mentioned are from among those cited in the study of pedicel length and mapped in Figure 41.

⁶ *Thrinax morrisii* is excluded from these figures as it was not included in the original intensive study. Considering the extensive range of the species, the small amount of data available would perhaps be misleading by comparison. More complete data and bargraphs depicting the range of variation and means of the individual localities for *Thrinax parviflora* can be found in Read (1968).

petiole bases persist below the crown long after the fibrous wrapping has deteriorated.

The apical portion of the *Thrinax* sheath is of great diagnostic importance within the genus. That of *T. parviflora*, *T. excelsa*, and *T. morrisii* is linguiform (Figure 10A,B) extending upward from the point of attachment on the petiole and becoming long pointed. This tonguelike extension is cloth-like, often separating between the fibers and then appearing as a net. The sheath apex of *T. radiata* on the other hand is not at all linguiform (Figures 10c, 11A) but takes an exactly opposite form with the margins descending from their attachment along the solid petiole in a V-form. The sheath of *T. radiata* soon tears away from the petiole, even as the leaf expands (Figure 11A), and the fibers

readily separate into ragged fibers around the "bud" region. The lateral margins of the sheath may be inserted on the petiole base at the same or different levels.

The lower portion of the sheath of all four species is covered with a dense velvety tomentum (Figure 9A,c) but is usually lost on exposure. As the young inner growth expands, the sheath fibers pull apart permitting the tubular portion to expand with internal growth pressures. The division of the petiole also separates. Even in the very immature leaf sheath, a groove is present in the otherwise solid portion of the sheath. As the "bud" expands, the groove separates and in mature plants the opening of the split exposes the young inflorescence (Figure 9A), but of course this is normally

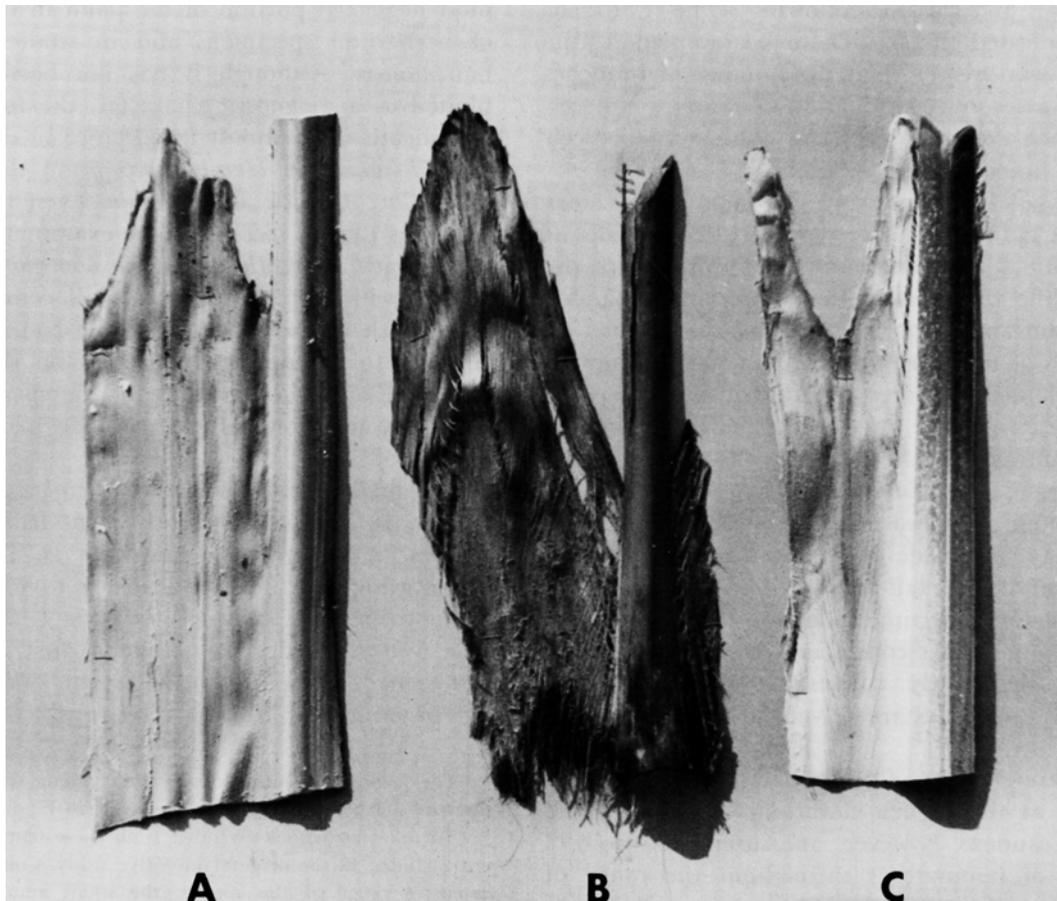


FIGURE 10.—Leaf sheaths of the three Jamaican species of *Thrinax* showing: A, B, the long linguiform apex of *T. excelsa* and *T. parviflora* respectively; C, the deep V-form, nonlinguiform sheath of *T. radiata*.

obscured by the older, dead, outer leaf bases. As the inflorescence develops and elongates, it continues to separate the sides of the split petiole and extends through the opening. At maturity the inflorescence normally (in Jamaica) appears below the petiole of the leaf to which it is in fact axillary. Rarely does the inflorescence emerge above the subtending leaf petiole.

Petiole: Petioles of *Thrinax* are slender, and extremely strong and flexible. They vary considerably in length, width, and form, even within a species. However, the length of the petiole in relation to the length of the longest leaf segment is an excellent character for distinguishing between *T. radiata*, wherein the petioles are shorter than the longest segment, and *T. parviflora*, with petioles

longer than the longest segment of the leaf. The range of variation of petiole length of 218 samples of *Thrinax parviflora* from among 26 different localities is (35-)40 to 155 cm. The mean lengths for each locality varied from 40 to 135 cm. These figures are to be compared to (36-)44 to 88 (-94) cm (\bar{x} =61.6 cm) for *T. radiata* (50 samples), and 125 to 200 cm (\bar{x} =165 cm) for *T. excelsa* (6 samples). The range of variation in petiole width of the same individuals of *T. parviflora* mentioned above is 0.9 to 2.4 cm. The mean widths for each locality varied from 0.9 to 2.0 cm. These figures are also to be compared to 2.1 to 3.2 cm (\bar{x} =2.5 cm) for *T. radiata* and 2.5 to 3.9 cm (\bar{x} =3.4 cm) for *T. excelsa*.

Throughout most of their length petioles of

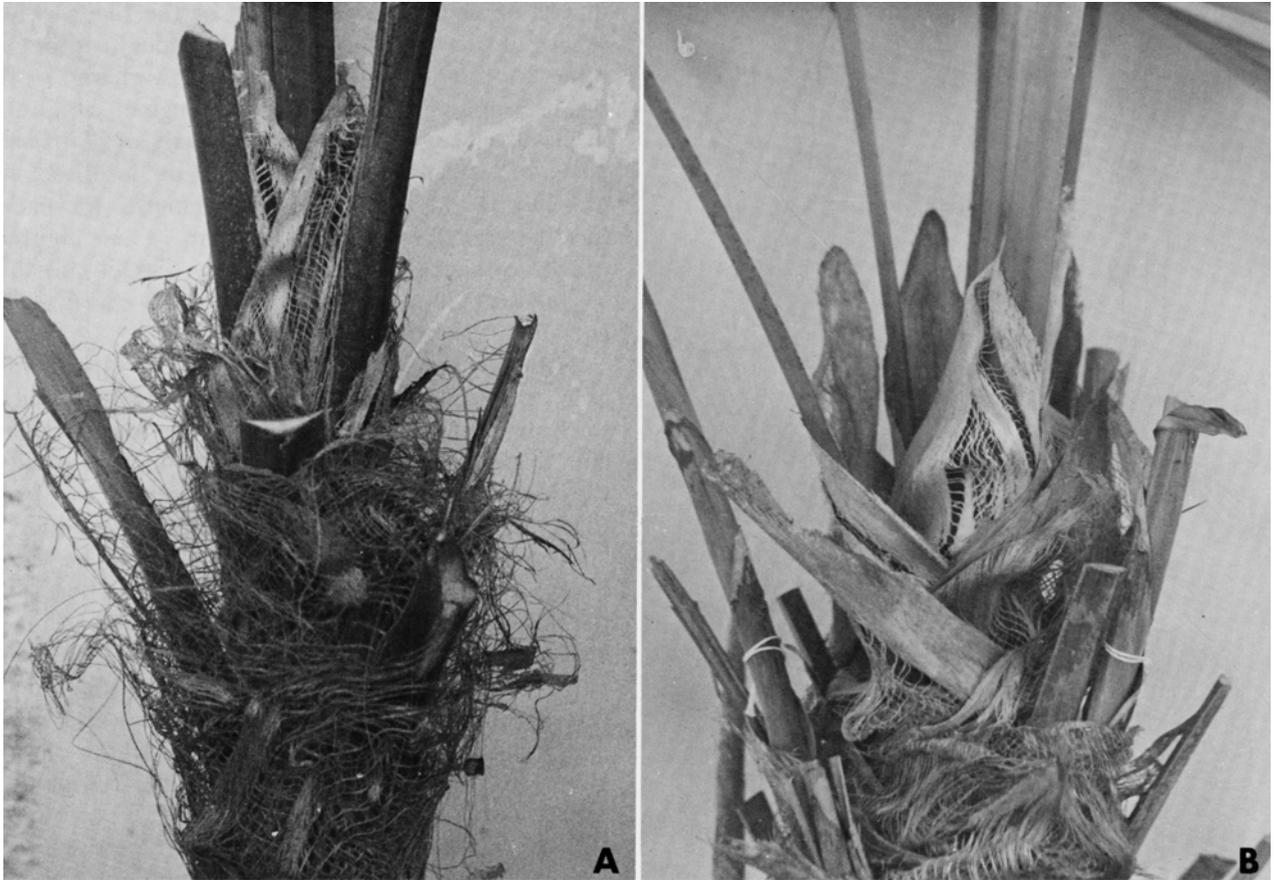


FIGURE 11.—Bud regions: A, *Thrinax radiata*; B, *T. parviflora*, showing the strongly linguiform sheath of the latter. Note the minute scattered scales on the petioles in "A" and the absence of them in "B."

Thrinax are ancipitous and biconvex; however, the solid portion within the sheath is usually concave adaxially. At the junction between the petiole and the sheath they may be flat or slightly concave in *T. parviflora* and *T. excelsa* or with a median ridge in *T. radiata*. The petiole is widest at the junction with the sheath and narrowest a short distance below the hastula, where its margins may be variously bent and distorted as the blade expands (Figure 12).

The adaxial surface of the petiole is glabrous or glabrescent. The abaxial surface of the emerging petiole is densely floccose lepidote initially, but the degree of persistence of the indumentum varies among the species depending on exposure. The petioles of *T. parviflora* lose their scales very soon after exposure (Figure 10B), while a conspicuous amount of scattered scales persists on the petioles

of *T. radiata* (Figure 10C) and *T. morrisii*. The abaxial surface of the petioles of *T. excelsa* remains velvety for a considerable time (Figure 10A).

Hastula: The first mention of the hastula, or ligule as it had been known to Beccari and others, as a key character was by J. A. & J. H. Schultes (1830:1301). They stressed that the difference between their newly described *T. argentea* and the earlier *T. parviflora* was that the former had a "prominentia centrali minore." They also distinguished their new *T. pumilio* by its "defectu prominentia in centro frondis." All members of the genus *Thrinax* exhibit a prominent adaxial hastula of one form or another.

The hastula appears as an extension of the apex of the petiole into the laminar portion of the leaf. It is always in a plane with the petiole and overlaps the region of segment insertion but may bend, twist, or become semitubular depending on the degree of expansion or folding of the blade. The length of the hastular overlap was thought to be of some importance, but as a generic key character, it has been found of little use. The range of variation in hastula length of 164 individuals of *Thrinax parviflora* from among 26 different localities is (0.1–)0.4 to 4.6 cm. The mean lengths for each locality varied from 0.6 to 3.2 cm. These figures can be compared to 1.0 to 2.0 cm (\bar{x} =1.4 cm) for *T. radiata* (20 samples) and 1.8 to 2.6 cm (\bar{x} =2.1 cm) for *T. excelsa* (6 samples).

Although the shape of the hastula is quite variable, the general outline and proportions hold fairly true for each species but are extremely difficult to describe. It is important to point out that the hastula is distorted by expansion of the leaf blade and is thus best observed on the unexpanded "bud leaf." Occasionally the hastula may be torn by expansion of the blade. The shape and form of the hastula may be seen in Figure 12A,C,D,F.

Abaxially the apex of the petiole usually terminates in a short overlapping collar of tissue which may exhibit one or two small prominences 1 to 2 mm long. Throughout the habitats at the lower elevations, however, *Thrinax parviflora* commonly exhibits abaxial hastular projections of considerable size (Figure 12E) occasionally exceeding the adaxial hastula in length. Such prominent abaxial hastulas have not been observed in any other species of the *Thrinax* alliance. Leaves of a plant in the population of *T. parviflora* at Cockpit, Claren-

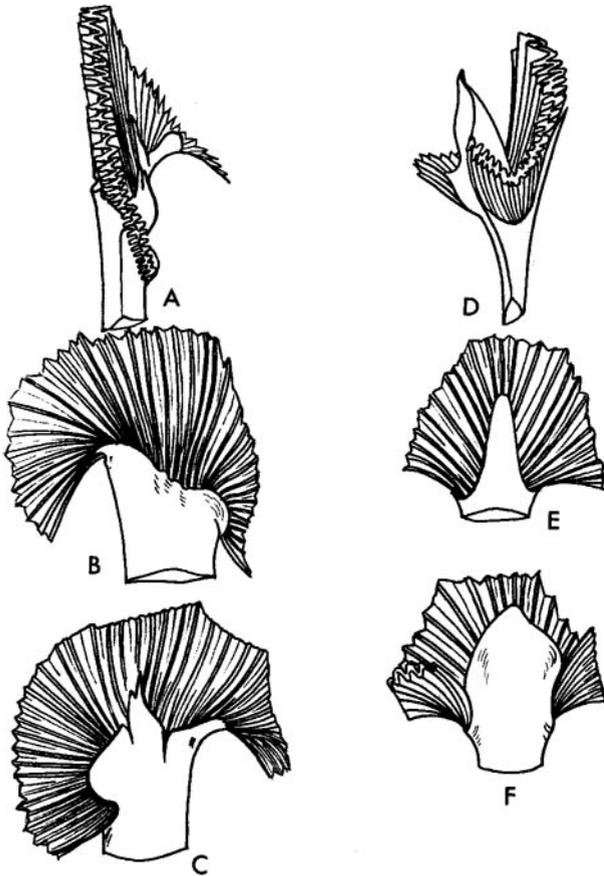


FIGURE 12.—Three different views of the hastular region: A-C, *Thrinax radiata*; D-F, *T. parviflora*. (A, D = side views; B, E = abaxial views; C, F = adaxial views.)

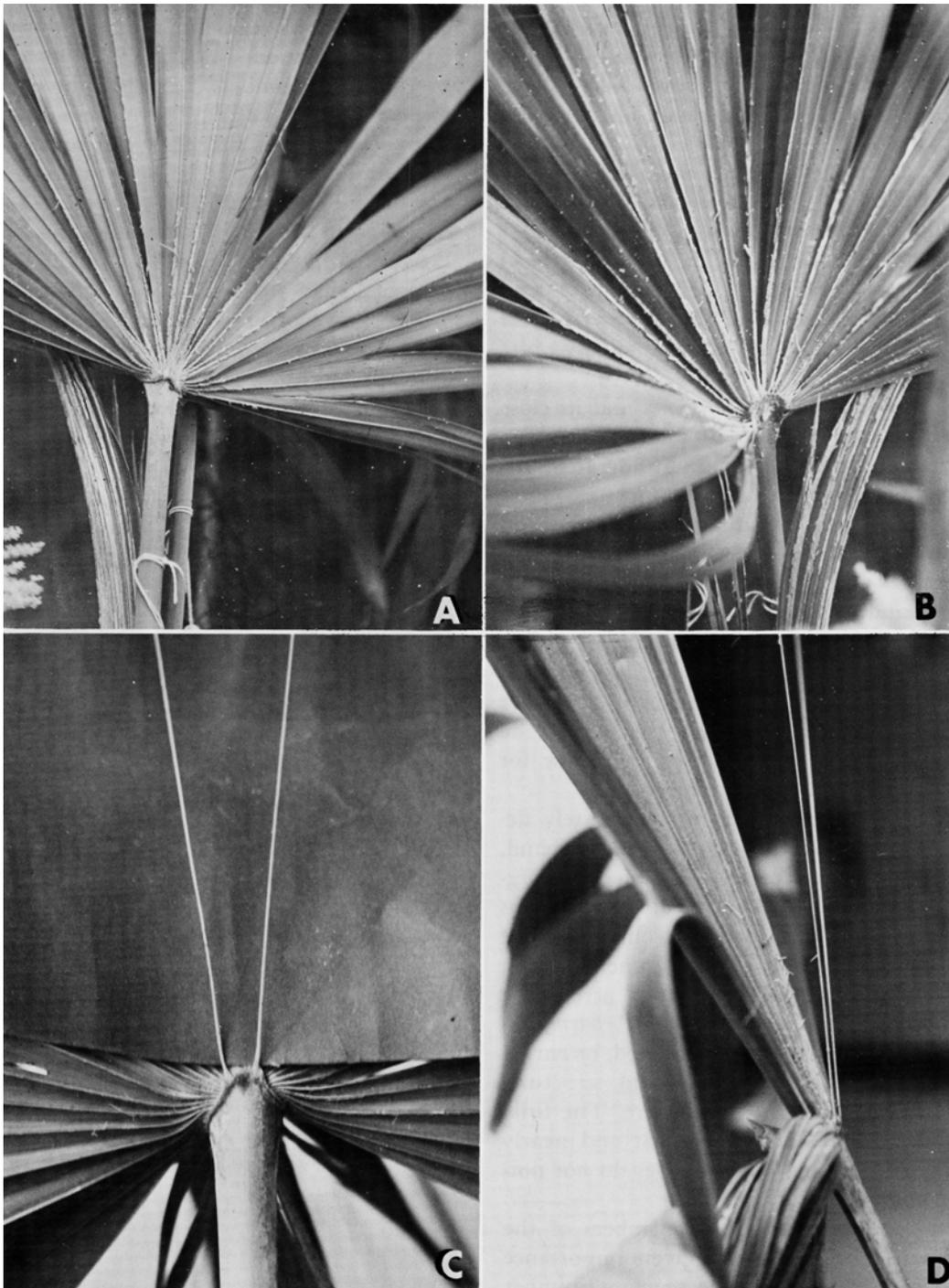


FIGURE 13.—*Thrinax parviflora*, newly expanded leaf blade, with adhering scales: A, abaxial surface; B, adaxial surface. C, D, Abnormal processes from the abaxial hastular region, on plants found at Cockpit, Clarendon, Jamaica.

don, Jamaica, were found to possess exceedingly long, slender, rigid filaments arising from the abaxial hastula (Figure 13c,d). The filaments appear to be extensions of the retuse or slightly bifid minor prominences mentioned above. No explanation can be offered for this curious phenomenon at present.

In bud, and upon emergence, the abaxial hastular region of the young leaf is densely covered with floccose lepidia, which are normally lost soon after exposure. The hastular collar is usually fringed with larger more persistent scales (Figure 13A,B). The newly exposed hastula of the *T. morrisii* leaf is always densely velutinous with silvery-white tomentum.

Lamina: The leaf blade of *Thrinax* and its close allies is completely palmate in form, having no central costa or primary midrib. Although of basically the same structure throughout the genus, the leaf blade assumes a number of different and characteristic forms. They also vary considerably in size, texture, and indumentum.

The unexpanded leaf blade as it emerges from the "bud region" is a compressed bundle of tightly folded plicate segments with only the major nerves and segment margins exposed. The exposed surface is at first appressed lepidote, but after the blade expands as in Figure 13A,B, the scales persist for only a short time on the principal nerves.

The leaf blade often has been inaccurately described as peltate because as the segments expand, as a result of pulvinus-like regions along the largest nerves in *T. radiata* and occasionally shade forms of *T. parviflora* and *T. morrisii*, a complete circle is formed by the position of the segment apices, and the outermost segments overlap across the petiole (Figure 14). Leaves of mature *T. parviflora* are normally so folded, crumpled, twisted, or curled that they present a three dimensional structure, which is described more fully elsewhere. The fully expanded leaves of *T. excelsa* are flat and nearly circular in outline, but the outer lobes do not normally meet nor overlap.

Segments: Segment number in members of the *Thrinax* alliance has also been given importance as a key character. Although the segment number is fairly constant for the leaves of any given plant of *T. parviflora*, varying from three to five about the mean, the variation within a single population may be as much as 22 segments between the greater

and smaller numbers. The measurements at locality No. 33 in Jamaica were found to cover nearly the entire range of segment numbers throughout the entire population in Jamaica and considerably overlap the numbers recorded for leaves of *T. radiata* and *T. excelsa*. There is no direct relationship between the size of a leaf and the segment number. *Thrinax excelsa* with a leaf 3 m broad may have 52 segments, while a leaf of *T. parviflora* only 1.5 m broad may have a similar number. Leaves of juvenile plants normally have fewer segments than those of mature plants.

The range of variation in segment number for 264 samples of *T. parviflora* leaves, from among 28 different localities, is 35 to 60. The mean number of segments for each locality varied from 37 to 56. These figures can be compared to 51 to 63 seg-



FIGURE 14.—*Thrinax parviflora* at Palmer's Cross, Clarendon, Jamaica. The region where the segments are joined is the palman; note the tubular hastula.

ments ($\bar{x}=56$) for *T. radiata* (50 samples) and (52–)55 to 65 segments ($\bar{x}=59$) for *T. excelsa* (41 samples).

Individual segments may vary in size, outline, and degree of fusion at the margins. The segments directly in line with the petiole are the longest and broadest within the leaf. Those on either side become progressively smaller away from center. The degree of segment fusion is also greater at the center where two or three segments may be fused for more than three quarters of their length or the two central segments may be fused for their entire length.

Apart from the greater fusion of the central segments the amount of fusion between segments elsewhere across the blade is somewhat irregular. For purposes of comparison a specific region of the blade was selected to represent the leaf. Segments to be measured were chosen by grasping the central four segments in the hand and counting the next three segments on each side of the group held. The third segment on each side of the central group of segments (thus two segments per leaf) were selected and removed for measuring. In order to collect a maximum amount of information, concerning the leaf blade, with a minimum of bulk, the most satisfactory method was to strip the selected segments from the leaf, down to the hastula. The remainder of the blade was then discarded, except for the hastula, which was trimmed out and retained if undamaged. The segments thus selected from the same region on each leaf provided comparative information regarding the length, breadth, form, texture, indumentum, and length of connation. The hastular region (Figure 12) and accompanying segment bases provided additional information regarding the petiole width, hastula form and length, and the number of segments per leaf.

The leaf segments have been described variously as lanceolate, ensiform, linear, etc., but these terms are more applicable to leaves or leaflets with curved margins. The margins of *Thrinax* leaf segments are straight throughout their greater length particularly in the proximal half. They may, however, have near the broadest region a pinching in or "shoulder" (Figure 15A,C,E). The chart of simple symmetrical plane shapes published by the Systematics Association Committee for Descriptive Biological Terminology (*Taxon* 11, 1962) provides a much more accurate terminology of palm leaf-

segment outline. In the chart,⁷ numbers 25, 54, and 63 correspond closely to the outlines of the leaf segments in *Thrinax*. These are basically narrowly rhomboid, but vary from trullate to obtrullate (Figure 15A,B).

The leaf segments of *T. parviflora* are more often than not conspicuously pinched in just above the broadest part (Figure 15A,C,E). This character is not peculiar to *T. parviflora*, however, for it is found in *T. radiata* as well, but it is not so prominent in the latter.

Segment apices may be bifid to varying depths or not at all. In the leaf segments of *T. parviflora* the apices are usually acute and often not at all bifid. When bifid the apical points may be strongly divergent (Figure 15A,F). In *T. radiata* the segment apices are long and slender (Figure 15B,D), usually deeply bifid and attenuated into a filament which is readily lost. The outermost segments in all species may exhibit long, slender, fiberlike filaments up to twice their length. The occurrence of filaments in the sinuses between the segments (such as is typical of *Sabal* and *Washingtonia*) is rare; however, several leaves of *T. parviflora* have been found where similar but more delicate filaments were produced. What may appear to be a greater number of anomalies in *T. parviflora* should rather be taken as an indication that the greater the number of specimens examined in the field, the greater number of anomalies will be found.

Although segment width as such is of little diagnostic significance, the position of the broadest part along the segment is very important. In *Thrinax parviflora* the broadest part of the segment is well above the sinus (Figure 15A). In both *T. radiata* and *T. excelsa* the broadest point is at the sinus (Figure 15B), or very close to it. The measurement of segment width was always made at the broadest point. The range of variation of segment width of 398 samples of *T. parviflora* from among 29 different localities is 2.4 to 6.4 cm. The mean segment widths for each locality varied from 2.4 to 5.6 cm. These figures are to be compared to (4.6–)4.8 to 6.2 (–6.4) cm ($\bar{x}=5.6$ cm) for *T. radiata* (50 samples) and (4.4–)4.6 to 7.2 (–7.4) cm ($\bar{x}=6.2$ cm) for *T. excelsa* (20 samples).

The range of variation in leaf-segment length for

⁷ Reproduced in W. T. Stearn, *Botanical Latin*, pages 318–319, 1966.

T. parviflora is very great and overlaps considerably with *T. radiata*, which in general exhibits much longer segments. Those of *T. excelsa* on the other hand are very long and even at the lower limits of the range of variation measurements overlap with those of *T. radiata* only at the 5 percent level. The range of variation in segment length for 428 samples of *T. parviflora* from among 30 different localities is 39 to 96 cm. The mean segment lengths for each locality varied from 42 to 92 cm. These figures can be compared to (73–)79 to 113(–115) cm (\bar{x} =92.9 cm) for *T. radiata* (50 samples) and 114 to 173 cm (\bar{x} =144 cm) for *T. excelsa* (16 samples).

Palman: The region of the leaf blade wherein the segments are fused together by their margins, measured from the hastula to the sinus between

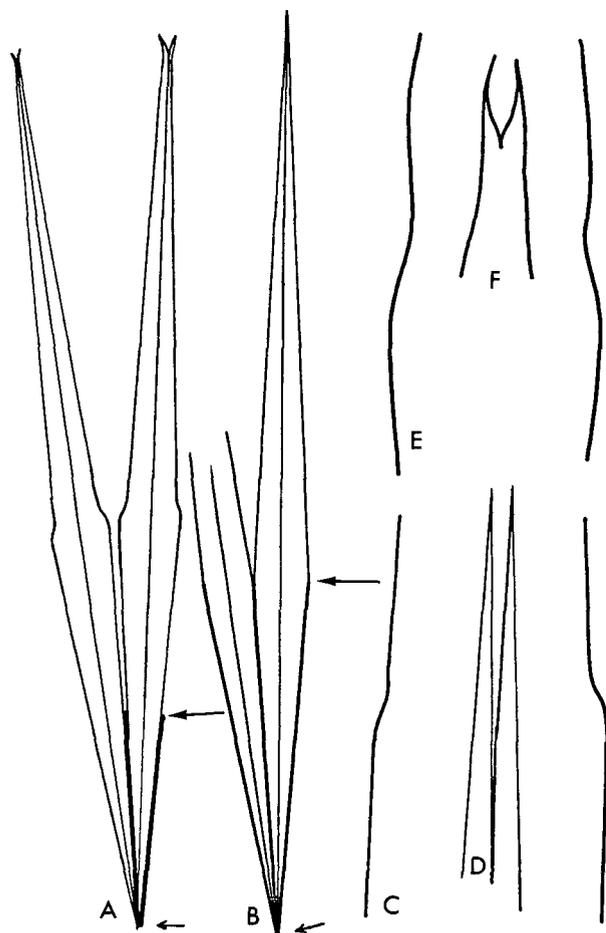


FIGURE 15.—*Thrinax* leaf segment outlines showing fusion (indicated by arrows): A, *T. parviflora*; B, *T. radiata*. C, E, Two types of constrictions on segments are depicted; D, F, bifid apices.

the segments, is known as the palman (Figure 15A,B, between points indicated by arrows) like the palm of the hand from the wrist to between the fingers. The palman has been described variously as one-third or two-thirds the length of the segments; however, in *T. parviflora* it is so variable, depending on the age of the plant or exposure, that such descriptions are of no practical value. Actual measurements of the palman do, however, have some comparative value among the taxa. Measurements of the palman of each of the three Jamaican species are compared as follows: the range of variation in palman length of 749 samples of *T. parviflora* from among 29 different localities is 7 to 34(–42) cm compared to (30–)33 to 54(–55) cm for *T. radiata* (50 samples) and (48–)52 to 84(–100) cm for *T. excelsa* (16 samples). The mean lengths for the palmans for each locality of *T. parviflora* varied from 9 to 28 cm compared to 44 cm for *T. radiata* and 71.8 cm for *T. excelsa*. The length of segment fusion or palman depth was measured using the same segments described under length and width of leaf segments.

Because, as previously mentioned, the central segments are fused for a greater length than the outer ones, the palman is narrower distally and toward the base than it is at the side. A common characteristic of the leaves of *T. radiata* is the complete fusion of the margins between the central two segments. Elsewhere in the blade the palman outline, formed by the sinuses, is fairly uniform. This latter is also true for leaves of *T. excelsa* and *T. morrisii*. In *T. parviflora*, however, apart from the cluster of central segments with conspicuously longer fusion, the length of the fusion between the segments is very irregular throughout the blade.

Undoubtedly, the largest palman measurements for the genus are those of *T. excelsa*. They clearly exceed even the largest measurements of *T. parviflora* and overlap the very largest of the measurements of *T. radiata* by only a few centimeters; and the overlap in palman depth measurements between *T. parviflora* and *T. radiata* occurs only at the 5 percent level. Therefore palman width or depth can be used in part as a diagnostic character in Jamaica, providing of course only fully mature specimens are used and the measurements are made in precisely the same manner as those here.

Indumentum: The adaxial laminal surface, except for the major nerves, is for the most part

glabrous or glabrescent. Minute scales may be found occasionally on the adaxial surface near the apical portion of the segments, especially on freshly opened leaves. Although a waxy surface is characteristic of palms throughout the *Thrinax* alliance, it appears that the leaves of *T. parviflora* and especially *T. morrisii* have a particularly great amount. One of the first peculiarities noted by the author in regard to *T. parviflora* was an abundance of white "hairlike" material on the surface of the leaves in a number of herbarium specimens. On closer examination the material appeared as minute needlelike crystals, which dissolved in absolute alcohol. When drops of alcohol were washed across a leaf segment and allowed to dry on a piece of glass, a quantity of white waxlike substance resulted. The same held true for both fresh and dried

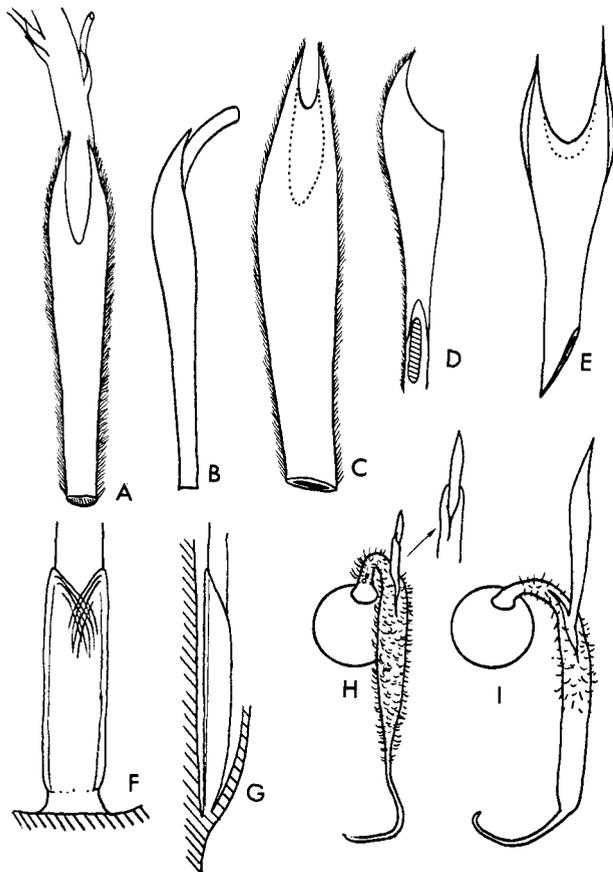


FIGURE 16.—Inflorescence bracts, the ultimate tubular bifid bracts on each primary branch: A, B, *Thrinax parviflora*, adaxial and side views; C, *T. radiata*, adaxial view; D, E, *T. excelsa*, side and adaxial views respectively; F, G, prophyll in position, on inflorescence axis, in the axil of the leaf sheath. Seed germination: H, *T. excelsa*; I, *T. parviflora*.

leaves of *T. parviflora*. When the same experiment was run using leaf segments of *T. radiata* the amount of wax deposited was negligible by comparison.

Abaxially the laminar surface is variously lepidote, the differences providing excellent diagnostic characters. Although the abaxial surface of the leaves of *T. parviflora* appears to be glabrous, it is in fact glabrescent with widely scattered microscopic scales which are readily lost with age. Unlike the other species, the scales on some specimens of *T. parviflora* appear to be reduced to simple hyaline hairs or "Y-shaped" scales which become detached quite readily. A magnification of about 25 times is necessary in order to see the scales on *T. parviflora*.

The scattered scales on the leaves of *T. radiata* are quite conspicuous and may be seen easily with the unaided eye as tiny flecks over the abaxial surface. On a fresh leaf the individual scales may be shortly fimbriate from an oval glandlike center. On drying or with age the fimbria may be lost leaving the conspicuous central portion which can be readily seen on herbarium specimens as well, especially with a 10-power lens. The abaxial leaf surface of *T. radiata* may, in addition to the scales, be glaucescent, but it is never silvery white.

Thrinax excelsa is readily distinguished from the aforementioned by having the abaxial surface of the leaf blade densely covered with interlocking fimbriate hyaline scales. Fully mature leaves of this species are conspicuously white to silvery white below as a result of the dense covering of hyaline scales. The leaves of juvenile plants of this species appear glabrescent but nearly always exhibit patches of interlocking scales and hairs.

Among the widely distributed populations of *Thrinax morrisii*, the degree and development of abaxial scales varies considerably. Whether this is a reflection of the ecology or is truly genetically determined remains a question for further study of the living plants throughout their total range of distribution. Specimens from Anguilla, the type locality, appear depauperate and exhibit very small, poorly developed scales; one specimen nearly lacking scales altogether. Specimens from Puerto Rico through the Bahamas and Florida exhibit increasingly greater numbers of scales with greater and greater degrees of fimbriation on individual scales. In the Cuban plants the fimbria are

greatly extended and often become interlocking much like the scales on leaves of *T. excelsa* but are not quite as densely arranged.

INFLORESCENCE.—Axis and Bracts: The inflorescences of the four species of *Thrinax* are basically of similar structure but differ markedly in size, puberulence of the branches, and color at anthesis. Originating in the axil of a leaf, at a point immediately below the petiolar groove, the inflorescence is adnate to the leaf for about 1 cm (Figure 16G). The first inflorescence bract is inserted about 2 cm above the base (Figure 16F). It is bicarinate, flattened adaxially and convex or rounded abaxially, and is completely closed at first. The apex is pierced by elongation of the second bract.

The inflorescence of *Thrinax* and its close allies consists of a short weak axis with between 7 and 22 primary branches supported mainly by large, fibrous tubular bracts telescoped one inside another from the apex to the base. Each bract, with the excep-

tion of one to several empty basal bracts, subtends a primary branch, enclosing the basal portion of a primary branch and the lower portion of the next higher bract. The apical aperture of each principal bract is oblique. The bracts are densely appressed lepidote varying in color among the species. In *T. radiata* and *T. morrisii* the scales are gray or white becoming tan with age; those of *T. parviflora* are light brown or tan at first darkening with age; and in *T. excelsa* the scales on the bracts are dark rusty brown.

Measurements of the variation in inflorescence length within *Thrinax parviflora* are recorded in Figure 18. The inflorescence in *T. parviflora* usually equals the petiole in length but may occasionally exceed it, extending up among the leaf blades, but is not known to exceed the leaf in length. Inflorescences of *T. radiata* and *T. morrisii* are always longer than the leaves and extend conspicuously well above the crown of leaves. The

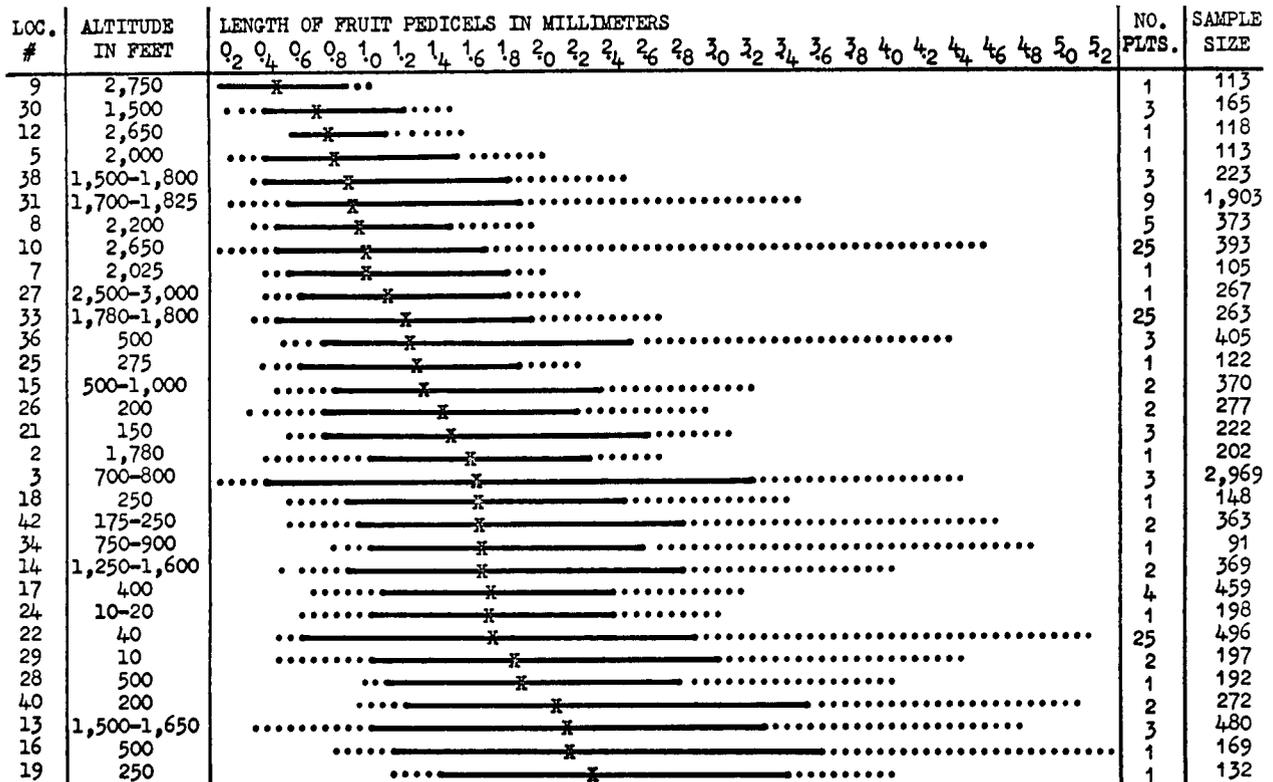


FIGURE 17.—Pedicel length, *Thrinax parviflora*, arranged by increasing means, top to bottom, showing the wide range of variability of this once "important" taxonomic character. The x in bar graphs represents mean length, solid line 90% of all measurements, and dots indicate 5% of total off each end of range.

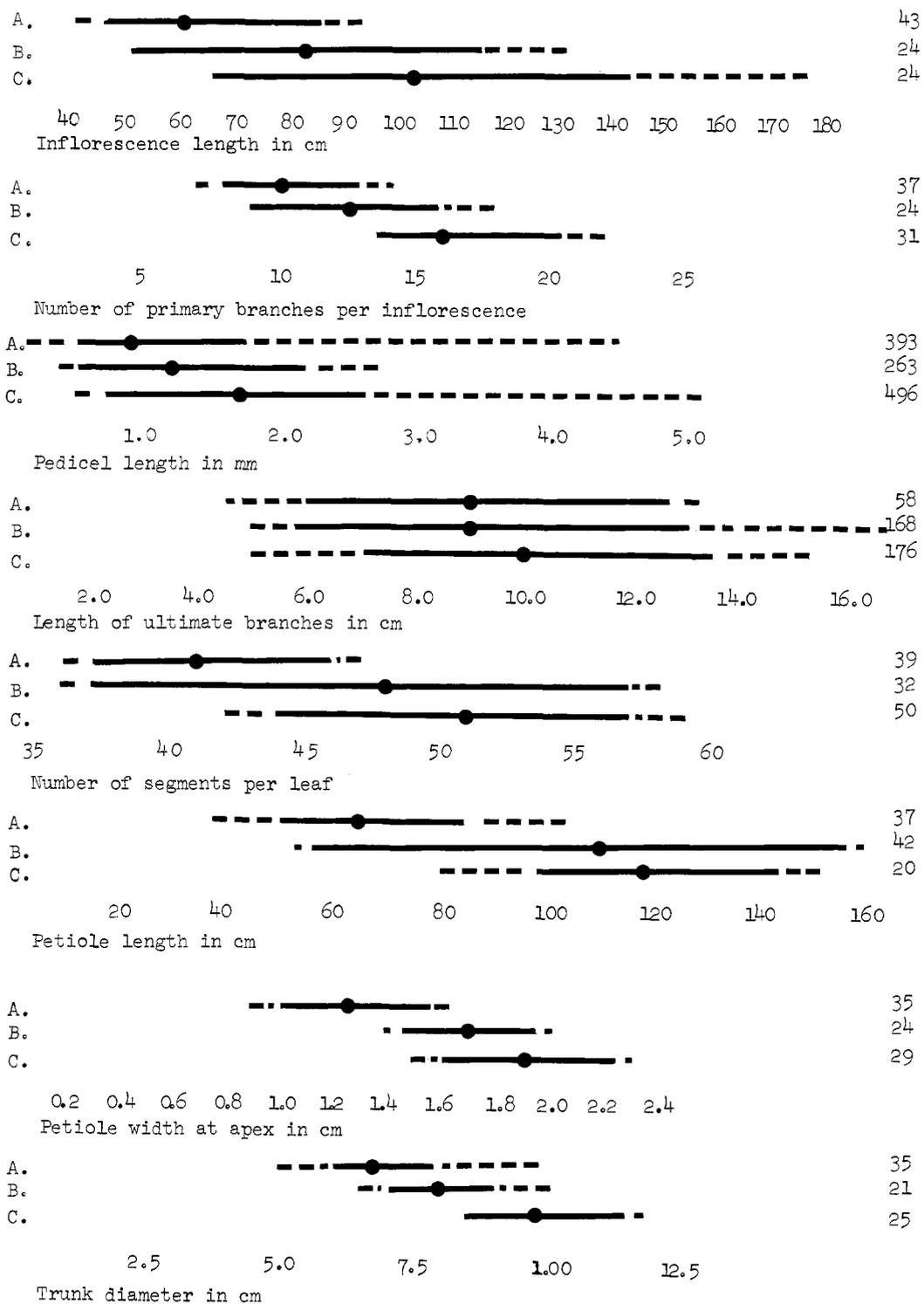


FIGURE 18.—Measurements of characters from the three intensively studied populations in Jamaica: A, Hollymount Hill; B, Mango Tree Hill; C, Cockpit, Clarendon. Sample size on right; bar graph as in Figure 41.

inflorescence in *T. excelsa* rarely equals the petiole, it is usually strongly curved and much shorter than the petiole.

Each primary branch of the inflorescence supports a bicarinate bifid bract (Figure 16A-E) with ciliate margins, midway along its peduncle and partially included within the tubular primary bract. During development of the inflorescence and before the flowers are exposed from the primary bracts the bifid bract completely encloses the primary branch and its flower buds. Early on the day in which anthesis takes place, the primary branch including its branchlets elongates rapidly, extending 15 to 20 cm in length during a 10-hour period. The branched portion of the primary branch is pushed out beyond the bifid bract and becomes pendulous (Figure 9D).

The color of the primary branches and branchlets at flowering is characteristic of the species, particularly in *T. excelsa*. All parts of the branches and the flowers of *T. excelsa* are a bright rosy pink or purple, while in *T. parviflora* they are creamy white to yellowish. In *T. radiata* and *T. morrisii*

they are white, only becoming cream colored or yellow with age.

The primary branches throughout the genus are known to be once branched; however, in *T. parviflora* an occasional plant may produce a primary branch that has the lower branches secondarily branched. The primary branches of *T. parviflora* are typically densely puberulent throughout most of its range. Nevertheless at the higher elevations puberulence becomes less pronounced and at the highest elevations is restricted to protected areas in the axils of the branches and in lines on the peduncle. The primary branches of *T. radiata*, *T. morrisii*, and *T. excelsa* are entirely glabrous.

Flowers: The bisexual flowers of the *Thrinax* alliance are exceptional in the Palmae in having a single whorl of perianth, variable stamen number from 5 to 15 or more, and a unilocular unilocular gynoecium. The flowers of *Thrinax* are very like those of the rest of the alliance. Except for the peculiar stamen character in *Hemithrinax* there is little of practical diagnostic significance in the flower. The flowers and associated inflorescence

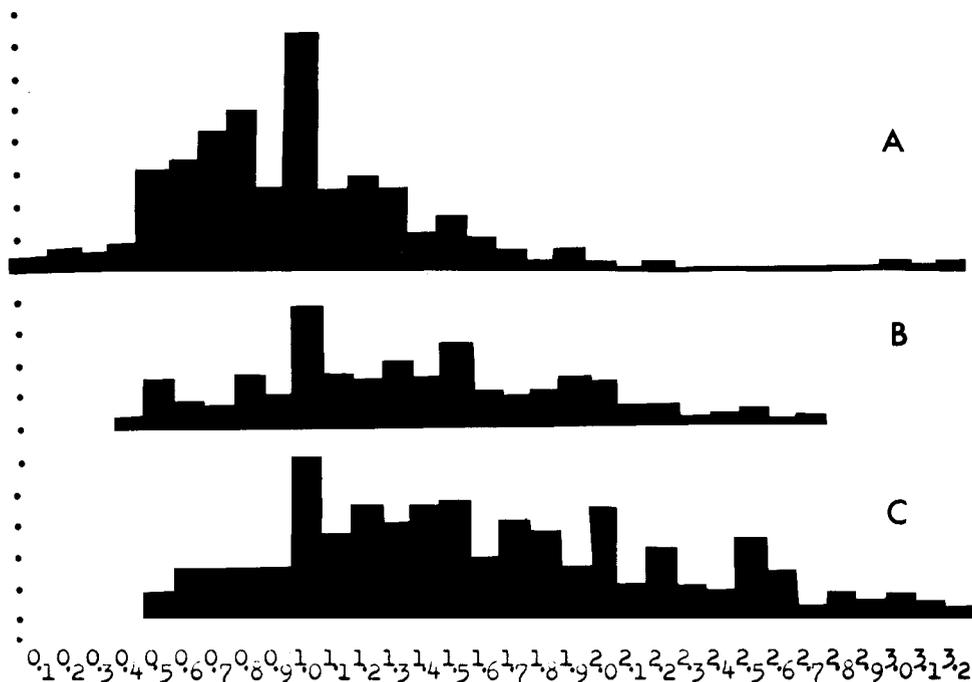


FIGURE 19.—Frequency and distribution of pedicel lengths in the three areas of intensive study in Jamaica: A, Hollymount Hill; B, Mango Tree Hill; C, Cockpit, Clarendon. Each point on the ordinate represents 10 measurements; pedicel length on abscissa in mm.

parts vary greatly in size and form even within a single species. Those of *T. parviflora* are the most variable among Jamaican species. *Thrinax radiata* flowers are very like the larger *T. parviflora* flowers. *Thrinax excelsa* flowers are rather uniform in size and form and differ from the aforementioned species primarily in the pink perianth and a simple horizontal stigmatic opening.

All *Thrinax* flowers are to some degree pedicelled, although in *T. morrisii* the pedicels may be very short and disklike. Much artificial division of the genus has resulted from the use of pedicel length, its presence or absence, primarily because of inaccurate conclusions based on inadequate material. Based partly on this character specimens of *T. parviflora* have been described as distinct taxa and placed in two different subgenera. Beccari (1907, 1933) considered *T. tessellata* and *T. harrisiana* to be distinct. He distinguished them from *T. parviflora* in his keys by their very short pedicels. Bailey (1938) also considered *T. tessellata* and *T. harrisiana* to be distinct but referred them to Sargent's subgenus "Sessiliflorae" with "sessile" flowers. Both names are synonymous with *T. parviflora* Sw., not of Bailey. Measurements of the variation of pedicel length of plants in the type locality of *T. tessellata* (Hollymount) are recorded in Figures 17 and 19, as locality #10, where they can be compared with the variation throughout the species. From a study of a large number of specimens it becomes evident that the flowers are more frequently long pedicellate than "sessile." No inflorescences have been found where conspicuously long pedicels are lacking, and none are truly sessile.

The perianth is a single series in cupular form and has a slight basal depression where it fits over the apex of the pedicel (Figure 20A,B). The upper margin is irregularly "6-lobed" or with 6 triangular, acute or attenuate prominences (Figure 21c,g,p, and others). According to a study of the anatomy of coryphoid palms, Morrow (1965)⁸ stated that in *Thrinax* there are 14 vascular traces to the perianth determined at one level as compared to 3 in *Hemithrinax*. Stamen filaments are mostly free but are always dilated slightly at the base where they are usually very shortly connate

⁸ The material utilized by Morrow in his anatomical studies was unfortunately wrongly identified as *T. excelsa*. This was the *T. excelsa* of Bailey, not Lodd. ex Griseb. It should therefore be called *T. radiata*.

beneath the ovary (Figures 21B,L; 22K; 23C,E; 24G,J,K); although in a key utilizing corolla-androecium structure Morrow (1965:341) stated: "C. Filaments free of adnation and connation" by which he distinguished *Thrinax* from other members of the alliance which possess, "C. Filaments in a ring, becoming free of connation higher up." The stamen filaments of *Thrinax* may be fused in varying lengths up to the apex (Figure 24G,J). One unit may in fact appear as a single broad filament with two or three anthers affixed (Figure 26). It is to be regretted that in Morrow's discussion of the "Evolution in the Calyx and Corolla of Coryphoid Palms," he neglected any mention of the peculiar and unique form exhibited by *Thrinax* and its allies, apart from an exception to his argument against a polyphyletic origin of the calyx of coryphoid palms on page 335. The occurrence of a perianth in a single whorl must have some evolutionary significance, either as a very primitive condition or a highly advanced one in which adnation and connation of calyx and corolla parts are carried to the extreme.

From the earliest description of the genus the androecium has been said to have 6 stamens, and although flowers are commonly observed with 6 stamens the most frequently occurring numbers are 7 or 8 in *T. parviflora*, 7 for *T. radiata*, and

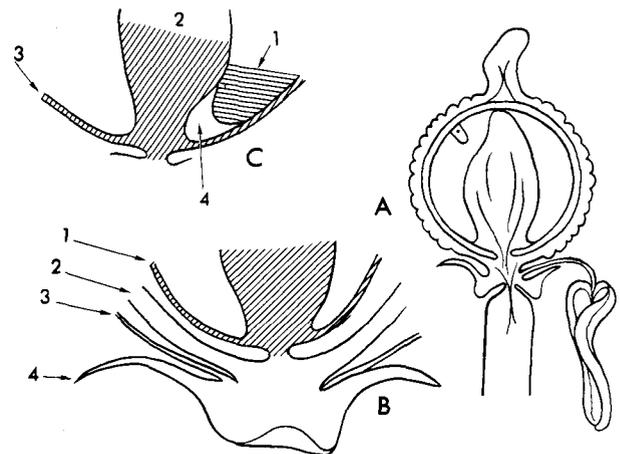


FIGURE 20.—Schematic drawings of developing fruit: A, immature fruit on pedicel, longitudinal section; B, base of fruit and perianth, B1, testa, B2, pericarp, B3, stamen filament, B4, perianth; c1, endosperm c2, 3, testa, c4, vacancy by shrinking endosperm.

8 or 9 for *T. excelsa*. Five stamens per flower is by no means a rare condition and the number of stamens quite often exceeds 10 or 12. The range of variation in anther number of 784 flowers of *T. parviflora* from among 11 different collections is

5 to 10 (-15). The mean number of anthers varied from 6.5 to 8.8 among the 11 collections. These figures are to be compared to 5 to 8 (-10) ($\bar{x}=6.5$) for *T. radiata* (127 samples) and (6-7) to 10 (-11) ($\bar{x}=7.5$) for *T. excelsa* (50 samples).

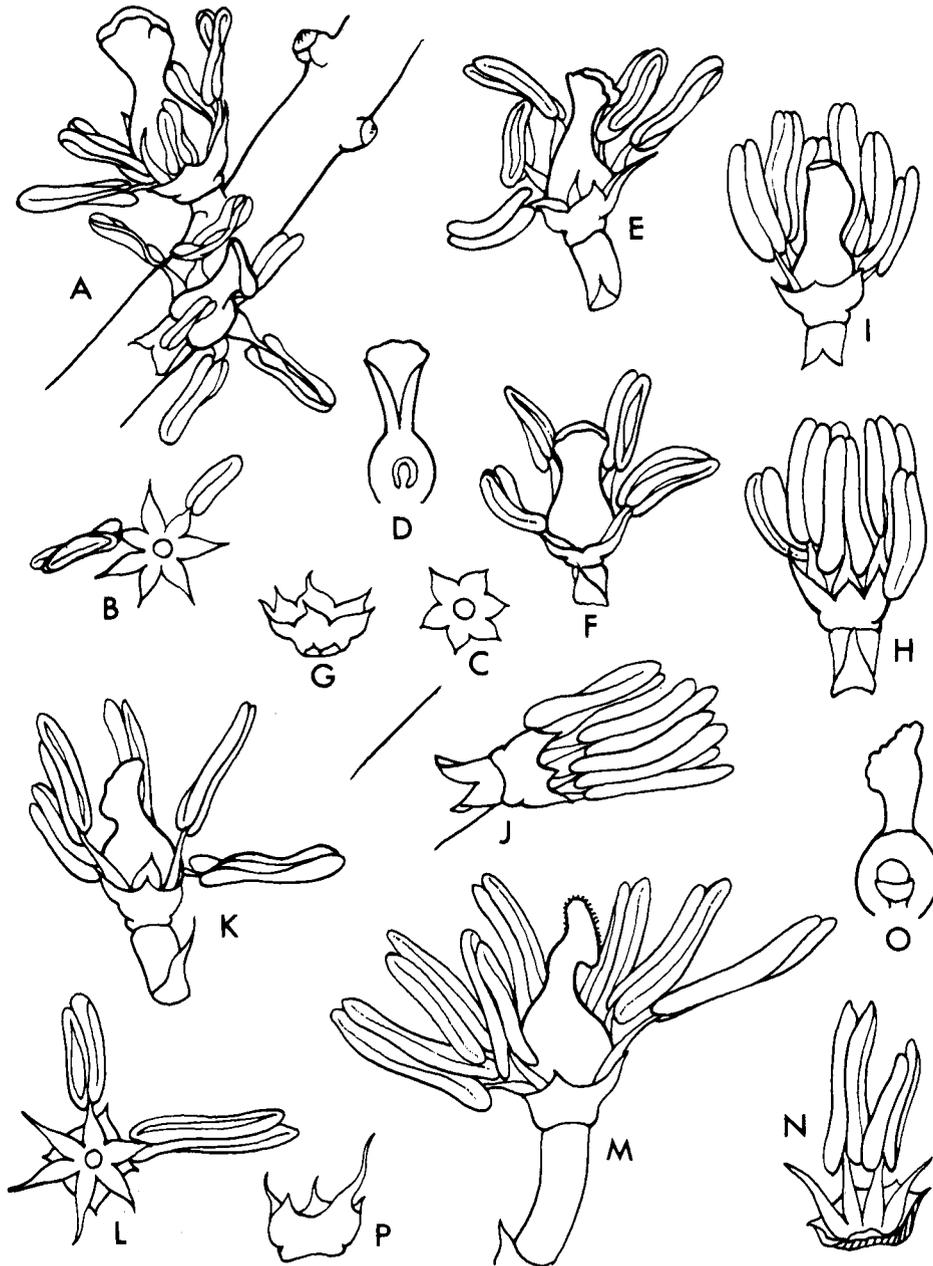


FIGURE 21.—*Thrinax parviflora*, variability of flowers: A-C, Hollymount Hill; H-I, Devils Backbone; J-P, Cockpit; B, L, filament bases; D, O, longitudinal section of pistil; C, G, P, perianth; N, cross section showing perianth and filaments.

The anthers are basifixed, and although the sacs are normally joined by a very narrow connective the condition has been observed where one sac is attached only at its apex while the other is affixed normally along the length of the filament. The

anthers are always slightly divided or retuse at both apex and base. The individual sacs are commonly apiculate and unequal in length. The range of variation in anther length of 1107 anthers randomly selected from among 12 different collections

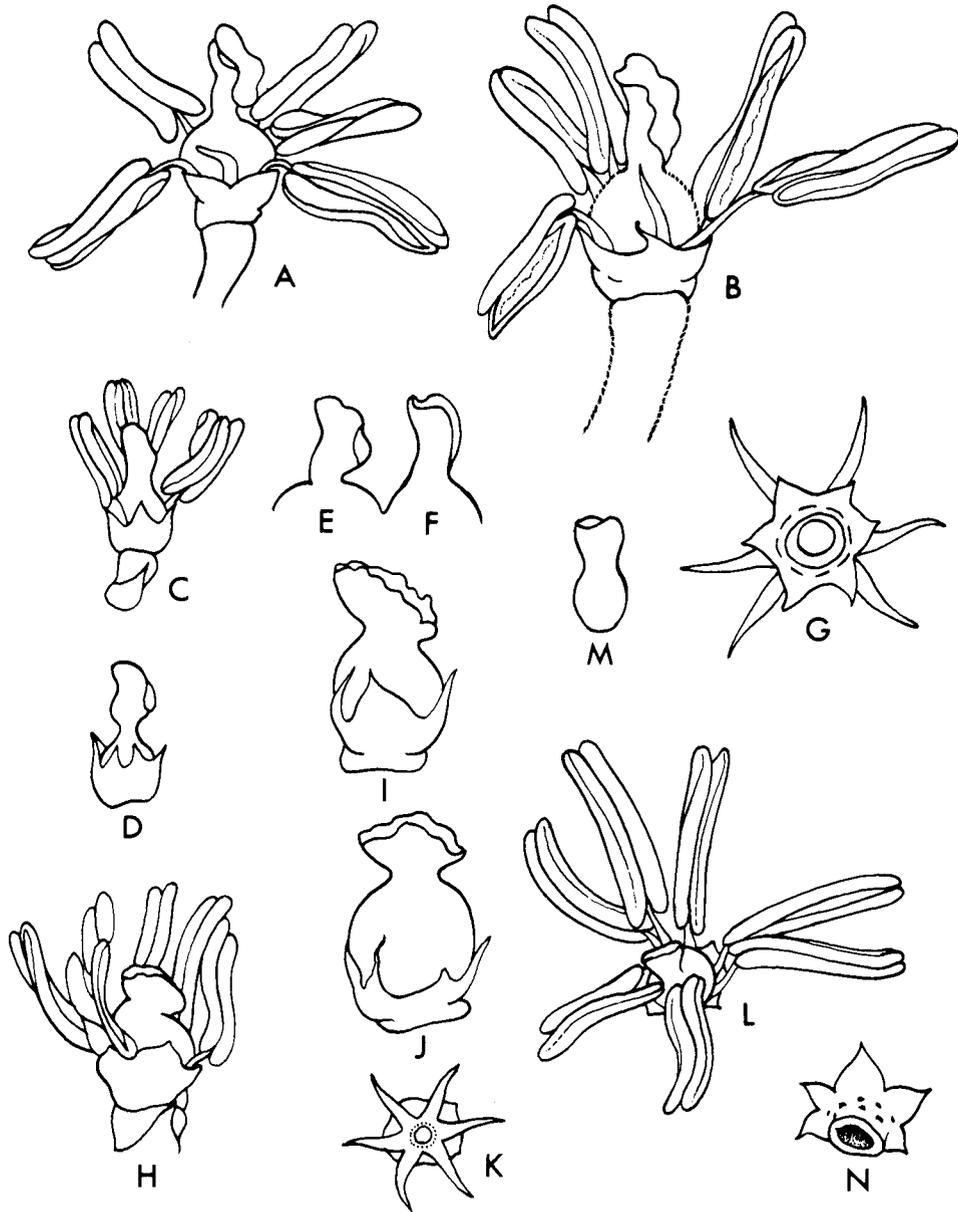


FIGURE 22.—*Thrinax parviflora*, variability of flowers: A-C, Long Mountain; H-K, Mango Tree Hill; L-N, Palmers Cross; E, F, M, pistil form; G, N, perianth, basally; K, filaments and perianth from above.

of *T. parviflora* is (1.1-)1.2 to 4.0 (-4.2) mm. The range of means varied from 1.6 to 3.4 mm. These figures can be compared to (2.0-)2.2 to 3.4 (-3.6) mm (\bar{x} =2.8 mm) for *T. radiata* (199 samples) and (1.2-)1.4 to 2.0 (-2.3) mm (\bar{x} =1.6 mm) for *T. excelsa* (100 samples).

The gynoecium is unilocular, "bearing a single basal bitegmic ovule. The orientation of the micropyle is slightly oblique but it is more orthotropous than campylotropous" (Morrow, 1965:108). "The funicular aril is developed to the same extent in *Thrinax* as in *Coccothrinax* and *Hemithrinax*

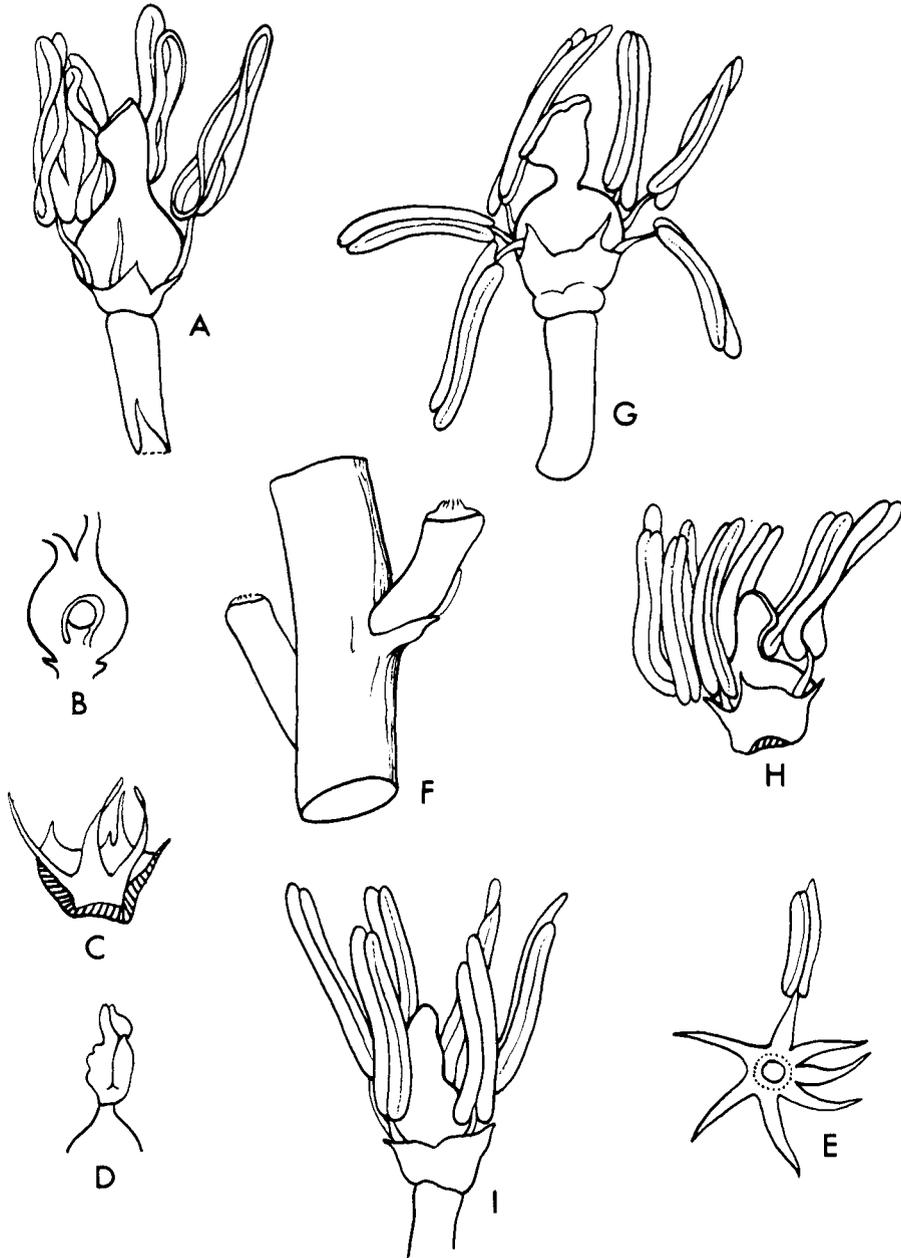


FIGURE 23.—*Thrinax radiata*: A, G-I, variability of flowers; B, base of the ovary in vertical section showing ovule; C, base of filaments and perianth; D, stigma; E, filaments; F, branchlet and pedicels.

(1965:110). The ovary is globose to slightly pyriform, usually abruptly constricted into a short style, which flares out into an infundibuliform stigmatic region in flowers of *T. parviflora* and *T. radiata*, and is usually quite oblique or sometimes lateral. In *T.*

excelsa the stigma appears as a simple conical depression in the apex of the style. The margins of the stigmatic region in *T. parviflora* and *T. radiata* are frequently undulate and ciliate.

Observations over a period of time on a plant of

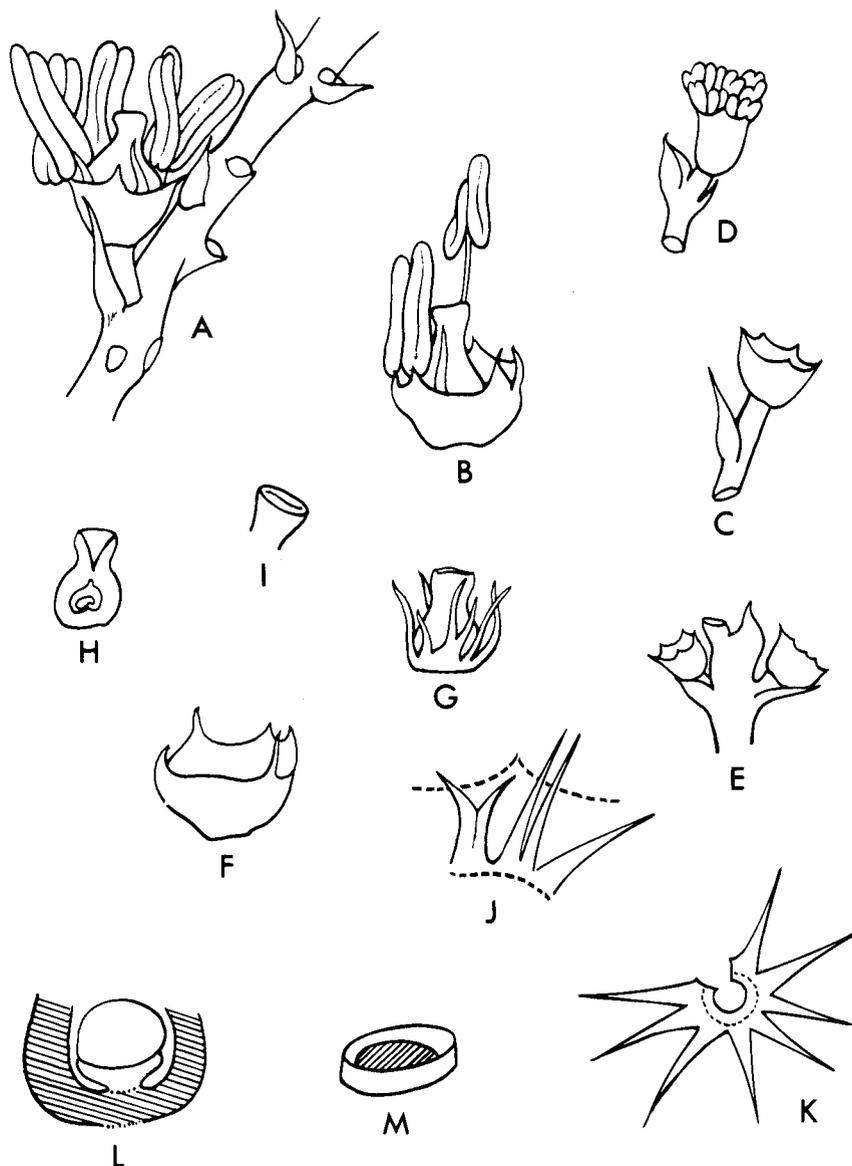


FIGURE 24.—*Thrinax excelsa*: A, B, flowers at anthesis; C, D, apical portion of branchlet showing the relationship of terminal flower and apex; E, shows an apical flower with its subtending bract; F, perianth cupule; G, filaments surrounding the base of the ovary, some variously connate; H, longitudinal section of pistil showing v-form stigmatic region, and ovule; I, stigmatic region in the apex of the style; J, connation of filaments; K, stamen filaments dissected from flower; L, base of ovary in cross section, showing ovule and funicular aril; M, funicular aril removed from ovule.



FIGURE 25.—Immature fruits of *Thrinax parviflora* showing variation of stigmatic remains; both from the same collection on the Devils Backbone, Jamaica.

T. parviflora reveal that the stigma is tightly compressed laterally obscuring the stigmatic surface at anthesis. Within twelve hours all anthers had dehisced and the released pollen was adhering to all surfaces of the inflorescences, but the stigmas were still closed. Twenty-four hours following anthesis the stigmas were open in the form of a funnel. Pollen was still plentiful on the inflorescence branches and by shaking the inflorescence a large quantity was dislodged. A second plant in the immediate vicinity was at anthesis at the time the stigmas were receptive.

The length of the style-stigma is quite variable and although fairly constant among the flowers on a single plant, it varies considerably among the plants in a single population. The stigmatic remains are most prominent during development of

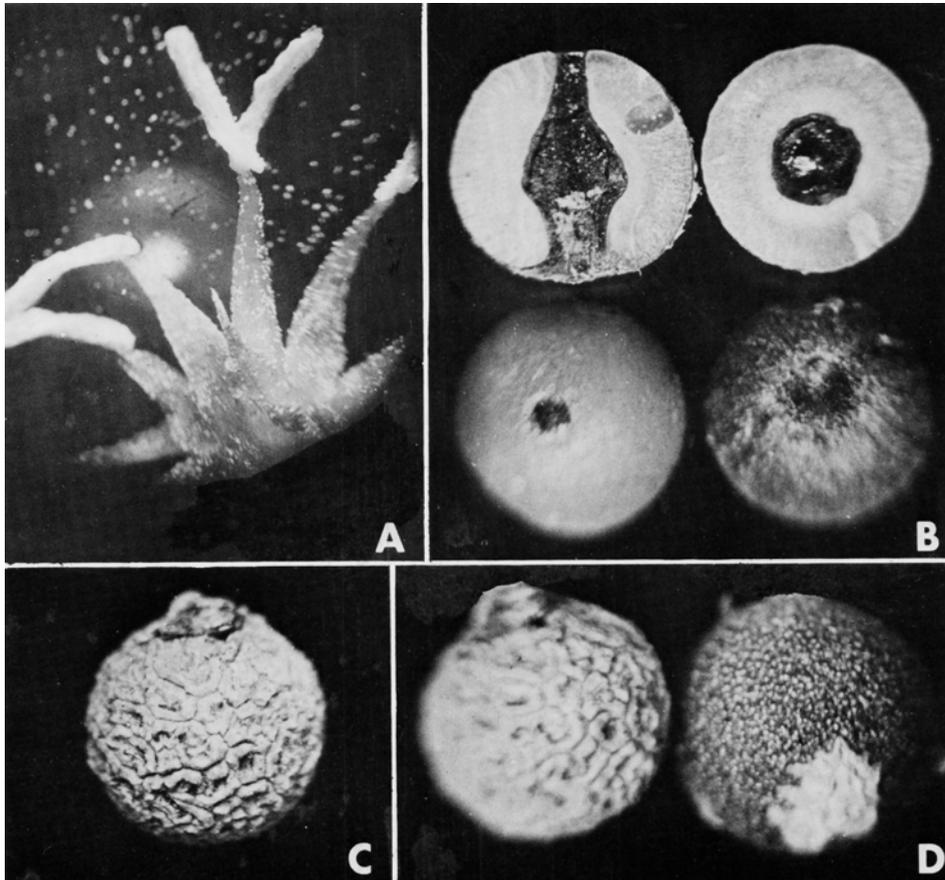


FIGURE 26.—*Thrinax parviflora*: A, abnormal flower with two anthers on a single filament; B, seed dissections showing intrusion of the testa (upper row longitudinal and cross sections through the embryo, bottom row apical and basal intrusion, left to right respectively); C, D, developing fruit exhibiting symptoms of fungal infection.

the fertilized ovary and in the young fruit. Figure 25 illustrates the variability of the length of the stigmatic remains on the young fruit of plants of *T. parviflora* growing side by side on the Devils Backbone.

The ovary enlarges rapidly following anthesis and therefore provides a very poor character for comparative studies. The surface of the ovary in all three Jamaican species is smooth at first but following fertilization considerable change takes place, especially in *T. parviflora*. As the ovary enlarges, the surface rapidly becomes slightly papillate and is soon completely covered by minute granulations (Figures 25, 26D).

In a discussion of the nature and evolution of the unilocular gynoeceum that Morrow queries as "unicarpellate or multicarpellate," he (1965) suggests that

there are at least three possibilities:

1) The unilocular gynoeceum is a single carpel, produced from ontogenetic or phylogenetic abortion of two other carpels.

2) The unilocular gynoeceum is a single carpel but has captured the vascular supply of two carpels which abort.

3) The unilocular gynoeceum is composed of three carpels, which grew together in such a manner as not to be recognizable.

He further suggested that "first . . . the unilocular forms have skipped a developmental step; and second, the development of the ovary occurs prior to anthesis."

Morrow (1965:355) stated that, "Normally unilocular species (*Thrinax* et al.) have been seen with 2 locules," and in this connection it seems appropriate to describe a curious phenomenon ob-

served in a number of specimens of *Thrinax parviflora*. A herbarium specimen at the Institute of Jamaica had on it a flower that seemed to be bicarpellate, but since soaking and dissection would have destroyed the flower, investigation was delayed until fresh material could be obtained. Fresh flowers at anthesis were collected on Portland Ridge, Jamaica, in which apparent fusion of flowers was in process. Figure 27D shows the apex of a rachilla upon which the apical flower possessed two distinct carpels and nearly double the normal number of stamens. The perianth formed a single 12-lobed whorl surrounding the base of the androecium. The possible explanation became apparent when the flower illustrated in Figure 27A-C was studied and dissected. On one side the perianth, although partly fused at the base, turned in apically and continued partly between the two carpels (Figure 27B). On the opposite side the perianth was a continuous "normal appearing" cupule enclosing both halves of the "flower" (Figure 27A). Two of the stamen filaments obviously originated between the two carpels. The arrangement of androecia and gynoecea diagrammed in Figure 27C clearly indicates that two flowers are partially fused on the apex of the rachilla. Fusion of the perianth is only partially complete. Other flowers have been observed in which the two carpels are apparently situated side by side without stamen filaments between them and with the perianth completely enclosing the base as a single multilobed unit. A situation of this sort could possibly explain the 2-locular ovary cited by Morrow.

Fruit: The fully developed but not fully mature fruit of *T. parviflora* may exhibit any one of several different characters. Fruit not infected or damaged by fungus attack (see section on Phytomorphosis) may be granulate, densely papillate, or even tuberculate and they often become scurfy as the fruit matures. Young fruit of *T. radiata* and *T. excelsa* are generally smooth to slightly pustulate or with widely spaced papillae. Fully mature fruits of all four species are smooth and white or creamy white.

The seed of *Thrinax* is subglobose with a subapical embryo and is intruded partly or completely by the testa. The seeds of all three Jamaican species are completely intruded from base to apex. The seeds of *T. morrisii* differ in that the seeds are not completely intruded by the testa, rather the testa

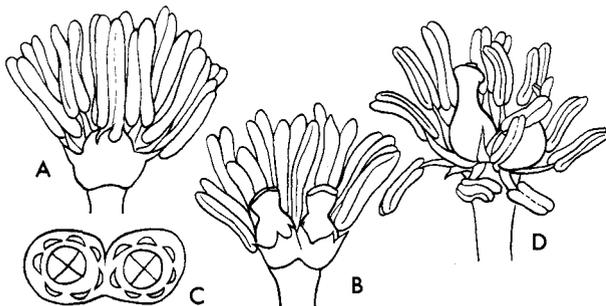


FIGURE 27.—Anomalous flowers of *Thrinax parviflora*; apical flowers exhibiting partial fusion of parts. Explanation in the text.

intrudes little more than halfway from base to apex. In fruit not quite fully developed (Figure 20B), the endosperm (c1) is rubbery and the intrusion of testa is easily observed as a dark fleshy tissue (c2) continuous with the very thin testa (c3) surrounding the endosperm. In longitudinal section the drying endosperm has pulled away from the central intrusion of testa (Figure 20c4; see also Figure 26B).

GERMINATION OF SEEDS.—The mode of germination of the seeds of *Thrinax* is similar to that of *Phoenix* as described by Gatin (1906) and Tomlinson (1960). The cotyledonary haustorium remains in the endosperm and the cotyledonary petiole (Figure 16H,1) by elongation pushes the radical out and down, burying the plumule and cotyledonary sheath a few centimeters into the substrate. The plumule then emerges through a split in the upper surface of the cotyledonary petiole.

Of interest, taxonomically, is the fact that in *T. excelsa* and *T. morrisii* the cotyledonary sheath

is pubescent throughout but that of *T. parviflora* is pubescent for only half its length, the lower portion remaining naked.

The first postcotyledonary leaf is tubular, sheath-like and bladeless, and usually pointed at the apex. The first seedling leaf, termed an eophyll by Tomlinson (1960), has a narrowly lanceolate green blade. Several successive seedling leaves are lanceolate, but leaves with three, and eventually more, segments are soon produced. The leaves produced henceforth become more and more complex as they appear with increasing numbers of segments.

POLLEN.—*Thrinax* pollen is pale cream colored to white, elliptic to broadly elliptic in outline, and monosulcate. The exine, when viewed by means of the light microscope, appears to be fairly uniformly psilate-foveolate among the four species; however, photographic studies by means of the scanning electron microscope clearly suggest the possibility of distinguishing between species by means of pollen-exine morphology. Further studies

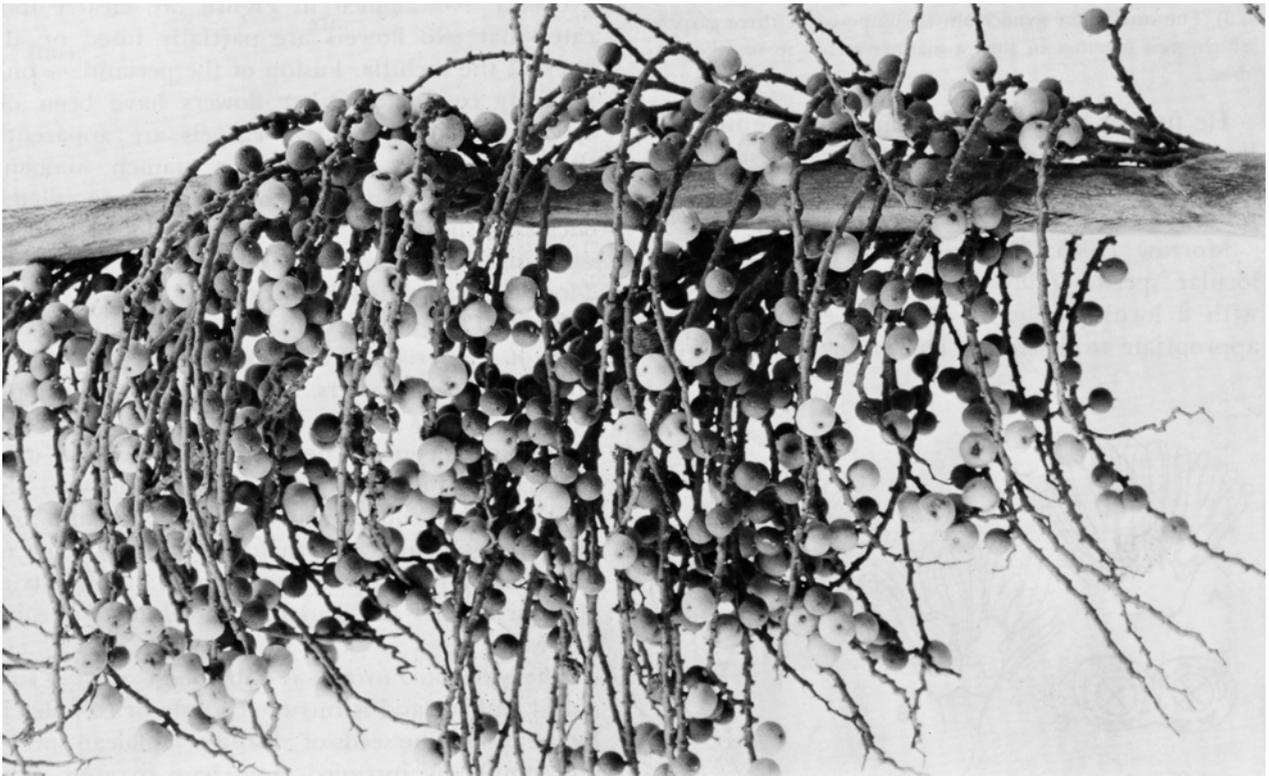


FIGURE 28.—Portion of fruiting inflorescence of *Thrinax morrisii*; fruit about natural size; note the bumplike pedicels.

of pollen from the extremes of the ranges and ecologies of the four species and their subspecies would be necessary in order to establish whether or not the types illustrated here are in fact really different or if they merely represent isolated parts of a range of variation. Certainly the character of the exine of *T. parviflora* is somewhat distinct from that of *T. excelsa*, and the exine morphology of *T. radiata*

and *T. morrisii*, while differing somewhat from the others, appears to be simply variations on a similar theme.

Anatomy

In his studies on the anatomy of palms, Tomlinson (1961:3) was correct in his observation that "specific identifications have never been very relia-

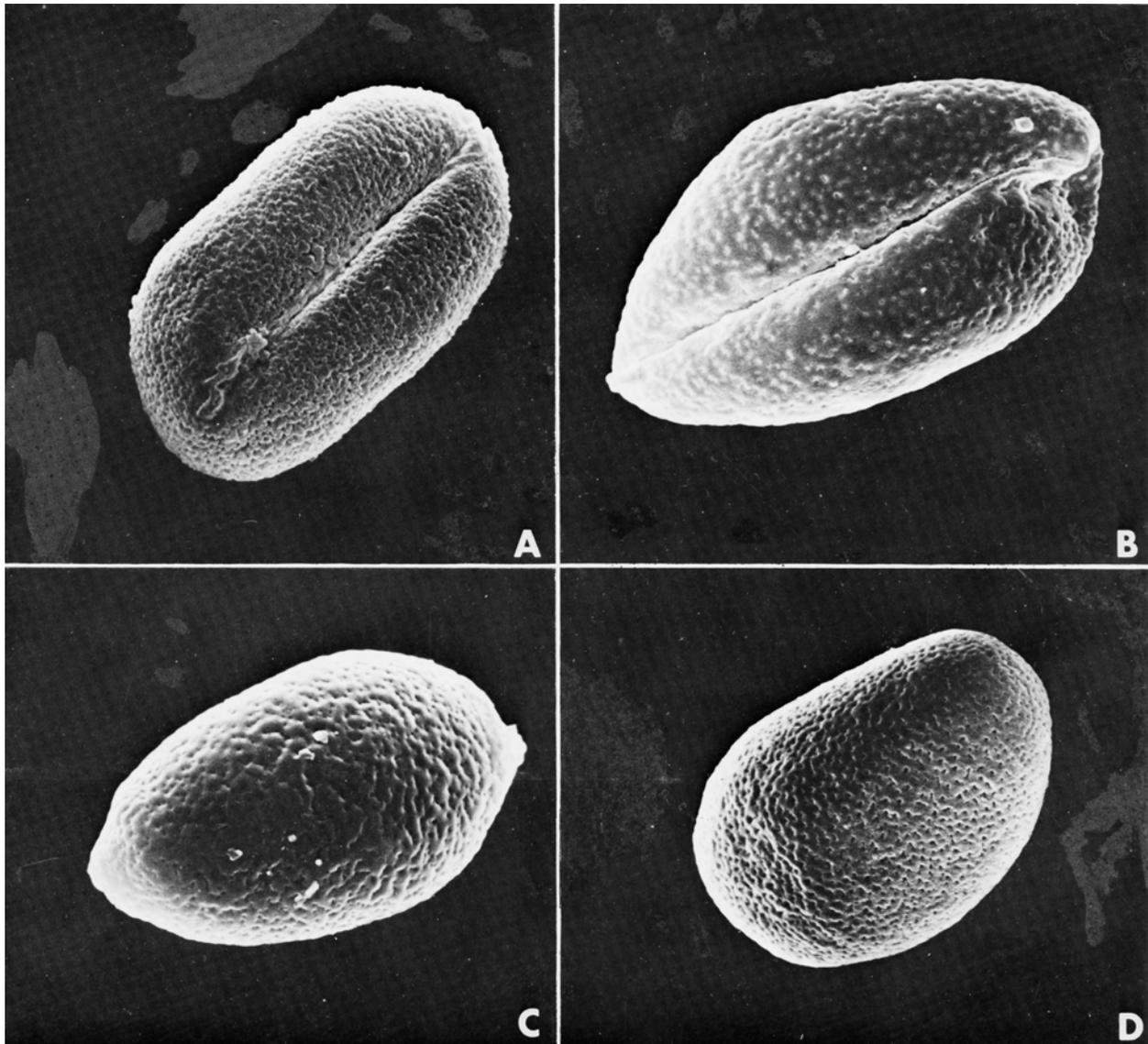


FIGURE 29.—Scanning electron micrographs of *Thrinax* pollen enlarged about 2600 times: A, *T. parviflora*; B, *T. radiata*; C, *T. excelsa*; D, *T. morrisii*. (Photographs courtesy of the SEM laboratory staff, from samples prepared by the Botany Palynology Laboratory at Smithsonian Institution.)

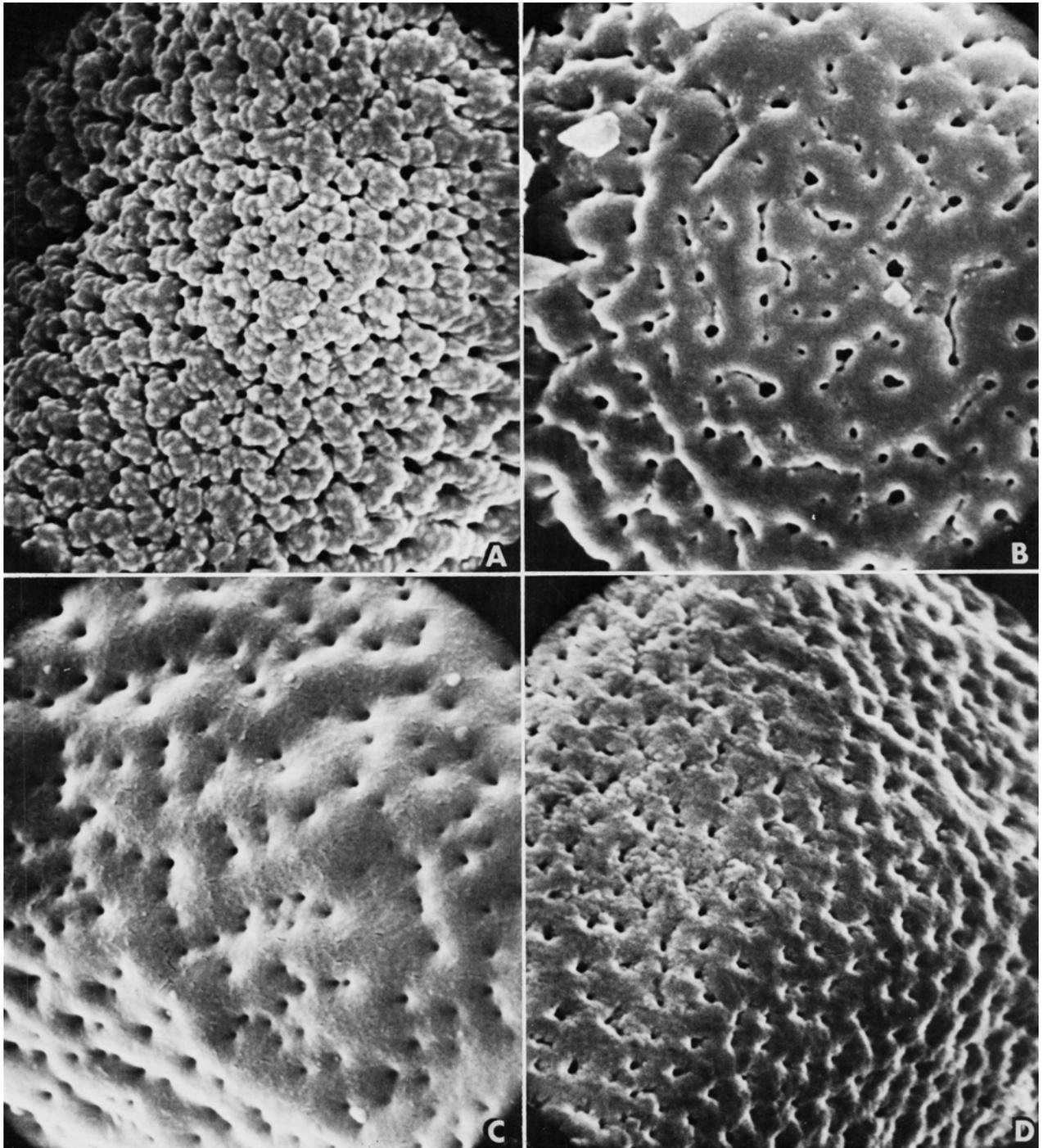


FIGURE 30.—Scanning electron micrographs of *Thrinax* pollen magnified about 10,000 times. A, *T. parviflora*; B, *T. radiata*; C, *T. excelsa*; D, *T. morrisii*. Note how different the surface pattern appears under the much greater magnification.

ble." But he states: "In many genera this is no disadvantage since interspecific differences are often only quantitative and are obscured by anatomical variation within a single species." This statement may be true for other palms but in the genus *Thrinax*, once the taxonomy is worked out, certain

anatomical characters follow the same pattern as the key morphological characters. It is now possible to identify accurately each species of the genus simply by comparing the anatomical characters of the lamina with the following key or the accompanying illustrations.

Anatomical Key to the Species of *Thrinax* Using Laminar Characters

1. Laminar cross section composed almost entirely of palisade cells; stomata deeply sunken; abaxial outer epidermal cell walls greatly thickened, surface very irregular *T. morrisii*
1. Laminar cross section composed of either distinct layers of palisade and mesophyll, or palisade cells few and scattered; stomata not sunken; abaxial epidermal cell walls not greatly thickened nor is the surface highly irregular.
 2. Palisade and mesophyll layers quite distinct; hairs when present large and complex with numerous surface cells in cross section.
 3. Stomate guard cells in cross section, hooklike in appearance *T. radiata*
 3. Stomate guard cells in cross section, not at all hooklike in appearance *T. excelsa*
 2. Palisade cells absent or rather uncommon and widely scattered if present; hairs when present, small and with few surface cells; stomate guard cells, in cross section hooklike in appearance *T. parviflora*

MATERIAL AND METHODS.—In most cases samples of 2 sq cm each of dry herbarium material were selected and soaked overnight in aerosol (Ayensu, 1967). Thin sections were then made by hand using a sharp razor blade with the specimen supported by elderberry pith. The sections were then stained using a 0.05 percent solution of toluidine blue in 0.15 M phosphate buffer for a few seconds and mounted in ethylene glycol under glass cover slips. Neither soaking in sodium hypochlorite solution nor heating in hydrochloric acid seemed to make the material easier to section. The material to be sectioned was selected from the midportion of leaf segments, about halfway between apex and hastula, between the major veins.

The following account of the anatomy of the lamina of *Thrinax* is based in part on a treatment of the genus by P. B. Tomlinson (1961), but it has been modified significantly by more recent personal observations. Tomlinson's treatment was unfortunately based on a mixture of both *Coccothrinax* and *Thrinax*, closely allied but distinct genera. He (p. 296) concluded that

from the material . . . examined, although some of it has not had a reliable name and may have been confused with *Coccothrinax*, there appears to be considerable variation in the anatomy of the lamina, particularly in the structure and distribution of the hairs and the distribution of the veins

and fibrous strands. Since the taxonomy of *Thrinax* and related genera seems to be rather confused, little reliance can be placed on the anatomical information which has so far been recorded until a detailed survey can be made upon a large number of species from accurately established sources.

The elements that do not agree with observations on verified *Thrinax* materials have been removed, and in addition to my own new observations those that do apply to the genus *Thrinax* have been retained.

LAMINA ⁹.—*Hairs* frequent in abaxial costal regions, each with sunken, elliptical, sclerotic, multicellular bases. *Cuticle* thick. *Epidermis* wholly cutinized, outer wall somewhat thickened. Adaxial epidermis fairly uniform, costal regions differentiated only above largest veins, cells rather variable, mostly more or less cubical or slightly longitudinally extended, walls not sinuous. Abaxial epidermis differentiated into narrow costal and wider intercostal regions. Costal cells rectangular, longitudinally extended, narrow, shallow; intercostal cells less regular, shorter, wider, deeper, and slightly papillose. *Stomata* restricted to abaxial intercostal regions, those of both *T. ra-*

⁹ Grateful appreciation is extended to Mrs. Lisa Keys, graduate student at the University of Massachusetts, for her freely volunteered help in the preparation of materials and hand sections used in the laminar anatomy.

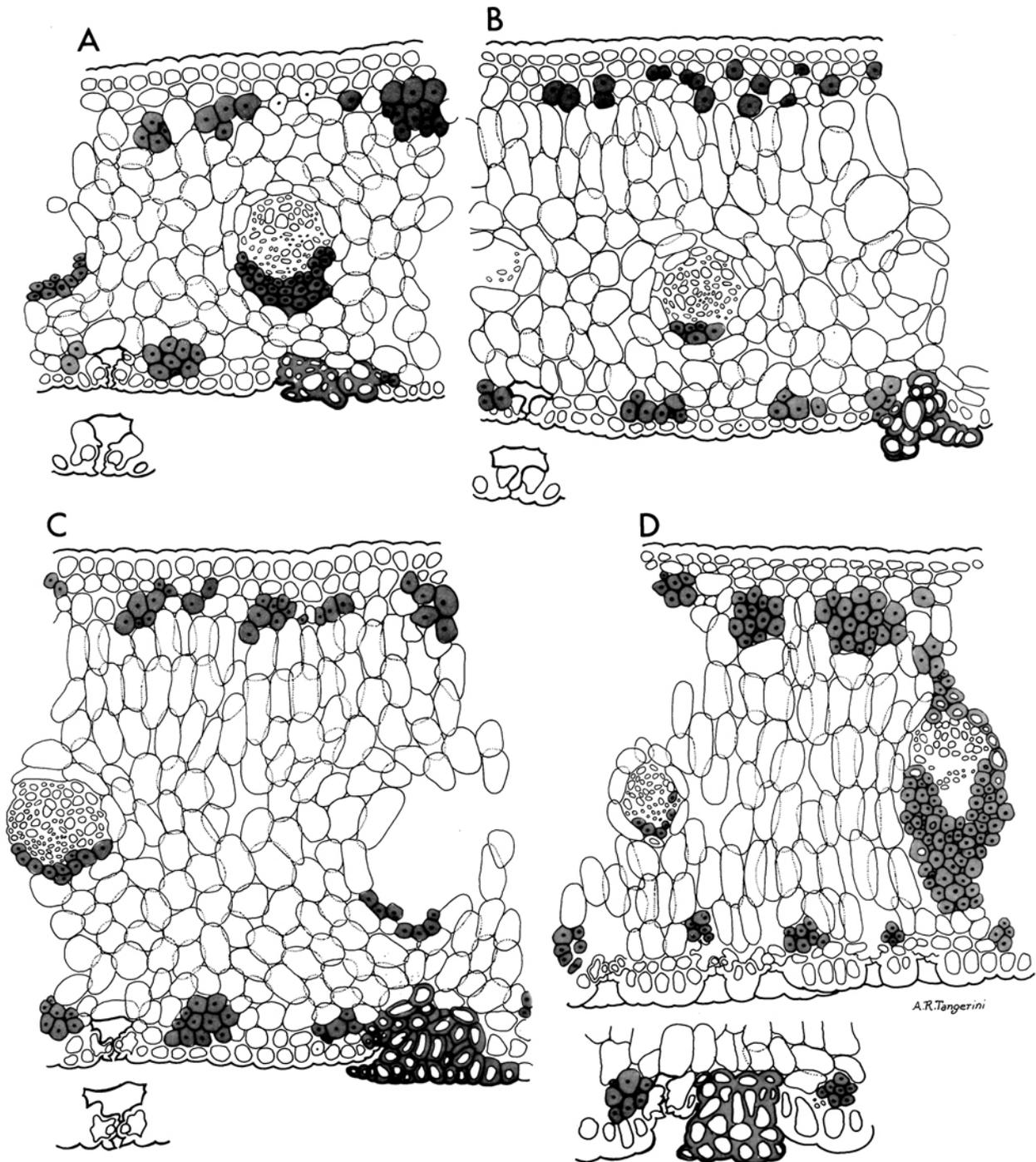


FIGURE 31.—Camera lucida drawings of *Thrinax* leaf sections: A, *T. parviflora* (Read 1736, Devils Backbone); B, *T. excelsa* (Read 1936b, John Crow Mountains); C, *T. radiata* (Read 1862, Morant Point); D, *T. morrisii* (Read 798, Grassy Key, Fla.).

diata and *T. parviflora* similar in cross section as in Figure 31A,C, while *T. excelsa* and *T. morrisii* share similar guard-cell types which differ from the other two species (Figure 31B,D). *Hypodermis* 1- to 2-layered below each surface but adaxial hypodermis mostly 2-layered; cellfiles often replaced by fibers. Adaxial cells rectangular, longitudinally extended. Abaxial cells more cubical, irregular in intercostal regions. *Chlorenchyma* with a fairly distinct 2- to 3-layered adaxial palisade (except *T. parviflora* which has only widely scattered infrequent palisade cells, the chlorenchyma being primarily composed of mesophyll). *Thrinax morrisii* is distinctive in having the chlorenchyma composed almost entirely of palisade cells. Abaxial mesophyll cells more or less isodiametric, compact. Fibers frequent, mostly in strands below each surface. Adaxial strands irregular, with 1-21 (rarely more) fibers per strand irregularly intruding the chlorenchyma, these adjacent to the epidermis or separated from the epidermis by a layer of small hypodermal cells. Abaxial strands with fewer fibers, sometimes cylindrical, mostly adjacent to adaxial epidermis. *Veins* mostly in abaxial mesophyll or equidistant from either surface. Outer parenchymatous sheath complete around, or interrupted below small veins, always interrupted both above and below large veins; sheath-cells cubical, often containing chloroplasts. Inner sclerotic sheath completely fibrous around large veins, usually including sclerotic parenchyma adjacent xylem of small veins. Phloem of large veins not subdivided, rarely slightly sclerotic. *Transverse commissures* usually in abaxial mesophyll, rather infrequent, wide. *Ribs* most prominent adaxially in proximal part of lamina. Surface layers similar to those of lamina, with few small hypodermal fibrous strands. Central ground parenchyma containing several vascular bundles: those in adaxial ribs with well-developed, somewhat confluent, fibrous sheaths; those in abaxial ribs more or less surrounded by a common sclerotic cylinder. *Expansion cells* in bands, including fibrous strands, within each fold of the lamina.

These studies have provided the only positive means of identifying *Thrinax radiata* with living taxa.

Leaf Axis: Epidermis with more or less cubical cells; walls thickened, cutinized. *Stomata* occasional, slightly sunken. *Hypodermis* 1-layered, inconspicuous, sometimes slightly lignified. Peripheral *chlo-*

renchyma indistinct. Fibrous bundles occasional in chlorenchyma. *Vascular bundles* uniformly scattered, not congested at the periphery; each with a complete fibrous sheath, usually including 2 wide metaxylem vessels and an undivided, not sclerotic, phloem strand.

Cell Inclusions: Stegmata of leaf in short, often continuous, files mostly adjacent to vascular fibers. Silica bodies spherical, spinulose, diameter 12 microns; basal wall of silica cell slightly thickened. Enlarged cells filled with raphid bundles are fairly common between the smaller veins.

Vascular Elements: Vessels: elements of leaf with scalariform perforation plates on oblique end walls. *Sieve tubes:* elements of leaf with compound sieve plates on more or less transverse end walls. It was noted by Parthasarathy (1968) that the *Thrinax* alliance and *Licuala* are exceptional among coryphoid palms in possessing more areoid than typically coryphoid sieve plates. Furthermore, he stated that *Thrinax* in common with other closely allied genera is also set apart from most coryphoid palms by having but a single phloem strand, and sclerotic parenchyma cells in the metaphloem of many vascular bundles.

Literature: The greatest criticism concerning studies by earlier workers is that most of the material was unreliably identified, as mentioned by Tomlinson (1961). Furthermore the material was either obtained from botanical gardens which are questionably reliable, unless vouchered materials are available at the institution, or the materials were obtained from herbarium specimens without citation of specimen numbers or collector. Thus the unvouchered materials used by past workers cannot now be identified with certainty.

Tomlinson (1961:296) cited as his material, "*T. argentea* Lodd. -Kew. Leaf," which is probably a *Coccothrinax*; and "*T. tessellata* Becc. Jamaica. Leaf," which name is now in synonymy of *Thrinax parviflora* Sw. Drabble (1904) treated *T. excelsa* Lodd. and *T. parviflora* Sw., the former name having been applied to *T. radiata* in Jamaica and the latter to *T. radiata* in Florida. Gillain (1900) treated *T. argentea* Lodd. and *T. graminifolia* Wendl., the first a *Coccothrinax* and the second a nomen incertum. Jost (1887) and Zawada (1890) simply cited "*Thrinax* sp." And of the nine taxa attributed to *Thrinax* in the study by Pfister (1892) only "*T. excelsa* Lodd." could be a *Thrinax* but certainly

not of that species. Rudolph (1911) and Solereder and Meyer (1928) worked only with species of *Coccothrinax*.

Cytology¹⁰

The species of *Thrinax* in Jamaica, in addition to many other similarities already mentioned, have a chromosome complement similar in number and morphology to other members of the alliance. The results of the present study when compared with previous work (Read, 1963, 1964, 1965a, b) lead to the conclusion that, as far as can be determined, it is not possible to distinguish between genera of the *Thrinax* alliance by means of their chromosome karyotypes. The relatively large size, 1–3.0 (–3.5) microns in length, of the chromosomes places *Thrinax*, together with its closest allies, in a group of palm genera having chromosomes of a similar size but which differ primarily in having a 2-whorled perianth and a 1- to 3-carpellate ovary (i.e., *Schippia*, *Cryosophila*, *Trithrinax*, and *Chelyocarpus*). Except for the genera just mentioned and several genera of dioecious palms, which also have large chromosomes, all other coryphoid palms studied thus far have mostly very small chromosomes, 0.5 to 1.5 (–2.0) microns long.

The karyotype for each species exhibits an almost complete gradation of sizes from smallest to largest with some recognizable differences in morphology. With such small chromosomes, however, and with the present technique it has proved unsatisfactory to attempt a classification of size or morphological groupings. Chromosome size may vary considerably among the preparations of a single species or individual depending on the timing of pretreatments or fixation and especially the degree of squashing. And although certain chromosomes are recognizable as having subterminal, submedian or median constrictions, it is extremely difficult to differentiate between real and apparent differences. For example with such small chromosomes, as so often happens, they do not always lie flat or parallel with the level of resolution. It is then possible to misinterpret a chromosome which

may have part of its arms bent down or under; thus a submedian or subterminal primary constriction may appear as a median or submedian respectively. An ideal preparation would require squashing to less than 0.5 micron in order to flatten the chromosomes sufficiently. This has not been possible because of the presence of the pollen grains in the preparation.

MATERIAL AND METHODS.—All material used in the present study was collected from wild plants in the field in Jamaica.

A detailed description of the technique has already been published (Read, 1965), therefore only a brief review need be given here. Portions of inflorescence were collected at anthesis or as soon before as possible. The pollen was collected by allowing it to shed on a piece of paper in a draft free room. It was then stored in gelatin capsules and placed in an airtight container with dry silica gel and a color indicator, at room temperature (about 26°C). It was necessary at times to dissect the unopened anthers from the flowers and permit them to dry in the gelatin capsules and silica gel. It was important not to store more pollen in a capsule than would effectively coat the walls when dry, otherwise the possibility of fungal and bacterial contamination became serious.

Pollen was sown on a nutrient medium (100 ppm H_3BO_3 in water; 0.02% colchicine in distilled water; 10% lactose or sucrose and 10% gelatin) for the study of pollen-tube mitosis. After heating medium slightly it was applied to cover glasses by means of a small cotton swab. The pollen was dusted lightly over the surface of the dry medium and the cover glass then overturned onto a Van Tieghem cell lined with moist absorbent paper. An improved method was to place the rings that form the Van Tieghem cells directly on a layer of moist absorbent paper lining the bottom of a plastic tray. After the prepared cover glasses were in place the container was closed to prevent drying. The tray was maintained at room temperature (about 26°C) and germination was usually found to have proceeded sufficiently within 8 to 10 hours.

When examination of sample slides indicated that mitosis was in process, the cover glasses were stained with acetocarmine and made permanent by the vapor transfer method. All counts and drawings were made on freshly prepared slides. The tapping and differential squashing necessary to produce the

¹⁰From work related to a project supported by National Science Foundation grants G-18770 and extension GB-1354. While in Jamaica the Botany Department of the U.W.I. acquired phase-contrast attachments especially for use by the author in his research on palm cytology.

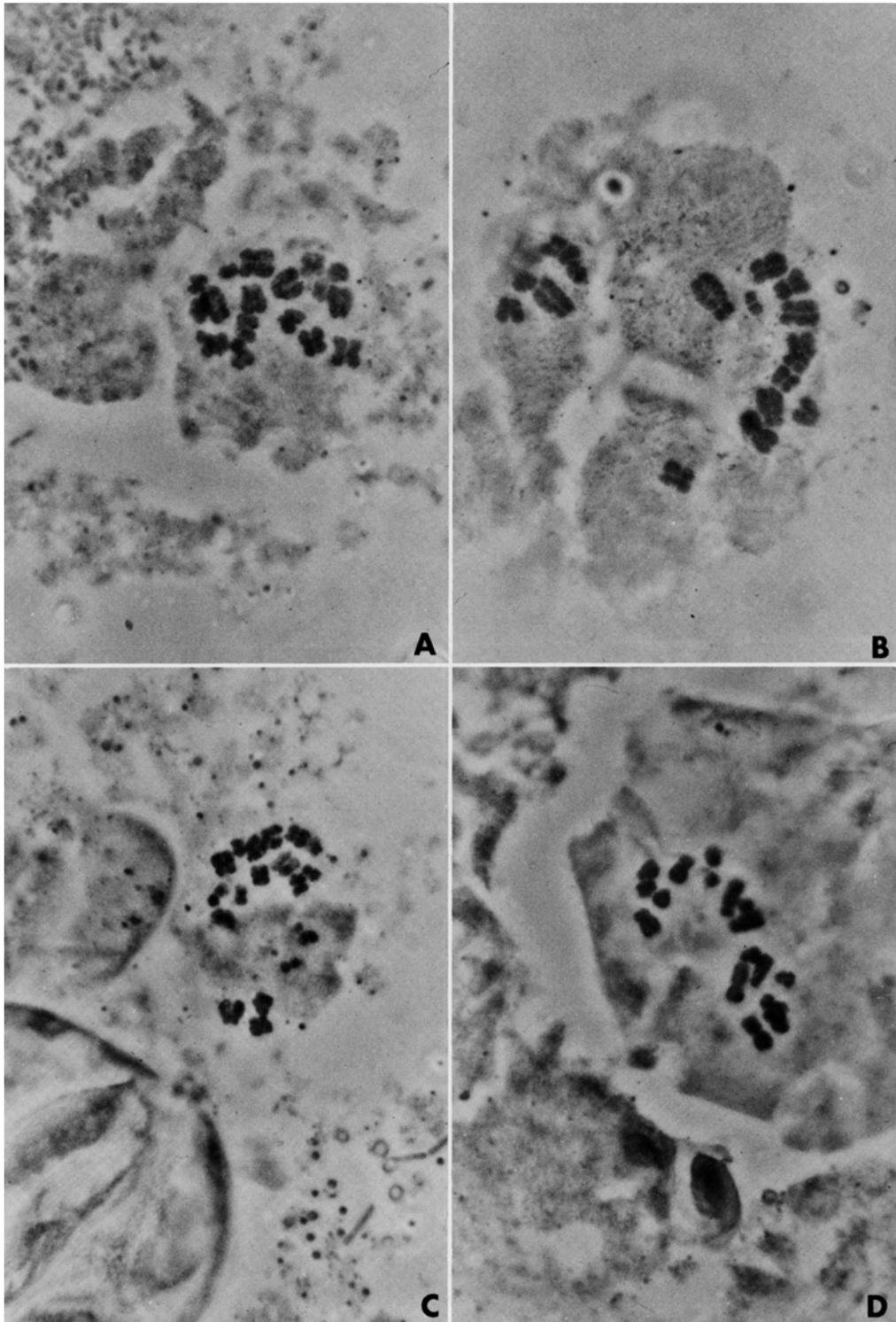


FIGURE 32.—Photomicrographs of the chromosomes of species of *Thrinax* at pollen tube mitosis: A, B, *T. parviflora*, Read 1657; C, *T. parviflora*, Read 1675c; D, *T. excelsa*, Read 1625. (\times ca. 2500.)

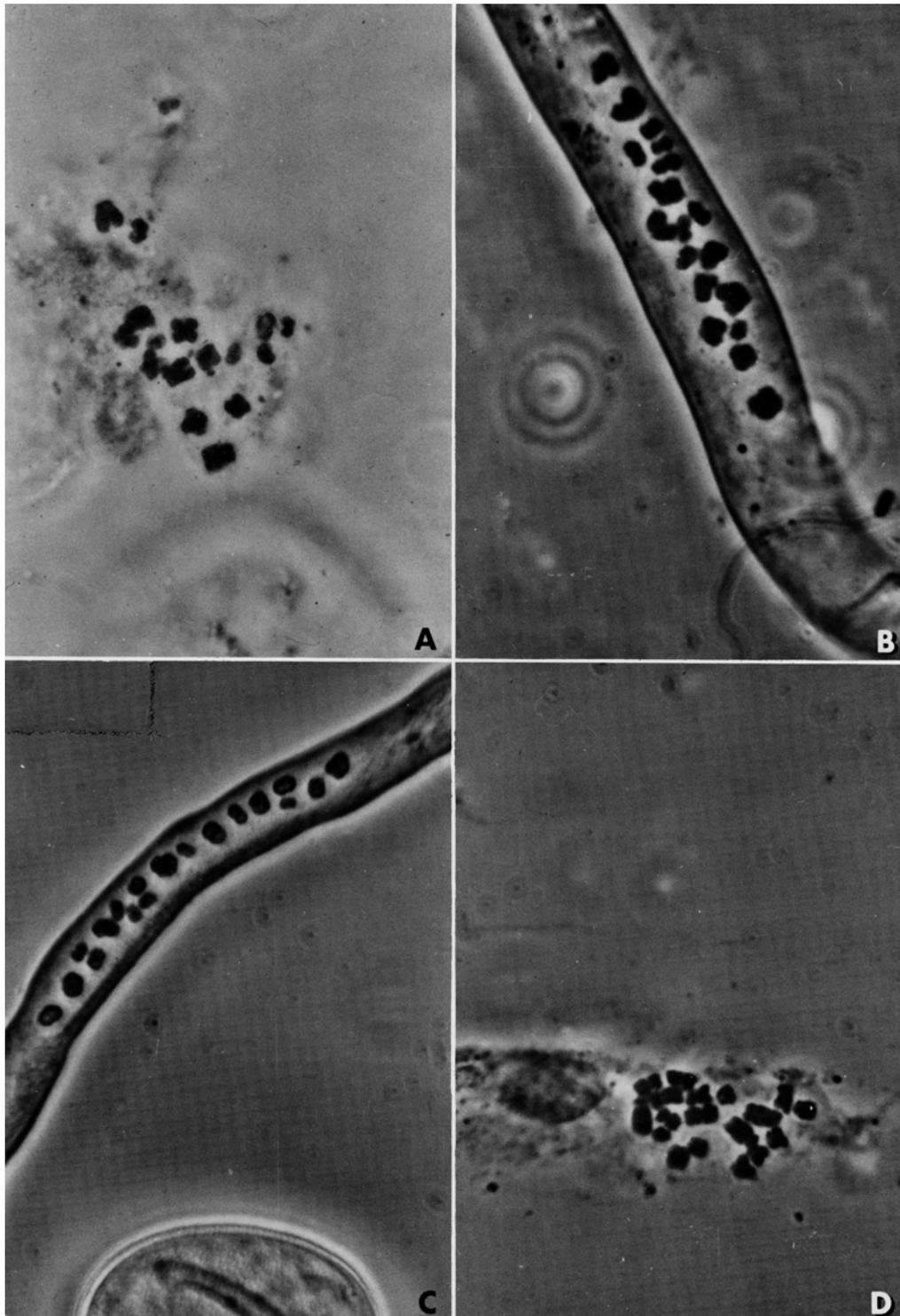


FIGURE 33.—Photomicrographs of the chromosomes of species of *Thrinax* at pollen tube mitosis: A, B, *T. radiata*, Read 1671; C, D, *T. morrisii*, Read 1437a. (\times ca. 2500.) Note the chromosomes obviously still within the developing pollen tube in Figures B, C.

best figures was not possible after a few hours. Drawings were made with the aid of a camera lucida, and the photographs were made on 35 mm film either in black and white or color (Kodachrome II). The use of phase-contrast aided immeasurably in distinguishing between closely situated chromosomes and also produced photographs of better quality.

Before the present study was undertaken, reports of chromosome numbers in *Thrinax* were already in the literature; however, as a result of the present revision of the nomenclature among the Jamaican taxa, it is necessary to revise the names cited for the species for which chromosome numbers have been reported. *Thrinax excelsa* as reported by Venkatasubban (1945) and Read (1963) should be named *T. radiata*. *Thrinax parviflora* and *T. floridana* as reported by Read (1964, 1965a respectively) should likewise be named *T. radiata*. *Thrinax*

microcarpa as reported by Read (1963, 1964, 1965a) should be named *T. morrisii*.

Thrinax radiata has been reexamined using native material from its natural habitat. Authentic *T. excelsa* also has been studied from material collected in the field. It was particularly interesting, early in the research, to compare the chromosomes of *T. parviflora* from plants growing in the extreme climates in which the two biotypes occurs. The chromosome number in each case has been determined to be $n=18$, agreeing with all other coryphoid palms studied to the present. Idiograms of each species in Jamaica are illustrated in Figure 34. *Thrinax parviflora* from a lowland habitat at Cockpit, Clarendon, is represented by *a, b*, and the high elevation phenotype from plants on the Devils Backbone is represented by *c, d, e*. *Thrinax radiata* is represented by idiograms *f, g*, and *T. excelsa* by idiograms *h, i*.



FIGURE 34.—Idiograms of *Thrinax* showing their comparative karyotypes. *a, b*, *T. parviflora*, Read 1675c; *c-e*, *T. parviflora*, Read 1736; *f, g*, *T. radiata*, Read 1671; *h, i*, *T. excelsa*, Read 1625.

Phytomorphosis and Zoomorphosis in *Thrinax parviflora*

The specific epithet "*tessellata*" was applied by Beccari (1907:271) to a specimen from Hollymount at the upper elevations on Mt. Diablo. The name was given in allusion to the fruit which Beccari described as having the "*epicarpio distincte suberoso-tessellato*," a condition common in the cool moist environments where a fungus infection radically alters the exocarp of the fruit producing the condition shown in Figure 26c. The fruit can become infected at almost any stage of development. Figure 26b shows two stages in the development of the fungus on young fruits. The fruit on the right has a small area where the epidermis has only begun to erupt as a result of the fungal activity. The fruit on the left has no trace of epidermis remaining as in Figure 26c. Fruits exhibiting both partial and complete alteration of the epidermis are part of the isotype of *T. tessellata*, herein treated as synonymous with *T. parviflora*. The fungus,

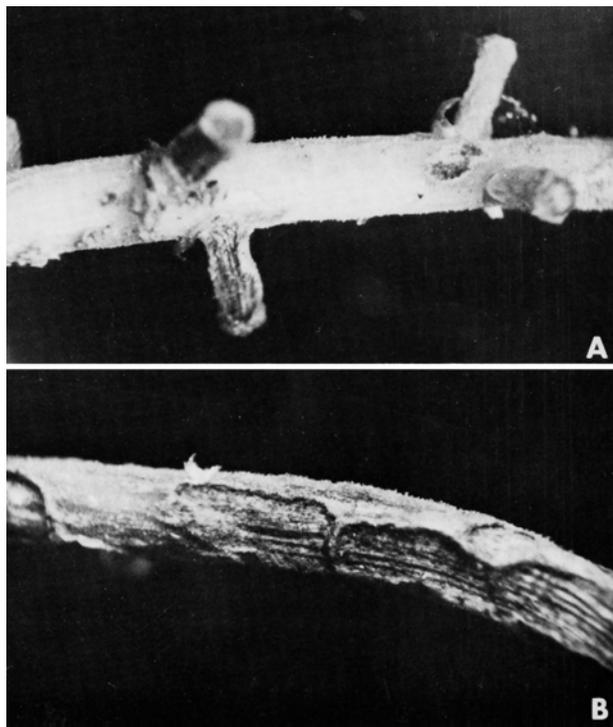


FIGURE 35.—Grazing by caterpillars has produced varying amounts of damage to the inflorescence branches of *Thrinax parviflora*. Vascular bundles are exposed in "B."

although observed in situ, has not yet been isolated and identified.

In the same environment where fungal damage is common on the fruit, the branches of the inflorescence also undergo a dramatic change. Extensive grazing by caterpillars causes considerable damage to the epidermis and outer tissues of the branches (Figure 35). So extensive is the damage in some areas, it is seldom possible to find healthy or unutilized epidermal tissue anywhere on the inflorescence branches. The grazing creates a distinctive pattern of trenches, exposing the fibrovascular bundles, intersected with narrow ridges of ungrazed tissue in Figure 35b. At the lower elevations only occasional damage by larval grazing is encountered on specimens and this is usually of minor importance (Figure 35a). At the higher elevations, however, it is seldom possible to determine the nature of the epidermis (e.g., degree of puberulence), or for that matter even to find ungrazed epidermis at all on fruiting material.

The apex of the petiole in the region of the abaxial hastula and infrequently even the adaxial hastula are often grazed extensively. Often the abaxial hastular region of the youngest leaf on a plant is completely grazed of epidermal tissue exposing a network of fibrovascular bundles.

Breeding System

The breeding system is very difficult to understand completely, primarily as a result of the difficulties of observing anthesis in the field. Individual plants may bear as many as 6 to 10 inflorescences each year and at one time. The most conspicuous feature of an inflorescence at anthesis is the predominance of anthers. Lacking conspicuous and enclosing perianth parts, the anthers are exposed immediately as the primary branches are extended beyond the primary bracts. The anthers in turn obscure the pistil. Each inflorescence may have between 7 and 21 primary branches. These decrease in size and the number of secondary branches successively toward the apex. Those at the apex may have only 6 to 10 secondary branches. The primary branches below the apex may possess from 17 to 47 secondary branches and each of these may have from about 40 to 115 flowers. Therefore it is possible for each plant to produce between 100,000 and 300,000 flowers over a 24-hour period. Consid-

ering also that each flower may possess from 5 to 15 stamens, each of which produces an abundance of light dry pollen, it can easily be seen that the production of pollen by a single plant is phenomenal indeed. The anthers dehisce almost immediately as the sun rises and atmospheric moisture decreases.

Normally all parts of the inflorescence are covered with scattered pollen very shortly after anthesis. When an inflorescence was permitted to reach anthesis overnight in a closed office, all surfaces, books, and objects in the room were visibly coated with pollen within an hour.

The light, dry pollen of *Thrinax* is conceivably carried over very long distances by the wind and has been determined to remain viable for periods up to 3 or 4 months at room temperature (about 26°C). Pollen of *T. parviflora* collected on 12 January 1967 was maintained dry in gelatin capsules that were kept in containers of silica gel with a color indicator at room temperature. Samples of this pollen were sown and germinated on the medium used in the cytological studies at intervals over a 4-month period. Pollen viability was excellent at first (between 70 and 80 percent) on 15 January. It dropped to 41 percent by 9 February, and on 27 February had further dropped to 37 percent. On 1 April viability was only 1 percent. It is conceivable then, considering the great quantity of pollen produced by a single plant at one time, that crossing need not be a rare occurrence.

An attempt was made to test inhibition to selfing. Pollen from two different plants was to be placed on the stigmas of emasculated flowers of one of the plants. A difference in the rate of pollen germination (determined by fixing and staining an hour or so after pollination) favoring the outcrossed flowers would indicate a resistance to selfing. If this were the case, pollen from nearby plants would conceivably be able to germinate and compete with the mass of pollen from the flower's own anthers.

Attempts at emasculation of flowers on fully developed inflorescences in the field proved futile. Within seconds following removal of the enclosing bracts the anthers dehisced and scattered pollen over the pistils. Further attempts were made on inflorescences removed and placed in containers of water in the laboratory. It was possible to remove the unopened anthers by spraying them with water. It was observed, however, that pollination was ef-

fectively prevented by the lateral compression of the stigmatic surfaces. Before pollination could be achieved with certainty the flowers fell without having exposed their stigmatic surfaces.

Other attempts were made using inflorescences still attached to the crown of a plant which was cut at the apex of the caudex and removed to the laboratory. Most of the leaves were removed and the cut portion was placed in a container of water. Several fully developed inflorescences proceeded to reach anthesis during the following night in the laboratory, but again the flowers fell without having exposed their stigmatic surfaces.

Further observations on plants in the field confirmed that the stigmas are tightly compressed at anthesis and follow roughly the following schedule:

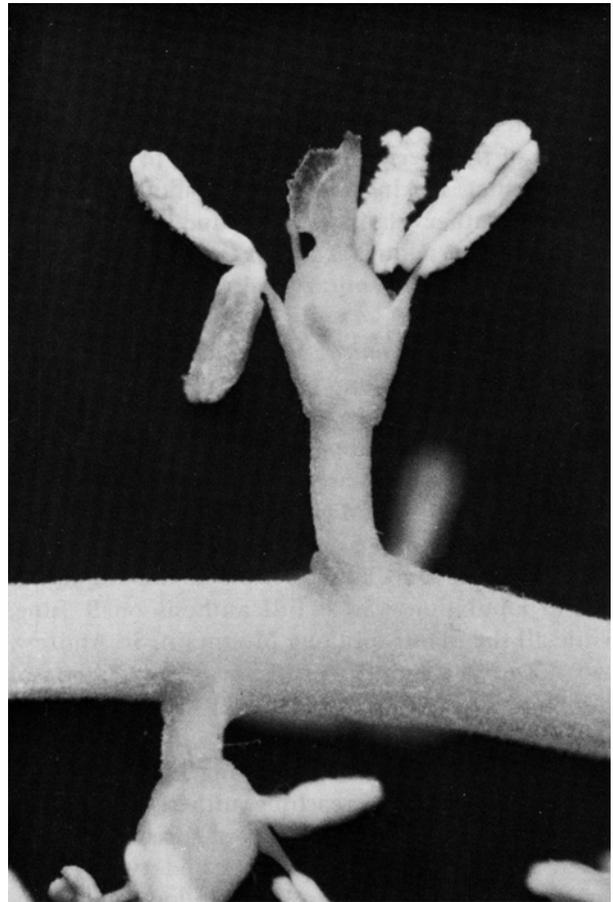


FIGURE 36.—Flower of *Thrinax parviflora*. Photographed with a Contaflex camera, hand held on a binocular-dissecting microscope and using Kodachrome II film exposed for 10 seconds. Note the form of the stigmatic region.

- 21 Sept. 7:30 P.M. A few rachillae and flowers exposed.
 22 Sept. 8:00 A.M. All rachillae and flowers exposed; flowers creamy-white including ovary; anthers dehisced; stigmas tightly compressed.
 22 Sept. 8:00 P.M. Pollen covering all inflorescence parts; stigmas still compressed.
 23 Sept. 9:30 A.M. Ovary yellow, conspicuous; quantities of pollen still present; stigmas open, funnellike.

That this is not always the situation is borne out by pickled material in which the anthers are not fully dehisced while the stigma is fully open and by the photograph (Figure 36) showing a flower at anthesis with its stigma fully open and apparently receptive.

The fact that the stigmatic surfaces are often closed during anthesis, effectively preventing selfing, permits a period during which pollen from surrounding plants can mix either in the air or on the inflorescence before receptivity of the stigma occurs. Thus although the chances for selfing are far greater, outcrossing is not ruled out altogether. Success of the species seems, however, to depend on the fact that, lacking pollen from another population or another plant, seed production is assured in quantity by selfing, as evidenced by the excellent fruit production of solitary individuals in the field or in cultivation.

Flowering in Jamaica: In January 1966, several plants of *T. parviflora* on Mango Tree Hill, in Trelawny, were observed to have inflorescences exposed in bud for about 20 cm. Subsequent and frequent trips to the area found the inflorescence unchanged until 14 May when the same inflorescences were at a stage one or two days past anthesis. At Cockpit and Palmers Cross in Clarendon the entire population was at full anthesis on 9 June, while all the plants on Long Mountain, St. Andrew, had flowered a month earlier on 8 May.

It was observed, in 1966, that most inflorescences of a single plant reached anthesis within a 48-hour period. This is notable considering that the 4 to 6 or more inflorescences reaching anthesis at the same time had developed in the axils of successively produced leaves over a 12-month period two seasons earlier. Apparently each solitary inflorescence produced within each leaf axil remains at a particular stage until several reach the same stage. They then proceed development together and reach anthesis at the same time. Each plant presumably has 3

seasons of inflorescence production at any one time. The 3 or more older leaves subtend 3 or more spent inflorescences; the 3 or more younger leaves subtend inflorescences at or past anthesis, or in fruit; and, apically, 3 or more youngest leaves subtend resting or developing immature inflorescences. Each season a select number reaches anthesis at once, during which time the next season's inflorescences will be reaching a certain stage of equal development.

In Table I the localities, within each subspecies grouping, are arranged in descending elevation from the top toward the bottom. It can be seen that in any one year, widely separated populations flow-

TABLE I.—*Flowering and fruiting dates for Thrinax parviflora arranged by phenotypic expression (localities 27–30 represent subspecies parviflora; 33–29 represent subspecies puberula)*

Locality number	Anthesis	Immature fruit	Mature fruit
27		Feb 1955	
10	Jan 1967 Mar 1967	Mar 1967	Jun 1966
8	Jan 1967		
7	Jan 1967		
5	Jan 1960	Jan 1958	
32		Jan 1956	Apr 1966
31	Jan 1967		May 1966
30	Nov 1964		
33	May 1966 Jul 1967		Nov 1966
2			Nov 1965
14b	May 1966 Jul 1967		
38	Apr 1963	Apr 1955 Mar 1960	Nov 1955
34			Oct 1955
3	May 1966 Jun 1967 Sep 1967		
36	May 1966	Aug 1955	Aug 1955
17			Nov 1965
40	May 1966		
26		Jul 1966	
42	May 1966		Nov 1955
21	Jun 1966		Nov 1965
4	Jun 1966		
22	Jun 1966		
24	Jun 1967	Feb 1967	
29		Aug 1966	

ered several weeks to a month apart. This was especially true in 1966.

A plant removed from a hill near Silver Spring, Hanover, and planted in the palm collection at Mona, produced an inflorescence, and reached anthesis on 26 May, but the pollen was sterile. Additional plants were collected at Charlton, Windsor Cave, and Negril Hill on 4, 5, and 6 June respectively. These were a week or more past anthesis, when collected, providing some overlap in flowering among widely spaced populations. Nearly all populations of the warm, dry, lower elevations reached anthesis between 8 May and 9 June 1966. During the first half of 1966, no plants were found at anthesis or even postanthesis anywhere in the higher elevations. The presence of mature fruit on 29 June at Hollymount Hill suggested that the plants may have bloomed during the winter.

In 1967 several individuals from throughout the higher elevations were collected at or near anthesis between January and March. Flowering and seed production must be very irregular and rarely plentiful among the plants at the higher elevations, for after having collected the few available inflorescences for herbarium specimens and study, no fruiting specimens have since been found among the thousands of plants observed. In January on the Devils Backbone one of the plants with fully developed inflorescences was cut below the crown and removed to the laboratory. At 9:00 P.M. on 12 January not one flower was exposed, but by 8:00 the following morning all primary branches were fully exposed and all flowers were shedding pollen.

Although most of the lowland plants have been observed to flower during the summer months, a single plant of *T. parviflora* near Portland Point was found at postanthesis in February 1967. It is not known if fruit set as a result, because no fruit was found later in the year.

Widespread drought and widely scattered, irregular, late, and below normal rainfall in 1967 no doubt had a strong effect on the flowering of *Thrinax parviflora*, because the pattern of flowering at the lower elevations in 1967 was markedly different from that described for 1966. A trip to Mango Tree Hill in late May, where all plants had finished bloom by the same date in 1966, yielded not a single inflorescence. None were ex-

posed for more than a few centimeters. Two plants on Long Mountain, which flowered in early May in 1966, flowered on 22 and 23 June 1967. Several other plants on Long Mountain had inflorescences exposed, but they did not reach anthesis until late September, several weeks following a period of heavy rain which broke the 8-month drought.

At Cockpit and Palmers Cross, Clarendon, not one inflorescence was observed on 24 June 1967 when nearly every plant in the Portland Ridge area, a few miles to the south, was at full anthesis.

Genetic exchange between distant populations of *T. parviflora* by means of pollen exchange is probably very low. Since nearly all plants in a population shed their pollen during a 48-hour period, and since populations widely removed from one another may flower a week or more apart, it is unlikely that pollen from one population can be carried through wind and rain and still be able to compete a week later with the greater mass of pollen already available on an inflorescence in another population. Except for this unlikely but possible exchange of pollen, genetic exchange between local populations most likely results from the indiscriminate distribution of seed by birds and the resulting plants crossing with their neighbors in the new locality.

Plants of *T. radiata* have been observed in flower or fruit throughout the year. Most of the plants in a given population are usually at the same stage of bloom or fruit, but there seems to be no definite season. *Thrinax excelsa* has been observed in flower from April to September, and fruit has been collected from July through September.

Seed Distribution: Doves and pigeons are common throughout the range of *Thrinax* in Jamaica, and have been reported by the country people as most plentiful when the "thatch" is in fruit. It was said of the hills near Silver Spring, Hanover, that, "Bald Plates" [sic] are seen in flocks feeding on the thatch "peas." At the time of my visit to the area, the palms were not in fruit and no "Bald Plates" were in evidence. There are eleven species of doves or pigeons indigenous to Jamaica and the Baldpate or White Crowned Pigeon is common throughout the distribution range of *T. radiata* in the northern Caribbean. Several of the others are common to Jamaica and neighboring islands but the Baldpate is said to move freely among the islands (Bond, 1961).

Variation of *Thrinax parviflora*

Thrinax parviflora is a highly variable and polymorphic species and occurs over an equally variable and complex system of environments from near sea level to about 914 m (3000 ft) elevation. Considerable effort has been expended in attempting to correlate variability of phenotype with environment. Lacking experimental evidence, however, of any genetic bases for the variation, it is not possible to do more than describe the range of variation in the various environmental zones. Until such a time as plants from the different areas are grown under identical conditions and/or with reciprocal trans-

plants, the true extent of genetic differentiation cannot be known.

The extent of variability can be and has been measured by field studies on plants in 42 localities throughout the entire range of distribution of the species, and in nearly every ecological situation over a 2-year period.

In the two extremes of climatic conditions there are what appear to be two distinct biotypes which, although lacking really significant qualitative differences, look quite different as a result of the combined effect of a number of apparently minor quantitative differences. Two localities, each hav-

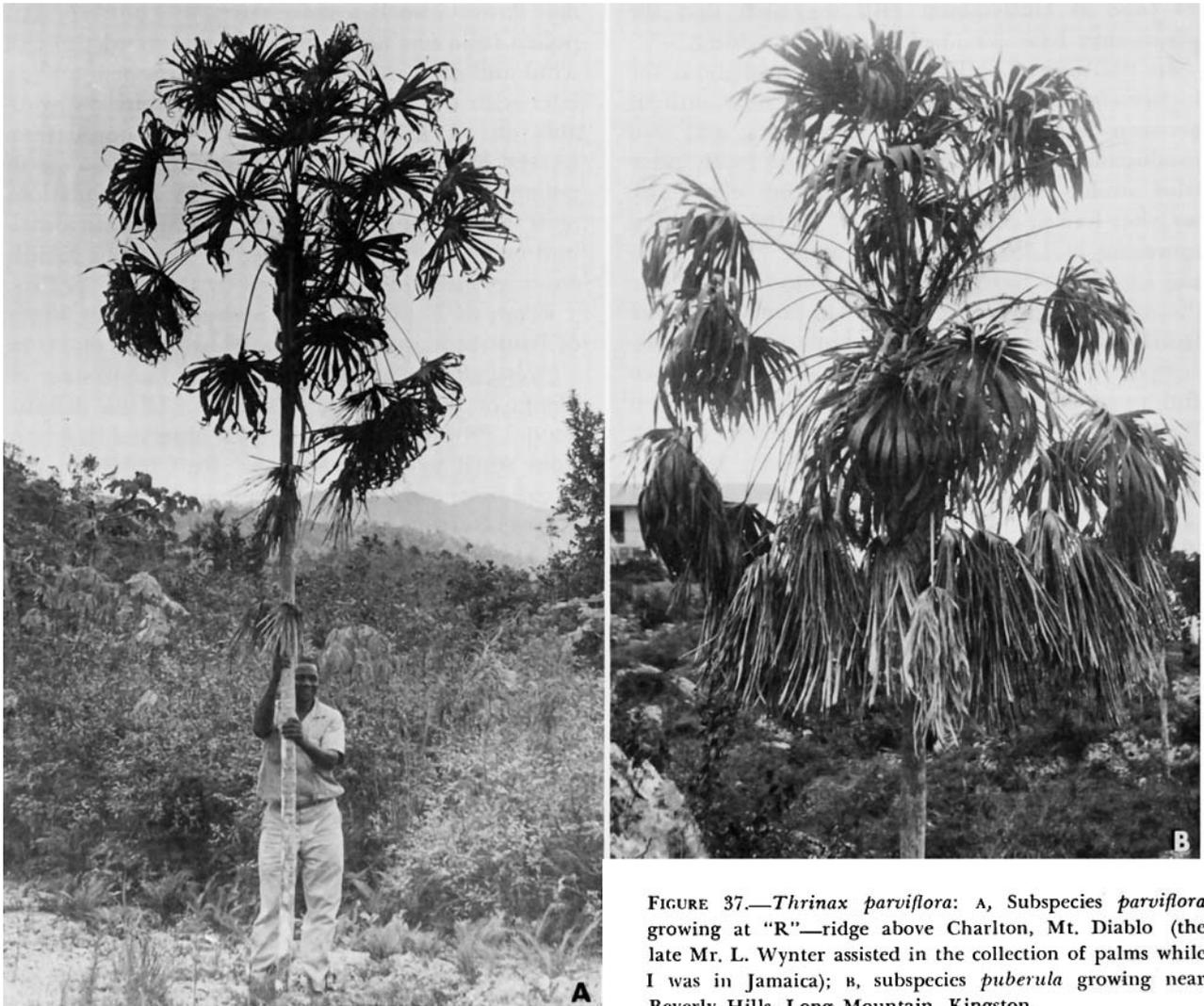


FIGURE 37.—*Thrinax parviflora*: A, Subspecies *parviflora* growing at "R"—ridge above Charlton, Mt. Diablo (the late Mr. L. Wynter assisted in the collection of palms while I was in Jamaica); B, subspecies *puberula* growing near Beverly Hills, Long Mountain, Kingston.

ing a large number of individuals in a nearly uniform environment and representing as nearly as possible (1) the hottest, driest, lowest elevation and (2) the coolest, wettest, highest elevation, were selected for intensive study of the widest range of variation in the species. Each population was selected primarily for its ecological situation and for having an adequate sample of individuals in a relatively accessible area. See the section on Morphology for an explanation of the method of selection of plants and parts for measurement and study.

It will be demonstrated under the section on the typification of *Thrinax parviflora* that the characters of *Thrinax*, at the higher elevations of Mt. Diablo, most closely correspond with characters drawn from the type specimen and original diagnosis of the species. These plants, typified by a large sample taken at collection locality #10 on Hollymount Hill at 792.4 m (2600 ft) elevation, represent one extreme in the overall variation of the species. Figure 37A illustrates the typical "pin-wheel" form of the leaf and the open crown on tall slender trunks. In addition the very short, blunt or acutely pointed hastula and the relative absence of an abaxial hastula, glabrous to glabrate (Figure 40c,d,e) inflorescence branches, generally short pedicellate flowers or fruits, and short anthers are char-

acteristic of the plants in this locality. Inflorescences are shorter than the petioles, erect except in fruit, and the lowermost branches of the lower primary branches are occasionally branched more than once. Flowering is very irregular but occurs between December and March.

Also characteristic of all plants at the higher elevations are certain biotic changes of the inflorescence and fruit (described under Phytomorphosis and Zoomorphosis in *Thrinax parviflora*). These changes have led to considerable confusion and misinterpretation. In fact one specific epithet, now in synonymy, is descriptive of the change in the character of the fruit, and the plants to which it applied have been suggested as having some significance in evolutionary theory. In a discussion of the durian theory in relation to palms, Corner (1966:180) wrote: "Perhaps in this durian complex, there should be added *Thrinax tessellatus* [sic] of Jamaica, the fruits of which appear to have small flattened warts as in *Pholidocarpus*."

In contrast with the Hollymount Hill "biotype" the plants of the lower elevations, below 365.76 m (1200 ft) from the base of Mt. Diablo south to Portland Ridge, and typified by collection locality #22 at Cockpit, Clarendon, have quite a different aspect somewhat resembling the plant in Figure 37B. The heavy crown, with relatively broad leaves

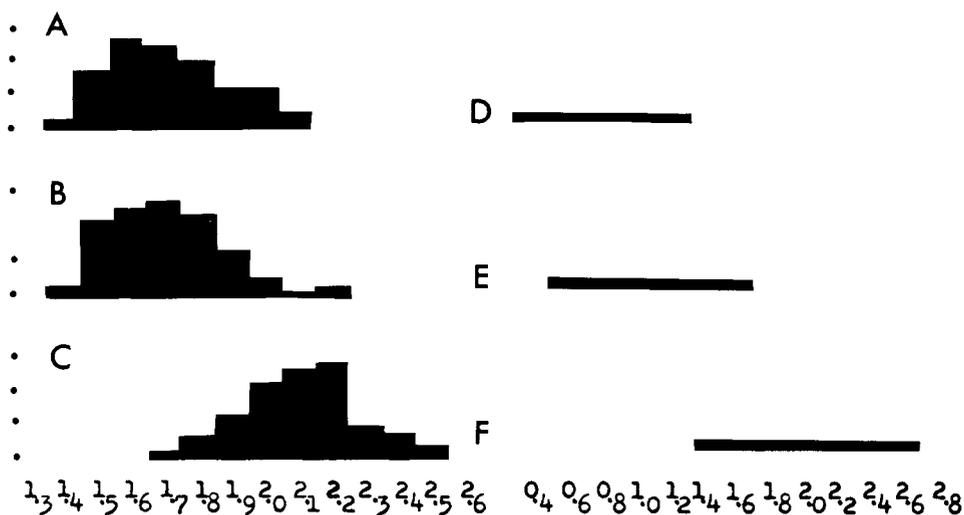


FIGURE 38.—A-C, Frequency distribution of anther lengths; D-F, range of pedicel lengths. A, D are *Thrinax parviflora* from Devils Backbone; B, E are from the Swartz type specimen; and C, F are from *T. radiata* Morant Point, Jamaica. (Histograms are based on 100 measurements; bar graphs are based on 25 measurements. Measurements in mm.)

and slightly drooping segments, supported on a short trunk is typical. The adaxial hastula is prominent, long pointed, and often tubular when the leaf is fully expanded. The abaxial hastula is also conspicuous, frequently forming a triangular projection up to 1.6 cm long. The arching inflorescences equal or exceed the petiole in length, and all branching parts including the elongate pedicels are densely puberulous (Figure 40A,B).

The length of the pedicels, in flower or fruit, and the length of the anthers have frequently been used as key characters for distinguishing between taxa. These characteristics have been given some emphasis in this study to test their usefulness and to emphasize the danger inherent in the use of small samples such as are available on herbarium specimens of palms. It can readily be seen in the histograms in Figures 19, 38 that pedicel length is certainly not a good character.

Figure 38A,C illustrates the variability of anther length in *Thrinax parviflora* and *T. radiata*. If only two localities are considered, the character might appear useful; however, plants with very short or very long anthers occur in the same population. This situation occurs in nearly all the characters tested. Given only two extreme localities, which were the basis of Beccari's work, because they represent classical collecting areas, two quite distinct taxa are the result. Additional collections however, from many localities over the entire range of the species throughout the island fill in the gaps and blend the overlapping measurements, resulting in a kind of clinal variation of nearly all characters. Accumulation of mutations expressed as certain of the extreme variations, with subsequent introgression, might be achieved as a result of the fact that the highland biotype flowers from November to March, while the lowland plants flowered from April through September.

Throughout the range of *T. parviflora*, definite trends in leaf form and trunk size exist which appear to follow certain gradual changes in climatic conditions. The most significant variations in the physical environment that appear to influence the phenotype are changes of moisture availability in the areas of different rainfall and of temperature with differences in elevation. Consistent east-west trends may also be due to combinations of these factors. Several features such as branching and puberulence of the inflorescence rachillae and hastula form,

although different at the two principal environmental zones, seem to vary little throughout the range of the species and appear to be characteristic of particular ecotypes.

Caudex: The caudex diameter and height of mature individuals are extremely variable even within a small local population, but the largest mean diameters and shortest trunks occur in the hot, dry, exposed areas of St. Andrew, St. Catherine, and Clarendon. Plants with trunks having smaller mean diameters are found in regions of greater rainfall toward the west and in the cool moist gorges (i.e., Cane River, Rio Cobre), or at the median elevations of the hills or Cockpit Country. The very tall plants of smallest trunk diameters are found only at the cool, moist, high elevations or in exceptional areas of unusual climatic



FIGURE 39.—Polymorphic leaves of *Thrinax parviflora*: G. R. Proctor, of the Institute of Jamaica, holds a leaf from a juvenile plant in his right hand, and a leaf from a flowering size plant in his left hand; near Ramgoat Cave, in the Cockpit country of Jamaica.

conditions such as that described under Donkey Trail and "R"-ridge.

Leaf Polymorphism: Among the plants of *Thrinax parviflora* growing at the higher elevations, there is a striking change in leaf morphology from seedling to maturity and eventual exposure of the crown at the canopy. The seedling stages up to the formation of the trunk are typical for the genus. The change in leaf form, however, subsequent to the first appearance of a trunk is possibly unique among fan-leaved palms (Figure 39).

The leaves produced at the time of trunk formation are circular in outline and rather flat or slightly funnel shaped with the free part of the segments rigid. As the trunk elongates the leaves attain their greatest diameter, have a broad palman, and the segments arch slightly. With increased age of the plant the palman is slightly smaller and the longer segments tend to droop. When the plant reaches maturity the leaves appear to be much smaller as a result of the much reduced palman and the fact that the drooping segments begin to curl.

Fully mature plants in the full dense shade below the canopy may have leaves with a fairly broad flat palman and drooping curled segments such as are illustrated in Figure 37B; however, when the plants are exposed either on a cliff face or above the canopy they assume a strikingly different form. The basal portion of the blade folds up and forward, the palman is very small and uneven, and the segments are twisted and tightly coiled (Figures 8, 39). At this latter stage the blade often appears as a "pinwheel" on an excessively long slender petiole. The petiole in fact is shorter on older plants, but the much contorted blade creates an illusion of a longer petiole.

Variability of the Leaf Elsewhere: The form of the leaf blade throughout the range of the species is the most highly variable characteristic of the entire complex of variation, reflecting in effect different phases of the polymorphism exhibited during the development of plants at the highest elevations. The change in shape or form is in fact simply the result of quantitative changes in the component parts of the leaf. The form of the leaf, which must not be confused with outline, is three dimensional resulting from varying degrees of folding, twisting, and curling of the palman and segments. The overall trend appears to be a decrease

in size of parts with maturity, aging, increased height and exposure and with change from hot and dry to wet and cooler climates.

The change in leaf form during maturation of individuals, throughout the greater portion of the population, is simply the production of larger leaves accompanied by increases in the number, width, and length of segments, and the breadth of the palman. Mature plants, not yet having reached the canopy, produce larger, more heavily textured leaves, juvenile types showing a tendency for the lower portion of the blade to be folded upward.

In the hot dry plains of Clarendon near Palmers Cross the mature leaf blade (Figure 7) has a broad uneven palman and wide very leathery segments. Elsewhere in the dry evergreen thicket formations of St. Andrew, St. Catherine, and Clarendon, the leaf blade is not quite so leathery, the broad palman is relatively flatter but with the basal part of the blade folded up and forward (Figure 37B), and the segments arching or drooping. The leaves of plants exposed at the canopy or in a clearing exhibit a narrower palman and increasingly lax segments. Tall, very old plants have leaves in which the changes just described are even more strongly expressed. In certain areas of lower temperatures and/or higher moisture availability (i.e., Cane River Gorge, Rio Cobre Gorge, Fern Gully, and westward from Clarendon) mature plants have leaves with proportionally smaller palman and narrower segments which twist or curl slightly (Figure 37A).

In regions of higher rainfall in the west and northwest of the island such as at Negril Hill, Silver Spring, Lances Bay, Dolphin Head, and Windsor Cave, the species exhibits a markedly reduced leaf with a narrow uneven palman, and narrow twisted segments. This form of leaf blade is expressed to different degrees depending on maturity or exposure but appears almost intermediate between the two extremes discussed earlier. During the early part of the study, plants having the latter leaf form were classified along with plants of the highest elevations until it was realized that the dense puberulence on the inflorescence branches placed the plants more consistently among those of the lower elevations. In Cockpit Country, plants of median elevations (but on exposed drier locations) resemble the lowland forms most closely.

In regions of still greater moisture availability and cooler temperatures, as on the upper levels of

Dolphin Head, Somerset, Top Hill, Albion Mountain, and Mt. Diablo, the leaf blade of mature plants is smaller and more tightly curled and twisted in proportion to increased elevation and exposure at the canopy. The greatest extreme in reduction in size of leaf parts accompanied by a great amount of folding, twisting, and curling occurs on the highest levels of Mt. Diablo where the plants (Figure 8) exhibiting these characteristics are very tall and exposed above the canopy.

Hastula: Although quite variable throughout the range of the species, at the higher elevations the hastula is generally short and blunt adaxially and lacking or vestigial on the abaxial surface. This is one of the few characters of which measurements do not appreciably overlap.

With the exception of the plants at the highest elevations, the adaxial hastula is quite prominent, long pointed, and frequently tubular. The abaxial hastula is also conspicuous whether as a flap of tissue projecting from the apex of the petiole or as a well-defined triangular extension with a retuse apex. In the sample studied at Cockpit in Clarendon, a specimen was collected in which the abaxial hastula was developed into two slender processes projected up along the undersurface of the blade for 20 to 30 cm (Figure 13c,d). Although not noticed at the time the specimens were collected, two leaves taken from the same plant exhibited the same anomalous condition, suggesting perhaps that all leaves produced by the plant possessed similar processes.

Inflorescence: The usually arching inflorescence equals or exceeds the petioles among the plants of lower elevations but varies considerably in length and aspect at the higher elevations where it may be erect and much shorter than the petiole.

Of particular interest is the occurrence of primary branches which are twice branched, a unique condition so far as is known among members of the *Thrinax* alliance. As a rule the individual primary branches are once branched. At the lower elevations the ultimate branches are commonly forked but never as elaborately branched as those at the highest elevations. Several specimens have been collected on Mt. Diablo in which the lowermost primary branches are twice branched producing a secondary condition resembling the primary branch from which it originates. These highly branched secondary branches, however, are subtended by the same

triangular nonsheathing bracteoles as are the simple unbranched ultimate branches.

Pedicels: One of the key characters used to distinguish between the "species" of the *Thrinax parviflora* complex, and among species of other genera as well, is the length of the floral and fruit pedicels. As was mentioned earlier the importance given to the length of the pedicels by the various workers in the genus has necessitated particular attention to testing its reliability. The results presented in graph form in Figures 17 and 19 illustrate the uselessness of the character in Jamaica and emphasize the need for adequate samples from throughout the entire range of the species complex. It also points out the danger of basing taxonomic conclusions on too few characters and in certain cases upon the wholly inadequate presently available herbarium specimens.

Samples from 144 plants in 32 different localities totaling some 12,000 measurements are tabulated in Figures 17 and 19. It can be seen readily that any attempt to correlate pedicel length with a particular phenotype or locality is futile. The frequency histograms (Figure 19), representing only three localities, alone show so much overlap at the higher frequencies that one can conclude the shortest pedicels do occur at Hollymount Hill and the longest occur at Cockpit, but these extreme areas share the identical lengths with such great frequency as to be of hardly any taxonomic significance. When all 32 localities are considered together as in Figure 17 the ranges and means of variation overlap considerably. They show a general tendency to increase gradually from high to low elevations.

Puberulence: The entire population of *Thrinax parviflora* is divided into two fairly distinct expressions of puberulence on inflorescence branches. This character, never having been mentioned in any study of the genus, provides the only fairly consistent means, apart from the hastula, for separating the species into two biotypes. Throughout the range of distribution of the species, with the exceptions to be mentioned below, all parts of the inflorescence branches are densely puberulous. This, as far as can be ascertained, is another unique character in the *Thrinax* alliance; certainly no other members of the genus have been reported to have puberulent rachillae. Although the presence of puberulence can sometimes be determined by the naked eye, it is usually necessary to use a lens of

at least $\times 8$. The degree of puberulence does not vary much at the lower elevations (Figure 40A,B).

On the upper peaks and ridges where cool mists and clouds prevail (e.g., Hollymount Hill, Union Hill, Grier Mount, Devils Backbone, Dolphin Head, Somerset, Stirling Castle, Ramgoat Cave, etc.), there is a striking change in the puberulence. The plants here produce inflorescences with appar-

ently glabrous (Figure 40E) or glabrate (Figure 40D) branches. Frequently the puberulence is limited to widely scattered hairs in lines or patches usually on the rachis or peduncle. It is doubtful that any plants produce inflorescences which have truly glabrous branches, but it is difficult to see the hairs at anthesis and pollen grains can easily be mistaken for puberulence. Occasionally inflores-

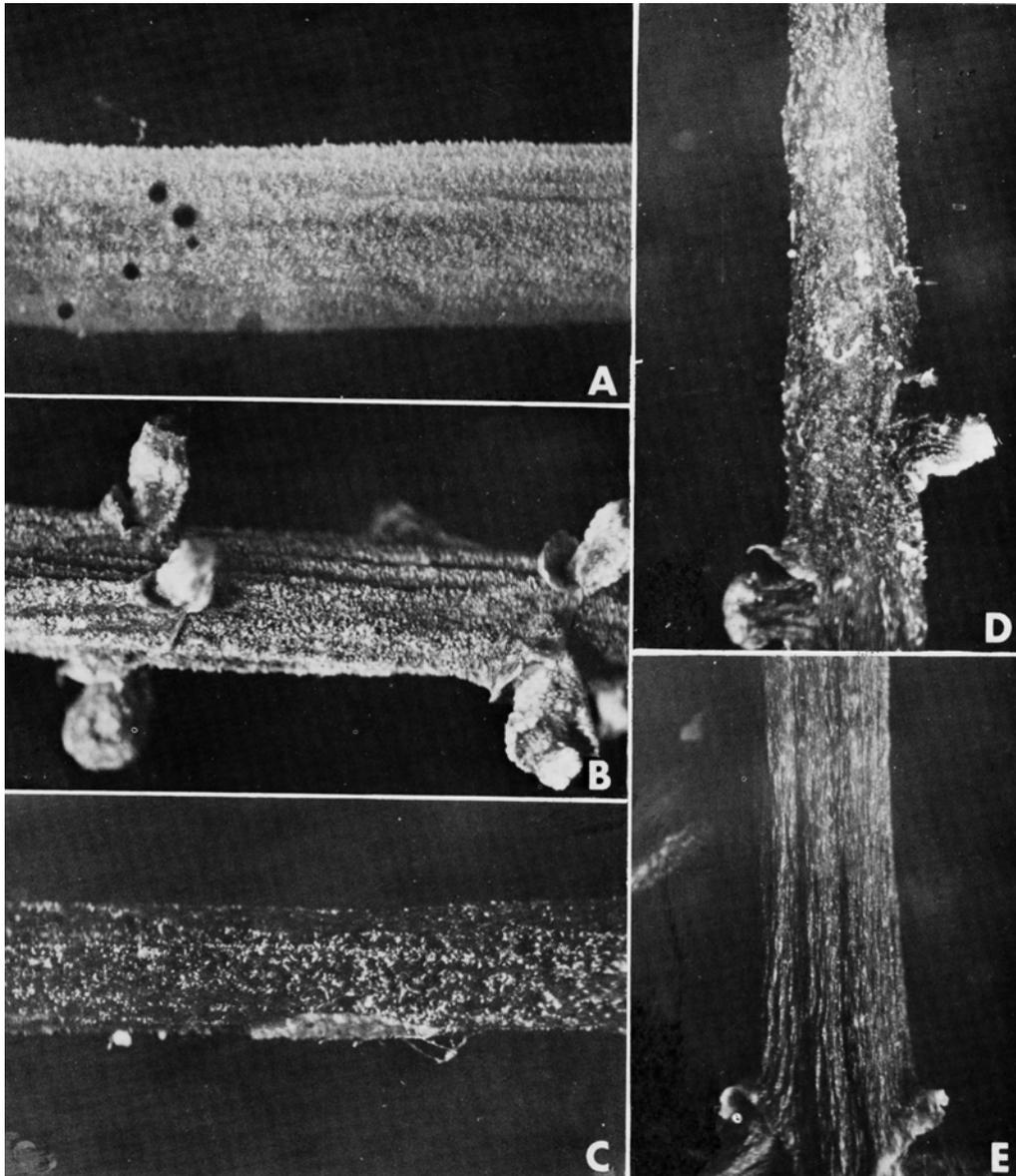


FIGURE 40.—Different degrees of puberulence exhibited by inflorescences of *Thrinax parviflora*, ultimate branches: A, Cockpit, Clarendon; B, Spring Garden, St. Catherine; C, Devils Backbone; D, E, Hollymount Hill.

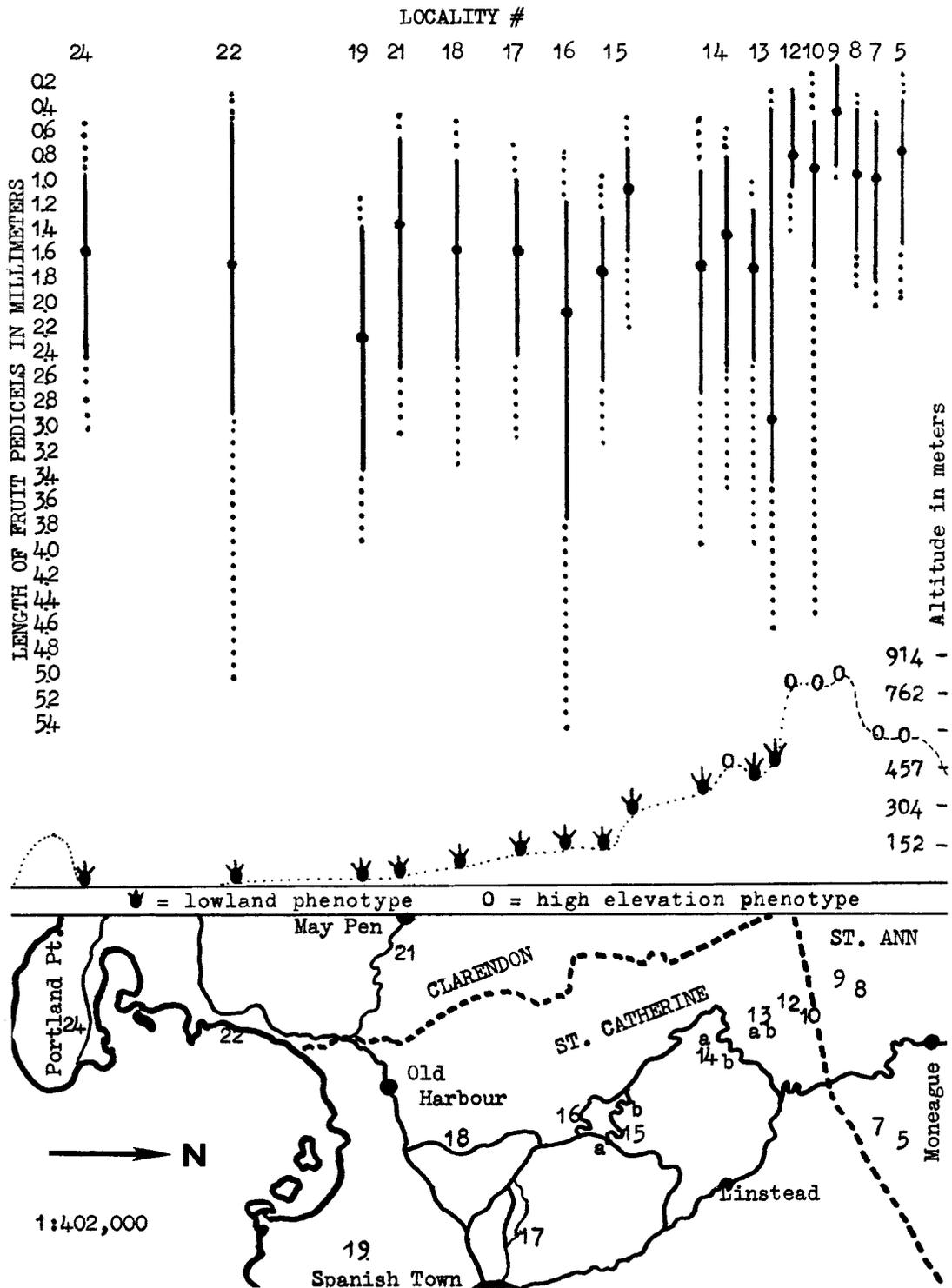


FIGURE 41.—Transect across central Jamaica, showing pedicel length and phenotype, from lowest to highest elevations where *Thrinax parviflora* occurs. The large dot in the bar graphs represents the mean length of the pedicels, the solid line represents 90% of all measurements, and the broken line indicates 5% of the total taken off each end of the range.

cences of plants in exposed localities produce branches with considerable puberulence (Figure 40c). Insect grazing on the branches of plants at the higher elevations often entirely denudes the epidermis preventing accurate determination.

In certain localities such as at Dolphin Head and Windsor Cave phenotypically similar plants growing in the same general area may produce inflorescences with dense puberulence or almost glabrous branches. Transplant experiments would be most helpful to test the effect of climate on the degree of puberulence.

Transplant Experiment: An attempt was made to transplant mature individuals from the highest elevations into a garden at the University of the West Indies Botany Department to be grown with individuals removed from low elevations. The elevation at Mona is approximately 600 feet, and the area frequently suffers from prolonged dry periods. The primary purpose was to obtain flowering material for cytological studies dependent on the production of inflorescences within the year or two following transplanting. Only one plant produced inflorescences and this was very soon after having been transplanted. The flowers produced nonviable pollen.

Another possible and valuable result of the experiment would have been the observation of the degree of puberulousness on the inflorescence branches of plants removed from the high elevations. It was strongly suspected that there would be an increase in puberulousness if the high-elevation plants formed inflorescences in the hot dry climate of Mona. Leaf form and pedicel lengths produced at Mona would also have provided valuable information about possible genetical differences between the two apparent biotypes. This experiment has been terminated as a result of an abnormally long drought and a severe water shortage from January to September of 1967. Most of the plants remained green and in fact produced new leaves during the growing season of 1966; however, watering was stopped in the spring of 1967, and during two weeks of particularly hot drying winds, without rain or water, nearly all leaves rapidly turned brown and the trunks began to wrinkle from shrinkage. All plants have since died due to the continued drought and lack of water.

Seeds from many remote areas have been germinated and the resulting plants will be trans-

planted in a test garden. The comparative results of seedling transplants will take many years because of the extremely slow growth rate characteristic of palms in this genus. Seedling palms grown in containers will become established more easily if root damage is minimized and water is available. It is the earnest desire of the author to bring together in one test garden seedlings of all taxa in the genus for comparative studies at some future date.

TRANSECT FROM PORTLAND RIDGE TO HOLLYMOUNT, JAMAICA.—A line drawn from Portland Ridge, in the south, to the northern slopes of Mt. Diablo (Figure 41) passes through regions of low to high elevations from sea level to about 914 m (3000 ft), and from hot, dry nearly xerophytic conditions to cool, moist mesophytic woodlands and high pinnacles frequently bathed with mist. The rainfall varies from less than 126 cm (50 inches) per year at Portland Ridge to more than 178 cm (70 inches) per year on the heights of Mt. Diablo. Along the line, changes in temperature and moisture availability are mostly gradual up to the middle elevations on Mt. Diablo where, as a result of the combined effect of exposure, elevation, and the very steep escarpment, the changes are more abrupt. At the elevation where cloud formation most frequently occurs, noticeable differences in the climate and flora are evident over a very short distance. *Thrinax parviflora* grows on practically every natural outcrop of limestone along the transect line.

During the present study numerous collections were made in nearly every accessible area along an irregular line from south to north, and on Mt. Diablo, in an attempt to obtain adequate material over a range of variable ecology. The collections were also part of an investigation to determine the distinctions for maintaining two taxa in the region, one in the lower elevations (*T. parviflora*) and one at the highest elevations (*T. tessellata*). The principal means of distinguishing between these two species had been the supposed absence of pedicels and the appearance of the fruit in the latter. The tessellated appearance of the fruit at the higher elevations, resulting from fungal infection described earlier, and the length of the fruit pedicels are poor characters which were based on wholly inadequate material.

The transect runs through two of the three intensive study areas. Samples of inflorescences were taken from every available plant at both Cockpit

and Hollymount Hill. In addition pedicel measurements were taken from every collection locality along the route of the transect. These measurements are all compared in Figure 41, and it is obvious (as has already been shown) from the results that the length of the pedicels cannot be used for separating taxa. Although the high-elevation plants have a predominance of short pedicels, those of lower elevations exhibit an abundance of pedicels in the same length ranges, and there is considerable overlap at the 90 percent level.

Only two apparently reliable characters can be used to characterize the high- and low-elevation phenotypes along the transect: the hastula and the degree of puberulence on the primary branches of the inflorescence. The designation in Figure 41 for lowland phenotype represents plants with long, pointed hastulas and densely puberulous primary branches, accompanied usually by large leaves and relatively short and stout caudices. The designation for high-elevation phenotype represents plants with short, acute or blunt hastulas and glabrate (Figure 40E) to lightly puberulent (Figure 40C,D) primary branches.

Additional measurements are included in Figure 18 comparing variability at the three intensive study areas. Bar graphs giving the range of variation and means for the various organs of plants along the transect route may be found in Read (1968).

Blue Mountain Trail: Along the southern face of Mt. Diablo an exceedingly steep escarpment rises nearly 609 m (2000 ft) above the valley. Along most of the escarpment, which faces south, climatic conditions up to about 502.92 m (1650 ft) elevation are very similar to those at lower elevations. Full exposure to the sun, particularly in the winter months, perfect drainage, and average rainfall permit a dry evergreen, thicket-type vegetation in which the palms are almost indistinguishable from plants growing near sea level on Portland Ridge. At approximately 609 m elevation the vegetation changes to open woodland in protected valleys and gorges, and tall, slender plants of the typical high-elevation palm dominate the exposed ridges and rocky pinnacles. There does not appear to be a transition zone for the palms along the trail, because suitable rocky outcrop was not encountered between 502.92 and 762 m elevation. It is important to note that the point between 518.16 and 609 m

(1700 and 2000 ft) elevation is the altitude at which clouds generally form and obscure the peaks and ridges, commonly throughout the year, but more frequently in the late summer and winter months. The clouds and mists common above 609 m elevation on Mt. Diablo result partly from and contribute to the higher moisture availability and cooler temperatures reflected in a different flora.

The greatest extremes in phenotypic expression are coincidentally found growing on the south-facing escarpment of Mt. Diablo above an area known as Charlton. At locality #13, between 457.20 and 502.92 m (1500 and 1650 ft) elevation, several palms exhibit among themselves the largest trunk and leaf dimensions, and although two of the plants in the group had pedicel lengths averaging within the normal range of means for lowland forms, the third plant exhibited exceptionally long pedicels which caused the mean for the group to be among the longest pedicel lengths (Figures 17, 41) of any population on the island.

Near the upper limit of the escarpment, overlooking the group of exceptional plants just mentioned, typical high-elevation plants occur between 609 and 807.72 m (2000 and 2650 ft), in the cloud zone. The very tall, slender-stemmed palms with very small tightly folded and curled leaf blades grow among somewhat dwarfed thicket wherein occur numerous epiphytes, ferns, and herbaceous plants.

"R"-ridge: A short distance to the west of the Blue Mountain trail, a spur extends southward from Mt. Diablo and descends to 457.2 m (1500 ft) elevation at a pass over which the Ewarton-Worthy Park road crosses. Apparently the spur and ridge provide a barrier to moisture-laden prevailing winds from the east, for the appearance of the vegetation seems to indicate a rapid increase in moisture availability as one ascends a short distance along the road to the pass. At approximately 365.76 m (1200 ft) the road passes from an area of exceedingly dry, nearly xerophytic rocky outcrop to an area of mesophytic woodland on an east-facing slope. *Thrinax parviflora* exhibiting the lowland phenotype are common on the slope. A short distance uphill, but beyond a bend in the road, the vegetation changes to dense woodland where tall, slender palms of the high-elevation phenotype are found. Patches of mesophytic woodland alternate with xerophytic scrub between 396.24 and 457.20 m

(1300 and 1500 ft) elevation along the road, and it is possible to observe both phenotypic expressions of *T. parviflora* growing a short distance apart but still apparently in different habitats. Near the pass at 457.2 m (1500 ft) the vegetation mostly resembles moist woodland, which is usually limited to much higher elevations on Mt. Diablo. The whole of the ridge area is one of strong ecological contrasts.

On a small limestone and marl ridge, at the highest elevation along the road, there is a strange mixture of both high mountain and lowland species of plants other than palms (e.g., *Sloanea jamaicensis* and *Bursera simaruba*) growing side by side. Here too was found the unique situation where both phenotypes of *T. parviflora* are growing very near one another. Retaining their peculiar individuality, the two phenotypes are distinguished by the tightly congested leaf blade with twisted segments and more slender trunk of the high-elevation form (Figure 42B,C) as compared with the larger, flat or simply folded leaf blade with straight or drooping segments and much heavier trunk of the lowland

form (Figure 42A). In attempting to verify these apparent differences it was found that the old inflorescences, taken from plants exhibiting the characteristics of the high-elevation phenotype, were so completely damaged by insect grazing that they were useless for comparison with the densely puberulous inflorescences taken (collected in young fruit in July) from plants exhibiting characteristics of the lowland phenotype. The occurrence of two different phenotypes (differing it must be stressed only in quantitative characters which overlap considerably with plants elsewhere on the island) in the same population, while proving nothing and raising numerous unanswerable questions, certainly suggests the existence of two genotypes, at least in that particular locality.

Among a group of tall, slender plants growing on a steep slope in a depression behind the ridge, where even the lowland form attains considerable height (up to 9 or 10 m), two plants were observed which might represent intermediates between what may now be considered two genetic biotypes. Both



FIGURE 42.—Phenotypes of *Thrinax parviflora* found growing within a short distance of one another on "R"-ridge, at about 457 m elevation, along the Ewarton-Worthy Park road. The two plants at the left are typical of the two extreme forms; the plant on the far right could possibly be a hybrid between the two biotypes.

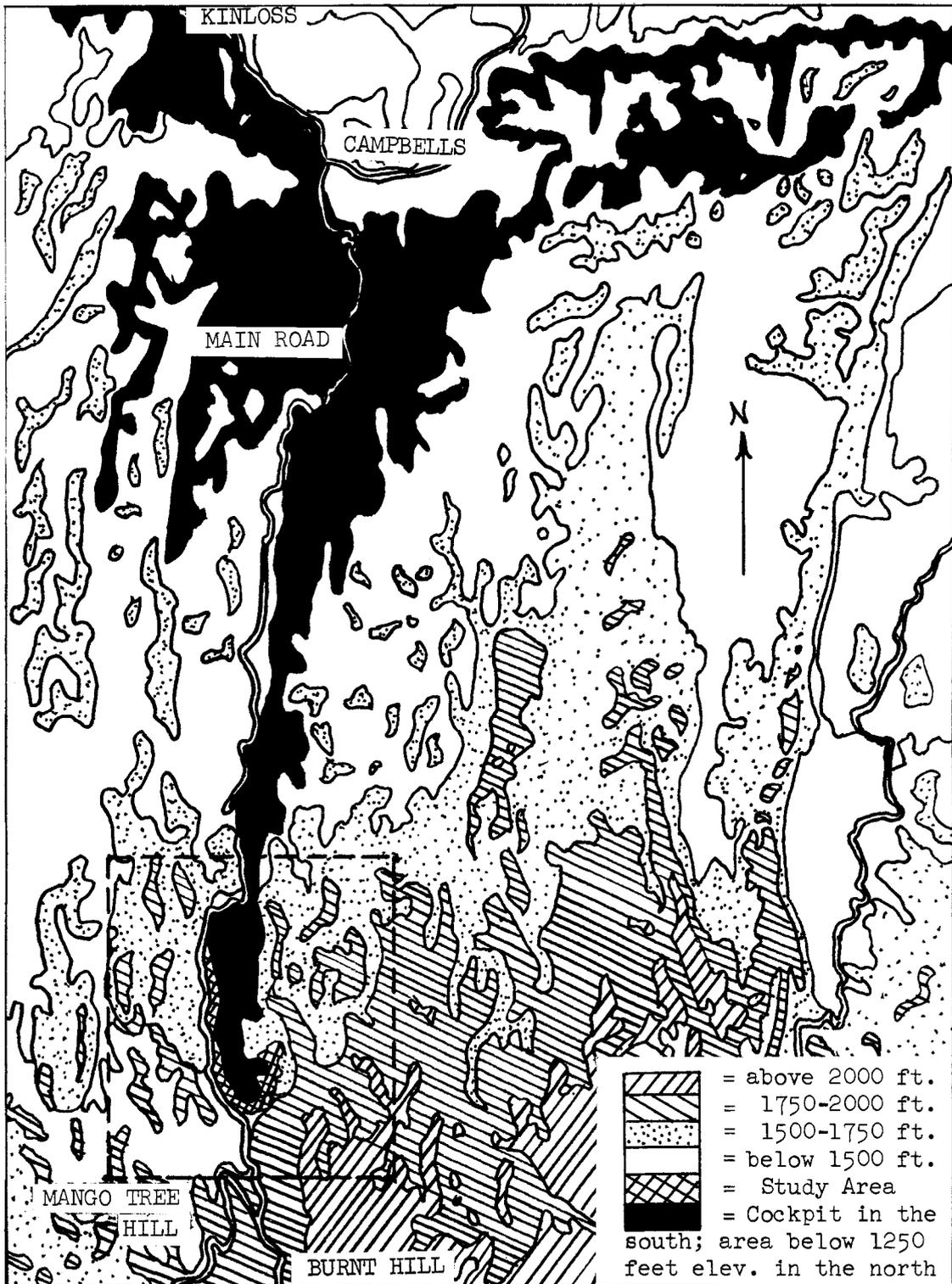


FIGURE 43.—Region of the Cockpit country showing extent of deep continuous box canyon running from Barbecue Bottom to Burnt Hill. Adapted from the topographic maps of the Directorate of Colonial Surveys, D.C.S. 1st edition 1954. Jamaica 1/50,000. Further explanation will be found in the text.

of the intermediates exhibited flatter leaf blades, intermediate in size, with rigid segments (Figure 41D), and the trunks were intermediate between plants exhibiting the clearly recognizable phenotypes of high or low elevations. It should be mentioned that apart from the area just described it is almost impossible to be certain about the position of certain plants growing in exposed situations at middle altitudes without resort to examination of the puberulence on the inflorescence branches. In the population described above both forms appear most robust and the differences between them appear somewhat exaggerated.

The area here in question was not found until very late in the study and, although of great significance, it is regretted that time and circumstances did not permit additional field work. It remains an exceedingly interesting area for future concentrated study when plants of both forms can be compared by study of inflorescences at anthesis and in fruit.

DONKEY TRAIL TRANSECT.—In the northeastern corner of the “Cockpit Country” in Jamaica, a series of large interconnected cockpits extends four miles southward along the road from Kinloss to within half a mile of Burnt Hill intersection. The cockpits (indicated by solid shading in Figure 43), including the one at Barbecue Bottom, vary from nearly a mile wide in the vicinity of Campbells, to only 100 or 200 m wide at the southern end. The formation resembles a “box canyon” with walls 100 to 200 m high throughout its length and opens to the north where it is exposed to the prevailing northeasterly winds. Figure 43 illustrates the major topographic features of the region.

In mountainous regions, increase in elevation is normally accompanied by a gradual decrease in temperature, and cloud formation is usually restricted to the higher peaks and ridges. An anomalous situation occurs in these cockpits where the usual climatic conditions are inverted. High ridges surrounding the southernmost cockpit (Figure 44), although rising above 548.64 m (1800 ft), support an open, dry evergreen thicket which resembles that on the lower slopes of Mt. Diablo. Likewise, plants of *Thrinax parviflora* growing on the ridge very closely resemble those of much lower elevations elsewhere. As one descends into the cockpit the air temperature decreases noticeably in a very short distance and the vegetation changes from dry evergreen woodland on the upper slopes to wet

forest on the lower slopes and in the bottom *Thrinax parviflora* growing inside the cockpit (Figure 44B) exhibits the phenotype usually associated with the highest and wettest elevations of Mt. Diablo.

Because extremely different phenotypes were found growing a short distance from one another, a transect study was made in order to compile additional information in support of ecoclimatic variation in *Thrinax parviflora*. During a 48-hour period from 25 to 27 May 1967, a climatological and morphological study was made along a transect projected through a population of *T. parviflora* on the south side of the cockpit at “B” in Figure 44.

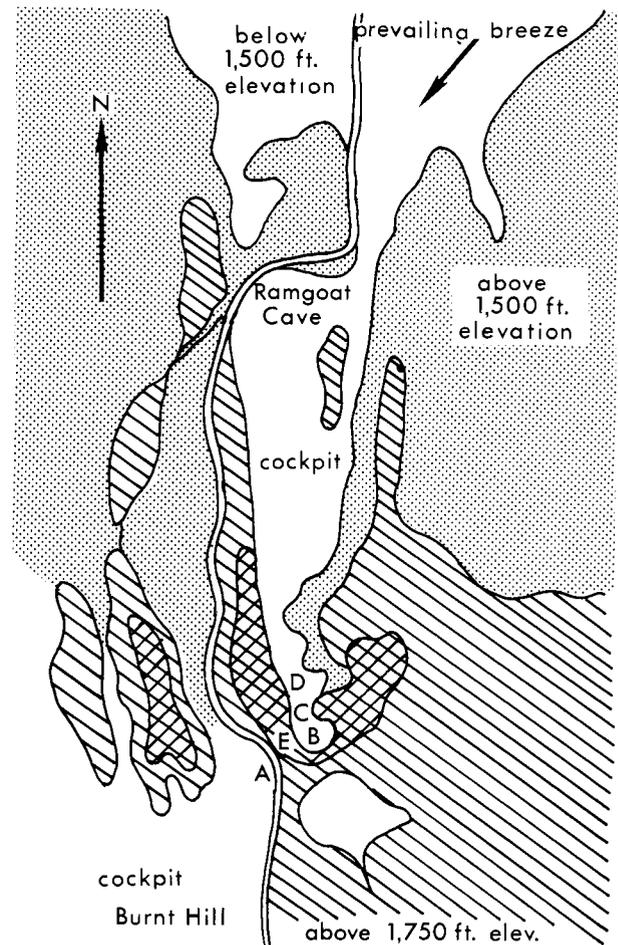


FIGURE 44.—Donkey Trail special area, enlarged from section indicated in Figure 43: A, start of the donkey trail; B, C, points at which climatological readings were made. Further explanation in the text.

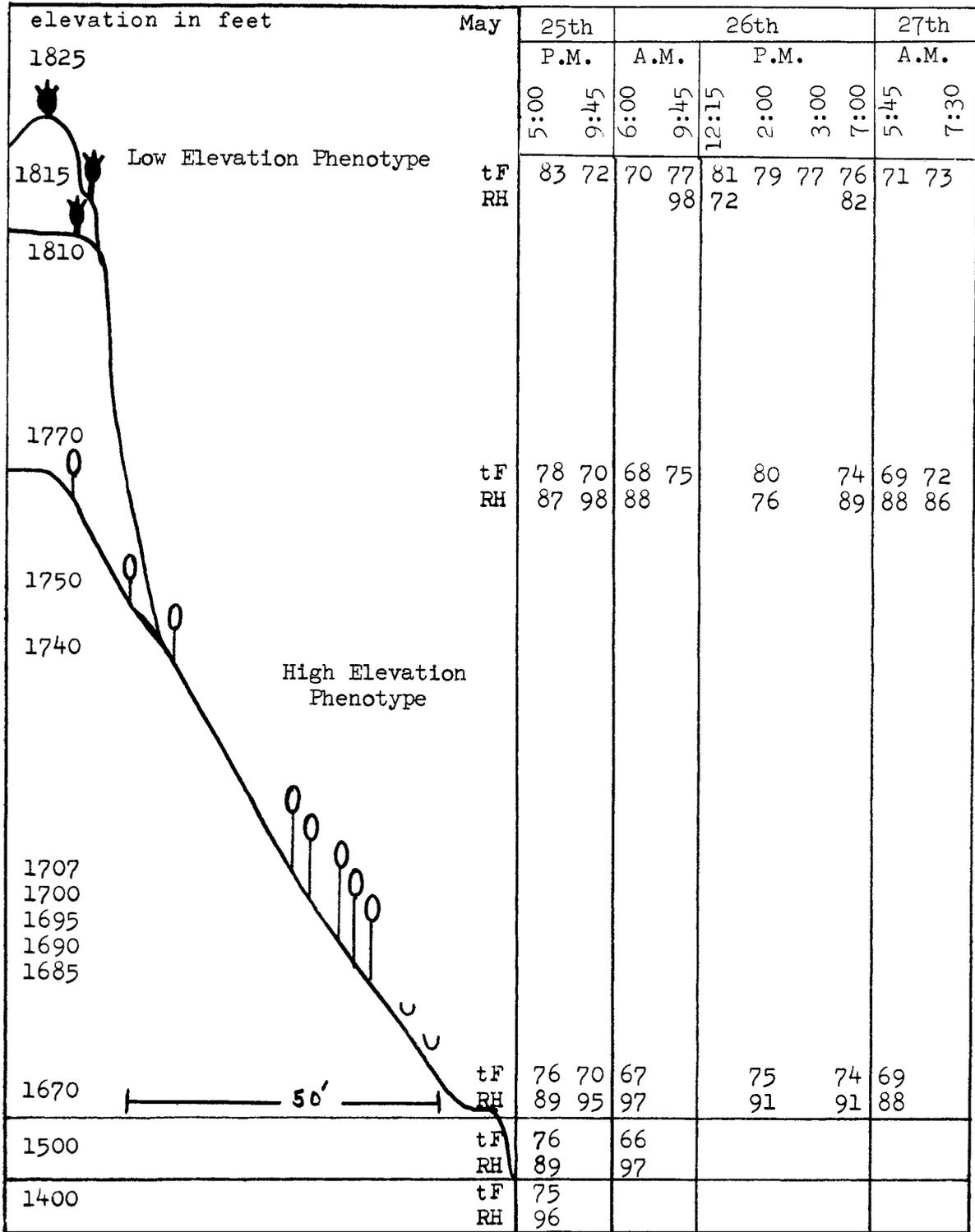


FIGURE 45.—Donkey Trail Cockpit profile (tF = temperature in degrees F; RH = the relative humidity; o = mature plants; u = juvenile plants; vertical scale, 1 cm = 10 ft; angle of slope 55-60 degrees).

The transect originated on the highest ridge at 556.26 m (1825 ft) elevation ("E" in Figure 44) and extended down into the cockpit for 47.24 m (200 ft) to 509.02 m (1670 ft) elevation along a belt 3.05 m on each side of a string stretched between the two points. The upper 15 m of the transect consisted of nearly vertical exposed cliffs above the donkey trail. Below the pass a scree slope at an angle of 55° comprised the remaining 32 m. The donkey trail originates at point "A" in Figure 44, passes over the ridge at 539.49 m (1770 ft), and continues diagonally across the path of the transect providing access to the stations where climatological information was gathered (Figure 44B,C,D,E).

A constant recording thermometer was placed at the highest (most inaccessible) point at 556.26 m (1825 ft) elevation, near the base of a large palm. A maximum-minimum recording thermometer was placed at the 509.02 m (1670 ft) level. Periodic recordings of temperature and relative humidity were made using a sling psychrometer and the percentage relative humidity was computed with the aid of the Psychrometric Tables compiled by C. F. Marvin.¹¹ The information obtained is recorded in Figure 45 and is compared with the distribution of phenotypes on the side of the cockpit.

Mango Tree Hill, one of the original areas of intensive study, is about a mile to the southwest of the Donkey Trail study area. The palms mostly exhibit the lowland phenotype and closely resemble those on the uppermost ridge at the Donkey Trail area. A maximum-minimum recorded thermometer was also maintained on Mango Tree Hill throughout the 48-hour period for comparison with temperatures recorded on the Donkey Trail ridge (Table 2).

Although the sample studied at the Donkey Trail site is small and the period covered by the climatological data is short, certain significant trends and features are thought to be worth noting. A marked difference in climate between the ridge and slope of the cockpit is not only evident in the differences in temperature and percentage of relative humidity, but is also reflected in the distribution of species of certain plants. *Hohenbergia remota*, *H. polyccephala*, and *Tillandsia* sp. aff. *fasciculata* are plentiful on the ridge but entirely absent on the slope

below. *Guzmania lingulata*, ferns, and herbaceous plants occur on the slopes but are entirely absent on the ridge. Were it not for the fact that the sky was overcast during part of the study, the disparity in the temperature and relative humidity readings between the ridge and the slope might have been even greater. At all times a strong cool breeze blew through the Donkey Trail pass at 539.49 m (1770 ft) elevation where the temperature was as much as 1.68°C lower on the northern side, a distance of only twenty feet. Dew and fog began to form in the bottom of the cockpit soon after 7:00 P.M. The fog persisted up to the 487.68 m (1600 ft) level until after 8:00 A.M., when the sun's rays reached the lower levels of the cockpit. During the winter months when the angle of the sun would be to the south, longer periods of shade and fog, along with a greater difference in temperature between the ridge and the north-facing slope of the cockpit would be expected. The conditions just described for the inside of the cockpit resemble conditions prevailing above 609 m (2000 ft) elevation on the Mt. Diablo range of mountains.

It can be seen from a study of Table 3 that in each organ studied size differences occur, but they are not great enough to be considered important; however, the more congested and twisted leaf blades and taller, more slender caudices of the plants in the cockpit create a distinct impression of two distinct biotypes. In Table 3 each elevation recorded represents a single plant along the transect. Each measurement, with the exception of caudex height and diameter, represents the average of four measurements for each plant. All characters studied, with the exception of the caudex height, tend to decrease gradually in size with decrease in elevation within the cockpit and could probably be correlated with the lower temperature and increased humidity. Although numerous seedlings of *Thrinax parviflora*

TABLE 2.—Comparison of temperatures recorded on Mango Tree Hill and Donkey Trail Ridge

Locality	Temperatures maxi- mini- mum mum	Flowering season
Mango Tree Hill	84° F 66° F	May through August
Transect 1825'	83° F 70° F	May through August
Transect 1670'	76° F 67° F	January through March

¹¹ Published by the U.S. Weather Bureau, Washington, D.C. (W.B. No. 235, U.S. Department of Commerce, 1941).

TABLE 3.—Comparison of selected characters among individuals collected at different elevations (in feet) in the Donkey Trail Cockpit study area

Selected characters	1825	1815	1810	1750	1740	1707	1700	1695	1690	1686
Petiole length in cm	72	79	143	68	68	75	67	78	72	85
Petiole width at the sheath in cm	2.1	1.8	2.5	1.3	1.1	1.5	1.2	1.6	1.6	1.7
Petiole width at the apex in cm	1.8	1.5	2.0	1.0	1.0	1.1	1.1	1.2	1.2	1.4
Hastula (adaxial) length in cm	2.5	3.4	2.1	0.9	1.3	1.0	0.6	—	0.9	0.8
Hastula (abaxial) length in cm	0.5	0.4	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Leaf segment number	54	43	55	41	38	45	44	42	41	44
Leaf segment length in cm	74.0	62.0	85.0	50.5	51.5	53.0	46.5	50.0	54.0	63.0
Segment width at the widest point in cm	4.2	5.3	6.6	3.5	3.2	4.6	4.3	3.8	4.3	3.8
Palman length in cm	11.2	21.2	32.5	14.5	14.5	14.7	19.5	9.5	14.5	21.2
Caudex diameter in cm	10.0	8.0	11.0	7.7	6.0	6.5	6.2	6.2	6.1	5.5
Caudex height in m	5.0	1.4	1.0	3.3	3.6	4.0	4.0	4.0	5.0	5.0
Pedicels of fruit, mean length in mm	1.3	1.7	—	1.0	0.6	1.0	0.6	1.1	1.1	0.6
Degree of puberulence relates to Figure 40.....	B	B	—	—	C	—	D	—	E	E

occur below 502.92 m (1650 ft) elevation, inside the cockpit mature plants are absent, and below 487.68 m (1600 ft) even seedlings were exceedingly rare.

Thrinax Swartz

Thrinax Sw., Prodr. pp. 4, 57. 1788.—Linn., Gen. Pl. ed. 8 (Schreb. ed.) 2:772. 1791.—Sw., Fl. Ind. Occ. 1:613, t. 13. 1797.—Linn., Gen. Pl. ed. 9 (Spreng. ed.) 1:255. 1830.—Mart., Hist. Nat. Palm. 3:254, pro parte. 1838.—Drude in Engler & Prantl, Nat. Pflanzenf. 2(3):34. 1887.—Baillon, Hist. Pl. 13:317. 1894.—Sarg., Silva 10:49–50, pro parte. 1896; Bot. Gaz. 27:83–84. 1899; Silva 14:79–80. 1902.—Cook, Bull. Torr. Bot. Club 28:534–535. 1901.—Becc., Webbia 2:9–10, 247–250. 1907.—Britt., Torreyia 8:240–241. 1908.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13: 327–336. 1933 [“1931”].—Dalgren, Index Amer. Palms 272–278. 1936.—Bailey, Gent. Herb. 4:129–149. 1938; 8:94–99. 1949.

Simpsonia O. F. Cook, Science, n. s. 85:332–333. 1937 [name invalid (sine descr. dat.); type-species: *Thrinax microcarpa* Sargent].

Section *Porothrinax* Drude ex Sargent, Silva 10:49. 1896 [type-species: *Thrinax microcarpa* Sargent].

TYPE-SPECIES.—*Thrinax parviflora* Swartz.

Small to medium, solitary, erect, palmate-leaved,

unarmed, hermaphroditic, coryphoid palms; caudex columnar, tan to gray, smooth or fibrous, obscurely ringed with leaf scars, base usually a mass of roots forming a mound on rock substrate.

Leaves palmate; the sheath fibrous, unarmed, at first tubular, velutinous, the petiole with a predetermined abaxial groove below the insertion of the sheath which splits on expansion of the bud permitting egress of the inflorescence (at least in Jamaican taxa), the petiole above the sheath mostly flat adaxially, conspicuous, various in outline, abaxially a ridge, flap, or small projection; blade flabellate, entirely lacking a central costa, adaxial surface glabrous, abaxial surface variously lepidote; segments narrowly rhomboid, trullate, or obrullate, fused variously toward the base forming a plicate palman, mostly bifid at the apex.

Inflorescences interfoliar, elongate, erect to arching, divided into numerous, pendulous, primary branches, these mostly simply branched; lowermost primary bract bicarinate, inserted about 1 cm above the base of the peduncle, others tubular with an oblique aperture, all primary bracts densely appressed lepidote, each enclosing the base of the next higher bract and the peduncle of a primary

branch with its bract, the latter bicarinate and bifid, and partially enclosing the flowers prior to anthesis, inserted midway along the flattened peduncle of the primary branch; each ultimate branch subtended by a narrow triangular bract.

Flowers bisexual, mostly protandrous, solitary on prominent or very short bracteolate pedicels; perianth a single series, forming a 6-lobed or dentate cupule, not enclosing reproductive parts; stamens (5-)6-12 (-15); filaments usually straight, slender, mostly free; anthers auriculate basally, retuse apically, basifixed, locules linear to oblong, dehiscent introrsely by lateral slits; pistil unilocular, uniovulate, with a narrow very short style flaring upward to a laterally compressed infundibuliform stigma; ovule with a well-developed funicular aril, erect at the base of the locule.

Fruit small, depressed-globose to globose, white at maturity, often with persistent apical stigmatic remains and persistent basal perianth; epidermis smooth at maturity when fresh; mesocarp thin, mealy; seed depressed-globose, smooth, tan when fresh, depressed basally at the hilum; endosperm homogeneous but intruded partially or completely through the center from base to apex by the testa; embryo lateral to subapical.

DISCUSSION OF THE GENUS *Thrinax*.—The name *Thrinax*, derived from the Greek word for "trident," was conceived by Linnaeus the younger in a manuscript before his death in 1783. Olof Swartz (1788) published the name, accompanied by a 10-word diagnosis, omitting any reference to Linnaeus. Considering the brevity of Swartz's original description it is noteworthy that the description in the eighth edition of Linnaeus' *Genera Plantarum* published in 1791 comprises a quarter of a page. When Swartz published his *Flora* in 1797, he acknowledged that Linnaeus *filius* had provided the generic name. It is evident from a comparison of the Swartz description of 1797 with the Linnaean manuscript that much of the former's information is in fact based on his own observations in Jamaica. In the ninth edition of Linnaeus' *Genera Plantarum*, editor Sprengel cited, "L. fil. (1781)" as authority for the genus. The reason for citing "1781" is not clear except as it may refer to the unpublished manuscript.¹² Swartz clearly indicated that the flowers

were pedicellate, but Sprengel wrote that they were sessile.

For 42 years the genus comprised but a single named species. In 1830, three additional species were published by J. A. & J. H. Schultes: *T. argentea*, *T. pumilio*, and *T. radiata*. Of these three species only one remains in the genus, for *T. argentea* has been transferred to the genus *Coccothrinax* and *T. pumilio* became the type for a new genus, *Porothrinax*, a name which cannot be applied (see Appendix II). Eight years later Martius described two more species, *T. multiflora* and *T. barbadensis*, both of which were later referred to *Coccothrinax*.

If the numerous nomina nuda are included, about 23 binomials had been published in the genus by 1866. The first attempt to remove discordant elements from the genus was made in 1866 when Grisebach listed: "5. *Porothrinax pumilio* Wendl. ined. (*Thrinax* Lodd.); Wr. 3219e:" without a generic diagnosis but by implication based on the description of *T. pumilio* Lodd. ex. J. A. & J. H. Schultes. Since *T. pumilio* cannot with any certainty be applied to any known taxon, it is considered a nomen incertum. *Porothrinax*, based upon this taxon, was not validly published because it lacked a separate generic diagnosis at the time of publication.

In 1887, Otto Drude created three subgenera: *Eu-thrinax*, *Hemithrinax*, and *Porothrinax*. *Eu-thrinax* was characterized as having long-pedicellate flowers with introrsely dehiscent anthers and a vertically sulcate ruminant albumen in the seed, and comprising *T. radiata*, *T. parviflora*, and *T. multiflora*. Subgenus *Hemithrinax* was characterized by a single species, *H. compacta*, which has nearly sessile or short-pedicelled flowers, sessile anthers with extrorse dehiscence and seeds with the uniform albumen penetrated by a broad deep basal cavity. *Porothrinax* was typified by *P. pumilio* of uncertain identity.

Although Drude's treatment was accepted in the *Silva* in 1896, Sargent soon recognized that certain discordant elements could be removed by utilizing the character of the seed. Thus in 1899:82 he divided the genus into *Coccothrinax*, with seeds "vertically sulcate by the infolding of the testa into the ruminant albumen," and *Thrinax*, the seeds of which have a uniform albumen more or less deeply penetrated by a broad basal cavity. At that time no other satisfactory characters were known for dis-

¹² The Linnaeus *filius* unpublished manuscript was cited by W. H. Aiton in the Preface (p. vi) of *Hortus Kewensis* in 1789.

tinguishing the two genera when seed was unavailable. For currently reliable characters, see Table 4. Bailey (1939) did not believe the color of the ripe fruit to be reliable, but, except for one unconfirmed report of a white-fruited species of *Coccothrinax* and the fact that the fruits of *Thrinax* "*harrisiana*" were erroneously reported to be purplish, the character holds quite well. León (1956) wrote that it is possible

to distinguish without hesitation a species of *Thrinax* from one of *Coccothrinax*: in the latter case, the sheath is clearly cylindrical, commonly formed of more or less rigid fibers which are strongly interwoven and in every case persistent

on the trunk for many years. . . . In *Thrinax*, the sheath is more irregular and not long persistent on the trunk.

Unfortunately León missed the true character of the *Thrinax* sheath that provides the most useful field character: the petiole of *Thrinax*, as indicated in Figure 9c, is split in the sheath, which is not so in *Coccothrinax*.

At the same time he described *Coccothrinax*, Sargent further divided the remaining elements of *Thrinax* into two sections: the *Pedicellatae*, including the type for the genus and recognized by having long pedicels, and the *Sessiliflorae*, containing species with the flowers having the appearance of being

Key to the Species of *Thrinax*

1. Inflorescence branches exhibiting numerous conspicuous pedicel remains, exceeding 1 mm in length following fruit set (except occasional specimens of subspecies *parviflora* of *T. parviflora*); adaxial hastula glabrous or with closely appressed inconspicuous scales on emergence from the bud region; abaxial leaf surface lacking rows of minute, waxy dots associated with sunken stomata.
 2. Leaves of mature plants densely covered abaxially with white or silvery, overlapping and interlocking, hyaline, fimbriate scales (leaves of young plants have similar scales but may appear green beneath because the scales are less densely disposed); petioles of adult plants tan velutinous, abaxially; inflorescence branches and flowers pink to purple at anthesis, primary bracts densely covered with rufous appressed scales; (leaf sheath long linguiform, densely, tan, velutinous, Figure 10A) grows naturally only in the interior of eastern Jamaica 3. *T. excelsa*
 2. Leaves of mature plants concolorous or very slightly lighter green beneath, scales when present widely spaced, not touching; petioles of adult plants very soon glabrescent abaxially; inflorescence branches and flowers white, ivory, or yellowish at anthesis, scales on primary bracts not rufous colored.
 3. Leaves of mature plants concolorous, glabrescent; scales when present minute (difficult to see with the aid of an 8 power lens); segments broadest well beyond the palman; sheath long linguiform (Figure 10B), (observed best in the region of newly emerging leaves (Figure 11B); inflorescence branches and flowers ivory to yellowish at anthesis, the axes densely granulose-puberulose (except subspecies *parviflora* in which the inflorescence branches are usually glabrous-glabrate but then the pedicels toward the apex of the branches are very short); grows naturally only southwest and west of the Blue Mountains in Jamaica 1. *T. parviflora*
 3. Leaves of mature plants lighter green beneath, with scattered but conspicuous fimbriate scales which have a conspicuous translucent central region; segments broadest at the point of fusion; sheath not linguiform, rather deeply V-form (Figures 10c, 11A); inflorescence and flowers white at anthesis, the axes glabrous; common, but grows naturally only in close proximity to the sea, below 250 ft elevation on islands throughout the northern Caribbean and the Bahamas, and islands off the coasts of Florida, Mexico, and British Honduras 2. *T. radiata*
1. Inflorescence branches exhibiting only small inconspicuous, wartlike, or disklike, pedicel remains, less than 1 mm (averaging about 0.4 mm) in length, following fruit set; adaxial hastula densely velutinous with white, silky, scales on emergence from the bud region; abaxial leaf surface usually exhibiting rows of numerous, minute, white, waxy, dots associated with sunken stomata. (Inflorescence arching, exceeding the leaves, branches white to yellowish with age; leaves often blue green to whitish abaxially and often exhibiting closely arranged, pale, hyaline, fimbriate scales abaxially.) 4. *T. morrisii*

sessile. Shortly thereafter Beccari (1907) published his comprehensive study of American *Coryphea* in which he also divided the genus *Thrinax* into two sections adopting the groupings described by Sargent but under different names. Beccari's division, however, was based on the degree of intrusion of the testa into the endosperm: *Euthrinax*, having the seed completely perforated, and *Typhlothrinax*, having the testa intruding only part way into the endosperm. Since Sargent's interest was only with palms of North America it remained for Beccari to raise *Hemithrinax* to full generic status again, which, with *Coccothrinax* and *Thrinax*, comprised the three genera of the subtribe *Thrinaceae*. In a supplement, in English, Beccari (1933) dealt with *Thrinax* in much the same manner as earlier but the addition of floral dissections made it a valuable adjunct to his earlier work.

In 1937, Cook of the Bureau of Plant Industry, United States Department of Agriculture, proposed a new genus, *Simpsonia*, which was based on Sargent's *Thrinax microcarpa*, but since the proposal does not conform to Article 36 of the International Code of Botanical Nomenclature it is not validly published. Bailey (1938:131) revived the use of Sargent's *Pedicellatae* and *Sessiliflorae* because "the species may vary within themselves in the extent of the centralium in the seed."

Common Names: As might be expected the common names applied to the members of the genus, as well as to the genus as a whole, are almost as difficult to straighten out as are the scientific names. The first common name to appear in the literature was that applied by Sloane (1696). He called the palms "thatch," a name also applied to any other palm used in the roofing of shelters, but in many cases the distinction is made by the addition of a prefix or qualifying word. In 1937, Cook

referred to a group of sturdy wind-resistant palms, including a *Thrinax*, as hurricane palms. Bailey (1938) referred to members of the genus as peaberry palms, and in 1949 he included members of *Thrinax* along with *Coccothrinax* under the name broom palms.

1. *Thrinax parviflora* Swartz

Thrinax parviflora Sw., Prodr. 57. 1788.—Ait., Hort. Kew. 3:473. 1789.—Sw., Fl. Ind. Occ. 1:614, t.13. 1797.—Linn., Sp. Pl. sec. (Willd. ed.) 2:202. 1799.—Pers., Synops. Pl. 1:383. 1805.—Lam., Encycl. Méth. 7:635. 1806.—Ait., Hort. Kew. 2nd ed. 2:307. 1811.—Titford, Hort. Bot. Amer. p. 112. 1811.—Lunan, Hort. Jam. 2:28. 1814.—Pers., Synops. Pl. (Diet. ed.) 2:1091. 1830.—Linn., Syst. Veg. sec. (J. A. & J. H. Schult. ed.) 7(2):1300. 1830.—Mart., Hist. Nat. Palm. 3:255, t.103, pro parte. 1838.—Kunth, Enum. Pl. 3:253. 1841.—Griseb., Fl. Brit. W. Ind. p. 515. 1864.—Cook, Bull. Torr. Bot. Club 28:535, pro parte. 1903.—Becc., Webbia 2:251, pro parte. 1907; Annal. Roy. Bot. Gard. Calcutta (Martelli ed.) 13:327, pl. 28: fig. 3, pro parte. 1933 ["1931"].—Read in Adams, Fl. Pl. Jam. pp. 75-76. 1972.

TYPE.—Swartz *s.n.* Jamaica (a single sheet with juvenile leaf and packet of flowers).

Small to medium palm, 1-10 (-13) m high, caudex columnar, often very slender, 5-14 (-15) cm in diameter, internodes 1.0-6.5 cm apart on lower trunk, reduced to lines above.

Leaf sheath 45-70 cm long, apex long linguiform 7-22 cm long, netlike, entire, becoming ragged and fibrous with age, tan, velutinous, glabrescent with age on exposed surfaces; petiole (35-)50-145 (-160) cm long, abaxial surface densely tan lepidote, soon glabrescent on exposure, (1.0-)1.2-2.2 (-2.4) cm wide at the sheath, (0.8-)1.0-2.2 (-2.4) cm wide at apex; hastula triangular or rounded acute (0.1-)0.5-3.4 (-4.6) cm long, may become tubular with expansion and folding of blade, abaxially with a distinct ridge 0.1-0.5 (-1.0) cm long or a triangular projection 1.0-1.7 cm long; leaf in bud densely tan-brown lepidote on all exposed surfaces, often persistent on principal nerves and exposed portion of lower segments.

Leaf blade when expanded very variable, circular and flat on young plants and in the shade, the basal lobes folded up away from the petiole when in the sun, and on older plants, or variously folded and contorted on tall slender plants, abaxial surface with microscopic widely scattered scales; palman

TABLE 4.—*Characters known to be reliable in separating Coccothrinax from Thrinax*

Characters	<i>Coccothrinax</i>	<i>Thrinax</i>
Petiole	solid in the sheath	split in the sheath
Fruit	fleshy, purple-black	pulpy, white or ivory
Seed	cerebriform	smooth
Endosperm	infolded ruminant	nonruminant, partially or completely intruded by the testa

variously folded and very irregular in outline, (7-)8-34 (-42) cm broad; segments rhomboid (35-)37-57 (-60) in number, (38-)40-90 (-96) cm long, (2.3-)2.8-6.0 (-6.4) cm wide, widest beyond point of fusion, the middle two or three segments always fused for a greater length but rarely totally.

Inflorescence erect to arching, 40-175 cm long, bracts greenish with brown appressed scales, each inflorescence with 7-22 primary branches, those in the lower half with 17-45 ultimate branches, these ivory to yellowish at anthesis, densely puberulous to glabrescent or glabrous, several of the lowermost branches occasionally forked or highly branched but subtended by a narrow triangular bract; flowers ivory to yellowish, fragrant, (15-)32-60 (-84) per branch; stamens 5-10 (-15) per flower, anthers linear to oblong (1.1-)1.2-4.0 (-4.2) mm long; infundibuliform stigma oblique to lateral, ciliate; developing ovary papillate to granulate.

Fruit papillate to scurfy granulate, tan before maturation, become white and smooth or slightly punctate, except when infected by a fungus, then tessellated, 6.4-7.3 (-7.5) cm in diameter; pedicels bracteolate, (0.1-)0.5-2.8 (-5.2) mm long; primary branches yellow to orange at maturity of fruit (green or insect grazed at high elevations); rachis 6-25 cm long; ultimate branches 4.5-17.0 cm long, 1.1-1.5 mm thick at point of insertion on rachis; seed tan to dark brown 5.4-6.2 (-6.5) mm in diam., normally completely perforated by the testa. Haploid chromosome number, $n=18$.

TYPIIFICATION OF *Thrinax parviflora*

The original publication of *Thrinax parviflora* by Olof Swartz (1788) consisted of a very short diagnosis, which characterized the genus, and a reference to Patrick Browne's account of the species published 32 years earlier. There was no reference to his own collections or to the younger Linnaeus' unpublished manuscript. Patrick Browne's (1756) description of the palm growing and thriving on all the rocky hills of Jamaica clearly indicated the palm intended. Swartz (1797) reproduced the Browne diagnosis and elaborated on it considerably with his own observations made while in Jamaica from 1784 to 1786. The description of such characters as long, glabrous, compressed-terete petioles which were longer than the 1-2-ft-long leaf blades,

inflorescences shorter than the leaves and pale yellowish anthers leaves no doubt which Jamaican taxon was being described. Only one taxon in Jamaica exhibits these characters. An illustration in Swartz (1797: pl. 13) shows dissections of the flower and fruit, but they are very schematic. The drawing unquestionably portrays *Thrinax* which, if interpreted on the basis of the scurfy-looking fruit, provides additional support for the present determination of the species.

In the herbarium at the Naturhistoriska Riksmuseet in Stockholm, where many of Swartz's collections are maintained, three herbarium specimens attributed to him have caused considerable confusion over the past 186 years. Through the courtesy of Professor Dr. Tycho Norlindh of the Riksmuseum, I was able to make a careful study of the specimens while they were on loan to Dr. H. E. Moore at the Liberty Hyde Bailey Hortorium, Cornell University, in New York. The three specimens represent two distinct taxa, both Jamaican, but it is obvious that only one of the sheets can be the type for Swartz's *Thrinax parviflora*. The three specimens each have inscriptions in the hand of J. E. Wikström, the director of the Botanical Museum and Botanical Garden of the Royal Academy of Sciences from 1818 to 1856. These inscriptions, according to correspondence between Dr. E. Asplund of the Riksmuseum and Dr. L. H. Bailey in 1937, "often giving valuable information regarding the provenience [sic] of the specimen, but sometimes being only a repetition of what is already present on the label (in old time mostly on the back of the sheet)." Each sheet has a quite different history and so will be discussed separately.

The first specimen (Figure 46b) containing a short section of a *Thrinax* inflorescence also contained a portion of a *Bactris* inflorescence; the latter has been removed to another sheet. This sheet retaining the *Thrinax* specimen and labeled "*Sabal umbraculifera* Mart." could not have been collected by Swartz, for as Professor Norlindh has explained in correspondence:

It once belonged to the Linnean Herbarium and can possibly have been collected by Swartz, who made his collections in the West Indies in 1784-86. Dr. Dahl obtained it from Linnaeus (pater), thus before 1778, and then it was incorporated in the herbarium of Baron Clas Alströmer and later left to the Royal Academy of Science, the supervisor of Riksmuseum.

According to the letter from Asplund to Bailey, "*Sabal umbraculifera* Mart." below the right specimen is written by Wikström. On the back of the sheet Wikström has repeated the same determination and also written "Herb. Alstroemeri". In another hand is written "Palmeto Dahl.", "Corypha umbraculifera", "Dahl a Linné P.", and "Jamaica". Those words may be written by Clas Alströmer or Andreas Dahl (or perhaps by a copyist, since they are obviously written in text hand). After "umbraculifera" is added "Jacq.", probably by Wikström. The specimens on this sheet were given by Linnaeus to Dahl and came from him to Alströmer. Alströmer and Dahl were pupils of Linnaeus. . . . The former was a member of the Swedish aristocracy and had a botanical garden and museum in Gothenburg, of which he had employed Dahl as a keeper. His herbarium came to this museum in 1848. The father of Alströmer and Linnaeus were among

the founders of the Royal Academy of Sciences.—There is nothing indicating that Swartz did ever see this specimen.

The second specimen (Figure 46A) containing three pieces of a *Thrinax* inflorescence, including a terminal portion with six primary branches attached, is labeled "No. 4 *Sabal umbraculifera* Mart. Jamaica Swartz" and "Herb. Swartzii" in Wikström's hand. This and the preceding specimen belong to the same taxon, although probably not from the same source. It seems unlikely that, had either of these specimens been seen or utilized by Swartz, they would have been incorrectly labeled. The annotations by Wikström were made 40 to 60 years after the publication of *Thrinax* by Swartz,

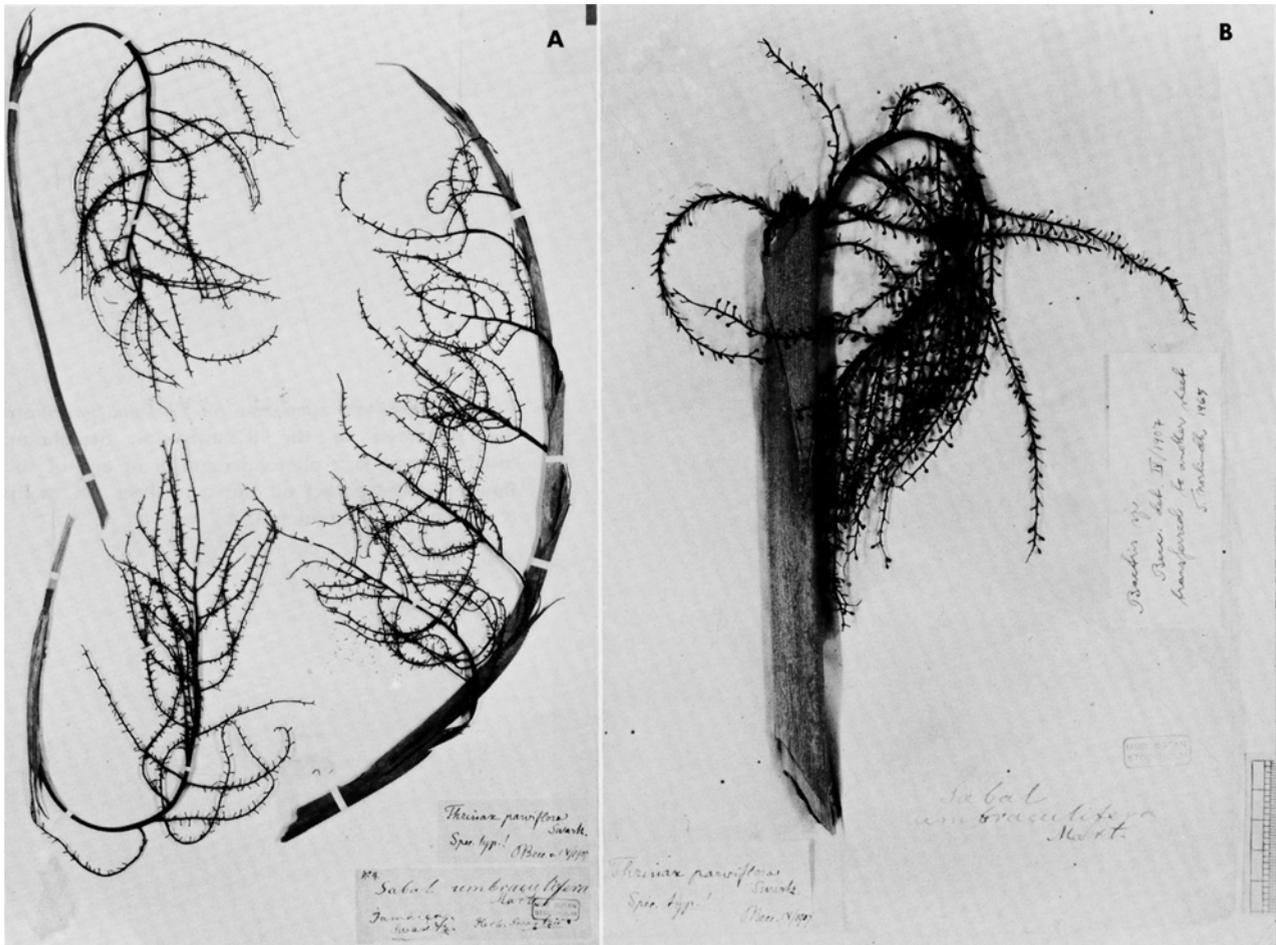


FIGURE 46.—Two herbarium sheets often erroneously considered as part of the Swartz type for *Thrinax parviflora*. Discussion in the text. (Supplied by courtesy of Prof. Norlin, Riksmuseum, Stockholm.)

yet there is no indication that they ever were associated with the genus until Beccari annotated the sheets in 1907 and identified them with *Thrinax*.

The third specimen (Figure 47) has a small flabellate leaf and a packet containing fragmentary rachillae and flowers. This specimen is labeled by Wikström as "Jamaica Swartz." and "*Thrinax parviflora* Swz." thus as early as the 1800s this specimen was recognized as one of Swartz's own. In addition the packet contains flowers wrapped in paper labeled "*Thrinax parviflora*," below which is written in a different hand, "Swartz scripsit." The latter is

no doubt Wikström's handwriting for it is the same as on the other sheets. Thus Wikström provided us with the earliest indication of a specimen seen and perhaps even labeled by Swartz.

In 1907, Beccari annotated all three sheets as "Spec. typ.!", apparently not recognizing that two taxa were involved, also ignoring that only one of the sheets had been labeled *Thrinax* by Swartz. Dr. L. H. Bailey (1938:138), when writing about these same specimens, concluded, as has the present author, that the last sheet described (Figure 47) "undoubtedly may be considered authentic *Thrinax*



FIGURE 47.—Type specimen of *Thrinax parviflora* Sw. preserved in the Riksmuseum, Stockholm, Sweden. Inset is a photomicrograph of one of the flowers in the packet on the type sheet (\times ca 6). (Courtesy of Riksmuseum.)

TABLE 5.—Comparison of Swartz's type and description of *Thrinax parviflora* with two of the Jamaican taxa

Characters	Swartz type and description	<i>Thrinax parviflora</i> subsp. <i>parviflora</i>	<i>Thrinax radiata</i>
Petiole length	longer than blade	longer than blade	shorter than blade
Blade width	1-2 feet	2-3 ft or more	3-6 ft
Pedicel length at anthesis	(0.5)0.7-1.5 (1.7) mm long	(0.3)0.5-1.5 (1.7) mm long	(1.4)1.6-2.4 (2.7) mm long
Flower color	yellowish	ivory to pale yellow	white
Anther length	(1.4)1.5-2.0 (2.2)	(1.1)1.2-2.0 (2.2)	(1.7)1.8-2.3 (2.5)

parviflora of Swartz." Bailey had corresponded with both the Linnean Society of London and the herbarium of the Royal Botanic Gardens at Kew, in 1937, but failed to turn up Swartzian *Thrinax* in either herbarium.

An undated sheet containing an inflorescence of *Thrinax* located in the Banks herbarium of the British Museum was examined, at my request, by Dr. William T. Stearn, who made the following comments (in correspondence) concerning Banks and Swartz:

There is one sheet from Bank's herbarium which Swartz almost certainly saw during his long period of work in London on his West Indian collections. If Banks already possessed a specimen from the West Indies, obviously, according to the attitude of the time, he did not need another, and the specimen he possessed was simply annotated with Swartz's determination. If, on the other hand, Banks lacked a representative of the species, then Swartz gave him one and his specimen was mounted immediately and annotated according to Swartz, thus obviating error. Swartz did not mount his own specimens. He was a very generous man and evidently gave away many specimens. After his death his specimens were mounted at Stockholm and written up for the most part by Wikström; presumably Swartz had written the name on the covers, as was then usual with loose specimens, and presumably, as was also usual, alas! the covers were then thrown away. The sheet here collected in Jamaica by Robins was photographed by Moore in 1950 (this photograph B. M. 2577).¹³ In the capsule are two fruits presumably given to Banks by Swartz, as the sheet is annotated as having on it Jamaican material from "Dr. Swartz" and these fruits are the only ones to which this note could apply.

¹³ The specimen in the herbarium of the British Museum (Herbarium Banks) "Jamaica. Robins" has been chosen as the lectotype of *Thrinax martii*, as it is the only known specimen of those cited by Martius, upon which *T. martii* is based.

There is no doubt now that the only specimen considered authentic Swartz material, and therefore the holotype, is the single sheet, illustrated in Figure 47, in the Riksmuseum in Stockholm, which has a small but complete leaf and a packet of flowers. The other two sheets, until now considered identical, are removed from the species and are treated under *T. radiata*. The Robins specimen in the Banksian herbarium also represents *T. radiata*, with the exception of the fruits which cannot at this time be placed with any certainty.

In Jamaica there are three distinct and well-defined taxa in the genus *Thrinax* that have been recognized as a result of extensive field work and numerous collections. One of these must of course be associated with *Thrinax parviflora* Sw. All three taxa have a 6-dentate perianth, an emarginate stigma, and a 1-seeded fruit. Apart from the information in the *Flora*, the type specimen provides additional evidence in support of the present determination of the species. The juvenile leaf on the sheet is unfortunately of little significance, although it has certain indefinable characteristics such as texture and general appearance which suggest a similarity to the seedlings collected in the mountains. The leaf lacks lepidia of any sort (*T. radiata* seedling-leaves usually exhibit scattered lepidia on the abaxial surface). The attached packet contains fragments of flowers and small pieces or rachillae, pedicels, and numerous anthers. Measurements of the anthers and pedicels are compared with similar measurements taken from plants at Devils Backbone and Morant Point in Figure 38. Although Swartz placed the genus in the *Hexandria*, flowers in the packet had as many as 7 stamen filaments still attached. Many flowers of *Thrinax* in Jamaica have

been found with 6 stamens; however, it is more common to find any number up to 12 or 15.

Comparing the Swartz type and description with the taxa in Jamaica as presently understood, one taxon is immediately eliminated from consideration because two of the characters mentioned by Swartz in the *Flora* certainly do not apply. *Thrinax excelsa* of the John Crow Mountains in eastern Jamaica has leaves no less than 6 to 12 feet across and very striking pink flowers. Another taxon, *Thrinax radiata*, of littoral areas, has leaves measuring more than 3 feet across and the petioles are much shorter than the blade, the flowers are white and the floral pedicels are more than 1.6 mm long even at anthesis. Thus *Thrinax radiata*, which has erroneously been known as *T. excelsa* in Jamaica, *T. wendlandiana* in Cuba, *T. parviflora* in the Bahamas, and *T. floridana* in Florida, can also be ruled out. Recent anatomical findings agree.

Although *Thrinax parviflora* Sw. is an extremely variable species (see section on variability) the population above 609 m (2000 ft) elevation on Mt. Diablo has been found to resemble Swartz's type and description most closely. It is this population, seen on all the cliffs and rocky hills along the main route across Jamaica (now subspecies *parviflora*), which was chosen to represent one of the two Jamaican taxa in Table 5 comparing them with the Swartz material.

In 1838, Martius published an amplified account of *T. parviflora* consisting of information from several sources. The description, including elements of several taxa, in fact appears to contain characteristics of his newly described *T. multiflora*. Grise-

bach's description (1864) only contributed to the growing confusion concerning the application of *T. parviflora*.

For the first time in 199 years, identification of the species with a taxon in Jamaica came close when Beccari (1907) recognized the Harris collection from Ferry River as true *T. parviflora*. Unfortunately, elements of a second taxon from the littoral of the north coast were also included in the description of the species. The illustrations of flowers and fruits that appeared in the 1933 supplement do not accurately depict authentic *T. parviflora*. On pl. 28: III, figure 1 (taken from the Swartz type) and figures 2 and 4 (taken from a Harris specimen collected along Ferry River) represent true *T. parviflora*, but the remaining figures most likely represent *T. radiata*. As a result, rather than straightening out the problem, Beccari further obscured the true nature of the species. In 1907, he also described *T. tessellata* based on a phytomorphic form from Mt. Diablo. *Thrinax harrisiana* described by Beccari (1908) was based on a non-tessellated and immature-fruited specimen collected on the heights of Dolphin Head.

When L. H. Bailey (1938) undertook the challenge to revise the genus, he did not fully understand *T. parviflora* in Jamaica. Although Dr. Bailey collected and correctly identified material of authentic *T. parviflora* from Salt River, Clarendon, and the Port Royal Mountains, in St. Andrew, he nevertheless chose to typify the species by using the Florida taxon. Although Florida and Jamaican plants of *T. radiata* differ only in minor quantitative characters such as leaf segment and fruit size,

Diagnostic Key to the Subspecies of *Thrinax parviflora*

1. Adaxial hastular projection 0.3–1.2 cm long*, lacking or vestigial abaxially; branches of the inflorescence glabrous, glabrate, or lightly puberulose; inflorescence erect and shorter than the petioles at anthesis; fresh anthers short (1.2–2.0 mm long); mature plants with leaves forming an open crown of conspicuously twisted and curled leaf segments subspecies *parviflora*
2. Adaxial hastular projection very prominent or even long pointed, 1.5–4.4 cm long, prominent and up to 1.6 cm long abaxially; branches of the inflorescence densely granulose puberulose throughout; inflorescence arching, equaling or longer than the petioles at full anthesis; fresh anthers elongate (ca. 2–4 mm long); mature plants generally with leaves forming a dense crown of broad blades with more or less flat to curved or slightly twisted leaf segments subspecies *puberula*

* Measured from beneath the hastula, against the lamina.

it is curious that Bailey should have chosen those from Florida as representative of *T. parviflora* while at the same time referring the Jamaican plants to *T. excelsa*. Specimens of true *T. parviflora*, which Bailey collected in Jamaica, were not considered in his final analysis.

Following Bailey's revision of the genus in 1938 nearly all references to *T. parviflora* that appear in the taxonomic literature actually refer to *T. radiata*.

Common Names: Sloane's early common name for the species in 1696 was simply "thatch," but in Patrick Browne's description in 1756 the names "palmeto-royal" or "palmeto-thatch" were cited. L. H. Bailey cited "iron-thatch" as the common name on a specimen collected at Alligator Pond, in the Parish of Manchester, in 1931. Presently the species is called thatch, thatch-pole, or broom palm.

Thrinax parviflora Swartz subsp. *parviflora*

Thrinax parviflora Sw. subsp. *parviflora*, Prodr. 57. 1788. [Type: Olof Swartz, Jamaica (S).]

Thrinax tessellata Becc., Webbia 2:271. 1907. [Type: W. R. Maxon & G. N. Collins 5, 26 May 1904. Hollymount, Jamaica, 2600 ft (792.4 m) elev. (B, specimen destroyed?; US, neotype, W. R. Maxon 2353).]

Thrinax harrisiana Becc. in Fedde, Repert. 6:94. 1908. [Type: Harris 9273. Dolphin Head, Jamaica, 1500–1600 ft. (457.2–487.7) elev. (B, specimen destroyed?; UCWI, isotype).]

SPECIMENS EXAMINED AND COLLECTING LOCALITIES (Parish and locality number in Jamaica).—Abbreviations for herbaria are those of J. Lanjouw and F. A. Stafleu in *Index Herbariorum, Reg. Veg.* 31(1) ed. 5, 1964, with the addition of FTG, for the Fairchild Tropical Garden, Coral Gables, Florida, and DA, for L'École National d'Agriculture, Damien, Port-au-Prince, Haiti.

Locality numbers correspond with those given on the map of Jamaica (Figure 48).

ST. ANN

5. Stirling Castle Forest Reserve: 609 m, Jan. 1958, R. A. Howard & G. R. Proctor 15055 (GH, IJ); Jan. 1960, R. A. Howard et al. 20513 (IJ).
6. Lydford Post Office: 457.2 m, Dec. 1953, R. A. Howard & G. R. Proctor 13506 (BH).
7. Devils Backbone, 616.62 m, ridge along parish boundary east of Mt. Diablo: Jan. 1967, R. W. Read 1736, 1737, 1738 (S, UCWI, US).
8. Union Hill: 669.96 m, Apr. 1908, N. L. Britton & A. Hollick 2753 (NY, US); Jan. 1967, R. W. Read 1939 (BH, IJ, US).
9. Grier Mount, 838.2–914 m: Dec. 1953, R. A. Howard & G. R. Proctor 13611 (BH); Jan. 1966, R. W. Read 1573 (US).

ST. CATHERINE

10. Hollymount Hill, 807.72 m, the first pinnacle on right side of Hollymount road after reaching 762 m elevation:

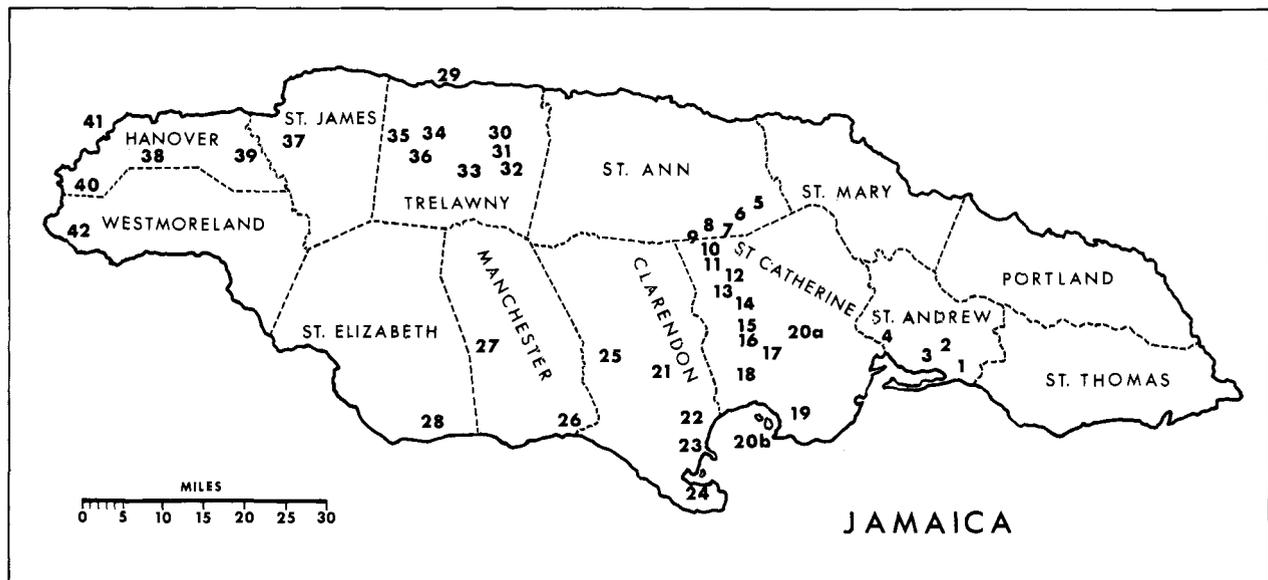


FIGURE 48.—Distribution of *Thrinax parviflora* in Jamaica. The locality numbers refer to list of Specimens Examined under treatment of the species.

Apr. 1963, *R. W. Read & G. R. Proctor 1146* (FTG); Feb. 1966, *R. W. Read 1595, 1596* (US); June 1966, *R. W. Read 1681* (BH, IJ, S, UCWI, US); Jan. 1967, *R. W. Read 1761* (US); Mar. 1967, *R. W. Read 1835 & 1836* (US).

11. Hollymount: May 1903, *W. R. Maxon 1961, 1962* (US); 838.2 m, May 1904, *W. R. Maxon & G. N. Collins no. 5* (B, holotype of *T. tessellata*, not seen); May 1904, *W. R. Maxon 2353* (UCWI; US, neotype); Feb. 1905, *W. Harris no. 6* (UCWI); Sept. 1906, *N. L. Britton 734* (NY); Aug. 1931, *L. H. Bailey 710* (BH).
12. Blue Mountain, Mt. Diablo, top of south escarpment: 807.72 m, May 1967, *R. W. Read 1895* (GH).
13. Mt. Diablo: Mar. 1916, *E. P. Killip 420* (US); south slope; 457.2–502.92 m, May 1967, *R. W. Read 1896* (FTG); 502.92–533.40 m, May 1967, *R. W. Read 1897* (FTG).
- 14b. Charlton to Worthy Park road: 27-mile marker, 487.68 m, May 1967, *R. W. Read 1898* (US).

MANCHESTER

27. Somerset: 762–914 m, Feb. 1955, *G. R. Proctor 11604* (IJ).

TRELAWNY

30. Ramgoat Cave: 457.2 m, Apr. 1963, *R. W. Read & G. R. Proctor 1148* (FTG); Nov. 1964, *G. R. Proctor 25675* (IJ).
31. Donkey Trail, ½ mile north of Burnt Hill intersection: 518.16–556.26 m, May 1966, *R. W. Read 1663* (US); June 1967, *R. W. Read 1757* (S), *1758* (FTG).
32. Burnt Hill: Jan. 1956, *R. A. Howard et al. 14678* (IJ); ¼ mile north of intersection, 533.4 m, Apr. 1966, *R. W. Read 1640* (US).
- 36b. Weather Station (south of Windsor Cave): over 400 m elev., Apr. 1967, *C. D. Adams s. n. (Read 1877)* (US).

ST. JAMES

37. Fray Woods: 502.92–548.64 m, Mar. 1908, *W. Harris 10341* (B, not seen; UCWI, US).

HANOVER

38. Dolphin Head: above Askenish, 457.2–548.64 m, May 1906, *W. Harris 9273* (B, holotype of *T. harrisi*, not seen; UCWI, isotype); Mar. 1908, *W. Harris 10264* (B, not seen; UCWI, US); Mar. 1908, *N. L. Britton & A. Hollick 2217* (US); Feb. 1931, *L. H. Bailey 15053* (BH); Sept. 1951, *R. G. Robbins 2878* (UCWI); Apr. 1955, *G. R. Proctor 10054* (IJ); Mar. 1960, *G. R. Proctor 20683* (IJ); Sept. 1960, *C. D. Adams 7995* (M, UCWI); Apr. 1963, *R. W. Read & G. R. Proctor 1150* (FTG).
39. Bubby Hill: 441.96 m, Aug. 1965, *G. R. Proctor 26675* (IJ).
- 41b. Hills near Kemshot: Mar. 1908, *N. L. Britton 2426* (US).

SOURCE UNKNOWN

Olof Swartz, Jamaica (S, holotype of *T. parviflora* Sw.).

Thrinax parviflora Swartz *puberula*, new subspecies

A subspecies *parviflora* differt hastula adaxialiter 1.5–4.4 cm longa et aliquantum prominente, abaxialiter usque ad 1.6 cm longa, inflorescentiae ramulis dense granuloso-puberulis.

TYPE: *R. W. Read 1565* Palmers Cross, Parish of Clarendon, Jamaica, Nov. 1965 (US).

SPECIMENS EXAMINED AND COLLECTING LOCALITIES (Parish and locality number in Jamaica).—

ST. ANDREW

1. Cane River Gorge, 76.2–182.88 m: Mar. 1931, *L. H. Bailey 15089* (BH); Apr. 1963, *R. W. Read & G. R. Proctor 1139, 1140* (FTG); Mar. 1966, *R. W. Read 1603* (US).
2. Dallas Mountain: Apr. 1963, *R. W. Read & G. R. Proctor 1141* (FTG); 542.54 m, Nov. 1965, *R. W. Read & C. D. Adams 1559a* (US).
3. Long Mountain: Mona Hill, Sept. 1906, *N. L. Britton 373* (NY, US); vicinity of water tank, Montclair Dr., Beverly Hills, 213.36–243.84 m, May 1966, *R. W. Read 1657, 1658c* (BH, US); June 1967, *R. W. Read 1950* (US); Mona Mt., May 1904, *W. R. Maxon 2147* (US).
4. Ferry Hill: along river side, 30.48 m, May 1904, *W. Harris 4* (B, not seen); Ferry River, *G. N. Collins s. n.* (US); May 1904, *W. R. Maxon 2190 & 2197* (US).

ST. CATHERINE

- 14a. Charlton to Worthy Park road (26-mile marker): 381 m, June 1966, *R. W. Read 1672* (FTG).
- 14b. Charlton to Worthy Park road (26.5-mile marker): 487.68 m, June 1967, *R. W. Read 1941, 1944* (US).
15. Mendez Hill to Spring Vale: 152.4–304.8 m, May 1967, *R. W. Read 1899* (FTG), *1900* (NY).
16. Cudjoe Hill: 152.4 m, Mar. 1966, *R. W. Read 1602* (BH).
- 17a. Johnston Pen vicinity, near rock quarry, 2–4 miles south from Spanish Town, off the Friendship Rd.: 121.92 m, Nov. 1965, *R. W. Read 1655a, 1655b* (US).
- 17b. Guanaboa Vale, 9 miles NW of Spanish Town: Nov. 1965, *R. W. Read 1551* (US).
18. Spring Garden: 76.2 m, Mar. 1966, *R. W. Read 1600, 1601* (BH).
19. Hellshire (Healthshire) Hills: near Salt Island, 76.2 m, Sept. 1908, *W. Harris & N. L. Britton 10524* (UCWI, US).
- 20a. Rio Cobre Gorge: near Bog Walk, ca 182.88 m, Feb. 1931, *L. H. Bailey 15065* (BH).
- 20b. Great Goat Island: Apr. 1920, *W. R. Maxon & E. P. Killip 1593* (US).

CLARENDON

21. Palmers Cross: in a sisal field, 45.72 m, Apr. 1963, *R. W. Read & G. R. Proctor 1147* (FTG); Nov. 1965, *R. W. Read 1565* (BH, S, UCWI, US, holotype of *T. parviflora* subspecies *puberula*); June 1966, *R. W. Read 1676b* (BH, S, UCWI, US).

22. Cockpit: 4.75–12.19 m, June 1966, *R. W. Read 1675a, 1675b* (US); Feb. 1967, *R. W. Read 1827b* (US).
 23. Salt River: ca 15.24 m, Nov. 1935, *L. H. Bailey 202* (BH).
 24. Portland Point: 3.05–6.1 m, Feb. 1967, *R. W. Read 1825* (US).
 25. Clarendon Park: 83.82 m, Feb. 1966, *R. W. Read 1583* (BH).

MANCHESTER

26. Round Hill: 60.96 m, July 1966, *R. W. Read 1689* (US).
 Alligator Pond: Feb. 1931, *L. H. Bailey 15080* (BH).

ST. ELIZABETH

28. Bull Savanna: 152.4 m, July 1962, *E. T. Robertson 9326* (UCWI).

TRELAWNY

29. White Bay: 3.05 m, Aug. 1966, *R. W. Read 1702a, 1702b* (US).
 31. Donkey Trail, ½ mile north of Burnt Hill intersection: 518.16–556.26 m, May 1967, *R. W. Read 1946* (US).
 33. Mango Tree Hill (Carambi Hill): 542.54–563.88 m, Jan. 1966, *R. W. Read 1574* (US); May 1966, *R. W. Read 1662* (US).
 34. Sherwood Content: 228.6–247.32 m, Oct. 1955, *G. R. Proctor 11065* (IJ).
 35. Mt. Pantrepant: ca. 91.44 m, Nov. 1935, *L. H. Bailey 215* (BH).
 36. Windsor Cave: 152.4 m, Aug. 1955, *G. R. Proctor 10540, 15631* (IJ).

HANOVER

40. Silver Spring: near Fish River, 60.96 m, Mar. 1966, *R. W. Read & Ivor Cornman 1614* (K).
 41a. Lances Bay: 15.24 m, June 1966, *R. W. Read 1669* (S).

WESTMORELAND

42. Negril Hill: New Hope Estate, 53.34–76.2 m, Nov. 1955, *G. R. Proctor 11206* (IJ); inland from Revival, June 1966, *R. W. Read 1670* (US).

SOURCE UNKNOWN

1849 *Wulsschlagel #573* "Borassus flabelliformis L.?" (M);
 1878 *W. 1512*, 2 sheets (UCWI).

2. *Thrinax radiata* Lodd. ex J. A. & J. H. Schult.

Thrinax radiata Lodd. ex J. A. & J. H. Schult. in Linn. Syst. Veg. sec. 7(2):1301. 1830.—Mart., Hist. Nat. Palm. 3:257. 1838.—Kunth, Enum. Pl. 3:253. 1841.—Becc., Annal. Roy. Bot. Gard. Calcutta (Martelli ed.) 13:335. 1933 ["1931"]. [Type: Specimen in Herbarium Regium Monacense "e horto paris" (M).]

Coccothrinax radiata (Lodd. ex J. A. & J. H. Schult.) Sarg. ex K. Schum. in Just's Bot. Jahresb. 27 (1):469. 1901. [As to the type only, not subsequent usage and associations.]

Thrinax floridana Sarg., Bot. Gaz. 27:84. 1899; Silva 14:81, t. 735. 1902.—Small, Fl. S.E. U.S. p. 221. 1903.—Becc., Webbia 2:262. 1907.—Small, Fl. Fla. Keys p. 26. 1913.—Sarg., Manual Trees N. Amer. p. 97. 1926.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:328. 1933 ["1931"].—Read, Amer. Hort. Mag. (Ledin ed.) 40:28. 1961.—Read in Moore, Principes 7:168. 1963. [Type: *Sargent, Thrinax* no. 2, 14 Nov. 1898 ("cultivated at Miami from Long Key"), Florida (AAH).]

T. wendlandiana Becc., Webbia 2:265. 1907. nom. illeg.? Pomona Col. Journ. Econ. Bot. 3:403, f. 168. 1913.—Sarg., Manual Trees N. Amer. p. 97. 1926.—Burret, Sv. Vet.-akad. Handl. ser. 3, 6(7):10. 1929.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:332. 1933 ["1931"].—León, Fl. Cuba. 1:260. 1946. [Type: *Wright no. 3219* (1860–1864), Cuba (G).]

T. martii Griseb. et H. Wendl. ex Griseb., Cat. Pl. Cub. p. 221. 1866 [excluding elements of *Coccothrinax*]. [Type: *Jamaica. Robins* (Inflor.) Herb. Banks (BM).]

T. pumilio sensu Mart., Hist. Nat. Palm. 3:256, as to tab. 103, f. IV, 1–4. 1838 [et auct. non Lodd. ex J. A. & J. H. Schult. in Linn. Syst. Veg. sec. 7(2):1301. 1830].

Porothrinax pumilio H. Wendl. ex Griseb., Cat. Pl. Cub. p. 221. 1866 [pro parte, as to the specimen cited, not the type].

T. parviflora auct. non Sw.: Mart., Hist. Nat. Palm. 3:255, pro parte. 1838.—Sauv., Anal. Acad. Ci. Habana 7:563. 1871.—Vasey, Cat. For. Trees U.S., USDA Rept. no. 11. 1875:186. 1876.—Chapm., Bot. Gaz. 3:12. 1878; Fl. South. U.S. p. 651. 1883.—Sarg., Gard. & For. 9:162. 1896.—Becc., Webbia 2:255, pro parte. 1907.—Small, Journ. N. Y. Bot. Gard. 26:49. 1925; 31:58. 1930; Sci. Monthly 32:242. 1931.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:327, pro parte. 1933 ["1931"].—Small, Manual S. E. Flora p. 241. 1933.—Bailey, Gent. Herb. 4:135. 1938.—Buswell, U. of Miami Bull. 19(6):49. 1945.—Bailey, Gent. Herb. 8:991. 1949.—Bomhard, U. S. Dept. Agric. Inf. Bull. no. 22, p. 21. 1950.—Asprey & Loveless, Journ. Ecology 46:547–570. 1958.—Alain, Principes 5:68. 1961.—Long & Lakela, Fl. Trop. Florida p. 245. 1971.

T. excelsa sensu Bailey, Gent. Herb. 4:134. 1938 [non Lodd. ex Griseb., Fl. Brit. W. Ind. p. 515. 1864].

T. multiflora sensu Read in Adams, Fl. Pl. Jam. p. 76. 1972 [non Mart., Hist. Nat. Palm. 3:255, t. 103, f.l.a., t. 163. 1838].

Medium palm, (1.5–)2.0–10.0 (–12.0) m tall, caudex columnar, 8.1–11.6 (–13.0) cm in diameter, tapering out to an enlarged base and mound of roots, internodes 4–7 cm apart on lower trunk.

Leaf sheath 58.4–62.2 cm long, apex oblique down from petiole, tearing away from petiole and soon becoming coarsely fibrous, indumentum persistent on fibers; petiole 36–94 cm long, adaxially flat to slightly convex, 2.2–3.1 cm wide at sheath, rounded abaxially, 1.6–2.3 cm wide at narrowest and 2.1–3.2 cm wide at apex, abaxially with scattered scales, soon glabrescent or with few persistent

scales; hastula acuminate or sharply triangular, 1.0–1.9 cm long, often tending to decurve or split with the expansion of the blade, abaxially a short (0.1–0.4 cm long, flap or ridge, often with one or two rounded or toothlike prominences; unopened blade glabrescent on the adaxial nerves, scattered floccose scales on abaxial nerves and exposed surfaces.

Leaf blade, when expanded, circular in outline, 1.2–1.6 m in diameter, abaxial surface lighter in color than adaxial surface, abaxially dull, often glaucescent, flecked with conspicuous gray lepidia, zone around hastula yellow green, translucent when viewed from below against the light; principal nerves yellow green; palman 30–55 cm broad, relatively flat or slightly folded; segments 51–63 in number, narrowly trullate, often acuminate, with long slender apical filaments which are readily lost, (73–)79–113 (–115) cm long, (4.6–)5.1–6.2 (–6.4) cm wide, widest at sinus or rarely slightly above; fusion 30–55 cm long in palman, relatively uniform throughout blade, but gradually longer toward upper middle; center two segments near apex of blade often fused throughout their length, basal segments commonly overlapping.

Inflorescence erect, or arching slightly at anthesis, 1.2–2.2 m long, bracts green, with white or gray scales, 13–21 glabrous primary branches, the lowermost primary branches with (24–)27–37 ultimate branches, these white at anthesis, up to 12 cm long; pedicels at anthesis (1.4–)1.6–2.3 (–2.7) mm long; flowers white, fragrant, 46–56 per branch; stamens (5–)6–8 (–10) in number, anthers linear (2.0–)2.2–3.5 (–3.6) mm long when fresh, (1.7–)1.8–2.3 (–2.5) mm long when dry, filaments very narrowly connate basally, angle of connation acute or rounded.

Fruit 7.0–8.2 mm in diameter smooth, white at fresh maturity, green and slightly papillate shortly before; seed light brown 6.0–6.8 mm in diameter completely perforated; primary branches yellowish green at fruit maturity, pedicels (1.2–)2.0–5.0 (–5.2) mm long. Haploid chromosome number, $n=18$.

SPECIMENS EXAMINED.—JAMAICA. ST. THOMAS. Morant Point along the road to the lighthouse, on limestone near White Bay: Mar. 1954, *G. R. Proctor 8393* (IJ); Aug. 1955, *G. R. Proctor 10443* (IJ); Aug. 1954, *G. Webster & K. Wilson 5236* (IJ); Apr. 1963, *R. W. Read & G. R. Proctor 1142, 1143, 1144* (FTG); Feb. 1967, *R. W. Read 1791* (BH, US); July 1967, *R. W. Read 1959, 1960, 1961, 1962* (IJ, UCWI, US). HOLLAND BAY: 1952, *G. F. Asprey 2879* (UCWI). ST. MARY. Galina Point on dry coastal limestone, forming a woodland:

date unknown, *G. R. Proctor 15546* (IJ); Apr. 1956, *W. T. Stearn 775* (BH, UCWI); Apr. 1956, *A. R. Loveless 2879A* (UCWI); without date, *Collins 153* (US). CRAB WOODS, west of Galina: Nov. 1965, *R. W. Read 1553 & 1554* (US). ST. ANN. Queen's Highway between Discovery Bay and Bengal Bridge: Aug. 1955, *G. R. Proctor 10568* (IJ); Feb. 1957, *G. R. Proctor 16152* (IJ). ST. ANN'S BAY: Feb. 1931, *L. H. Bailey 15058* (BH). TRELAWNY. Near Salt Marsh on sea side of road: Apr. 1963, *R. W. Read 1149* (FTG). HANOVER. West of Lucea near the sea: Apr. 1963, *R. W. Read 1151* (FTG). RUTLANDS PEN, near Bloody Bay: Mar. 1966, *R. W. Read 1611* (US). WESTMORELAND. Near Negril Lighthouse: Nov. 1955, *G. R. Proctor 11132* (IJ). NEGRIL, on rocks near the sea: Mar. 1962, *C. D. Adams 10978* (UCWI). ST. ELIZABETH. Long Acre Point, west of Black River: Sept. 1907, *W. Harris 9957* (UCWI, US). LOCALITY UNKNOWN. "*Jamaica. Robins*" s. n. (BM, lectotype of *T. martii* Griseb. et H. Wendl. ex Griseb.).

HAITI. LA GONAIVE. Pointe Latanier: Aug. 1927, *E. L. Ekman H. 8841* (DA, IJ, S); "E troite": Aug. 1927, *W. J. Eyerdam 292* (US). DEPT. DU STD. Massif de la Hotte: western group, Les Roseaux, Oct. 1928, *E. L. Ekman H. 10782* (S).

CUBA. PROV. PINAR DEL RIO. Near Sabalo: Nov. 1920, *E. L. Ekman 11443* (S). Las Pozas: Apr. 1934, *G. Naleson for León 16102* (BH). PROV. HABANA. Vedado: 1929, *Brother León 14191* (BH). Batabanó: Nov. 1904, *Van Hermann 3928* (NY, US). Playa de Marianao: Feb. 1910, *N. L. Britton & P. Wilson 4557* (US); Mar. 1929, *L. H. Bailey 12529* (BH). Manano (?): scattered on high sand dunes, July 1905, *Van Hermann 898* (NY, US). PROV. CAMAGUEY. Cayo Guajaba: Nov. 1909, *J. A. Shafer 2846* (US). PROV. LAS VILLAS. Punta Diablo, Cienfuegos Bay: Mar. 1910, *N. L. Britton & P. Wilson 6044* (US). PROV. ORIENTE. Punta de Maisi: Mar. 1931, *L. H. Bailey 15145* (BH); Oct. 1934, *Hermano León 16192* (BH). Manati: June 1932, *Hermano León 15670* (BH). North of "Raimon," Nipe Bay: May 1909, *J. A. Shafer 1785* (US). "In Cuba Orientali, 1859, 1860": *C. Wright 2329* (AAH, GH, NY, US, syntypes of *T. wendlandiana*); 1860–1864, *C. Wright 3219* (G, lectotype of *T. wendlandiana*, F, GH, K, isotypes). Vicinity of P[B]aracoa: Feb. 1902, *C. L. Pollard, E. Palmer & W. Palmer 192* (US). ISLA DE PINOS. Boqueron, Ensenada de Signanea: Feb. 1916, *N. L. Britton, P. Wilson & A. D. Selby 14491* (US). Playa Bibijagua: Feb. 1956, *E. P. Killip 45604* (US).

MEXICO. YUCATAN. Downs of Progreso: Dec. 1865, *Schott 293* (US); (without date), *G. F. Gaumer 1100* (NY, US); May 1952, *H. E. Moore 6366* (BH). Santa Clara: 1959, *S. Kiem 329* (BH). Izamal: Mar. 1916, *G. F. Gaumer & Sons 23317* (NY, US); Mar. 1916, *G. F. Gaumer & Sons 23265* (NY). QUINTANA ROO. Puerto Juarez, sand dunes beside sea opposite Isla Mujer: Oct. 1959, *H. E. Moore 8086* (BH).

CENTRAL AMERICA. COUNTRY UNKNOWN. 1886, *G. F. Gaumer* s. n. (US). BRITISH HONDURAS. All pines: Aug. 1930, *W. A. Schipp 661* (NY). Belize District: Mile 29 Cayo Road, May 1960, *S. Kiem 605* (BH). HONDURAS. Forest near Bolet's plantation: Feb. 1903, *P. Wilson 360* (NY).

FLORIDA. DADE COUNTY. "Cultivated at Miami from Long Key": Nov. 1898, *C. S. Sargent no. 2* (AAH, holotype of *T. floridana*); Nov. 1898, *C. S. Sargent 202* (NY). Miami, cult.

from Keys: Oct.-Nov. 1901, *J. K. Small & G. V. Nash 347* (NY, US). COLLIER COUNTY. Cape Romano: May 1898, *C. S. Sargent s. n.* (AAH). Caximbas Island: Apr. 1892, *J. H. Simpson 180* (NY). Cape Sable: Oct. 1878, *A. P. Garber 43* (NY, US). Northwest Cape: Apr. 1916, *J. K. Small 7699* (NY, US). MONROE COUNTY. Sands Key: Mar. 1904, *N. L. Britton 344* (NY). Elliott Key: (cult. at Little River, Miami), Apr. 1932, *O. F. Cook s. n.* (US). Key Largo: Jan. 1909, *J. K. Small & J. J. Carter 2953* (NY). Lower Matecumbe Key: Apr. 1932, *O. F. Cooke & J. T. Presley s. n.* (US). Long Key: Jan. 1963, *R. W. Read 799* (US). Grassy Key: Feb. 1937, *E. P. Killip 32109* (US). Vacca Key: Jan. 1909, *J. K. Small & J. J. Carter 2959* (NY). Boot Key: Apr. 1909, *N. L. Britton 542* (NY). Big Pine Key: Jan. 1952, *E. P. Killip 41842* (US). Torch Key: May 1890, *A. H. Curtiss s. n.* (AAH). Water Key: Apr. 1932, *O. F. Cook & J. T. Presley s. n.* (NSC, NY, US). Racoon Key: Mar. 1898, *C. L. Pollard, G. N. Collins & E. L. Morris 101* (NY, US). Stock Island: Nov. 1955, *E. P. Killip 45097* (US). Area Unknown: Hammock, May 1917, *F. W. Pennell 9617* (US); Sykes Hammock, Sept. 1929, *H. O'Neill s. n.* (US).

BAHAMAS: Cat Cay, May 1905, *L. J. K. Brace 3753* (US).

SOURCE UNKNOWN: Specimen in *Herbarium Regium Monacense "E horto . . . paris"* (M, holotype of *T. radiata*).

DISCUSSION.—The name *Thrinax radiata* is the second oldest binomial published in the genus *Thrinax*. Having first been published by Renato Desfontaines (1829) without a description (but with a reference to Martius' unpublished work), the name therefore had no botanical standing. The following year, however, the father and son team of J. A. and J. H. Schultes took up the name but cited Loddiges, the English nurseryman, instead of Desfontaines as the earlier source of the name. Their short diagnosis, based solely on a small leaf, also included a reference to "Martius in litt." and Desfontaines' "Cat. h. paris." Among the specimens of the Herbarium Regium Monacense at Munich is a specimen of a juvenile leaf labeled "*Thrinax radiata* Lodd. E. horto . . . paris" (Figure 50), which is undoubtedly the one described and indicated in the Schultes publication as *Thrinax radiata*. No specimens were cited by either Martius or the Schultes team, but the reference to Martius and the original diagnosis pertaining to a juvenile leaf clearly indicate the specimen at Munich. A specimen of an inflorescence studied by León in 1939 at Paris (Herbario de Houliet) could not have been seen at the time of the original publication, since no mention of an inflorescence was made in the original diagnosis. The specimen at Munich, which I am designating as holotype, measuring 27 cm across, appears certainly to be either a *Thrinax* or

a *Coccothrinax* on sight; however, it was not possible until this past year to ascertain exactly its specific identity. Beccari had annotated the specimen as "*Thrinax ponceana* O. F. Cook?" but did no more. Following a thorough study of the laminar anatomy of all four species of *Thrinax*, their various biotypes and juvenile plants, it is now possible with known materials to identify unquestionably the true specific identity of the type specimen of *T. radiata*.

Eight years following the publication by the Schultes team, Martius' publication (1838) ap-

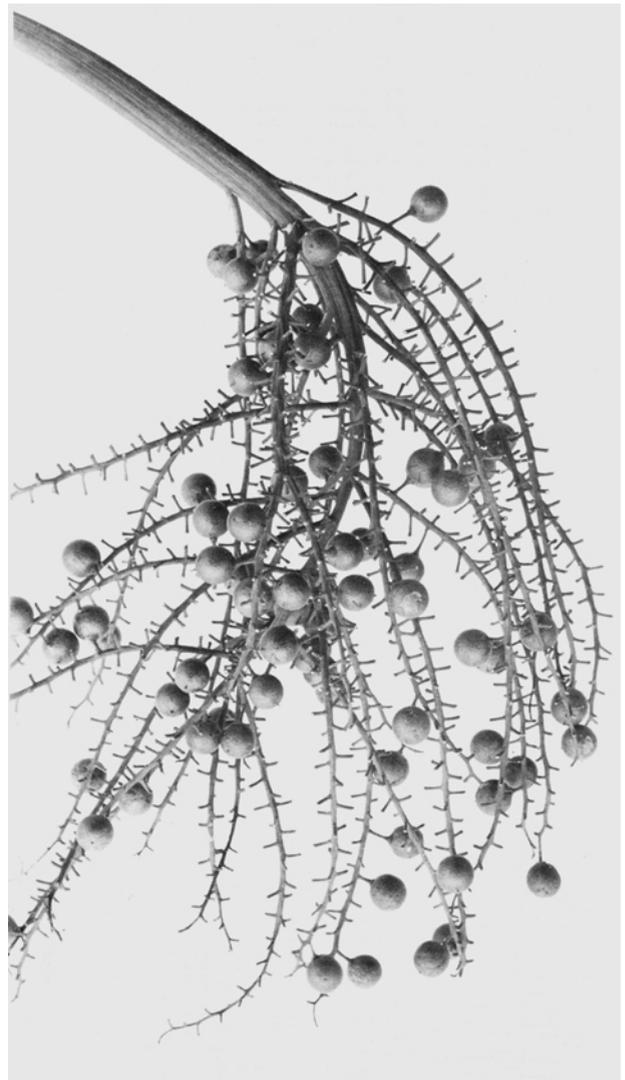


FIGURE 49.—A primary branch of the fruiting cluster with nearly mature fruits of *Thrinax radiata*.

peared with but little more to aid in the disposition of the name. The name *Thrinax radiata* appeared in Grisebach (1866) and again in Sauvalle (1871) but with no indication concerning its application in Cuba. Drude (1887) treated *Thrinax radiata* in his subgenus "I *Eu-Thrinax*" along with *T. parviflora* and *T. multiflora*. The subgenus was erected on the basis of seeds, but since no seeds of the original collection are known and no mention of seeds or fruits appeared in the original description, it is surprising to find *T. radiata* so treated.

The next significant publication concerning *Thrinax radiata* appeared when Sargent (1899)

created the new segregate genus *Coccothrinax*. For no indicated reason Sargent (p. 89) stated simply that, "*Thrinax argentea* R. & S.; *Thrinax radiata* R. & S.;" also "belong in *Coccothrinax*." Perhaps he was aware of another specimen of *Coccothrinax* flowers which has apparently been erroneously associated with the *T. radiata* type specimen. It remained for K. Schumann (1901) to make the correct combination in that genus. In 1933, Beccari treated the name as an "Imperfectly known or doubtful species." In 1939, Brother León, apparently unaware of the earlier transfer, published the "new combination" and elaborated on the original diagnosis with information from the specimen he had studied in Paris.

It is obvious that the description of *Thrinax parviflora*, which appeared in Martius (1838), contains several elements not applicable to the Swartz concept. Grisebach (1866) recognized this when he published *T. martii* based on "*T. parviflora* Mart. non Sw." Martius' literature citations apply to *T. parviflora* Swartz, but references to the leaves being "subtus parce floccosocanescentibus" (p. 225) and "Indumentum in pagina laminae inferiore parcum, e floccis albis decumbentibus constans" (p. 256) quite likely refer to *Coccothrinax*. The major portion of the description, however, applies to *Thrinax*, probably *T. radiata*. The locality citation: "Crecit in insula Jamaica, praesertim orientali, colles saxosos praediligens, nec tamen a locis depressis maritimis exulans," clearly indicates *T. radiata*, as does pl. 103 (the inflorescence to the left). This illustration corresponds amazingly well with the Robins' Jamaica specimen "spadices floridos in herbariis . . . et Banksiano asservatos" (p. 255) from which much of Martius' description was derived.

Since *Thrinax martii* (Griseb. & Wendl. was based primarily on the description and illustration by Martius (1838), and the "Jamaica Robins" specimen is the only one in the Banks herbarium which could represent the material used by Martius, it seems logical and in the best interest of nomenclatural stability to select that specimen as lectotype.

In 1907, Beccari founded a new species, *Thrinax wendlandiana*, partly based on collections made by Charles Wright in Cuba. A specimen in the Geneva Herbarium labeled "Plantae Cubensis Wrightianae No. 3219, coll. C. Wright, 1860-1864" was annotated by Beccari in 1907 with a note stating that

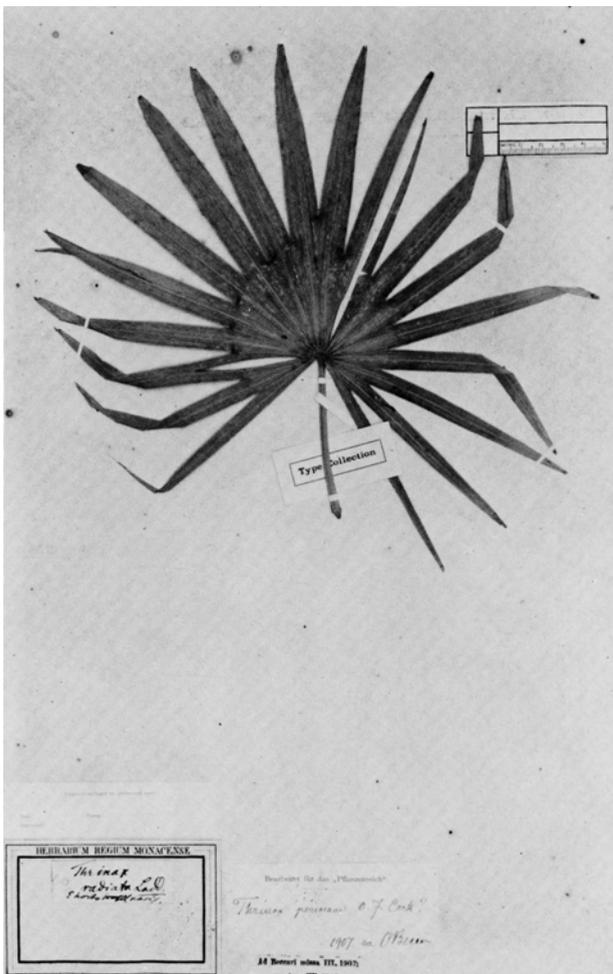


FIGURE 50.—The type specimen of *Thrinax radiata* from the Herbarium Regium Monacense, Munich.

Wright's number 3219¹⁴ was used in support of "Porothrinax pumilio (fructus) . . . *Thrinax Martii* (flores) . . . *Thrinax argentea* Mart. (folium) Griseb. Cat. Cub. p. 221." This sheet has an annotation label identifying it as "*Thrinax wendlandiana* Becc." and has also been labeled "Typus" but I am not certain by whom. Thus he further contributed to an already confusing nomenclatural mess.

Although Beccari cited "*Thrinax Martii* Gris. et Wendl. in Gris . . . (pro parte?)" for *Coccothrinax martii* Becc., he seems to have treated "Th. Martii Gris. et Wendl." in its entirety under *T. wendlandiana*. Therefore under the rules of priority *Beccari* should have taken up the epithet "*martii*" instead

¹⁴The Wright specimens are a source of considerable confusion, partly because some of the specimens have the same number, with a series of letters. These specimens must be examined at length and independently in order to determine their correct identity.

of using *T. wendlandiana*. All the Wright material cited under number 3219 has so far represented but a single taxon of *Thrinax*. It appears that Beccari (pp. 268 and 308) was separating out what he considered *Thrinax* elements under *T. wendlandiana* and referring the epithet to the genus *Coccothrinax*. It is obvious, however, from a study of the specimens cited, and lectotypified by Wright No. 3219, that *T. wendlandiana* is conspecific with *T. radiata*.

Vasey (1876) reported a palm from Florida, which he called *Thrinax parviflora*. A. W. Chapman (1878) confirmed this report when he reported the occurrence of the palm on the "Keys along the Florida Reef, extending up the west coast as far as Cape Romano." When Sargent (1896) published his first palm study he too used the name *T. parviflora*. The illustration (pl. 510) published at the same time depicted the inflorescence and fruit of what is presently known as *Coccothrinax argentea*,



FIGURE 51.—*Thrinax radiata* at Morant Point, Jamaica: A, leaf blade showing the broad flat palman, hastular region, and overlapping lower segments; B, plant with inflorescences in fruit with several new ones emerging from the crown.



FIGURE 52.—*Thrinax radiata* in natural habitat on the Florida Keys.

with a leaf of *Thrinax* in the background. Sargent (1899) later became convinced that the palm in Florida was not *T. parviflora* Sw., "but distinct from that species, as collected by Charles Wright in Cuba (no. 2329) and determined by H. Wendland." He therefore published a new binomial, *T. floridana*, based on its having "longer and stouter fruiting pedicels, smaller fruit and deeper seminal cavity." This new name again appeared in his revised palm study (1902), along with an illustration (fig. 735) clearly depicting the palm native to Florida.

Beccari accepted Sargent's new species and included it in his 1907 publication. It is important to note here that two names, which in the present study are considered synonymous, appeared in Beccari's key separated from one another and from *T. parviflora* by the use of such characters as perianth-lobe form, anther length, fruit, and seed size. Several noncomparative quantitative characters were also mentioned. As Small (1925) pointed out, "the diagnostic characters on record for the distinguishing of the two supposed species—*Thrinax floridana* and *T. Wendlandiana*—in Florida, may be found on the same plant." Beccari (1933) even went so far as to state that his *T. wendlandiana* also occurred in southern Florida at Madeira Hummock and at Pumpkin Key.

In 1925, Small wrote that, "judging from recent information and study," the Florida taxon "proves to be the same as *Thrinax parviflora* of the West Indies." Thus coming full circle to the original incorrect determination by Vasey half a century earlier. Although Small had not arrived at the correct conclusion concerning the name of the taxon, he had, however, concluded that the reason for the confusion lay in the fact that "decisions were based on too scanty material, where ample specimens should have been or could have been secured"; and, "secondly, the main studies were made in the closet instead of in the field."

When Bailey (1938) published his study of *Thrinax*, he followed Small's application of *T. parviflora*. Although Bailey used the incorrect name, he was the first to recognize that the palms collected and described under various names from the littoral of Haiti, Jamaica, Cuba, Florida, The Bahamas, Mexico, and British Honduras were members of a single taxon. When Bailey examined the three specimens of "*Thrinax parviflora*" in the col-

lection of the Stockholm herbarium, he believed them to represent a single taxon; however, he selected one sheet about which he stated: "That sheet undoubtedly may be considered authentic *Thrinax parviflora* of Swartz." It was unfortunate that he chose to draw his information and characterization of that species from an altogether different sheet, for the sheet Bailey chose (1938: fig. 81) contained a large portion of an inflorescence (figure 45A) which was labeled as "*Sabal umbraculifera*" as recently as 1907. (See discussion of Swartz' type and typification under *T. parviflora*.)

Bailey's key (1938) to the species of *Thrinax* utilized quantitative characters such as size of fruit and leaf segments, and differences in the dried epidermis of the fully developed but not necessarily "mature" fruit. The so-called differences in the abaxial surface of the leaf¹⁵ vary on a single plant depending on the age of the leaf selected. The hastula was mentioned in support of "*T. parviflora*" and the "spathelets" were mentioned in support of "*T. excelsa*," but they are not reciprocally compared. *Thrinax radiata*, although distributed over 1000 miles across the northern Caribbean and on many different islands, varies slightly in quantitative characters but maintains its peculiar individuality as a single species. Although Bailey found no appreciable differences between the Florida plants and those of Cuba, Haiti, and Central America, he nevertheless selected a plant collected by Britton in coastal thickets of Jamaica as typical of *T. excelsa*.

At the turn of the century misconceptions and confusion regarding *Thrinax* pervaded every attempt to revise the genus. Britton collected *Thrinax radiata* in both the Bahamas and Jamaica, and identified the plants as *T. parviflora*, although he (1908) stated that *Thrinax excelsa* "from Jamaica, is abundant on that island and distinct from *T. parviflora*, to which it is doubtfully referred by Beccari." It is difficult to know what plants were considered *T. excelsa* by Britton, for his specimens from Morant Point, Jamaica, were identified as *T. parviflora*, and the specimens from the John Crow Mountains formed the type of his new species

¹⁵Varying reports of the color of the abaxial leaf surface seem to stem from different impressions and the use of vague descriptive terminology such as "indifferently lighter colored," "whitish or silvery," "glaucous or whitish," "silvery-white," all of which have at one time or another been applied to the Florida taxon.

T. rex. Bailey accepted Britton's identification of the Bahamian material but referred the Jamaican collections to *T. excelsa*. Bailey was unfamiliar with "*T. excelsa*" in Jamaica, for he wrote in 1938 that the taxon was

known to me as a living plant only in cultivation in Jamaica, Cuba, Trinidad, Ciudad Bolivar on the Orinoco, and British Guiana. It is conspicuous in its ample bright green or yellowish-green leaves lighter colored underneath, full broad segments, and white or nearly white soft-fleshed bead-like large berries; petiole broad, obtuse at margins and compressed. It is a handsome palm. I have seen it in cultivation under the names *T. parviflora* and *T. floridana*.

While working on the genus in Jamaica the present author decided on the basis of available information that the taxon under consideration was actually conspecific with Martius' *Thrinax multiflora*. It was clear then, as now, that the text and plates published in support of *T. multiflora* contained several taxa. Since no type specimen was known at the time, an attempt to sort out the recognizable taxa resulted in the designation of the only known species of *Thrinax* from Haiti (excluding Navassa) as *T. multiflora* and relegating the miscellaneous described or figured taxa to other names. Alas a type specimen does exist, with a label in what appears certainly to be Martius' own hand, in the Herbarium Regium Monacense, Munich. There is now no doubt about its being a *Coccothrinax*, but not the same as the one identified as *Thrinax argentea* by Martius.

COMMON NAMES.—This palm has been known in Florida under a variety of names such as Florida thatch, Jamaican thatch, or just plain thatch. Small (1925) called the palm "silk-top thatch." In Jamaica the palm may be called sea thatch or simply thatch, pronounced "tatch." In Cuba the names "guano de costa," "miraguano de lana," and "guano campeche" were reported by León (1946). The species may also be known as "latanier-la-mer" or "guanillo" in Haiti and the Dominican Republic. A note on a specimen collected in 1959, by Dr. H. E. Moore indicates that the palm was called "chit" at the Downs of Progreso, Mexico, where it was collected.

3. *Thrinax excelsa* Lodd. ex Grisebach

Thrinax excelsa Lodd. ex Griseb., Fl. Brit. W. Ind. p. 515. 1864.—Hook., Bot. Mag. t. 7088. 1889.—Read in Adams,

Fl. Pl. Jam. pp. 75–76. 1972. [Type: Specimen from the plant illustrated in Bot. Mag. t. 7088 (K).]
T. rex Britt. & Harris, Bull. Torr. Bot. Club 37:352. 1910.—Howard, R. A., *Principes* 4:133. 1960. [Type: *Britton 4151*. "Eastern slopes of John Crow Mountains at 450 to 600 meters altitude," Jamaica (NY).]

Large palm, 3–11 m tall, caudex columnar 12.5–16.0 (–20.0) cm in diameter; leaf sheath 70–90 cm long, apex long linguiform, soon tearing away from petiole, not netlike, densely tan velvety throughout; petiole (1.2–)1.6–2.2 m long, densely persistent white to tan velvety lepidote abaxially, 4.0–4.5 cm wide at sheath, 2.5–3.9 cm wide at apex; hastula irregularly truncate to broadly acute 1.8–2.5 cm long, 3.4–3.9 cm wide, abaxially often with a retuse prominence to 4 mm long near the middle; unexpanded blade portion densely white to tan lepidote on all surfaces.

Leaf blade when expanded (2.0–)2.3–3.5 m in diameter circular in outline but with the outer segments not overlapping, free portion of segments drooping slightly; palman relatively flat 45–100 cm broad; segments (52–)55–65 in number, narrowly obovate, 114–172 cm long, 4.4–7.4 cm wide, widest at the sinus, fused for 45–100 cm in the palman, rather uniformly throughout the blade, slightly longer toward the upper center, bifid at apex, 3.10 cm deep, abaxial surface white to silvery densely lepidote with interlocking fimbriate hyaline scales.

Inflorescences 140–170 cm long, always arching at anthesis, primary bracts brown with rufous appressed scales, primary branches (10–)15–17 in number, about 27–30 cm long at anthesis, with 37–47 rachillae each, glabrous, pink to purple at anthesis; flowers rosy pink, fragrant (odor of rum and spice), pedicelled, 90–114 per rachilla, bracteoles shorter than the pedicels; stamens (6–)7–10 (–11) in number, anthers (1.2–)1.4–1.9 (–2.1) mm long, exceeding pistil in length, stigmatic area a simple slit in the apex of the style.

Fruit 8.0–10.1 (–11.0) mm in diameter, pedicels 0.4–3.5 mm long; rachillae up to 17.7 cm long, lowermost 3.7–4.5 mm thick at the point of insertion on rachis; seed 5.9–6.0 in diameter, completely intruded from base to apex by testa. Haploid chromosome number, $n=18$.

SPECIMENS EXAMINED.—JAMAICA. ST. THOMAS. "Woodlands, eastern slopes of south end on John Crow Mountains," "520 m alt.": Mar. 1909, N. L. Britton 4151 (NY, lectotype: *Thrinax rex*); Mar. 1909, Wm. Harris & N. L. Britton 10759

(NY, UCWI, US; syntypes: *Thrinax rex*). Southwestern slopes of Winchester Peak, between Wheelerfield and Johnson Mountain: Feb. 1966, R. W. Read 1581 (US); Mar. 1966, R. W. Read 1625 (BH, K, UCWI); Mar. 1966, R. W. Read 1621 (US); July 1966, R. W. Read 1682 (BH, IJ, K, UCWI); Feb. 1967, R. W. Read 1792 (US); 29 Aug. 1967, R. W. Read & H. E. Moore 1963 (BH, US). PORTLAND. Uncommon Hill above Fruitful Vale: Apr. 1954, G. R. Proctor 8537 (IJ). Eastern slopes of John Crow Mountains above Ecclesdown: Aug. 1955, G. R. Proctor 10483 (IJ); Mar. 1961, C. D. Adams 9387 (UCWI); Apr. 1963, R. W. Read & G. R. Proctor 1145 (FTG).

CULTIVATION: Kew Gardens, May 1889 (K, holotype; specimen from plant illustrated in *Bot. Mag.*, pl. 7088).

DISCUSSION.—The specific epithet *excelsa* first appeared, without a description, in a catalog of palms published in 1845 by Conrad Loddiges & Sons,

nurserymen. This very old firm, at Hackney near London, introduced and gave names to a number of palms up to that time. Many of the names that appeared in their earlier catalogs had been taken up by several botanists before 1845; however, as far as can be determined the palms were all juvenile plants, and it was seldom possible to identify the names with living plants. The Loddiges catalog attributed *T. excelsa* to Cayenne.

August H. Grisebach (1864) published the name *Thrinax excelsa* Lodd. with a description based on a plant grown at Kew and notes supplied by Dr. Joseph Hooker. Presumably the plant at Kew was already labeled with the Loddiges name. *Thrinax excelsa* was described by Grisebach as being 7 feet 7 inches tall and had a trunk 8 inches thick at the



FIGURE 53.—*Thrinax excelsa*: A, in its natural habitat on the John Crow Mountains of eastern Jamaica; B, an average-size leaf held by Winston Barrett, an assistant to George Proctor of the Institute of Jamaica.

time it flowered at Kew. The Kew Report for 1882 recorded that the plant of *T. excelsa* had grown to 20 feet tall, an increase of 12 feet 5 inches in about 18 years. Grisebach (p. 515) further described the palm as having

leaves pale-green above, hoary-glaucous beneath by minute, appressed down, divisions united to about one-third: "ligule bluntly deltoid;" sheath densely coated with buff-coloured cotton. . . . leaves 4'-5' long, about 50-fid: divisions about 2' long, 3"-1" broad; "ligule 15" long;" spadix branches spreading-recurved, its axis 1' long, naked below; spathe

rusty-tomentose; berry globose, 3''' diam.—Hab. Jamaica!, Hort. Kew.

Hooker (1889: pl. 7088) depicted *Thrinax excelsa* as a plant with a broad circular leaf, white on the undersurface and having a pink inflorescence. A comparison between plants now growing in the John Crow Mountains in eastern Jamaica, with Grisebach's description and pl. 7088, leaves no doubt that they are true *T. excelsa*. Unfortunately the color of the inflorescence was not mentioned by



FIGURE 54.—Ripe fruit and flowers post anthesis of *Thrinax excelsa*. Notice the silvery undersurface of the leaf blade, lower left.

Grisebach and little notice was taken of the color illustration in *Botanical Magazine*.

It is not known how the nurserymen in the United States first came to apply the name *T. excelsa* erroneously to a form of *T. radiata* being cultivated in Florida, but the name has been common among the nursery trade for many years, up to the present. When discussing his newly described *T. floridana*, Sargent (1899) stated that, "This is the *Thrinax excelsa* of Florida nurserymen but not of Grisebach in Jamaica, . . . the number of stamens is said to be nine although this fact does not appear in the recent description of the species in the *Botanical Magazine* (115:pl. 7088)."

In 1907, Beccari apparently became confused by the name *T. excelsa* as it appeared in the literature. He listed *T. excelsa*, of *Botanical Magazine* t. 7088, as equivalent to *Coccothrinax argentea* with a question mark, no doubt because of the white undersurface of the leaf. In the same list of names excluded from the genus he stated that the *T. excelsa* listed by Wendland in Kerchov de Denterghem (1878) was said to have originated in French Guiana, although nothing in that work has been found to confirm this. Then as a final gesture to what is without a doubt the most magnificent palm in the genus, he relegated "*T. excelsa* (Lodd.?) Grisebach" to synonymy with *Thrinax parviflora*.

A year after the publication of Beccari's work, Britton (1908) wrote in a review of the work that "*Thrinax excelsa* Lodd., as described by Grisebach, from Jamaica, is abundant on that island and distinct from *T. parviflora*, to which it is doubtfully referred by Beccari." Britton's criticism of Beccari's work for the most part was just, but in regard to *Thrinax*, which he referred to as "probably the most difficult of the American genera," he did not understand the complexities of the genus. Beccari did not "doubtfully" refer the species to *T. parviflora*, he only questioned the Loddiges authorship. Britton was correct that the species is distinct from *T. parviflora*, although present indications are that he was not thinking of *T. parviflora* Sw. but of other authors, and what he thought to be true *T. excelsa* of Jamaica is in fact the same *T. excelsa* of Florida nurserymen (i.e., *T. radiata*). Britton and Wm. Harris (1910) jointly published a "Hitherto Undescribed Species of Jamaica," *Thrinax rex*, discovered on the "Eastern slopes of the John Crow Mountains at 450 to 600 meters altitude."

In the report on the Jamaican collecting trip, Britton wrote (1909:102) that

the most noteworthy tree is a magnificent fan-leaved palm of the genus *Thrinax*, with leaves of young plants over ten feet in diameter, the old trees with trunks up to 60 feet high or perhaps even higher and nearly a foot in diameter, truly the monarch of the genus, and a splendid addition to our knowledge of it.

In the 1933 posthumous publication of Beccari's *Coryphea*, the only alteration in the disposition of "Imperfectly known species" was the citation "*Thrinax excelsa* Lodd. ex. Grisebach Fl. Brit. W. Ind. 515. = *Thrinax Harrisiana*. Becc.?" If indeed this were so then the converse would be more correct, *Thrinax harrisiana* Becc. would be a synonym of *T. excelsa* because it is a later name. Thus it remained in the confusion that has persisted up to the present.

Bailey (1938) accepted *Thrinax rex* without question, and the name *T. excelsa* was used for an altogether different taxon in Jamaica. The taxon to which Bailey applied *T. excelsa* is the same as that mentioned earlier by Sargent as the *T. excelsa* of the nursery trade and if not identical to the Florida taxon at least of the same species. (For a discussion of Bailey's use of *T. parviflora* and *T. excelsa* see the discussion of *T. radiata*). The specific epithet *excelsa* is still commonly misapplied to the common Thatch Palm in landscaping, nursery trade, and botanical gardens around the world.

The palm described so enthusiastically by Britton (1909) and Britton and Harris (1910) was not collected again until 1951 when George R. Proctor of the Institute of Jamaica "rediscovered" it while on a journey into the mountains. It was collected again in 1959 when Dr. R. A. Howard of the Arnold Arboretum climbed the John Crow Mountains in search of living material for introduction into cultivation. He wrote of his experiences in 1960. Although he felt that "*T. tessellata*" (*T. parviflora*) was "quite common and generally undistinguished," his impression concerning *T. excelsa* was quite different for he wrote that, "*Thrinax rex* [sic], however lives up to its name and even the most hardened botanical travellers pay quiet homage in looking up to this giant of the genus" which, he further commented, "exists in isolated splendor in one of the most humanly difficult environments of Jamaica."

The latest extension of the known range of *T.*

excelsa was discovered in July of 1973 when the author and Dr. Ornduff of the University of California were on a raft trip down the Rio Grande in Portland, Jamaica. Numerous large and small plants were observed growing on the cliffs of limestone called "Two Rocks" overhanging a section of the river. The most unusual aspect of this discovery is that the species is found well below its normal elevation at about 60 m above sea level and only a couple miles from the mouth of the Rio Grande near Port Antonio.

COMMON NAMES.—*Thrinax excelsa* grows in a region of tumbled, jagged crags of honeycomb limestone where few people manage to enter. Because of the inaccessibility of the region, the palm is not well known even among the native people and therefore lacks a definite common name. Upon questioning some workmen in the area only one person knew of a palm on the ridge, which he called "broad thatch."

4. *Thrinax morrisii* H. Wendland

- Thrinax morrisii* H. Wendl., Gard. Chron. (ser. 3) 11:104, f. 20, 21. 1892.—Britt. & Wilson, Sci. Sur. Porto Rico . . . 5:117. 1923.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:334. 1933 ["1931"].—Bailey, Gent. Herb. 4:143. 1938. [Type: *H. A. Alford Nicholls*, Nov. 1891. Blowing Point, Anguilla, West Indies (K).]
- T. microcarpa* Sarg., Gard. For. 9:162. 1896; Silva 10:53, t. 511. 1896; Bot. Gaz. 27:87. 1899; Silva 14:80. 1902.—Small, Fl. S.E. U.S. p. 222. 1903.—Sarg., Manual Trees N. Amer. p. 105. 1905.—Becc., Webbia 2:277. 1907.—Britt., Torreya 8:240. 1908.—Britt. & Wilson, Sci. Sur. Porto Rico. 5:117 (pro parte). 1923.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:333. 1933 ["1931"].—Bailey, Gent. Herb. 4:141. 1938. [Type: *A. H. Curtiss* 2679***, June 1879. No Name Key, Florida (NY).]
- Simpsonia microcarpa* (Sarg.) O. F. Cook, Science (n. s.) 85: 333. 1937. [Nom. illeg. Type: *Thrinax microcarpa* C. S. Sargent.]
- T. keyensis* Sarg., Bot. Gaz. 27:86. 1899; Silva 14:83. 1902.—Small, Fl. S.E. U.S. p. 222. 1903.—Sarg., Manual Trees N. Amer. p. 104. 1905.—Becc., Webbia 2:274. 1907.—Britt., Torreya 8:240. 1908.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:333. 1933 ["1931"]. [Type: *C. S. Sargent* 1886. "North shore of the largest of the Marquesas group of islands . . ." Florida (AAH).]
- T. ponceana* O. F. Cook, Bull. Torr. Bot. Club. 28:536. f. 45. 1901.—Becc., Webbia 2:282. 1907.—Britt., Torreya 8:240. 1908.—Urban, Symb. Antill. 4:128. 1911.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:334. 1933 ["1931"]. [Type: *O. F. Cook* 1005, "dry limestone hills which skirt the southern coast . . . to the west of Ponce." Puerto Rico—the specimen in the USNM does not have a number attached, but the parts are labeled, presumably by O. F. Cook, as "*Thrinax ponceana* CK (Type)," (US).]
- T. praeceps* O. F. Cook, Bull. Torr. Bot. Club. 28:536. 1901.—Becc., Webbia 2:287. 1907.—Urban, Symb. Antill. 4:128. 1911.—Becc., Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:335. 1933 ["1931"]. [Type: *L. M. Underwood & R. F. Griggs* 850, 13 July 1901, "precipitous mountain-side . . . between Utuado and Arecibo . . ." Puerto Rico (US).]
- T. bahamensis* O. F. Cook in Northrop, Mem. Torr. Bot. Club. 12:20. 1902.—Britt., Torreya 8:240. 1908. [Type: "Big Cabbage Creek, Andros Island," Bahamas, June. No specimen was cited but there is material in the USNM with a label that reads "No. 668 *Thrinax bahamensis* CK type," collected by *Dr. & Mrs. John D. Northrop*.]
- T. drudei* Becc., Webbia 2:269. 1907; Pomona Coll. Journ. Econ. Bot. 3:404. 1913; Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:332. 1933 ["1931"].—Bailey, Gent. Herb. 4:148. 1938. [Type: "Cuba. Plantae Cubenses Wrightianae n. 3965 col. nome di *Thrinax multiflora* nell' Erbario di Berlino ed in quello della Harvard University" (B, destroyed, GH, lectotype).]
- T. punctulata* Becc., Webbia 2:280. 1907; Pomona Coll. Journ. Econ. Bot. 3:405. 1913; Annal. Roy. Bot. Gard., Calcutta (Martelli ed.) 13:334. 1933 ["1931"].—Bailey, Gent. Herb. 4:146. 1938. [Type, *Van Hermann* no. 4245, 10 December 1904. Prov. Pinar del Rio, Monte Guanajay, Cuba (identified as *Thrinax multiflora*) (B, destroyed, NY lectotype).]
- T. ekmanii* Burret, Sv. Vet. akad. Handl. ser. 3, 6(7):27. 1929.—Bailey, Gent. Herb. 4:147. 1938. [Type: *E. L. Ekman* H. 10839, 23 Oct. 1928. Navassa Island, near the lighthouse, Haiti (identified on sheet as "*Thrinax wendlandiana* Becc. var *glauca* Ekm. et Burret") (S).]

Small to medium palm, 1–10.5 m tall; caudex columnar, slightly tapering upward, ashy gray, smooth, but leaf and inflorescence scars prominent, becoming rimose with age, (5–)8–35 cm in diameter at the base; leaf sheath 28–60 cm long, at first long linguiform, soon breaking apart, and separating from the petiole apically, becoming somewhat netlike, densely tan to white velutinous at first, soon becoming glabrescent; petiole 27–84 cm long, at first densely white lepidote abaxially, soon glabrescent, (1.0–)1.5–2.0 (–2.1) cm wide at the sheath, 0.7–1.6 (–2.0) cm wide apically; hastula ovate-obtuse, rarely pointed, erect, thin, 0.2–0.8 cm long, ca 3 cm wide, densely velutinous, ciliate, often with dense conspicuous tufts of white or silvery indumentum when first exposed, soon becoming glabrescent; abaxial hastula rather inconspicuous, densely, white lepidote; unexpanded bud leaf (blade portion) densely appressed lepidote on all surfaces; expanded leaf usually glossy green adaxially; variously lepidote abaxially, with spreading,

interlocking, fimbriate, hyaline scales (especially when freshly expanded), becoming glabrescent in age, otherwise glaucous, blue green as a result of numerous minute white dots in rows associated with sunken stomata, the abaxial leaf color variously interpreted, depending on age and exposure; blade ca 75–150 or more cm in diameter, nearly circular in outline, the segments rarely lying in the same place (except in juveniles), the outer or lower segments often folded up and forward toward the apex of the blade; palman ca 12–42 cm broad; segments, rigid or lax, ca 33–58 in number, narrowly trullate to rhombic, pinched or not about midway; the longer middle segments 55–75 cm long, (2.3–) 3.5–4.8 cm wide (at widest part), widest at point of fusion, apically bifid, 2–8 cm deep.

Inflorescence 55–150 cm long, erect or arcuate, equaling or greatly exceeding the leaves in length;

primary bracts silvery white to tan lepidote, often with apical tufts of long white scales; primary branches glabrous, pendant, or tufted-arcuate (when not fully exposed in some specimens), 9–21 in number, (8–)9–30 (–35) cm long at anthesis; ultimate branches 20–50 in number, 5.5–14.5 (–20) cm long, subtended by a narrowly triangular bract which is conspicuously tufted apically with white hyaline scales; flowers white; becoming pale yellowish or even pale orange with age, situated on inconspicuous disklike pedicels; bracteoles triangular; perianth lobes mostly acute, triangular, apiculate, rarely attenuate or abruptly rather long apiculate; stamens mostly 6 in number; filaments broadly connate basally into a cup or ring often equaling the perianth; anthers (0.8–)1.0–1.8 (–2.0) mm long, exceeding the pistil in length; stigmatic area infundibuliform, often ciliate, the ovary often becoming orange post-

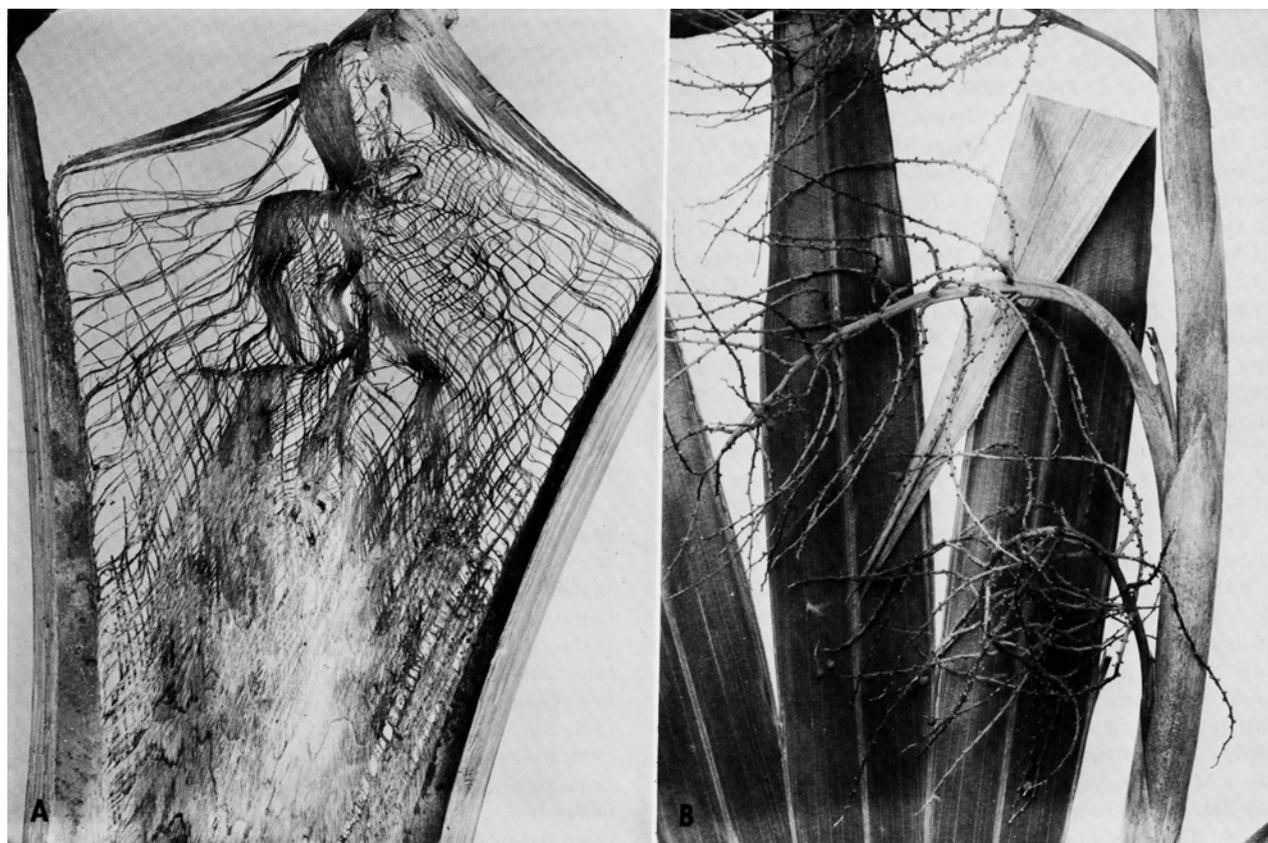


FIGURE 55.—*Thrinax morrisii*: A, leaf sheath; B, leaf segments and a portion of the inflorescence with its bumplike pedicels. Notice the white undersurface of the folded down segment. (Photographs from the O. F. Cook files.)

anthesis; fresh ripe fruit (3.5–)4.0–4.5 (–8.0) mm in diameter (varying as much as 2 mm diameter on a single inflorescence), globose, with a persistent style; pedicels (0.0–)0.1–0.6 (–0.8) mm long; seed depressed globose, mahogany brown, (2.3–)2.7–4.2 (–5.0) mm in diameter, mostly only partly intruded by a conical cavity basally.

SPECIMENS EXAMINED OR CITED.—LESSER ANTILLES. Barbuda. Near river landing: May 1937, *H. E. Box 668* (BH, US). Southwestern part of island: South of the lagoon, sea level, Apr. 1956, *A. C. Smith 10459* (BH, US). Near sand dunes: Jan. 1947, *L. R. Hutson 2* (BH). ANGUILLA. Blowing Point: Dec. 1890, *D. Morris* (K, not seen, syntype of *T. morrisii*); Nov. 1891, *H. A. A. Nicholls* (K, not seen, lectotype of *T. morrisii*); Jan. 1950, *I. Velez 3749* (US). Long Bay Hill: June 1974, *R. W. Read 74–213* (US).

PUERTO RICO AND OFFSHORE ISLANDS. PUERTO RICO. Dry limestone hills west of Ponce: *O. F. Cook "1005"* (US, holotype of *T. ponceana*); Nov. 1902, *A. A. Heller 6125* (G, US); Jan. 1949, *L. H. Bailey 603* (BH). Ponce to Penuelas: Mar. 1906, *N. L. Britton & J. F. Cowell 1300* (US). Tallahoa, near Ponce: May 1932, *L. H. Bailey 30 & 30x* (BH). Near Fajardo: May 1885, *P. Sintenis 1324* (US). Yauco: May 1935, *F. H. Sargent 666* (US). Salinas de Cabo Rojo: Feb. 1885, *P. Sintenis 100* (G). Guanica: Mar. 1915, *N. L. Britton, J. F. Cowell & S. Brown 4917* (US); Jan. 1886, *P. Sintenis 3500* (G, US). Road from Utuado to Arecibo: July 1901, *L. M. Underwood & R. F. Griggs 850* (US, holotype of *T. praeceps*); Mar. 1914, *N. L. Britton & J. F. Cowell 2049* (US). South of Arecibo: May 1932, *L. H. Bailey 64* (BH). Camuy to Quebradillas: Mar. 1914, *N. L. Britton & J. F. Cowell 1953* (US). Lares: June 1901, *L. M. Underwood & R. F. Griggs 38* (US); Apr. 1913, *N. L. Britton, E. G. Britton & W. E. Hess 2750* (US). Between Toa Baja and Espinoza: Apr. 1921, *E. E. Barker s. n.* (BH). West of Vega Baja: Mar. 1922, *N. L. Britton, M. S. Brown & C. E. Chardon 6811* (US). Corozal: Mar. 1923, *N. L. Britton & E. G. Britton 7829* (BH, US). Near Bayamón on Mogotes: June 1968, *R. W. Read 2058, 2059* (US). Guajateca Beach: Jan. 1962, *Bro. Alain 9090* (IJ). MONA ISLAND. Mar. 1955, *E. L. Little & M. L. Kuns 16528* (US). VIEQUES ISLAND. Feb. 1914, *J. A. Shafer 2796* (US).

TURKS AND CAICOS ISLANDS. FIVE CAYS. Providenciales: July 1954, *G. R. Proctor 9181* (IJ).

BAHAMA ISLANDS. GREAT BAHAMA. Apr.–May 1905, *L. J. K. Brace 3709* (US). NEW PROVIDENCE. Nov. 1937, *L. H. Bailey 1054* (BH); Nassau: Mar. 1903, *A. H. Curtiss 101* (US); July 1903, *W. C. Coker 539* (US). HOG ISLAND (Paradise Island). Freshwater Pond: Feb., 257 (? syntype of *T. bahamensis*); July 1962, *R. W. Read 840* (US). ELEUTHERA. Feb.–Mar. 1907, *E. G. Britton 6515* (US). ANDROS. Big Cabbage Creek: *Dr. & Mrs. J. D. Northrop 668* (US, holotype of *T. bahamensis*). Margin of Fresh Creek Lagoon: Mar. 1966, *E. Y. Dawson 26650* (US). Key near Mastic Key: Nov. 1937, *L. H. Bailey 1046* (BH). Near Fresh Creek: *J. K. Small & J. J. Carter 8757* (US). Deep Creek: Aug.–Sept. 1906, *L. J. K. Brace 5183* (US). West Side, in Loggerhead Creek region: Nov. 1937,

L. H. Bailey 1009 (BH). GREEN CAY. July 1903, *W. C. Coker 250* (US). WATLINGS ISLAND (San Salvador). July 1903, *W. C. Coker 529* (US); date unknown, *W. C. Coker 481* (US). MAYAGUANA. Feb. 1973, *W. Gillis & G. R. Proctor 11585* (GH, IJ, US).

FLORIDA. MONROE COUNTY. Key Largo: May 1923, *J. K. Small, C. A. Mosier & J. B. DeWinkeler 10950* (US); Jan. 1925 *L. H. & E. Z. Bailey 6162* (BH); Aug. 1929, *J. K. Small & C. A. Mosier "a" & "c"* (BH). Lower Matecumbe Key: Apr. 1932, *O. F. Cook & J. T. Presley* (US). Long Key: Jan. 1963, *R. W. Read 797* (US). Grassy Key: Jan. 1963, *R. W. Read 798* (US). Ram Rod Key: Apr. 1932, *O. F. Cook & J. T. Presley* (US). Saddle Bunch Key: Mar. 1898, *C. L. Pollard, G. N. Collins & E. L. Morris 23* (US). Big Pine Key: Apr. 1932, *O. F. Cook & J. T. Presley* (US); Aug. 1935, *L. H. Bailey 42* (BH); Aug. 1929, *J. K. Small & C. A. Mosier "b"* (BH); Feb. 1937, *E. P. Killip 32025* (US); Feb. 1935, *E. P. Killip 31436* (US); Jan.–Feb. 1940, *R. F. Martin, 1328* (US); Mar. 1936, *E. P. Killip 31717* (BH US); June 1963, *R. W. Read 923* (US). No Name Key: June 1879, *A. H. Curtiss 2679**** (NY, holotype of *T. microcarpa*, US); May 1891, *J. H. Simpson 268* (US); 1881, *A. H. Curtiss No. H* (NY, US); June 1895, *A. H. Curtiss* (US); July 1927, *H. O'Neill* (US); Nov. 1929, *O. F. Cook* (US); Apr. 1932, *O. F. Cook & J. T. Presley* (BH, US). Marquesas Keys: north shore of the largest, 1898, *C. S. Sargent* (AAH, not seen, holotype of *T. keyensis*); Aug. 1935, *L. H. Bailey 44* (BH). CULTIVATED. Royal Palm Hotel, Miami: Feb. 1925, *L. H. & E. Z. Bailey 6350* (BH); Mar. 1925, *L. H. Bailey 6474* (BH). C. T. Simpson's place, Little River: Feb. 1925, *L. H. Bailey 6342* (BH); Apr. 1932, *O. F. Cook & J. T. Presley* (US); June 1928, *O. F. Cook* (US). USDA Plant Introduction Station, Miami: Feb. 1952, *H. E. Moore 6010* (BH); Sept. 1962, *R. W. Read 782, 781*, (US); *R. W. Read 1437* (BH). Fairchild Tropical Garden, Coral Gables: June 1962, *R. W. Read 771* (US); Apr. 1965, *R. W. Read 1409* (BH, FTG, Voucher for chromosome number); June 1969, *DeArmand Hull H-41* (BH, Voucher for M Sc. Thesis). SOURCE UNKNOWN. Florida 1915 (US).

HAITI. NAVASSA ISLAND. Oct. 1928, *E. L. Ekman H. 10839* (S, holotype of *T. ekmanii*; US); June 1956, *G. R. Proctor 15468* (IJ, US); Feb. 1960 *S. Kiem* (BH).

CUBA. PROV. CAMAGUEY. Cayo Cruz: Oct. 1909, *J. A. Shafer 2800* (US). Cayo Romano: Punta Jucaro, Oct. 1909, *J. A. Shafer 2602* (US). Cayo Ballenato Grande: Mar. 1909, *J. A. Shafer 947* (US). PROV. MATANZAS. Curva de Guerrero between Caliso and San Miguel de los Baños: Dec. 1931, *Bro. León 15328* (BH). San Miguel de los Baños: Mar.–Apr. 1931, *J. T. Roig* (BH). PROV. HABANA. Lomas de Capasse: June 1930, *Bro. León 14583* (BH). Loma de la Jaula, Capasse: Dec. 1929, *Bro. León 14723* (BH). Loma Peregrina, Capasse: May 1928, *Bro. León 13336* (BH). Sierra de Anafe: Dec. 1936, *Bro. León 16667* (BH, US). Sierra de Esperón: Nov. 1932, *L. H. Bailey 1088* (BH). PROV. PINAR DEL RIO. Mt. Guanajay: Dec. 1904, *Baker & Van Hermann 4245* (B, destroyed; F; NY, Lectotype of *T. punctulata*); 1859–1860, *Wright 3965* (AAH; B, destroyed; F; GH, lectotype of *T. drudei*; NY, US). Sierra de Esperón ("O Anafe," Mt. Guanajay of Van Herman):

Dec. 1936, *Bro. León 16667* (BH). Sierra de Anafe: Dec. 1911, *P. Wilson 11504* (US). Vicinity of Sumidero: July 1912, *J. A. Shafer 13414* (US). Sierra del Sumidero: Mar. 1932, *L. Howell for Bro. León 15563* (BH). La Guira: Aug. 1912, *J. A. Shafer 13752* (US). Hills between Río Cayaguaje and Sierra Guane: Nov. 1911, *J. A. Shafer 10469* (US). Santa Cruz de los Pinos: Arroyo Piedras, July 1930, *Bro. León 14590* (BH, US). Vinales: Dec. 1930, *E. P. Killip 13596* (US); Apr. 1930, *Bro. León 14369* (US). Sierra de la Guassa: Mar. 1932, *L. Howell for Bro. León 15562* (BH). Mogote de la Baudea: Dec. 1930, *Bro. León 14721* (BH). Cayos de San Filipe: Oct. 1932, *Bro. León 15860* (BH, US). Arroyo Mamey-Pan de Quajaiabón: Aug. 1934, *G. Nateson for León 16142* (BH). Sierra del Ancón: Mar. 1932, *L. Howell for Bro. León 15561* (BH). Sierra del Rangel: Arroyo Aspiro, Dec. 1930, *Bro. León 14724* (BH).

DISCUSSION.—Almost from its conception, *Thrinax morrisii* has been treated as a distinct but poorly known species restricted to two tiny remote islands at the extreme northeastern margin of the Caribbean Sea. As a matter of fact it was the most thoroughly known of any *Thrinax* described up to that time. It was the only one for which the description and illustrations had been drawn up from excellent material, including mature leaves, inflorescence, and mature fruit. Treated simply as a dwarf, narrowly endemic species on the islands of Anegada and Anguilla, the name *Thrinax morrisii* frequently appeared in the literature but never in synonymy. It wasn't even associated with *T. pumilio*, a name which means "small," from which it was said to differ (Wendland, 1892:104) "in the greater number of segments of the lamina and in the shortness of the lamina itself."

Thrinax morrisii was first discovered in December 1890 by D. Morris, then Assistant Director of Kew, near a place called Blowing Point on the southwestern part of the island of Anguilla. In a report published by Morris (June 1891:131) the palm (without a name) was described as "present in fairly large quantities, and the fan-shaped leaves were used for thatching native huts." Morris explained that "the chief interest attached to this palm is connected with its dwarf habit. The largest and apparently most matured specimen did not measure more than about 30 to 35 inches in height." He was unable to find fruit or flowers at the time, but "30 to 40 plants . . . were carried away . . . to be established at the Botanical Stations at Antigua and St. Lucia." Figure 56 is an old photograph, depicting a group of plants in a botanic garden,

possibly Antigua. It is not known if these are from the original Morris collection, but I suspect that they are, since the photograph dates from between 1902 and 1931.

Sargent (1896) published a new species of *Thrinax* from the Florida Keys which he called *T. microcarpa* in allusion to the small fruits ($1\frac{1}{8}$ inch in diam.). Instead of 30–35 inches, however, as in *T. morrisii*, this new species measured 20–30 feet in height. He also described (p. 162) a palm growing on the Marquesas Keys (Florida), to which he erroneously attributed specimens of fruits with a "fleshy succulent pericarp." For this, he later (1899) published the name *T. keyensis*. *Thrinax micro-*



FIGURE 56.—Small plants of *Thrinax morrisii*, possibly from the original collection, in the Botanic Garden, Antigua. (Photo by M. M. Joseph, Dominica, in the L. H. Bailey collection at the Bailey Hortorium, Cornell, 1937?)

carpa was said to differ, from this species (p. 87) "in its taller and more slender trunk without a basal enlargement, in its shorter spadix and smaller fruit with darker colored seeds, and in its smaller and thinner leaves." But characters such as "taller," "more slender," "shorter," "smaller," "darker," and "thinner" are not considered adequate in the present treatment. Sargent (1902:80) separated the two species in a key only on the basis of seed and leaf size.

Thrinax praeceps and *T. ponceana* appeared simultaneously in O. F. Cook's synopsis in 1901.



FIGURE 57.—*Thrinax morrisii* growing naturally on Big Pine Key, Florida. (Photograph from the O. F. Cook collection, now deposited in the Department of Botany, Smithsonian Institution.)

Considering the results of studies on *Thrinax parviflora* in Jamaica, the following observations by Cook (1901:537) are certainly of interest:

Several species of *Thrinax*, of which *T. Morrisii* Wendland may serve as an example, have been described chiefly with reference to the relative size of the leaf segments and the extent of their separation. If the palms under observation near Ponce belonged as was believed, all to one species, it is not only true that the individual *Thrinax* passes all the stages from the narrow and grass-like almost completely separated segments of the very young plant to the more than half united leaf of the large tree, but it also appears to be true that under unfavorable conditions a *Thrinax* may not be able to attain full maturity of size and form but may at the same time produce flowers and seeds. In the narrow chinks and crevices of the bare rocks were very small, stunted trees, obviously of great age, while but a few feet distant a deeper fissure might hold vegetable debris and moisture sufficient to nourish vigorous specimens several times the size of their less fortunate companions. The stunted trees retain in proportion to their size, but apparently with little reference to their age, the small deeply divided leaves of young plants and have short few branched inflorescences, another difference of supposed systematic importance.

Yet examination of the Cook types and his original diagnoses reveal little more than quantitative differences between his two new species, and no reference to *T. morrisii* other than that quoted above. Unpublished notes in the Washington files left by Dr. Cook (in the Department of Botany, Smithsonian Institution) state that *T. praeceps* "differs from *T. ponceana* in longer and slightly more slender and more tomentose leaf sheaths; smaller, smoother leaves with longer petioles and smaller, more acute ligule." These "diagnostic" characters are, as has been repeatedly stated, the real problem in palm taxonomy. The only sure way of separating them remains the admonition by Cook in the same paper (p. 526) where he stated that

a locality definitely indicated would often go further toward establishing the identity of a species than much of the descriptive matter prepared for this purpose. For the present at least, the geographical idea should be kept uppermost in systematic studies of the palms, since it is generally much easier and far more logical to extend the limits of supposed species, than to cope with the confusion caused by the miscellaneous reporting of species far outside their natural ranges.

The test of time has shown that good diagnostic qualitative characters, as in many other groups of plants, seem to be the easiest means of distinguish-

ing taxa in the Palmae; however, this has required a thorough understanding of ecological tolerances and phenotypic plasticity within the species.

The following year (1902) Cook described yet another new species, this time from the Bahamas. Based on specimens collected by Northrop at Big Cabbage Creek, Andros Island, *Thrinax bahamensis* was said to compare favorably with Sargent's *T. keyensis* "in view of the short pedicels, distinctly lobed calyx, broad filaments and short styles." But "this species is evidently much smaller in all its parts than *Thrinax Keyensis*" (p. 20). And "in comparison with *Thrinax Ponceana* . . . the leaves of the present species are smaller with the petioles less flattened and more distinctly ribbed on the upper side near the apex."

In 1907, Beccari treated ten "good" species and three dubious species in the genus *Thrinax*. I now treat six of the ten good species as conspecific with *T. morrisii*. Two of these, *T. drudei* and *T. punctulata*, were described as new and apparently distinguished solely by the extent of the intrusion of the testa into the center of the seed, for they were placed in two subgenera separated by this character. While seemingly a good distinction between *T. radiata* and *T. morrisii*, this character appears to be variable in *T. parviflora* subspecies *parviflora* in Jamaica and requires further investigation with more adequate material in *T. morrisii* in Cuba, especially since the fruits upon which the species in Cuba were based are immature. I find no other significant differences between the type of *T. drudei* (Wright no. 3965) and the type of *T. punctulata* (van Hermann no. 4245). Beccari (1913:407) felt the resemblance between the two species to be great enough to suggest that ". . . it is necessary to obtain better specimens with flowers of both to establish these species on more sure diagnostic characters." Descriptions of new species of palms, based on

single incomplete specimens, have usually proved to be extremely questionable at best.

When N. L. Britton and Percy Wilson (1923) presented their findings, they did not accept Cook's two species but treated them under the earlier *T. microcarpa* of Sargent and distinguished this species from *T. morrisii* by the (p. 116) "mature leaves silvery beneath" for the former and "leaves green on both sides, or faintly glaucescent beneath" for the latter.

Thrinax ekmanii was described by Max Burret (1929) based on collections made by E. L. Ekman on the island of Navassa. A limestone island with steep cliffs rising high out of the sea, Navassa lies just off the westernmost peninsula of Haiti between Hispaniola and Jamaica. While *Thrinax morrisii* does not occur on either of the larger islands it does occur naturally, as presently circumscribed including *T. ekmanii*, on this tiny island. Interestingly Navassa supports another palm, *Pseudophoenix sargentii*. Although no really good diagnostic characters are known which can be used to maintain *T. ekmanii* as a distinct species the most conspicuous thing, characterizing both palm taxa on Navassa, is the extremely silvery white condition of the abaxial surface of the leaves. Until further extensive observations of this character in the field are accomplished the nature of its variability throughout the entire range of the species must be treated as uncertain.

COMMON NAMES.—Known variously in the literature as "brittle-thatch," in Florida; "palmita" or "miraguano," in Cuba; "buffalo-top," in the Bahamas or "buffalo-thatch" in the Caicos Islands; the name "pimetta" was noted on specimens from Barbuda. Various herbarium specimens collected in Cuba bear the names, "miraguano de sierra," "guano blanco de sierra," and "guanita de sierra." It is called "broom palm" in Anguilla.

Appendix I

Binomials Published in the Genus *Thrinax*

(Arranged in chronological order)

- T. parviflora* Sw., Prodr. 57. 1788.
T. radiata Mart. ex Desf., Cat. Pl. Hort. Reg. Paris, ed. 3, 31. 1829. nom. nud.
T. argentea Lodd. ex Desf. loc. cit. nom. nud.
T. argentea Lodd. ex J. A. & J. H. Schult., Syst. Veg. 7 (2): 1300. 1830. = *Coccothrinax argentea* (Lodd. ex J. A. & J. H. Schult.) Sarg. ex K. Schum.
T. pumilio Lodd. ex J. A. & J. H. Schult. loc. cit. 1301. nom. incert.
T. pumila Fulch.? ex J. A. & J. H. Schult. loc. cit. nom. nud., in synonym.
T. radiata Lodd. ex J. A. & J. H. Schult. loc. cit.
T. gracilis Hort. ex J. A. & J. H. Schult. loc. cit. pro syn.
T. elegans Hort. ex J. A. & J. H. Schult. loc. cit. pro syn.
T. aurantia Fulch. ex J. A. & J. H. Schult. loc. cit. nom. nud.
T. multiflora Mart., Hist. Nat. Palm. 3:255. 1838. = *Coccothrinax* sp.
T. aurata Hort. ex Mart. ibid. p. 257. pro syn.
T. barbadensis Lodd. ex Mart. loc. cit. = *Coccothrinax* sp.? [not necessarily *C. barbadensis* Becc.].
T. maritima Lodd., Cat. Palm. 1845. nom. nud.
T. montana Lodd. loc. cit. nom. nud.
T. stellata Lodd. loc. cit. nom. nud.
T. ferruginea Lodd. loc. cit. nom. nud.
T. excelsa Lodd. loc. cit. nom. nud.
T. mexicana Lodd. loc. cit. nom. nud.
T. rupestris Lodd. loc. cit. nom. nud.
T. ? chuco Mart., Palm. Orbis. p. 45. 1846. = *Chelyocarpus chuco* (Mart.) H. E. Moore.
T. yuraguana A. Rich. ex Sagra, Hist. Fis. Pol. Nat. Cuba, pt. 2. 11:278. 1850. nom. illeg. = *Coccothrinax miraguama* (H. B. K.) León [as to type, not as to plant described, which = *C. yuraguana* León].
T. miraguano Mart., Hist. Nat. Palm. 3:320. 1853. = *Coccothrinax miraguama* (H. B. K.) León.
T. ? miraguama (H. B. K.) Walp., Annal. Bot. Syst. 5:818. 1858.
T. excelsa Lodd. ex Griseb., Fl. Brit. W. Ind. p. 515. 1864.
T. martii Griseb. et H. Wendl. ex Griseb., Cat. Pl. Cub. p. 221. 1866. = *T. radiata* Lodd. ex J. A. & J. H. Schult.
T. rigida Griseb. et H. Wendl. ex Griseb. loc. cit. = *Coccothrinax rigida* (Griseb. & H. Wendl.) Becc.
T. crinita Griseb. et H. Wendl. ex Sauv., Anal. Acad. Ci. Habana 7:563. 1871. = *Coccothrinax crinita* (Griseb. & H. Wendl.) Becc.
T. acuminata Griseb. et H. Wendl. ex Sauv. op. cit. = *Coccothrinax miraguama* (H. B. K.) Becc.
T. grandis Hort. ex Kerchove, Les Palm. 258. 1878. nom. nud.
T. garberi Chap., Bot. Gaz. 3:12. 1878. = *Coccothrinax argentata* (Jacq.) Bailey.
T. graminifolia Hort. ex Kerchove, Illust. Hort. 31:187. 1884. nom. incert.
T. arborea Hort. ex Kerchove, ibid. p. 187. nom. nud.
T. tunicata Hort. ex Kerchove, loc. cit. nom. nud.
T. elegantissima Hort. ex Hook., f. Kew Rept. 1882:66. 1884. pro syn.
T. morrisii H. Wendl. ex Anonymous, Gard. Chron. ser. 3, 10:700. 1891. nom. nud.
T. morrisii H. Wendl., Gard. Chron. ser. 3, 11:104. 1892.
T. microcarpa Sarg., Gard. & For. 9:162. 1896. = *T. morrisii* H. Wendl.
T. floridana Sarg., Bot. Gaz. 27:84. 1899. = *T. radiata* Lodd. ex J. A. & J. H. Schult.
T. keyensis Sarg. ibid. p. 86. = *T. morrisii* H. Wendl.
T. praeceps O. F. Cook, Bull. Torr. Bot. Club 28:536. 1901. = *T. morrisii* H. Wendl.
T. ponceana O. F. Cook, loc. cit. = *T. morrisii* H. Wendl.
T. bahamensis O. F. Cook, Mem. Torr. Bot. Club 12:20. 1902. = *T. morrisii* H. Wendl.
T. wendlandiana Becc., Webbia 2:265. 1907. = *T. radiata* Lodd. ex J. A. & J. H. Schult.
T. drudei Becc. ibid. p. 269. = *T. morrisii* H. Wendl.
T. tessellata Becc. op. cit. 271. = *T. parviflora* Sw.
T. punctulata Becc. op. cit. p. 280. = *T. morrisii* H. Wendl.
T. harrisiana Becc. in Fedde, Repert. 6:94. 1908. = *T. parviflora* Sw.
T. rex Britt. & Harris, Bull. Torr. Bot. Club 37:352. 1910. = *T. excelsa* Lodd. ex Griseb.
T. longistyla Becc. in Urb., Symb. Antill. 7:170. 1912. = *Coccothrinax* sp.
T. ekmanii Burret, Kungl. Sv. Vet-Akad. Handl. ser. 3, 6 (7): 27. 1929. = *T. morrisii* H. Wendl.
T. altissima Hort. ex Bailey, Gent. Herb. 4:149. 1938. nom. nud.
T. aurantiaca Fulch.? ex Bailey, ibid. nom. nud.
T. compacta Griseb. & Wendl. ex Bailey, ibid. nom. nud.
T. havenensis Hort. ex Bailey, ibid. nom. nud.

Appendix II

Nomina Incerta et Dubia

Thrinax pumilio Lodd. ex J. A. & J. H. Schult., Linn. Syst. Veg. sec. 7 (2):1301. 1830. nom. incert.

T. pumila Fulch. ? ex J. A. & J. H. Schult. loc. cit. in synonym.

T. pumilio Lodd. Cat. Palm. 1845. nom. nud.

Porotherinax H. Wendl. ex Griseb. Cat. Pl. Cub. p. 221. 1866. nom. nud.

The original description of *Thrinax pumilio* by J. A. & J. H. Schultes (1830) was based on material from a young plant sent to the Munich Herbarium by Loddiges. No specimen has since been found there that could be identified with the description. It could represent almost any palmate genus since Loddiges included plants of both *Coccothrinax* and *Thrinax* under *Thrinax*. It is impossible to apply the very ample description to any known species or for that matter to ascribe it to any genus. A description drawn from a young palmate leaf with only 10 to 14 segments is impossible to identify lacking a specimen. The statement that a hastula is not present is disconcerting, for even very young *Thrinax* and *Coccothrinax* exhibit this organ. Moreover it would seem that a *Thrinax* leaf blade 2 feet in diameter should have more than 14 segments. The additional statement (p. 1301) that

T. pumilio "Differt a *Thr. parviflora* et *argentea* praesertim defectu prominentiae in centro frondis a prolongatione stipites" suggests a generic difference rather than a specific one. The mention of the embryo must be disregarded, since it came from Martius and no doubt does not apply to the taxon in question because it is a juvenile plant by definition.

Specimens cited at the time of the publication of *Porotherinax pumilio* by Grisebach (1866:221) are merely associated with the name and are not to be considered as the type. The mention of the seed having "the albumin centrally perforate, the margin not at all ruminant" is taken from associated specimens, not from type material and thus must be ignored in typifying *Thrinax pumilio*. *Porotherinax* H. Wendl. ex Griseb. was not accompanied by a separate diagnosis and is therefore not validly published (Articles 41 and 42 of the International Code of Botanical Nomenclature).

Thrinax section *Porotherinax* ascribed to Drude (1887) and validated by C. S. Sargent (1896) is a new name based on *Thrinax microcarpa* and should not be confused with the earlier invalid name published by Grisebach.

Literature Cited

- Aiton, W.
1789. *Hortus Kewensis*. Volume 3. London.
- Aiton, W. T.
1811. *Hortus Kewensis*. 2nd ed., volume 3. London.
- Asprey, G. F.
1959. Vegetation in the Caribbean Area. *Caribbean Quarterly*, 5:245-263.
- Asprey, G. F., and A. R. Loveless
1958. The Dry Evergreen Formations of Jamaica, II: The Raised Coral Beaches of the North Coast. *Journal of Ecology*, 46:547-570.
- Asprey, G. F., and R. G. Robbins
1953. The Vegetation of Jamaica. *Ecological Monographs*, 23:359-412.
- Ayensu, E. S.
1967. Aerosol OT Solution, an Effective Softener of Herbarium Specimens for Anatomical Study. *Stain Technology*, 42:155-156.
- Bailey, L. H.
1938. *Thrinax*—The Peaberry Palms. *Gentes Herbarum*, 4:129-149, figures 75-84.
1939. *Coccothrinax* in the Southern Greater Antilles. *Gentes Herbarum*, 4:247-259.
1949. Palms Uncertain and New. *Gentes Herbarum*, 8: 95-99.
- Beard, J. S.
1955. The Classification of Tropical American Vegetation-types. *Ecology*, 36:89-100.
- Beccari, O.
1907. Le Palme Americane della Tribu delle Corypheeae. *Webbia* 2:1-288.
1908. Palmae Novae Antillanae, XXIV. In *Repertorium Novarum Specierum Regni Vegetabilis* (auctore F. Fedde), 6:94-95.
1912. The Palms Indigenous to Cuba. *The Pomona College Journal of Economic Botany*, 2:402-407, figures 164-167.
1933. Asiatic Palms—Corypheeae. *Annals of the Royal Botanic Garden, Calcutta*, 13:327-336, plates 24, 28, 29. [Published posthumously, revised and edited by Prof. Ugolino Martelli; dated 1931].
- Bentham, G., and J. D. Hooker
1883. *Genera Plantarum*. Volume 3.
- Bond, J.
1961. *Birds of the West Indies*. London.
- Britton, N. L.
1908. Beccari's American Palms. *Torrey*, 8:238-241.
1909. Botanical Exploration in the West Indies and Florida. *Journal of The New York Botanical Garden*, 10:99-114.
- Britton, N. L., and W. Harris
1910. Studies of West Indian Plants, 14: Hitherto Undescribed Species of Jamaica. *Bulletin of the Torrey Botanical Club*, 37:352.
- Britton, N. L. and P. Wilson
1923. Scientific Survey of Porto Rico and the Virgin Islands. *New York Academy of Sciences*, 5:116-117.
- Browne, P.
1756. *The Civil and Natural History of Jamaica*. London.
- Burret, M.
1929. Palmae Cubenses et Domingenses A. CL. E. L. Ekman. *Kungl. Svenska Vetenskapsakademiens Handlingar*, series 3, 6 (7):27.
- Chapman, A. W.
1878. An Enumeration of Some Plants. *Botanical Gazette*, 3:12.
1883. *Flora of the Southern United States*. Supplement, 2nd ed. New York.
- Cook, O. F.
1901. A Synopsis of the Palms of Puerto Rico. *Bulletin of the Torrey Botanical Club*, 28:525-569, plate 45.
1902. Palms from the Bahamas. In Alice R. Northrop, *Flora of New Providence and Andros. Memoirs of the Torrey Botanical Club*, 12:20-21.
1937. Hurricane Palms in Florida, Including a New Genus *Simpsonia*. *Science*, 85:332-333.
- Corner, E. J. H.
1966. *The Natural History of Palms*. Berkeley and Los Angeles: University of California Press.
- Desfontaines, R.
1829. *Catalogus Plantarum Horti Regii Parisiensis*. 3rd ed. Paris.
- Drabble, E.
1904. On the Anatomy of the Roots of Palms. *Transactions of the Linnean Society of London, Botany*, series 2, 6:427-490.
- Drude, O.
1887. Palmae. In Engler and Prantl, *Die Natürlichen Pflanzenfamilien*, 2 (3):34.
- Gatin, C. L.
1906. Germination des Palmiers. *Annales des Sciences Naturelles, Botanique, Paris*, series 9, 3:192-314.
- Gillain, G.
1900. Beiträge zur Anatomie der Palmen- und Pandanaceen-Wurzeln. *Botanisches Centralblatt*, 83:339-345.
- Grisebach, A. H.
1864. *Flora of the British West Indian Islands*. London.
1866. *Catalogus Plantarum Cubensium*. Leipzig.
- Hooker, J. D.
1884. *Kew Report for 1882*. London.
1889. *Thrinax excelsa*. *Curtis's Botanical Magazine*, tabula 7088.

- Hooker, J. D., and T. Thomson
1855. Introductory Essay. In *Flora Indica*. xv + 285 pages. London.
- Howard, R. A.
1960. *Thrinax rex*—A Regal Palm of Jamaica. *Principes*, 4:133-137.
- Jost, L.
1887. Ein Beitrag zur Kenntniss der Athmungsorgane der Pflanzen. *Botanische Zeitung*, 45:600-606; 617-628; 633-642.
- Kerchove de Denterghem, O.
1878. *Les Palmiers*. Paris.
- Kunth, C. S.
1841. *Enumeratio Plantarum*. Volume 3. Stuttgart and Tübingen.
- León, Hno.
1939. Contribucion al Estudio de las Palmas de Cuba, III. *Memorias de la Sociedad Cubana de Historia Natural*, 13:153.
1946. Flora de Cuba, 1. *Contribuciones Ocasionales del Museo de Historia Natural del Colegio de la Salle*, 8:260-262.
1956. Identifying *Coccothrinax*. *Principes*, 1:16.
- Ligon, R.
1657. *A True & Exact History of the Island of Barbados*.
- Linnaeus, C.
1753. *Species Plantarum*. Stockholm.
- Loddiges, C., and Sons
1845. *Palms in the Collection of Conrad Loddiges and Sons, Hackney Near London with Their Native Countries*. London.
- Loveless, A. R., and G. F. Asprey
1957. The Dry Evergreen Formations of Jamaica, I: The Limestone Hills of the South Coast. *Journal of Ecology*, 45:799-822.
- Martius, C. F.
1838. *Historia Naturalis Palmarum*. Volume 3. Leipzig.
- Moore, H. E.
1963. The Typification and Species of *Palma Miller* (1754). *Gentes Herbarum*, 9:242-244.
- Morris, D.
1891. Report of a Botanical Mission to the West Indies. *Royal Gardens, Kew, Bulletin of Miscellaneous Information*, 1891:131.
- Morrow, L.
1965. Morphology and Anatomy of Coryphoid Palm Flowers. A thesis, Cornell University.
- Parthasarathy, M. V.
1968. Observations on Metaphloem in the Vegetative Parts of Palms. *American Journal of Botany*, 55(10): 1152-1167.
- Pfister, R.
1892. Beitrag zur vergleichenden Anatomie der Sabalceblätter. 51 pages. Dissertation, Zurich.
- Ray, J.
1688. *Historia Plantarum*. Volume 2. London.
- Read, R. W.
1963. Palm Chromosomes. *Principes*, 7:85-88.
1964. Palm Chromosome Studies Facilitated by Pollen Culture on a Colchicine-lactose Medium. *Stain Technology*, 39:99-106.
1965. Chromosome Numbers in the Coryphoideae. *Cytologia*, 30:385-391.
1965b. Palm Chromosomes by Air Mail. *Principes*, 9:4-10.
1966. *Coccothrinax jamaicensis*—The Jamaican Silver Thatch. *Principes*, 10:133-141.
1968. A Study of *Thrinax* in Jamaica. A thesis, The University of the West Indies, Mona, Jamaica.
- Rudolph, K.
1911. Der Spaltöffnungsapparat de Plamenblätter. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften . . . Klasse*, 1 (120):1049-1086.
- Sargent, C. S.
1896. *Thrinax* in Florida. *Garden and Forest*, 9:162.
1896. *Silva of North America*. Volume 10. Cambridge, Mass.: The Riverside Press.
1899. New North American Trees. *Botanical Gazette*, 27: 83-87.
1902. *Silva of North America*. Volume 14. Cambridge, Mass.: The Riverside Press.
- Sauvalle, F. A.
1871. Flora Cubana. *Anales de la Academia de Ciencias Médicas, Físicas y Naturales de la Habana*, 8:152.
- Schreber, J. D. C. (editor)
1791. *Caroli a Linné . . . Genera Plantarum*. Editio Octavo. Frankfurt.
- Schultes, J. A. and J. H. (editors)
1830. *Caroli a Linné . . . Systema Vegetabilium*. Volume 7, part 2.
- Schumann, K.
1901. Neue Arten der Siphonogamen 1899, VIII. *Just's Botanischer Jahresbericht*, 27(1):469.
- Shreve, F.
1914. A Montane Rain-Forest. *Carnegie Institution of Washington*, Publication number 199.
- Sloane, H.
1696. *Catalogus Plantarum Quae in Insula Jamaica*. London.
1725. *A Voyage to the Islands Madera, Barbados, Nieves, S. Christopher*. Volume 2. London.
- Small, J. K.
1925. Silk-top Thatch—*Thrinax parviflora*. *Journal of the New York Botanical Garden*, 26:49-54.
- Snedecor, G. W.
1948. *Statistical Methods*. Iowa State College Press.
- Solereder, H., and F. J. Meyer
1928. *Palmae*. Volume 3 in *Systematische Anatomie der Monoktyledonen*. Berlin.
- Sprengel, C. (editor)
1830. *Caroli Linnaei . . . Genera Plantarum*. Editio nona, volume 2. Göttingen.

Swartz, O.

1788. *Nova Genera & Species Plantarum seu Prodrromus*. Stockholm, Uppsala.
1797. *Flora Indiae Occidentalis*. Volume 1. Erlangen.

Tomlinson, P. B.

1960. Essays on the Morphology of Palms, I: Germination and the Seedling. *Principes*, 4:56-61.
1961. Palmae. Volume 2 in *Anatomy of the Monocotyledons*. Oxford: The Clarendon Press.

Vasey, G.

1876. A Catalogue of the Forest Trees of the United States. *U.S. Department of Agriculture Report*, number 11.

Venkatasubban, K. E.

1945. Cytological Studies in Palmae, Part I: Chromosome Numbers in a Few Species of Palms of British India and Ceylon. *Proceedings of the Indian Academy of Sciences*, 22:193-207.

Wendland, H.

1892. New or Noteworthy Plants. *The Gardners' Chronicle*, ser. 3, 11:104, figures 20, 21.

Willdenow, C. L. (editor)

1799. *Caroli a Linné . . . Species Plantarum*. Editio Quarta. Berlin.

Zawada, K.

1890. Das Anatomische Verhalten der Palmenblätter dem System dieser Familie. 40 pages. Dissertation. Erlangen.