The Genus Pandanus in Micronesia
I. The Marianas Species

Benjamin C. STONE

School of Biological Sciences,
University of Malaya, Kuala Lumpur, Malaysia

Preparation of a Flora of Guam has brought to a critical point the question of the pandans of Micronesia, a subject with which I have been concerned for more than ten years. The taxonomic treatment of the Marianas species presented here is an attempt to summarize what has been learned in the course of considerable field study as well as the study of herbarium materials. Early work was made possible through a National Science Foundation grant (1834) to Prof. H. St. John, and I am grateful to Dr. St. John for his encouragement in studying the Pandanaceae. More recently while at the College of Guam I was able to enlarge my familiarity with the Guam species, and through the generosity of the College, especially the President, as well as through the interest of the Department of Agriculture of the U.S. Pacific Trust Territory, especially Mr. Manuel Sproat, I was able to undertake additional field work in Palau, Truk, Ponape, Saipan, and Rota. To all these institutions and persons I would like to acknowledge my gratitude.

Micronesian Pandanus: how many species?

Botanical publications devoted to Micronesian pandans have generally taken one of two positions: the earliest, and a few of the more recent, are of the view that there are very few species of the genus in Micronesia. This is the position taken by the pre-1900 publications; it is the view of Safford (1905), concerning only Guam; and it is the view of Dr. F. R. Fosberg, who has personally visited perhaps as many, or more, of the islands in Micronesia as any other person. The other viewpoint found its highest expression in the writings of Prof. Ryozo Kanehira during the 1930's and was espoused by several other botanists. This position is simply that there are many local endemic species of *Pandanus*, in Micronesia.

At first I assumed that Kanehira and the others who shared his view were correct. But a thorough study of the Marshall Islands pandans showed that many of these so-called species were simply cultivated forms, as myriad and variable, or more so, than the various kinds of apples of more northern climes. This discovery led to a rather profound skepticism of the "species" from elsewhere in Micronesia. Field studies tended to reinforce this skepticism. The result is a considerable reduction in the number of species which I believe can reasonably be recognized from the Micronesian region. Most of the names which I consider as synonyms were proposed for plants of the Section *Pandanus*, which are certainly the most widespread and the most abundant in individuals in Micronesia. A few however proved to be reducible to species representing other sections of the genus. Several of the synonyms were names based on manifestly immature

specimens—unripe fruits—indicating a need for cautious study of specimens to ascertain their relative maturity. Evidently unripe fruits can look so unlike ripe fruits (of the same species, or same individual) that the "new species" has even been placed in the wrong section of the genus.

In one paper, Prof. Kanehira (1935) mapped the distributions of the various sections of the genus, and reached the conclusion that Micronesia must be one of the "centers of origin" of the genus. Unfortunately this cannot be substantiated, and the pandans of Micronesia are seen to be, as is true of probably all of the other Micronesian genera, fewer in species than those of the rich islands of Malaysia, Indonesia, the Philippines, New Guinea, and the Solomon Islands. This is not of course to deny the fact that Micronesia does have its endemic species. These are as interesting and as unique as ever; one at least (*Pandanus patina*) defies a rational placement in the known sections of the genus. But the conclusion is nonetheless satisfying as it removes what seemed to be a striking exception to the general conclusions reached on the basis of analysing the endemism and phytogeographic relationships of the remainder of the vascular flora of Micronesia. This was especially true in the Marshall Islands, where more than 20 species were supposed to be endemic in a region of highly monotonous topography, very little substrate variation, fairly uniform climate, and no other species of any genus of flowering plants except *Lepturus* was considered to be endemic.

A fuller discussion of the importance of the cultivars in taxonomy of the Micronesian pandans is given under Section *Pandanus* below.

In various other papers I have attempted to describe some aspects of variability in fruit morphology, which is the main basis of classification for species of *Pandanus*. Assumptions by various authors as to the reliability of particular characters have proved, in many cases, to be untrue or at least exaggerated. Absolute size, meristic characters such as carpel number, variations in shape, extent of carpel separation, and various less tangible features have all been invoked at one time or another as ostensibly "specific" characters. In evaluating the reliability of these characters (Stone 1959; 1961; 1967) I believe I have presented sufficient evidence concerning them, and just how far they may be used, so that I do not need to repeat all justifications here. However, this is not to say that the characters listed are without value. Indeed, "clusters" of just these characters may be diagnostic of local populations of pandans in Micronesia. In many cases, however, these are ranked at less than specific level, often as forms or even cultivars. In Western Micronesia, especially in Palau, Yap, and the Marianas, where cultivation has played a relatively small role, the pandans often display a distinct "local stamp" of features (as Martelli put it when discussing Hawaiian pandans in 1930) which sometimes permit a sound basis for recognizing them as taxa. Where cultivation and attendant introduction are common however, it is often more difficult to place a particular specimen.

The Sections of the Genus.

Pandanus, with perhaps 600 species, would be very difficult to work with if sectional divisions had not been set up. There are now over two dozen of these (St. John 1960 et seq.), and some others exist which are as yet undescribed.

Some of these were first proposed as distinct genera by Gaudichaud (1841), De Vriese (1854), and others, but tradition has never upheld these genera. Some of these sections would certainly have been sanctioned as genera if the pandans had received as much study or had been as popular as, for example, the palms. Fortunately, perhaps, the pandans have been rather neglected, and those botanists who worked the most on the genus—Warburg, Martelli (1913–14), Kanehira, St. John, and others—all reconfirmed its unity.

Not all of the proposed sections are perhaps clearly distinct, but those present in Micronesia are easily distinguished, provided that reasonably mature fruits are available. It is less easy, but still possible in our area, to distinguish sections on the basis of staminate flowers or vegetative material. For species identification however, ripe fruit is necessary.

The sections found in Micronesia are as follows:

SECTIONS OF *PANDANUS* OCCURRING IN MICRONESIA

a. Carpels usually free, ripening as drupes, or a few connate in few-celled phalanges, these usually intermingled with 1-celled drupes.
   b. Cephalia spicately or racemosely disposed; staminate spikes also racemosely disposed.
      Stigmas plane, often excentric; drupes small. JEANNERETIA
   B. Cephalia solitary; staminate spike now solitary, now ravemose.
      c. Cephalia subglobose; stigmas vertical; mesocarp thick, pithy; staminate spikes racemose. HOMBRONIA
      C. Cephalia oblong-cylindric; stigmas mostly horizontal; mesocarp fibrous; staminate spike solitary. MICROSTIGMA
      C′. Cephalia subglobose; stigmas horizontal, very broad; mesocarp pithy-fibrous; staminate flower...? (*P. patina*, endemic species in Ponape; section uncertain, possibly undescribed).

A. Carpels connate, ripening as phalanges, or a very few (always terminal) 1-celled; seeds enclosed in a unitary osseous endocarp, not rarely only the innermost normal.
   d. Cephalia solitary (very rarely a second cephalium on the peduncle, this always strongly reduced and often infertile). PANDANUS
   D. Cephalia racemose, those of one inflorescence subequal in size, all with fertile seeds. Staminate flower...? (*P. kanehirae*, endemic in Palau; probably a subsection of Sect. Pandanus).

Brief Descriptions of the Sections

Genus PANDANUS Stickm.

Section *Pandanus*.

Cephalia solitary racemose. Carpels connate into phalanges with a unitary endocarp. Stigmas more or less horizontal on the apex of each carpel, U- or V-shaped or reniform, with a groove on the interior side. Stigmas arranged more or less concentrically, the grooved side directed toward the interior (centripetally). Staminate spikes in bracteate racemes. Staminate phalanges more

or less columnar, with the filaments all along the distal length of the column, or crowded umbellately at the apex; anthers free, oblong, shortly apiculate at apex. Staminodia and pistillodia very rare.

Type species: *Pandanus odoratissimus* L. f.

Represented throughout Micronesia; the most widely distributed section in our area. In the Marshall Islands represented by many cultivars, mostly grown for their pulpy edible fruits; some grown for leaves. Cultivars with unarmed leaves and with white-striped leaves are known in Guam.

Although more than half a dozen species of this section have been claimed to exist in the Marianas, I consider that there is only one truly wild. However, seven forms are distinguished by characters of the phalanges, which are recognized here.

Section *Pandanus*, a subsection nov.? Represented by *Pandanus kanehirae* Martelli, endemic to Palau. While this species fits reasonably well into Sect. *Pandanus*, it has some apparently unique features and quite likely should be made the type of a subsection. Cephalia are racemose; carpels are connate into several-celled phalanges; stigmas are small and more or less horizontal. However, the staminate flowers are unknown.

Section *Hombronia* (Gaudichaud) Warburg.

Cephalia solitary or racemose. Carpels mostly connate into phalanges, these often mingled in the same cephalium with few to many free carpels; carpels connate in rows, not concentrically arranged; stigmas mostly vertical, all facing the apex of the cephalium, or facing each other (if two) or the two end stigmas of a row facing each other; mesocarp usually solid and pithy, not chambered. Staminate spikes racemose; staminate phalanges columnar, with free anthers.

Type species: *Pandanus dubius* Sprengel (Syn. Hombronia edulis Gaud.).

Represented in Micronesia by two very similar species, of uneven distribution; present in Palau, Yap, Truk, Kusaie, the Marianas (Guam-Tinian-Rota-Saipan), but absent in the Marshall Islands, in Ponape, and most Caroline Atolls; present however in Nukuoro and Kapingamarangi, where they may be introduced.

Section *Jeanneretia* (Gaudichaud) Stone. (Jeanneretia Gaud., Bot. Voy. Bonite. t. 25. 1841).

Cephalia racemose, usually rather small. Carpels all or nearly all free, rarely 2-4-celled. Stigmas horizontal, often slightly or markedly excentric. Staminate spikes racemose; stamens in groups of 3–5.

Type species: *Pandanus polycephalus* Lamarck (Jeanneretia littoralis Gaud.).

Represented in Palau and Yap, but not elsewhere in Micronesia, by about four species.

Section *Microstigma* Kurz.

Cephalia solitary or racemose, often elongate or cylindric. Carpels all or nearly all free. Stigmas horizontal, most central. Staminate spikes solitary or racemose; stamens arising singly from axis of spike, not in phalanges.

Type species: *Pandanus montanus* Bory (Syn. Sussea conoidea Gaud.).

Represented in Truk and Ponape, but not elsewhere in Micronesia. One species.

Section? (probably new): represented by *Pandanus patina* Martelli, which is endemic to Ponape, found there only on the summits of the highest peaks. The species was assigned to Sect. *Lophostigma*, but this seems very unlikely. It shows some resemblance to Sect. *Microstigma*, but since the staminate flowers are unknown, it cannot be positively placed there. It also has some points of resemblance to Sect. *Hombronia*, but the stigmas are horizontal. The cephalium is solitary and globose; the carpels are all free; the stigma is large and somewhat excentric. It is quite possible that it should be made the type of a section; but it is necessary to know the characters of the staminate inflorescence.

Micronesian species

During the period of the Japanese Mandate in Micronesia, the two most active botanists concerned with the flora of the numerous mandated islands were Ryozo Kanehira, of the Faculty of Agriculture of the Imperial Kyushu University in Fukuoka, who was concerned with forestry as well as with taxonomy, and Takahide Hosokawa, then of the Taihoku (Formosa) Imperial University (now at Kyushu University), who was both taxonomist and ecologist. It was especially the late Prof. Kanehira's opinion that Micronesia held a large number of endemic species, particularly in this the typical section of the genus. During the decade 1930–1940, Prof. Kanehira described species from Micronesia. In his *Flora Micronesica* of 1933 (primarily concerned with trees of the area) Kanehira depended on Count Martelli, the world authority on Pandanaceae, for an account of the pandans, but subsequently he became greatly interested in them and published many papers concerned not only with Micronesian species but also with those of other regions, including Borneo, New Guinea, and Malaya. Dr. Hosokawa also proposed a few new species based on his own collections in Micronesia. In proposing these species, both Kanehira and Hosokawa depended (it would seem) rather heavily on the precedents set by Martelli, on reasonably dependable grounds. These precedents arose from a dual cause, first from the overwhelming majority of herbarium material which consisted largely or entirely of fruits, which in turn led to a great reliance on characters of the fruit in classification; and second, from the tradition of earlier botanists up to Warburg's monograph in the Pflanzenreich of 1900 that characters of the fruits were dependable and accurate.

These precedents still prevail, to a great extent, and are still basically sound. However, as I have shown elsewhere (1961), variation in the fruits of cultivated forms can make virtually useless the classical grounds for specific delimitation based on the morphology of syncarps, phalanges, and carpels. Both Kanehira and Hosokawa were familiar with the Marianas and Caroline Islands, but neither botanist had concerned himself with the Marshall Islands, or the smaller Caroline atolls, and it was precisely in those places that the pandans displayed the greatest range of variation as a result of their importance in the daily life of the indigenous people, which led them over the course of centuries to select numerous special cultivars, propagating them as clones, and chiefly emphasizing increasing bulk and sweetness of the mesocarp pulp, sometimes with concomitant reduction or even disappearance of endocarp and viable seed. This led in the Marshall Islands to an array of over 130 known cultivars and in the Gilbert Islands to

more than 200 (Stone, 1963; Luomala, 1953). In the Caroline atolls, particularly those nearer the Marshall Islands, there occur from as many as two dozen to about three or four cultivars (Stone, 1960; 1963). These cultivars, as represented by a few dry phalanges in herbaria, with or more often without a few dry leaves, misled the two Japanese botanists, who, most particularly Prof. Kanehira, believed that they represented new species. Thus by 1940 there came to exist on paper an astonishing number of endemic species of Sect. *Pandanus* in Micronesia; and 22 of them allegedly were restricted to the Marshall Islands.

During an intensive study of Marshallese pandans it soon became obvious that these "species" were merely cultivars, usually clones, valued for their fruit. I now believe that all the Marshallese forms can be reduced to one common species (though in 1961 I distributed the forms among two species), and one rare form which apparently represents a chance hybridization of the local species with an individual of *P. pedunculatus* R. Br. (sensu lato), which occurs in Australia and Melanesia, and fruits of which presumably occasionally drift into the Marshalls (along the course I have discussed in connection with the presence of *Pandanus pistillaris* in Mokil; Stone 1959).

It is interesting to note that the islands west of Truk do not include known and used cultivars of pandans, with the usual exception of those used for their textile-quality leaves. Around Truk there occur a small number of edible cultivars, including the seedless form called by Kanehira *Pandanus cylindricus*. The atolls around Ponape, and their "immigrant" establishments on Ponape itself, have a large number of cultivars; Mokil and Pingelap in particular have a good representation, as does Kapingamarangi (Stone, 1967). It is interesting to find in these atolls several cultivars which are clearly of Marshallese origin, which in some cases is acknowledged by the inhabitants; but there are also some clones not found in the Marshall Islands. But no areas can boast of as many clones as the Marshall and Gilbert Islands. In Yap and Palau, on the contrary, it is virtually unthinkable to eat pandan fruits—except for the seeds of *P. dubius* or *P. compressus*, of Sect. *Hombronia*, which do not concern us here.

The realization that cultivated clones had been misconstrued as species resulted in a striking reduction in the number of species supposedly endemic in Micronesia and of course in the percentage of endemism for the region (which these spurious species of *Pandanus* had inflated to a considerable degree). On the other hand, there are still a small number of insular populations, more or less free of the influence of cultivation, which display an at times bewildering amount of variation. As before this variation chiefly involves the fruits, although some features of leaves and male inflorescences also vary. Fortunately I have had a good deal of field experience, partly during the tenure of a research assistantship to Dr. H. St. John and financed through the National Science Foundation grant (G-1834) in 1956 and 1957, and partly through my stay in Guam as Head of the Department of Biology of the College of Guam, 1961-65, in many of the Micronesian islands, particularly in Guam, Saipan, Rota, Tinian, in Palau, in Truk and the Hall Islands, in Ponape, Kusaie, and the atolls of the Ponape District, as well as many of the Marshall Island atolls. My impression is that on the high islands there occur forms which at least for the time being can usefully be

discriminated, and therefore are here deemed species. It is true, however, that the diagnostic features of these species are still largely those of the fruits. It would come as no surprise if further study, particularly of deliberate controlled hybridizations or cytogenetic investigations, appeared to support the idea that these populations, or some of them, should be ranked at a lower level taxonomically, as varieties or forms. Yet it is equally true that once an appreciation of the different kinds of variation that occur in these populations (and of course of the range of each kind of variation) is obtained, there remain several "clusters" of forms which in some cases at least show a satisfactory geographic delimitation as well as often being restricted to one island or two adjacent islands. It is these "clusters", often insular populations, which I have ranked as species.

A separate but confused and confusing issue is that of nomenclature. Briefly, it involves three problems. (1): The typification of the name *Pandanus tectorius*, usually ascribed to Solander ex Parkinson (1773); (2): the question of whether any of the relevant pandans of Micronesia are taxonomically identical with *P. tec orius*; and (3): the question of whether any Micronesian pandans can be referred to *Pandanus odoratissimus* L. f. (1781). I have elsewhere discussed this problem (Stone, 1967), and have attained sufficient understanding of *P. odoratissimus* to state with fair conviction that it does not occur anywhere in Micronesia. As to *P. tectorius*, I consider first that no Micronesian plants are really identical with this Tahitian species, and second that the name is illegitimate as of 1773, and dates only from 1900 as *P. tectorius* Sol. ex Warburg. This means that even if the Tahitian and Micronesian plants are thought to be conspecific, the name *P. tectorius* is by no means the earliest epithet, and that the name *P. fragrans* Gaud. (based on Guam specimens) is probably the earliest *relevant* available name. The rather frequent mention of Micronesian pandans under the name *P. tectorius* is thus here considered erroneous both on taxonomic and purely nomenclatorial grounds.

The species of Pandanus in the Marianas Islands.

Gaudichaud illustrated a phalange collected in Guam with the name *Pandanus fragrans* in the Atlas of the Voyage of "La Bonite" (1841). Although he provided no formal description, the name stands as a valid one under the International Code of Botanical Nomenclature since it was accompanied by an illustration "with analyses" and was used in combination with an already established generic name. This name was not taken up by later authors (except Brongniart, who applied it to a plant from New Caledonia, probably erroneously). The next treatment of Marianas species was that of Martelli, who described *Pandanus kafu* and *P. guamensis* (1914), and illustrated *P. fragrans* (in Kanehira, 1934). Kanehira shortly afterward described *Pandanus charancanus*, *P. hosokawai*, and *P. saipanensis* (1936), all from Saipan. Hosokawa described *Pandanus rotensis*, *P. pseudomenne*, and *P. koidzumii* (1943) from Rota, Saipan and Tinian.

Safford (1905) had mentioned *Pandanus tectorius* Parkinson (of Tahiti) as occurring in Guam, but stated "I am not sure of the identity of the Guam plant" (p. 344). The plants he referred to by this name are the "aggak" of the Guamanians, used for their leaves, and often planted around houses; but I see no reason to suppose that they are anything but domesticated plants of the wild *P. fragrans*. Safford also mentions a plant (p. 345) called "paingot" in Guam,

said to be used as a pot-herb. I have seen no such plant in Guam. However, there is such a plant, used (for example) in Malaya to flavor coconut-tapioca puddings and such foods; it is a plant with soft, unarmed leaves, which Ridley named *Pandanus odorus*. It has never been found in flower or fruit. This is perhaps, or could formerly have been, in Guam.

It should be mentioned here that Safford's photographs are mislabelled. His Plate 60 (facing p. 344) with the legend "Pandanus fragrans" is in fact a photo of *Pandanus dubius*. On Plates 2, 8, and 23, however, plants of *Pandanus fragrans* are shown; and the "aggak" or textile pandan is shown on his Plate 7.

Merrill (1914) in his Enumeration of the Plants of Guam, did not reach any conclusions about the pandans, but suggested tentatively that perhaps *Pandanus fragrans* should be the name properly to be used, and that probably only one species existed in Guam, but was polymorphic. In this he was correct on both counts. Furthermore, *P. fragrans* occurs on the other Marianas Islands. Its polymorphic nature led to the recognition of six forms, some at first proposed as species.

The only other wild species of *Pandanus* definitely known in the Marianas is *Pandanus dubius*. These two species may be quickly discriminated as follows:

Key to *Pandanus* in the Marianas

a. Leaves commonly well over 10 cm broad, thick, the tip bluntly rounded with a short acumen; male inflorescences with yellow bracts; cephalium depressed-globose, commonly over 20 cm wide; drupes mostly 1-celled, with one vertical stigma, or a few 2-4-celled with 2-4 stigmas; strongly glaucous and somewhat purplish; pithy, with thin endocarp and large seeds; often 15 cm long or longer. ..... *P. dubius*

A. Leaves usually less than 10 cm broad, relatively narrower, the tip produced gradually into an elongate whiplike extension; texture firm but thin; male inflorescence with white bracts; cephalium subglobose, globose, or ovoid, mostly 15–20 cm wide; phalanges generally 2–8-celled, with 2–8 horizontal or oblique often rather small stigmas; not or scarcely glaucous; ripening to orange or vermilion; upper mesocarp chambered; seeds embedded in dense bony endocarp, rather small; often 4–8 cm long, rarely longer. ..... *P. fragrans*

Note: *Pandanus carolinianus* Martelli occurs, or occurred, in Saipan, as cultivated plants. Two of these cultivars were described by Kanehira as *P. saipanensis* and *P. hosokawai*. They may be distinguished (if still persisting) by their multilocular phalanges with 5–20, commonly 10–16 cells per phalange, and the relatively thick, mild, sweet pulp. See further notes below.

Sect. *Pandanus*

Pandanus fragrans Gaudichaud, Bot. Voy. Freyc. t. 22, f. 10. 1851.
Safford 1905: 344. Merrill, Philipp. J. Sci. Bot. 9: 48. 1914.
Martelli, in Kanehira, Bot. Mag. Tokyo 48; 117. f. 2. 1934.
Kanehira, J. Jap. Bot. 12: 499–500. f. 4–5. 1936; J. Dept. Agric. Kyushu Univ. 4: 261. 1935.

Not of Brongniart, Ann. sc. Nat. Bot. ser. 6, 1: 274. 1875.
P. guamensis Martelli, Webbia 4: 404. t. 42, f. 4–6. 1914.
Kanehira, J. Dpt. Agric. Kyushu Univ. 4: 261. 1935.
Bot. Mag. Tokyo 49: 67, f. 7. 1935; J. Jap. Bot. 12: 546, f. 11–12. 1936; ibid. 13: 322, f. 7. 1937.
P. kafu Martelli, Webbia 4: 405. t. 19, f. 1–3. 1914.
Merrill, Philipp. J. Sci. Bot. 9: 47.1914. Kanehira, Bot. Mag. Tokyo 45: 273. 1931; Flora Micronesica 62. f. 4. 1933; J. Dpt. Agric. Kyushu Univ. 4: 261. 1935.
P. charancanus Kanehira, Bot. Mag. Tokyo 50: 523, f. 47–48. 1936; J. Jap. Bot. 549, f. 19–20. 1936.
P. rotensis Hosokawa, Acta Phytotax. Geobot. 13: 166. f. 3. 1943.
P. pseuda-Menne Hosokawa, ibid. 164, f. 2. 1943.
P. koidzumii Hosokawa, ibid. 163, f. 1. 1943.

Holotype: *Gaudichaud* (P). Type locality: Guam.
Endemic in the Mariana Islands.

Vernacular name (Chamorro): "kafu" (for wild trees); "aggak" (for trees used for their leaves).

General description of P. fragrans.

Tree occasionally to 12 m tall, sparingly branched, branches each with a terminal crown of elongated ensiform leaves. Trunk with basal proproots up to 1–2 m long, rarely more; bole and branches grayish, rather pale, studded with scattered short conic rather blunt projections rarely much over 5–8 mm long, or these few or sometimes absent; branches di- or trichotomously arranged, somewhat dorso-ventrally flattened and slightly amplexicaul in appearance at basal junction. *Leaves* mostly 1–3 m long, rarely over 8–10 cm wide (these dimensions exceeded in leaves of vigorous unbranched juvenile plants), M-shaped in cross-section, prickly along the margins and the costa dorsally, otherwise unarmed; prickles antrorse, the largest near the leaf-base, greenish, somewhat incurved, seldom over 3 mm long, decreasing in size but becoming more crowded toward the leaf-apex which is gradually tapered and drawn out into a long trigonal nearly linear closely and minutely prickly flagella. Attitude of leaves at first erect, but soon the tip or distal third dropping. Upper surfaces dark green, slightly glossy; lower surface paler, duller, not or scarcely glaucous or sometimes glaucous. *Male inflorescence* pendent, a branching spadix with narrow subfoliaceous white bracts and white cylindric-compressed multistaminate spikes to 15–18 cm long. Staminate phalanges of many stamens borne subracemosely, the usually 10–16 stamens with a short distinct filament, oblong shortly apiculate anthers each about 4–5 mm long; spikes about 9–11 per inflorescence; lowest bracts empty, with green leaflike tips. *Female inflorescence* in anthesis erect, solitary, subglobose, terminal, closely invested by white ephemeral bracts crowded at the apex of the peduncle, slightly spreading at anthesis, afterward closely appressed (by growth of the cephalium) but withering to brown and in fruit caducous and mostly fallen from the then pendent cephalium; peduncle trigonal, commonly 20–40 cm long; cephalium subglobose or ellipsoid, when mature about 15–25 cm long, 14–25 cm broad, composed of about 80 (mostly 50–100) phalanges, these mostly 4–8 cm long, mostly 2–11-

celled, the apical ones occasionally simple, those adjacent to the peduncle sometimes "doubled"; phalange sides smooth or sometimes with sulci demarcating the carpels, these seldom over 0.5 mm deep; carpel apex conic or truncate or slightly concave, adjacent apices usually separated by shallow sometimes almost obsolete sulci; free apex of carpel rarely to 1 cm long, mostly 0.5–5 mm; stigmas apical, approximately central or on peripheral carpels inwardly somewhat excentric, U- or V-shaped or reniform or variously distorted, horizontal or oblique, sessile or very slightly raised, mostly 1–2 mm broad. Pericarp and lower mesocarp when fully ripe orange to vermilion, the carpel apices sometimes remaining greenish or brownish; upper mesocarp within chambered, each chamber corresponding to a carpel apex, traversed longitudinally by a few fibers and transversely by thin plates of pith; endocarp unitary, with the same number of seeds (or at least ovarian cells) as carpels, reddish brown, very dense, bony, traversed by a few longitudinal fibers reaching the interior side of the stigmatic apex of each carpel. Lower mesocarp fibrous and pulpy, scarcely or not shouldered at middle of phalange. Seeds slenderly ellipsoid, mostly about 10–12 mm long, with soft white endosperm; basal embryo, germinating by growth outward through (parallel with) the fibers of the base of the phalange.

Key to formae

1. Phalanges mostly 2–4-celled, sometimes 1-celled.
   2. Phalange sides creased and ribbed longitudinally; carpel apices low-conic; outer series in-arched ..... f. *marianus*
   2. Phalange sides smooth,
      3. Phalanges nearly all 2-celled; carpel apices truncate, slightly concave; stigmas about 2 mm wide ..... f. *tinianensis*
      3. Phalanges either 2-celled or 3-celled, about equal numbers of each.
         4. Stigmas 1–2 mm wide; carpel apices conic.
            5. Carpel apices 6-9 mm high ..... f. *koidzumii*
            5. Carpel apices 1–5 mm high ..... f. *fragrans*
         4. Stigmas mostly 2.5–3 mm wide; carpel apices truncate to slightly concave ..... f. *megastigma*

1. Phalanges mostly 3–8-celled, commonly 4–5-celled.
   6. Phalanges mostly 4–6.5 cm long, often laterally compressed.
      7. Carpel apices truncate and slightly concave, outer series of carpels erect to divergent ..... f. *rotensis*
      7. Carpel apices low-conic; outer series strongly incurved ..... f. *fragrans*
   6. Phalanges mostly 7–10 cm long, stout and robust, tending to be subterete; carpel apices conic or truncate-conic, sometimes 1 cm high .. f. *savannarum*

Descriptions of formae.

(a) forma *fragrans*. The commonest form in Guam on limestone; also throughout the Marianas, at least in the southern part.

Phalanges without lateral sutures; turbinate-pyriform; carpels not ribbed or creased longitudinally, usually 2 to 5 connate in each phalange; stigmas 1 mm broad.

GUAM: Tumon (*3933**); Barrigada Hill (*4003*); Mt. Almagosa (*4457*); Apra (*4357*).

SAIPAN: Hillside just south of Laderon Rueda (*1368*; *1369*); between Susupe and San Vicente above the quarry (*1370*); summit of Mt. Tagpochau (*1374*).

(b) forma *marianus* B. C. Stone, forma nova.

Forma *fragrans* simillima sed superficies carpidii longitudinaliter sulcatis.

Phalanges without lateral sutures, carpels with longitudinal ribs and creases; carpels usually 1–3, rarely 4–6; phalanges about 5×2 cm; stigmas 1 mm broad; phalange apex truncate, with shallow apical sutures.

Holotype: GUAM: In limestone forest, Yigo-Atdosco (*Stone 4266*, GUAM).

GUAM: Just south of Naval Hospital opposite Fonte River (*1361*).

(c) forma *savannarum* B. C. Stone, forma nova.

Superficies carpidii non-sulcatis; sed sulci intercarpidales profunduli. Phalanges 3–8-carpidiatis.

Phalanges with conspicuous lateral sutures separating the carpels somewhat; apices of carpels conic; carpels mostly 3–5, or up to 8, per phalange; phalanges robust, stout.

Holotype: GUAM: In volcanic savanna hills at Manengon (*Stone 3865*, GUAM).

GUAM: Cetti Bay Hillsides (*3905*); Upper Harmon (*3845*); hillsides s. of Agat, S. W. of Mt. Lamlam (*1362*; *1363*); S. of Mt. Lamlam (*1364*).

To this form precisely belong *P. guamensis* Martelli, Webbia 4: 16, t. 2, f. 4–5. 1914; and *P. pseudo-Menne* Hosokawa, Acta Phytotax. Geobot. 13: 163. 1943.

PAGAN: *Hosokawa 7691-a* (Taihoku=Taiwan), holotype of *P. pseudo-Menne*. This form grew in volcanic soil in a savanna.

TINIAN: *Hosokawa 7708* (Taihoku)

(d) forma *megastigma* B. C. Stone, forma nova.

Forma *tinianensis* simillima, sed phalangibus plerumque 3-carpidiatis, stigmata magna 2–3 mm lata.

Holotype: Guam: Forests opposite gate of Andersen A. F. B. (*Stone 4248*, GUAM).

GUAM: Same locality, *4249*, *4250*, GUAM.

The holotype has phalanges mostly 3-celled, some 1–2-celled or 4-celled; averaging over 6.2 cm long, and 4–6 cm wide; carpel apices truncate, slightly concave; stigmas 2–3 mm broad. The ripe pulp was vermilion.

(e) forma *koidzumii* (Hosokawa) B. C. Stone, comb. and stat. nov.

Syn. *P. koidzumii* Hosok. Acta Phytotax. Geobot. 13: 163, f. 1. 1943.

Phalanges without lateral sutures; carpels unribbed, mostly 3 per phalange, apices truncate, apical sutures very shallow or obsolete; stigmas about 2 mm broad.

Holotype: TINIAN, *Hosokawa 7805* (now apparently lost), Taihoku (=Taiwan).

Known only from Tinian so far.

(f) forma *tinianensis* B. C. Stone, forma nova.

Forma *koidzumii* simillima sed phalangibus 2-carpidiatis.

* This and remaining such numbers refer to the author's collections in the College of Guam herbarium.

Phalanges as in the previous form, but constantly 2-celled, only 1 or 2 apical ones 1-celled, and 1 or 2 basal ones 3-celled.

Holotype: TINIAN: Central part of the island, alt. 100 ft., on ridge near pumping station (*Stone 1372*, BISHOP).

TINIAN: Near San José (*1373*, BISHOP).

(g) forma *rotensis* (Hosokawa) B. C. Stone, comb. and stat. nov.

Syn. *P. rotensis* Hosokawa, Acta Phytotax. Geobot. 13: 166. f. 3. 1943.

Phalanges mostly 5-celled, rarely 4-6-celled; carpel apices pyramidal, all or mostly 6–9 mm high; stigmas about 2 mm wide. Phalanges about 7×4 cm.

Holotype: ROTA: Seacoast (*Hosokawa 7670*, Taihoku (=Taiwan)).

Like f. *tinianensis* but with 4–6-celled phalanges.

General notes on *Pandanus fragrans*.

Flowering time. Observations of the pandans in Guam over several years showed that a rather exact periodicity is involved in flowering, which is gregarious in various localities, though not necessarily involving the whole island. Since the fruits are the most commonly noticed structures, with male inflorescences seen on occasion but female inflorescences rarely seen (because they are more hidden by the leaves and erect), data on flowering time is scanty for most species. The population of f. *fragrans* on Barrigada Hill exhibited gregarious flowering in late February or early March, and for one to three days in this period there was a dense display of male inflorescences. I believe that an equal number of female plants also flowered then, but these can only be seen by careful observation, unless it is possible to look more or less directly down at the crowns. At this time the bracts around the cephalium spread somewhat, presumably allowing access for the pollen. Bees were seen to visit the male inflorescences, but I could not ascertain whether they visited the females. After a few days, almost all male inflorescences had withered to a dryish mass or had fallen. Almost exactly 2 months later, flowering again occurred, in late April or early May. This 2-monthly interval was repeated until late August-early September. There was no flowering in late November, December or January.

I did not see male inflorescences in Saipan or Tinian. However, it appears that the timing of the flowering is affected by local conditions, altitude, and probably by local rainfall. During the gregarious flowering of the Barrigada plants, others appeared in flower in Yigo and around Dededo, but the plants of the savanna hills between Agat and Manengon were not flowering. It would be most interesting to have further data on this periodicity, especially to see if the 2-monthly interval between large gregarious flowering is normal.

Ripe fruits. The ripe fruits are orange to red-orange. They fall from the receptacle of the cephalium one by one or in clusters as the receptacle itself rots. The pulp is sought by various animals, especially by fruit-bats and by the African snails (*Achatina fulica*). There are indications that rats also seek the fallen fruits. Germination seems generally to be prolific, but very few seeds reach maturity as trees. Those trees near the sea or near streams may drop their phalanges into the water. Dry phalanges are relatively common objects in the drift along beaches; some of which, no doubt, were brought from distant areas. These are rarely found germinating; the voracity of the hermit-crabs may be one reason.

The seeds are edible for human purposes also, but the difficulty in extracting them from the hard endocarp is enough to discourage most persons. The pulp is edible in emergencies, but otherwise is so thin and rich in piercing, irritant crystals of calcium oxalate, that it is best left to the bats, rats and snails.

Mosquitoes. It may be of interest to point out that a local species of mosquito, *Aedes pandani* Stone, breeds in the small amount of water held by the leaf-axils of the Marianas pandans (*P. dubius* also). This is the common day-flying, day-biting mosquito that infests all the shady forests of the islands.

Pandanus carolinianus Martelli, Webbia 4: 400, t. 34. f. 1-3. 1914.

Kanehira, Bot. Mag. Tokyo 49: 61, f. 2. 1935; J. Dpt. Agric. Kyushu Univ. 4: 260. 1935; J. Jap. Bot. 12: 545, f. 6-7. 1936.

New synonyms: *P. saipanensis* Kanehira, Bot. Mag. Tokyo 50: 521, f. 43-44. 1936; J. Jap. Bot. 12: 549, f. 16-17. 1936.

P. charancanus Kanehira, l. c. 1936; in part; as to photographs of syncarp only (excl. descr., holotype, and fig. of phalanges).

P. hosokawai Kanehira, Bot. Mag. Tokyo 50: 522. 1936; J. Jap. Bot. 12: 549. 1936.

SAIPAN: "Donny" (where?) *Kanehira 3584* (P.s.); Donny, *Kanehira 3679* (P.c.)

It is evident from the specimens of the species proposed by Kanehira listed above as new synonyms that these were collected from planted or escaped trees near Carolinian settlements in Saipan. No doubt these cultivars were introduced to Saipan by Caroline Islanders (probably from Truk or Truk district). In fact, Trukese (including the peoples of outlying atolls in the Truk area, such as Namonuito, Hall Islands, Mortlock Islands, etc.) are known to have had occasional canoe contact with the Marianas Islands, probably long before Spanish discovery of the Marianas, as well as sporadically afterward. At least a small number of Carolinians lived permanently in Saipan and Guam. That they would bring with them a favorite edible pandan cultivar is understandable, especially after they discovered that the pandans of Sect. *Pandanus* wild in the Marianas had very poor edible qualities, and had never been deliberately utilized by the Chamorro-speaking peoples.

These cultivars can be recognized by their multilocular large phalanges with a large amount of basal mesocarp pulp, which when ripe is relatively low in calcium oxalate, high in sugar content, rather juicy, and palatable. The cephalia furthermore are usually ellipsoid or oblong, rather than subglobose as in *P. fragrans*.

I did not find these cultivars in Guam; nor in Saipan, Tinian, or Rota, during the various collecting trips made to these islands between 1956 and 1965. It is possible that they have died out.

It is worth repeating that care should be taken in collecting pandans in Micronesia to ascertain whether they are cultivated or at least used. Description of further "new species" in the Sect. *Pandanus* is highly likely to be erroneously based on cultivars of polymorphic species such as *P. carolinianus* and *P. fischerianus*.

Sect. *Hombronia*

Pandanus dubius Sprengel, Syst. Veg. 3- 897. 1826. Kurz, J. Bot. 5: 127, t. 64,

f. 1–2. 1867. Warburg, in Krieger, Neuguinea, t. 7. 1899; in Pflanzenr. 4, 9: 50, f. 14 A & C (only). 1900. Martelli, Webbia 4: 12. 1913. Merrill, Philipp. J. Sci. Bot. 9: 48. 1914. Kanehira, Bot. Mag. Tokyo 45: 273. 1931; Flora Micronesica 61, f. 2. 1933; J. Dpt. Agric. Kyushu Univ. 4: 260. 1935; J. Jap. Bot. 14: 170–173, f. 1–5. 1938. Stone, Proc. Biol. Soc. Wash. 80:54. 1967; Flora of Guam (in prep.).
New synonym: *P. kafu* var. *confluentus* Kanehira, Bot. Mag. Tokyo 50: 525. f. 49–50. 1936.
Holotype: Plate 80 of Rumphius' Herbarium Amboinense, vol. 4. 1753.
For synonymy see Kanehira 1938; Stone 1967.

Distinctive because of its relatively broad, bluntly rounded, shortly acuminate-caudate leaves, yellow bracts; and glaucous-purplish large fruits, the segments usually 1–2-celled, rarely also 3–4-celled, with solid soft pithy interior, thin endocarp and relatively large seeds centrally situated in the drupe or phalange. Staminate inflorescence pendent, racemose, each spike subtended by a somewhat fleshy bract; spikes white, oblong-cylindric, usually somewhat flattened ventrally; staminate phalanges columnar-racemose, bearing numerous filaments (about 10–20) each with oblong 5–6 mm apiculate anther; pollen white.

This plant forms occasionally extensive thickets in the Marianas, almost invariably on limestone soils; individual trunks may attain a height of 10 or 12 m, and are sparsely branched; but frequently the trunks, or their proximal part, are decumbent, supported on numerous proproots, which sometimes form impenetrable masses. The pendent cephalia may attain a diameter of 35 cm, and are subglobose or somewhat oblate. The colors of the fruits as they change through stages of ripening are striking. Two such stages may be compared as follows.

	Full-sized but unripe phalanges	*Fully ripe phalanges*
Apex:	Glaucous greenish-white	Orange
Midline:	Orange-brown	Maroon
Base:	Slightly purplish-green	Strongly glaucous purplish

The phalanges tend to remain connate until past full ripeness.

The relatively large white seeds have a pleasant flavor (if ripe) resembling that of coconut meat. Hence the fruits are still, and formerly were frequently, sought out by the Marianas people as food. Unlike the dense endocarp of *P. fragrans*, that of *P. dubius* is easily cut open, so that the seeds may be picked out and eaten. In Rota (at least) there is a traditional Sunday pastime involving the eating of these seeds.

It is difficult to decide whether *P. dubius*, known in the Mariana islands as "pahong"* or "pafung", is authentically wild or is introduced. The problem is that both explanations are very easily defended. The phalanges or drupes of *P. dubius* are buoyant; the species occurs in Yap and Palau and farther to the southwest in Malaysia; drift fruits could easily account for its occurrence in the Marianas. However, it would be equally easy to concede that the fruits could have been brought to the Marianas by voyagers who enjoyed eating them and perhaps also utilized their leaves, which may be made into water-repellent mats. I am inclined toward the former explanation, but cannot exclude the latter; and of course, both postulated events may really have occurred.

* Spelled "pahoun" by Gaudichaud.

A related point of interest is the vernacular name "pahong" and its variants. This word shows a remarkable similarity to words applied in other regions either to *P. dubius* or to *P. compressus* (P. tetrodon Balf. f. sensu Kanehira; non Ridley) or to other similar species. For example:

Region	*Vernacular name*	*Applied to*
Palau	pohk; poko	P. dubius, P. kanehirae
Truk	poak	P. compressus (?)
Kusaie	mweu-yok (note: mweu=pandan, general term).	P. dubius
Nukuoro	pakoa	P. dubius
Kapingamarangi	paho	P. compressus
New Hebrides (Efaté)	vaku	P. dubius (?) P. compressus
New Ireland	waum	P. dubius
Solomon Is. (Santa Ysabel)	meongehe, meou	P. dubius, (?) P. compressus
Mauritius	baquois (French spelling; pron. "ba-kwah")	various species with mat-quality lvs.
Malaya	mengkuang; bengkuang	various species, with mat-quality lvs.
Amboina	haun	P. dubius

Recent Collections of P. dubius in the Marianas Islands (all *Stone* collns.).

GUAM: N. C. S. beach below Harmon (*3801-a*); Barrigada Hill (*4025*; staminate); Yigo-Atdosco (*4264*; *4265*; staminate); Barrigada Hill (*4672*; staminate); Mt. Almagosa (*4901*). All collns. GUAM.

SAIPAN: E. of Rapagau (*1366*); Tagpochau (*1367*; *1371*; *1383*). All collns. BISHOP.

Note on new synonym: *Pandanus kafu* var. *confluentus* Kanehira, Bot. Mag. Tokyo 50: 525. f. 49–50. 1936.

It is very difficult to understand how Kanehira could have failed to interpret his no. *3688* from "Charanca" (=Chalan Kanoa), Saipan, as anything other than *Pandanus dubius*. The cephalium (shown in the photograph in J. Jap. Bot. 12: 554, f. 21, 1936, and again in Bot. Mag. Tokyo 50: 525, f. 49. 1936) is somewhat smaller than average, with fewer drupes, but their form, the structure of the stigmas, the pithy mesocarp, the central seed with thin endocarp, all show the indisputable identity of the plant. *Pandanus kafu* (=*P. fragrans*) therefore is not to be considered as including a variety with "confluent stigmas" on which character Kanehira based his diagnosis.

I have examined the holotype in Herb. Kyushu Univ. in 1963.

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Explanation of Plates

Plate I. *Pandanus fragrans* Gaud. A grove of adult individuals at Barrigada Hill, Guam.

Plate II. *Pandanus fragrans* Gaud. Phalanges of various formae. a–c. f. *marianus* (*Stone 1361*). d. f. *savannarum* (*Stone 1362*). e–f. f. *savannarum* (*Stone 1363*).

Plate III. *Pandanus fragrans* Gaud. Phalanges of various formae. a–b. forma *megastigma* (*Stone 4248*). c. f. *savannarum* from Saipan (*Stone 1365*). d–e. f. *tinianensis* (*Stone 1372*). f. f. *fragrans* (*Stone 1368*).

Plate IV. *Pandanus fragrans* Gaud. Phalanges of various formae. On left: f. *koidzumii* (*Hosokawa 7805*). Center top): f. *rotensis* (*Hosokawa 7670*). Right, and top center: f. *savannarum* (P. pseudo-Menne) *Hosokawa 7961–a*; slightly reduced. Others natural size.

Plate V. *Pandanus fragrans* Gaud. Cephalia. a. f. *fragrans* (*Stone 4003*). b. f. *savannarum* (*Stone 1362*). c. the same, showing cephalium cut in half and separated phalanges.

Plate VI. *Pandanus dubius* Sprengel, showing leaves and cephalia, from Guam, near Ritidian Point.

Plate VII. Upper left: *Pandanus fragrans* Gaud., with male inflorescence; Barrigada Hill, Guam. Upper right: *P. fragrans*, nearly ripe phalanges; Guam; (*Stone 1690*). Lower left: *Pandanus dubius* Sprengel, male inflorescence (*Stone 2495*), Ysabel, Solomon Is. Lower right: *P. dubius*, ripe drupes (*Stone 1689*), Guam.

Plate I.

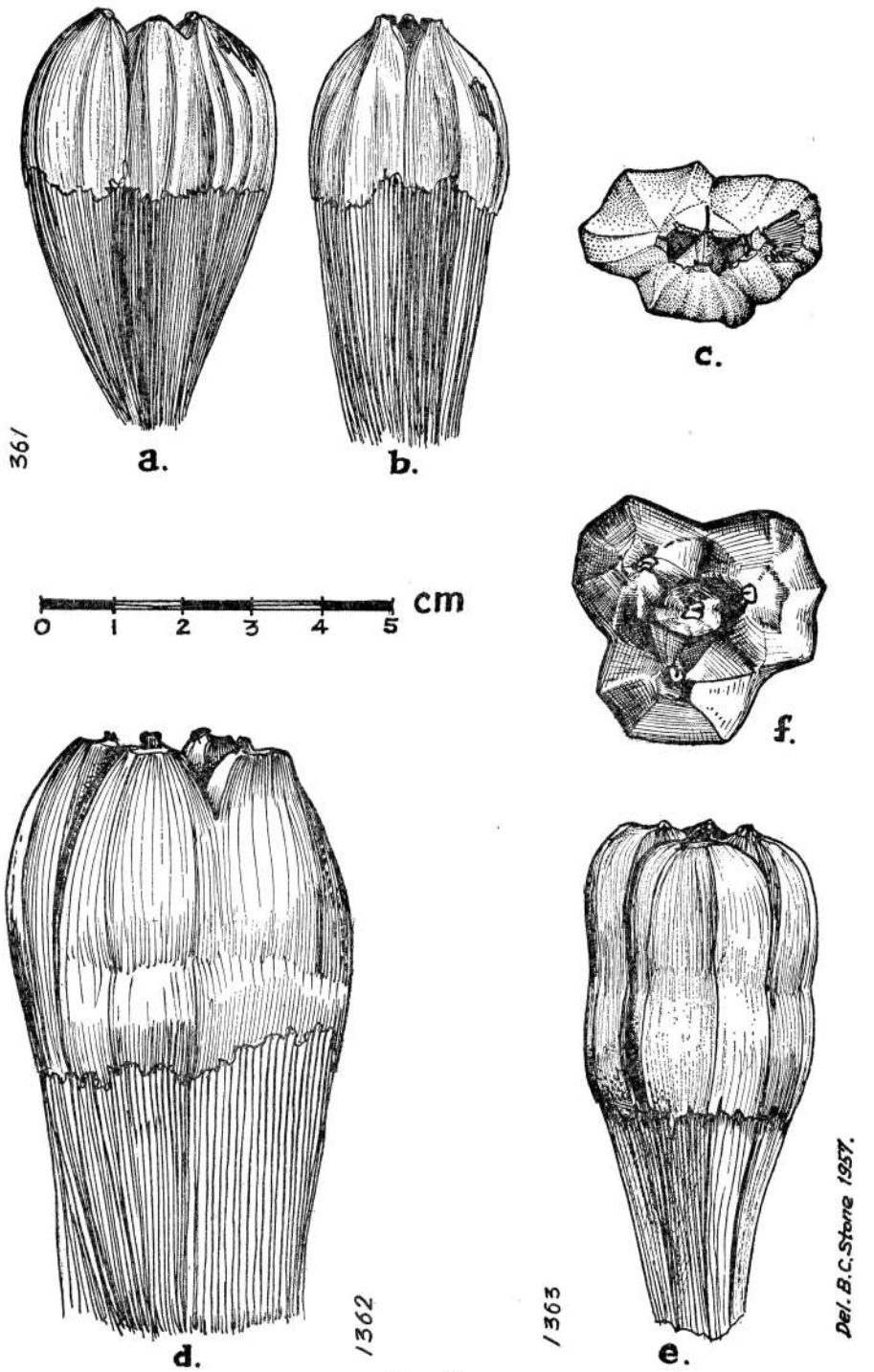

Plate II.

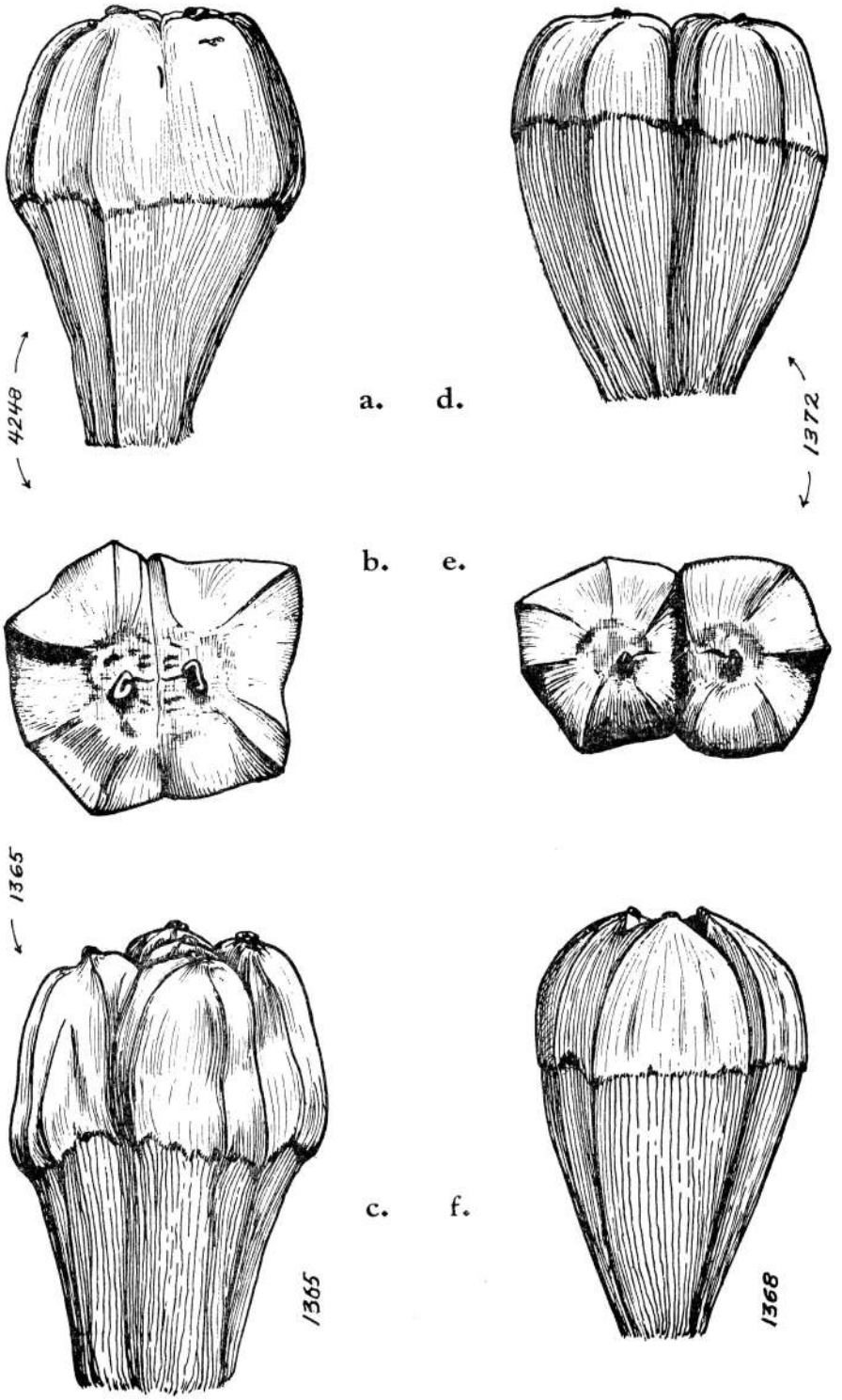

Plate III.

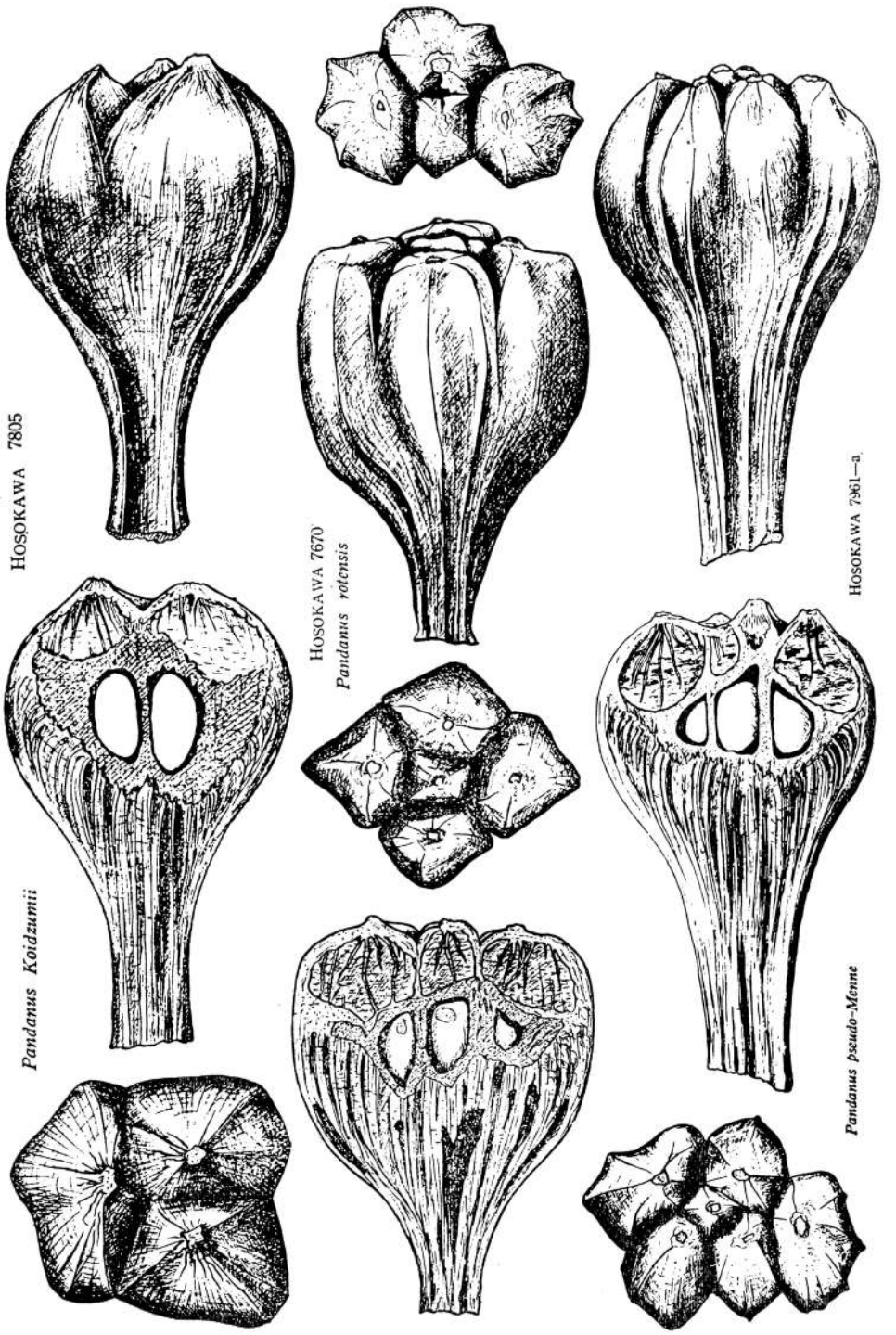
HOSOKAWA 7805
HOSOKAWA 7670
Pandanus rotensis
HOSOKAWA 7961—a
Pandanus Koidzumii
Pandanus pseudo-Menne

Plate IV.

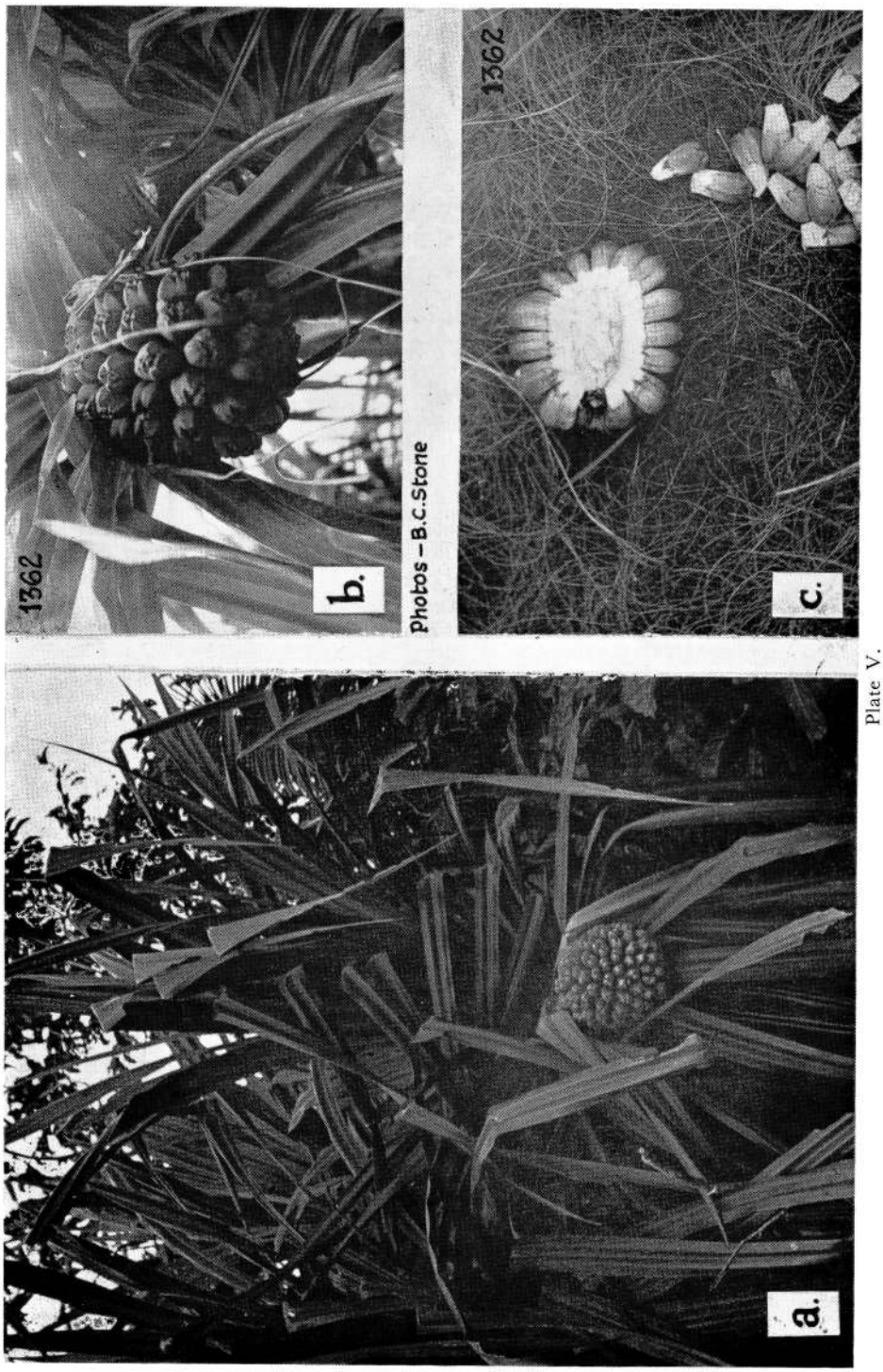

Plate V.

Plate VI.

Plate VII.