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The Biology and Economics of the *Oenocarpus-Jessenia* (Palmae) Complex.

A thesis presented

by

Michael Jeffrey Balick

to

The Department of Biology

in partial fulfillment of the requirements

for the degree of

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in the subject of

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TABLE OF CONTENTS

Introduction 1

Acknowledgements 5

1. Ethnobotany of the *Oenocarpus-Jessenia* Complex. 7

2. Nutritional Studies of *Jessenia bataua*. 60

3. Chemotaxonomic Studies. 77

4. Morphology and Growth 106

5. Taxonomy. 202

6. Economics of *Oenocarpus-Jessenia* Domestication:
   Use as a Tropical Oilseed Crop. 346

INTRODUCTION

The Oenocarpus-Jessenia complex is a group of magnificent pinnate-leaved palms found over much of the northern half of lowland South America. They range from diminutive understory elements to large canopy trees in the neotropical rain forest. In certain inundated areas, Oenocarpus and Jessenia palms can be found in vast monospecific stands, while in terra firma (higher, well drained) zones, these palms are usually found scattered throughout the forest.

Indigenous societies in the Amazon Valley have long utilized Oenocarpus and Jessenia palms for food, magic, medicine, fiber, in recreation and in some areas have brought individual species into a semi-domesticated state. From the Indian's perspective, in many areas of the Amazon, Oenocarpus and Jessenia constitute the most important palms of the forest. Consequently, a wealth of ethnobotanical and anthropological lore has developed around these two genera, offering an interesting challenge to the field scientist.

The study of Amazonian palms involves a significant number of problems, primarily of a logistical nature. These large organisms, up to several tons in weight, must be felled, dissected, carefully sampled and photographed in order that complete biological data be obtained. This comprehensive examination process, in combination with the remote location and distribution of the family, clearly supports Bailey's contention that palms are the "big game" of the plant kingdom.

Students of the palms have always considered the family a difficult group to work with in the field. In a letter dated 8 October 1850, Richard Spruce wrote from Santarem, Brazil, that "Palms are very scarce here but had they been abundant I should have found it impracticable to dry many spadices on account of our quintal being so stocked with goats, poultry and other "porcaria"."

As important elements of the tropical flora, palms have, in general, been ignored by tropical botanists. The devotion of one-hundred percent of one's field time and attention to a single family is often too great a sacrifice for all but the most dedicated palm specialist. Unfortunately, those who collect "numbers" rather than botanical specimens and attempt to include palms in their accumulations too often end up with fragmentary bits and pieces that are virtually useless to the serious specialist. Clearly, these neglected trees require much additional attention and in-depth study, especially in view of the current rate of tropical rain forest destruction.

The Oenocarpus-Jessenia complex holds special interest as an object of scientific study because of its oleaginous fruits. These fruits are the source of a high quality oil, similar in taste and chemical composition to olive oil. Given that the palms can grow in swampy habitats otherwise unsuited for conventional agricultural production, the botanist with an economic perspective is offered an exciting challenge. As a potentially new crop plant, these palms provide some hope

for an alternative use of marginal lands and the generation of income for people who have traditionally had limited access to the cash economy. Thus, this study has concentrated equally on both the theoretical and applied aspects of the biology and economics of Oenocarpus and Jessenia domestication.

I have been privileged to travel to various parts of the globe over the last decade, as is the style of many in my generation, and to have observed and lived with several cultures outside of my own. During these journeys, I have continually been impressed with the phenomenon that, in this hungry world, there is a tremendous but unnecessary migration from the forests, where most people develop and thrive, to the concentrated aggregation of dwellings known as cities, where, far from receiving the promised plethora of materialistic goods, these same people deteriorate and starve. It became my goal to search for a dissertation topic which could somehow improve the living standards of just a few people to start, and potentially many more, if the idea proved successful. At the same time, the invaluable personal discipline gained from interaction with a theoretical topic such as plant systematics, was also deemed important.

My quest ended with the Oenocarpus-Jessenia complex and my liaison with Centro de Desarrollo Integrado "Las Gaviotas", a Colombian development institution interested in domesticating and utilising these palms to the advantage of local settlers and Guahibo Indians living in the Llanos of Colombian Orinoquia. Perhaps the advice offered by Oakes Ames to his young student Richard E. Schultes serves to clarify

my feelings: "[Systematic botany]...should be humanized and and the fundamental implications of taxonomy should be emphasized through their broad application to human affairs." In addition, he noted, "I don't know of any better subject in the botanical field on which to build such a (intellectual) personality than economic botany with its tremendously important human implications and its call for searching investigations among things that really matter. If I were a young man beginning my career all over again, I should try through intensive research in economic botany and ethnobotany to bring more light into the intellectual realm and take my place, not in a laboratory cubicle, but in the world..."[1]

Thus, it is in this spirit, with hope that my research may someday prove both economically and scientifically significant, that I offer this modest contribution on the *Oenocarpus*-*Jessenia* complex.

Footnotes

1. Plimpton, P. A. 1979. Oakes Ames, Jottings of a Harvard botanist. Harvard University Press. Cambridge.

Acknowledgements

This investigation would not have been possible without the assistance generously offered from many persons and organizations. I am grateful to Professor Richard Evans Schultes, who, from the beginning, was most supportive of this project and unselfishly gave his time to guide and oversee it to completion. The original idea of an Oenocarpus -Jessenia domestication study was suggested by Dr. Paolo Lugari Castrillon, Director of the Centro de Desarrollo Integrado "Las Gaviotas", who provided both financial and logistical assistance in Colombia.

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(Ethnobotany); S. Gershoff (Nutrition); G. Cooper-Driver (Chemotaxonomy); P. B. Tomlinson (Morphology and Growth); H. E. Moore, Jr. (Taxonomy) and W. P. Mason (Economics). Thus, in some cases the chapters are a collaborative effort, necessitated by this multidisciplinary treatment.

W. Kittredge, J. J. Lupo, W. Wilbert, S. Wilder, E. Seling and E. W. Smith all participated in the production of the illustrations and graphics. I am most grateful to C. Hesterberg for her preparation of the manuscript.

My parents offered both moral and financial support of my university education and fieldwork, a debt which can never be properly repaid.

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Chapter 1

ETHNOBOTANY OF THE OENOCARPUS-JESSENIA COMPLEX

Palms play a major role in the lives of many tropical -dwelling aboriginal societies, providing food, clothing, shelter and various ameliorants (Anderson 1978; Balick 1979; Schultes 1977; Wallace 1853a; Wilbert 1976). Those in advanced societies may not fully realize the importance of palms in their own lives; products often imported from remote lands arrive pre-processed, bottled, tinned or, when fresh, are so enveloped in plastics as to be almost unrecognizable from their virgin state. In contrast, aboriginal man not only recognizes the value of the palms in his immediate environment, but often holds them in such high esteem as to surround them with magical beliefs or religious significance (Schultes 1974; Wilbert 1976). These societies carefully survey, name and inventory their palms, and use them to the fullest during their productive seasons. Indeed, the "ownership" of individual palm trees in vast, seemingly uninhabited rain forest or in sparsely populated desert lands is not uncommon. An eloquent discourse on the importance of palms to tropical-dwelling man is offered by Moore (1973):

> "The versatility of palms in the hands of man is astonishing. Houses, baskets, mats, hammocks, cradles, quivers, packbaskets, impromptu shelters, blowpipes, bows, starch, wine, protein from insect larvae, fruit, beverages, flower, oil, ornaments, loincloths, cassava graters, medicines, magic, perfume--all are derived from palms. The importance of man as a biotic factor in the tropical ecosystem has been argued (Richards, 1952, 1963; C. O. Sauer, 1958). However, to whatever extent man has been involved in the

tropical ecosystem, palms have certainly been a major factor in making possible this involvement and even today, despite, the advent of the corrugated tin roof and the rifle, they are of primary importance to many primitive American cultures."[1]

In the Amazon Valley of South America, the Oenocarpus -Jessenia complex is of great importance to local peoples for its sundry economic uses. This is evidenced by the local folk-taxonomy. As an important group of plants, the palms have a common name in each locality. In fact, over a hundred names have been recorded for this single complex throughout South America.

Palm usage, obtained from in situ observations during a year of field work in the Amazon Valley, will be discussed in the following pages. This included in-depth studies during expeditions to three lowland tribal areas: 1. the Colombian Vaupés--Tukano and Kubeo observed in the vicinity of the Rio Vaupés and some of its tributaries (approx. Lat. 1°08'N., Long. 70°04'W.); 2. the Colombian Llanos (Vichada) --the Guahibo, inhabitants of savannah and gallery forest (approx. Lat. 4°30'N., Long. 70°40'W.); 3. the Peruvian Amazon--studies among Bora, who migrated from the Colombian Putamayo area to the Peruvian Rio Yaguasyacu, an affluent of the Rio Ampiyacu, Departamento de Loreto (approx. Lat. 2° 40'S., Long. 72°00'W.) Data from the literature and from interviews with knowledgeable informants are also included.

Beverage Production

The first genus mentioned, Oenocarpus, literally means "wine fruit", from the Greek (oinos=wine; karpos=fruit). The

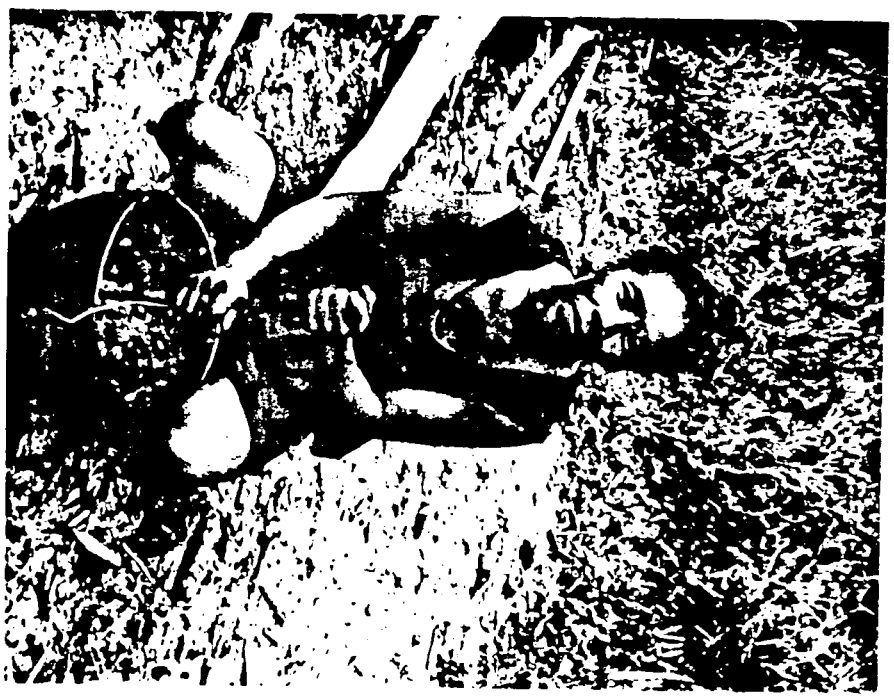
production of a refreshing, oil-rich drink from the fruits was a primary use noted by sundry explorers of the Amazon (Barbosa Rodrigues 1903; Spruce 1908; Wallace 1853). Wallace considered the beverage of Oenocarpus bacaba to be ". . .of delicious flavour, somewhat resembling filberts and cream."[2] The closely related palm Oenocarpus [=Jessenia] bataua was, ". . .of even superior flavour."[3]

Local peoples collect various species to prepare this nutritious drink depending on the region. Choice may be restricted by the number of palm species in a particular area or influenced by individual preference. The most important are Jessenia bataua, Oenocarpus bacaba, O. mapora, O. minor, and O. distichus. All have a similar fruit structure--a thin epicarp, pulpy mesocarp a few millimeters thick, and hard seed laterally covered with flattened fibers (Fig. 1.1).

The method of beverage preparation depends on regional proclivity or tradition, rather than on the particular species. My observations of a Kubeo Indian family in the northwest Amazon of Colombia (Rio Kubiyú, an affluent of the Rio Vaupés) illustrate one basic process. Ripe fruits of Jessenia bataua, dark purple and soft to the touch, are collected and placed in a tin cauldron. This is filled with sufficient water merely to cover the seeds. The fruits simmer in warm (but not hot) water for approximately 10 minutes. At this point, the children may be given some of the fruit as a treat. The still diluted fruit mix is churned with a multiforked stick carved from Virola (Myristicaceae) wood (Fig. 1.2). The

Fig. 1.1. Ripe fruit of *Oenocarpus mapora* with the dark purple epicarp partially removed to reveal the lavender, oil-rich mesocarp.

Fig. 1.2. Kubeo Indian woman churning heated *Jessenia bataua* fruits to release oily constituents and coloring for beverage preparation.

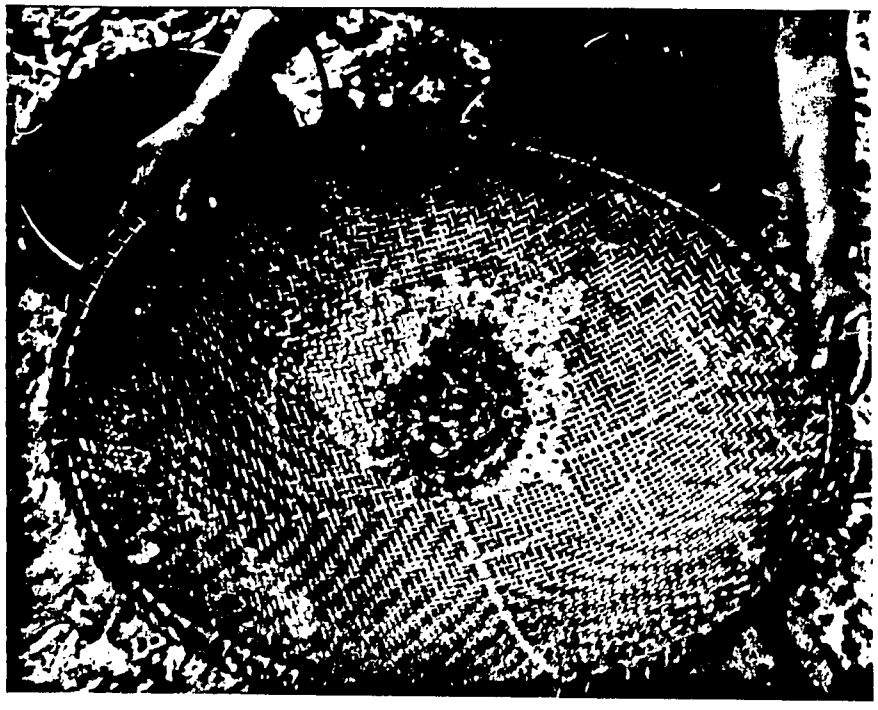


fruit pulp breaks into pieces, releasing the desired oily constituents and coloring. Additional water, added carefully cup by cup, produces a rather slimy, opaque purple, sweet smelling preparation. A woven basket constructed from Ischnosiphon (Marantaceae) fiber with a frame of Desmoncus (Palmae) is used to strain out the many remaining pieces of epicarp and unpalatable, fiber-covered seed (Fig. 1.3). Family members consume the drink as is (fig. 1.4), or add a few handfuls of toasted cassava (Manihot esculenta) granules (fariña) to make a complete meal. The nutritional composition of this protein-rich beverage is discussed in chapter two.

The inhabitants of Guacamayas, Vichada, Colombia --primarily a region of open savannah and gallery forest--also use ripe Jessenia and Oenocarpus fruits to make a non-alcoholic drink locally known as chicha de seje. The procedure differs only slightly from that previously described. The water-filled cauldron is heated to a higher temperature, approximately $50^{o}C+$, for a shorter time (ca. 5 minutes), and excess water poured off. A very large and heavy manija in a mortar-like pilón of solid wood is used to mash the fruits, until the oily mesocarp separates from the seed (Fig. 1.5). The pilón does not effectively remove all of the pulp residue, so the rest is separated by hand. Upon completing this step, the contents are spilled into a tin and diluted with water. Finally, a nylon net sack is used to sieve out the unwanted pulp pieces, and these are fed to the domestic animals (pigs, chickens and dogs). The entire process of preparation takes from 20-30

Fig. 1.3. An indigenous basket made from a Desmoncus sp. circular frame and woven Ischnosiphon sp. fiber, used to strain out large pieces and fibers from the Jessenia bataua drink.

Fig. 1.4. The milk-like beverage produced from the fruit of Jessenia bataua, consumed from a laminated drinking gourd.



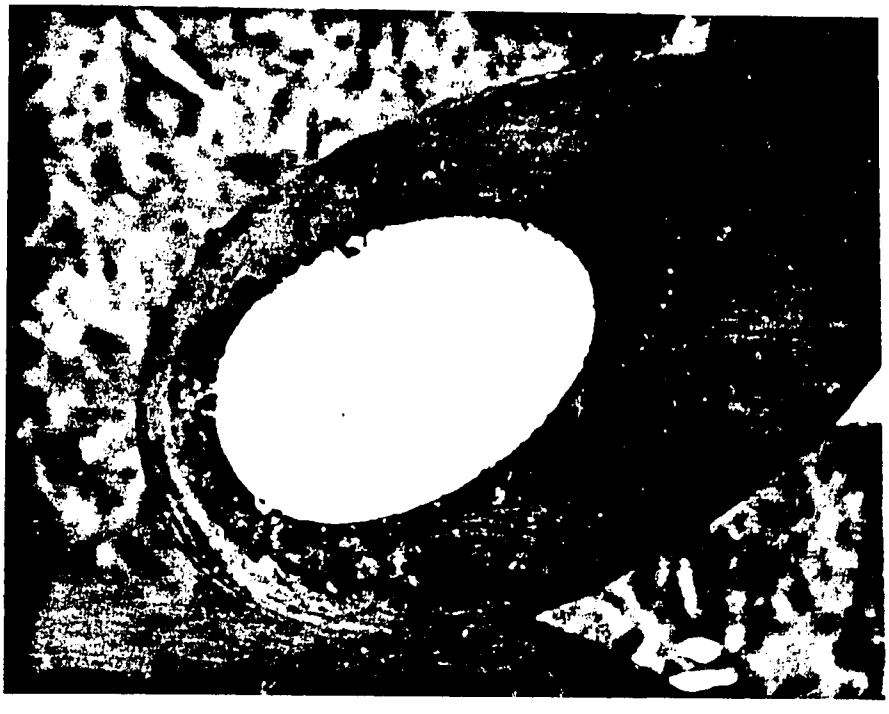
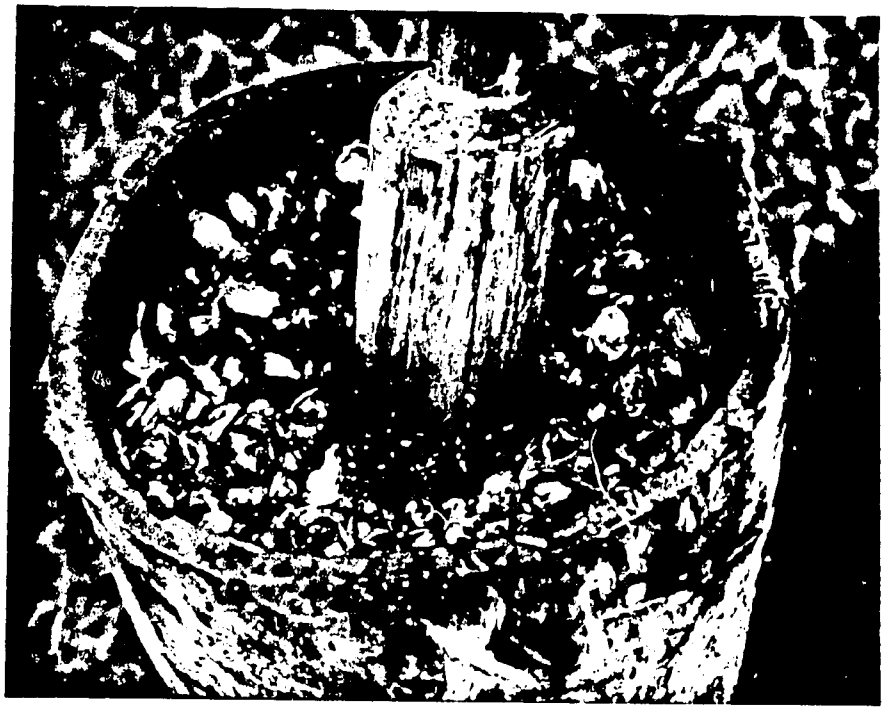


Fig. 1.5. Steamed *Jessenia bataua* fruit in a mortar-like *pilón* of solid wood, mashed with a heavy pestle-like *manija* to remove the oily mesocarp from the seed.



minutes, when the beverage is sweetened with panela (raw cane sugar) to produce an almost chocolate flavor which I find more agreeable than the Amazon version.

According to a Quechua Indian in the essentially Kofán-dominated area of lowland forest around Lago Agrio, Ecuador, a fermented version of this drink is made. The fresh beverage, stored for 24 hours, is subsequently mixed with lightly fermented cassava drink or banana mash. A few days of storage yields a libation only mildly alcoholic.

Oil Preparation

The oil extracted from these palms is similar both chemically and in taste to olive oil. As Richard Spruce observed in a letter written in 1854 to Sir William Hooker:

> "All of the palm drinks are exceedingly nutritive, and several are slightly purgative owing no doubt to the oil they contain . . . .After the Caire [Elaeis oleifera] as to the quantity of oil come the various species of Oenocarpus. The oil of these is apparently of finer quality than that of the Caire; it is colorless and sweet tasted, and not only excellent for lamps but for cookery. . . I can bear testimony that for frying fish, Bacaba [Oenocarpus] is equal to either olive oil or butter . . ."[4]

A more modern comment is offered as an enticement to potential investors in the July 1972 edition of the Brazilian Bulletin:

> "If U.S. gourmets ever tasted pataua [Jessenia bataua] oil, they would give up olive oil. Pataua oil . . . is like an essence of olive oil and about the same color, though a little greener. It is prized as a salad and cooking oil and gives a taste to food which would be envied by Italian cognoscenti."

Depending on the region, several different processes of oil extraction are employed. Each system involves agitation or pressure on the oil-rich mesocarp layer. Small-scale extraction techniques include expression in a crude press or maceration and subsequent flotation-separation in water. As with beverage preparation, the methodology depends on culture and tradition. However, when the oil plays an important role in the local economy, more efficient procedures are preferred.

The Guahibo of Colombia and Venezuela are adept at oil-making and have numerous uses for the product. In pre-Conquest times, when the tribe was far larger and more powerful, production of high quality palm oil was a major occupation and an important item of commerce. While many local palm species helped sustain their nomadic existence, oils from Oenocarpus and Jessenia palms were of particular delight to the Guahibo (Balick 1979).

The traditional processing technique used by these people was observed at "Las Gaviotas", Vichada, Colombia. About 20 kgs of ripe Jessenia bataua fruit, gathered during an afternoon in the surrounding gallery forest, are piled in a central collection area. These are covered with leaves (or plastic) and left overnight to ripen further. Whether or not this cover traps any gasses given off by the fruit that might stimulate further ripening, as is the case of some crops, is not known. Early in the morning, water is heated to approximately 50°C in a large pot (20-30 gallons). The pile of fruit is added and the pot set aside for several hours.

During this time, warm water penetrates and softens the epicarp and mesocarp. The contents are drained and shifted to a smaller pot, while the large vessel is filled with water and heated to just below the boiling temperature. The fruits are again spilled into the large pot, and fissures soon develop in the epicarp. A few kilograms of fruit are transferred to the large pilón (Guahibo=wahubo) and mashed with a heavy manija (Guahibo=wahubo makato) as previously described. After a few minutes of continued maceration, the pulp separates from the seed ("kernel") which is quickly sieved out with a 1/2 inch screen. Today the screen is often of metal. The pulp is allowed to fall onto plastic sheeting. In the past, however, the screen as described by my informant was manufactured of interlaced marantaceous fibers, and large palm or plantain leaves covered the ground on which the hot pulp fell. After screening, the pulp is immediately put into a woven tubular press, known here as a sebucán. This tube is the same type of press used to prepare cassava throughout the Amazon Valley. It operates on the principle of the children's toy known as a "Chinese finger tube"--a narrow woven straw tube which when placed on the two index fingers of both hands and pulled, constricts drastically in diameter, applying pressure to the contents (fingers). The pulp in a sebucán is constricted in a similar manner. One end of this device (known elsewhere as a tipi-tipi) is hung from the ceiling. Several men pull the tube by sitting on a stick attached to a corner post through the other end of the sebucán. Because of this leveraged force, the oil discharges

through the narrow slits in the weave of the press (Fig. 1.6) flowing directly into a pot placed below it. At this stage the exudate contains a significant volume of water. When the liquid is placed in a glass bottle, two layers form. The top, cloudy dark yellow layer is oil; the lower dark purple section comprises water. The preparer then boils the liquid in the collecting pot until all water evaporates. Any large pieces of pulp or epicarp that remain are removed by hand. After boiling, the oil is fairly pure and ready to bottle. The finished product varies from light green to yellow, depending on the species used and the effectiveness of final purification. It holds its excellent smell and taste without going rancid for a year or more. In contrast, some of the other palm oils are subject to an immediate increase in the free fatty acid content--the cause of rancidity--and are therefore less esteemed. A method of prolonging shelf life used in Brazil is the addition of a clove of garlic to the oil during the final boil. I discussed this process with an informant but never observed it in the field and therefore cannot evaluate its effectiveness. In 1978, a liter of Jessenia oil sold for 120-150 Colombian pesos (ca. US $5-6.00) in the Vichada area.

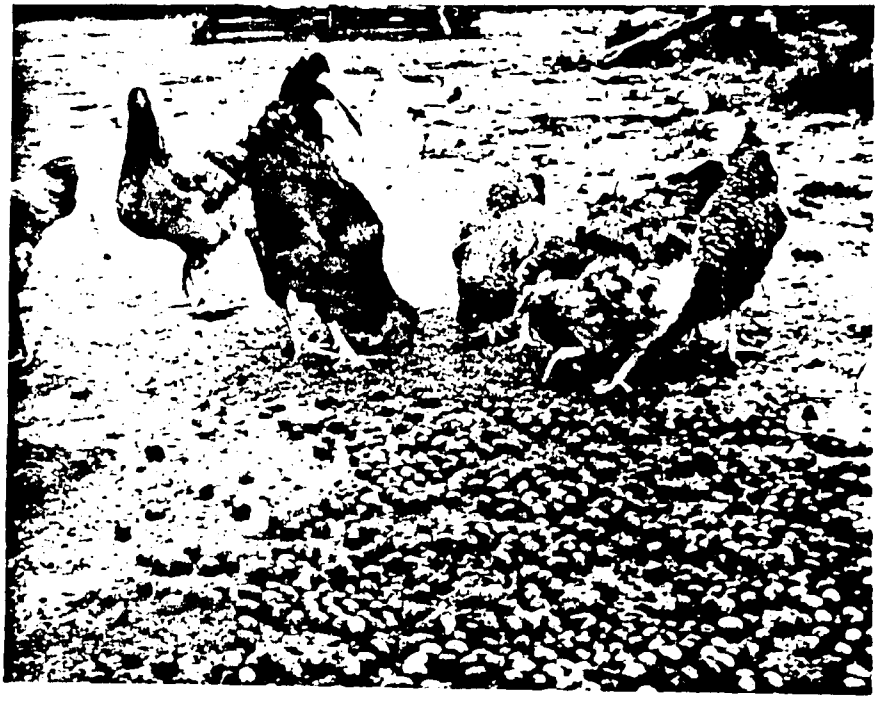
As with the beverage, a byproduct of oil processing, the pulp, is used as a feed for domestic animals (Fig. 1.7, 1.8).

In other locations, people not familiar with the cassava press use a far less efficient method. It entails preparation of the seeds in the same manner until the stage at which the fruits are macerated and screened. The fruits are crushed in the same pot, mixed with water and brought to a violent boil.

Fig. 1.6. Oil expressed in the sebucan is forced out through narrow slits in the weave and flows down to a collecting bowl.

Fig. 1.7. Appearance of *Jessenia bataua* pulp (epicarp + mesocarp) after oil extraction.

Fig. 1.8. Rooster and chickens consuming fresh *Jessenia bataua* pulp and residue following its use in beverage preparation.



With constant stirring and agitation, the oil contained in the mixture slowly rises to the top, is carefully skimmed off with a cup or spoon and poured through a makeshift filter to remove unwanted fibrous matter. Some Indians use the tail feather of a bird to skim off the oily layer, periodically wiping the oil from the feather into a bowl. It is collected and later reboiled for about an hour to remove both excess water and remaining impurities. A tedious and wasteful method at best, it is reported still to be practiced in some parts of the Peruvian Amazon.

A more modern approach to oil extraction utilizes a small scale hydraulic press, insuring the removal of as much of the oil as is reasonably possible. This process, based largely on the principles described above for the sebucán method is treated in chapter six.

Indians extract Oenocarpus-Jessenia oil throughout the natural range of these palms. Depending on relative abundance, the same species exploited for beverage production are utilized in oil-making. Where civilization has interceeded, only the older inhabitants have knowledge of and skill in this art. There are many other uses for the oil beyond its food value. Some of these are discussed in the following pages; others most certainly remain to be documented.

Additional Utilization as Food

Heart of palm or palmito is a regional delicacy obtained from the young growing tips of various species of Euterpe. This has been developed into a sizable export commodity in

the Amazon Valley. With the elimination of many native populations of Euterpe, interest in finding other sources of palm heart for commercial production has grown. The palm heart of all species of Oenocarpus and Jessenia is edible. The heart of J. bataua provides a kilogram or more of edible material (Fig. 1.9) with a slightly 'nutty' flavor not characteristic of the genus Euterpe. It is of great value to Indians as a foraging food. There appears, however, little value in cultivating the slow growing, solitary J. bataua solely for the one-time harvest of its heart. On the other hand, a faster growing, caespitose species such as O. mapora might prove feasible for plantation culture. It has a much smaller trunk, but because of its tufted habit and earlier maturity, produces more than Jessenia. In addition, its smaller stature allows for the inclusion of a greater number of trees in plantation rows. The young inflorescences of all the species are a delicious survival food and, in the same manner as the heart, might hold promise as a tinned delicacy.

Entomophagy--the consumption of insects--is common among aboriginal tribes in the Amazon Valley. Bergier (1941) explored the utilization of insect foods by many 'primitive' societies in his classic work Peuples Entomophages et Insects Comestibles and devoted an entire chapter to the Americas. Wallace (1853b), who undertook extensive Amazonian explorations, mentioned Neuroptera, Hymenoptera, Homoptera, Coleoptera, Aptera and Annelida as the 6 orders of insects consumed by the Indians in that area.

Fig. 1.9. A portion of the edible palm heart from *Jessenia bataua*.

Among the Bora, one of the most delectable insect foods is a weevil grub, know as *surí*. This is frequently found in newly felled trunks of *Jessenia bataua* as well as in damaged or exposed stem sections of living specimens. The Bora exploit this insect, even encouraging its infestation, by removing the hard outer portion of the fallen stems, providing many entrance areas for the adult weevils to bore into and lay their eggs. The harvest of an edible protein source, in the form of weevil larvae, is a secondary product of the palm, after the fruits are used as food. Upon razing, the trunk is covered somewhat, to conceal it from other people, and abandoned for a two or three month period. The cutter then relocates the fallen trunk, which by now has partially rotted. He can harvest a kilogram or more of the large (5 cm + long) fat, white grubs that develop throughout the stem (Fig. 1.10). These grubs (*Rhynchophorus palmarum* Latr.) are considered a delicacy and eaten raw or fried. During a Bora festival that I attended, the wife of the chief hosting the celebration selected a string of *surí* from among the wide range of animal and plant foods offered, as the most esteemed gift at the feast (Fig. 1.11). Tasting somewhat slimy and greasy when eaten raw, *surí* have a mild "ham and nutmeg" savor when fried. According to an informant familiar with this area, these insects can also be boiled, or wrapped in marantaceous leaves and baked on a fire.

A final food obtained from *Jessenia bataua* comprises bits of pulp that have been deep-fried in the oil during its preparation. An informant from the Chocó region of Colombia

Fig. 1.10. A weevil larva, known as *suri*, found in *Oenocarpus* and *Jessenia* wood, consumed as a food in the Amazon Valley.

Fig. 1.11. Wife of a Bora chieftan with a string of *suri* (*Rhynchoporus palmarum*) a gift that she received during a festival.

compared these in consistency to chicharrones, a form of fried pork skin. He noted their color to be light tan when cooked and presumed their origin to be from the suspension of the macerated pulp mixture in the oil. I was unable to confirm this preparation elsewhere.

Ethnopharmacology

In addition to the sundry uses of these palms as food, they constitute an important component of the ethnopharmacopoeia of tropical South America. Both in isolated regions and in population centers, the products are known, especially among the older inhabitants. Consequently, there exists a definite demand for them, even in the capital cities far from the rain forests. This is obvious when one browses through the herbal or folk medicine stalls in central markets and upon conversing with local curanderos or healers.

Curatives

A number of Oenocarpus-Jessenia derivatives are used in the belief that they cure or control diseases and infirmities. A common use of the oil, said to be particularly effective, is against certain bronchial and pulmonary afflictions. For a cough lacking other symptoms, tablespoonfuls of oil, often mixed with a small amount of lemon and honey, are taken at any time during the day or night, until relief is obtained. Bronchitis, asthma and chest colds are said to require a somewhat larger quantity of oil for best result. Indians in the Amazon Valley point out the importance of this oil as a 'cure' for tuberculosis. Further investigation into the

literature indicates that this use is widespread. Both Ranghel Galindo (1945) and Garcia Barriga (1974) discussed the importance of Oenocarpus-Jessenia oil in the treatment of tuberculosis, with the latter reference noting that it can be administered orally or by injection. The latter reference is not specific as to the method or dose of the injection, and caution would thus be advised. Schultes (1951) observed that the Witoto of Colombia also consider that if eaten as a food, the fruits of J. bataua act as a cure for this disease. Ranghel Galindo (1945) offered three studies by medical doctors on this claim:

> "The medicinal properties of Colombian Seje oil [Jessenia bataua] were studied by the following doctors:
>
> a) Carlos J. Cuartas, Bogotá, 1938. Study of Finikoff's Treatment, modified in the sense of augmenting the organic defenses of the patient in cases of surgical tuberculosis and tuberculosis of the joints, using Seje oil. In this work, Dr. Cuartas also demonstrated the application of iodized Seje oil in cases of pulmonary tuberculosis, as in Pott's Disease, white tumors, osteomyelitis of the base of the skull and lupus vulgaris.
>
> b) Roberto Peñuela del Castillo presented a thesis in 1925 entitled 'The ethyl esters of the fatty acids of Seje oil' as a requirement for the degree of Doctor of Medicine. According to this work, it is probable that the esters of Seje oil are able to be employed in tuberculosis and also in the treatment of the terrible leprosy.
>
> c) Ramón Cabrales Pacheco presented a work entitled 'Iodized Seje oil and calcium therapy in surgical tuberculosis.'"[5]

Further work is necessary for confirmation. It is especially important now because of the epidemic proportions of tuberculosis among the Indians where these palms are common. This

research would answer the question of whether the oil is simply a highly concentrated nutritional supplement or does indeed possess an anti-tubercular agent.

In the Tingo Maria area of Peru, Jessenia bataua oil and aceite de almendras dulces (sweet almond oil) are mixed and given for the treatment of convulsive cough and bronchitis. A small jar of this almond oil (30 ml.) (Fig. 1.12) mixed with one tablespoon or more of the palm oil, is given to children in one-half teaspoon doses, three times a day before eating. Adults require twice the dose of this widely used and apparently effective remedy. For a purgative effect, the oil can be taken by the tablespoonful at various times during the day as needed. Similarly, the Bora Indians of Amazonian Peru mix one handful of green fruits of Oenocarpus mapora with two cups of hot water, and consume this preparation for use as a laxative.

A curious ethnopharmacological use among the Bora is against hematoxicosis from the bite of certain venomous snakes. When a member of the group suffers a snakebite in an isolated area, he searches out the seedlings of Jessenia bataua. Only young seedlings are said to be of value (eg. those ca. 30 cm tall) and these seedlings must still be attached to the seeds. Ten plants are collected, each seed removed, and these soaked in about two cups of water. After agitating the seeds for a few minutes, the liquid is immediately consumed. This treatment is a last resort only, for use in the absence of any other remedy, when one finds

Fig. 1.12. Two commercial products used in Peru as admixtures to *Jessenia bataua* oil for folk-medicinal purposes.

ACEITE
DE ALMENDRAS
DULCES
ELABORADO EN LOS
LABORATORIOS
FROTACION
CHARCOT
QUITA DOLORES
ANALGESICO
USO EXTERNO

oneself at a great distance from home base in the rain forest. No explanation was offered for this curious use of the seeds nor for the special preference of this species. I never observed the application of this treatment in the field. It may be merely ceremonial or serve as psychological support. On the other hand, it is conceivable that the germinating seeds could produce a compound that has an effect on the action of the snake venom. Seemingly outlandish aboriginal preparations often prove valueless upon closer inspection. Quite the contrary, some such treatments have upon study been shown to be of minor or even major importance, with potential impact in our own medical system; this one deserves further investigation.

Many middle-aged and older persons living in small rural villages in the Neotropics suffer from arthritic conditions of pain and joint inflammation. In Tingo Maria, a healer offered the following alleviation: one bottle of Frotación Charcot (30 ml.) (Fig. 1.12) mixed with one teaspoon of *Jessenia bataua* palm oil. Charcot's "linimento", as it is locally called, can be purchased in Peruvian pharmacies and has the following composition according to the label: "Lindocaina-1 gm; Alcanfor-4.2 gm; Mentol-0.314 gm; Chloroformo -0.524 gm; Salicilato de Metilo-8.4 gm; Esencia eucaliptos-1.05 gm; Esencia de Trementina c.s.p.-100 gm.: The Charcot-palm oil mixture, at room temperature or warmed slightly, is massaged directly into the aching areas of the body. A typical treatment consists of two to three rubs per day, over a three-day period or until the pain subsides. The mixture has a shelf

life of three to four months, and can be used as often as needed. Doubtlessly at a minimum, the anesthetic constituents of the Frotación Charcot themselves help alleviate the pain for a short time; the addition of palm oil may assist in the absorption of the preparation through the skin.

Preventatives

Most cultures display concern for the appearance, health and retention of scalp hair. Throughout my fieldwork, the use of this palm oil for preventing hair loss and even for stimulating its growth was continually mentioned. The daily treatment is more or less the same everywhere. A small amount of oil is poured on the hand and massaged vigorously into the scalp. It is used by both sexes and, in some tribal groups, is generously applied merely to give the hair a deep sheen.

For protection against the hot tropical sun, Indians in Peru paint their faces with the residue from a ripe huito fruit (Genipa sp.). The resulting black dye is kept fast by a daily application of Jessenia bataua oil to prevent its dessication and cracking. One informant in Iquitos stated that this practice was common among the Bora, Witoto, Andoke, Ocaina, Yagua and Tikuna tribes. She also mentioned of the value of the chicha prepared from Jessenia fruit for "renewing the blood." The oil is likewise employed during childbirth: as soon as the child emerges, a clean, oil-soaked cloth is used to cleanse the infant's mouth. Simultaneously, a small amount (½ tsp.) is given to "stimulate" the newborn's digestion.

Ethnotoxicological Beliefs

There are several beliefs and cautions concerning the harmful effects of consuming the palm beverage or even the ripe Oenocarpus and Jessenia fruits themselves. Wallace (1853a) wrote that O bacaba drink could "...bring...[intermittent fevers] on, and ... [was] particularly hurtful to persons recovering from that disease."[6]

During a Projeto Flora Amazonia expedition to Brazil, a local member of the team explained that some people are unable to drink the beverage of these palms or eat the fruits, as they have a "bad" liver. After eating pataua (Jessenia bataua) for the first time, for example, they would become ill with symptoms of dysentery. Upon further questioning and discussions, it became apparent that many natives believe that palm fruits are inedible or harmful when consumed with other foods. The following table presents some of these combinations which are said to result in discomfort, serious illness or even death.

Table 1.1

Harmful Palm Combinations

Combination	Remarks
Liver of Tapir with Jessenia bataua fruits or beverage.	Said to quickly cause a "horrible death."
Beverage made from Oenocarpus bacaba with that made from Euterpe oleracea.	Never mix and drink these two together; consequences not elaborated.
Ripe mango with J. bataua or O. bacaba; Boiled or fried eggs with Oenocarpus or Jessenia	These pairs should never be eaten together; the result will be serious illness.

drink; Fresh milk with fruits from *Mauritia* sp.; *E. oleracea* with *cachaça* (locally produced cane alcohol); *E. oleracea* with citrus fruits (specifically lime, orange and lemon cited).

E. oleracea palm drink. Never drink much before sleeping as it will make one sick during the night and prevent sleep.

The importance of observing these caveats was strongly emphasized during my field research in Amazonas and Pará. The Brazilian counterparts on this expedition continuously discussed and reiterated these "rules", each one claiming to know of persons who died after eating one of the various "harmful combinations."

Fiber and Construction

Rain forest peoples regard these palms as an important source of fiber and construction materials. Wallace (1853a) chronicled one of the more unusual uses of *Jessenia bataua*: the exploitation of its sheath fibers as the darts for Indian blowpipes. These darts, or "arrows" as he called them, were the type covered with curare and utilized in hunting. Figure 1.13, taken from his classic book, *Palm Trees of the Amazon and Their Uses*, depicts the darts, a carrying quiver and sketch of the palm tree adorned with the sheath and petiole spines that always enclose the immature stem. The darts are made from these spines.

Actual preparation of the darts was observed at "La

Fig. 1.13. A drawing from Palm Trees of the Amazon and Their Uses, depicting a young spinose tree of *Jessenia bataua*, darts prepared from these spines (left), and a carrying quiver for hunting (right).

Macarena", a Kubeo Indian village about one-half day by motor canoe upriver from Mitú, Vaupés, Colombia. Ample supplies of cotton-soft Bombax sp. (Bombacaceae) seed-fibers and spines of Jessenia bataua, ca. 50 cm long, are collected. A small roll of string from the cumari palm, Astrocaryum vulgare is also prepared. The kapok-like fiber, placed in a basket made from Desmoncus and Ischnosiphon, is whipped with the spines to separate the individual fibers. A number of the stoutest J. bataua spines are cut down to about 40 cm and sharpened to a slender point on one end. The other end, blunted and moistened with saliva, is inserted into a basket of fluffed fiber, and twirled. This end catches the first few hair-like fibers on the spine, and with further twirling, the base soon is covered with a loose mass of fiber. The mass is matted down by tightly spinning it against the inside of the hand and securing it to the shaft with a piece of cumari string. The finished darts are notched a few centimeters from the tip and covered with the arrow poison. The superbly accurate blowpipe, locally called serbatana, is here constructed from the trunk of another palm, Iriartella setigera. The example observed in use by the Cubeo was said to have been obtained from the Kuripako, a group expert in the manufacture of blowpipes and curare.

These weapons are a miracle of aboriginal engineering and craftsmanship. Light in weight, they can be transported and aimed with ease, operate silently and are deadly accurate. In addition, only locally available materials are used in construction, so manufacture or replacement is not difficult.

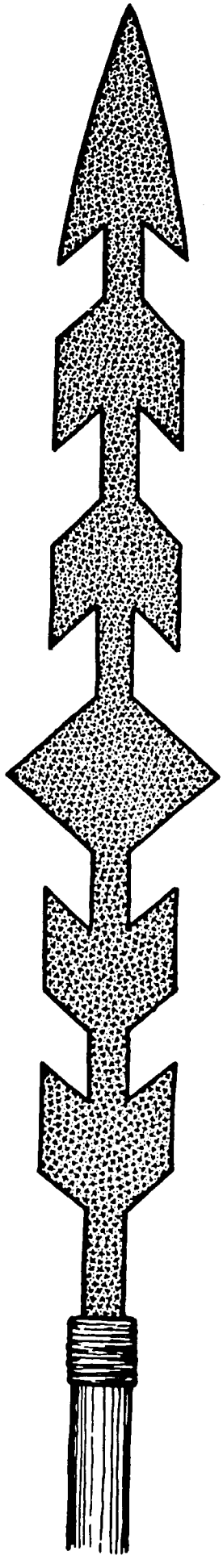
In the field, darts fired from the blowpipe penetrate deeply into the quarry. If an animal attempts to remove the imbedded spine, the notched, poisoned tip breaks off and remains in the body. Subcutaneous exposure of the curare delivered by the dart causes paralysis of the voluntary muscles, resulting in death by asphyxiation or failure to escape from the waiting hunter.

Other implements for hunting and warfare are made from these palms. Anderson (1978) reported that the Xiriana-teri group of the Yanomama tribe in Amazonian Brazil occasionally still use Jessenia bataua wood for making fighting clubs. He observed that "...the dense wood of this palm must make such clubs terribly effective."[7] This reference also described the manufacture of a hunting bow from the same wood, the resultant product noted to be "...strong, durable, and very difficult to draw."[8] Figure 1.14 shows a Yanomama Indian engaged in this activity.

The Guahibo in the Llanos of Colombia hold the wood of Jessenia bataua in high regard for the manufacture of bows and arrow points. They refer to a single folk cultivar of J. bataua, known as ataito, as specific for this task alone. The rare tree that yields ataito wood is a tall and robust individual. Bows and arrow points made from this wood are prized for hunting, although the latter are uncommon now, having been replaced by metal. A diagram of a barbed tip carved from this wood is illustrated in Figure 1.15. Balick (1979) described its effectiveness: "The point would enter the animal (or enemy?) and catch on the squared central

Fig. 1.14. Yanomama Indian carving a hunting bow from the trunk of *Jessenia bataua*. Photograph courtesy of A. B. Anderson, reprinted from *Principes* 22(1). 1978.

Fig. 1.15. Drawing of the barbed point of a Guahibo hunting arrow made from *Jessenia bataua* wood. Drawn by E. W. Smith.



portion. The arrow could then be neither pulled out or pushed through, and thus impeded the victim's movement, leaving a trail of blood for easy tracking and capture."[9]

Intertwined among the upright, durable sheath-petiole spines of Jessenia bataua is a mass of soft, hairlike brown fiber. I have never observed this in use by rain forest Indians. Dodge (1897), however, described its utility: "Oenocarpus [=Jessenia] bataua is found in the state of Pará, Brazil, where it is said 'to furnish the strongest ropes for the navy.'"[10] In the same reference, O. bacaba is described to "...yield a piassaba-like fiber."[11] Piassaba (Leopoldinia piassaba), although a much rarer species in the Amazon, produces fiber in far greater abundance than O. bacaba, which undoubtedly precludes any widespread commercial interest in the latter.

The large, arched pinnate leaves of Oenocarpus and Jessenia palms are used as shelter and thatch by various tribes in the Amazon Valley. Common practice in many localities is to "cap" the uppermost portion of a thatched roof with leaves of Jessenia and Oenocarpus species, making it watertight, while still permitting smoke from cooking fires to escape. Among the Guahibo, J. bataua and O. mapora serve this purpose. The Xiriana-teri produce decorative mats from J. bataua (Anderson 1978). I have seen Kubeo living along the Rio Vaupés in Colombia fabricating walls and other partitions from this species (Fig. 1.16). At one village, a cone-shaped coop, fashioned from Jessenia leaves, served to

Fig. 1.16. House of a Kubeo Indian family on the Río Vaupés, Colombia, with walls and inner partitions fabricated from woven leaves of *Jessenia bataua*.

Fig. 1.17. A pack basket woven from *Jessenia bataua* leaves, containing a young child to demonstrate the strength and capacity of this type of provisional carrier.

protect chickens from nocturnal attacks by vampire bats. On the Rio Yaguasyacu, the Bora employ both O. multicaulis and J. bataua for construction purposes. The trunk of the former species, known as chicyora, is used both as the main framework of the house and the roof crossbars, on which Lepidocaryum sp. thatch is woven. Temporary shelters of chicyora leaves are also made while traveling in inclement weather. In Vaupés, these quick lean-tos are called miatissabas.

During a foraging trip with the Bora, a tree of Jessenia bataua was felled for fruit collection. These people rarely carry pack baskets into the forest--the reason soon becoming evident. Selecting a single long palm leaf, our guide folded it into a 'U' shape, wove the pinnae into an interlocking sequence, creating a pack basket in about five minutes. After being filled with the fruit cache, it was secured to the head by a cord of twisted vine bark affixed to the upper sides of the basket. Upon seeing our interest, a second man quickly wove a smaller basket of 2 separate rachis pieces, in which a braid of the woven pinnae rests against the head for support. The larger basket easily accomodated a small child weighing 30-40 kg (Fig. 1.17) and was said to be able to carry the heavy carcass of a slain animal with no hardship to the bearer. Such provisional baskets are discarded after use, and my wish to take one back to Cambridge as a specimen was regarded as rather absurd.

Even the spent inflorescence of Jessenia bataua is not wasted by the Bora. After consuming the fruits, they salvage the large peduncle and rachis and carve it into the form of a

small child. The clasping base represents the legs, and the apex with a few trimmed rachillae, a head with hair. Small children are furnished these training 'toys' which, when placed on their hips, accustom them to carrying siblings later on. The wa-wa, as they call it, enables Bora children to become skilled at the task at an early age.

Sundry other miscellaneous uses for these palms exist, a selection of which, either from the literature or observed in the field, appear in Table 1.2.

Table 1.2

Miscellaneous Uses of the *Oenocarpus*-*Jessenia* complex in South America

Use	Comments	Reference
To preserve meat	Roasted meat can be stored up to 1 month without refrigeration when submerged in a pail of *J. bataua* oil and kept in this manner. Technique reported used in Amazonian Brazil.	Personal communication M. B. Israel 1978
Motor oil-engine lubricant	In various places in the Amazon Valley where petroleum is at at premium, *Oenocarpus* and *Jessenia* oils are occasionally used in outboard motors as a lubricant with satisfactory results.	Personal observation

Anti-rust agent	In the Llanos of Colombia, people rub these oils on guns to prevent rust, especially during the rainy season.	Personal observation
Torch	The "Motilones use these needles for torches" in Norte de Santander, Colombia, dated 9/26/46.	M. B. Foster et al Herb. spec. #1789
Dye	The Xiriana-teri make a dark blue dye from the fruit of J. bataua to paint their bodies.	Anderson (1978)
Love amulet	Ripe, dried seeds, known as cuya-cuya, were offered for sale in an herbal stall of the Huancayo market in Peru. It was said that these should be carried at all times and would serve not only to attract lovers but increase their desire.	Personal observation
Ornamental plants terraria and dish gardens	Seedlings of J. bataua were planted in dish gardens and terraria and offered for sale in a Lima nursery. These were noted to be good pot plants, lasting a long time in the home.	Personal observation

Dried pulp as an edible food	O. bacaba and O. distichus pulp can be dried, made into a concentrated paste and carried on extended trips into the jungle. Reconstituted by mixing with water, it produces a grayish or cream -colored drink.	Pio Correa (1926)
Necklaces	Seeds of Oenocarpus mapora were dried and strung on a cord with other plant and animal products for sale in Manaus.	Personal observation

The importance of this particular palm complex is evident from the foregoing discussion. Yet it is only one of the many groups of native Amazonian palms of value and use to local peoples. Further studies of additional genera will document this family as one of the most important to aboriginal civilizations of the wet tropics.

Footnotes

1. Moore (1973) p. 64-65.
2. Wallace (1853a) p. 29.
3. Wallace (1853a) p. 32.
4. Spruce (1908)1. p. 479.
5. Ranghel Galindo (1945) p. 43. Translated by Balick.
6. Wallace (1853a) 29.
7. Anderson (1977) p. 37.
8. Anderson (1977) p. 36.
9. Balick (1979) p. 373-374.
10. Dodge (1897) p. 253.
11. Dodge (1897) p. 253.

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Chapter 2

NUTRITIONAL STUDIES OF *JESSENIA BATAUA*

Most scientists and national policy makers foresee increasing difficulty in feeding the ever-expanding world population, particularly in tropical countries (Mayer 1976). Various recommendations are advanced; in the agricultural sector the majority are based on improving yields of conventional crops through an increased dependence on petroleum-derived fuels, fertilizers, pesticides and other agricultural chemicals (Barrons 1975). Current realities regarding diminished energy sources appear to require somewhat more unconventional approaches towards food production specifically aimed at low input technologies. One such is the identification and cultivation on a mass scale of plant foods presently possessing only regional importance, but having high nutritional or economic value in these areas (National Academy of Sciences 1975). Minor crops of local origin, when studied and introduced into neighboring or distant areas could provide several substantial benefits. They can be grown in rural centers with significant and direct impact upon local diets, requiring only simple cultivation, harvest and processing technology. Many will flourish on lands otherwise of marginal value for conventional agricultural: eg. swamps, hillsides and belts of impoverished soils. An increase in the number of crops utilized broadens the base upon which food production systems are built, lessening the chance for agricultural calamity in a particular area if supplies of

energy inputs were to be reduced through inflation or scarcity. The major grain and legume crops traditionally introduced through development programs frequently require complex technology, significant capital outlay, fertile soils and a constant flow of petroleum based products for greatest success. All too often peasant farmers subsisting at the periphery of the national economy are unable to reap resultant benefits of such programs.

Indians living in the Amazon Valley of South America have always relied upon the local flora to provide a major portion of their daily nutritional uptake. Generations of experience in gathering foods from the forest qualifies them as "botanical experts" able to search out the best kinds of edible plants growing in the jungle environment. Through ethnobotanical studies by Schultes (1963), Prance (1972), Pinkley (1973) and others, we have some indication of the vast quantity and variety of plant foods that sustain these people.

Palms in particular play an important role in the indigenous diets of this area. Examples include Bactris gasipaes (Seibert 1950), Manicaria saccifera (Wilbert 1976) and Astrocaryum tucuma (Wallace 1853). Perhaps among the most utilized but least known groups of palms are the genera Oenocarpus and Jessenia, providing not only food but also fiber, construction materials, medicines, toys, weapons and other items of daily importance.

The ripe fruits of Oenocarpus and Jessenia are purplish

black with a firm epicarp under which there is a soft pulp (mesocarp). This pulp is rich in oil; some species contain up to 50% (National Academy of Sciences 1975). Fruits are borne on large panicles, which in Jessenia bataua may comprise 1000 or more fruits, each weighing 10-15 gm. Indians have long exploited these, deriving a beverage from the pulp, extracting and purifying the oil, consuming the fruits directly or feeding them to domestic animals.

During field work in the Amazon Valley, it was observed that the daily consumption of Oenocarpus and Jessenia fruits during their season of abundance had a profound effect on the local inhabitants. They gained weight, appeared healthier with more endurance and reported fewer respiratory infections. Such effects seemed to be directly related to the consumption of the fruit and its products, a conclusion which was supported in discussions with other workers.[1]

The present study was designed to measure some of the nutritional qualities of these palm fruits. As their domestication for commercial exploitation is being considered in a number of tropical regions, such nutritional information is crucial.

Materials and Methods

Samples for analysis were collected during various expeditions to the Amazon Valley (1976, 1977, 1978). These collections included fresh fruit, oil and dried outer pulp (mesocarp + epicarp). From the fresh fruit, we prepared a beverage identical to the one made by Indians in the Amazon

Valley.[2]

In this laboratory, fatty acid content of three oil samples was determined by gas chromatography, and the nitrogen content of several pulp samples by micro-kjeldahl analysis. Subsequently all samples, including the initial ones, were sent to R. Kleiman[3] who performed the following analyses: fatty acids (gas chromatography), amino acids (amino acid analyser), oil content (Butt extration with petroleum ether) and nitrogen content (micro-kjeldahl). Proximate analyses[4] and tryptophan determinations (Matheson 1974) of pulps were also carried out.

On the basis of these data, rat feeding studies were undertaken. Four groups of eight male weanling Charles River CD rats in group cages were fed the diets in Table 2.1, ad libitum, for five weeks. Each diet contained identical quantities of fiber (15.3%), ash (4.6%) and oil (10.6%). Diets A, C, and D had 61.4% carbohydrate. Diet B contained an additional 2.8% carbohydrate as a substitute for its lower protein content. Diet A contained 5% protein from casein and 2.8% protein from dried Jessenia bataua fruit pulp. Diet B contained 5% casein and diets C and D contained 7.8% casein. Diet C contained 10.6% corn oil. Diet D contained 5% corn oil and 5.6% free Jessenia bataua palm oil. Diet A also contained 5.6% palm oil from the dried palm pulp.

Results

Table 2.2 presents the results of fatty acid analyses done on 12 samples of Jessenia bataua oil and compares the

Table 2.1

Diets used in Rat Studies on Products from *Jessenia bataua**

% Component	A Experimental	B Basal	C Control	D Control + Palm Oil
Casein	5	5	7.8	7.8
Cellulose	--	15.3	15.3	15.3
Dried Pulp**	50	--	--	--
Salts IV (Chu and Hegsted 1976)	4.0	4.6	4.6	4.6
Choline	0.3	0.3	0.3	0.3
Corn Oil	5.0	10.6	10.6	5.0
Jessenia Oil	--	--	--	5.6
Sucrose	35.7	64.2	61.4	61.4

*Vitamins were added so that each 100 gm of diet contained 0.4 mg thiamin hydrochloride, 0.8 mg riboflavin, 0.4 mg pyridoxine hydrochloride, 4 mg niacin, 0.02 mg biotin, 2 mg calcium pantothenate, 0.1 mg folic acid, 0.005 mg vitamin B12, 0.1 mg menadione, 10 mg α-tocopherol, 180 IU vitamin D and 1800 IU vitamin A.

**The palm pulp used was a mixture of pulp obtained from 3 different samples. By analysis its composition on a dry weight basis (in %) was: protein 5.6, oil 11.1, carbohydrate 51.5, fiber 30.6 and ash 1.2.

data to a published analysis of olive oil (Boniforti and Salvi 1963). It can be seen that the chemical composition of *Jessenia bataua* oil is similar to that of olive oil, both containing approximately 75-80% oleic acid. The only significant chemical difference of nutritional importance is that olive oil has about three times more linoleic acid than *Jessenia bataua* oil. There were a small amount of additional fatty acids in the samples designated as other.

As the percentages were usually minor, these were grouped together. The mean for the 12 samples was 1.6%, with a range of 0.2-4.6%. Fatty acids included in this category were myristic, arachidic and eicosenoic (gadoleic). Others appeared to be oxygenated derivatives of fatty acids.

Table 2.2

A Comparison of the Fatty Acid Composition of *Jessenia bataua* Oil and Olive (*Olea europaea*) Oil.

Fatty Acid	*Jessenia bataua** Samples, %	Olive Oil Samples, %
Palmitic	13.2 ± 2.1	11.2
Palmitoleic	0.6 ± 0.2	1.5
Stearic	3.6 ± 1.1	2.0
Oleic	77.7 ± 3.1	76.0
Linoleic	2.7 ± 1.0	8.5
Linolenic	0.6 ± 0.4	0.5
Other	1.6 (range 0.2-4.6)	--

*Values given as the mean ± standard deviation of 12 separate samples.

Table 2.3 presents an amino acid analysis of the *Jessenia bataua* protein. When the amino acid content of this protein is compared to the FAO/WHO provisional amino acid scoring pattern, the limiting amino acids are tryptophan and lysine but that, on the basis of this analysis, these are present at 90% and 96% of the recommended levels. These data suggest that *Jessenia bataua* protein quality is comparable

Table 2.3

Amino Acid Analysis of *Jessenia bataua* Protein

Amino Acid Component	Mg of Amino Acid per Gram of Protein: mean ± standard deviation*	Amino Acid Scoring Pattern**	%of FAO/WHO Scoring Pattern
Isoleucine	47 ± 4	40	118
Leucine	78 ± 4	70	111
Lysine	53 ± 3	55	96
Methionine	18 ± 6		
Cystine	26 ± 6		
Methionine + Cystine	44 ± 9	35	126
Phenylalanine	62 ± 3		
Tyrosine	43 ± 5		
Phenylalanine + Tyrosine	105 ± 7	60	175
Threonine	69 ± 6	40	173
Valine	68 ± 4	50	136
Tryptophan	9 ± 1	10	90
Aspartic Acid	122 ± 8		
Serine	54 ± 3		
Glutamic Acid	96 ± 5		
Proline	75 ± 8		
Glycine	69 ± 4		
Alanine	58 ± 4		
Histidine	29 ± 4		
Arginine	56 ± 2		

*Values represent mean ± standard deviation for 7 separate samples with the exception of tryptophan, for which only 3 samples were analysed.

**FAO/WHO provisional Amino Acid scoring pattern. The scoring pattern represents an "ideal protein" containing all the essential amino acids to meet requirements without excess (Food and Agriculture Organization of the United Nations/World Health Organization 1973).

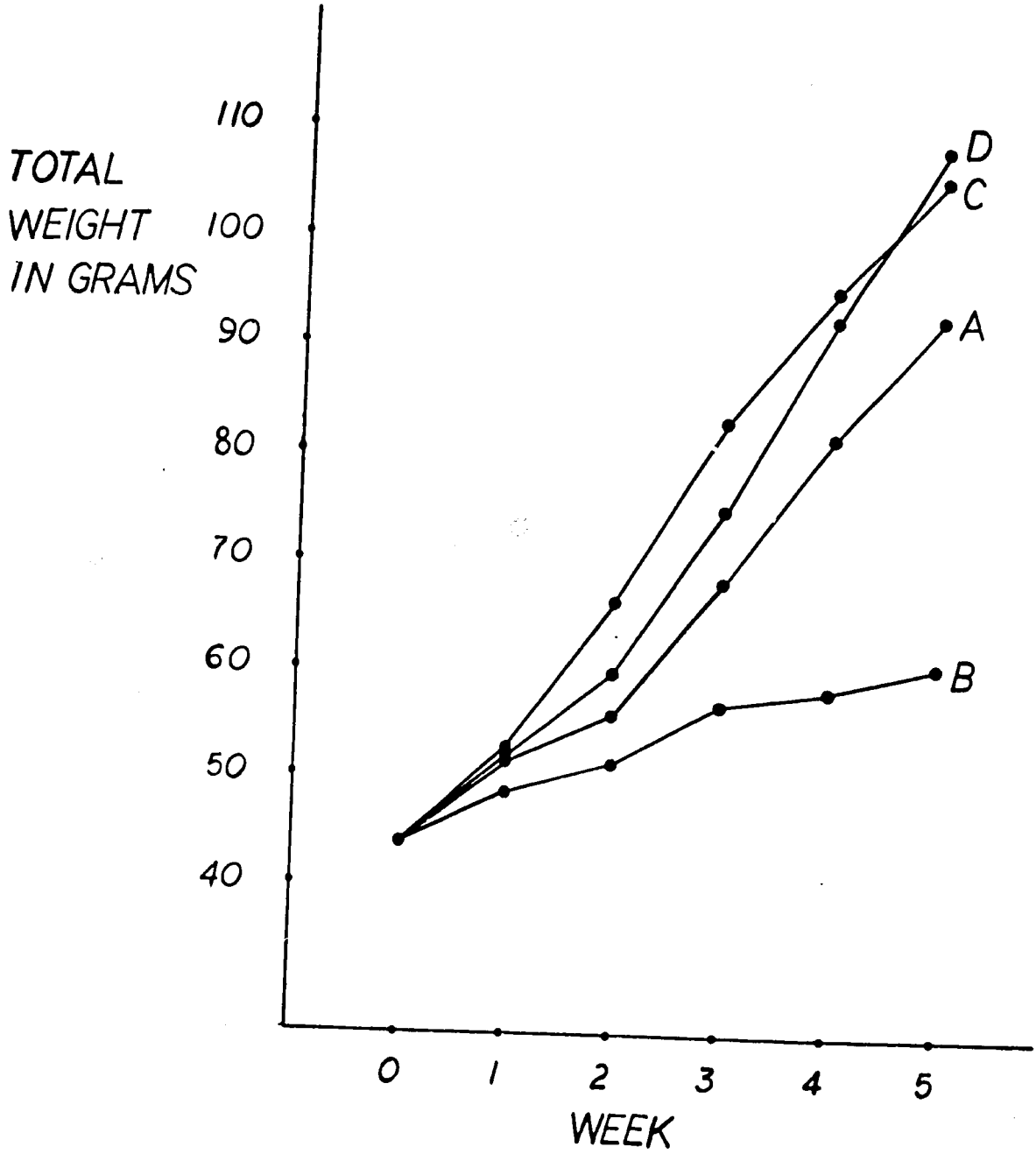
to that of good animal proteins and considerably better than most grain and legume proteins.

Figure 2.1 presents the results of a five week feeding study in which Jessenia bataua protein was compared to casein and Jessenia bataua oil to corn oil. Diet A contained 50% Jessenia bataua dried pulp ground in a large blender. During the first two weeks, the weanling rats appeared to have difficulty in consuming the diet, which may have been related to the physical characteristics of the pulp, or to its taste or smell. During the last three weeks of feeding, this difficulty disappeared and the animals grew at a rate similar to animals fed Diet C containing 7.8% casein. This feeding test suggests that the biological value of the Jessenia bataua protein was similar to that of casein. Final weights of rats fed Jessenia bataua oil was similar to those of rats fed diets containing only corn oil. Autopsy of the rats revealed no abnormalities associated with feeding either the Jessenia bataua oil or the pulp.

Discussion

The present study furnishes data on the nutritional value of a plant not in commercial cultivation. It is clear from the studies done here and from the experience of Indians in the Amazon Valley, that Jessenia bataua fruit may have untapped nutritional potential for man. Jessenia bataua is a neotropical palm distributed over much of the northern half of South America, including Panama and Trinidad. It is restricted to the lowlands, up to an altitude of about 1000 m. This palm has never been cultivated on a wide scale, and

Fig. 2.1. Growth of rats fed with diets described in Table 1. Diet A contained 5% casein with 2.8% protein and 5.6% oil from *Jessenia bataua* pulp; Diet B with 5% casein; Diet C with 7.8% casein; Diet D with 7.8% casein and 5.6% *Jessenia bataua* oil. Final mean rat weights ± standard error in grams for the diets were as follows: A. 93±5; B. 60±3; C. 106±6; D. 108±4.


TOTAL
WEIGHT
IN GRAMS
110
100
90
80
70
60
50
40
D
C
A
B
0
1
2
3
4
5
WEEK

thus basic agronomic data such as growth requirements, yields, and longevity of the tree, are lacking. There is no information on the time required to produce fruit under cultivation, although growth is known to be slow in the wild. Lack of knowledge concerning this oleaginous palm is reminiscent of the similar situation involving the African Oil Palm (Elaeis guineensis) at the beginning of this century before it was domesticated--indeed many parallels can be drawn between the two species.

On analysis, Jessenia bataua oil is similar to olive oil. Interestingly, the analyses done by liquid-gas chromatography, confirm the observations and chronicles of Italian and Spanish missionary priests living in the Amazon before modern nutritional science developed, who described Jessenia bataua as new world olive oil. The oil of this plant, if it could be produced on a large scale or a system developed for its rational exploitation from the wild, would provide a product of appeal not only to people in developing countries but to those in the industrialized world as well.

Because the major nutritional problem of people living in developing countries, most of which are tropical, is protein-calorie malnutrition, we have been particularly concerned with the oil and protein content and quality of this fruit. Surprisingly, the protein, both by amino acid analysis and rat feeding trials, has a biological value equivalent to that of the best animal proteins. Unfortunately, the level of protein in the pulp following oil removal is relatively low. However, as shown from first hand observations

in the Amazon Valley, it is an excellent food for poultry and pigs.

A milk produced from the fruit pulp is widely consumed in the Amazon. Analysis of the calorie content of the milk prepared in the laboratory--compared to human, cow and soybean milk--is presented in Table 2.4.

Table 2.4

A Comparison of Fat-Protein-Carbohydrate Content of Milk or Milk-Like Beverages

Approximate percentage calories from each component	*Jessenia bataua* milk	Human milk*	Cow milk*	Soybean milk*
Fat	55.3	45.9	49.8	37.6
Protein	7.4	5.6	20.9	37.9
Carbohydrate	37.3	48.5	29.3	24.5

*Data from United States Department of Agriculture (1963).

It is clear from data concerning the quality of the protein and oil that the beverage made from this plant is of high nutritional value. *Jessenia bataua* milk is most comparable in fat-protein-carbohydrate composition to human milk. Since the human protein requirement can be met by a diet containing less than 10% of its calories from high quality protein, the protein level in *Jessenia bataua* milk is more attractive than that supplied by soybean milk. Furthermore, the biological value of the *Jessenia bataua* protein is about 40% higher than that of soybean. On the basis of our very

limited rat feeding studies and anecdotal information acquired during field work in regions where Jessenia bataua oil and milk are consumed by people and its pulp by animals, there is presently no evidence that this food contains toxic materials.

An increasing concern of nutritionists who have done studies among rice-, corn-, and wheat-eating populations in which approximately 70% of the calories are supplied by grain, has been the low caloric density of the diets consumed. Even when adequate supplies of grain exist, children may not eat sufficient food to meet their caloric requirements. For this reason, a food with the high caloric density of Jessenia bataua is very attractive. Studies in man and animals indicate that the intake of essential fatty acids required to prevent deficiency lie within the range of 1-2% of total calories (National Academy of Sciences 1974). Jessenia bataua milk contains approximately 1.5% of its calories from linoleic acid.

Those nutritionists who feel that health advantage accrues from a high ratio of polyunsaturated fatty acids to saturated fatty acids may be slightly disappointed by the composition of Jessenia bataua oil, even though most of the fatty acid contained in the oil is the atherogenic neutral oleic acid. It may be possible that other species of palm fruit in the closely related genus Oenocarpus will provide oil with higher levels of polyunsaturated fatty acids. We obtained one sample of Oenocarpus mapora, and analysis showed

the protein to be of the same high quality as in *Jessenia bataua*. However, the fatty acid content of its oil was somewhat different, with the major changes being 19.6% palmitic acid, 64% oleic acid and 10.9% linoleic acid.

In conclusion, we feel that studies by botanists, agronomists and nutritionists designed to evaluate little-known foods consumed in developing countries may provide important new sources of food proteins for combating world hunger. This work has languished in the past, while full attention and support were directed towards developing the standard grain and legume crops for introduction into rural development schemes. The mixed successes achieved makes it apparent that the world food supply can not be totally dependent on only a few crops. The foundation upon which agriculture is built must be widened to include marginally used crops with further potential such as shown in the example of *Jessenia bataua*.

Footnotes

1. Personal communication R. E. Schultes, H. García-Barriga and D. L. Dufour.

2. Methodology for preparation of beverage from Jessenia bataua fruits in the laboratory: Heat 250 ml water to 70°C. Add 25 fruits (ca. 11-15 gm each) to water, bringing the volume up to ca. 540 ml. Heat continually at 70°C for 20 minutes. Macerate to separate "pulp" from seeds. Allow to settle for 10 minutes. Strain out seeds, pulp pieces and fibers, bottle and refrigerate for 24 hours. Sample then frozen.

3. R. Kleiman, Research Leader, Instrumental Analysis Research, Horticultural and Special Crops Laboratory, United States Department of Agriculture, Northern Regional Research Center, Peoria, Illinois.

4. Raltech Scientific Services, Inc., Madison, Wisconsin.

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Chapter 3

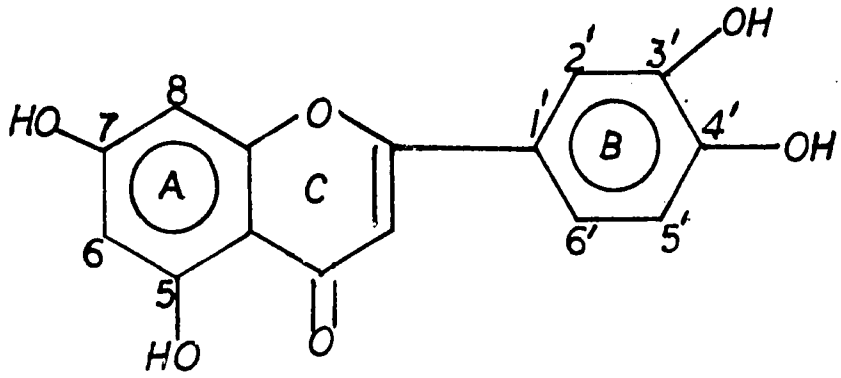
CHEMOTAXONOMIC STUDIES

Introduction

Many studies have shown that variation in the distribution of different classes of chemical compounds can be used for systematic botanical purposes (Bohm and Wilkins 1978, Cooper-Driver and Swain 1977, Crawford 1970, Giannasi 1975, Whalen 1979). Chemotaxonomy may be undertaken at the macromolecular level, as in the amino acid sequencing of a specific protein (for example cytochrome C (Boulter 1974)) or at the micromolecular level using secondary plant products (for example alkaloids, terpenoids and flavonoids (Smith 1976)).

Flavonoids constitute one of the most useful groups of secondary plant compounds for chemotaxonomic purposes because of their widespread distribution and diversity of structure (Harborne 1977). They are chemically stable structures, allowing for the analysis of either freshly collected material or dried herbarium specimens. In fact, recent studies on fossil leaves have isolated flavonoid glycosides, still intact after millions of years (Giannasi and Niklas 1977). Flavonoids are also easy to detect and identify using relatively simple and inexpensive apparatus (Harborne _et al_. 1975). All flavonoids are structurally related to the parent compound flavone (Fig. 3.1), and individual classes of flavonoids--flavanones, chalcones, flavones, isoflavones, flavonols, aurones, anthocyanidins, etc.--differ from each other only in the state of oxidation of the central pyran ring. Within classes, compounds

Fig. 3.1. Basic structure of the parent compound flavone--the example shown is Luteolin.


HO
7
8
O
A
C
6
5
HO
O
1'
2'
3'
OH
B
4'
OH
6'
5'

vary depending on the number and orientation of phenolic hydroxyl groups attached to the aromatic rings, on the degree of O- and C-alkylation, and on the number and nature of sugars attached to the hydroxyl groups (O-glycosides) or directly to the aromatic nucleus (C-glycosides).

There are three levels at which it is possible to study the distribution of flavonoids for chemotaxonomic purposes (Giannasi 1978). 1) By examining the distribution of flavonoid compounds following 2-dimensional chromatography of an alcoholic extract of plant material (usually in solvent systems TBA:tert-butanol-acetic acid-water and 15% acetic acid). The position and number of the flavonoid compounds can be determined from R_f values and color reactions under ultra-violet light in the presence and absence of ammonia. While this method is of great use in overall surveys of plant families or genera, as it requires far less time than isolating and identifying individual compounds, difficulties may occur in locating the compounds, due to overlap or to lack of visibility under u.v. light (eg. flavanones). However, the examination of flavonoid distribution provides basic information on overall differences between plant taxa (Anderson 1980). 2) By acid hydrolysis. The plant extract is hydrolyzed with 2N hydrochloric acid and the parent flavonoid compounds (aglycones) separated and identified by paper or thin layer chromatography. As much of the information concerning flavonoids as chemotaxonomic markers concerns substitution patterns on the aglycone (eg. glycosylation, methylation) this method

also has its limitations but does give chemical evidence for differences in flavonoid groupings between plant taxa. 3) Complete or nearly complete identification of all the major flavonoid compounds present. This provides much more detailed and pertinent information for separating plants both taxonomically and phylogenetically on the basis (presence or absence) of flavonoid groups and patterns of substitution (hydroxylation, glycosylation) as described above (Bohm and Wilkins 1978, Crawford and Mabry 1978).

Chemotaxonomic studies usually rely upon both herbarium and freshly collected materials. In such studies, there is the underlying assumption that the two types of material are interchangeable from a chemical standpoint and that reliable data may be obtained from each. Plant parts collected in temperate regions are frequently quickly dried, as herbarium facilities are often close by, and collections are made usually during the warm spring or summer seasons. Tropical botanical collections, on the other hand, must often be exposed to one of a number of chemicals for field preservation before drying (Hodge 1947, Moore 1950, Schultes 1947).

Therefore, before proceeding with chemotaxonomic studies on the palm genera Oenocarpus and Jessenia, it was decided to test the effects of various chemical preservatives on the phenolic acid and flavonoid content of the leaves of Jessenia bataua (Cooper-Driver and Balick 1978).

Both the generic and specific limitations of Oenocarpus and Jessenia are unclear. While many people accept Karsten's

genus. Jessenia (Burret 1928, Dahlgren 1936, Moore 1973, Dugand 1976), Wessels Boer (1965, 1972) considered it to be synonymous with Oenocarpus. The taxonomic history and associated problems of these genera are further discussed in Chapter 5. At the specific level, many delimitations have been made, often based on fragmentary collections, with little biological understanding of true specific characteristics versus those arising from phenotypic plasticity. As a second part of this study, an examination was made of the distribution of flavonoids in some Oenocarpus and Jessenia taxa. The flavonoid data obtained, together with the information from more traditional systematic studies was then used in order to answer the following questions:

1. Is Jessenia a widespread but monotypic genus?
2. Is Jessenia distinct from Oenocarpus?
3. Assuming Oenocarpus and Jessenia to be distinct genera, what are the specific relationships within Oenocarpus?

This chemotaxonomic investigation was undertaken by examining flavonoid patterns on two-dimensional chromatograms and, whenever possible, by the isolation and characterization of some of the major compounds present. Not all flavonoids in the species examined could be fully identified, due to limitations on time, lack of materials and my own degree of expertise.

Materials and Methods

A. Preservation Studies

Fresh leaf material was obtained from seedlings of *Jessenia bataua* which had been grown in a phytotron to 20 cm high. These were then divided into eight groups, and each group subjected to the following individual treatments: 1) sun dried; 2) dried in an herbarium oven at 105° F; 3) soaked in water; 4) soaked in 95% ethanol; 5) soaked in white rum (86 proof, ca. 44% ethanol); 6) soaked in an FAA mixture (90% ethanol: 5% glacial acetic acid: 5% formalin); 7) soaked in formalin (100% formalin, ca. 40% formaldehyde) and water in a 1:1 mixture; 8) soaked in formalin alone. The leaves for treatments 3-8 were stored in the dark for four weeks at room temperature and then removed from the solution and air dried. The solutions were kept refrigerated.

Two samples of dried leaves from each of the eight treatments were finely macerated, extracted with boiling 80% methanol, and the solution concentrated and made up to a final volume of 10 ml. The u.v. spectrum (220-400 nm) of the methanol extracts (suitably diluted) was determined, and the amount of phenolic compounds calculated, using caffeic acid (a cinnamic acid) and rutin (quercetin 3-0 rhamnoglucoside, a flavonol) as standards. Identical amounts of the methanol extract were examined also by two dimensional chromatography, using the solvent systems n-butanol-acetic acid-water 6:1:2 (BAW) in one direction, followed by 5% aqueous acetic acid (HOAc) in the second direction. The solutions in which the

leaves had been soaked were concentrated to a standard volume and subjected to two-dimensional chromatography by the procedure described above.

B. Chemotaxonomic Studies

During field work in South America and Trinidad, fresh palm leaf material was collected. With each specimen of Oenocarpus, Jessenia or other palm, I removed 50-200 gms of pinna material, for the most part from a single leaf, and dried it in the sun. This usually took from 2-4 days, depending on the intensity and duration of sunlight on a particular day. All materials, packaged in plastic bags and sealed, were shipped back to the laboratory. The specimens used in this study are listed in Table 3.1. Complete herbarium specimens, from 1-5 in number, were made both as vouchers for the chemosystematic work and for other taxonomic studies.

Extraction of Flavonoid Compounds

Extracts of the leaf material were prepared from 2 grams of dried leaves, finely macerated, put into a 150 ml beaker and mixed with 50 ml of 80% methanol. After boiling gently for five minutes, the macerated material in aqueous alcohol was stored for 24 hours. The mixture was filtered and the leaf residue washed with additional 80% methanol.

2-Dimensional Chromatography of Flavonoid Compounds

The solution was concentrated, using a rotary evaporator, to approximately 5 ml. About 100 µl of this extract was

Table 3.1

Specimens Examined for Flavonoid Content

Species	
Jessenia bataua subsp. *oligocarpa*	*Balick et al. 1231*, Valencia, Trinidad.
Jessenia bataua subsp. *bataua*	*Balick et al.* nos. *1148*, Tingo Maria, Peru; *952*, Itaituba, Brazil; *1013*, Pebas, Peru; *1187*, Lago Agrio, Ecuador; *955*, Belém Brazil; *s.n.* Tingo Maria, Peru; *1189* Lago Agrio, Ecuador; *929* (seedlings), Santarém-Cuiabá Highway, Brazil; *929*, Santarém-Cuiabá Highway, Brazil *933*, Santarém-Cuiabá Highway, Brazil; *1190a* Rio Palenque, Ecuador; *1188*, Lago Agrio Ecuador.
Oenocarpus mapora	*Balick et al.* nos. *975*, Iquitos, Peru; *987*, Pebas, Peru, *1158*, Tocache, Peru: *1199*, Vichada, Colombia.
Oenocarpus distichus	*Balick et al.* nos. *910*, Santarém-Cuiabá Highway, Brazil, *915* Santarém-Cuiabá Highway, Brazil; *930*, Santarém-Cuiabá Highway, Brazil; *957*, Belém, Brazil.
Oenocarpus minor	*Balick et al.* nos. *968*, Reserva Ducke, Brazil; *969*, Reserva Ducke, Brazil.
Oenocarpus bacaba	*Balick et al.* nos. *954*, Belém-Brazilia Highway, Brazil; *1201*, Vichada, Colombia.

applied to a sheet of 46 x 57 cm Whatman No. 3 Chromatography paper. The paper was then run 2-dimensionally, descending in solvents TBA (tert. butanol-acetic acid-water 3:1:1) first direction, and 15% acetic acid in water, second direction. After drying, fluorescence spots of the phenolic compounds were observed under u.v. light (ca. 350 nm) and marked as to position and color. Fuming with ammonia caused color changes in some spots, and the appearance of "new" spots, all of which were recorded.

Isolation of Flavonoid Compounds

After careful examination of all the papers under u.v. light, taxonomically important spots were selected for each species. These were chosen on the basis of being unique to a particular taxa or being common to several taxa and present in high concentrations. The selected compounds were isolated by two methods. In the first method, about 20 sheets of Whatman No. 3 paper were spotted with extract containing the equivalent of up to 40 gms of leaf material. These were run 2-dimensionally, the individual spots cut out, eluted in 80% methanol, concentrated, and refrigerated. In the second method, leaf extracts were streaked in bands on Whatman No. 3 paper, run in TBA, the fluorescent bands cut out, eluted in methanol, concentrated, and then restreaked on Whatman No. 3 paper and run in 15% acetic acid. Again the bands of the unknown compounds were cut out, eluted, concentrated and refrigerated.

Identification of Flavonoid Compounds

Thin layer chromatography

Thin layer chromatography was used for the separation of isolated flavonoids. Silica gel TLC plates (Eastman Chromatogram Cellulose sheets), spotted with the unknown compounds, were run in a maximum of three solvent systems: 15% acetic acid; distilled water; and TBA. R_f values were measured under u.v. light after fuming with ammonia.

U.V. Spectroscopy

A Beckman u.v. Spectrophotometer was used for spectral analysis. Spectral peaks and shoulders were observed of unhydrolysed compounds in 80% methanol. Further data were obtained through the addition of: 1) 1N potassium hydroxide, 2) solid sodium acetate, 3) 0.5 M aluminum chloride and 4) aluminum chloride with 2N hydrochloric acid. These stock solutions were added to both sample and blank. Spectral shifts are interpreted as follows (Cooper-Driver 1975):

1. Potassium hydroxide (KOH), a strong base, serves to ionize to some extent all the hydroxyl groups on the flavonoid nucleus. Therefore, flavones and flavonols, with a free 4'-hydroxyl group, show large bathochromic shifts in Band I (long wavelength band) of about 40-65 nm and smaller shifts of Band II (short wavelength band). In flavonols with free hydroxyl groups at both 3 and 4' positions, these shifts may not occur, as such compounds are unstable in strong base and break down with accompanying changes in the Band I absorption peaks within a number of minutes. More rapid changes are

found in compounds with the 3,3', 4' trihydroxy groups and also occur in both flavones and flavonols having 5,6,7-;5,7,8,- and 3',4',5'-trihydroxylation groups.

2. The addition of sodium acetate (NaOAc) ionizes completely only the more acidic hydroxyl groups: eg. 3 and 7 hydroxyl groups primarily responsible for Band II absorption. When NaOAc is added, flavones and flavonols with free 7-hydroxyl groups exhibit a diagnostic 5-20 nm bathochromic shift of Band II. Flavonoids with a 4'-hydroxyl (or 3',4'-di OH) group but no free 7-hydroxyl group usually have a pronounced shoulder on the long wavelength side of Band I.

3. With the addition of aluminum chloride ($AlCl_3$), acid-stable five or six membered ring complexes are formed with the 4-CO group and hydroxyl groups at C-3 or C-5, respectively, and acid-labile five-membered ring complexes with ortho-dihydroxy systems. In flavones or flavonols, adding $AlCl_3$ gives 30-60 nm bathochromic shifts of Band I due to carbonyl chelation. This reaction may be augmented by ortho-dihydroxy group chelate formation.

4. The presence of an ortho-dihydroxyl group in the B ring of flavones and flavonols can be detected by a comparison of the spectrum of the flavonoid in the presence of $AlCl_3$ and $AlCl_3$+HCl. When the acid is added, a hypsochromic shift occurs; the $AlCl_3$ complex between the C-4 keto function and either the 3- or 5- hydroxyl group is stable in the presence of acid.

Results and Discussion

A.A. Preservation Studies

The amount of phenolic compounds remaining in the leaf material following the various preservation treatments is shown in Table 3.2.

Table 3.2

Treatment	Phenols (as caffeic acid) mgm/gm dry weight
1. Sun dried	12.5
2. Herbarium dried	11.5
3. Water	3.0
4. 95% ethanol	2.4
5. White rum	2.4
6. FAA	0.9
7. Formalin:water, 1:1	1.8
8. Formalin	1.6

A 2-dimensional chromatogram was made of the leaf extract of Jessenia bataua from treatment 1 and eight u.v. fluorescent spots were noted. Upon examination of the other 2-dimensional chromatograms obtained from treatments 2-8, varying intensities in spot patterns under u.v. light could be determined. Spot patterns obtained from leaf extracts which have undergone these different extraction procedures are given in Table 3.3. Some of these treatments (4-8) resulted in a significant amount of leakage of phenolic compounds from the leaf.

Table 3.3

Spot Patterns Obtained from Leaf Extracts

Treatment	Phenolic Compounds Present							
	1	2	3	4	5	6	7	8
1. Sun dried	++	++	++	++	++	++	++	++
2. Herbarium Dried	++	++	++	++	++	++	++	++
3. Water	+	+	+	+	+	+	+	+
4. 95% Ethanol	tr	tr	tr	tr	tr	tr	tr	tr
5. White Rum	tr	tr	tr	tr	tr	tr	tr	tr
6. FAA	-	-	-	-	-	-	-	-
7. Formalin-water 1:1	-	-	-	-	-	-	-	-
8. Formalin	-	-	-	-	-	-	-	-

(++ = very positive; + = positive; tr = trace; - = negative)

The 2-dimensional chromatograms from the solutions in which the leaves had been soaked showed that varying amounts of the compounds had been extracted from the leaves and were present in the solution. Results of these chromatograms are presented in Table 3.4, and show a correlation with Table 3.3: e.g. soaking leaves in 95% ethanol results in phenolic compounds being leached from the leaves and being present in the soaking solution (preservative).

Table 3.4

Spot Patterns Obtained from Preservative Solutions

Treatment	Phenolic Compounds Present							
	1	2	3	4	5	6	7	8
3. Water	+	+	+	+	+	+	+	+
4. 95% Ethanol	++	++	++	++	++	++	++	++
5. White rum	++	++	++	++	++	++	++	++
6. FAA	+	+	+	+	+	+	+	+
7. Formalin-water 1:1	-	-	-	-	-	-	-	-
8. Formalin	-	-	-	-	-	-	-	-

(++ = very positive; + = positive; - = negative)

There is no doubt from the results in Tables 3.3 and 3.4 that palm material must be preserved only by sun or subsequent artificial drying, if it is to be of use in chemotaxonomic investigation for flavonoids or closely related phenolic compounds. Soaking in preservatives containing 95% ethanol, white rum and FAA changes cell permeability, resulting in a consequent leakage of phenolic material into the preservative solution. Preservatives containing formaldehyde in high concentration (nos. 7 and 8) which cross link with proteins, carbohydrates and phenolic compounds, give insoluable precipitates and show no free phenolic compounds in either methanolic leaf extracts or in the preservative solutions. While water does not harm phenolic constituents in the material to the extent of the other chemicals, it is of no value as a preservative as it lacks fungicidal and bacteriocidal

properties. Thus, on the basis of the above results, palm leaf material (and presumably that of other plants), if it is to be used in chemotaxonomic analysis, must be sun- or herbarium-dried. In addition, labels of herbarium specimens should clearly indicate the way in which the specimen was collected and preserved prior to mounting. If chemical preservation is unavoidable, as is often the case in remote tropical localities, then 10-50 gm of plant material (leaf or flower or both, depending on the plant) should be collected, sun- or blotter-dried separately, and stored in an air-tight bag for later use. Concurrent but independent investigations by Coradin and Giannasi (1980) studying the effect of preservatives on temperate species of plants, have resulted in a similar conclusion to those obtained above (Cooper-Driver and Balick 1978). Thus, the proper treatment of herbarium collections is of extreme importance, if chemotaxonomy is to continue to grow as an important research tool for tropical systematic botany.

B.B. Chemotaxonomic Studies

The 2-dimensional chromatographic patterns of species examined are given in Fig. 3.2, and the chromatographic and spectral properties of isolated compounds given in Tables 3.5 and 3.6.

All samples of Jessenia gave similar 2-dimensional chromatographic patterns. Material from Peru, Brazil and Ecuador yielded identical spot patterns, while that from Trinidad was somewhat distinct. The flavonoid patterns for

the two populations--Amazon Valley and Trinidad--are presented in Fig. 3.2 a.b. Approximately 50% of the flavonoid compounds in Jessenia are common to both populations. In conjunction with other evidence, primarily morphological and phytogeographic, I have determined that all populations represent a single species, Jessenia bataua, of which two subspecies are delimited: J. bataua subsp. bataua (Amazon Valley and J. bataua subsp. oligocarpa (Trinidad and the northeastern edge of South America).

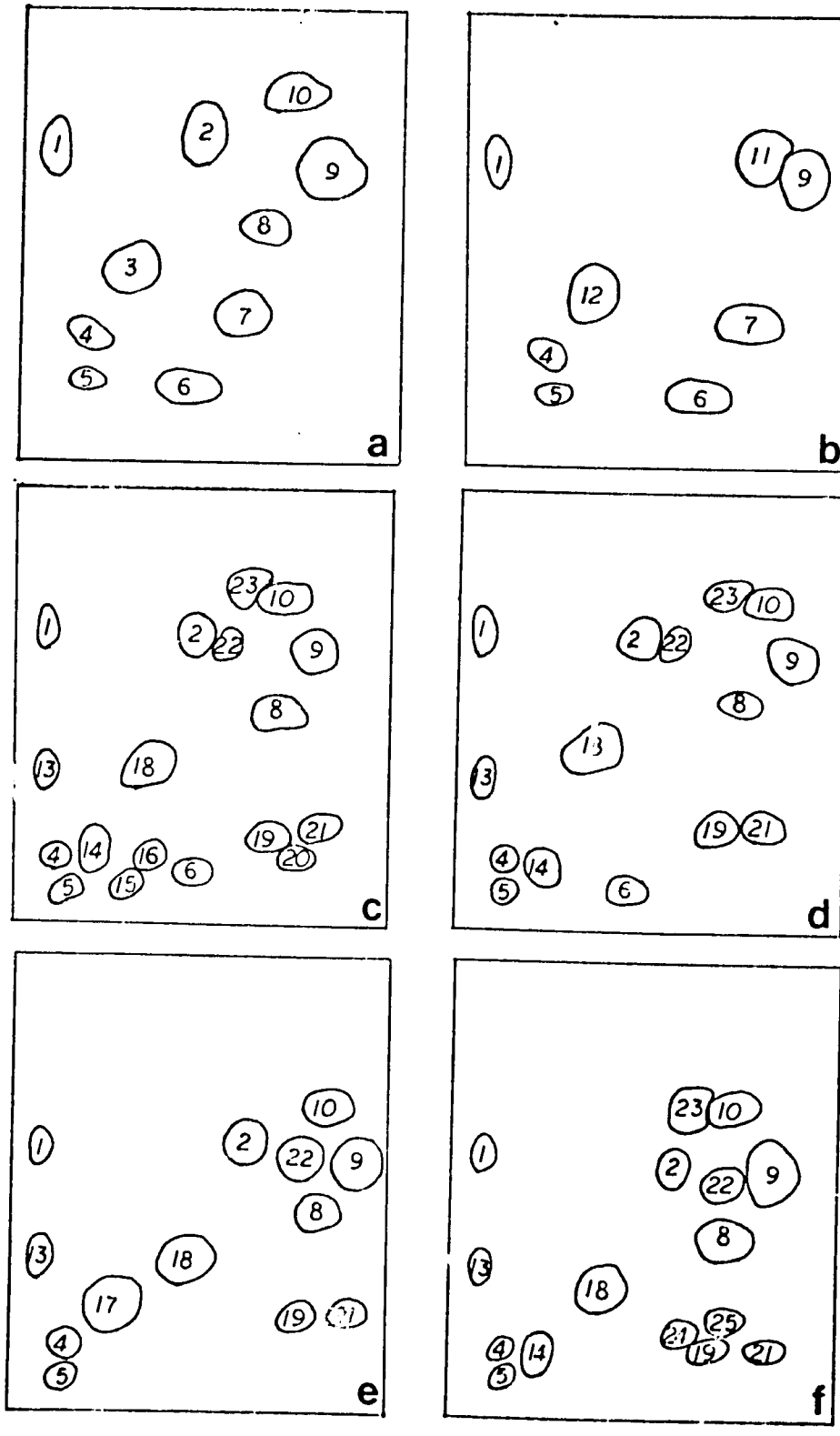
Characteristic 2-dimensional chromatogram spot patterns were also obtained with Oenocarpus. Individual patterns from the four species studied are shown in Fig. 3.2 c-f. While Oenocarpus and Jessenia are, from the flavonoid patterns, clearly distinct generic concepts, a certain number of compounds are found common to both (1,4,5,8,9,10--Table 3.5). Oenocarpus and Jessenia share 25% of the compounds present, offering some biochemical evidence for their taxonomic affinity.

In Oenocarpus, O. bacaba and O. distichus have a large number of shared compounds (82%), whereas Oenocarpus bacaba shares a smaller number with O. minor (50%) and O. mapora (58%), suggesting a close relationship between O. bacaba and O. distichus. Oenocarpus minor shares 71% of its compounds with O. mapora and 76% with O. distichus. Oenocarpus mapora shares 69% of its compounds with O. distichus. From a morphological standpoint, the closest relationship among the above four species is between O. bacaba and O. distichus, an affinity borne out somewhat by the percentage of shared flavonoid

Fig. 3.2. Chromatographic spot patterns of Oenocarpus and Jessenia species examined. Chromatograms correspond to the following species: a. Jessenia bataua subsp. bataua; b. J. bataua subsp. oligocarpa; c. Oenocarpus bacaba; d. O. distichus; e. O. mapora; f. O. minor.

Color reactions under u.v. light (before fuming with NH_4--after fuming with NH_4) are as follows: 1. purple--purple; 2. dark brown--yellow; 3. white--yellow; 4. green--green; 5. green--green; 6. dark--yellow green; 7. dark--green; 8. pink--pink; 9. blue--blue; 10. pink--pink; 11. dark--dark; 12. dark brown--yellow brown; 13. purple--purple; 14. dark--light green; 15. purple--purple; 16. purple--purple; 17. light green--light green; 18. dark--yellow; 19. dark--yellow; 20. purple--purple; 21. green--light yellow; 22. dark--yellow; 23. dark--dark; 24. yellow green--yellow green; 25. yellow green--yellow green.

TBA



15% HOAc

Table 3.5

Compounds Present in 2-dimensional Chromatograms of Alcoholic Extracts of *Jessenia* and *Oenocarpus*.

Species	Spot Number																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Jessenia bataua subsp. *bataua*	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Jessenia bataua subsp. *oligocarpa*	+	-	-	+	+	+	+	-	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Oenocarpus distichus	+	+	-	+	+	+	-	+	+	+	-	-	+	+	-	-	-	+	+	-	+	-	+	-	-
Oenocarpus bacaba	+	+	-	+	+	+	-	+	+	+	-	-	+	+	+	+	-	+	+	+	+	-	+	-	-
Oenocarpus mapora	+	+	-	+	+	-	-	+	+	+	-	-	+	-	-	-	+	+	+	-	+	+	-	-	-
Oenocarpus minor	+	+	-	+	+	-	-	+	+	+	-	-	+	+	-	-	-	+	+	-	+	+	+	+	+

(+ = positive; - = negative)

compounds.

Over the last two decades, the investigation of flavonoid patterns in plants has developed as an important taxonomic tool. These compounds are used to delimit taxa at many levels (for example, see Cooper-Driver and Swain 1977, Crawford 1970 , Giannasi 1975, and Whalen 1979). Works in the Palmae have so far mostly been limited primarily to broad surveys (Bate-Smith 1968, Williams et al. 1973). Williams et al. offered chemical evidence for the separation of several closely related taxa at various levels. The subfamilies Phoenicoideae and Caryotoideae (Moore 1973 gives these as categories without rank) possessed distinct flavonoid patterns, while similar chemical evidence supported the separation of the Phytelephantoideae and Nypoideae. Separation of the genera Cocos and Butia was based on the presence of negatively charged flavonoids in Butia and their absence in Cocos. At the varietal level, Butia capitata var. capitata contained quercetin, while var. pulposa did not.

Williams et al. found the following compound classes present in her broad survey of the Palmae: Flavone-C-glycosides (in 84% of sample); Flavone-O-glycosides including Tricin (in 50%), Luteolin (in 30%) and Apigenin (in 50%); Flavonol-O-glycosides including Quercetin (in 24%) and Kaempferol (in 10%); Potassium Bisulphate Salts (in 50%); Leuco-anthocyanadins (in 66%). Specific to the Arecoid palms, the following percentages were obtained: Negatively charged flavonoids (in 41%); Flavone-C-glycosides (in 76%); Tricin (in 19%); Luteolin (in 26%); Apigenin (in none); Quercetin (in 24%);

Kaempferol (in 12%); Leuco-anthocyanadins (in 57%).

While the determinations in Table 3.6 are only tentative, it appears that many of the compound classes found in Williams *et al.*, eg. Flavone-*C*-glycosides, Luteolin and Kaempferol, occur also in *Oenocarpus* and *Jessenia*.

Based on the results of the present study, the questions presented at the beginning can be answered. *Jessenia* and *Oenocarpus* are to be treated as distinct genera. While they share a certain number of characteristic compounds, the patterns are relatively distinct, given the diversity exhibited both within and between genera. The four species of *Oenocarpus* examined differed somewhat. All species, excepting *O. distichus*, had, in addition to the shared spots, from one to three individual characteristic spots. While five species have, in the past, been recorded for *Jessenia*, chemical and other evidence gathered in our study indicates this genus to a widespread monotypic genus consisting of two subspecies. Material from Brazil, Ecuador and Peru, corresponding to *J. bataua* and *J. weberbaueri* was shown to be identical. In addition, seedlings of *J. polycarpa* used in the preservation studies gave a pattern very comparable to that of *J. bataua*. The Trinidad population, usually called *J. oligocarpa*, differed only in a few spots and, along with more traditional systematic evidence, may be relegated to the subspecific level (for further discussion of this concept see Chapter 5).

A curious condition was observed in palm leaf material

Table 3.6

Color, R_f and Spectral Data of Flavonoids Isolated from *Jessenia* and *Oenocarpus* species.

Spot No.	Species	Color u.v./u.v. + NH_4	R_f Values TBA	15%HOAc	H_2O
2.	*Jessenia bataua* subsp. *bataua*	dark brown/yellow	0.70	0.45	0.05
3.	" "	white/yellow	0.50	0.25	0.3
6.	" "	dark/yellow-green	0.10	0.30	n.d.
7.	" "	dark/green	0.35	0.55	0.11
9.	" "	blue/blue	0.55	0.80	0.68
10.	" "	pink/pink	0.80	0.60	n.d.
12.	*Jessenia bataua* subsp. *oligocarpa*	dark brown/ yellow brown	0.40	0.12	n.d.
14.	*Oenocarpus distichus*	dark/light green	0.30	0.10	n.d.
20.	*Oenocarpus bacaba*	purple/purple	0.25	0.65	n.d.

Spectral Data for Selected Compounds

Spot No.	MeOH	MeOH/KOH	MeOH/NaOAc	MeOH/$AlCl_3$	$AlCl_3$/HCl	Flavonoid Compound Isolated
2.	268,304sh,336	276,296sh,372	274,304sh,334	273,344	273,340	luteolin-O-glycoside
3.	262,330	272,370	262,338	266,336	266,336	luteolin-O-glycoside
6.	270,340	289,400	270,340	270,340	n.d.	flavone-C-glycoside
7.	271,302sh,335	282,330sh,400	282,300sh,380	271,333	n.d.	flavone-O-glycoside
9.	240,300sh,326	268,300sh,372	300sh,326	296,326	n.d.	caffeic acid glycoside
10.	253,322	277,370	243sh?,320	254,320	254,320	?
12.	249,266,350	249,260,412	266,350	269,294sh, 306sh,352	272,284sh, 300sh,354	quercetin-diglycoside
14.	268,285sh,336	272,338	277,395	273,338	273,338	flavone-C-glycoside
20.	278	292	278	278	278	flavonone

(sh=shoulder; n.d.=no data obtained)

collected in the Museu Emilio Goeldi garden in Belém, Pará, Brazil. While properly collected and sun dried, no significant flavonoid patterns were obtained from any of the five samples tested. The absence of phenolic material in these cultivated palms is most perplexing, especially as palms collected just a few miles away yielded patterns identical to those usually found. While this divergence does not imply that all cultivated material be suspect, it certainly warrants investigation on a wider scale. Other workers have used cultivated palm specimens (Williams *et al.* 1973) with no apparent problems.

Conclusion

Within the *Oenocarpus-Jessenia* complex, chemical evidence may be used to delimit genera and species. Chemical studies produce support for a general uniting of several of the species in the two genera. Specimens collected under various epithets from different localities proved to be identical in flavonoid composition. This evidence, along with indications from more traditional types of study, has led to the conclusion that, while many species have been described in both *Oenocarpus* and *Jessenia*, far fewer true species actually exist. Compounds are abundant and distinctive enough to warrant a large scale chemical survey of these two genera. A primary requirement of any further work rests in the procurement of sun-dried, vouchered material of all species, including those four not yet examined (*O. macrocalyx*, *O. discolor*, *O. tarampabo*, *O.*

circumtextus), a task which can be carried out only with additional comprehensive field work in the Amazon Valley.

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Chapter 4

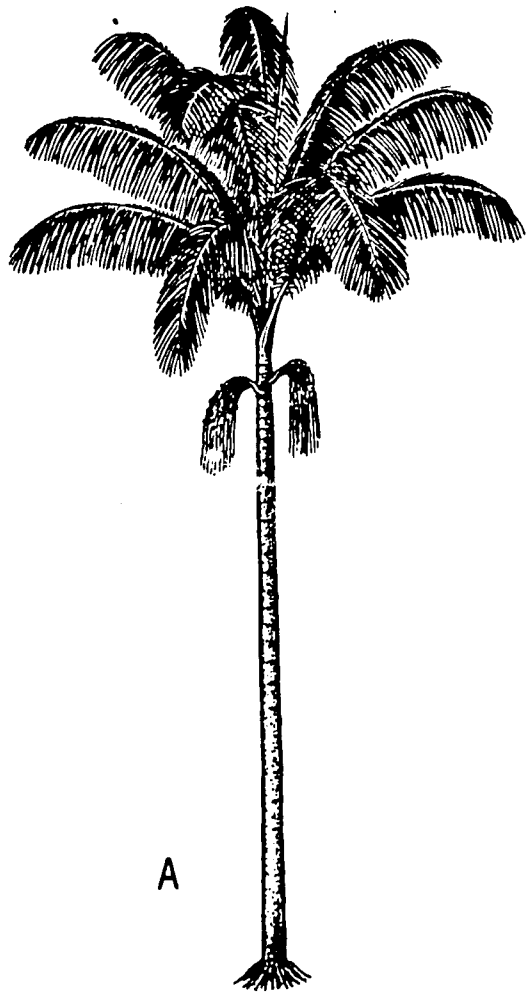
MORPHOLOGY AND GROWTH

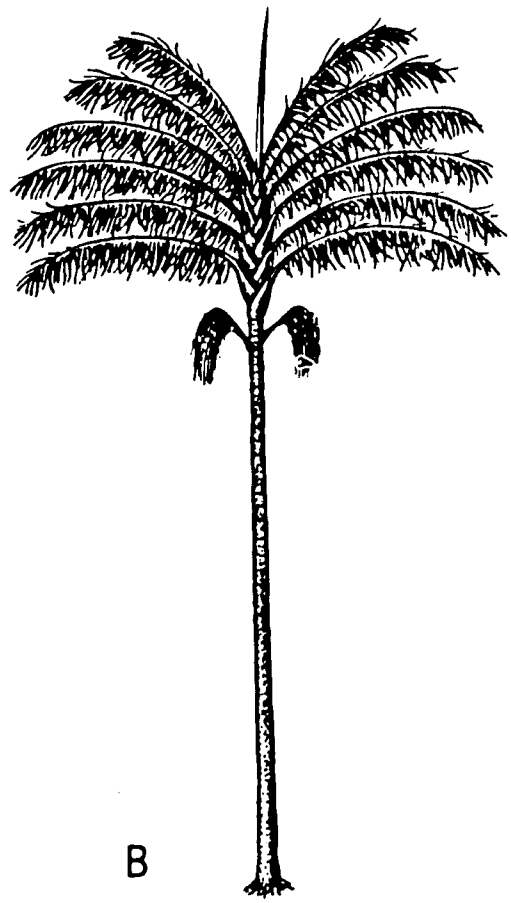
Habit

For a group so limited in number of species, palms in the Oenocarpus-Jessenia complex are surprisingly varied in habit. The species may be divided into two groups conforming to the two architectural models presented in Halle et al. (1978). The most common in this complex is Corner's Model (p. 109), in which the vegetative growth is from a single aerial meristem producing an unbranched vegetative axis with axillary inflorescences (Fig. 4. 1A,B). This model is common in the palms, representative of trees with indeterminate growth. In the Oenocarpus-Jessenia complex, the species within this model may be further subdivided into two groups, based on phyllotaxis. The more predominant are those species with spiral phyllotaxis--J. bataua, O. minor subsp. minor, O. bacaba, O. circumtextus and O. mapora (Corner's Model, in part). Three species--O. distichus, O. discolor and O. tarampabo--have a two-ranked leaf arrangement.

The second major group of species in Oenocarpus and Jessenia conform to Tomlinson's Model (p. 118), i.e. to caespitose species, where basal branches ("...initially restricted to the epicotyledonary region of the seedling axis...and the basal nodes in subsequent axes.") repeatedly develop as equivalent orthotropic modules. In this model, the inflorescences may be terminal or lateral, although only lateral inflorescences are found in the Oenocarpus -Jessenia complex. The two taxa characterized by this model are O. minor subsp. intermedius and O. mapora (Fig. 4. 1C).

Fig. 4.1. Habits of palms in the Oenocarpus-Jessenia complex. A. Jessenia bataua, representing Corner's Model, with spiral phyllotaxis; B. Oenocarpus distichus, representing Corner's Model, with a two-ranked leaf arrangement; C. Oenocarpus mapora, in this case a caespitose specimen representing Tomlinson's Model; D. Oenocarpus mapora, a solitary specimen representing Corner's Model. Note the dimorphic habit of Oenocarpus mapora. Drawn by E. W. Smith.


A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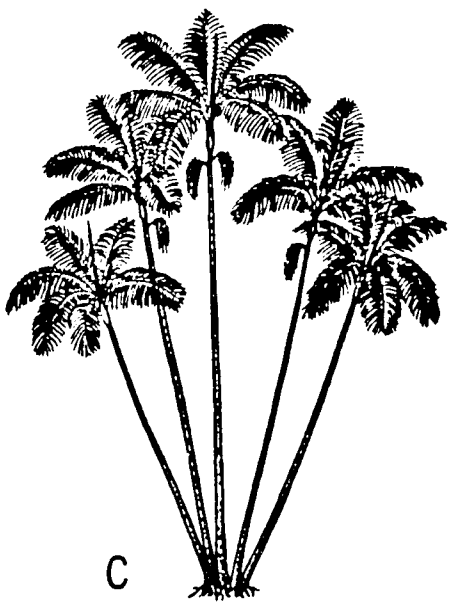

C

D

Oenocarpus mapora is dimorphic in habit, since it can also conform to Corner's Model (Fig. 4. 1D). Halle et al. (1978) stated that Tomlinson's Model may include apparently solitary-stemmed palms if the sequence of branch production allows only one aboveground axis at a time. There are some indications that the solitary habit of O. mapora is correlated with a more regular pinna arrangement than that of the caespitose individuals, but this cannot now be formally proposed or substantiated.

Stem

Most monocotyledons, including all palms, lack an active cambium. Growth is entirely primary. Two types of stem growth are possible. Stems of the first type do not increase in girth below the crown. A uniform diameter throughout the stem is characteristic of both Oenocarpus and Jessenia. Alternatively, some palms, such as Archontophoenix cunninghamiana, increase substantially in girth below the crown, caused by intercellular tissue expansion from cell enlargement, cell division and the formation of schizogenous lacunae (Waterhouse and Quinn 1978). This non-meristematic activity is known as diffuse secondary growth (Tomlinson 1961) or sustained primary growth (Waterhouse and Quinn 1978).

Palms are lacking also in cork cambium, although they have other forms of shielding tissue, such as sheaths and spines. These provide the same protective function as the periderm of dicotyledons.

Jessenia bataua may reach a height of 20-25 m or more.

The erect trunk, often only 25 cm in diameter, has a substantial base for support, provided by the inverted subterranean basal cone, formed before the erection of the aboveground bole during establishment growth. Seedlings develop these stem bases through the production of short, progressively wider, congested internodes (Tomlinson 1960a). When the base reaches a certain width (presumably one sufficient to support the aerial section) internodal elongation begins and a characteristic trunk can be observed. In some palm groups, a limited amount of taxonomic information can be obtained from the nodes (leaf scars) based on their appearance (swollen vs. smooth) and spacing. In the Oenocarpus-Jessenia complex, the scars are smooth and flush with the stem towards the base and middle but become progressively more prominent and swollen towards the apex. In these two genera nodal appearance or spacing is not useful for the separation of species.

Waterhouse and Quinn (1978) studied the expansion of nodal girth in Archontophoenix cunninghamiana and found conflicting results in three different specimens, showing apical internodes either to increase or decrease in diameter over time. In general, on an individual tree, apical stem diameter was less than basal stem diameter. Mean internode length was measured and found to be greater in older palms, but no statements were made regarding trends on a single stem, other than that internodal elongation ceased after exposure by leaf fall.

Wessels Boer (1965) observed Oenocarpus bacaba to have nodes spaced 30-50 cm apart, but did not mention any dimensional trend associated with position on the stem itself. Bannister (1970) found that leaf scars were very closely spaced in the uppermost few meters of trunk in Euterpe globosa: she attributed this to the influence of canopy light. From my field observations in Brazil, the development of a uniform and logical trend in nodal spacing was revealed.

If the palm stem is considered to be constructed of a quantity of cylinders affixed end to end in an upright fashion, then the volume contained within each internodal area can be determined. This may be used to measure any significant change that occurs over the entire length of the stem correlating with the age of the palm. A specimen of Oenocarpus minor subsp. intermedius was felled (Balick #968) and the spacing of nodes on the aerial stem was measured. This, when combined with the knowledge that the stem diameter is uniform throughout (in this case 7 cm), allowed computation of the individual values of volume for each internodal cylinder. On this particular specimen, a "middle-aged", healthy tree, 45 individual internodes were measured, including those still covered by leaf bases. The volume of these internodes, from the base (1) to just below the apex (45), is presented in Table 4.1.

Adding the values for the five basal internodes and comparing them with the values for the five apical internodes,

Table 4.1

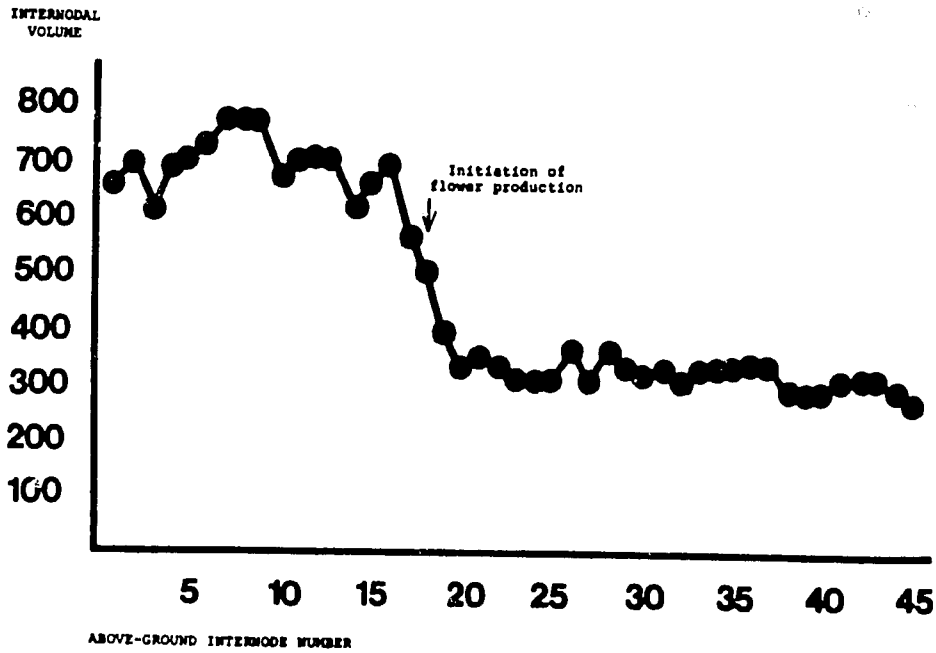
Internode Number	Length cm	Volume cm^3	Internode Number	Length cm	Volume cm^3
1.	17	654	34.	8.5	327
2.	18	692	35.	8.5	327
3.	16	615	36.	9	346
4.	18	692	37.	9	346
5.	18	692	38.	7.5	288
6.	19	730	39.	7.5	288
7.	20	769	40.	7.5	288
8.	20	769	41.	8	308
9.	20	769	42.	8	308
10.	17	654	43.	8	308
11.	18	692	44.	7.5	288
12.	18	692	45.	7	269
13.	18	692			
14.	16	615			
15.	17	654			
16.	18	692			
17.	15	577			
18*	13*	500*			
19.	10	384			
20.	8.5	327			
21.	9	346			
22.	8.5	327			
23.	8	308			
24.	8	308			
25.	8	308			
26.	9.5	365			
27.	8	308			
28.	10	385			
29.	8.5	327			
30.	8	308			
31.	8.5	327			
32.	8	308			
33.	8.5	327			

*Level of first inflorescence.

a sum of 3345 cm^3 vs. 1481 cm^3 is obtained, a difference of 1864 cm^3. Clearly, there is a trend towards shorter, less voluminous internodes over the life of the aerial portion of the Oenocarpus stem. While dissecting and measuring the stem, the node at which the first inflorescence had appeared, no. 18 was marked. When the individual internodal values are graphed against their position on the stem, a dramatic drop is demonstrated at the point of production of the first inflorescence (Figure 4.2). The weight of stem wood as calculated from a sample taken at the base of this specimen is 1.7 gm per cm^3. This is substantially greater than wood sampled just below the crown, found to be 1.0 gm per cm^3. The differential is due in part to the larger mass of fibrous sheaths surrounding the vascular bundles at the base of the stem.

In the absence of physiological studies, it may be hypothesized that, once floral initiation occurs in Oenocarpus, resources are diverted from volumetric stem production to bract, inflorescence and fruit production. The following growth pattern for the stem is envisioned: 1) seedling palm concentrating on its subterranean base; 2) young individual devoted to the extension of the aerial stem in competition for light, necessary nutrients and a position in the overall ecosystem; and 3) seed-bearing adult, reducing its vertical expansion both because of the limited height to which it can be supported by its base (Holttum 1955) and diversion of resources to the reproductive

Fig. 4.2. Changes in volumetric production of the aerial stem with age in *Oenocarpus minor* subsp. *intermedius*. Note that with the onset of inflorescence formation, stem production, as measured by internodal volume, is significantly reduced.


INTERNODAL VOLUME
800
700
600
500
400
300
200
100
Initiation of flower production
5
10
15
20
25
30
35
40
45
ABOVE-GROUND INTERNODE NUMBER

function. A general growth cycle for the Oenocarpus stem can be represented by a hypothetical diagram (Fig. 4.3). This supposition, based entirely on observations in Oenocarpus, may hold true for other palms. Observations on Jessenia bataua subsp. bataua in Ecuador have shown that, under cultivation, when fully exposed to light and fertilized presumably at a young age, the plant produces first inflorescences almost at ground level. In the forest, flowering does not occur until the trunk has reached a height of 5-10 meters.

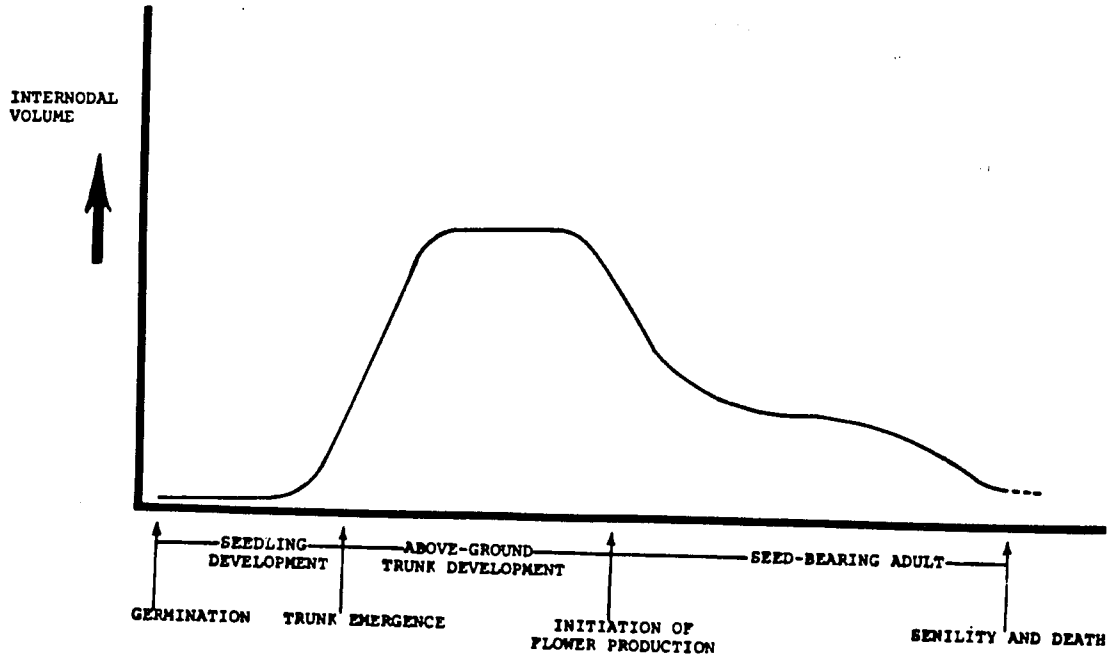
The change from wholly vegetative growth to purely reproductive growth as measured by the palms stem is poorly understood. Further in situ observations in this family may provide additional strategies to use in studying various genera. In this fashion, data might be compared for the diverse habits (eg. vining, caespitose, understory, "acaulescent", etc.) and a better understanding of growth might thus be available.

Leaf

The Oenocarpus-Jessenia leaf is pinnately compound and for descriptive purposes may be divided into three distinctive sections: sheath, petiole and rachis. The sheath is the tubular base of the leaf enclosing the stem, and usually is smooth, olive-green and variously lepidote.

In Jessenia, the ventral portion of the sheath is often conspicuously split, especially in adult leaves, and the whole leaf is easily pushed off by mechanical pressure exerted by the developing axillary inflorescence. Spines

Fig. 4.3. Hypothetical trends in volumetric stem production over the lifetime of the *Oenocarpus* palm. The highest rate of stem production is during initial development of the aerial trunk.


INTERNODAL VOLUME
SEEDLING DEVELOPMENT
ABOVE-GROUND TRUNK DEVELOPMENT
SEED-BEARING ADULT
GERMINATION
TRUNK EMERGENCE
INITIATION OF FLOWER PRODUCTION
SENILITY AND DEATH

line.the upper sheath margin. These spines are durable, resilient and knitting needle-like, up to 1 m long and extend to the petiole base (Fig. 4.4). Interspersed among these elongate spines is a smooth, soft, brown fibrous mass composed of hair-like strands each up to 20 cm long.

The sheath of Oenocarpus is somewhat thinner and more tightly clasping, although neither can be considered closed, forming a crownshaft as in Euterpe. Spines on the Oenocarpus sheath are of a single type: short (reaching a maximum of 20 cm long), wiry, and flexible, although the quantity and form varies in each species.

Because Oenocarpus and Jessenia lack protective regenerative stem tissue, the stem is vulnerable to mechanical injury, especially when young. Spines and related structures offer the stem of Oenocarpus and Jessenia some degree of protection. When a falling tree or similar accident removes a section of the sheath-spine cover, the soft exposed trunk is swiftly invaded by boring weevils. This was observed on Jessenia bataua in Manaus; within a few hours after cutting, swarms of weevils (Rhynchophorus palmarum) had located the fallen trunk and begun boring into the cut face.

Together with attached spines and fibrous mat, the sheaths persist along the trunk until the reproductive phase in the life cycle is reached. Then as if from some biological or mechanical cue uniformly communicated throughout the stem, the sheaths and spines cleanly absciss. Oenocarpus circumtextus, the only exception, retains the covering throughout

Fig. 4.4. An example of the spines produced by the sheath base and upper petiole margins in Jessenia bataua. The long, upright, durable, knitting needle-like spines protrude out from the mass of hair-like fiber (an unnumbered specimen collected from the Río Vaupés, Colombia).

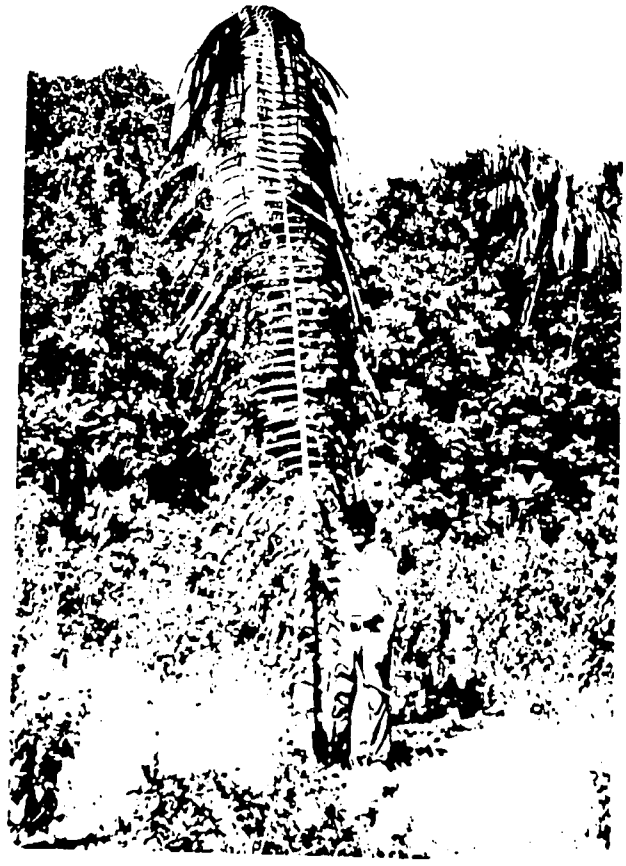
its lifetime. Among Jessenia populations in the rain forest, a pile of recently fallen spines lying at the base of a tree is always a sign of inflorescence initiation and development.

The petiole is the portion of the leaf axis devoid of pinnae, lying directly above the sheath. In this complex, its length usually is related to that of the rachis. In Oenocarpus mapora for example, the rachis ranges from (.95)2.8-5.5 m long, while the petiole ranges from 15-95 cm in length. The adaxial face is trough-shaped, the abaxial face convex. As previously noted, the base of the petiole may be somewhat fibrous. The petiole is variously lepidote, depending on the species, age and degree to which it has been exposed.

The rachis is the portion of the leaf axis on which the pinnae are inserted. In this complex it is usually green, deeply to shallowly trough-shaped at the base, 3-4-sided towards the center, trigonal towards the apex, longitudinally ribbed and variously lepidote throughout. Rachis length depends on height, condition and age of the tree. In a population studied in Manaus, the rachis of a young palm with a barely emergent trunk measured 6.7 m long, that of a palm with a 3.5 m trunk still concealed by fibers was 9 m long and the rachis of a senescent individual with a 16.25 m trunk was only 4.95 m long.

Jessenia has regularly inserted pinnae, borne in a single plane with variously opposite to alternate arrangement (Fig. 4.5). Those of Oenocarpus vary from regular insertion on a

Fig. 4.5. The gracefully arched pinnate leaf of *Jessenia bataua* showing the rachis and fibrous petiole base. (*Zarucchi et al. no. 1874*)



single plane to an irregular grouping at various angles to the rachis. Pinnae are narrowly to somewhat broadly linear-lanceolate at the center of the rachis (Jessenia and Oenocarpus Subgen. Oenocarpus) to ovate-oblong or oblong -lanceolate at the center of the rachis (Oenocarpus Subgen. Oenocarpopsis). Depending on the species, these are variously covered with waxes and trichomes (mostly abaxially). Both Oenocarpus and Jessenia have reduplicate pinnae.

Trichomes

A wealth of trichome diversity characterizes this complex. Different trichome types occur on the sundry morphological structures of an individual species: eg. leaves, rachis, bracts and inflorescence. Examination of these trichomes was accomplished with the aid of the dissecting, light and scanning electron microscopes. Several are described here, especially those having taxonomic importance.

In the Oenocarpus-Jessenia complex, trichomes exhibit a varying degree of complexity in form and construction. The simplest are short (ca. 75-100 μ long) stubby, hair-like, unicellular trichomes appressed to the abaxial surface of the pinna, between the intermediate veins. This type, occurring in many species of Oenocarpus, is sharply pointed with a base two to several times as wide as the apical portion. In some species, the bases are simple (Fig. 4.6A), while in others they possess small, secondary projections, indicating perhaps the early development (or degeneration?) of a stellate structure (Fig. 4.6B).

Fig. 4.6. Scanning electron microscope photographs of the abaxial pinna trichomes in Oenocarpus and Jessenia. A. Oenocarpus mapora subsp. mapora (Balick et al. 1188); B. Oenocarpus bacaba (Balick et al. 966); C. Oenocarpus mapora subsp. dryanderae (Anderson 18); D. Jessenia bataua subsp. bataua (Cook 73); E. Jessenia bataua subsp. bataua (Zarucchi et al. 1805); F. Jessenia bataua subsp. bataua (Zarucchi et al. 1805); G. Jessenia bataua subsp. bataua (Cook 73); H. Jessenia bataua subsp. bataua (Zarucchi et al. 1805). White scale bar is 100 μ long.

A second kind of pinna trichome studied consists of one to several narrow, flattened hair-like rays emerging from a central axis (Fig. 4.6 C). These rays are unicellular, twisted along their length (ca. 400-600 μ) sharply pointed at the apex and common on the abaxial lamina between the intermediate veins of Oenocarpus mapora subsp. dryanderae.

Jessenia bataua exhibits the most unusual pinna trichomes. This single species produces a range of multicellular trichomes from peltate to sickle-shaped or variously modified, each ca. 220-420 μ long. The peltate trichomes have a series of approximately five concentric rings of cells united so as to have an elliptic or ovate outline (Fig. 4.6 D). A doubly sickle-shaped trichome represents the splitting of one-half a peltate trichome and subsequent emergence of two tapering arms. Figure 4.6E illustrates this condition with Fig. 4.6F a probable intermediate form. A further derivation is the sickle-shaped trichome, where the scale completely opens up and the ribbing becomes somewhat linear or curved, rather than circular (Fig. 4.6G). There are many intermediate and aberrant stages in the trichomes of J. bataua. Perhaps the most unusual is a combination of the inrolled and linear forms (Fig. 4.6H) where part of the trichome appears to be more or less peltate but the other portion develops into a loriform structure with a split, multi-ribbed, twisted apex. This condition is believed to originate from the simpler forms, but forms not commonly seen in this species.

In addition to these several types, various other complex

trichomes develop on the undersurface of the primary and intermediate veins in Oenocarpus and Jessenia, but are not considered here, as their diagnostic utility, if any, is not presently understood.

The leaf rachis frequently is covered with maroon to grey indumentum. High magnification reveals these structures all to be simply variations on the same theme: basically flattened, lepidote scales with a number of twisted and curved, peripheral arms (Fig. 4.7). Some species appear more flattened (Oenocarpus distichus, Fig. 4.7A) while others possess a crinkled appearance (O. mapora subsp. mapora, Fig. 4.7B; O. mapora subsp. dryanderae, Fig. 4.7C; O. minor subsp. minor, 4.7D).

Of the taxa examined, trichomes of O. distichus appear to have the largest diameter (to ca. 1 mm) while those of O. minor subsp. minor have the smallest (to ca. 0.5 mm). The indumentum in J. bataua subsp. oligocarpa (Fig. 4.7E, G) appears somewhat more dense and the individual trichomes slightly larger than in subsp. bataua (Fig. 4.7F, H). These structures degenerate with time and exposure. Examination of the type of O. macrocalyx, taken from an older leaf, revealed breakage of the peripheral arms, general reduction in overall density and the formation of a grainy covering (perhaps from wax, dirt or pulverized trichomes).

The bract of a single specimen of Oenocarpus minor subsp. minor was examined, revealing a different type of trichome structure than that of either the rachis or pinna.

Fig. 4.7. Scanning electron microscope photographs of the indumentum on the leaf rachis. A. Oenocarpus distichus (Balick et al. 930); B. Oenocarpus mapora subsp. mapora (Balick et al. 1188); C. Oenocarpus mapora subsp. dryanderae (Anderson 18); D. Oenocarpus minor subsp. minor (Balick et al. 903); E. Jessenia bataua subsp. oligocarpa (Balick et al. 1231); F. Jessenia bataua subsp. bataua (Zarucchi et al. 1809); G. Jessenia bataua subsp. oligocarpa (Balick et al. 1231); H. Jessenia bataua subsp. bataua (Zarucchi et al. 1809). White scale bar is 100 μ long.

A
B
C
D
E
F
G
H

These trichomes appear as slender, horizontally ribbed, multicellular, spirally coiled, flattened strips. While no other bracts were examined with the SEM, light microscopy confirmed the presence of this type of multicellular trichome on at least one other species (O. bacaba).

The fibrous spines of Jessenia bataua are covered with trichomes near their insertion with the sheath. In this species, the mat of tissue that forms a basal webbing over the spines is thickly covered with brown, tufted hairs.

Taxonomic Implications

Studies of trichomes in the Oenocarpus-Jessenia complex revealed a significant amount of useful taxonomic information. Examples presented here must be considered only an introductory treatment with further studies certain to yield additional diagnostically useful data.

Sterile leaf material of any species in this complex may be assigned at least to genus, and in some cases to species and subspecies, on examination of the abaxial surface, as evidenced by the following simple key:

1. Abaxial surface of the leaf lacking trichomes . . . . . most Oenocarpus species
1. Abaxial surface of the leaf containing trichomes.
    2. Trichomes unicellular, slender and stubby or hair-like.
        3. Mostly elongate, frequently twisted, hair-like, tufted trichomes between the intermediate veins

. . . . . Oenocarpus mapora subsp. dryanderae

3. Mostly solitary, stubby trichomes between the intermediate veins . . . . . some Oenocarpus species, excepting the above subsp.

2. Trichomes multicellular, relatively broad, peltate to sickle-shaped.

4. Waxy covering present, mostly peltate to rounded trichomes weakly interspersed throughout the surface . . . . . Jessenia bataua subsp. oligocarpa

4. Waxy covering absent, peltate to sickle-shaped trichomes densely formed over the surface . . . . . Jessenia bataua subsp. bataua

Species in Oenocarpus are either completely devoid of trichomes or have mostly stubby, hair-like or modified, frequently tufted groupings sparsely formed throughout. The presence of the latter type between the intermediate veins of the abaxial surface separates O. mapora subsp. dryanderae (Fig. 4.8A) from the other species in Oenocarpus (Fig. 4.8B). In several species of this genus, tufted, hair-like trichomes can be found abaxially on the primary and intermediate veins. No pattern in their distribution or structure was discovered and hence the indumentum of the areas between the veins is felt more diagnostically useful.

Trichomes of Jessenia range from peltate to sickle-shaped and are also much broader than in Oenocarpus. While a hair-like Oenocarpus trichome may be ca. 12-20 μ wide, those of

Fig. 4.8. Basic types of abaxial pinna trichomes mentioned in the key: A. Unicellular, slender, elongate, twisted, hairlike and tufted--*Oenocarpus mapora* subsp. *dryanderae* (*Anderson 18*); B. Unicellular, sporadically dispersed, slender, solitary and stubby--*Oenocarpus bacaba* (*Balick et al. 1201*); C. Multicellular, broad, peltate to sickle-shaped, densely arranged--*Jessenia bataua* subsp. *bataua* (*Cook 73*); D. Multicellular, broad, mostly peltate, weakly interspersed over a waxy surface--*Jessenia bataua* subsp. *oligocarpa* (*Balick et al. 1231*). White scale bar is 100 μ long.

Jessenia range from 50 μ (sickle-shaped) to 130 μ (peltate) wide. An intermediate form not pictured here consists of a more or less peltate base with a single hair-like apex. This type has been found on a suspected hybrid between J. bataua and O. bacaba in the Colombian Llanos.

In Jessenia bataua, sterile leaf material can be separated into its component subspecies on the basis of the abaxial trichome density and the occurrence of a surrounding waxy covering. Jessenia bataua subsp. bataua (Fig. 4.8C) has a much higher density of trichomes than subsp. oligocarpa. Jessenia bataua subsp. oligocarpa in many cases consists of a greater percentage of peltate or rounded trichomes with a much thicker waxy coating (Fig. 4.8D). Calculations of the trichome density shown in the two photographs yields a figure of 44 trichomes per mm^2 in J. bataua subsp. bataua versus 12 trichomes per mm^2 in J. bataua subsp. oligocarpa. This particular distinction is less clear in interface populations of the two subspecies in Venezuela.

Trichomes on the rachis are less useful for diagnostic purposes. Overall density often depends on age and condition of the leaf. Limited comments based on size and complexity of individual trichomes are possible, but no overall taxonomic scheme can be proposed at this time. The large, grey, flattened trichomes of Oenocarpus distichus are distinctive, and these can easily be separated from other species such as O. minor and O. mapora, based on color, shape and size. As adequate material of several species in this complex is

lacking, further investigation at the present time would be difficult and probably unproductive.

Inflorescence

Oenocarpus and Jessenia both produce axillary inflorescences. During this study, a substantial effort was made towards understanding the morphological variation in the Oenocarpus-Jessenia inflorescence, because of its function in fruit production. Further, the unusually constructed and characteristic inflorescence in this complex separates it from all other palms of the Amazon Valley.

The Oenocarpus-Jessenia inflorescence consists of a flattened axis with simple rachillae inserted laterally and abaxially, so that the profile of an expanded or fruiting inflorescence reminds one of a horse's tail (Fig. 4.9). The hippuriform panicle, as it is called, easily distinguishes the complex from the closely related Amazonian arecoid genera Hyospathe and Euterpe. The primary inflorescence axes of Euterpe and Hyospathe have rachillae inserted on all sides rather than solely laterally and abaxially.

Two bracts, consisting of a prophyll and peduncular bract, enclose the inflorescence in Oenocarpus and Jessenia (Fig. 4.10). The bracts of all species are similarly constructed, except in O. circumtextus. The first (outer) bract on the axis, a somewhat flattened, bicarinate prophyll, has dentate margins. It serves as a protective sheath for the inflorescence and young peduncular (inner) bract during early development, and in J. bataua completely encloses these

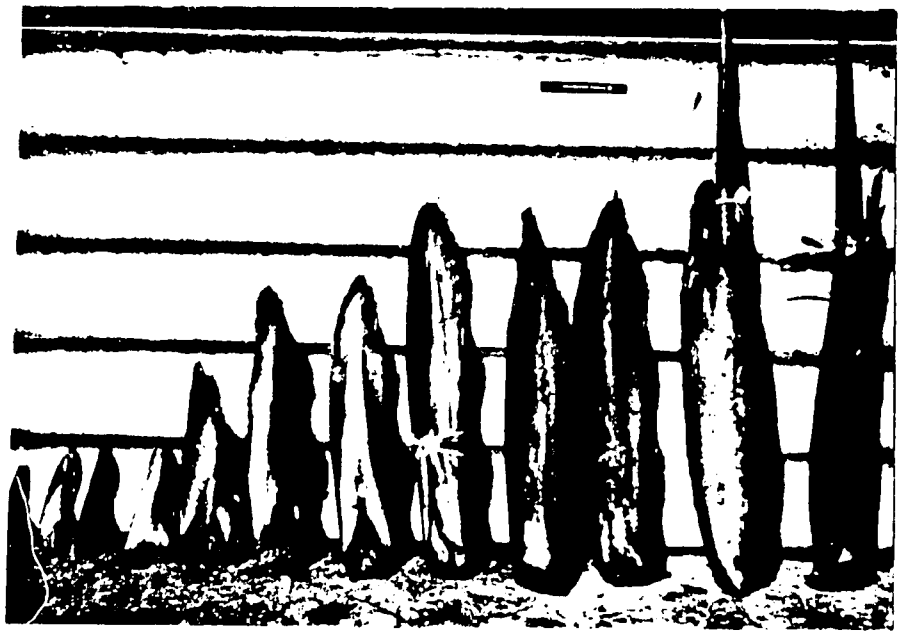
Fig. 4.9. The characteristic hippuriform panicle, in this case of Oenocarpus bacaba. From a specimen photographed near Mitú, Vaupés, Colombia.

Fig. 4.10. Young inflorescence of Jessenia bataua still enclosed by bracts. The specimen on the left consists of a prophyll and peduncular bract while that on the right is only a peduncular bract with the prophyll removed to show the narrowing of the base. Note the difference in size between these two specimens of similar age collected from the same locality. (Zarucchi and Balick 1793 (left); Zarucchi and Balick 1805 (right)).

other parts until it reaches ca. 30-60 cm in length (Fig. 4.11). When more or less fully expanded (expansion size variable depending on relative size of the inflorescence), the sharply pointed peduncular bract breaks through the prophyll apex and enlarges to adult size. The prophyll splits lengthwise along one or both of its flattened planar faces, leaving the dentate margins entire, and usually falls away before anthesis. The tubular, olive green, often lepidote peduncular bract, after reaching maximum size, swells in the middle due to mechanical pressure from the developing inflorescence. The enlarging panicle forces the peduncular bract to split along most of its length. After abscissing at its base, the bract falls from the tree, its protective function completed. The sole exception is O. circumtextus, where the peduncular bract splits only along about one-half of its length and persists. This bract is tapered at the base, corresponding to the narrowly elongate shape of the peduncle. In a dried state it is brown and longitudinally somewhat ribbed.

Prophyll and peduncular bract size vary according to the usual overall inflorescence length of a particular species. In Oenocarpus minor subsp. minor, with its relatively small inflorescence, prophyll and peduncular bract may range from 20-35 cm and 28-42 cm in length respectively. The prophyll of this subspecies may grow to two-thirds of the peduncular bract length. In Jessenia bataua the prophyll is usually only one-half as long as the peduncular bract; the

Fig. 4.11. Series of developing inflorescences removed from the leaf axils of two specimens of *Jessenia bataua*. Note that the peduncular bract cuts through the covering prophyll and elongates to the size shown in Fig. 4.9. Scale shown is 15 cm long. (*Zarucchi et al. 1838. 1839*).



prophyll may reach 0.75-1.0 m long and the peduncular bract 1.0-2.3 m long.

The axis of the inflorescence consists of a peduncle and branched rachis with simple rachillae. The peduncle is defined as that part of the inflorescence along which no branches are inserted. It is initially appressed to the stem and has a shallowly "U" shaped base that does not completely enclose the entire circumference of the trunk. The thin line of contact between the peduncular base and the stem is the entire support mechanism for an inflorescence that, when fruiting, may weigh up to 15-20 kg or more, as in Jessenia bataua subsp. bataua. All of the species have a short, stout, adaxially flattened peduncle, with the exception of Oenocarpus circumtextus, in which the peduncle is elongate and narrow, as might be expected from the tapered shape of the inner bract.

A variable number of lateral branches are inserted into the distal portion of the main inflorescence axis. The section of the main axis above the prophyll and peduncular bract scars is usually short and stout, adaxially flattened and has rachillae inserted only laterally and abaxially. The adaxial surface of the main axis differs in Oenocarpus and Jessenia. In Jessenia, the adaxial surface is frequently covered with warts or bumps, while in Oenocarpus is usually somewhat smooth.

The rachillae inserted into the inflorescence axis are first order branches. They are pendulous and proximally

covered with triads of flowers. Each triad includes a single pistillate and two staminate flowers (Fig. 4.12). Distally there are pairs of staminate or solitary staminate flowers through abortion of the pistillate flower in a triad. In Jessenia, the rachilla apex may be a slender sterile extension ca. 5-10 cm long, tipped by one or more staminate flowers or rudimentary buds. In Oenocarpus, this apical extension is either sterile, or entirely covered with densely congested staminate flowers. Burret (1928) considered the form of the rachilla apex--either attenuate or bluntly pointed--as diagnostically important in Oenocarpus. I am inclined to give lesser importance to this seemingly variable character.

The inflorescence is protandrous, the pistillate flowers opening a minimum of several weeks after anthesis of the staminate flowers. When the pollen is shed, it adheres to the rachillae and turns red with time, a phenomenon especially obvious in species of Oenocarpus. Fruits develop only along the proximal portion of each rachilla. In Jessenia bataua, the two subspecies usually differ in percentage of an individual rachilla axis occupied by pistillate flowers or fruits. Rachillae of J. bataua subsp. bataua ordinarily have pistillate flowers, fruits or scars from abscissed pistillate flowers along 40-60% of their length, while those of subsp. oligocarpa usually are covered by only 10-15%. A rare exception to this is the entirely staminate inflorescence that can develop in any member of the complex.

Aside from the prophyll and peduncular bracts, a number

Fig. 4.12. A portion of the rachilla of *Jessenia bataua* showing the floral triads of 1 pistillate (P) and 2 staminate (S) flowers. The section of the rachilla distal to this is entirely covered with staminate pairs (or solitary staminate flowers) through abortion of the central pistillate flower, or the axis lacks flowers entirely (*Zarucchi et al. 1838*).

p
s
7
8
9
10
11

of other bracts are present on the inflorescence. Small, flat, triangular, scale-like fertile bracts subtend rachillae. On the flattened adaxial face, the bracts cover sites of aborted rachillae. In Jessenia bataua, small, triangular, pointed bracts subtend pairs of staminate flowers on the distal portion of the rachis. This character is especially evident in J. bataua subsp. oligocarpa, and can be used to distinguish it from subsp. bataua with its less obvious, blunted bracts.

Both staminate and pistillate flowers are subtended by a series of obscure bracteoles. When the flowers are still attached, these bracteoles are not apparent. With abcission of the flower, one to several small, more or less triangular bracteoles can be observed along the periphery of the floral scar, especially evident at the sites of pistillate flower insertion. Bracteoles of staminate flowers frequently deteriorate after floral abcission, and are difficult to locate. While varying somewhat in shape, these bracteoles are present on all species of Oenocarpus and Jessenia.

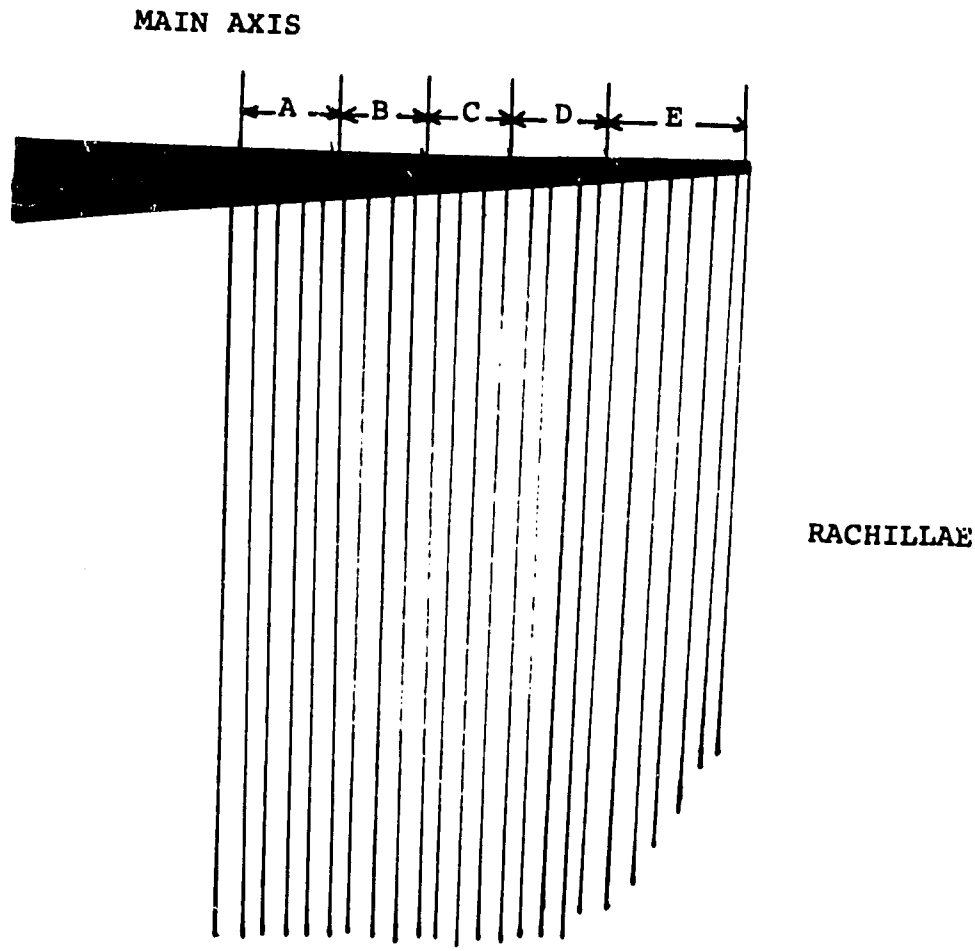
The inflorescence characteristic to these two genera appears to be derived from a Euterpe-like ancestor. In the closely related genus Euterpe, the peduncle is short and thin with an elongate axis bearing erect rachillae inserted on all sides over its entire length. Oenocarpus and Jessenia lack branches along the adaxial surface of the main inflorescence axis. Instead, a series of triangular bracts subtend the sites of aborted rachillae, providing evidence for an

ancestral inflorescence with uniformly distributed rachillae. Thus, the evidence suggests that the unusual hippuriform inflorescence of Oenocarpus and Jessenia has been derived through the loss of branches on the adaxial face of the main axis of the inflorescence.

The hippuriform panicle seems to have great structural advantage in the support of a larger weight of fruit. Erect rachillae on the adaxial face of the main axis, such as in Euterpe, require thickening if they are to bear increased fruit weights. On the other hand, pendulous rachillae such as in Oenocarpus and Jessenia must only be capable of tensile support, where reduction in girth and subsequent elongation is possible, allowing for a greater mass of fruits to be carried.

In a panicle from a tree in the Colombian Vichada, the 170 attached rachillae were divided into five groups of 34 each as diagrammed in Fig. 4.13. Letters indicate the position on the main axis of the inflorescence, A being closest to the stem and E at the apex. All rachillae were removed from the main axis and each measured for the following variables: overall rachilla length, length of attachment of floral triads (two staminate and one pistillate flowers), length of attachment of staminate pairs and solitary staminate flowers, and number of pistillate flowers. The results are presented in Fig. 4.14. Beginning at the base (proximal section) of the main axis, rachillae gradually decrease in length towards the apex. The number of pistillate flowers

Fig. 4.13. Breakdown of groupings for dividing the peduncle into sections to measure rachillae variation. Section A is closest to the peduncle attachment and section E is distal.


MAIN AXIS
A
B
C
D
E
RACHILLAE

per rachilla appears more or less consistent throughout, with a slight increase noted on the central portion of the main axis. The length of the rachilla occupied by floral triads increases from the base (A) to the middle (C), then decreases slightly towards the apex (E). The portion of the rachilla occupied by staminate pairs and solitary staminate flowers decreases towards the apex. It was also observed that rachillae inserted laterally were slightly shorter than those inserted abaxially, regardless of position (proximal vs. distal) on the axis. These observations and trends are not true for all inflorescences of Jessenia bataua. In some panicles, the number of pistillate flowers per rachilla decreases slightly in those rachillae inserted towards the apex of the inflorescence axis.

On the basis of data from the previously discussed panicle it would appear, with a constant or somewhat decreasing number of pistillate flowers per rachilla (counting from the base of the main axis to its apex), that fruit production could be expected also to be uniform or decrease exiguously in this direction, assuming identical reproductive efficiency throughout the first order branches of a single panicle. To investigate this point, an inflorescence of Jessenia bataua (Zarucchi et al. 1840A) was divided into three sections (proximal base (A); middle (B); rachis apex (C)), and ten rachillae removed from each of the three sections. The data, graphed in Fig. 4.15, indicate that a greater number of fruits formed on the rachillae

Fig. 4.14 Dimensions of rachillae and variation of component parts with regard to position on the main axis of the inflorescence in Jessenia bataua (measured from Balick and Hoyos 76-18).

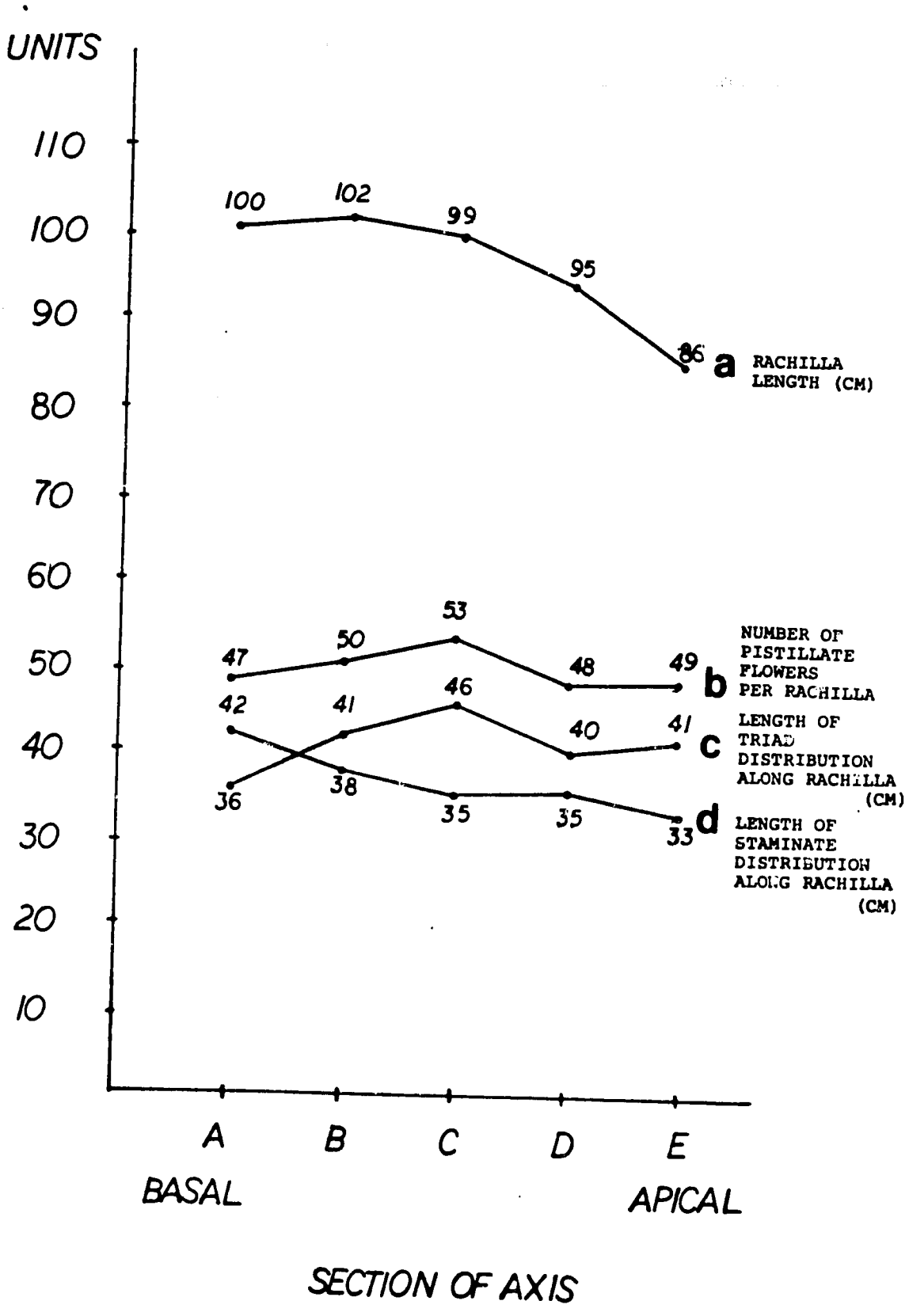
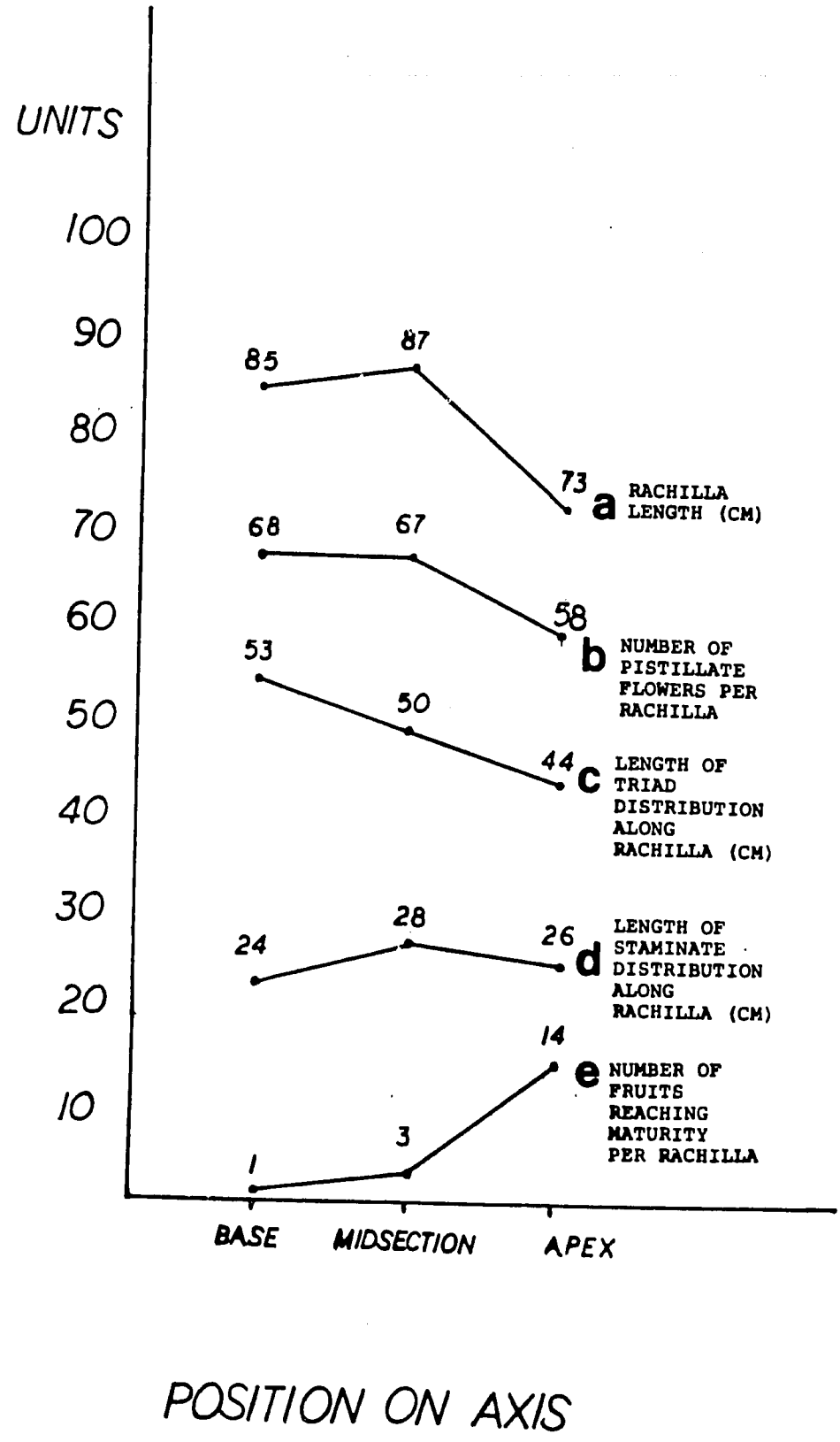

UNITS
110
100
90
80
70
60
50
40
30
20
10
100
102
99
95
86
a
RACHILLA LENGTH (CM)
47
50
53
48
49
b
NUMBER OF PISTILLATE FLOWERS PER RACHILLA
42
41
46
40
41
c
LENGTH OF TRIAD DISTRIBUTION ALONG RACHILLA (CM)
36
38
35
35
33
d
LENGTH OF STAMINATE DISTRIBUTION ALONG RACHILLA (CM)
A
B
C
D
E
BASAL
APICAL
SECTION OF AXIS

Fig. 4.15. Dimensions of rachillae and variation of component parts and fruit production with regard to position on the main axis of the inflorescence. (measured from Zarucchi et al. 1840A).


UNITS
100
90
80
70
60
50
40
30
20
10
85
87
73
a RACHILLA LENGTH (CM)
68
67
58
b NUMBER OF PISTILLATE FLOWERS PER RACHILLA
53
50
44
c LENGTH OF TRIAD DISTRIBUTION ALONG RACHILLA (CM)
24
28
26
d LENGTH OF STAMINATE DISTRIBUTION ALONG RACHILLA (CM)
1
3
14
e NUMBER OF FRUITS REACHING MATURITY PER RACHILLA
BASE
MIDSECTION
APEX
POSITION ON AXIS

closest to the apex of the main axis (C), while very few pistillate flowers developed into fruits on the basal rachillae (A). Other panicles must certainly be examined in order to make an unqualified statement about fruit development versus position on the axis. However, in this single example, while the rachillae towards the axis apex had fewer pistillate flowers, these developed a far greater number of fruits as compared to the rachillae at the base of the inflorescence axis. This phenomenon might have been caused by physiological factors, mechanical interference to pollination or unexplained developmental mechanisms elucidated only following further field work.

A great deal of variation was found in the distribution of pistillate flowers along the rachillae and in overall rachillae length in different panicles. Throughout my field work, special attention was given to Jessenia bataua, and in many herbarium collections made, rachillae were randomly selected from the middle of the inflorescence axis, preserved and examined. Table 4.2 contains measurements of rachillae of 13 panicles. A population from Mitú and vicinity in the Colombian Vaupés was the most intensively studied, and a great range of measurements was encountered. The variation exhibited by three panicles from a single tree (Balick 933, Pará, Brazil) should be noted in this context.

Staminate Flowers

Flowers in this complex are unisexual. Staminate flowers are sessile, asymmetrical, with three ovoid-lanceolate

Table 4.2
Variation in Rachillae Size and Construction
as Measured on Selected Panicles

(Given as mean + range)

Collection	Locality	Length of Triad Distribution per rachilla (cm)	Length of Staminate Distribution along rachilla (cm)	Number of pistillate flowers per rachilla	Approx. Length of Sterile section (cm)	N
Zarucchi et al.						
1809	Vaupés, Col.	36(31-41)	27(21-30)	50(40-58)	10	10
1811	Vaupés, Col.	37(33-41)	29(35-45)	52(47-58)	10	10
1838	Vaupés, Col.	60(49-68)	63(56-68)	78(66-89)	5	10
1840	Vaupés, Col.	49(36-58)	26(13-35)	64(45-77)	5-10	30
1841	Vaupés, Col.	42(40-46)	53(46-59)	73(63-78)	6	10
1849	Vaupés, Col.	61(49-68)	30(18-38)	81(58-85)	6	20
1850	Vaupés, Col.	62(52-72)	24(14-32)	84(68-93)	10-15	10
1851	Vaupés, Col.	46(41-45)	34(26-39)	58(50-68)	8	10
1874	Vaupés, Col.	51(34-62)	23(14-37)	90(71-104)	10	60
Balick et al.						
929	Pará, Braz.	41(25-55)	42(34-51)	58(41-76)	30	30
933A*	Pará, Braz.	32(11-44)	37(30-44)	47(9-69)	15	30
933B*	Pará, Braz.	19(2-29)	35(26-41)	34(2-60)	15	30
933C*	Pará, Braz.	24(8-35)	44(36-50)	31(5-57)	17	30

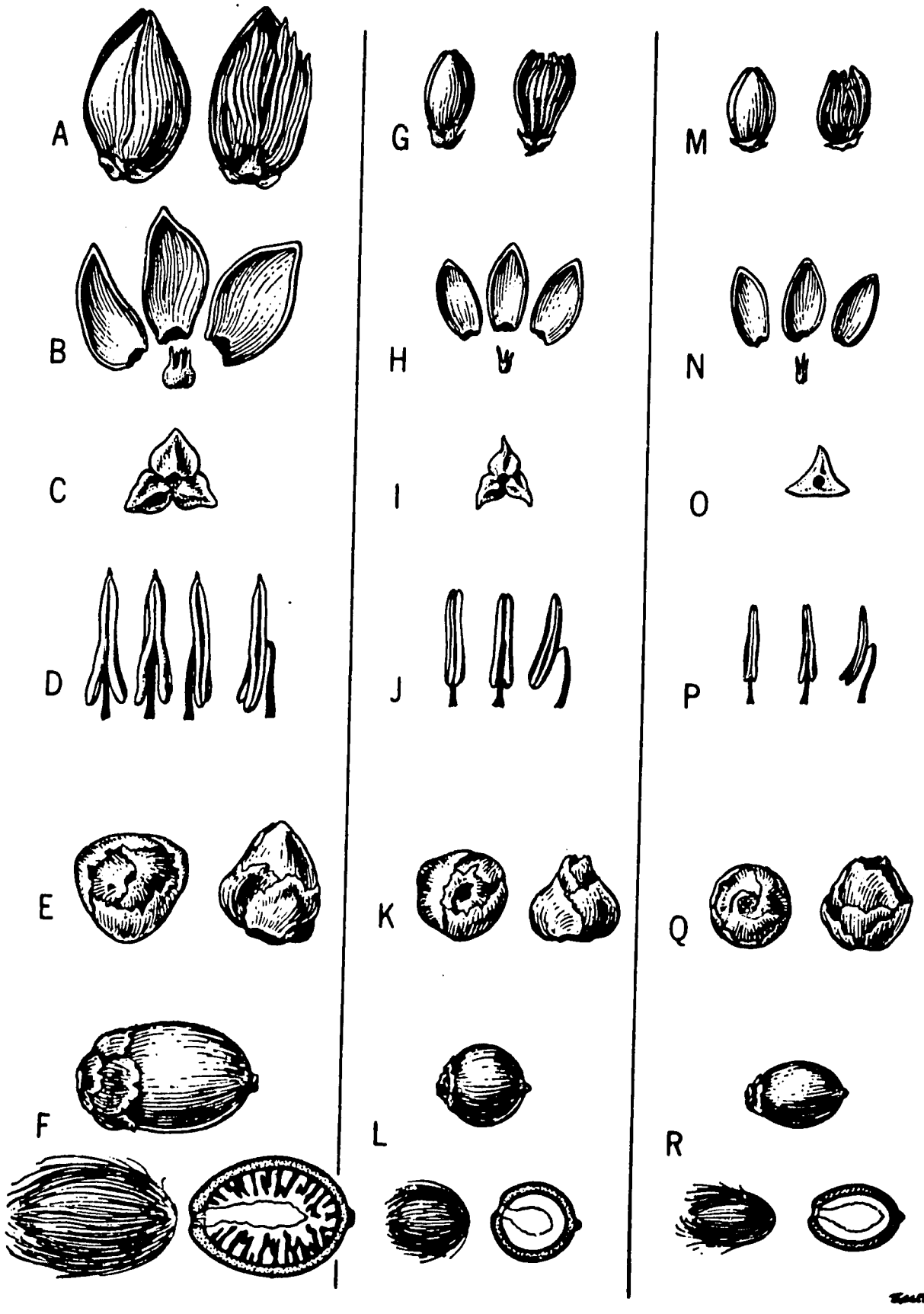
*Three panicles from the same tree.

to obtuse, acute sepals (Fig. 4.16 (A,B,G,H,M,N). Usually the sepals are imbricate, briefly connate basally or valvate (Fig. 4.16C,I). Oenocarpus circumtextus has the most unusual sepals, which are fused into a flattened triangle with concave sides (Fig. 4.16 O). In general, each sepal is thickened in the center, much thinner marginally, and they range from 1.0-1.75 mm in length.

Stamen number varies from 6 in Oenocarpus to (7-)9-20 in Jessenia. In the Jessenia populations, individual panicles usually possess a somewhat consistent stamen number, with a narrow range. Stamen number per flower in Colombian populations sampled varied from 8.8 ± 0.8 to 17.3 ± 1.16 (mean ± standard deviation, N=20), with most samples fallin near these two extremes.

In addition to stamen number, these two genera can usually be separated by morphology of both anther and filament. Filaments in Oenocarpus are strongly inflexed at the apex in bud (Fig. 4.16 J,P), while those of Jessenia usually are linear or rarely somewhat curved apically (Fig. 4.16 D). Stamens of Jessenia possess a definite connective extension beyond the locules of the anthers, a condition lacking in Oenocarpus. Both genera possess linear, versatile, dorsifixed anthers with two bilocular thecae. In Jessenia, the anther apex tapers to a fine point, while in Oenocarpus it is usually rounded or blunted. The two longitudinally extrorse dehiscent thecae can be separated far more easily in Oenocarpus than in Jessenia. In the latter species, the

Fig. 4.16. Flowers and fruits in the Oenocarpus -Jessenia complex. JESSENIA: Jessenia bataua subsp. bataua (Zarucchi and Balick 1851): A. Staminate flower, x 3.5; B. Petals and rudimentary ovary, x 3.5; C. Calyx, x 6; D. Stamens, x 5.5. Jessenia bataua subsp. oligocarpa (Balick et al. 1231): E. Pistillate flowers almost at anthesis, x 1.8. Jessenia bataua subsp. bataua (Zarucchi et al. 1851): F. Fruits, upper with epicarp and cupule intact, lower left showing fibrous seed covering, lower right a cross section showing elongate embryo and ruminate endosperm. SUBGENUS OENOCARPUS: Oenocarpus bacaba (Steyermark 56066): G. Staminate flower, x 3.5; H. Petals and rudimentary ovary, x 3.5; I. Calyx, x 6; J. Stamens, x 5.5; K. Pistillate flowers almost at anthesis, x 3.6. Oenocarpus bacaba (Black 47-1522): L. Fruits, x 0.9. SUBGENUS OENOCARPOPSIS: Oenocarpus circumtextus (Ducke 12305): M. Staminate flower, x 3.5; N. Petals and rudimentary ovary, x 3.5; O. Calyx, x 6; P. Stamens, x 5.5. Oenocarpus circumtextus (Huebner 41): Q. Pistillate flowers almost at anthesis, x 3.6; R. Fruits, x 0.9. Drawn by E. W. Smith.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R

connective strongly unites the thecae throughout their length. At the center of each staminate flower, a small pistillode is found (Fig. 4.16 B,H,N).

Pistillate Flowers

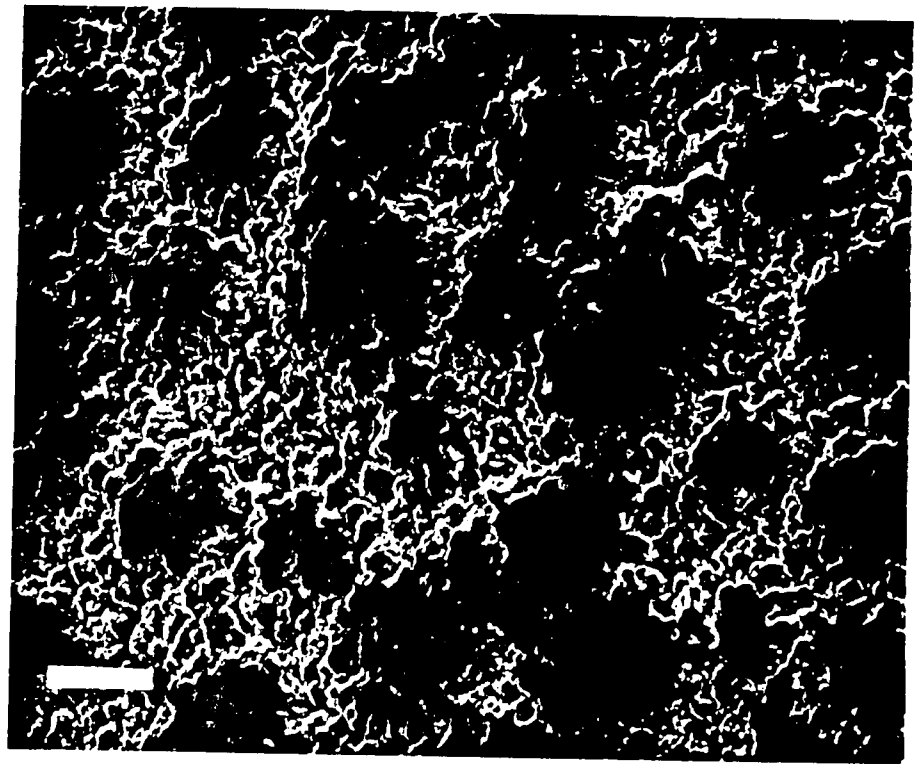
The sessile, symmetrical pistillate flowers (Fig. 4.16 E,K,Q) have three imbricate, fleshy, hooded-concave sepals enclosing the corolla in bud. These are suborbicular, longitudinally striate and often marginally fringed. Petals are similarly constructed, although not so fleshy when young. As with staminate flowers, the receptive pistillate flower has a slight fragrance. Both the sepals and petals thicken and enlarge during development of the fruit. Staminodes were not observed in pistillate flowers.

A basally attached, anatropous ovule develops within the trilocular, uniovulate gynoecium. In some species and in certain individuals suspected to be of hybrid origin, the ovule aborts. The style is very short and thick, and the three stigmas present are reflexed at anthesis and adaxially somewhat papillate.

Fruit

Fruits of Oenocarpus and Jessenia have the same construction (Fig. 4.16 F,L,R). They are globose to ovoid -ellipsoid in outline. The stigmatic residue is usually apical or slightly excentric. The smooth, minutely warted epicarp often is covered with a layer of wax (Fig. 4.17). The fleshy, variously colored (greenish, white, lavender)

Fig. 4.17. Scanning electron microscope photograph of epicarp of Oenocarpus bacaba fruit (Ledoux 56-1502). Note warted surface covered with waxy layer. White scale bar is 100 μ long.



mesocarp has a high oil content--in some species ca. 30% or more of dry weight. Fruits usually are one-seeded; occasionally in Jessenia bataua, two ovules form, but the resultant two-seeded fruit apparently lacks viable embryos. Flattened longitudinal fibers completely surround and sheath the seed. With removal of the epicarp and mesocarp, when rotted or eaten off by humans or animals for example, the fibers are strongly reflexed from the seeds. This condition appears to serve as an aid in germination and early growth --the seed anchoring itself to the ground with the reflexed fibers. The fibers also may afford protection from potential predators wishing to crush the seed for the oily embryo or eat off any remaining mesocarp. The endocarp, a very thin brown layer, encloses a homogenous (Oenocarpus) or ruminate (Jessenia), horny endosperm. The Oenocarpus endosperm is white; that of Jessenia is white with brown rays. The clavate embryo extends laterally along the length of the seed; up to ca. three-fourths the length in both Oenocarpus and Jessenia. The large mass of embryo tissue relative to overall seed size is unusual in the Palmae.

Depending on the species, fruits vary somewhat in size. Small fruited species include Oenocarpus bacaba, O. minor, O. circumtextus and O. distichus. In Oenocarpus, O. mapora subsp. dryanderae has the largest fruits, while those of Jessenia bataua are the largest and heaviest in the complex, some reaching a length of 4.0-4.75 cm and a weight of 15 gm or more. Because of interest in the fruit for oil production,

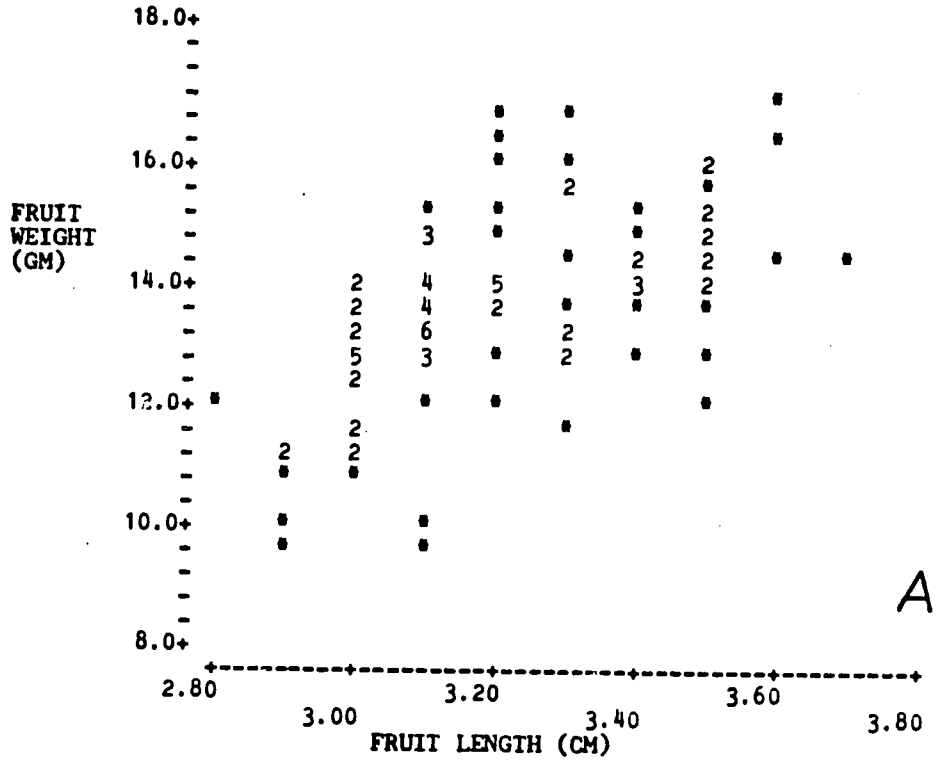
a large number of samples were measured and weighed. It was found that even in a single population there exists great variation in fruit. Fig. 4.18 illustrates the difference in size and weight between two fresh fruit collections of J. bataua from the same population in Pebas, Peru.

Measurements of the fruit (length x width) from each specimen of Jessenia bataua collected were made in the field. Some of these are presented in histogram form in Fig. 4.19. No geographical correlations can be deduced from these measurements. This variation in fruit size from tree to tree in any given population depends probably on factors such as age, health, genotype, drainage and other localized soil conditions, and density of trees per hectare.

The reproductive efficiency of a particular panicle is influenced by external factors, as well as by physiology and morphology. Estimates of reproductive efficiency in wild trees were made by counting numbers of mature or well developed fruits on randomly selected rachillae as indicated by pistillate flower scars (Table 4.3). The small number of panicles studied was a result of difficulties in sampling, since fruit usually tended to drop off when trees were felled.

The results from this one small area in the Vaupés of Colombia gives some idea of the range and limits of reproductive efficiency of trees in the wild. The highest percentage was determined by measuring all the rachillae and fruits from a single panicle on a particularly productive tree (#1840). Determination of how reproductive efficiency varies

Fig. 4.18. A comparison of length and weight between two samples of *Jessenia bataua* fruit, collected from two trees in the same population. The differences in fruit length and weight are a result of phenotypic plasticity, rather than indicative of specific or subspecific distinction. Asterisks represent a single value; numbers indicate quantity of fruits in a particular length-weight class. A. *Plowman 7311*, Pebas, Loreto, Peru. Length (average (cm) $\pm$ standard deviation, n = 100): 3.2 $\pm$ 0.20 Weight (gm): 13.6 $\pm$ 1.57. B. *Plowman 7312*, Pebas, Loreto, Peru, n = 102. Length (cm): 3.6 $\pm$ 0.15; Weight (gm) 11.3 $\pm$ 1.33.


FRUIT WEIGHT (GM)
18.0
16.0
14.0
12.0
10.0
8.0
2.80
3.00
3.20
3.40
3.60
3.80
FRUIT LENGTH (CM)
A

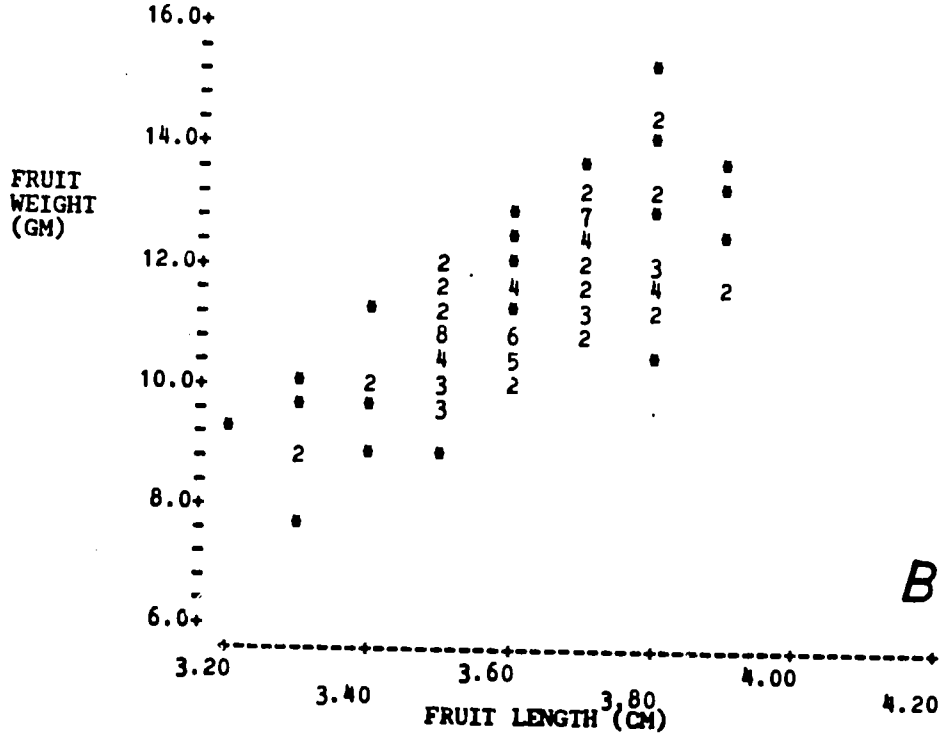

FRUIT WEIGHT (GM)
16.0
14.0
12.0
10.0
8.0
6.0
3.20
3.40
3.60
3.80
4.00
4.20
FRUIT LENGTH (CM)
B

Fig. 4.19. Histograms of fruit lengths from various populations of Jessenia bataua in the Vaupés and the Vichada of Colombia. Measurements of groups are given in cm (average ± standard deviation). Asterisks in G and H each represent two observations; in all other histograms each asterisk represents a single observation. Collections A-I are Zarucchi et al. numbers and J-M are Balick and Hoyos numbers. A. 1793, 3.04 ± 0.11; B. 1809, 2.57 ± 0.09; C. 1811, 2.70 ± 0.23; D. 1813, 3.08 ± 0.16; E. 1814, 3.37 ± 0.13; F. 1838, 3.26 ± 0.18; G. 1840, 3.09 ± 0.22; H. 1842, 3.55 ± 0.09; I. 1851, 3.11 ± 0.13; J. 76-18, 3.58 ± 0.15; K. 76-20, 2.52 ± 0.12; L. 76-21, 2.87 ± 0.20; M. 76-23, 3.03 ± 0.12.

A

middle of interval	number of observations	
2.80	4	******
2.85	0	
2.90	8	********
2.95	0	
3.00	48	**********
3.05	0	
3.10	22	**********
3.15	0	
3.20	14	**********
3.25	0	
3.30	4	******

B

middle of interval	number of observations	
2.50	27	**********
2.60	14	**********
2.70	6	******
2.80	3	***

C

middle of interval	number of observations	
2.1	1	*
2.2	0	
2.3	4	******
2.4	1	*
2.5	31	**********
2.6	10	**********
2.7	14	**********
2.8	11	**********
2.9	2	**
3.0	22	**********
3.1	1	*
3.2	1	*

D

middle of interval	number of observations	
2.6	1	*
2.7	1	*
2.8	10	**********
2.9	10	**********
3.0	17	**********
3.1	22	**********
3.2	27	**********
3.3	11	**********
3.4	1	*

E

middle of interval	number of observations	
3.00	2	**
3.05	0	
3.10	4	***
3.15	0	
3.20	14	**********
3.25	0	
3.30	24	**********
3.35	0	
3.40	25	**********
3.45	0	
3.50	30	**********
3.55	0	
3.60	2	**

F

middle of interval	number of observations	
2.7	2	**
2.8	0	
2.9	2	**
3.0	4	****
3.1	12	**********
3.2	29	**********
3.3	11	**********
3.4	17	**********
3.5	9	**********
3.6	4	****

G

each * represents 2 observations

middle of interval	number of observations	
2.3	1	*
2.4	2	**
2.5	4	***
2.6	4	**
2.7	0	
2.8	7	****
2.9	12	******
3.0	51	**********
3.1	41	**********
3.2	43	**********
3.3	19	**********
3.4	16	********
3.5	7	****
3.6	1	*

H

each * represents 2 observations

middle of interval	number of observations	
3.20	1	*
3.25	0	
3.30	2	**
3.35	0	
3.40	17	**********
3.45	0	
3.50	87	**********
3.55	0	
3.60	44	**********
3.65	0	
3.70	24	**********
3.75	0	
3.80	2	**

I

middle of interval	number of observations	
2.80	3	***
2.85	0	
2.90	5	*****
2.95	0	
3.00	24	**********
3.05	0	
3.10	30	**********
3.15	0	
3.20	24	**********
3.25	0	
3.30	9	**********
3.35	0	
3.40	5	*****

J

middle of interval	number of observations	
3.30	8	********
3.35	0	
3.40	8	********
3.45	0	
3.50	26	**********
3.55	0	
3.60	23	**********
3.65	0	
3.70	21	**********
3.75	0	
3.80	13	**********
3.85	0	
3.90	1	*

K

middle of interval	number of observations	
2.30	9	**********
2.35	0	
2.40	19	**********
2.45	0	
2.50	36	**********
2.55	0	
2.60	24	**********
2.65	0	
2.70	8	********
2.75	0	
2.80	4	****

L

middle of interval	number of observations	
2.4	1	*
2.5	2	**
2.6	11	**********
2.7	16	**********
2.8	18	**********
2.9	16	**********
3.0	18	**********
3.1	8	********
3.2	7	*******
3.3	2	**
3.4	1	*

M

middle of interval	number of observations	
2.70	1	*
2.75	0	
2.80	7	*******
2.85	0	
2.90	12	**********
2.95	0	
3.00	35	**********
3.05	0	
3.10	26	**********
3.15	0	
3.20	17	**********
3.25	0	
3.30	2	**

in the complex throughout South America and the identification of factors that could result in higher yields under cultivation should be given high priority in further domestication studies of these palms.

Table 4.3
Reproductive Efficiency in *Jessenia bataua*

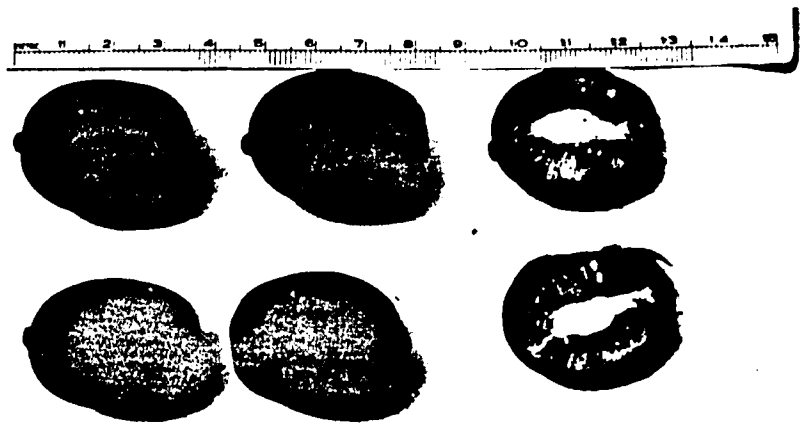
Tree #	Fruits Collected ÷ Pistillate Flowers Produced	Reproductive Efficiency	Rachillae Sample Size
Zarucchi et al.			
1840	1143/7863	14.5%	133
1849	186/1539	12.0%	20
1850	59/1721	3.4%	20
1851	84/1166	7.2%	20

Double-seeded fruits, while rare in this complex, were found in populations of *Jessenia bataua* in the Colombian Vaupés and Vichada (Fig. 4.20). In an entire fruit crop from a single panicle, 82 of the 1108 fruits contained two seeds. The double-seeded fruits had smaller embryos and endosperm per seed, but presented a greater surface area (and amount of oily mesocarp) than fruits with single seeds (Fig. 4.21). This phenomenon was observed exclusively on young trees with recently shed spinose coverings, an indication of the beginning of full inflorescence production. No middle-aged or senescent palms with double-seeded fruits were ever found, indicating possibly that this condition is limited to the

Fig. 4.20. Specimens of both double- and single-seeded fruits of Jessenia bataua from the same tree. Note the smaller embryo in double-seeded fruits relative to the single seeded fruits. (Zarucchi et al. 1850).

Fig. 4.21. Single-seeded fruits, the more common condition in Jessenia bataua (Zarucchi et al. 1814).

1850



1814

early seed-bearing years of the life cycle of Jessenia bataua.

Cytology

A number of root tips were collected from seedlings grown in Cambridge and prepared according to Radford et al. (1974), but counts could not be obtained. An attempt was made at mailing pollen from the field to the laboratory (see Read 1965) for germination on a colchisine-lactose medium. However, the delay in getting material from the rain forest to a city where it might be mailed was apparently too great, as none of the 10-15 samples sent in this way germinated.

Read (pers. comm.) indicated that palm chromosome numbers rarely vary between closely related genera, and thus no numerical difference could be expected between Oenocarpus and Jessenia. According to Moore (1973), the Euterpe alliance, of which Oenocarpus and Jessenia are members, has a chromosome complement of n=18.

Pollen

Martius (1823), described the pollen of Oenocarpus (in the broad sense) as yellow, uniformly globose-elliptic, longitudinally sulcate and fissured. In his classic text Pollen Morphology and Plant Taxonomy, Erdtman (1952) offered a few comments and illustrations of J. bataua pollen. More recent studies by Thanikaimoni (1970) of the entire family listed both qualitative and quantitative observations for

Oenocarpus and Jessenia. Sowunmi (1972) studied 120 genera of palms and classified them according to pollen morphological groupings. Jessenia was listed in the Arecoideae, subgroup Areca, Roystonea type. She characterized this particular subgroup on the basis of monocolpate grains, semitectate sexine, reticulate tectum and as lacking processes. The Roystonea type, consisting of Cyphophenix, Normanbya, Manicaria, Jessenia and Roystonea, has an irregular sexine pattern and minutely reticulate or punctate to vermiculate to negatively reticulate tectum. No mention was made of Oenocarpus in this investigation.

Pollen was acetolysed (Erdtman 1952) and examined also with the aid of the AMR 1000 Scanning Electron Microscope (SEM) of the Museum of Comparative Zoology at Harvard University. The following notes on the two genera have been compiled from both laboratory observations and the literature.

Oenocarpus

Solitary, heteropolar grains, monosulcate (elliptic in outline) or trichotomosulcate (somewhat triangular in outline) in polar view. Longest axis 38-68 μ (acetolysed samples). Sulcus narrowly elliptic (monosulcate) or triradiate (trichotomosulcate). Tectum undulate, perforate, vermiculate to faveolate.

Jessenia

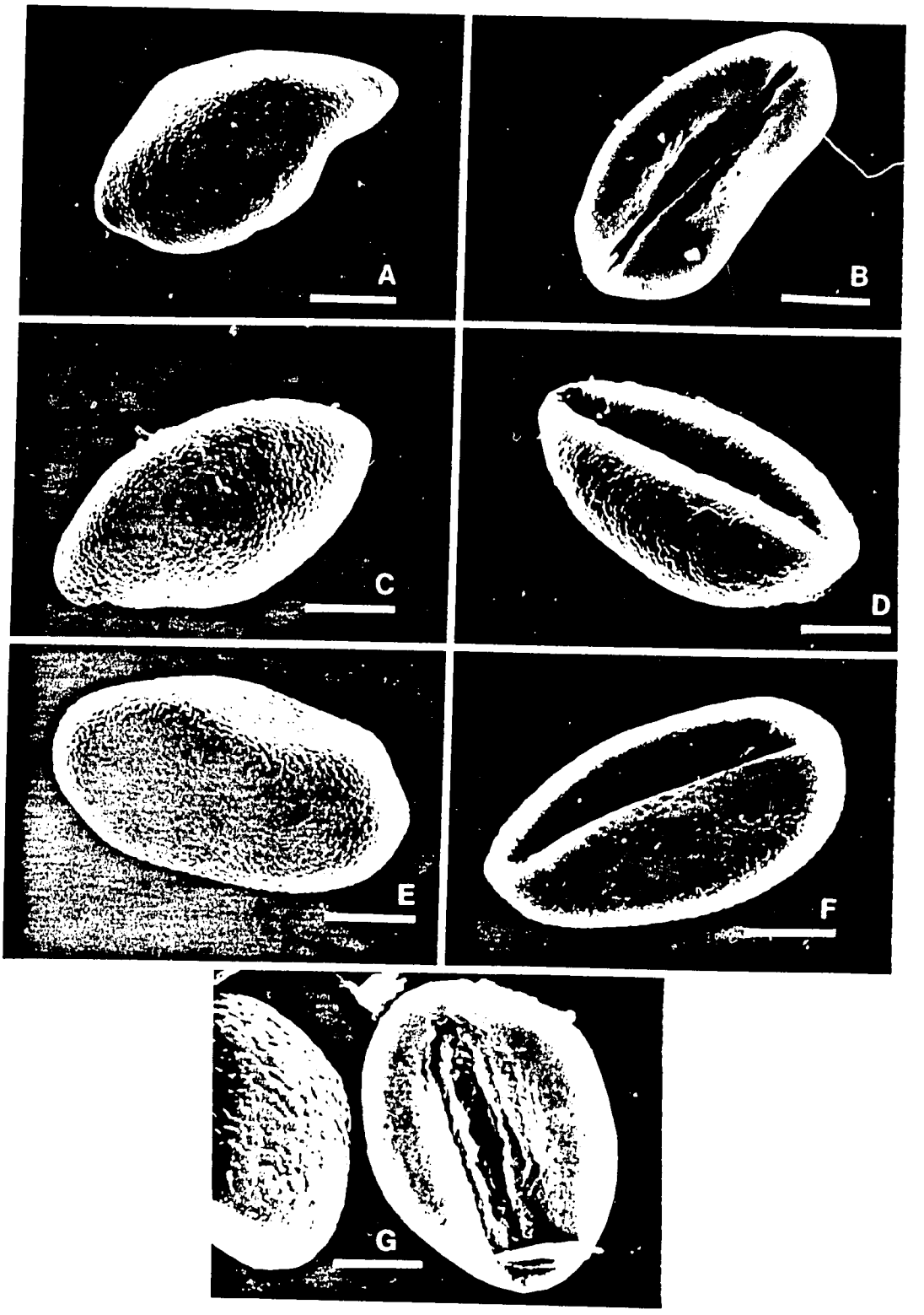
Solitary, heteropolar grains, usually monosulcate (elliptic to somewhat globose elliptic in outline) or rarely trichotomosulcate (somewhat triangular in outline) in polar

view. Longest axis 33-57 μ (acetolysed samples). Sulcus narrowly elliptic (monosulcate) or triradiate (trichotomotosulcate). Tectum undulate, perforate, vermiculate to foveolate.

General shape and sculpturing can be seen from the SEM photographs. The grains have different ornamentation in the distal and proximal polar views. In Jessenia bataua subsp. bataua, the outline is more narrowly elliptic than in the globose-elliptic grains of J. bataua subsp. oligocarpa (Fig. 4.22 E-G). Furthermore, the pollen of J. bataua subsp. bataua contains a few small grana imbedded on the inside of the apices of the sulcus. These grana are not clearly formed in J. bataua subsp. oligocarpa nor in the species of Oenocarpus examined. The proximal polar surface pattern in J. bataua subsp. oligocarpa (Fig. 4.23A) is somewhat more fused, having broader vermiculate streaks and apparently fewer perforations than J. bataua subsp. bataua (Fig. 4.23 B). The distal polar surface shows much less sculpturing, mostly of the foveolate type. This variable pattern is seen also in Oenocarpus mapora subsp. mapora (Fig. 4.22 A,B) and O. circumtextus (Fig. 4.22 C,D).

A magnified view of the proximal polar surface in Oenocarpus mapora subsp. dryanderae (Fig. 4.23 C) and O. circumtextus (Fig. 4.23 D) reveals an important difference. Pollen of the first named species generally has a vermiculate surface like that in Jessenia, although the streaks are somewhat thinner. Examination of additional species (O. bacaba,

Fig. 4.22. Proximal polar and distal polar views of Oenocarpus and Jessenia pollen. A-B. Oenocarpus mapora subsp. mapora (Balick et al. 1157); C-D. Oenocarpus circumtextus (Ducke 12305); E-F. Jessenia bataua subsp. bataua (Zarucchi et al. 1851); G. Jessenia bataua subsp. oligocarpa (Wessels Boer 1514). White scale bar is 10 μ long.


A
B
C
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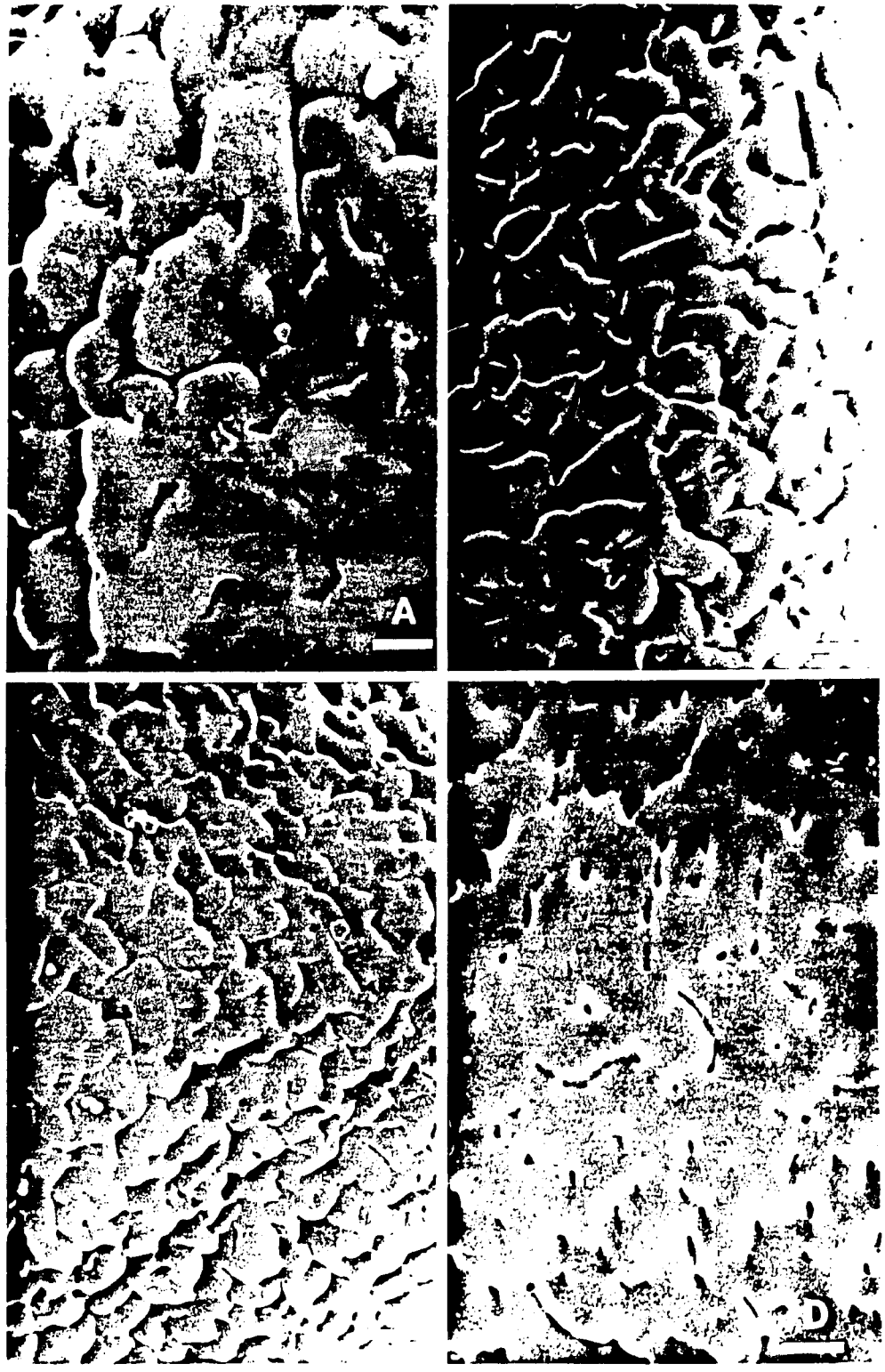
E
F
G

Fig. 4.23. Magnified view of the proximal polar surface of Oenocarpus and Jessenia pollen. A. Jessenia bataua subsp. oligocarpa (Wessels Boer 1514); B. Jessenia bataua subsp. bataua (Zarucchi et al. 1851); C. Oenocarpus mapora subsp. dryanderae (Anderson 18); D. Oenocarpus circumtextus (Ducke 12305). White scale bar is 1 μ long.


A
D

O. minor) confirmed the widespread presence of a vermiculate surface in Oenocarpus. However, the proximal polar surface of O. circumtextus is foveolate, with distinct, small, irregularly circular to elliptic pits, ca. 0.25-0.5 μ long, to channeled or mildly vermiculate. Consequently, palynological evidence appears to offer some support for a taxonomic separation of O. circumtextus from the other species in the genus (see Chapter 5).

Table 4.4 presents data from Thanikaimoni (1970) comparing pollen shape, aperture type, overall size and ektexine dimensions in acetolysed grains of Oenocarpus and Jessenia. The range in size and shape of pollen in the complex is evident from the table. Pollen of J. bataua subsp. oligocarpa is smaller than that of subsp. bataua, while in O. circumtextus it is noted to be far larger than that of the other species of Oenocarpus studied. With the small number of specimens sampled, limitations clearly exist in any use of this table. In addition, the SEM photographs do not confirm certain measurements: for example, the great differential in size between O. circumtextus and the other species. My own measurements on four specimens of J. bataua show the following lengths for acetolysed pollen (mean ± standard deviation, N=25): Zarucchi et al. 1851 (Vaupés) 43.08 μ ± 2.65; Balick and Hoyos 76-18 (Vichada) 43.32 μ ± 3.22; Balick and Hoyos 76-20 (Vichada) 46.32 μ ± 4.18; Balick and Hoyos 76-22 (Vichada) 49.02 μ ± 2.69.

Table 4.4

A Comparison of the Pollen in Some Members of the *Oenocarpus*-*Jessenia* Complex*

Species	Shape	Length along longitudinal axis in polar view (μ)	Longitudinal diameter in polar view (μ)	Transversal diameter in equatorial view (μ)	Maximum tectum thickness (μ)	Maximum bacula height (μ)	Maximum thickness of foot layer (μ)
J. bataua[1] subsp. *bataua*	monosulcate rarely trichotomosulcate	48-57	33-45	20-40	1.0	0.8-1 0	0.7
J. bataua[2] subsp. *oligocarpa*	monosulcate	33-38	26-30	22-25	1.0	0.8	0.7
O. bacaba[3]	always trichotomosulcate	38-40	40	30-35	1.0	0.5	0.5
O. circumtextus[4]	monosulcate	60-68	40-55	30-35	0.6	1.0	0.4
O. distichus[5]	monosulcate sometimes trichotomosulcate	40-50	30-37	23-30	0.6	0.5	0.5
O. sp.[6]	majority trichotomosulcate	40-48	30-45	22-32	0.8	0.8	0.6

1. Huebner 34 (B): Coelho and Prance 9532 (INPA); without collector (COL).
2. Wessels Boer 1933 (U).
3. Steyermark 58066 (F).
4. Ducke 12305 (U).
5. Hopp 15, without herbarium.
6. Coelho sn, INPA #1168 (INPA).

*From Thanikaimoni (1970)

Germination and Early Growth

Seeds in this complex have hypogeal, adjacent ligular germination. The cotyledon does not grow away from the seed; rather, the seedling develops while still closely attached to the seed. The seedling emerges from a cotyledonary ligule. Concurrently, a single, narrow, primary root grows from the side of the cotyledonary ligule. A wider root forms, growing downward from the plumule base to replace the primary root. Later, side roots emerge from the compressed nodal areas of the underground stem to supplant this first large root. Tomlinson (1960b) speculated that this kind of germination was characteristic of palms inhabiting dark, moist environments where seedlings do not require protection by underground burial, a speculation which is indeed true for Oenocarpus and Jessenia.

According to Braun (1968), Jessenia bataua requires 20-40 days to germinate. A high percentage of fresh seed germinates. Jordan (1970) found 80 and 99% germination after 79 and 83 days respectively, in J. bataua and 88 and 97% after 74 and 67 days for Oenocarpus mapora. During my field work, some seed lots collected in the Amazon Valley and sent to the Palm Society Seed Bank in Florida sprouted in high numbers, while others appeared to suffer and deteriorate during transport. Well packed, Oenocarpus and Jessenia seeds, cleaned of the epicarp and mesocarp, wrapped in slightly moistened newspaper and sealed in plastic bags, were found to survive a maximum of six weeks from collection,

through shipment and planting. As the palms grow in what is a relatively favorable, constantly moist environment, there appears to be little advantage in developing a complex or delayed system of germination.

During beverage production, fruits are placed in warm water ($50^{o}C+$) for a half hour or so to soften and remove the epicarp and mesocarp. When fruits are not as ripe as desired, they may be soaked in water overnight at room temperature, to make the epicarp pliant. While preparing the drink, the fibrous seeds are cleaned of their oily content, strained out of the mix and discarded. Anecdotal information offered by Indians in the Vaupés and Vichada of Colombia revealed that this practice of soaking seeds (especially in warm water) hastens germination and growth, resulting also in an increase of the overall percentage of fruits sprouting per seed group.

While various types of pre-treatments are known for palm seeds (Loomis 1958), I was unable to find reference to such a positive effect from the combination of warm water and pericarp removal. Clearly an increase in germination and early growth rate of this slow developing palm would have important implications for cultivation.

In an experiment devised to test this supposition, five groups, of 50 Jessenia bataua seeds each, were collected and planted in germination boxes in Manaus, after being given the following treatments: 1) control--no treatment, with epicarp and mesocarp left intact; 2) soaked in water at room temperature for one week with epicarp and mesocarp left

intact; 3) epicarp and mesocarp removed, seeds then soaked in water at room temperature for one week; 4) soaked in warm water (ca. 50°C+) for one-half hour, epicarp and mesocarp left intact; 5) epicarp and mesocarp removed and seeds soaked in warm water for one-half hour.

After 52 days the germination and growth data were tabulated (Table 4.5).

Table 4.5
Germination and early growth of *Jessenia bataua* seed following various treatments

Seed lot and Treatment	Percentage Germination	Percentage with first bifid leaf apparent
1. Control--no treatment, epicarp and mesocarp left intact.	42	4
2. Cool water soak--epicarp and mesocarp left intact.	72	46
3. Cool water soak--epicarp and mesocarp removed.	98	92
4. Warm water soak--epicarp and mesocarp left intact.	22	0
5. Warm water soak--epicarp and mesocarp removed.	98	90

This simple *in vitro* test demonstrated indigenous observations to be correct. After a period of time when untouched seeds in the forest presumably would have shown a low germination rate with few seedling leaves actually produced, seeds used in beverage production (or gnawed or

passed through the digestive tract of an animal) and subsequently discarded in the surrounding forest would have an increase in both germination and early growth rate. It could be argued, therefore, that the oily mesocarp layer, when offered to humans or animals as an attractive food, is also of adaptive value in guaranteeing better germination and growth for the seed.

The appearance of a small seedling leaf with a green lamina follows the production of the ligule and bladeless plumular sheath. Tomlinson (1960c) used the term "eophyll" (from the Greek "early leaf) to describe this first blade and the similar few that follow. He assigned taxonomic importance to the morphology of the eophyll and classified them as entire, bifid or compound. Seeds of Oenocarpus and Jessenia produce bifid or deeply emarginate eophylls. The two genera can be separated from each other on the basis of the abaxial surface of the eophyll, which is either waxy-white in Oenocarpus or has peltate to sickle-shaped trichomes in Jessenia--and distinguished from other Amazonian palms by the presence of the seed with its flattened fibrous cover and large embryo.

Growth and Bioenergetics

Palms occurring naturally in forest stands exhibit variety in size and form, depending on age and environment. Natural populations of Jessenia bataua were carefully studied in the Reserva Florestal Ducke near Manaus and a number of life stages delimited. These life stage classifications

concern observations on a species throughout its lifetime: conclusions are drawn on how various components (eg. root, trunk, inflorescence and leaf) vary with time. Banninster (1970) referred to these as size classes in her study of Euterpe globosa (= Prestoea montana), delimiting four such categories: seeds, seedlings (to 0.5 m tall), young trees (0.5-6.0 m tall) and mature trees (over 6.0 m tall). In view of the plasticity in Oenocarpus and Jessenia and the inability to make absolute correlations regarding size and age, these groups are here called "life stages."

Six major life stages were identified in Jessenia bataua, and these are divided into a total of 11 stages and substages. Certain difficulties arose when attempting to compile detailed quantitative data for the groups. Because of its size (often 25-30 m tall), the palm is rather awkward to work with, and thus it became necessary to estimate parameters in some calculations. While these may or may not be entirely accurate, they are nevertheless the best possible under existing circumstances. In studies of the adult root, it was impossible to dig into the ground beyond a depth of .75 m, due to inundation by the water table. Consequently, little was learned about the adult root system in this species. Furthermore, a large accumulation of unanalyzed data and specimens were destroyed as the result of a press fire in Manaus. To determine weights, all materials were dried at 80°C in an oven of the type used in nutritional analysis for a minimum of 48 hours. The following life stages in J.

<u>bataua</u> were delimited:

1. Seed.

Seeds were collected from an adult palm. A single panicle yielded ca. 1650 seeds with an average dry weight of 5.5 gm each.

2a. Seedlings with only the first bifid eophyll formed.

Of 10 collections made, 80% were still attached to the seeds, which, by this stage, weighed 1.4-2.6 gm each ($\bar{x}$=2.0). The plants were 14-33 cm in height, with one-half the bifid eophyll measuring 14-17.5 cm long by 1.5-2.5 cm wide. Roots penetrated 7-22 cm below the surface and consisted of a single main root and 1-3 secondary units. The aboveground portion of the seedling (excluding the seed) weighed 0.2-1.4 gm ($\bar{x}$=0.7), while the root system totalled 1.0-5.0 gms ($\bar{x}$=2.5 gm).

2b. Seedlings possessing several bifid leaves.

In only 50% of 10 collections were seeds still attached and these seeds now weighed only 0.8-2.0 gm each ($\bar{x}$=1.46), a significant drop from the first two stages. It could, however, be expected, if the loss of epicarp, mesocarp, some of the nutritive tissue and overall decomposition were to be considered. The young plants have a range of 30-47 cm in height, with one-half the bifid leaf measuring 20-30 cm long by 2.0-4.0 cm wide. The petiole bearing the rachis measured 14.5-33 cm, and the young sheath barely 5.0 cm long. Each plant had from 2-4 leaves. Roots, 3-4 per plant (those with a diameter $\geq$ 3 mm) measured 14-24 cm long and some were

well branched. Excluding the attached seeds, aboveground mass was 1.9-5.4 gm per plant ($\bar{x}$=2.78) while roots weighed 0.3-1.1 gm ($\bar{x}$=.68).

3a. Sapling with leaves each bearing no more than 4 segments.

By this stage the seeds have completely separated from the young plants which now were 80-120 cm high (n=5). Leaf segments, 34-40 cm long by 3.0-5.5 cm wide, were borne on a rachis measuring 3-15 cm, a petiole 44-74 cm and sheath 10-12 cm long. There were 3-5 leaves per plant. Roots were 15-40 cm long, a measurement now subject ot error due to breakage upon excavation from the ground. From this point on, the below-ground system became too complex to measure individual root lengths. Approximately 6-10 roots $\geq$ 3 mm thick were counted per plant. Above-ground biomass amounted to 16.6-33.6 gm ($\bar{x}$=28.5), while that below ground amounted to ca. 1.9-5.7 gm ($\bar{x}$=3.35).

3b. Sapling with short, juvenile, pinnate leaves and no aerial trunk.

Of five specimens studied, heights ranged from 1.0-1.6 m. Petiole and sheath measured together were 63-103 cm and rachis 33-70 cm. The 3-5 leaves per plant each carried 9-21 pinnae. No estimate of biomass or additional data were obtained for this sample due to the unfortunate fire previously mentioned.

3c. Sapling with intermediate-sized pinnate leaves.

From this point on, as work was carried out in a forest reserve, we cut only one tree per category. The 4 leaves on

this plant measured ca. 4.4 m each, including sheath, petiole and rachis. Because of their graceful curve, the plant itself was only 4.0 m tall. Central pinnae measured ca. 60 cm long by 5 cm wide. The above-ground weight of 6.88 kg was far larger than that below ground, 1.16 kg. None of the durable black spines so characteristic of this species were formed by this stage--only a few soft green hair-like spines arose from the sheath.

4a. Adolescent palms, leaves expanded almost to full size, beginning of aerial trunk formation.

This palm was 5 m tall with 6 leaves, each measuring ca. 8.5 m long. The 191-199 individual pinnae per leaf had reached adult size, ca. 1 + m long by 6-10 cm wide. The young trunk weighed 3.2 kg, bringing the above ground biomass to 32.7 kg, while below-ground comprised only 2.17 kg.

4b. Adolescent palm with small spinose trunk.

Reaching a height of ca. 12 m, the 4.5 m long apical trunk bore 18 leaf scars. Leaves were beginning to change from a more or less vertical orientation to one slightly less so.

4c. Adolescent palms with fibrous covering completely dropped from the trunk.

At an overall height of ca. 17 m, the entire spinose covering had abscissed from the trunk. The stem measured 8.7 m long with 29 leaf scars. No axillary inflorescence buds were found. More commonly, such inflorescences are usually produced by this stage and, in fact, frequently are

found mature enough to flower and fruit.

5a. Seed-bearing adult.

This specimen reached a height of 23 m, with 11 leaves in the crown oriented at an angle of ca. 45° to the stem. The aerial stem measured 14.7 m to the lowermost sheath, and had 133 leaf scars to this point. Dissection of the 17 sheaths present revealed axillary inflorescences formed in 2 series of 3 and 5 each, spaced between several axils having aborted inflorescences. This indicates that inflorescence production was not continuous. In specimens examined from other locations, axillary inflorescence production was found to range from inflorescences present in all axils to only in very few. The number of buds produced, as can be expected, appears dependent on health and environment of a particular individual.

5b. Senescent palm.

The senescent palm showed a reduction in growth rate, reproductive capacity and biomass generation as compared to the previous life stage. Only 6 leaves were present in the crown and these had shortened considerably, with a rachis only ca. 5 m, petiole ca. 20 cm and sheath 95 cm long. Even the number of pinnae on an individual rachis showed a slight decrease from the seed-bearing adult, with 190 on the oldest and 181 on the newly emerging leaf. No young axillary inflorescence buds were found under the sheaths dissected. This palm had a strongly bent trunk measuring 16.25 m to the lowermost sheath, with 131 leaf scars present. From field

experience in other areas, this individual was judged to have deteriorated unusually early in its life cycle, due to a hostile environment, physical damage to the stem or other unexplained factors. The number of leaves produced on the aerial stem (131) was less than that on the previous specimen (133), a very healthy individual. Under more favorable conditions, the palm probably can produce 150 or more leaves on an aerial trunk during its lifetime.

No estimate of ages can be attached to any of the life stages as tagging and subsequent necessary years of observation were not undertaken. However, measurements within the defined life stages reveal several important growth trends. A comparison of above and below ground biomass over time reveals a decreased percentage of root versus shoot with growth. In seedling stages roots comprise 20-25% of total weight; in sapling stages this drops to 10-15%, while in the adolescent stage (the last calculation believed to have any accuracy) is only 6%. While Tomlinson and Soderholm (1975) used a final root biomass of 10% in their calculations of bioenergetics of Corypha elata, the trend shown here, should it be proven to hold throughout all stages, would appear to indicate a somewhat smaller number necessary for Jessenia bataua. Unfortunately, I know of no way that this could be accurately calculated; therefore, I retain the estimate made by these workers in my own calculations.

The leaf is a good indicator of a palm's life stage. Seedlings and juvenile pinnae stages are easily recognized

when contrasted to adult stages. In the senescent stage, slightly smaller and far fewer leaves are present in the crown than in the adult seed-bearing stage. As mentioned earlier, leaf orientation also varies with adult age. Leaves in a young adult often display a more vertical orientation, while a horizontal slant is indicative of an older specimen. Although bracts, inflorescences, fiber and fruits are known to vary in size and number over time, we were unable to obtain any quantitative data for documentation. This would require felling entire populations of trees in a completely isolated area, a task which must be reserved for a later date.

An important consideration of reproduction and growth strategy in tropical trees is the amount of dry matter produced by a plant throughout its lifetime in relation to the percentage of dry matter allocated for reproductive effort. Determination of such proportions allow for comparisons in productivity when combined with other data and shed light on the reasons why a plant has evolved its specific reproductive strategy.

The total biomass of Jessenia bataua has been estimated in the following manner:

1. Root biomass. As no reasonable measurements could be made on living material, 10% of total leaf and trunk biomass was used as an estimate for this parameter. Tomlinson and Soderholm (1975) suggested this figure in similar studies of Corypha elata.

2. Trunk biomass. As construction of Jessenia bataua

is rather uniform, it can be treated as an elongated cylinder and volume calculated using a standard algebraic formula. Weight per cm^3 of volume was determined from a sample portion of dried trunk.

3. Leaf biomass. Production of mature leaves was determined by counting the number of visible leaf scars on the aerial stem. While the total amount of production in seedling, sapling and adolescent stages was believed to be difficult to approximate, it was considered more or less balanced by the general reduction in size and weight of senescent leaves towards the end of the palm's lifetime. Thus, a single weight for all leaves, as evidence by leaf scars, was used in the calculations.

4. Inflorescence biomass. A representative panicle with 130 rachillae was selected and weighed. In the wild, panicles vary greatly in size and this representative weight was felt to be a usable approximation. While estimates of fruit production are also difficult, due to variation with time and environment, an average of 1000 fruits per panicle was selected. An estimate of staminate flower production was obtained by counting the number of staminate flowers on a group of rachillae; this resulted in an average value of 240 such flowers per rachilla. For weighing, staminate flowers just before anthesis were chosen. To measure pistillate flower production, inflorescences were examined and these determined to have an average of 60 pistillate flowers per rachilla. Assuming a reproductive efficiency of 10%, only

about 6 pistillate flowers per rachilla would be expected to develop into fruit; the other 54 would fall off, and therefore must be considered in the calculations. Receptive pistillate flowers were used in weight calculations. Values for prophyll and bract were obtained by weighing representative samples and using these throughout the calculations, even though they may vary as much as, or more than do panicles.

Several additional problems arose during biomass estimates with this species. We had no knowledge of the actual lifetime of a healthy palm; so that an approximation of 150 leaf scars was selected, based on an educated guess made from field experience. Average trunk height at senescence was estimated at 18 m. A figure of 50% of the 150 visible leaf scars was used to estimate total panicle production, first subtracting 30 leaf scars formed during the adolescent life stage. This calculation yielded a value of 60 panicles produced over the lifetime of a wild palm, most likely a conservative estimate in some areas.

Tomlinson and Soderholm (1975) used a 10% correction factor for a measurement of energy lost via respiration during vegetative growth in Corypha elata. The total vegetative biomass of Jessenia bataua, eg. trunk, root and leaf, was increased by this correction factor.

The following values were calculated:

Trunk biomass	314 kg
Leaf biomass	1155 kg

Root biomass	147 kg
Inflorescence biomass	434 kg
Fruit biomass	330 kg

From these values the reproductive effort can be calculated:

Total biomass of *Jessenia bataua*	2380 kg
Total biomass of fruits	330 kg
Total biomass of inflorescence	434 kg
Total reproductive biomass	767 kg
Percentage of total biomass in reproductive biomass	32%

A value of approximately 32% of the total dry mass of *Jessenia bataua* is directed toward reproductive effort. The hapaxanthic (once-flowered) *Corypha elata* under cultivation in Florida was found to direct 15-20% of its dry matter into reproductive effort (Tomlinson and Soderholm 1975). For *Euterpe globosa* in Puerto Rico, these authors calculated a reproductive effort of 4.5%, using data presented in Bannister (1970). Clearly, *J. bataua*, even with our probable high margin of error, approaches the upper limits known for this value in the Palmae. This high value appears due, in part, to the weight of the inflorescence bracts. Both prophyll and peduncular bract are large and heavy but perform a vital function in the protection of developing panicles. Addition of this weight almost doubled the total estimate obtained from the panicles alone. *Oenocarpus* and *Jessenia* have chosen the largest kind of inflorescence bract through

their linear orientation of rachillae during enclosure. From a structural viewpoint, palms having rachillae folded and twisted within the enclosing bracts (as in some species of Geonoma) seem to economize with regard to biomass, because relatively smaller bracts can be produced. This speculation can not be confirmed by measurements at present; however, a simple examination of living material of as many species as possible in the field is all that would be required.

It appears curious that the reproductive biomass of the closely related and similarly constructed arecoid palm Euterpe globosa is so much lower than that for Jessenia bataua. There is no specific mention in Bannister (1970) that the bracts were included in the calculations, and this may be the reason for the resulting low percentage allocated to reproductive effort.

Hardon et al. (1972) showed the fruit bunch vs. dry matter ratio produced during any one year in Elaeis guineensis to be approximately 51%. While this figure seems high for a crop species, an account of fruit bunch production over total dry matter production during the entire lifetime, including non-productive and senile phases, would decrease the value obtained to one more comparable to Jessenia bataua or Corypha elata. Workers using plants in diverse families and genera have found widely ranging values. Calculations made from data in Hirose (1971) for Solidago altissima resulted in an estimate of 2% for this perennial herb. Harper and Ogden (1970) found most of the annual composites they

examined to have reproductive efforts of 20-30%. Studies in Amphicarpus purshii, an annual grass, showed about 30% of overall shoot biomass allocated to reproduction (McNamara and Quinn 1977). This study was particularly interesting, because the reproductive efforts are divided about 2:1 among subterranean and aerial propagules on the same plant. Unfortunately, after measuring subterranean spikelets, remaining roots were clipped off and not included in the calculations, leaving us unable to use this example for direct comparison.

In the wild, Jessenia bataua is a very successful species, colonizing vast areas of inundated and terra firme sites. It is most aggressive on inundated lowland and swampy areas, where other dicotyledonous competitors are unable to grow. An estimated minimum of 60,000 fruits are produced over the lifetime of a wild Jessenia bataua, far fewer than the 242,800-355,290 for Corypha elata (Tomlinson and Soderholm 1975) or 150,000 for Euterpe globosa (Bannister 1970). Jessenia bataua seeds have a high germination rate and are widely dispersed by man and animals (due to the oily mesocarp). No significant seed predators were ever noted in the field. This lack of predators, along with the more aggressive and generally successful nature of the species, may explain the production of the relatively small number of seeds.

According to Tomlinson and Soderholm (1975), Corypha elata produces approximately 10 million flowers on flower-bearing axes 5,280 m in length. Rough estimates for Jessenia

bataua reveal that approximately 2 million staminate flowers and 0.5 million pistillate flowers are produced on 7,800 m of first order branches over the lifetime of the palm.

Calculations of biomass production and reproductive effort over the lifetime of *Jessenia bataua* are admittedly highly speculative. As it is a pleonanthic species, many assumptions were made for growth, flowering, and fruit production--factors which are known to vary greatly in each locality. However, this modest effort, as incomplete and presumptious as it may be, represents the most inclusive study possible at this time, given the massive size of the organism (more than 2 metric tons) and its remote location in the Amazon Valley. In general, the value for reproductive effort obtained in this analysis agrees with that for *Corypha elata*, if it is remembered that rough calculations were used in both studies. Investigations of other genera are necessary before comparisons can be made between forest palms. However, the data so far obtained suggests that, in some palms at least, growth strategy is characterized by a relatively high reproductive effort.

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Chapter 5

TAXONOMY

A Taxonomic History of the *Oenocarpus*-*Jessenia* complex

Martius described the genus *Oenocarpus* in his epic work *Historia Naturalis Palmarum* in 1823. It was so named because the fruits provided Amazonian Indians with a beverage or "wine" (from the Greek: oinos=wine, karpos=fruit). Five species were included: *O. distichus*, *O. bataua*, *O. bacaba*, *O. minor* and *O. circumtextus*. He characterized the genus on a number of morphological features, including a two-parted woody "spathe" (two bracts enclosing the inflorescence), sessile flowers, staminate flowers with six stamens and one-seeded fruits with either homogenous or ruminate endosperm. In *Palmarum familia ejusque genera denuo illustrata* (1824) he qualified his summary in the previous work, by noting the endosperm in the seeds of *Oenocarpus* to be ruminate.

Karsten (1857) described *Jessenia* with no mention of any affinity with *Oenocarpus*. He designated *J. polycarpa* from Colombia as the type species. The genus was named in honor of Dr. Carl Jessen, a professor of botany in Eldena, Prussia. The descriptions of the two genera are similar, with the exception of the number of stamens, given as 16-20 in *Jessenia*.

Oenocarpus and *Jessenia* were maintained as distinct generic concepts through a number of publications (Walpers, 1848-49; Drude, 1882; Bentham and Hooker, 1883; Engler and

Prantl, 1889). Burret (1928) re-evaluated the two genera and examined the taxonomic relationships of the species described. His work was based both on new material received from the field and on Martius' original drawings and descriptions. George Huebner sent Burret a complete collection of O. bataua from Manaus, which he compared to Martius' original data in Historia Naturalis Palmarum. The material proved to be identical, with the exception of the staminate flowers. Flowers in Huebner's collection had 14-15 stamens, as opposed to Martius' six. In addition, the apices of the anthers were distinctly pointed, while rounded apices are characteristic in Oenocarpus. Burret recognized this collection to be unmistakably related to Jessenia polycarpa from both its vegetative and sexual components. He made the new combination Jessenia bataua (Martius) Burret, which re-defined the genera into more uniform and natural generic concepts. Many of the Martius specimens were composed of fragmentary, poorly labelled and mixed collections (Burret, 1928; Wessels Boer, 1965). In this case, staminate flowers of another species of Oenocarpus (perhaps O. distichus, as Burret suggested) were mixed with the specimen of O. bataua, producing the apparent similarity of flowering material within Oenocarpus as described by Martius (1823). As O. bataua was the only species in the genus with ruminate endosperm--all others being homogenous--this character is a significant and stable taxonomic distinction for generic separation between Oenocarpus and Jessenia.

As mentioned above, Burret was able to divide the genera on the basis of sterile material. In Jessenia, he noted the abaxial surface of the pinnae to be covered with sickle-shaped to doubly sickle-shaped trichomes; these were lacking in Oenocarpus.

This complex has been variously partitioned into sections, subsections and subgenera by different workers. Table 5.1 outlines the major divisions and their component taxa as proposed by these workers.

Martius did not designate a type species for this genus. Moore (1963) eliminated Oenocarpus bataua, O. distichus, O. minor and O. circumtextus for various reasons, and named O. bacaba as the lectotype of the genus. In the same work, he mentioned an earlier use of Jessenia (Linnaea 25:519. 1853) than that of Karsten. It was then, only a name used in synonomy of Hyalosperma Steetz (= Helipterum DC. (Compositae)), not validly published. It is, therefore, of no nomenclatural consequence and thus Karsten's Jessenia is based upon legitimate grounds.

The mention of "Patavoua" and "Comun" by Aublet (1775) in Historie des plantes de la Guiane Francoise resulted in some concern to Martius (1823) and Burret (1928) that these might be earlier specific epithets for elements respectively, of Jessenia and Oenocarpus. Martius listed these names as binomials with Palma as the genus. Cook (1940) identified figures depicted in the frontispiece of Volume 1 of Aublet's work as belonging to Oenocarpus. The question arises as to whether

TABLE 5.1

Major Subdivisions and their Component Taxa of Historical Importance in the *Oenocarpus*-*Jessenia* complex.

Drude (1882)*

Oenocarpus

Sect. I. *Distichophyllum* Dr.

1. *O. distichus*
2. *O. tarampabo*

Sect. II. *Bataua* Dr.

3. *O. bataua*

Sect. III. *Bacaba* Dr.

4. *O. bacaba*
5. *O. mapora*
6. *O. multicaulis*
7. *O. minor*
8. *O. circumtextus*

Barbosa Rodrigues (1903)*

Oenocarpus

Sect. I. *Yandybácaba* Barb. Rodr.

1. *O. distichus*
2. *O. discolor*
3. *O. tarampabo*

Sect. II. *Bacába* Dr. *ex parte*

4. *O. bacaba*

Sect. III. *Bacábay* Barb. Rodr.

5. *O. minor*
6. *O. multicaulis*
7. *O. circumtextus*

Sect. IV. *Patauá* Barb. Rodr.

8. *O. bataua*

Burret (1928)

Oenocarpus

Sect. I. *Euoenocarpus* Burret

Subsect. 1. *Distichophyllum* Dr.

1. *O. distichus*
2. *O. discolor*
3. *O. tarampabo*

Subsect. 2. *Bacaba* Dr. *ex parte*

4. *O. bacaba*
5. *O. mapora*
6. *O. minor*
7. *O. microspadix*
8. *O. huebneri*
9. *O. intermedius*
10. *O. multicaulis*

Sect. II. *Oenocarpopsis* Burret

11. *O. circumtextus*

Jessenia

12. *J. bataua*
13. *J. polycarpa*
14. *J. oligocarpa*
15. *J. repanda*

Balick (1980)

Oenocarpus

Subgen. I. *Oenocarpus*

1. *O. distichus*
2. *O. discolor*
3. *O. tarampabo*
4. *O. bacaba*
5. *O. macrocalyx*

6a. *O. mapora* subsp. *mapora*

6b. *O. mapora* subsp. *dryanderae*

7a. *O. minor* subsp. *minor*

7b. *O. minor* subsp. *intermedius*

Subgen. II. *Oenocarpopsis* (Burret) Balick

8. *O. circumtextus*

Jessenia

9a. *J. bataua* subsp. *bataua*

9b. *J. bataua* subsp. *oligocarpa*

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* A consideration of Brazilian species only

or not Aublet made an effort to describe two species in Jessenia and Oenocarpus. Indeed, "Patavoua" is the common name for Jessenia bataua in French Guiana, according to the label of Sagot 851(P), from that country, as "Comun" is for Oenocarpus bacaba, according to Poiteau s.n.(P), from French Guiana. There is little doubt in my mind that Aublet was referring to J. bataua and O. bacaba as "Patavoua" and "Comun". These, however, were not taxonomically described; they were, rather, discussed in an ethnobotanical context --the local edible uses for the fruits. Thus, these can not be considered earlier binomials for J. bataua and O. bacaba. This judgement agrees with that of Moore (1963) who stated "...Aublet considered a number of palms under their vernacular names with no attempt to erect genera or to provide binomials... ."

In recent times, Wessels Boer (1965) chose to define Oenocarpus in the broad sense of Martius, to include Jessenia. The decision was based in part on a reference to a single specimen of Jessenia, Tutin 167(BM) with an herbarium label noting flowers with 6 stamens. However, Wessels Boer admitted that it was impossible to verify this count, as the herbarium specimen itself contained no flowers. The issue was also raised to the value of ruminate versus homogenous endosperm as a generic character (cf. Euterpe). In the concluding remarks on these palms in Surinam, he admitted that he had no good first hand field experience other than with O. bacaba and J. oligocarpa. Yet, he chose

to unite the genera on the basis of the characteristic leaf sheath and inflorescence. The synonymous nature of Jessenia was maintained in later papers, as he accrued further field experience (Wessels Boer 1971, 1972). Others, including Moore (1973) and Dugand (1976), considered the two as distinct genera.

I am unable to agree with the conclusion of Wessels Boer. For the present work, several years of herbarium and field study have been dedicated solely to the scrutiny of members of these two genera. They have been observed and collected with a monographic perspective throughout much of their range. In my opinion, Wessels Boer's floristic surveys of geographically limited areas, while providing good inventories and a wealth of botanical information about the plants present, did not allow an understanding of the group to the depth required for a proper taxonomic evaluation of the two genera. In most cases, his conclusions in these works have been towards a widespread uniting of neotropical genera (cf. Attalea and Iriartea in Wessels Boer 1965), an action subject to debate among students of this family.

In this study, I have tried to clarify the differences and outline a valid taxonomic scheme for the complex, within the limitations of current knowledge. As presently understood, the complex consists of two genera. Jessenia comprises a single species with two subspecies; Oenocarpus contains eight species and four subspecies. The following outline illustrates many of the essential morphological differences

between the two genera.

Oenocarpus	Jessenia
Solitary to caespitose, medium to large, slender to stout palms.	Solitary, usually stout, large palms.
Pinnae regularly inserted along the rachis in a single plane to irregularly grouped and inserted at various angles to the rachis.	Pinnae regularly inserted along the rachis in a single plane.
Lower surface of pinnae slightly vestite or whitish -waxy.	Lower surface of pinnae with peltate to sickle -shaped to doubly sickle -shaped trichomes.
Leaf sheath with strawlike or wiry fibers to ca. 30 cm long.	Leaf sheath with thin, short hairlike fibers and stout knitting-needlelike fibers to 1 m in length.
Staminate flowers with 6 stamens.	Staminate flowers with 7-20 stamens.
Anthers with connective not produced.	Anthers with connective produced.
Endosperm homogenous.	Endosperm ruminate.

KEY TO THE GENERA IN THE OENOCARPUS-JESSENIA COMPLEX

1. Seeds with homogenous endosperm; staminate flowers with 6 stamens; pinnae lacking trichomes abaxially or trichomes, if present, needlelike or hairlike . . . . . 1. Oenocarpus.

1. Seeds with ruminate endosperm; staminate flowers with (7-)9-20 stamens; pinnae covered abaxially with peltate to sickle-shaped or doubly sickle-shaped trichomes . . . . . 2. Jessenia.

1. Oenocarpus Martius, Hist. Nat. Palm. 2:21-22. 1823.

Large to medium, solitary to caespitose, erect, pleonanthic, monoecious arecoid palms; stem slender to massive, whitish grey to black, smooth to fibrous, or, when young, covered with remains of sheaths and sheath fibers; base sometimes producing a small mass of slender roots.

Leaves pinnate, spirally to distichously arranged in suberect (when young) or horizontally spreading (when mature) coma; sheaths clasping, somewhat split opposite petiole, thick, coriaceous, lightly furrowed on the inside, smooth on the outside, upper portion fibrous, these reaching to petiole base; petiole concave-channeled and smooth adaxially, convex and smooth abaxially; rachis trough-shaped at base, more or less 3- or 4-sided near center, flattened to concave adaxially, flattened to semi-convex abaxially, changing to trigonal towards apex, smooth, more or less ribbed longitudinally, frequently lepidote when young; pinnae numerous, regularly to irregularly inserted along rachis in a single plane or at various angles to rachis; adaxial surface glossy green; abaxial surface light green to white, linear-lanceolate to oblong-lanceolate at center of rachis, plicate, acute to long acuminate, reflexed at attachment, 1-ribbed with prominent intermediate veins, smooth adaxially, the abaxial surface smooth, usually with waxy coating (at least when newly unfolded) and, in some species, sparsely to densely covered with needlelike to twisted, hairlike trichomes.

Inflorescence interfoliar in bud, protandrous, weakly

to strongly hippuriform (shaped like a horse's tail); peduncle short to elongate, flattened adaxially, bracteate, bearing a sharply 2-edged, flattened prophyll with dentate margins (except in Oenocarpus circumtextus where the prophyll is of unknown construction) and a larger, tubular peduncular bract swollen in the middle, longitudinally somewhat striate, tapering to sharp point and opening lengthwise; rachis flattened adaxially, frequently lepidote, rachillae simple, inserted laterally and abaxially, arched to pendulous at anthesis, short to elongate, linear to slightly undulate, slender, attenuate.

Flowers unisexual, sessile, borne in triads of 2 staminate and 1 pistillate flower proximally on the rachillae, in pairs of staminate or solitary staminate distally or rarely staminate throughout; staminate flowers asymmetrical, sepals 3, ovate-lanceolate, acute, centrally somewhat thickened, marginally thin or even somewhat translucent, basally briefly connate to valvate or briefly imbricate; petals 3, valvate, longitudinally striate, linear to oblong-lanceolate, acute, slightly fleshy, one or two in each flower often somewhat dissimilar, incurved, stamens 6, filaments subulate, slender, linear or sometimes curved and bent, apically inflexed in bud, connective not extending beyond locules; anthers dorsifixed at lower junction of thecae, more or less hastate, rounded or blunt apically, versatile, with 2 easily separated, bilocular thecae, longitudinally and extrorsely dehiscent; pistillode small,

trifid; pistillate flowers symmetrical; sepals 3, imbricate, fleshy, suborbicular, hooded-concave, enclosing corolla in bud; petals 3, imbricate (except the briefly valvate apex when mature), suborbicular, hooded-concave, somewhat thin when young, becoming larger and fleshier at maturity; staminodes lacking; gynoecium unilocular, uniovulate; ovule erect, anatropous, rarely aborted; style short, thick; stigmas 3, reflexed at anthesis, papillate adaxially.

Fruit green when young, covered with a varying degree of wax, becoming dark purple when ripe, globose to ovoid-ellipsoid, obtuse to acute, basally with a shallow, bowl-like cupule of indurate perianth; stigmatic residue apical to slightly excentric; epicarp smooth; mesocarp fleshy, rich in oil, with thin, flattened longitudinal fibers adnate to and completely covering seed; seed ovoid-elliptic to globose; endosperm horny, white, homogenous; embryo white, clavate, ca. 2/3 as long as seed.

Type species. *Oenocarpus bacaba* Martius.

KEY TO THE SUBGENERA OF *OENOCARPUS*

1. Trunk smooth in adults; pinnae linear-lanceolate to somewhat broadly linear-lanceolate at center of rachis and lacking a significant acumen; peduncle of inflorescence short and stout; peduncular bract opening along entire length and falling away . . . . . 1. subgen. *Oenocarpus*.

1. Trunk covered with a fibrous reticulum, even in adult stage; pinnae ovate-oblong or oblong-lanceolate at center of rachis, terminating apically in a long narrow acumen 10-22 cm long by 2-3 mm wide; peduncle of inflorescence long and slender; peduncular bract opening along about one-half its length and persistent . . . . . 2. subgen. *Oenocarpopsis*.

1. Oenocarpus subgen. Oenocarpus

Oenocarpus Sect. Distichophyllum Drude, in Martius, Fl. Bras. 3,2:467. 1882.

Oenocarpus Sect. Bacaba Drude, in Martius, Fl. Bras. 3,2:467. 1882 (in part).

Oenocarpus Sect. Yandybacaba Barbosa Rodrigues, Sert. Palm. Bras. 1:41. 1903.

Oenocarpus Sect. Bacabay Barbosa Rodrigues, Sert. Palm. Bras. 1:42. 1903 (in part).

Oenocarpus Sect. Euoenocarpus Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10:292. 1928.

Large to medium, solitary to caespitose palms; stem smooth or, when young, covered with remains of sheaths and sheath fibers, obscurely ringed with leaf scars. Pinnae linear-lanceolate to somewhat broadly linear-lanceolate at center of rachis. Inflorescence strongly hippuriform; peduncle short and stout, bearing sharply 2-edged, flattened prophyll with dentate margins and a larger, tubular peduncular bract swollen in middle, tapering to sharp point and opening along its entire length; both bracts caducous. Staminate flowers with 3 valvate to briefly imbricate sepals.

Type. Oenocarpus bacaba Martius.

KEY TO THE SPECIES OF SUBGENUS OENOCARPUS

1. Leaves distichously arranged; solitary palms. Brazil, Bolivia, and perhaps Venezuela.
   2. Stems thick, 13-25 cm in diameter; central pinnae acute to acuminate, 0.7-1.15 m long, 3.5-5.5 cm wide. Brazil (Maranhao, Mato Grosso, Para and possibly Minas Gerais); and perhaps Venezuela (Bolivar).
      3. Pinnae lanceolate-acute, dark green abaxially, a small swelling present at insertion; petals of staminate flowers oblong-obtuse. Brazil (Maranhao and Para) and perhaps Venezuela (Bolivar). . . . . 1. Oenocarpus distichus.
      3. Pinnae lanceolate-acuminate, glaucous abaxially, inserted directly into rachis with no swelling; petals of staminate flowers lanceolate-acute. Brazil (Mato Grosso, Maranhao and possible Minas Gerais) . . . . . 2. Oenocarpus discolor.
   2. Stems slender, less than 13 cm in diameter; central pinnae very narrowly acuminate, 40-50 cm long, 2 cm wide. Brazil (Rondonia) and Bolivia (Beni) . . . . . 3. Oenocarpus tarampabo.
1. Leaves spirally arranged; solitary to caespitose palms. Costa Rica, Panama, Colombia, Guyana, Surinam, French Guiana, Ecuador, Brazil, Peru and Bolivia.

4. Axis of inflorescence distal to peduncular bract scar greater than 4.5 cm long; pinnae either grouped on the rachis or more or less regular with an occasional grouping of 2-3, usually at midleaf.

5. Rachillae 100-200 or more, usually longer than 80 cm; ripe fruit globose to globose-elongate; pinnae mostly in groups along much of the rachis, except near the apex. Much of the northern half of South America, to an altitude of ca. 1000 m . . . . . .4. Oenocarpus bacaba.

5. Rachillae fewer than 100, 75 cm or less in length; ripe fruit ellipsoid-acute to subovoid; pinnae usually (although not always) regularly arranged except for a few and these often at midleaf.

6. Ripe fruit 1.5-1.7 cm long (not including cupule), by 1.1-1.2 cm wide, ellipsoid-acute. Brazil (Amazonas). . . 5. Oenocarpus macrocalyx.

6. Ripe fruit 1.8-2.9 cm long (not including cupule) by 1.4-2.25 cm wide, ellipsoid to ovoid. Much of the northern half of South America, Panama and Costa Rica, to an altitude of 1000 m . . . . . .6. Oenocarpus mapora.

4. Axis of inflorescence distal to peduncular bract scar less than 4.0 cm long; pinnae mostly regularly inserted along the rachis, rarely with an occasional grouping of 2-3. Brazil (Amazonas and Pará) and elsewhere?. . . . . 7. Oenocarpus minor.

1. Oenocarpus distichus Martius, Hist. Nat. Palm 2:22-23, t. 22-23. 1823.

Trunk large, solitary, columnar, 10-20 m high, 13-25 cm in diameter.

Leaves 9-15 per coma, robust, distichous; sheath ca. 70-95 cm long, outer surface dull olive-green, inner surface brown, glossy, upper margins lined with reticulum of slender, flexible brown fibers; petiole green to green-brown, grey(?)-lepidote at first, becoming more or less glabrous; rachis green to dark green, more or less unequally 4-sided towards center with shallow keel protruding upwards along center of adaxial face, extending along part of rachis, 3.5-5 m long, grey-lepidote when young, this vesture frequently falling away with age; pinnae 89-109 per side, fewer on younger specimens, inserted at regular intervals and more or less in same plane at apex, irregularly arranged towards middle and base either singly or in groups of 2-7 at various angles to rachis, pale green abaxially, linear to linear-lanceolate, acute; basal pinnae ca. 0.7-1.1 m long, ca. 2-3.5 cm wide; central pinnae ca. 0.7-1.15 m long, ca. 3.5-5 cm wide; apical pinnae (fourth from apex measured) ca. 38-71 cm long, ca. 2.5 cm wide.

Inflorescences 1 to few apparent at any one time, creamy white at anthesis, changing to reddish powdery in fruit; prophyll olive-green, to ca. 93 cm long, ca. 24 cm wide (a single robust example measured, norm much smaller), grey-brown-lepidote when young; peduncular bract of similar

color, ca. 1-2 m long, red-brown-lepidote when young, the indument turning grey with age or falling away, axis distal to peduncular bract scar 25-35 cm long, 2.6-3.5 cm wide at this scar, variable in size depending on individual; rachillae ca. 69-186, ca. 0.9-1.2 m long, 4-5+ mm wide, triads of 2 staminate and 1 pistillate flower on proximal 50-65% of individual rachillae, this variable; staminate flowers creamy white; sepals ca. 1.25 mm long; petals ca. 4 mm long, filaments brown, slender; pistillate flowers creamy white in bud, (20)51-165 per rachilla, ca. 4 mm long, ca. 4.5 mm wide at time of anthesis of staminate flowers.

Fruit globose to somewhat globose-elongate when mature, variable in size, 1.8-2.1 cm long (including cupule), 1.4-1.6 cm wide, 2-3 gms in weight when ripe, stigmatic residue apical to slightly excentric, sharply pointed, ca. 1.5 mm long, ca. 2 mm wide; cupule tan, ca. 4 mm deep, ca. 9 mm wide; epicarp grainy-waxy; mesocarp pulpy, greenish to purple; fibers ca. 0.5 mm wide.

Type. Brazil. Pará, 1818-1820, Martius 2615 (M, isotype P).

Distribution. Known mainly from Pará and Maranhão, Brazil; possibly in Bolivar, Venezuela.

Representative specimens

BRAZIL. Pará: Belém, rear of Instituto farm, fr, 26 Nov 1946, Bailey 341 (BH); Santarém-Cuiabá highway, BR 163, km 878 from Santarém, Cachoeira do Curua, Serro do Cachimbo, 4 Nov 1977, Balick et al. 910 (BH, ECON, MG, NY), km 876

from Santarém, fr, 6 Nov 1977, Balick et al. 915 (ECON, MG, NY), km 1231 from Santarém, 17 Nov 1977, Balick et al. 930 (ECON, MG, NY).

CULTIVATED. Brazil. Pará: Belem, EMBRAPA Station, 13 Dec 1977, Balick & Rosa 957 (ECON, MG).

This palm, characterized by its distichous leaf arrangement, produces a strikingly beautiful and easily recognized fan-shaped crown. From afar, it has the appearance of being closely related to Oenocarpus bacaba, except for the distinctive ranking of the leaves.

Barbosa Rodrigues (1903) distinguished two varieties, bacaba branca and bacaba vermêlha based solely on the color of the pulpy mesocarp. The former has whitish mesocarp and the latter reddish. Such differences in mesocarp pigmentation occur in other species of this complex. When processed, bacaba branca yields a creamy white beverage considered superior in taste, while that from bacaba vermêlha is reddish yellow.

In his original description, Martius (1823) noted that this species occurs in Pará and Maranhão. Huber (1902) wrote of it in Bragança and the lower Amazon, stating that it accompanied the great river to the frontiers of Goiás and Mato Grosso. He also noted its complete absence from the upper Amazon and Rio Negro.

A single specimen was collected from Estado Bolívar in Venezuela by Steyermark in the "dense forest along Río Karuai between base of cerro and forest ridge above Río Karuai

[Steyermark 60591]". The altitude of this particular locality (1220-1325 m) approaches the upper limit for the genus, making this a significant collection. Wessels Boer (1972) discussed the collection (from F), concluding that the leaf fragments and inflorescence with well developed pistillate flowers could not positively be identified as Oenocarpus distichus. His conclusion is based mainly on the fact that the field label fails to mention the characteristic leaf arrangement. Wessels Boer apparently overlooked Steyermark's comments (1957) on the specimen, which give some credence to the possible correct identification. In this case, it is important to rely on the published report as a supplement to the incomplete label description. After examining the collection, now apparently consisting of only a single panicle, I find the inflorescence structure to be more like O. bacaba than O. distichus. My experience with the latter species is mostly from Pará, where the axis shows a definite elongation in relation to its width compared to the more widespread O. bacaba. The axis in the Venezuelan collection lacks this characteristic elongation. Further field work is needed to prove positively the presence of this species in Venezuela.

Oenocarpus distichus thrives in the sandy soil of terra firme areas in Pará, where it was seen along the Santarém -Cuiabá highway, and in Belém and its environs. A magnificent stand, growing in plantation rows, can be found at the EMBRAPA agricultural research station in Belém. This represents, to my knowledge, the only attempt at cultivation of the species

on a medium-sized experimental scale. As it is in a protected area, the stand can be further studied, and new data obtained as the palms mature.

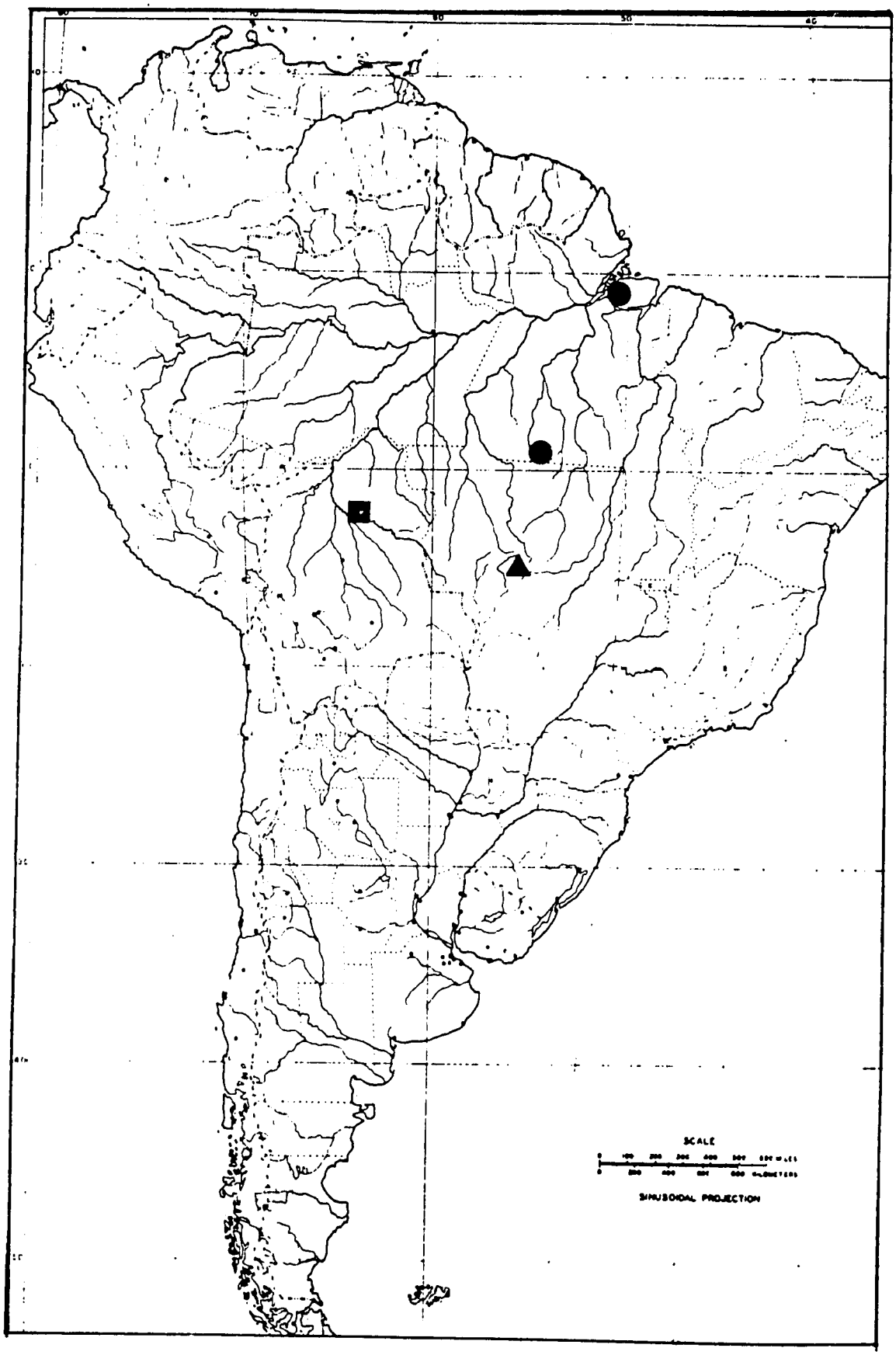
Only a few herbarium collections of this species exist. Knowledge about its distribution, variation and habit is surprisingly lacking, especially in view of the regional utilization of the pericarp for oil and a beverage, both in the past and at present.

Fig. 5.1. Oenocarpus distichus Martius along the Santarém-Cuiabá highway in Pará, Brazil (Balick et al. 915).

Fig. 5.2. Oenocarpus distichus Martius: A. Prophyll and peduncular bract enclosing the inflorescence (Balick et al. 910): B. Crown of a felled palm showing two-ranked arrangement of sheaths (Balick et al. 915); C. Fruiting panicle (Balick et al. 915); D. Cross section of the crown showing two-ranked arrangement of sheaths (Balick et al. 910).

B

Fig. 5.3. Approximate distribution of the distichous-leaved species of Oenocarpus, as presently understood: ▲ = Oenocarpus discolor; ● = Oenocarpus distichus; ■ = Oenocarpus tarampabo.


SCALE
SINUSOIDAL PROJECTION

7. Oenocarpus discolor Barbosa Rodrigues, Palmae Matto-grossenses. 8, t.3. 1898.

Trunk medium, solitary, columnar, ca. 8 m high, ca. 15 cm in diameter.

Leaves ca. 10 per coma, robust, distichous; sheath ca. 25 cm long, somewhat gibbous dorsally; petiole ca. 1.2 m long, channeled adaxially, grey tomentose (with age?); rachis more or less unequally 4-sided towards center, with a shallow keel protruding upwards along center of adaxial face, extending along part of rachis; rachis ca. 4-5 m long; pinnae numerous, inserted at regular intervals and more or less in same plane at apex, aggregated in groups of 2-6 at various angles to rachis towards middle and base, somewhat erect and deflexed-pendulous, narrowly to broadly linear, weakly acuminate; basal pinnae ca. 1 m long, ca. 1 cm wide; central pinnae ca. 1.1 m long, ca. 5.5 cm wide; apical pinnae ca. 30-40 cm long, ca. 1.5 cm wide.

Inflorescences 1 to several apparent at any one time; prophyll ca. 50-70 cm long, ca. 20 cm wide, reddish to light brown-lepidote; peduncular bract ca. 0.7-1.1 m long, ca. 15 cm wide, lepidote like prophyll; axis with many deflexed -pendulous rachillae ca. 50 cm long, these red powdery in fruit, with densely arranged flowers; staminate flowers with sepals lanceolate-acuminate, ca. 1.25 mm long(?); petals ca. 3.25 mm long(?), oblong-acute, stamens about one-half as long as petals.

Pistillate flowers and fruits unknown.

Type. Brazil. Mato Grosso, Barbosa Rodrigues 239 (destroyed); Barbosa Rodrigues, Palmae Mattogrossenses (1898) t. 3 (lectotype).

Distribution. Mato Grosso Maranhão and possibly in Minas Gerais, Brazil.

It is very difficult to evaluate properly the taxonomic status of this distichous-leaved palm, since herbarium material is entirely lacking. Barbosa Rodrigues (1898) mentioned collecting 12 adult and several young plants from the type locality in Mato Grosso. These specimens are presumed to have been destroyed. I was unable to locate them in Brazil. In addition to his own collecting, Barbosa Rodrigues wrote of the efforts of George Riedel, who found this species near the village of Guimarães. Concerning this lack of material, Barbosa Rodrigues concluded "...Creio que o Dr. Riedel não colheu examplares ou então dormen em algum herbario da Russa, sem determinação; o que não admira porque milhares de plantas nossas estão n'este caso."

My own description of this species is based entirely on Barbosa Rodrigues' descriptions, comments, and plates appearing both in Palmae Mattogrossenses Novae vel Minus Cognitae (1898) and Sertum Palmarum Brasiliensium (1903). The lectotype, designated by Glassman (1972), is Plate 3 of the former text. This designation would seem to be the best possible solution. In fact, the plates in Barbosa Rodrigues' publications are frequently used to typify his species. The

type locality is a moist forest canyon at Morrinhos, reaching to the Serra da Chapada in Mato Grosso. In the discussion accompanying the original description, Barbosa Rodrigues also suspected a range extension of the palm (locally known as "pindo" or "pindoba") into the highlands of the Municipio de Monte Claros in Minas Gerais. He based this suspicion on certain linguistic evidence. Due to the lack of available materials or recent studies, neither an accurate record of the distribution of this species nor an understanding of its variation can be obtained.

The original description by Barbosa Rodrigues was examined quite carefully, because of the aforementioned lack of other material, and several errors found. Some discrepancies exist between the measurements in the type plate and the text. In the description, the peduncular bract is interpreted to be 40-50 cm wide, while from the plate the more likely figure of 15 cm can be calculated from the one-tenth reduction. In addition, the solitary anther (fig. 10) is depicted as far larger than the staminate flower that actually contains it (fig. 7). These are minor flaws, which indicate only that a caveat be applied to such measurements throughout the manuscript.

A more serious error appears in the floral description. Both the original description (1898) and the text of the later work (1903) clearly state that Barbosa Rodrigues never saw the pistillate flowers or fruits of Oenocarpus discolor. However, in the updated plate (1903) in the later work, complete and dissected pistillate flowers are depicted (figs.

6-13). If indeed the pistillate flowers were known, this important information should have been added to the written description. Otherwise one is led to conclude that the drawings are from a mixed collection consisting of O. discolor and perhaps another species. This would appear to have been the case, as Barbosa Rodrigues commented in the later text, that the pistillate flowers in this genus are all so similar before anthesis that it is very difficult to separate them. Therefore, I suggest that these few particular figures be ignored and that any future workers who may collect this species concentrate on obtaining complete material, including pistillate flowers and fruits, for proper description.

Burret (1940) mentioned three photographs of this species at Berlin. These were taken at a northern Mato Grosso forest site within the Amazon drainage area, and apparently accompany Hopp 3012. Curiously, the palm is known locally as bacaba, a name more frequently applied to Oenocarpus distichus, rather than "pindo" or "pindoba" mentioned as the usual name for O. discolor. The true identity of this collection cannot be determined, since it was among the material destroyed as a result of the Second World War.

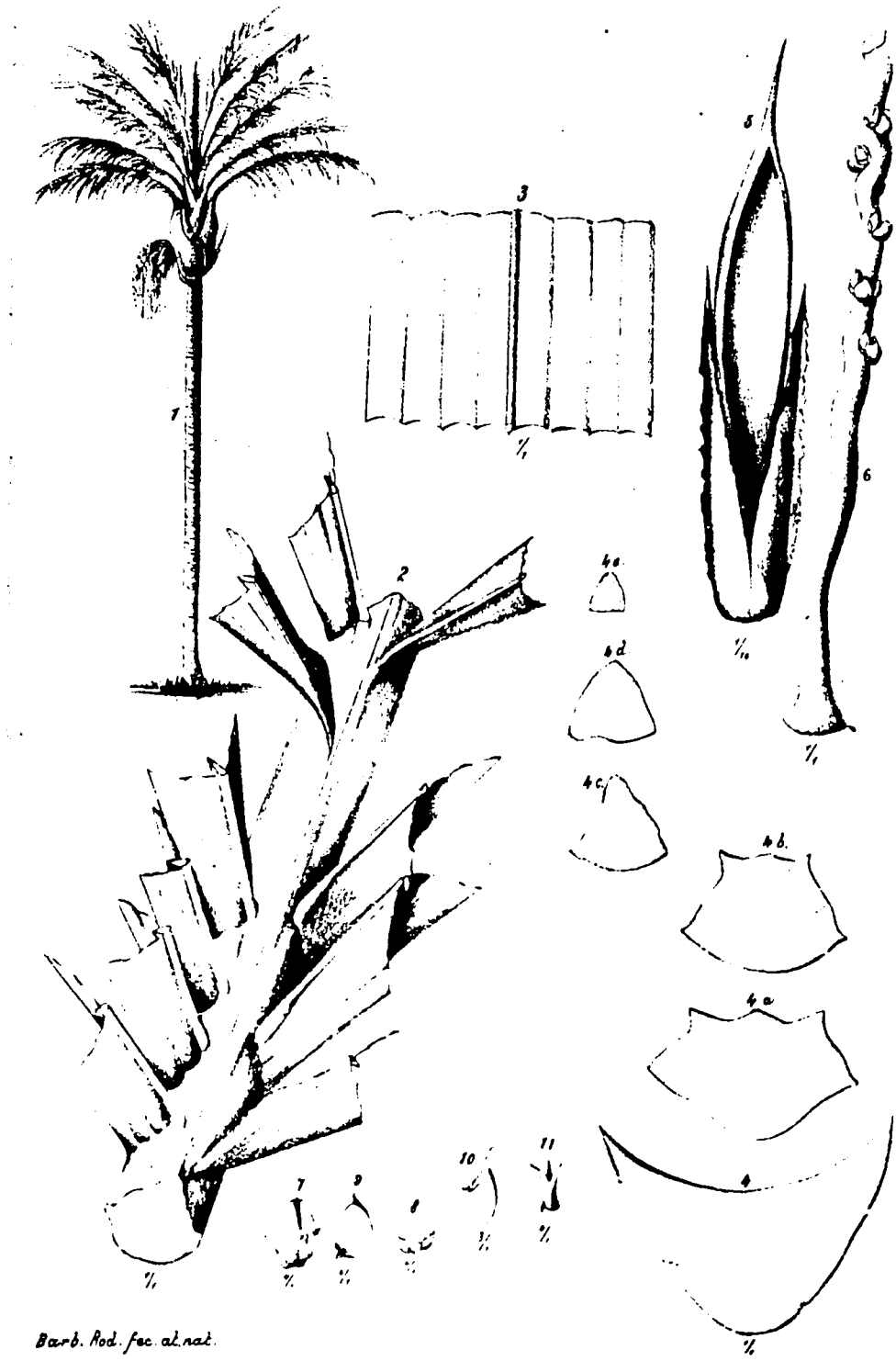
Oenocarpus discolor exhibits a remarkable affinity to O. distichus; and, without comparative material, an acceptable delimitation of this species is impossible at present. As Barbosa Rodrigues suggested, if the fruit of his new species, when finally located, turns out to be equivalent to that of O. distichus, then a reevaluation of his species would be called for; in which case, he noted, O. discolor may deserve

simply varietal status. To assist in a field distinction between the two, the following characteristics, selected from among those compiled by Barbosa Rodrigues (1898), may be helpful:

O. distichus	*O. discolor*
Stem 6-12 m long by 22 cm wide.	Stem 6-8 m long by 15 cm wide.
10-15 crispate leaves 5-6 m long.	10 elegant leaves 4-5 m long.
Pinnae narrowly lanceolate -acute, dark green on both sides.	Pinnae narrowly lanceolate -acuminate, dark green adaxially, truly glaucous abaxially.
Petals of staminate flowers oblong-obtuse.	Petals of staminate flowers lanceolate-acute.
Anthers erect, obtuse.	Anthers subsagittate, oblique to horizontal.
Small swelling present at insertion of pinna.	Small swelling lacking at insertion of pinna.

As a final note, Barbosa Rodrigues' original comments included mention of finding panicles with three bracts, the third entirely covering the first and subsequently falling away. I have never found the development of a third bract on an inflorescence in any member of this complex, and thus this must remain a problem for future field work to resolve.

Fig. 5.4. Lectotype of *Oenocarpus discolor* Barbosa Rodrigues, *t. 3*, from *Palmae Mattogrossenses* (1898).



Barb. Rod. fec. al. nat.

3. Oenocarpus tarampabo Martius, Palmet. Orbign. 12, t.8 fig. 3, t18b. 1842.

Trunk medium, solitary, slender, ca. 8-9 m high.

Leaves 14-15 per coma, elegant, arched-spreading, distichous; petiole 45-60 cm long; rachis rather broad and thick, ca. 2.5-3.5 m long; pinnae in groups of 2-5, linear-lanceolate, narrowly long-acuminate, deep green adaxially, ca. 40-50 cm long, ca. 2 cm wide.

Inflorescences several per tree, creamy white at anthesis; peduncular bract fusiform, longitudinally striate; axis distal to peduncular bract scar ca. 10 cm long; rachillae ca. 30-40 cm long, clustered tightly at base, attenuate; petals of staminate flowers oblong-lanceolate, acute.

Fruit subglobose, ca. 1.5 cm in diameter; stigmatic residue somewhat eccentric.

Type. Bolivia. Beni, d'Orbigny 28 (destroyed); Martius, Palmet. Orbign. (1842) t.18B (lectotype).

Distribution. Reported from Beni in eastern Bolivia and from Rondônia, Brazil.

There is no herbarium material of this species available. Glassman (1972) suggested that the type, d'Orbigny 28, might be at Paris. According to Lourteig (pers. comm.) it is apparently not. Moore (pers. comm.) informed me that many of Martius' types (other than his own Brazilian collections) are in his personal herbarium at Bruxelles, but that there is no

record of this specimen at that institution. Consequently, it must be presumed missing or destroyed. Therefore, one plate accompanying the original description (t.18b) showing various parts of the palm is chosen as the lectotype.

The above description, based on Martius (1842) and Drude (1882), is unfortunately very incomplete, but it must remain so until additional collections are made. Burret (1928) studied a single sheet from Munich, a d'Orbigny collection from Bolivia labelled as Oenocarpus tarampabo. He concluded it to belong to the genus Jessenia. I have seen this same sheet and feel it is more likely a species of Oenocarpus. However, as this particular sheet consists of only two young rachillae lacking either flowers or fruits, it is of little taxonomic value, cannot be positively identified as O. tarampabo, and is best ignored.

Oenocarpus tarampabo is found in eastern Bolivia in the area of San Joaquín, Beni (ca. Lat. 13° S, Long. 65° W) and on the Rio Guaporé near Principe da Beira, Rondônia, Brazil (ca. Lat. 12°25' S, Long. 64°25' W). It is said to thrive in the wet forest along river margins. It flowers from April to May. Indigenous groups refer to these trees as trampabo or tarampabo.

Zarucchi (pers. comm.) confirmed the existence of a distichous-leaved Oenocarpus in Rondônia Brazil, seen during a Projeto Flora Amazônia expedition to that area. As neither herbarium material nor photographs were obtained, its positive identity cannot be established, although it is likely O. tarampabo.

Fig. 5.5. Lectotype of *Oenocarpus tarampabo* Martius, *t. 18b*, from *Palmetum Orbignianum* (1842).

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Fig. 5.6. Drawing of the habit of *Oenocarpus tarampabo* (right) t. 8, fig. 3, from *Palmetum Orbignianum* (1842). Other palms shown are *Thrinax chuco* (left) and *Euterpe precatoria* (center).

4. Oenocarpus bacaba Martius, Hist. Nat. Palm. 2:24-25. t.26. 1823.

Oenocarpus bacaba var. xanthocarpa Trail, in Im Thurn, Timehri 3:230. 1884.

Oenocarpus baccata, in Cuervo-Marquez, Trat. Elem. Bot. 458. 1913. nomen nudum.

Oenocarpus hoppii Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11:1041. 1934. Type. Brazil. Pará: cultivated in the gardens of the Museu Goeldi, Oct. 1932, Hopp 8(B).

Oenocarpus grandis Burret, Notizbl. Bot. Gart. Berlin-Dahlem 12:612. 1935. Type. Brazil. Amazonas: Manicoré, middle Rio Madeira. 1934, Hopp 1324(B).

Oenocarpus bacaba var. bacaba, in Wessels Boer, Acta. Bot. Venez. 6:327. 1971. nomen nudum.

Oenocarpus bacaba var. grandis (Burret) Wessels Boer, op. cit. 6:327. 1971. nomen nudum.

Oenocarpus bacaba var. parvus Wessels Boer, op. cit. 6:327. 1971. nomen nudum.

Trunk large, solitary, columnar, 8-20(-25) m high, (12-) 15-25 cm in diameter.

Leaves 7-17 per coma, robust, spirally arranged, fewer in younger or senescent plants; sheath ca. 0.75-1.10 m long, outer surface dull olive green, inner surface glabrous, brown,

upper margins lined with strawlike, brown, flexible fibers; petiole green to green-brown, ca. 0.6-1.0 m long, grey-lepidote at first, becoming more less glabrous; rachis green to dark green, unequally 4-sided in cross section towards center, 3.5-6.0 m long, maroon-lepidote when young, vesture becoming darker or grey with age and frequently falling away; pinnae 75-117 per side, inserted at regular intervals and all in same plane at apex, usually irregularly arranged towards middle and base either singly or in groups of 2-6(7) at various angles to rachis, linear to linear-lanceolate, acute, somewhat pendulous; basal pinnae (0.65-)0.7-1.2 m long, 1.5-4.0 cm wide; central pinnae (0.7-) 0.9-1.6 m long, 3-7 cm wide; apical pinnae (fourth from apex measured) (23-)30-70(-83) cm long, 1.5-2.25 cm wide.

Inflorescences 1 to several apparent at any one time, creamy-white at anthesis, changing to reddish powdery in fruit; prophyll olive green, 0.3-1.0 m long, 9-20 cm wide; peduncular bract similar in color, 0.8-2.0 m long, ca. 10+ cm wide, frequently somewhat brown-lepidote; axis distal to peduncular bract scar (7.5-)15-40 cm long, (2.35-)3.5-10 cm wide at scar, axis variable in size depending on individual; rachillae ca. 113-200 (-230), (55-)80-120(172) cm long, 4-7 mm wide, triads of 2 staminate and 1 pistillate flower on proximal 43-90% of individual rachillae but variable; staminate flowers creamy-white in bud; sepals ca. 1.5-1.75 mm long; petals ca. 3-5 mm long, ca. 1.5-3 mm wide; anthers ca. 3 mm long, filaments brown; pistillate flowers creamy

white in bud, ±110-190 per rachilla, ca. 4 mm long, ca. 4 mm wide at time of anthesis of staminate flowers.

Fruit globose to somewhat globose-elongate when mature, variable in size, (1.5)1.6-2.1(2.2) cm long (including cupule), (1.2-)1.4-2.1 cm wide, (1-)3-6 gms in weight when ripe, stigmatic residue apical to somewhat excentric, pointed, ca. 1 mm long, 2 mm wide; cupule tan, ca. 4-6 mm deep; epicarp grainy-waxy; mesocarp pulpy, light purple; fibers ca. 0.5 mm wide.

Type. Brazil. Amazonas, Martius s.n. (M ?, n.v.).

Distribution. Amazon and Orinoco Valley in Colombia, Venezuela, Guyana, Surinam, French Guiana, Peru, and Brazil.

Representative specimens.

COLOMBIA. Amazonas-Vaupés: Río Apaporis, entre los Ríos Kananarí y Pacoa, alt. 250 m, fr, 1-15 Dec 1951, H. García-Barriga 13914 (US). Meta: about 20 km SE of Villavicencio, alt. ca. 500 m, fr, 17 Mar 1939, Killip 34275 (US). Vichada: San Luis, 2 hours by car from Las Gaviotas, fr, 18 May 1978 Balick & Vargas 1201 (ECON, COL). Vaupés: Caño Cuduyarí, tributary of Río Vaupés, alt. 200 m, fl, 15 Oct. 1939, Cuatrecasas 7221 (COL, US); across from La Makarena, Río Vaupés, upriver from Mitú, fl, 9 Jul 1976, Zarucchi et al. 1815 (ECON).

VENEZUELA. Amazonas: near Macuruco, river above Santa Bárbara del Orinoco, fr, 29 May 1975, Berry 791 (BH, VEN); near Río Manapiare at camp at Caño Santo, fl, 7 Nov 1975,

Berry 1655 (BH, VEN); Santa Barbara del Orinoco Experimental Station, 1-2 km S of Trapichote, alt. 130 m, 26 Feb-12 Mar 1976, Berry & Chesney 2118 (BH, VEN); Cerro Duida, SE slopes along Cano Negro, tributary of Cano Iguapo, alt. 260 m, fl, 28-29 Aug 1944, Steyermark 56066 (F); Sierra Parima, vicinity of Simarawochi, Rio Matacuni, 6-7 km W of Venezuela-Brazil frontier, 18 April-23 May 1973, Steyermark 107569a (BH, VEN); near Puerto Ayacucho between airport and Rio Cataniapo, young fr, 25 Jul 1967, Wessels Boer 1875 (U); near San Carlos de Rio Negro, fr, 18 Jan 1968, Wessels Boer 2276 (U); Brazo Casiquiare near Solano, 8 Feb 1968, Wessels Boer 2408 (U); Yavita, alt. 128 m, fr. 1942, Williams 14129 (F, VEN); San Carlos de Rio Negro, alt. 100 m, 28 Feb 1942, Williams 14521 (US, VEN); Capihuara, Alto Casiquiare, alt. 120 m, fr, 27 May 1942, Williams 15586 (US, VEN). Barinas: 20 km N of Barrancas, Mun. Cruz Paredes, Dist. Obispos, alt. 300-600 m, fr, 29 Mar 1972, Marcano-Berti & Torres-Lezama 3002 (VEN). Bolivar: near El Palmar, alt. ca. 75 m, young fr, 24 Jun 1967, Wessels Boer 2080 (U). Delta Amacuro: lower Orinoco, Catalina, May 1896, Rusby & Squires 414 (M, NY, US).

GUYANA. East Berbice-Corentyne: Corentyne River, Mataroo Swamp, fl, fr, 12 Oct 1880, Im Thurn 3 (K); Corentyne River, fl, Jul 1880, Jenman 521 (FDG, K). Mazaruni-Potaro: Mazaruni Station, 16 Aug 1940, For. Dept. Fld. no. F542 (K, NY), seedling, 25 Jan 1944 For. Dept. Fld. no. F1558 (K); Potaro Road, km 37, seedling, 28 Sep 1951, For. Dept. Fld. no. 3089 (K); basin of Cuyuni River, Essequibo tributary, about 240 km from mouth, fr, 21-26 Nov 1937, Smith 2584 (A, F, K, NY, P, U, US).

SURINAM. Brokopondo: village of Brokopondo, fl, 6 May 1965, van Donselaar 2365 (U); near Powakka, 8 Oct 1962, Wessels Boer 157 (U); Afobaka Road, km 81 S of Paramaribo, fr, 18 Dec 1962, Wessels Boer 361 (U); near Berg en dal, fr, 19 Dec 1962, Wessels Boer 390 (U); Brownsberg, Mazaruni top, 4 Feb 1963, Wessels Boer 620 (U). Marowijne: Apetina on Tapanahoni River, ca. 100 m, 5 Jul 1977, Moore et al. 10319 (BH); Gonini River, 1 Nov 1962, Wessels Boer 253 (U); Lawa River, 3 Nov. 1962, Wessels Boer 265 (U); Afobaka, without date, Wessels Boer 358 (U); Mapane region, Camp 8, fr, 9 Jan 1963, Wessels Boer 473 (U); Oelemari airstrip near Brazil border, fr, 16-19 Mar 1963, Wessels Boer 905 (U); near Oelemari, fr, 19-20 Mar 1963, Wessels Boer 1014 (U). Nickerie: Palaime Creek, fr, 19-22 Feb 1963, Wessels Boer 709 (U). Saramacca: Stondansi, upper Nickerie, young fr, 9 Dec 1962, Wessels Boer 333 (U); hill near right branch of Coppename River, fl, fr, without date, Wessels Boer 1379 (U). Suriname: S of Paramaribo, near Mijnzorgweg, fr, fl, 19 Nov 1962, Wessels Boer 283 (U).

FRENCH GUIANA. Charvein, fr, 28 Jan 1914, Benoist 693 (P); Karounany, fr, 1855, Sagot 851 in part (P).

BRAZIL. Amazonas: Tefe, fr, 25 Sep 1947, Black 47-1522 (IAN); Manaus, Campo Salles, fr, Oct 1926, Huebner 83 (B); Experimental Station at Mazagão, Ilha das Barreiras, fr, 17 Jan 1956, Ledoux 56-1502 (IAN); Reserva Florestal Ducke, km 26 on Manaus-Itacoatiara Highway, fr, 6 Sep 1966, Prance et al. 2187 (BH, INPA, NY). Pará: Bôa Vista on the Tapajós River, fl, May-June 1929, Dahlgren & Sella 131 (F); lower

Trombetas, Achpicá Lake, fr, fl, 20 Sep 1910, Ducke 10973 (MG).

Cultivated.

BRAZIL. Pará: Botanical Garden of Museu Paraense Emilio Goeldi, cult. pl. no. 108, Dec 1977, Balick 966 (ECON).

Oenocarpus bacaba is a common, often social palm found in many terra firme areas from the lowlands up to an elevation of about 1000 m. Pio Correa (1926) noted that O. bacaba also grows in a high density palm swamp forest formation known as bacabal. I have seen this species growing only in areas that are rarely, if ever, flooded and with a density somewhat lower than other, more social species such as Jessenia bataua and Mauritia flexuosa. However, Indians and other local inhabitants relish the ripe fruits of O. bacaba and frequently cut the large trees for harvest, causing widespread depauperation in many areas that formerly may have contained large populations.

The type collection by Martius came from the forest near the confluence of the Rio Solimoes and Rio Negro. Here the local name is bacaba or bacaba-assú, the basis of his specific epithet. He noted that it flowers throughout the year, with fruits appearing in the months of November and December. As with all the palms of this complex, flowering and fruiting schedules vary from region to region. According to Wessels Boer (1965), the Surinam populations flower from November to February and fruit from February to May. Information associated with Huebner 83, discussed in Burret (1928),

noted October fruiting in Manaus. I have observed this species fruiting in the gallery forests of the Vichada, Colombia, from April to August, and sporadically at other times.

Burret (1928) discussed the chronology of descriptive errors that appear throughout the early literature on this species. Wallace (1853) depicted the palm to have regularly arranged pinnae, whereas in fact they are clustered. The entire fruits, as illustrated and described by Drude (1882), are somewhat larger than usual. Burret also mentioned that the thick fruit apex represented was a character that did not agree with his material. The section of the original description concerning the placement of the flowers on the rachis "Flores in ima ramorum basi solummudo foeminei" is in error, contradicting the drawing, in this case accurate, showing pistillate floral buds on the rachilla always surrounded by two staminate floral buds. A final error is noted in the plate of Oenocarpus bacaba by Barbosa Rodrigues (1903), where a small caespitose palm (page 45) is ascribed to that species. This plate more likely represents O. mapora, even in the view of Barbosa Rodrigues who, in the same work, described O. bacaba as "caudex excelsus...solitarius."

Two species described by Burret--Oenocarpus hoppii and O. grandis--are considered here to be synonymous with O. bacaba. I examined the extant type material of both species, which is presently at Berlin. Oenocarpus hoppii can be separated largely on its somewhat narrowed-elongate fruit

with a "stretched" appearance. When it is dissected, this unusual shape is shown to result from the aborted embryo and consequent narrowly-elongate seed, a condition that I have observed in the field only rarely in this complex. As the specimen was collected from a cultivated plant, some variation might be expected due to an unnatural environment. Careful comparison of the material, including foliage and inflorescence parts, seems to indicate with little doubt that it belongs to O. bacaba.

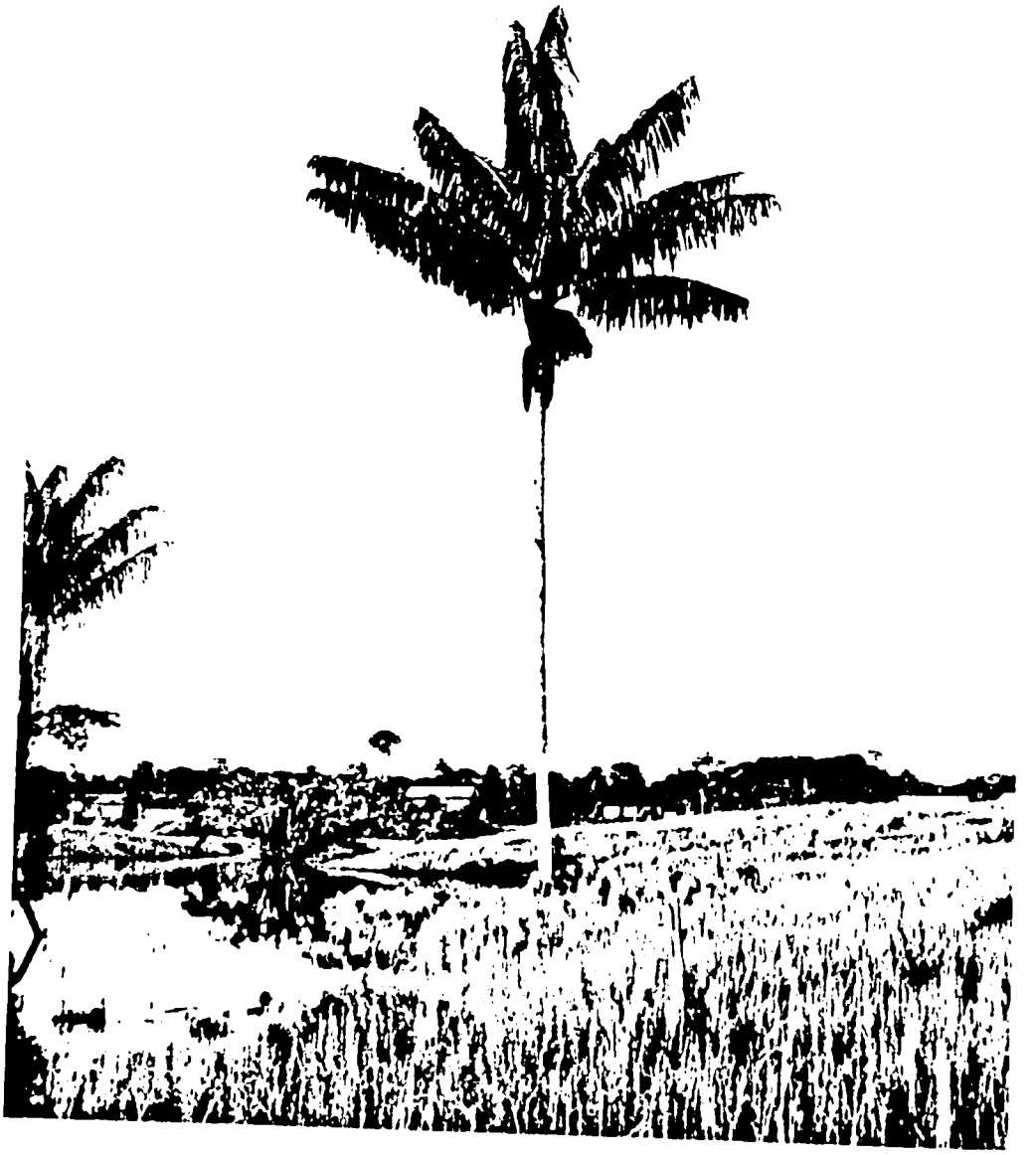
In the original description of Oenocarpus grandis, the species was placed in subsection Distichophyllum, characterized by two-ranked leaf arrangement. Distinction was drawn between that species and O. distichus on the basis of several fruit and leaf characteristics. I am unable to understand why this species was put into subsection Distichophyllum, when no mention of leaf arrangement was made in the original description nor on the label. Burret's final comment noted the unfortunate lack of a photograph, from which one could determine leaf arrangement. The type specimen of O. grandis (Hopp 1324), in fact, represents O. bacaba. The inflorescence has a short, broad rachis common in this species. The thick, undulate rachillae are not worthy of special distinction but rather frequently are indicative of an unusual local environmental condition or even of a disease. The dimensions of the fruit, rachis, and rachillae, and the percentage of pistillate flowers borne proximally on each rachilla (ca. 64%) all fall within the limits of the highly variable O. bacaba.

A number of varieties of Oenocarpus bacaba have been erected. The earliest, var. xanthocarpa, has no particular distinction and here placed in synonomy. One unusual note on this variety by Im Thurn (1884) is the occurrence of flowers usually with 6 stamens but apparently rarely having only 5. I have never seen any flower of this genus with fewer than 6 stamens; consequently, the populations from Corentyne, Guyana may prove quite interesting if this "character" is found to be frequent. Most likely, however, it was the result of breakage of a stamen or other mechanical damage.

In his key to the palm flora of that country, Wessels Boer (1971) listed three varieties of Oenocarpus bacaba from Venezuela: var. bacaba, var. parvus W. Boer, and var. grandis (Burret) W. Boer. The first, var. bacaba, distinguished by its "normal-sized" inflorescence with rachillae about 1 m long, represents the most widespread variety. A smaller tree (ca. 10 m high), var. parvus, has a stem diameter of 10 cm and leaves about 5 m long. The peduncle diameter measures about 3 cm between the bract scars, and the rachillae are about 60 cm long. Apparently this variety has been seen only in the upper Rio Negro in Territorio Amazonas. The taller, var. grandis, based on Burret's species, is of much larger stature, a stem diameter to 30 cm, leaves 8 m long, and a peduncle measuring 10 cm in diameter between the bract scars. Wessels Boer recorded that it is planted close to human settlements in the area of the upper Rio Negro. In his key,

none of the varieties is given a Latin description nor does he cite voucher specimens. To delimit varieties within species based solely on frequently plastic characters of size when only incomplete collections exist and photographs are lacking is difficult and unproductive and will not be attempted here. It is true that many forms exist: these vary in trunk, peduncle, rachillae, and fruit dimensions. In the future, it may be possible to recognize varieties and to describe them.

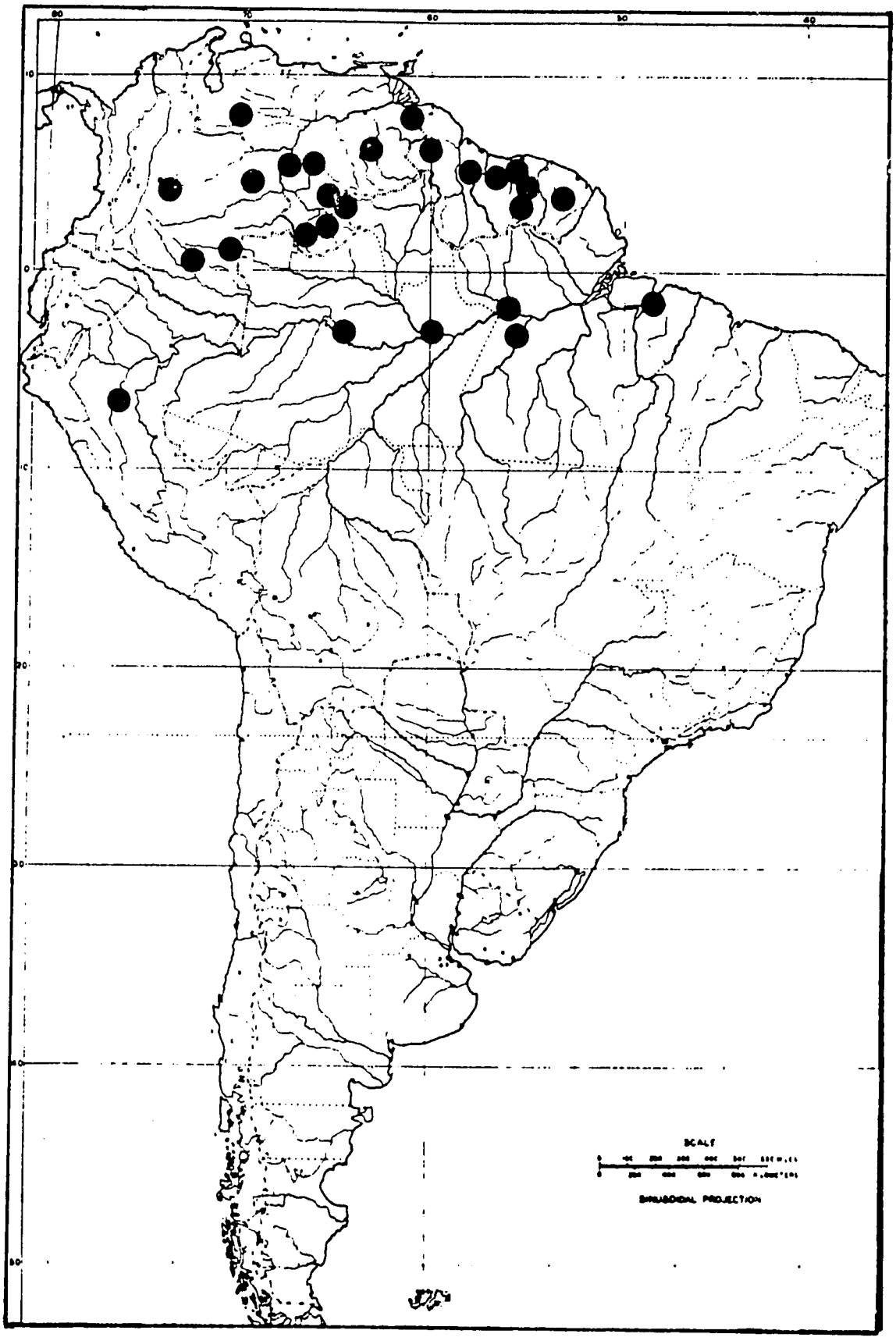
5.7 Oenocarpus bacaba Martius in a grassy field along the Río Vaupés, across from Mitú, Vaupés, Colombia.



5.8. Oenocarpus bacaba Martius: A. Mature prophyll and bract just below the crown of leaves, showing the vertical orientation common before the bract splits open (Balick et al. 954); B. Fruiting panicle (Balick et al. 972 Manaus, Brazil, destroyed); C. Young developing fruits along the rachillae (Vaupés, Colombia); D. Stem section at approximately 1 m from the ground (Balick et al. 954).

A
B
C
D

Fig. 5.9. Distribution of *Oenocarpus bacaba* Martius.


SCALE
SINUSOIDAL PROJECTION

5. Oenocarpus macrocalyx Burret, Notizbl. Bot. Gart. Berlin-Dahlem 11:1043, 1934.

Trunk large, stem diameter and habit unknown, to 30 m tall.

Leaves spirally arranged (?); sheath ca. 45 cm long, ca. 20 cm in diameter at base, maroon-lepidote abaxially, upper margins lined with a dense mass of slender, short, more or less rigid fibers; petiole and rachis ca. 2.9 m long; rachis at base 3 cm wide, more or less unequally 3-sided in cross section near middle (?), maroon-lepidote; pinnae numerous, usually inserted at regular intervals and all in the same plane but some grouped in pairs and inserted at various angles to the rachis; central pinnae to 75 cm long, 2.5-3.5 cm wide, linear-lanceolate, gently acuminate.

Inflorescences creamy white at anthesis; prophyll ca. 27 cm long; peduncular bract probably ca. 50 cm long; axis distal to peduncular bract scar 4.5-5 cm long, ca. 1.6-1.8 cm wide at scar; rachillae ca. 44, 26-44 cm long, ca. 3-5 mm wide at center; triads of 2 staminate and 1 pistillate flower on proximal 44-77% of individual rachillae, this variable depending on individual. Flowers unknown.

Fruit ellipsoid-acute, ca. 1.3-1.7 cm long (including cupule), 1.0-1.2 cm wide; stigmatic residue apical, ca. 1 mm high, ca. 1 mm wide; cupule tan, 3-4 mm deep, 6-10 mm wide; epicarp grainy, mesocarp thin, pulpy, fibers ca. 3-4 mm wide.

Type. Brazil. Amazonas: Livramento near border of Mato Grasso, Jan 1932, Hopp 1155 (B).

Distribution. Known only from Amazonas, Brazil.

Representative specimens.

BRAZIL. Amazonas: Mun. Humaytá, between Rio Livramento and Rio Ipixuna, fr, 7-18 Nov 1934, Krukoff 7052 (A, BH, F, K, LE, MO, NY, U, US).

This poorly known species has been collected only twice. The type (Hopp 1155), preserved at the Botanical Museum Berlin-Dahlem (B), consists of a fruiting panicle and a leaf. The other specimen, Krukoff 7052, comes from the basin of the Rio Madeira, on a plateau between Rio Livramento and Rio Ipixuna in Amazonas, Brazil.

Burret considered the length of the calyx an important character in this species. He distinguished *Oenocarpus macrocalyx* from the closely related *O. minor* by noting that in the new species the calyx extends to about 2/3 of the corolla, while in the latter species it is less than 1/2 as long. A much better criterion for separation of the two species, however, can be found in the inflorescence. The type specimen measures 5.25 cm in length from the peduncular bract scar to the rachis apex. In contrast, the usual range in *O. minor* is between 1.3-4.0 cm long. The rachillae are also somewhat larger than in the "normal" *O. minor* subsp. *minor* while the fruits are only slightly smaller.

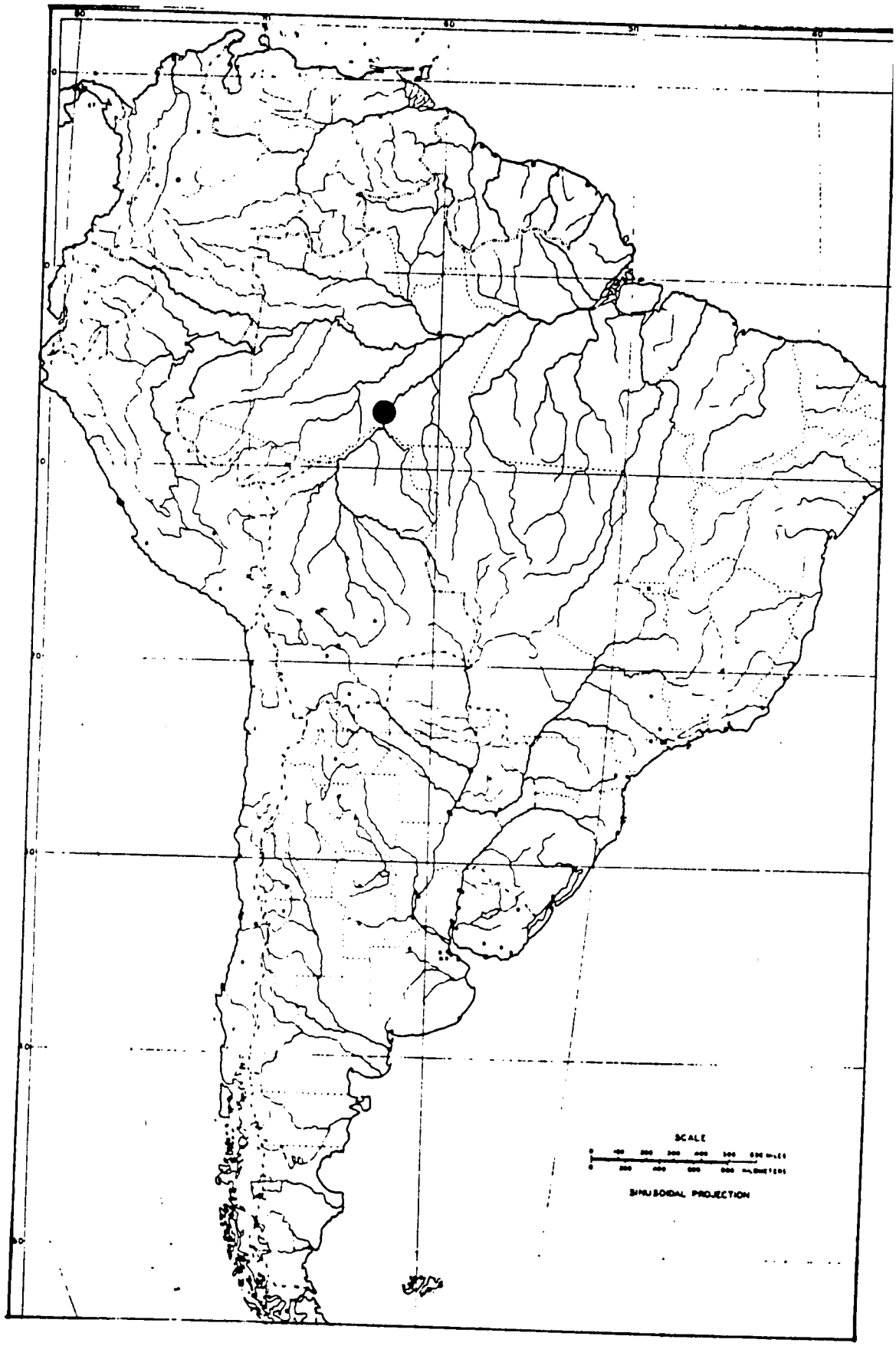
A comparison of *Oenocarpus macrocalyx* with *O. mapora*

reveals differences in both size and shape of the fruit. Fruits of O. macrocalyx are smaller (ca. 1.3-1.7 cm long by 1.0-1.2 cm wide, not including cupule), more narrowly ellipsoid, and sharply pointed, while those of O. mapora are larger (2.2-2.9 cm long by 1.4-2.25 cm wide, not including cupule) ellipsoid to ovoid, and frequently more or less apically rounded. In addition, the cupule of O. macrocalyx, ca. 3-4 mm deep, is somewhat smaller overall than that of O. mapora, ca. 5-9 mm deep.

There is no question that Oenocarpus macrocalyx is a very poorly understood species. Most of the Krukoff duplicates consist of immature fruit, causing difficulty in a distinction based on fruit. However, the specimen from GH has a few ripe fruits, conforming to Burret's general description and dimensions for O. macrocalyx, and can be clearly distinguished on this basis from O. mapora. Variation has been noted in rachis (of the inflorescence) dimensions, assuming that the Krukoff duplicates are all from the same species, posing further questions.

From a biological viewpoint, before Oenocarpus macrocalyx can be unquestionably maintained as a separate species, it must be recollected and photographed in its entirety. Using the local name bacabinha, it should be possible to relocate and study this palm, and work towards a solution of the taxonomic problems discussed.

Fig. 5.10. Distribution of *Oenocarpus macrocalyx* Burret.


SCALE
SINUSOIDAL PROJECTION

6. Oenocarpus mapora Karsten, Linnaea 28:274. t.55. 1857.

Trunk medium to large, caespitose, 2-12 per cluster or more rarely solitary, columnar, 3-16 (25) m high, 9-15 cm in diameter.

Leaves ca. 6-8 per coma, arching, spirally arranged; sheath ca. 45-95 cm long, outer surface dull olive green to leaden grey, inner surface glabrous, brown, upper margins lined with wiry brown fibers, petiole green to green-brown, ca. 15-95 cm long, ca. 2.5-3+ cm wide at apex, light brown to maroon-lepidote at first, indumentum becoming grey and frequently deciduous, then glabrous; rachis green, unequally 3-sided in cross section towards center, (.95)2.8-5.5 m long, lepidote; pinnae 60-71 + per side, inserted at regular intervals and all in the same plane at apex, often more or less irregularly arranged towards center and base, either singly or in groups of 2-4, at various angles to rachis (some to ca. 75°), linear-lanceolate, acute; basal pinnae ca. 55-75 cm long, 2.0-3.5 cm wide; central pinnae 0.6-1.0 m long, 3.5-5.5(-7.8) cm wide; apical pinnae (fourth from apex measured) 20-33 cm long, 1.25-2.75 cm wide.

Inflorescences 1 to several apparent at one time, creamy white at anthesis, changing to reddish powdery in fruit; prophyll olive green, ca. 25-45(57) cm long, somewhat lepidote; peduncular bract of similar color, 50-85+ cm long, ca. 4-8+ cm wide at center, light orange-lepidote when young, becoming dark orange-maroon with age; axis distal to peduncular bract scar 6-20 cm long, 1.9-4.75 cm wide at scar, axis variable in

size depending on the individual; rachillae ca. 64-98, 36-73 cm long, ± 2-5 mm wide, triads of 2 staminate and 1 pistillate flower on proximal 50-60% of individual rachillae; staminate flowers creamy white, sepals ± 1.5-1.75 mm long; petals 3-4 mm long, 1.5-2.0 mm wide, anthers ± 1.75-2.75 mm long, filaments brown, slender, straight to somewhat undulate; pistillate flowers creamy white in bud, 54-97 per rachilla, ± 3.0-3.5 mm long, 4.5-6.0 mm wide at time of anthesis of staminate flowers.

Fruit ellipsoid to ovoid, variable in size, 2.2-2.9 cm long (not including cupule), 1.4-2.25 cm wide, stigmatic residue more or less apical, ca. 2 mm long, 1-3 mm wide; cupule tan, ca. 5-9 mm deep, ca. 9-20 mm wide; epicarp grainy-waxy, mesocarp pulpy, lavender to purple, fibers ca. 0.5 mm wide.

KEY TO THE SUBSPECIES OF OENOCARPUS MAPORA

1. Abaxial surface of pinnae generally devoid of solitary and tufted, twisted trichomes between the intermediate veins, these, if present sparsely placed only on the intermediate veins; ripe fruits 1.8-2.5 cm long (not including cupule) by 1.4-2.0 cm wide. Costa Rica, Panama, and throughout much of the northern half of lowland South America . . . . . 6a. subsp. mapora.

1. Abaxial surface of pinnae densely covered with silvery, solitary and tufted, twisted trichomes between and on the intermediate veins; ripe fruits 2.5-2.9 cm long (not including cupule) by 1.75-2.25 cm wide. Colombia: Valle--Buenaventura and immediate vicinity. . . . . 6b. subsp. dryanderae.

6a. Oenocarpus mapora Karsten subsp. mapora.

O. multicaulis Spruce, Journ. Linn. Soc. 11:142. 1871.

Type. Peru. San Martin: Tarapoto, without date, Spruce hb. palm. 63, (K? n.v.).

O. huebneri Burret, Notizbl. Bot. Gart. Berlin-Dahlem 10:297. 1928.

Type. Brazil. Amazonas: Manaus, Jan 1927, Huebner 87 (B).

O. panamanus Bailey, Gent. Herb. 3:71, fig. 50-53. 1933.

Type. Panama. Canal Zone: Summit, experimental garden, 1 Jul 1931, Bailey 441 (BH).

Trunks caespitose, growing 6-12 together or solitarily. Pinnae generally devoid of trichomes between the intermediate veins abaxially, or if trichomes present, these mostly simple and bristlelike and appressed to the lamina, or else on the intermediate veins. Fruit ellipsoid to subovoid, variable in size, 1.8-2.5 cm long (not including cupule), 1.4-2.0 cm wide; cupule ca. 5-6 mm deep, 9-16 mm wide.

Type. Venezuela. Zulia: Perija de Maracaibo, without date, Karsten s.n. (isotype, LE).

Distribution. A widespread species occurring in Costa Rica, Panama and throughout much of the northern half of South America, up to an altitude of about 1000 meters.

Representative specimens.

COSTA RICA. Puntarenas: S of Río Terraba, E of Palmar Sur near sea level, 11 Mar 1953, Moore 6541 (BH).

PANAMA. Darién: Uriti River, fr, without date, Duke & Bristan 219 (MO); vicinity of La Palma, alt. 0-50 m, Jan & Feb 1912, Pittier 5484 (US). Panama: Arraiján, 15 Jun 1923, Maxon & Cook 7034 (US); along El Llano-Carti Road, 16-18.5 km by road N of Pan American Highway at El Llano, alt. ca. 400-450 m, fr, 28 Mar 1974, Nee & Tyson 10979 (MO). Canal Zone: Barro Colorado Island, Shore S, 9 Jun 1931, Bailey & Bailey 75 (BH); Barro Colorado Island, fr, 2 Sep 1929, Bangham 554 (A, US); forest reserve near crossing of Cruces trail and Madden Dam Road, fr, 29 Jun-12 Jul 1940, Bartlett & Lasser 16407 (MICH); Juan Mina, fr, 22 Jun 1923, Cook & Martin 39 (US); Barro Colorado Island, Frijoles, seedlings, 13 Jul 1923, Cook & Martin 58 (US); Las Cascades plantation beyond Summit, seedlings, 14 Jun 1923, Cook 7101 (US), fl, 11 Apr 1925, Cook s.n. (US); Barro Colorado Island, Fred Miller Trail 360, fl, 6 Dec 1967, Croat 4119 (MO), Gross Trail 260, S side of trail, fl, 16 Dec 1967, Croat 4366 (MO), Snyder-Molino Trial 290, young fr, 9 Apr 1968, Croat 4537 (MO), shoreline from SW edge of Peña Blanca Point to W edge of first deep cove (central cove), young fr, 23 Apr 1968, Croat 5042 (MO), AVA Trail 1650, fr, 11 May 1968, Croat 5503 (MO), along sandy beach NW of Colorado Point, 13 May 1968, Croat 5527 (MO), in and around clearing, seedlings, 12 Sep 1968, Croat 5960 (MO), Snyder-Molino Trail 325, fl, 22 Feb 1969, Croat 8093 (MO), Armour Trail 2600, 14 Mar 1969, Croat 8646 (MO), forest across stream from Smith house, 26 Mar 1970, Croat 9126 (MO), Zetek Trail 195, seedling, 22 Jun 1970, Croat 10977 (MO), N of Snyder-Molino Trail 200, seedling,

10 July 1970, Croat 11187 (MO); drowned forest of Río Puente, near junction with Río Chagres, alt. 66 m, fl, 7 Dec 1934, Dodge et al. 16827 (BH, US); Barro Colorado Island, fr, 18 Aug 1927, Kenoyer 169 (US); railroad relocation between Gorgona and Gatun, alt. 10-50 m, 7 Jan 1911, Pittier 2293, 2295 (US); around Las Cruces, alt. 20-100 m, 1 Feb 1911, Pittier 2628 (US); Barro Colorado Island, fr, 2 Sept 1929, Salvoza 954 (A).

COLOMBIA. Antioquía: Porcesito, valley of Río Medellín, alt. 110 m, fl, 19 May 1946, Hodge 6863 (BH, GH); Peñas Blancas, fl, 29 Apr 1926, Juzepczuk & Woronow 4636 (LE), fl, 5 May 1926, Juzepczuk 4709 (LE), fl, 25 Apr 1926, Woronow & Juzepczuk 4537 (LE). Caqueta: Hetucha near Río Orgeguaza, fl, 30 Jul 1926, Woronow & Juzepczuk 6320 (LE). Chocó: Cabo Marzo, 13 Sep 1970, Moore et al. 9873 (BH). Meta: Cabuyaro, Jan 1937, H. García-Barriga 5103 (US); SE of Villavicencio, fr, without date, Killip 34275 (US). Nariño: delta of Río Mira, near Tumaco, sea level, fl, June 1966, Schulz & Rodríguez P. 492 (U), fr, June 1966, Schulz & Rodrígues P. 502 (U); Norte de Santander: Bellavista on pipeline fl, alt. ca. 830 m, 15 Sep 1946, Foster & Foster 1672 (GH); Petrolea, beginning of pipeline, ca. 60 m, fr, 24 Sep 1946, Foster & Foster 1785 (BH, GH). Vaupés: selve entre Calamar y San José del Guaviare, alt. 240 m, fl, 1 Nov 1939, Cuatrecasas 7368 (US). Vichada: Guacamayas, fr, 26 Jul 1976, Balick & Hoyos 76-19 (COL, ECON); Topochera, Las Gaviotas, fr, 9 May 1978, Balick & Vargas 1199 (COL, ECON). Santander: Puerto

Wilches and vicinity, alt. 100 m, 28 Nov-2 Dec 1926, Killip & Smith 14808 (GH, NY, US); km 16 between Puerto Wilches and Puerto Santos, alt. 110-115 m, 29 Nov 1926, Killip & Smith 14845 (A, NY, US); Puerto Wilches, between La Gómez and km 80 of Atlantic railroad, alt. 100-200 m, 19 Apr 1960, Romero Castañeda 8313 (MO, NY).

VENEZUELA. Apure: Reserve Forestal San Camilo, S of San Camilo (El Nula) to Río Sarare, young fr, 27 Mar 1968, Steyermark et al. 101380 (BH, VEN). Barinas: along Highway 5, between Río Acequia and junction with road to Ciudad Bolivia, 4 km SW of junction, alt. 175 m, fl, young fr, 25-26 Aug 1966, Steyermark & Rabe 96507 (F, U, US, VEN); near Barinitas, alt. ca. 200 m, fl, 6 May 1967, Wessels Boer 1774 (U); near crossing of Barinas-San Cristóbal road and Río Bumbún, alt. ca. 250 m, young fr, 15 June 1967, Wessels 1855 (U), fl, 16 Jun 1967, Wessels Boer 1857 (U). Zulia: Sierra de Perija, near Quebrada Koshida (Kosida) S of Misión de Los Angeles de Tokuku (Tocucu), SW of Machiques, alt. 325-350 m, fl, 13 Aug 1967, Steyermark 99963 (BH, US, VEN); along Pan American Highway, 30 km N of Caño Zancudo, alt. ca. 100 m, 5 Dec 1967, Wessels Boer 2115 (U), fl, 5 Dec 1967, Wessels Boer 2117 (U).

ECUADOR. Napo: 16 km from Lago Agrio on road to Quito, fl, 10 Apr 1978, Balick & Allon 1188 (ECON, QCA).

PERU. Loreto: along road near Lake Quistachocha, Iquitos, fr, Feb 1978, Balick et al. 975 (AMAZ, BH, ECON, MO, USM); Maynas, Río Yaguasyacu, affluent of Río Ampiyacu,

Brillo Nuevo and vicinity, fl, 30 Jan 1978, Balick et al. 987 (AMAZ, BH, ECON, MO, USM); Yurimaguas, lower Río Huallaga, alt. ca. 135 m, fl, 23 Aug-7 Sep 1929, Killip & Smith 27648 (F, NY, US); Coronel Portillo, 6-8 kms beyond Aguaytía on road to San Alejandro, alt. ca. 330 m, fl, 29 Apr 1960, Moore et al. 8376 (BH); Coronel Portillo, 6-10 kms from Pucallpa, fl, 7 May 1960, Moore et al. 8406 (BH). San Martin: Mariscál Cáceres, Tocache Nuevo, alt. 300 m, fl, 6 Mar 1978, Balick et al. 1157 (ECON, USM); near km 15, road from Tarapoto to Yurimaguas on Cerro de Escalero, alt. ca. 920 m, young fr, 26 May 1960, Moore et al. 8525 (BH).

BRAZIL. Acre: near mouth of Rio Macauhan, tributary of Rio Yaco, fl, 5 Sep 1933, Krukoff 5803 (K, NY); Amazonas: basin of Rio Madeira, Humayta near Tres Casas, fl, 14 Sep-11 Oct 1934, Krukoff 6402 (K, NY).

BOLIVIA. Pando: W bank of Río Madeira opposite Abuña, fr, 19 Nov 1968, Prance et al. 8677 (BH, INPA, NY).

CULTIVATED SPECIMENS

BRAZIL. Pará: Botanical Garden of Museu Paraense Emílio Goeldi, cult. pl. nos. 239-240, fr, Dec 1977, Balick 964 (ECON), cult. pl. no. 450, Dec 1977, Balick 965 (ECON), without cult. pl. no. fl, 30 Jun 1965, Cavalcante 1419 (MG).

DOMINICA. Dominica Botanical Garden, fr, 15 May 1968, Read 2012 (US).

PERU. Loreto: Coronel Portillo, in garden by Forestry Office, Pucallpa, 11 May 1960, Moore et al. 8412 (BH).

PHILIPPINE ISLANDS. Laguna Province, Los Baños College,

College of Agriculture Campus, beside Language Building, 15 Sep 1966, Moore & Pancho 9398 (BH); Luzon, in College of Agriculture grounds, fr, 27 Aug 1958, Pancho 2036 (BH).

SRI LANKA. Peradeniya, Royal Botanical Garden, fl, 20 Nov 1963, Moore 9032 (BH).

Oenocarpus mapora was described by Karsten from Perija, near Lake Maracaibo, Venezuela. The type specimen was a solitary individual. Spruce, in 1871, named a caespitose palm, O. multicaulis, from the Peruvian Amazon. It was not apparent to him that O. mapora was actually a widespread species found, even within the same population, both solitary and caespitose. Studies in the gallery forests of the Colombian Llanos show that individual trees are extremely variable. For example, arrangement of pinnae may be more or less regular in a single plane, with an occasional grouping of 2 or 3 pinnae or, irregular in clusters of up to 4 pinnae together and inserted at many angles to the rachis. Plants may be solitary, or comprise up to 12 trunks growing in a tight cluster.

The true status of Oenocarpus mapora was not clear to me, until I studied the Venezuelan collections of Wessels Boer from Zulia and Barinas. These are identical to the specimens seen and collected throughout the Amazon, there recognized as O. multicaulis. While O. multicaulis is a more distinctive name for this usually caespitose palm, it must be considered synonymous with the earlier O. mapora and the latter epithet now used.

In this treatment, three species previously described are considered synonymous with Oenocarpus mapora subsp. mapora. Burret (1928) described O. huebneri from a collection on the Rio Uripiranga near Manaus. According to the field label, the specimen was purchased as a small seedling in Manaus and later planted. It is known only from cultivation. I made an herbarium specimen from what is likely a progeny of the type tree (or the type tree itself?) growing in the gardens of the Museu Emilio Goeldi in Belém. Burret's type was also seen, now consisting of only a sheath and bracteate inflorescence. The living material of these two species looks very similar. One possible superficial distinction might be the somewhat narrower central pinnae (ca. 5.5-6.5 cm) of material from Museu Goeldi garden nos. 239-240 ("O. huebneri") in comparison with the wider (ca. 7.0-7.8 cm) pinnae of no. 450 (O. mapora). However, as O. mapora shows such wide variation in habit, stem, leaf, and inflorescence size throughout its great range, a specific delimitation cannot be made on this single character. One curious condition in the Huebner type is undulate filaments of the staminate inflorescence. This is uncommon in O. mapora, and if additional populations along the Rio Uripiranga are located and further studied, perhaps support for legitimate distinction at some level could be found.

Bailey's description (1933) of Oenocarpus panamanus represents the first technical account of the genus from Panama. Hitherto, the name usually applied to the Panamanian

species was Oreodoxa regia (cf. Seemann 1854, p. 203). Bailey distinguished his new species from O. multicaulis (= O. mapora) on the basis of what he felt were its smaller staminate flowers ("...minoribus floribus staminatis differens."). Panama is a relatively well studied tropical region. Abundant herbarium material from the Canal Zone, Darien and Panama Provinces, and Barro Colorado Island is available. Bailey took a number of photographs (eight on Barro Colorado Island; seen from BH and F) as did Cook (Cook neg. nos. 27285-27294 at Las Cascades, C.Z., seen from U.S.). In my opinion, the Panamanian populations represent nothing more than a range extension for Oenocarpus mapora. All leaf, stem, flower, and fruit dimensions fall well within the normal limits of this species. The same two arrangements of pinnae, more or less regular or somewhat irregularly grouped, occurring in Amazonian specimens can also be seen in Panamanian material. In his discussion accompanying the description, Bailey cites the need for additional collections and close field observation before "...the group is well understood or the limits of species clarified." The broader geographic outlook taken during the present study, throughout the range of this species, indicates the identity of Bailey's species as O. mapora.

While Croat (1978) listed exact flowering and fruiting times as unknown on Barro Colorado Island, it is suggested that plants flower more than once a year. He has observed fruiting to be from March to July, and noted that plants

often bear fruiting and flowering inflorescences at the same time. The following table offers a selection of those specimens seen in fruit.

Specimen	Location	Date
Krukoff 5803	Rio Purus, Acre, Brazil	September 5, 1933
Steyermark 96507	Río Acequia, Barinas, Venezuela	August 25-26, 1966
Balick 964	Cultivated in Belém, Brazil	December 1977
Balick et al. 975	Iquitos, Peru	January 1978
Balick et al.987	Río Yaguasyacu, Loreto, Peru	January 30, 1978
Balick et al. 1199	Las Gaviotas, Vichada, Colombia	May 9, 1978

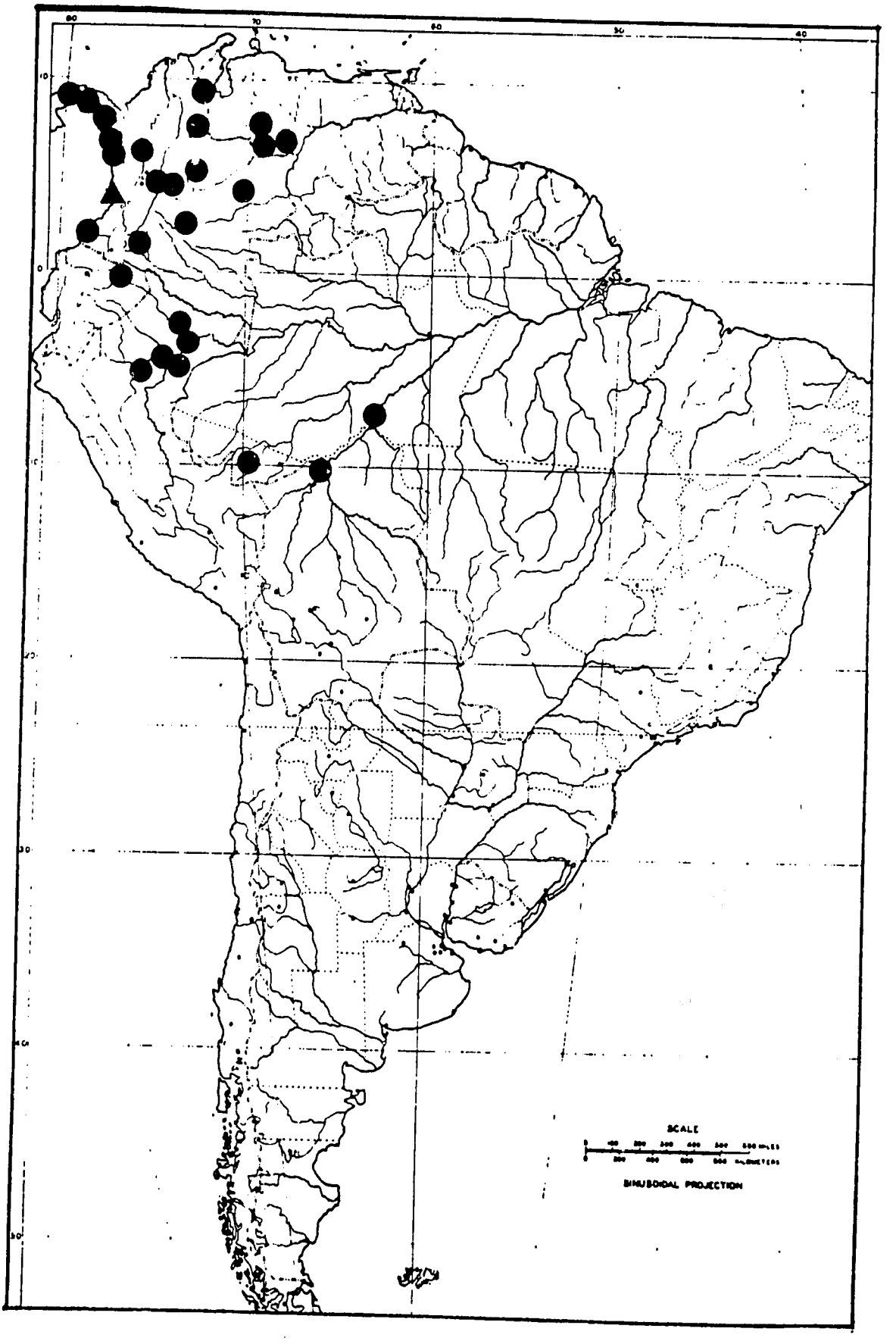
Future research should give a more exact picture of differences in the regional phenology of this widespread species.

Fig. 5.11. Oenocarpus mapora Karsten subsp. mapora, showing caespitose habit (Vichada, Colombia).

Fig. 5.12. Oenocarpus mapora Karsten subsp. mapora: A. Developing inflorescence, enclosed by prophyll and bract, below the crown of leaves. Note the ripe fruiting panicle ca. 2 nodes below the inflorescence (Balick et al. 987); B. Inflorescence enclosed by prophyll and bract. Note dentate margins of prophyll (Balick et al. 987); C. Panicle with ripe fruit (Vichada, Colombia); D. Arrangement of pinnae on the rachis (Balick et al. 975).

c
d

Fig. 5.13. Distribution of *Oenocarpus mapora*: ● = subsp. *mapora*; ▲ = subsp. *dryanderae*. Costa Rican distribution of sub. *mapora* not shown.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6b. Oenocarpus mapora Karsten subsp. dryanderae (Burret) Balick stat. nov.

Oenocarpus dryanderae Burret, Notizbl. Bot. Gart. Berl. 11:865. 1933.

Trunks caespitose, growing fewer than 5 together or rarely solitary (?). Pinnae densely covered with silvery, solitary and tufted, twisted trichomes abaxially both between and on the intermediate veins. Fruit more or less ovoid, variable in size, 2.5-2.9 cm long (not including the cupule), 1.75-2.25 cm wide; cupule ca. 8-9 mm deep, 15-20 mm wide.

Type. Colombia. Valle: Buenaventura, without date, Dryander 11 (B).

Distribution. At present known only from Buenaventura and vicinity. Valle, Colombia.

Representative specimens.

COLOMBIA. Valle: Station Bajo Calima, 4 km upstream from Bajo Calima (Pto. Patiño) on Río Bajo Calima, ca. 32 km NE of Buenaventura, fl, fr, 6 Mar 1975, Anderson 18 (INPA); Buenaventura, 3 May 1926, Cook 74 (US), fr, 26 May 1926, Cook 152 (US); Forests in concession of Carton Colombia, vicinity of Buenaventura, 10 Feb 1967, Moore et al. 9459 (BH); slope by road near Río Anchicayá, vicinity of Buenaventura, fr, 13 Feb 1967, Moore et al. 9479 (BH).

Burret based his original species on an unnumbered

collection made by Mrs. E. Dryander from an island in the Bay of Buenaventura, Colombia. Subsequently, other material of the species was collected in this vicinity and a better understanding of the plant obtained. In the description, Burret admitted that the new species was closely related to Oenocarpus multicaulis (=O. mapora). Upon further study of the newly collected material it appears that delimitation at the specific level is not warranted. Rather, the palm seems more worthy of subspecific status. It is distinguished by characteristic abaxial tomentum of the pinnae and fruit somewhat larger than O. mapora subsp. mapora. There appears to be an interface population between the two subspecies, as fragmentary collections of palms with modified abaxial pinnae vesture have been noted in Colombian material.

The species that Dugand (1976) referred to as the sole representative "apparently pertaining" to this subspecies at COL (Killip 35513) is in reality a specimen of Euterpe. Two basic common names are recorded for this species, milpesillo (O. F. Cook 152) and Don Pedrito or San Pedrito (A. B. Anderson 18).

Fig. 5.14. Oenocarpus mapora Karsten subsp. dryanderae (Burret) Balick stat. nov., showing habit (Anderson 18). Photograph by A. B. Anderson.

7. Oenocarpus minor Martius, Hist. Nat. Palm. 2:25-26. t. 27. 1823.

Trunk medium, solitary to caespitose, columnar, 4-10 m high, 4.4-8.0 cm in diameter.

Leaves ca. 6-10 per coma, gracefully arched, spirally arranged; sheath ca. 30-60 cm long, outer surface green-brown, red-brown-lepidote at first, becoming more or less glabrous; inner surface glabrous, brown, upper margins lined with brown, slender, wiry fibers; petiole green, ca. 20-40 cm long; rachis green, more or less unequally 3-sided and abaxially convex towards center, 1.8-4.0 m long, maroon-lepidote when young; pinnae 49-79 per side, inserted at regular intervals and all in the same plane or rarely with an occasional grouping of 2-3, linear-lanceolate, abruptly acuminate to somewhat irregularly attenuate; basal pinnae ca. 40-70 cm long, 1.2-1.75 cm wide; central pinnae ca. 40-72 cm long, 2.5-4.5 cm wide; apical pinnae (fourth from apex measured) ca. 20-38 cm long, 1.5-2.5 cm wide.

Inflorescences 1 to several apparent at any one time, creamy white at anthesis, changing to reddish powdery in fruit; prophyll light olive-green, ca. 20-35 cm long, 4-6(-10) cm wide, more or less glabrous; peduncular bract green, ca. 28-68 cm long, 4-6 cm wide, orange-red to maroon-lepidote; axis distal to peduncular bract scar 1.3-4.0 cm long, 0.9-2.4 cm wide at scar, axis variable in size depending on individual; rachillae ca. 25-72, (17-)26-56 cm long, slender, 4-7 mm wide, triads of 2 staminate and 1

pistillate flowers on proximal 35-66% of individual rachillae; staminate flowers creamy white, sepals ca. 1.0-1.5 mm long; petals 3.0-4.5 mm long, 1.5-2.0 mm wide; anthers ca. 2.0-2.5 mm long, filaments brown, slender, straight to somewhat undulate; pistillate flowers creamy white in bud, 25-104 per rachilla, ca. 2.5-3.5 mm long, 3.5-4.0 mm wide at anthesis of staminate flowers.

Fruit globose-ovoid to ellipsoid, acute, ca. 1.6-2.3 cm long (including the cupule), 1.0-1.6 cm wide; stigmatic residue apical to subapical, ca. 1-2 mm long, 1.0-1.5 mm wide; cupule tan, 3-5 mm deep by ca. 1 cm wide; epicarp smooth, somewhat grainy-waxy, mesocarp pulpy, light purple, fibers ca. 0.5 mm wide.

KEY TO THE SUBSPECIES OF OENOCARPUS MINOR

7a. Stems solitary; axis of inflorescence distal to peduncular bract scar 1.3-2.1 cm long, 0.9-1.9 cm wide at scar; rachillae 25-35. Brazil (Amazonas and Pará) and elsewhere? . . . . . .7a. subsp. minor.

7b. Stems caespitose; axis of inflorescence distal to peduncular bract scar 1.5-4.0 cm long, 1.8-2.4 cm wide at scar; rachillae 54-72. Brazil (Amazonas and Pará) and elsewhere? . . . . . .7b. subsp. intermedius.

7. Oenocarpus minor Martius subsp. minor.

Ö. microspadix Burret, Notizbl. Bot. Gart. Berlin-Dahlem 12:297. 1928. Type. Brazil. Amazonas: Manaus, Campos Salles, Oct 1926, Huebner 82 (B).

Trunk solitary. Rachis 2-3 m long; pinnae 51-60+ per side. Prophyll ca. 4-6 cm wide; peduncular bract 28-42 cm long; axis distal to peduncular bract scar 1.3-2.1 cm long, 0.9-1.9 cm wide at scar; rachillae 25-35, (17-)26-40 cm long; pistillate flowers 25-85 per rachilla, ca. 2.5-3.0 mm long at anthesis of staminate flowers.

Type. Brazil. Amazonas: Manaus, 1810-1820, Martius 3121B (M. isotype P).

Distribution. Centered in Amazonian Brazil, although reported in the literature as occurring elsewhere.

Representative specimens.

BRAZIL. Amazonas: Reserva Florestal Ducke, Manaus-Itacoatiara highway, km 26, fl, 25 Oct 1977, Balick et al. 903 (BH, ECON), fl, 27 Dec 1977, Balick et al. 969 (ECON), 4 Apr 1967, Byron & Elias 67-2 (INPA); Cuieiras-Manaus trail, km 1, fr, 6 Apr 1974; Campbell et al. P21875 (INPA, NY); Manaus, estrada velha da BR 17, km 40, fl, 11 Nov 1955, L. Coêlho 2886 (INPA); Caviana, Rio Purus, fl, 29 Jan 1955, Ernani 765 (INPA); Manaus, Campos Salles, fl, Oct 1926, Huebner 81a (B); Manaus -Porto Velho road, km 245, 3 km S of Igapó Açu, fr, 13 Mar 1974, Prance et al. 20470 (BH, INPA); Manaus, Igarapé do Cachoeira, 1855, Spruce hb. palm 3 (K); Rio Tarumá near Manaus,

fr, 1855, Spruce hb. palm 57 (K). Pará: Rio Jamundá, São Jorge, Faro, fl, 10 Nov 1950, Black & Ledoux 50-10686 (IAN). Rondônia: Basin of Rio Madeira, 8 km NE of Porto Velho, 9 Nov 1968, Prance et al. 8278 (BH, INPA, NY).

CULTIVATED. BRAZIL. Pará: Botanical garden of Museu Paraense Emilio Goeldi, Belém, cult. pl. nos. 27-28, Dec 1977, Balick 963 (ECON, MG), cult. pl. no. 880, Oct 1965, Cavalcante 1422 (MG).

According to the literature, Oenocarpus minor is a wide ranging species. It is, however, poorly represented by voucher collections. Martius (1823) described the type collection from the Rio Negro. Here it was said to be found freely dispersed but rarely social in the forests of the interior. Wallace (1853), whose herbarium specimens and drawing of this tree were lost, reported it to be common in the dry virgin forests of the Upper Rio Negro. Drude (1882) gave its range as the entire Amazon Valley, in shady, moist primary forest. Others wrote that the plant occurs in the Vaupés of Colombia (Cuatrecasas, 1958), the upper Essequibo of Guyana (Im Thurn, 1884), throughout the Orinoco region (Jahn, 1908) and "probably" in Peru (MacBride, 1960). This last reference appears to have been based solely on Dahlgren's listing of the species from Peru in his Index of American Palms. Wessels Boer (1971) made no mention of it in his key to the palms of Venezuela. In going through his Venezuelan collections now preserved at Utrecht (U), I did not find this species.

Most of these localities cannot be verified by existing

herbarium material or from personal observation. All of the specimens seen are from Brazilian territory, and it is likely that many of the other distribution records in the literature are based on misinformation or confusion with closely related species.

Burret (1928) commented that the fruiting panicle illustrated in the original description is not drawn proportionally to the actual plant. In addition, he felt that the stigmatic residue on the ripe fruit (fig 13) was too blunt. Examination of the material at hand gives some credence to these observations.

Reports by Pio Correa (1926), Barbosa Rodrigues (1903), and Huber (1909) of varying panicle length in Oenocarpus minor all ascribe this to the existence of several different varieties. Huber, however, mentioned a specimen of his (8891) with an inflorescence axis measuring about 10 cm in length and rachillae about 50 cm long as belonging to this species; probably it represents another species, such as O. mapora. Barbosa Rodrigues observed that the several varieties ("plusieurs variétés") could be distinguished by their appearance and, in addition, the panicle length. Such differences in size or appearance may be due to age, environmental conditions or actual heritable characters.

Burret (1928) described a new species, Oenocarpus microspadix, from an apparently depauperate tree of O. minor subsp. minor, basing it on the especially small panicle (ca. 18.5-20 cm long) and staminate flowers (ca. 3 mm long). The

type specimen grew in the same forest as O. minor subsp. minor in an area near Manaus. My own field experience provides justification for treating O. microspadix as a synonym of O. minor subsp. minor. Specimens of this subspecies growing only a few meters apart, collected in Reserva Florestal Ducke, Manaus, had extremely variable panicles that were exactly comparable to the situation described above. This difference was felt to be a function of exposure or location, rather than to specific or varietal limits. As Burret had only limited field experience in the Amazon Valley, he often did not recognize such examples of phenotypic plasticity and instead described deviant forms as new species.

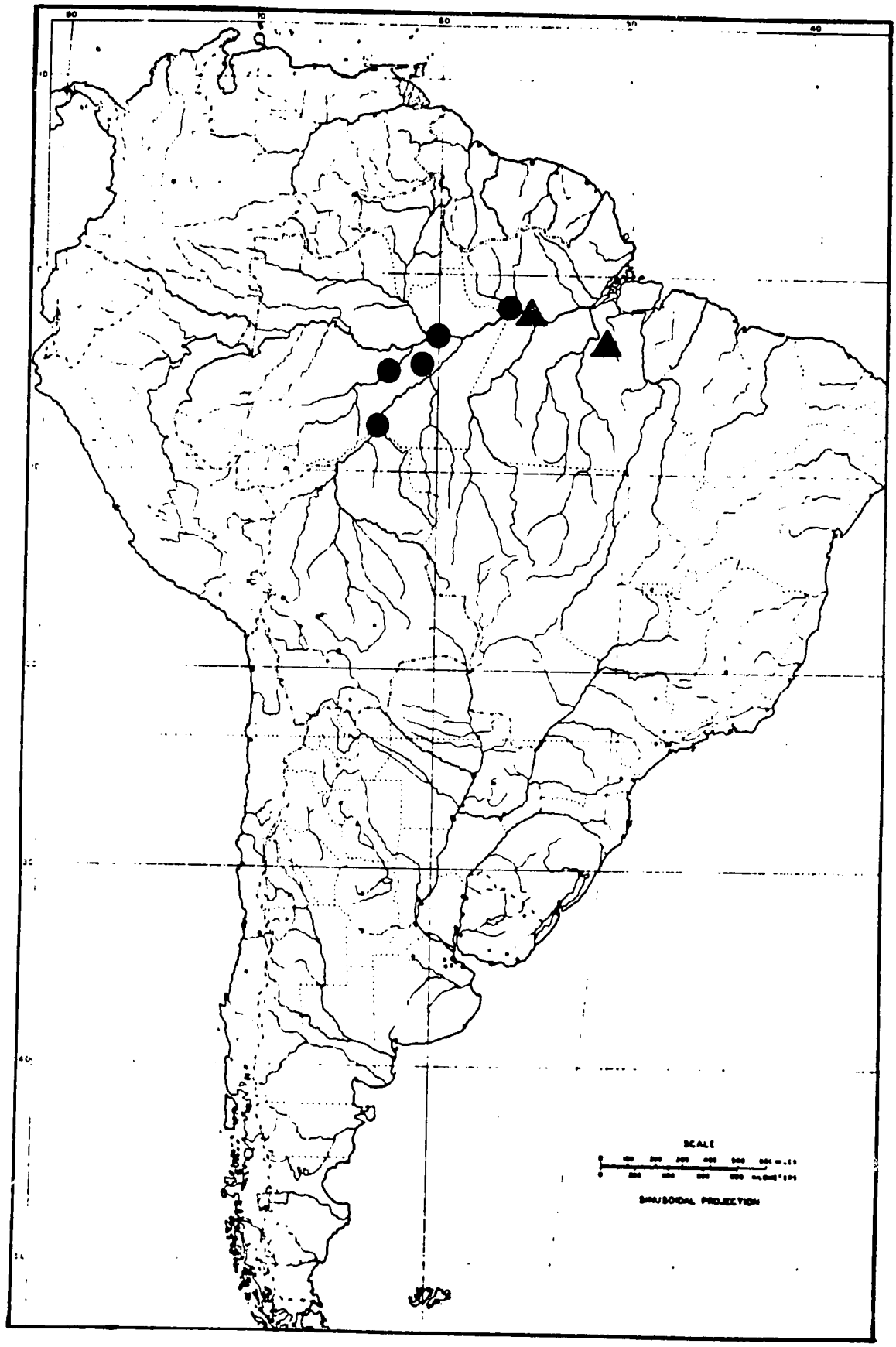
The unusual statement that this is a "pot-bellied" species was made by Pio Correa (1926). I have never known this condition to occur in Oenocarpus, and his report is probably the result of confusion with another genus.

According to Martius (1823), Oenocarpus minor flowers throughout the year. His fruiting and flowering material from Pará was collected between October and December. I made similar collections during the same time of the year in Manaus. Other specimens with ripe fruits include Cavalcante 1422 from cultivation in Belém (October 1965) and Campbell et al. P21875, from the Cuieiras-Manaus trail (April 6, 1974).

Although the fruits of Oenocarpus minor are small, Barbosa Rodrigues (1903) pointed out that they contain relatively more pulp than do some of the other species. In his opinion, the wine-colored drink produced from these fruits is very agreeable.

Fig. 5.15. Oenocarpus minor Martius subsp. minor, ca. 4.5 m tall, growing in Reserva Florestal Ducke, Manaus (Balick et al. 903).

Fig. 5.16. Distribution of *Oenocarpus minor* Martius: ● = subsp. *minor*; ▲ = subsp. *intermedius*.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7b. Oenocarpus minor Martius subsp. intermedius (Burret) Balick stat. nov.

Oenocarpus intermedius Burret. Notizbl. Bot. Gart. Berlin-Dahlem 10:298. 1928.

Trunks caespitose. Rachis 1.8-4.0 m long; pinnae 49-79 per side. Prophyll ca. 10 cm wide; peduncular bract ca. 38-68 cm long; axis distal to peduncular bract scar 1.5-4.0 cm long, ca. 1.8-2.4 cm wide at this scar; rachillae 54-72, ca. 31-56 cm long; pistillate flowers 32-104 per rachilla, ca. 3.0-3.5 mm long at anthesis of staminate flower.

Type. Brazil. Amazonas: Manaus, Campos Salles, Jan 1925, Huebner 1(B).

Distribution. Known to date only from Amazonas and Pará in Brazil, but perhaps wider ranging.

Representative specimens.

BRAZIL. Amazonas: Reserva Florestal Ducke, Manaus -Itacoatiara highway, fr, 27 Dec 1977, Balick et al. 968 (ECON, MG, NY); Colonia Santo Antonio, Manaus-Itacoatiara highway, km 7, fr, 16 Mar 1967, Moore et al. 9540 (BH, INPA, NY). Pará: 1 km W of Ruropolis on BR 230, fl, 29 Nov 1977, Balick et al. 953 (ECON, MG, NY).

A single panicle consitutes the entire remaining collection of Huebner 1, designated by Burret as the type specimen. This is recorded from a terra firme location, as

is Balick 953, of the same species. In contrast, Moore 9540 was collected in a swampy area on sandy soil. Along with the type collection, Burret received a photograph of this palm (Huebner photograph No. 1), which I unfortunately was unable to locate at Berlin during my visit to that institution.

Oenocarpus subgen. *Oenocarpopsis* (Burret) Balick stat. nov.

Oenocarpus Sect. *Oenocarpopsis* Burret, *Notizbl. Bot. Gart. Berlin-Dahlem* 10:292, 300. 1928.

Medium, solitary palms; stem covered throughout with a dark brown, tightly woven fibrous network, even in adult state. Pinnae ovate-oblong or oblong-lanceolate at center of rachis. Inflorescence weakly hippuriform; peduncle elongate and thin, bearing a small cryptic prophyll (not seen) completely obscured by fibrous network and a larger, tubular peduncular bract with a long slender base forming a manubrium and tapering to a sharp point at apex, splitting along only about one-half its length and persisting. Staminate flowers with 3 briefly connate sepals.

Type. *Oenocarpus circumtextus* Martius.

This subgenus consists of a single species, *Oenocarpus circumtextus*.

8. Oenocarpus circumtextus Martius, Hist. Nat. Palm. 2:26, t. 26, fig. 3-4. 1823.

Trunk medium, ca. 3-6 m high, ca. 10-14 cm in diameter.

Leaves spirally arranged; sheaths completely obscured by fibrous reticulum; petiole and rachis ca. 3 m long, at first somewhat lepidote, then more or less glabrous; rachis towards apex rounded abaxially and keeled adaxially; pinnae fewer in number than in other species, inserted at regular intervals and all in the same plane, ovate-oblong or oblong-lanceolate; central pinnae ca. 50-70 cm long and 10-12 cm wide, last 10-22 cm forming a long, narrow acumen ca. 2-3 mm wide which is abaxially lepidote; apical pinnae (fourth from apex measured) ca. 24 cm long, ca. 6.75 cm wide.

Inflorescences 1 to several apparent at one time; prophyll (not seen on herbarium material) presumably much reduced and obscured by fibrous reticulum; peduncular bract light brown-tomentose, ca. 90+ cm long including manubrium, ca. 1.5-3 cm wide at middle when closed, ca. 1.1-1.5 cm wide towards base, longitudinally shallowly furrowed. Panicle with peduncle base obscured, axis distal to peduncular bract scar ca. 50+ cm long, ca. 1.0-1.4 cm wide at center, transversly elliptic in cross section. Rachillae 21-32, ca. 28-38 cm long, 3-5 mm wide, attenuate, traids of 2 staminate and 1 pistillate flowers on proximal 21-56% of individual rachillae, variable depending on the individual. Staminate flowers creamy white, sepals ca. 1 mm long, petals ca. 3-4.25

mm long, ca. 1.5-2.0 mm wide, anthers ca. 2-2.5 mm long, filaments brown; pistillate flowers creamy white, (5-)21-76 per rachilla, sepals ca. 3.5 mm long at time of anthesis of staminate flowers.

Fruit oblong-cylindrical, ca. 1.7 cm long (including the cupule), 1.1 cm wide; stigmatic residue slightly excentric; cupule tan, ca. 5 mm deep (according to drawing); epicarp somewhat grainy; mesocarp pulpy; fibers ca. 0.5 mm wide.

Type. Colombia. Amazonas: Cerro de La Pedrera, 1810-1820, Martius s.n. (M). The specimen is on four sheets, ticketed 108-111, the first three of which were originally designated as O. bacaba and, in 1880, corrected by Drude.

Distribution. Known only from a single locality in Amazonas, Colombia, although originally cited as Brazilian.

Representative specimens.

COLOMBIA. Amazonas: Cerro de La Pedrera, fl, 24 Nov 1912, Ducke 12305 (MG, US, U), alt. ca. 300 m, fl, Feb 1926, Huebner 41 (B).

Oenocarpus circumtextus is a poorly known but distinctive species of which only a few collections have been made. The single known locality, Cerro de La Pedrera, lies in Colombian territory. It was formerly called Serra de Cupatí. The original description listed the palm from Brazil, in the mountain of the latter location. However, as Dugand (1942)

pointed out, this area is now Colombian, following the establishment of a definitive border between Colombia and Brazil. Cerro de La Pedrera is located across and slightly upstream from the village of La Pedrera, about 30 kms west of the Brazilian frontier and is known for its endemic flora.

Martius, Ducke, and Huebner are the only ones to have collected this species. While most of their collections consist of leaf and inflorescence fragments, Huebner 41, from B, contains an upper stem section. The thick, persistent fibrous network that sets this species apart from all others in Oenocarpus, is clearly illustrated by the Huebner specimen. In his field label Huebner compared this palm, known locally as resina, to Leopoldinia pulchra, with its similarly fibrous trunk.

In Flora Brasiliensis (1882), Oenocarpus circumtextus was included in the section Bacaba, along with O. bacaba, O. mapora and O. minor. This was distinct from section Distichophyllum, with distichously arranged leaves, and section Bataua having seeds with ruminate endosperm. Barbosa Rodrigues (1903) established a new section, Bacábay, containing O. circumtextus, O. mapora and O. minor. The other sections described at that time were Yandybacába and Pataná. Burret (1928) felt there to be only two sections in Oenocarpus, and named them Oenocarpopsis and Euoenocarpus. The former section consisted only of O. circumtextus. The major difference pointed out in Oenocarpopsis was the persistent peduncular bract with its long, narrow, tubular base. During my

investigations, a number of significant differences have been noted, and I consequently raise the section to subgeneric status. These differences are evident from both the key and subgeneric descriptions.

Oenocarpus circumtextus has never been collected outside of its type locality. Wessels Boer (1971), however, included it in his key to the palms of Venezuela, due probably to the fact that a duplicate specimen of Ducke 12305 is in the herbarium at Utrecht. Because Wessels Boer was unaware of its limited geographic distribution, he assumed that the species must occur in other Amazonian regions. As was written in the key, "Aun no conocido en Venezuela, pero puede esperarse del Territorio Amazonas."

No phenological data is given in the original description. Ducke 12305, containing staminate flowers, was collected on November 24, 1912. As with most specimens in this genus, flowering probably occurs sporadically throughout the year.

Fig. 5.17. Oenocarpus circumtextus Martius: A. Section of the leaf rachis with folded pinnae. Note the long, narrow acumen of the central pinnae characteristic to this species, as highlighted by the white card (Ducke 12305); B. Inflorescence, note narrow, elongate peduncle distinguishing this species from all others in the complex (Martius s.n.); C. Apex of the stem, showing fibrous reticulum (left); bract enclosing inflorescence (right), note narrow base (Huebner 41); D. Close up of the intricately woven fibrous reticulum (Huebner 41). Thin black scale line is ca. 5 cm long.

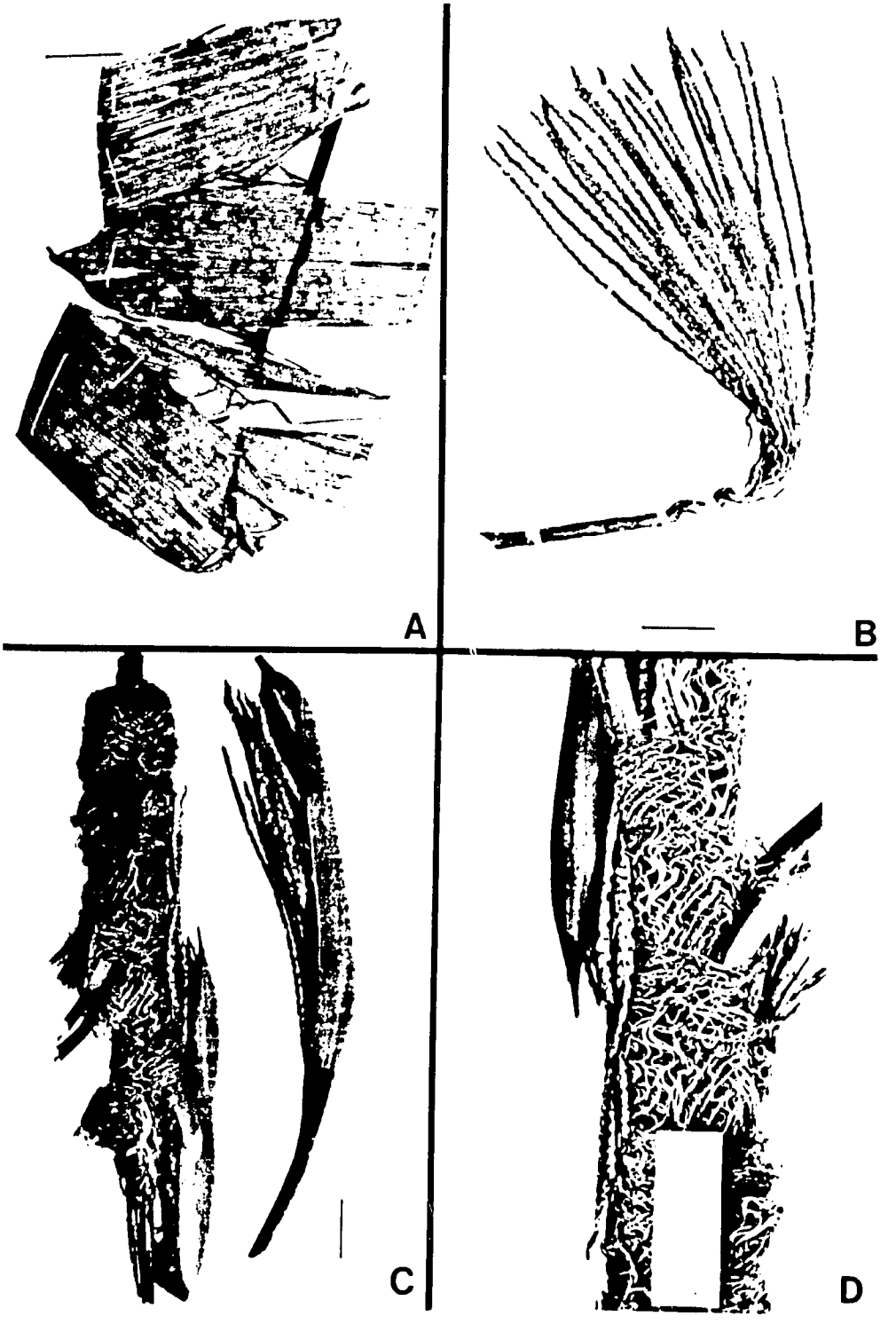
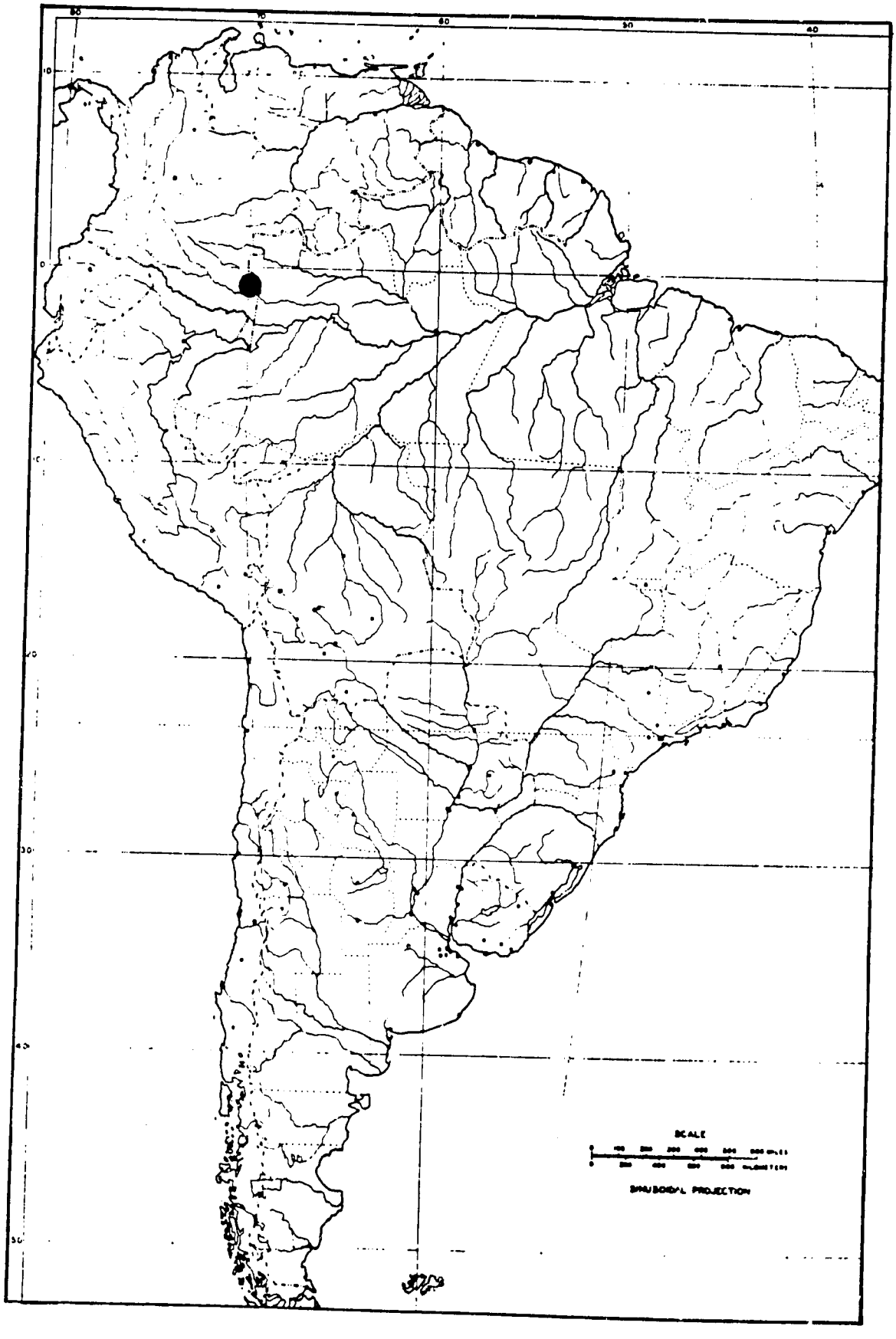

A
B
C
D

Fig. 5.18. The single known locality of *Oenocarpus circumtextus* Mart.


SCALE
SINUSOIDAL PROJECTION

Jessenia Karsten, Linnaea 28:387. 1857.

Large, solitary, erect, pleonanthic, monoecious arecoid palms; stem columnar, frequently massive, grey to black, smooth or, when young, covered with remains of sheaths and sheath fibers and spines, obscurely ringed with leaf scars; base frequently producing a small mass of slender roots.

Leaves pinnate, spirally arranged in a suberect (when young) or horizontally spreading (when mature) coma; sheaths partially clasping, somewhat split opposite petiole, thick, coriaceous, lightly furrowed on the inside, smooth on the outside, upper portion lined with mat of brown fibers, of which some are thin, hairlike and interwoven, others stout, needlelike, and marginally persistent on the sheath and extending into the center and along lower margins of petiole; petiole smooth, channeled adaxially convex abaxially, rachis trough-shaped at base, more or less 4-sided near center, flattened to concave adaxially, abaxially flattened to semiconvex, changing to trigonal towards apex, smooth, ribbed longitudinally, lepidote when young; pinnae numerous, regularly arranged and inserted along rachis in a single plane, subalternate towards base, opposite to subopposite centrally, subopposite to subalternate towards apex, broadly linear -lanceolate at center of rachis, plicate, acute, basally reflexed at attachment, 1-ribbed with prominent intermediate veins, smooth adaxially, covered with pale (or rarely reddish) peltate to sickle shaped or doubly sickle-shaped trichomes abaxially.

Inflorescence interfoliar in bud, protandrous, hippuriform; peduncle short, flattened adaxially, bracteate, bearing a sharply 2-edged, flattened prophyll with dentate margins and a larger, thick, tubular peduncular bract swollen in middle, tapering to sharp point and opening lengthwise, both bracts deciduous; rachis flattened adaxially, frequently lepidote, with simple rachillae inserted laterally and abaxially, arched to pendulous at anthesis, elongate, linear to slightly undulate, slender, attenuate.

Flowers unisexual, sessile, borne in triads of 2 staminate and 1 pistillate flower proximally on rachillae, in pairs of staminate or solitary staminate distally, usually devoid of flowers in ultimate portion, occasionally the slender apex of rachillae terminating in several solitary, small, staminate flowers, inflorescence rarely entirely staminate; staminate flowers asymmetrical, sepals 3, obtuse, acute, imbricate, petals 3, valvate, longitudinally striate, more or less lanceolate, acute, slightly fleshy, one or two in each flower often dissimilar, incurved, stamens (7,8)9-20, filaments awl shaped, slender, straight or undulate and rarely curved at apex in bud, inserted at lower junction of thecae and extending along juncture with a connective produced; anthers dorsifixed, linear, tapering to a point, versatile, with 2 divergent bilocular theceae, sagittate basally for half their length, longitudinally and extrorsely dehiscent, stillode rudimentary, trifid; pistillate flowers symmetrical; sepals 3, imbricate, fleshy, suborbicular,

hooded-concave, completely enclosing the corolla in bud; petals 3, imbricate (except the briefly valvate apex when mature), suborbicular, hooded-concave, somewhat thin when young, becoming larger and fleshier at maturity; staminodes lacking; gynoecium usually unilocular, uniovulate, rarely 2-locular and with 2 ovules; ovule erect, anatropous; style short, thick, stigmas 3, reflexed at anthesis, papillate adaxially.

Fruit one-seeded or rarely two-seeded, ovoid-ellipsoid, obtuse with a shallow bowl-like cupule of indurate perianth at its base; stigmatic residue apical to slightly excentric; epicarp slightly grainy-waxy, smooth, thin; mesocarp fleshy, rich in oil, with thin, flattened longitudinal fibers adnate to and completely covering the seed; seed ovoid-ellipsoid, endosperm horny, ruminate; embryo white, cylindrical-clavate, ca. 2/3 as long as seed.

Type species. *Jessenia polycarpa* Karsten

1. Jessenia bataua (Martius) Burret, Notizbl. Bot. Gart. Berlin-Dahlem, 10:302. 1928.

Trunk columnar, 14-25(-28) m high, (12-)19-25(-27) cm in diameter, internodes spaced 20 cm or more apart on lower portion of stem, much closer towards apex.

Leaves 8-16 per coma, fewer in younger or senescent plants; sheath 0.6-1.4 m long, outer surface dull olive green, inner surface brown, with stout needlelike fibers to 1 m long; petiole green, 0.2-1.0 m long, ca. 5-8 cm wide apically, ca. 8-12 cm wide basally; rachis light green to dark green, 3-8+ m long, red to light-brown-lepidote when young, vesture becoming grey with age and falling away; pinnae 65-108 per side, glossy dark green adaxially; basal pinnae ca. 6.0-1.5 m long, 2.5-2.75+ cm wide; central pinnae (0.75-)1.0-1.7(-2.0) m long, (4.5-)6-11(-14) cm wide; apical pinnae (fourth from apex measured) 15-70 cm long, 1.5-3.5 cm wide.

Inflorescences 1-3(4+) apparent at any one time, creamy white at anthesis; prophyll olive green, variable in size but often ca. 75+ cm long, ca. 20-25 cm wide; peduncular bract of a similar color but frequently thinly striped with yellow or brown, 1-2.3 m long (8-)9-18(-19) cm wide, often somewhat lepidote; axis distal to peduncular bract scar (15-)22-40(-50) cm long, (4.6-)7-11(-20) cm wide at scar, axis variable in size depending on individual, sometimes developing a reddish-velvety tomentum that is deciduous with age; rachillae (116-)135-350(423), (50-)70-120(-140) cm long,

(2-)4-6(7-9) mm wide; staminate flowers creamy white in bud, fragrant; sepals ca. 1.5 mm long; petals 4-7(8) mm long, ca. 2-4 mm wide; stamens ca. 5-6 mm long; anthers ca. 2.5-5 mm long, filaments brown; pistillate flowers creamy white in bud, subtly fragrant at anthesis; sepals ca. 4-6 mm long at time of anthesis of staminate flower.

Fruit green with a waxy cast when young, becoming dark purple-black when ripe, rounded at the apex, variable in size, (2.3-)2.5-4.0(-4.75) cm long (not including the cupule), 2.0-2.75 (3.0 in the rare 2-seeded fruits) cm wide at center, (5)6-15(16+) gms in weight when ripe; stigmatic residue ca. 1-2 mm long, 2-3 mm wide; cupule tan, ca. 5-10 mm deep; mesocarp pulpy, purple or lavender-white; fibers ca. 1 mm wide; endosperm white, penetrated by light to dark brown rays, embryo white.

KEY TO THE SUBSPECIES OF *JESSENIA BATAUA*

1. Pinnae covered with many trichomes on abaxial surface; rachillae uniformly tapering gently throughout; pistillate flowers usually 40-90, borne on proximal 40-60% of rachilla; staminate flowers ca. 4-7(-8) mm long, stamens (7-)9-20. Panama and the Amazon and Orinoco Valley, Andean foothills, and Pacific coastal territory . . . . . 1a. subsp. *bataua*.

1. Pinnae with whitish waxy covering on abaxial surface, trichomes generally few and scattered; rachillae thickened proximally on portion bearing pistillate flowers; pistillate flowers usually 3-54 in number, borne on proximal 10-25% of rachilla; staminate flowers ca. 4-5 mm long, stamens (7-)9-10(11). Restricted to northern and northeastern Venezuela, Trinidad, Guyana, and Surinam . . . . . .1b. subsp. *oligocarpa*.

1a. Jessenia bataua (Martius) Burret subsp. bataua.

Oenocarpus bataua Martius, Hist. Nat. Palm 2:23. t. 24, 25. 1823.

Type. Brazil. Amazonas, without date, Martius s.n. (M? n.v.).

Jessenia polycarpa Karsten, Linnaea 28:388. 1857.

Type. Colombia. Meta: Llano de San Martin, 1853, Karsten s.n. (isotype LE).

Jessenia repanda Engel, Linnaea 33:691, t.3, fig. 6. 1865.

Type. Venezuela. Tachira: La Grita, Linnaea 33:691, t.3, fig. 6. (lectotype).

Oenocarpus seje, Cuervo Marquez, Trat. Elem. Bot. 458. 1913. nomen nudum.

Jessenia weberbaueri Burret, Notizbl. Bot. Gart. Berlin-Dahlem, 10:840. 1929. Type. Peru. San Martin: Moyobamba, 18 Aug 1904, Weberbauer 4561 (B).

Pinnae with abaxial surface light green to grey, usually densely covered with peltate to sickle-shaped to doubly sickle-shaped trichomes (more apparent in newly emerged leaves). Rachillae more or less uniform in thickness throughout, lacking strongly pronounced bracts subtending staminate pair or solitary flower, rachillae (116-)135-270(-285) in number, with triads of 2 staminate and 1 pistillate flower on proximal (20)40-60(-65)% of individual rachillae, this quite variable depending on individual. Staminate flowers 5-7(8) mm long

with (7-)9-20 stamens. Pistillate flowers usually (15-)40-90(-119) per rachilla.

Type. Brazil. Amazonas, without date, Martius s.n. (M? n.v.).

Distribution. Panama and lowland areas over much of the northern half of South America.

Representative specimens.

PANAMA. Darien: Río Urut', young fr, without date, Duke & Bristan 218 (BH); without locality or date, Pittier 5678 (US).

COLOMBIA. Amazonas: 1 km E of Puerto Nariño, Río Loreto-Yacu, alt. 100 m, 2 Feb 1973, Glenboski C-253 (US). Antioquia: Porce, Mun. Gomez Plata, fr, 1 Oct 1940, Ranghel Galindo 7, 23 (COL). Caquetá: Florencia, Cerros La Estrella, alt. 400 m, 30 Mar 1940, Cuatrecasas 8871 (COL); Hetuchá, Río Orteguaza, fl, fr, 21 Jul 1926, Woronow 6106 (LE). Chocó: 7 km W of Totenendo, on road to Quibdo, alt. ca. 100 m, young fr, 12 Aug 1976, Gentry & Fallen 17601 (BH); junction of Río Condoto and Río San Juan, alt. 100-150 m, seedling, 20 Apr 1939, Killip 35673 (BH, COL); Cabo Marzo, 13 Sep 1970, Moore 9872 (BH). Meta: Llanos Orientales, Caño Quenane, alt. 400 m, fl, fr, 22-23 Feb 1941, Dugand & Jaramillo 2897 (COL); Llano de San Martin, alt. 250 m, 1851-1857, Triana 716 (P). Norte de Santander: Petrolea, beginning of pipeline, alt. ca. 60 m, fr, 26 Sep 1946, Foster & Foster 1789 (BH). Vaupés: Mitú, fl, alt. 200 m, 18 Oct 1939, Cuatrecasas 7266 (BH

(photo), COL, US); Río Guayabero, alt. 240 m, fl, 8 Nov 1939, Cuatrecasas 7539 (COL, US); Río Caraparana, between Las Bocas and El Encanto, alt. 150 m, 22-28 May 1942, Schultes 3864 (BH); Río Apaporis, Jinogojé, at mouth of Río Piraparaná, alt. ca. 230 m, 18 Jun 1952, Schultes & Cabrera 16754 (BH); Río Kubiyú, fl, fr, 30 Jun 1976, Zarucchi & Balick 1793 (ECON), fr, 1 Jul 1976 Zarucchi & Balick 1805 (ECON); Río Vaupés near stream across from Mitú, fr, 3 Jul 1976, Zarucchi & Balick 1809 (ECON); along road S of Mitú, fr, 5 Jul 1976, Zarucchi et al. 1811 (ECON); Tukunaray, below Mitú on Río Vaupés, fr, 6 Jul 1976, Zarucchi et al. 1813 (ECON); Río Vaupés, La Makarena Village upriver from Mitú, fr, 9 Jul 1976, Zarucchi et al. 1814 (ECON), Río Kubiyú, fr, 12 Jul 1976, Zarucchi et al. 1838 (HUA, ECON), fr, 12 Jul 1976, Zarucchi et al. 1840 (COL, ECON), fr, 12 Jul 1976, Zarucchi et al. 1842 (ECON), fr, 15 Jul 1976, Zarucchi et al. 1850 (ECON); Río Vaupés, La Makarena Village upriver from Mitú, fl, fr, 17 July 1976, Zarucchi et al. 1851 (COL, ECON); Río Vaupés, on trail that leads to Santa Lucia on Río Querari, fr, 7 Aug 1976, Zarucchi et al. 1874 (ECON). Valle: Buenaventura, 3 May 1926, Cook 73 (US), fr, 5 May 1926, Cook 79 (US), seedling, 7 May 1926, Cook 93 (US), 23 May 1926, Cook 135 (US), fl, 30 May 1926, Cook 178 (US); Río Naya, Puerto Merizalde, alt. 5-20 m, fl, fr, 20-23 Feb 1943, Cuatrecasas 13962 (COL, F, MO); Río Calima, La Trojita, alt. 5-50 m, 19 Feb - 10 Mar 1944, Cuatrecasas 16319 (COL); Río Cajambre, alt. 5-80 m, fr, 5-15 May 1944, Cuatrecasas

17379 (COL, F); 18 km E of Buenaventura, alt. ca. 50 m, young fr, 14 Feb 1939, Killip & García-Barriga 33255 (BH, US); Buenaventura, 9 Feb 1967, Moore et al. 9454 (BH); Agua Dulce, an island in Buenaventura Bay, 12 Feb 1967, Moore et al. 9476 (BH); Río Calima, Quabrada de la Brea, alt. 30-40 m, 19 May 1946, Schultes & Villarreal 7377 (BH). Vichada: Las Gaviotas, Topochera, fl, young fr, 25 Jul 1976, Balick & Hoyos 76-18 (ECON); Guacamayas, fr, 26 Jul 1976, Balick & Hoyos 76-20 (ECON); Las Gaviotas, 27 Jul 1976, Balick & Hoyos, 76-22 (ECON). Santander: 20 km S of Barrancas Bermeja, alt. ca. 100 m, fr, July 1966, Schulz & Rodríguez P. 509 (U).

VENEZUELA. Amazonas: along river 8 km above Santa Bárbara del Orinoco, fl, 28 May 1975, Berry 788 (BH, VEN); San Carlos de Río Negro, alt. 115 m, seedling, 18 Sep 1975, Berry 1421 (VEN); 4 km from San Carols de Río Negro off road to Solano, seedling, 22 Sep 1975, Berry & Brünig 1506 (VEN); San Carlos de Río Negro, alt. 115 m, fr, 23 Sep 1975, Berry 1537 (BH, VEN); Santa Bárbara del Orinoco Experiment Station, 1-2 km S of Trapichote, alt. 130 m, 26 Feb-2 Mar 1976, Berry & Chesney 2106 (VEN); mouth of Río Ventuari between Macuruco and Santa Bárbara del Orinoco, alt. 130 m, fr, 24 Mar 1976, Berry 2133 (VEN); Piedra Blanca, Macuruco, Río Orinoco, alt. 130 m, fl, 25 Mar 1976, Berry 2155 (BH, VEN); 3 km S of Trapichote, alt. 130 m, fl, 29 Mar 1976, Berry 2196 (BH, VEN); Cerro Duida, SE slopes along Caño Negro, tributary of Caño Igapo, alt. 260 m, 28-29 Aug 1944, Steyermark 58065 (F); near Sanariapo, 26 Jul 1967, Wessels Boer 1891 (U); near San Carlos de Río Negro

19 Jan 1968, Wessels Boer 2280 (U); near Santa Rosa de Amanadona, 30 Jan 1968, Wessels Boer 2369 (U); Puerto Ayacucho, alt. 100 m, young fr, 18 May 1940, Williams 12994 (F, US, VEN); Maroa, Río Guainía, alt. 127 m, 14 Feb 1942, Williams 14345 (F, US, VEN). Bolivar: Meseta de Jaua, Cerro Sarisariñama, Cumbre, alt. 700 m, seeds in cave, 12-15 Feb 1974, Steyermark et al. 109005 (VEN); around Las Paras encampment, vicinity of Salto Para, Río Caura, alt. 230-280 m, fr, 15-17 Jan 1977, Steyermark et al. 113113 (BH, VEN); near El Palmar, alt. ca. 75 m, 23 Nov 1967, Wessels Boer 2062 (U). Delta Amacuro: Atabuina, Caño Arature, to the foot of Sierra de Imataca, alt. 750 m, fr, 10 Apr 1959, Buza 304 (VEN). Merida: road from La Azulita to Caño Zancudo near Caño Zancudo, alt. ca. 250 m, 29 Aug 1967, Wessels Boer 2005 (U). Miranda: Parque Guatopo, seedling, 14 Mar 1976, Berry 2131 (VEN), several km N of the Junction of Río Santa Clara with the road, alt. ca. 300 m, 30 Apr 1976, Berry 2202 (VEN), on steep slopes bordering Río Santa Cruz, between Santa Teresa and Altagracia de Orituco, 14.5 km from Los Alpes, 12 km from Rancheria Mi Querencia, 29 Nov 1971, Steyermark & Braun 104041 (BH, VEN). Monagas: Guácharo Cave, 6 km NW of Guácharo, alt, 950 m, seedling, 23 Apr 1945, Steyermark 62304 (VEN). Zulia: 1 km NW of Machiques-Colón Highway, between Río Tokuko and Río Aricuizá, ca. 90 km S of Machiques, alt. 50-100 m, fr, 22 Aug 1967, Steyermark & Fernández 99604 (BH, VEN); along Carretera Panamericana, ca. 30 km N of Caño Zancudo, alt. ca. 100 m, 5 Dec 1967, Wessels Boer 2112 (U).

FRENCH GUIANA. Charvein, 28 Jan 1914, Benoist 694 (P); Karounany, 1855, Sagot 851 in part (P).

ECUADOR. Imbabura: between El Pajon and Cachaco, alt. 600 m, without date, Acosta Solis 12742 (F); Lúrimagúa, alt. 600 m, fr, 10 Oct 1934, Heinrichs 787 (F, M). Napo: 16 km from Lago Agrio on Quito Road, fl, 10 Apr 1978, Balick et al. 1187 (ECON, QCA); Auca Territory, drilling site of Texaco Oil Company, 12 Apr 1978, Balick & Allon 1189 (ECON, QCA). Pichincha: Río Palenque Scientific Station, 56 km N of Quevado on Quito-Guayaquil Road, alt. 230 m, 19 Apr 1978, Balick & Allon 1190.

PERU. Huánuco: Leoncio Prado, Quebrada de Saugapilla, near Aucayacu, alt. 600 m, fl, 4 Mar 1978, Balick et al. 1148 (ECON); Tingo Maria, Naranjillo, 720 m alt., 10 Jul 1957, Ellenberg 2267 (U). Junín: La Merced, alt. ca. 700 m, 29 May-4 Jun 1929, Killip & Smith 23999 (BH (photo), F, NY, US), 24008 (F, NY, US). Loreto: Maynas, Río Yaguasyacu, tributary of Río Ampiyacu, Brillo Nuevo and vicinity, fr, Feb 1978, Balick et al. 1013 (AMAZ, ECON); El Sacremento, 89 km from Pucallpa, 240 m alt., 22 Jul 1957, Ellenberg 2462 (U); 40 km S of Pucallpa, 230 m alt., seedling, 24 Jul 1957, Ellenberg 2544a (U); Santa Rosa, lower Río Huallaga below Yurimaguas, alt. ca. 135 m, seedling, 1-5 Sep 1929, Killip & Smith 28845 (BH (photo), F, NY, US); Coronel Portillo, beyond vivero of Forestry Service toward Río Manatay, km 4, Pucallpa, alt. ca. 220 m, 5 May 1960, Moore et al. 8402 (BH); Iquitos, alt. 120 m, seedling, Oct. 1929, Williams 3548 (F); Fortaleza,

Yurimaguas, young fr, 1929, Williams 4963 (MO).

BRAZIL. Acre: near mouth of Rio Macauhan, tributary of Rio Yaco, fl, 3 Sep 1933, Krukoff 5758 (BH (photo), F, K, M, MICH, MO, NY, US). Amazonas: Yanomamu tribe at Tototobí, basin of Rio Denemi, 23 Aug 1975, Anderson 188 (BH): Reserva Florestal Ducke, Manaus-Itacoatiara Highway, seedling, 25 Oct. 1977, Balick 902 (ECON, INPA, NY); Manaus, Cachoeira alta do Tarumã, 28 Jun 1955, Chagas 1261 (INPA); Jutica, Varadouro, 16 Nov 1928, Luetzelburg 23043 (R); Reserva Florestal Ducke, fl, 15 Mar 1967, Moore 9532 (BH, INPA, NY); Rio Negro, Arivau, 1 Sep 1967, without collector, SPF herbarium no. 7 (IAN). Mato Grosso: Machado Angusturo, young fr, Dec 1931, Krukoff 1603 (BH, F). Pará: Santarém-Cuiabá Highway, BR 163, km 1136 from Santarém, fl, fr, 16 Nov 1977, Balick et al. 929 (ECON, MG, NY), km 1234 from Santarém, young fr, 18 Nov 1977, Balick et al. 933 (ECON, MG, NY); 42 km E of Itaituba on Trans-Amazon Highway, fl, young fr, 28 Nov 1977, Balick et al. 952; EMBRAPA field station, Igapó de localidad Jogo, fl, 11 Dec 1977, Balick & Rosa 955 (ECON, MG, NY); without locality, fl, Jul 1923, Ducke 18615 (RB); Belém, fr, 5 Nov 1945, Pires & Black 571 (IAN), fr, 14 Oct 1950, Pires 2643 (IAN), seedling, 14 Oct 1950, Pires 2644 (IAN). Roraima: Bôa Vista, Jan 1933, Capucho 536 (F, IAN).

Discussions of this sub-species, and those now considered synonymous with it, have been fraught with confusion and conflict, beginning with the early description of Martius. Burret (1928) treated Oenocarpus and Jessenia in a lengthy article, outlining some of the early errors. Martius (1823) described what is recognized as the first species, under the name Oenocarpus bataua. The critical features involving staminate floral morphology are in error, as the type specimen was apparently based on a mixed collection of that species with another truly of the genus Oenocarpus. Because of the seeming similarity in floral morphology to his other species, Martius failed to realize that he was dealing with two generic concepts. In the original text, flowers are described with 6 stamens and linear, obtuse anthers. This, along with the illustrations in Tab. 25, Figs. 4-6, shows the staminate material to be from Oenocarpus and not Jessenia bataua, as here recognized. The fruits depicted in the same plate have a ruminate endosperm, a character authenticating them as J. bataua. Thus, because of this mixed collection, Martius circumscribed the genus Oenocarpus to include what is presently known as Jessenia, with no major floral characteristics on which to base a distinction.

Karsten (1857) described the type species of the genus: Jessenia polycarpa. His discussion pointed out the similarities between Jessenia and Oenocarpus. The first hint is offered that O. bataua might be similar to J. polycarpa, but again a distinction is made, based on the erroneous mention of 6

stamens and the plate depicting O. bataua as having excentric stigmatic residue. This is in contrast to the fruit of Karsten's J. polycarpa, where the stigmatic residue is apical. In truth, placement of stigmatic residue in Jessenia is now known to be a variable character and was somewhat exaggerated in the Martius plate. Had the original description of O. bataua not been in error, the affinity of these two species might have been realized even at this early date. The description of J. polycarpa had no accompanying illustration. In a later work (1860), Karsten offered an expanded discussion and magnificently detailed plate. The major inconsistency lies in the unusually large number of leaves in the coma. A minimum of 24 leaves are pictured; in reality the number of leaves per coma is from 8-15. Also, according to Burret (1928), the anthers as drawn by Karsten, are not sufficiently pointed. Except for these two features, the drawing is reasonably accurate and, somewhat modified, was used in Engler and Prantl's Die Natürlichen Pflanzenfamilien (1889).

Burret (1928), recognizing Martius' error, made the combination Jessenia bataua (Mart.) Burret. At the same time, he reported only two apparent differences between that species and J. polycarpa. In three flowers examined from the type material of J. polycarpa, 17-19 stamens were counted. Seven flowers from a Huber collection of J. bataua had 14-15 stamens each. The second distinction raised by Burret was the absence of any mention of spiniform leaf fibers in the description of J. polycarpa. Martius' phrase

"margin in fibras transversus rigidus duras nigricantes dissoluti" accounts for these fibers in J. bataua. Burret (1928, 1929) based his separation, in part, on this supposed difference. In reading the original description by Karsten (1857), the phrase "rachi parte inferiore caniculata reticulatim appendiculata" is sufficient evidence, in my opinion, for the presence of these fibers in the type specimen. Throughout my fieldwork, an effort was made to find a specimen lacking spinose fibers on the sheath and petiole bases. In no case was this possible. Each specimen had both the soft, hairlike, brown fibers and longer, spiniform fibers. This does not suggest that the spineless condition may not exist; rather, that it was never seen and would appear to be, therefore, rather rare. While refusing to unite the two species, Burret (1928) commented on their similarity, furthermore suggesting that perhaps J. polycarpa was only to be distinguished as var. polycarpa.

A mat of sheath remains and fibers always encloses the young trunk of Jessenia bataua. This appears to be a protective mechanism for the young, soft trunks which, at this stage, can easily be damaged by insects. Indeed, in the rain forest, I observed a portion of the young trunk, scraped clean and devoid of fiber that had been subsequently attacked by weevils. With further growth, the peripheral vascular bundles in the stem become heavily lignified, and entry is made difficult. After the development of the first inflorescence, the sheath-fiber cover falls away, revealing

the smooth glossy trunk. Dugand (1944) published a photograph of the coma of J. polycarpa, stating that the fibers were lacking. They are apparent to me and can be seen running parallel to the petiole. This specimen, Dugand and Jaramillo 2897, is from the Llanos of Meta. Presumably it is the same species found in the bordering Llanos of Vichada. Jessenia has been carefully studied in the Vichada and never once were the stout fibers lacking. In a later paper, Burret (1929) reports receiving new material and photographs of J. polycarpa from Caquetá, at Hetuchá on the Río Orteguaza. He claims that the photograph shows soft fibers. The stout spiniform fibers are missing or obscured. Unfortunately, this photograph, never published by Burret, is no longer available at Berlin for confirmation. The only photograph of this species that I was able to locate in Berlin, Hubner No. 30a(?), clearly shows a young tree with spinose fibers present. It is conceivable that these fibers could vary in durability, depending perhaps on the age of the tree. For example, in a depauperate or senile tree, perhaps such fragile spines may appear. Much of the above confusion has resulted from the specimen's appearance during its early growth. The young trunks are often many meters tall, and with their fibrous cover are strikingly apparent in the forest. As Spruce (1871) comments:

> "The OE. Bataua Mart. Palm. 23...is surely distinct from the palm that Mr. Wallace and myself have heard called "Pataua" by the Brazilians, "Seje" by the Venezuelans; for no mention is made in Martius's descriptions of the trunk being encased

> in the spiniform remnants of the leaf sheath, and only becoming dénuded in the tallest specimens after the fashion of the Piassaba; on the contrary, it is classed among the species "caudice nudo"."

Steyermark (1957) published a letter from Dugand, in which the correct judgment is given that the dimorphism of spinose vs. spineless trunks is a function of age (cf. Barbosa Rodrigues (1903) Plate 41 and Wallace (1853) Plates 10, 11). Indeed, from the field studies undertaken, there can be no doubt that this condition is purely dependent on the age of the palm. However, the overall height at which the trunk fibers are dropped is environmentally influenced. Palms in a dark forest environment tend to have elongate trunks and to retain their covering, until considerably taller that those in a bright, exposed area. In any case, it is apparent from the literature, herbarium material and field examples studied that there are no criteria on which to separate these two species. Because of this, Burret's combination, using the earlier description by Martius as the basionym, is correct. Steyermark (1957) selected J. polycarpa as the correct epithet, based on the fact that Burret transferred O. bataua, after Karsten had described J. polycarpa, but the rules of nomenclatural priority do not support this choice.

Engel (1865) described Jessenia repanda from the moist forest of Catatumbo, Sardinata and Guamás, along the Río Magdalena in Colombia and in Venezuela. His species was distinguished primarily by its enlarged yellow-orange trunk

rings formed by the leaf scars, as depicted in Fig. 6 accompanying the description. Burret (1928, 1929) accepted the ring character, along with the long, flexible fibers pictured, as being distinctive features. After careful examination of the illustration and description of Engel, I do not consider this to be a distinct species. Rather, it appears to be a part of the broader distribution of J. bataua subsp. bataua over northern South America. The drawing offered by Engel looks much too stylized to base an accurate description upon it, especially in the absence of a type specimen. Rings produced by the swollen leaf scars are a common feature in the upper part of the trunk of J. bataua and become enlarged when growing in an exposed area. The illustration fails to show the lower part of the trunk, which is most likely not so strongly undulate. Furthermore, sheaths shown in the coma are far too congested to form the distinctly spaced rings. These sheaths are also too small to be representative of anything in this genus as it appears in nature. Their length can be estimated as barely more than equal to the trunk diameter, a maximum of 25 cm. In a living specimen, the sheath is approximately four times that length. The insertion of this organ is portrayed as strictly basal, instead of the true state--partially clasping. An unusually high number of attached, but apparently dead, sheaths appear in the figure, again contrary to the natural state. The weight of a dead leaf plus the swelling of a new inflorescence bract pulls-pushes the sheath off so that only a limited

number can be present at any one time. Because this drawing is so suspect in its accuracy, I fail to find support for the use of the long flexible fibers as a distinct character. Such a depiction is more likely stylized hair-like fiber, elongated by the pen of the artist rather than by the evidence from nature.

Burret (1929) described Jessenia weberbaueri, based on the large fruit (ca. 4 cm long including perianth) and thick rachillae. The type specimen comes from a dry mountain forest in Moyobamba, Loreto, at 900 m altitude. The panicle and fruit are to be found in Berlin, and were carefully examined. In addition, I visited two sites about 240 km south of the type locality (Tocache Nuevo and Puerto Pisano on the Río Huallaga) where Jessenia is common. Because the inflorescence of J. bataua is so variable, field and herbarium botanists often believe specific delimitation is justified. This is not the case. Differences such as noted in Burret's species were observed within the same population in the Vaupés of Colombia. Thickened rachillae are often found in palms growing in exposed, stressed sites and fruits vary in size depending on many factors. In this treatment, based on field experience, examination of the type specimen and general familiarity with the group, J. weberbaueri must be considered a synonym of J. bataua subsp. bataua.

Jessenia bataua grows in a variety of habitats. It frequently colonizes wet, swampy areas subject to periodic flooding, where the dicotyledonous species of the rain forest

are unable to grow. Along with other palms such as Mauritia and Euterpe, it gains advantage by the lack of competition and forms pure stands extending over acres or even throughout tracts many times that size. It is also found on upland sites free from inundation. In these locations, competition with other rain forest vegetation is more intense, and rarely are pure stands found. Of the specimens observed in upland sites, many are of a large size infrequent in the inundated locations. The palms require water and a humid environment. In the Llanos of Colombia, for example, they never grow in the savannah, but instead are confined to the gallery forest along the streams and rivers. In my field work, a magnificent palm, growing in an open area of a farm in Ecuador, was found with its earliest fruiting panicle scars only a half meter up from the soil level. This is in striking contrast to the usual rain forest habit of first flowering at about 4-5 m from ground level. A low flowering height as this is thought to be the result of an exposed, well illuminated, fertile environment, similar to the dimorphic habit of Elaeis guineensis growing under cultivation versus its forest habit.

Fruiting times vary throughout the broad geographic range of the species, due to the many localized environments. Fruits often appear most prolifically during alternate years, a trend that warrants further investigation. In many populations, flowers or fruits in some stage of development can usually be found throughout the year. Fruiting is consistently heavier over a period of several months or longer. Of the

specimens cited, the following representative collections contain ripe fruit, and might be used to obtain a limited idea of when fruiting is apparent in selected regions: Balick et al. 76-18, 929, 1013; Berry 1537, 2133; Buza 7502; Cook 79; Cuatrecasas 16319; Pires 571, 2643; Ranghel Galindo 7; Steyermark 99604, 113113; Zarucchi et al. 1793, 1874. A caveat should be applied against generalizing regional schedules from the few selected examples, especially as intermittent production can often be found throughout the year.

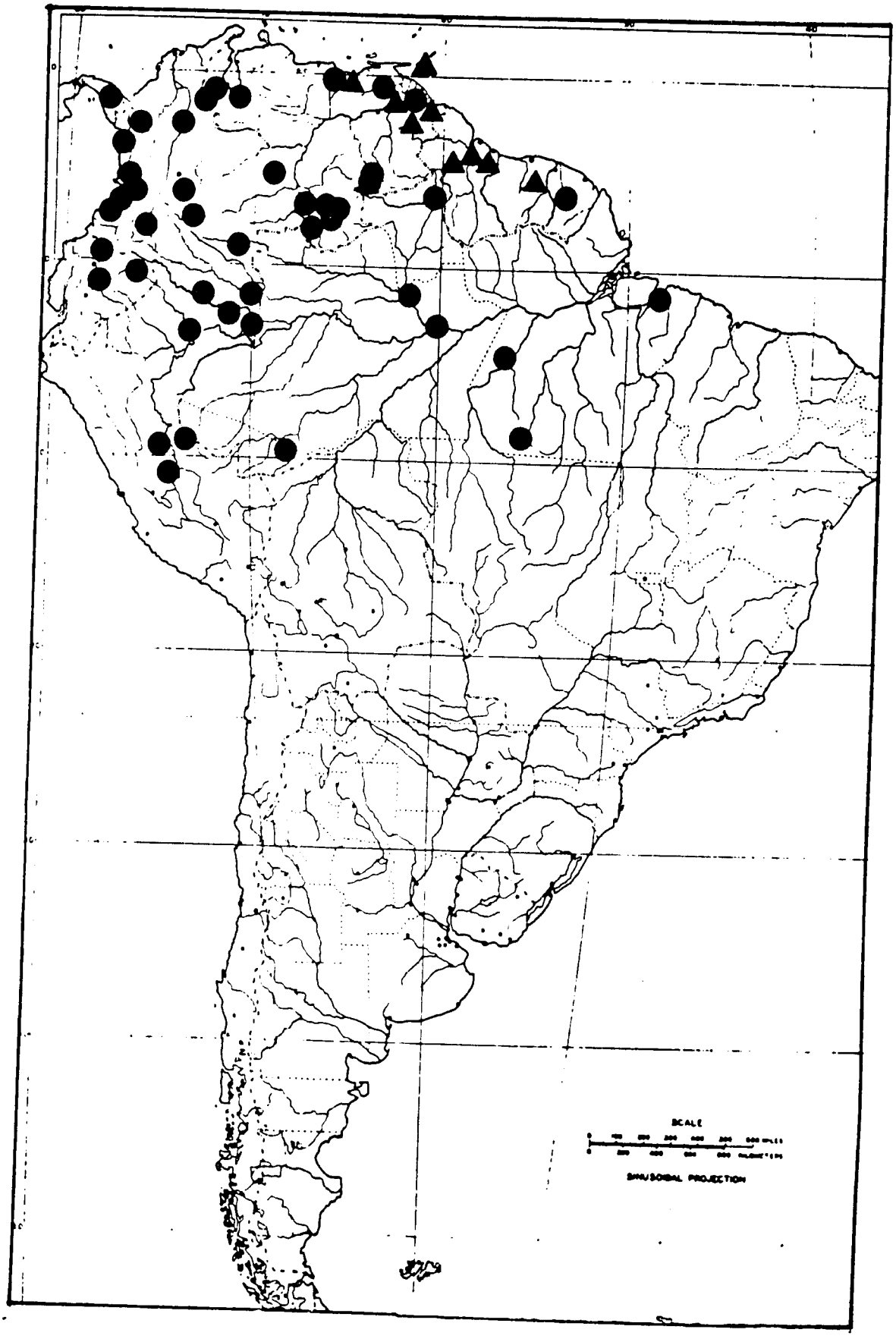
Mesocarp coloration, either reddish-pink or white, is used as a distinguishing character by certain local peoples in the Amazon Valley. This was pointed out by both Bora and Guahibo Indians in two areas that I studied. As reported in Balick (1979), the coloration "...does not seem to be simply a different stage in the maturity of the fruits, as the Indians note that the trees bear consistently either one or the other of the different forms annually."

Barbosa Rodrigues (1903) gives the origin of the specific epithet as a German pronunciation of the Indian name "pataua." This name derived from the Geral term"pacaúa", the fruit of the paca (paca=Agouti sp.+ úa=fruit). Many other forest animals and birds relish the ripe fruits of this species, and their activities may assist in its distribution.

Fig. 5.19. *Jessenia bataua* Karsten subsp. *bataua* growing in Reserva Florestal Ducke, Manaus, Brazil.

Fig. 5. 20. Jessenia bataua Karsten subsp. bataua; A. Mature prophyll and peduncular bract, enclosing the inflorescence, shortly before splitting open (Balick et al. 1148); B. Inflorescence with developing pistillate flowers (Balick et al. 939); C. Fruits along the rachillae (Balick et al. 955); D. Cross section of the crown, showing spiral phyllotaxis (Balick et al. 955).

Fig. 5.21. Distribution of Jessenia bataua Karsten: ● = subsp. bataua; ▲ = subsp. oligocarpa.


SCALE
SINUSOIDAL PROJECTION

1b. Jessenia bataua (Martius) Burret subsp. oligocarpa (Grisebach & Wendland) Balick stat. nov.

Jessenia oligocarpa Grisebach & Wendland in Grisebach, Fl. Brit. West. Ind. 516. 1864. Type. Trinidad. 1857-63, Crueger 74 (GOET n.v.; BH(photo)).

Oenocarpus oligocarpa (Grisebach) Wessels Boer, Ind. Palms Suriname 58. 1965.

Oenocarpus oligocarpa (Grisebach) Burret in Wessels Boer, Acta. Bot. Venez. 6:326. 1971.

Pinnae with abaxial surface white-glaucous to grey, usually with peltate to sickle-shaped to doubly sickle-shaped trichomes weakly interspersed throughout a waxy coating (more apparent in newly emerged leaves). Rachillae thickened proximally on the part bearing the pistillate flowers, distal portion bearing staminate flowers distinctly thinner with small or sharply pointed bracts subtending each staminate pair or solitary flower, rachillae 178-350 (423) in number, with triads of 2 staminate and 1 pistillate flower on proximal ca. (1)6-25% of individual rachillae, this quite variable depending on individual. Staminate flowers 4-5 mm long with (7-)9-10(11) stamens. Pistillate flowers (1)3-54(57) per rachilla.

Type. Trinidad. 1857-63, Crueger 74 (GOET n.v., BH (photo)).

Distribution. Trinidad, northern and northeastern Venezuela, Guyana and Surinam.

Representative specimens.

VENEZUELA. Bolivar: Near El Palmar, alt. 75 m, fl, 23 Nov 1967, Wessels Boer 2062 (U). Delta Amacuro: Sur de Ibaruma, 23 Mar 1948, Tamayo 3562 (VEN). Miranda: San Pablo, cerca de Caripito, 9 Mar 1948, Tamayo 3563 (VEN). Monagas: Reserva Forestal de Guarapiche near confluence of Río Guarapiche with Caño Colorado, fr, 25 May 1967, Wessels Boer 1825 (U).

TRINIDAD. Without locality, 17 Feb 1921, Bailey & Bailey s.n. (BH); Cumito, fr, 19 Jan 1946, Bailey 105 (BH); Valencia, fl, young fr, 10 Jun 1978, Balick et al. 1231 (BH, ECON, TRIN) 25 Mar 1920, Britton et al. 1006 (K, NY, US); without locality, without date, Crueger s.n. (K); Aripo Valley, 13 Feb 1932, Loomis 49 (US); Valencia along road, 23 Aug 1963, Wessels Boer 1623 (U).

GUYANA. East Berbice-Corentyne: Corentyne River, fl, Nov 1879, Jenman 519 (FDG, K). East Demerara-West Coast Berbice: Essequibo River, Moraballi Creek near Bartica, sea level, fl, 28 Oct 1929, Sandwith 528 (K). Mazaruni-Potaro: Essequibo, 1863-67, Appun 239 (K); Partang River, ca. 19 km above mouth, alt. 580 m, fl, Maguire & Maguire 43911 (U); Partang River, Merume Mountains, alt. 580 m, fl, 23 Jun 1960, Tillett et al. 43911 (NY).

SURINAM. Brokopondo: W slope of Emma Keten, alt. ca. 200 m, fl, May 1963, Wessels Boer 1433 (U); Kappel Savannah, fl, 8 Jun 1963, Wessels Boer 1514 (U); Taffelberg, 11 Jun 1963, Wessels Boer 1543 (U).

Jessenia oligocarpa was described by Grisebach and Wendland from an unspecified population in Trinidad. Several ambiguous characters--such as pinna shape and arrangement, and stamen number--were used to separate this new species from J. polycarpa and Oenocarpus bataua. The most valid criterion in the original description distinguishing J. oligocarpa as unique, and accounting for the derivation of the specific epithet, is the small number of pistillate flowers on each rachilla. Pistillate floral number is a somewhat dubious way of establishing a difference; at the beginning of this study I was more inclined to consider Jessenia as a widespread genus consisting of a single, more or less uniform species. During my time spent in Trinidad, where I observed Jessenia populations in the forest around Valencia, it became apparent that these differed from the populations in the Amazon Valley. The differences are not always consistent, however, and within the interface of the two concepts, eg. the northern edge of South America, a gradation of certain characteristics can be observed. Examples of this are in the number of pistillate flowers per rachilla and the abaxial vesture of the pinna, making distinction at times a problem. I feel these concepts to be deserving of subspecific delimitation. The following table outlines my present understanding of the basic contrasts between the two subspecies.

Jessenia bataua subsp. *oligocarpa* (on Trinidad)	*Jessenia bataua* subsp. *bataua* (in the Amazon Valley)
Leaf	
Whitish color on abaxial surface of pinnae, especially apparent on young leaves, due to waxy "bloom" and scattered scales.	Greyish color on abaxial surface of young leaves due to presence of many scales; waxy "bloom usually absent.
Inflorescence	
Rachillae thickened proximally on portion bearing pistillate flowers; distal portion bearing staminate flowers distinctly thinner with pronounced bracts.	Rachillae more uniform throughout, or at least distal portion not so strikingly thinner than the proximal portion as in the other subspecies, bracts not so pronounced.
Triads of 2 staminate and 1 pistillate flower usually borne on proximal 10-25% of individual rachillae. Apparently a somewhat larger percentage in populations outside of Trinidad.	Triads of 2 staminate and 1 pistillate flower usually borne on proximal 40-60% of individual rachillae.
Usually most pistillate flowers develop into fruits, forcing many rachillae to spread apart.	Usually a maximum of 8-10% of the pistillate flowers develop into fruits; as these are more evenly distributed, the rachillae do not spread apart as much.
Panicle with a large number of rachillae to a usual maximum of 350.	Panicle with a smaller number of rachillae to a usual maximum of 270.
Staminate flowers ca. 4-5 mm long.	Staminate flowers 5-7(8) mm long.

Stamens (7-)9-10(11).	Stamens (7-)9-20; more than in other subspecies.

Jahn (1908) repeats most of the information contained in the original description of Jessenia oligocarpa, but he adds that, since the species is in Trinidad, it probably also occurs in eastern Venezuela. No herbarium specimens are offered to document this statement. Wessels Boer (1971) published a key to the palms of Venezuela, in which Jessenia bataua and J. oligocarpa were recognized as separate. As he tended towards the unification of many palm genera, Jessenia is treated as a part of Oenocarpus. Some of the separations between J. bataua and J. oligocarpa, such as 12-22 stamens in J. bataua versus 7-11 stamens in J. oligocarpa are invalid. In fact, as few as 7 stamens have infrequently been noted in Colombian populations of J. bataua.

NOMINA DUBIA AND EXCLUDED TAXA

Oenocarpus

Oenocarpus altissimus Klotzsch ex Wendl. Ind. Palm. 30. 1854. = Martinezia sp. according to Burret (1928).

Oenocarpus bolivianus Hort. Kew. ex Wendl. Ind. Palm. 30. 1854. = perhaps O. caracasanus (= Euterpe sp.) as suggested by Wendland (1854).

Oenocarpus calaber Hort. ex Wendl. Ind. Palm 30. 1854. = O. caracasanus (= Euterpe sp.) according to Wendland (1854).

Oenocarpus caracasanus Mart. Hist. Nat. Palm. 3:310. 1849. = Euterpe sp., according to my field observations in Venezuela.

Oenocarpus chiragua Hort. ex Wendl. Ind. Palm. 30. 1854. = perhaps a Syagrus sp. according to Burret (1928).

Oenocarpus cubarro Hort. ex Wendl. Ind. Palm. 30. 1854. = perhaps O. caracasanus (= Euterpe sp.) according to Wendland (1854).

Oenocarpus dealbatus Hort. ex Wendl. in Kerch. Les Palm. 252. 1878. = Mauritia armata according to Wendland (1878).

Oenocarpus edulis Hort. ex Watson, Gard. Chron. Ser. 3(2):157. 1887. = perhaps Jessenia oligocarpa (= J. bataua subsp. oligocarpa) according to Burret (1928).

Oenocarpus excelsus Mart. Hist. Nat. Palm. 3:310. 1849. Nomen.

Oenocarpus frigidus (HBK.) Spreng. Syst. Veg. 2:140. 1825. = Euterpe frigida according to Burret (1929).

Oenocarpus glaucus Mart. Hist. Nat. Palm. 3:310. 1849. = Oenocarpus caracasanus (= Euterpe sp.) according to Burret (1928).

Oenocarpus gracilis Hort. ex Wendl. in Kerch. Les Palm. 252. 1878. Nomen.

Oenocarpus iriartoides Triana, Neuv. jen i espec. Neo-Granad 15. 1854. Species incerta.

Oenocarpus laguayra Hort. ex Walp. Ann. Bot. Syst. 5:807. 1860. Nomen.

Oenocarpus lutescens Mart. Hist. Nat. Palm. 3:310. 1849. Nomen.

Oenocarpus pulchellus Linden Illustr. Hort. 28:32. 1881. = Euterpe sp. according to Burret (1928).

Oenocarpus regius (HBK.) Spreng. Syst. 2:140. 1825. = Roystonea regia according to Dahlgren (1936).

Oenocarpus sancona (HBK.) Spreng. Syst. 2:140. 1825. Species incerta.

Oenocarpus tenuis Mart. Hist. Nat. Palm. 3:310. 1849. Nomen.

Oenocarpus utilis Klotzsch Linnaea 20:447. 1847.

= Prestoea acuminata according to Moore (1963).

Jessenia

Jessenia amazonum Drude ex Mart. Fl. Bras. 3(2):474. 1882. = Archontophoenix cunninghamiana, according to Burret (1928).

Jessenia glaziovi..na Dammer ex Engl. Bot. Jahrb. 31(70):21. 1902. = Archontophoenix alexandrae according to Burret (1928).

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Chapter 6

ECONOMICS OF *OENOCARPUS*-*JESSENIA* DOMESTICATION: USE AS A TROPICAL OILSEED CROP

"The National Soybean Producers Association...demands duties and quotas on palm oil imports into the U.S., and wants the U.S. to pressure the World Bank to stop making loans to increase palm oil production even more."

Business Week
March 22, 1976

"..Since palm oil is a successful export from poor nations, the World Bank and A.I.D. seem to have done something skillful, and something nice, too. Some of the people producing palm oil have annual incomes smaller than the monthly payments on an American farmer's Buick."

George F. Will
Washington Post
News Service
Evening Journal
Wilmington, Delaware
March 18, 1976

"..And he gave it for his opinion, that whoever could make two ears of corn...to grow upon a spot of ground where only one grew before, would deserve better of mankind, and do more essential service to his country than the whole race of politicians put together."

Jonathan Swift
Gullivers Travels
1726

This chapter concerns some of the economic aspects that must be considered before any attempts are made at commercializing Oenocarpus and Jessenia oils. Data and yield calculations involve a single species, Jessenia bataua. This is presumed to be one of the most productive species of the complex. Because there has never been a major attempt at plantation cultivation and scientific domestication of Jessenia bataua, some of the calculations and assumptions presented are based on speculation and extrapolation from educated guesses developed mainly from first-hand field observations or available literature studies. The ambiguous nature of these data is clearly indicated as such, and caution would be advised in developing long range economic forecasts using the figures given.

The focus of the study is on Latin America, where the palms are presently located and immediately usable. The technology is transferrable to any tropical location--by planting the seeds elsewhere. Interest presently exists in commercializing the palms in both the Old World and New World. This chapter offers a summation of current knowledge in the hopes that such domestication efforts will be furthered.

Edible fats and oils play a vital role in human nutrition. As appealing foodstuffs, they provide energy, serve as a carrier for certain fat soluable vitamins (A,D,E,K) and are used in the construction, repair and maintenance of body tissue.

Tropical America, as is true of other tropical areas, suffers from a serious edible oil shortage (Table 6.1), directly affecting both the health of the local people (especially the poor) and the economies of the countries involved. Shortages of edible oils are frequent in these areas, and prices often wildly fluctuate. Local governments allocate valuable foreign exchange to purchase such oils. The encouragement and development of local oilseed industries would lessen the outflow of currency, permitting the apportionment of funds for other necessities. Among the social benefits accruing from a local increase in oilseed production would be the creation of additional jobs, lessening of rural flight to urban areas, an increase in the G.N.P., the stabilization of land ownership and the encouragement of colonization efforts in previously unused land.

Animal fats and oils were once more popular than those from vegetable products. Presently, for health reasons and ease of production, interest has declined in such animal products. Edible vegetable oil output of both the United States and the world has grown at a greater rate over the past few years than has that for animal fats (Fig. 6.1, 6.2). It thus appears that we should turn to the plant kingdom for the solution of this Latin American "oil crisis."

The most important world oilseed crops are soybeans, cottonseed, groundnut (peanut), sunflower and rapeseed (Fig. 6.3, Table 6.2). Of a 47,837,000 metric ton (MT) 1978 world production of oil crops (oil equivalent), Latin America

Table 6.1

Latin American Imports of Oils and Oilseeds[1]

	(100 Metric Tons) 1975	1976	1977	1978	% of World[2] Imports
Coconut Oil	196	184	1	50	0.5%
Cottonseed	27	1,081	403	446	30.0%
Cottonseed Oil	527	392	525	434	12.3%
Groundnuts[3]	484	210	200	20	0.3%
Groundnut Oil	358	530	1,284	523	12.3%
Olive Oil	97	111	112	80	5.0%
Palm Oil	0	104	110	84	0.4%
Soybeans	1,039	4,185	6,098	6,493	2.8%
Soybean Oil	947	1,705	1,990	2,311	11.4%
Total	3,675	8,502	10,723	10,441	

(1) If not included in the table, Latin America did not import in measurable quantities.

(2) 1978

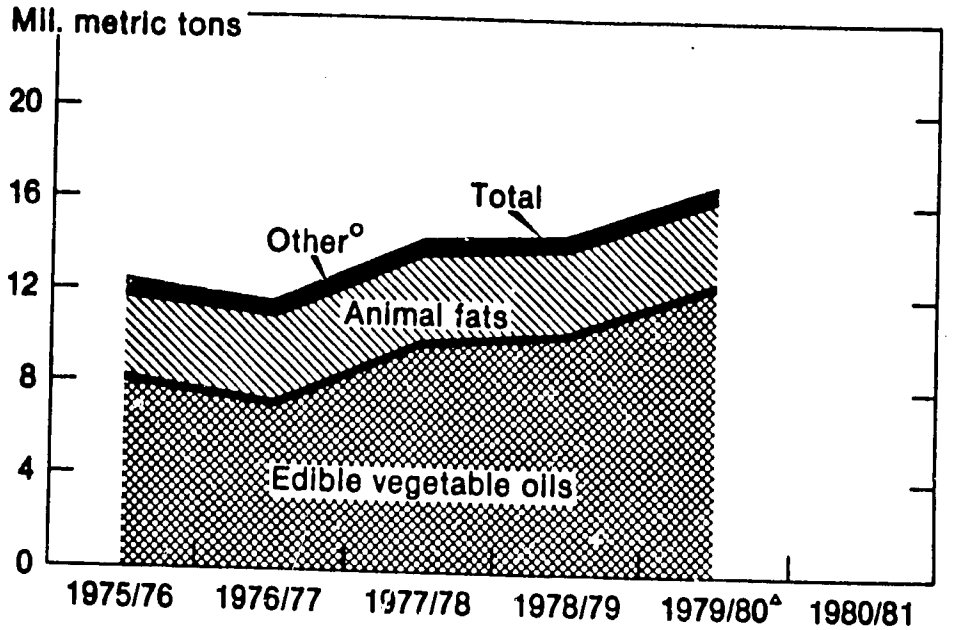
(3) shelled basis

Source: Food and Agriculture Organization of the United Nations 1979.

Fig. 6.1. Oils and fats production in the United States--recent trends in animal fat, vegetable oil and fish oil production. Source: United States Department of Agriculture 1979a, Neg. ESCS 154-79(9).

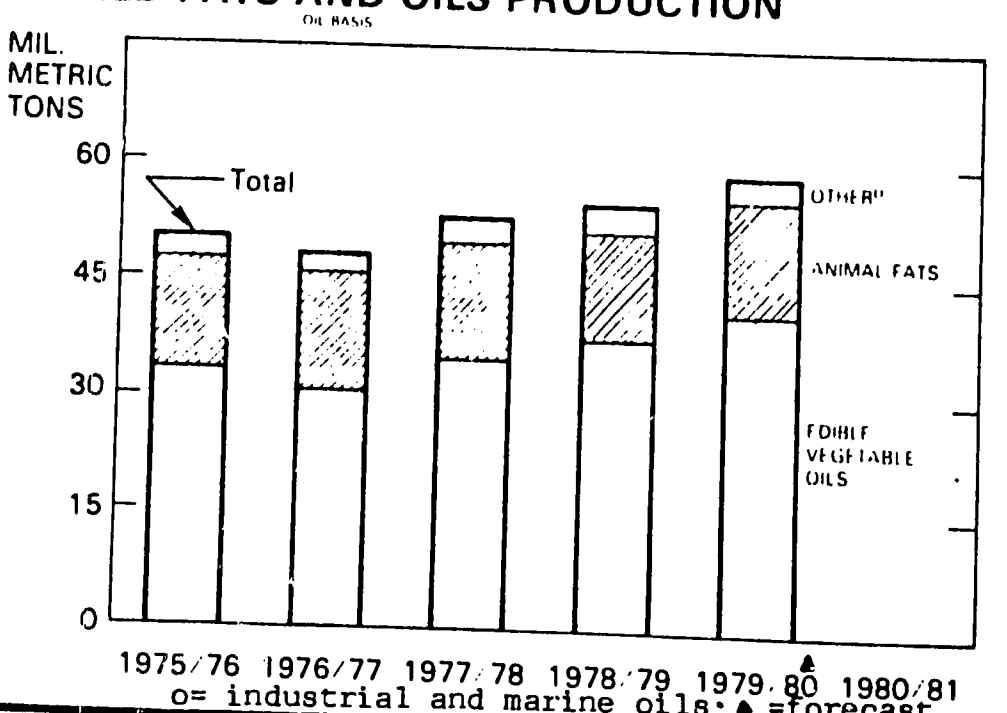
Fig. 6.2. World fat and oil production. Trends in animal fat, vegetable oil and fish oil production. Source: United States Department of Agriculture 1979a, Neg. ESCS 145-79(9).

U.S. Oils and Fats Production*



*Excludes tall oil. °Linseed oil and fish oil. △Projected.

WORLD FATS AND OILS PRODUCTION



o= industrial and marine oils; ▲ =forecast

Fig. 6.3. Major world oilseed crops by volume produced. Source: United States Department of Agriculture 1979a, Neg. ESCS 148-79(9).

WORLD OILSEED PRODUCTION

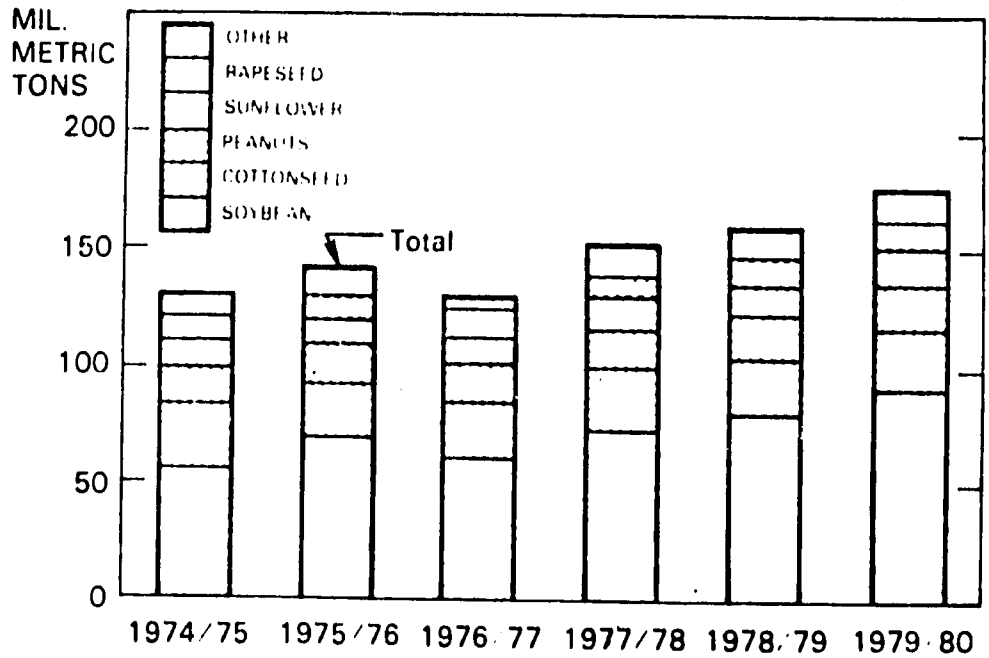


Table 6.2

World Production of Oilseeds and Fats

(1,000 Metric Tons)

	1969-71 (Av.)	1976	1977	1978
Castor Beans	844	626	707	971
Copra	3,837	5,163	4,783	5,053
Palm Kernels	1,160	1,474	1,479	1,541
Palm Oil	1,971	3,495	3,829	4,014
Cottonseed	22,492	22,665	25,736	24,380
Olives	7,650	8,119	9,239	9,560
Olive Oil	1,550	1,519	1,804	1,773
Groundnuts	18,217	17,880	17,982	18,678
Linseed	3,481	2,575	2,993	2,758
Rapeseed	6,617	7,557	7,981	10,187
Sesame Seed	2,013	1,869	1,935	1,972
Soybeans	46,747	63,064	79,207	79,239
Sunflower Seed	9,876	10,133	11,954	12,812
Tung Oil	109	110	103	98
Lard	3,798	3,933	4,094	4,253
Tallow	4,315	4,985	5,197	5,210
Total:	134,677	155,167	179,023	182,499

Source: Food and Agriculture Organization of the United Nations 1979.

produced 5,441,000 MT. For only the oilseeds listed in Table 6.1, Latin American imports amounted to 1,044,100 MT, a significant percentage of local consumption. Dollar value for these commodities is rather high. Venezuela alone imported 73 million dollars worth of fixed vegetable oils and fats and 36.4 million dollars worth of oilseed nuts and kernels in 1976.

While the problems are obvious, we must thoughtfully consider how positive solutions towards lessening the Latin American dependence on imported edible oils should be implemented, if at all. Simple transfer of technology and crops from the developed to the developing world has proven to be a poor long term solution. Each area must be considered independently and regional plans carried out in a large part by local peoples, preferably on a small scale during the beginning stage.

The Oenocarpus-Jessenia complex consists of nine species and six subspecies. Each taxon varies in height, form, size of fruits, yield and many other characteristics. The geographic range of this complex includes the Amazon Valley and much of northern South America, up to an altitude of about 1000 meters, where the palms are found on the Andean foothills. The verdant rain forests of the Amazon Valley contain the highest density of exploitable plants.

Jessenia bataua, a massive palm in the rain forest environment, often attains a height of 20-25 meters. Fruits form in bunches, known botanically as panicles, and hang on

the smooth trunk just below the tuft of leaves. The palm, variously called "pataua", "seje" or "milpesos", depending on the locality, has sundry other minor and indigenous names. Pataua is primarily an inhabitant of wet areas. Thriving in heat and humidity and able to grow equally well on either seasonally flooded or upland areas, its ability to withstand inundations of water is certainly an advantage for exploitation. In the wild, dense, pure stands of palms covering large areas frequently are found. These zones are immediately usable for commercial exploitation. Unfortunately, the practice of felling instead of climbing the plentiful trees for harvest and of burning forest land for colonization has eliminated useful palm populations in some areas.

Market Potential

Indigenous populations have long extracted the fruit pulp (mesocarp) oil for use as a food. Such a procedure is simple: the fruits are heated, pulp removed and oil expressed in a woven basket press. While requiring no elaborate equipment, the primitive methodology used cannot remove all mesocarp oil from the fruit.

Pataua oil also has presumed medicinal qualities, being widely valued as a folk remedy for asthma, tuberculosis, bronchitis and other respiratory ailments. Thus, in addition to its value as a food oil, it can command an even greater local price by marketing it as a curative.

The many uses and high prices (up to $15.00 per liter in Venezuela for medicinal purposes) now in effect for the

limited production in the Amazon Valley give an indication of the value of the oil. The most widespread use, however, is as a high quality edible and salad oil. Chemically, the composition of this oil is surprisingly similar to that of olive oil. Early explorers and missionaries in the Amazon were astounded at the resemblance of this locally produced oil to that of the olive. Similarities and differences can be seen by a comparison of the oil to other commercial species (refer also to Chapter 2).

Table 6.3

A Comparison of Fatty Acids Contained in Selected Fats and Oils

Species:	Pataua	Olive (Spanish)	African Palm	Soybean
Fatty Acid %				
Oleic	76.5	80.5	43.1	33.6
Linoleic	3.4	6.9	7.5	51.8
Palmitic	8.8	9.4	39.0	6.8
Stearic	5.6	1.4	3.5	4.4
Myristic	-	.02	2.4	-
Linolenic	-	-	-	2.3

Source: Jamieson 1943.

The most striking similarity is the high percentage of oleic acid, 80.5% in olive oil and 76.5% in pataua oil. While under current marketing and trading laws pataua oil could never be surreptitiously labelled as olive oil and sold, with its similar, even superior flavor, the introduction, if properly managed and marketed, would undoubtedly be successful. For the economic aspects of this study, the substitutability of pataua and olive oils has been assumed.

Given this similarity, some idea of the potential volume and value of the pataua oil industry can be obtained by examining statistical information available on olive oil.

Olive oil is obtained by crushing ripe olives, which yield 15-20% oil by weight. The first pressing releases the most valuable substance, known as virgin olive oil. Subsequent extractions yield a lower grade oil. Olive oil is used mostly as a salad and cooking oil, although other uses are in soap making and wool combing. As a high quality oil, olive oil commands a significantly greater price than other edible oils. Table 6.4 outlines comparative prices in recent years.

Table 6.4
Wholesale Prices for Fats and Oils in the U.S.

¢/pound	Calendar year 1972	Calendar year 1977	March 1978	December 1979
Olive oil (imported f.o.b. N.Y.)	42.7	86.7	86.7	83.3
Coconut oil (imported f.o.b. N.Y.)	10.7	28.4	32.9	41.6
Soybean oil (refined N.Y.)	12.1	29.0	31.7	30.9
Palm oil (bulk U.S. ports)	--	24.3	27.4	30.1
Palm kernel oil (bulk U.S. ports)	--	33.3	36.9	42.8
Peanut oil (refined N.Y.)	20.4	36.3	41.2	36.6

Safflower oil (drums N.Y.)	31.4	52.0	52.0	--na--
Cottonseed oil (tanks N.Y.)	15.8	30.5	32.0	34.8
Corn oil (refined f.o.b. N.Y.)	19.3	36.5	49.5	34.8

Source: United States Department of Agriculture 1978a, 1978b, 1980.

Depending on the figures and the years, olive oil is approximately three or more times more costly than African Palm Oil, which in tropical American countries is being widely planted in many of the lowland areas.

A report by the World Bank shows a similar price differential in favor of olive oil, a spread projected to exist at least until 1990. Index calculations for 1977 and 1990 lead one to expect a stable fourfold difference during this time (Table 6.5).

Table 6.5

Selected Fats and Oils--Actual and Projected Prices (current U.S. $ per metric ton)

Year	Soybean	Olive	Palm	Palm Kernel
1960	$ 225	$ 585	$ 228	$ 317
1975	619	2,436	434	409
1977	576	2,234	530	620
1980	668	2,753	611	1,010
1985	1,089	3,778	882	1,298
1990	1,402	5,417	1,139	1,695
Index (1977)	26%	100%	21%	31%
Index (1990)	26%	100%	24%	28%

Source: World Bank 1980.

Because of the influence of the Spanish and Portuguese cultures, a strong tradition of olive oil use in Latin American cookery exists. None of these areas are important producers of olive oil, with the exception of Argentina. Table 6.6 lists olive oil imports by selected countries for this region.

Table 6.6
Use of Olive Oil by Selected Countries
(U.S. tons)

	1973	1974
Brazil	17,365	30,000
Colombia	190	270
Ecuador	140	170
Guatemala	159	200
Costa Rica	56	58
Mexico	119	112
Venezuela	787	1000
U.S.A.	32,705	41,240

Source: Wilkie, 1977.

There is a basic need and market for olive oil in Latin America, and pataua oil could successfully compete in this market.

The health factor also plays a part in trends of edible oil consumption. Those seeking to lower serum cholesterol in the diet may choose unsaturated oils such as safflower, sunflower and corn oil over saturated oils such as coconut, African palm, lard and cottonseed. Olive oil and probably Jessenia oil are most likely neutral in this regard because of their high concentrations of oleic acid, and have a comparative advantage for the producer in this portion of the market.

Current world producers of olive oil are for the most

part European countries. Lesser amounts are also grown and exported from Asia, Africa and Argentina (Table 6.7, 6.8).

Because of the strong consumer demand for olive oil, there appear to be few short term effects from the development of a pataua oil industry on olive oil producing countries. A very small amount of pataua oil, relative to overall olive oil production, could be expected to be produced during the next decade if exploitation efforts were immediately to begin.

History of Past Trading

A small international commercial market for pataua oil developed during the volatile trading years of the Second World War. With European sources cut off, the Amazon was able to supply moderate quantities of "olive oil" for commerce. The program in Brazil was limited and not well organized--at the cessation of hostilities production dropped and imports and the widespread use of olive oil began once again. The reason for this decrease is not known but could be based on supply and price of pataua oil, the desire to rebuild war-ravaged European economies or other factors. Table 6.9 illustrates the pataua export figures for Brazil. Since most of the oil produced was said to have been for the export market, these figures are also a general approximation of total commercial production. There is, of course, no way to know the entire annual volume for any single year or at present, as bottles are continually being produced for individual use or barter.

Table 6.7

World Production of Olive Oil*

(1,000 Metric Tons)

	1969-71	1976	1977	1978
Africa	173	154	213	184
Libya	8	11	21	26
Morocco	41	41	32	36
Algeria	21	11	21	26
Tunisia	103	91	139	96
North and Central America	2	2	2	3
Mexico	1	1	1	1
U.S.A.	1	1	0	1
Other	0	0	1	1
South America	18	13	12	11
Argentina	17	12	12	10
Other	1	1	0	1
Asia	128	282	143	264
China	1	1	1	1
Cyprus	2	3	3	2
Iran	1	1	1	1
Israel	1	1	1	2
Jordan	3	5	2	7
Lebanon	11	11	7	10
Syria	23	58	42	60
Turkey	86	201	86	181
Other	0	1	0	0
Europe	1228	1067	1434	1312
Albania	4	7	7	7
Greece	178	251	259	262
Italy	553	325	737	496
Portugal	70	40	33	33
Spain	419	442	395	510
Other	4	2	3	4
Total	1549	1518	1804	1774

*As some figures are unofficial or estimates, the data do not necessarily total correctly and, in addition, may represent minor production from other sources.

Source: Food and Agriculture Organization of the United Nations 1979.

Table 6.8

Olive Oil--Percentage of World Production by Area

	1969-71	1976	1977	1978
Africa	11.0%	10.1%	11.8%	10.3%
North and Central America	0.1	0.1	0.1	0.2
South America	1.1	0.9	0.7	0.6
Asia*	8.3	18.6	7.9	14.9
Europe	79.5	70.3	79.5	74.0
Total	100.0%	100.0%	100.0%	100.0%

*includes the Middle East

Source: Food and Agriculture Organization of the United Nations 1979.

Table 6.9
Exports of Brazilian Pataua Oil

Year	Amount in Kgs	Cruzeiros Value
1939	14,870	70,000.70
1940	71,265	364,107.00
1941	70,914	571,632.00
1942	121,934	1,297,568.00
1943	103,849	1,336,897.70
1944	214,674	2,845,232.00
1945	150,109	2,002,107.80
1946	95,503	1,970,082.50
1947	26,727	661,587.70
1948	29,891	538,436.00
1949	24,656	408,260.00

Source: Pereira-Pinto 1951.

Records exist for some importations of pataua oil into the United States, contained in the following document: U.S. Court of Customs and Patent Appeals, No. 4614, filed December 7, 1948. The Nylos Trading Company of New York imported 63 drums of pataua oil from Brazil for use by the Conti Products Corporation in the manufacture of soap. A dispute arose over the classification of oil for import tax purposes. The Tariff Act of 1930 (paragraph 1732) provides for the free importation of palm oil. However, the U.S. Customs claimed that this oil was not "palm oil" but "patava oil" (semantically equivalent to "pataua oil") and thus assessible for duty at 20% ad valorem, according to the provision in paragraph 53 of said Act, providing duty "for all other expressed or extracted oils, not specifically provided for."

Various authorities in the field, including a botanist, chemist and oil trader offered testimony during the case. The Court ruled that "palm oil" was specifically to refer to the product of Elaeis guineensis, the African Oil Palm. Even though "patava oil" was an oil from a palm tree, its commercial classification was to be, from that time on, distinct from "palm oil." Thus, the precedent was established for excluding "patava oil" from the legal and commercial category of "palm oil." This distinction might today be a useful one if "palm oil" projects are not acceptable to funding sources in the United States.

Several assumptions can be made concerning the short-lived production of pataua oil for the export market. Because of the crisis situation involving the loss of traditional supplies of olive oil, the pataua oil "industry" developed quickly and with no real organization. It is likely that most of the trees were felled during oil collection, to obtain as many fruits as possible in the least amount of time, without regard for future production (once a palm tree is cut down, it does not grow back in the manner of dicotyledonous trees). Hence, large areas of palms were destroyed, explaining the absence today of this once widespread tree near many rural villages. Consequently, future attempts will require a more rational exploitation such as cultivation of plantation trees, in a system comparable to that used for the African Oil Palm.

The extraction during this short period of production

was by primitive methods, owing to the isolated locations of the palms. An efficient and economical procedure was not used. For the proper development of an industry today, mechanical presses are vital for removing all of the mesocarp oil possible.

Summarizing lessons learned from this wartime experience, several objectives and requirements may be stated for a proposed pataua domestication project:

1. A good organization and infrastructure is required. Sites for exploitation must be situated near rivers, roads or other means of economical transport. Semi-skilled labor is required for operation of the extraction facility, overall project organization and supervision. As fruits deteriorate rapidly when ripe, the flow rate from field to press must be uniform and carried out in a minimal amount of time.

2. Existing palms in the wild must be conserved by prohibiting the felling of trees for harvest. This will assure no decline in the number of productive trees; rather overall total will increase through natural propagation: eg. seed production and dispersal. In addition, germ plasm will be preserved in the wild until such time as large scale collection and preservation can be undertaken. Future domestication work will rely upon the available variation in palms for genetic manipulation.

3. Additional areas should be replanted with Oenocarpus and Jessenia palms. A replacement of forests and other tracts now devoid of exploitable products: e.g. wood, latex, nuts, etc., with economic species such as pataua palms will increase the value of the land. The palms thrive on swampy or wet sites not suitable for most other species, and best use of such zones can be made through a massive reforestation program using Oenocarpus and Jessenia.

4. Extraction must be done mechanically. Use of the basket press does not remove enough mesocarp oil for maximum financial return. A simple hydraulic hand unit can express a far greater percentage of oil.

Current Yield Levels

As stated before, present utilization of the Oenocarpus-Jessenia complex is on a very limited basis, with oil extracted at the request of an individual for use as food or medicine. In 1950, two agronomists, Luciano Sirotti and Gino Malagutti, undertook a study of the feasibility of the exploitation of Venezuelan populations of "seje" (Jessenia bataua and Oenocarpus bacaba). Their detailed field observations provide an idea of what a grove of these palms is able to produce.

The "sejales"--almost pure stands of these palms--are composed of plants in various life cycle stages: seedlings, young, mature (fully productive) and senescent (dying or

non-productive) individuals. This kind of forest is a dynamic system, with inputs from young plants adding to the overall population, and losses from senescent plants dying out. The rate of population flow and changes over a certain period are unknown. The mature, producing, versus the mature senescent or sterile non-productive Jessenia bataua trees were calculated by Sirotti and Malagutti (1950) in terms of productive and non-productive plants. Of the populations studied in the Venezuelan Amazon, it was found that 71.6% of the mature plants were productive and 28.4% were not. Of these, the average fruiting panicle weighed 14.5 kgs (range 12-18 kgs), of which 10.43 kgs (range 8-15 kgs) was pure fruit. Of the 71.6% productive plants, 29.9% produced 1 panicle, 42.1% produced 2 panicles and 36.8% produced 3 panicles. In a natural grove then, from 100 mature plants, an average of 154.6 panicles with approximately 10.43 kg of fruit each, can be obtained--a total of 1612 kg of fruit.

According to the observations of these two agronomists, the number of plants per hectare in an exploitable sejal was as follows:

Seedlings (under one year)	1000
Young plants (1-4 years)	400-500
Bearing plants	400-500

Variable percentages of oil composition are listed for the fruit of this palm, ranging from 5-10%. At 8% the amount of oil that could be expected from these 100 plants would be 129 kg annually (282.8 lbs). At 7.63 pounds per gallon, a

production of 37.2 gallons of oil might be expected from each 100 trees of Jessenia bataua growing under wild conditions. With a current wholesale price of 83.3 ¢/lb for olive oil, the total return per 100 wild forest plants would be $236 each year. Taking an average of 450 bearing plants per hectare, a yield of 580.5 kg of oil is extractable each year, assuming a reasonable consistency in the forest structure, and the integrity of the original calculations. At the wholesale price mentioned, 83.3 ¢/lb, a return of $1064.00 per hectare can be obtained for the oil extracted. While this is not by any means a large sum of money, it must be remembered that great numbers of these palms exist today in many areas of the Amazon, although not all at the stated 400-500 trees per hectare density. These calculations were not able to take into account the harvest of Oenocarpus bacaba growing in the same areas as Jessenia bataua, and yielding equivalently oleaginous fruits, but ripening at a different season, also adding value to the land. Based on my own field measurements, a density of 450 bearing trees per hectare in the wild seems rather high, although there is no real reason to consider the calculations of Sirotti and Malagutti as suspect.

As has been mentioned, many areas where these palms were formerly abundant no longer exist. At present, clearing is proceeding at lightning speed, for colonization, local use and for whatever rationale is involved in man's destruction of his own habitat. Consequently, the feasibility of

plantation cultivation must be considered for this palm, initiated at first by government, private sector and international agencies, perhaps in combination with other agricultural projects.

Agronomists often cite the high yields of Elaeis guineensis as good reason not to begin exploitation of Jessenia bataua or other oilseed crops. The current value of the African palm is praised as if it had always been a domesticated plant, especially as latest United States Department of Agriculture estimates show yields of 3480 kg of palm oil and 421 kg of palm kernel oil respectively per hectare (U.S.D.A. 1976). Those skeptical of the value of Oenocarpus and Jessenia would be well advised to study the history of Elaeis domestication and consider what it once was, before making a quick decision regarding the utilization of other oil palms. To present fairly both cases, we must go back to the native locations of the African Oil Palm and also investigate its original production.

Elaeis guineensis is of African origin. Zeven (1967) supported this origin with fossil pollen evidence from the Miocene and younger (25 million years ago) in the Niger Delta. Early explorers and traders mention these palms in their journals as being useful for food. Much movement of the plant has continued, through domestication and use by man, and it is now common in tropical regions worldwide.

The habitat of many jungle palms is similar. While they can survive in the rain forest, through competition with other

plants, they thrive in swampy and waterlogged areas because of a physiological ability to adapt to the low degree of soil aeration. In Africa, E. guineensis is found in great stands on areas too wet for the usual rain forest vegetation. Zeven lists its habitats as: fresh water swamps, sources and banks of water courses, moist valleys, banks of lakes, swamps, alluvial plains, low-lying islands in rivers and forest fringes, especially in savannah areas. In these latter zones, palms can develop and multiply as they are not cut off from the sun by overhanging trees. The phenotype of the wild oil palm is thought to be thin-trunked with a covering of epiphytes and old leaves, and very small fruit bunches in comparison with those known today from plantation cultivation.

The biology and life cycle of the wild palm groves is most revealing. In a semi-wild environment, it may take 20-30 years for the palms to reach a fruiting age. In contrast, only four years are presently required until fruiting begins in the domesticated African Oil Palm. For wild groves of Jessenia bataua, 8-12 years is cited as the time required for first fruiting. The percentage of yielding trees of Elaeis guineensis growing wild in Africa is also of interest. Zeven (1967) noted that the number of mature palms bearing fruit in any one year varied from 54-63% in an Abak grove in eastern Nigeria. This compares to the 71.6% found for J. bataua in Venezuela. Examining the size of African Oil Palm bunches from the wild in Benin, Nigeria, Zeven calculated the average number of all stemmed

palms per hectare as 59.6, each producing 1.9 bunches of fruit, weighing an average of 27.8 kg, or 14.3 kg for each bunch. Of this, the fruit:bunch ratio was a mean of 58:42, or an average calculated value of 16 kgs fruit, of which 6.72 kg was mesocarp (pulp) and 2.24 kgs kernel. In the same reference, an assumption is made of the oil:bunch ratio as 16%, which gives about 4.45 kg of oil per palm present. The yields of a grove near Abak range between 12.0 kg of bunches per plant (at 254 plants per hectare over an observation period of 1949-52) to 28.2 kg per plant (at 175 plants per hectare during 1949-59). Using the same oil:bunch ratio, yields range from 1.9-4.5 kg of oil per tree. Our previous calculation with Jessenia bataua gave a value of approximately 1.3 kg per tree, much lower than these values. However, keeping in mind the higher price of olive oil, a return of 3-4 times that of E. guineensis oil may be expected per kg. Using the pre-domestication biological data for the African Oil Palm, the great increase in oil production over time can be seen (Table 6.10). The African Oil Palm is a low yielding plant in the wild, with small fruits and few bunches. Under cultivation, Bunting et al. (1934) estimated fruit yields of 7-8 year old African Palms at 6,287 kg hectare, with 1527 kg of palm oil obtainable. Recent U.S.D.A. data for Malaysian palms suggest a yield of 3901 kg of oil (palm + palm kernel) per hectare. Highest yielding experimental results presented in Corley et al. (1976) list a maximum of 37,200 kg of fruit per hectare in some trials with up to 8,420 kg of oil produced

Table 6.10

Present and Historical Yields of the African Oil Palm

	Kg Fruits/Hectare	Kg Palm Oil/HA	Oil:Bunch (%)
Wild State (Zeven 1967)			
Benin (per 125 plants)	2,000	556	ca. 16
Abak (per 125 plants)			
Minimum:	870	240	ca. 16
Maximum	2,044	564	ca. 16
Malaysia (Bunting *et al*. 1934)			
Ca. 1930, 7-8 year old palms, 136 per hectare	6,287	1,572	not noted
Malaysia 1971-75 av. (U.S.D.A. 1976) (density not noted)	ca. 15,604	3,480 (+ 421 kg palm kernel oil)	ca. 25
Malaysia, experimental high-yielding plantation (Corley *et al*. 1976) (density not noted)			
Spacing trial	28,500	6,760	23.7
Fertilizer trial	37,200	6,280	16.9
Progeny trial	30,400	8,420	27.7

per hectare in others. This last reference represents a total increase of just under twentyfold for overall fruit production over wild trees, resulting from the intensive program of domestication and selection of Elaeis guineensis. The reasons for this include artificial pollination, selection for disease resistance and higher yields and proper cultural care--in short, creation of an ideal habitat for the reproduction of the palm through its seed productivity.

Present State of Domestication

At present, the Oenocarpus-Jessenia palms are not domesticated in the agronomic sense of the word; eg. taken from the original habitat and cultivated for successive generations by man (Seibert 1948). Diversity of these organisms is poorly understood, as no study has ever been made over their entire geographic range. This investigation represents the most inclusive work to date, but many important localities remain to be investigated.

One indigenous achievement has been the partial, subconscious domestication of the pataua palm through its everyday use as a food. Indians in each area recognize a number of different "forms" of Oenocarpus and Jessenia, always assigning a hierarchal preferance ranking to each. As foragers, these people have an extensive knowledge about the composition of their rain forest and collect only those "forms" considered superior in taste, oil content, coloration, ease of harvest, etc. Panicles from such trees are brought back to the village and the fruit is prepared for consumption.

As mentioned in Chapter 4, heating the seeds and removing their oily mesocarp increases germination percentage and actually hastens growth rate. After preparation, the seed from the preferred palms is discarded in the area surrounding the house, where it germinates and grows. Within a few years, the forest around a settlement contains a high composition of pataua palms. Even after abandoning a site, people return to harvest fruits from this select group of trees. Today, disturbed forest areas having concentrations of these palms indicative of past settlement are, consequently, choice locations in which to collect germ plasm of superior, subconsciously selected variants.

The Las Gaviotas Model of Utilization in Colombia

Centro de Desarrollo Integrado "Las Gaviotas" is a non-profit development agency located in the Llanos of the Comisaría del Vichada. An area of savannah and gallery forest, the region is, in general, unsuitable for conventional agriculture, so alternative solutions for development are being sought. The original objective of Las Gaviotas was to select a poorly populated area of Colombia, colonize it and build a permanent settlement dedicated to developing low-cost technology and uses for the region. The rational exploitation of native plants from the gallery forests, specifically extracting fats and oils from palm trees, is a prime goal of the agricultural program.

Guahibo and other residents of the region commonly destroy the forests for swidden agriculture. Las Gaviotas

now purchases fruits of Oenocarpus and Jessenia palms as a raw material for its small-scale, mechanized processing and extraction facility. For the first time, a financial incentive exists for an individual farmer to conserve palms on his land for long-term fruit production, instead of clearing them for several short-lived annual grain or legume crops.

As the presses and extraction facilities have been donated by international organizations, most of the costs involved in processing are variable, and these costs constitute primarily labor. Thus, an individual landowner is able to receive a fair price for his sacks of fruit sold to Las Gaviotas. The collection scheme involves the organization of fruit harvests on a specific day in each locality. Then, people bring the harvest to their village center--perhaps on market day--for collection by the Las Gaviotas truck. The truck transports fruit back to the facility for processing (see Appendix 1 for description of this procedure).

One constraint for increasing production in this area appears to be the total supply of Oenocarpus-Jessenia palms, which have traditionally been cut for harvest. According to Blaak (pers. comm.), local residents are now climbing the palm to collect fruit panicles, ensuring a yearly financial reward, instead of simply cutting them down. A requisite for expansion of the project is repopulation of the gallery forests of the Vichada with Oenocarpus and Jessenia palms --specifically O. bacaba, O. mapora and J. bataua. This

demonstration that man can practically and economically harvest the products of his tropical forests, especially in such an impoverished area, is an excellent model on which to base further development of agro-forestry in other zones presently being decimated.

Proposed Plantation Cultivation

If a Jessenia bataua plantation is well cared for, an immediate increase in production can be assumed. If all palms of a single species are grown under uniform conditions, each should yield during the same season, and calculations will not have to be adjusted for non-productive (senescent or diseased) plants. I have seen individual plants under semi-cultivated conditions with as many as 5 panicles apparent at one time, in various stages of fruit and flowering. Thus, it is felt that the number of panicles could be increased from two per year to a higher figure. For example, if it is assumed that the average is 2.5 panicles per year, then the yield of fruit will be somewhat increased. Another factor is reproductive efficiency: that is, the actual number of fruits formed versus the potential number. Field studies have shown a reproductive efficiency of only 3-15% in Jessenia bataua on a heavily fruited panicle. The total amount of fruits that could be formed would be about 6-8 times the present 10.4 kg. The reproductive efficiency could perhaps be increased through better pollination, disease control and physiological methods. This area of biology is poorly understood, and reasons for the relatively

low efficiency are not now known; perhaps, indeed, there is no way to increase it. However, in plantation cultivation, through the skills of the breeder and agronomist, it is more likely that there would be a rise in the percentage of fruit set. As simple a procedure as hormone sprays during floral anthesis--as is done with vegetable crops--might be the answer.

It might be helpful to recalculate some of the figures for the proposed Jessenia bataua plantation, using the field observations of Sirotti and Malagutti. On the scale of 100 well grown plants, the annual fruiting based on observations in the wild would be approximately as follows:

1 panicle 21%

2 panicles 42%

3 panicles 37%

total: 216 or 2.16 panicles per plant

In the triangular spacing method of Hartley (1967), about 216 African Oil Palms are planted per hectare at an approximate spacing of 7.32 x 6.34 meters. Judging from the size of Jessenia bataua, this spacing could be possible, especially as the leaves are held upright on the palms during their early development and the first years of bearing. Only at full maturity do the leaves assume a horizontal orientation. This habit would allow for intercropping of the young plantation, adding a greater economic incentive to production.

An estimate of the oil yield per hectare from this

planting, assuming no increase in reproductive efficiency or in the number of panicles produced, might be obtained as follows: 2.16 panicles x 216 palms x 10.4 kg of fruit per panicle = 4852.22 kg of fruit annually per hectare. At an 8% recoverable oil content, 388 kg (or 854 lb) of oil might be produced annually on a well managed planting of 216 trees per hectare. At 83.3 ¢/lb the value would be $711.4 per hectare. It must be remembered that Latin American prices for olive oil are far higher than world market prices because of the duties and transportation costs involved. Therefore, a much greater price could be expected from sales of pataua oil in this region.

If an increase to 2.5 panicles annually produced is calculated, the total fruit harvested per hectare would be 5616 kg, yielding 449.3 kg (988.4 lb) of oil, or $823 per hectare. Finally, if reproductive efficiency is increased, and palms produced 12 kg of fruit per panicle, the per hectare yield becomes 6480 kg of fruit, 518.4 kg of oil (1140.5 lb) and a value of $950 (Table 6.11).

Table 6.11

Forecasted Yields and Values of *Jessenia bataua* in a Domesticated State, Based on Values calculated for Wild Palms

	# Palms/ Hectare	Kg Fruit Yield/ Hectare	% Oil	Kg Oil/ Hectare	Price Kg	Value/ Hectare
Low Estimate	216	4852.22	8%	388	83.3¢	$711
Medium Estimate	216	5616	8%	449.3	83.3	823
High Estimate*	216	6480	8%	518.4	83.3	950

*But still a conservative estimate, as increases in yield due to domestication and selection are unknown and not accurately predictable.

Admittedly, the previous calculations on a proposed plantation involve much speculation on unknown factors. Because there has never been a real attempt at cultivation, these figures are the only ones available. The census of 500 trees per hectare by Sirotti and Malagutti is an extremely high density of palms with a lower per tree production but an overall higher dollar yield. Whether these stands can be maintained and produce fruit over a long period of time in such a high density is questionable. As mentioned, my own experience in Jessenia palm groves shows the number of bearing trees to be much lower than the Sirotti and Malagutti figures. Furthermore, not taken into account here is the cyclical nature of pataua fruit production over a period of years. The tree begins yielding in great quantities, but, as it approaches senescence, yields begin to taper off. Sirotti and Malagutti use a lifespan of 50 years in their calculations, with the first few plants (density of 200 per hectare) bearing at years 7-10; 100% production being achieved during years 15-42, 60% production during years 43-46, and 25% production during years 47-50. Their estimate of 50 viable years may or may not be accurate and can only be investigated through long-term ecological studies.

A calculation of 22 kg of oil per tree is often cited in the literature (see for example National Academy of Sciences 1975) but no sources or methods are ever given as to how this number has been ascertained. I have traced these calculations to a publication by the well known Colombian

botanist Armando Dugand. Upon re-examining the figures, they appear to be incorrect, and the actual figures should be a maximum of 2.22 kgs per tree per year, using his given variables. Because of their importance, the paragraph in which these calculations appear is reproduced in Appendix 2 along with the recalculations. In the Dugand figures, there was a probable misplacement of the decimal point, but it has since come to have been accepted, unfortunately, as fact.

In addition to Jessenia bataua, other species within this complex could be exploited. The genus Oenocarpus is characterized by an oily mesocarp. Oenocarpus minor and O. mapora might be of value as, according to anecdotal information, they begin to fruit within 3-4 years of planting, a substantially shorter period than in Jessenia bataua. These two species of Oenocarpus are smaller in stature, and caespitose. Oenocarpus distichus has a higher percentage of pulp in relation to kernel than Jessenia and, furthermore, develops its leaves along a single vertical plane, allowing for more intensive spacing per hectare. Oenocarpus bacaba is a species highly esteemed throughout the Amazon Valley for its oil production.

One additional use of Oenocarpus and Jessenia is for possible crossing with different groups of palms, using the DNA recombinant technique now under development. If an "olive oil" producing palm could be crossed with a high-yielding African Oil Palm, perhaps a race could be developed of high-yielding "olive oil" palms. Although at

present this technology is a long way off, one should be aware of the possibility.

Present technology would allow for the crossing of Oenocarpus and Jessenia as a first step. In the wild, natural hybrids between O. bacaba and J. bataua have been found. The resultant progeny produces a miniature kernel with no embryo and has a higher relative mass of fleshy mesocarp to seed. When Indians in the Vaupés of Colombia locate trees of such parentage, they climb rather than cut the palms for harvest, as the hybrids are recognized and highly esteemed for good quality fruit production.

The only experimental plantation of species in this complex to my knowledge is at the EMBRAPA agricultural research station in Belém, Brazil. I had the opportunity of visiting the site, where Oenocarpus distichus is planted on sandy soil in the very high density spacing of 4 x 4 meters. Unfortunately, the experiment was abandoned for an unknown period of time, and the usual growth rates under normal plantation cultivation could not be calculated. After 16 years, however, with adverse conditions and poor soil, some trees were producing their first crop. The plants looked healthy and bore low enough to the ground to be harvested easily. There is no way of knowing the amount of secondary growth allowed to flourish in the planting and how this affected the experiment. A need remains for monitored repetitions with all species. Because various species fruit at different seasons, perhaps a year-round or extended

harvesting scheme could be worked out--another aspect necessitating further study.

A singular problem noted in the Oenocarpus distichus plantation was weevil larvae found boring into the fleshy parts of palm, eg. the leaf sheath and inflorescence. This pest was identified as Rhynchophorus palmarum, an injurious predator found also in wild palm populations and deemed a possible insect threat to cultivation. The weevil attacks both coconut and African Oil Palm plantations in tropical America, burrowing into the trunk and crown, especially on young trees. Techniques have been developed to prevent and control infestations.

In summary, utilization of this palm complex for oil production might proceed in two directions. 1) The existing stands of palms in Latin America are immediately exploitable. 2) Greater opportunity is through rational domestication, as Oenocarpus-Jessenia palms hold much promise as oilseed crops for tropical regions. Low yields at present and no knowledge of what future production rates could be are needlessly preventing the widespread domestication and use of this plant. However, it has been shown through the example of Elaeis guineensis that palm fruit yields increase greatly when selected for superior characteristics and given good agronomic conditions. There is no reason to doubt that an increase in production would occur when Jessenia bataua is grown in plantations although perhaps not so dramatically as has happened with the African Oil Palm. Only consistent,

scientifically based trials will provide the answer. If successful, such an increase in the number of oilseeds cultivated and the areas under cultivation will provide both economic and social benefits to producer countries and their inhabitants.

U.S. Oilseed Industry

The oilseed industry in the United States is large and powerful, providing an immense dollar volume of export products. Due to the current trade imbalance, these products are increasingly important. In fact, oilseeds are second only to grain and feed exports, with a total of $6,350,000,000 in oilseeds and products exported in 1977. This represents a threefold increase in the dollar value of such exports since 1970.

Of the domestic oilseed industry, soybeans constitute the major crop (Fig. 6.4, 6.5). Other important crops include peanuts, corn and cottonseeds. Soybeans are by far the most important of these, as can be seen from the preliminary export records for 1978, given in metric tons (U.S.D.A. 1979b):

Soybeans -- 20,704,536 MT, an increase of 260% since 1964.

Soybean oil -- 929,282 MT, an increase of 50% since 1964.

Soybean oilseed cake and meal -- 5,914,576 MT, an increase of 270% since 1964.

Peanuts (shelled and unshelled) -- 394,852 MT, an increase of 850% since 1964.

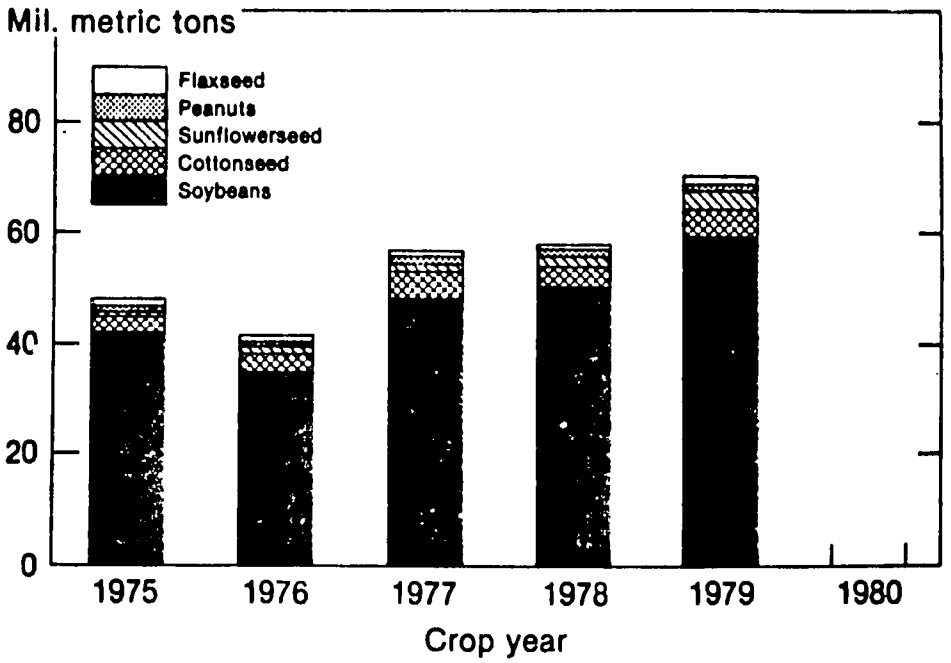
Peanut oil -- 40,339 MT, an increase of 9% since 1964.

Cottonseed -- 42,908 MT, an increase of 4.5% since 1964.

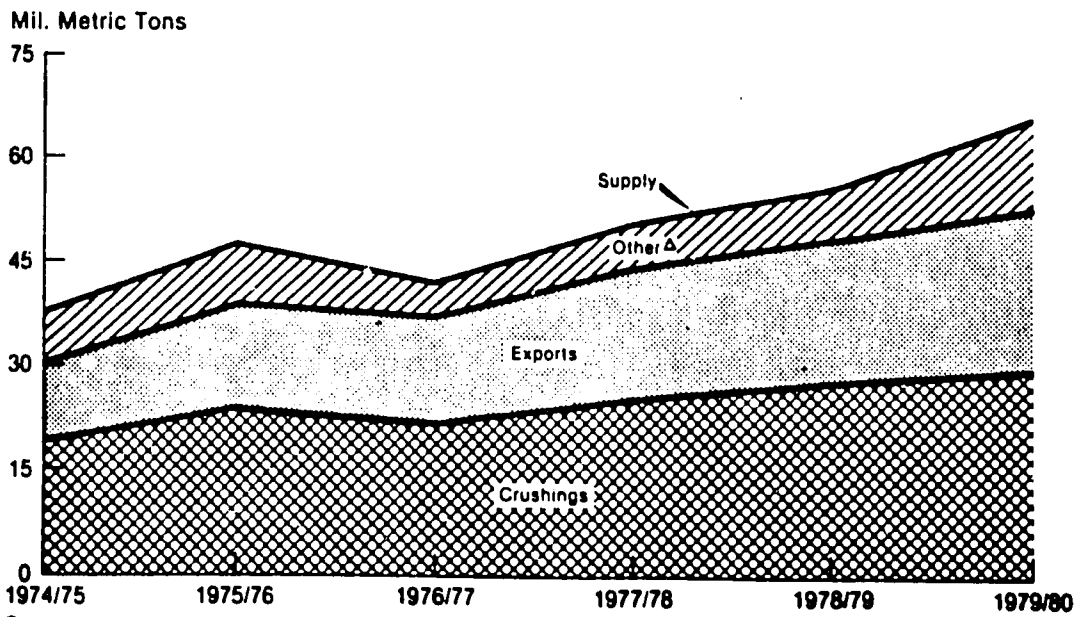
Fig. 6.4. Oilseed production in the United States by crop; trends in recent times. Source: United States Department of Agriculture 1979a, Neg. ESCS 155-79(9).

Fig. 6.5. Use of the soybean crop of the United States. Note the increased importance of the export market. Source: United States Department of Agriculture 1980, Neg. ESCS 2511-80(1).

U.S. Oilseed Production



U.S. Soybeans°



°Crop year beginning September 1. △Other uses include seed, feed, and stock changes.

.Cottonseed oil -- 330,765 MT, an increase of 2% since 1964.

The rapidly expanding production of the African Oil Palm has posed a threat to the soybean industry over the last few years. The palm can produce far greater quantities of oil per acre than soybean, in an astounding ratio of 12:1 (Table 6.12). Soybean does produce more seed meal per acre, 578 kg as compared to palm meal, 227 kg. At an average price taken from 1971-75, the total value per hectare for the African palm is $1643, while the soybean is a relatively poor $400. In most years, the price of palm oil is lower than that for soybean oil.

Tropical countries are expanding palm oil plantations at a remarkable pace. The African Oil Palm is viewed as a key to development. Low maintenance cost, strong market, and long, reliable yielding life (ca. 30 years), are major reasons for this interest.

Palm oil imports into the U.S. have declined over the past few years, but worldwide production continues to increase. Tree crops, once planted, generally bear reliably each year, and, in this case, yield a substantial "permanent" crop which cannot be held out of production as can an annual crop such as soybean or sesame.

In 1976, during a conference of the American Agricultural Editors Association, President Gerald Ford was questioned about the rise in palm oil production and whether he had any plans for action with regard to the threat to the U.S. soybean industry. He reminded the conference that world exports

Table 6.12

Comparative Value of African Oil Palm and Soybean

(1971-75 Average)[1]

	Yield Per Hectare/Kg.		Value Per Hectare/$		
	Oil	Meal	Oil	Meal	Total
African Palm (W. Malaysia)	3,901[2]	561	$1,576	$67	$1,643
Soybean (U.S.A.)	323	1428	153	247	400

1. 1971-75 average prices for Europe.

2. Includes 3,480 kg palm oil and 421 kg palm kernel oil

Source: United States Department of Agriculture 1976.

were a "two-way street" and that there was a 12 billion dollar net gain from farm exports in 1975. However, written later into the 1978 Foreign Assistance Act was a clause restricting the use of U.S. funds in financing development projects involving the African Oil Palm.

The proposed pataua domestication program could conceivably be subject to criticism as a palm oil project, and the previous few paragraphs have been included to explain the reasons for such a possible attitude. As explained in the beginning of this chapter, pataua is non-competitive with palm or even soybean oil. It is in the chemical class of olive oil with its high composition of oleic acid. There truthfully can be no justified criticism of this program by agribusiness interests in the U.S., as the products will not be competitive. Indeed, the only competition will be with the olive oil producing countries, as olives and their oil are a negligible portion of U.S. Agribusiness. It could even be offered as a good argument in support of a pataua program, as it will occupy tropical acres that could have been used for African Palm, to produce pataua oil instead.

U.S. Oilseed Support Prices

The next section briefly summarizes the status of the U.S. oilseed industry, in terms of price support and protection. An idea might be obtained from this for the formulation of a foreign support model for pataua.

Six oilseed commodities are currently eligible for price support by the U.S.D.A.: soybeans, cottonseed, peanuts, tung

oil, flaxseed and castor beans. Other oil-producing commodities such as corn, that are supported as feed grains, are not considered here.

Soybeans are supported at a 1978 price level of $4.50 per bushel, for grade #1, with 12.8-13.0% moisture. Support is implemented through loans and outright purchases of farm and warehouse stored soybeans.

Support for cottonseed is established only when the President or Vice-President of the Commodity Credit Corporation determines the need. For example, in 1973 there was no support program. When a support program is announced, it is provided through direct purchases from, or loans to producers.

Peanuts were supported in 1976 by a level of $414 per short ton, 75% of the parity price as of August 1, the beginning of the 1976-77 market year. With an acreage allotment of 1,614,312 acres, the marketing quota for 1976 was 2,004,400 tons. Penalties were applied to farmers exceeding their allotment. All peanuts within the eligibility requirements were given support, primarily in the form of non-recourse warehouse storage loans to approved grower associations. Supports also existed through loans to producers for on-farm stored peanuts and outright purchases. Peanuts found to contain the Aspergillus flavum toxin were not eligible for support.

Tung nuts were supported in 1975 through the support of tung oil (15-22% by weight of the seed), at a level of 29.2¢

per pound. Non-recourse warehouse loans were granted to eligible producers. No acreage allotments or marketing quotas exist for this oil. Due to recent adverse weather conditions, the tung oil industry in the U.S. has declined.

In 1974 the average crop support price for U.S.-grown flaxseed (grade #1) was $2.50 per bushel. Funds are granted through loans and purchases. A special purchase program exists in the humid areas of Texas, where some flaxseed is grown, because seed cannot be stored for more than short periods of time. There are no acreage allotments or marketing quotas for flaxseed.

Castor beans were brought under support in a limited price support program in 1968 in a program intended to bring production levels up to 20% of U.S. needs. At that time the support was about 5.5¢ per pound, to a maximum of 30 million pounds. Castor beans are also intended for use on acreage that has been taken out of production from feed grains.

The general aim of these support programs is to encourage domestic production of vegetable oils and in addition provide alternative crops for feed grain producers. However, the oilseed market is growing significantly, and is now about one-half the size of the feed grain export market. Farmers have been able to produce oilseeds on certain acreage taken out of feedgrains, with an increase in farm income. In addition, farm surpluses are reduced under this system of management.

The "double use" of some oilseed crops also helps to stimulate their production. For example, soybeans can be crushed for oil but the meal that remains is of higher value. Cottonseed oil is a byproduct of cotton fiber and corn oil a byproduct of corn wet milling. This is not the case in flaxseed, as flax grown for seed is not usable for fiber.

Domestic Protection through Quotas and Tariffs

A system of tariffs and import quotas on certain commodities protects and stimulates the domestic oilseed market. Obviously, any great flood of a single commodity, unchecked, has disastrous effects on local producers. This has actually happened with African Palm Oil imports, and tighter import controls have resulted in a recent drop in overall imports. Table 6.13 shows general tariffs and import controls listed in June, 1968.

Another program involving oilseeds is the Agricultural Trade Development and Assistance act of 1954 (Public Law 480, 83rd Congress). Under this law, exports of domestically produced oils are used as trade commodities and for famine and disaster relief. Exports of soy and cottonseed oil have been subsidized by the government, an additional benefit for the producer.

As has been shown, the domestic production of oilseeds is stimulated by government in three major ways: price supports, import tariffs and restrictions, and international (and national) "giveaway" programs. A proposed pataua industry could be helped off the ground by a local government

Table 6.13: Selected Tariff and Import/Export Data

Commodity	Rate prior to Jan. 1, 1968	U.S. concessions in 1964-67 trade conf. effective Jan. 1, 1972	Domestic Prod. recent average	Imports Recent avg.	Exports	Notes
Apricot and peach kernels	3¢/lb.	1.5¢/lb.	4.1 million lbs.	140,000 lbs.	756,000 lbs.	imports/ exports fluctuate yearly
Castor bean	.25¢/lb.	free	prod. support up to 30 mill. lbs.	0-5 mill. lbs. (1963 -67)	oil under 1 mill. lbs. annually	same as above
Castor oil	value over 20¢/lb. -1.5¢/lb. value under 20¢/lb. -1.5¢/lb.	1.5¢/lb. 7.5% ad. val.	24 mill. lbs, most from domestic beans	105 mill. lbs per year	same as above	same as above
Coconut Oil (many different schedules and classes depending on geographic origin and type of commodity.)	1¢/lb. if entered after July 3, '74.	none	353 mill. lbs from imported copra in 1967.	506 mill. lbs. 1967.	4 mill. lbs.	
Cottonseed	1/3¢/lb.	none	6,266,000,000 lbs. (1967)	--	9,174,000 lbs	U.S. leads in world prod.
Cottonseed oil	3¢/lb.	none	1,107,500,000 lbs (1967)	17,454,000 lbs (1967)	72,000,000 lbs (1967)	

Flaxseed	50¢/bu.	none	1,116,136,000 lbs (1967)	148,000 lbs (1967)	337,642,000 lbs (1967)	
Linseed oil	4.5¢/lb.	none	365,800,000 lbs (1967)	12,000 lbs (1967)	45,360,000 lbs (1967)	
Palm Kernel Oil (edible)	.5¢/lb.			104,342,000 lbs (1967)		imports for Palm Oils higher in recent times
Palm Kernel Oil (inedible)	free					
Palm Oil (edible)	free				64,261,000 lbs (1967)	see above
Soybean Certified Seed	1.4¢/lb	1¢/lb.	58,362,000,000 lbs (1967)	36,000 lbs		
Soybean other	2¢/lb	1¢/lb.		16,000 lbs	15,805,000,000	
Soybean Oil	45% ad. val.	22.5% ad. val.	5,992,000,000 lbs. (1967)	5,000 lbs.	1,129,000,000 lbs. (1967)	

Source: United States Tariff Commission 1968.

using any or all of these ways.

Support for Agricultural Production in Latin America

Latin American governments offer varying degrees of protection and support for national agriculture. The following synopsis illustrates efforts made by Brazil, Colombia, Ecuador and Venezuela.

Brazil, with its strong interest in agricultural development, has built a large system of grower-assistance programs and supporting agencies. A minimum pricing policy offers growers the choice of withholding their crops from the market at government or private warehouses until the price rises, or, if necessary, direct product acquisitions. A good credit policy exists giving low interest loans of 13-22%. With an annual inflation rate far above this figure, the results are loans at negative interest rates. The crop insurance program (PROAGRO) offers security against possible failure. A number of agencies assist agricultural development at the regional level, including POLOCENTRO (Goias, Mato Grosso and Minas Gerais), POLONORDESTE (N.E. Brazil) and POLOAMAZONIA (Amazon Basin). Individual commodities have specific incentive schemes: for example, PROALCOOL to increase alcohol production for fuel. Other support agencies include one for the establishment of farmer cooperatives (PRONACOOP), colonization and land reform (INCRA), research (EMBRAPA), technical assistance and rural extension (EMBRATER) and food supply and policy (CONAB, SUNAB, COBAL). Lastly, import and export restrictions on locally produced and competitive foreign

goods exist.

Colombia has used purchase plans and subsidized credit to stimulate oilseed production, although the overall program in the past few years has not been so effective as desired, particularly in 1976, when a shortage of fats and oils occurred in that country. Some oilseed crops, such as African Palm and coconut are given a lower priority, while others such as soybeans, sesame and cottonseed are considered more important in national agricultural policy. About 40% of Colombian edible fat and oil needs were imported in 1978.

Agriculture's share of the national economy of Ecuador (gross domestic production) is getting smaller, due to the income from petroleum production and other industries. The government does provide for support, subsidies, storage and outright purchase of raw agricultural products. Some duties and controls of both imports and exports are also in force. Other programs include agricultural credit, irrigation and mechanization projects, colonization and agrarian reform. Interestingly enough, the development of oilseed production --specifically soybeans and peanuts--was designated as a first priority by the Ecuadorian national policy office in 1977.

Basic Venezuelan policy has been towards the substitution of oilseed imports. There is both a duty on such imported products and support prices for the principle oilseeds produced. Support prices are guaranteed by the Agricultural Marketing Board (CMA) which will purchase

products at specified locations throughout the country. CMA is also responsible for vegetable oil purchases on the world market, after estimating local production and requirements. Wholesale and retail prices for vegetable oils are fixed by the government.

One danger pointed out in some Latin American countries was the over-stimulation of African Palm Oil production by artificially high support prices. When full production is reached, world price drops and the market is saturated, a reliance on such high prices may result in substantial problems in this sector of the agricultural economy.

In recent times, two diseases, known as spear rot and sudden wilt, have begun to severely plague the African Oil Palm industry in South America. Monoculture of the African Oil Palm may encourage the spread of this disease.

An expanded management program for oil production in Latin America appears necessary. National planners should study projects such as the pataua program for their own countries and not rely on a single oil palm. Latin American governments must begin to consider alternative oil crops such as pataua for regional development schemes, especially in the lowland areas.

Conclusion

Oenocarpus and Jessenia are at present such a high risk crop that peasant farmers should not be expected to initiate cultivation on a large scale. Primary efforts, outside of the small-scale exploitation of extant populations

in the Amazon Valley and elsewhere, should be directed towards the selection and domestication of desirable forms for plantation agriculture. Because of the high demand and rate of return that could be expected for pataua oil, it appears to be a potentially important crop for the tropics. No great short-term results or returns may be expected. A serious commitment of capital and research talent should be made by a major international organization which can utilize the most up-to-date genetic and agronomic techniques for the production of an acceptable crop meeting the criterion necessary for domestication--high growth rate and yield, rapid maturation, low stature, thicker mesocarp, etc. Special marketing and support mechanisms must be set up by each local government; perhaps as a tax imposed on imported olive oil, while at the same time, offering a subsidy to those developing pataua plantations. If properly domesticated, the *Oenocarpus*--*Jessenia* complex could represent a substantial contribution as an important oilseed crop for tropical regions.

Appendix 1

Extraction Procedures at "Las Gaviotas"

Mechanized processing of Oenocarpus and Jessenia fruit as undertaken at "Las Gaviotas" involves five stages--fruit reception, sterilization, digestion, pressing and clarification.

The fruits are first removed from the panicles, examined as to their state of maturity (ripe fruits have the highest recoverable oil content) weighed and stored under cover. Excessive amounts of humidity or heat over a several-day period will cause deterioration in the quality of stored, ripe fruits. Sterilization inactivates the mesocarp enzymes, which otherwise could initiate oil deterioration through lipolysis --also termed rancidity: an increase in the free fatty acid content. Sterilization at "Las Gaviotas" is with steam derived from a boiler fired with bagasse from fiber and seed of previously processed Jessenia and Oenocarpus fruits. Fruits are heated for 1-2 hours in 2 kettles, each containing 1200 kg. The sterilized fruit, transferred to a digestor, is crushed and the oil-rich cells of the mesocarp broken. The digestor takes about 3 minutes to complete its task, and is operated by a small diesel engine. The next step--pressing --is done in lots of 20 kg of digested fruit. A Stork hydraulic hand press with a total capacity of 300 kg per hour expresses the oil from the mesocarp. Fibrous mats are included within the press container to prevent the stony kernels from bunching up together and interfering with the

extraction procedure. Semi-purified oil is released and flows into collecting drums. Clarification, the final stage, follows pressing and involves heating the oil to about 80-90°C to separate the water and fiber from the pure oil. A final heating of 100°C drives all water from the oil, which is then put into drums for shipment and sale. The total fuel requirement, with the exception of the diesel engine mentioned, is met by burning the dried seed fiber left over from processing. Byproducts of oil production include an oily layer in the sludge suitable for soap manufacture, additional seeds with potential use as fuel (charcoal) and pulp residue as an animal feed.

Cost of the Stork presses used in extraction at "Las Gaviotas" have been priced by the manufacturer (pers. comm.) at Dfl. 16,000 for a hand operated hydraulic press with hand pump and fuel tank or Dfl. 27,000 for a hand operated hydraulic press with mechanical driven pump, special valve and fluid tank. Auxiliary equipment for the hand presses and a covering building amount to Dfl. 7,000 and Dfl. 6,000 respectively. A mechanical digester for the output of two mechanized hand presses is estimated at Dfl. 46,000. Due to current high rates of inflation and subsequent problems in currency conversion calculations, figures are given in Dutch guilders (Dfl.). As of March 24, 1980, the U.S. dollar was equivalent to approximately 0.48 Dfl. The prices listed for equipment do not include shipping, inland transport, foundation, erection, trials or other supporting structures (office, workshop, store).

Appendix 2

The original text from Dugand's publication "Las Palmeras y El Hombre," (1972) in which the mistaken annual calculation of 22 kg of oil produced per pataua palm (here called milpesos) is presented in the following paragraph.

> "A los que gusten de números les interesará saber que la pulpa oleosa del fruto de la palmera colombiana llamada unamo o milpesos (Jessenia polycarpa), separada la semilla, constituye entre 36 y 39% del peso del fruto entero, una vez evaporada la mayor parte de la humedad. De tal cantidad el 18% o 19% es aceite aprovechable. Por lo tanto, de cada kilogramo de frutos enteros, tales como se recogen de la támara, resultan entre 65 y 70 gramos de aceite por término medio. El peso promedio de los frutos támara, excluído el del racimo mismo (o sea el pedúnculo y ramificaciones) es de 13 a 16 kilogramos, siendo el de cada fruto moderadamente seco, 8 a 9 1/2 gramos. Cada palmera adulta produce por término medio dos racimos anualmente (a menudo hasta tres), o sea unos 30 kilogramos de frutos, de los cuales se pueden extraer 22 kilogramos de aceite que equivalen a 24 litros, estimando la densidad en 0.915 (ver G. Pereira Pinto 1951:71). Dejo a los entendidos en economía la aplicación de valores comerciales a estos simples datos numéricos."

Using his variables, the numbers should appear as follows: 30 kg fruit x 36-39% mesocarp content = 10.8-11.7 kg pure mesocarp; 10.8-11.7 kg mesocarp at 18-19% oil content = 1.944-2.223 kg pure oil from 30 kg fruit.

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