

A MONOGRAPH OF *SABAL* (ARECACEAE: CORYPHOIDEAE)

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ABSTRACT

This monographic study of the New World genus *Sabal* (Arecaceae: Coryphoideae) recognizes 15 species. In addition to defining species limits and distributions, the study addresses broader questions concerning likely modes of speciation in the group and biogeographic radiation. The systematic treatment incorporates results from extensive field work and studies of leaf anatomy and flavonoid phytochemistry, ecology and biogeography, and morphology. Distribution maps and a key to the taxa are provided. Solutions are offered for the many nomenclatural problems that existed in the genus. A phylogenetic hypothesis, the first for the genus, is proposed. Moreover, phytochemical and anatomical features are examined in an ecological perspective, and hypotheses about their function and evolutionary significance are presented.

Key words: anatomy, Arecaceae, Caribbean, Mexico, morphology, Palmae, phytochemistry, *Sabal*.

INTRODUCTION

One of the most common genera of palms in and around the Caribbean basin is the genus *Sabal* (Arecaceae: Coryphoideae). It is widespread and often weedy, thriving in anthropogenic habitats from Bermuda to Sonora, from Texas to Trinidad. Likewise, it is common in the southeastern United States and is likely one of the palms best known to north temperate botanists. *Sabal* is widely cultivated as an ornamental in gardens around the world; in its native habitats, it sustains thatch, basketry, and hat-making industries. Yet despite its familiarity, *Sabal* has remained poorly studied and poorly understood.

Previous workers (Bailey 1934, 1944; Beccari 1907) confined their efforts to morphological taxonomic studies of genus. Faced with the general morphological sameness of the species and confounded by inadequate collections, they were most concerned with defining species boundaries. *Sabal*, the sole member of the subtribe Sabalinae of the tribe Corypheeae (Uhl and Dransfield 1987), was clearly circumscribed at the genus level, but species boundaries were ill-defined. At the root of much of the past taxonomic confusion lay narrow species concepts in which nearly every separate population was recognized as a distinct species. Only with an appreciation for the ease with which *Sabal* has dispersed over long distances do we begin to develop a meaningful species concept for this group.

The present monograph has incorporated morphological, anatomical, and phytochemical data in an evolutionary and ecological framework. In addition to a key to the taxa, distribution maps, species descriptions and full synonymies, a phylogenetic hypothesis is provided. It is the first phylogeny proposed for the genus. Three additional questions are addressed: What has been the likely mode of speciation in the group? What can the phylogenetic hypothesis and present day distribution reveal about past biogeographical events and patterns? What adaptations are present in *Sabal* that allow it to succeed so well in a variety of environments in and around the Caribbean?

Distribution and Ecology

The distribution of *Sabal* is primarily Mexican, southeastern United States, and Caribbean (including Bermuda), with an outlying species found in Costa Rica, Panama, Venezuela, Colombia, and Trinidad (Fig. 1). Several disjunctions in the distribution are immediately apparent.

Sabal mauritiiformis is known from southern Mexico, southeastern Costa Rica, eastern Panama and the adjacent northern coast of South America. It is also found in southern Trinidad and has been reported by Wessels Boer (1988) from the islands of Curaçao and Bonaire. Its present distribution is probably recent, since it grows in lowland wet tropical forests that were submerged until quite recently.

Four other disjunctions are also readily attributable to overwater dispersal of seeds: those of *S. maritima*, *S. palmetto*, *S. causiolum*, and *S. yapa*. *Sabal maritima* is found on both Cuba and Jamaica (and is the only species of *Sabal* on Jamaica). Its present distribution—on recent soils on both islands—may also be recent, or it may have moved into these soils as other soils on the islands weathered. *Sabal causiolum* is found on Hispaniola and Puerto Rico; it inhabits lowland disturbed areas on both islands. *Sabal palmetto* is found in Cuba, the Bahamas, and the southeastern United States; *S. yapa* occurs on the Yucatán Peninsula (in Mexico and Belize) and western Cuba.

Island endemism is common in the genus, with one quarter of the species endemic to the Greater Antilles and Bermuda. Two species of Florida, *S. etonia* and *S. miamiensis*, are endemic to islandlike areas, the Central Florida Ridge and the Everglades Keys, respectively.

Most widespread species of *Sabal* (*S. mauritiiformis*, *S. mexicana*, *S. palmetto*, and *S. yapa*) as well as island endemics (*S. causiolum*, *S. domingensis*, and *S. maritima*) are small-fruited trees of the forest canopy. They thrive in high light intensity environments and commonly persist after forests are cleared for agricultural purposes. Recruitment in *S. palmetto* is a case in point. The species grows readily in oak forests in northern Florida, but seedlings under a closed canopy remain suppressed and form no aboveground stem. Stem elongation and sexual maturation await gap formation in the canopy. Along forest margins, on dunes, and in fields, growth and recruitment are immediate with no suppressed stage.

These species, as well as *S. bermudana*, *S. rosei*, and *S. pumos*, are "weedy" species, colonizing gaps and patchy habitats. They withstand burning and thrive in anthropogenic habitats. *Sabal uresana*, a species of xerophyllous woodlands of northwestern Mexico, appears to survive less well in disturbed habitats and, as noted by Gentry (1942), appears to be declining in the wild. This species never forms large stands in cleared fields as do its congeners *S. rosei* and *S. pumos*.

Sabal minor is an understory species of deciduous forests, while *S. etonia* and *S. miamiensis* are understory species of pine-oak associations in Florida.

MATERIALS AND METHODS

Field Studies

In the years 1984–86, I studied 13 populations of species occurring in Florida in the field. During the summers of 1986 and 1987, natural populations and cultivated individuals of *Sabal* were studied throughout Mexico. In 1988, field studies were undertaken in Panama, Cuba, Bermuda, the Dominican Republic, Trinidad, and Jamaica, as well as in southern Florida.

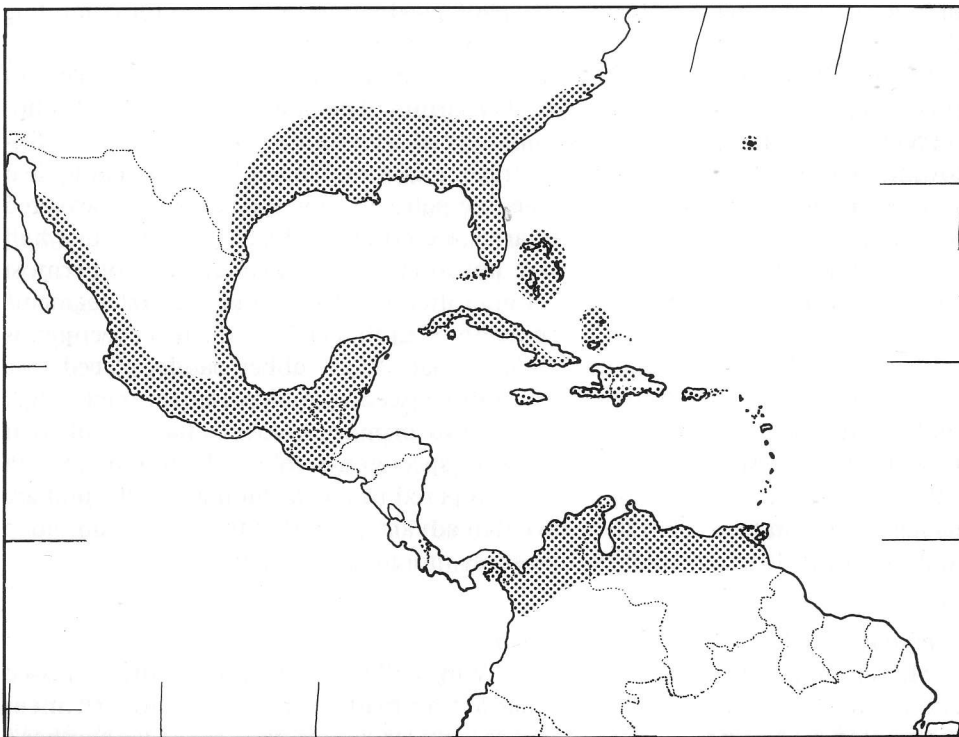


Fig. 1. Distribution of *Sabal*, a strictly New World genus.

At each population, complete voucher specimens were gathered and a separate collection number was given to each individual collected. Specimens collected prior to September, 1985, are deposited at FLAS, with duplicates distributed to various herbaria. Specimens collected after September, 1985, are deposited at RSA, with duplicates to be distributed.

Field observations of characteristics not readily visible from dried specimens include: species abundance, altitude, soil type, associated species and vegetation type, trunk height, diameter and surface texture, leaf number and color, petiole length, inflorescence number, length and posture, flower color and fragrance, insect visitors, fruit color, seed dispersers, and seed predators.

In addition, collections of flowers, fruits, and leaf samples were preserved in FAA and later transferred to glycerine-alcohol (Martens and Uhl 1980). These specimens were used for anatomical and morphological investigations. Dried bulk samples of leaf material were collected for phytochemical analysis. Living seed, when available, was collected and distributed to the Seed Bank of the International Palm Society, Fairchild Tropical Garden (Miami, Florida), Huntington Botanical Garden (San Marino, California), and Jardín Botánico (Mexico City, Mexico).

Herbarium Studies

Over 500 herbarium specimens were examined in the course of this study. Four herbaria (BH, FI, MEXU, P) were visited, and numerous herbaria (see Acknowledgments) lent material for study. Study of herbarium material was essential not

only for determining the range of morphological variation but also for compiling data on geographic and altitudinal distribution and common names.

Bailey (1934, 1940, 1944) has written eloquently and often on the problem of preparing specimens of *Sabal* for the herbarium. The large stiff leaves and inflorescences resist the press and demand special techniques. I have found the following method of preparation and storage to be suitable for *Sabal*: a healthy leaf is selected and removed from the tree, the petiole below the hastula is measured and then discarded (petiole length varies according to shade received), one half of the lamina is cut away taking care not to cut the hastula, and the outermost segments of the other half of the lamina (often wind-torn and the first segments to senesce) are trimmed away. Once trimmed in this fashion the leaf specimen is folded to fit the herbarium case, held in place with rubber bands, placed in a press, and dried. The inflorescence (or infructescence) is likewise trimmed of half its branches, and only the lower one or two primary branches (and all of their branches) are preserved. The inflorescence specimen is folded, held in place with rubber bands, and pressed. Specimens prepared in this fashion are bulky and are usually stored in boxes, but they have that advantage in that they can be unfolded and examined from all sides, unlike sheet-mounted specimens.

Methods for Measurement of Specimens

Measurements were taken from both living or pickled material and dried pressed specimens. Measurements of floral parts were made from herbarium specimens rehydrated by boiling. Measurements of large structures were made with either a metric scale measuring tape or ruler, and those of small structures were made with rotary dial micrometer (SPI 31-414).

Tree height was estimated visually; trunk diameter was measured on living specimens. Petiole and blade lengths were measured at the time of collection prior to pressing. All other vegetative measurements were taken from dried specimens. Petiole width was measured at the juncture of the petiole and hastula. Leaf segment measurements were taken from a segment midway along one side of the hastula. Segment width and lamina thickness were taken immediately above (distal to) the point of segment connation. Only one set of measurements was made for each collection.

Inflorescence length was either estimated visually or measured at the time of collection. Its natural position relative to the leaves was recorded. Rachilla diameter and length and bracteole length were taken from pressed specimens; all other floral measurements were made from rehydrated flowers. Rachillae length and number were measured (one for each collection) from basal branchlets (penultimate branches), and thus represent maxima for these characters; rachillae tend to be shorter and fewer in number on terminal penultimate branches. Rachilla thickness was taken midway along a rachilla from a middle rachilla; for both thickness and length, in no case was a terminal rachilla used. Petals, because their margins are involute, were measured at their widest points by folding them transversely, thus inducing their margins to unroll. Only one set of floral measurements was made for each collection.

Fruits and seeds were measured in the dry condition. From each collection, five fruits and seeds, selected at random, were measured, tabulated, and averaged; every effort was made to include only mature fruits and seeds.

MORPHOLOGY

Stem and Root

Stem formation begins underground in *Sabal*. A germinating seedling shows a peculiar geotrophic behavior, forcing the plumule downward. The eophyll emerges from the upturned tip of the plumule through a short series of tubular bracts (actually bladeless eophylls). The germination mode is remote and is figured by Bailey (1944, fig. 189). Aerial stem formation does not commence until many years' growth underground. In species that typically have no aerial stem, such as *S. etonia*, continued stem formation underground results in the curiously twisted or sigmoid underground stem illustrated by Bailey (1934, fig. 147; 1944, fig. 192). The underground stem allows *Sabal* to withstand disturbance (viz., fire) and is a key factor in the ability of *Sabal* to colonize open areas.

The aerial trunk of *Sabal* ranges from 3 m (in some populations of *S. minor*) to 25 m tall. Most caulescent species are 5–15 m tall. Trunk diameter can range from 15 cm (*S. yapa*) to 60 cm (*S. causiarum*), with most species falling in the 35–45 cm range. The surface of the trunk (when not clothed in persistent leafbases) may be smooth and white-gray or rough, vertically fissured, and gray-brown. In *S. pumos* and *S. rosei*, peg-like remains of petioles may persist on the trunk. The trunk may be green early in the life of the palm, and some species (*S. yapa*, *S. bermudana*) have nodal rings clearly to obscurely visible.

Aerial stem formation is an unreliable taxonomic character and has been the source of much taxonomic confusion in the past. The presence of an aerial stem was used by Cook (1901) to segregate the genus *Inodes* from *Sabal*, and several names have been proposed for populations of *S. minor* with aerial stems. Species that typically form large aerial stems can sometimes achieve reproductive maturity prior to aerial stem formation. This behavior is known in *S. mexicana*, *S. palmetto*, and *S. yapa*.

Roots of *Sabal* are large, numerous, and arise adventitiously along the stem. They arise uniformly around the base of aerial stems, but may arise only on the lower surface of sigmoid underground stems (see Bailey 1944, fig. 192).

Leaf

Petioles are 30–250 cm long, the length often depending on the amount of shade received and hence the amount of etiolation. Petioles are always unarmed in *Sabal*. The petiole is convex abaxially, but the adaxial side is concave or channeled, with a ridge formed in the channel of the distal half of the petiole.

Specific distinctions based on the presence or absence of persistent leafbases have no validity. Upon senescence, a leaf typically breaks off midway along the petiole; the petiole stub may persist (sometimes retaining photosynthetic ability) or abscise. The petiole sheathes the stem for a short distance, and as the stem expands, the persistent petiole base splits longitudinally forming a characteristic crisscross pattern (Fig. 30). Over time, the remains of the petiole base fall or rot away, but while present, they provide a foothold for epiphytes and hemiepiphytes, as well as a home for insects and other small animals.

The petiole is inserted into the blade at the hastula (Fig. 2A). The hastula forms on the adaxial surface in *Sabal* and may be short and obtuse or long and acuminate. It is usually asymmetrical in that one side is longer than the other. The margin

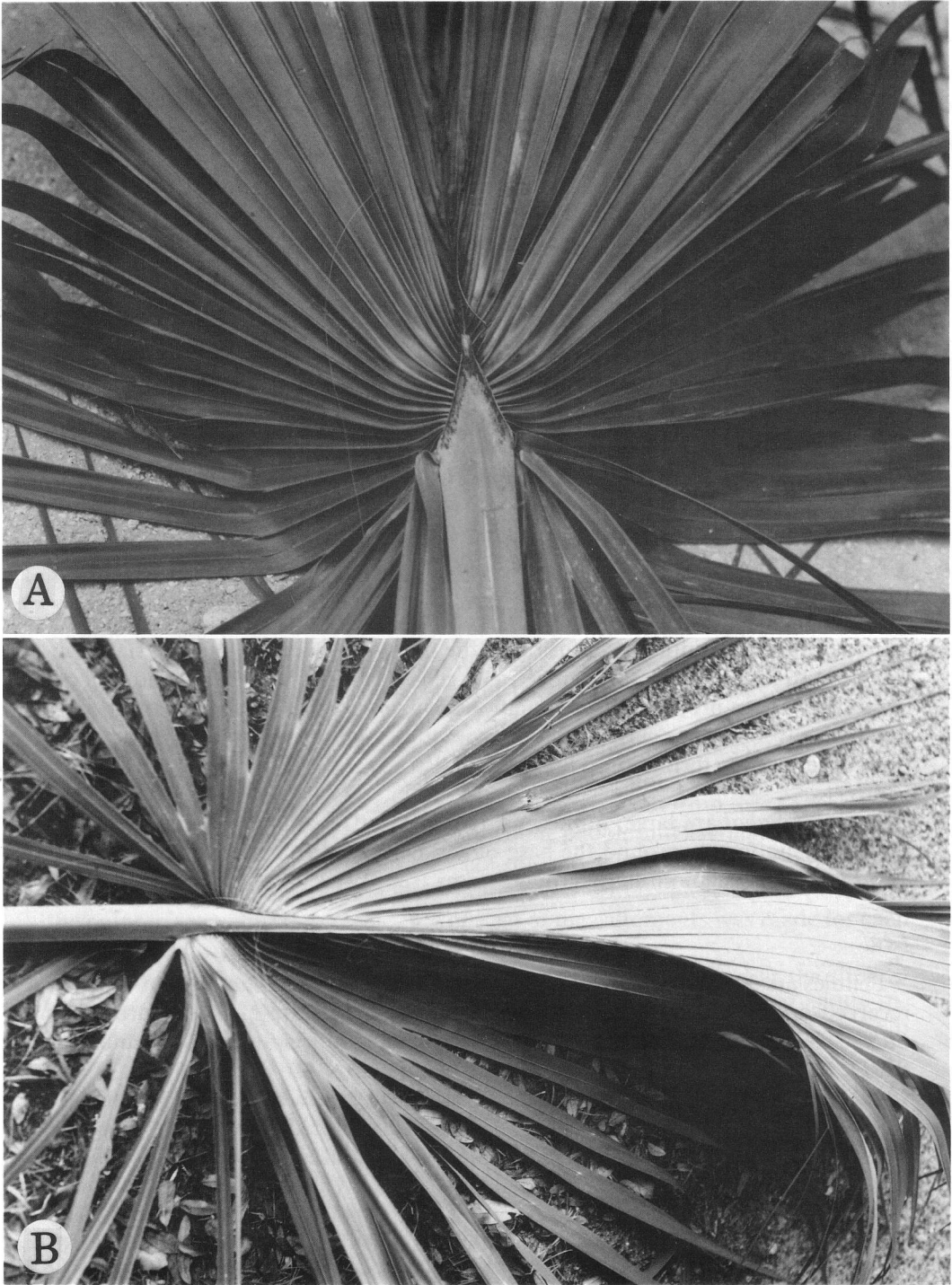


Fig. 2. Leaf morphology in *Sabal* (*S. palmetto*).—A. Adaxial surface showing hastula at apex of petiole.—B. Abaxial surface showing the costa, the extension of the petiole into the blade.

of the hastula may be entire or undulate, erect, involute, or revolute. The size and shape of the hastula are useful taxonomically only in the most general way (Moore 1971a).

In some populations of some species (viz., *S. mexicana* in Veracruz, Mexico, and *S. mauritiiiformis* in Trinidad) the hastula is highly involute, so much so that the adaxial surface of the hastula is no longer visible. The curled abaxial edge of the hastula may bear the impressions of the underlying leaf segments giving the hastula a ridged appearance.

The leaves of *Sabal* are alternate and spirally arranged, flabelliform, composed of 15–120 segments (in the range of 60–75 for most species), and weakly to strongly costapalmate. The costa in a strongly costapalmate species typically curves downward (Fig. 2B), giving the leaf its characteristic rigid curvature. Segments are induplicate with a strong central vein, the midvein, and along their margins of connation, a strong suture vein is formed. Segments may be lax or rigid, bifid at the apex or not. Filamentous fiber extensions may be inserted between the segments (at the termination of the suture vein) and at the termination of the midvein in bifid segments. The leaves of *Sabal* may be glaucous or evenly green.

Segments are short (less than 100 cm) in some species (*S. etonia*, *S. minor*) or long (up to 200 cm), and the apical bifurcation may be shallow, deep, or absent. Lamina thickness ranges from less than 0.1 mm (in some species) to 0.5 mm. Segments may be connate for 15–50% of their length, with the least amount of connation among the outermost segments and the greatest among the terminal segments (those adjacent to the costa). The size of the palman (the proximal fused laminar portion of the leaf) shows some variation both within and among species.

In some species, leaf segments are grouped in twos or threes, with connation within groups nearly complete and connation between groups very slight. In *S. mauritiiiformis*, splitting between segment groups occurs along a midvein, giving some segments a reduplicate appearance. This phenomenon is also known to occur in *Licuala* Thunb. (Corner 1966) and other coryphoid palms (Uhl and Dransfield 1987).

Peltate, multiseriate trichomes are present on young leaves of all species. They are brown with a lacinate margin and give young leaves a scurfy vesture. Usually, they are rapidly caducous. The trichomes persist longest along the abaxial side of the midveins. Only *S. maritima* frequently retains its trichomes for the life of the leaf.

Inflorescence

The paniculate inflorescence in *Sabal* is interfoliar, and its posture early in development and degree of ramification are diagnostic for some species (Fig. 3). The inflorescence may be erect (emerging 90° from horizontal), ascending (emerging less than 90° but greater than 45° from horizontal), arching (emerging ca. 45° from horizontal and arching downward), or cernuous (emerging more or less horizontally and hanging downward). Normally, ascending or arching inflorescences may sag under the weight of developing fruits, so inflorescence posture is best observed early in the development of the inflorescence before the rachillae have fully emerged. The inflorescence ranges in length from 0.4 to 3 m, and it is sparingly to densely branched. There are 2–4 orders of branching enumerated according to the system of Tomlinson and Zimmermann (1968). The inflorescence

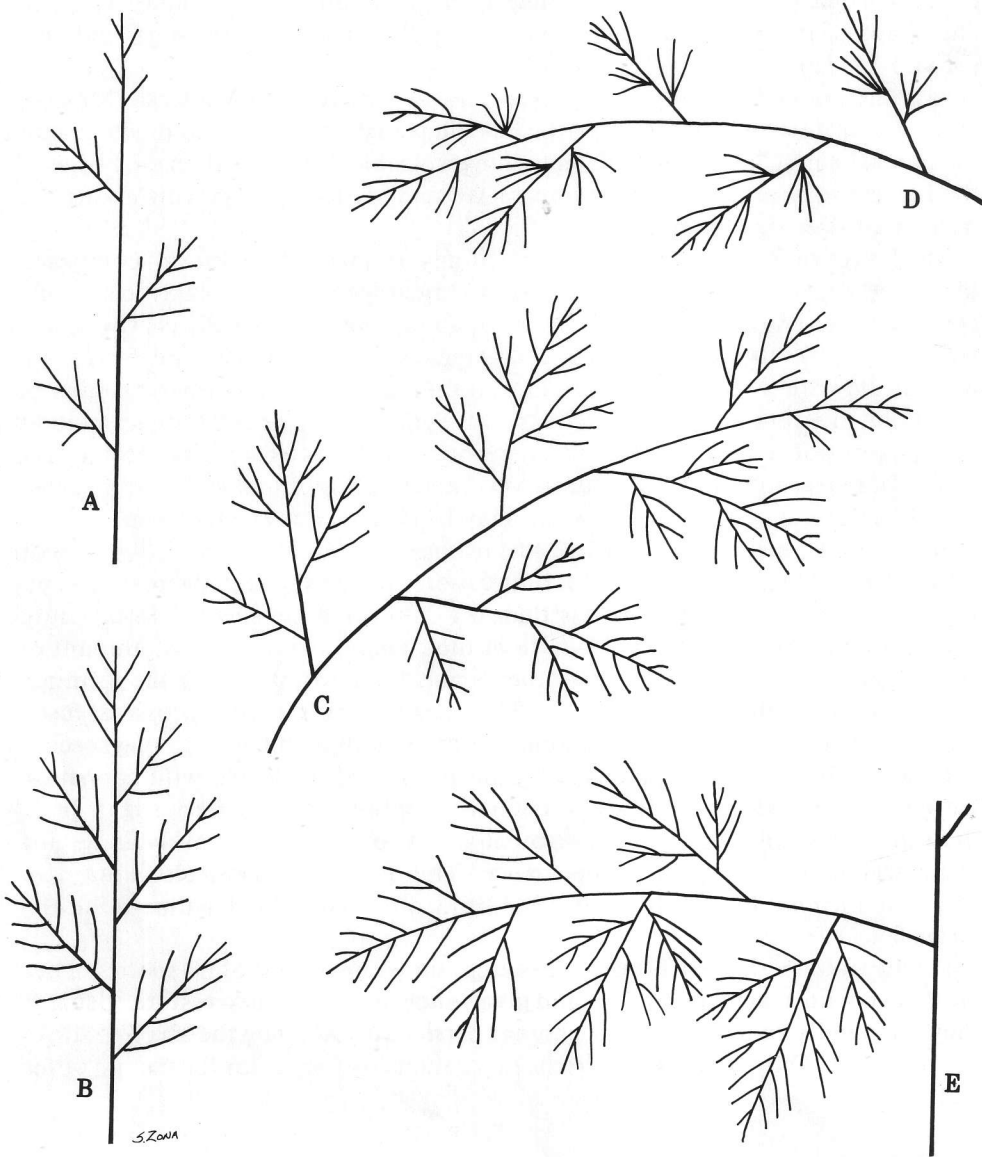


Fig. 3. Schematic diagrams of inflorescence branching patterns in *Sabal*.—A. *S. minor*.—B. *S. etonia*.—C. *S. causiarum*.—D. *S. bermudana*.—E. *S. mauritiiformis*.

is clasped by a sheathing bicarinate prophyll and 2–5 tubular bracts, according to the vigor of the plant. Branches up to and including the penultimate branches are each subtended by a bicarinate bract. Tubular bracts, with straight or oblique openings, clasp all branches up to and including the antepenultimate branches. The bicarinate bract of the penultimate branches may be exerted or inserted within the tubular bracts of the antepenultimate branches. The ultimate branches (the rachillae) are borne in the axils of solitary small triangular bracts. Flowers are subtended by one small bract, and a pedicellar bracteole is borne obscurely on each flower (Morrow 1965).