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A

ANATOMICAL AND PHYLOGENETIC STUDIES  
OF *BACTRIS* AND BACTRIDINAE (PALMAE: COCOEAE)

By

EVANDRO JOSÉ LINHARES FERREIRA

A dissertation submitted to the Graduate Faculty in Biology  
in partial fulfillment of the requirements for the degree  
of Doctor of Philosophy, The City University of New York

2001

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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## Abstract

ANATOMICAL AND PHYLOGENETIC STUDIES  
OF *BACTRIS* AND THE SUBTRIBE BACTRIDINAE (PALMAE: COCOEAE)

By

Evandro José Linhares Ferreira

Adviser: Dr. Andrew Henderson

Anatomical study of leaves of representative species of Bactris and five other palm genera in the subtribe Bactridinae was carried out. Anatomical descriptions and additional morphological information were used in a phylogenetic analysis intended to provide new insights into the generic relationships within Bactridinae, specific relationships within Bactris, and the origin of B. gasipaes var. gasipaes, the only neotropical domesticated palm. The results of the anatomical descriptions showed that Bactris is more diverse than previously thought and five major leaf anatomical types can be identified. The phylogenetic analysis of anatomical and morphological data sets performed independently supports the monophyletic status of

Bactridinae but failed to resolve relationships within Bactridinae and Bactris. Relationships are resolved only when the data sets are analyzed in a combined analysis. In this, all Bactridinae genera are monophyletic and new relationships are found among them. Bactris is monophyletic and its internal structure is composed of several clades. Only one of these groups correspond to formally segregated genera and the fragmentation of Bactris into several smaller genera is not supported. The place of origin, number of domestication events, and ancestors of the domesticated B. gasipaes var. gasipaes is not completely explained because the phylogenetic analysis was hampered by computational limitations.

### Dedication

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provided all these years.

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## I. Introduction

The genus Bactris (palmae) is one of the largest and most widespread in the Neotropics. The first species were described by Jacquin (1763) before the genus was formally described by Scopoli (1777), a confusing situation corrected by Moore (1963).

Conflicting interpretation of characters (Martius, 1824; Karsten, 1857; Barbosa Rodrigues, 1902; Bailey, 1947) and narrow species concepts (Barbosa Rodrigues, 1902; Burret, 1933-1934; Bailey, 1947) resulted in the division of the genus into several segregate genera (Guilielma, Pyrenoglyphis, and Yuyba) and overdescription of species. Furthermore, comprehensive monographic studies were not available in the past. The result was taxonomic confusion.

A recent monographic treatment of the genus is now available (Henderson, 2000). Several important aspects were addressed in his study. For example, the species concept adopted are clear and most nomenclatural conflicts are solved. Henderson studied 405 of the 460 types of names known in Bactris. Accepted species, synonyms, doubtful and invalid names are all cited and discussed. The species and species complexes, as well as some informal groups, were clearly identified. Although it did not

provide a phylogeny for Bactris, Henderson's treatment defined boundaries among the taxonomic entities within the genus. Such information was not available previously and provides the necessary background for a phylogenetic study of the genus.

Sanders (1991) produced a preliminary phylogeny of Bactris and its segregate genera Amylocarpus (=Yuyba), Guilielma and Pyrenoglyphis. An important result of Sanders' analysis is that Bactris is monophyletic only when the segregate genera are included within it. This seems to be accepted by most recent taxonomists (Henderson, 1995; Henderson et al., 1995; de Nevers et al., 1996; Ferreira, 1997). Other results of Sanders, however, are disputed and disagreements regarding character interpretation have recently been raised. De Nevers et al. (1996) could not see the tubercles or papillae at the bases of the endocarp fibers in most Central American members of the Tuberculate clade proposed by Sanders. They also discuss several of Sanders characters, saying they are difficult to see or to interpret in the same way Sanders saw or interpreted them. Henderson (2000) believes Sanders has misinterpreted the stem diameter and connation of staminate petals when defining the position of the Balanophora clade. He suggests that B. balanophora is similar to B. ptariana, a

species placed by Sanders in the distant Latibracteate clade. For these reasons, Sanders' preliminary phylogeny of Bactris should be used with caution.

The uncertainties regarding phylogenetic relationships within Bactris has left some important questions unanswered. The most important of these is the identity of related species to the pupunha palm (B. gasipaes), the only domesticated palm native to the New World. This species is widely cultivated and plays an important economic role in rural communities throughout Central and South America. The identification of its wild ancestor or closely related group of species is crucial because they have the potential to be used as source of germplasm to improve cultivated plants.

## II. Literature Review

The palm family shares with other monocots leaves with sheathing bases and parallel venation, flowers with a trimerous plan, and sympodial or monopodial habit. Palms are easily distinguished from other plant families because most have a distinct, often unbranched trunk with a terminal crown of leaves. Although considered the more diverse group within the monocots, palm morphological

structures are often referable to simple patterns (Uhl & Dransfield, 1987).

The family has a pantropical distribution and grows in different environments within their latitudinal range. Rhapidophyllum and Washingtonia at 33°N in North America and Rhopalostylis at 44°18'S in New Zealand represent the extreme latitudinal ranges of palm distribution. Palms are adapted to grow in deserts, tropical rain forests, savannas, and mangroves. Some species of the Neotropical genera Ceroxylon and Geonoma (Rodrigo Bernal, pers. comm.) can be found growing at high elevations (3000 m) in the Andes.

#### 1. Economic importance of palms

Several palm species are economically important and the list of species and their uses is extensive (Balick & Beck, 1990). Most species are exploited in their natural environment, but at least three are considered major agricultural crops worldwide.

The oil palm (Elaeis guineensis) is widely cultivated in Asia, South America, and Africa for its oil. In 1997, it accounted for 19% of the world vegetable oil production (OW, 1992).

The date palm (Phoenix dactylifera) has been cultivated since about 4000 BC (Zohary & Hopf, 1993) and its fruits are a popular food source all over the world. In some Middle Eastern countries, dates are the principal agricultural export product.

The coconut palm (Cocos nucifera) is not only a landmark of tropical landscapes, but also one of the most cultivated plant species worldwide. Its different plant parts provide a source for a wide variety of products used for human and animal food, construction material, fuel, medicine, and clothing.

Among the non-cultivated palms, the rattans (Calamus spp.) have worldwide economic importance. These climbing palms are native to Southeast Asia and their canes are used by the furniture industry. Rattan trade is a multimillion-dollar industry and overall the global trade is worth \$4 billion by the time the finished product reaches the consumer (INBAR, 2000). Cultivation of rattan is now being attempted in Malaysia, Philippines, Thailand, and Indonesia.

Other non-cultivated palms have only regional or local importance. In South America, the jussara palm (Euterpe edulis) and the açai palm (Euterpe oleracea) are exploited for its hearts of palm. Around 140,000 tons of canned

products are marketed annually in Brazil (Mora-Urpí et al., 1997).

In Brazil, Venezuela, and Ecuador, fibers of palm leaves are used in broom and basketry production (Ferreira, subm.). These palms are commonly known as piassava palms and three of them have major importance in each country: Attalea funifera (Brazil), Leopoldinia piassava (Brazil and Venezuela), and Aphandra natalia (Ecuador).

Many other palm species are exploited for different products. The sago palm (Metroxylon spp.), from Southeast Asian and the Pacific, is a major source of carbohydrate for millions of people in that region. Sap of the palmyra palm (Borassus flabellifer) is used to make sugar in India and Malaysia. In South America, fresh fruits from several species are widely marketed, most notably the tucumã palm (Astrocaryum aculeatum), the buriti palm (Mauritia flexuosa), and the uricuri palm (Attalea phalerata).

The uses and economic importance of the pupunha palm are discussed elsewhere in this and the following chapters.

## 2. Classification of palms

The palm family comprises 189 genera (Dransfield & Uhl, 1998; Uhl & Dransfield, 1999) and approximately 1500-



2800 species worldwide (Moore, 1973; Henderson et al., 1995; Uhl and Dransfield, 1987).

## 2.1. Uhl and Dransfield's classification of palms

Uhl and Dransfield (1987), based on the ideas of Moore (1973), proposed the current classification of palms. This classification used morphological aspects of reproductive and vegetative parts and was not based on cladistic study. The family was divided into six subfamilies, ordered according to their level of specialization: Coryphoideae, Calamoideae, Nypoideae, Ceroxyloideae, Arecoideae, and Phytelphantoideae. Although recent molecular evidence suggest the necessity of changes in the current classification of palms (Uhl et al., 1995; Lewis et al., 2000), Uhl and Dransfield's classification remains the only formal classification available and will be presented below. The latest molecular results on palm classification will be discussed elsewhere.

The Coryphoideae is the most primitive subfamily and comprises 40 genera organized in three tribes and six subtribes. It commonly distributed in subtropical areas worldwide. Its main distinguishing vegetative character is palmate or costapalmate, induplicately folded leaves.

The Calamoideae includes 22 genera, organized into two tribes and eight subtribes. They have a pantropical distribution, and are usually found in areas of high precipitation. In the Neotropics, some of its members are frequently found in swampy areas. The subfamily is characterized by the presence of closely overlapping scales covering the ovaries and fruits.

The Nypoideae includes the monotypic genus Nypa. It is distributed in Asia and the Western Pacific. Nypa is the only palm that is adapted to grow in mangrove areas. It can be recognized by its unique, dichotomously branched and prostrate stem bearing an erect inflorescence with a terminal head of pistillate flowers and lateral spikes of staminate flowers.

The Ceroxyloideae includes 10 genera organized into three tribes. It has a predominant Neotropical distribution, but two genera occur in Madagascar, one in the Mascarene Island, and one in Australia. The main distinguishing character of the subfamily is an inflorescence with numerous peduncular bracts, except in the Neotropical genus Wendlandiella.

The biggest subfamily of palms is the Arecoideae. It is a pantropical group comprised of 113 genera. This subfamily is divided in six tribes and twenty-three

subtribes. The morphological character that best defines the Arecoideae is the arrangement of its staminate and pistillate flowers in triads along the rachillae. Bactris is a member of this subfamily and is included in the tribe Cocoeae, subtribe Bactridinae.

The Phytelephantoideae is the more advanced subfamily in Uhl and Dransfield's classification. It is comprised of three neotropical genera and can be identified by its multiparted flowers that cluster in condensed monopodial units. The high number of stamens (approaching 1200 in the genus Ammandra) also characterizes all members of the subfamily.

## 2.2. Recent phylogenetic studies of the palm family

A phylogenetic analysis of palms using morphological and molecular data (Uhl et al., 1995), supported new relationships of tribes and subtribes within the subfamilies and three major evolutionary groups in palms. The first is represented by the Nypoideae, which may represent the earliest diverging lineage in the family. The second is the Calamoideae. The last group includes the other subfamilies. The subfamilies Calamoideae, Coryphoideae and Phytelephantoideae are monophyletic. The

Ceroxyloideae is polyphyletic - although its tribes are monophyletic. The Arecoideae appears to be paraphyletic or polyphyletic.

Asmussen et al. (2000) and Baker et al. (1999) used only molecular data in their studies. Their results support relationship of subfamilies suggested by Uhl et al. (1995). The clade comprising Arecoideae, Ceroxyloideae, Coryphoideae, and Phytelephantoideae has a higher support than Uhl et al.'s.

An molecular study of Lewis et al. (2000) has found that only two groups, corresponding to the subfamilies Calamoideae and Phytelephantoideae, are well defined. Their position within the family, however, needs further investigation. Its results do not support Nypoideae as sister group to all other palms and the subfamilies Arecoideae, Ceroxyloideae, and Coryphoideae do not form discrete groups. In fact, if the groups of Lewis et al.'s analysis were to be considered at subfamily level, only Calamoideae and Nypoideae could be so considered. Lewis et al.'s results indicate a clear antagonism between morphological and molecular results.

From the few results presently available, it is clear that much research remains to be done in the field of molecular studies of palms. The rate of DNA evolution in

palms is unusually slow (Lewis et al., 2000) and molecular studies have used DNA sequences from several different regions of the plastid, mitochondria and nucleus without much success (Hahn, 1999). It seems that a formal classification of palms based entirely on molecular data will require a few more years of research.

### 3. Higher level classification of Bactris

#### 3.1. Tribe Cocoeae

Cocoeae, a member of the subfamily Arecoideae, is divided into five subtribes and includes 22 mostly neotropical genera. Members share the following features: a trilocular gynoecium, a thick bony endocarp with three clearly defined pores, inflorescence branched to one order, prophyll hidden within the leaf sheaths, and one well-developed and frequently woody peduncular bract. Uhl and Dransfield (1987) placed all genera bearing spines in the subtribe Bactridinae, which is commonly known as spiny Cocoeae (Table 1).

#### 3.2. Subtribe Bactridinae

Table 1. High level classification of palms<sup>12</sup> (Uhl and Dransfield, 1987) and the placement of Bactris (main levels are highlighted)

---

|      |                                      |
|------|--------------------------------------|
| I-   | Coryphoideae (subfamily level)       |
| II-  | Calamoideae (subfamily level)        |
| III- | Nypoideae (subfamily level)          |
| IV-  | Ceroxyloideae (subfamily level)      |
| V-   | <b>Arecoideae (subfamily level)</b>  |
|      | Caryoteae (tribe level)              |
|      | Iriarteeae (tribe level)             |
|      | Podococceae (tribe level)            |
|      | Areceae (tribe level)                |
|      | Cocoeae (tribe level)                |
|      | Beccariophoenicinae (subtribe level) |
|      | Butiinae (subtribe level)            |
|      | Attaleinae (subtribe level)          |
|      | Elaeidinae (subtribe level)          |
|      | <b>Bactridinae (subtribe level)</b>  |
|      | <u>Acrocomia</u> (generic level)     |
|      | <u>Gastrococos</u> (generic level)   |
|      | <u>Aiphanes</u> (generic level)      |
|      | <u>Bactris</u> (generic level)       |
|      | <u>Desmoncus</u> (generic level)     |
|      | <u>Astrocaryum</u> (generic level)   |
|      | Geonomeae (tribe level)              |
| VI - | Phytelephantoideae (subfamily level) |

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The subtribe Bactridinae is confined to the New World and is most diverse in South America. Also found in Central America and the Caribbean, it includes the genera Acrocomia, Aiphanes, Astrocaryum, Bactris, Desmoncus, and Gastrococos. Their habit ranges from massive caulescent

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<sup>1</sup> Tribes and subtribes omitted in all but the subfamily Arecoideae

palm to acaulescent, and to small climbing palms. Leaves are simple or pinnate and the leaflets apices acute or praemorse. The inflorescence can have a few (rarely one) or numerous rachillae. The pistillate flowers can be as few as one or dozens per rachilla.

Acrocomia includes two species occurring in open or disturbed areas. One species, A. aculeata, is a large palm widely distributed from Mexico to Argentina. The other species, A. hassleri, is a small palm confined to central Brazil and Paraguay. Hahn (1991) and Henderson et al. (1995) give the most recent taxonomic accounts of the genus.

Gastrococos is a monotypic genus found only in Cuba. They are large palms, vegetatively similar to Acrocomia. The most recent taxonomic account of the genus is that of Moore (1967).

Aiphanes has 22 species in the Lesser Antilles, Central and South America. It is most diverse in South America. Plants are small and acaulescent or medium sized caulescent palms and grow in either low or high altitudinal humid forest. All species are characterized by their pinnae with praemorse apices. The genus was recently revised by Borchsenius and Bernal (1996).

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<sup>2</sup> Genera omitted in all but the subtribe Bactridinae

Desmoncus is widespread in the Americas and is the only genus with climbing stems in the neotropic. There are 61 published names (Uhl & Dransfield, 1987) but only seven species are accepted by Henderson et al. (1995). They are mostly small palms growing in primary or disturbed forests. There is no modern revision of the genus.

The genus Astrocaryum probably includes between 18-25 species distributed from Mexico to South America. They are small to large palms occurring in open areas, disturbed or primary forests, usually at low elevations. The most recent taxonomic accounts is that of Kahn and Millán (1992).

The genus Bactris is discussed in detail below.

### 3.3. Evolution and relationships in Bactridinae

In their classification of palms, Uhl and Dransfield (1987) suggested that inflorescence structure and conation of perianth parts in the pistillate flowers are the more important characters to define the evolutionary stage among the genera of Bactridinae. Using these criteria, Acrocomia is the least specialized genus because its staminate flowers are superficially inserted in the rachilla and its pistillate perianth has free parts. Astrocaryum is the



most advanced genus, with staminate flowers inserted in deep pits in the rachilla and pistillate perianth parts united into a tube. They also suggested that Gastrococos was closely related to Acrocomia, a conclusion also shared more recently by Henderson et al. (1995). Moore (1967), however, had proposed that Gastrococos was the closest genus to Aiphanes. He based this on the similarities of distal distribution of staminate flowers in the rachillae, conation of pistillate petals, adnation of staminodial ring to the petals, and posture of stamen filaments.

Borchsenius and Bernal (1996) revised Aiphanes and found several floral similarities with Acrocomia. They did not present a phylogeny for the genus, nor did they make clear their point of view regarding this disagreement. The remaining members of Bactridinae, Bactris, Desmoncus and Astrocaryum, are considered by Uhl and Dransfield (1987) to form the more advanced group because of their tubular pistillate corolla.

Sanders (1991) suggested that Bactris, Desmoncus, and Astrocaryum formed a strong clade within Bactridinae. This clade shared the following characteristics: cespitose stems, connate calyces and corollas in the pistillate flowers, and non-mucilaginous mesocarp. This suggestion was based on a preliminary study he conducted to define the

outgroup of his cladistic study of Bactris. He used a generalized non-spiny genus (no generic name was specified) of Cocoeae as outgroup, and no information on characters, data matrix and phylogenetic trees were given.

#### 4. The genus Bactris

The characters that best distinguish Bactris are the presence of spines, a thick endocarp, connate pistillate petals, and triads of flowers regularly or irregularly distributed along the rachillae. The closely related Desmoncus has similar features but can be readily distinguished by its climbing habit. Stems of Bactris are usually cespitose and aerial; however, solitary, short and subterranean stems can also be found. Leaves are pinnate or simple. Leaflets are inserted regularly or irregularly along the rachis, spreading in one or several planes. Inflorescence is interfoliar, subtended by a prophyll and one peduncular bract. There are one or several rachillae. Plants are monoecious; the flowers are arranged in triads of one central pistillate and two laterals staminate. Staminate flowers have a trilobed calyx and a corolla with three petals basally connate. Pistillate flowers have a connate, slightly trilobed calyx and corolla. A

staminodial ring may be found inside the pistillate corolla. The gynoecium is syncarpous, trilocular and triovulate. The one-seeded fruits have a variable shape, but the stigmatic residue is always apical. The glabrous or spinulose epicarp is purple-black, orange-red or yellowish to straw colored. The mesocarp is juicy, mealy, and less often starchy. The endocarp is hard, sometimes covered by fibers, and has three pores usually located above the equator. The endosperm is homogeneous and germination is adjacent-ligular. The first leaf is commonly bifid, although it may also be pinnate.

#### 4.1. Diversity and distribution

Bactris comprises at least 73 species distributed from Southern Mexico to Paraguay, including a few in the Greater Antilles (Henderson, 2000). The greatest diversity is in the Amazon region where half the species occur. Central America and the Atlantic coastal forest of Brazil are characterized by a high level of endemic taxa. Fewer species are found in central Brazil, Paraguay and the Andes; most of these are also present in adjacent regions. The habitat in which Bactris is most commonly found is lowland forests along river margins. Only a few species

are found in savannas and disturbed areas. Bactris grows from sea level to 1700 m of elevation in the Andes.

#### 4.2. Taxonomic history

The first species of Bactris was described by Jacquin in 1763, but the genus was not validly published until 1777 by Scopoli (Moore, 1963).

Several authors have contributed to the taxonomy of the genus. Martius (1824, 1826, and 1847), Spruce (1871), Barbosa Rodrigues (1875, 1888), Trail (1877), Karsten (1857), and Burret (1933-1934) described the majority of the species from the Amazon region and adjacent areas. Oersted (1859) and Bailey (1933, 1938, 1943, and 1947) described the majority of species from Central America and the Caribbean region. Unfortunately some of these authors had a very narrow species concept and described new species based on rather small morphological differences or geographical location of the plants. Barbosa Rodrigues, Burret, and Bailey were the more prolific describing almost every new specimen as a new species.

The genus was initially divided by Martius (1824) when he created Guilielma. The first species described was G. speciosa, a cultivated pupunha palm he collected in the

eastern Brazilian Amazon. However, the pupunha palm had already been described a few years earlier by Kunth (1816) as Bactris gasipaes. Instead of making a new name combination, Martius placed Kunth's species as synonym of his "new" species. Spruce (1871) commented that speciosa was not the correct epithet for this taxon and that Guilielma was indistinguishable from Bactris, G. speciosa was a nomen illegitimum and the correct name should be G. gasipaes. Martius never stated clearly what characters he used to distinguish Guilielma from Bactris. It seems that a combination of a large stem size, petiolar spines in three ranks, and endocarp with adnate fiber bands were the characteristics used to segregate Guilielma. Nevertheless, Guilielma was widely accepted and in the years following its publication, 15 species and varieties were described or transferred to it.

The next segregated genus was Augustinea (Karsten, 1857). Here, another mistake led to a nomenclatural problem. At the time Karsten published Augustinea, this name was already applied to a genus in the family Melastomataceae. A new name, Pyrenoglyphis, was validly published in 1866. Karsten's genus was distinguished by the presence of a staminodial ring in the pistillate calyx and corolla. It was a monotypic genus and included the

species B. major he had transferred from Bactris. Pyrenoglyphis was accepted by Burret (1933-1934), who described a few species and transferred to it all Bactris species with the staminodial ring in the pistillate corolla.

The segregated genus Amylocarpus was created by Barbosa Rodrigues (1902). Here, too was another nomenclature conflict because Amylocarpus was already used as a fungal name since 1857. Bailey (1947) corrected this problem, adopting the name Yuyba, a divisional designation in Barbosa Rodrigues' publication. Bailey transferred all of Barbosa Rodrigues' Amylocarpus species to the new genus. Almost half of the species placed or described in this new genus were related to the B. simplicifrons species complex, one of the most widespread and variable taxa of Bactris. Although Bailey shared a narrow species concept with Barbosa Rodrigues, the main reason that led him to support Barbosa Rodrigues' new genus was a different one. Bailey did not believe that a Bactris species found in the Caribbean could also be found in the Amazon region. Consequently, a specimen of B. simplicifrons he found in Trinidad was described as new in the genus Yuyba.

The first attempt of a taxonomic revision of Bactris was that of Burret (1933-1934), a German botanist at Berlin

Table 2. Burret's taxonomy of Bactris and segregated genera (1933-1934), sensu Sanders (1991)

---

|     |                                        |
|-----|----------------------------------------|
| I   | - <u>Guilielma</u> (generic level)     |
| II  | - <u>Bactris</u> (generic level)       |
|     | Bactris (subgeneric level)             |
|     | Bactris (sectional level)              |
|     | Aiphanoides (sectional level)          |
|     | Amylocarpus (subgeneric level)         |
|     | Amylocarpus (sectional level)          |
|     | Piranga (sectional level)              |
| III | - <u>Pyrenoglyphis</u> (generic level) |

---

during the 1920s and 1930s who did most of his work in the herbarium. He collected very few specimens in the field and most of the time studied specimens sent to him by other field collectors. In his treatment, three segregated genera were recognized, Bactris, Guilielma, and Pyrenoglyphis (Table 2). Bactris was further subdivided in two subgenera and four sections. No keys, illustrations or discussion about relationships of the different species or groups of species were provided. Burret's treatment included 144 previously published species and 45 new species described by him. Sanders (1991) commented that Burret treatment is a compendium of names, not a taxonomic treatment.

Wessels Boer (1965) was the first botanist to suggest that Bactris was a genus with an excessive number of

species. According to him, this overdescription was a result of morphological plasticity in some species. This was evident in his treatment of B. simplicifrons.

The most recent taxonomic studies in the genus were carried out by de Nevers et al. (1996) and Henderson (2000). The first treated only Central American Bactris. The second included the entire genus. Unlike the previous study by Burret (1933-1934), Henderson's monograph was based on the examination of the species in the field as well as the herbarium. According to Henderson, there are at least 73 species and 21 varieties of Bactris. Given the quantity of species proposed by Burret, this is a remarkably small number of species and this can be attributed to the broad species concept adopted by Henderson. He acknowledges the preliminary nature of his work and that taxonomic problem remains to be solved in Bactris. The problems are found within five species complexes (B. corossilla, B. hirta, B. maraja, B. major, and B. simplicifrons). These are extremely variable and widespread taxa, some of them with several segregates at the specific or subspecific level. Henderson's treatment does not present a phylogeny of the genus; it recognizes informal groups of species (Table 3). Nevertheless, there



Table 3. Henderson (2000) groups of Bactris<sup>1</sup>

| Groups               | Species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|----------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <u>Amylocarpus</u>   | <u>B. aubletiana</u> , <u>B. cuspidata</u> , <u>B. hirta</u> , <u>B. killipii</u> , <u>B. schultesii</u> , <u>B. simplicifrons</u> , <u>B. syagroides</u>                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| <u>Guilielma</u>     | <u>B. cubensis</u> , <u>B. gasipaes</u> , <u>B. jamaicana</u> , <u>B. plumeriana</u> , <u>B. riparia</u> , <u>B. setulosa</u>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                  |
| Orange-fruited       | <u>B. balanophora</u> , <u>B. campestris</u> , <u>B. caudata</u> , <u>B. charnleyae</u> , <u>B. coloradonis</u> , <u>B. dianeura</u> , <u>B. gracilior</u> , <u>B. grayumii</u> , <u>B. hondurensis</u> , <u>B. kunorum</u> , <u>B. mexicana</u> , <u>B. militaris</u> , <u>B. neomilitaris</u> , <u>B. oligoclada</u> , <u>B. panamensis</u> , <u>B. ptariana</u>                                                                                                                                                                                                                                                             |
| <u>Piranga</u>       | <u>B. acanthocarpa</u> , <u>B. acanthocarpoides</u> , <u>B. barronis</u> , <u>B. glandulosa</u> , <u>B. halmoorei</u> , <u>B. pliniana</u> , <u>B. raphidacantha</u> , <u>B. tefensis</u> , <u>B. timbuiensis</u>                                                                                                                                                                                                                                                                                                                                                                                                              |
| Purple-fruited       | <u>B. bahiensis</u> , <u>B. bidentula</u> , <u>B. caryotifolia</u> , <u>B. coloniata</u> , <u>B. constanciae</u> , <u>B. corossilla</u> , <u>B. elegans</u> , <u>B. faucium</u> , <u>B. ferruginea</u> , <u>B. fissifrons</u> , <u>B. glassmanii</u> , <u>B. glaucescens</u> , <u>B. guineensis</u> , <u>B. hatschbachii</u> , <u>B. horridispatha</u> , <u>B. longiseta</u> , <u>B. macroacantha</u> , <u>B. maraja</u> , <u>B. pickelii</u> , <u>B. pilosa</u> , <u>B. setiflora</u> , <u>B. setosa</u> , <u>B. soeiroana</u> , <u>B. sphaerocarpa</u> , <u>B. tomentosa</u> , <u>B. turbinocarpa</u> , <u>B. vulgaris</u> . |
| <u>Pyrenoglyphis</u> | <u>B. bifida</u> , <u>B. brongniartii</u> , <u>B. chaveziae</u> , <u>B. concinna</u> , <u>B. gastoniana</u> , <u>B. major</u> , <u>B. martiana</u> , <u>B. oligocarpa</u>                                                                                                                                                                                                                                                                                                                                                                                                                                                      |

<sup>1</sup> Highlited species are included in this study

is no doubt Henderson's treatment is far more comprehensible than that of Burret.

#### 4.3. Current phylogeny of Bactris

Sanders (1991) was the first to propose a phylogenetic hypothesis for Bactris. His study was based on 106 morphological characters from stems, leaves, inflorescence, flowers, and fruits. Sanders recognized that "not all characters were reliable in this preliminary character evaluation and cladistic analysis and these homoplasious characters may need to be eliminated from future analyses of the whole genus".

Sanders found that Bactris would be monophyletic only if the segregated genera Guilielma and Pyrenoglyphis were included. If these genera were treated as separate entities, Bactris would fragment into eight or more poorly defined genera. The situation would be even more complex if Amylocarpus was to be segregated because it was placed at a subsectional level in Sanders' phylogeny.

In Sanders' analysis, the basic structure of Bactris has four major clades at the subgeneric level and several more inclusive clades either at sectional or subsectional levels (Table 4).

Table 4 - Internal structure of Bactris (Sanders, 1991).

---

Bactris (Generic Level)

- I - Balanophora clade (subgeneric level)
  - II - Non-Ocreate clade (subgeneric level)
    - Guilielma clade (sectional level)
    - Antillean clade (sectional level)
  - III - Latibracteate clade (subgeneric level)
    - Nonfibrous clade (sectional level)
      - Many plesiomorphic clades (subsectional level)<sup>1</sup>
      - Amylocarpus clade (subsectional level)
    - Exserted-anther clade (sectional level)
      - Few plesiomorphic clades (subsectional level)<sup>2</sup>
      - Piranga clade (subsectional level)
      - Campestris clade (sectional level)
      - Caudata clade (sectional level)
  - IV - Tuberculate clade (Subgeneric level)
    - Militaris clade (Sectional level)
    - Setulosa clade (sectional level)
    - Corossilla clade (sectional level)
      - Turbinocarpa clade (sectional level)
      - Constanciae clade (sectional level)
      - Atropurpureous clade (sectional level)
      - Bidentate clade (sectional level)
      - Long-prophyll clade (sectional level)
      - Tubiflorous clade (sectional level)
        - Pilosa clade (Subsectional level)
        - Pyrenoglyphis clade (Subsectional level)
- 

The first major clade is the Balanophora clade. It contains a single species, B. balanophora, considered the least specialized in the genus. Sanders pointed out that

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<sup>1</sup> Although not giving a formal list, he cites B. hondurensis and B. coloradonis complexes.

B. balanophora has flattened and adnate endocarp fibers and a large stem size. Both characters have been traditionally used to circumscribe the pupunha palm and closely related species. In Sanders' phylogenetic tree the Balanophora clade is sister to the clade containing the pupunha palm.

The second major clade is the Non-Ocreate clade. The synapomorphies of the Non-Ocreate clade are the loss of the ocrea in adult leaves, petiolar spines in three ranks, staminate petals rounded and a thick starchy mesocarp. The petiolar spines in three ranks are a variable character because some cultivated plants are spineless. The Non-Ocreate clade is composed of two small inclusive clades at the sectional level: the Antillean and the Guilielma clades. The Antillean clade includes the Bactris species found in the Antilles. The Guilielma clade includes the pupunha palm and two closely related species.

For many years, the pupunha palm was included in the segregated genus Guilielma. In some cases it was considered a subgenus of Bactris (MacBride, 1960; Clement, 1988). In Sanders' analysis, Guilielma cannot be treated as a subgenus unless the members of the Antillean clade are included. Ferreira (1997), using leaf anatomical and morphological data, found that B. riparia and B. setulosa

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<sup>2</sup> The same case here, only B. mexicana and B. oligoclada are listed.

are closely related to the pupunha palm. In Sanders' analysis, these two species were placed in two distinct and inclusive clades of the Tuberculate clade.

The third major clade, Latibracteate, is the least well-supported in Sanders' analysis because the defining synapomorphies (few outer mesocarp fibers, stigma recessed, and rachis bract transversely oblong to linear) suffer from homoplasy. The Latibracteate is composed of four inclusive clades, the Nonfibrous, Exserted-Anther, Campestris, and Caudata clades. It is worthwhile to note that two large species complexes (B. simplicifrons and B. hirta) are included in this clade.

The last major clade is the Tuberculate. It includes five inclusive clades (Militaris, Setulosa, Corossilla, Turbinocarpa, and Constanciae). The Tuberculate is considered the more advanced major clade. It has two synapomorphies (tuberculate endocarp and asymmetric endocarp pores). De Nevers et al. (1996) found it difficult to interpret these synapomorphies. It seems that the degree of variability of them is greater than suggested by Sanders' analysis.

##### 5. The domestication of pupunha palm

The origin, parent species, number of times, and place of domestication of the pupunha palm have been a source of disagreement among researchers. Barbosa Rodrigues (1898), Burret (1933-1934), Clement (1988), Henderson (1995), and Ferreira (1999a) suggested it has a monophyletic origin. Huber (1904) and Mora-Urpí (1993) support the polyphyletic hypothesis. Mora-Urpí (1983) believes pupunha palm is a result of multiple domestication events while Clement (1988) suggested a single event followed by artificial dispersion. The only apparent agreement seems to be with regard to where the domestication event took place. Most authors cited above believe it occurred in a large area along the Andes cordilleras, from northern to the southeastern South America. Ferreira (1997) suggested the pupunha palm was domesticated in a single event in the southwestern Amazon region, from a single ancestor, the wild B. macana.

### III. Morphology and Anatomy of Bactris and its Taxonomic and Phylogenetic Significance

The morphological approach has been the rule in taxonomic and phylogenetic studies of palms. Sanders (1991) and Henderson (2000) suggested several morphological

Features of Bactris with taxonomic or phylogenetic importance. Anatomical information has been used as accessory data, usually to support taxonomic decision based almost entirely on morphology. The reasons for the limited use of anatomy in palm taxonomy are the difficulties involved in obtaining the data (Tomlinson, 1990; Pinheiro, 1997; Ferreira, 1997), which requires special techniques, a considerable amount of time and "most botanist avoid them, leaving the field for the eccentric" (Tomlinson, 1990). Pinheiro (1997) was the first to conduct a broad and extensive survey of leaf anatomy of a large palm group, the Attaleinae. He was also the first to do a cladistic study of palms using exclusively anatomical data.

## 1. Morphology

The more promising morphological characteristics are those from fruits, inflorescence, staminate flowers, and a few from the leaf and its indument.

### 1.1. Fruits

In most taxonomic and phylogenetic studies of Bactris (Martius, 1824; Karsten, 1857; Barbosa Rodrigues, 1902;

Burret, 1933-1934; Bailey, 1947; Sanders, 1991; Henderson, 1995, 2000; Salzman & Judd, 1995; de Nevers et al., 1996; Ferreira, 1999), the fruits are frequently the source of the most reliable morphological information. It is possible to group species according to their fruit color or the presence of a staminodial ring in the calyx and corolla. In the past, the endocarp fibers were used to segregate Guilielma from Bactris (Martius, 1824; Burret, 1933-1934).

In Sanders' phylogeny, fruits define major clades and evolutionary trends within Bactris. He proposed a trend in the evolution of fruit characters in the genus, suggesting that primitive fruits are elongate with a red, orange or yellowish epicarp, with flattened, adnate, anastomosing endocarp fibers, and that more advanced fruits are purple-black with terete, free endocarp fibers.

Henderson (2000) suggested that fruit size, color, and spininess, as well as the nature of the mesocarp and endocarp are the most useful characters to identify Bactris. Indeed, fruits are more useful than staminate flowers in identifying herbarium specimens because the latter are extremely ephemeral and rarely collected. Moreover, the fruits are usually readily available and easy to observe using simple instruments.



#### a. Fruit color

The genus can be divided into two major groups according to epicarp color. Nearly half of the species have red, yellowish, or orange fruits. The others have purple-black or black fruits. Henderson (2000) has identified some relationships of fruit color and indument to some groups. The epicarp in the Piranga group (reddish color) is spinulose, while many species of the purple-black group are scaly or minutely spinulose.

#### b. Fruit mesocarp

The mesocarp of Bactris is starchy, juicy or mealy. However, the fibers are the most important feature of mesocarp for species segregation. Within the Non-Ocreate clade proposed by Sanders, the Antillean species have elongated fibers attached to the fruit apex and base. The Guilielma species have short, stout and free fibers (Ferreira, 1999a).

#### c. Fruit endocarp

The endocarp in the majority of Bactris species is fibrous and rarely smooth. It is blackish to brownish and has three pores. One of them, the fertile pore, is located over the embryo. The position of the pores is a useful character to distinguish some groups of species. For example, the pupunha palm and two closely related species all have the fertile pore distally displaced; it is also bigger than the other pores. When the endocarp is fibrous, fibers usually radiate from the pores, and these fibers are useful to segregate species within the genus. The pupunha palm and a few closely related species have pore fibers flattened and adnate to the endocarp (Ferreira, 1997). In other species, the pore fibers do not radiate towards the endocarp surface, instead, non-pore fibers may be present, either totally or partially free. In species with juicy mesocarp, the endocarp fibers have attached juice sacs, as the case of many species with purple-black fruits. Henderson (2000) has found that species with fiberless endocarp or with only few fibers usually have red or orange epicarp.

#### d. Perianth

Few features of the fruit perianth have been used to segregate species or groups of species within Bactris. One of them is the presence of a staminodial ring in the corolla. Staminodial rings are found only in the species with purple-black fruits. Although this character is not widespread among all purple-black species, it may be used to segregate groups within these species. For example, species in the Pyrenoglyphis group have this ring. A rare feature is the staminodial ring found inside the calyx of some specimens of B. major.

## 1.2. Inflorescence

Inflorescences in Bactris are quite variable. Henderson (2000) found that all *Piranga* species have filamentous rachillae. He also suggested that floral triad arrangement on the rachillae is useful taxonomically. For example, in the *Piranga* species the triads are more or less regularly arranged on the proximal ca. half of the rachillae. All *Amylocarpus*, many *Pyrenoglyphis* and a few Purple-fruited species have triads regularly arranged throughout the rachillae. Most of the remaining species have triads scattered in an irregular pattern.

### 1.3. Staminate flowers

Staminate flowers, although less frequently present in herbarium specimens, exhibit a few morphological features of taxonomic value. For example, all species of the former genera Guilielma have cucullate petals and a long receptacle. The stamen filaments shape, insertion on receptacle, and folding are also useful to segregate species. More importantly, the staminate flowers do not change shape and size after anthesis. On the other hand, the pistillate flowers, commonly found in herbarium specimens, rapidly change size and shape after anthesis, making it difficult to circumscribe potential cladistic characters.

### 1.4. Leaves

A few morphological characters from the leaves are useful. For example, most *Pyrenoglyphis* species have a metallic sheen on abaxial surface after drying. The presence of spines presence, shape, and distribution on leaves are also useful to segregate groups of species.

## 2. Anatomy

In general, anatomical characters from leaves of palms are of diagnostic value not only at the generic level (Tomlinson, 1961; Wessels Boer, 1968), but also at the specific level (Glassman, 1972; Uhl, 1972, 1978; Read, 1975; Barfod, 1988; Borchsenius & Bernal, 1996; Barrow, 1998). Martens and Uhl (1984) suggested that 50-60 anatomical characters from the leaves might have taxonomic, evolutionary, or biological importance.

Tomlinson (1961) described in detail the anatomy of palm leaf. The main structures described include hairs, cuticle, epidermis, hypodermis, mesophyll, vascular and non-vascular fibers, venation, transverse commissures, midrib, and expansion cells. Some of these have traditionally been assumed to be plastic. Stomata, cuticle, hypodermis, and the mesophyll are classical examples of variable anatomical characters. For example, Borchsenius and Bernal (1996) associated the position (superficial or sunken) of stomata in Aiphanes with the height of the plant and the habitat in which they grow. Pinheiro (1997), on the other hand, has found that stomata position is consistent, without regard to plant height or habitat. Barfod (1988) found xeromorphic anatomical features in some Phytelphantoid palms not growing in dry

habitats. Rudall (1987) has stated that these adaptive features, often based on physiology, are in most cases assumed and less often proven. Since there are few anatomical studies in palms, it is not surprising that Pinheiro and Barfod found exceptions to these assumptions. For this reason, it seems that any survey of anatomical characters for cladistic analysis should consider them plastic until they are proven consistent by sampling.

## 2.1. Leaf anatomical studies of Bactris

Except for the description by Tomlinson (1961), no other detailed anatomical description of Bactris has been published. Tomlinson's results however, are limited and do not reflect the anatomical diversity of the genus, as demonstrated by Ferreira (1997). The fiber sclereids, suggested by Tomlinson as the most important feature segregating Bactris from Guilielma, were not found in any of the non-Guilielma species studied by Ferreira. There were also differences in shape, position and size of non-vascular fiber bundles; specific variations in shape and position of primary veins; hypodermal cells shape and wall thickness.

#### IV. Research Rationale

There are several reasons justifying this research.

The first is the lack of an extensive study of leaf anatomy of Bactris. The description by Tomlinson (1961) was based on the survey of only four samples. The lack of anatomical data covering a large number of species within the genus has hampered the use of anatomical characters in phylogenetic studies of the genus (Sanders, 1991; Salzman & Judd, 1995; Ferreira, 1999a).

The second is the clear evidence that Sanders' phylogeny requires a modern review (de Nevers et al., 1996; Ferreira, 1997; Henderson, 2000). Because his study was undertaken before a comprehensive revision of the genus was available, many species included in his analysis were poorly known. An important aspect that needs to be addressed carefully is the phylogenetic relationships among the genera of Bactridinae. Sanders (1991), Salzman and Judd (1995), and Ferreira (1999a) have used Desmoncus or Astrocaryum as outgroups while doing phylogenetic studies of Bactris, but the other Bactridinae genera could well be used for this purpose.

A third reason is the fact that a new phylogeny of Bactris is necessary not only for scientific purposes, but

also for economic reasons. The pupunha palm is currently the subject of an intensive international program for crop improvement in Costa Rica, Brazil, and Colombia (Clement & Mora-Urpí, 1987). Germplasm collections of cultivated plants are being made, ex situ collections have already been established, and cultivation by farmers is being promoted. This effort has resulted in an impressive increase in its cultivation (Clement, 1995).

Finally, the production of heart of palm from the cultivated pupunha palm is the best economical and ecological alternative to the destructive exploitation of heart of palm from native species (Mora-Urpí et al., 1997). In Brazil, exploitation of the jussara palm (Euterpe edulis) has driven this species to economic extinction in the Atlantic coastal forest. Heart of palm exploitation from wild palms in Brazil is now centered in the Amazon River estuary. Although not as destructive, extensive populations of the native açai palm (Euterpe oleracea) are being exploited.

Thus, a more accurate phylogeny of Bactris would indicate the closely related species or even the wild ancestors of the domesticated pupunha palm. This information is fundamental for a continued progress in the agronomic development of more productive and disease



resistant varieties of the pupunha palm. Indirectly, developing the cultivation of the pupunha palm will likely relieve the pressure on the destructive exploitation of heart of palm from native species.

#### V. Objectives and Hypothesis Tested

This research has two main goals. The first is to produce a detailed leaf anatomical description of Bactris. The second is to investigate phylogenetic hypotheses of relationships within Bactris. An indirect result of this last objective will be a phylogenetic study of Bactridinae; to achieve this, a detailed anatomical description of selected species of each Bactridinae genera will also be produced.

The hypotheses tested during this study were the following:

Hypothesis I. Bactris is monophyletic and its internal organization includes several large groups of species. Some of these groups may correspond to the formerly segregated genera. The alternate hypothesis would support the segregation of Bactris into several smaller genera.

Hypothesis II. The domesticated pupunha palm was the result of multiple events of domestication (Mora-Urpí, 1993, 1984), and has several wild ancestors. The alternate hypothesis is that domestication was limited to one event and that there is only one wild ancestor of pupunha palm.

## VI. Material and Methods

### 1. Selection of species

There were 46 taxa included in this study (Appendix I). The primary aspect influencing their selection was the investigation of phylogenetic relationships within Bactris; the secondary was the investigation of phylogenetic relationships among the genera of Bactridinae. For this reason different approaches had to be used in each case.

#### 1.1. The Bactridinae and outgroup species

Whenever possible, more than one, but not more than three species from each Bactridinae genus were selected. The reason was to avoid using each genus as a terminal taxon. This prevented the introduction of large amounts of polymorphisms in the data matrix because some genera (e.g.

Aiphanes, Astrocaryum and Desmoncus) are diverse and variable. Within each genera, the species were selected to represent their current or former taxonomic status. As a result, Aiphanes includes A. aculeata, a member of the former subgenus Macroanthera (Burret, 1932) and A. ulei, representing the remaining species in the genus (Borchsenius & Bernal, 1996). The genus Astrocaryum is represented by three species, each from a different subgenus proposed by Kahn and Millán (1992). The three Desmoncus species were selected randomly since little is known about their phylogeny. From Acrocomia, the species selected was the widely distributed A. aculeata. Finally, Gastrococos is represented by its sole species. The genus Bactris is represented by all species selected for the study.

To test the potential outgroups for Bactridinae, two palm species, Syagrus comosa and Maximiliana maripa, were selected. A palm was selected as outgroup because a cladistic analysis of the whole palm family that indicates Nypa as the sister of all other palms (Uhl et al., 1995). The species selected as outgroup in this study belongs to different subtribes related to Bactridinae within the tribe Cocoeae. Syagrus belongs to the subtribe Butiinae and Maximiliana to the subtribe Attaleinae. These tribes are

easily distinguished from Bactridinae by their lack of spines. These two species were also selected because extensive and reliable anatomical information is now available (Pinheiro, 1997).

### 1.2. The Bactris species

A recently published revision of Bactris (Henderson, 2000) was the basis for the selection of the 33 species used in this study. They were selected to represent each of the six groups of species proposed by Henderson. In some cases selection was also influenced by the number of collections available in herbaria in order avoid including rare or poorly collected species and inherent sampling problems therein.

The only difference between the species proposed by Henderson and the ones used in this study is the status of the wild variety of Bactris gasipaes. Here, B. gasipaes var. chichagui is further subdivided into two distinct populations. The mostly southwestern Amazonian population, formally considered at the specific level as B. dahlgreniana (Glassman, 1972; Clement, 1988) and a population found along the Andes in northern Venezuela and Colombia, originally described as B. macana. The reason

for this split is that these populations are distinct and may have had distinct roles in the domestication of the pupunha palm (Ferreira, 1999a). Treating them as a single entity, under the criteria adopted for specimen selection (see 2), would result in the inclusion of members from only one or another population, not both. This would mask the taxa diversity and prevent testing the second hypothesis of this study.

## 2. Selection of specimens

All Bactris specimens examined were identified by A. Henderson and most were included in his treatment of Bactris. Species belonging to different genera were identified by several palm taxonomists, including A. Henderson, R. Bernal, and F. Kahn.

The main criterion used in the selection of specimens was their common or similar geographical origin. This was done to reduce variability within the members of a single species. Therefore, the resulting selected specimens were in fact a sampling of local or regional populations. This is particularly important in the case of widely distributed species or species complexes, such as Acrocomia aculeata, Bactris simplicifrons, B. maraja, and B. major.

### 2.1. Number of specimens used for anatomical studies

For each taxon studied, three specimens were examined resulting in a total of 138 specimens being prepared and examined. Since several anatomical techniques were used (see 3) and, in several instances, duplicate slides prepared, a collection of more than 600 permanent slide mounts was made.

Specimens used in the anatomical study are listed after the anatomical description of each taxon. Anatomical descriptions of the two outgroup species were previously published by Pinheiro (1997) and are not presented here. Additional anatomical observations of these taxa were made only if particular information was not included in Pinheiro's description. The list of specimens examined includes data on their distribution, locality description, date of collection, and collector name and number. The abbreviation appearing in brackets indicates the Herbarium where the specimen is deposited.

### 2.2. Number of specimens used for morphological survey

All specimens used for anatomical studies were also examined for the morphological survey. However, because most palm collections are fragmentary, due mostly to the large size of their leaves and inflorescence, it was necessary to include additional specimens in this survey. Most collections examined had 1-3 leaf parts, consisting of a leaf base with portion of the petiole and few pinnae, a middle portion with rachis and pinnae, and the apical portion with rachis and pinnae. The more common situation was for the collection to have only the middle leaf part. Some collections included a complete or incomplete inflorescence. When incomplete, the inflorescence had a basal, middle and an apical portion. A collection would usually, but not always, be more or less complete according to the size of the palm. Small palms, such as B. bifida, B. simplicifrons, B. tomentosa, and B. killipii were often represented by complete collections, while larger palms like B. gasipaes, B. setulosa, and Acrocomia aculeata were more fragmentary. Consequently, the number of specimens examined for each species is variable and usually larger in the case of medium to large sized palms. Another factor affecting the number of collections surveyed was the presence of flowers and fruits. In most cases a single

collection would have either fruits or flowers, rarely both.

The list of specimens used during the morphological survey is presented in the Appendix I.

### 3. Anatomical Methods

Leaf clearings, epidermal peels, leaf cross sections, and flower clearings were used in this study. The presentation of anatomical descriptions follows Tomlinson (1961). Since morphometric methods are not used in this study, measurements were not made during the anatomical survey.

#### 3.1. Sampling

##### a. Sampling of leaves

Only the middle portion of leaflets located along the middle part of leaves were sampled. For species with entire leaves, samples were taken from the middle portion of the lamina. This ensured the accuracy and uniformity of data collection. For all sample types, 3-5 spare sample



were prepared and kept in Glycerin-Alcohol ready to be used in case of material loss.

Scissors were used to cut the leaves. While samples for leaf clearings were trimmed directly from herbarium specimens, the smaller samples used for epidermal peels and cross-section were trimmed after a small leaf portion (4-5 cm long) was rehydrated. This was necessary because dry leaves are too brittle and cutting them usually resulted in longitudinal fissures or separation of midrib or main vein.

A 2-3 cm long section of leaflet with midrib and one of the margins was used to prepare leaf clearings of pinnate leaves. For species with simple leaves (B. bifida, B. killipii, and B. simplicifrons) a marginal section 2-3 cm long, including at least one main vein, was used.

Epidermal peel samples were trimmed to 1 cm<sup>2</sup> and required one untrimmed margin to assure a positive identification of adaxial and abaxial surfaces.

Leaf cross-section samples of pinnate leaves were 1-2 cm long and included the midrib and one leaflet margin. When the leaflet was too wide to make workable-sized paraffin blocks, such as those from Bactris setulosa, Aiphanes aculeata, and A. ulei, the sample was subdivided.

#### b. Sampling of flowers

For each specimen examined, 3-4 staminate flowers were cleared and kept in Hemo-De until dissection and eventual permanent mount.

### 3.2. Rehydration and fixing

All samples were rehydrated using the solution recommended by Martens and Uhl (1984). The rehydration procedure took 12-24 hours using a vacuum chamber (12 p.s.i.). After samples were removed from the vacuum chamber, they were washed with three changes of deionized water (15 minutes each), and fixed in FAA (Formalin, Acetic Acid, 50% Ethanol) for at least 48 hours.

### 3.3. Leaf clearings

Leaf clearings were performed using a method slightly modified from Ferreira (1999b) (Appendix II). The timing of samples in 5% NaOH solution in an oven at 58-60°C was variable. Some samples were cleared after 24 hours while others required up to one week and at least one change of NaOH after the first 24 hours. There were no differences in

stain intensity between samples stained for only 30 minutes or overnight. All samples were permanently mounted.

#### 3.4. Epidermal peels

O'Brien and McCully (1981), Ferreira (1997), and Pinheiro (1997) were followed for the preparation of epidermal peels (Appendix III). Samples were initially placed in half-filled 20 cc glass vials with Jeffrey's solution. There was one change of Jeffrey's solution after the first 24 hours. The epidermis separated after 4-5 days and, in most cases, no additional cleaning with paintbrush was necessary. Because Jeffrey's solution becomes dark after 2 days and epidermal samples are small and fragile, water was added while changing solutions to clear the solution and prevent sample. Moving the samples from the petri-dish to the slide was accomplished by filling the petri-dish with Hemo-De, submerging the slide, and guiding the floating samples towards the slide center. The slide was slowly raised out of the Hemo-De and the sample centered and stretched with a paintbrush.

#### 3.5. Leaf cross-section

The methods of Martens and Uhl (1984), Ferreira (1997), and Pinheiro (1997) were modified and used to prepare the cross-sections samples.

a. Hydrofluoric Acid (HF) treatment

The samples were first soaked for 4-9 days in a 2:1 mixture of Glycerin-Alcohol 70% (1:6) and HF. The length of time the samples could be soaked in HF without being damaged was variable. A general rule was that they would be damaged after 10 days. As a result, large sample batches were initially soaked for longer periods. If damaged occurred, they were submitted to shorter treatment.

b. Embedding, sectioning, and staining

The samples were placed in small glass vials and embedded in Paraplast plus according to a protocol using a Hemo-De series (Appendix IV). Since Hemo-De is less volatile than Toluene or Butyl-Alcohol, it was necessary to make two additional changes of 100% melted Paraplast, at 24-hour intervals. The blocks were trimmed (exposing the leaf edge) and soaked for additional softening in Glycerin-Alcohol 70% (2:6) for up to 2 months.

An A. O. Spencer 820 rotary microtome was used to obtain 15-20 $\mu$  thick sections. They were fixed in 1" x 3" glass slides using Haupt adhesive and kept overnight in 43°C warming plates.

The staining procedure followed a modified Safranin-Astra Blue protocol (Appendix V). Permanent mounts were made with Kleermount and the slides were left on a warming plate (43°C) for 2-3 days. Observations and photos were made using a Nikon light microscope.

### 3.6. Flower clearings

The flowers were cleared using a slightly modified version of the protocol used to prepare leaf clearings.

The dissection of the different flower parts occurred only at the end of the dehydration procedure to avoid loss of material.

## 4. Morphological Survey

The morphological observations of vegetative and reproductive structures of herbarium specimens were made with an Olympus SZ60 stereomicroscope with magnification up to 63x. After rehydration, Wild M5 dissecting microscope

with up to 500x magnification was used to dissect flowers and fruits.

## 5. The characters used in the cladistic analysis

Only qualitative characters were used in the analysis. The 66 morphological and anatomical characters were searched for among the ingroup and outgroup taxa. Complex multistate characters were avoided Whenever possible, and variation broken down and reduced into binary states (a reductive approach).

### 5.1. Character list

#### Stem habit

1. Stem habit: (0) climbing, (1) non-climbing.

The climbing habit evolved independently in several palm groups (Tomlinson, 1990). Within Bactridinae, only Desmoncus has developed such capacity. D. stans is one exception but had to be excluded because of the lack of specimens. It is known, however, that many adult species of Desmoncus have a free-standing juvenile stage and non-

climbing habit has been found in several Desmoncus specimens from South America (Grayum and De Nevers, 1988).

### Armature

2. Spines: (0) absent, (1) present.

The definition of spines used here is that of Tomlinson (1990). State (1) refers to the presence of spines emerging from superficial tissue in any plant part. The members of Bactridinae are one of the few palm groups to be conspicuously and consistently spiny (Tomlinson, 1990).

3. Spines on petiole forming: (0) longitudinal ranks, (1) clustered to shortly transverse lines, (2) irregularly distributed.

Spines were surveyed on petiole not only for their distinct arrangement there, but also because most herbarium specimens had a short portion of petiole attached to the basal part of the leaf rachis. There are two distinct pattern of spine distribution in the petiole. In the first (state 0), the spines usually form three longitudinal lines extending from the leaf-sheath to the first basal leaflet. It is found in six species of the Non-Ocreate clade sensu

Sanders (1991), of which, B. gasipaes var. gasipaes, B. jamaicana, and B. plumeriana are polymorphic, having states (0) and (2). In the second pattern (state 1), the spines form small clusters that eventually spread diagonally to form short transverse lines, such as the ones found in B. setulosa. The state (2) was the best solution to allow the inclusion of the remaining species whose spines are not arranged in any discernible pattern.

#### Leaf morphological characters

4. Leaf blade: (0) simple, (1) pinnate.

One intermediate state, leaf blade pinnate only at the base, is found only in B. sphaerocarpa. It was not included here because uninformative character were excluded from the final data matrix.

5. Pinnae apex shape: (0) narrowing, (1) broadening.

This character is applied only to species with pinnate blade. The state (1) is found in Aiphanes and in Bactris caryotifolia. In these species, the pinnae apex is always praemorse.



6. Midrib position on narrowed pinna apex: (0) terminal, (1) subterminal.

In state (0) the pinna apex is equally or unequally divided into two distinct, more or less similarly shaped teeth. In most Bactris one segment is always longer, with the midrib continuing as inner margin of it (1).

7. Metallic sheen on leaf abaxial surface: (0) absent, (1) present.

The state (1) is found only in three species of Bactris. It can only be observed on herbarium specimens.

8. Distinct scale band at the leaf margin: (0) absent, (1) present.

Scales are frequent in the leaves of juvenile stages of many Bactridinae palms, but in most instances they are ephemeral. In a few species, however, they form a band near the leaflet margin that persist throughout the adult stage.

#### Leaf anatomical characters

9. Fiber sclereids: (0) absent, (1) present.

Fiber sclereids are found in several species of Bactris. They are elongated fiber-like structures irregularly matted throughout the mesophyll. Tomlinson (1961) used the sclereids to segregate Bactris from Guilielma.

10. Short longitudinal non-vascular bundles: (0) absent, (1) present.

These non-vascular bundles are not reported in Tomlinson (1961). Although similar in appearance to small sclereids, they are distinct in that they lack lignin.

11. Branched longitudinal vascular bundle: (0) absent, (1) present.

Although palms are more commonly recognized by their parallel venation, a closer observation of leaf clearings has revealed that venation divergence is frequent. It seems to be more common in species with wide pinnae, such as Aiphanes, a few Bactris, and most taxa with broad lanceolate to elliptical pinnae.

12. Transversely extended adaxial epidermal cells: (0) absent, (1) present.

The adaxial epidermis in palms can be longitudinally, obliquely or transversely extended. Among these three situations, only the last is clear cut.

13. Persistent epicuticular wax on abaxial epidermis: (0) absent, (1) present.

This is a character found only in Astrocaryum and can be observed in cross-section and leaf clearings samples. It was unusual to find epicuticular wax in cross-section samples because all of them were treated with the solvents Xylem and Hemo-De.

14. Adaxial epidermal cell files alternately oblique and transverse: (0) absent, (1) present.

When transversely extended most epidermal cells form distinct longitudinal files (except in Astrocaryum gynacanthum). These files are often interrupted by obliquely arranged cells forming a rather irregular file.

15. Abaxial intercostal cells in same file as stomata: (0) not forming distinct rows, (1) forming distinct rows.

Non-stomata cells on abaxial surface are either irregularly arranged (0) or form distinct longitudinal rows between two stomata (1).

16. Stomata position: (0) superficial, (1) sunken.

17. Stomata on adaxial surface: (0) absent, (1) present.

Tomlinson (1961) suggested adaxial stomata were absent from palms that were later included in the subtribe Bactridinae by Uhl & Dransfield (1987). During this survey it was found that many Bactridinae species have adaxial stomata, often on costal regions.

18. Abaxial stomata in distinct files or short rows: (0) absent, (1) present.

In Acrocomia, Gastrococos, and Astrocaryum the abaxial stomata form distinct files or short rows. It was thought that non-stomata cells in these lines would also form distinct rows and that character 18 would be correlated with character 15. This was not the case.

19. Terminal subsidiary cells: (0) non-lobed, (1) lobed.

When present lobes are usually located at the extremities of the subsidiary cells. Tomlinson (1961) had not reported them in any of the current Bactridinae palm.

20. Lateral subsidiary cells overarching guard cells: (0) absent, (1) present.

This character is not correlated with state (1) of character 16, nor are these cells lobed as in character 19. Lateral subsidiary cells are deeper and narrower than all adjacent cells.

21. Leaf main vein: (0) several midribs, (1) single midrib.

22. Non-vascular fiber bundles on peripheral chlorenchymatous layer: (0) absent, (1) present.

The peripheral chlorenchymatous layer surrounding the midrib is defined by Tomlinson (1961) as an extension of the lamina. In some cases, this layer is well-developed and non-vascular fiber bundles can be found on the adaxial region.

23. Vascular bundles on peripheral chlorenchymatous layer: (0) absent, (1) present.

In Acrocomia aculeata and Gastrococos crispera, vascular bundles replace the non-vascular bundles found in the other species.

24. Primary veins protruding pattern: (0) both surfaces, (1) only abaxial.

The reason for state (0) is the fact none of the species studied had primary veins protruding only adaxially. To define the character states as either adaxial or abaxial would add unnecessary polymorphism to the data matrix while scoring species with primary veins protruding in both surfaces.

25. Buttress: (0) absent, (1) present.

These structures are fibrous extensions of the bundle sheath, usually linking a vascular bundle to the hypodermis or epidermis. Their main function seems to be mechanical support, although in some cases the fibrous extensions do not reach the epidermis. Rudall (1992) refers to buttresses sensu Tomlinson as girder or bundle sheath extensions.

26. Adaxial hypodermal layer continuous and uniform: (0) absent, (1) present.

The adaxial layer is uniform and continuous along the whole lamina (0) or compressed or interrupted by the veins (1).

27. Palisade mesophyll: (0) absent, (1) present.

General inflorescence characters

28. Inflorescence: (0) protandrous, (1) protogynous.

29. Peduncle shape in cross-section: (0) terete, (1) flattened.

30. Spiny peduncular bract: (0) absent, (1) present.

Here, spines are of the same nature as the ones considered in character 1. In B. major var. socialis spines leave a shallow groove-like impression on the bract surface.

31. Outer surface of peduncular bract: (0) non-grooved, (1) grooved.

This character is uninformative within the ingroup but was included because state (1) is found in both outgroups.

32. Zigzag rachillae: (0) absent, (1) present.

Rachillae in a zigzag pattern (1) is found only in Desmoncus.

33. Filamentous rachillae: (0) absent, (1) present.

The rachillae are very thin and pendulous in their distal portion (1) or, the more common situation, the rachillae are thick, stout, and stiff, erect or not.

#### Staminate flowers characters

34. Staminate flowers on rachillae: (0) superficial, (1) deeply sunken, (2) in shallow pits subtended by bracts.

State (0) and (1) are very contrasting. State (2) refers to the way flowers of Acrocomia develop on rachillae surface, a unique characteristic among the Bactridinae palms.

35. Distribution of floral triads on rachillae: (0) completely regular, (1) completely irregular, (2) regular on one side only, (3) few triads at the base, (4) regular on 1/2 rachillae length.

In Bactridinae, staminate and pistillate flowers form triads of one central pistillate and two lateral staminate flowers, but the organization of these triads on the rachillae is variable. The more frequent situation in Bactris is for the triads to be either regularly (0) or irregularly (1) distributed along the whole rachillae.



There is, however, an exception. In some species, the triads are more or less regularly arranged on only one side of the rachillae (2). The states (3) and (4) were included to accommodate the pattern found in Astrocaryum, Acrocomia and Gastrococos.

36. Shape of staminate flowers: (0) asymmetrical, (1) symmetrical.

There is a close association between symmetrical shape of flowers and state (1) of character 37, however, the flowers of Aiphanes have ovate to triangular petals.

37. Shape of staminate petals: (0) ovate to triangular, (1) boat shape.

There is no correlation between character 37 and 38. The majority of cucullate petals are ovate to triangular.

38. Apex of staminate petals: (0) non-cucullate, (1) cucullate.

In state (1) there is an abrupt folding of the apical portion of the petals. In flowers with cucullate petals, the folding are frequently located in the side not facing the rachillae.

39. Fiber bundles on staminate corolla surface: (0) non-prominent, (1) prominent.

State (1) is clear cut even in rehydrated flowers.

40. Receptacle: (0) prominent, (1) non-prominent.

The receptacle is clearly distinct if the petals are removed (0) or obscure, being disintegrated as the petals are removed (1).

41. Filament shape: (0) triangular, (1) filamentous.

State (0) seems to be associated with shorter filaments.

42. Filament disposition: (0) non-folded, (1) folded.

State (1) refers to the single to multiple folds observed at the filament mid portion. This is a common state within Bactris, but it is not known if folded filaments cause the anther to become exerted during anthesis.

43. Filament apex: (0) non-inflexed, (1) inflexed.

#### Staminate flower anatomical character

44. Anastomosed fiber bundle on margin of staminate petal:  
(0) absent, (1) present.

Pistillate flowers characters

45. Pistillate calyx: (0) tubular or annular, (1) aposepalous.
46. Pistillate corolla: (0) tubular, (1) apopetalous.
47. Apopetalous corolla: (0) petals broadly imbricate, (1) non-imbricate.
48. Lobes of pistillate corolla at anthesis: (0) spreading, (1) non-spreading.
49. Stigmas at anthesis: (0) reflexed, (1) non-reflexed.
50. Ovules attachment: (0) lateral, (1) central.

General fruit characters

51. Fruit shape: (0) globose, (1) obovoid to depressed-globose, (2) ellipsoid, (3) ovoid.

The establishment of discrete states for this character is somewhat arbitrary but it is based on the actual fruit shapes observed from the specimens studied. States (0), (2), and (3) are clear cut. State (1) includes two distinct shapes that share some similarity: both are wider or depressed in their distal regions. Moreover, depressed-globose fruits are more distinct from true globose than from obovoid.

52. Staminodial ring in fruit corolla: (0) absent, (1) present.

This character refers to staminodial ring in fruits and not on flowers for the practical reason that the ring can be more easily observed in ripe fruits, a stage in which they reach maximum development.

53. Epicarp color: (0) reddish to orange, (1) yellowish to straw, (2) blackish to purplish-black, (3) brown.

Because developmental studies were not carried out, states (0), (1), and (2) may not reflect an accurate assessment of fruit color in Bactris. There are three basic fruit colors in the genus: red, yellow and purple-black. Each of these color categories displays variation (e.g. red: bright red, dark red). The states used here

are, for now, the best solution to avoid using numerous, specific color matching states that could add up to a dozen. State (3) was observed only in the outgroups.

54. Spinulose epicarp: (0) absent, (1) present.

Although emergent like the ones observed on petiole and peduncular bracts, the small spines of the fruit epicarp do not have distinct pulvinus.

55. Mesocarp consistency: (0) doughy, (1) juicy, (2) fleshy, (3) dry-fibrous, (4) hard-starchy.

This character was observed in fruits with the epicarp removed. State (1) is associated with the presence of juice sac attached to the non-pore endocarp fibers of many black to purple-black species. State (4) applies only to the fruits of B. gasipaes.

56. Outer mesocarp fibers: (0) absent, (1) present.

These fibers are located just underneath the epicarp and are easily observed in dehydrated fruits.

57. Outer mesocarp fiber arrangement: (0) free, (1) attached to endocarp poles, (2) bunched radiated.

Free fibers (0) are usually short and diagonally arranged, the innermost portion penetrating the mesocarp. The fibers attached to endocarp poles (1) are parallel and elongated, branching only near the poles. State (2) is found only in B. constanciae, the only species included here to have muricate epicarp.

58. Endocarp dimension in side view: (0) longer than wide, (1) round, (2) wider than longer.

It would be impossible to give a specific name to each variation of endocarp shape found in Bactris. Endocarps have pores of distinct shape, size, and location; are shallowly to deeply pitted or strongly tuberculate. To allow a segregation into distinct character states, a broad concept was adopted because most endocarps, without regard to their surface irregularities, fall in one or another of the proposed categories. As it turned out, this character was not correlated with character 51. For example, B. gasipaes var. gasipaes has a ovoid fruit, but its endocarps are in most cases wider distally (obovoid).

59. Endocarp pore position: (0) medial to apical, (1) basal to sub-basal.

State (0) applies to all Bactridinae species while state (1) is found only in the outgroup. The reason for the inclusion of a range in both states derives from the fact that in these two large groups, the position of the fertile pore can be variable (see character 60).

60. Fertile pore position: (0) longitudinally displaced, (1) not longitudinally displaced.

Besides being much bigger than infertile pores, the fertile pore can also be longitudinally displaced, sometimes located at the endocarp pole as in B. gasipaes var. gasipaes.

61. Endocarp shape in polar view: (0) circular, (1) non-circular.

62. Grooved endocarp: (0) absent, (1) present.

63. Endocarp fibers: (0) absent, (1) present.

This character is uninformative within the ingroup because they all have fibrous endocarp. It has been used because the two outgroup species have fiberless endocarp.

64. Non-pore endocarp fiber: (0) absent, (1) present.

65. Appressed to partially free non-pore endocarp fiber:  
(0) absent, (1) present.

These fibers are sometimes confused with the long, appressed pore fibers, however, they are usually of a lighter color, unbranched, and easily detachable. Their distal portion is frequently raised from the endocarp surface and rarely goes through the mesocarp.

66. Free non-pore endocarp fibers: (0) matted, (1) non-matted.

There is a correlation between density and fiber length with state (0) because fibers are always matted if they are long and densely arranged in the endocarp.

## 6. Data matrix construction

Morphological and anatomical variation of a single feature in a given organism is a common situation in nature. However, extremely variable features are something researchers try to avoid while doing cladistics studies because they have to be scored as polymorphic. In some cases extremely variable features are not considered useful (McClatchey, 1999). In the past, due to software



constraints, polymorphisms were coded as either missing or having the state presumed to be the ancestor within the taxa, leading to errors in the calculation of tree length and consistency index (Nixon & Davis, 1991). The recent cladistic software Winclada (Nixon, 1999) allows the coding of polymorphic character states in a restricted form. For the present study, two data matrices were used. In the first, restricted polymorphism coding was used. In the second, the polymorphic taxa were broken down into subtaxonomic units as proposed by Nixon and Davis (1991). The main reason for this was to better assess the relationships among the several subtaxonomic units resulting from the breaking down of the two varieties of Bactris gasipaes and to test the hypothesis II of this study.

In each of these two data matrices the assemblage of anatomical and morphological data sets were analyzed independently as well as together in a combined analysis.

#### 6.1. Data matrix 1 (Table 5)

The following procedure was used during the construction of the data matrix: missing data are indicated

Table 5. Data Matrix 1 for ingroup and outgroup taxa. Polymorphisms are indicated by alternative states enclosed in brackets

|                                   |               |            |               |               |               |                  |        |
|-----------------------------------|---------------|------------|---------------|---------------|---------------|------------------|--------|
| Maximiliana maripa                | 10-1010001    | 0000100100 | 111000171-    | 1000-00010    | 1000110100    | 313-010011       | 1000-- |
| Syagrus comosa                    | 10-1010001    | 0000100100 | 111010100-    | 1100400001    | 0010110100    | [23]13-311011    | 1000-- |
| Acrocomia aculeata                | 1121000000    | 0000110101 | 1110101101    | 000231111[01] | 1011110101    | 011000-001       | 001100 |
| Alphanes aculeata                 | 11211-0101    | 1000001000 | 1000001000    | 0000010001    | 0001111001    | 0100010201       | 011111 |
| A. ulei                           | 11211-0101    | 1000001000 | 1000001000    | 0000010111    | 0000111001    | 1100010001       | 1010-- |
| Astrocaryum gynacanthum           | 112100000[01] | 0010000110 | 1101111111    | 0001311101    | 001000-101    | 1100011000       | 101111 |
| A. jauari                         | 1121000000    | 0111000110 | 1001111111    | 0001311101    | 001000-101    | [12]110210001    | 011111 |
| A. murumuru                       | 1121000001    | 0111000110 | 1101111111    | 0001311111    | 101000-101    | 1111210001       | 101101 |
| Bactris acanthocarpa var. exscapa | 1121010100    | 0000000000 | 1101000101    | 0010200100    | 111000-111    | 1001011001       | 101111 |
| B. acanthocarpoides               | 1121010000    | 0000001000 | 1001000101    | 0010200110    | 111000-111    | 1011011201       | 101111 |
| B. balanophora                    | 1111010001    | 1000000000 | 1001000111    | 0000100010    | 111000-111    | [13]000010001    | 001111 |
| B. bifida                         | 1120--1010    | 0000001000 | 0100000100    | 0000000010    | 001000-111    | 2[01]20111000    | 001100 |
| B. brongniartii                   | 1121010010    | 0000001000 | 1000000111    | 0000100000    | 101000-111    | 1[01]20111201    | 101100 |
| B. campestris                     | 1111010001    | 1000000010 | 1000000111    | 0000100000    | 111000-111    | 1000011201       | 001111 |
| B. caryotifolia                   | 11211-0000    | 1000000000 | 1100000111    | 0000100100    | 111000-111    | 1020111201       | 001101 |
| B. coloradonis                    | 1121010001    | 1000001000 | 1001001111    | 0000100000    | 101000-111    | 1000011000       | 101111 |
| B. concinna                       | 1121011010    | 0000001000 | 1000001111    | 0000000110    | 001100-111    | 1121111000       | 101100 |
| B. constanciae                    | 1121010000    | 0000001000 | 1101000111    | 0000100000    | 101000-111    | 0000112201       | 101100 |
| B. cubensis                       | 1121010000    | 0000000000 | 1000101111    | 0000100101    | 111000-111    | 1000011001       | 001111 |
| B. ferruginea                     | 1121010001    | 0000000000 | 100000111[01] | 0000100100    | 001000-111    | 1020111201       | 101100 |
| B. gasipaes var. chichagui N      | 1101010001    | 0000001000 | 1001101111    | 0000100110    | 111000-111    | 0000410001       | 001111 |
| B. gasipaes var. chichagui S      | 1101010001    | 0000001000 | 100110111[01] | 0000100110    | 111000-111    | 0000410000       | 001111 |
| B. gasipaes var. gasipaes         | 11[02]1010001 | 0000001000 | 100110111[01] | 0000100110    | 111000-111    | 30[01]0410[01]00 | 00111- |
| B. glandulosa var. glandulosa     | 11-1010001    | 1000001000 | 1001000111    | 0010200100    | 111000-111    | 1000011201       | 101111 |
| B. glaucescens                    | 1121000000    | 0100010010 | 1000111111    | 0000100010    | 101000-111    | 1020111201       | 101100 |
| B. gracilior                      | 11-1010001    | 1000001000 | 1001000111    | 0000100000    | 101000-111    | 1000011001       | 001111 |
| B. guineensis                     | 1121010001    | 1000000000 | 1000100111    | 0000100010    | 101000-111    | 1020111201       | 101100 |
| B. hirta var. spruceana           | 1121010000    | 0000000000 | 1001000111    | 0000000110    | 111000-111    | [01]001011001    | 001111 |
| B. horridispatha                  | 1121010001    | 1000000000 | 1001000111    | 0000100100    | 101000-111    | 2021111000       | 001110 |
| B. jamaicana                      | 11[02]1010001 | 1000000000 | 1000000111    | 0000100101    | 111000-111    | 1000011201       | 101111 |
| B. killipii                       | 11-0--0001    | 1000001000 | 0001000100    | 0000000000    | [01]01000-111 | [02]000011001    | 111111 |
| B. major var. socialis            | 1121011010    | 0000001000 | 1000001111    | 0000100110    | 001000-111    | 2121111001       | 001110 |
| B. maraja var. trichospatha       | 1121010010    | 0000010000 | 1101000111    | 0000100000    | 101000-111    | 1021111201       | 101100 |
| B. mexicana var. mexicana         | 1121010001    | 1000000000 | 1001100111    | 0000100110    | 111000-111    | 1000011201       | 001111 |
| B. plumeriana                     | 11[02]1010000 | 0000000000 | 1000001111    | 0000100110    | 111000-111    | 1000011001       | 001111 |
| B. ptariana                       | 1111010001    | 1000000000 | 1001000111    | 0000100010    | 111000-111    | 101[01]011201    | 001111 |
| B. riparia                        | 1121010000    | 0000001000 | 1001001111    | 0000100110    | 111000-111    | 1000011201       | 001111 |
| B. setosa                         | 1121010001    | 0000001000 | 1000101111    | 0000100011    | 111000-111    | 1020111201       | 101100 |
| B. setulosa                       | 1111010001    | 0000001000 | 1001000111    | 0000100[01]00 | 111000-111    | 1000011201       | 001101 |
| B. simplicifrons                  | 1120--0001    | 1000001000 | 0000000110    | 0000000000    | 001000-111    | 0000011000       | 111111 |
| B. sphaerocarpa                   | 1121010010    | 0000001000 | 1000000111    | 0000000110    | 001000-111    | 1020111001       | 001100 |
| B. tomentosa                      | 1121010010    | 0000001000 | 1100000111    | 0000000010    | 001000-111    | 1021111201       | 101100 |
| Desmoncus macroacantha            | 0121000001    | 1000001000 | 1000000101    | 0100000001    | 000000-101    | [12]000011001    | 001111 |
| D. orthacanthos                   | 0121000000    | 1000001000 | 1001000101    | 01000000[01]1 | 100000-101    | 10[01]0011001    | 0010-- |
| D. polyacanthos                   | 0121000001    | 1000001000 | 1000000101    | 01000000[01]1 | 000000-101    | [12]000010001    | 0010-- |
| Gastrococos crispa                | 1121000000    | 0000110101 | 111000170[01] | 0000411011    | 0001011101    | 011000-101       | 001100 |

by a question mark (?), inapplicable character-states by a dash (-) and, polymorphic as an asterisk (\*) in the case of binary characters, or (\$) if the character is multistate.

## 6.2. Data matrix 2 (Table 6)

Taxa with polymorphism were subdivided into subunits (subtaxon) and when they were variable in more than one character several combinations were made. This procedure was discussed by Nixon and Davis (1991) and used by Struwe al. (1994). As a result, Bactris gasipaes var. gasipaes, which had 4 polymorphic characters, was split into 16 subtaxon ( $2^4$ , where 2 refers to the number of the states of the polymorphic character and 4 is the number of polymorphic character shown by the taxon). Each subtaxon unit was assigned a sequential number.

A shortcoming of this procedure are difficulties to indicate which of the subtaxonomic units occur in reality and to give them specific names (Stevenson et al., 2000). Here all combinations were used and there was no incorporation of autapomorphies, as suggested by Nixon (Struwe et al., 1994).

## 7. Cladistic analysis

Table 6. Data matrix 2 for ingroup and outgroup taxa. Polymorphic taxa are divided into subtaxonomic units

|                                   |            |            |            |            |            |            |        |
|-----------------------------------|------------|------------|------------|------------|------------|------------|--------|
| Maximiliana maripa                | 10-1010001 | 0000100100 | 111000171- | 1000-00010 | 1000110100 | 313-310011 | 1000-- |
| Syagrus comosa 1                  | 10-1010001 | 0000100100 | 111010100- | 1100400001 | 0010110100 | 213-311011 | 1000-- |
| S. comosa 2                       | 10-1010001 | 0000100100 | 111010100- | 1100400001 | 0010110100 | 313-311011 | 1000-- |
| Acrocomia aculeata 1              | 1121000000 | 0000110101 | 1110101101 | 0002311110 | 1011110101 | 011000-001 | 001100 |
| A. aculeata 2                     | 1121000000 | 0000110101 | 1110101101 | 0002311111 | 1011110101 | 011000-001 | 001100 |
| Alphanes aculeata                 | 11211-0101 | 1000001000 | 1000001000 | 0000010001 | 0001111001 | 0100010201 | 011111 |
| A. ulei                           | 11211-0101 | 1000001000 | 1000001000 | 0000010111 | 0000111001 | 1100010001 | 1010-- |
| Astrocaryum gynacanthum 1         | 1121000000 | 0010000110 | 1101111111 | 0001311101 | 001000-101 | 1100011000 | 101111 |
| A. gynacanthum 2                  | 1121000001 | 0010000110 | 1101111111 | 0001311101 | 001000-101 | 1100011000 | 101111 |
| A. javari 1                       | 1121000000 | 0111000110 | 1001111111 | 0001311101 | 001000-101 | 1110210001 | 011111 |
| A. javari 2                       | 1121000000 | 0111000110 | 1001111111 | 0001311101 | 001000-101 | 2110210001 | 011111 |
| A. murumuru                       | 1121000001 | 0111000110 | 1101111111 | 0001311111 | 101000-101 | 1111210001 | 101101 |
| Bactris acanthocarpa var. exscapa | 1121010100 | 0000000000 | 1101000101 | 0010200100 | 111000-111 | 1001011001 | 101111 |
| B. acanthocarpoides               | 1121010000 | 0000001000 | 1001000101 | 0010200110 | 111000-111 | 1011011201 | 101111 |
| B. balanophora 1                  | 1111010001 | 1000000000 | 1001000111 | 0000100010 | 111000-111 | 1000010001 | 001111 |
| B. balanophora 2                  | 1111010001 | 1000000000 | 1001000111 | 0000100010 | 111000-111 | 3000010001 | 001111 |
| B. bifida 1                       | 1120--1010 | 0000001000 | 0100000100 | 0000000010 | 001000-111 | 2020111000 | 001100 |
| B. bifida 2                       | 1120--1010 | 0000001000 | 0100000100 | 0000000010 | 001000-111 | 2120111000 | 001100 |
| B. brongniartii 1                 | 1121010010 | 0000001000 | 1000000111 | 0000100000 | 101000-111 | 1020111201 | 101100 |
| B. brongniartii 2                 | 1121010010 | 0000001000 | 1000000111 | 0000100000 | 101000-111 | 1120111201 | 101100 |
| B. campestris                     | 1111010001 | 1000000010 | 1000000111 | 0000100000 | 111000-111 | 1000011201 | 001111 |
| B. caryotifolia                   | 11211-0000 | 1000000000 | 1100000111 | 0000100100 | 111000-111 | 1020111201 | 001101 |
| B. coloradonis                    | 1121010001 | 1000001000 | 1001001111 | 0000100000 | 101000-111 | 1000011000 | 101111 |
| B. concinna                       | 1121011010 | 0000001000 | 1000001111 | 0000000110 | 001100-111 | 1121111000 | 101100 |
| B. constanciae                    | 1121010000 | 0000001000 | 1101000111 | 0000100000 | 101000-111 | 0000112201 | 101100 |
| B. cubensis                       | 1121010000 | 0000000000 | 1000101111 | 0000100101 | 111000-111 | 1000011001 | 001111 |
| B. ferruginea 1                   | 1121010001 | 0000000000 | 1000001110 | 0000100100 | 001000-111 | 1020111201 | 101100 |
| B. ferruginea 2                   | 1121010001 | 0000000000 | 1000001111 | 0000100100 | 001000-111 | 1020111201 | 101100 |
| B. gasipaes var. chichagui N      | 1101010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 0000410001 | 001111 |
| B. gasipaes var. chichagui S 1    | 1101010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 0000410000 | 001111 |
| B. gasipaes var. chichagui S 2    | 1101010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 0000410000 | 001111 |
| B. gasipaes var. gasipaes 1       | 1101010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3000410000 | 00111- |
| B. gasipaes var. gasipaes 2       | 1101010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3000410100 | 00111- |
| B. gasipaes var. gasipaes 3       | 1101010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3010410000 | 00111- |
| B. gasipaes var. gasipaes 4       | 1101010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3010410100 | 00111- |
| B. gasipaes var. gasipaes 5       | 1121010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3000410000 | 00111- |
| B. gasipaes var. gasipaes 6       | 1121010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3000410100 | 00111- |
| B. gasipaes var. gasipaes 7       | 1121010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3010410000 | 00111- |
| B. gasipaes var. gasipaes 8       | 1121010001 | 0000001000 | 1001101110 | 0000100110 | 111000-111 | 3010410100 | 00111- |
| B. gasipaes var. gasipaes 9       | 1101010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3000410000 | 00111- |
| B. gasipaes var. gasipaes 10      | 1101010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3000410100 | 00111- |
| B. gasipaes var. gasipaes 11      | 1101010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3010410000 | 00111- |
| B. gasipaes var. gasipaes 12      | 1101010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3010410100 | 00111- |
| B. gasipaes var. gasipaes 13      | 1121010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3000410000 | 00111- |
| B. gasipaes var. gasipaes 14      | 1121010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3000410100 | 00111- |
| B. gasipaes var. gasipaes 15      | 1121010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3010410000 | 00111- |

Table 6. continued

|                               |            |            |            |            |            |            |        |
|-------------------------------|------------|------------|------------|------------|------------|------------|--------|
| B. gasipaes var. gasipaes 16  | 1121010001 | 0000001000 | 1001101111 | 0000100110 | 111000-111 | 3010410100 | 00111- |
| B. glandulosa var. glandulosa | 11-1010001 | 1000001000 | 1001000111 | 0010200100 | 111000-111 | 1000011201 | 101111 |
| B. glaucescens                | 1121000000 | 0100010010 | 1000111111 | 0000100010 | 101000-111 | 1020111201 | 101100 |
| B. gracilior                  | 11-1010001 | 1000001000 | 1001000111 | 0000100000 | 101000-111 | 1000011001 | 001111 |
| B. guineensis                 | 1121010001 | 1000000000 | 1000100111 | 0000100010 | 101000-111 | 1020111201 | 101100 |
| B. hirta var. spruceana 1     | 1121010000 | 0000000000 | 1001000111 | 0000000110 | 111000-111 | 0001011001 | 001111 |
| B. hirta var. spruceana 2     | 1121010000 | 0000000000 | 1001000111 | 0000000110 | 111000-111 | 1001011001 | 001111 |
| B. horridispatha              | 1121010001 | 1000000000 | 1001000111 | 0000100100 | 101000-111 | 2021111000 | 001110 |
| B. jamaicana 1                | 1101010001 | 1000000000 | 1000000111 | 0000100101 | 111000-111 | 1000011201 | 101111 |
| B. jamaicana 2                | 1121010001 | 1000000000 | 1000000111 | 0000100101 | 111000-111 | 1000011201 | 101111 |
| B. killipii 1                 | 11-0--0001 | 1000001000 | 0001000100 | 0000000000 | 001000-111 | 0000011001 | 111111 |
| B. killipii 2                 | 11-0--0001 | 1000001000 | 0001000100 | 0000000000 | 001000-111 | 2000011001 | 111111 |
| B. killipii 3                 | 11-0--0001 | 1000001000 | 0001000100 | 0000000000 | 101000-111 | 8888811881 | 111111 |
| B. killipii 4                 | 11-0--0001 | 1000001000 | 0001000100 | 0000000000 | 101000-111 | 2000011001 | 111111 |
| B. major var. socialis        | 1121011010 | 0000001000 | 1000001111 | 0000100110 | 001000-111 | 2121111001 | 001110 |
| B. maraja var. trichospatha   | 1121010010 | 0000001000 | 1101000111 | 0000100000 | 101000-111 | 1021111201 | 101100 |
| B. mexicana var. mexicana     | 1121010001 | 1000000000 | 1001100111 | 0000100110 | 111000-111 | 1000011201 | 001111 |
| B. plumeriana 1               | 1101010000 | 0000000000 | 1000001111 | 0000100110 | 111000-111 | 1000011001 | 001111 |
| B. plumeriana 2               | 1121010000 | 0000000000 | 1000001111 | 0000100110 | 111000-111 | 1000011001 | 001111 |
| B. ptariana 1                 | 1111010001 | 1000000000 | 1001000111 | 0000100010 | 111000-111 | 1010011201 | 001111 |
| B. ptariana 2                 | 1111010001 | 1000000000 | 1001000111 | 0000100010 | 111000-111 | 1011011201 | 001111 |
| B. riparia                    | 1121010000 | 0000001000 | 1001001111 | 0000100110 | 111000-111 | 1000011201 | 001111 |
| B. setosa                     | 1121010001 | 0000001000 | 1000101111 | 0000100011 | 111000-111 | 1020111201 | 101100 |
| B. setulosa 1                 | 1111010001 | 0000001000 | 1001000111 | 0000100000 | 111000-111 | 1000011201 | 001101 |
| B. setulosa 2                 | 1111010001 | 0000001000 | 1001000111 | 0000100100 | 111000-111 | 1000011201 | 001101 |
| B. simplicifrons              | 1120--0001 | 1000001000 | 0000000110 | 0000000000 | 001000-111 | 0000011000 | 111111 |
| B. sphaerocarpa               | 1121010010 | 0000001000 | 1000000111 | 0000000110 | 001000-111 | 1020111001 | 001100 |
| B. tomentosa                  | 1121010010 | 0000001000 | 1100000111 | 0000000010 | 001000-111 | 1021111201 | 101100 |
| Desmoncus macroacanthos 1     | 0121000001 | 1000001000 | 1000000101 | 0100000001 | 000000-101 | 1000011001 | 001111 |
| D. macroacanthos 2            | 0121000001 | 1000001000 | 1000000101 | 0100000001 | 000000-101 | 2000011001 | 001111 |
| D. orthacanthos 1             | 0121000000 | 1000001000 | 1001000101 | 0100000001 | 100000-101 | 1000011001 | 0010-- |
| D. orthacanthos 2             | 0121000000 | 1000001000 | 1001000101 | 0100000001 | 100000-101 | 1010011001 | 0010-- |
| D. orthacanthos 3             | 0121000000 | 1000001000 | 1001000101 | 0100000011 | 100000-101 | 1000011001 | 0010-- |
| D. orthacanthos 4             | 0121000000 | 1000001000 | 1001000101 | 0100000011 | 100000-101 | 1010011001 | 0010-- |
| D. polyacanthos 1             | 0121000001 | 1000001000 | 1000000101 | 0100000001 | 000000-101 | 1000010001 | 0010-- |
| D. polyacanthos 2             | 0121000001 | 1000001000 | 1000000101 | 0100000001 | 000000-101 | 2000010001 | 0010-- |
| D. polyacanthos 3             | 0121000001 | 1000001000 | 1000000101 | 0100000011 | 000000-101 | 1000010001 | 0010-- |
| D. polyacanthos 4             | 0121000001 | 1000001000 | 1000000101 | 0100000011 | 000000-101 | 2000010001 | 0010-- |
| Gastrococos crispa 1          | 1121000000 | 0000110101 | 1110001?00 | 0000411011 | 0001011101 | 011000-101 | 001100 |
| G. crispa 2                   | 1121000000 | 0000110101 | 1110001?01 | 0000411011 | 0001011101 | 011000-101 | 001100 |

The cladistic analysis was performed with an IBM-compatible computer using the version 0.9.99 (Beta) of Winclada (Nixon, 1999). Winclada was used to build the data matrix; calculate the consensus tree, view, manipulate and print the trees; map, trace and examine character statistics in the tree. The data matrix was submitted to Nona (Goloboff, 1993), which also calculated tree length, consistency index (CI), and retention index (RI; Farris, 1989). All multistate characters were treated as nonadditive (unordered). Uninformative characters were excluded from the analysis and the remaining characters assigned equal weight. The following Winclada settings were used: heuristic search, HOLD=1,000 (HOLD=5,000 for data matrix 2), replications=100 (Mult\*N), starting trees per replication=10 (HOLD/). The search strategy selected was multiple TBR+TBR (Mult\*Max\*). Due to hardware limitation (computer memory overflow), the HOLD command was set to 5000 in the following analysis: a) anatomical data set using data matrix 1 and 2, b) morphological data set using data matrix 2, and c) combined data set using data matrix 2.

## VII. Results

## 1. Anatomical descriptions

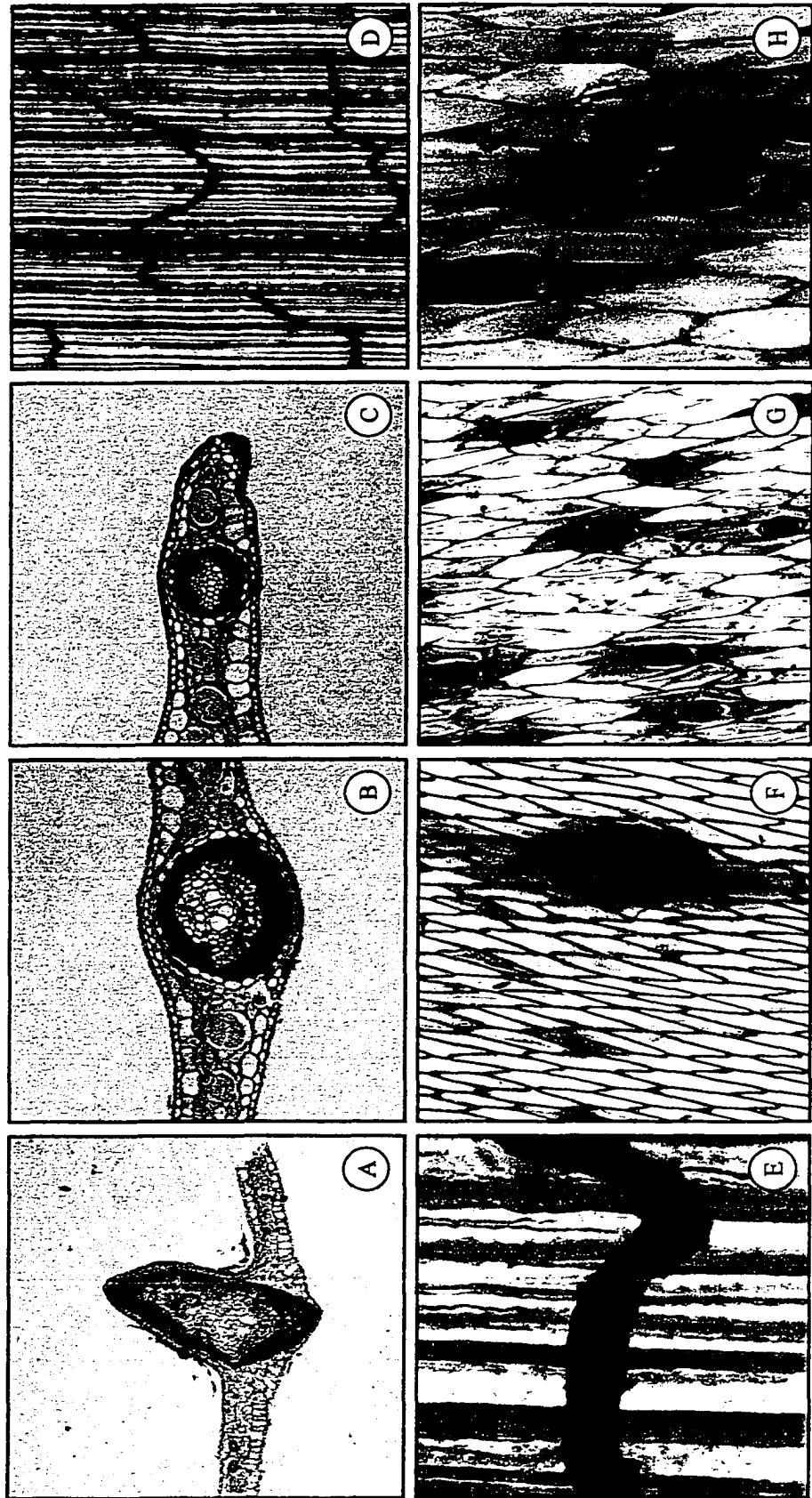
### 1.1. Bactris

#### 1.1.1. Bactris acanthocarpa var. exscapa (Fig. 1)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer conspicuous but shortly interrupted adaxially, with few small non-vascular fiber bundles; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally near the lamina; inner ground parenchyma with 2 large vascular bundles and several smaller phloem strands irregularly embedded in the innermost fibrous layers. **Expansion cells:** forming conspicuous, 1-2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina conspicuous ad- and abaxially. **Hairs:** on abaxial surface; hair base slightly sunken, uniseriate, cutinized, flask-shaped. **Epidermis:** ad- and abaxial cell walls not sinuous, outer wall thickened. **Adaxial epidermis:** intercostal cells, rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying, organized or not into distinct longitudinal files of cells; costal cells rectangular, longitudinally extended, large costal regions slightly

Figure 1. Leaf anatomy of Bactris acanthocarpa var. exscapa. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B13, x40), B. midsection (B13, x100), C. section tip (B13, x100), D. venation pattern (LC14, x25), E. transverse commissure (LC14, x200), F. adaxial surface (EP15, x200), G. abaxial surface (EP15, x200), H. stomata (EP15, x400).





raised, with 6-10 distinct longitudinal files of cells.

**Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral to almost spindle-shaped, less obliquely extended, not organized into distinct longitudinal files; costal cells narrower than intercostal cells, rectangular, longitudinally extended, the larger bands slightly raised, with up to 11 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, smaller but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** large. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells slightly transversely extended, shape rather variable, roundish to almost square-shaped. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll 4-5 layers of thick-walled cells. **Tannin cells:** numerous but the tanniniferous material not completely filling the cells, consisting of brown cellular deposits not saturating the mesophyll. **Fiber-sclereids:** absent.

**Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical and non-cylindrical strands of variable size and shape; large strands cylindrical and regularly distributed as a distinct layer level with small veins, smaller strands variously shaped and irregularly distributed in the mesophyll, attached mostly to the ad- and abaxial hypodermis. **Primary veins:** widely ovoid to obtrullate, prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, thick-walled and strongly lignified, well-developed ad- and abaxially, narrowed laterally, 1-3-layered near the lamina. **Secondary veins:** roundish, centered; outer sheath incomplete, only lateral; inner sheath complete, up to 3 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial, with a single layer of elongate mesophyll cells radiating from the outer parenchymatous cells, resembling Kranz anatomy typical of C4 plants; outer sheath complete; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins irregularly divided into several small strands by files of thin-walled fibers. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B13, LC13, EP13- BRAZIL.

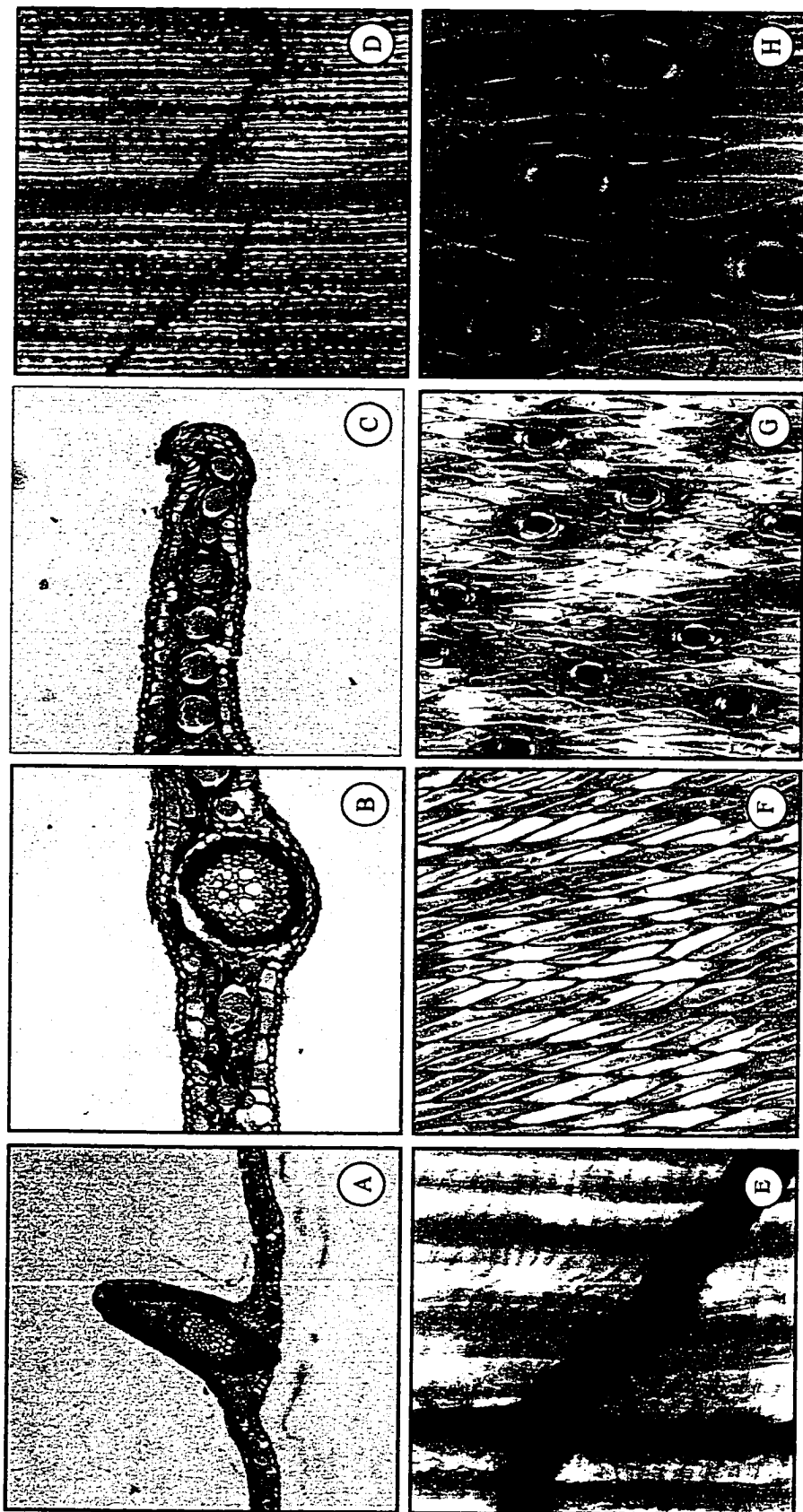
Rondônia: Mun. Guajará-Mirim, ca. 32 km SE of Guajará-Mirim, ca. 10°57'S, 65°4'W, 175 m, 12 Apr 1987, Nee 34801 (NY); B14, LC14, EP14- BRAZIL. ACRE: Mun. Brasiléia. Seringal Porongaba, 25 km N of km 4 on Brasiléia-Assis Brasil road, 23 May-2 Jun 1991, Scariot & Ferreira 561 (NY); B15, LC15, EP15- BRAZIL. AMAZONAS: Mun. Humaitá, BR 230, km 140, ca. 7°58'S, 62°2'W, 16 Apr 1985, Henderson et al. 251 (NY).

1.1.2. Bactris acanthocarpoides (Fig. 2)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete, conspicuous, shortly interrupted or not adaxially; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 1-2 large abaxial vascular bundles, several smaller bundles and few phloem strands irregularly embedded in the adaxial region of the fibrous layer.

**Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to midrib; few bands elsewhere ad- or adaxially in the lamina. **Hairs:** on ad- and abaxial surface; hair base sunken, uniseriate, cutinized,

Figure 2. Leaf anatomy of Bactris acanthocarpoides. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B20, x40), B. midsection (B21, x100), C. section tip (B21, x100), D. venation pattern (LC21, x20), E. transverse commissure (LC21, x200), F. adaxial surface (EP21, x200), G. abaxial surface (EP21, x200), H. stomata (EP21, x400).



ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer wall. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, organized into distinct longitudinal files of cells; costal cells rhombohedral to almost square-shaped but shorter and less obliquely extended than intercostal cells, large costal regions with 6-8 poorly distinguished longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells like those of the adaxial epidermis but less obliquely extended and not in distinct longitudinal files; costal cells narrower than intercostal cells, rhombohedral to rectangular, longitudinally extended, the larger bands raised, with up to 20 distinct longitudinal files of cells. **Stomata:** superficial, rare on adaxial costa, numerous, not in distinct longitudinal files and rather diffuse on abaxial intercostal bands; terminal subsidiary cells irregularly overarching the guard-cells, shorter and usually staining more than surrounding epidermal cells; guard-cells leveled with the epidermal surface, somewhat elongate, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above

and below the large veins; ad- and abaxial cells either slightly transversely extended and rectangular, or strongly transversely extended, becoming almost spindle-shaped.

**Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-5 layers of densely arranged, thick-walled cells. **Tannin cells:** numerous, densely arranged, the tanniniferous material not completely filling the cells, consisting of brown cellular deposits, not saturating the mesophyll. **Fiber-sclereids:** absent.

**Raphide-sacs:** absent. **Non-vascular fibers:** forming strands of variable size and shape; large strands cylindrical and organized in a distinct layer level with small veins; smaller strands roundish or diamond-shaped, irregularly distributed in the mesophyll near the ad- and abaxial hypodermis. **Primary veins:** widely ovoid, prominent abaxially; outer sheath incomplete, only a few cells laterally; inner sheath complete, consisting of 2-5 layers of thick-walled fibers; the abaxial fibrous area touching the hypodermis. **Secondary veins:** roundish, abaxial; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Quaternary veins:** absent. **Marginal**



**rib:** absent. **Phloem:** of large veins irregularly divided into several strands by rows of fibers or sclerotic partitions. **Transverse commissures:** wide, mostly elongate but a few short, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B19, LC19, EP19- SURINAME. Stoelmanseiland, 27 Oct 1962, Wessels Boer 198 (NY); B20, LC20, EP20- SURINAME. Road to Phedra, 16 Nov 1962, Wessels Boer 282 (NY); B21, LC21, EP21- SURINAME. Mapanie, 7 Jan 1963, Wessels Boer 467 (NY).

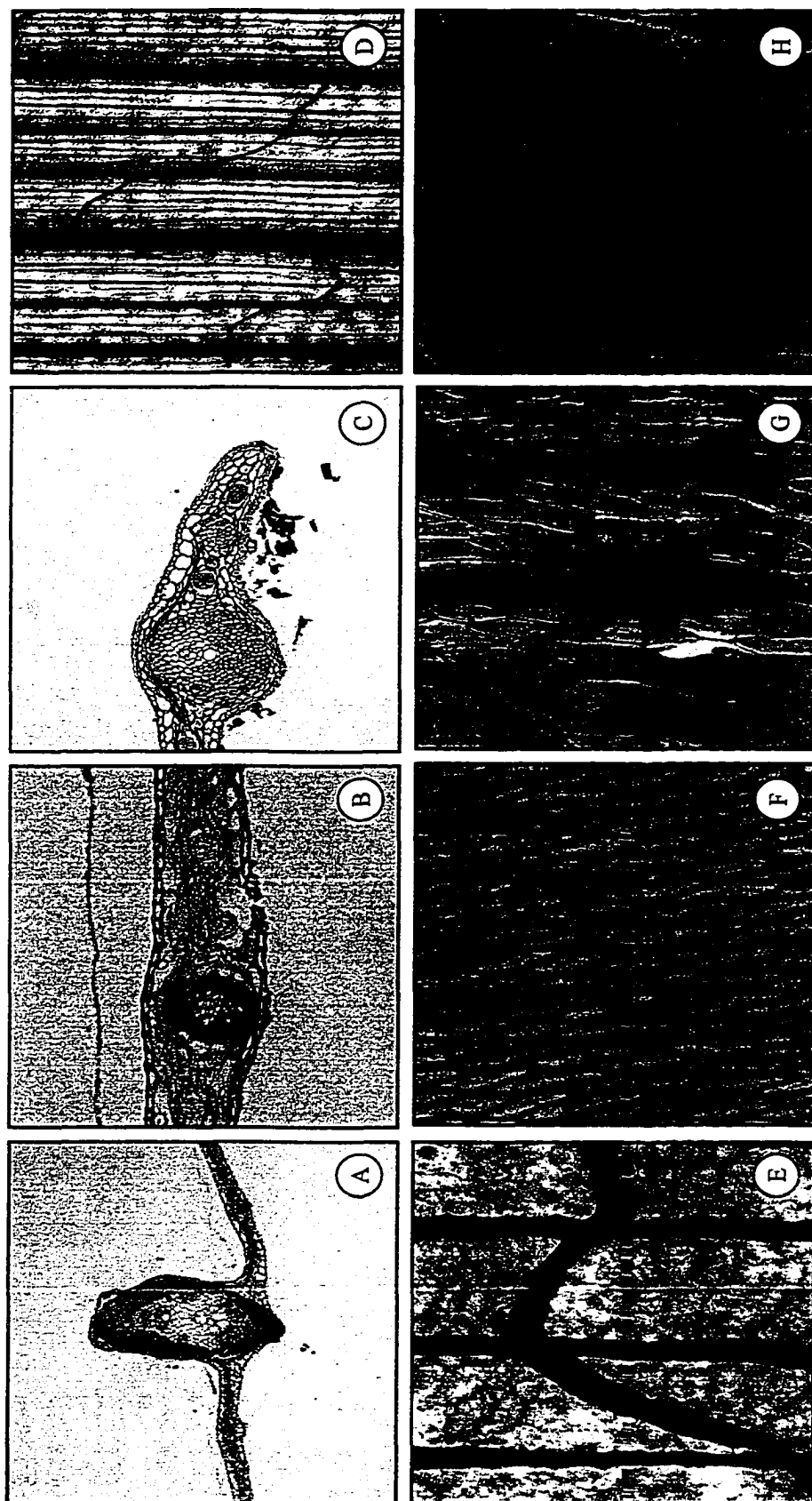
### 1.1.3. Bactris balanophora (Fig. 3)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete or incomplete, somewhat irregular, conspicuous; inner fibrous layer well-delimited, thick-walled and well-developed ad- and abaxially, narrowed laterally, 2-layered near the lamina; inner ground parenchyma with 3 large vascular bundles and few smaller lateral bundles. **Expansion cells:** forming conspicuous, 1-2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina not prominent. **Hairs:** on ad- and abaxial surface, mostly near the costa; hair base superficial,

Figure 3. Leaf anatomy of Bactris balanophora. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B67, x40), B. midsection (B69, x200), C. section tip (B68, x100), D. venation pattern (LC68, x25), E. transverse commissure (LC68, x200), F. adaxial surface (EP69, X200), G. abaxial surface (EP68, x200), H. stomata (EP68, X400).

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uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, not thickened. **Adaxial epidermis:** intercostal cells spindle-shaped, rhombohedral only near the costa, longitudinally extended, not in distinct files; costal cells smaller than intercostal cells, rhombohedral to rectangular, longitudinally extended, large costal regions with up to 12 distinct longitudinal files of cells. **Abaxial epidermis:** with cells slightly smaller, costal and intercostal bands conspicuously differentiated; intercostal cells wider than adaxial cells, mostly spindle-shaped but shape variable, not organized into distinct longitudinal files; costal cells smaller than intercostal cells, rectangular, rarely rhombohedral, longitudinally extended, the larger bands distinctly raised, with up to 31 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells not overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells almost level with epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** large. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and interrupted

below the large veins; ad- and abaxial cells slightly transversely extended, irregularly hexagonal.

**Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-5 layers of thick-walled cells.

**Tannin cells:** numerous, the brownish tanniniferous material not completely filling the cells and not saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** absent.

**Non-vascular fibers:** forming strands of variable size and shape; larger strands cylindrical and mostly centered, forming a poorly distinguished layer level with the small veins, smaller strands irregularly shaped and frequently attached to the adaxial hypodermis. **Primary veins:** obtrullate, prominent abaxially, the fibrous area touching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, well-developed, several layers of thick-walled fibers abaxially and laterally, 1-3 layers abaxially. **Secondary veins:** ovoid, slightly prominent ad- and abaxially, centered; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers.

**Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

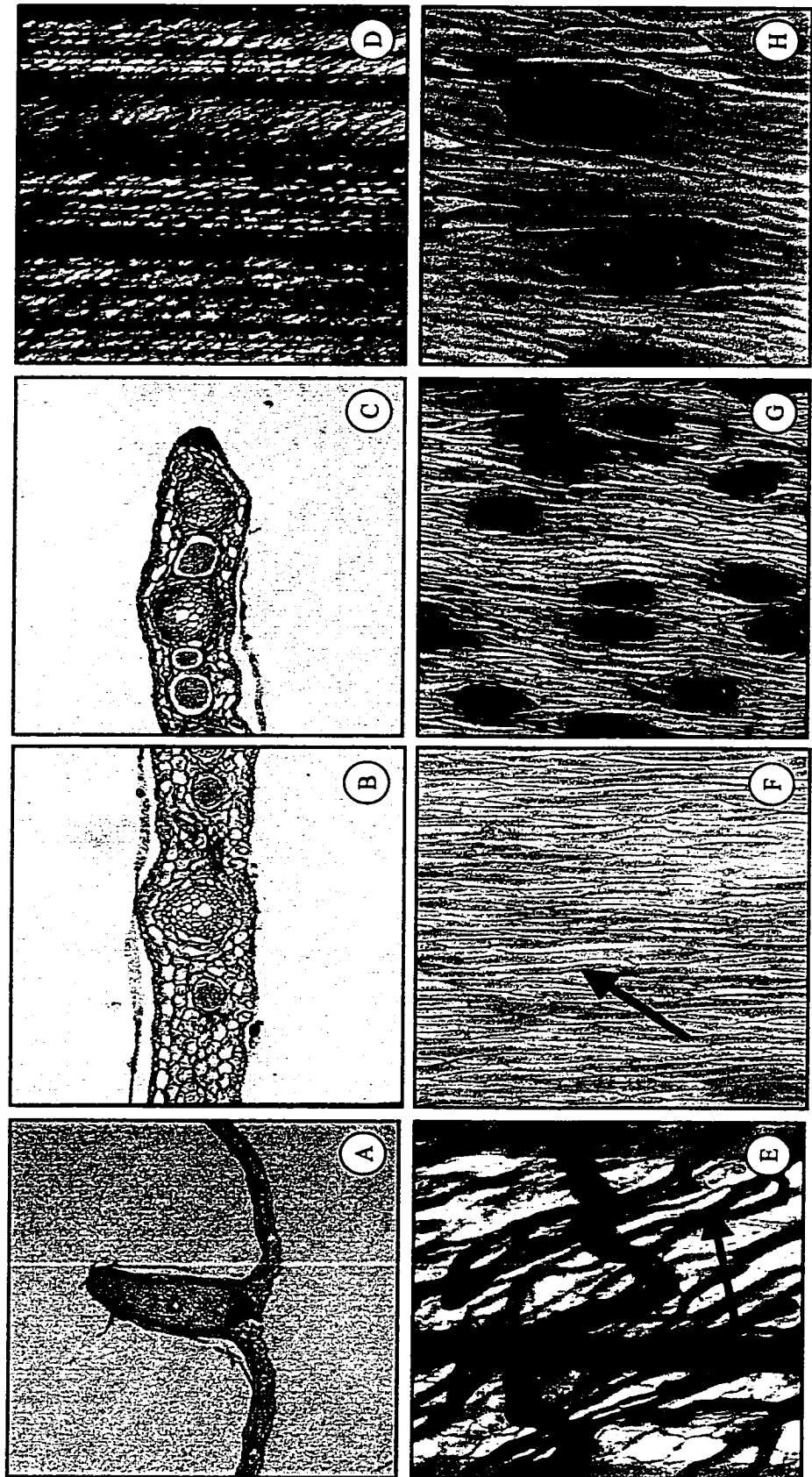
**Specimens examined.** B67, LC67, EP67- VENEZUELA.

AMAZONAS: 4 km E of San Carlos de Río Negro, 1°56'N, 67°10'W, 120 m, 21 Jan 1968, Wessels Boer 2310 (NY); B68, LC68, EP68- VENEZUELA. AMAZONAS: Dpto. Atures, Río Autana, 4°48'N, 67°27'W, 90-110 m, 5 Nov 1984, Guánchez 3223 (NY); B69, LC69, EP69- VENEZUELA. AMAZONAS: 4 km E of San Carlos de Río Negro, 1°56'N, 67°10'W, 120 m, 25 Nov 1977, Liesner 3834 (NY).

#### 1.1.4. Bactris bifida (Fig. 4)

**Midrib:** absent. **Main ribs:** midrib-like, prominent adaxial, abaxially pointed to rounded; peripheral chlorenchymatous layer complete and inconspicuous, with few fiber bundles; inner fibrous layer poorly delimited, well-developed and thick-walled ad- and abaxially, narrowed laterally, 1-2-layered near the lamina; inner ground parenchyma with 2-3 large vascular bundles and few phloem strands embedded in the innermost abaxial layers. **Expansion cells:** forming conspicuous, 1-2-layered confluent bands adjacent to main ribs; bands elsewhere in the lamina also conspicuous, ad-

Figure 4. Leaf anatomy of Bactris bifida. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B35, x40), B. midsection (B35, x100), C. section tip (B35, x100), D. venation pattern (LC34, x25), E. transverse commissure, note the diagonally arranged fiber sclereids (LC36, x200), F. adaxial surface, note the spindle-shaped and longitudinally extended intercostal cells (EP36, X200), G. abaxial surface (EP36, X200), H. stomata (EP36, x400).





or abaxially, frequent in folding areas. **Hairs:** on ad- and abaxial surface; hair base superficial, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer wall. **Adaxial epidermis:** intercostal cells spindle-shaped, longitudinally extended; costal regions unusually wide, the cells shorter and wider than intercostal cells, rhombohedral to rectangular, longitudinally extended, large costal regions with more than 25 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands not conspicuously differentiated, but the costal bands wider; intercostal cells like those of the adaxial epidermis; costal cells shorter and more irregularly shaped than adaxial cells, mostly rhombohedral, the larger bands not raised and with few distinct longitudinal files of cells. **Stomata:** superficial, frequent adaxially along costal regions, abaxially on intercostal and costal bands, not in distinct longitudinal files, diffuse; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered

beneath each surface, both layers absent above and below the main ribs, compressed above and below the secondary veins; ad- and abaxial cells oblate to irregularly oblong.

**Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-5 layers of tightly arranged, thick-walled cells. **Tannin cells:** absent or present; if present, the tanniniferous material completely fills the cells, saturating the mesophyll. **Fiber-sclereids:** numerous, forming a secondary, transversely extended, fibrous network in surface view. **Raphide-sacs:** absent. **Non-vascular fibers:** forming large cylindrical strands distributed in a single, centered, layer level with small veins. **Primary veins:** roundish, slightly prominent ad- and abaxially, centered; outer sheath incomplete, lateral only; inner sheath complete, 1-2 layers of thick-walled fibers abaxially and laterally, only a few thin-walled fibers adaxially. **Secondary veins:** similar to secondary veins, but smaller; roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Tertiary veins:** roundish, centered; outer sheath complete; inner sheath formed by a single layer of thin-walled fibers. **Quaternary veins:** absent.

**Marginal rib:** prominent ad- and abaxially; outer sheath incomplete, lateral only; inner fibrous sheath well-

developed, thin-walled. **Phloem:** of large veins divided into distinct strands by sclerotic partitions. **Transverse commissures:** wide, short, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

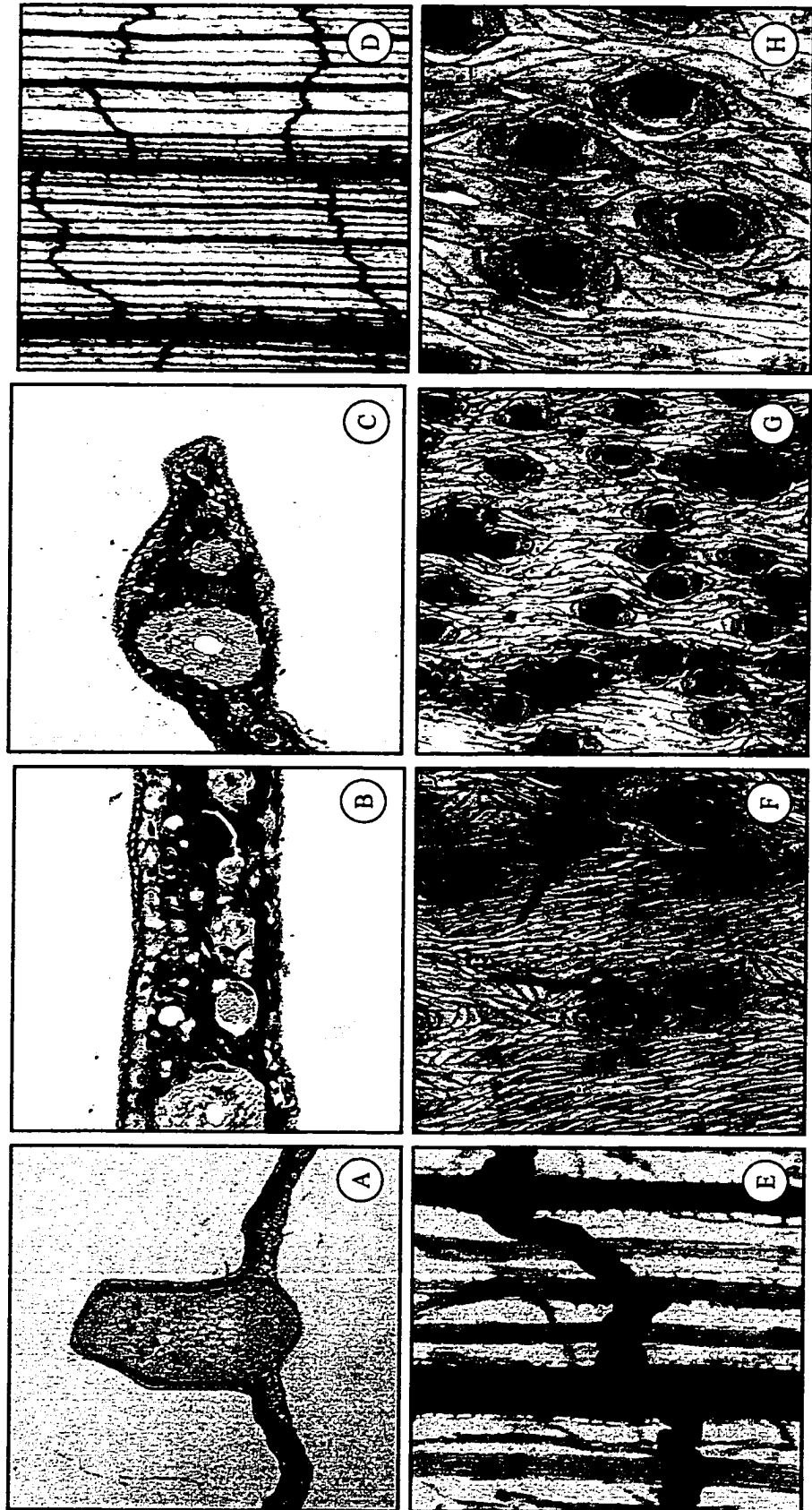
**Specimens examined.** B34, LC34, EP34- BRAZIL.

AMAZONAS: Mun. Tefé, right bank of Rio Solimões, Missão Tefé, 4 km from river, 13 Jan 1991, Henderson et al. 1548 (NY); B35, LC35, EP35- BRAZIL. AMAZONAS: Mun. Atalaia do Norte, Rio Javari, São Joaquim, just before confluence of Rio Javari-Mirim, 4°30'S, 71°45'W, 10 Jan 1989, Henderson et al. 867 (NY); B36, LC36, EP36- BRAZIL. AMAZONAS: Mun. Tefé, right bank of Rio Solimões, Missão Tefé, 4 km from river, 13 Jan 1991, Henderson et al. 1546 (NY).

#### 1.1.5. Bactris brongniartii (Fig. 5)

**Midrib:** abaxially rounded, adaxially prominent; peripheral chlorenchymatous layer conspicuous, complete and saturated with tanniniferous cells; inner fibrous layer well-delimited, thick-walled and well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 2-3 large and several smaller vascular bundles, few small phloem strands embedded in the

Figure 5. Leaf anatomy of Bactris brongniartii. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B52, x40), B. midsection (B54, x200), C. section tip (B54, x100), D. venation pattern (LC53, x25), E. transverse commissure (LC53, x200), F. adaxial surface, note several stomata adjacent to the costa (EP53, x200), G. abaxial surface (EP53, x200), H. stomata (EP53, x400).



fibrous layer. **Expansion cells:** forming conspicuous, 1-2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** on ad- and abaxial surface; hair base not seen in cross-section but distally the hair elongate, uniseriate, cutinized. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells mostly rhombohedral, but cell-shape variable, obliquely-longitudinally extended, but angle of obliquity varying, longitudinal files of cells fairly distinguished; costal cells shorter and less obliquely extended than intercostal cells, rhombohedral, large costal regions with 5-6 distinct longitudinal files of cells, but cell files usually poorly distinguished on most large costa. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells irregularly shaped, but mostly equilateral, longitudinally extended, not in distinct longitudinal files; costal cells narrower than intercostal cells, mostly rhombohedral but some irregularly shaped, longitudinally extended, the large bands slightly raised, with up to 12 distinct longitudinal files of cells. **Stomata:** superficial, unusually common along the costal and adjacent intercostal region on adaxial surface; abaxially numerous, rather diffuse on intercostal

bands, not in distinct longitudinal files; terminal subsidiary cells slightly overarchng the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells almost at the same level of epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells slightly transversely extended; the adaxial cells more or less rectangular, the abaxial more irregularly shaped.

**Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-5 layers of thick-walled cells.

**Tannin cells:** numerous, the red tanniniferous material completely filling the cells and saturating the mesophyll.

**Fiber-sclereids:** numerous, forming a secondary, transversely extended, fibrous network in surface view.

**Raphide-sacs:** rare, centered. **Non-vascular fibers:** forming cylindrical strands distributed in a single abaxial layer level with small veins. **Primary veins:** ovoid to pear-shaped, slightly prominent ad- and abaxially; outer sheath incomplete, lateral only; inner sheath complete, many thick-walled fibers ad- and abaxially, laterally only 2-3 layers. **Secondary veins:** ovoid, abaxial; outer sheath

incomplete, only lateral; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath incomplete, thin-walled fibers adaxially. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B52, LC52, EP52- VENEZUELA.

BOLÍVAR: Mun. Cedeño, Río Caura, 6°35'N, 64°45'W, 20 May 1996, C. Knab-Vispo 567 (NY); B53, LC53, EP53- BRAZIL.

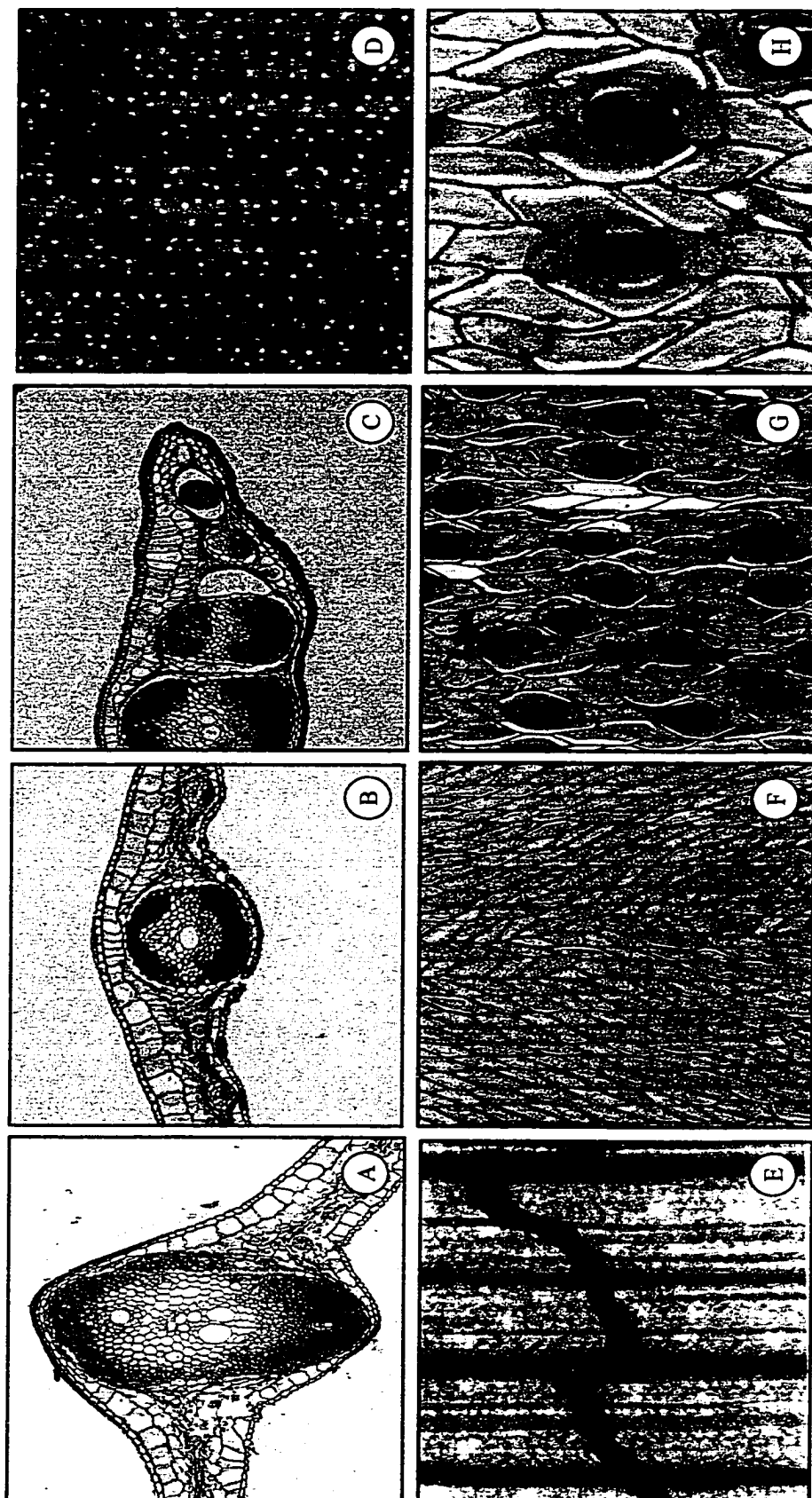
RORAIMA: Mun. Alto Alegre, Ilha de Maracá, 3°24'N, 61°26'W, 15 Jul 1986, Henderson & Lima 606 (NY); B54, LC54, EP54- VENEZUELA. AMAZONAS: Río Mavaca, 2°1'N, 65°7'W, 228 m, 7 Feb 1989, Henderson et al. 995 (NY).

#### 1.1.6. Bactris campestris (Fig. 6)

**Midrib:** abaxially rounded, equally prominent on both surfaces; peripheral chlorenchymatous layer inconspicuous; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 1-layered near the lamina; inner ground parenchyma with 1-2 large



Figure 6. Leaf anatomy of Bactris campestris. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B49, x20), B. midsection (B51, x100), C. section tip (B51, x100), D. venation pattern, the bright spots are stomata (LC49, x25), E. transverse commissure (LC49, x100), F. adaxial surface (EP50, x200), G. abaxial surface (EP50, x200), H. stomata (EP50, x400).



vascular bundles and rather rare small phloem strands attached to the innermost fibrous layers. **Expansion cells:** inconspicuous near midrib and primary veins due to the large size and multiple layers of hypodermal cells; bands elsewhere in the lamina also inconspicuous. **Hairs:** common along abaxial costal bands; hair base not seen. **Cuticle:** persistent on margin of leaf. **Epidermis:** the adaxial layer more regular in size and shape; ad- and abaxial cell walls not sinuous, outer wall more thickened on adaxial cells. **Adaxial epidermis:** intercostal cells rhombohedral to hexagonal, size variable, obliquely-longitudinally extended or mostly longitudinally extended; costal cells smaller than intercostal cells, rhombohedral to hexagonal, but shape variable, mostly longitudinally extended, the larger bands slightly raised, with 7 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells like those of the adaxial epidermis but smaller and not in distinct files; costal cells rectangular, longitudinally extended, cells narrower than intercostal cells, the larger bands slightly raised, with up to 8 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct longitudinal files, dense; terminal

subsidiary cells overarching the guard-cells, shorter, wider, with prominent lobes on each extremity, well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-2-layered beneath the adaxial surface, single-layered abaxially; the first adaxial layer wider than second layer, more uniform and continuous above the large veins; the second adaxial layer narrow, interrupted or not by non-vascular fiber bundles; the abaxial layer compressed below the large veins; in some regions of the lamina the hypodermal layers comprising 2/3 of the lamina; ad- and abaxial cells rectangular or square-shaped. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-5 layers of thick-walled cells. **Tannin cells:** numerous, densely arranged, the red tanniniferous material completely filling the cells and saturating the mesophyll, or filling partially the cells, appearing as brownish deposits, not saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** common, ad- or abaxial. **Non-vascular fibers:** forming cylindrical strands of variable size; the larger strands level with the veins; smaller strands irregularly distributed, many attached to

the first adaxial hypodermal layer. **Primary veins:** ovoid to almost roundish, slightly prominent ad- and abaxially, the adaxial fibrous area going through the second adaxial hypodermis layer; outer sheath incomplete, lateral only; inner sheath complete, consisting of 2-3 layers of thick-walled fibers. **Secondary veins:** roundish, centered; outer sheath incomplete abaxially; inner sheath complete, consisting of 1-2 layers of thick-walled fibers. **Tertiary veins:** roundish, centered; outer sheath complete; inner sheath incomplete, 1 layer of thick-walled fibers abaxially and thin-walled fibers adaxially. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of thick-walled fibers or thin sclerotic partitions. **Transverse commissures:** wide, mostly elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by 1-several sclerotic parenchymatous layers, the cells of the outermost layer inflated and protruding irregularly toward the mesophyll.

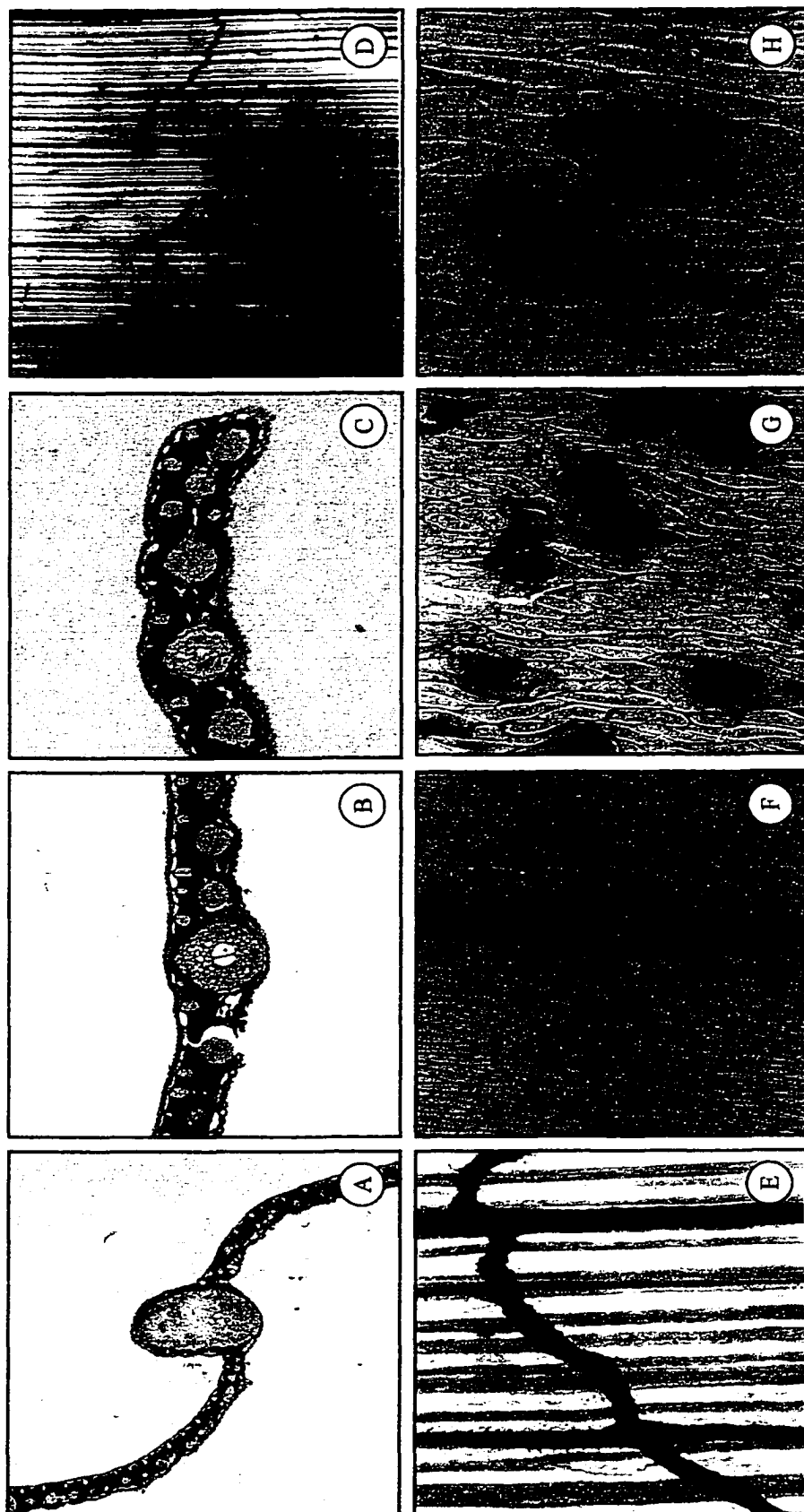
**Specimens examined.** B49, LC49, EP49- FRENCH GUIANA. Sinnamary, 5°22'N, 52°59'W, 31 Dec 1988, Sanders 1815 (NY); B50, LC50, EP50- BRAZIL. AMAPÁ: Mun. Calçoene, BR 156, 12 km W of Calçoene, ca. 2°28'N, 51°W, 8 Dec 1984, Mori & Cardoso 17287 (NY); B51, LC51, EP51- VENEZUELA. AMAZONAS:

Brazo Casiquiare near Solano, ca. 2°N, 67°W, 8 Feb 1968,  
Wessels Boer 2410 (NY).

1.1.7. Bactris caryotifolia (Fig. 7)

**Midrib:** abaxially rounded, adaxially prominent; peripheral chlorenchymatous layer conspicuous, shortly incomplete adaxially, with tannin cells and small roundish non-vascular fiber bundles; inner fibrous layer poorly-delimited, thick-walled and well-developed adaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 1-2 large and 1-2 smaller vascular bundles, few small phloem strands embedded in the innermost fibrous layers. **Expansion cells:** forming conspicuous, 1-2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina conspicuous ad- and abaxially. **Hairs:** not seen on adaxial surface, irregularly distributed abaxially; hair base not seen but distal structure uniseriate, cutinized. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells spindle-shaped, most slightly obliquely-longitudinally extended, not in distinct longitudinal files; costal cells smaller than intercostal cells, rhombohedral, longitudinally extended, large? costal bands

Figure 7. Leaf anatomy of Bactris caryotifolia. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B127, x40), B. midsection (B127, x100), C. section tip (B127, x100), D. venation pattern (LC127, x20), E. transverse commissure (LC127, x200), F. adaxial surface (EP127, x200), G. abaxial surface (EP128, x200), H. stomata (EP128, x400).





with up to 5 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells irregularly spindle-shaped, longitudinally extended, not in distinct longitudinal files, but cells irregularly shaped and extended near stomata; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 8 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter, slightly inflated, well-differentiated from the surrounding epidermal cells; guard-cells slightly below the epidermal surface, smaller than adjacent epidermal cells; each guard-cell with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** large. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells transversely extended, mostly hexagonal. **Chlorenchyma:** a true palisade mesophyll absent, however, areas of the mesophyll with adaxial columnar non-vascular fiber bundles usually show few, poorly distinguished, palisade-like cells; spongy mesophyll well-differentiated, 5-6 layers of thick-walled

cells. **Tannin cells:** numerous, the cells completely filled by reddish or brownish tanniniferous material, completely saturating or not the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical and columnar strands; the cylindrical strands abaxial, arranged in a single layer level with the veins; the columnar strands often attached to the adaxial hypodermis. **Primary veins:** ovoid, slightly prominent ad- and abaxially; the abaxial fibrous area touching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, 2-3 layers of fibers, these often thick-walled abaxially and thin or thick-walled laterally and adaxially. **Secondary veins:** ovoid to roundish, abaxial; outer sheath incomplete, lateral only; inner sheath complete, consisting of 1-2 layers of thin-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath consisting of a single layer of thin-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers. **Transverse commissures:** wide, elongate, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B127, LC127, EP127- BRAZIL.

BAHIA: Mun. Mucuri, ca. 10 km W of Mucuri, 18°5'S, 39°39'W,

1-20 m, 4 Feb 1989, Noblick & Brito 4802 (NY); B128, LC128, EP128- BRAZIL. ESPÍRITO SANTO: Santa Teresa, Valsugana Velha, 24 Nov 1988, Boudet Fernandes et al. 2647 (NY); B132, LC132, EP132- BRAZIL. RIO DE JANEIRO: Mun. Angra dos Reis, Serra do Ariró, 30 Oct 1988, Boudet Fernandes 2618 (BR).

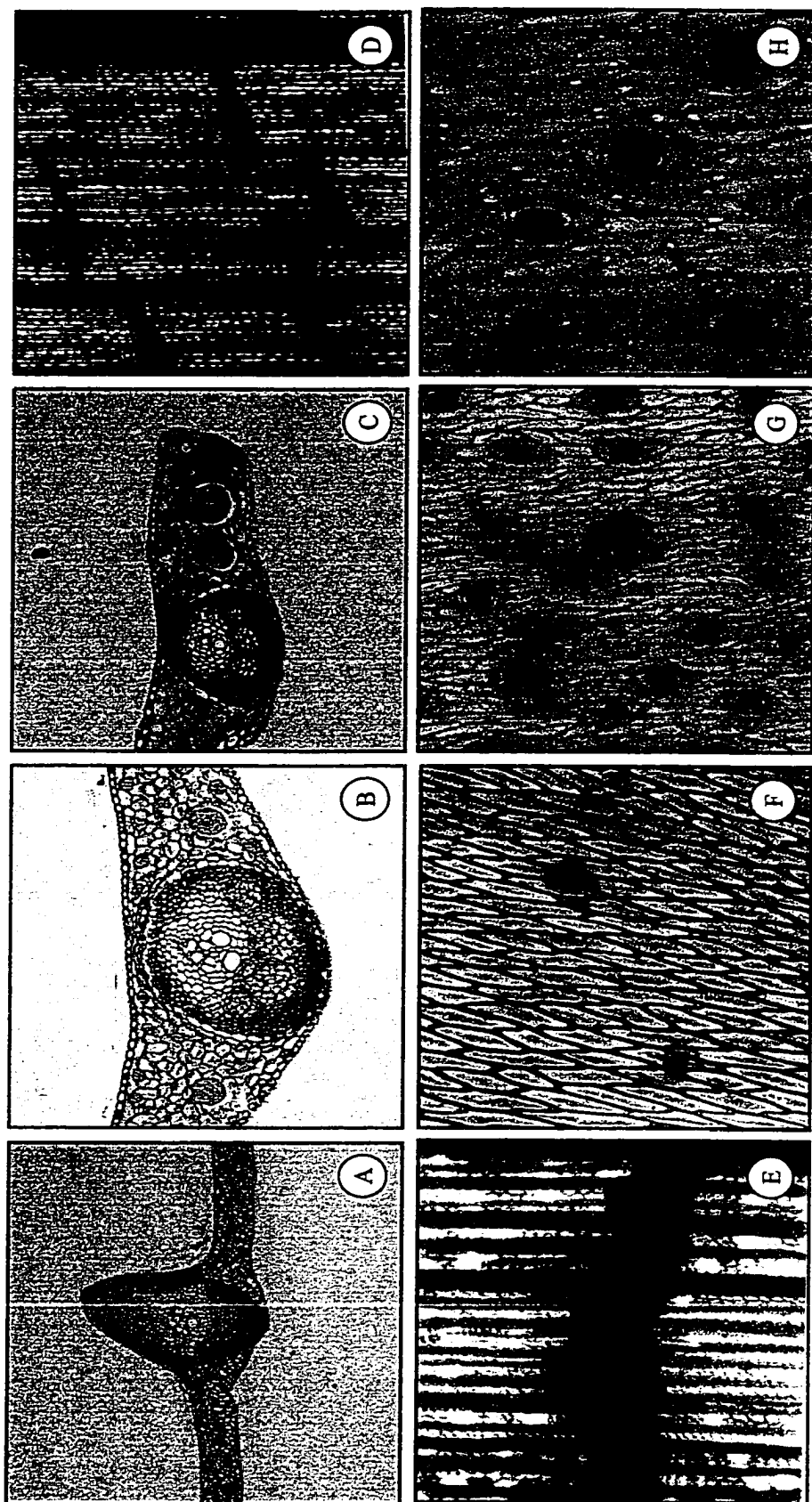
#### 1.1.8. Bactris coloradonis (Fig. 8)

**Midrib:** abaxially pointed to rounded, adaxially prominent; peripheral chlorenchymatous layer conspicuous and complete; inner fibrous layer well-delimited, thick-walled and well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 2-6 large vascular bundles and few small phloem strands irregularly distributed in the innermost fibrous layers.

**Expansion cells:** forming 1-2-layered bands adjacent to midrib; bands elsewhere in the lamina inconspicuous.

**Hairs:** rarely on adaxial surface, common on adaxial costal bands; hair base superficial, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, outer wall thickened; distinct silica bodies at the cell junction on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally

Figure 8. Leaf anatomy of Bactris coloradonis. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B45, x40), B. midsection (B45, x100), C. section tip (B45, x100), D. venation pattern (LC44, x20), E. transverse commissure (LC44, x200), F. adaxial surface (EP45, x200), G. abaxial surface (EP45, x200), H. stomata (EP45, x400).



extended, organized into short longitudinal files of cells; costal cells shorter than intercostal cells, more regularly shaped, rectangular to almost square-shaped, longitudinally extended, large costal regions with 9-11 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral, slightly obliquely extended, not in distinct files; costal cells narrower than intercostal cells, rectangular, longitudinally extended, the larger bands slightly raised, with up to 17 distinct longitudinal files of cells. **Stomata:** superficial, rare near costal region on adaxial surface, dense on abaxial intercostal regions; terminal subsidiary cells not overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small, rarely bigger than a single, surrounding mesophyll cell. **Hypodermis:** 1-layered beneath each surface, both layers compressed below the large veins and interrupted by strands of non-vascular bundles attached to the epidermis; adaxial cells slightly transversely extended, hexagonal; abaxial cells irregularly

roundish to oblate. **Chlorenchyma:** 1-layered palisade mesophyll well-differentiated but discontinuous along the whole lamina; spongy mesophyll well-differentiated, 5 layers of tightly arranged, thick-walled cells. **Tannin cells:** absent. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming strands of variable size and shape; the cylindrical strands larger and irregularly distributed abaxially in the mesophyll; the diamond to almost columnar-shaped strands smaller and usually near or attached to the hypodermis or epidermis. **Primary veins:** pear-shaped, prominent abaxially, the abaxial fibrous area going through the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, several layers of thick-walled fibers in the ad- and abaxial area, laterally only 2-3 layers. **Secondary veins:** ovoid, centered; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2-3 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, consisting of 1-2 layers of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view;

sheathed by 1-several sclerotic parenchymatous layers, the cells of the outermost layer inflated and protruding irregularly toward the mesophyll.

**Specimens examined.** B43, LC43, EP43- COSTA RICA.

LIMÓN: Dist. de Los Angeles de Jiménez, Finca Copasa, 18 Apr 1991, Mattos 2891 (NY)); B44, LC44, EP44- PANAMA.

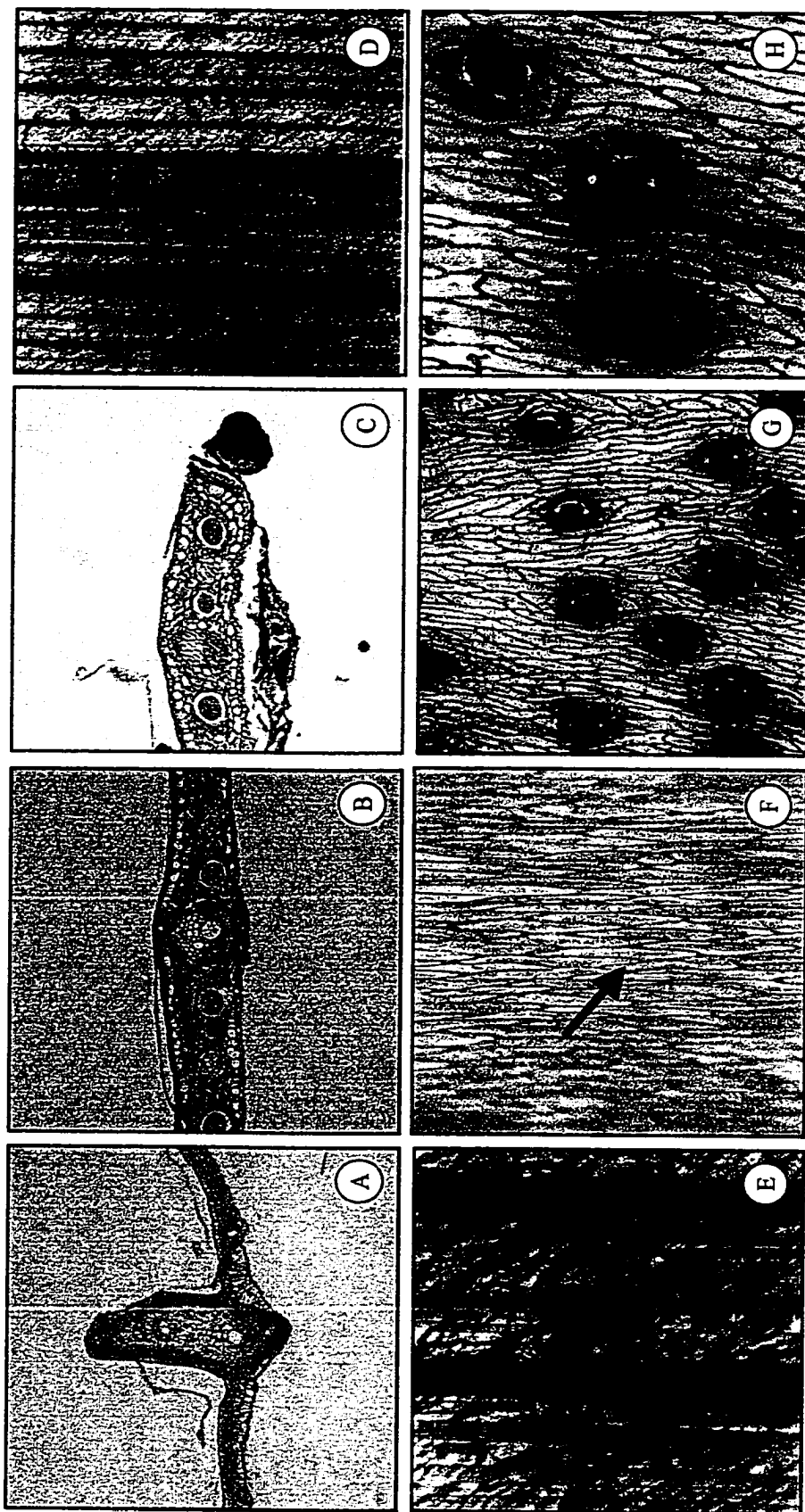
PANAMÁ: Pipeline road, 11 Mar 1983, Gentry & Hamilton 41119 (NY)); B45, LC45, EP45- PANAMA. SAN BLAS: El Llano-Cartí road, km 26.5, along Río Cartí Chico, 9°19'N, 78°55'W, 200 m, 11 Dec 1987, Henderson & Herrera 716 (NY).

#### 1.1.9. Bactris concinna (Fig. 9)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer conspicuous, shortly interrupted adaxially; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 2-layered near the lamina; inner ground parenchyma with 2-3 large and several smaller vascular bundles, but few phloem strands irregularly embedded in the innermost fibrous layers. **Expansion cells:** forming conspicuous, 2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina more conspicuous adaxially. **Hairs:** on ad- and abaxial surface; hair base not seen in



Figure 9. Leaf anatomy of Bactris concinna. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B39, x40), B. midsection (B39, x100), C. section tip (B39, x100), D. venation pattern (LC37, x20), E. transverse commissure (LC37, x100), F. adaxial surface, note the spindle-shaped and longitudinally extended intercostal cells (EP38, x200), G. abaxial surface (EP38, x200), H. stomata (EP38, x400).



cross-section. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer wall. **Adaxial epidermis:** intercostal cells spindle-shaped, longitudinally to slightly obliquely extended; costal cells shorter and slightly wider than intercostal cells, rhombohedral to rectangular, longitudinally extended, large costal regions with up to 20 distinct longitudinal files of cells.

**Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells spindle-shaped or rhombohedral; costal cells narrower than intercostal cells, rhombohedral or spindle-shaped, longitudinally extended, the larger bands not conspicuously raised, longitudinal files of cells poorly distinguished. **Stomata:** superficial, adaxially common near the costal region, abaxially numerous, not in distinct files, diffuse on intercostal and costal bands; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small.

**Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial oblong to roundish, but most cells irregularly shaped.

**Chlorenchyma:** 1-layered palisade mesophyll poorly differentiated; spongy mesophyll well-differentiated, 4-5 layers of tightly arranged, thick-walled cells. **Tannin cells:** numerous, the tanniniferous material partially filling the cells, appearing as brownish deposits, not saturating the mesophyll. **Fiber-sclereids:** numerous, forming a secondary, transversely extended, fibrous network in surface view. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands of variable size; the large and small strands forming a single abaxial layer level with small veins. **Primary veins:** pear-shaped, slightly prominent ad- and abaxially; outer sheath incomplete, lateral only; inner sheath complete, consisting of 2-3 layers of thick-walled fibers. **Secondary veins:** ovoid, centered; outer sheath incomplete abaxially; inner sheath complete, few thick-walled fibers ad- and abaxially, laterally conspicuously pitted parenchyma cells above the phloem. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath single layered, consisting of sclerotic and conspicuously pitted parenchyma cells. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers or thin sclerotic partitions. **Transverse commissures:** wide, short, regularly arranged and forming a

scattered pattern in surface view; sheathed by sclerotic parenchyma.

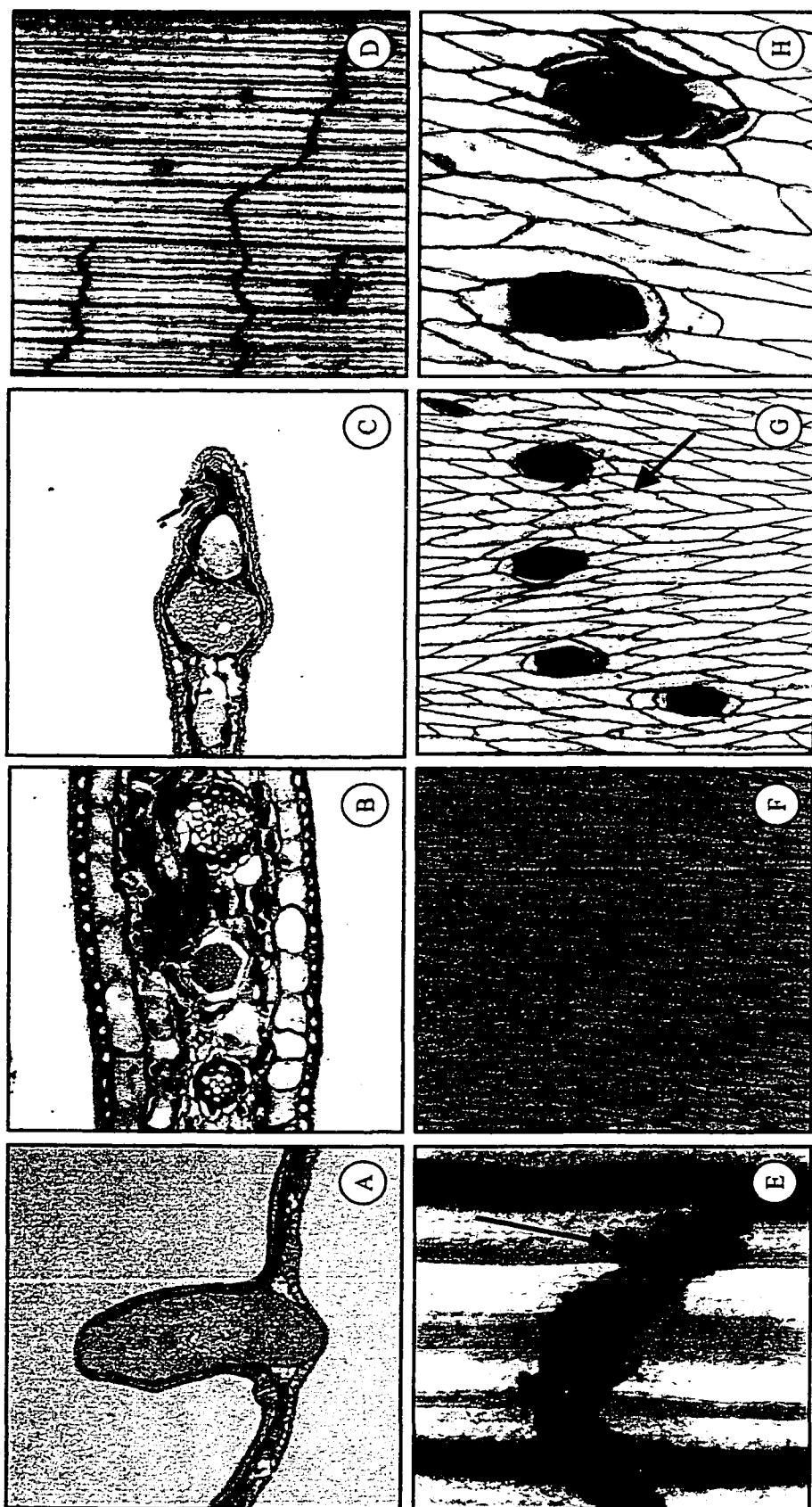
**Specimens examined.** B37, LC37, EP37- BRAZIL.

AMAZONAS: Barro Vermelho, left bank of Rio Juruá, 6°28'S, 68°46'W, 17 Oct 1991, Pardini 12 (NY); B38, LC38, EP38- BRAZIL. AMAZONAS: Mun. Benjamin Constant, Rio Javari, between Benjamin Constant and Atalaia do Norte, 4°20'S, 70°20'W, 3 Jan 1989, Henderson et al. 814 (NY); B39, LC39, EP39- BRAZIL. AMAZONAS: Ilha Amaraca opposite Tabatinga, 23 Jul 1973, Prance et al. 16726 (NY).

1.1.10. Bactris constanciae (Fig. 10)

**Midrib:** abaxially rounded, adaxially prominent; peripheral chlorenchymatous layer conspicuous, interrupted adaxially, with small non-vascular bundles; inner fibrous layer poorly-delimited, well-developed and thick-walled abaxially and laterally, adaxially thin-walled; inner ground parenchyma with 1-2 large vascular bundles and several smaller phloem strands irregularly distributed in the innermost fibrous layers. **Expansion cells:** forming conspicuous, 1-layered ad- and abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous, either ad- or abaxial. **Hairs:** not seen. **Epidermis:** ad- and

Figure 10. Leaf anatomy of Bactris constanciae. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B25, x40), B. midsection (B25, x200), C. section tip (B26, x100), D. venation pattern (LC27, x20), E. transverse commissure, note the inflated sheathing cells protruding towards the mesophyll (LC27, x200), F. adaxial surface, note that ad- and abaxial cell-walls are sinuous (EP25, x200), G. abaxial surface (EP25, x200), H. stomata (EP25, x400).



abaxial cell walls sinuous, the outer wall thicker than the cell lumen is deep. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended; costal cells slightly shorter than intercostal cells, rhombohedral, longitudinally extended, poorly organized into barely distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands not conspicuously differentiated; intercostal cells rhombohedral, less obliquely extended than adaxial cells; costal cells slightly narrower than intercostal cells, rhombohedral, longitudinally extended, the larger bands not raised, with 3 distinct longitudinal files of cells. **Stomata:** superficial, rare on adaxial surface, frequent on abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells slightly overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells slightly below the epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** large. **Hypodermis:** 1-layered beneath each surface, the adaxial layer wider than abaxial layer, continuous and uniform, not compressed above large veins; adaxial cells more transversely extended, somewhat rectangular; abaxial cells less regular,



oblate to oblong. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll 5-6 layers of tightly arranged, thick-walled cells. **Tannin cells:** numerous, densely arranged, the tanniniferous material completely filling or not the cells, appearing as a brown cellular deposit and not saturating the mesophyll or the cells completely filled with reddish tanniniferous material and saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming strands of variable size and shape; large strands cylindrical and organized into a distinct layer level with small veins; smaller strands irregularly shaped and usually attached to the ad- and abaxial hypodermis. **Primary veins:** roundish to ovoid, slightly prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, 2-3-layered, thick-walled fibers abaxially and laterally, thin-walled fibers adaxially. **Secondary and Tertiary veins:** almost indistinguishable, roundish, abaxial; outer sheath incomplete, only lateral; inner sheath incomplete, 1-2-layered, mostly thin-walled. **Quaternary veins:** absent. **Marginal rib:** prominent ad- and abaxially, inner sheath well-developed, thick-walled. **Phloem:** of large veins divided into distinct strands by sclerotic partitions, except in the veins of the margin of the lamina.

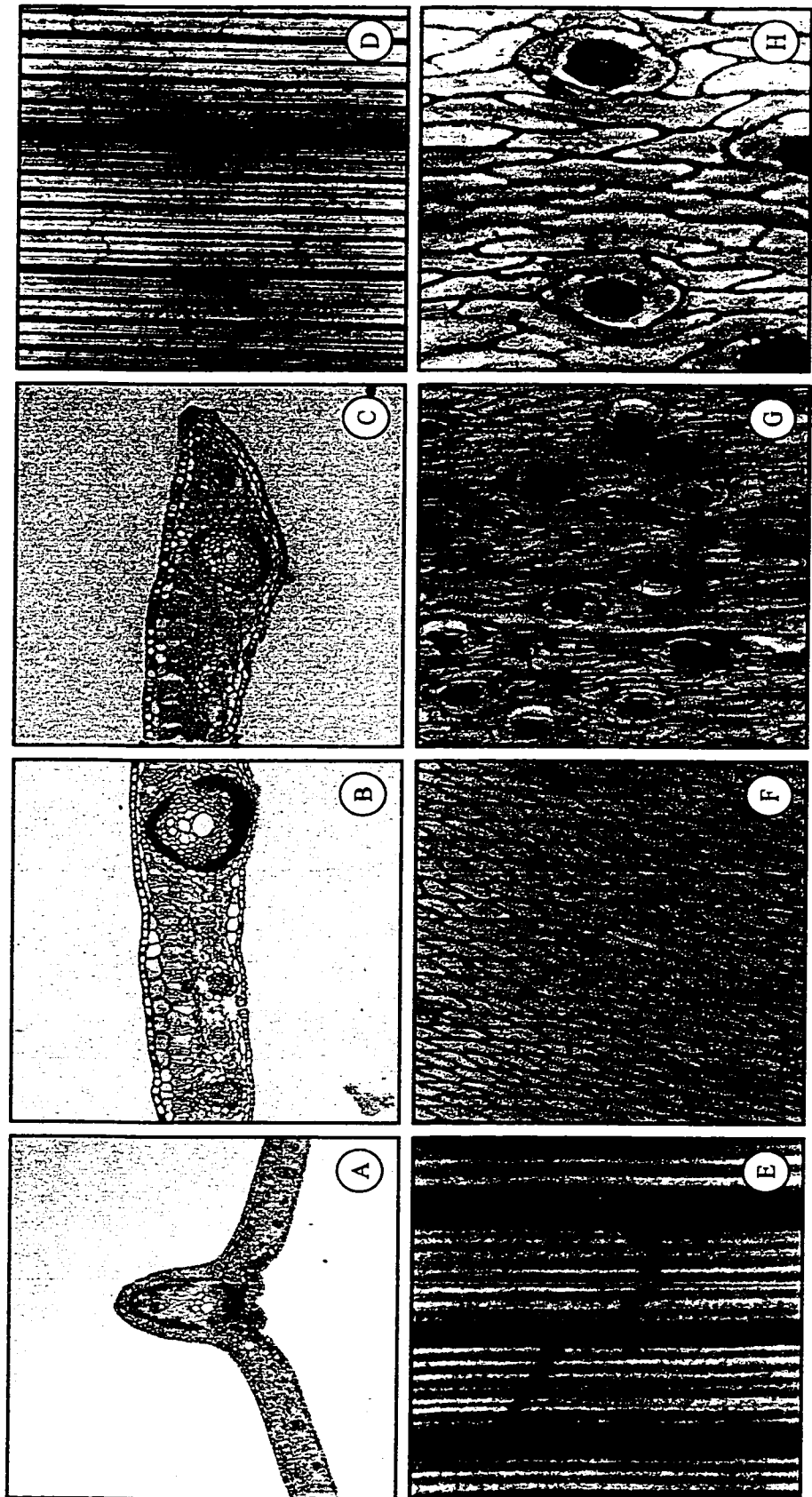
**Transverse commissures:** wide, elongate or short, irregularly arranged and forming a mixed continuous-scattered pattern in surface view; sheathed by sclerotic parenchyma, the cells inflated and protruding toward the mesophyll.

**Specimens examined.** B25, LC25, EP25- FRENCH GUIANA. Piste de St. Elie, 5°19'N, 53°1'W, 29 Dec 1988, Sanders 1811 (NY); B26, LC26, EP26- SURINAME: Alsborige, 23 Oct 1962, Wessels Boer 189 (NY); B27, LC27, EP27- FRENCH GUIANA. Station des Nouragues, Bassin de l'Approuague, Arataye, 4°03'N, 52°42'W, 300 m, de Granville et al. 10354 (NY).

#### 1.1.11. Bactris cubensis (Fig. 11)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete, conspicuous; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed or interrupted laterally, 0-2-layered near the lamina; inner ground parenchyma with 2 large and 2-3 smaller vascular bundles, few small phloem strands embedded in the fibrous layer. **Expansion cells:** forming conspicuous, 1-2-layered, confluent or not, abaxial bands adjacent to midrib; bands elsewhere in the lamina

Figure 11. Leaf anatomy of Bactris cubensis. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B120, x40), B. midsection (B119, x100), C. section tip (B120, x100), D. venation pattern (LC119, x20), E. transverse commissure (LC119, x200), F. adaxial surface (EP119, x200), G. abaxial surface (EP119, x200), H. stomata (EP119, x400).



conspicuous ad- and abaxially. **Hairs:** few on adaxial costal regions, abaxially numerous and regularly distribute on large and small costal bands; hair base sunken, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, organized into distinct longitudinal files but a few, narrowed, spindle-shaped and longitudinally extended cells occurring between the files of larger rhombohedral cells; costal cells smaller than intercostal cells, rhombohedral to rectangular in shape, longitudinally extended, large costal regions with up to 8 distinct longitudinal files of cells. **Abaxial epidermis:** cell size similar to the adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells irregularly shaped, few rhombohedral or trapezoidal, mostly transversely extended but irregular near stomata; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands slightly raised, with up to 8 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding

epidermal cells; guard-cells slightly below the level of epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** large. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells slightly transversely extended, hexagonal, but abaxial cells more irregular. **Chlorenchyma:** palisade mesophyll irregularly 1-2-layered, the first layer level with the columnar, non-vascular fiber bundles; spongy mesophyll well-differentiated, 5-6 layers of thick-walled cells. **Tannin cells:** absent. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical and columnar strands; the cylindrical strands abaxial and arranged in a single layer, level with the veins; the columnar strands large and often attached to the adaxial hypodermis. **Primary veins:** ovoid, slightly prominent ad- and abaxially; the abaxial fibrous area reaching the hypodermis through a poorly developed buttress; outer sheath incomplete, lateral only; inner sheath incomplete, 3-4 thick-walled layers ad- and abaxially, laterally the layers interrupted by sclerotic and conspicuously pitted parenchyma cells. **Secondary veins:** narrowly ovoid, abaxial; outer sheath incomplete, lateral only; inner

sheath incomplete, 1-2 ad- and abaxial layers of thick-walled fibers, the layer laterally interrupted near the phloem by sclerotic and conspicuously pitted parenchyma cells; the adaxial buttress completed by thick-walled, anticlinally extended palisade cells reaching the hypodermis. **Tertiary veins:** roundish, abaxial; outer sheath complete or incomplete abaxially; inner sheath incomplete, 1-layered, few thick-walled fibers abaxially, thin-walled fibers laterally and adaxially. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins poorly divided into distinct strands by sclerotic partitions. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B119, LC119, EP119- CUBA.

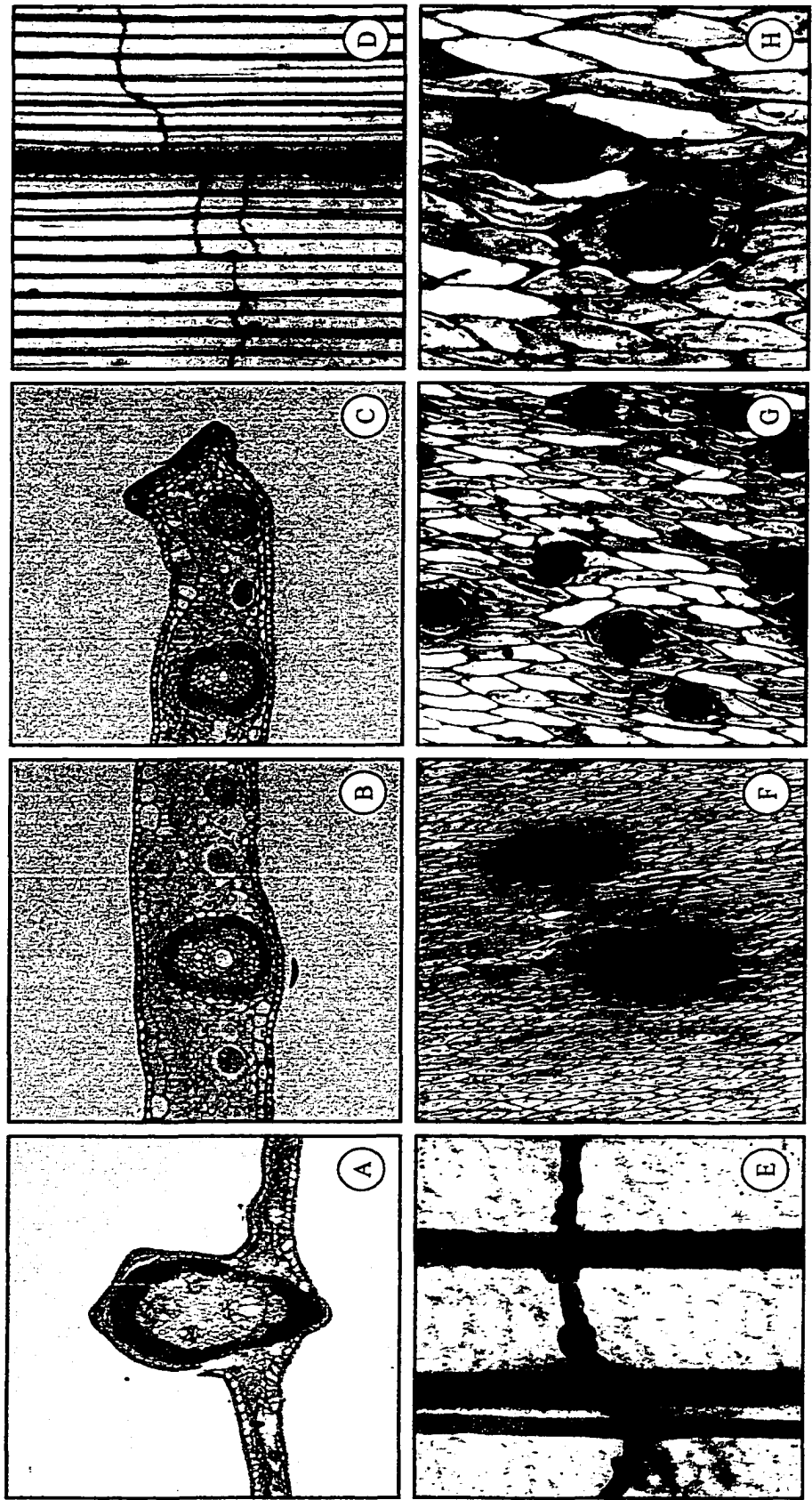
GUANTANAMO: Toa River, near Tabajo, 16.6 km N of Baracoa, 15 Aug 1993, Salzman 340 (FLAS); B120, LC120, EP120- CUBA. HOLGUIN; 13.8 km S of Moa, on Moa-Baracoa road, 18 Aug 1993, Salzman 393 (FLAS).

#### 1.1.12. Bactris ferruginea (Fig. 12)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete, conspicuous; inner fibrous

Figure 12. Leaf anatomy of Bactris ferruginea. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B33, x40), B. midsection (B33, x100), C. section tip (B32, x100), D. venation pattern (LC31, x25), E. transverse commissure (LC31, x200), F. adaxial surface (EP32, x200), G. abaxial surface (EP32, x200), H. stomata (EP32, x400).





layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, only a few layers near the lamina; inner ground parenchyma with 2-3 large vascular bundles and few phloem strands embedded in the innermost fibrous layers. **Expansion cells:** forming inconspicuous, 1-2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** on ad- and abaxial surface but more frequent abaxially along the costal bands; hair base sunken, uniseriate, cutinized, spherical.

**Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, angle of obliquity varying, longitudinal files of cells distinct or not; costal cells rhombohedral but smaller and less obliquely extended than intercostal cells, large costal regions with up to 5 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells like those of the adaxial epidermis but less obliquely extended and not organized into distinct longitudinal files; costal cells smaller than intercostal cells, rhombohedral, longitudinally to obliquely-longitudinally extended, the larger bands slightly raised, with up to 10 distinct longitudinal files

of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells slightly leveled with the epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** large. **Hypodermis:** 1-layered beneath each surface, the adaxial layer wider than abaxial layer, both layers compressed above and below large veins; ad- and abaxial cells slightly transversely, adaxial cells hexagonal, abaxial cells irregularly oblong. **Chlorenchyma:** a well-differentiated 1-layered palisade mesophyll; spongy mesophyll, 5 layers of densely arranged, thin-walled cells. **Tannin cells:** absent. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming strands of variable size and shape; the largest strands are cylindrical and distributed in a single abaxial layer level with small veins; smaller strands irregularly roundish, mostly attached to the adaxial hypodermis. **Primary veins:** pear-shaped, slightly prominent ad- and abaxially; outer sheath incomplete, lateral only; inner sheath complete, thick-walled, 2-4 layered, the layer thinner abaxially. **Secondary and Tertiary veins:** almost indistinguishable, the

secondary veins slightly larger than the tertiary; both veins roundish, abaxial; outer sheath incomplete abaxially in secondary and tertiary veins; inner sheath complete, consisting of 1-2 layers of thick-walled fibers.

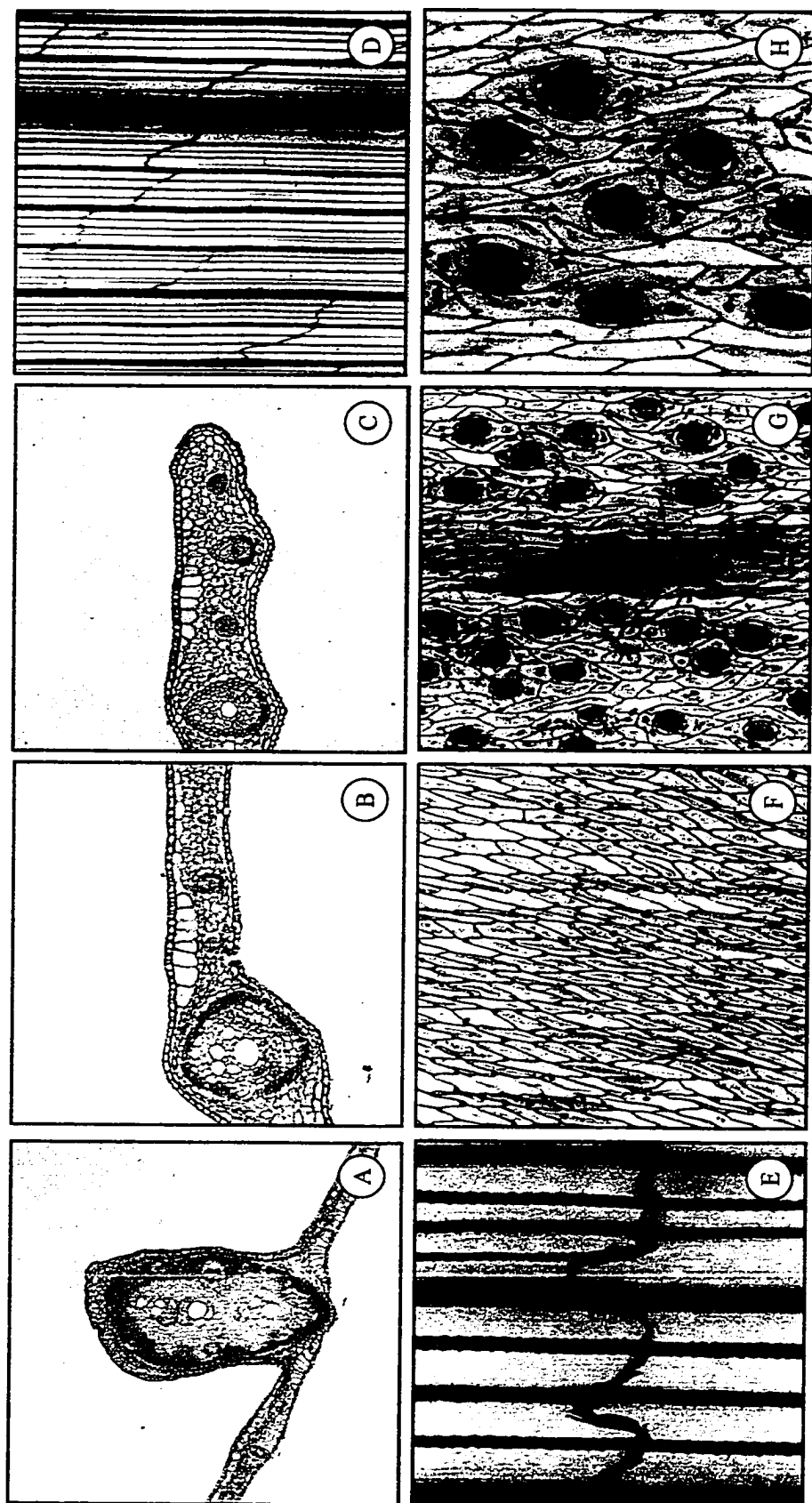
**Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers or thin sclerotic partitions. **Transverse commissures:** narrow, elongate, more or less regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B31, LC31, EP31- BRAZIL. BAHIA: Mun. Ilhéus, cidade de Ilhéus, 14°46'S, 39°04'W, 19 Sep 1994, Carvalho et. al 4837 (NY); B32, LC32, EP32- BRAZIL. BAHIA: Mun. Belmonte, 7 km E of Barralândia, 15°51'S, 38°54'W, 50-100 m, Noblick 4751 (NY); B33, LC33, EP33- BRAZIL. BAHIA: Mun. Una, 1 km W of Una, 15°18'S, 39°04'W, 12 Jan 1989, Noblick 4729 (F, FTG, K, NY).

#### 1.1.13. Bactris gasipaes var. gasipaes (Fig. 13)

**Midrib:** abaxially pointed, adaxially prominent; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 1-3 large and 4-7

Figure 13. Leaf anatomy of Bactris gasipaes var. gasipaes.  
A-C, cross-section; D-E, clearings; F-H, epidermal peels.  
A. midrib (B100, x40), B. midsection (B100, x100), C.  
section tip (B101, x100), D. venation pattern (LC102, x20),  
E. transverse commissure (LC102, x100), F. adaxial surface  
(EP101, x200), G. abaxial surface (EP101, x200), H. stomata  
(EP101, x400).



smaller vascular bundles, either within the ground parenchyma or deeply embedded in the fibrous layer, few phloem strands embedded in the adaxial innermost fibrous layers. **Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina ad- and abaxially prominent. **Hairs:** on adaxial costal regions, but more abundant on large abaxial costal bands, above the small bands the hairs organized into distinct single files; base sunken, uniseriate, cutinized, clavate. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, but cell in some areas almost longitudinally extended and becoming spindle-shaped, organized or not into distinct longitudinal files; costal cells shorter than intercostal cells, rectangular, longitudinally extended, large costal regions with up to 8 distinct longitudinal files. **Abaxial epidermis:** cells smaller than adaxial cells, more irregularly shaped than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells of irregular shape, many hexagonal, pentagonal and rhombohedral, the majority longitudinally extended, except those near the stomata, cells not organized into distinct longitudinal files; costal cells

smaller than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 30 distinct longitudinal files of cells. **Stomata:** superficial, rare on adaxial costal region, numerous, rather diffuse on abaxial intercostal bands, not in distinct files; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with the epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins, the adaxial layer wider than abaxial layer; ad- and abaxial cells transversely extended, hexagonal, but the abaxial cells more irregularly shaped. **Chlorenchyma:** a well-differentiate, 1-layered palisade mesophyll; spongy mesophyll well-differentiated, 4-5 layers of thick-walled cells. **Tannin cells:** absent. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming fairly uniform cylindrical strands distributed in a single layer level with the veins. **Primary veins:** widely ovoid to obtrullate, prominent abaxially; the ad- and abaxial fibrous area reaching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, well-



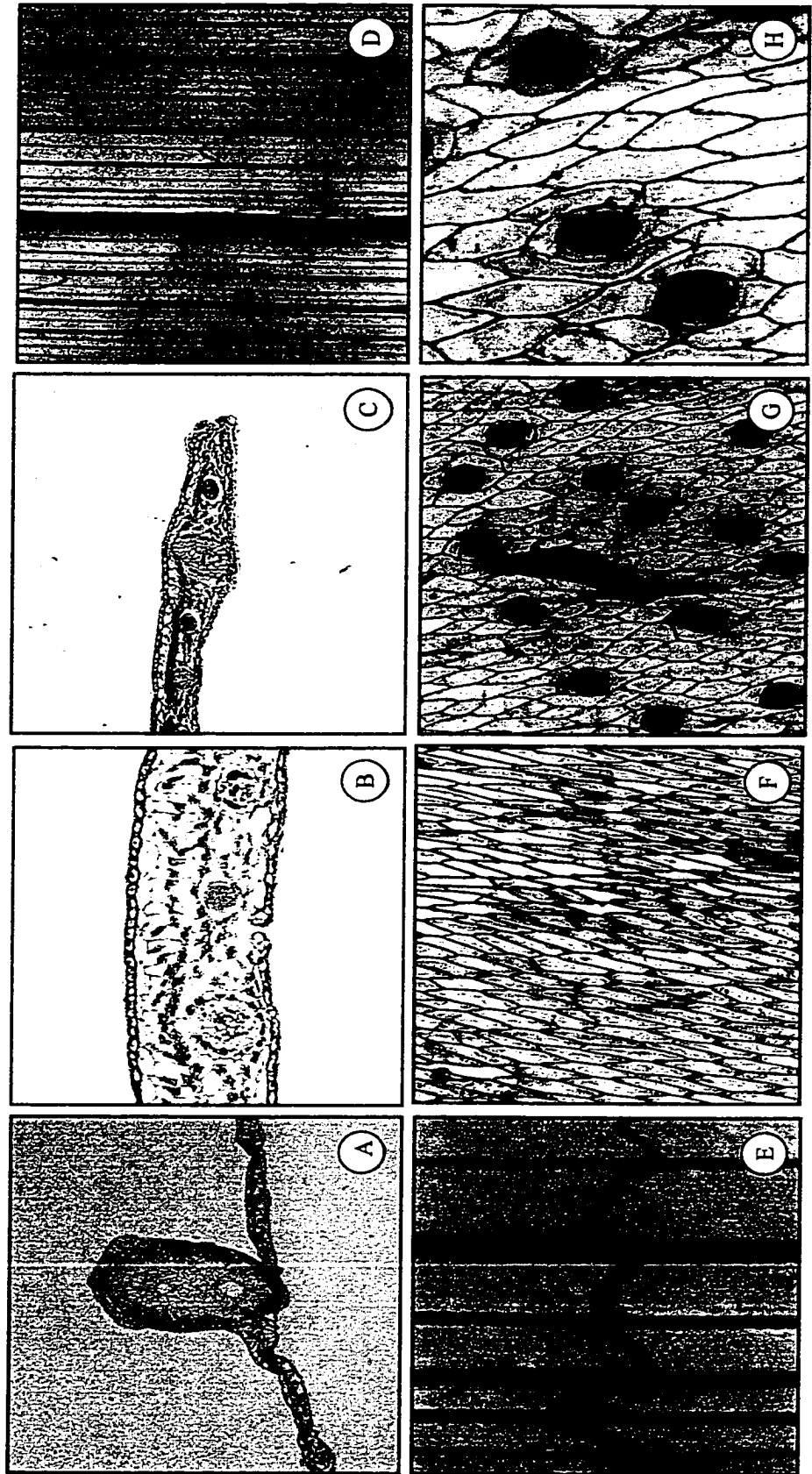
delimited, numerous thick-walled fibers in the ad- and abaxial area, laterally only 1-3 layers. **Secondary veins:** narrowly ovoid, slightly prominent ad- and abaxially, centered; outer sheath incomplete, only lateral; inner sheath complete, thick-walled, single layered, completed by a small adaxial buttress reaching the hypodermis. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, thick-walled, single layered. **Quaternary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, thin to thick-walled, single layered. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by sclerotic partitions. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B100, LC100, EP100- BOLIVIA. SANTA CRUZ: Parque Amboró, 17°39'S, 63°43'W, 22 Dec 1988, Saldias 533 (NY); B101, LC101, EP101- BOLIVIA. SANTA CRUZ: Parque Amboró, 17°39'S, 63°43'W, 22 Dec 1988, 10 Mar 1989, Saldias 683 (NY); B102, LC102, EP102- BOLIVIA. SANTA CRUZ: Parque Amboró, 17°39'S, 63°43'W, 3 Mar 1990, Saldias et al. 1004 (NY).

1.1.14a. Bactris gasipaes var. chichagui (northern population) (Fig. 14)

**Midrib:** abaxially pointed, adaxially prominent; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 1-3 large and 3 smaller vascular bundles, few phloem strands embedded in the innermost fibrous layers. **Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina very prominent ad- and abaxially. **Hairs:** on adaxial costal and intercostal regions, more numerous abaxially, specially on the large costal bands, but also uniformly distributed as a single line above the small costa; hair base sunken, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, but sometimes longitudinally extended and the cells almost spindle-shaped, organized or not into distinct longitudinal files; costal cells more regularly shaped and shorter than intercostal cells, rectangular, longitudinally extended, large costal regions raised, with up to 12 distinct longitudinal files of cells.

Figure 14. Leaf anatomy of Bactris gasipaes var. chichagui (Northern population). A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B99, x40), B. midsection (B98, x200), C. section tip (B98, x100), D. venation pattern (LC99, x20), E. transverse commissure (LC99, x100), F. adaxial surface (EP98, x200), G. abaxial surface (EP98, x200), H. stomata (EP98, x400).



**Abaxial epidermis:** cells smaller than adaxial cells, more irregularly shaped than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells of irregular shape, many hexagonal, pentagonal and rhombohedral, the majority longitudinally extended, except those near the stomata, cells not organized into distinct longitudinal files; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 25 distinct longitudinal files of cells. **Stomata:** superficial, rare on adaxial costal region, numerous, rather diffuse on abaxial intercostal bands, not in distinct files; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with the epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells transversely extended, hexagonal, but the abaxial cells more irregularly shaped. **Chlorenchyma:** palisade mesophyll well-differentiated, continuous, single layered; spongy mesophyll well-differentiated, 3-4 layers of thick-walled cells. **Tannin cells:** numerous adaxially, the cells

partially filled with the reddish tanniniferous material, the mesophyll not saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** rare, centered. **Non-vascular fibers:** forming cylindrical strands distributed in a single layer level with small veins. **Primary veins:** ovoid to obtrullate, prominent abaxially; outer sheath incomplete, lateral only; inner sheath complete, thick-walled fibers, well-developed, the ad- and abaxial fibrous area often reaching the hypodermis, laterally only 1-3 layers. **Secondary veins:** narrowly ovoid, slightly prominent ad- and abaxially, centered; outer sheath incomplete, only lateral; inner sheath complete, consisting of 1-2 layers of thick-walled fibers completed by an adaxial buttress. **Tertiary veins:** roundish, abaxial; outer sheath complete or incomplete ad- and abaxially; inner sheath complete, consisting of a single layer of thick-walled fibers. **Quaternary veins:** roundish, abaxial; outer sheath complete or lacking abaxially; inner sheath complete, consisting of a single layer of thick-walled fibers. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct to almost indistinct strands by thin sclerotic partitions. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B97, LC97, EP97- VENEZUELA.

ZULIA: Dist. Perijá, near Estación Hidrológica Aricuaisá,  
9°35'N, 72°54'W, 100-250 m, 28 Feb 1982, Bunting et al.

10981 (NY); B98, LC98, EP98- VENEZUELA. ZULIA: Dist.

Catatumbo, 2-4 km S of Casigua, 11 Oct 1982, Bunting 11777

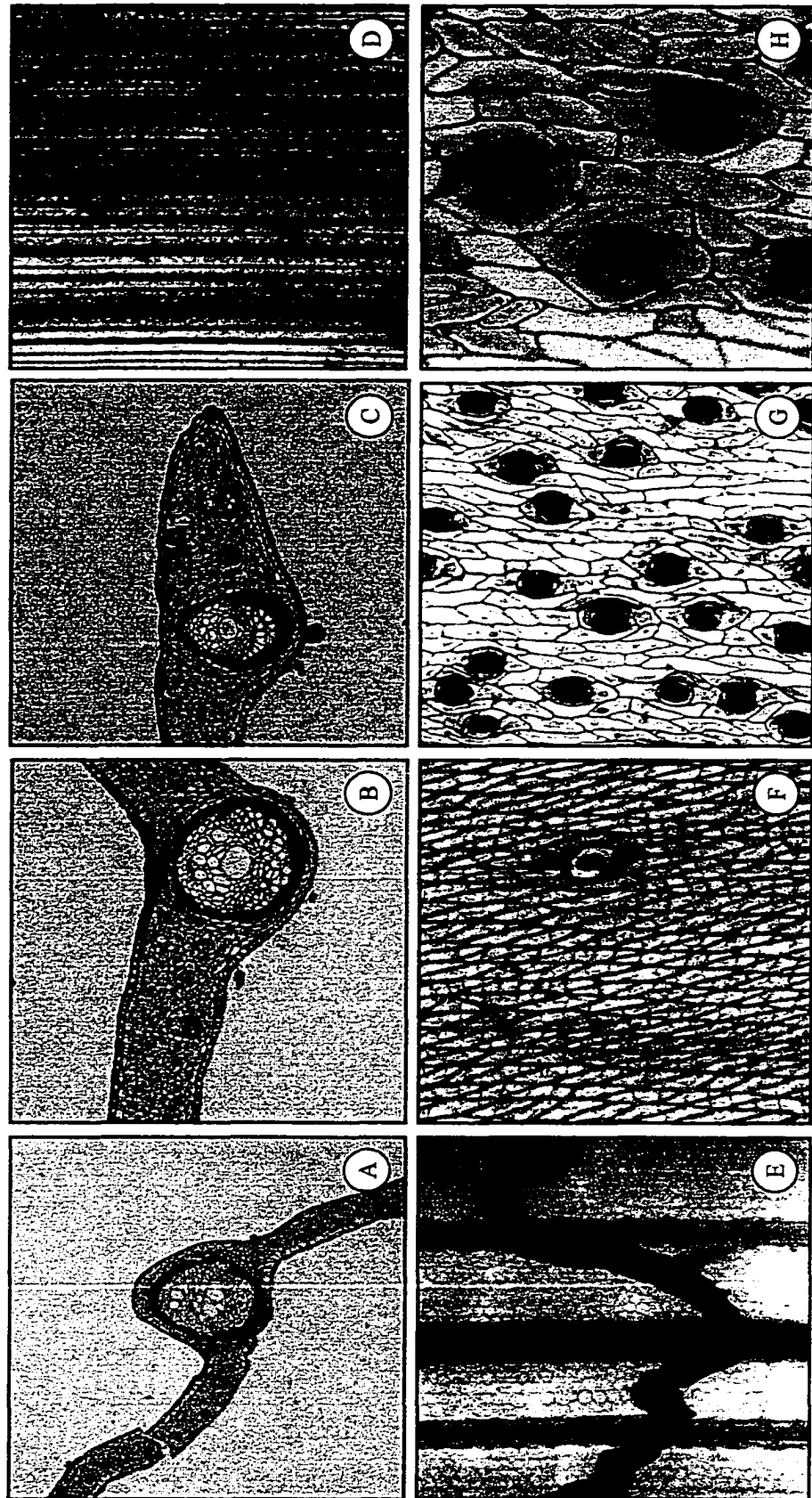
(NY); B99, LC99, EP99- VENEZUELA. BARINAS: Caimital, 8 km S  
of Barrancas, 24-25 May 1966, Schulz & Rodríguez 419 (NY).

1.1.14b. Bactris gasipaes var. chichagui (southern  
population) (Fig. 15)

**Midrib:** abaxially rounded, adaxially prominent; peripheral  
chlorenchymatous layer complete and conspicuous; inner  
fibrous layer well-delimited, thick-walled, well-developed  
ad- and abaxially, narrowed laterally, 2-3-layered near the  
lamina; inner ground parenchyma with 1-2 large and 3-4  
smaller vascular bundles, few phloem strands embedded in  
the innermost fibrous layers. **Expansion cells:** forming  
inconspicuous, 1-layered abaxial bands adjacent to midrib;  
bands elsewhere in the lamina conspicuous ad- and  
abaxially. **Hairs:** on ad- and abaxial surface but more  
frequent on abaxial costal bands, on small costal bands the  
hairs form a distinct single line; base sunken, uniseriate,  
cutinized, clavate. **Epidermis:** ad- and abaxial cell walls

Figure 15. Leaf anatomy of Bactris gasipaes var. chichagui (Southern population). A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B94, x40), B. midsection (B94, x100), C. section tip (B94, x100), D. venation pattern (LC94, x25), E. transverse commissure (LC94, x200), F. adaxial surface (EP95, x200), G. abaxial surface (EP95, x200), H. stomata (EP95, x400).





not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, organized into distinct longitudinal files; costal cells shorter than intercostal cells, rectangular, longitudinally extended, large costal regions with up to 11 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, more irregularly shaped than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells of irregular shape, many hexagonal, pentagonal and rhombohedral, the majority longitudinally extended, except those near the stomata, not into distinct longitudinal files; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 24 distinct longitudinal files of cells. **Stomata:** superficial, rare on adaxial costal region, numerous, rather diffuse on abaxial intercostal bands, not in distinct files; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with the epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above

and below the large veins, the adaxial layer slightly wider; ad- and abaxial cells transversely extended, hexagonal, but abaxial cells somewhat more irregular.

**Chlorenchyma:** palisade mesophyll 1-2-layered and well-differentiated; spongy mesophyll also well-differentiated, 4-5 layers of thick-walled cells. **Tannin cells:** absent.

**Fiber-sclereids:** absent. **Raphide-sacs:** rare, usually near the hypodermis. **Non-vascular fibers:** forming small cylindrical strands distributed in a single layer level with the veins. **Primary veins:** widely ovoid, prominent abaxially; the ad- and abaxial fibrous area reaching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, very well-delimited by thick-walled, strongly lignified fibers, laterally 2-3 layers, few fibers in the ad- and abaxial area; a poorly developed adaxial buttress present or not. **Secondary veins:** narrowly ovoid, slightly prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, consisting of 1-2 layers of thin to thick-walled fibers; the ad- and abaxial fibrous area reaching the hypodermis by a short buttress. **Tertiary veins:** roundish, abaxial; outer sheath complete or incomplete below; inner sheath incomplete, few thick-walled fibers abaxially, a single, thin-walled fibrous layer abaxially. **Quaternary veins:** roundish, abaxial; outer

sheath complete; inner sheath complete, consisting of 1 layer of thin-walled fibers. **Marginal rib:** absent.

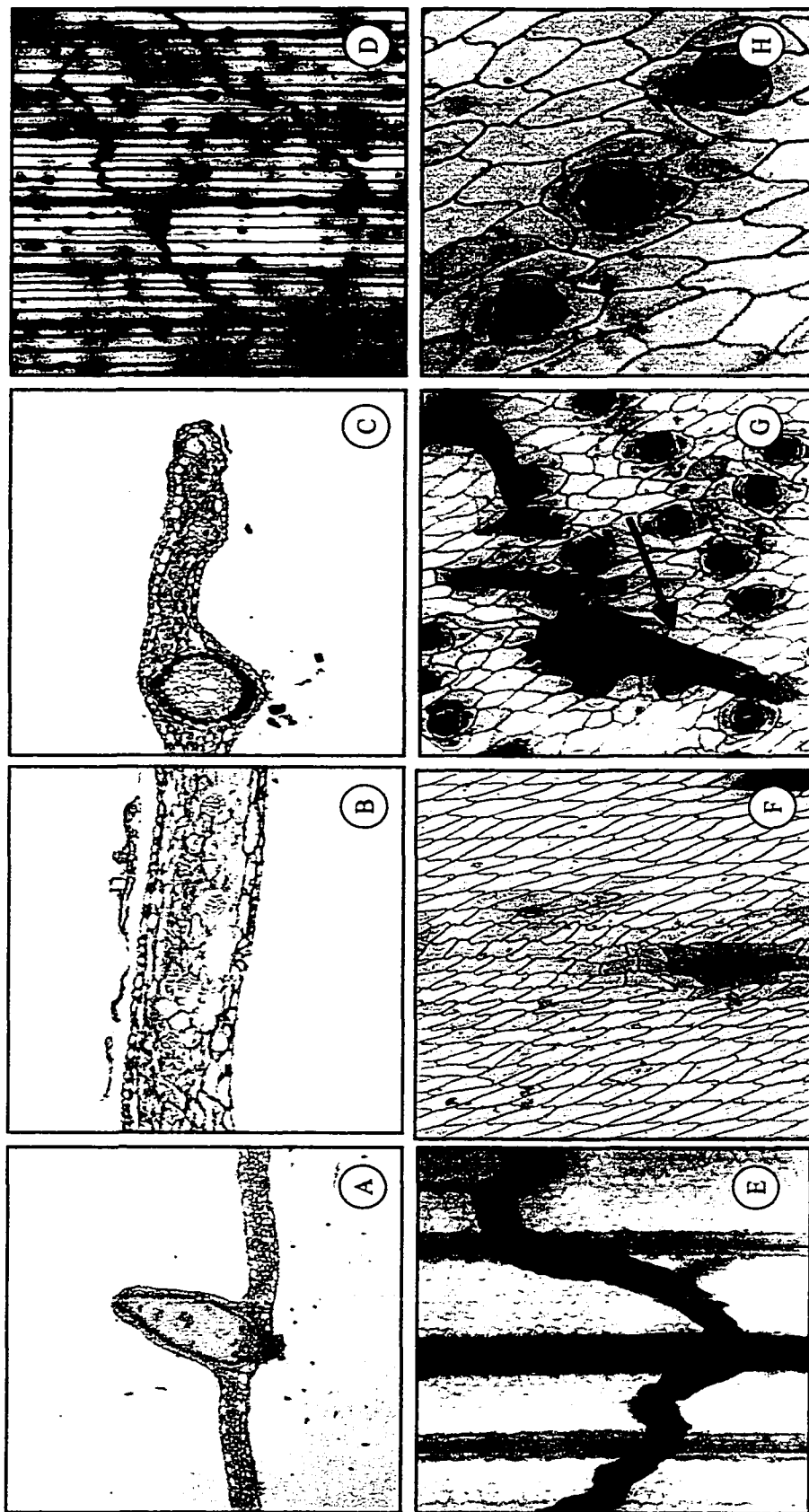
**Phloem:** of large veins divided into indistinct strands by thin sclerotic partitions. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B94, LC94, EP94- BRAZIL. ACRE: Mun. Taumaturgo, Reserva Extrativista do Alto Juruá, 08°57'S; 72°33'W, 120 m, 12 Mar 1992, E. Ferreira 133 (HPZ); B95, LC95, EP95- BRAZIL. ACRE: Mun. Tarauacá, igarapé "Joací", Colocação "Remanso", 08° 17'S, 69°58'W, 150 m, 8 Mar 1994, E. Ferreira 334 (HPZ); B96, LC96, EP96- Rio Juruá, above Cruzeiro do Sul, near Natal, 8°20'S, 72°15'W, 8 Feb 1992, A. Henderson et al. 1663 (NY).

1.1.15. Bactris glandulosa var. glandulosa (Fig. 16)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer conspicuous and complete; inner fibrous layer well-delimited, somewhat narrow, not well-developed, the outermost fibers thick-walled and the innermost thin-walled; inner ground parenchyma with a very large abaxial vascular bundle and several lateral and adaxial bundles. **Expansion cells:** forming inconspicuous,

Figure 16. Leaf anatomy of Bactris glandulosa var. glandulosa. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B62, x40), B. midsection (B61, x200), C. section tip (B61, x100), D. venation pattern (LC62, x25), E. transverse commissure (LC62, x200), F. adaxial surface (EP62, x200), G. abaxial surface, note a hair with a missing distal portion (EP62, x200), H. stomata (EP62, x400).



1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina ad- and abaxially prominent. **Hairs:** frequent on ad- and abaxial surface but more abundant near abaxial costal bands; hair base superficial, large, multiseriate, cutinized. **Epidermis:** ad- and abaxial cell walls sinuous, slightly thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, slightly obliquely extended, the files of cells easily distinguished; costal cell-shape similar to intercostal cells but smaller and more longitudinally extended, large costal regions with 7-8 distinct longitudinal files of cells. **Abaxial epidermis:** cell size similar to adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells shaped more irregularly than adaxial cells, mostly longitudinally extended; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands wide distinctly raised, with up to 30 distinct longitudinal files of cells. **Stomata:** superficial, few on adaxial surface near the costal regions, numerous on abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells slightly raised above the epidermis, each with

2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells transversely extended, irregularly hexagonal. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 5 layers of thick-walled cells. **Tannin cells:** absent. **Fiber-sclereids:** absent. **Raphide-sacs:** rare, centered. **Non-vascular fibers:** forming cylindrical strands of variable size irregularly distributed in the mesophyll. **Primary veins:** obovoid to obtrullate, prominent abaxially; the ad- and abaxial fibrous area touching or going through the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, thick-walled, ad- and abaxially well-developed, laterally only 1-2 fibrous layers. **Secondary veins:** ovoid, slightly prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, consisting of 1-2 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath incomplete, 1-layered, adaxial fibers thin-walled. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by sclerotic partitions. **Transverse commissures:** wide, elongate, irregularly



arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B61, LC61, EP61- COSTA RICA.

PUNTARENAS: ca. 5 km W of Rincón, 8°42'N, 83°31'W, 7 Jun 1992, Henderson et al. 1820 (NY); B62, LC62, EP62- PANAMA.

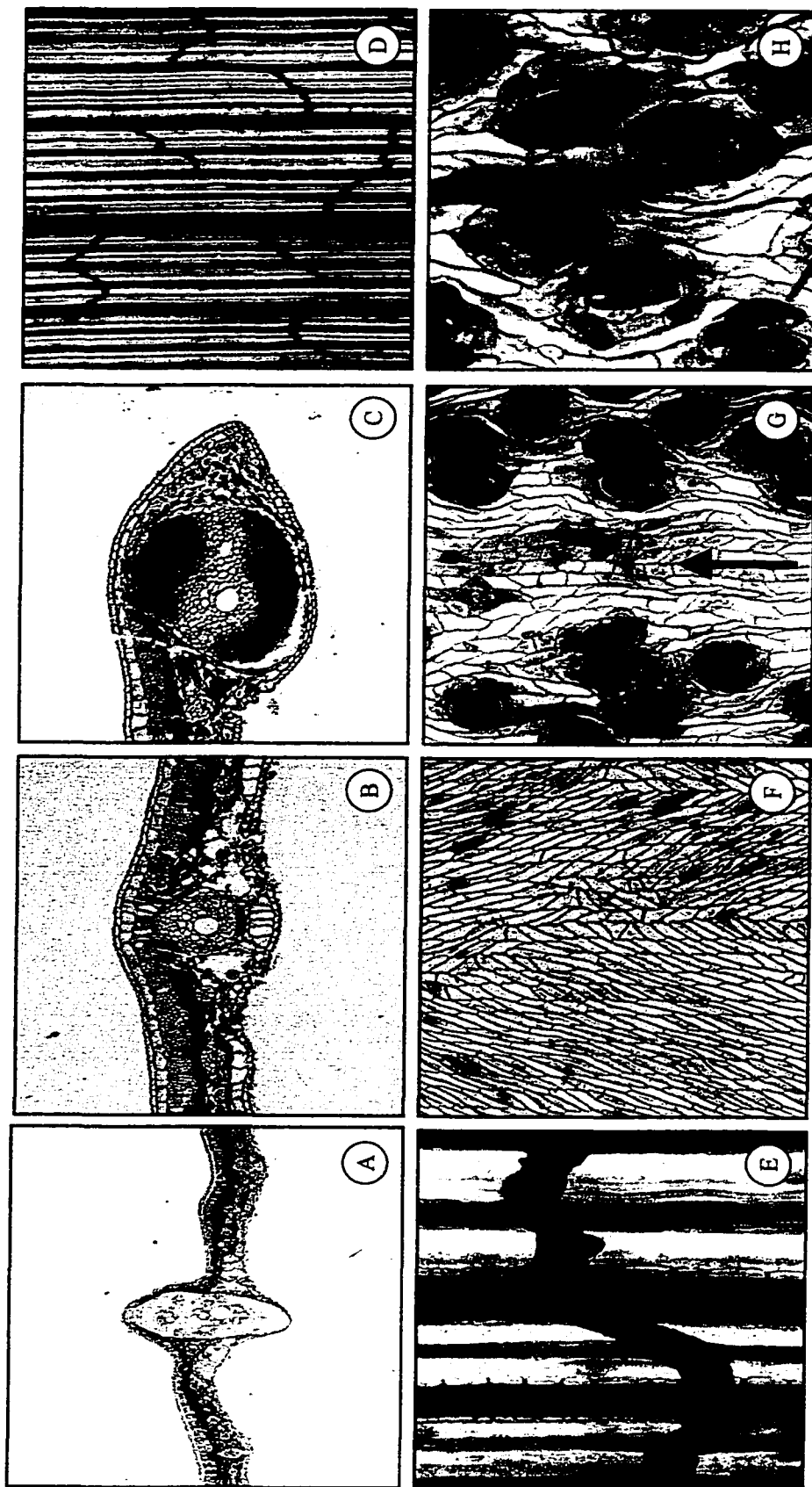
COCLÉ: El Valle de Antón, 27 Nov 1995, Henderson & Bernal 2037 (NY); B63, LC63, EP63- COSTA RICA. HEREDIA: Dist. Río Frio, Finca Fincagua, margem del Río Sarapaqui, 16 Sep 1990, Mattos & Mora-Urpí 2880 (NY).

#### 1.1.16. Bactris glaucescens (Fig. 17)

**Midrib:** abaxially pointed, equally prominent on both surfaces; peripheral chlorenchymatous layer conspicuous but interrupted adaxially; inner fibrous layer poorly-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 5-6 large vascular bundles.

**Expansion cells:** forming conspicuous, 2-layered abaxial bands adjacent to midrib; bands in the lamina usually below the veins. **Hairs:** more common on abaxial surface; hair base sunken below epidermis, uniseriate, cutinized, clavate. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer wall. **Adaxial epidermis:** cells

Figure 17. Leaf anatomy of Bactris glaucescens. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B22, x20), B. midsection (B23, x100), C. section tip (B23, x100), D. venation pattern (LC22, x25), E. transverse commissure (LC22, x20), F. adaxial surface (EP23, x200), G. abaxial surface, note the costal cells forming distinct files (EP23, x200), H. stomata (EP23, x400).



of irregular shape, but mostly rhombohedral, obliquely to transversely extended, but angle of obliquity varying; costal and intercostal cells organized into files of cells very similar; costal cells shorter than intercostal cells, irregularly shaped, but many more or less rectangular to rhombohedral, almost transversely extended. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells of irregular shape and size, not in distinct longitudinal files, some cells on abaxial surface inflated, specially those near the stomata; costal cells narrower than intercostal cells, rhombohedral to rectangular, longitudinally extended, the walls of costal cells not thickened as to make them conspicuously different from intercostal cells, the larger bands not raised, with few distinct longitudinal files of cells. **Stomata:** sunken, restricted to abaxial intercostal bands, not in distinct longitudinal files, dense; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells by distinct lobes on its extremities, the lobes overarching the guard-cells; guard-cells sunken below the adjacent epidermal cells, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal**

**chamber:** small. **Hypodermis:** 1-layered beneath each surface, the adaxial cells forming a continuous and uniform layer, not compressed above the large veins, the abaxial layer irregular, compressed below the large veins; adaxial cells transversely extended, rectangular to square-shaped; abaxial cells not transversely extended, rectangular, but more irregular than adaxial cells. **Chlorenchyma:** 1-2-layered palisade mesophyll, the first layer level with the columnar non-vascular fiber bundles, the second just above the small veins; spongy mesophyll well-differentiated, intercellular spaces easily distinct, 5-6 layers of loosely arranged, thick-walled cells. **Tannin cells:** numerous, densely arranged, the cells completely filled by a reddish tanniniferous material, saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** rare, centered. **Non-vascular fibers:** forming cylindrical and columnar strands; the cylindrical strands smaller, forming a single layer level with the small veins; the columnar strands larger and attached to the adaxial hypodermis. **Primary veins:** ovoid, ad- and abaxially prominent; outer sheath incomplete, lateral only; inner sheath incomplete, 2-3-layered, thick-walled fibers ad- and abaxially, laterally sclerotic and conspicuously pitted parenchyma cells; poorly developed ad- and abaxial buttresses completed by thick-walled, slightly

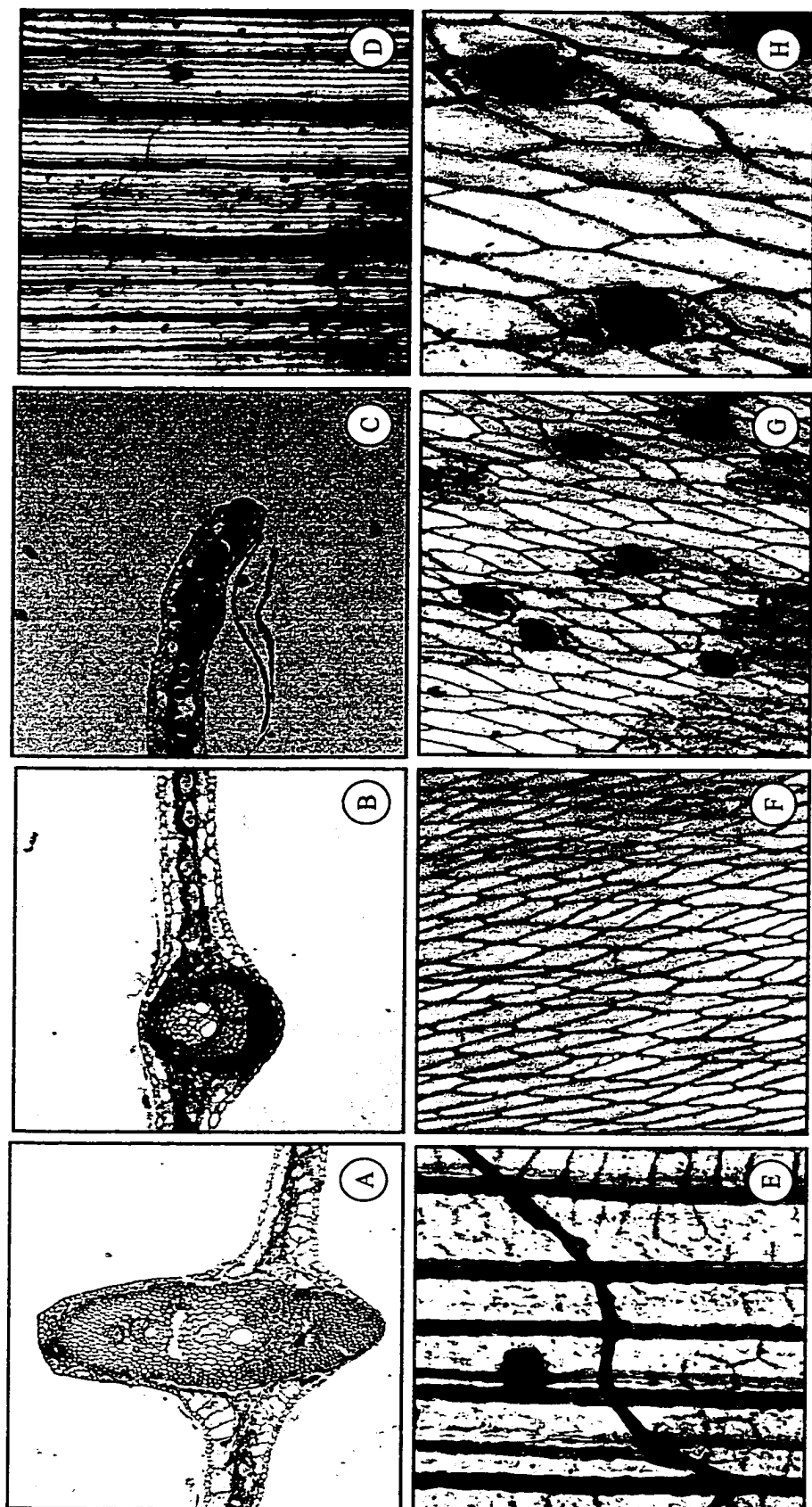
lignified, anticlinally extended mesophyll cells.

**Secondary veins:** roundish, abaxial; outer sheath incomplete, only lateral; inner sheath incomplete, 1-2-layered, few ad- and abaxial thick-walled fibers, laterally only sclerotic and conspicuously pitted parenchyma cells; buttress only adaxially, completed by thick-walled, extended mesophyll cells. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath incomplete, 1-layered, few thick-walled fibers abaxially, thin-walled fibers laterally and adaxially. **Quaternary veins:** absent. **Marginal rib:** prominent abaxially, inner sheath several-layered, thick-walled. **Phloem:** of large veins undivided. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B22, LC22, EP22- BOLIVIA. BENI: Prov. Yacuma, Espíritu, 15 Oct 1989, Moraes & Sarmiento 1091 (NY); B23, LC23, EP23- BRAZIL. RONDÔNIA: Rio Guaporé, Costa Marques, 12°26'S, 64°13'W, 150 m, 27 Mar 1987, Nee 34511 (NY); B24, LC24, EP24- BOLIVIA. SANTA CRUZ: Prov. Velasco, Florida, Río Paraguá, 2 Nov 1989, L. Moreno 24 (NY).

1.1.17. Bactris gracilior (Fig. 18)

Figure 18. Leaf anatomy of Bactris gracilior. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B42, x40), B. midsection (B42, x100), C. section tip (B42, x100), D. venation pattern (LC42, x25), E. transverse commissure (LC42, x200), F. adaxial surface (EP40, x200), G. abaxial surface (EP40, x200), H. stomata (EP40, x400).





**Midrib:** abaxially pointed to rounded, adaxially prominent; peripheral chlorenchymatous layer conspicuous and complete; inner fibrous layer poorly-delimited, well-developed, thick-walled only abaxially, adaxially thin-walled, narrowed laterally, 3-4-layered near the lamina; inner ground parenchyma with 1-2 large vascular bundles and 2-4 small adaxial and lateral bundles. **Expansion cells:** forming similar, 1-2-layered ad- and abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous.

**Hairs:** on ad- and abaxial surface; hair base not seen in cross-section. **Epidermis:** ad- and abaxial cell walls not sinuous, slightly thickened on outer wall. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended; costal cells shorter than intercostal cells, mostly rhombohedral, longitudinally extended, large costal regions with 5-7 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral, obliquely extended, organized into poorly distinguished longitudinal files; costal cells narrower than intercostal cells, rectangular, longitudinally extended, the larger bands distinctly raised, with up to 19 distinct longitudinal files of cells. **Stomata:**

superficial, rare adaxially, abaxially restricted to intercostal bands, not in distinct longitudinal files, diffuse; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers wide, making up to 50% of the lamina, both layers interrupted above and below the large veins; ad- and abaxial cells transversely extended, oblong to rectangular. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll not well-differentiated, 4 layers of tightly arranged, thick-walled cells. **Tannin cells:** numerous, densely arranged, the tanniniferous material completely filling the cells, saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming strands of variable size and shape; the cylindrical strands usually larger, centered; the irregularly shaped strands mostly attached to the adaxial hypodermis. **Primary veins:** pear-shaped, prominent abaxially, ad- and abaxial fibrous area going through the hypodermis, reaching the epidermis; outer sheath incomplete, lateral only; inner sheath complete, consisting

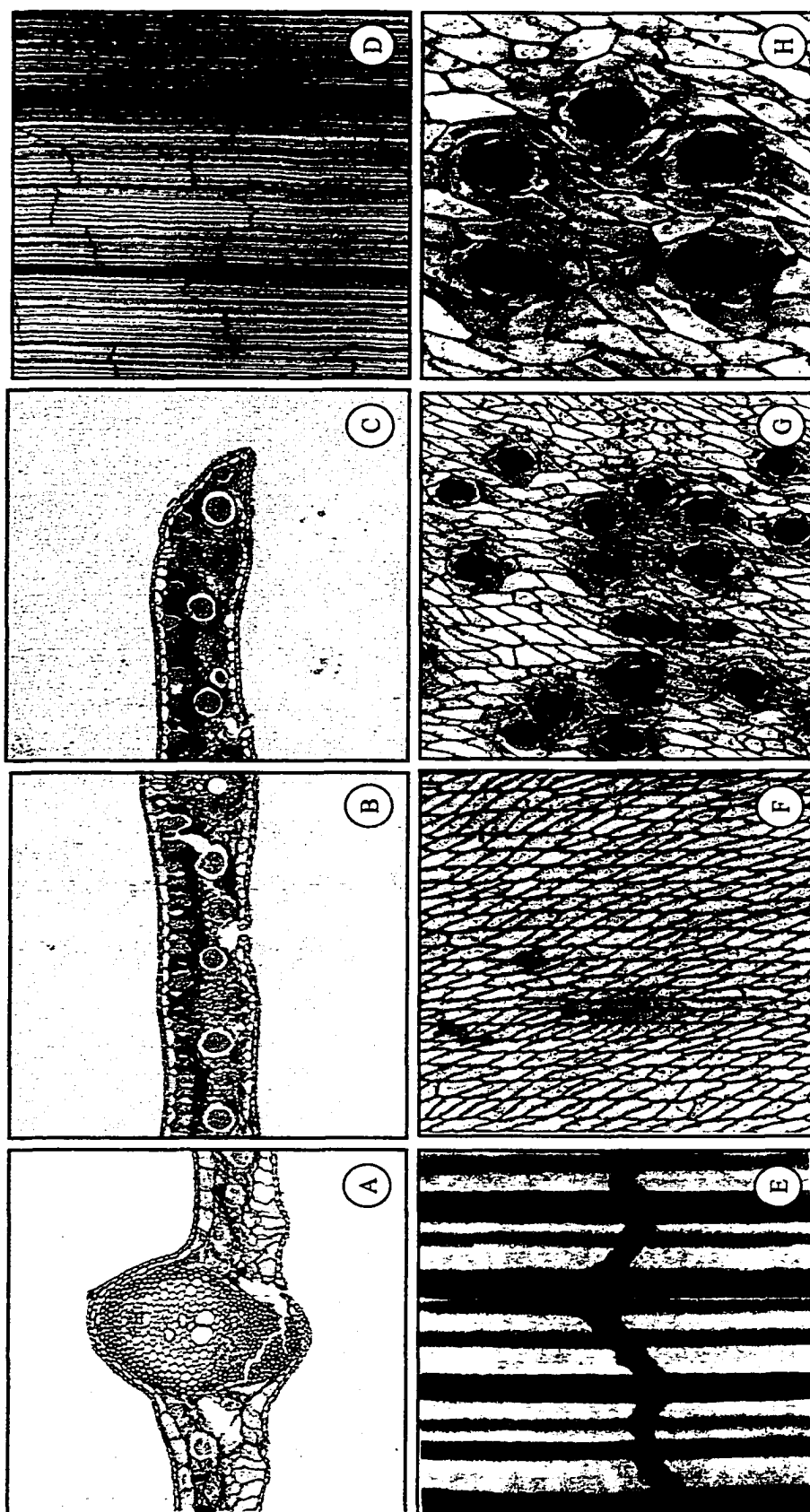
of 3-5 layers of thick-walled fibers. **Secondary veins:** ovoid, centered; outer sheath incomplete, only lateral; inner sheath complete, consisting of 1-2 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath complete, consisting of a single layer of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of thick-walled fibers. **Transverse commissures:** narrow, elongate, irregularly arranged and forming a scattered pattern in surface view; sheathed by thin-walled, parenchymatous cells.

**Specimens examined.** B40, LC40, EP40- PANAMA. SAN BLAS: El Llano-Cartí road, Nusigandi, 9°20'N, 79°W, km 16, 17 Jul 1985, de Nevers 5976 (NY); B41, LC41, EP41- COSTA RICA. HEREDIA: Finca El Bejuco, 6 km W of Puerto Viejo, 10°27'N, 84°4'W, 14 Dec 1984, Henderson et al. 60 (NY); B42, LC42, EP42- COSTA RICA. HEREDIA: between Corazón del Jesús and La Virgen, Moore 6629 (NY).

1.1.18. Bactris guineensis (Fig. 19)

**Midrib:** obovoid, pointed to rounded abaxially, prominent on both surfaces or only adaxially; peripheral

Figure 19. Leaf anatomy of Bactris guineensis. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B5, x100), B. midsection (B4, x100), C. section tip (B4, x100), D. venation pattern (LC5, x20), E. transverse commissure (LC5, x200), F. adaxial surface (EP6, x200), G. abaxial surface (EP6, x200), H. stomata (EP6, x400).



chlorenchymatous layer absent ad- and abaxially, inconspicuous laterally; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 1-2-layered near the lamina; inner ground parenchyma with 1-2 large vascular bundles, the adaxial bundles inversely oriented. **Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous.

**Hairs:** on abaxial surface; hair base superficial, uniseriate, thick-walled, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, not thickened. **Adaxial epidermis:** intercostal and costal regions not well-differentiated, cells rhombohedral, obliquely-longitudinally extended, forming distinct, elongate longitudinal files of cells; costal cells less obliquely extended than intercostal cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral to almost hexagonal, slightly obliquely extended and not organized into distinct longitudinal files; costal cells narrower than intercostal cells, rectangular to rhombohedral, obliquely to almost completely transversely extended. **Stomata:** restricted to abaxial intercostal regions, superficial; terminal subsidiary cells

overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins but the adaxial layer more uniform; adaxial cells mostly hexagonal and slightly transversely extended but cells near midrib square-shaped; abaxial cells rectangular near the veins, irregular elsewhere, not always transversely extended. **Chlorenchyma:** a distinct and continuous palisade mesophyll absent but palisade-like cells present in the spaces between the columnar, non-vascular fiber bundles; spongy mesophyll well-differentiated, up to 6 layers of loosely arranged, thin-walled cells. **Tannin cells:** few, scattered and easily distinct from other mesophyll cells, mostly in the adaxial region near the columnar strands, not saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** common, abaxial. **Non-vascular fibers:** forming cylindrical and columnar strands; the cylindrical strands distributed in a single layer level with the small veins, the columnar strands attached to the adaxial hypodermis. **Primary veins:** ovoid, slightly prominent ad- and abaxially; outer sheath

incomplete, only lateral; inner sheath incomplete, the 1-2-layered thick-walled fibrous ring interrupted above the phloem by sclerotic and conspicuously pitted parenchyma cells; the adaxial buttress completed above by thick-walled, extended hypodermal cells. **Secondary veins:** ovoid, centered; outer sheath incomplete, only lateral; inner sheath incomplete, 1-2-layered, few thick-walled fibers abaxially, sclerotic and conspicuously pitted parenchyma cells laterally, elongated adaxial buttress completed above by thick-walled, extended hypodermal cells. **Tertiary veins:** roundish, abaxial; outer sheath incomplete, lacking abaxially; inner sheath incomplete, 1-layered, few thick-walled fibers abaxially, laterally and adaxially completed by conspicuously pitted parenchyma cells. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins undivided. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B4, LC4, EP4- COLOMBIA. BOLÍVAR: near Cartagena, 10°28'N, 75°32'W, 10 m, 4 Jul 1984, Gentry & Cuadros 47621 (NY); B5, LC5, EP5- COLOMBIA. MAGDALENA: Mun. Santa Marta, Parque Nacional Natural Tayrona, 23 Sep 1976, Lozano & Schnetter 2952 (NY); B6, LC6, EP6- COLOMBIA.



CÓRDOBA: Mun. Tierralta, 7 km from Tierralta to Planeta Rico, 100 m, 30 Jul 1986, Bernal et al. 1210 (NY).

1.1.19. Bactris hirta var. spruceana (Fig. 20)

**Midrib:** adaxially prominent, abaxially pointed to rounded; peripheral chlorenchymatous layer absent ad- and abaxially, inconspicuous laterally; fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 1-4-layered near the lamina; inner ground parenchyma with 2 ad- and abaxially vascular bundles.

**Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to main ribs; bands elsewhere in the lamina mostly abaxially. **Hairs:** on abaxial surface; hair base superficial, uniseriate, cutinized, and ellipsoidal.

**Epidermis:** ad- and abaxial cell walls not sinuous, outer wall thickened only on adaxial cells. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended but angle of obliquity varying; costal cells smaller than intercostal cells, rhombohedral to square-shaped, longitudinally extended, large costal regions raised, with up to 6 distinct longitudinal files of cells.

**Abaxial epidermis:** cells smaller than adaxial cells; costal and intercostal bands conspicuously differentiated;

Figure 20. Leaf anatomy of Bactris hirta var. spruceana.

A-C, cross-section; D-E, clearings; F-H, epidermal peels.

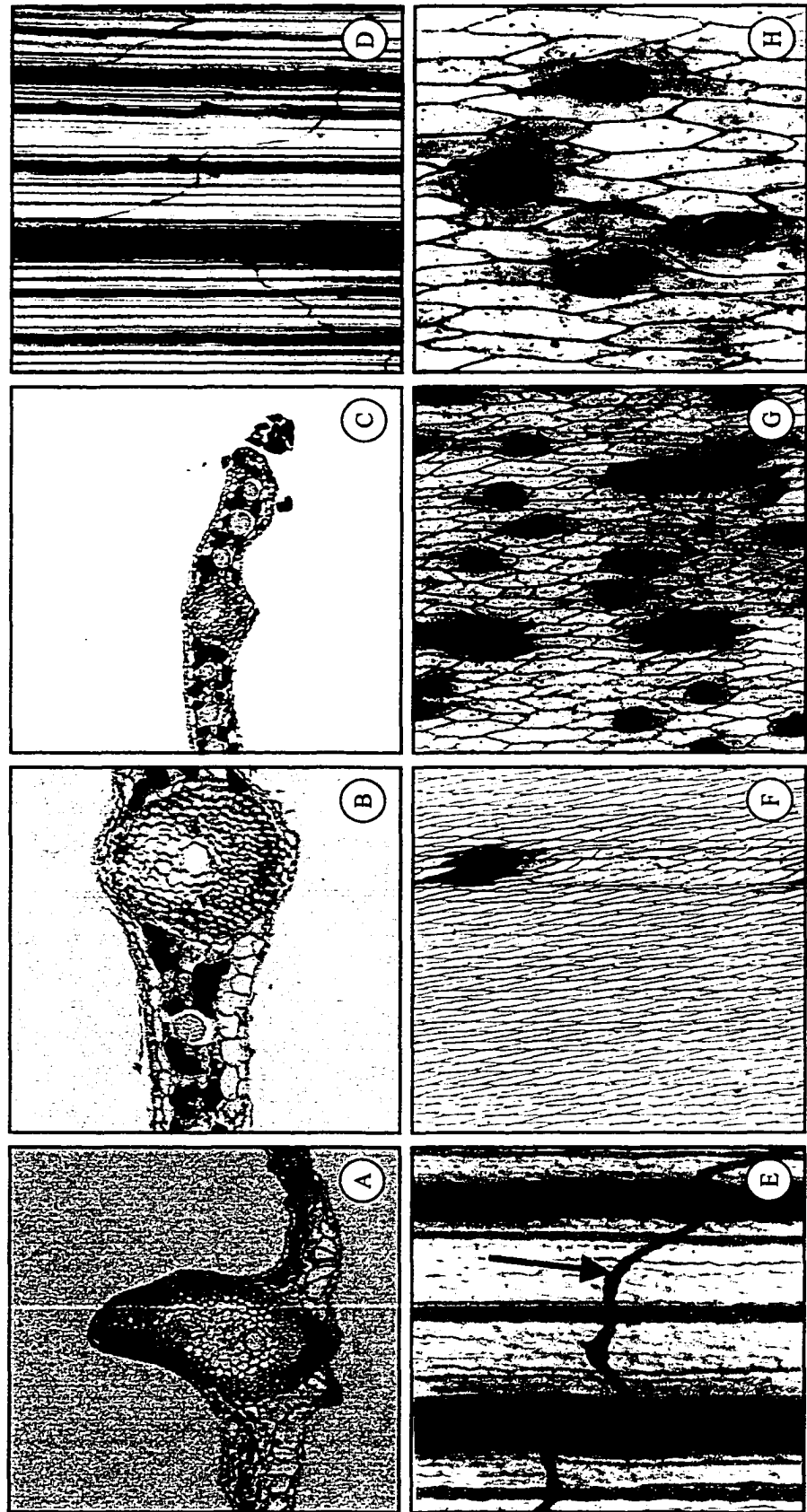
A. midrib (B1, x100), B. midsection (B3, x200), C. section

tip (B3, x100), D. venation pattern (LC1, x25), E.

transverse commissure, note it is sheathed by a single  
layer of thin-walled, translucent, parenchymatous cells

(LC1, x200), F. adaxial surface (EP1, x200), G. abaxial

surface (EP2, x200), H. stomata (EP2, x400).



intercostal cells like those of adaxial epidermis but less obliquely extended, inflated inward, almost interrupting the hypodermis; costal cells rectangular but narrower than intercostal cells, longitudinally extended, large costal bands with up to 11 distinct longitudinal files of cells.

**Stomata:** restricted to abaxial intercostal bands, superficial, not in distinct files, rather diffuse; terminal subsidiary cells not overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells slightly raised above the epidermis, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, wider abaxially, both layers absent above and below the main ribs, present and compressed above and below the secondary veins; ad- and abaxial cells irregularly oblong and transversely extended; abaxial cells roundish near the large veins. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll 3-4 layers of tightly arranged, thick-walled cells. **Tannin cells:** few, scattered and easily distinct from other mesophyll cells, or numerous, densely arranged and saturating the mesophyll.

**Fiber-sclereids:** absent. **Raphide-sacs:** absent or present and rare. **Non-vascular fibers:** large and numerous

cylindrical strands form a single layer level with small veins. **Primary veins:** ovoid, abaxially prominent; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2-4 layers of thick-walled fibers, ad- and abaxial region going through the hypodermis and reaching the epidermis. **Secondary veins:** ovoid, centered; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2-3-layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath incomplete, lacking abaxially; inner sheath complete, consisting of 1-2 layers of thick-walled fibers. **Quaternary veins:** absent.

**Marginal rib:** absent. **Phloem:** of large veins irregularly divided into as many as 4 strands by sclerotic partitions. **Transverse commissures:** unusually narrow, elongate, regularly distributed and forming a continuous pattern in surface view; sheathed by a single layer of thin-walled, translucent, parenchymatous cells.

**Specimens examined.** B1, LC1, EP1- VENEZUELA.

AMAZONAS: Río Mavaca, 2°1'N, 65°7'W, 228 m, 6 Feb 1989,

Henderson 978 (NY); B2, LC2, EP2- VENEZUELA. AMAZONAS:

Neblina base camp, 0°50'N, 66°10'W, 14 Feb 1984, Henderson

25 (NY); B3, LC3, EP3- VENEZUELA. AMAZONAS: Cucuy, 1°13'N,

66°51'W, 2 Feb 1968, Wessels Boer 2385 (NY).

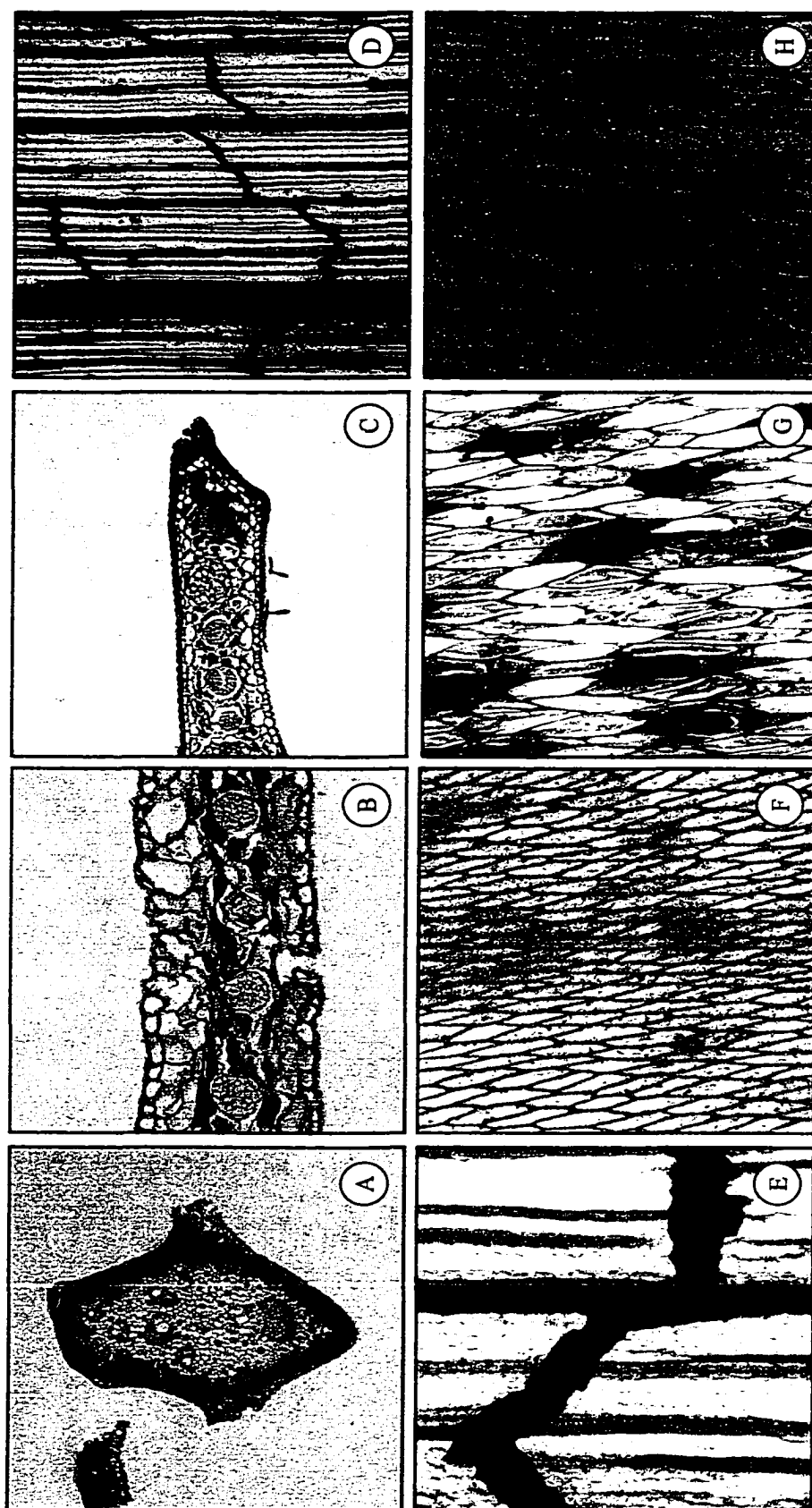
1.1.20. Bactris horridispatha (Fig. 21)

**Midrib:** abaxially pointed, adaxially or equally prominent on both surfaces; peripheral chlorenchymatous layer inconspicuous laterally, interrupted adaxially; inner fibrous layer well-delimited, thick-walled, well-developed on all sides; inner ground parenchyma with 2-6 large vascular bundles and few phloem strands irregularly embedded in the innermost fibrous layers. **Expansion cells:** forming inconspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous.

**Hairs:** on ad- and abaxial surface but more frequent abaxially along the costal bands; hair base not seen in cross-section but apparently multiseriate, cutinized, ellipsoidal from surface view. **Cuticle** persistent only near the margin of the lamina. **Epidermis:** ad- and abaxial cell walls not sinuous, outer wall slightly thickened.

**Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying, cells organized into poorly distinguished longitudinal files; costal cells shorter than intercostal cells, rectangular to rhombohedral, mostly longitudinally extended, large costal regions with 5-7 distinct longitudinal files of cells. **Abaxial epidermis:** cells

Figure 21. Leaf anatomy of Bactris horridispatha. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B28, x40), B. midsection (B30, x200), C. section tip (B30, x100), D. venation pattern (LC30, x25), E. transverse commissure (LC30, x200), F. adaxial surface (EP28, x200), G. abaxial surface (EP30, x200), H. stomata (EP30, x400).





smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells irregularly shaped, but mostly rhombohedral, longitudinally extended, not in distinct files; costal cells narrower than intercostal cells, rectangular, longitudinally extended, the larger bands slightly raised, with up to 18 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct longitudinal files, diffuse; terminal subsidiary cells slightly overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells slightly transversely extended and irregularly hexagonal. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll, 5 layers of thin-walled cells. **Tannin cells:** numerous, densely arranged, the tanniniferous material filling partially or completely the cells, saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** common, near abaxial hypodermis. **Non-vascular fibers:** forming cylindrical strands of variable

size; the larger strands form an abaxial layer, level with the small veins; smaller strands mostly attached to the adaxial hypodermis. **Primary veins:** roundish, prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, thick-walled, well-developed and reaching the hypodermis abaxially, laterally and adaxially only 2-3 layers. **Secondary and Tertiary veins:** almost indistinguishable, the secondary slightly larger; both veins roundish, abaxial; outer sheath incomplete abaxially in secondary veins, complete in the tertiary; inner sheath complete, thick-walled and 1-layered in both veins. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by files of fibers or thin sclerotic partitions. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

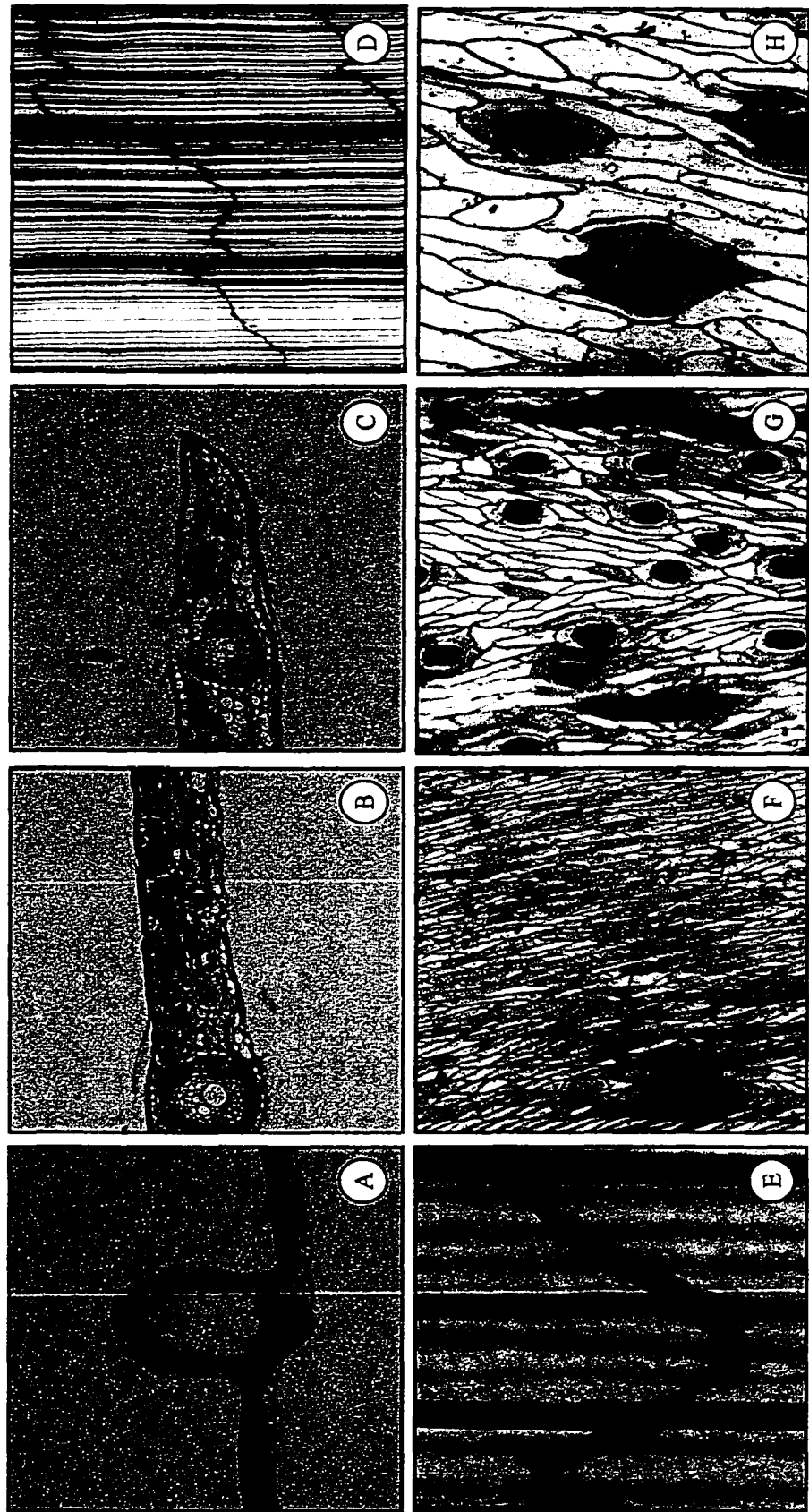
**Specimens examined.** B28, LC28, EP28- BRAZIL. BAHIA: Mun. Una, Estação Lemos de Maio, 15°18'S, 39°4'W, 20-100 m, 23 Dec 1996, Sant'Ana et al. 627 (NY); B29, LC29, EP29- BRAZIL. BAHIA: Mun. Una, km 46 on BA-001 Ilhéus-Una, 15°9'S, 39°5'W, 13-14 Jul 1993, Jardim et al. 178 (NY); B30, LC30, EP30- BRAZIL. BAHIA: Mun. Una, 1 km W of Una, 15°18'S, 39°04'W, 12 Jan 1989, L. Noblick 4730 (NY).

1.1.21. Bactris jamaicana (Fig. 22)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete and conspicuous; inner fibrous layer well-delimited, thick-walled, well-developed, 6 or more-layered ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 2 large and several smaller peripheral vascular bundles, few small phloem strands embedded in the adaxial region of the fibrous layers. **Expansion cells:** forming inconspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** on ad- and abaxial surface, but more numerous along abaxial costal bands; base superficial, uniseriate, cutinized, ellipsoidal.

**Epidermis:** ad- and abaxial cell walls not sinuous, thickened outer wall on adaxial cells only. **Adaxial epidermis:** intercostal cell-shape variable, almost spindle-shaped but a few cells clearly rhombohedral, obliquely-longitudinally extended but angle of obliquity varying, not arranged into distinct longitudinal files; costal cells shorter and wider than intercostal cells, mostly rhombohedral, but cells on center of costa rectangular, obliquely to longitudinally extended, large

Figure 22. Leaf anatomy of Bactris jamaicana. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B93, x40), B. midsection (B93, x100), C. section tip (B93, x100), D. venation pattern (LC93, x25), E. transverse commissure (LC93, x200), F. adaxial surface (EP91, x200), G. abaxial surface (EP91, x200), H. stomata (EP91, x400).



costal regions with up to 15 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells like those of the adaxial epidermis but less obliquely extended and more irregularly shaped; costal cells narrower than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 13 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, diffuse; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells and adjacent epidermal cells slightly raised above the epidermis, each guard-cell with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, the adaxial layer wider and continuous above the large veins, the abaxial layer compressed below; ad- and abaxial cells hexagonal, mostly transversely extended, except the adaxial cells near the margin of the lamina. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 5-6 layers of thick-walled cells. **Tannin cells:** numerous, a few individual cells readily distinct, completely filled by the

reddish tanniniferous material, other cells only partially filled with the tanniniferous material, the mesophyll not saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical and columnar strands; the cylindrical strands larger, arranged in a single layer level with the veins; smaller strands columnar and often attached to the adaxial hypodermis. **Primary veins:** ovoid, prominent ad- and abaxially; the abaxial fibrous area reaching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, consisting of 2-4 layers of thick-walled fibers. **Secondary veins:** ovoid, slightly prominent ad- and abaxially, centered; outer sheath incomplete, only lateral; inner sheath complete, consisting of 1-3 layers of thick-walled fibers. **Tertiary veins:** narrowly ovoid to roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, consisting of 1-2 layers of thick-walled fibers. **Quaternary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers. **Transverse commissures:** wide, elongate and short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B91, LC91, EP91- JAMAICA.

WESTMORELAND: between Kew Park and Rat Trap, 19 Sep 1963,

Wessels Boer 1663 (NY); B92, LC92, EP92- JAMAICA. ST.

THOMAS: Johnson Mountain Hills, 29 Jul 1966, Read 1692

(NY); B93, LC93, EP93- JAMAICA. CLARENDON: Mason River

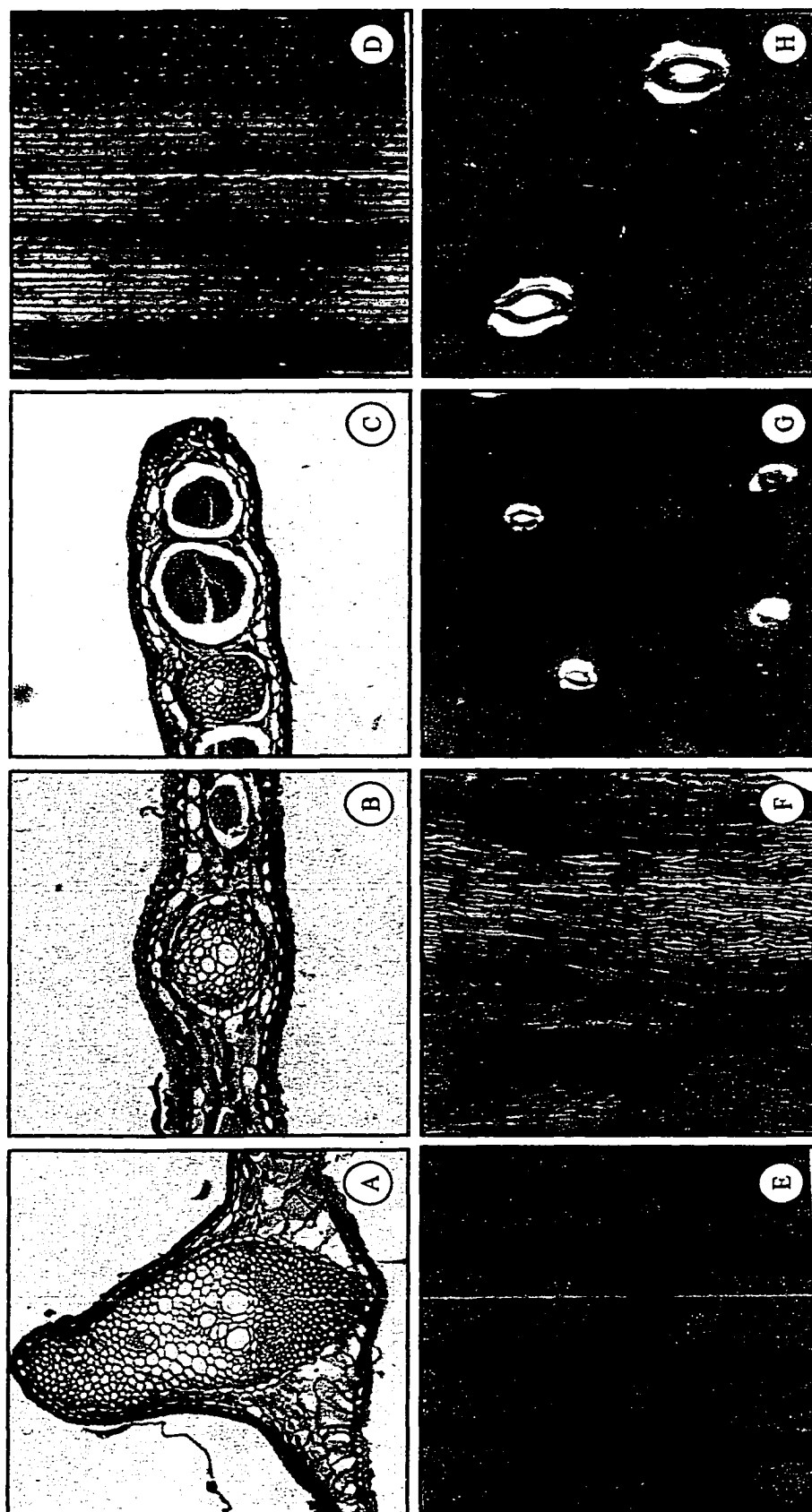
Field Station, 27 Jun 1992, Salzman 136 (FLAS).

#### 1.1.22. Bactris killipii (Fig. 23)

**Midrib:** absent. **Main ribs:** large, midrib-like, adaxially prominent, abaxially pointed; peripheral chlorenchymatous layer absent ad- and abaxially, inconspicuous; inner fibrous layer not well-delimited, well-developed and thick-walled abaxially, narrowed laterally, 1-2-layered near the lamina, thin-walled adaxially; inner ground parenchyma with 1-2 large vascular bundles, the adaxial bundle often inversely oriented. **Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to main ribs; bands elsewhere in the lamina frequently in folding regions, either ad- or abaxially. **Hairs:** on abaxial surface; hair base sunken, uniseriate, thick-walled, ellipsoidal to spherical. **Epidermis:** cuticle thick and persistent; ad- and abaxial cell walls not sinuous, thick cutinized layer on outer and anticlinal walls. **Adaxial epidermis:**



Figure 23. Leaf anatomy of Bactris killipii. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B9, x100), B. midsection (B7, x200), C. section tip (B7, x100), D. venation pattern (LC7, x20), E. transverse commissure (LC7, x200), F. adaxial surface (EP9, x200), G. abaxial surface (EP9, x200), H. stomata (EP9, x400).



intercostal and costal cells spindle-shaped, longitudinally extended; costal cells shorter than intercostal cells, more regularly shaped, rectangular to hexagonal, longitudinally extended, large costal regions with up to 7 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral, longitudinally extended; costal cells rhombohedral on small bands to almost rectangular in larger bands, longitudinally extended, these raised above the intercostal surface, large costal bands with up to 14 distinct longitudinal files of cells. **Stomata:** slightly above the epidermal surface but sunken below the cuticle layer; scattered on adaxial surface near the costal regions, and dense, not in distinct longitudinal files, on abaxial intercostal bands; terminal subsidiary cells not overarched the guard-cells, smaller and well-differentiated from the surrounding epidermal cells; guard-cells slightly raised above the epidermis, each with 2 cutinized ledges, the outermost enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers absent above and below the main ribs, present and compressed above and below the secondary veins; ad- and

abaxial cells slightly to strongly transversely extended, oblong and rectangular. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll 3-4 layers of tightly arranged, thin-walled cells. **Tannin cells:** numerous, the tanniniferous material not completely filling the cells and not saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming massive and numerous cylindrical strands distributed in a single layer level with the veins; the cylindrical strands especially large near the margin of the lamina. **Primary veins:** obovoid, prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, touching the hypodermis, consisting of 1-2 layers of thick-walled fibers, but the adaxial fibers have larger pits. **Secondary veins:** roundish, abaxial; outer sheath incomplete, only lateral; inner sheath complete, 1-2-layered, thick-walled fibers abaxially and thin-walled fibers adaxially. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath 1-layered, composed of sclerotic and conspicuously pitted parenchyma cells. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins irregularly divided into 2-4 strands by files of thick-walled fibers. **Transverse commissures:** wide, elongate,

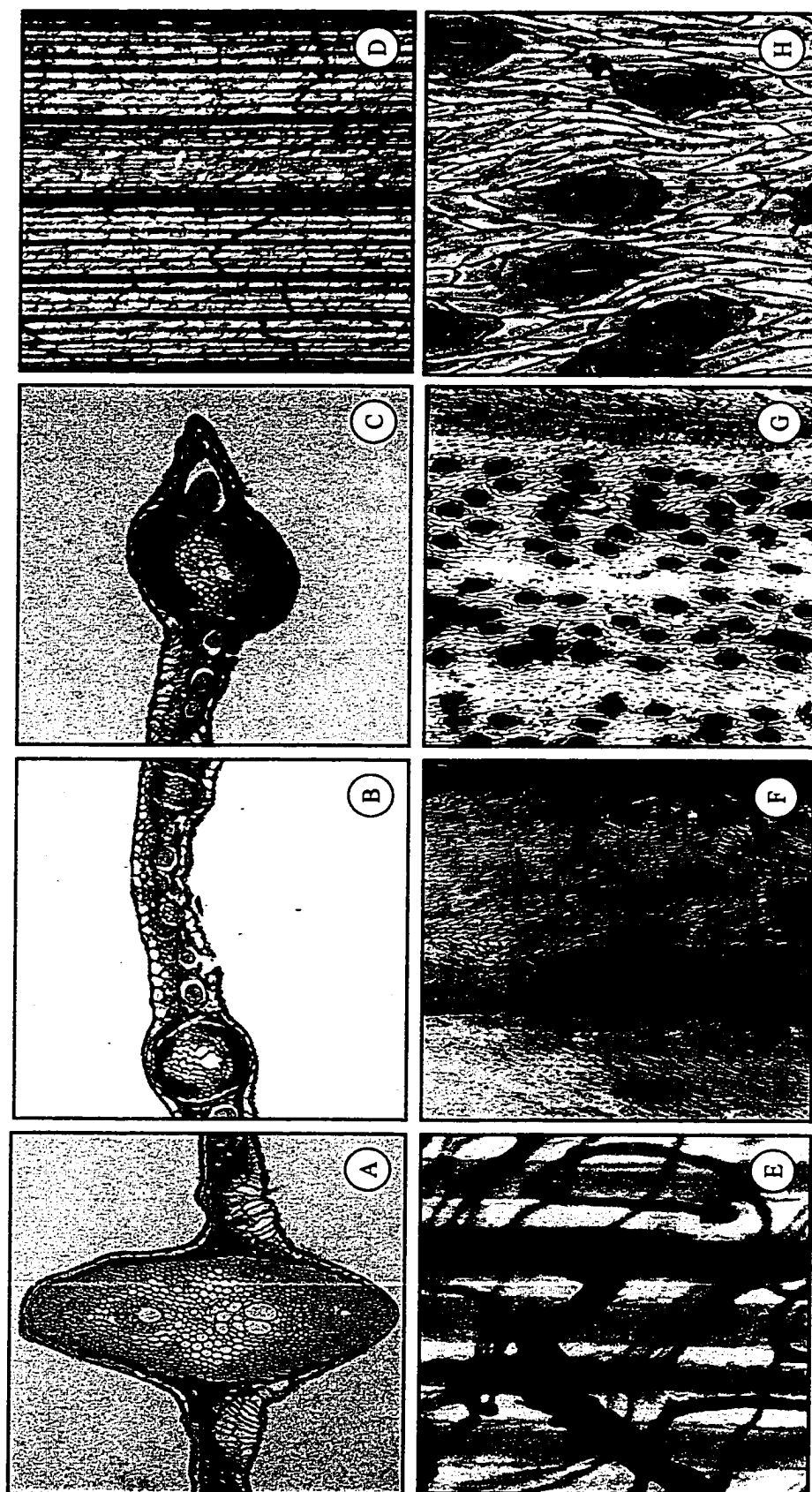
regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B7, LC7, EP7- BRAZIL. AMAZONAS: Mun. Tefé, Rio Curimatá de Baixo, ca. 3°55'S, 65°10'W, 18 Jan 1991, Henderson & Guedes 1573 (NY); B8, LC8, EP8- COLOMBIA. AMAZONAS: road from Leticia to Tarapacá, ca. 7 km from Leticia, 180 m, 17 Mar 1990, Galeano et al. 2107 (NY); B9, LC9, EP9- BRAZIL. AMAZONAS: Mun. Atalaia do Norte, Rio Javari, Paumari (or Natividad), 4°17'S, 70°18'W, 5 Jan 1989, Henderson et al. 838 (NY).

1.1.23. Bactris major var. socialis (Fig. 24)

**Midrib:** abaxially pointed, equally prominent on both surfaces; peripheral chlorenchymatous layer conspicuous laterally, incomplete adaxially; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 2-4 large and few smaller vascular bundles, several small phloem strands embedded in the innermost abaxial region of the fibrous layer. **Expansion cells:** forming 1-2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina ad- and abaxially prominent. **Hairs:** on abaxial costal and intercostal

Figure 24. Leaf anatomy of Bactris major var. socialis. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B58, x40), B. midsection (B60, x100), C. section tip (B60, x100), D. venation pattern (LC59, x25), E. transverse commissure (LC59, x200), F. adaxial surface, note some fiber sclereids have remain attached (EP59, x200), G. abaxial surface (EP59, x200), H. stomata (EP69, x400).



region, adaxially on intercostal bands or adjacent to costal bands; hair base sunken, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying and some cells almost spindle-shaped, files of cells poorly distinguished; costal cells shorter than intercostal cells, rectangular to rhombohedral, longitudinally extended, large costal regions with up to 15 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells irregularly shaped and extended, most rhombohedral cells not adjacent to stomata; costal cells smaller than intercostal cells, rhombohedral to rectangular, longitudinally extended, the larger bands only slightly raised, with up to 10 distinct longitudinal files of cells. **Stomata:** superficial, few near the adaxial costal regions, adaxially numerous, densely distributed on intercostal bands, not in distinct longitudinal files; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells slightly raised below the epidermal surface, each with 2 cutinized ledges of similar



size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; adaxial cells slightly transversely extended, square to rectangular in shape; abaxial cells transversely extended, rectangular. **Chlorenchyma:** palisade mesophyll single layered, poorly differentiated; spongy mesophyll well-differentiated, 5 layers of thick-walled cells. **Tannin cells:** few, mostly adaxial, the red tanniniferous material filling partially the cells and not saturating the mesophyll. **Fiber-sclereids:** numerous, forming a secondary, transversely extended, fibrous network in surface view. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands distributed in a single abaxial layer level with small veins. **Primary veins:** ovoid, slightly prominent ad- and abaxially; the abaxial fibrous area reaching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, many thick-walled fibers ad- and abaxially, laterally 2-3 layers of thin-walled fibers. **Secondary veins:** ovoid to oblong, centered; outer sheath incomplete, only lateral; inner sheath incomplete, ad- and abaxially with thick-walled fibers, laterally interrupted by sclerotic and conspicuously pitted parenchyma cells. **Tertiary veins:** roundish, abaxial; outer sheath complete;

inner sheath consisting of sclerotic and conspicuously pitted parenchyma cells. **Quaternary veins:** absent.

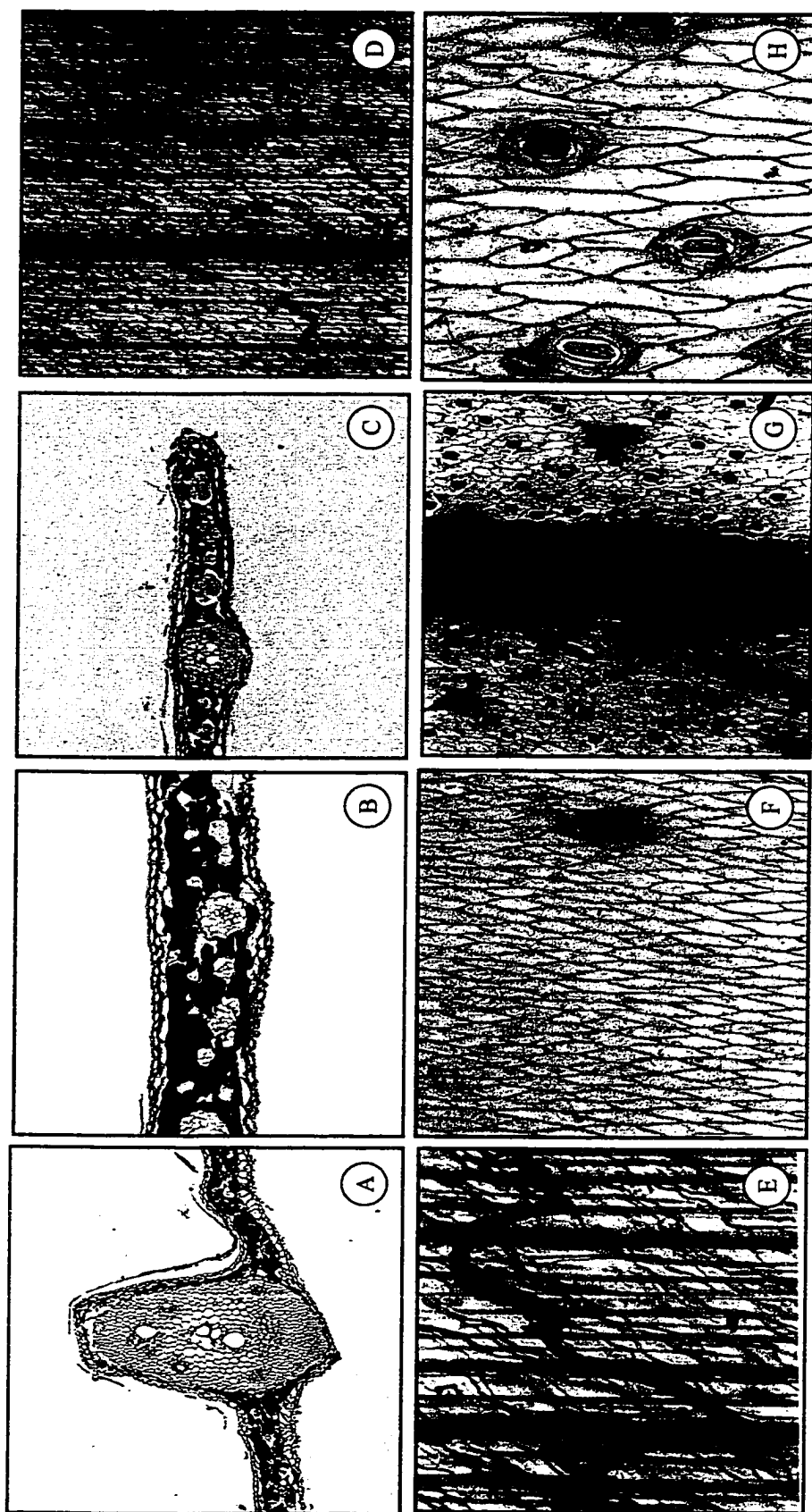
**Marginal rib:** prominent ad- and abaxially; inner fibrous layer with thick-walled fibers in the ad- and abaxial area, laterally thin-walled. **Phloem:** of large veins divided into distinct strands by lines of fibers or thin sclerotic partitions. **Transverse commissures:** wide, elongate, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B58, LC58, EP58- BOLIVIA. PANDO: Prov. Madre de Dios, Puerto Candelaria, Río Madre de Dios, 21 km S of Riberalta, 11°2'S, 66°15'W, 125 m, 19 Aug 1985, Nee 31432 (NY); B59, LC59, EP59- BOLIVIA. SANTA CRUZ: Prov. Ichilo, Parque Nacional Amboró, 17°30'S, 63°44'W, 400 m, 10 Mar 1989, Saldias 689 (NY); B60, LC60, EP60- BOLIVIA. SANTA CRUZ: Prov. Andrés Ibáñez, 18°30'S, 63°50'W, 400 m, 16 May 1988, Moraes & Henderson 1053 (NY).

1.1.24. Bactris maraja var. trichospatha (Fig. 25)

**Midrib:** abaxially rounded, adaxially prominent; peripheral chlorenchymatous layer conspicuous, complete or shortly interrupted adaxially, with small roundish non-vascular fiber bundles and tannin cells; inner fibrous layer well-

Figure 25. Leaf anatomy of Bactris maraja var. trichospatha. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B56, x40), B. midsection (B57, x200), C. section tip (B56, x100), D. venation pattern (LC57, x20), E. transverse commissure (LC57, x100), F. adaxial surface (EP55, x200), G. abaxial surface (EP55, x200), H. stomata (EP56, x200).



delimited, thick-walled, well-developed on all sides; inner ground parenchyma with 3-5 large and several smaller vascular bundles, few small phloem strands embedded in the innermost fibrous layers. **Expansion cells:** forming 1-layered abaxial bands adjacent to the midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** on adaxial intercostal region but more abundant on abaxial costal bands; hair base multiseriate, distal region multiseriate, cutinized. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, organized into distinct files of cells; costal cells smaller than intercostal cells, rectangular, longitudinally extended, large costal regions with up to 16 distinct longitudinal files. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells irregularly shaped, many rhombohedral, but also hexagonal or pentagonal, obliquely-longitudinally extended, not in distinct files; costal cells narrower and more regularly shaped than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with 8-18 distinct longitudinal files of cells. **Stomata:** superficial; adaxially few, near the costal regions; numerous on abaxial

intercostal bands, diffuse, not in distinct longitudinal files; terminal subsidiary cells partially overarchng the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with the epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells transversely extended, shape irregularly rectangular. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-6 layers of thick-walled cells. **Tannin cells:** numerous, the red tanniniferous material completely filling the cells and saturating the mesophyll. **Fiber-sclereids:** numerous, forming a secondary, transversely extended, fibrous network in surface view. **Raphide-sacs:** absent. **Non-vascular fibers:** forming small to large cylindrical strands, mostly abaxially, level with the veins. **Primary veins:** ovoid to pear-shaped, prominent abaxially; outer sheath incomplete, lateral only; inner sheath complete, consisting of 3 or more layers of thick-walled fibers. **Secondary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath incomplete, 1-2-layered, numerous thick-walled fibers abaxially and few

thin-walled fibers adaxially. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath incomplete, 1-layered, abaxially thick-walled, adaxially thin-walled.

**Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

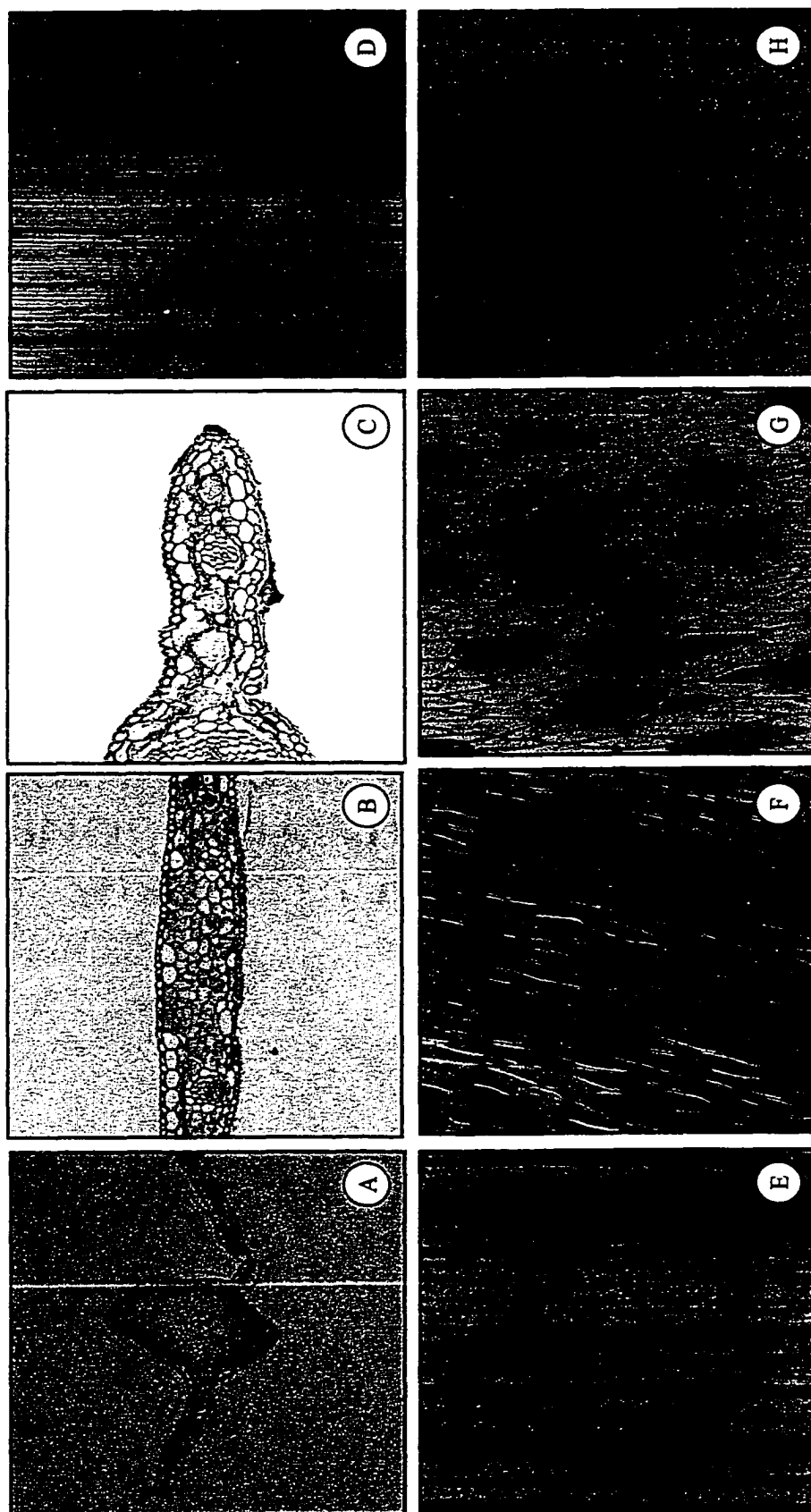
**Specimens examined.** B55, LC55, EP55- BRAZIL. ACRE: Rio Juruá, near Natal, 8°20'S, 72°15'W, 7 Feb 1992, Henderson et al. 1655 (NY); B56, LC56, EP56- BRAZIL. AMAZONAS: Altamira, Rio Juruá, 6°35'S, 68°54'W, 13 Nov 1991, Pardini 42 (NY); B57, LC57, EP57- BRAZIL. AMAZONAS: Mun. Tefé, Missão de Tefé on Rio Amazonas, 13 Jan 1991, Henderson et al. 1545 (NY).

1.1.25. Bactris mexicana var. mexicana (Fig. 26)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete or incomplete, irregular, conspicuous or inconspicuous; inner fibrous layer well-delimited, well-developed and thick-walled ad- and abaxially or thin-walled adaxially, narrowed laterally, 2-layered near the lamina; inner ground parenchyma with 2

Figure 26. Leaf anatomy of Bactris mexicana var. mexicana.  
A-C, cross-section; D-E, clearings; F-H, epidermal peels.  
A. midrib (B75, x40), B. midsection (B76, x100), C.  
section tip (B77, x100), D. venation pattern (LC73, x20),  
E. transverse commissure (LC73, x100), F. adaxial surface  
(EP74, x200), G. abaxial surface (EP74, x200), H. stomata  
(EP74, x400).





large and 2-3 smaller vascular bundles, rarely small phloem strands embedded in the innermost fibrous layers.

**Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** on ad- and abaxial surface, not numerous; hair base not seen. **Epidermis:** ad- and abaxial cell walls not sinuous, walls not thickened. **Adaxial epidermis:** intercostal cells obliquely-longitudinally extended, rhombohedral to almost spindle-shaped when angle of obliquity is too small, not organized into distinct longitudinal files; costal cells shorter than intercostal cells, rhombohedral, longitudinally extended, large costal regions with 3 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral but shape quite variable, longitudinally extended; costal cells shorter than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 15 files of distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells;

guard-cells raised above the level of epidermal surface, each with 2 cutinized ledges, the outermost much, the wall thickened below each ledge. **Substomatal chamber:** small.

**Hypodermis:** 1-layered beneath each surface, both layers interrupted or not above the large veins, compressed below; ad- and abaxial cells slightly transversely extended, hexagonal. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 5-6 layers of thick-walled cells. **Tannin cells:** numerous, mostly adaxial, the tanniniferous material not completely filling the cells and not saturating the mesophyll. **Fiber-sclereids:** absent.

**Raphide-sacs:** absent. **Non-vascular fibers:** forming strands of variable size and shape; large strands cylindrical and usually distributed in a single layer level with small veins; smaller strands more or less columnar and frequently attached to the adaxial hypodermis. **Primary veins:** trullate to obtrullate, prominent abaxially; the ad- and abaxial fibrous area reaching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, consisting of 2-4 layers of thick-walled fibers and a poorly developed adaxial buttress. **Secondary veins:** widely ovoid, slightly prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2-3 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer

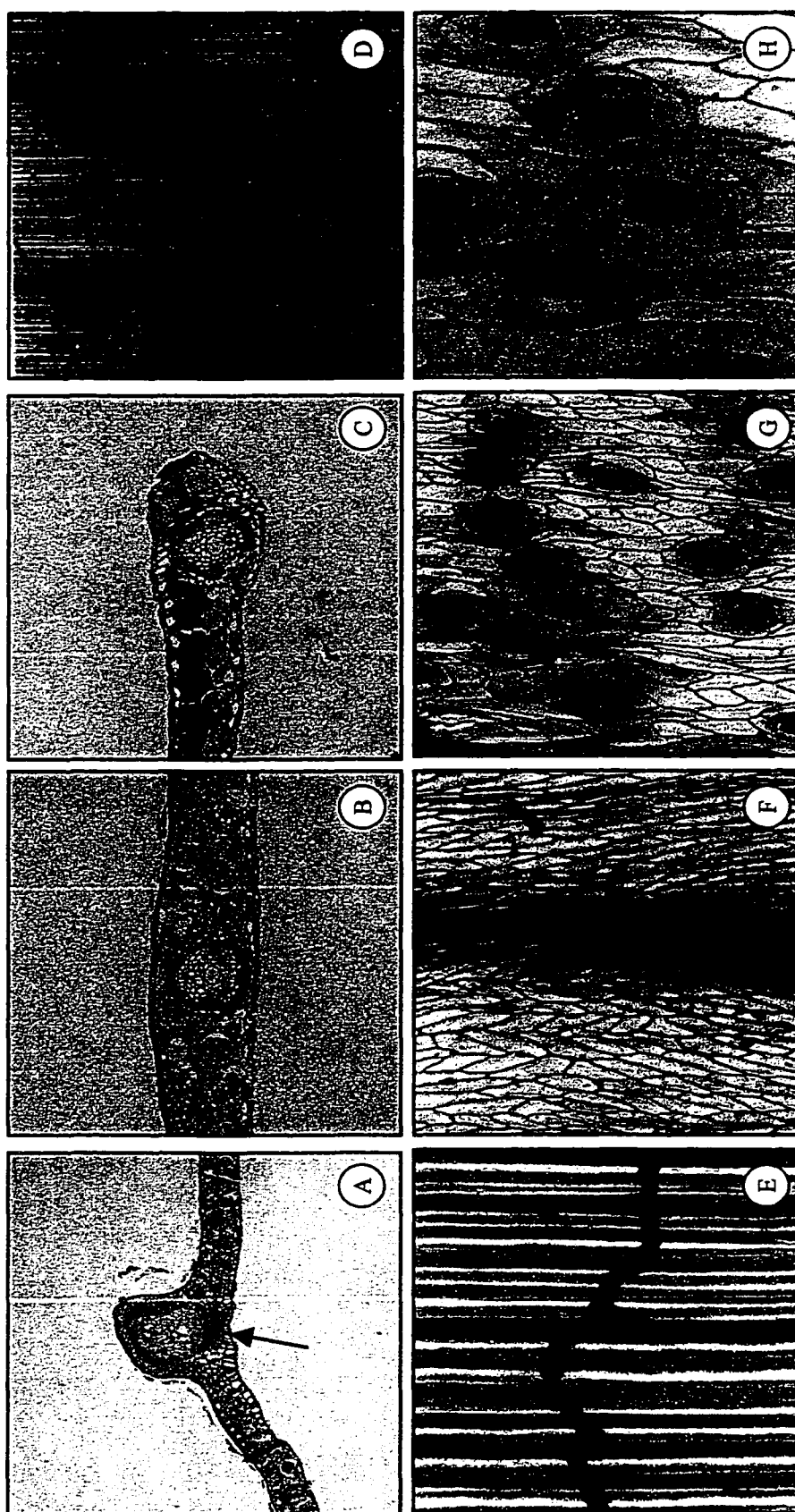
sheath incomplete abaxially; inner sheath consisting of 1-2 layers of thin-walled fibers. **Quaternary veins:** roundish, abaxial; outer sheath complete; inner sheath complete, consisting of 1 layer of thin-walled fibers. **Marginal rib:** absent. **Phloem:** of large veins divided into indistinct strands by sclerotic partitions. **Transverse commissures:** wide, elongate, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B73, LC73, EP73- MEXICO. OAXACA: 37 mi. from Empalme Balboa beyond Mathias Romero, 5 May 1952, Moore & Brossard 6353 (NY); B74, LC74, EP74- MEXICO. VERACRUZ: Pital, Liebmann s.n. (NY); B75, LC75, EP75- MEXICO. TABASCO: 8.2 km from Fco. Rueda, 20 Jun 1983, C. Cowan et al. 3985 (NY).

1.1.26. Bactris plumeriana (Fig. 27)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete, conspicuous, with numerous tannin cells; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 1-2-layered near the lamina; inner ground parenchyma with 2 large and 1-2 smaller vascular bundles,

Figure 27. Leaf anatomy of Bactris plumeriana. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib, note the confluent expansion cells (B118, x40), B. midsection (B118, x100), C. section tip (B116, x100), D. venation pattern (LC118, x20), E. transverse commissure (LC118, x200), F. adaxial surface (EP116, x200), G. abaxial surface (EP116, x200), H. stomata (EP116, x400).



few small phloem strands embedded in the fibrous layer.

**Expansion cells:** forming conspicuous, 1-layered and confluent abaxial band; bands elsewhere in the lamina inconspicuous. **Hairs:** rare on adaxial surface, frequent on large abaxial costal bands, few on small costa forming a poorly defined line; base sunken, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, not thickened. **Adaxial epidermis:** intercostal cells mostly rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying, thus the cell-shape is irregular in those areas; costal cells smaller than intercostal cells, rhombohedral to rectangular in shape, mostly obliquely-longitudinally extended, large costal regions with 3-5 poorly distinguished longitudinal files of cells. **Abaxial epidermis:** cells similar in size to those of adaxial epidermis, costal and intercostal bands conspicuously differentiated; intercostal cells more irregularly shaped than adaxial cells, many rhombohedral and somewhat longitudinally extended, except the ones near the stomata; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands slightly raised, with up to 10 distinct longitudinal files of cells. **Stomata:** superficial, numerous and restricted to abaxial intercostal bands, not in distinct files, rather

diffuse; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells slightly raised above the epidermis due to its bigger size, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells slightly transversely extended, hexagonal. **Chlorenchyma:** palisade mesophyll irregularly 2-layered, the first layer level with the columnar, non-vascular fiber bundles; spongy mesophyll well-differentiated, 4-5 layers of thick-walled cells. **Tannin cells:** absent or present; if present, numerous, adaxially most cells completely filled by the reddish tanniniferous material, abaxially the cells only partially filled with the tanniniferous material, the mesophyll completely saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands of variable size and columnar strands attached to the adaxial hypodermis; the larger cylindrical strands arranged in a single layer level with the small veins; other smaller cylindrical strands irregularly distributed in the mesophyll. **Primary veins:** ovoid, slightly prominent ad- and abaxially; the ad- and abaxial



fibrous area reaching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, ad- and abaxially well-developed, laterally only 1-2 layers of thick-walled fibers. **Secondary veins:** ovoid, abaxial; outer sheath incomplete, lateral only; inner sheath complete, single layered, abaxially and laterally thick-walled, adaxially thin-walled. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath incomplete, single layered, few thick-walled fibers abaxially, laterally and adaxially thin-walled. **Quaternary veins:** roundish, abaxial; outer sheath complete; inner sheath thin-walled, 1-layered. **Marginal rib:** prominent abaxially; outer sheath incomplete, lateral only; inner sheath complete, thick-walled and well-developed. **Phloem:** of large veins divided into distinct strands by lines of fibers or inconspicuous sclerotic partitions. **Transverse commissures:** wide, elongate, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

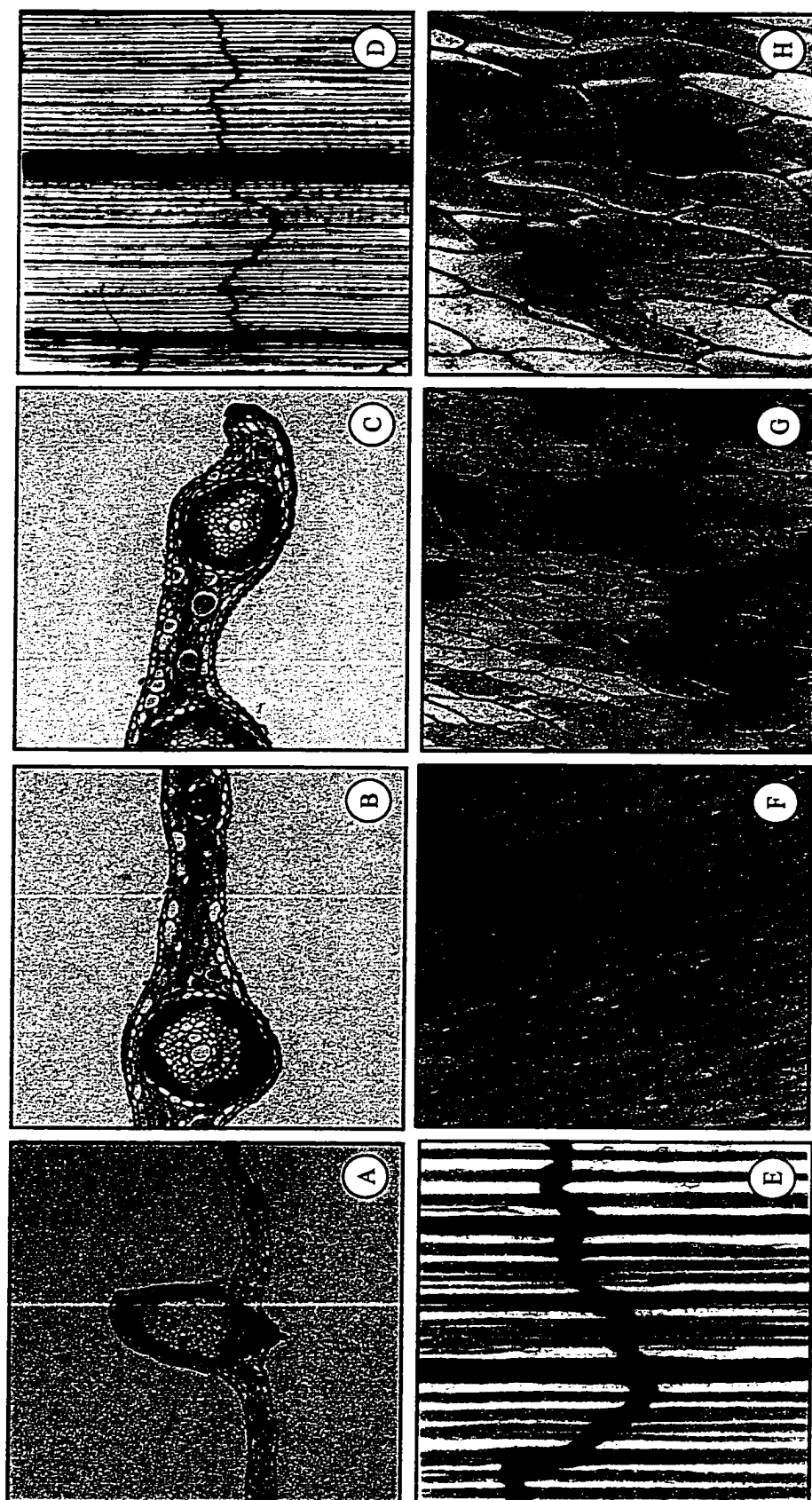
**Specimens examined.** B116, LC116, EP116- DOMINICAN REPUBLIC. DAJABÓN: road from Partido to Dajabón, 0.5 km W of Santiago de la Cruz, 10 Jul 1993, Salzman & Zona 260 (FLAS); B117, LC117, EP117- DOMINICAN REPUBLIC. ESPAILLAT: 6.2 km E of Gaspar Hernández, 19.6 km W of Río San Juan, 10

Jul 1993, Salzman & Zona 262 (FLAS); B118, LC118, EP118-DOMINICAN REPUBLIC. MONSEÑOR NOUEL: Loma El Caribe, 10 Jul 1993, Salzman & Zona 264 (FLAS).

1.1.27. Bactris ptariana (Fig. 28)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete or incomplete, somewhat irregular, conspicuous; inner fibrous layer well-delimited, thick-walled and well-developed ad- and abaxially, narrowed laterally, 2-layered near the lamina; inner ground parenchyma with 3 large vascular bundles and few smaller lateral bundles. **Expansion cells:** forming conspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** rare on adaxial surface, common abaxially along costal bands; hair base sunken, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, not thickened. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying, not in distinct longitudinal files of cells; costal cells smaller than intercostal cells, rectangular in shape, longitudinally extended, large costal regions with 6-12 distinct longitudinal files of cells. **Abaxial epidermis:**

Figure 28. Leaf anatomy of Bactris ptariana. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B70, x40), B. midsection (B70, x100), C. section tip (B70, x100), D. venation pattern (LC72, x20), E. transverse commissure (LC72, x100), F. adaxial surface (EP71, x20), G. abaxial surface (EP71, x200), H. stomata (EP71, x400).



with cells narrower than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral, pentagonal or hexagonal, but many irregularly shaped, longitudinally extended; costal cells rectangular, longitudinally extended, narrower than intercostal cells, the larger bands raised, with up to 10 distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells not overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells slightly raised above the epidermis, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells slightly transversely extended, hexagonal. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-5 layers of thick-walled cells. **Tannin cells:** numerous, the tanniniferous material not completely filling the cells and not saturating the mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming strands of variable size and shape; the larger strands cylindrical

and irregularly distributed in the mesophyll; smaller strands mostly columnar and frequently attached to the adaxial hypodermis. **Primary veins:** ovoid to trullate, prominent abaxially; the abaxial fibrous area touching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, several layers of thick-walled fibers, except the 1-2-layered lateral area. **Secondary veins:** ovoid, slightly prominent ad- and abaxially, centered; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2-4 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath incomplete, only lateral; inner sheath complete, consisting of 1-2 layers of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** narrowly oblong; outer sheath incomplete, only lateral; inner sheath complete, several layers of thick-walled fibers in the ad- and abaxial area, 1-2 layers laterally. **Phloem:** of large veins divided into indistinct strands by thin sclerotic partitions. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B70, LC70, EP70- GUYANA.

Demerara-Mahaica Region, from Timehri Airport to Kuru Creek, 6°25'N, 58°15'W, 10-30 m, Hahn et al. 3858 (NY);

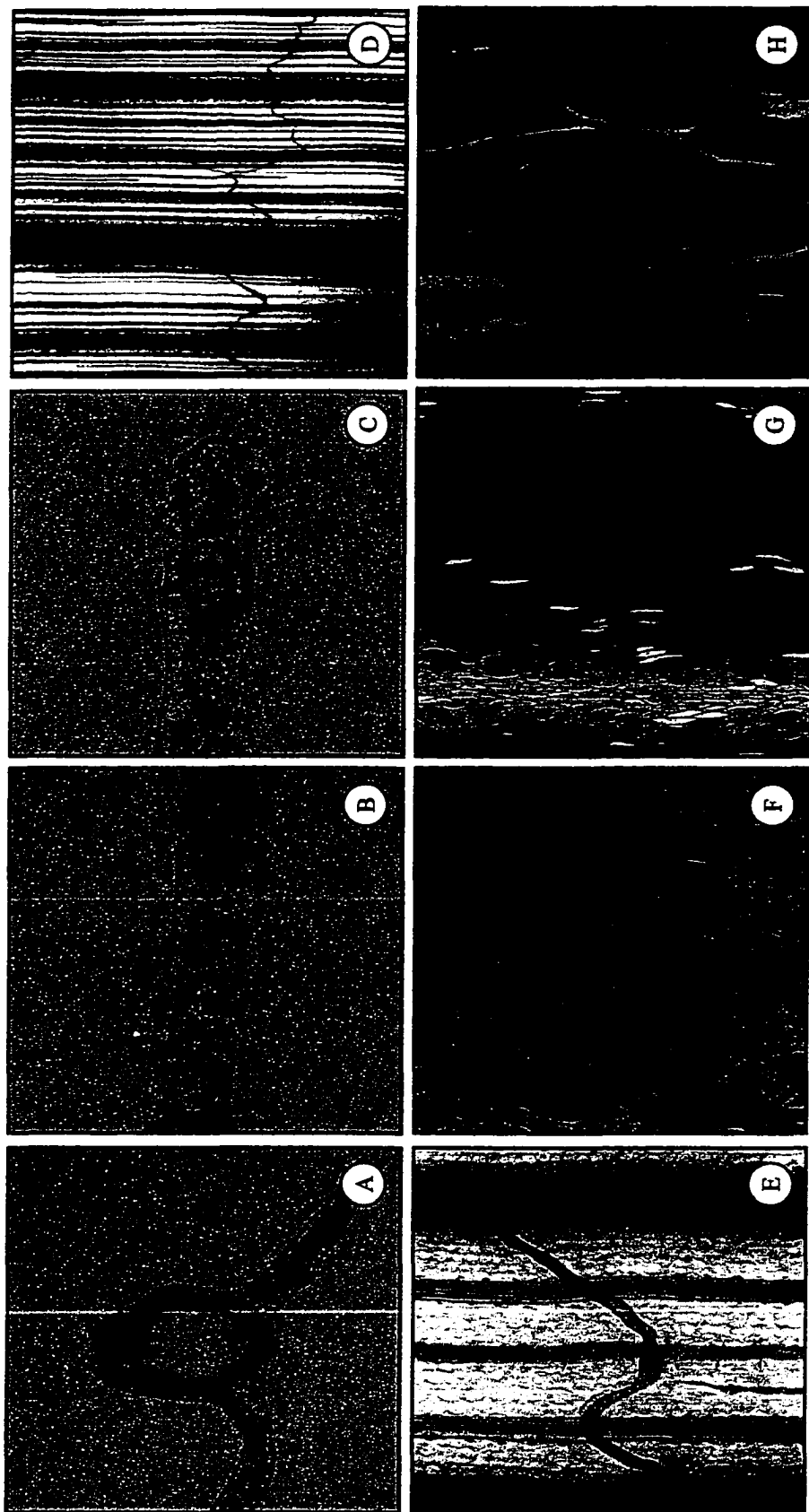
B71, LC71, EP71- GUYANA. Upper Demerara region, Mabura Hill, 5°25'N, 58°40'W, 50 m, 21 Apr 1989, Hahn 5810 (NY);  
 B72, LC72, EP72- VENEZUELA. BOLÍVAR: Cerro Venamo, 1395-1400 m, 31 Dec 1963, Steiermark et al. 92778 (NY).

1.1.28. Bactris riparia (Fig. 29)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer conspicuous and complete; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially but adaxially the layer wider, narrowed laterally, 2-layered near the lamina; inner ground parenchyma with 2-3 large and 4-8 smaller vascular bundles, either within the ground parenchyma or deeply embedded in the fibrous layer, few phloem strands embedded in the innermost adaxial region of the fibrous layers. **Expansion cells:** forming conspicuous, 1-2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina conspicuous ad- and abaxially. **Hairs:** very rare on abaxial surface, common on abaxial costal bands, on large bands irregularly distributed, on small bands they form a single line; hair base superficial, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, slightly thickened outer walls. **Adaxial**

Figure 29. Leaf anatomy of Bactris riparia. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B108, x40), B. midsection (B108, x100), C. section tip (B108, x100), D. venation pattern (LC108, x25), E. transverse commissure (LC108, x200), F. adaxial surface (EP107, x200), G. abaxial surface (EP107, x40), H. stomata (EP107, x200).





**epidermis:** intercostal cells rhombohedral, obliquely-longitudinally to longitudinally extended; costal cells smaller than intercostal cells, rectangular, longitudinally extended, large costal regions with up to 12 distinct longitudinal files of cells. **Abaxial epidermis:** cell size similar to adaxial cells; costal and intercostal bands conspicuously differentiated; intercostal cells irregularly shaped, but many hexagonal, pentagonal and rhombohedral, most cells longitudinally extended but variable near the stomata; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 38 distinct longitudinal files of cells. **Stomata:** superficial, few on adaxial surface near the costal regions, numerous on abaxial intercostal regions, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells slightly below the epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, the adaxial layer wider than abaxial layer, ad- and abaxial layers compressed above and below the large veins; ad- and abaxial cells slightly transversely extended, hexagonal. **Chlorenchyma:** palisade

mesophyll poorly differentiated, single layered; spongy mesophyll well-differentiated, 4-5 layers of thick-walled cells. **Tannin cells:** absent. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands of variable shape and size; large strands cylindrical, forming a single layer level with small veins; smaller strands irregularly shaped, many roundish, attached or not to the adaxial hypodermis. **Primary veins:** ovoid to ellipsoid, prominent abaxially; outer sheath incomplete, lateral only; inner sheath complete, well-delimited, thick-walled, 2-3 abaxial layers, 1-2 layers laterally and adaxially; the fibrous area touching the hypodermis. **Secondary veins:** roundish to ovoid, slightly prominent ad- and abaxially, centered; outer sheath complete; inner sheath complete, single layered, mostly thick-walled except a short, thin-walled lateral area. **Tertiary veins:** obovoid, abaxial; outer sheath incomplete, only lateral; inner sheath incomplete, single layered, almost completely thick-walled except for a short, lateral, thin-walled area. **Quaternary veins:** roundish, abaxial; outer sheath complete or incomplete below; inner sheath complete, single-layered, thick-walled abaxially, thin-walled adaxially. **Marginal rib:** absent. **Phloem:** of large veins poorly divided into distinct strands

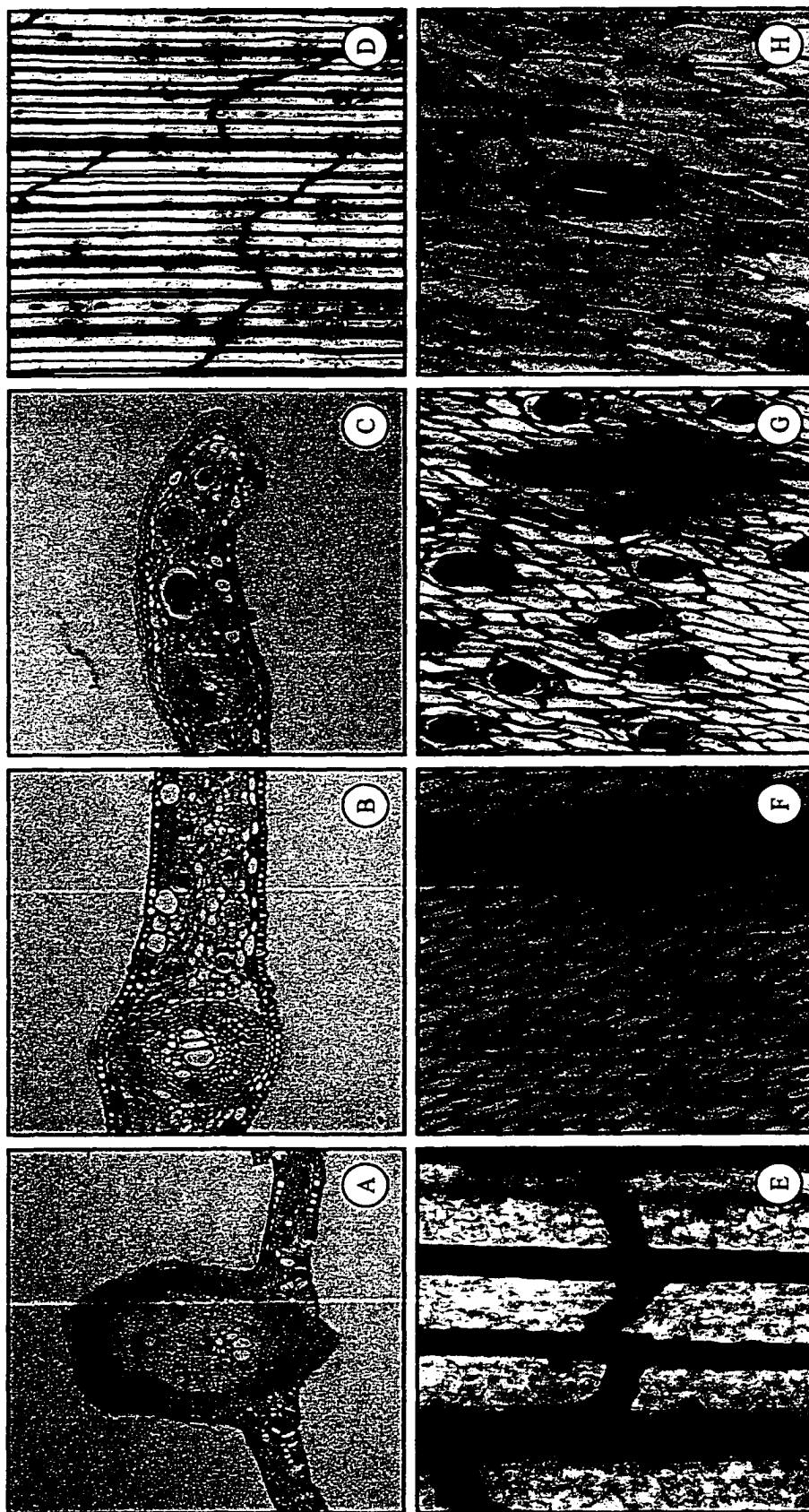
by thin sclerotic partitions. **Transverse commissures:** narrow, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by thin-walled, translucent, parenchymatous cells.

**Specimens examined.** B106, LC106, EP106- BRAZIL. ACRE: Rio Moa, between Seringal Belo Monte and Santa Barbara, 7°30'S, 73°W, 12 Feb 1992, Henderson 1676 (NY); B107, LC107, EP107- BRAZIL. ACRE: Rio Moa, between Seringal Belo Monte and Santa Barbara, 7°30'S, 73°W, 12 Feb 1992, Henderson et al. 1677 (NY); B108, LC108, EP108- PERU. LORETO: Padre Isla, opposite Iquitos, 11 Sep 1995, Henderson & Padilla 2020 (NY).

#### 1.1.29. Bactris setosa (Fig. 30)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer conspicuous but shortly interrupted adaxially; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 1 large abaxial vascular bundle, 3 smaller adaxial bundles inversely oriented and few smaller phloem strands regularly embedded in the innermost fibrous layers. **Expansion cells:** forming 1-2-layered, conspicuous abaxial

Figure 30. Leaf anatomy of Bactris setosa. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B18, x40), B. midsection (B18, x100), C. section tip (B18, x100), D. venation pattern (LC16, x25), E. transverse commissure (LC16, x200), F. adaxial surface (EP18, x200), G. abaxial surface (EP18, x200), H. stomata (EP18, x400).



bands adjacent to midrib, few bands elsewhere ad- or abaxially in the lamina. **Hairs:** on abaxial surface; hair base sunken, uniseriate, cutinized, clavate. **Epidermis:** ad- and abaxial cell walls not sinuous, outer wall thickened. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, organized into longitudinal files of cells; costal cells rhombohedral but shorter, narrower and less obliquely extended than intercostal cells, large costal regions with 6-12 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral, irregularly obliquely extended, outer wall irregularly shaped; costal cells narrower than intercostal cells, rhombohedral, longitudinally extended, the larger bands with up to 12 distinct longitudinal files of cells. **Stomata:** superficial, rare near costal adaxial regions, not in distinct files, rather diffuse; terminal subsidiary cells slightly overarching the guard-cells, shorter, wider and differentiated from the surrounding epidermal cells; guard-cells slightly sunken below the epidermis by the lateral subsidiary and adjacent epidermal cells; each guard-cell with 2 cutinized ledges of similar size, the wall slightly thickened below each ledge. **Substomatal**

**chamber:** small. **Hypodermis:** 1-layered beneath each surface, the adaxial layer always wider, both layers compressed above and below the large veins; adaxial cells slightly transversely extended, hexagonal to almost roundish; abaxial cells transversely extended, hexagonal to oblong. **Chlorenchyma:** a well-differentiated palisade mesophyll, mostly single-layered, but 2 layers present near the midrib; spongy mesophyll 5 layers of densely arranged, thick-walled cells. **Tannin cells** absent or present; if present, the tanniniferous material fills completely the cells which are either few or scattered, easily distinct from other mesophyll cells or densely arranged and saturating the adaxial mesophyll. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands of variable size; the larger strands level with small veins; smaller strands irregularly distributed near the adaxial hypodermis. **Primary veins:** ovoid, slightly prominent ad- and abaxially; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2-3 layers of thick-walled fibers and a small adaxial buttress reaching the hypodermis. **Secondary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, consisting of 1-3 layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath



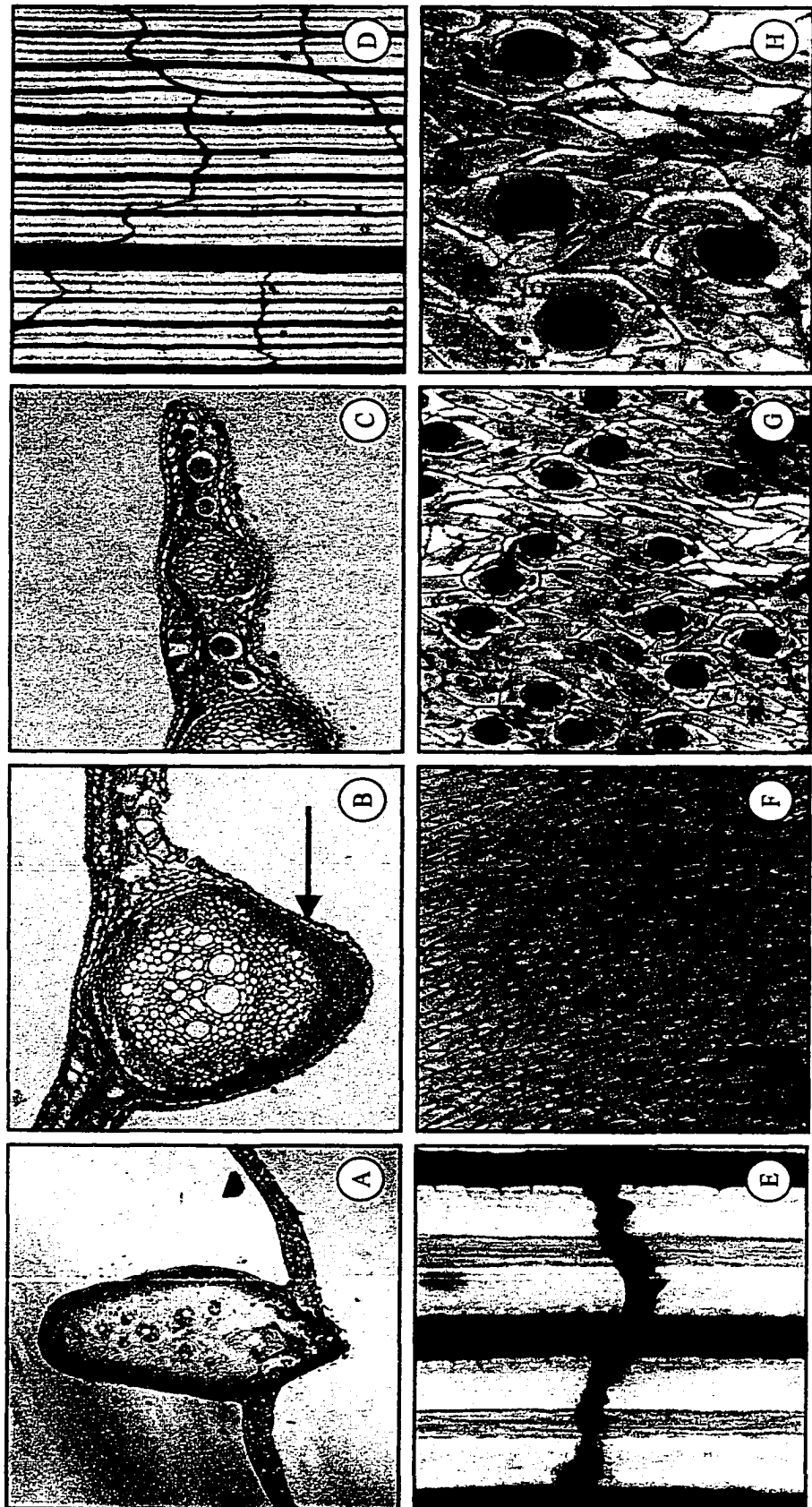
incomplete abaxially; inner sheath incomplete, 1, less frequently 2, layers of fibers, abaxially the fibers thick-walled, adaxially thin-walled. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins irregularly divided into 1-2 strands by sclerotic partitions. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B16, LC16, EP16- BRAZIL. BAHIA: Mun. Mucuri, ca. 2 km S of Rio Mucuri and 8 km W of BR 101, 18°05'S, 39°39'W, 40-80 m, 3 Mar 1989, Noblick & Brito 4794 (NY); B17, LC17, EP17- BRAZIL. RIO DE JANEIRO: between Recreio dos Bandeirantes and Barra de Tijuca, 11 Feb 1973, Krapovickas et al. 23226 (NY); B18, LC18, EP18- BRAZIL. BAHIA: Mun. Una, Res. Biológica do Mico-Leão, km 48 da rodovia BA-001, 15°09'S, 39°05'W, 23 Dec 1996, Sant'Ana et. al 630 (NY).

#### 1.1.30. Bactris setulosa (Fig. 31)

**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer complete and conspicuous; inner fibrous layer not very well-delimited, the outermost fibrous layer thick-walled and strongly lignified, the

Figure 31. Leaf anatomy of Bactris setulosa. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B103, x20), B. midsection, note the abaxially prominent primary vein (B103, x100), C. section tip (B103, x100), D. venation pattern (LC105, x25), E. transverse commissure (LC105, x200), F. adaxial surface (EP105, x200), G. abaxial surface (EP105, x200), H. stomata (EP105, x400).



innermost thin-walled, well-developed ad- and abaxially or all sides with similar width; inner ground parenchyma with 1-3 large vascular bundles, up to 9 smaller and mostly adaxial vascular bundles, few phloem strands embedded in the fibrous layer. **Expansion cells:** forming conspicuous, 1-3 layered abaxial bands adjacent to midrib; bands elsewhere in the lamina prominent ad- and abaxially.

**Hairs:** not seen on adaxial surface but abundant on large abaxial costal bands, above the small costal bands the hairs organized into distinct single files; base sunken? multiseriate? cutinized, roundish? **Epidermis:** ad- and abaxial cell walls not sinuous, thickened outer wall on adaxial cells only. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, but cells in some areas irregularly extended and thus irregularly shaped, organized or not into distinct longitudinal files; costal cells shorter than intercostal cells, rhombohedral, longitudinally extended, large costal regions with 4-6 poorly distinguished longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, the shape as irregular as on adaxial epidermis, costal and intercostal bands conspicuously differentiated; intercostal cells hexagonal, pentagonal and rhombohedral, but mostly irregularly shaped, longitudinally extended except those

near the stomata, not organized into distinct longitudinal files; costal cells smaller than intercostal cells, rectangular, longitudinally extended, the larger bands raised, with up to 30 distinct longitudinal files of cells. **Stomata:** superficial, rare on adaxial costal region, numerous, rather diffuse on abaxial intercostal bands, not in distinct files; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells slightly above the epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; ad- and abaxial cells transversely extended, rectangular to hexagonal, but region of cell junction irregularly shaped. **Chlorenchyma:** palisade mesophyll poorly differentiated, discontinuous over the whole section, except near hypodermal cells of hexagonal shape; spongy mesophyll well-differentiated, 3-4 layers of thick-walled cells. **Tannin cells:** numerous, a few individual cells readily distinct, completely filled by the reddish tanniniferous material, other cells only partially filled by the tanniniferous material, the mesophyll not saturated. **Fiber-sclereids:** absent.

**Raphide-sacs:** absent. **Non-vascular fibers:** forming a prominent abaxial layer of large cylindrical strands level with small veins, and smaller, numerous and irregularly shaped strands distributed near the adaxial hypodermis. **Primary veins:** widely obtrullate, prominent abaxially, the abaxial fibrous area often reaching the hypodermis; outer sheath incomplete, lateral only; inner sheath complete, thick-walled, well-developed ad- and abaxially, laterally only 2-3 layers. **Secondary veins:** roundish to ovoid, prominent abaxially; outer sheath incomplete, only lateral; inner sheath complete, thick-walled, 2-3-layered. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete, thick-walled, 1-2-layered. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers or thin sclerotic partition. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B103, LC103, EP103- VENEZUELA. BARINAS: road from Santo Domingo to Barinitas, 8°50'N, 70°30'W, 1000 m, 5 Jun 1967, Wessels Boer 1775 (NY). B104, LC104, EP104- VENEZUELA. ZULIA: Mara, Ríos Socuy-Guasare basin, La Paloma, 600 m, 4 Aug 1981, Bunting 10179 (NY);

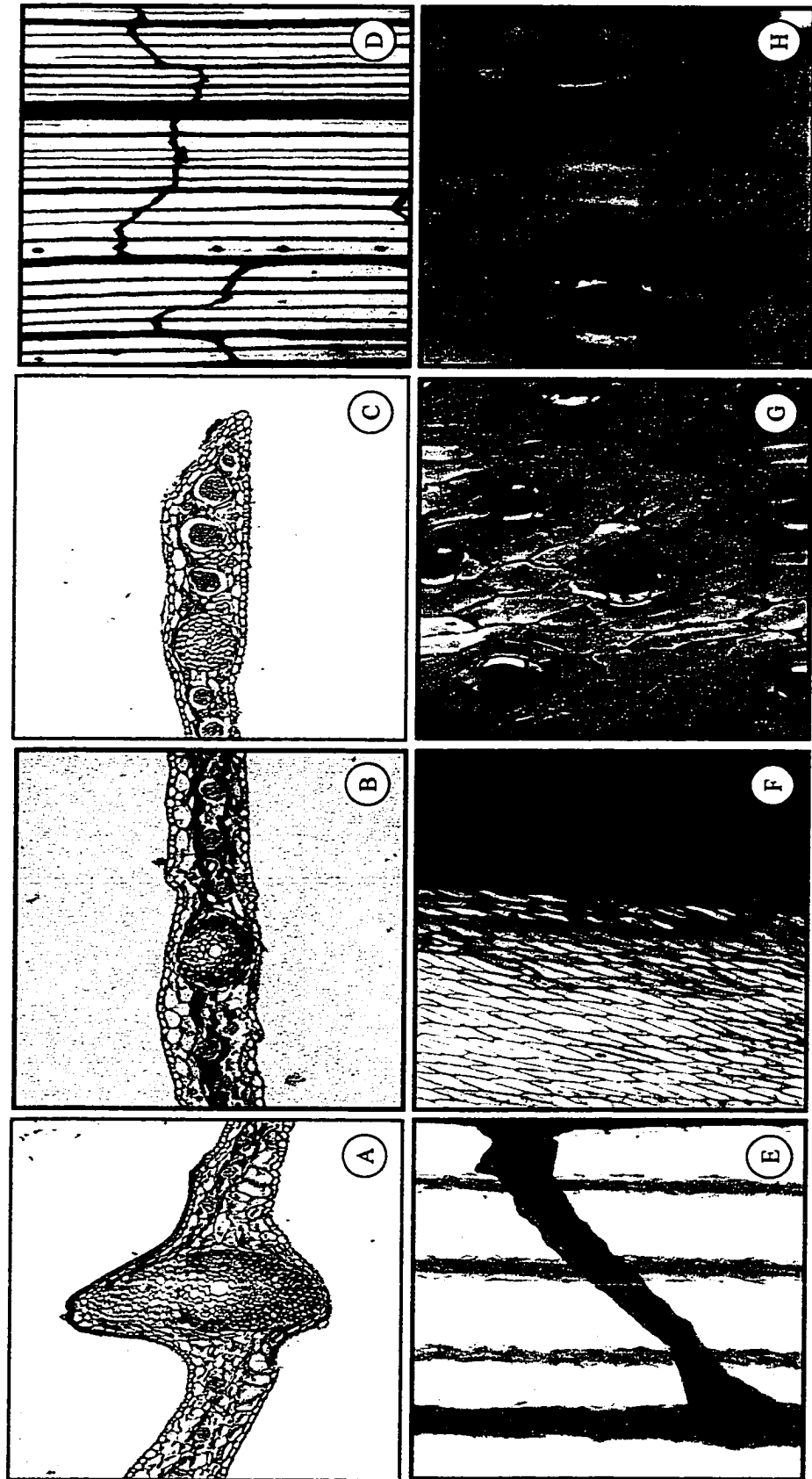
B105, LC105, EP105- YARACUY: Cerro La Chapa, N of Nirgua,  
10°15'N, 68°35'W, 11 Nov 1967, Wessels Boer 2043 (NY).

1.1.31. Bactris simplicifrons (Fig. 32)

**Midrib:** absent. **Main ribs:** midrib-like, prominent adaxially, pointed abaxially; peripheral chlorenchymatous layer conspicuous but incomplete; inner fibrous layer poorly-delimited, thick-walled ad- and abaxially, narrowed laterally, 2-3-layered near the lamina; inner ground parenchyma with 1 large vascular bundle. **Expansion cells:** forming prominent, 1-layered abaxial bands adjacent to primary veins; bands elsewhere in the lamina inconspicuous. **Hairs:** on ad- and abaxial surface; hair base superficial, uniseriate, cutinized, triangular. **Epidermis:** ad- and abaxial cell walls not sinuous, walls not thickened. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, organized into distinct longitudinal files; costal cells rhombohedral to rectangular but somewhat more irregular and smaller than intercostal cells, mostly longitudinally extended, large costal regions with up to 8 distinct longitudinal files of cells. **Abaxial epidermis:** cell size similar to adaxial cells, costal and intercostal bands conspicuously

Figure 32. Leaf anatomy of Bactris simplicifrons. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B47, x40), B. midsection (B47, x100), C. section tip (B46, x100), D. venation pattern (LC47, x25), E. transverse commissure (LC47, x200), F. adaxial surface (EP47, x200), G. abaxial surface (EP48, x200), H. stomata (EP48, x400).





differentiated; intercostal cells mostly rhombohedral, but shape irregular, obliquely extended, not in distinct longitudinal files; costal cells more regularly shaped and narrower than intercostal cells, rhombohedral to rectangular, longitudinally extended, the larger bands distinctly raised, with 11-15 distinct longitudinal files of cells. **Stomata:** superficial, rare near costal regions on adaxial surface, common on abaxial intercostal regions, not in distinct files, rather diffuse; terminal subsidiary cells not overarching the guard-cells, smaller and well-differentiated from the surrounding epidermal cells; guard-cells slightly level with epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged; the outer cell wall much thickened, the cutin? detachable.

**Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers absent above and below the main ribs, compressed above and below the large veins, both layers wide, making up to 1/3 of lamina; ad- and abaxial cells irregularly hexagonal. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll poorly differentiated, 4-5 layers of tightly arranged, thin-walled cells. **Tannin cells:** absent or present; if present, numerous, densely arranged, the tanniniferous material filling partially the cells, not saturating the mesophyll. **Fiber-sclereids:**

absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming a single layer of cylindrical strands centered, level with the veins. **Primary veins:** roundish to ovoid, prominent in both surfaces, the fibrous area reaching the hypodermis; outer sheath incomplete, only lateral; inner sheath complete, consisting of 2-4 layers of thick-walled fibers. **Secondary veins:** roundish, centered; outer sheath complete; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Tertiary veins:** roundish, centered; outer sheath complete; inner sheath complete, consisting of 1 layer of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by sclerotic partitions. **Transverse commissures:** wide, short to elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B46, LC46, EP46- GUYANA.

Mazaruni-Potaro District, Bartica-Potaro road, 24 mi. S of Bartica, 50-125 m, 15 Aug 1976, Mori et al. 8091 (NY); B47, LC47, EP47- GUYANA. Cuyuni-Mazaruni Region, Essequibo River near Dennison Camp, 5°21'N, 58°48'W, 10-15 m, 27 May 1989, Gillespie & Persaud 1439 (NY); B48, LC48, EP48- GUYANA. Cuyuni-Mazaruni Region, Pakaraima Mountains, Kurupung-

Membaru trail, 6°5'N, 60°23'W, 22 Jul 1992, Hoffman & Marco  
2132 (NY).

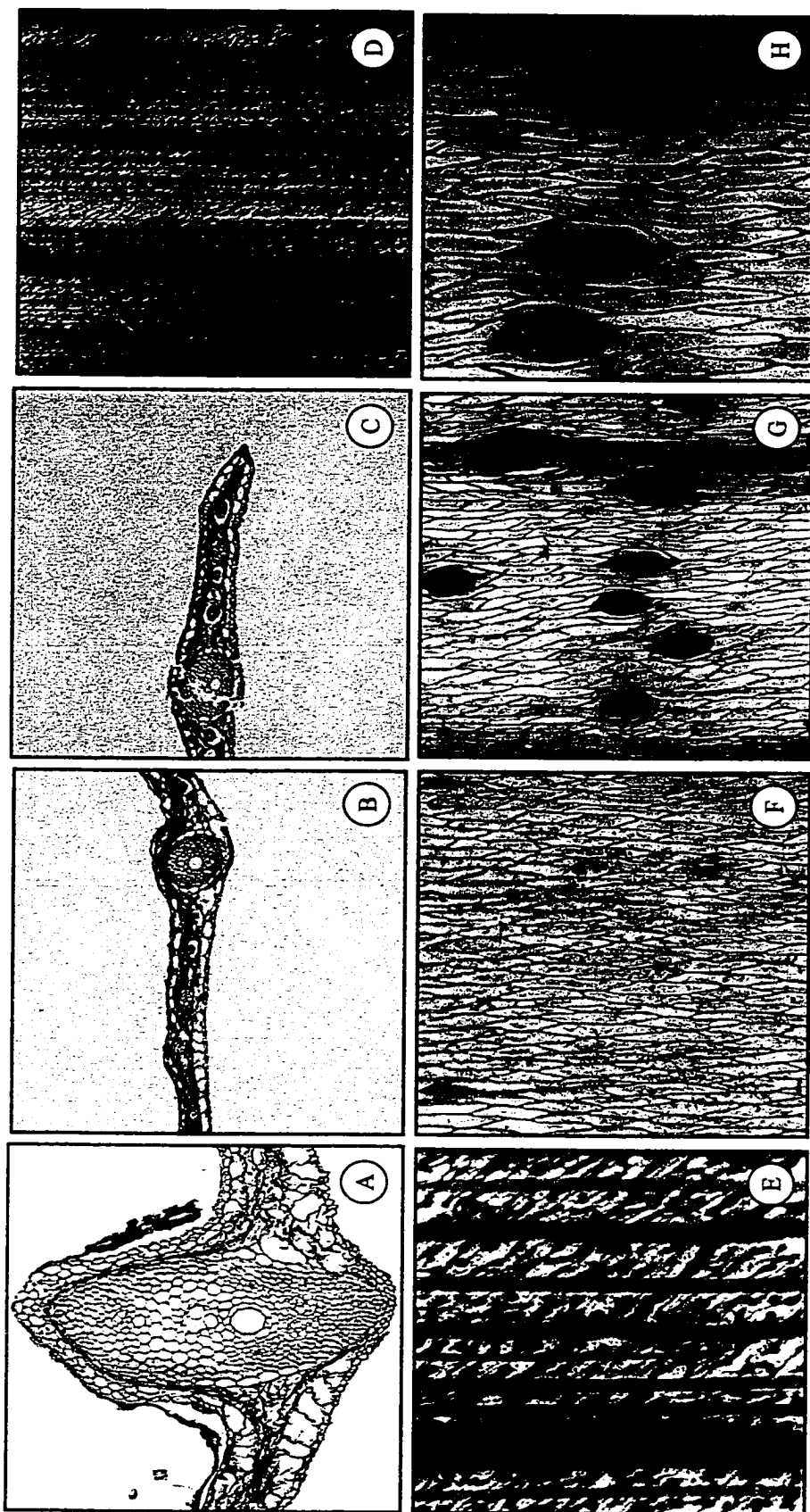
1.1.32. Bactris sphaerocarpa (Fig. 33)

**Midrib:** large, prominent adaxially, abaxially rounded; peripheral chlorenchymatous layer conspicuous, complete or incomplete; inner sclerotic layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 3-5-layered near the lamina; inner ground parenchyma with 1 large vascular bundle and several small phloem strands embedded in the innermost fibrous layers.

**Expansion cells:** in conspicuous, 1-layered abaxial bands adjacent to main ribs; bands elsewhere in the lamina not prominent. **Hairs:** on ad- and abaxial surface, but more frequent near large abaxial costal bands; hair base slightly sunken, uniseriate, cutinized, ellipsoidal.

**Epidermis:** ad- and abaxial cell walls not sinuous, slightly thickened on outer walls. **Adaxial epidermis:** intercostal cells spindle-shaped, longitudinally extended, not in distinct longitudinal files; costal cells smaller than intercostal cells, rectangular, longitudinally extended, large costal regions with up to 8 distinct longitudinal files of cells. **Abaxial epidermis:** cells similar in size

Figure 33. Leaf anatomy of Bactris sphaerocarpa. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B66, x40), B. midsection (B66, x100), C. section tip (B66, x100), D. venation pattern (LC65, x20), E. transverse commissure (LC65, x100), F. adaxial surface (EP66, x200), G. abaxial surface (EP64, x200), H. stomata (EP64, x400).



to adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells spindle-shaped, longitudinally extended, not in distinct longitudinal files; costal cells smaller than intercostal cells, rectangular, longitudinally extended, larger bands slightly raised, with up to 14 distinct longitudinal files of cells. **Stomata:** superficial, rare on adaxial surface, numerous, rather diffuse on abaxial intercostal regions, not in distinct longitudinal files; terminal subsidiary cells partially overarching the guard-cells, shorter and well-differentiated from the surrounding epidermal cells; guard-cells slightly level with the epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers absent above and below the main ribs, compressed above and below the large veins; ad- and abaxial cells slightly transversely extended, irregularly oblong. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 3-4 layers of thin-walled cells. **Tannin cells:** completely filled by tanniniferous material; few, individual cells readily distinct and not saturating the mesophyll, or numerous and completely saturating the mesophyll. **Fiber-sclereids:** numerous, forming a secondary,

transversely extended, fibrous network in surface view.

**Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands of variable size; the larger strands distributed in centered, irregular layers. **Primary veins:** ovoid, prominent ad- and abaxially; outer sheath incomplete, only lateral; inner sheath complete, consisting of 3-4 layers of thick-walled fibers. **Secondary veins:** roundish, centered; outer sheath complete or lacking abaxially; inner sheath complete, consisting of 1 layer of thin-walled fibers. **Tertiary veins:** roundish, centered; outer sheath complete; inner sheath consisting of a single layer of thin-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins irregularly divided into as many as 4 strands by thin-walled fibers. **Transverse commissures:** wide, elongate, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

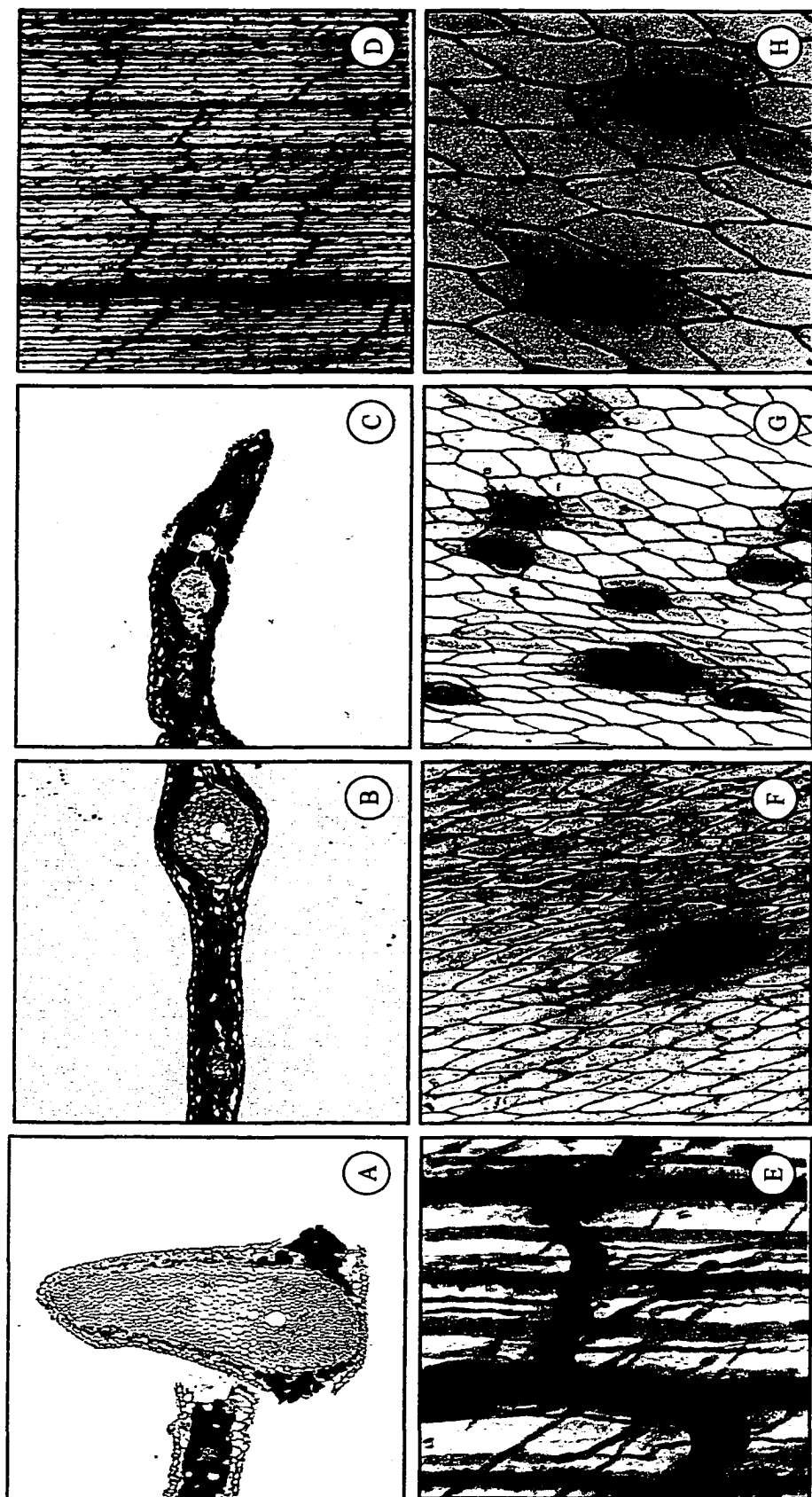
**Specimens examined.** B64, LC64, EP64- PERU. LORETO: Río Nanay, 3°52'S, 73°30'S, 8 Sep 1990, Vásquez et al. 14359 (NY); B65, LC65, EP65- PERU. LORETO: Río Sinchiyacu, 2°50'S, 76°55'W, 200 m, 25 Feb 1991, Pipoly et al. 13758 (NY); B66, LC66, EP66- BRAZIL. AMAZONAS: Mun. Atalaia do Norte, Rio Curuçá, tributary of Rio Javari, 4°30'S, 71°22'W, 150 m, 12 Jan 1989, Henderson et al. 881 (NY).



1.1.33. Bactris tomentosa (Fig. 34)

**Midrib:** abaxially pointed to rounded, prominent adaxially; peripheral chlorenchymatous layer absent abaxially, conspicuous adaxially and laterally, tannin cells present; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, narrowed laterally, 1-3-layered near the lamina; inner ground parenchyma with 2 large vascular bundles and several smaller phloem strands irregularly embedded or not in the innermost fibrous layers. **Expansion cells:** forming inconspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** dense or not on abaxial surface; hair base superficial, uniseriate, cutinized, ellipsoidal. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened outer wall on adaxial cells only. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, the angle of obliquity varying; costal cells shorter than intercostal cells, rectangular to rhombohedral, longitudinally extended, large costal regions slightly raised, with 6-12 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands

Figure 34. Leaf anatomy of Bactris tomentosa. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B11, x20), B. midsection (B11, x100), C. section tip (B11, x100), D. venation pattern (LC10, x20), E. transverse commissure (LC10, x200), F. adaxial surface (EP11, x200), G. abaxial surface (EP11, x200), H. stomata (EP11, x400).



conspicuously differentiated; intercostal cells like those of the adaxial epidermis but less obliquely extended; costal cells narrower than intercostal cells, rectangular to almost spindle-shaped, longitudinally extended, the larger and smaller bands slightly raised, larger bands with up to 12 distinct longitudinal files of cells. **Stomata:** superficial, adaxially few, along the costal regions, abaxially not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with epidermal surface, each with 2 cutinized ledges of similar size, the wall slightly thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers continuous above and below the large veins, compressed above the veins; ad- and abaxial cells slightly transversely extended, shape irregular, oblong to almost spindle-shaped. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll 5 layers of tightly arranged, thin-walled cells. **Tannin cells:** numerous, dense, the cells filled by a reddish tanniniferous material, completely saturating the mesophyll. **Fiber-sclereids:** numerous, forming a secondary, transversely extended, fibrous network in surface view. **Raphide-sacs:** rare, centered. **Non-vascular fibers:** forming

cylindrical strands of variable size; the larger strands abaxial, level with small veins; smaller strands irregularly distributed in the adaxial region of mesophyll, sometimes attached to the hypodermis. **Primary veins:** ovoid to obtrullate, prominent ad- and abaxially; outer sheath incomplete, only lateral; inner sheath complete, well-developed, thick-walled, 3-5 or more layers ad- and abaxially, only 2 lateral layers; the ad- and abaxial fibrous area touching the hypodermis. **Secondary veins:** roundish, abaxial; outer sheath incomplete, only lateral; inner sheath incomplete, 1-2-layered, thick-walled fibers abaxially and laterally, thin-walled fibers adaxially. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath incomplete, consisting of a single layer of thin-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into several small strands by files of thick-walled fibers. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B10, LC10, EP10- BRAZIL.

AMAZONAS: Mun. Manaus, Tarumã Alta, 14 km N of Manaus, 19 Dec 1982, Plowman et al. 12637 (NY); B11, LC11, EP11-

BRAZIL. AMAZONAS: 60 km N of Manaus on road to Caracarai, 4

Aug 1986, Henderson & Nascimento 642 (NY); B12, LC12, EP12-  
 BRAZIL. AMAZONAS: Reserva Ducke, 26 km N of Manaus, 10-21  
 Nov 1986, Henderson 665 (NY).

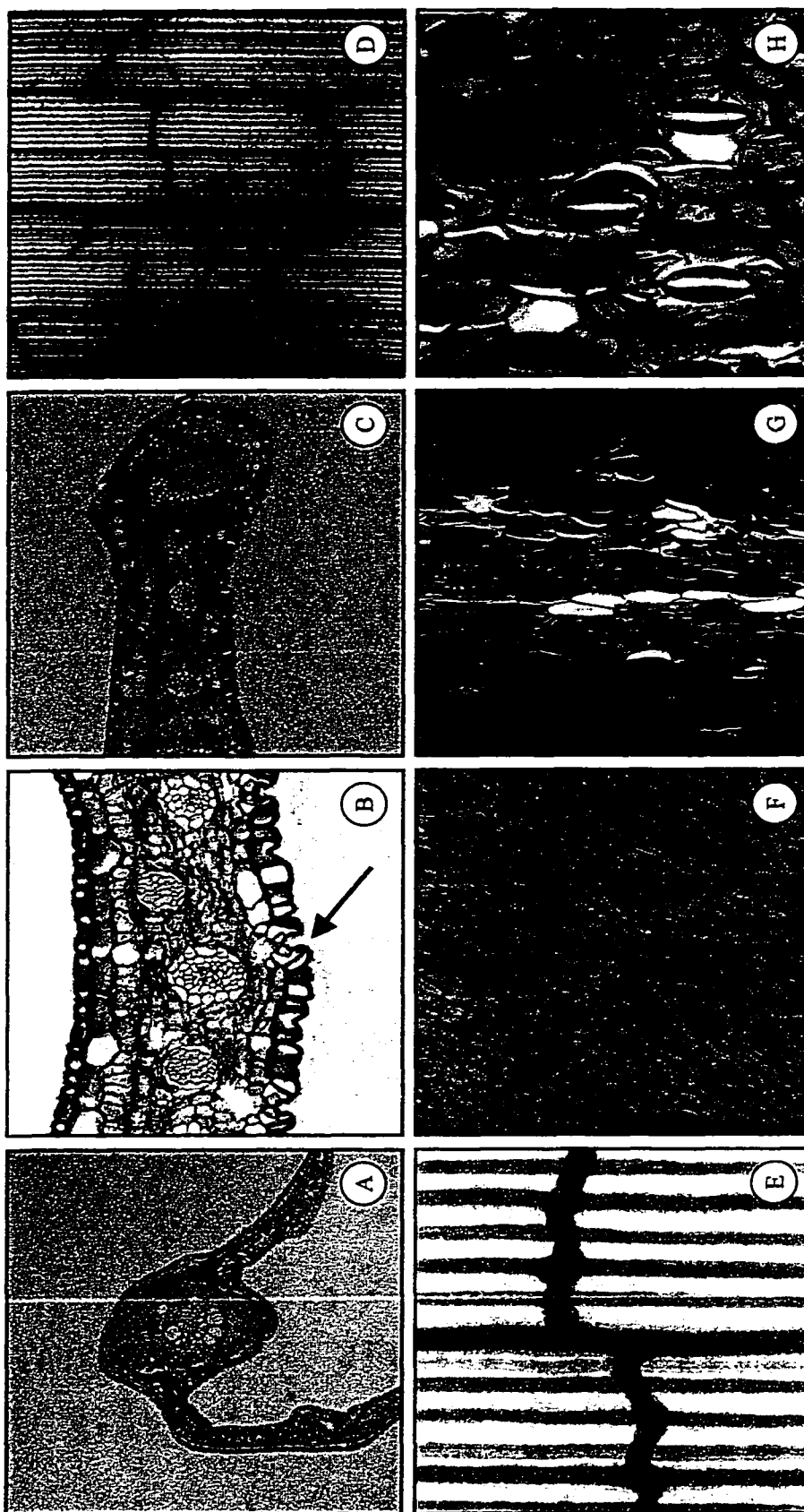
## 1.2. Acrocomia

### 1.2.1. Acrocomia aculeata (Fig. 35)

**Midrib:** abaxially pointed, prominent only adaxially or equally prominent on both surfaces; chlorenchymatous layer conspicuous but irregular, interrupted or not, with complete small vascular bundles; inner fibrous layer poorly to well-delimited, thick-walled and well-developed, narrowed and 2-3-layered or very wide laterally near the lamina; inner ground parenchyma with 4-5 large and several smaller vascular bundles, all partially surrounded by thick-walled fibers, several isolated phloem strands embedded in the outermost fibrous layers. **Expansion cells:** forming conspicuous, 2-3-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous.

**Hairs:** rare on adaxial surface, more frequent abaxially, organized into a distinct file at the edges of large costal bands and on small bands; hair base not seen in cross-section, but distal structure of smaller hairs uniseriate

Figure 35. Leaf anatomy of Acrocomia aculeata. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B115, x40), B. midsection, note the sunken stomata (B114, x200), C. section tip (B115, x100), D. venation pattern (LC115, x20), E. transverse commissure (LC115, x200), F. adaxial surface (EP113, x200), G. abaxial surface (EP114, x200), H. stomata (EP114, x400).





and cutinized, the larger hairs spine-like and multiseriate. **Epidermis:** ad- and abaxial cell walls not sinuous, wholly thickened. **Adaxial epidermis:** intercostal cells mostly rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying and then some cells almost spindle-shaped; costal cells smaller than intercostal cells, mostly rhombohedral, but also rectangular and hexagonal-shaped cells, obliquely extended, large costal regions with 9 or fewer distinct longitudinal files of cells, or sometimes the files not distinct. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated, cells around stomata distinctly smaller and shaped; intercostal cells mostly irregularly shaped, those in same file as stomata narrower than adjacent epidermal cells, oblong, forming short rows up to 3 cells long; costal cells smaller than intercostal cells, rectangular, hexagonal or rhombohedral, longitudinally extended, the larger bands slightly raised, with up to 11 distinct longitudinal files of cells. **Stomata:** sunken, restricted to abaxial intercostal bands, not in distinct files, but forming short rows of 2-5; terminal subsidiary cells larger and wider than the adjacent intercostal cells, well-differentiated from the surrounding epidermal cells, overarching the

guard-cells. Lateral subsidiary and adjacent epidermal cells wider and raised well above the guard-cells in cross-section view, overarching it in cross-section; guard-cells with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 2-layered beneath adaxial surface, 1-layered abaxially; the first adaxial layer continuous above the large veins, usually not compressed, the cells more transversely extended than the second layer, the shape rather variable, rectangular, oblong or hexagonal; the second layer interrupted above the large veins, the cells not transversely extended, rectangular; abaxial layer more irregular than adaxial layer, frequently interrupted or compressed by large and medium sized veins and the stomata, cell-shape rectangular, not transversely extended.

**Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 6-9 layers of thick-walled cells; numerous, large intercellular spaces irregularly distributed throughout the mesophyll. **Tannin cells:**

absent. **Fiber-sclereids:** absent. **Raphide-sacs:** absent.

**Non-vascular fibers:** forming cylindrical strands fairly uniform; the larger strands distributed in a distinct layer level with the veins; smaller strands irregularly distributed in the adaxial region, mostly attached to the

first hypodermal layer. **Primary veins:** ovoid, slightly prominent ad- and abaxially; outer sheath incomplete, only lateral; inner sheath incomplete, the 2-3-layered thick-walled fibrous ring interrupted above the phloem by sclerotic, conspicuously pitted parenchyma cells; the adaxial fibrous region reaching the first hypodermal layer, abaxially the fibrous region touching or not the hypodermis. **Secondary veins:** narrowly ovoid, slightly prominent, centered; outer sheath incomplete, only lateral; inner sheath incomplete, 1-3 layers of thick-walled fibers abaxially, laterally and just above the phloem the layers interrupted by sclerotic and conspicuously pitted parenchyma cells, adaxially an elongate buttress of thick-walled fibers reaching the second hypodermal layer; the buttress gives a characteristic apiculate shape to the adaxial region of the vein. **Tertiary veins:** roundish, abaxial; outer sheath complete or incomplete abaxially; inner sheath incomplete, 1-layered, abaxially few thin-walled fibers, completed laterally and adaxially by conspicuously pitted parenchyma cells. **Quaternary veins:** absent. **Marginal rib:** large, prominent abaxially; outer sheath poorly developed adaxially, lacking laterally and abaxially; inner sheath irregular, abaxially a mass of thick-walled fibers completed above by a single layer of

conspicuously pitted parenchyma cells. **Phloem:** of large veins divided into indistinct strands by thin sclerotic partitions, except in the poorly developed phloem of the veins in the margin of lamina. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B113, LC113, EP113- BOLIVIA.

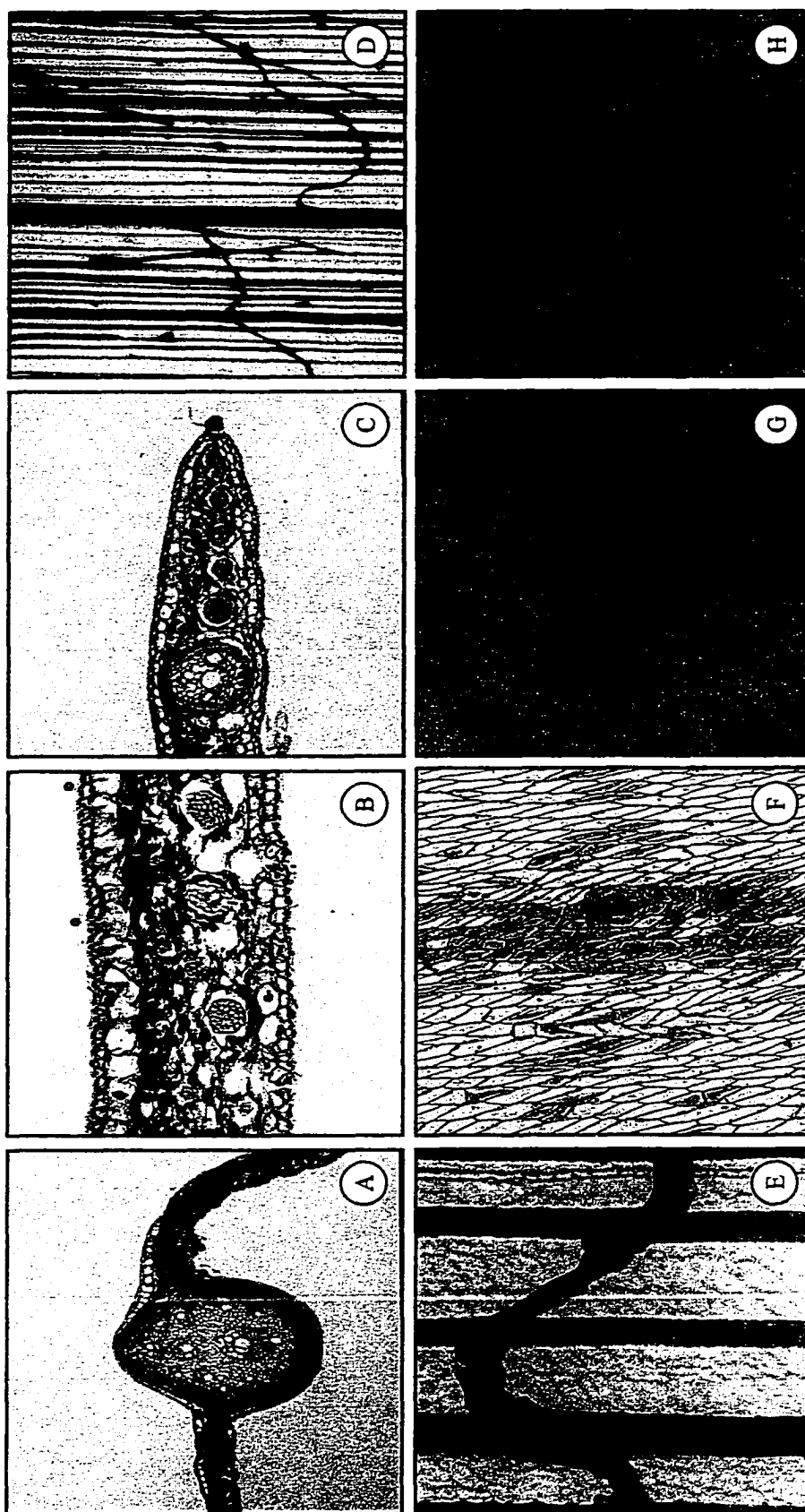
SANTA CRUZ: Prov. Andres Ibañez, Fortin Libertad-Rio Grande, 2 Dec 1990, Moreno 63 (NY); B114, LC114, EP114- BOLIVIA. SANTA CRUZ: Prov. Velasco, estancia Flor de Oro, W side of Río Iténez, 13°33'S, 61°00'W, 190 m, 29 Jun 1991, Nee 41521 (NY); B115, LC115, EP115- BOLIVIA. SANTA CRUZ: Prov. Andres Ibañez, 6 km NW of Terevinto, 17°41'S, 63°25'W, 450 m, 30 Nov 1988, Nee & Coimbra 36993 (NY).

### 1.3. Aiphanes

#### 1.3.1. Aiphanes aculeata (Fig. 36)

**Midrib:** abaxially rounded, abaxially prominent, ovoid, not narrowed at midpoint; conspicuous chlorenchymatous layer absent; inner fibrous layer well-developed, well-delimited, thick-walled, widened laterally near the lamina; inner ground parenchyma with 2 large and 9-11 smaller vascular

Figure 36. Leaf anatomy of Aiphanes aculeata. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B125, x40), B. midsection (B126, x200), C. section tip (B125, x100), D. venation pattern (LC124, x25), E. transverse commissure (LC124, x200), F. adaxial surface (EP125, x200), G. abaxial surface (EP125, x200), H. stomata (EP125, x400).



bundles partially surrounded by thick-walled fibers, either attached at regular interval to the innermost fibrous layers or scattered on ground parenchyma, few isolated phloem strands embedded in the abaxial outermost fibrous layers. **Expansion cells:** forming conspicuous, 1-2-layered abaxial bands adjacent to midrib; adaxially, less prominent, single layered bands; bands elsewhere in the lamina conspicuous only in folding regions. **Hairs:** long, on ad- and abaxial surface, adaxially near the costal regions, abaxially irregularly distributed in the intercostal region, in poorly distinguished files on small costal bands; hair base sunken, uniseriate, cutinized, roundish; the hair base robust, stiff, distal portion filiform. **Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** intercostal cells rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying; costal cells shorter than intercostal cells, mostly rhombohedral, obliquely extended, large costal regions with up to 13 poorly distinguished longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells hexagonal, pentagonal and rhombohedral, longitudinally extended; costal cells narrower than

intercostal cells, rectangular or rhombohedral, longitudinally extended, the larger bands slightly raised, with up to 10 distinct longitudinal files of cells.

**Stomata:** superficial, adaxially near the large costal regions, abaxially numerous on intercostal bands, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with the epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small.

**Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins, the adaxial layer wider than abaxial layer; ad- and abaxial cells slightly transversely extended, rectangular in shape.

**Chlorenchyma:** 2-layered palisade mesophyll, the 2 layers not well organized; spongy mesophyll well-differentiated, 5-7 layers of thick-walled cells; intercellular air space abundant, cells regularly roundish. **Tannin cells:**

numerous, the cells partially filled by reddish tanniniferous material, the mesophyll not saturated.

**Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands of variable size; the larger strands distributed in a distinct abaxial



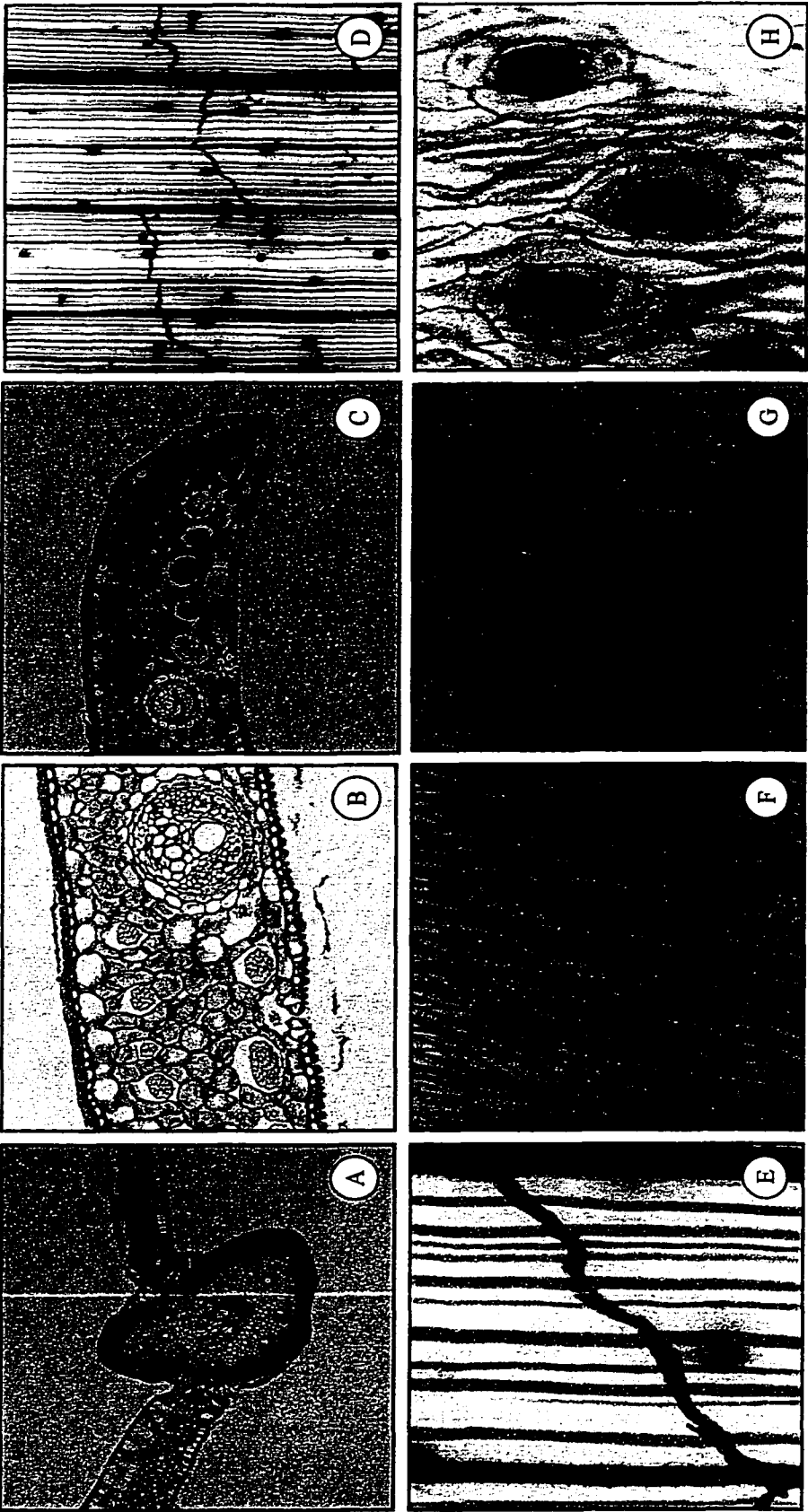
layer, the smaller irregularly distributed near the adaxial hypodermis. **Primary veins:** ovoid, ad- and abaxially prominent; outer sheath only abaxially; inner sheath complete, consisting of 1-2 very uniform layers of thick-walled fibers; the ad- and abaxial fibrous region not reaching the hypodermis. **Secondary veins:** roundish, abaxial; outer sheath lacking abaxially; inner sheath complete, 1, rarely 2, layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath complete, consisting of a single layer of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins undivided. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B124, LC124, EP124- BRAZIL. ACRE: Mun. Taumaturgo, RESEX Alto Juruá, ao longo do Rio Bagé, 8°55'S, 72°31'W, 120 m, 11 Mar 1992, E. Ferreira 121 (HPZ); B125, LC125, EP125- BRAZIL. ACRE: Mun. Mâncio Lima, Rio Moa, 5 minutes from confluence of Rio Azul, 17 Oct 1989, Henderson & Scariot 1145 (NY); B126, LC126, EP126- BRAZIL. ACRE: Mun. Brasiléia, Seringal Porongaba, Col. São José, 23 May-2 Jun 1991, Scariot & E. Ferreira 570 (NY).

1.3.2. Aiphanes ulei (Fig. 37)

**Midrib:** abaxially rounded, prominent abaxially or equally prominent on both surfaces, distinctly narrowing at midpoint; chlorenchymatous layer conspicuous but irregular; inner fibrous layer well-delimited, thick-walled, well-developed ad- and abaxially, the width of the layer irregular, narrowed laterally, 1-layered near the lamina; inner ground parenchyma with 1-2 large and several smaller vascular bundles, several phloem strands embedded at regular intervals in the innermost region of the fibrous layer. **Expansion cells:** forming conspicuous, 2-3-layered abaxial bands adjacent to midrib and single layered bands adaxially; bands elsewhere in the lamina conspicuous only in folding regions. **Hairs:** on adaxial costal regions, abaxially more numerous on large costal bands, not organized into distinct files on small costa; hair base sunken, uniseriate, cutinized, roundish. **Epidermis:** ad- and abaxial intercostal cells slightly undulate, thickened on outer walls. **Adaxial epidermis:** intercostal cells mostly spindle-shaped, but rhombohedral and hexagonal cells also common, the cells oblique or longitudinally extended, but angle of obliquity varying; costal cells shorter than intercostal cells, mostly rectangular, longitudinally

Figure 37. Leaf anatomy of Aiphanes ulei. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib, note it is abaxially prominent (B112, x40), B. midsection (B111, x200), C. section tip (B112, x100), D. venation pattern (LC112, x20), E. transverse commissure (LC112, x200), F. adaxial surface (EP112, x200), G. abaxial surface (EP112, x200), H. stomata (EP112, x400).



extended, large costal regions with up to 11 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; costal and intercostal cells irregularly shaped and extended, not in distinct files; costal cells rectangular, narrower than intercostal cells, longitudinally extended, large bands slightly raised, with up to 12 distinct longitudinal files of cells. **Stomata:** superficial, adaxially near the costal regions, abaxially numerous, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter but not otherwise well-differentiated from the surrounding epidermal cells; guard-cells level with the epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, both layers slightly compressed above and below the large veins, the adaxial layer wider than abaxial layer; adaxial cells hexagonal, slightly transversely extended, but short sections of hypodermis have cells transversely extended; abaxial cells more transversely extended than adaxial cells, mostly rectangular, except a few transversely extended cells. **Chlorenchyma:** 2-layered palisade mesophyll well-differentiated from spongy

mesophyll but the 2 palisade layers not very well organized; spongy mesophyll well-differentiated, cells loosely arranged, 5-7 layers of roundish, thick-walled cells; intercellular air space abundant, cells regularly roundish. **Tannin cells:** absent or present; if present, poorly distinguished, the cells partially filled by a brownish tanniniferous material, the mesophyll not saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming small cylindrical strands distributed into 2 distinct ad- and abaxial layers; the abaxial layer within the palisade mesophyll; the adaxial layer near the abaxial surface, level with the small veins. **Primary veins:** widely ovoid, ad- and abaxially prominent; outer sheath incomplete, lateral only; inner sheath complete, 1-3 very uniform layers of thick-walled fibers, the abaxial fibrous area reaching the hypodermis. **Secondary veins:** roundish, abaxial; outer sheath lacking abaxially; inner sheath complete, 1, rarely 2, layers of thick-walled fibers. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath complete, usually a single layer of thick-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins clearly divided in 2 distinct strands by thin-walled fibers. **Transverse commissures:** wide, elongate, regularly

arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B110, LC110, EP110- ECUADOR.

PASTAZA: Southern bank of Río Pastaza, opposite to Mera, 1°27'S, 78°08'W, 1300 m, 25 Oct 1987, Skov & Borchsenius 64776 (NY); B111, LC111, EP111- ECUADOR. MORONA-SANTIAGO: Sendero del Taisha al Kankeim, 30 km al SW del Río Pastaza, 2°25'S, 77°30-40'W, 400-600 m, 22 Mar 1986, Baker 6805 (NY); B112, LC112, EP112- ECUADOR. MORONA-SANTIAGO: one hour walk west of Taisha, along trail to Cangaime, 2°25'S, 77°30'W, 400 m, 13 May 1986, Balslev et al. 62200 (NY).

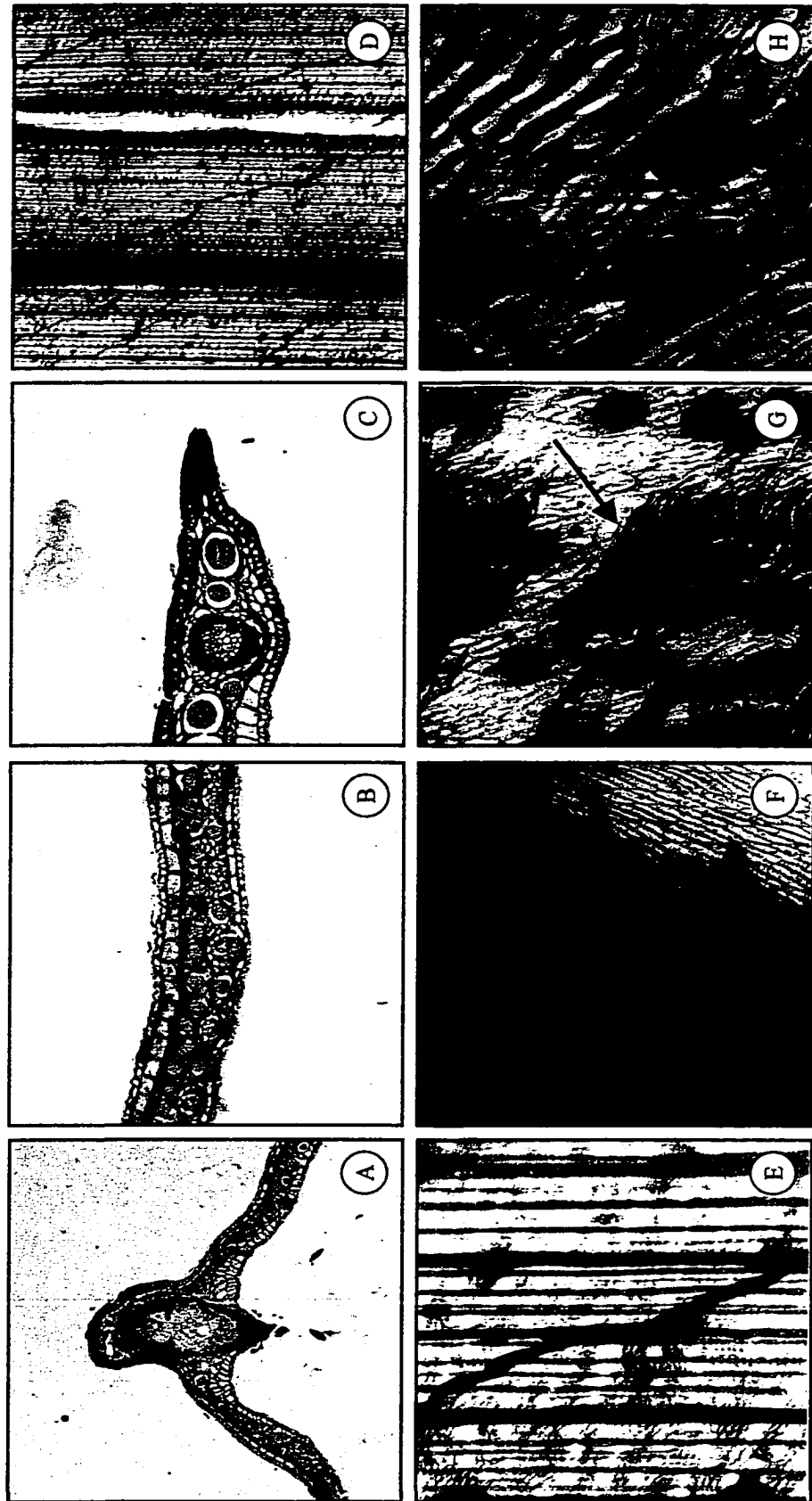
1.4. Astrocaryum

1.4.1. Astrocaryum gynacanthum (Fig. 38)

**Midrib:** abaxially rounded to pointed, adaxially prominent; peripheral chlorenchymatous layer conspicuous and complete on adaxial region, with roundish bundles of non-vascular fibers and tannin cells; inner fibrous layer well to poorly-delimited, well-developed ad- and abaxially, thick-walled but width of the layer irregular, narrowed laterally, 1-3-layered near the lamina; inner ground parenchyma with 2-4 large and few smaller bundles, rarely

Figure 38. Leaf anatomy of Astrocaryum gynacanthum. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B82, x40), B. midsection (B82, x100), C. section tip (B82, x100), D. venation pattern (LC83, x20), E. transverse commissure (LC83, x200), F. adaxial surface (EP83, x200), G. abaxial surface, note the persistent epicuticular wax surrounding the stomata (EP84, x200), H. stomata (EP84, x400).





phloem strands embedded on fibrous layer. **Expansion cells:** forming conspicuous, 2-3-layered abaxial bands adjacent to midrib; adaxial bands absent; bands elsewhere in the lamina inconspicuous. **Hairs:** absent on adaxial surface, frequent abaxially on large and small costal bands; base superficial, uniseriate, sclerotic? ellipsoidal.

**Epicuticular wax** persistent ad- and abaxially, the units filamentous, almost spindle-shaped, transversely extended.

**Epidermis:** ad- and abaxial cell walls not sinuous, thickened on outer walls. **Adaxial epidermis:** costal and intercostal cells almost indistinct, rhombohedral to spindle shaped, obliquely-longitudinally extended, but angle of obliquity varying, costal and intercostal cells organized into distinct longitudinal files, but files on costal regions not distinct from those on intercostal.

**Abaxial epidermis:** cells smaller than adaxial cells, the walls much thickened in surface view, costal and intercostal bands conspicuously differentiated; intercostal cells rhombohedral, obliquely-longitudinally extended, clearly organized into distinct files, even the cells not in the same files of stomata; costal cells narrower than intercostal cells, rectangular, rhombohedral, longitudinally extended, the larger bands raised, with up to 17 distinct longitudinal files of cells. **Stomata:**

superficial, restricted to abaxial intercostal bands, forming short rows of 2-8; terminal subsidiary cells overarching the guard-cells, shorter, wider, conspicuously inflated and well-differentiated from the surrounding epidermal cells; guard-cells slightly raised above the epidermis, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge.

**Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface; adaxial layer wider, uniform and continuous along the whole lamina, rarely compressed above large veins, abaxial layer often compressed below large veins, ending almost inside the substomatal chamber; ad- and abaxial cells transversely extended, rectangular, the cell junctions obscure or not. **Chlorenchyma:** 1-layered, poorly developed palisade mesophyll; spongy mesophyll well-differentiated, 4-6 layers of tightly arranged, thick-walled cells. **Tannin cells:** numerous, the cells partially filled by a brownish material and mesophyll not saturated or cells completely filled by a reddish tanniniferous material, the mesophyll completely saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical strands distributed into two distinct layers; the first layer adaxial, above the veins, the second layer abaxial, level with the small veins.

**Primary veins:** ovoid when inner sheath is complete or widely obovoid to heart-shaped when inner sheath is incomplete; in both cases the veins prominent abaxially; outer sheath incomplete, only lateral; inner sheath incomplete or complete; if complete, it is thick-walled, 5-layered ad- and abaxially, and 2-layered laterally; if incomplete, the inner sheath has 2 abaxial layers of thick-walled fibers and a single lateral layer of thin-walled fibers, complete above by a poorly developed buttress reaching the hypodermis. **Secondary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath complete or incomplete; if complete, 1-2 layers of thick-walled fibers; when incomplete, the inner sheath thick-walled, 1-2-layered abaxially, and thin-walled, 1-layered laterally and adaxially. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath incomplete, few thick-walled abaxial fibers completed above by thin-walled fibers. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of thin-walled fibers. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

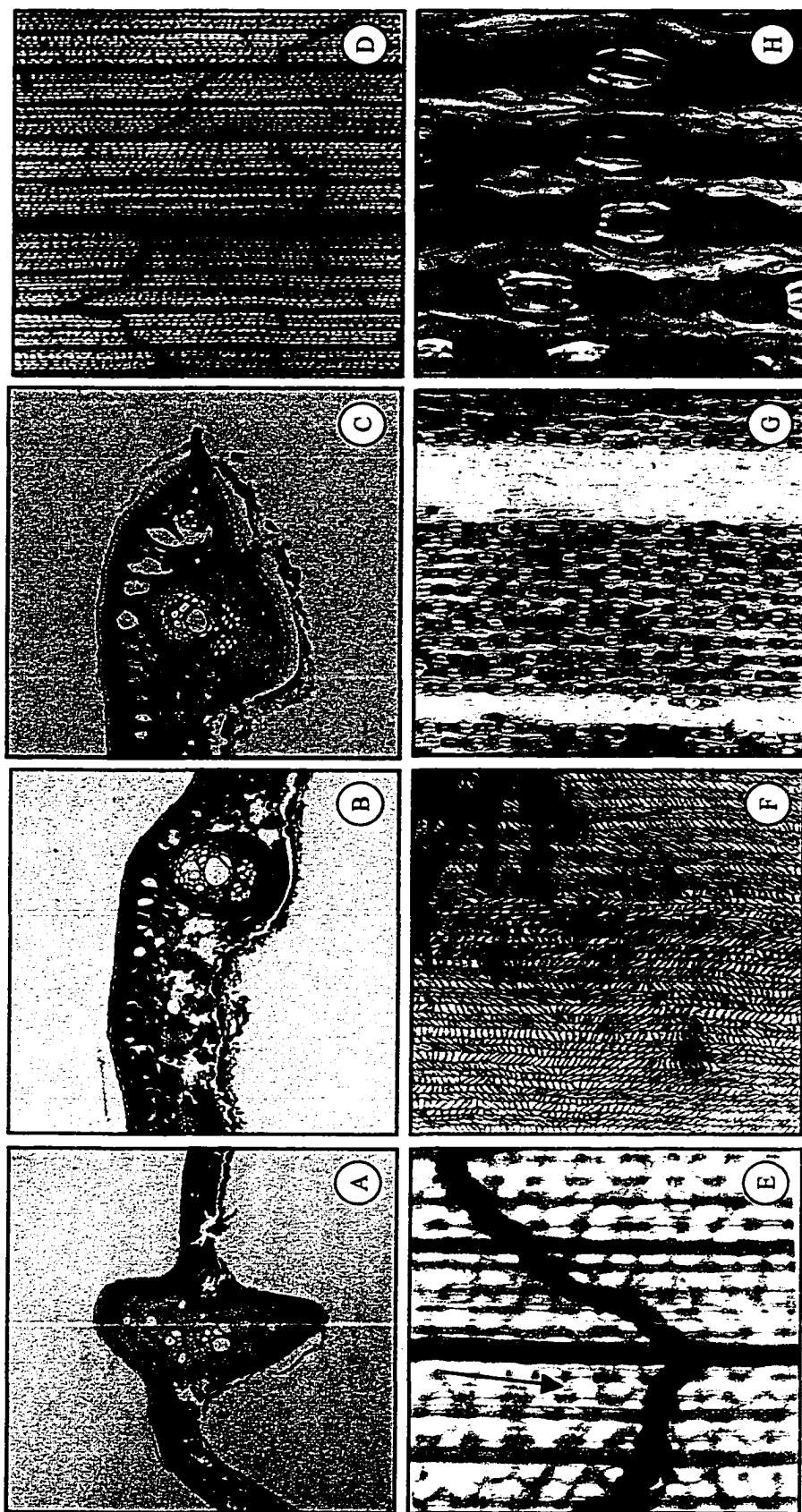
**Specimens examined.** B82, LC82, EP82- VENEZUELA.

AMAZONAS: 6 KM n of Puerto Ayacucho on the road to Puerto Páez, 5°40'N, 67°40'W, 200-300 m, 22 Jun 1994, Noblick et al. 4945 (NY); B83, LC83, EP83- VENEZUELA. BOLÍVAR: Río Paragua, en los alrededores de El Caruto Viejo, 6°39'N, 63°29'W, 13 May-13 Jun 1987, Stergios 10802 (NY); B84, LC84, EP84- VENEZUELA. BOLÍVAR: Dpto. Sifontes, concesión minera Oro Uno, 7 km al N-O de la Clarita, 6°13'N, 61°27'W, 180 m, 3 Aug 1985, Aymard et al. 3958 (NY).

#### 1.4.2. Astrocaryum jauari (Fig. 39)

**Midrib:** abaxially rounded to pointed, more prominent abaxially; conspicuous peripheral chlorenchymatous layer, with tannin cells; inner fibrous layer well-delimited, thick-walled, well-developed and several-layered ad- and abaxially, narrowed laterally, 1-2-layered near the lamina; inner ground parenchyma with 3-4 large and 3-4 smaller vascular bundles, these somewhat underdeveloped. **Expansion cells:** forming conspicuous, 1-2-layered abaxial bands adjacent to midrib; adaxial bands absent; bands elsewhere in the lamina inconspicuous. **Hairs:** absent. **Epicuticular wax** persistent ad- and abaxially, the units filamentous, spindle-shaped, transversely extended. **Epidermis:** adaxial

Figure 39. Leaf anatomy of Astrocaryum jauari. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B78, x40), B. midsection (B78, x100), C. section tip (B78, x100), D. venation pattern (LC77, x20), E. transverse commissure, note the persistent epicuticular wax (LC77, x100), F. adaxial surface, note the persistent epicuticular wax (EP76, x100), G. abaxial surface (EP76, x100), H. stomata (EP76, x400).



cell walls not sinuous, costal abaxial cells slightly undulate; ad- and abaxial outer wall not thickened.

**Adaxial epidermis:** costal and intercostal regions almost indistinct, the cells mostly rectangular, organized into distinct files alternately obliquely-longitudinally extended and transversely extended. **Abaxial epidermis:** cells narrower but more elongate than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells not in the same file as stomata spindle-shaped and longitudinally extended; costal cells mostly rectangular but also irregularly-shaped, longitudinally extended, the larger bands raised, without the distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, dense and organized in distinct files; terminal subsidiary cells overarching the guard-cells, oval to oblong, conspicuously inflated, much stained (thick-walled?) than surrounding epidermal cells, attached to other terminal subsidiary cells and forming distinct files of stomata. Lateral subsidiary cells also inflated; guard-cells level with the epidermal surface, smaller than all surrounding cells, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** large. **Hypodermis:** 1-layered beneath each surface, adaxial



layer wider, uniform and continuous along the whole lamina, abaxial layer compressed below the large veins and ending almost inside the substomatal chamber; ad- and abaxial cells transversely extended, rectangular, cell junctions obscure. **Chlorenchyma:** 2-layered palisade mesophyll well-differentiated, the first layer interrupted by the columnar non-vascular fibers; spongy mesophyll well-differentiated, 6-9 layers of thick-walled cells, abundant intercellular spaces in the mesophyll. **Tannin cells:** numerous, the cells partially filled by reddish tanniniferous material, the mesophyll not saturated. **Fiber-sclereids:** absent.

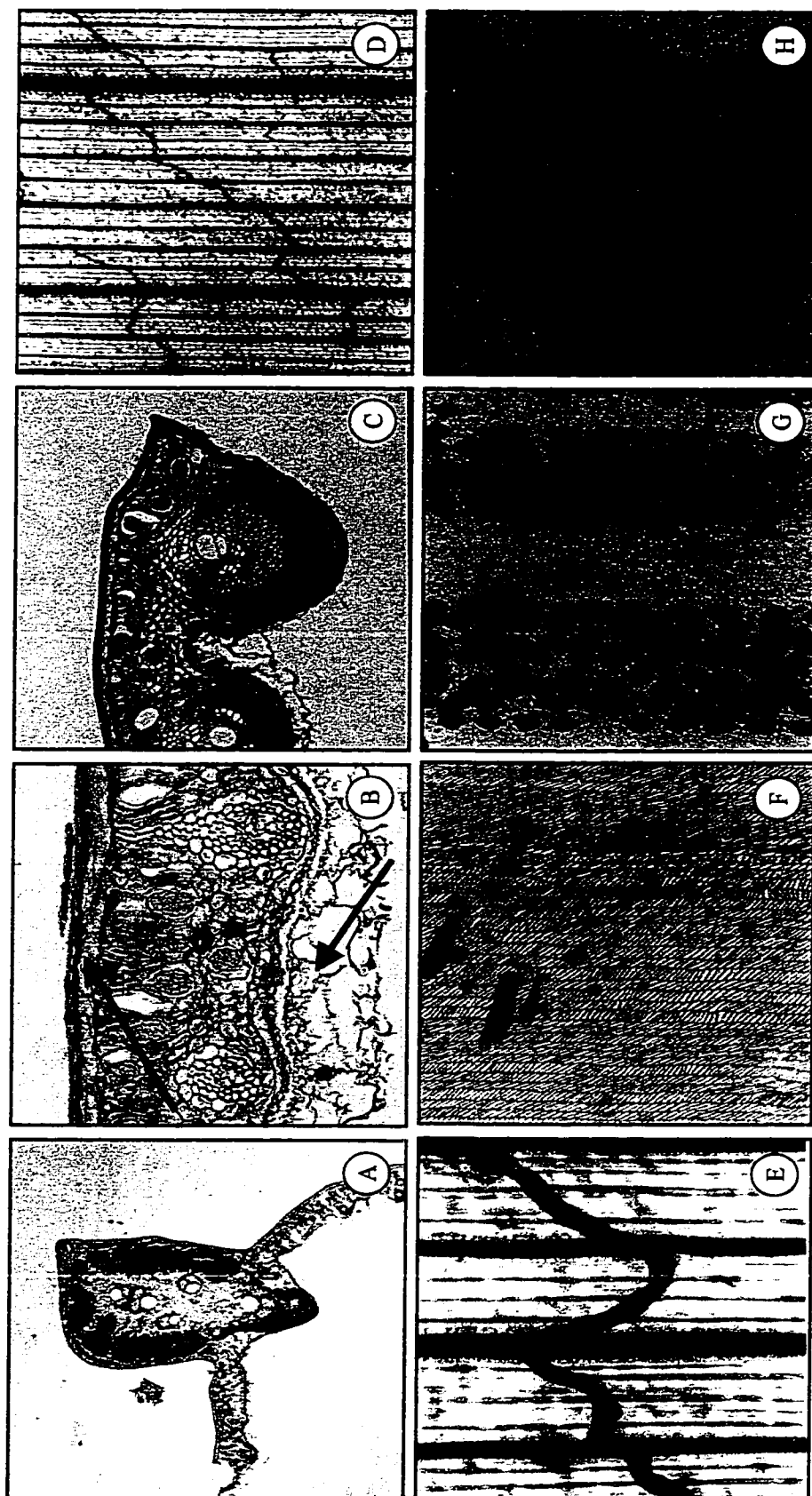
**Raphide-sacs:** absent. **Non-vascular fibers:** forming cylindrical and columnar strands; the cylindrical strands distributed in a single layer near the abaxial surface, level with the small veins; the columnar strands often attached to the adaxial hypodermis. **Primary veins:** obovoid, prominent abaxially; outer sheath incomplete, lateral only; inner sheath complete, thick-walled, 3-5 abaxial layers, laterally single layered, adaxially completed by a buttress reaching the hypodermis. **Secondary veins:** obovoid, abaxially prominent; outer sheath incomplete, lateral only; inner sheath complete, 1-2 layers of thick-walled fibers, adaxially a small buttress completed by thick-walled, often anticlinally extended,

mesophyll cells touching the hypodermis. **Tertiary veins:** roundish to slightly obovoid, centered; outer sheath complete or lacking abaxially; inner sheath incomplete, single layered, thick-walled fibers abaxially and laterally, thin-walled adaxially. **Quaternary veins:** absent. **Marginal rib:** ovoid, prominent abaxially; outer sheath incomplete, lateral, almost adaxial; inner sheath complete, thick-walled, 6 layers on abaxial region, 1-layered laterally, adaxially a small buttress not reaching the hypodermis. **Phloem:** of large veins divided into distinct strands by lines of thick-walled fibers. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B76, LC76, EP76- BRAZIL. AMAPÁ: Mun. Cupuxi, 45 km WSW of Porto Grande, 0°36'N, 51°52'W, 7 Jan 1985, Mori & Cardoso 17732 (NY); B77, LC77, EP77- SURINAME. Masowyne near Granks, 26 Oct 1962, Wessels Boer 196 (NY); B78, LC78, EP78- BRAZIL. RORAIMA: Mun. Alto Alegre, Ilha de Maracá, 3°24'N, 61°26'W, 15 Jul 1986, Henderson & Lima 605 (NY).

#### 1.4.3. Astrocaryum murumuru (Fig. 40)

Figure 40. Leaf anatomy of Astrocaryum murumuru. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B79, x25), B. midsection, note the continuous adaxial hyodermis (B81, x200), C. section tip (B81, x100), D. venation pattern (LC80, x20), E. transverse commissure (LC80, x100), F. adaxial surface (EP80, x100), G. abaxial surface (EP80, x100), H. stomata (EP80, x400).



**Midrib:** abaxially pointed, adaxially prominent; peripheral chlorenchymatous layer conspicuous, with fiber bundles; inner fibrous layer well-delimited, thick-walled, well-developed and several-layered ad- and abaxially, narrowed or interrupted laterally, 0-2-layered near the lamina; inner ground parenchyma with 2-5 large and several smaller vascular bundles often partially surrounded by thick-walled fibers, several phloem strands embedded at irregular intervals in the outermost region of the fibrous layer.

**Expansion cells:** forming conspicuous, 2-3-layered abaxial bands adjacent to midrib; adaxial bands absent; bands elsewhere in the lamina inconspicuous. **Hairs:** absent.

**Epicuticular wax** persistent ad- and abaxially, the units filamentous, almost spindle-shaped, transversely extended.

**Epidermis:** adaxial cell walls not sinuous, costal and intercostal abaxial cells slightly undulate; ad- and abaxial outer walls not thickened. **Adaxial epidermis:** costal and intercostal regions almost indistinct, the cells rhombohedral and rectangular, wider than longer, organized into distinct files, the cells alternately obliquely-longitudinally extended and transversely extended. **Abaxial epidermis:** costal and intercostal bands conspicuously differentiated; intercostal cell's shape and extension irregular, but few cells spindle-shaped; costal cells

mostly rectangular, longitudinally extended, the large and small bands raised, without the distinct longitudinal files of cells. **Stomata:** superficial, restricted to abaxial intercostal bands, not in distinct longitudinal files, but rather forming short rows of 2-6; terminal subsidiary cells overarching the guard-cells, shorter, wider, inflated, lobed? and well-differentiated from the surrounding epidermal cells. Lateral subsidiary cells exceeding and overarching the guard-cells in cross-section; guard-cells slightly below the level of epidermal surface, each with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface; adaxial layer wider, uniform and continuous along the whole lamina; abaxial layer compressed below the large veins, ending almost inside the substomatal chamber; ad- and abaxial cells transversely extended, rectangular, the cell junctions obscure.

**Chlorenchyma:** 2-layered, well-differentiated palisade mesophyll; spongy mesophyll, 4-5 layers of tightly arranged, thick-walled cells, intercellular air spaces absent. **Tannin cells:** few cells completely filled by a reddish tanniniferous material, the mesophyll not saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** absent.

**Non-vascular fibers:** forming cylindrical to ovoid-shaped

strands; the strands usually distributed in the adaxial region of the mesophyll, above the level of the small veins. **Primary veins:** prominent abaxially, roundish; outer sheath on higher lateral area, almost adaxial; inner sheath incomplete, 1-2 layers of thick-walled fibers abaxially, laterally single-layered, thin-walled fibers and conspicuously pitted parenchyma cells, adaxially thin-walled fibers forming a small buttress, these distally apiculate and not reaching the hypodermis. **Secondary veins:** obovoid to ellipsoidal, prominent abaxially; outer sheath on high lateral area, almost adaxial; inner sheath incomplete, 1-2 layers of thick-walled fibers abaxially, conspicuously pitted parenchyma cells laterally, adaxially a small buttress of thin-walled fibers or conspicuously pitted parenchyma cells; the buttress not reaching the hypodermis. **Tertiary veins:** roundish to slightly obovoid, prominent abaxially; outer sheath incomplete abaxially; inner sheath incomplete, 1-2 abaxial layers of thin-walled fibers completed above by conspicuously pitted sclerotic parenchyma cells. **Quaternary veins:** absent. **Marginal rib:** large, prominent abaxially; outer sheath only on high lateral area; inner sheath complete, 6-layered and thick-walled abaxially, 3-layered laterally and an obscure layer of thin-walled fibers adaxially. **Phloem:** of large veins

divided in distinct strands by lines of thick-walled fibers. **Transverse commissures:** wide, short, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B79, LC79, EP79- BRAZIL. PARÁ: Mun. Abaetetuba, praia de Beja, 1°35'N, 48°45'W, 1-5 m, 19 Oct 1994, Noblick et al. 5024 (NY); B80, LC80, EP80- FRENCH GUIANA. Trail from Saül airstrip to Roche Bateau, 3°37'N, 53°12'W, 22 Jun 1988, Prance et al. 30662 (NY); B81, LC81, EP81- BRAZIL. PARÁ: Ilha de Marajó, Rio Anajás, 3 Nov 1987, Beck & Souza 273 (NY).

### 1.5. Desmoncus

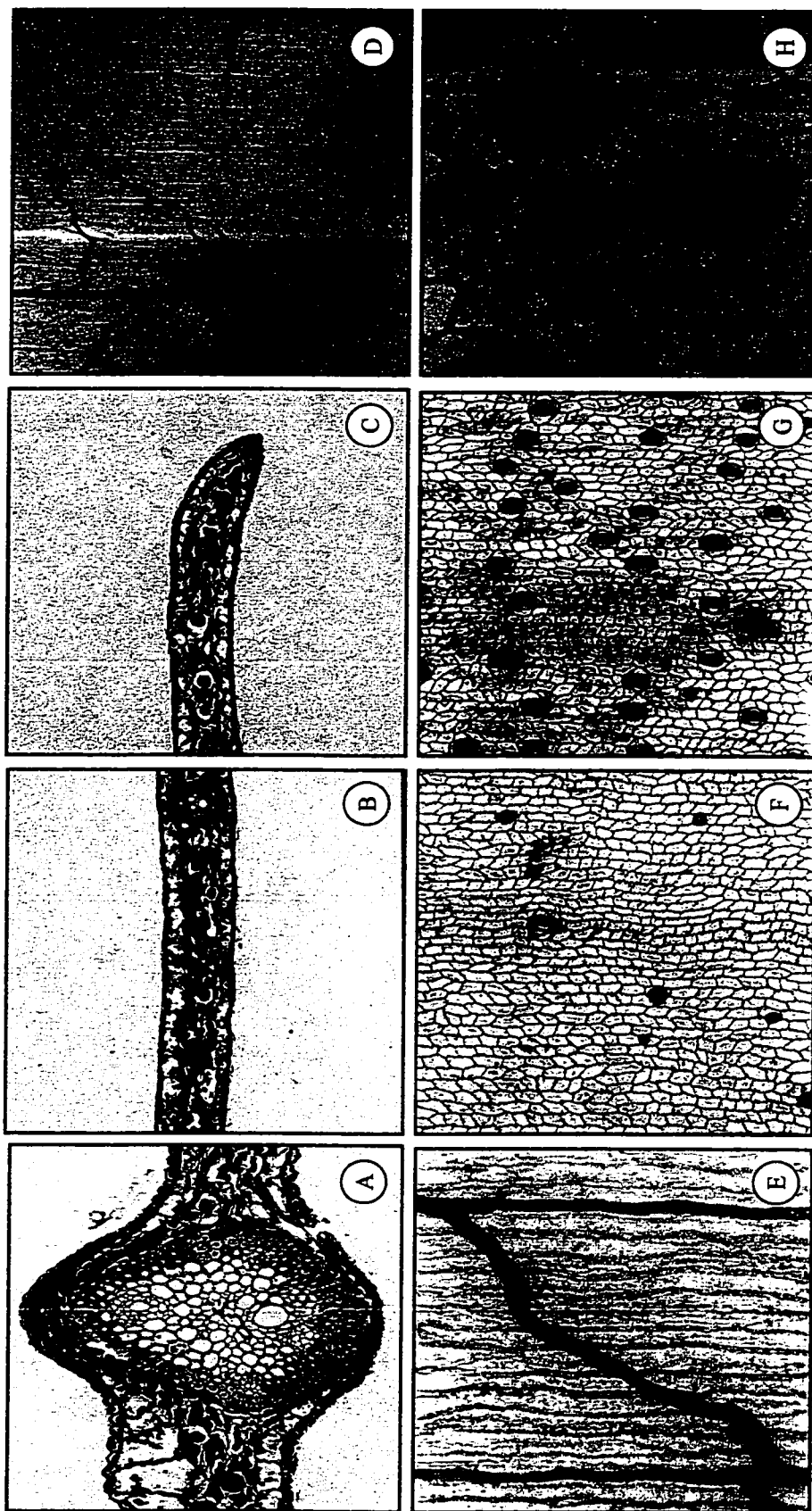
#### 1.5.1. Desmoncus macroacanthos (Fig. 41)

**Midrib:** abaxially rounded, adaxially prominent; peripheral chlorenchymatous layer conspicuous on adaxial region, tannin cells absent or present; inner fibrous layer well to poorly-delimited, thick-walled but width of the layer irregular, often narrowed near the lamina; inner ground parenchyma with 2 large and few smaller vascular bundles, few phloem strands embedded in the fibrous layer absent.

**Expansion cells:** forming inconspicuous, 1-layered adaxial



Figure 41. Leaf anatomy of Desmoncus macroacanthos. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B85, x40), B. midsection (B85, x100), C. section tip (B85, x100), D. venation pattern (LC87, x20), E. transverse commissure (LC87, x100), F. adaxial surface (EP85, x100), G. abaxial surface (EP85, x100), H. stomata (EP85, x400).



bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** on ad- and abaxial surface, mostly on large costal regions; hair base not seen in cross-section, but apparently multiseriate. **Epidermis:** ad- and abaxial cell walls sinuous, not thickened. **Adaxial epidermis:** with cells somewhat more irregularly shaped than abaxial cells in cross-section view; costal and intercostal regions only slightly distinct, the cells organized into distinct longitudinal files; intercostal cells mostly rectangular, longitudinally extended; costal cells narrower than intercostal cells, rectangular. **Abaxial epidermis:** costal and intercostal bands not conspicuously differentiated, both with cells organized into distinct longitudinal files; intercostal cells like those of the adaxial epidermis; costal cell rectangular, walls more sinuous than adjacent cells, the larger bands not raised, with up to 6 distinct longitudinal files of cells. **Stomata:** superficial, few adaxially along the large costal bands; abaxially numerous, not in distinct files, rather diffuse and distributed in both costal and intercostal bands; terminal subsidiary cells not overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells slightly below the epidermal surface, each with 2 cutinized ledges, the

outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface; ad- and abaxial layer compressed above and below the large veins; ad- and abaxial cells hexagonal, transversely extended. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-5 layers of tightly arranged, thick-walled cells. **Tannin cells:** either numerous and distinct from each other or numerous and not distinct, the cells completely or partially filled by a reddish tanniniferous material, in both cases the mesophyll is not saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** common, frequent on adaxial mesophyll. **Non-vascular fibers:** forming small cylindrical strands regularly or irregularly distributed as a single layer or not in the mesophyll; sometimes the strands in contact with the hypodermis. **Primary veins:** ovoid, slightly prominent ad- and abaxially; outer sheath incomplete, only lateral; inner sheath complete, 1-layered, either thin or thick-walled, the ad- and abaxial fibrous area not reaching the hypodermis. **Secondary veins:** roundish, centered; outer sheath complete; inner sheath complete, the fibers thin or thick-walled. **Tertiary veins:** roundish, centered; outer sheath complete; inner sheath complete, thin-walled. **Quaternary veins:** absent. **Marginal**

**rib:** absent. **Phloem:** of large veins undivided. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

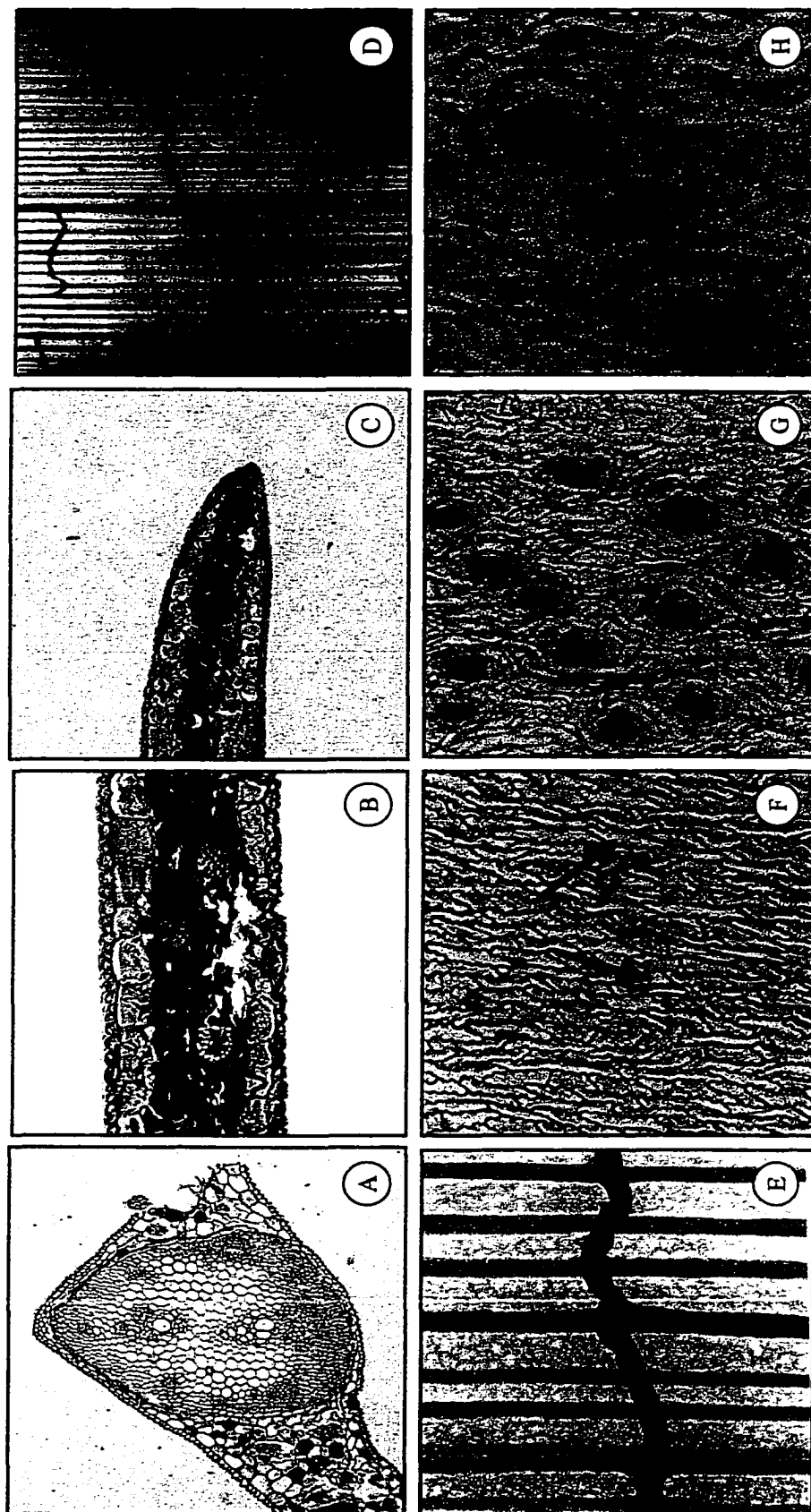
**Specimens examined.** B85, LC85, EP85- GUYANA.

Mazaruni-Potari District, Bartica-Potari road, 24 km S of Bartica, 6°13'N, 61°27'W, 180 m, 3 Aug 1985, Mori et al, 8100 (NY); B86, LC86, EP86- VENEZUELA. AMAZONAS: Dpto. Antures, vicinity of and upstream from damsite, 5°35'N, 67°15'W, 100 m, 13 May 1980, Steyermark et al. 122423 (NY); B87, LC87, EP87- GUYANA. Demerara-Mahaica Region, along Linden-Soesdyke Hwy, 6°30'N, 58°11'W, 1-50 m, 9 Dec 1986, Pipoly & Ameer 9236 (NY).

#### 1.5.2. Desmoncus orthacanthos (Fig. 42)

**Midrib:** abaxially rounded, equally prominent on both surfaces; chlorenchymatous layer inconspicuous; inner fibrous layer poorly-delimited adaxially, outermost layers on abaxial region thick-walled, laterally and adaxially thin-walled, layer width irregular but often narrowed near midpoint; inner ground parenchyma with 2 large and 4-5 smaller vascular bundles attached to the innermost fibrous layers. **Expansion cells:** forming inconspicuous or almost

Figure 42. Leaf anatomy of Desmoncus orthacanthos. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B122, x40), B. midsection (B123, x200), C. section tip (B123, x100), D. venation pattern (LC122, x20), E. transverse commissure (LC122, x200), F. adaxial surface, note the sinuous cell-wall (EP121, x100), G. abaxial surface (EP121, x200), H. stomata (EP121, x400).



indistinct, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** not seen. **Epidermis:** ad- and abaxial cell walls sinuous, thickened on outer walls, cell-shape rather irregular in cross-section view. **Adaxial epidermis:** intercostal cells with walls strongly sinuous, the cell-shape irregular, but many rectangular, longitudinal to obliquely-longitudinally extended, but angle of obliquity varying and some cells spindle-shaped, not organized in distinct longitudinal files; costal cells more regularly shaped, mostly rectangular, longitudinally extended, large costal regions with distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated; intercostal cells like those of the adaxial epidermis; costal cells narrower than intercostal cells, rhombohedral, longitudinally extended, the larger bands not raised, without the distinct longitudinal files of cells. **Stomata:** superficial, few adaxially along the large costal regions, abaxially numerous, not in distinct files, rather diffuse; terminal subsidiary cells overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells slightly sunken below the epidermal surface, each with 2 cutinized ledges, the



outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small. **Hypodermis:** 1-layered beneath each surface, the adaxial layer wider than abaxial layer, both layers compressed above and below the large veins; ad- and abaxial cells rectangular, except near the margin of the lamina. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 5-6 layers of loosely arranged, thick-walled cells. **Tannin cells:** numerous, the cells completely or partially filled by a reddish tanniniferous material, the mesophyll completely or partially saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** common on adaxial region. **Non-vascular fibers:** forming small cylindrical strands distributed in two distinct, ad- and abaxial layers. **Primary veins:** ovoid, slightly prominent in both surfaces; outer sheath incomplete, only lateral; inner sheath incomplete, 1-2-layered, either thick-walled or the layer completely formed by conspicuously pitted parenchyma cells; fibrous area touching the abaxial hypodermis. **Secondary veins:** roundish, abaxial; outer sheath complete; inner sheath incomplete, 1-layered, completely formed by conspicuously pitted parenchyma cells or shortly thick-walled abaxially. **Tertiary veins:** roundish, abaxial; outer sheath complete; inner sheath incomplete, 1 layer of conspicuously pitted

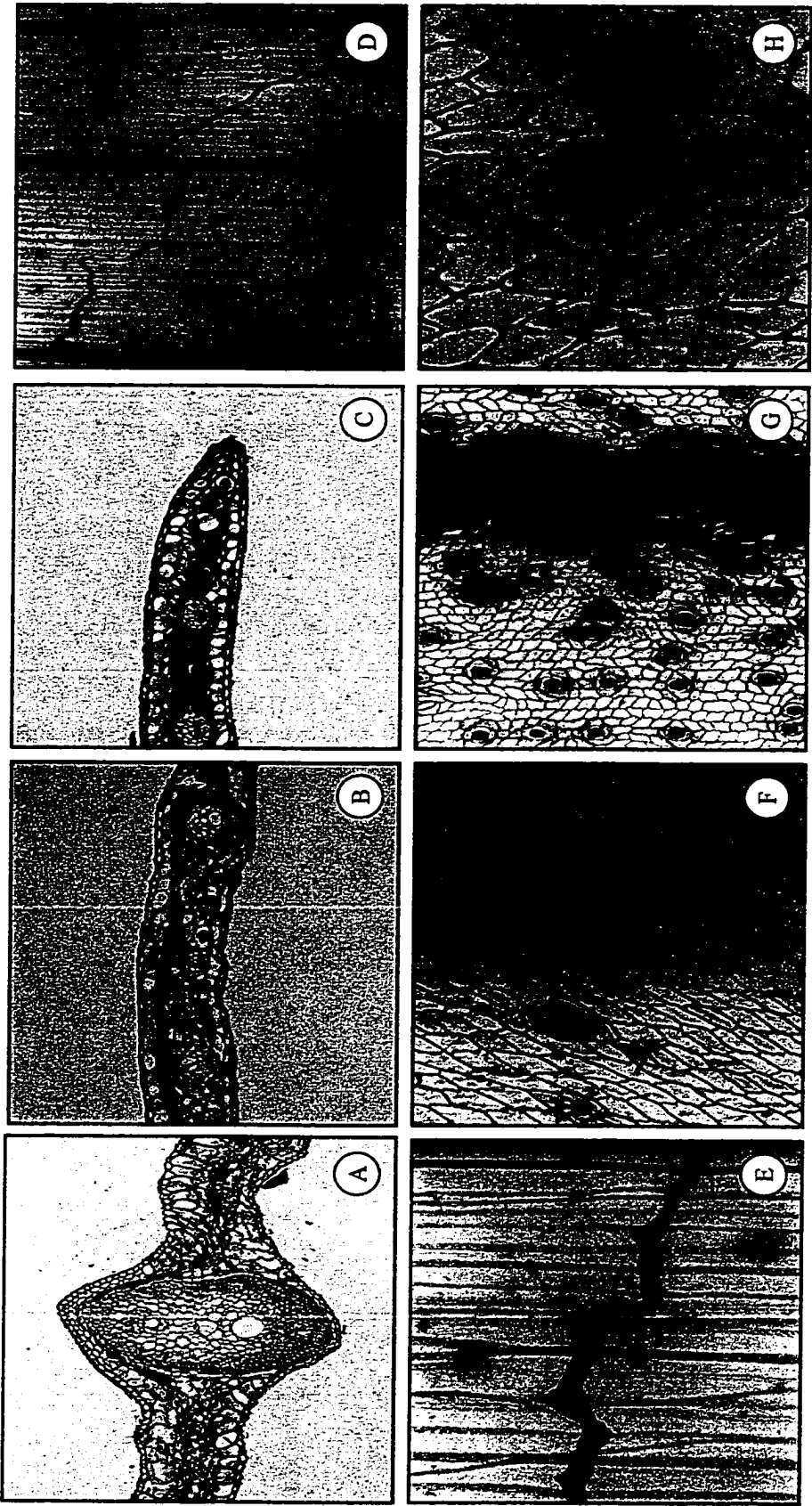
parenchyma cells or the layer shortly thick-walled abaxially. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins partially divided into distinct strands by sclerotic partition. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B121, LC121, EP121- VENEZUELA. DELTA AMACURO: Dpto. A. Diaz, Caño Daudacana, 8°47'N, 61°00'W, 0 m, 19 Aug 1982, Malave & Canales 23 (NY); B122, LC122, EP122- SURINAME. Dikkshoop near Groningen, Saramacca River, 29 Apr 1963, Wessels Boer 1335 (NY); B123, LC123, EP123- SURINAME. Cultuurtuin-Paramaribo, 24 Jan 1961, Kramer & Hekking 123 (NY).

#### 1.5.3. Desmoncus polyacanthos (Fig. 43)

**Midrib:** abaxially rounded, equally prominent on both surfaces; peripheral chlorenchymatous layer conspicuous on adaxial region; inner fibrous layer poorly-delimited, abaxial and outermost layers thick-walled, the innermost on lateral to adaxial regions thin-walled, but layer width irregular, although often narrowed near the lamina; inner ground parenchyma with 1 large and 4-5 smaller vascular

Figure 43. Leaf anatomy of Desmoncus polyacanthos. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B88, x40), B. midsection (B88, x100), C. section tip (B88, x100), D. venation pattern (LC90, x20), E. transverse commissure (LC90, x100), F. adaxial surface (EP89, x200), G. abaxial surface (EP88, x100), H. stomata (EP89, x400).



bundles, few phloem strands embedded in the adaxial fibrous layer. **Expansion cells:** forming inconspicuous, 1-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** few, ad- and abaxially along the large costa; hair base sunken, multiseriate? cutinized. **Epidermis:** ad- and abaxial cell walls sinuous, not thickened. **Adaxial epidermis:** with cells somewhat more irregularly shaped than abaxial cells in cross-section view; costal and intercostal region distinct and organized into longitudinal files of cells, large costal regions with up to 15 lines of cells; intercostal cells mostly rhombohedral, longitudinally extended; costal cells narrower than intercostal cells, rectangular, longitudinally extended; the walls of costal cells more sinuous than adjacent cells. **Abaxial epidermis:** large costal and intercostal bands conspicuously differentiated, both organized into distinct longitudinal files of cells; intercostal cell-shape more irregular than adaxial cells, rhombohedral, hexagonal, longitudinally to obliquely-longitudinally extended; costal cells rectangular to rhombohedral, walls much sinuous than adjacent cells, the larger bands not raised, with up to 10 distinct longitudinal lines of cells. **Stomata:** superficial, adaxially along the large costal bands; abaxially numerous,

not in distinct files, rather diffuse; terminal subsidiary cells not overarching the guard-cells, shorter, wider and well-differentiated from the surrounding epidermal cells; guard-cells level with the epidermal surface, each with 2 cutinized ledges, the outermost slightly enlarged, the wall thickened below each ledge. **Substomatal chamber:** small.

**Hypodermis:** usually 1-layered beneath each surface but an additional, discontinuous layer sometimes present near the margin of the lamina; the adaxial layer wider than abaxial layer, both layers compressed above and below the large veins; adaxial cells hexagonal, non-transversely to slightly transversely extended; abaxial cells rectangular, rarely hexagonal to oblong, more transversely extended than adaxial cells. **Chlorenchyma:** palisade mesophyll absent; spongy mesophyll well-differentiated, 4-6 layers of tightly arranged, thick-walled cells. **Tannin cells:** numerous, the cells completely or partially filled by a brownish tanniniferous material, the mesophyll completely or partially saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** common, frequent on adaxial region. **Non-vascular fibers:** forming small cylindrical strands regularly or irregularly distributed in the mesophyll; when regularly distributed they form an abaxial layer, in contact or not with the hypodermis. **Primary veins:** roundish to slightly

ovoid, abaxially prominent or not; outer sheath incomplete, only lateral; inner sheath complete, thick-walled, 2 layered. **Secondary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath incomplete, 1-layered, abaxially thick-walled, laterally thin-walled and adaxially either thin-walled or the layer completed by conspicuously pitted parenchyma cells. **Tertiary veins:** roundish, centered; outer sheath incomplete abaxially; inner sheath incomplete, 1-layered, abaxially thick-walled, laterally thin-walled and adaxially the layer completed by conspicuously pitted parenchyma cells. **Quaternary veins:** absent. **Marginal rib:** absent. **Phloem:** of large veins divided into distinct strands by lines of fibers. **Transverse commissures:** wide, elongate, regularly arranged and forming a continuous pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B88, LC88, EP88- SURINAME.

Oelemari River bank, 20 km above airstrip, 19 Mar 1963, Wessels Boer 1037 (NY); B89, LC89, EP89- SURINAME. Blaka watra creek, 18 Oct 1962, Wessels Boer 177 (NY); B90, LC90, EP90- SURINAME. Some miles South of Present Hope, 24 Jan 1962, Hekking 1248 (NY).

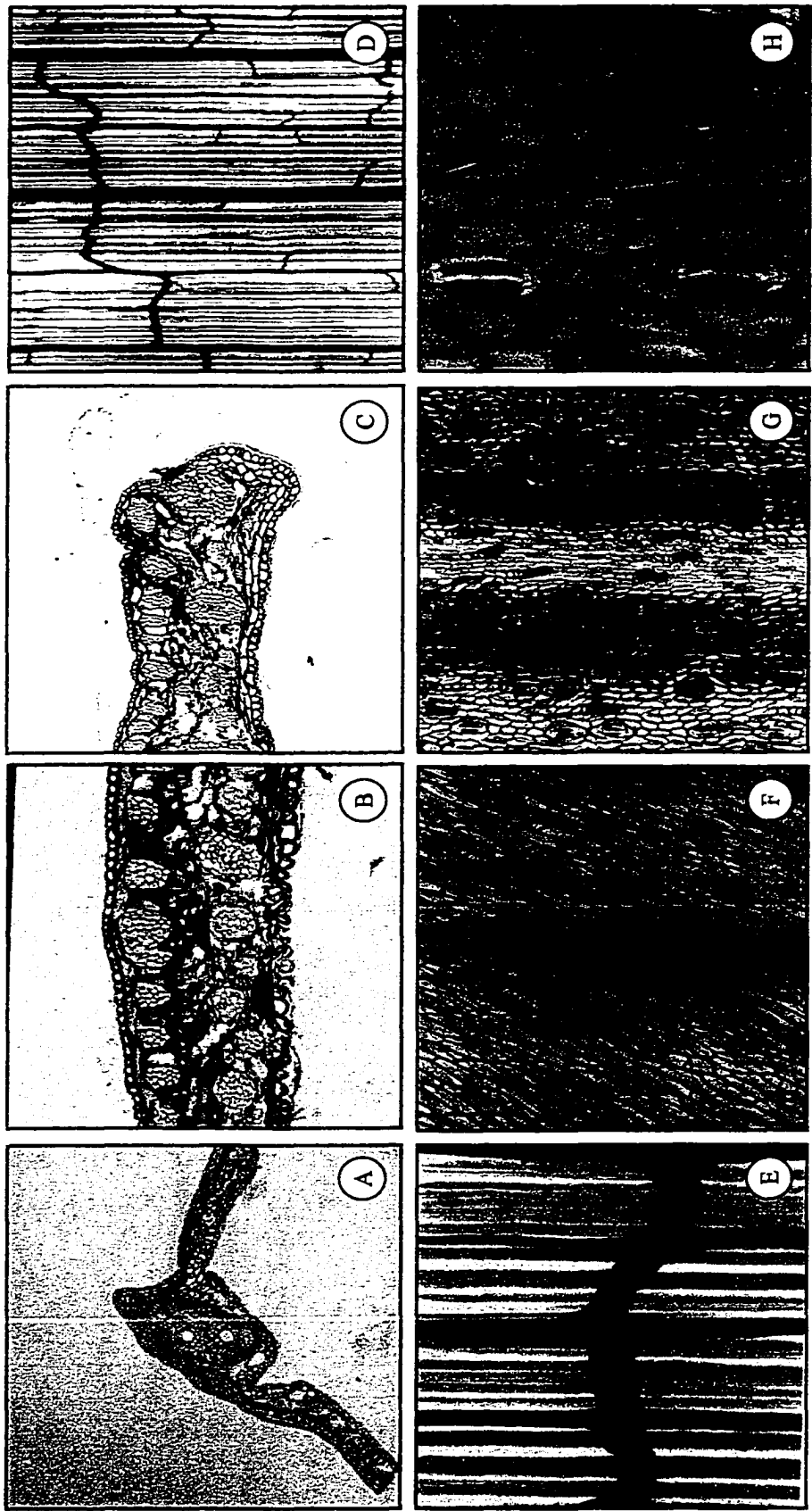
#### 1.6. Gastrococos

1.6.1. Gastrococos crista (Fig. 44)

**Midrib:** abaxially pointed or rounded, equally prominent on both surfaces; chlorenchymatous layer conspicuous but irregular, interrupted or not; inner fibrous layer well-developed, poorly-delimited, thick-walled, narrowed and 2-4-layered or very wide laterally near the lamina; inner ground parenchyma with 3-6 large and several smaller vascular bundles, all partially surrounded by thick-walled fibers, several isolated phloem strands embedded in the outermost fibrous layers. **Expansion cells:** forming conspicuous, 2-layered abaxial bands adjacent to midrib; bands elsewhere in the lamina inconspicuous. **Hairs:** rare on adaxial surface, more frequent abaxially, irregularly distributed on large costal bands, but in distinct files on small bands; hair base not seen in cross-section, but distal structure of smaller hairs uniseriate and cutinized; large hairs not seen. **Epidermis:** ad- and abaxial cell walls not sinuous, wholly thickened. **Adaxial epidermis:** intercostal cells mostly rhombohedral, obliquely-longitudinally extended, but angle of obliquity varying and some cells spindle-shaped, organized into distinct longitudinal files; costal cells smaller than intercostal



Figure 44. Leaf anatomy of Gastrococos crispa. A-C, cross-section; D-E, clearings; F-H, epidermal peels. A. midrib (B131, x40), B. midsection (B130, x200), C. section tip (B130, x100), D. venation pattern (LC130, x20), E. transverse commissure (LC130, x200), F. adaxial surface (EP131, x20), G. abaxial surface (EP131, x100), H. stomata (EP131, x400).



cells, mostly rectangular, longitudinally extended in the center of the costa, outermost cells obliquely extended, large costal regions with up to 12 distinct longitudinal files of cells. **Abaxial epidermis:** cells smaller than adaxial cells, costal and intercostal bands conspicuously differentiated, cells around stomata distinctly smaller and somewhat rectangular; intercostal cells mostly irregularly shaped, those in same file as stomata narrower and more elongate than adjacent epidermal cells, oblong, forming short rows up to 4 cells long; costal cells smaller than intercostal cells, rectangular or hexagonal, longitudinally extended, the larger bands slightly raised, with up to 24 distinct longitudinal files of cells. **Stomata:** sunken, restricted to abaxial intercostal bands, forming short rows of 2-7; terminal subsidiary cells overarching the guard-cells, larger, wider and well-differentiated from the surrounding epidermal cells. Lateral subsidiary and adjacent epidermal cells wider and overarching the guard-cells in cross-section view; guard-cells with 2 cutinized ledges of similar size, the wall thickened below each ledge. **Substomatal chamber:** large, merging with adjacent intercellular spaces? **Hypodermis:** 1-layered beneath each surface, both layers compressed above and below the large veins; adaxial cells hexagonal, transversely extended;

abaxial cell-shape rather irregular, but many of them rectangular, transversely extended. **Chlorenchyma:** 2-layered palisade mesophyll, the first layer interrupted by columnar non-vascular fiber bundles attached to the hypodermis, the second layer less developed, just below the columnar strands; spongy mesophyll well-differentiated, 5-6 layers of loosely arranged, thick-walled cells; numerous, large intercellular spaces irregularly distributed in the mesophyll. **Tannin cells:** mostly adaxial, between the columnar non-vascular fiber bundles, few cells readily distinct, completely filled by the reddish tanniniferous material, other cells only partially filled, the mesophyll not saturated. **Fiber-sclereids:** absent. **Raphide-sacs:** rare, centered. **Non-vascular fibers:** forming cylindrical and columnar strands; the cylindrical strands distributed in a distinct abaxial layer level with the small veins; the columnar strands always attached to the adaxial hypodermis. **Primary veins:** ovoid to widely ovoid, prominent ad- and abaxially; outer sheath incomplete, only lateral; inner sheath complete, thick-walled, 4-layered abaxially, laterally 1-2-layered and 3-4 layers adaxially; the ad- and abaxial fibrous region not reaching the hypodermis. **Secondary veins:** narrowly ovoid, centered; outer sheath incomplete, lateral above the phloem; inner sheath

complete, abaxially thick-walled and 2-layered, laterally a single layer of thin-walled fibers, adaxially a short, triangular-shaped buttress of thick-walled fibers reaching the hypodermis. **Tertiary veins:** roundish, abaxial; outer sheath incomplete abaxially; inner sheath incomplete, 2 layers of thick-walled fibers abaxially, 1-layered laterally and adaxially, but only thin-walled fibers on adaxial region. **Quaternary veins:** roundish, abaxial; outer sheath complete; inner sheath mostly conspicuously pitted parenchyma cells, but a few thin-walled fibers present abaxially. **Marginal rib:** small, not prominent; outer sheath only adaxial; inner sheath complete, thick-walled, 4-layered abaxially, dwindling adaxially to a single layer. **Phloem:** of large veins divided into distinct strands by lines of thick-walled cells, except in the poorly developed phloem of the veins in the margin of lamina. **Transverse commissures:** wide, short and elongate, irregularly arranged and forming a scattered pattern in surface view; sheathed by sclerotic parenchyma.

**Specimens examined.** B129, LC129, EP129- CUBA.

MATANZAS: hills South of Matanzas, 10 Sep 1903, Britton & Wilson 470 (NY); B130, LC130, EP130- CUBA. HABANA: vecindad de Santiago de Las Vegas, 1 Mar 1900, Baker 4556 (NY);

B131, LC131, EP131- CUBA. HABANA: Punta Brava, 29 May 1914,  
Ekman 1171 (NY) .

## 2. Notes on anatomical methods

### 2.1. HF treatment for leaf cross-section samples

Among the genera studied, Desmoncus could not be left for more than 4 days in HF solution without being damaged. Acrocomia, Gastrococos, Astrocaryum, and Aiphanes were not damaged if left for 9 days. The timing for Bactris species was quite variable. Species belonging to the Guilielma group (Henderson, 2000), were the most resistant. All Pyrenoglyphis species and two of three Amylocarpus species (B. hirta and B. simplicifrons) were damaged after 4 days.

### 2.2. Flower clearings

All species with thick petals, including all Astrocaryum, Acrocomia aculeata, Gastrococos crista and the Bactris of the Guilielma group, required a longer time in 5% NaOH to have the petals cleared. It often resulted in overly macerated floral parts, making their handling difficult. The tannin-rich staminate flowers of Bactris

horridispatha, B. major, B. brongniartii, B. bifida, B. maraja, and all Astrocaryum species required two changes of the NaOH solution.

### 3. Cladistic Analysis

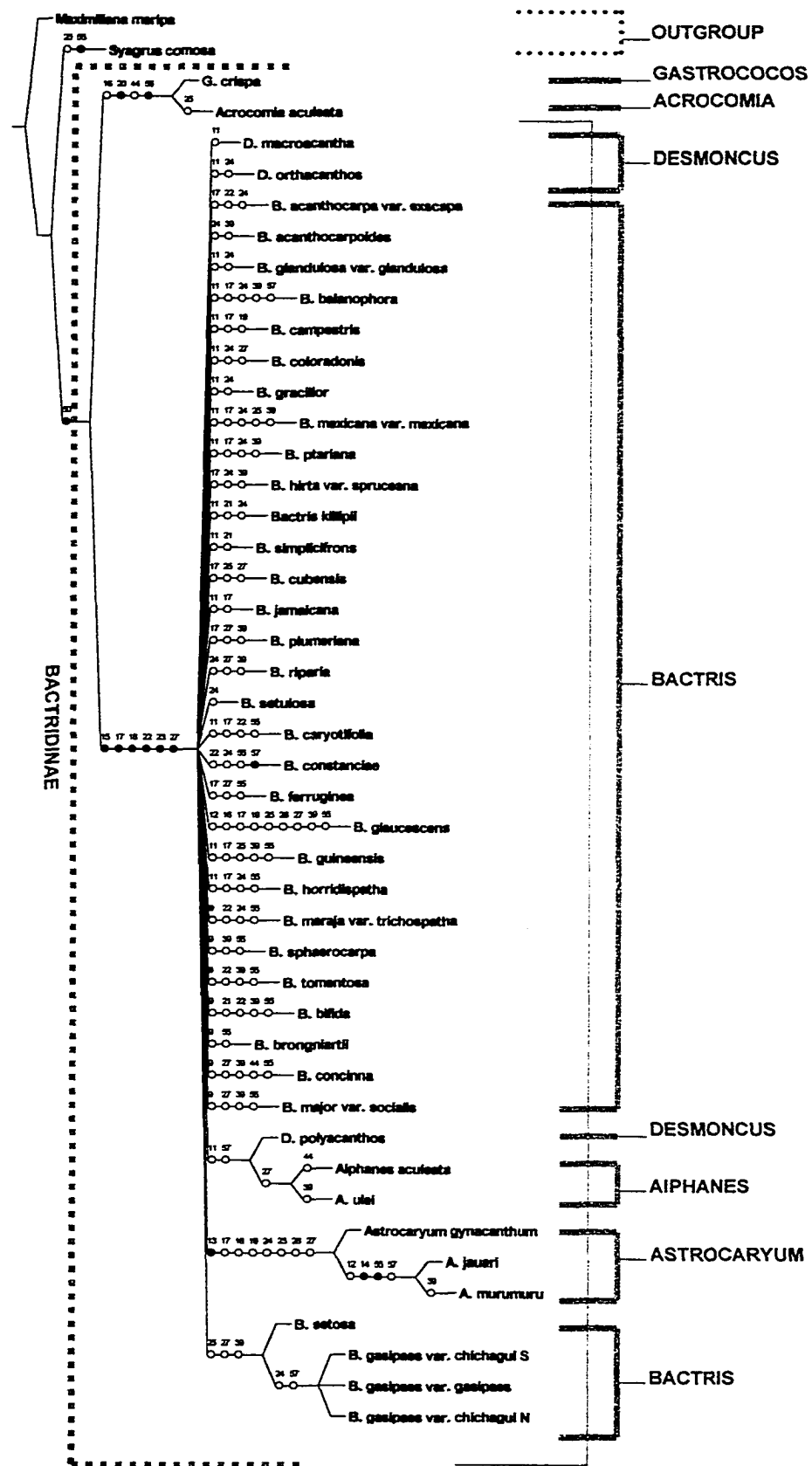
#### 3.1. Anatomical data set

##### 3.1.1. Data Matrix 1 - restricted polymorphisms

After 100 replications, 5000 trees (each L=81, CI=0.35, RI=0.74) were retained in memory. The consensus tree (Fig. 45) was almost completely unresolved (L=171, CI=0.16, RI=0.30). The monophyly of Bactridinae is supported but the relationships among its genera remain largely unresolved. A clade formed by Gastrococos and Acrocomia is positioned outside a large polytomy comprising all the remaining genera. Within this polytomy, only three major clades are supported. The best supported of these is the Astrocaryum clade, defined by a single synapomorphy: persistent epicuticular wax on the abaxial surface (ch. 13). A second clade, supported only by homoplasious characters, includes the two Aiphanes and Desmoncus polyacanthos. A third clade includes B. setosa,

Figure 45. Strict consensus tree from the analysis of anatomical data set, matrix 1: taxa with restricted polymorphisms.





which is sister to an unresolved group formed by two B. gasipaes varieties.

Figure 46 represents a tree randomly chosen among the 5000 trees retained by Winclada. In this tree Gastrococos, Acrocomia, and Astrocaryum form monophyletic groups. This is not the case, however, of Bactris and the other Bactridinae genera. The species of Desmoncus do not form a monophyletic group. In one clade, D. polyacanthos is sister to the species of Aiphanes. Desmoncus macroacanthos is sister to Bactris simplicifrons. Desmoncus orthacanthos is the basal taxon to a branch with several clades including some Bactris, the two other Desmoncus and the Aiphanes species.

### 3.1.2. Data Matrix 2 - polymorphic taxa divided into subtaxonomic units (Fig. 47)

The results of the analysis are similar to the ones obtained with the data matrix 1. The longer consensus tree (L=210) and higher RI (0.53) reflect the larger number of terminals and decrease in character conflict or missing information (-) in the data matrix.

As can be seen from Fig. 47, the subtaxonomic units of Acrocomia and Gastrococos are not supported as monophyletic

Figure 46. Randomly chosen tree of the analysis of anatomical data set, matrix 1: restricted polymorphisms.

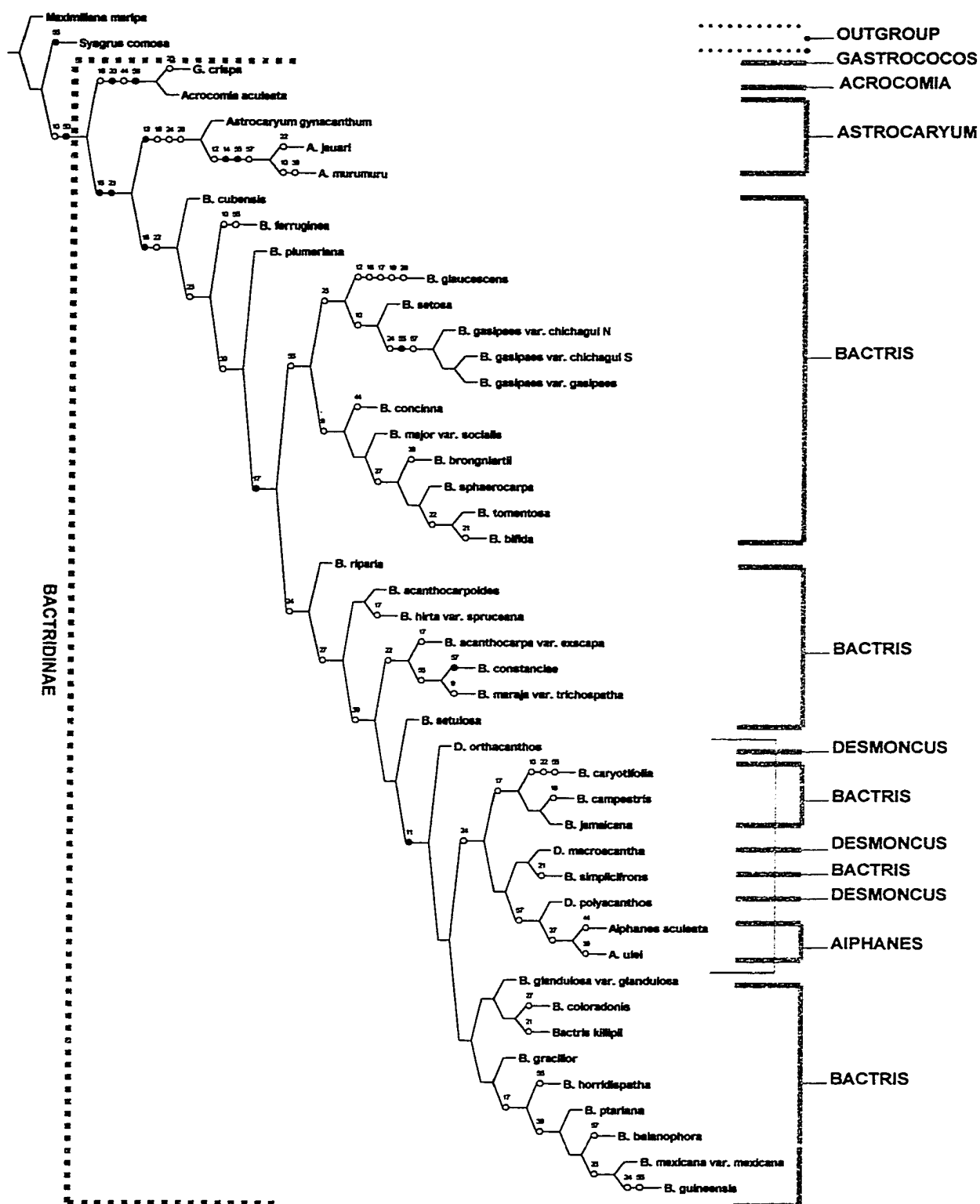
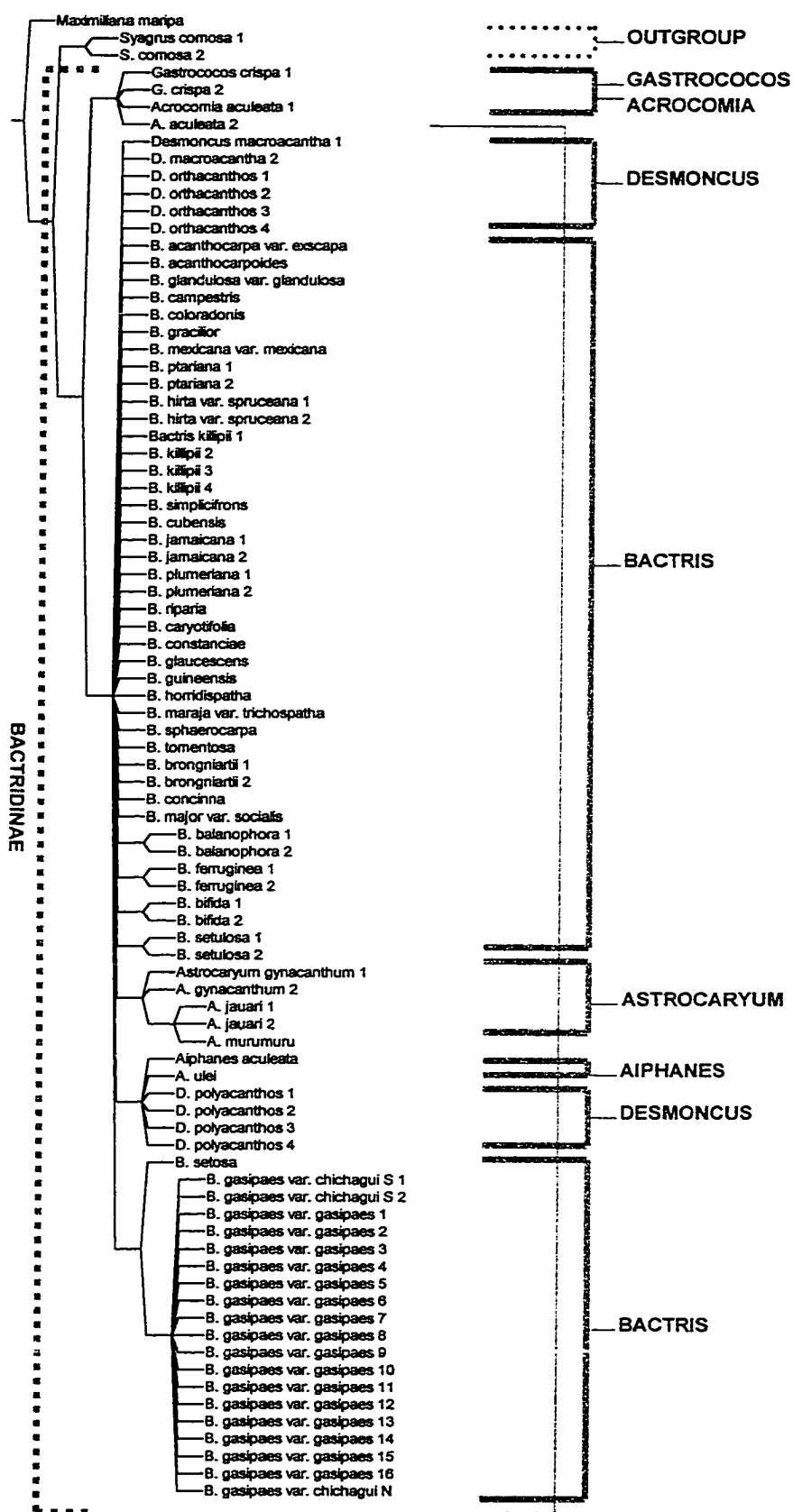


Figure 47. Strict consensus tree from the analysis of anatomical data set, matrix 2: polymorphic taxa divided into subtaxonomic units.



groups and the segregation of these two genera is not possible. As with the analysis of data matrix 1, Aiphanes and the four subtaxonomic units of Desmoncus polyacanthos form a clade with unresolved relationships. Relationships among the subtaxonomic units of Astrocaryum do not conflict with those inferred from the analysis of data matrix 1.

Figure 48 represents a tree randomly chosen among the 5000 trees retained by Winclada. In this tree the subtaxonomic units of Gastrococos and Acrocomia are well resolved. Astrocaryum form a clade nested in a branch with a few subtaxonomic units of Bactris. In this clade, Bactris glaucescens is sister to the Astrocaryum taxa. Aiphanes and Desmoncus position in this tree are similar to that of Fig. 46.

### 3.2. Morphological data set

#### 3.2.1. Data Matrix 1 - restricted polymorphisms

Cladistic analysis resulted in 613 equally most parsimonious trees, each 136 steps long, CI=0.37, and RI=0.71. However, as in the analysis of the anatomical data, the strict consensus tree (L=239, CI=0.21, RI=0.36) was largely unresolved (Fig. 49). The monophyly of

Figure 48. Randomly chosen tree from the analysis of anatomical data set, matrix 2: polymorphic taxa divided into subtaxonomic units.



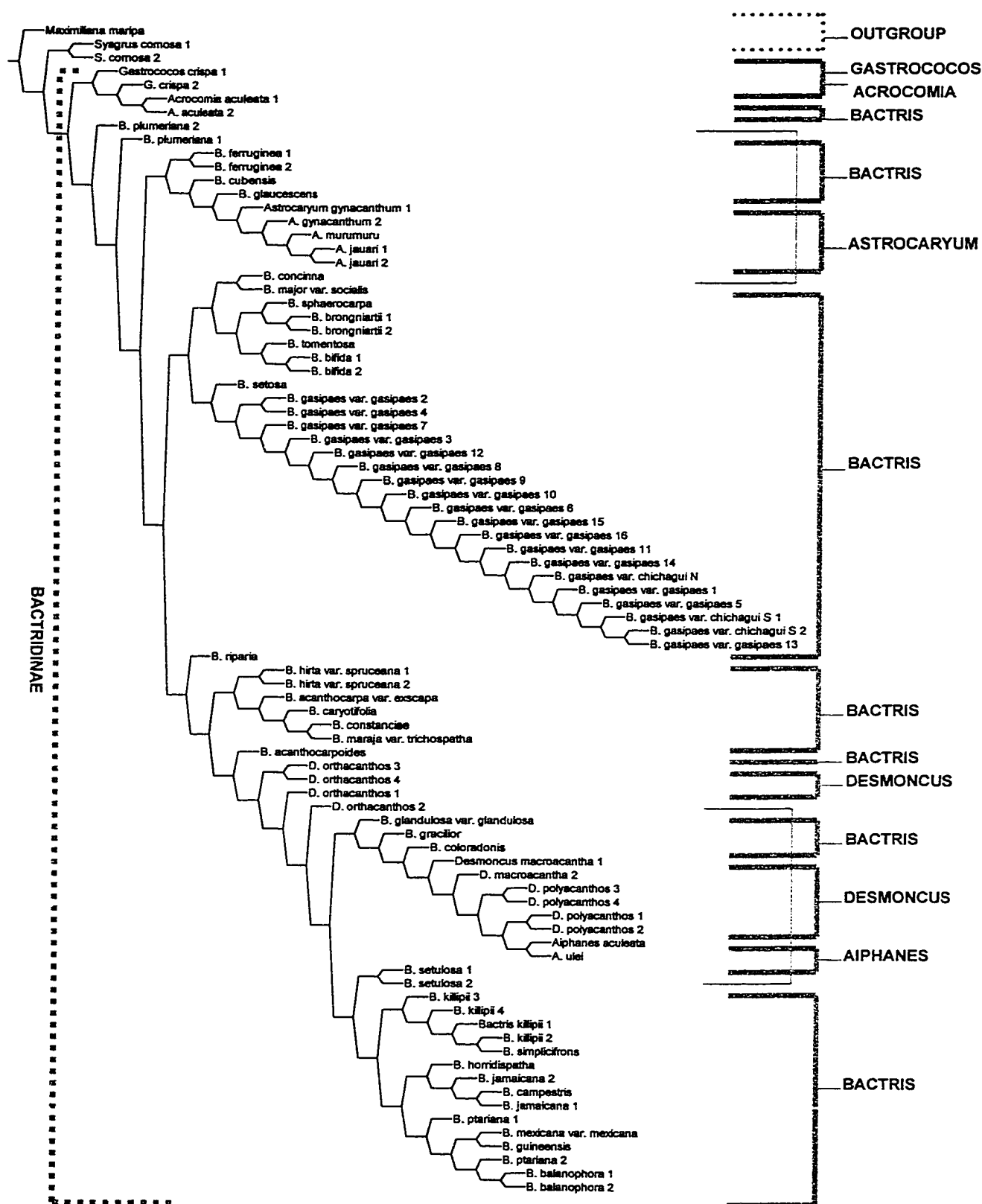
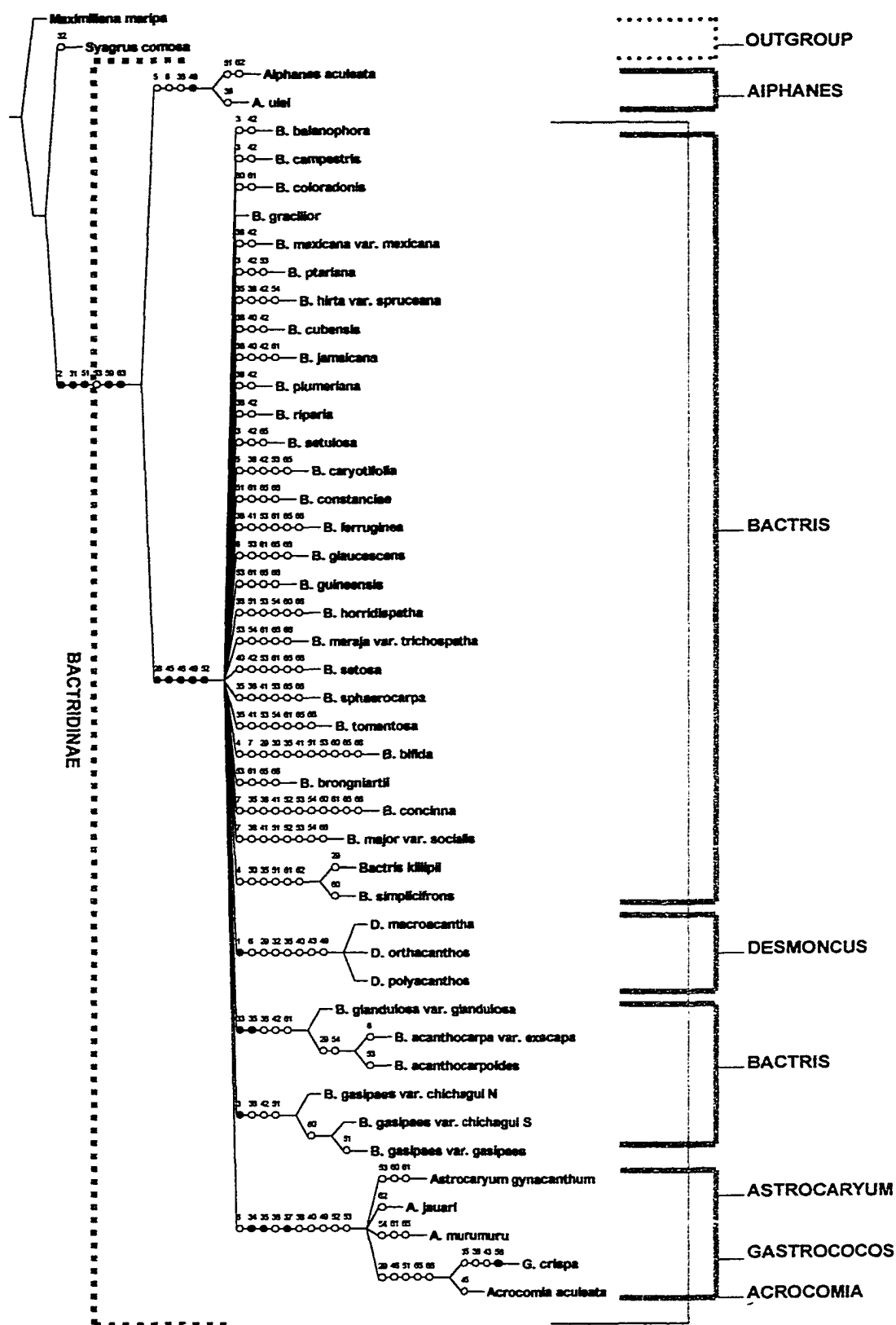


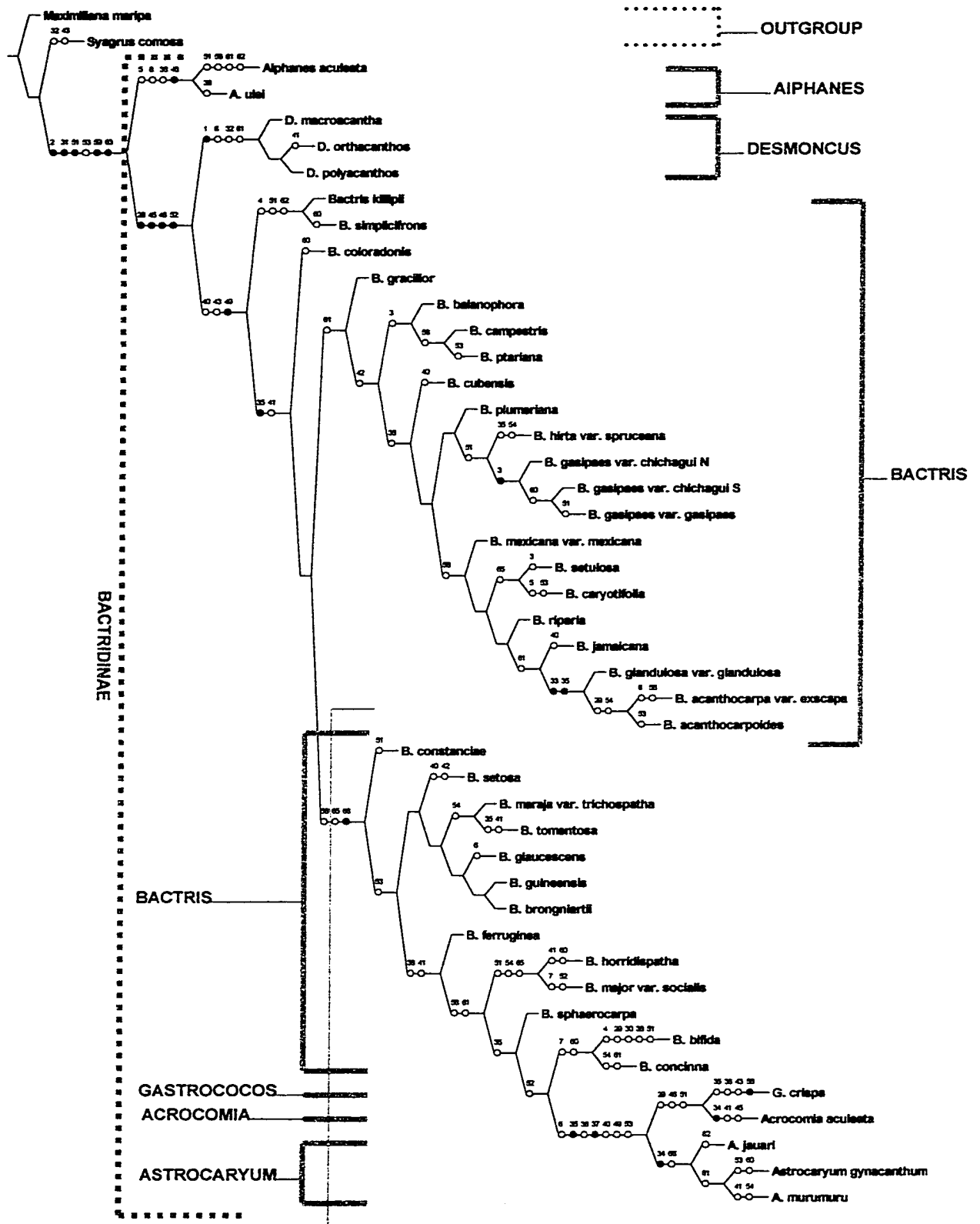
Figure 49. Strict consensus tree from the analysis of morphological data set, matrix 1, taxa with restricted polymorphisms.



Bactridinae is supported but the relationships among its genera is not resolved. Aiphanes is the sister clade to the large clade including the remaining taxa. Within this large clade, five smaller clades are present. The first, supported by homoplasious characters, includes Bactris simplicifrons and B. killipii. The second includes all taxa of Desmoncus, supported by a single synapomorphy: stem with climbing habit (ch. 1). The third includes B. glandulosa, B. acanthocarpa, and B. acanthocarpoides, supported by two synapomorphies: 1) filamentous rachillae (ch. 33), and 2) flower triads regularly arranged on one side of rachillae (ch. 35). The fourth clade includes the two varieties of B. gasipaes, supported by a homoplasious synapomorphy: petiolar spines forming longitudinal ranks (ch. 3). The last and best supported clade is formed by Acrocomia, Gastrococos and the three Astrocaryum species.

Figure 50 represents a tree randomly chosen among the 613 most parsimonious trees retained by Winclada. In this tree Aiphanes and Desmoncus form monophyletic groups. Gastrococos and Acrocomia form a clade sister the Astrocaryum taxa. All of them are monophyletic, but are nested in a clade including several species of Bactris.

Figure 50. Randomly chosen tree from the analysis of morphological data set, matrix 1, taxa with restricted polymorphisms.



### 3.2.2. Data Matrix 2 - polymorphic taxa divided into subtaxonomic units

The resulting consensus tree (Fig. 51) was 314 steps long, with a CI=0.16, and a RI=0.57. The monophyletic status of Bactridinae is supported but the cladogram is mostly unresolved.

The two Aiphanes species form a small clade sister to a largely unresolved clade that includes the remaining taxa. Within the larger clade, there are several small clades; four of these corresponds to the subtaxonomic units of Bactris ptariana, B. bifida, B. hirta, and B. jamaicana, suggesting that each of these species is monophyletic. The Desmoncus clade, Acrocomia-Gastrococos-Astrocaryum clade, and the clade containing Bactris glandulosa, are also supported. A clade formed by Bactris simplicifrons and B. killipii is also present, but the relationships among its subtaxonomic units are unresolved. The final clade includes one subtaxonomic unit of Bactris plumeriana (#1) and all the subtaxonomic units of the varieties of B. gasipaes. It is worth noting that the relationships among the subtaxonomic units of the southern population of var. chichagui and the var. gasipaes are not clear.

Figure 51. Strict consensus tree from the analysis of morphological data set, matrix 2, polymorphic taxa divided into subtaxonomic units.



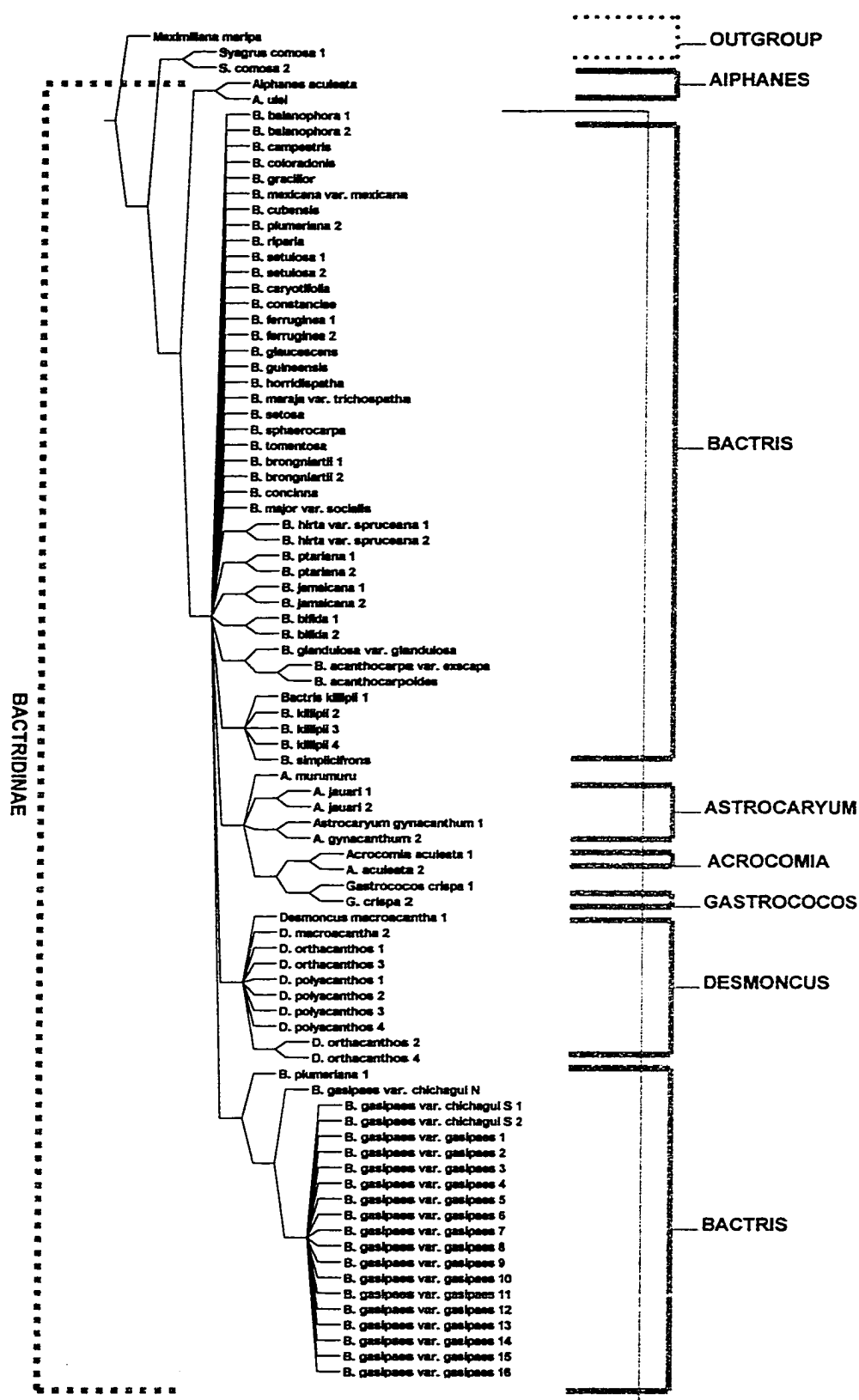


Figure 52 represents a tree randomly chosen among the 5000 trees retained by Winclada. In this tree, Aiphanes and Desmoncus form monophyletic groups sister to Bactris. The position of the subtaxonomic units of Acrocomia, Gastrococos, and Astrocaryum are similar to that obtained in Fig. 50.

### 3.3. Combined anatomical and morphological data sets

#### 3.3.1. Data Matrix 1 - restricted polymorphisms

The analysis resulted in two most parsimonious trees, 241 steps long, CI=0.33, and RI=0.67. The strict consensus tree (Fig. 53) was 250 steps long, with a CI=0.32, RI=0.66. With the exception of a polytomy within Bactris, the resolution is greater than in any of the analysis of separated data sets.

#### a) Relationships among the genera of Bactridinae

The subtribe Bactridinae is monophyletic and supported by five uncontradicted synapomorphies: 1) presence of spines (ch. 2); 2) non-grooved outer surface of the peduncular bract (ch. 31); 3) ovules centrally attached

Figure 52. Randomly chosen tree from the analysis of morphological data set, matrix 2, polymorphic taxa divided into subtaxonomic units.

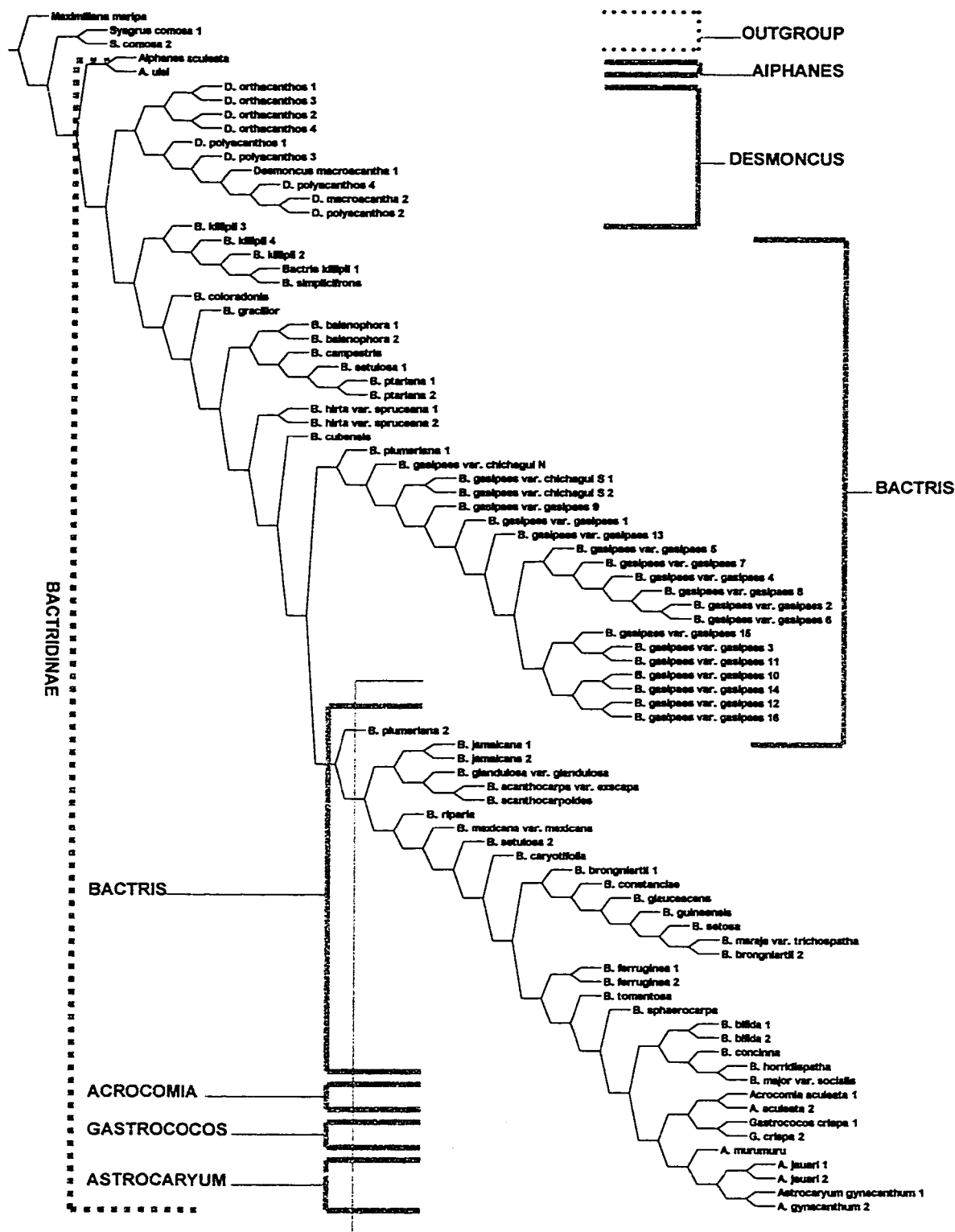
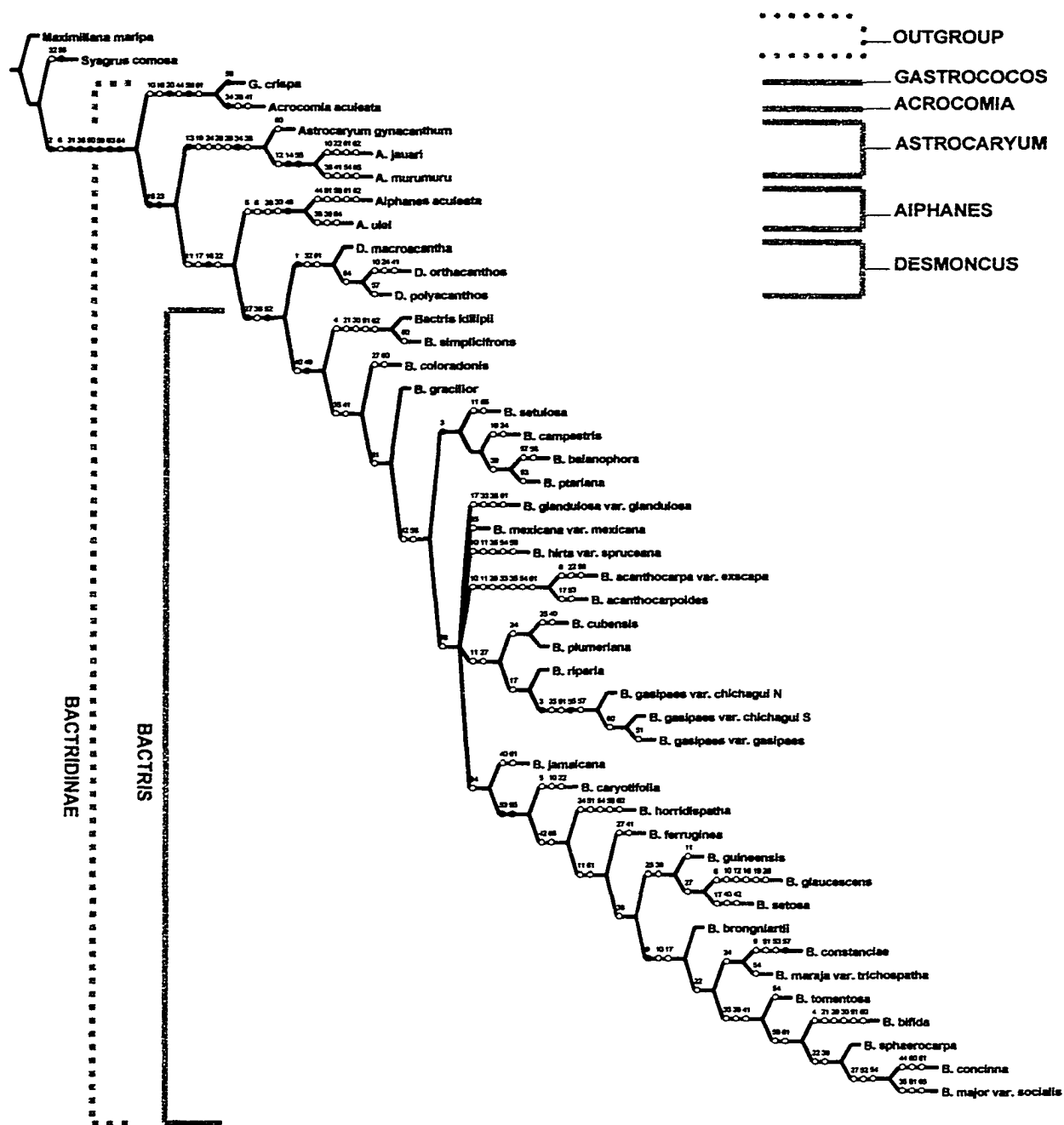


Figure 53. Strict consensus tree from the analysis of combined data set, data matrix 1, taxa with restricted polymorphisms.



(ch. 50); 4) medial to apical endocarp pores (ch. 59); and 5) a fibrous endocarp (ch. 63). Two additional homoplasious synapomorphies also support the clade: 1) symmetrical staminate flowers (ch. 36), and 2) fibrous endocarp (ch. 64).

Gastrococos and Acrocomia form a basal clade supported by two synapomorphies: 1) lateral subsidiary cells overarching the guard cells (ch. 20), and 2) absence of outer mesocarp fibers (ch. 56). Acrocomia can be distinguished from Gastrococos by its staminate flowers developed in shallow pits and subtended by bracts on the rachillae surface (ch. 34). The remaining Bactridinae form a clade supported by two uncontradicted synapomorphies: 1) abaxial epidermal cells forming distinct rows when in the same files as stomata (ch. 15), and 2) the presence of vascular bundles in the peripheral chlorenchymatous layer of the midrib (ch. 23).

The three species of Astrocaryum form a monophyletic clade supported by two synapomorphies: 1) epicuticular wax persistent on abaxial epidermis (ch. 13), and 2) staminate flowers developing in deep pits (ch. 34). Astrocaryum jauari and A. murumuru form a clade, sister to A. gynacanthum, supported by two synapomorphies: 1) adaxial epidermal cells in distinct files alternately oblique and

transversely arranged (ch. 14), and 2) a fleshy mesocarp (ch. 55). The clade formed by Aiphanes, Desmoncus and Bactris is supported by one uncontradicted synapomorphy: abaxial stomata not arranged in distinct files or short rows (ch. 18).

Aiphanes is monophyletic and sister to the clade formed by Desmoncus and Bactris. The Aiphanes clade is supported by one synapomorphy: lobes of the pistillate corolla spreading during anthesis (ch. 48).

The clade formed by Desmoncus and Bactris is supported by two homoplasious synapomorphies: 1) absence of palisade mesophyll (ch. 27), and 2) absence of staminodial ring in fruit corolla (ch. 52). The Desmoncus clade is supported by one uncontradicted synapomorphy: a stem with a climbing habit (ch. 1). Within this genus, D. orthacanthos and D. polyacanthos form a clade weakly supported by one homoplasy: lack of non-pore endocarp fibers (ch. 64).

Bactris is supported by only one uncontradicted synapomorphy: stigmas non-reflexed during anthesis (ch. 49).

#### b) Relationships within Bactris



There are five major clades within Bactris and although it is mostly resolved, the majority of the clades are poorly supported.

The basal clade is formed by B. killipii and B. simplicifrons. It is supported by five homoplasious characters: 1) simple leaf blade (ch. 4); 2) leaf with several main veins (ch. 21); 3) spines absent in the peduncular bract (ch. 30); 4) fruits globose (and also ellipsoid in B. killipii, Ch. 51); and 5) grooved endocarp (ch. 62). The second and third clades are formed by one species each: B. coloradonis and B. gracilior.

The fourth clade comprises four species: B. setulosa, B. campestris, B. balanophora and B. ptariana. Its synapomorphy is petiolar spines clustered or in short rows (ch. 3).

The fifth clade is polytomy. Although the relationships within this clade are not clear, it includes three poorly supported and more inclusive clades.

The first is formed by B. acanthocarpa var. exscapa and B. acanthocarpoides. The second includes B. cubensis and B. plumeriana, forming a clade sister to the clade comprising B. riparia, and the two varieties of B. gasipaes. These varieties form an inclusive clade supported by two synapomorphies: 1) petiolar spines forming

longitudinal ranks (ch. 3, but var. gasipaes is polymorphic), and 2) mesocarp hard-starchy (ch. 55). The third clade includes 15 taxa. Excluding the basal taxon, B. jamaicana, all the remaining taxa share one uncontradicted synapomorphy, the juicy fruits (ch. 55), and one homoplasious synapomorphy, black to purple-black fruits (ch. 53, except B. constanciae). The species of the distal portion of the branch form a terminal clade supported by a homoplasious synapomorphy: presence of fiber-sclereids (ch. 9, absent in B. constanciae).

The topology of Bactris is fully resolved in the trees on Figures 54 and 55, the two equally most parsimonious trees found.

In Fig. 54 the taxa included in the unresolved fifth clade of the strict consensus tree are rearranged into three clades, resolving the positioning of B. glandulosa, B. mexicana, and B. hirta.

Bactris glandulosa is sister to the remaining taxa included in the unresolved fifth clade. These remaining taxa are organized into two large clades. The first includes B. mexicana and B. hirta. There, B. hirta becomes part of a clade including B. acanthocarpa and B. acanthocarpoides. This small clade is supported by one homoplasy: spinulous epicarp (ch. 54) and is sister to a

Figure 54. Tree one of two obtained from the analysis of combined data sets, data matrix 1, taxa with restricted polymorphisms.

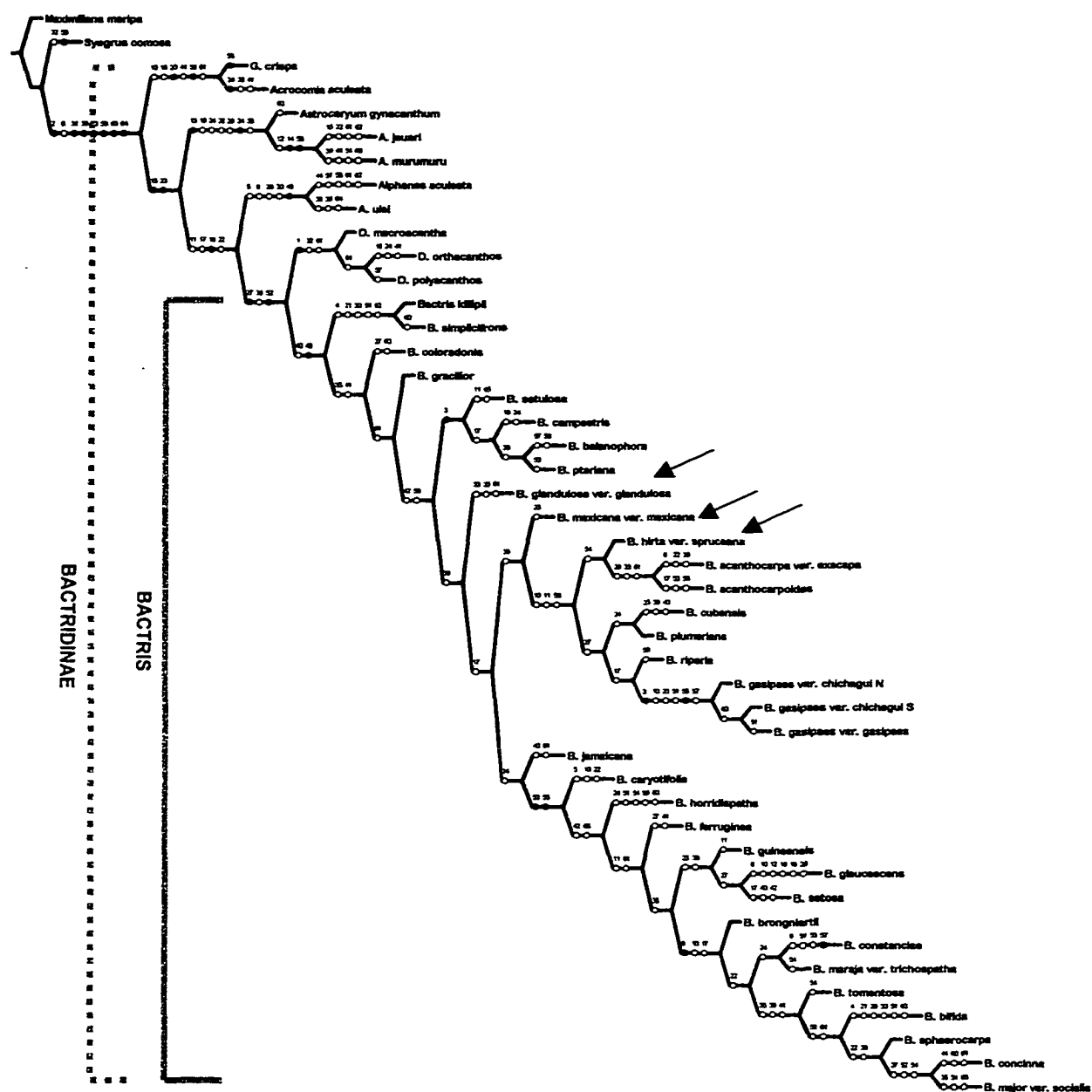
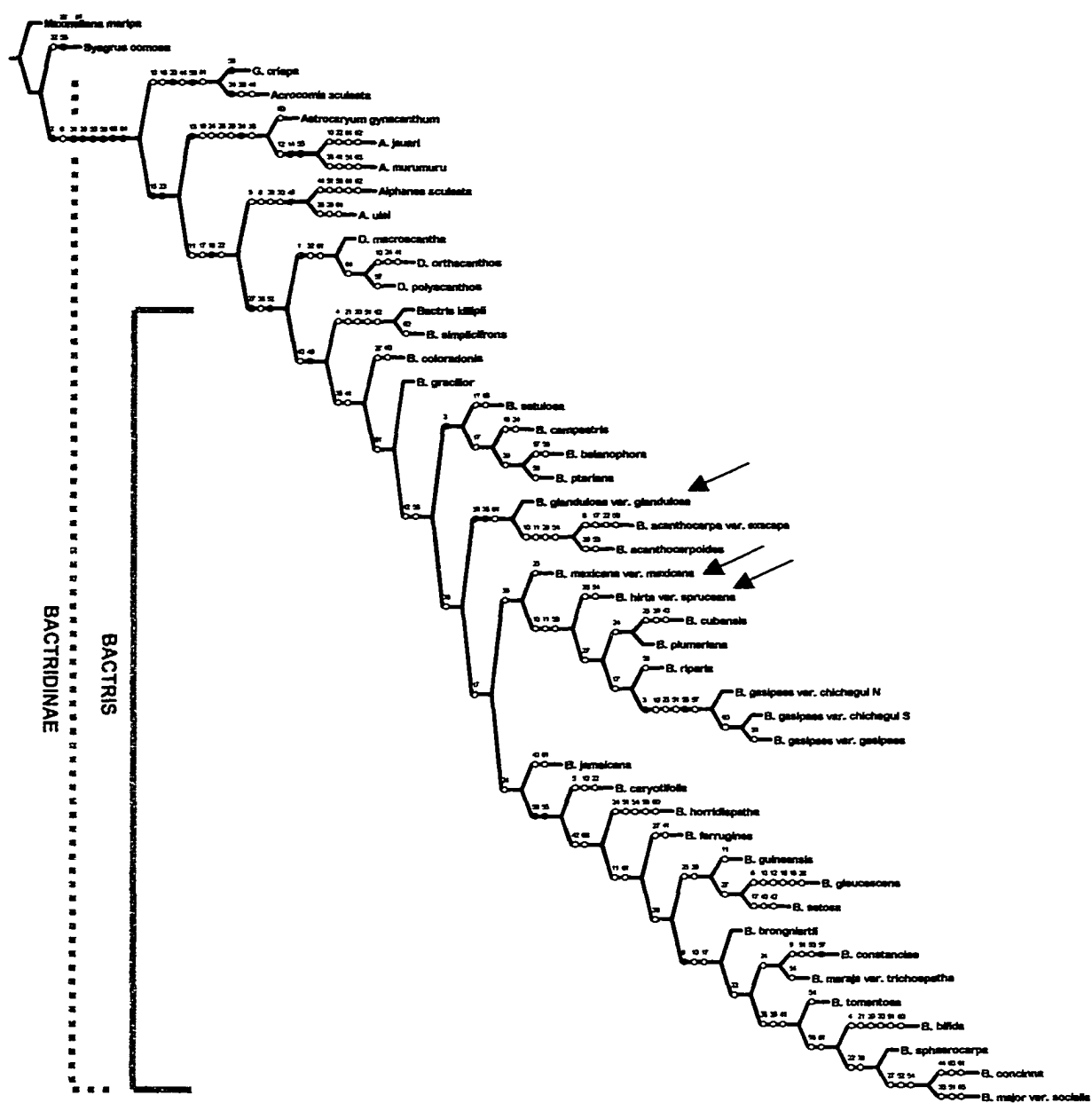


Figure 55. Tree two of two obtained from the analysis of combined data sets, data matrix 1, taxa with restricted polymorphisms.



larger clade including B. cubensis, B. plumeriana, B. riparia, and the two varieties of B. gasipaes. Bactris mexicana is sister to all these taxa.

In Fig. 55, the position of B. glandulosa, B. mexicana, and B. hirta is different. Bactris glandulosa becomes part of the clade including B. acanthocarpa and B. acanthocarpoides. This small clade Figure 50. Tree one of two equally most parsimonious trees from the analysis of combined data set, matrix 1, taxa with restricted polymorphisms. This small clade is supported by one uncontradicted synapomorphy: filamentous rachillae (ch. 33) and a homoplasious synapomorphy: floral triads regularly distributed on one side of the rachillae (ch. 35).

Bactris mexicana and B. hirta are included in a poorly supported clade formed by B. cubensis, B. plumeriana, B. riparia, and the two varieties of B. gasipaes.

### 3.3.2. Data Matrix 2 - polymorphic taxa divided into subtaxonomic units

Each of the 5000 trees retained by the program was 281 steps long and had a CI=0.28, and RI=0.79. The strict consensus tree (Fig. 56) was 318 steps long, with a CI=0.25, and RI=0.76.

a) Relationships among the genera of Bactridinae

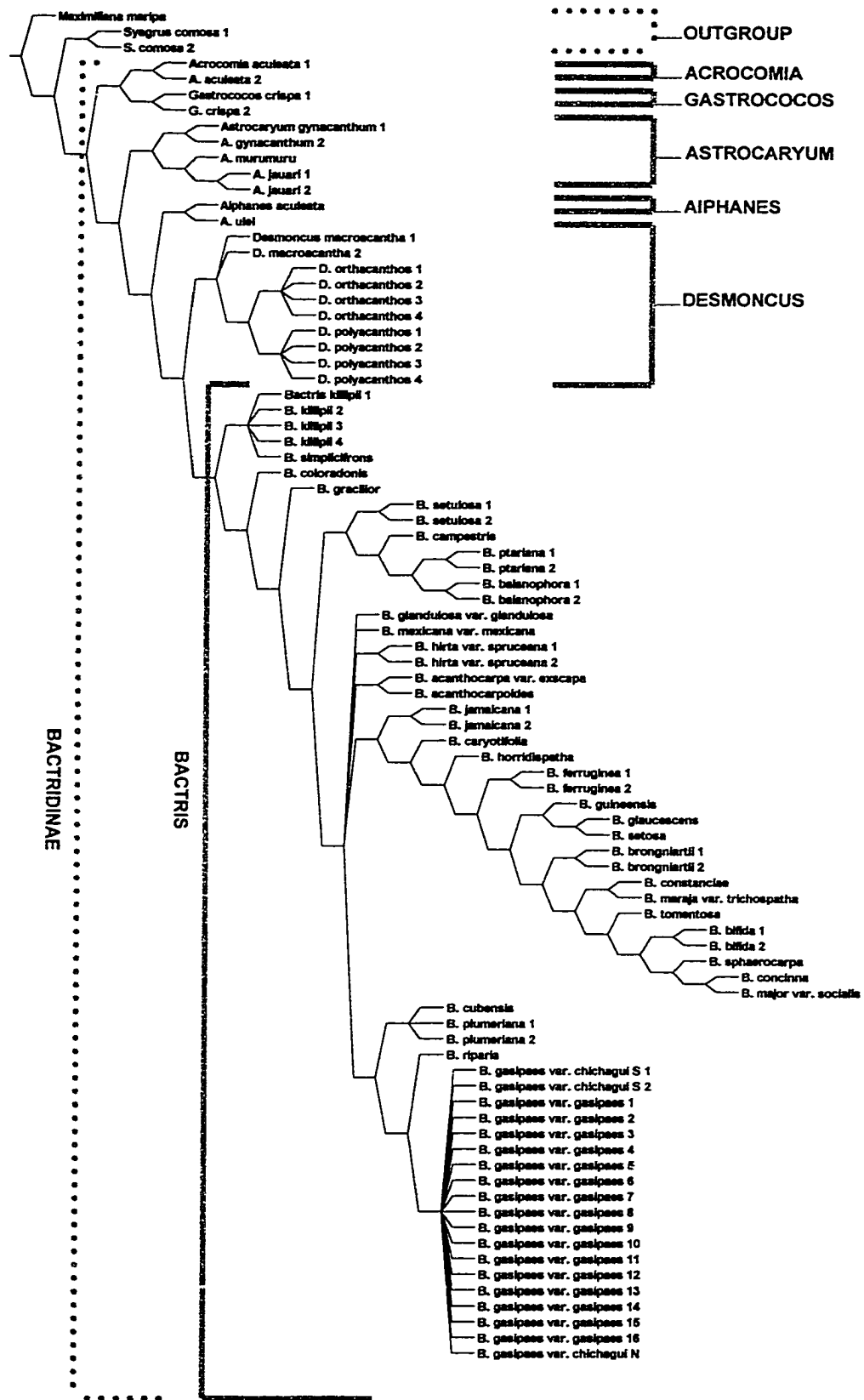
Cladistic analysis of data matrix 2 supports the monophyly of Bactridinae. Relationships among its genera are identical to those inferred from data matrix 1. In Desmoncus and Bactris the relationships among the subtaxonomic units are not resolved within some clades. In the former, the two D. macroacanthos subtaxonomic units do not form a distinct clade. The other two species, D. orthacanthos and D. polyacanthos, form distinct clades but there is no resolution among their subtaxonomic units.

b) Relationships within Bactris

The general structure of Bactris remains unchanged and the five previously discussed major clades are also present here. The relationships among the subtaxonomic units within some clades, however, are not always resolved. These are the cases of the clades comprising B. killipii and B. simplicifrons, the clade including B. plumeriana, and the clade including the varieties of B. gasipaes.



Figure 56. Strict consensus tree from the analysis of combined data set, matrix 2, polymorphic taxa divided into subtaxonomic units.



The fifth clade is a polytomy in which the subtaxonomic relationship is similar to that resulting from the analysis of data matrix 1. The relationships in this clade are, however, resolved in the tree in Fig. 57, chosen arbitrarily among the 5000 equally most parsimonious trees. The subtaxonomic units included in the fifth clade of the strict consensus tree are rearranged into three clades and the resulting topology is equivalent to that obtained in the tree presented in Fig. 54.

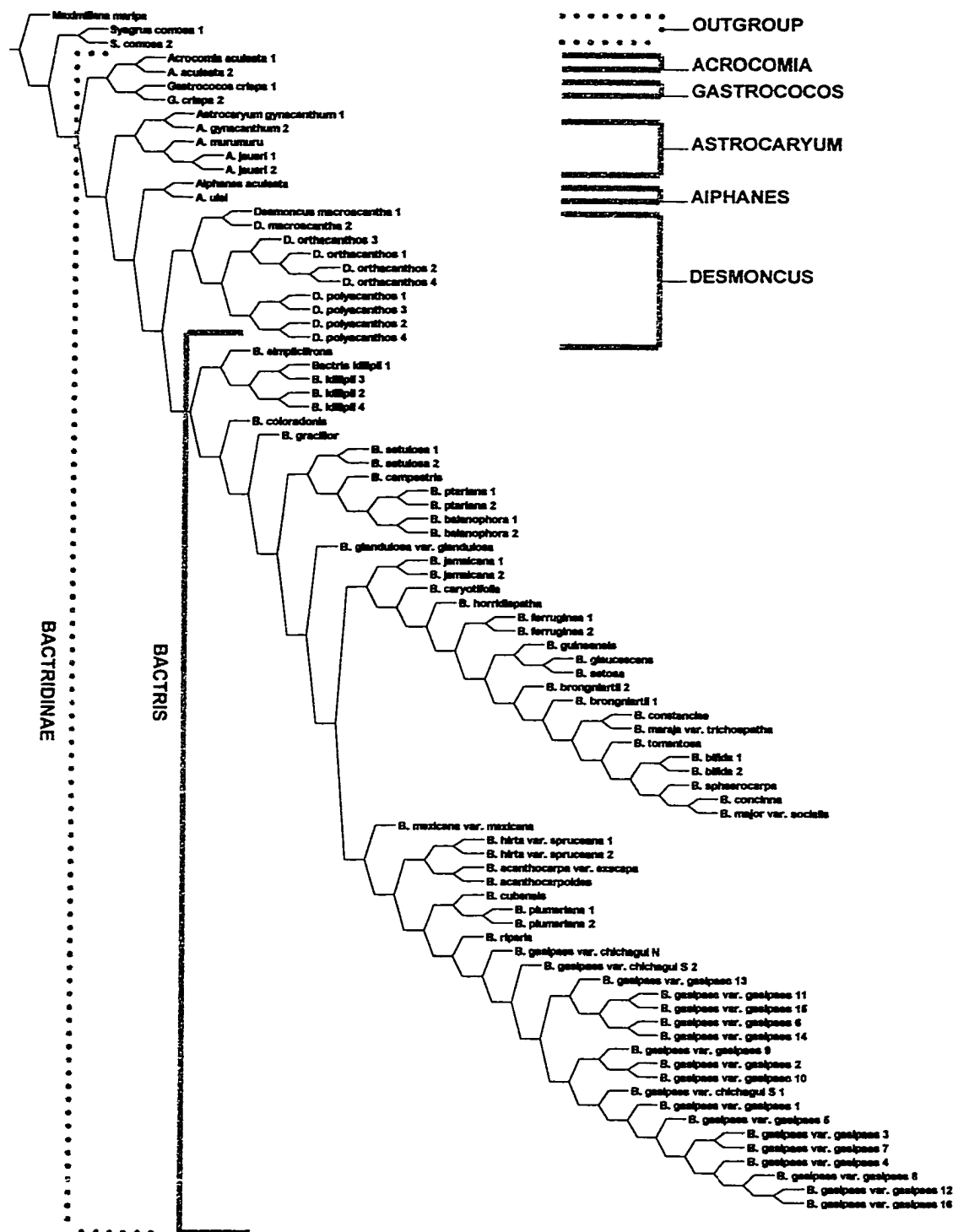
The relationships of subtaxonomic units of the two B. gasipaes varieties are fully resolved, suggesting the southern population of var. chichagui as the most closely related variety to the domesticated var. gasipaes. The domesticated var. gasipaes is segregated from the southern population of var. chichagui by its ovoid fruits (ch. 51) and both are distinct from the northern population of var. chichagui by their longitudinally displaced fertile endocarp pore.

## VIII. Discussion

### 1. Anatomy

The results of this work demonstrates that Bactris is

Figure 57. One of the 5000 trees, arbitrarily chosen, resulting from the analysis of combined data set, matrix 2, polymorphic taxa divided into subtaxonomic units.



more diverse anatomically than previously thought (Tomlinson, 1961). The use of fibers sclereids as a diagnostic character for Bactris is not supported because it was found that a large number of its species lack this feature. Fiber sclereids (Fig. 58a) were found in only seven of the 32 species used in the present study, all of which had black to purple-black fruits. The fact that Tomlinson (1961) generalized his finding to the whole genus is difficult to understand because two of the three species used in his study (B. acanthocarpa and B. minor (= B. guineensis)) do not have fiber sclereids. Only B. major (Fig. 58b) has this feature, and it may mean that he based the anatomical description solely in this species.

#### 1.1. Leaf anatomical types in Bactris (Table 7)

Based on the anatomical observations of cross-section samples it is possible to segregate Bactris into at least five leaf anatomical types. These anatomical types are divided according to the following: presence of adaxial non-vascular fiber bundles, the number of hypodermal layers, the position of main veins, the presence of lignified and anticlinally extended mesophyll cells, and the relative size of small veins and roundish non-vascular

Figure 58. Fiber sclereids in Bactris. A. densely arranged fiber sclereids on inner side of abaxial epidermis of B. brongniartii (EP54, x200). B. fiber sclereids diagonally arranged on inner side of adaxial epidermis of B. major var. socialis (EP58, x 200)

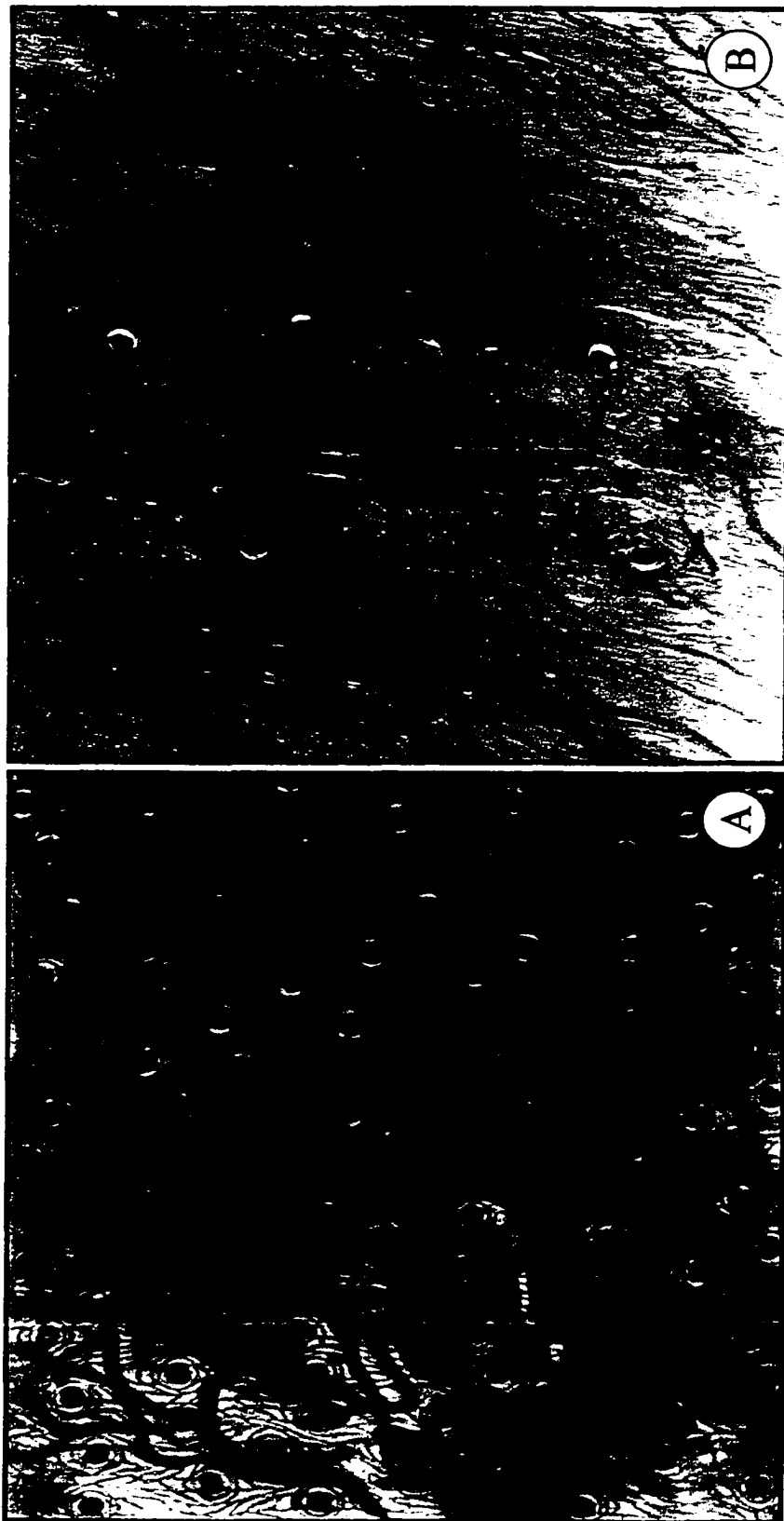




Table 7. Leaf anatomical types in Bactris

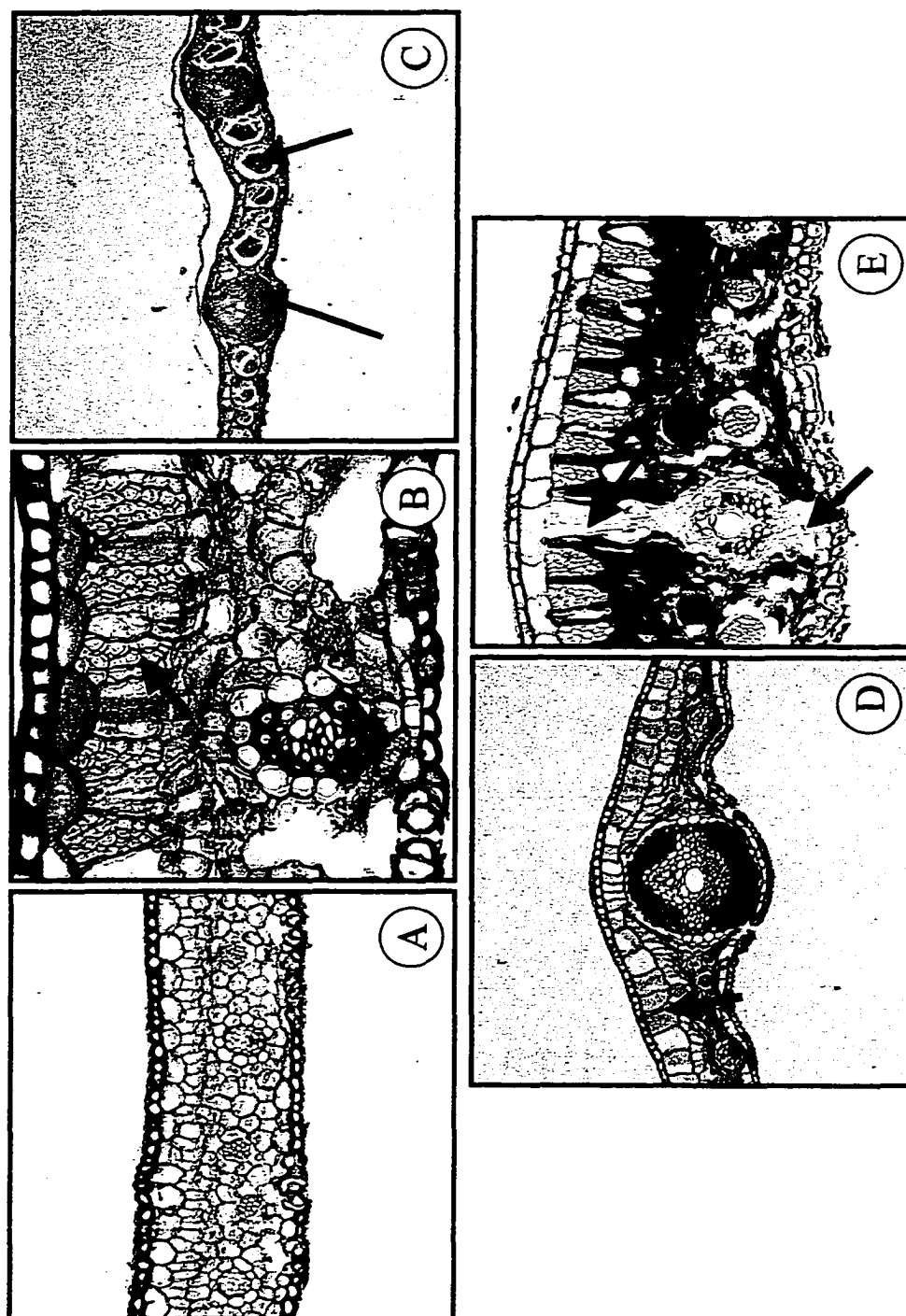
| Types       | Species                                                                                                                                                                                                                                                                                                                                                                                                           |
|-------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Gasipaes    | <u>B. acanthocarpa</u> , <u>B. acanthocarpoides</u> , <u>B. balanophora</u> , <u>B. brongniartii</u> , <u>B. concinna</u> , <u>B. constanciae</u> , <u>B. ferruginea</u> , <u>B. gasipaes</u> , <u>B. glandulosa</u> , <u>B. gracilior</u> , <u>B. horridispatha</u> , <u>B. major</u> , <u>B. maraja</u> , <u>B. mexicana</u> , <u>B. ptariana</u> , <u>B. riparia</u> , <u>B. setosa</u> , <u>B. setulosa</u> , |
| Cubensis    | <u>B. caryotifolia</u> , <u>B. coloradonis</u> , <u>B. cubensis</u> , <u>B. guineensis</u> , <u>B. jamaicana</u> , <u>B. plumeriana</u> .                                                                                                                                                                                                                                                                         |
| Killipii    | <u>B. bifida</u> , <u>B. hirta</u> , <u>B. killipii</u> , <u>B. simplicifrons</u> , <u>B. sphaerocarpa</u> , <u>B. tomentosa</u>                                                                                                                                                                                                                                                                                  |
| Campestris  | <u>B. campestris</u>                                                                                                                                                                                                                                                                                                                                                                                              |
| Glaucescens | <u>B. glaucescens</u>                                                                                                                                                                                                                                                                                                                                                                                             |

fiber bundles to the overall section thickness. They are described as follow:

a. Gasipaes (Fig. 59a)

It corresponds to Tomlinson's (1961) anatomical description of the genus and includes the majority of the species surveyed in this study. It is characterized

Figure 59. A-E. Anatomical leaf types in Bactris. A. Gasipaes type (B95, x200); B. Cubensis type (B119, x400), note the adaxial columnar-shaped non-vascular fiber bundles; C. Killipii type (B9, x40), note the large size of non-vascular and vascular bundles; D. Campestris type (B51, x100), note the thick hypodermal layer; E. Glaucescens type (B22, x200), note the anticlinally extended mesophyll cells above the small vein, the adaxial columnar-shaped non-vascular fiber bundles.



by a thick section in which most small vascular and non-vascular bundles do not protrude prominently. In most species, the vascular and non-vascular bundles are abaxially located. In B. gasipaes var. gasipaes and var. chichagui, the roundish non-vascular fiber bundles are few and very small. Bactris gracilior seems to be an intermediate form between the Gasipaes anatomical type and the Killipii type described below. This is an unusual species because almost 50% of its section thickness is made up by adaxial and abaxial hypodermis.

b. Cubensis (Fig. 59b)

The main distinguishing feature of this type is the presence of columnar, adaxial non-vascular fiber bundles. Similar structures are also found in Gastrococos and Astrocaryum. As a consequence of the position of these adaxial bundles, all the other vascular and non-vascular bundles in the section are usually small and abaxially located. Bactris coloradonis is included here but its adaxial bundles are much smaller than the ones found in other species. There are six species in this major type.

c. Killipii (Fig. 59c)

This type is characterized by the relatively large and centrally located vascular and non-vascular bundles. This is a consequence of the slender leaves found in all species included here, which are among the smallest species in the genus.

d. *Campestris* (Fig. 59d)

This type includes only one species, *B. campestris*. It is characterized by its 1-2 layered adaxial hypodermis that can make up to 2/3 of the section thickness. This unusual hypodermis arrangement could be linked to the fact the species is more commonly found in poorly drained areas, usually sandy soils in open savannas or low forest (Henderson, 2000).

e. *Glaucescens* (Fig. 59e)

This type is represented by only one species, *B. glaucescens*. Its general structure resembles the *Cubensis* type, but unlike that group, this is the only *Bactris* species with buttresses made up of lignified and

anticlinally extended mesophyll cells, a feature found only in Astrocaryum.

## 2. Phylogeny

### 2.1. Anatomical and morphological data sets

Although the monophyly of Bactridinae was supported by all analyses, the separate analysis of anatomical and morphological data sets, using either data matrix 1 or data matrix 2, could not completely resolve the generic and specific relationships.

In the anatomical data set analysis, only Acrocomia and Gastrococos were clearly resolved outside a large polytomic clade. The clade containing Astrocaryum was supported by one synapomorphy, but its relationship to the other genera in the tribe is unresolved. One of the Desmoncus taxa is closely related to Aiphanes in a poorly supported clade and two others are completely unresolved among a large number of Bactris. In this latter genus, the only clade formed is that including the varieties of B. gasipaes plus B. setosa. Dividing the polymorphic taxa into subtaxonomic units produced a tree topology similar to that obtained using restricted polymorphism. However, not

all polymorphic taxa in Bactris proved to be monophyletic as in the cases of B. bifida, B. setulosa, B. balanophora, B. ferruginea, and B. gasipaes.

The analysis of the morphological data set also supported the monophyletic status of Bactridinae, but it did not help resolve the generic or specific relationships in the subtribe. The only genus clearly resolved is Aiphanes, while the others are included in a large polytomic clade. Within this clade, Desmoncus forms a putative monophyletic group supported by one synapomorphy, but relationships among its taxa are not resolved. Astrocaryum, Acrocomia, and Gastrococos are included in a clade supported by one synapomorphy, but the relationships between them is also unresolved. Among the taxa of Bactris, morphological support to monophyletic groups yielded two additional clades besides the one including B. gasipaes. The first comprises B. simplicifrons and B. killipii and the second, B. glandulosa, B. acanthocarpa, and B. acanthocarpoides. Dividing the polymorphic taxa into subtaxonomic units indicates that seven out of eleven polymorphic taxa of Bactris are putatively monophyletic. This number is higher when compared to the results of the anatomical analysis. However, only the placement of B. bifida and B. gasipaes are common to both results.

## 2.2. Combined data sets

The analysis of the combined data set supported not only the monophyletic status of Bactridinae, but also resolved the relationships among its genera suggesting that each of them is monophyletic. Another important result is that Bactris is mostly resolved, although the clades are often poorly supported.

The tree topology is the same using either a data matrix with restricted polymorphisms (data matrix 1) or a data matrix with polymorphic taxa divided into subtaxonomic units (data matrix 2). The only differences were, as expected, a higher tree length and consistency index after the analysis of data matrix 2. This reflects the higher number of terminals and reduction in character conflict.

The topologies of all phylogenetic trees obtained are well resolved and each generic clade is well-supported. In this regard, Astrocaryum is the best supported genus. The clade Gastrococos-Acrocomia is also well-supported but within this clade, the former is only weakly supported by a homoplasious character, its roundish endocarp (ch. 58). Aiphanes and Desmoncus are each supported by a single



synapomorphy. In Bactris there are only three clades supported by synapomorphies.

Subdividing the polymorphic taxa into subtaxonomic units did not help clarify the question regarding the origin of the domesticated B. gasipaes var. gasipaes because in the strict consensus tree the relationships among the subtaxonomic units of the two B. gasipaes varieties are completely unresolved. It, however, suggests that B. gasipaes is a putative monophyletic species, even if some of the subtaxonomic units included in the analysis do not represent natural entities.

Because the characters supporting the topology of Bactris are mostly homoplasious, no attempt to discuss character evolution is made here.

### 2.3. Main clades in Bactris

The different clades identified within Bactris are discussed below, but no formal names will be given to them because the tree topology is weakly supported. If the clade has only one taxon, the clade name corresponds to that taxon. If it has two, the name is arbitrarily chosen between them. If it has more than two, the name selected is that of the basal taxon.

a. Simplicifrons

This clade do not corresponds to the former genus Amylocarpus because B. hirta is not included. Although it appears in the phylogenetic tree as sister to the remaining species of Bactris, this clade is supported only by homoplasious characters. In Sanders (1991), these species were included in the more inclusive Amylocarpus clade within the major clade Latibracteate. It corresponds to the Amylocarpus group proposed by Henderson (2000).

b. Coloradonis

This clade does not correspond to any previously proposed clade, group of species, or segregate genera. In Henderson (2000), this species is included in the orange-fruited group. In Sanders (1991), it was placed in the more inclusive Nonfibrous clade within the major clade Latibracteate.

c. Gracilior

This is the least supported clade and also does not correspond to any previously proposed clade, group of species or segregate genera. It was included in the Exserted-Anther clade, in the major clade Latibracteate of Sanders (1991), and in the orange-fruited group of Henderson (2000).

d. Setulosa

This is one of the best supported clades and four species are included here: B. setulosa, B. campestris, B. balanophora, and B. ptariana. These species were previously placed in different clades or groups of species by different authors. Ferreira (1999), and Henderson (2000), had considered Bactris setulosa closely related to the pupunha palm. Here, B. setulosa is placed in a distant clade. The other three species in the clade were included in the orange-fruited group by Henderson (2000). In Sanders (1991), these four species were scattered among three different major clades. Bactris balanophora was included in the Balanophora clade, Bactris campestris and B. ptariana in the Latibracteate clade, and B. setulosa was included in the Tuberculate clade. The fact B. ptariana appears here as sister to B. balanophora indicates Sanders

(1991) tentative placement of several taxa within some clades on the basis of apomorphies drawn from the literature was not always a suitable method.

e. Gladulosa

This well-supported clade includes three species. They are included in the Piranga group by Henderson (2000), which is the equivalent of the Piranga clade of Sanders (1991).

f. Mexicana

This clade is formed by eight taxa, most of them also found in Non-Ocreate clade of Sanders (1991) and the phylogenetic tree presented by Ferreira (1999). The differences are the inclusion of B. mexicana and B. hirta, and the exclusion of B. setulosa and B. jamaicana. The tree topology above B. hirta is very similar to that of Ferreira (1999), except for the absence of the two species cited above. Bactris cubensis and B. plumeriana form a clade sister to B. riparia, B. gasipaes var. gasipaes, B. gasipaes var. chichagui (northern population), B. gasipaes var. chichagui (southern population).

g. Jamaicana

Two aspects could be used to characterize this mostly pectinate and poorly supported clade: most species have juicy and black to purple-black fruits. The exceptions are the presence of B. jamaicana at the base and B. constanciae forming a more inclusive clade with B. maraja. In Sanders (1991), these latter two species were members of the major clade Tuberculate, but apart from each other. In Henderson (2000), they were included in the purple-fruited group. The inclusive clade formed by B. guineensis, B. glaucescens and B. setosa is also found in Sanders (1991) as part of the Bidentate clade. Henderson (2000) placed these species in the Purple-fruited group. Henderson's and Sanders' proposed Pyrenoglyphis group and clade are not supported because Purple-fruited or Tubiflorous clade species appears mixing with Pyrenoglyphis species in the distal portion of the branch.

## IX. Conclusion

The results of this research have clearly demonstrated that leaf anatomy of Bactris is more diverse than

previously though. Besides the morphological model proposed by Tomlinson (1961), four additional anatomical types can be found among the different taxa examined during the present study. Some of these major types have features typically found in other genera of Bactridinae or if one will, the other Bactridinae genera have features typically found in Bactris. If Pinheiro's (1997), reasoning were followed here, the so-called intermediate types could be easily singled out among the members of the Cubensis and Glaucescens types. However, the study of hybrids and putative hybrids is beyond the scope of this study and further discussion on this topic is given.

The phylogenetic analysis of anatomical characters, although supporting the hypothesis of monophyly of Bactridinae, failed to produce a fully resolved and well-supported hypothesis of phylogenetic relationships not only among the genera of Bactridinae, but also, within the species of Bactris. However, this failure maybe more a result of hardware limitation than any other cause. On the other hand, the failure may not be really a failure, but a consequence of the way each taxon was treated here: never as a hybrid, or a putative hybrid. Perhaps excluding some of the taxa from the analysis, as Pinheiro (1997) has done, might have resulted in a fully resolved and fairly

supported hypothesis of phylogeny could have been inferred resulting in a lumping of some of the Bactridinae genera.

The analysis of morphological data, just like the anatomical data, yielded support for the monophyletic origin of Bactridinae, but failed to resolve the relationships among its genera and within Bactris. The grouping of taxa, however, is different. This alone is a strong indication that phylogenetic hypotheses based on a single set of characters, either anatomical, morphological, or molecular, are the least desirable because evolutionary lines drawn from each type of data will likely be different.

Although the analysis of the combined data set of anatomical and morphological data could not completely resolve species relationships, it produced a phylogenetic tree better resolved and supported than the ones from the analysis of each of these data sets alone. This hypothetical phylogeny provides strong evidence for the monophyletic status of Bactridinae and each of its genera.

Relationships among the genera of Bactridinae are understood better now. Gastrococos and Acrocomia are closely related, supporting the suggestions of Uhl and Dransfield (1987), and Henderson (1995). Bactris and Desmoncus are closely related, as previously found by

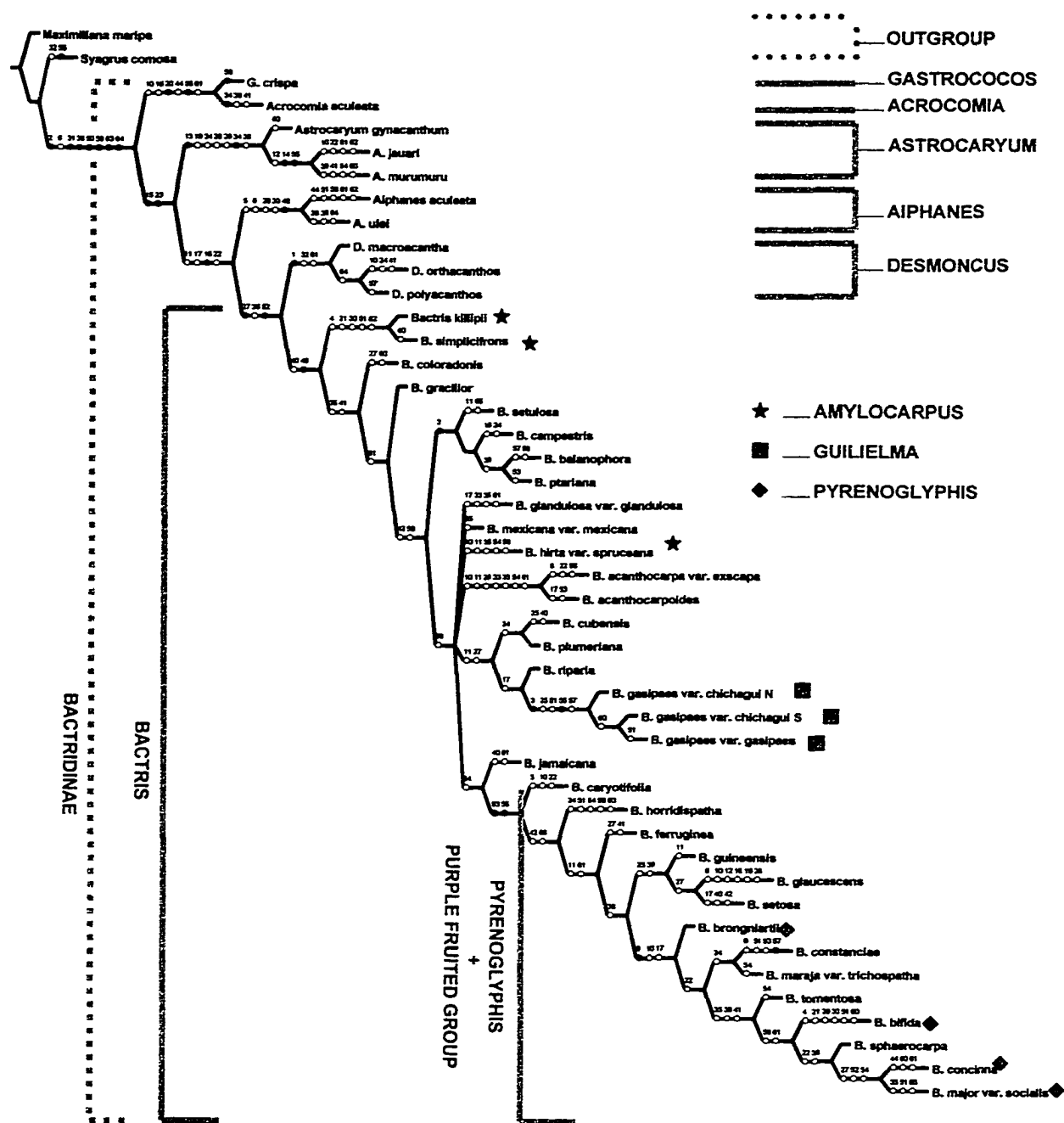
Sanders (1991). The position of Aiphanes as the sister genera to Bactris and Desmoncus is a novel result.

Regarding the phylogeny of Bactris, it was found to be monophyletic and its internal organization includes several groups of species. The segregation of Bactris into several smaller genera is not supported (Fig. 60). The species of Pyrenoglyphis are scattered in a single branch of a polytomic clade within Bactris, making its segregation difficult since relationships within this clade are fully resolved only if an arbitrary tree is drawn from the thousands of trees found by the program. The former species of Guilielma are nested in a well-supported but inclusive clade within a polytomic clade of Bactris. It is worth noting that this was the only monophyletic group within Bactris present in every phylogenetic tree produced during this study.

The resolution of the controversy regarding the origin of the domesticated B. gasipaes var. gasipaes can not be fully explained here. Reliable resolution in the cladistic analysis was obtained only with the use of data matrix 1 (restricted polymorphism). Based on this result, it seems that the var. gasipaes ancestor was an extinct taxon sister to the Northern population of var. chichagui. This hypothetical ancestor was likely widespread in a region



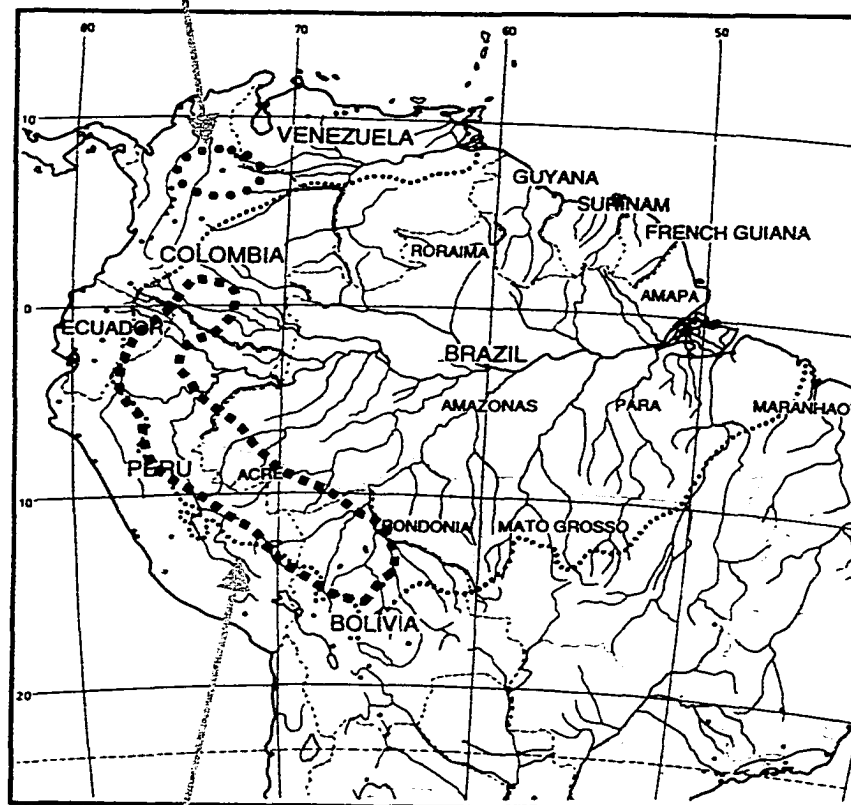
Figure 60. Phylogeny of Bactris (this study) and the position of the species belonging to the former genera Amylocarpus, Guilielma, and Pyrenoglyphis.



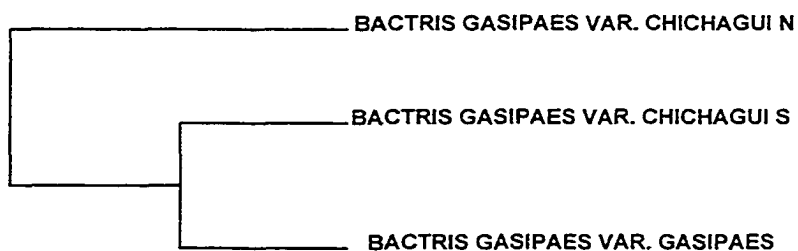
bordering the Southern part of the Amazon, along the Andes mountains, where the Southern population of var. chichagui is found today (Fig. 61). Another possibility, also not fully supported here, is that var. gasipaes is a domesticated variety whose earlier germplasm was collected directly from wild plants of the Southern population of var. chichagui. In this case, ancestor and descendant are still alive, sharing the same geographical space. However, the domesticated plants have been changed so drastically that the possibility to reverse to the wild condition or survive without human help is no longer possible (Clement et al., 1999). In this case, the recent proposal of Henderson 35(2000), that the domesticated and wild plants are a single taxonomic entity, segregated at variety level only, is perhaps the best solution in light of the current information available.

Figure 61. Distribution of the two populations of Bactris gasipaes var. chichagui included in this study. The results of the phylogenetic study indicates that the domesticated B. gasipaes var. gasipaes was likely domesticated within the area of distribution of the southern population of var. chichagui

NORTHERN POPULATION OF  
BACTRIS GASIPAES VAR. CHICHAGUI



SOUTHERN POPULATION OF  
BACTRIS GASIPAES VAR. CHICHAGUI



## Appendices

## Appendix I. List of taxa

## Ingroup taxa

1. Bactris

- 1.1. Bactris acanthocarpa Martius var. exscapa Barbosa Rodrigues, Enum. palm. nov. 31. 1875.
- 1.2. Bactris acanthocarpoides Barbosa Rodrigues, Enum. palm. nov. 33. 1875.
- 1.3. Bactris balanophora Spruce, J. Linn. Soc. Bot. 11: 146. 1871.
- 1.4. Bactris bifida Martius, Hist. nat. palm. 2: 105. 1826.
- 1.5. Bactris brongniartii Martius in d'Orbigny, Voy. Amérique mér. 7(3). Palmiers 59. 1846.
- 1.6. Bactris campestris Poeppig ex Martius, Hist. nat. palm. 2: 146. 1837.
- 1.7. Bactris caryotifolia Martius, Hist. nat. palm. 2: 106. 1826.
- 1.8. Bactris coloradonis L. H. Bailey, Gentes Herb. 3: 104. 1933.
- 1.9. Bactris concinna Martius, Hist. nat. palm. 2: 99. 1826.
- 1.10. Bactris constanciae Barbosa Rodrigues, Enum. palm. nov. 37. 1875.

- 1.11. Bactris cubensis Burret, Kongl. Svenska Vetensk.  
Acad. Handl. ser. 3. 6(7): 25. 1929.
- 1.12. Bactris ferruginea Burret, Repert. Nov. Spec. Nov.  
Regni Veg. 34: 222. 1934.
- 1.13. Bactris gasipaes Kunth var. gasipaes Henderson, Flora  
Neotrop. Monogr. 79: 71. 2000.
- 1.14a. Bactris gasipaes Kunth var. chichagui (H. Karsten)  
Henderson, Fl. Neotrop. Monogr. 79: 73. 2000. Bactris  
macana (Martius) Pittier, Manual Plant. Usual. Ven.  
276. 1926. (Northern population)
- 1.14b. Bactris gasipaes Kunth var. chichagui (H. Karsten)  
Henderson, Fl. Neotrop. Monogr. 79: 73. 2000. Bactris  
dahlgreniana Glassman, A Revision of B. E. Dahlgren's  
Index of American Palms 34. 1972. (Southern  
population)
- 1.15. Bactris glandulosa Oersted var. glandulosa de Nevers,  
Henderson & Grayum, Proc. Calif. Acad. Sci. 49: 183.  
1996.
- 1.16. Bactris glaucescens Drude in Martius, Fl. bras. 3(2):  
345. 1881.
- 1.17. Bactris gracilior Burret, Repert. Spec. Nov. Regni  
Veg. 34: 216. 1934.
- 1.18. Bactris guineensis (Linnaeus) H. E. Moore, Gentes  
Herb. 9: 251. 1963.



- 1.19. Bactris hirta Martius var. spruceana (Trail)  
Henderson, Flora Neotrop. Monogr. 79: 92. 2000.
- 1.20. Bactris horridispatha Noblick, Flora Neotrop. Monogr.  
79: 98. 2000.
- 1.21. Bactris jamaicana L. H. Bailey, Gentes Herb. 4: 177.  
1938.
- 1.22. Bactris killipii Burret, Bot. Jahrb. Syst. 34: 175.  
1933.
- 1.23. Bactris major Jacquin var. socialis Drude in Martius,  
Fl. bras. 3(2): 359. 1881.
- 1.24. Bactris maraja Martius var. trichospatha (Trail)  
Henderson, Flora Neotrop. Monogr. 79: 119. 2000.
- 1.25. Bactris mexicana Martius var. mexicana de Nevers,  
Henderson & Grayum, Proc. Calif. Acad. Sci. 49: 204.  
1996.
- 1.26. Bactris plumeriana Martius in d'Orbigny, Voy.  
Amérique mér. 7(3). Palmiers 64. 1844.
- 1.27. Bactris ptariana Steyermark, Fieldiana Bot. 28: 77.  
1951.
- 1.28. Bactris riparia Martius, Hist. nat. palm. 2: 97.  
1826.
- 1.29. Bactris setosa C. Martius, Hist. nat. palm. 2: 94.  
1826.
- 1.30. Bactris setulosa H. Karsten, Linnaea 28: 408. 1857.

1.31. Bactris simplicifrons Martius, Hist. nat. palm. 2:  
103. 1826.

1.32. Bactris sphaerocarpa Trail, J. Bot. 6: 8. 1877.

1.33. Bactris tomentosa Martius, Hist. nat. palm. 2: 100.  
1824.

## 2. Acrocomia

2.1. Acrocomia aculeata (Jacquin) Lodd. ex Martius, Hist.  
Nat. palm. 3: 286. 1849.

## 3. Aiphanes

3.1. Aiphanes aculeata Willdenow, Samml. Deutsch. Abh.  
Königl. Akad. Wiss. Berlin 1803: 251. 1806.

3.2. Aiphanes ulei (Dammer) Burret, Notizbl. Bot. Gart.  
Berlin-Dahlen 11: 568. 1932.

## 4. Astrocaryum

4.1. Astrocaryum gynacanthum Martius, Hist. nat. palm. 2:  
73. 1824.

4.2. Astrocaryum jauari Martius, Hist. nat. palm. 2: 76.  
1824.

4.3. Astrocaryum murumuru Martius, Hist. nat. palm. 2: 70.  
1824.

## 5. Desmoncus

5.1. Desmoncus macroacanthos Martius, Hist. nat. palm.  
2: 86. 1824.

5.2. Desmoncus orthacanthos Martius, Hist. nat. palm. 2:

87. 1824.

5.3. Desmoncus polyacanthos Martius, Hist. nat. palm. 2:

85. 1824.

6. Gastrococos

6.1. Gastrococos crispa (Kunth) H. E. Moore, Principes 11:

121. 1968.

#### Outgroup Taxa

1. Maximiliana

1.1. Maximiliana maripa (Aublet) Drude in Martius Fl.

bras.: Cyclantaceae et palmae I, fasc. 85, vol. 3(2):

452.

2. Syagrus

2.1. Syagrus comosa (Martius) Martius in d'Orbigny, Voy.

Amérique mér. 7(3). Palmiers 134. 1844.

Appendix II. List of specimens examined for morphological survey

1.1. Bactris acanthocarpa Martius var. exscapa

**PERU. MADRE DE DIOS:** Tambopata Nature Reserve, 12°50'S, 69°17'W, 250 m, 4 May 1991, Chávez 740 (NY), 23 Feb 1984, Gentry et al. 46074 (NY), 25 Feb 1984, Gentry et al. 46204 (NY), 22 Jul 1985, Gentry et al. 51143 (NY), 30 May 1987, Gentry & Jaramillo 57953 (NY), 2 Nov 1991, Henderson & Chávez 1629 (NY), Urcos-Puerto Maldonado road, ca. 200 m, 28 Sep 1987, Kahn & Llosa 2111 (NY).

**BRAZIL. ACRE:** Mun. Mâncio Lima, ca. 5 km W of Mâncio Lima, ca. 7°40'S, 72°55'W, 17 Feb 1992, Henderson et al. 1704 (NY); Mun. Xapurí, Seringal Cachoeira, 12 Oct 1989, Pinard 843 (NY); Mun. Brasiléia, Seringal Porongaba, 23 May-2 Jun 1991, Scariot & Ferreira 561 (NY). **AMAZONAS:** Mun. Humaitá, BR 230, km 140, ca. 7°58'S, 62°2'W, 16 Apr 1985, Henderson et al. 251 (NY). Borba, Rio Madeira, 3 km S of town, 29 Dec 1990, Henderson & Pardini 1507 (NY). **RONDÔNIA:** Mun. Guajará-Mirim, ca. 32 km SE of Guajará-Mirim, ca. 10°57'S, 65°4'W, 175 m, 12 Apr 1987, Nee 34801 (NY).

**BOLIVIA. BENI:** Prov. Vaca Díez, vicinity of Alto Ivón, 11°45'S, 66°2'W, ca. 200 m, 8 Dec 1983, Boom 4129 (NY), 16

Feb 1984, Boom 4462 (NY). **PANDO**: Prov. Abuna, Campamento 18, 10°39'S, 66°46'W, 2 Jul 1992, Gentry et al. 77670 (NY); Prov. Federico Román, Río Negro, 9°52'S, 65°42'W, 15 Jul 1992, L. Vargas et al. 975 (NY). **SANTA CRUZ**: Prov. Velasco, Río San Ramón, 320 m, 29 Oct 1989, L. Moreno 14 (NY).

## 1.2. Bactris acanthocarpoides

**GUYANA**. Essequibo River, 1°39'N, 58°38'W, 240-260 m, 5 Sep 1989, Jansen-Jacobs 1490 (NY); Kamo River, 1°32'N, 58°50'W, 260 m, 14 Sep 1989, Jansen-Jacobs 1583 (NY), 21 Sep 1989, Jansen-Jacobs et al. 1734 (NY); Rupununi District, Kuyuwini River, 2°10'N, 59°15'W, 200 m, 5 Feb 1991, Jansen-Jacobs et al. 2388 (NY).

**SURINAME**. Coesewijne River, 5 Oct 1962, Wessels Boer 153 (NY); Stoelmanseiland, 27 Oct 1962, Wessels Boer 198 (NY); road to Phedra, 16 Nov 1962, Wessels Boer 282 (NY); Stondansi Valley, 8 Dec 1962, Wessels Boer 324 (NY); Mapanie, 7 Jan 1963, Wessels Boer 467 (NY); Antoweg, Brownsloegheer, 12 Feb 1963, Wessels Boer 644 (NY); Toeval Meertje, 12 Feb 1963, Wessels Boer 649 (NY).

**FRENCH GUIANA**. Station de Nouragues, Arataye, 4°3'N, 52°42'W, 100 m, 6 Sep 1989, de Granville 11078 (NY).

### 1.3. Bactris balanophora

**COLOMBIA. AMAZONAS:** Araracuara, road to Puerto Arturo, "Guácharos", ca. 360 m, 18 Sep 1987, Galeano & Huitoto 1280 (NY); Quebradón del Tigre, ca. 250 m, 20 Sep 1988, Galeano & Miraña 1848 (NY); trail from Río Vaupés to Santa Lucia, 9 Aug 1976, Zarucchi et al. 1889 (NY).

**VENEZUELA. AMAZONAS:** Sipapo, 4°22'N, 67°6'W, May 1989, Foldats & Velazco 9200 (NY); Dpto. Atures, Río Autana, 4°48'N, 67°27'W, 90-110 m, 5 Nov 1984, Guánchez 3223 (NY); 4 km E of San Carlos de Río Negro, 1°56'N, 67°10'W, 120 m, 25 Nov 1977, Liesner 3834 (NY), 21 Jan 1968, Wessels Boer 2310 (NY); Cerro Aracamuni, 1°24'N, 65°38'W, 600 m, 21 Oct 1987, Liesner & Delascio 22256 (NY).

### 1.4. Bactris bifida

**PERU. LORETO:** Prov. Maynas, Río Momón, 130 m, 13 Sep 1995, Henderson & Padilla 2025 (NY); Prov. Maynas, Indiana, Yanamono Explorama Lodge, 3°28'S, 72°50'W, 106 m, 19 Feb 1989, Vásquez & Jaramillo 11713 (NY).

**BRAZIL. ACRE:** Mun. Mâncio Lima, Rio Moa near Barão, 7°25'S, 73°55'W, 9 Oct 1989, Henderson et al. 1103 (NY); Rio Juruá, above Cruzeiro do Sul, near Natal, 8°20'S,

72°15'W, 8 Feb 1992, Henderson et al. 1665 (NY). **AMAZONAS:** Mun. Atalaia do Norte, Rio Javari, just before confluence of Rio Javari-Mirim, 4°30'S, 71°45'W, 10 Jan 1989, Henderson et al. 867 (NY); Mun. Tefé, right bank of Rio Solimões, Missão Tefé, 13 Jan 1991, Henderson et al. 1546 (NY); 13 Jan 1991, Henderson et al. 1548 (NY); Mun. Tefé, Lago Tefé, NW shore, ca. 3°19'S, 64°49'W, 10 Dec 1982, Plowman et al. 12418 (NY).

#### 1.5. Bactris brongniartii

**VENEZUELA. AMAZONAS:** Esmeralda, 2°58'N, 65°21'W, 16 Feb 1990, Aymard & Delgado 7869 (NY); Río Ocamo, 3°3'N, 67°29'W, Jan 1990, Fernández 6618a (NY); Río Mavaca, 2°1'N, 65°7'W, 228 m, 7 Feb 1989, Henderson et al. 995 (NY).

**BOLÍVAR:** Mun. Cedeño, Río Caura, 6°35'N, 64°45'W, 20 May 1996, C. Knab-Vispo 567 (NY). **DELTA AMACURO:** between Amacuro and Deadwater Creek, 7 Nov 1960, Steyermark 87406 (NY).

**GUYANA.** Kanuku Mts., Nappi Creek, 3°21'N, 59°34'W, 130 m, 3 Nov 1987, Jansen-Jacobs 684 (NY); Rupununi District, Kuyuwini Landing, 2°10'N, 59°15'W, 8 Feb 1991, Jansen-Jacobs 2478 (NY); Sama Creek, Apr 1889, Jenman 5924 (NY).

**FRENCH GUIANA.** Fleuve Ouaqui, Saut Macaque, 10 Jul 1973, de Granville 1770 (NY); Fleuve Grand Inini, Dégrad Fourmi, 250 m, 12 Aug 1985, de Granville 7444 (NY).

**BRAZIL. AMAZONAS:** Mun. Maraã, Rio Japura, Mutum, 1°50'S, 65°17'W, 12 Jan 1991, Henderson et al. 1544 (NY). **PARÁ:** Rio Jari, base of Serra Arumanduba, 1°30'S, 53°N, 35-50 m, 24 Jul 1961, Egler & Irwin 45951 (NY). **RORAIMA:** Mun. Alto Alegre, Ilha de Maracá, 3°24'N, 61°26'W, 15 Jul 1986, Henderson & Lima 606 (NY).

#### 1.6. Bactris campestris

**VENEZUELA. AMAZONAS:** 2°39'N, 66°50'W, 24 Apr 1991, Aymard 9014 (NY); Dept. Atabapo, Cucurital de Caname, 3°40'N, 67°22'N, ca. 100 m, 30 Apr-1 May 1979, Davidse et al. 16915 (NY); Brazo Casiquiare near Solano, ca. 2°N, 67°W, 8 Feb 1968, Wessels Boer 2410 (NY).

**GUYANA.** Potaro-Siparuni Region, Kaieteur National Park, along Potaro River, 5°10'N, 59°29'W, 420 m, 8 May 1989, Gillespie et al. 1357 (NY); E. Berbice-Corentyne Region, Digitima savanna, Canje River, 5°53'N, 57°40'W, 10-20 m, 29 Oct 1989, Gillespie 2569 (NY); along Canje River, 5°41'N, 57°15'W, 11 Apr 1987, Pipoly 11411 (NY); Atkinson, St. Cuthbert's trail, 26 Feb 1969, U. G. Biol. 82 (NY).



**SURINAME.** Between Cola Creek and Zanderij, 27 Jan 1961, Kramer & Hekking 2734 (NY); Kappel Savanna, 27 Feb 1961, K. Kramer & Hekking 3052 (NY); Tafelberg mountain, ca. 800 m, 23 Aug 1944, Maguire 24461 (NY); Brownsberg, 9 Feb 1963, Wessels Boer 594 (NY).

**FRENCH GUIANA.** Cayenne-Regina highway, Piste de St. Elie, km 4, 18 Apr 1985, Prévost 1844 (NY); Sinnamary, 5°22'N, 52°59'W, 31 Dec 1988, Sanders 1815 (NY).

**BRAZIL. AMAPÁ:** Mun. Calçoene, BR 156, 12 km W of Calçoene, ca. 2°28'N, 51°W, 8 Dec 1984, Mori & Cardoso 17287 (NY). **RORAIMA:** Mun. Caracaraí, between km 522 and 524 of Manaus-Caracaraí highway, 1°18'N, 60°35'W, 25 Aug 1987, Cid 9181 (NY).

#### 1.7. Bactris caryotifolia

**BRAZIL. BAHIA:** Mun. Mucuri, ca. 10 km W of Mucuri, 18°5'S, 39°39'W, 1-20 m, 4 Feb 1989, Noblick & Brito 4802 (NY). **ESPÍRITO SANTO:** Santa Teresa, Valsugana Velha, 24 Nov 1988, Boudet Fernandes et al. 2647 (NY). **RIO DE JANEIRO:** Mun. Angra dos Reis, Serra do Ariró, 30 Oct 1988, Boudet Fernandes 2618 (BR).

#### 1.8. Bactris coloradonis

**COSTA RICA. LIMÓN:** Dist. de Los Angeles de Jiménez, Finca Copasa, 18 Apr 1991, Mattos 2891 (NY).

**PANAMA. COCLÉ:** continental divide above El Copé, 1 Dec 1995, Henderson & Bernal 2049 (NY); El Valle, 8°38'N, 80°06'W, 744 m, 9 May 1999, Henderson & E. Ferreira 3042 (NY). **COLÓN:** Barro Colorado Island, 19 Jun 1970, Croat 10946 (NY); Balboa, 2.5 mi. N of Goofy Lake, 26 Jul 1970, Croat 11550 (NY); Pipeline road, 11 Mar 1983, Gentry & Hamilton 41119 (NY). **DARIÉN:** Kuna Wargandi Reserve, 9°01'N, 78°03'W, 100 m, 30 Mar 1998, Dalle 204 (NY). **PANAMÁ:** Cerro Campana, 25 Mar 1969, Porter et al. 4209 (NY). **SAN BLAS:** El Llano-Cartí road, km 26.5, 9°19'N, 78°55'W, 200 m, 13 Apr 1985, de Nevers et al. 5351 (NY), 11 Dec 1987, Henderson & Herrera 716 (NY).

#### 1.9. Bactris concinna

**PERU. LORETO:** Prov. Maynas, Quebrada Tamshiyacu, 25 Jul 1982, Ayala et al. 3595 (NY); Pacaya-Samaria, 4°40'S, 74°20'W, 200 m, 15 Sep 1991, Chávez 753 (NY); Yaquerana Dist., Galvez River, 5°17'30"S, 73°09'50"W, 150 m, 12 Nov 1999, Fleck 807 (NY); Maynas, Rio Nanay, 3°40'S, 73°15'W, 120 m, 27 May 1991, Gentry & Ortiz 74233 (NY); Iquitos, 3-

11 Aug 1929, Killip & A. Smith 27007 (NY); Maynas, Manitií, 3°42'S, 72°50'W, 13 May 1988, Vásquez 10594 (NY).

**BRAZIL. AMAZONAS:** Mun. Benjamin Constant, Rio Javari, between Benjamin Constant and Atalaia do Norte, 4°20'S, 70°20'W, 3 Jan 1989, Henderson et al. 814 (NY); Barro Vermelho, left bank of Rio Juruá, 6°28'S, 68°46'W, 17 Oct 1991, Pardini 12 (NY); Jainú, right bank of Rio Juruá, 6°28'S, 68°46'W, 23 Oct 1991, Pardini 34 (NY); Altamira, right bank of Rio Juruá, 6°35'S, 68°54'W, 8 Nov 1991, Pardini 43 (NY); Ilha Amaraca opposite Tabatinga, 23 Jul 1973, Prance et al. 16726 (NY).

#### 1.10. Bactris constanciae

**SURINAME:** Kabalebo Dam, Nickeri Distr., 23 km S of Aranavero Dam, 18 Nov 1976, Heyde & Lindeman 174 (NY); Alsborige, 23 Oct 1962, Wessels Boer 189 (NY).

**FRENCH GUIANA.** Kourou, Piste de St. Elie, 15 Sep 1987, Hahn 3737 (NY), 1 May 1985, Prévost 1854 (NY); Station des Nouragues, Arataye, 4°3'N, 52°42'W, 300 m, de Granville et al. 10354 (NY); Rivière Camopi, 1 km from Saut Chien, 3 Feb 1968, Oldeman & Sastre 15 (NY); Piste de St. Elie, 5°19'N, 53°1'W, 29 Dec 1988, Sanders 1811 (NY).

1.11. Bactris cubensis

**CUBA. GUANTANAMO:** near Baracoa, s.d., Hoene 3051 (NY), 24-29 Jan 1902, Pollard et al. 101 (NY); Toa River, near Tabajo, 15 Aug 1993, Salzman 340 (FLAS); Sevilla Estate, near Santiago, 17 Sep 1906, N. Taylor 467 (NY); El Yunque, Mt. Baracoa, Mar 1903, Underwood & Earle 729 (NY). **HOLGUIN:** 13.8 km S of Moa, on Moa-Baracoa road, 18 Aug 1993, Salzman 393 (FLAS); Pinales, SE of Paso Estancia, 1-2 May 1909, Shafer 1750 (NY); Sierra Nipe, near Woodfred, 500-650 m, 15 Jan 1910, Shafer 3555 (NY); valley of Río Yamanigüey, 27 Feb-1 Mar 1910, Shafer 4227 (NY). **SANTIAGO DE CUBA:** Loma del Gato, Sierra Maestra, 11 Jul-14 Aug 1921, León et al. 10561 (NY).

1.12. Bactris ferruginea

**BRAZIL. BAHIA:** Mun. Ilhéus, cidade de Ilhéus, 14°46'S, 39°04'W, 19 Sep 1994, Carvalho et. al 4837 (NY); Mun. Guaratinga, road from BR 101 to Cajuita, 16°43'S, 39°40-50W, 150-200 m, 8 Feb 1985, Gentry & Zardini 49934 (NY); Mun. Lauro de Freitas, ca. 5 km W of the city, 12°54'S, 38°19'W, 28 Sep 1988, Noblick & Soeiro 4606 (F); Mun. Alagoinhas, 8-10 km S of Araçás, 12°10'S, 38°26'W, 50-100,

22 Nov 1988, Noblick & Soeiro 4683 (F); Mun. Entre Rios, 16 km SE of Entre Rios on road to Subaúma, 11°56'S, 38°05'W, 50-150 m, 29 Nov 1988, Noblick & Soeiro 4693 (NY); Mun. Cardeal da Silva, 6-7 km N of Cardeal da Silva, 50-100m, 1 Dec 1988, Noblick & Soeiro 4701 (F); Mun. Esplanada, 5 km S of Esplanada, 11°47'S, 37°57'W, 100-200 m, 2 Dec 1988, Noblick & Soeiro 4705 (F); Mun. Jandaíra, 3-4 km S of Jandaíra, 11°34'S, 37°47'W, 100-150 m, 3 Mar 1988, Noblick & Soeiro 4707 (F); Mun. Cairu, ca. 0.5 km NE of Cairu, 13°30'S, 39°03'W, 0-15 m, 9 Dec 1988, Noblick 4714 (F); Mun. Una, 1 km W of Una, 15°18'S, 39°04'W, 12 Jan 1989, Noblick 4729 (NY); Mun. Belmonte, 7 km E of Barralândia, 15°51'S, 38°54'W, 50-100 m, Noblick 4751 (NY).

1.13. Bactris gasipaes var. gasipaes

**BOLIVIA. BENI:** Prov. Vaca Diez, vicinity of Alto Ivón, 11°45'S, 66°2'W, 200 m, 8 Apr 1984, Boom 4984 (NY); Prov. Ballivián, Río Chimane, near Fátima, 5 Jun 1981, Davis 1173 (NY). **SANTA CRUZ:** El Cairo, 17°28'S, 63°42'W, 21 Aug 1987, Nee et al. 35683 (NY), Nee et al. 35684 (NY); Parque Amboró, 17°39'S, 63°43'W, 22 Dec 1988, Saldias 533 (NY), 10

Mar 1989, Saldias 683 (NY), 11 Mar 1989, Saldias 694 (NY),  
3 Mar 1990, Saldias et al. 1004 (NY).

1.14a. Bactris gasipaes var. chichagui (Northern  
population)

**VENEZUELA. BARINAS:** Caimital, 8 km S of Barrancas, 24-  
25 May 1966, Schulz & Rodríguez 419 (NY); between Barinas  
and Barinitas, 10 km NW of Barinas, 8°42'N, 70°18'W, 350 m,  
15 Jun 1967, Wessels Boer 1854 (NY); crossing of road  
Barinas-San Cristóbal and Río Bumbún, 8°13'N, 70°44'W, 16  
Jun 1967, Wessels Boer 1860 (NY). **ZULIA:** Dist. Bolívar,  
between El Pensado and Las Tres Marías, 26 Jul 1980,  
Bunting 9430 (NY); Dist. Bolívar, Embalse Burro Negro  
(Pueblo Viejo), 10 km E of Churuguarita, 250-300 m, 5-8 Aug  
1980, Bunting 9538 (NY); Dist. Perijá, near Estación  
Hidrológica Aricuaisá, 9°35'N, 72°54'W, 100-250 m, 28 Feb  
1982, Bunting et al. 10981 (NY); Dist. Catatumbo, 2-4 km S  
of Casigua, 11 Oct 1982, Bunting 11777 (NY); road  
Machiques-Colón, 50-100 m, 22 Aug 1967, Steyermark &  
Fernández 99565 (NY); Perijá, near Misión Los Angeles del  
Tucuco, 9°50'N, 72°50'W, 300-400 m, 6 Apr 1968, Wessels  
Boer 2452 (NY), 6 Apr 1968, Wessels Boer 2453 (NY).

1.14b. Bactris gasipaes var. chichagui (Southern population)

**PERU. HUÁNUCO:** Prov. Pachitea, 26 km S of Puerto Inca, 9°37'S, 74°56'W, 260 m, 20-22 Aug 1989, Listabarth 11-20889 (NY). **MADRE DE DIOS:** Manú National Park, Cocha Cashu Biological Station, 11°50'S, 71°25'W, 18 Aug-Sep 1989, Núñez et al. 11394 (NY)

**BRASIL. ACRE:** Mun. Taumaturgo, Reserva Extrativista do Alto Juruá, 08°57'S; 72°33'W, 120 m, 12 Mar 1992, E. Ferreira 133 (HPZ); Mun. Tarauacá, igarapé "Joací", Colocação "Remanso", 08° 17'S, 69°58'W, 150 m, 8 Mar 1994, E. Ferreira 334 (HPZ); Mun. de Sena Madureira, Rio Caeté, Colônia Santo Antonio, 09°12'S, 68° 44'W, 6 Apr 1994, E. Ferreira 435 (HPZ); Rio Juruá, above Cruzeiro do Sul, near Natal, 8°20'S, 72°15'W, 8 Feb 1992, A. Henderson et al. 1663 (NY).

**BOLIVIA. SANTA CRUZ:** Velasco, 14°31'S, 61°21'W, 250 m, 27 Mar 1994, Guillén et al. 1198 (NY); Prov. Nuflo de Chávez, 12 km NW of San Javier, 16°10'S, 62°34'W, 768 m, 12 May 1990, Saldias 1076 (NY); Prov. Nuflo de Chávez, Reserva Rios Blanco y Negro, 15°37'S, 64°42'W, 250 m, 10 Jul 1992, Saldias et al. 1544 (NY); Prov. Nuflo de Chávez, San Pablo,

ca. 60 km W of Concepción, 300 m, 19 May 1993, Saldias & Mostacedo 2529 (NY).

1.15. Bactris glandulosa var. glandulosa

**COSTA RICA. HEREDIA:** Dist. Río Frio, Finca Fincagua, margem del Río Sarapaqui, 16 Sep 1990, Mattos & Mora-Urpí 2880 (NY). **PUNTARENAS:** 5 km W of Rincón de Osa, 8°42'N, 83°31'W, 9-12 Jan 1970, Burger & Liesner 7297 (NY); ca. 15 km W of Rincón, 8°42'N, 83°33'W, 6 Jun 1992, Henderson et al. 1812 (NY); 7 Jun 1992, Henderson et al. 1820 (NY); Jardín Botánico Robert and Catherine Wilson, 1212 m, 30 Jan 1991, Mattos & Espinoza 2884 (NY).

**PANAMA. COCLÉ:** El Valle de Antón, 27 Nov 1995, Henderson & Bernal 2037 (NY); El Valle, 8°38'20"N, 80°06'54"W, 9 May 1999, Henderson & E. Ferreira 3040 (NY).

1.16. Bactris glaucescens

**BRAZIL. MATO GROSSO:** Mun. Cáceres, 3 km W of Cáceres on road to Vilhena, 11 Dec 1988, Henderson 812 (NY); Transpantaneira highway, Rio Pazaim, 15 Jun 1979, Prance et al. 26233 (NY); Poconé, 16°45'S, 56°50'W, 4 Oct 1986,



Scariot 10 (NY). **RONDÔNIA**: Rio Guaporé, Costa Marques,  
12°26'S, 64°13'W, 150 m, 27 Mar 1987, Nee 34511 (NY).

**BOLIVIA. BENI**: Prov. Yacuma, Espíritu, 14°8'S,  
66°24'W, 200 m, 15 Oct 1989, Moraes & Sarmiento 1091 (NY);  
Prov. Cercado, 7 km SW of Trinidad, 14°52'S, 64°57'W, ca.  
200 m, 7 Jan 1989, Nee 37545 (NY). **SANTA CRUZ**: Prov.  
Velasco, Florida, Río Paraguá, 2 Nov 1989, L. Moreno 24  
(NY).

#### 1.17. Bactris gracilior

**NICARAGUA. ZELAYA**: Caño Costa Riquita, ca. 1.8 km SW  
of Colonia Naciones Unidas, ca. 11°43'N, 84°18'W, 150-180  
m, Stevens 5083 (NY).

**COSTA RICA. HEREDIA**: 8 km SW of Puerto Viejo on road  
to San José, 10°26'N, 84°2'W, 7 Jan 1967, Burger & Mata  
4303 (NY); La Selva, Finca El Bejuco, 6 km W of Puerto  
Viejo, 10°27'N, 84°4'W, 14 Dec 1984, Henderson et al. 60  
(NY); between Corazón del Jesús and La Virgen, Moore 6629  
(NY). **LIMÓN**: 7 km SW of Bribrí, 100-250 m, 4 May 1983,  
Gómez et al. 20454 (NY).

**PANAMA. COCLÉ**: Coclecito road, 8°42'N, 80°28'W, 200 m,  
11 Jan 1986, de Nevers & McPherson 6709 (NY). **SAN BLAS**: El

Llano-Cartí road, km 16, 17 Jul 1985, de Nevers 5976 (NY),  
km 19.1, 3 Nov 1985, de Nevers et al. 6168 (NY).

1.18. Bactris guineensis

**COLOMBIA. BOLÍVAR:** Mun. San Martin de Loba, "El  
Garcero", 9°00'N, 74°05'W, 70 m, 6 Jul 1993, Arango 4647  
(NY); near Cartagena, 10°28'N, 75°32'W, 10 m, 4 Jul 1984,  
Gentry & Cuadros 47621 (NY); near Bonda, below 400 m, Jul  
1925, Smith 2762 (NY); Torrecilla, near Turbaco, 150-300 m,  
Killip & Smith 14421 (NY). **CÓRDOBA:** Mun. Tierralta, 7 km  
from Tierralta to Planeta Rico, 100 m, 30 Jul 1986, Bernal  
et al. 1210 (NY). **MAGDALENA:** Mun. Santa Marta, Parque  
Nacional Natural Tayrona, 23 Sep 1976, Lozano & Schnetter  
2952 (NY).

**VENEZUELA. GUÁRICO:** 12 km SE of Calabozo, 8°56'N,  
67°25'W, 75 m, 10 Sep 1987, N. Ramírez 2369 (NY).

**PORTUGUESA:** road from Guanare to Papelón, 9°N, 69°40'W, 16  
Aug 1967, Wessels Boer 1981 (NY).

1.19. Bactris hirta var. spruceana

**VENEZUELA. AMAZONAS:** Neblina base camp, 0°50'N,  
66°10'W, 5 Feb 1984, Henderson 10 (NY), 14 Feb 1984,

Henderson 25 (NY), 8 Mar 1984, Henderson 38 (NY); Río Mavaca, 2°1'N, 65°7'W, 228 m, 6 Feb 1989, Henderson 978 (NY); Cerro Sipapo, 800 m, 2 Feb 1949, Maguire & L. Politi 28701 (NY), 70 km SSW of Ocamo, 2°10'N, 65°34'W, 990-1670 m, 24-28 Feb 1984, Steyermark et al. 130208 (NY); Cucuy, 1°13'N, 66°51'W, 2 Feb 1968, Wessels Boer 2385 (NY).

#### 1.20. Bactris horridispatha

**BRAZIL. BAHIA:** Mun. Una, km 46 on BA-001 Ilhéus-Una, 15°9'S, 39°5'W, 13-14 Jul 1993, Jardim et al. 178 (NY); Mun. Una, 1 km W of Una, 15°18'S, 39°04'W, 12 Jan 1989, Noblick 4730 (NY); Mun. São Sebastião do Passé, ca. 3 km N of Lamarão do Pasé, 12°31'S, 38°28'W, 29 Sep 1988, Noblick & Soeiro 4607 (FTG), Noblick & Soeiro 4608 (FTG); Mun. Una, Estação Experimental Lemos de Maia, 15°18'S, 39° 04'W, 20-100, 29 Sep 1994, Noblick & Brito 4999 (FTG); Mun. Una, Estação Lemos do Maio, 15°18'S, 39°4'W, 20-100 m, 23 Dec 1996, Sant'Ana et al. 627 (NY).

#### 1.21. Bactris jamaicana

**JAMAICA. CLARENDON:** Mason River Field Station, 27 Jun 1992, Salzman 136 (FLAS). **PORTLAND:** John Crow Mountains, 9-

11 Mar 1909, N. Britton 4171 (NY), 22 Jun 1992, Salzman et al. 110 (FLAS). **ST. ANN:** N of Green Park, S of Lime Hill, 27 Jun 1992, Salzman 150A (FLAS). **ST. THOMAS:** Johnson Mountain Hills, 29 Jul 1966, Read 1692 (NY). **TRELAWNY:** Cockpit country, 13-18 Sep 1906, N. Britton 539 (NY). **WESTMORELAND:** between Kew Park and Rat Trap, 330-360 m, 19 Sep 1963, Wessels Boer 1663 (NY).

#### 1.22. Bactris killipii

**COLOMBIA. AMAZONAS:** Araracuara, trail to Río Yarí, 200-300 m, 18 Apr 1986, Galeano & Torres 899 (NY); road from Leticia to Tarapacá, ca. 7 km from Leticia, 180 m, 17 Mar 1990, Galeano et al. 2107 (NY).

**PERU. LORETO:** Prov. Maynas, Puerto Almendras, 3°48'S, 73°25'W, 122 m, 10 Sep 1995, Henderson & Padilla 2015 (NY), 30 May 1986, Vásquez & Jaramillo 7585 (NY).

**BRAZIL. AMAZONAS:** Mun. Atalaia do Norte, Rio Javari, Paumari (or Natavidad), 4°17'S, 70°18'W, 5 Jan 1989, Henderson et al. 838 (NY); Mun. Tefé, Rio Curimatá de Baixo, ca. 3°55'S, 65°10'W, 18 Jan 1991, Henderson & Guedes 1573 (NY).

#### 1.23. Bactris major var. socialis

**BOLIVIA. BENI:** La Esperanza, 16.5 km S of Riberalta, 11°10'S, 66°8'W, 230 m, 31 Jul 1982, Balick et al. 1360 (NY); Prov. Ballivián, km 35 on Yucumo-Rurrenabaque road, 14°50'S, 67°5'W, 28 Feb-2 Mar 1990, D. Smith et al. 14060 (NY). **PANDO:** Prov. Madre de Dios, Puerto Candelaria, Río Madre de Dios, 21 km S of Riberalta, 11°2'S, 66°15'W, 125 m, 19 Aug 1985, Nee 31432 (NY); Prov. Manúripí, Río Madre de Dios, 12°16'S, 68°26'W, 140 m, 27 Aug 1985, Nee 31607 (NY). **SANTA CRUZ:** 64 km N of San Julian, 14 Aug 1982, Balick et al. 1428 (NY); Prov. Nuflo de Chávez, Ascención de Guarayos, 30 Sep 1985, S. Beck 12305 (NY); Nuflo de Chávez, Serranía San Lorenzo, 10 km W of San Javier, 16°15'S, 62°40'W, 500 m, 22 Oct 1987, Killeen 2829 (NY); Prov. Andrés Ibáñez, 18°30'S, 63°50'W, 400 m, 16 May 1988, Moraes & Henderson 1053 (NY); Prov. Santiesteban, Montero, 17°21'S, 63°16'W, 295 m, 12 Jan 1987, Nee 33453 (NY); Prov. Andrés Ibáñez, W side of Santa Cruz, 17°47'S, 63°12'W, 400 m, 22 Jan 1987, Nee 33730 (NY); Prov. Ichilo, Parque Nacional Amboró, 17°30'S, 63°44'W, 400 m, 10 Mar 1989, Saldias 689 (NY), 5 Mar 1990, Saldias et al. 1032 (NY); Prov. Ichilo, Potrero San Rafael, 17°29'S, 63°39'W, 360 m, 2 Oct 1996, Saldias et al. 4812 (NY).

1.24. Bactris maraja var. trichospatha

**PERU: LORETO:** Río Yaguasyacu, Brillo Nuevo, 2°40'S, 72°W, Feb 1978, Balick et al. 1050 (NY); San Miguel, 2 km below Indiana, 3°30'S, 73°2'W, 130 m, 12 Feb 1989, Gentry et al. 65696 (NY); Maynas, Río Momóm, 13 Sep 1995, Henderson & Padilla 2024 (NY); Puerto Almendras, 3°45'S, 73°25'W, 7 Dec 1982, Vásquez & Jaramillo 3506 (NY).

**BRAZIL. ACRE:** Rio Juruá, near Natal, 8°20'S, 72°15'W, 7 Feb 1992, Henderson et al. 1655 (NY). **AMAZONAS:** Mun. Maraã, left bank of Rio Japura, Santa Galo, 9 Jan 1991, Henderson et al. 1525 (NY); Mun. Tefé, Missão de Tefé on Rio Amazonas, 13 Jan 1991, Henderson et al. 1545 (NY); Barro Vermelho, Rio Juruá, 6°28'S, 68°46'W, 18 Oct 1991, Pardini 18 (NY); Altamira, Rio Juruá, 6°35'S, 68°54'W, 13 Nov 1991, Pardini 42 (NY), 11 Nov 1991, Pardini 61 (NY).

#### 1.25. Bactris mexicana var. mexicana

**MEXICO. CHIAPAS:** 80 km SW of Palenque on road to Ocosingo, 14 Jan 1982, Breedlove & Almeda 57205 (NY).

**OAXACA:** Mun. Santa María Chimalapa, Loma Bonita, 4 Apr 1945, Hernández 600 (NY); 37 mi. from Empalme Balboa beyond Mathias Romero, 5 May 1952, Moore & Brossard 6353 (NY).

**TABASCO:** 8.2 km from Fco. Rueda, 20 Jun 1983, C. Cowan et

al. 3985 (NY). **VERACRUZ**: Mun. Hidalgotitlán, Río Soloxuchil, 100 m, 21 Jun 1986, Aguilar 151 (NY); Est. Biológica Los Tuxtlas, 18°34'N, 95°04'W, 100 m, 12 Sep 1984, Ibarra 1984 (NY); Pital, May 1841, Liebmann s.n. (NY); Agustín Melgar, 17°15'N, 94°33'W, 100 m, 2 Mar 1984, Nee 29759 (NY).

#### 1.26. Bactris plumeriana

**DOMINICAN REPUBLIC. DAJABÓN**: road from Partido to Dajabón, 0.5 km W of Santiago de la Cruz, 10 Jul 1993, Salzman & Zona 260 (FLAS). **EL SEIBO**: 22.3 km E of river at Miches, Arroyo Claro, 18°58'N, 68°59'W, 20 m, 5 Aug 1981, Zanoni et al. 15910 (NY). **ESPAILLAT**: 6.2 km E of Gaspar Hernández, 19.6 km W of Río San Juan, 10 Jul 1993, Salzman & Zona 262 (FLAS). **LA VEGA**: SE of Bonao, Arroyo Hato Viejo, 18°54'N, 70°20'W, 200 m, 21 Apr 1981, Zanoni et al. 12778 (NY). **MONSEÑOR NOUEL**: Piedra Blanca, 7 Jul 1993, Salzman & Zona 258 (FLAS); Loma El Caribe, 10 Jul 1993, Salzman & Zona 264 (FLAS). **SAN CRISTÓBAL**: Los Martínez de Villa Maimón, on Villa Maimón-Yamasa road, 18°53'N, 70°14'W, 100 m, 2 Dec 1980, M. Mejía & Zanoni 9652 (NY); 12 km from Comatillo on road to Trinidad Mejía, 18°51'N, 69°32'W, 140 m, 3 Sep 1981, Zanoni & M. Mejía 16283 (NY).

**HAITI. NORD:** Pilboreau Mountains, Camp Coq, 24 May 1941, Bartlett 17383 (NY); Pilate to Plaisance, 22 Aug 1903, Nash 632 (NY). **SUD:** road between Cavaillon and Cayes, near Boumier, 18°17'N, 73°41'W, 50 m, 16 May 1989, Henderson et al. 1029 (NY); road from Camp Perrin to Jérémie, near Beaumont, Morne Nafont, 8 Dec 1989, Henderson & Aubry 1183 (NY).

1.27. Bactris ptariana

**VENEZUELA. BOLÍVAR:** Cerro Venamo, 1395-1400 m, 31 Dec 1963, Steyermack et al. 92778 (NY).

**GUYANA.** Mabura region, Pibiri, 5°1'N, 58°37'W, 6 Apr 1993, Ek et al. 801 (NY); Potaro-Siparuni region, Kaietur Falls National Park, 5°10'N, 59°29'W, 420-450 m, 5 May 1989, Gillespie et al. 1262 (NY); Demerara-Mahaica Region, from Timehri Airport to Kuru Creek, 6°25'N, 58°15'W, 10-30 m, Hahn et al. 3858 (NY); Potaro-Siparuni region, Kaietur Falls National Park, 5°10'N, 59°29'W, 500 m, 17 Apr 1988, Hahn et al. 4729 (NY); Kartabo, 6°21'N, 58°50'W, 22 Jan 1989, Hahn & Tiwari 5130 (NY); Upper Demerara region, Mabura Hill, 5°25'N, 58°40'W, 50 m, 21 Apr 1989, Hahn 5810 (NY); Potaro-Siparuni region, Iwokrama rain forest reserve, 4°19'N, 58°48'W, 800 m, 25 Mar 1997, Mori et al. 24594



(NY); Ciong valley, 9 km N of Kato Village, 4°42'N, 59°5'W,  
 1 Jun 1995, Mutchnick 1454 (NY); Mabura Hill, 5°25'N,  
 58°40'W, 19 Nov 1986, Pipoly & Boyan 8848 (NY); Mt.  
 Ayanganna, Upper Mazaruni River basin, 700-800 m, 4 Aug  
 1960, Tillett 45037 (NY).

#### 1.28. Bactris riparia

**COLOMBIA. AMAZONAS:** Río Cahuinari, 220 m, 15 Sep 1988,  
Galeano & Miraña 1797 (NY).

**PERU. LORETO:** Padre Isla, opposite Iquitos, 11 Sep  
 1995, Henderson & Padilla 2020 (NY).

**BRAZIL. ACRE:** Rio Moa, between Seringal Belo Monte and  
 Santa Barbara, 7°30'S, 73°W, 12 Feb 1992, Henderson 1676  
 (NY), 12 Feb 1992, Henderson et al. 1677 (NY). **AMAZONAS:**  
 Mun. Tefé, Rio Solimões, ca. 2 hours upstream from Tefé, 22  
 Jan 1991, Henderson & Guedes 1604 (NY); Altamira, right  
 bank of Rio Juruá, 6°35'S, 68°54'W, 8 Nov 1991, Pardini 46  
 (NY).

#### 1.29. Bactris setosa

**BRAZIL. BAHIA:** Mun. Ilhéus, BA001 km 10, 24 Ago 1978,  
Morawetz et al. 111-24878 (F); Mun. Una, Estação

Experimental Lemos de Maia, 15°18'S, 39° 04'W, 12 Jan 1989, Noblick 4731 (F); Mun. Belmonte, Est. Experimental Gregório Bondar, 15°51'S, 38°54'W, 50-100 m, 17 Jan 1989, Noblick 4742 (F); Mun. Mucuri, Faz. Martinica, 18°05'S, 39°39'W, 40-80 m, 3 Mar 1989, Noblick & Brito 4794 (F); Mun. Una, Res. Biológica do Mico-Leão, 15°09'S, 39°05'W, 23 Dec 1996, Sant'Ana et. al. 630 (NY). **RIO DE JANEIRO**: between Recreio dos Bandeirantes and Barra de Tijuca, 11 Feb 1973, Krapovickas et al. 23226 (NY). **SÃO PAULO**: Piassaguera, 6 Jan 1911, Luederwaldt 12243 (NY); Sete Barros, Fazenda Intervalles, Saibadela, 13 Jul 1992, Pardini et al. 78 (NY).

### 1.30. Bactris setulosa

**VENEZUELA. BARINAS**: road from Santo Domingo to Barinitas, 8°50'N, 70°30'W, 1000 m, 5 Jun 1967, Wessels Boer 1775 (NY). **YARACUY**: Cerro La Chapa, N of Nirgua, 10°15'N, 68°35'W, 11 Nov 1967, Wessels Boer 2043 (NY). **PORTUGUESA**: Mun. Ospino, Parque Nacional Guache, 9°29'54"N, 69°34'34"W, 20 Apr 1996, 1100 m, Licata et al. 751 (NY). **ZULIA**: Mara, Ríos Socuy-Guasare basin, La Paloma, 600 m, 4 Aug 1981, Bunting 10179 (NY). **UNKNOWN PROVINCE**: 14 Jan 1963, Wessels Boer 506 (NY).

1.31. Bactris simplicifrons

**GUYANA.** Surama Village, 4°5'N, 59°4'W, 23 Feb 1990, Acevedo 3369 (NY); U. Takutu-U. Essequibo, Gunn's strip, 1°39'N, 58°37'W, 240 m, 18 Aug 1998, Clarke et al. 7065 (NY); Cuyuni-Mazaruni Region, Essequibo River near Dennison Camp, 5°21'N, 58°48'W, 10-15 m, 27 May 1989, Gillespie & Persaud 1439 (NY); Cuyuni-Mazaruni Region, Pakaraima Mountains, Kurupung-Membaru trail, 6°5'N, 60°23'W, 22 Jul 1992, Hoffman & Marco 2132 (NY); Kanuku Mts., Moco Region, 3°18'N, 59°39'W, 150 m, 17 Jul 1995, Jensen-Jacobs et al. 4558 (NY); Partang River, Merume Mountains, Imbaimadai Savanna, 488 m, 16 Jun 1960, Maguire et al. 43868 (NY); Potaro-Siparuni region, Mathews ridge, 7°26'N, 60°11'W, 28 Apr 1991, McDowell et al. 4482 (NY); Mazaruni-Potaro District, Bartica-Potaro road, 24 mi S of Bartica, 50-125 m, 15 Aug 1976, Mori et al. 8091 (NY); Potaro-Siparuni region, Iwokrama rain forest reserve, 4°37'N, 58°45'W, 70 m, 17 Mar 1997, Mori & Heald 24398 (NY); Cuyuni-Mazaruni Region, Essequibo River, Twasinki Falls, ca. 5°5'N, 28 Sep 1937, A. Smith 2143 (NY); upper Mazaruni River, Mount Ayanganna, 700-800 m, 5, 16-17 Aug 1960, Tillett 45046 (NY); Kamarang River, 21 Oct 1960, Tillett 45725 (NY).

1.32. Bactris sphaerocarpa

**PERU. LORETO:** Maynas, El Milagro, km 16 on Iquitos-Nauta road, 15 Sep 1995, Henderson & Padilla 2032 (NY); Río Sucusari, 3°20'S, 72°55'W, 6 Nov 1989, Vásquez & Jaramillo 13070 (NY); Río Sinchiyacu, 2°50'S, 76°55'W, 200 m, 25 Feb 1991, Pipoly et al. 13758 (NY); Río Nanay, 3°52'S, 73°30'S, 8 Sep 1990, Vásquez et al. 14359 (NY). **MADRE DE DIOS:** Pakitza PNM, Río Manú, 11°53'S, 70°58'W, 400 m, 4 Nov 1990, Chávez 694 (NY).

**BRAZIL. ACRE:** Rio Juruá-Mirim, Escuro, 8°7'S, 72°40'W, 9 Feb 1992, Henderson et al. 1666 (NY); Rio Moa, mouth of Rio Azul, 7°25'S, 73°10'W, 13 Feb 1992, Henderson et al. 1678 (NY); Mun. Manoel Urbano, Seringal Terra Nova, 9°06'S, 69°47'W, 23 Nov 1996, Silveira et al. 1536 (HPZ, NY).

**AMAZONAS.** Mun. Atalaia do Norte, Rio Curuçá, tributary of Rio Javari, 4°30'S, 71°22'W, 150 m, 12 Jan 1989, Henderson et al. 881 (NY). Altamira, right bank of Rio Juruá, 6°35'S, 68°54'W, 13 Nov 1991, Pardini 62 (NY).

1.33. Bactris tomentosa

**BRAZIL. AMAPÁ:** Serra do Navio, 16 Nov 1954, R. Cowan 38340 (NY). **AMAZONAS:** 60 km N of Manaus on road to Caracarai, 4 Aug 1986, Henderson & Nascimento 642 (NY); Reserva Ducke, 26 km N of Manaus, 10-21 Nov 1986, Henderson 665 (NY), Henderson 679 (NY); BDFF Reserve Km 41, ca. 90 km N of Manaus, 41 km E on ZF 3, 24 Aug 1989, Henderson et al. 1049 (NY), 2 Sep 1989, Henderson et al. 1060 (NY), 25 Dec 1990, Henderson & Pardini 1501 (NY); Mun. Manaus, Tarumã Alta, 14 km N of Manaus, 19 Dec 1982, Plowman et al. 12637 (NY); Rio Cuieras below mouth of Rio Brancinho, 28 Sep 1971, Prance et al. 15005 (NY); Reserva Ducke, 2°53'S, 59°58'W, 16 Nov 1995, Vicentini et al. 1148 (NY). **PARÁ:** Mun. Altamira, Igarapé Ipixuna, 4°49'S, 52°31'W, 1 Apr 1986, Balée 2091 (NY); Mun. Altamira, BR 22, km 96, vicinity of Cachoeira, 30 Oct 1965, Prance & Pennington 1864 (NY).

## 2. Acrocomia

### 2.1. Acrocomia aculeata

**BOLIVIA. SANTA CRUZ:** Nuflo de Chavez, Estância San Josecito, 16°02'S, 62°05'W, 500 m, 11 Nov 1985, Killeen 1435 (NY); Andrés Ibañez, carretera hacia Warnes, 17°35'S,

63°09'W, 400 m, 17 May 1988, Moraes & Henderson 1055 (NY),  
 Fortin Libertad-Rio Grande, 2 Dec 1990, Moreno 63 (NY);  
 Prov. Velasco, estancia Flor de Oro, W side of Río Iténez,  
 13°33'S, 61°00'W, 190 m, 29 Jun 1991, Nee 41521 (NY); Prov.  
 Andres Ibañez, 6 km NW of Terevinto, 17°41'S, 63°25'W, 450  
 m, 30 Nov 1988, Nee & Coimbra 36993 (NY); Ichilo Prov.,  
 carretera Santa Cruz-Villa Tunari, 17°25'S, 63°45'W, 355 m,  
 7 Jul 1989, Smith et al. 13623 (NY).

### 3. Aiphanes

#### 3.1. Aiphanes aculeata

**BRAZIL. ACRE:** Mun. Taumaturgo, ao longo do Rio Bagé,  
 8°55'S, 72°31'W, 120 m, 11 Mar 1992, E. Ferreira 121 (HPZ);  
 Mun. Mâncio Lima, Rio Moa, 5 minutes from confluence of Rio  
 Azul, 17 Oct 1989, Henderson & Scariot 1145 (NY); Rio Moa,  
 near mouth of Rio Azul, Meia Doze, 7°25'S, 73°15'W, 14 Feb  
 1992, Henderson et al. 1683 (NY); Mun. Xapurí, Seringal  
 Cachoeira, 13 Oct 1989, Pinard 847 (NY); Mun. Brasiléia,  
 Seringal Porongaba, Col. São José, 23 May-2 Jun 1991,  
Scariot & E. Ferreira 570 (NY).

**BOLIVIA. PANDO:** Madre de Dios, Puerto America, 165 m,  
 18 Feb 1991, Moreno 71 (NY).

### 3.2. Aiphanes ulei

**ECUADOR. MORONA-SANTIAGO:** Sendero del Taisha al Kankeim, 30 km al SW del Río Pastaza, 2°25'S, 77°30-40'W, 400-600 m, 22 Mar 1986, Baker 6805 (NY); one hour walk west of Taisha, along trail to Cangaime, 2°25'S, 77°30'W, 400 m, 13 May 1986, Balslev et al. 62200 (NY). **NAPO:** Añangu, South bank of Río Napo, 0°32'S, 76°23'W, 28 Jul 1985, Balslev et al. 60733 (NY). **PASTAZA:** road from Puyo towards Arajuno, 1°25'S, 77°50'W, 1200 m, 28 Sep 1983, Balslev & Balslev 4418 (NY); Southern bank of Río Pastaza, opposite to Mera, 1°27'S, 78°08'W, 1300 m, 25 Oct 1987, Skov & Borchsenius 64776 (NY).

**BRAZIL. AMAZONAS:** Mun. Atalaia do Norte, Estirão do Equador, 4°33'S, 71°40'W, 150 m, 8 Jan 1989, Henderson et al. 846 (NY), 11 Jan 1989, Henderson et al. 868 (NY).

## 4. Astrocaryum

### 4.1. Astrocaryum gynacanthum

**VENEZUELA. AMAZONAS:** Depto. Atabapo, Cucurital de Caname, 3°40'N, 67°22'W, 100 m, 30 Apr-1 May 1979, Davidse

et al. 16973 (NY); Dpto. Rio Negro, Neblina base camp, Rio Mawarinuma, 140 m, 29 Feb 1984, Henderson 35 (NY); 6 KM N of Puerto Ayacucho on the road to Puerto Páez, 5°40'N, 67°40'W, 200-300 m, 22 Jun 1994, Noblick et al. 4945 (NY); Dpto. Atures, road between Paso el Diablo & Caño Culebra, 100 m, 12 May 1980, Steyermark 122373 (NY); Dpto. Atabapo, camino entre culebra y la falda del extremo, 3°40'N, 65°45'W, 180-300 m, 28-30 Jan, 1 Feb 1982, Steyermark 125886 (NY). **BOLÍVAR**: Dpto. Sifontes, concesión minera Oro Uno, 7 km al N-O de la Clarita, 6°13'N, 61°27'W, 180 m, 3 Aug 1985, Aymard et al. 3958 (NY); Río Paragua, en los alrededores de El Caruto Viejo, 6°39'N, 63°29'W, 13 May-13 Jun 1987, Stergios 10802 (NY).

#### 4.2. Astrocaryum jauari

**BRAZIL. AMAPÁ**: Mun. Cupuxi, 45 km WSW of Porto Grande, 0°36'N, 51°52'W, 7 Jan 1985, Mori & Cardoso 17732 (NY).

**RORAIMA**: Mun. Alto Alegre, Ilha de Maracá, 3°24'N, 61°26'W, 15 Jul 1986, Henderson & Lima 605 (NY).

**SURINAME**. Kabalebo by Mattapie, 26 Oct 1962, Wessesls Boer 196 (NY).

#### 4.3. Astrocaryum murumuru



**FRENCH GUIANA.** Saül, bords de la crique cochon, 26 Mar 1981, de Granville 4481 (NY); Trail from Saül airstrip to Roche Bateau, 3°37'N, 53°12'W, 22 Jun 1988, Prance et al. 30662 (NY); 5 km WSW of Cayenne, 2 Jan 1989, Sanders 1817 (NY).

**BRAZIL. PARÁ:** Ilha de Marajó, Rio Anajás, 3 Nov 1987, Beck & Souza 273 (NY); Mun. Abaetetuba, praia de Beja, 1°35'N, 48°45'W, 1-5 m, 19 Oct 1994, Noblick et al. 5024 (NY); Mun. Anajás, mouth of igarapé Francês, 29 Oct 1984, Strudwick et al. 5003 (NY).

## 5. Desmoncus

### 5.1. Desmoncus macroacanthos

**VENEZUELA. AMAZONAS:** Dpto. Antures, vicinity of and upstream from damsite, 5°35'N, 67°15'W, 100 m, 13 May 1980, Steyermark et al. 122423 (NY).

**GUYANA.** Mazaruni-Potaro District, Bartica-Potaro road, 24 miles S of Bartica, 50-125, 13 Aug 1976, Mori et al. 8063 (NY), 24 km S of Bartica, 6°13'N, 61°27'W, 180 m, 3 Aug 1985, Mori et al. 8100 (NY); Demerara-Mahaica Region,

along Linden-Soesdyke Hwy, 6°30'N, 58°11'W, 1-50 m, 9 Dec 1986, Pipoly & Ameer 9236 (NY).

## 5.2. Desmoncus orthacanthos

**VENEZUELA. DELTA AMACURO:** Orinoco Delta, 28-29 Jan 1911, Bond et al. 63 (NY); Dpto. A. Diaz, Caño Daudacana, 8°47'N, 61°00'W, 0 m, 19 Aug 1982, Malave & Canales 23 (NY).

**GUYANA.** Mabaruma, Aruka river, 28 Apr 1945, Forest Department 5212 (NY); Berbice, n.d., Jenman 7726 (NY).

**SURINAME.** Cultuurtuin-Paramaribo, 24 Jan 1961, Kramer & Hekking 123 (NY); In the middle of the Cultuurtuin-Panamaribo, 24 Jan 1962, Kramer & Hekking 2708 (NY); Dikkshoop near Groningen, Saramacca River, 29 Apr 1963, Wessels Boer 1335 (NY).

## 5.3. Desmoncus polyacanthos

**SURINAME.** Powaka, 12 Oct 1962, Wessesls Boer 174 (NY); Blaka watra creek, 18 Oct 1962, Wessels Boer 177 (NY); Oelemari River bank, 20 km above airstrip, 19 Mar 1963, Wessels Boer 1037 (NY); Some miles South of Present Hope,

24 Jan 1962, Hekking 1248 (NY); Road Zanderij-Phedra, near road to Berlijn, 27 Mar 1961, Krammer & Hekking 3146 (NY).

## 6. Gastrococos

### 6.1. Gastrococos crispa

**CUBA. CAMAGÜEY:** between Jatibonico and Ciego de Avila, 27 Jun 1931, León 14966 (NY); Sierra Cubitas to Santa Rosa, 21 Feb 1909, Shafer 552 (NY). **HAVANA:** vecindad de Santiago de Las Vegas, 1 Mar 1900, Baker 4556 (NY); Punta Brava, 29 May 1914, Ekman 1171 (NY); Santiago de Las Vigas, 10 Mar 1905, Herman 719 (NY); Buena Vista, Shafer 242, (NY).

**MATANZAS:** hills South of Matanzas, 10 Sep 1903, Britton & Wilson 470 (NY). **ORIENTE:** vicinity of Santiago, 14-15 Mar 1909, Britton et al. 1854 (NY); Enseada de Mora, 26-29 Mar 1912, Britton et al. 13020 (NY). **SANTA CLARA:** Rio San Juan, 24-25 Mar 1910, Britton et al. 5924 (NY); Soledad, Cienfuegos, 20 Mar 1930, Jack 7802 (NY); West of Manajomabo, 3 Aug 1915, León & Gustave 5292 (NY). **SANTIAGO:** Mar 1903, Underwood 1698 (NY). **UNKNOWN PROVINCE:** San Pedro and vicinity, 12 Feb-22 Mar 1916, Britton & Wilson 14458 (NY).

Appendix III. Leaf clearings protocol for herbarium material.

01. Rehydrate in Glycerin-Alcohol 70% (1:6):10% Aerosol OT:deionized water (10:3:87), overnight in a vacuum chamber (12 p.s.i). Use small glass vials.
02. Wash in deionized water: three times, 5 min. each.
03. Leave in 5% NaOH, in an oven at 58-60°C, for 1-7 days, changing the NaOH solution if necessary (when too dark).
04. Wash in deionized water: three times, 5 min. each.
05. Place samples in a 1/3 strength commercial bleach until they are cleared, which can occur after 15 minutes or up to 3 hours.
06. Wash in deionized water: three times, 10 min. each.
07. Stain the samples with 0.5% aqueous Safranin, 30 min. or overnight.
08. Wash the samples 1-2 times in deionized water to take out the excess of Safranin.
09. Dehydrate the samples using the following series:  
Alcohol 50%, 70%, 95%, 100%, Alcohol 100%:Hemo-De (7:3), Alcohol 100%:Hemo-De (1:1), Alcohol 100%:Hemo-De (3:7), Hemo-De, Hemo-De. Leave the samples 10 minutes in each step.

10. Mount using Kleermount. Leave slides in warming plate (43°C) for several days.

Appendix IV: Epidermal peels extraction protocol for herbarium material.

01. Rehydrate in Glycerin-Alcohol 70% (1:6):10% Aerosol OT:deionized water(10:3:87), overnight or up to 24 hours in a vacuum chamber (12 p.s.i). Use small glass vials
02. Wash in deionized water: three times, 15 min. each.
03. place samples in Jeffrey's solution. Change for a new Jeffrey's solution within 24-48 hours (when solution is dark). Do not change more than once since it can over-macerate the samples.
04. Shake gently the vials, once a day during 3 minutes, to help the separation. Separation may occur in 3-5 days.
05. Wash the samples three times in deionized water, 15-30 min. each. Use a small glass pipette to change the liquids.
06. Move the epidermis to a new set of vials with 0.5% aqueous Safranin. Stain 30 minutes or overnight. Safranin has to cover the samples, but do not fill the vials completely.
07. Complete the vials with deionized water (Safranin solution will turn light-red) and shake them gently.
08. Wash the samples 1-2 times in deionized water, 1-2

minutes each.

09. Dehydrate using the following series: Alcohol 50%, 70%, 95%, 100%, Alcohol 100%:Hemo-De (7:3), Alcohol 100%:Hemo-De (1:1), Alcohol 100%:Hemo-De (3:7), Hemo-De, pure Hemo-De. Leave the samples 2-3 minutes in each step. Use different paintbrush to move the samples along the series, change the solutions when necessary.
10. Mount the epidermis using Kleermount. Leave slides, with weights on top, in warming plate (43°C) for several days.

# Appendix V: Paraffin embedding with Hemo-De protocol.

- |     | EtOH: | Hemo-De               |
|-----|-------|-----------------------|
| 01. | 50%   |                       |
| 02. | 70%   |                       |
| 03. | 95%   |                       |
| 04. | 100%  |                       |
| 05. | 90% : | 10%                   |
| 06. | 70% : | 30%                   |
| 07. | 50% : | 50%                   |
| 08. | 30% : | 70%                   |
| 09. | 10% : | 10%                   |
| 10. | '     | 100%                  |
| 11. |       | 100% (fill half vial) |
12. Add paraffin chips until saturated, leave at room temperature 12 hours or overnight with the lid on.
  13. Move the vial to a warming plate at 43°C (the lid off), 12 hours or overnight.
  14. Replace half the liquid with melted paraffin, leave the vial in the oven (58°C) 12 hours, with the lid off.
  15. Repeat the step 14 twice, using a 24 hour interval.
  16. Make the blocks transferring the samples to a tray with melted paraffin.



Appendix VI: Modified staining series with Astra Blue and Safranin.

01. Xylene 100% (10 minutes).
02. Xylene 100% (10 minutes).
03. 100% EtOH (5 minutes).
04. 95% EtOH (5 minutes).
05. 70% EtOH (5 minutes).
06. 1% Alcoholic Safranin: overnight.
07. Wash in water until no more stain dissolves from slide.
08. Stain in 0.5% aqueous Astra Blue: 1 hour.
09. Wash in deionized water: dip slides slowly 3-5 times.
10. 50% EtOH: dip slides slowly 3-5 times.
11. 70% EtOH: 3-5 quick dips.
12. 95% EtOH: 5 seconds.
13. 100% EtOH: 10 seconds.
14. 100% EtOH-100% Hemo-De (1:1): 10 seconds.
15. 100% Hemo-De: 10 minutes.
16. 100% Hemo-De: 10 minutes or overnight.

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