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CLADISTICS OF BACTRIS (PALMAE): SURVEY OF CHARACTERS AND REFUTATION OF BURRET'S CLASSIFICATION

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Abstract. In 1934, M. Burret published a classification of *Bactris* in which he segregated *Guilielma* and *Pyrenoglyphis* and in which he recognized two subgenera, four sections, and two subsections within *Bactris* s. str. His support of *Guilielma,* which includes the edible species centered around *B. gasipaes,* has sustained a long-standing controversy. Herein, this classification is tested by applying parsimony-based cladistic analyses to 49 representative species-level OTU's, scored for 106 characters, which were polarized by the outgroup genera, *Astrocaryum* and *Desmoncus. Bactris* is monophyletic only if neither *Guilielma* nor *Pyrenoglyphis* is segregated. Burret's subgenus and section *Bactris* are paraphyletic because his other taxa are nested within them. The cladistic analysis suggests there are four major clades, none of which corresponds directly to Burret's groups. Three of the four are strongly supported by autapomorphies. Because the interrelationships among the major clades are based on a few, homoplasious synapomorphies, segregation of any clade is unwarranted. Several other well-marked constituent clades, some of which correspond to Burret's groups, are nested within the major clades. The analysis reveals that Burret weighted too heavily certain characters and incorporated too few of the cladistically most reliable characters. The reliable characters are components of diverse organs but are concentrated in a suite associated with the fruits; they include: presence of an ocrea, petiolar spines in three ranks, structure of leaflet apices, structure of rachis bracts and rachillae, arrangements of the reduced cincinni, structure of staminate petals and stamens, shape and indument of pistillate corollas, presence of a staminodial ring, fruit shape, epicarp color, mesocarp composition, endocarp shape, and the structure and attachment of endocarp fibers. The remaining characters are consistent only at lower taxonomic levels and deserve more detailed analysis in future monographic studies.

Bactris Jacq. ex Scop., the largest genus of American palms with over 250 described species, urgently needs taxonomic revision at both the specific and infrageneric levels (Clement, 1988; Uhl & Dransfield, 1987). General collectors have tended to avoid species of *Bactris* because not only are they usually spiny, but they also are bulky like many other palms. Hence, there is insufficient material with which to discern intraspecific variational patterns. Nomenclatural types of numerous species named by Wallace, Barbosa Rodrigues, and Burret have been destroyed. Furthermore, comprehensive monographic studies have never been published. The combination of these three factors has led to taxonomic chaos.

The taxonomic confusion is most critical in the economic members of *Bactris,* taxa centered around *B. gasipaes* H.B.K. The cultivated plants and their wild and semi-wild relatives are widespread throughout the lowland tropics. Nine local variants from widely separated parts of this range have been named as species. To further complicate matters, Martius (1823–1850), who has been followed by several more recent authors, segregated these taxa as *Guilielma* Martius. Karsten (1856) later homonymously published *Guilielma* Karst. non Mart. for species with a staminodial ring. Hence, species included in *Guilielma* Mart. were completely excluded from *Guilielma* Karst. Epithets published under both homonyms have been applied indiscriminately to the cultivated plants, and there has been little regard for the correct names when treated as combinations in *Guilielma* vs. *Bactris* (Mora-Urpí & Clement, 1981; Clement, 1988).

Any recent taxonomist, ecologist, or agronomist who must deal with these intractable problems in *Bactris* has had to consult a compendium by Burret (1933–1934). This work resulted from the need for the numerous specimens that had accumulated in European herbaria by the 1920's to be identified. In the decade preceding the Second World War, Burret proposed increasing numbers of new species in an attempt to sort out the variation he found. Perhaps he perceived impending political upheaval in Europe; this may explain why he did not make a long-term commitment to completing a comprehensive monograph with comparative descriptions and keys. To provide the taxonomic context for his 45 new species, he instead published a synopsis (Burret, 1933–1934). It comprised: 1) the division of *Bactris* into several large taxa (Figure 1), 2) descriptions validating 38 of his species, 3) literature citations to the 144 previously published names that he accepted, and 4) specimen citations to both. In the absence of more comprehensive

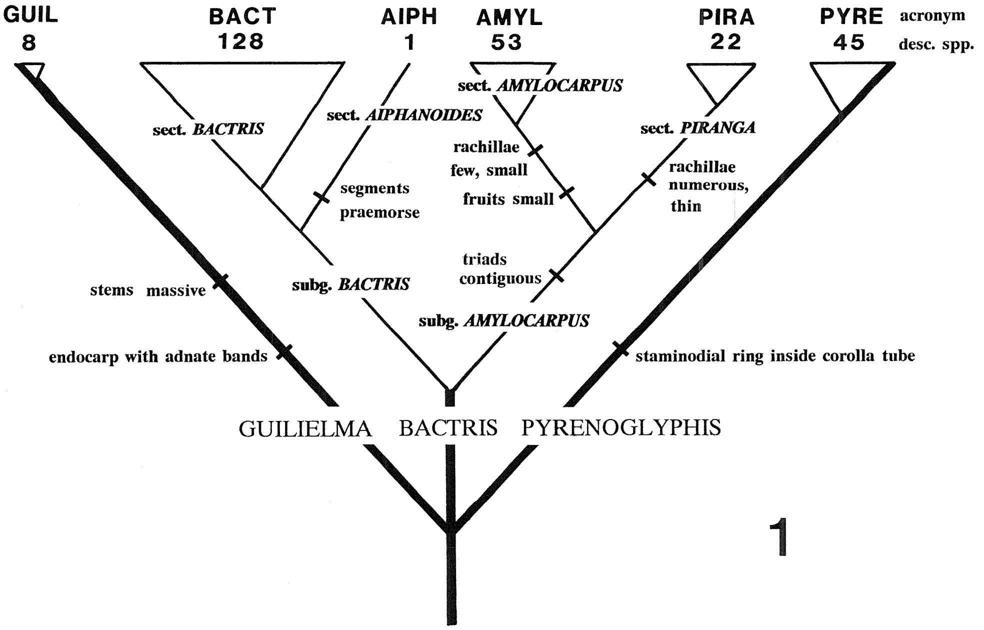


FIGURE 1. Phylogenetic interpretation of classification of *Bactris* s.l. published by Burret (1933–1934). For the type line of *Bactris,* autonyms, rather than Burret's names, have been used, in accordance with the ICBN (Greuter, 1988). Acronyms for Burret's groups are from TABLE 1. Indicated for each of the groups is the total number of species that were accepted by Burret or have been published since 1934. The bars and characters indicate the major diagnostic characters used by Burret to distinguish the groups.

work, it has become the standard taxonomic reference on *Bactris.*

Burret dealt with the disposition of the segregate genera that had been proposed by earlier workers and with the generic integrity of *Bactris* itself (FIGURE 1). He agreed with Martius that *Guilielma* should be recognized as a distinct genus based on the characters of massive stems and flattened fibers adnate to the endocarp. To deal with those *Bactris* species having a staminodial ring, which Karsten had placed in the homonymous *Guilielma* Karst., Burret transferred them into the segregate genus *Pyrenoglyphis* Karst. Karsten (1856, 1857) had originally erected *Pyrenoglyphis* as a monotypic genus for *Bactris major* Jacq. which, according to Karsten (1856; see also footnote to APPENDIX III), had both a staminodial ring *and* an intracalycine ring. Burret expanded the circumscription of *Pyrenoglyphis,* defining it by the staminodial ring only. Perhaps he hoped this would end the confusion created by the publication of *Guilielma* Karst. non Mart.

Burret retained other segregates in *Bactris* s. str., which he subdivided by combining ideas of Spruce (1871), Trail (1877), Drude (1882), and Barbosa Rodrigues (1903). He recognized four sections distributed among two subgenera (FIGURE 1; sect. *Amylocarpus* Barb. Rod. ["Eu-amylocarpus"] was further divided into two subsections which are not illustrated but are discussed below). All of these, except the monotypic sect. *Aiphanoides* Drude (*B. caryotifolia* Mart.), comprised numerous, similar species. Burret presented *Bactris* s. str., subgenus *Bactris* ("Eubactris") and sect. *Bactris* ("Acmophyllum"), the largest groups at their respective levels, as the core groups conforming to a typological concept of *Bactris.* These were simply contrasted with the alternate groups, which were defined by one or a few atypical characters. Unfortunately, Burret did not explicitly characterize his concept of the typical bactrid.

FIGURE 1 summarizes Burret's groups as branches of the phylogenetic tree that can reasonably be said to be implicit in his formal taxonomy. The advantage of transforming his taxonomy into a hypothesis of relationships in a phylogenetic context is that the important elements of his classification can be evaluated by phylogenetic analyses. Indeed, the impetus to appraise the relationships suggested by Burret come from the germ plasm explorers and agronomic plant breeders who desire a resolution of the taxonomic controversy over the specific and generic relationships of *B. gasipaes.* Particularly, "What are the limits, taxonomic position, closest relatives, and origin of the edible *Bactris* spp. and

TABLE 1. Species and specimens examined to obtain data for this study. The OTU acronyms are used elsewhere throughout this article. Herbarium (HERB) acronyms follow Holmgren et al. (1981).

Name	OTU	Specimens	HERB
ASTROCARYUM G. F. W. Meyer (outgroup 1)	ASTR		
alatum H. F. Loomis		*Hubbuch & Nemenyi 54,* associated living FTG 78424	FTG
		Nemenyi 2, assoc. living FTG 87165	FTG
aureum Griseb. & H. Wendl.		*Sanders & Budhoo 1759*	FTG
mexicanum Liebm.		*Fantz 3461,* assoc. living FTG 60415	FTG
		Hubbuch & Nemenyi 56, assoc. living FTG 59650	FTG
standleyanum L. H. Bailey		*Hubbuch & Nemenyi 55,* assoc. living FTG 87157	FTG
DESMONCUS Mart. (outgroup 2)	DESM		
chinantlensis Liebm. & Mart.		*Coons 1844*	FTG
		Kellerman s.n. 9 Aug 1940	BH
		Moore & Bossard 6361	BH
		Moore & Hartshorn 10121	BH
isthmius L. H. Bailey		*Bartlett 16728*	BH
longifolius Mart.		*Schunke 6927*	BH
macroacanthos Mart.		*Amaral et al. 706*	NY
		Liesner & González 5694	BH
		Mori & Bolten 8100	BH, NY
orthacanthos Mart.		*Stahel s.n. Aug 1947*	BH
polyacanthos Mart.		*Croat 21619*	BH
pumilus Trail		*Davidse 27712*	NY
BACTRIS Jacq. ex Scop.			
GUILIELMA GROUP	GUIL		
dahlgreniana Glassman	dah	*Clement 501-CR-88*	FTG
gasipaes H.B.K.	gas	*Davis & Marshall 1173*	NY
		Dunlap 1948	BH
		Foster & Foster 2118	BH
		Gentry & Cuadros 47512	MO
		Kayap 370	BH
		Read 1413	BH, FTG
macana (Mart.) Pittier	mac	*Foster & Foster 1731*	BH
PYRENOGLYPHIS GROUP	PYRE		
bifida Mart.	bif	*Plowman et al. 12418*	NY
		Schunke 8374	BH
concinna Mart.	cnc	*Croat 19329*	BH, MO
		Gentry et al. 52256	NY
		Prance et al. 16725	NY
cruegeriana Griseb. & H. Wendl.	cru	*Beard 131*	BH
		Seifriz 7	BH
gastoniana Barb. Rod.	gst	*Moore et al. 10340*	BH
gaviona Drude	gav	*Wessels Boer 1585*	BH
major Jacq. complex	maj	*Bailey & Bailey s.n. Feb 1921*	BH
		Bernal et al. 1209	FTG
		Hull H-1	FTG
		Moore & Putz 10511	BH
		Sanders 1753	FTG
		Sanders 1766	FTG
		Sanders & Watson 3	FTG
incl. *augustinea* L. H. Bailey		*Bailey 437*	BH
incl. *balanoidea* (Oerst.) H. Wendl.		*Moore 6543*	BH
incl. *superior* L. H. Bailey		*Bailey 162*	BH
maraja Mart.	mar	*Moore & Palmtak 10359*	BH
oligocarpa Barb. Rod.	oli	*Balick et al. 937*	BH
ottostapfeana Barb. Rod.	ott	*Fantz 3464*	FTG

Table 1. Continued.

Name	OTU	Specimens	HERB
Bactris Group	BACT		
balanophora Spruce	bal	*Berry 1468*	BH
		Schultes 3938	BH
		Schultes et al. 18304	BH
campestris Poepp.	cam	*Davidse et al. 16915*	NY
		Mori & Cardoso 17287	NY
caudata H. Wendl. ex Burret	cau	*Langlois 1*	BH
		Moore 6633	BH
		Moore & Córdoba 6700	BH
coloniata L. H. Bailey	cln	*Bernal et al. 1099*	FTG
coloradonis L. H. Bailey	clr	*Bernal et al. 1086*	FTG
		Bernal et al. 1097	FTG
corossilla Karst. complex	cor	*Steyermark et al. 101415*	BH
incl. *duplex* H. E. Moore		*Allen 3357*	BH
elegans Barb. Rod.	ele	*de Granville 2591*	BH
		Moore et al. 10331	BH
guineensis (L.) H. E. Moore	gui	*Bailey 253*	BH
		Bernal et al. 1210	FTG
		Essig 70000711-1	BH
		Gentry & Cuadros 47621	MO
hondurensis Standl.	hon	*Beach 1368*	BH
		Hammer 39, 86	FTG
		Holdridge 5123	BH
		Holm & Iltis 920, 923	BH
		Moore et al. 10127	BH
jamaicana L. H. Bailey	jam	*Bailey 216*	BH
		Evans 175	FTG
		Read 1692	BH, US
incl. *plumeriana* Mart. (combined with *B. jamaicana* due to missing data and nearly identical states in known char.)		*Jiménez s.n. 1 Sep 1960,* assoc. living FTG 60647	FTG
		Sanders et al. 1712	FTG
		Watson 1284	FTG
longiseta H. Wendl. ex Burret	lon	*Holdridge 5118*	BH
		Moore 6575	BH
mexicana Mart.	mex	*Sanders 1767*	FTG
militaris H. E. Moore	mil	*Hammer 67*	FTG
monticola Barb. Rod. complex	mon	*Moore & Palmtak 10315*	BH
		Mori & Cardoso 17734	NY
		Steyermark & Liesner 127352	MO
incl. *actinoneura* Drude		*Krukoff 8127*	NY
incl. *diviscupula* L. H. Bailey		*Johnston 1552*	BH
incl. *sigmoidea* Burret		*Bernal et al. 1096*	FTG
oraria L. H. Bailey	ora	*Allen 2580*	BH
pilosa Karst.	pil	*Bernal et al. 807*	NY
		Bernal et al. 1134	FTG
		Steyermark 99952	BH
porschiana Burret	por	*Hammer 84*	FTG
		Holdridge 5121	BH
savannarum Britt.	sav	*Bailey 156*	BH
		Sanders & Budhoo 1746	FTG
setosa Mart.	set	*Bailey 459*	BH
		dos Santos & Mattos 33168	BH
setulosa Karst. complex	stl	*Moore et al. 9837*	US
		Steyermark 99128	BH
		Steyermark & Agostini 91399	BH
		Steyermark & Liesner 118954	MO
incl. *cuesa* Griseb. & H. Wendl.		*Bailey 108*	BH
		Bailey s.n. 26 Feb 1946	BH
		Bailey & Bailey s.n. 13 Mar 1921	BH
		Beard 107	BH
		Delan & Swabey 13142	BH
aff. turbinocarpa Barb. Rod.	trc	*Bernal et al. 1103*	FTG

TABLE 1. Continued.

Name	OTU	Specimens	HERB
Aiphanoides Group	AIPH		
caryotifolia Mart.	car	*Bailey 328*	BH
		Luetzelburg 27028	BH
Amylocarpus Group	AMYL		
aubletiana Trail	aub	*Mori & Boom 14731*	NY
geonomoides Drude	geo	*Berry & Uhl 1538*	BH
		de Granville 3775	BH
		Egler & Irwin 46414	BH
hirta Mart.	hir	*Schultes & Cabrera 12806*	BH
pectinata Mart.	pec	*Costa 680075*	BH
		de Granville 2272	BH
simplicifrons Mart. complex	sim	*Asunción 196*	MO
		Dominguez 75	MO
		Prance & Huber 28496	NY
		Vásquez & Jaramillo 569	MO
incl. *arenaria* Barb. Rod.		*Moore et al. 9542*	BH
incl. *leutzelburgii* Burret		*Steyermark & Bunting 102440*	BH
incl. *trinitensis* (L. H. Bailey) Glassman		*Popenoe s.n. 23 Nov 1978*	FTG
		Sanders & Budhoo 1447	FTG
		Tomlinson 9-7-62B	FTG
tenuis Wallace	ten	*Berry 591*	BH
		Croat 20722	MO
		Schultes & Black 46-219	BH
		Schultes & Black 46-314	BH
turbinata Spruce	tur	*Steyermark 90198*	MO
		Steyermark et al. 130208	MO
Piranga Group	PIRA		
acanthocarpa Mart.	aca	*Balick et al. 924*	BH, NY
		Sperling et al. 5802	NY
acanthocarpoides Barb. Rod.	acd	*Moore et al. 10321*	BH
alleniana L. H. Bailey	all	*Allen 1804*	MO
		Allen 2951	BH
		Croat 12462, 22303	MO
		Croat & Porter 16404	MO
barronis L. H. Bailey	bar	*Allen 9, 2538*	BH
		Bernal et al. 1019	FTG
		Croat 6541, 10297	MO
		Duke 5612	MO
		Juncosa 1859	MO
constanciae Barb. Rod.	cns	*Sanders 1811, 1816*	FTG
glandulosa Oerst.	gla	*Córdoba 131*	BH
humilis (Wallace) Burret	hum	*Boom 4129*	NY
		Costa 670040	BH
		Steyermark 88407	BH
		Steyermark & Gibson 95769	BH
rhaphidacantha Wessels Boer	rha	*Liesner & González 11252*	NY
		Wessels Boer 1224	BH

their progenitors?" (Mora-Urpí & Clement, 1981; Clement & Mora-Urpí, 1987; Clement, 1988; Clement, pers. comm.; Mora-Urpí, pers. comm.).

The underlying goal of this paper is to use cladistic methodology to ascertain: 1) the phylogenetic basis for the relationships of *B. gasipaes* and 2) whether its segregation as the genus *Guilielma* Mart. is consistent with cladistic results. Because this would involve the examining of the monophyletic status of *Bactris* s.l. itself, a more useful approach is to test the monophyletic status and relationships of all of Burret's groups, such that a sampling of all major lines in *Bactris* s.l. should be included. To do so requires using not only those characters upon which Burret relied, but also a wide range of additional ones for constructing a broadly based, parsimonious cladistic hypothesis. This paper represents the first phase

TABLE 2. Data matrix used in this study, with OTUs (see TABLE 1 and APPENDIX I for abbreviations, specimens studied, and representation of taxa) scored for 106 characters, given sequentially starting with character 1 in first column on left (see APPENDIX II for detailed definitions).

ASTR	21?0000000	0000000000	0000000001	?000X10000	0001110000
DESM	?000001000	0000000000	000000?000	0000000000	0000?00000
ACA	1000001000	000010?000	00000?000?	0001100011	101?010001
ACD	1000001000	0000100???	???0000001	0001100011	101???????
ALL	1000001100	0000100000	0110010001	1001100011	1011111011
AUB	0010001000	1010?00010	0000111100	0110101010	011???????
BAL	?01000?001	0000100000	0000001000	0000X10012	1010011000
BAR	?001001000	0000100000	0000010001	0001100011	1011010001
BIF	101?001000	0110?01000	0001101110	0110000110	1030111000
CAM	112101100?	0000100000	000?000000	0000100012	1010000001
CAR	1010011000	000001?000	0011001000	0000100012	1010110?0
CAU	1000001100	0000100000	000001?000	0000100012	1010011010
CLN	1000001000	0000101000	0110101000	0000100012	1010020000
CLR	1001001000	0000100000	0000000000	0000100012	101???????
CNC	101000?000	0000101000	0000101110	0010000110	1030112010
CNS	1001001000	0000100000	0000000000	0000100012	101???????
COR	100000?001	000010?0?0	01000?0000	0000000012	101???????
CRU	101000?000	000010?000	00000?1000	0000000112	101???????
DAH	2000002010	0000000000	0001000001	0000100012	101???????
ELE	0010001000	0001100100	0000101110	0000100012	1010110000
GAS	2000002010	0000000000	0001000001	0000100012	1011000111
GAV	101100?000	00001000?0	00001?1100	0010000112	102???????
GEO	00?0001000	1010?00010	0000111?0	0110X10110	0110??????
GLA	0000001100	0000100000	0110010001	1001100011	1011110011
GST	001000?000	1000100000	0000101110	0110000110	103???????
GUI	1010011000	0000000000	0011000000	0000100012	1010111000
HIR	0000001000	1010?00010	0000111100	0110X10110	011???????
HON	1000001000	1010100000	0010111000	0100100011	1010010001
HUM	?000001000	0000100000	000?01000?	0001100011	1010010011
JAM	20?0002010	0000000000	0000000001	0000100012	1011100101
LON	1001001100	0000101000	01000?0000	0000100012	1010010011
MAC	2000002010	000000????	???1000001	0000100012	101???????
MAJ	1010001000	0?00100000	0000101000	0010000112	102011?01?
MAR	1120011000	0000100???	00100?0000	0000000112	101???????
MEX	1000001000	0000100000	0000010000	0000100012	101011?011
MIL	1000001000	0110?00000	0001000000	0000100012	10101100??
MON	112?0?1000	000010100?	000?00?000	0000?00012	101001?00?
OLI	0010001000	100010000?	0001101110	0110000110	?03???????
ORA	?010111000	0000000000	0011001000	0000100012	1010121000
OTT	1010001000	000010?000	0000000000	0000000112	102???????
PEC	0000001000	0000100010	0000111100	0?10X10110	011???????
PIL	101?0?1000	0000100000	00000?0000	0000000012	1010020001
POR	1000001100	000010?000	0000020001	0000100012	1010110000
RHA	?000001000	0000100000	0000010001	0001100011	101???????
SAV	1121011001	0000100000	0010020000	0000100012	1010000001
SET	?01001??00	0000000000	0011000000	0000100012	1010021000
SIM	0??0001000	1010?00010	1001111?0	0110101010	0110110000
STL	201?00?001	0000100000	000000000?	0000100012	1010010001
TEN	0??0001000	1000100010	1001111?0	0110101010	011???????
TRC	100?001000	00?0?00000	00?00?1000	0000100012	1010110000
TUR	0000001000	0000100010	0000111100	0?10X10110	011???????

TABLE 2 (continued). Designations are: 0 = primitive; 1 (2 or 3) = derived (or multistate ordered); exceptions are the unordered characters 1, 45, 46, 65, 75, and 76. ? = the relevant structure missing from available specimens or variable within the OTU. X = the precursor state unknown.

0000000?0	0100000??0	1000000?00	00010?1000	0100000000	000000
0000000000	000?000??0	0000000000	0000000000	0000000000	000000

0011011101	??00010010	100001000?	1000011000	0000020011	100000
????0?????	?00?010?00	1000210001	1000011000	00?0020011	100000
0011011101	1000010010	1000010000	1000100000	0000030111	100000
??????????	?010010?0	10000?0020	000010000?	1100030111	100000
0001011100	0011000100	0100011000	0000101000	0?00100000	010100
0001011101	1000010010	1000010000	1000011000	?000120011	100000
0000100010	0100010000	1011110001	0200001100	0010022010	000101
0001011100	0010000011	1000010000	0000101000	0000020101	?00000
00000100??	0000010010	10001?0000	20?0000100	?010022???	10000?
0000011100	0000000010	0000000000	?000000000	0000020101	100000

0000111010	0100000011	0001000101	0101011100	00?0022001	0000?1
??????????	??????????	??0????0??	0000000000	0000030111	101000
1100100010	010001??0	?011111001	0201001100	0010022010	000101
??????????	?000010000	00001?0010	1001000010	0010022010	100001
??????????	??????????	??0????0??	?001000?00	1100021011	100001
??????????	?100010100	1011110001	1001001100	0010022000	100001
??????????	??????????	??0????0??	0000000000	0101100000	000100
0000000010	0100010010	1000000101	1000000100	1010022011	100001
0000011100	0001000010	0001111001	0001000000	0001100000	000100
??????????	?????????0	??1????0??	0201001100	0010022010	000101

??????????	?010010011	1100010010	1000111001	1100030111	100010
0011011100	1000010010	1000?10000	1000100000	0000030111	100000
??????????	?????????0	??1????0??	0200000100	0010022010	000101
0000010000	0000010000	0000100000	201?000100	1010022001	100001
??????????	?010010??	110001????	?000111001	??000?01??	???0??
000001100?	0010000010	0001100000	0000000000	0000030111	100000
0011011101	1?00010010	100001000?	?000011000	0000?200?1	100000
0001010110	0000000010	0001111000	2000000000	1001110001	100000
0000011010	0000010010	0001100101	1000000100	0010022101	101001
??????????	??????????	??0????0??	1000000000	0001100001	100000

0000100010	0100000?00	1011110001	0101001100	0010022010	00010?
??????????	?????????0	??1????0??	2000001100	0010022000	100001
0000011101	1010010000	0001111001	1000000000	0000030001	100000
?0??011?00	0010010000	?0011??001	1000000000	0000021001	101001
0000?11?00	010??10010	1000000101	1000000100	0010022001	100001
??????????	?????????0	??1????0??	0200000100	0010022010	000101
0000010000	0000000000	0000100?00	2010000100	1010022001	100001
??????????	?100000100	1011110001	1001001100	0010022010	100001
??????????	?010010010	1100010???	?00011??00	??000?01??	???0??
0000011010	0100000100	1001100100	2000000100	0010022001	100001

0011011000	0000000010	0001101000	0000000000	0000030101	101000
??????????	?000010010	100001?000	1000011000	0000020111	100000
0001011100	0010000010	1000011000	1000100000	0000020101	100000
0000111010	0010000010	0000000001	2000000100	0010022111	100001
0000011100	0100010000	0000000100	?000100000	1100030111	101000
0000011010	0000001001	0?00110020	1000000000	?000021001	100001
??????????	?100010000	0000000100	100010?000	1100030111	101000
000?0??0?0	01001?0000	?00011000?	0101001000	0110021010	100101
??????????	?010010010	1100010000	1000111000	1100030111	100010

of recognizing all major monophyletic lineages within *Bactris* s.l. and of detecting important systematic characters in the genus. It is hoped that this paper, by providing a phylogenetic context for the investigation of smaller, monophyletic groups, will be the catalyst for the future monographic studies in *Bactris.*

Material and Methods

All of the relevant infrageneric groups, segregate genera and outgroups (see below) were sampled with representative species (Table 1, Appendix I). Morphological data were observed directly from 157 specimens (Table 1) that were selected to provide as complete as possible comparative data for vegetative, floral (both staminate and pistillate), and fruiting structures. To assure identifications of the *Bactris* species, specimens with annotations by palm specialists were given priority, and all specimens were compared to the species' protologues. Thus, 139 specimens representing 61 species of *Bactris* were treated as operational taxonomic units (OTU's) in the initial stages of this study. Based on personal field experience, on the comments of other field workers (e.g., Wessels Boer, 1965; Croat, 1978; Galeano & Bernal, 1987; De Nevers, 1988), and on the formation of monophyletic groups of two to four highly similar species in the initial analyses, certain potentially synonymous taxa were combined as single OTU's. This yielded 49 OTU's within *Bactris* for the final analyses (Tables 1, 2).

Characters were obtained at magnifications up to 30× from direct observation of dried, fresh, or liquid preserved material or from manipulation and dissection of rehydrated fragments. Originally, 246 features of gross morphology were surveyed. As an increasingly larger sample of specimens was recorded, features that were unstable within OTU's or invariant among OTU's were deleted. Gap coding was used to transform descriptive and quantitative characters into discrete states. Depending on the apparent relationships of the states, characters were coded as binary (simple linear), linear ordinal multistate, additive binary multistate, or branched multistate (nonadditive binary or mixed ordinal/nonadditive) following Pimentel and Riggins (1987). The state occurring in both outgroup genera was judged to be ancestral. Characters that varied between or within the outgroup genera were left unordered. The characters initially appearing stable within OTU's were used in an initial PAUP analysis. Those with a unit consistency (C) less than 0.1 were deleted. The ultimate data set comprised 57 linear and 22 branched characters, yielding 106 cladistic characters (Table 2, Appendix II). The rejected characters and features are summarized in Appendix III.

Cladograms were constructed by the Wagner-tree algorithm (Farris, 1970; Kluge & Farris, 1969) using the software PAUP (Swofford, 1985) on a microcomputer. Because the data set was large, searches for successively shorter trees were conducted by alternating between local and global branch-swapping (SWAP = ALT). For subsets of usually nine or fewer OTU's (see below), the shortest tree was found with the branch-and-bound option (BANDB). Optimization was by the MINF (minimum tree length), FARRIS (median-state value, maximizing reversals over parallelisms), and DELTRAN (delayed transformation, maximizing parallelisms over reversals) options; rooting was by the ANCESTOR option.

To determine the outgroup, a preliminary cladistic analysis was conducted for the entire Bactridinae J. D. Hooker. Data for each genus were extracted from the literature (particularly Uhl & Dransfield, 1987) and from living and herbarium material at FTG. The character states in the nonspiny Cocoeae were compiled for a generalized outgroup. In all resulting cladograms, *Bactris, Desmoncus,* and *Astrocaryum* together formed a clade strongly supported by the following synapomorphies: stems (primitively) caespitose, pistillate sepals connate, pistillate petals strongly fused into cup or tube, mesocarp not mucilaginous, endocarp pores supramedial. However, the interrelationships among the three genera were equivocal. The autapomorphies for *Desmoncus,* liane habit and cirrus, and the probable autapomorphies for *Astrocaryum,* staminate flowers congested into a terminal rachilla portion and sunken in pits, suggest that these two genera are each monophyletic. Therefore, *Astrocaryum* and *Desmoncus* were each treated as OTU's (Table 1), tagged as outgroups, and analyzed together with *Bactris* OTU's in the parsimony analyses.

As advocated by Farris (1969), a character's cladistic reliability is considered to be directly proportional to the character's consistency. Thus, the characters were weighted based on their unit consistencies in an initial analysis without weighting. To facilitate input, the consistency values were rounded to the nearest tenth and multiplied by 10 (Appendix II). The only exception was character 96 (adnation/freedom and structure of endocarp fibers), with a C value of 0.7. It was given a weight of 10 because the change from primitive (endocarp pale with fibers blackish, strongly flattened and adnate to the endocarp) to derived (endocarp black, with fibers dark to pale, terete and free from endocarp) is very complex, and a reversal is considered to be highly unlikely.

The initial unweighted and weighted runs were

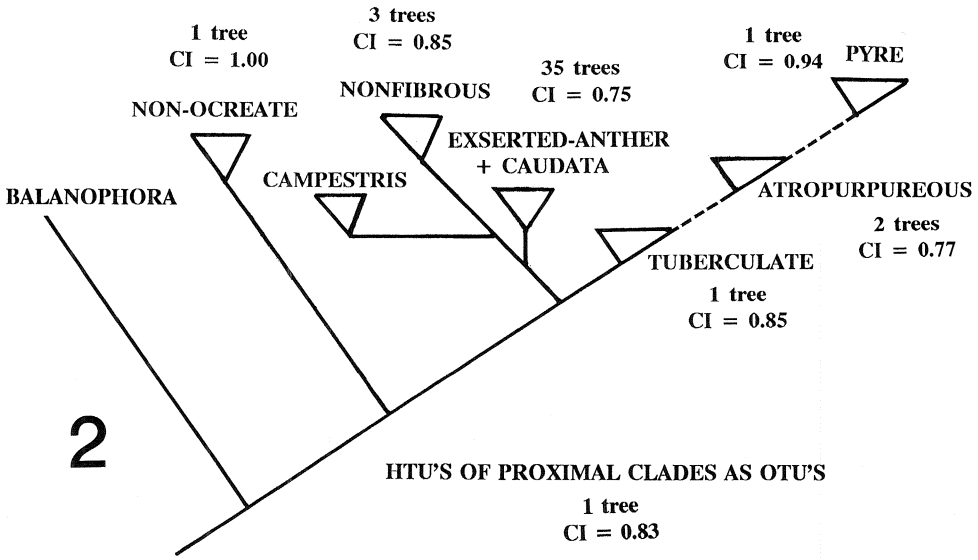


FIGURE 2. Branch-and-bound (BANDB) analysis of proximal and/or major clades within *Bactris.* Monophyletic clades of 9 or fewer OTU's were analyzed to obtain the shortest tree(s) for each clade and, in turn, were replaced by hypothetical ancestors (HTU's) for subsequent iterations until these proximal clades were obtained. Given is the Consistency Index (CI) of the most parsimonious tree or equally parsimonious trees obtained in each analysis. In all cases, equally parsimonious trees result from missing data. In cases of multiple BANDB trees, the strict consensus tree of each clade provides the topology depicted in FIGURE 3.

conducted with the initial set of 63 OTU's (61 *Bactris* spp. + 2 outgroup OTU's). PAUP 2.4 accommodates only 50 OTU's; also, the MULPARS option is greatly slowed by missing data. Therefore, the approach chosen was to: 1) obtain a preliminary cladogram based on a major subset of OTU's; 2) identify well supported monophyletic groups; 3) use BANDB to analyze each subclade of nine or fewer OTU's (the approximate maximum OTU's accommodated by BANDB) to find all possible shortest trees for each; 4) replace each by a hypothetical ancestor (HTU) in the data set; 5) use BANDB to analyze the next most inclusive clade in a repeated fashion until all clades could be run in a single BANDB analysis; and 6) reconstruct the total cladogram as a composite of cladograms of the subclades.

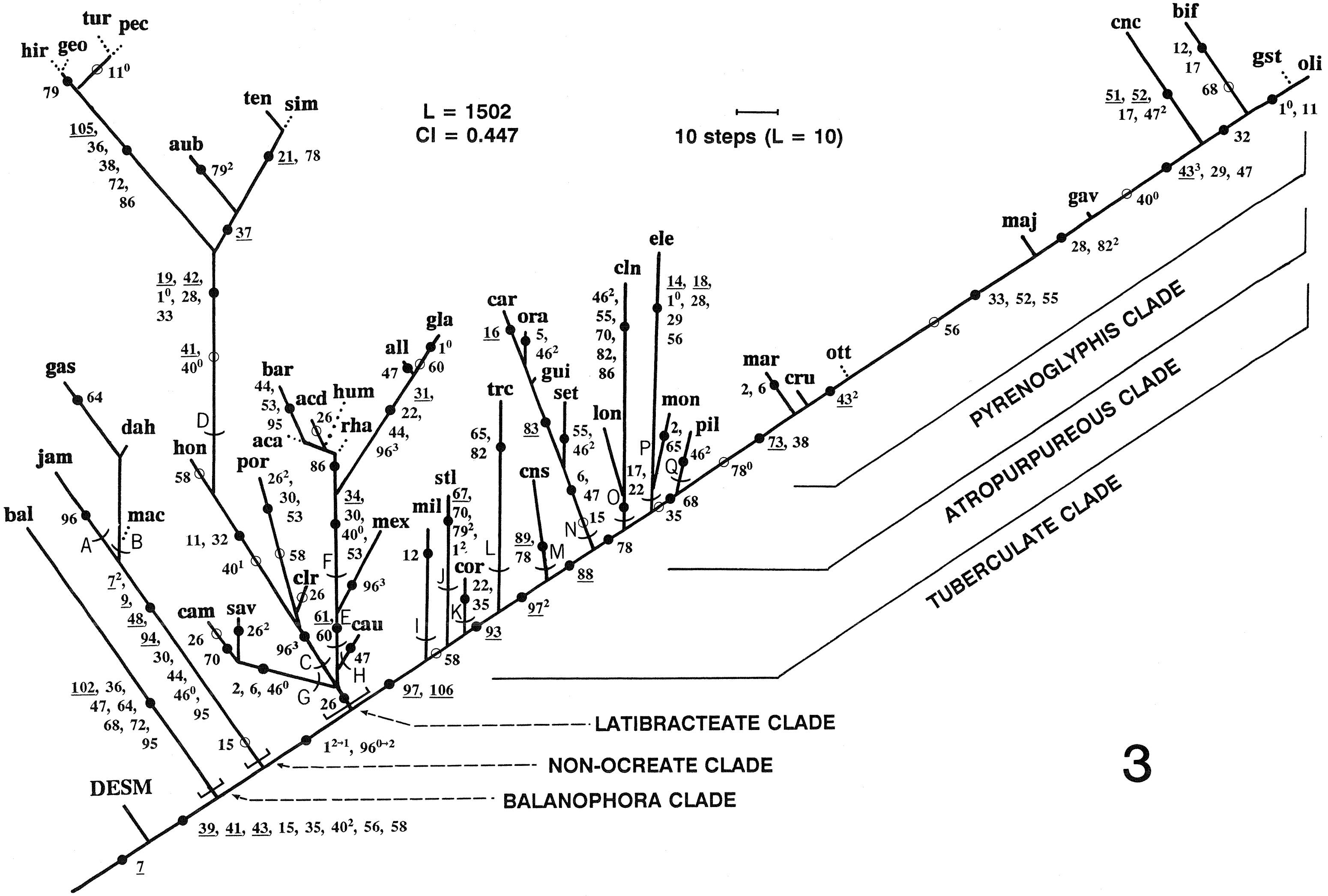
To get an initial structure of the whole genus, a subset of 37 preliminary OTU's, which had complete (or the least missing) data or that were similar to OTU's with more missing data, were analyzed. Upon the recognition of subclades, the remaining preliminary OTU's were included in the BANDB analyses. As indicated above, several initial OTU's were combined at this stage to yield the ultimate 49 OTU's. To score characters of the HTU's, HTU matrices were output using both the MINF and FARRIS options. If the two optimizations disagreed, the HTU was assigned missing data for the character. If more than one topology resulted from BANDB, the strict consensus tree was inserted in the composite cladogram.

To check the extent of total homoplasy, the structure of the composite cladogram was specified, analyzed with the data set of the ultimate 49 OTU's plus the HTU of *Bactris* s.l., and optimized by both FARRIS and DELTRAN. To search for shorter trees, branches of the composite cladogram were swapped globally and locally (SWAP = ALT).

RESULTS AND DISCUSSION

Topologies, Clades, and Synapomorphies

The initial, weighted cladogram yielded several distal monophyletic groups including AMYL (acronyms in small upper case correspond to the species and groups in TABLE 1), PIRA, GUIL, and a group of species in PYRE with spicate inflorescences. Further nesting of these was as follows: AMYL within the NONFIBROUS CLADE (marked predominantly by the loss of endocarp fibers, 96^3 [number and superscript follow notation in APPENDIX II and FIGURE 3]), PIRA within the EXSERTED-ANTHER CLADE (named for the unique synapomorphy, 61), GUIL with JAM to form the NON-OCREATE CLADE (named for the loss of the well developed ocreae in adult leaves, 7^2), and the spicate species within PYRE (FIGURE 2). PYRE


L = 1502
CI = 0.447
10 steps (L = 10)
PYRENOGLYPHIS CLADE
ATROPURPUREOUS CLADE
TUBERCULATE CLADE
LATIBRACTEATE CLADE
NON-OCREATE CLADE
BALANOPHORA CLADE
DESM
bal
jam
mac
gas
dah
hon
cam
sav
por
clr
bar
acd
aca
hum
rha
mex
cau
all
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bif
gst
oli
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
39, 41, 43, 15, 35, 40², 56, 58
7
1²⁻¹, 96⁰⁻²
97, 106
93
97²
88
78
68
35
78⁰
73, 38
43²
56
33, 52, 55
28, 82²
40⁰
43³, 29, 47
32
1⁰, 11

3

was nested along with several OTU's within the ATROPURPUREOUS CLADE (named for the synapomorphy of purple-black epicarps, 88), which was further nested within the TUBERCULATE CLADE (named for the tuberculate endocarp surface, 97).

Together, the NONFIBROUS CLADE, EXSERTED-ANTHER CLADE, CAM + SAV (CAMPESTRIS CLADE), and CAU (CAUDATA CLADE) form a more inclusive clade (LATIBRACTEATE CLADE) united by transversely elongate rachis bracts (char. 26). In all BANDB analyses of this inclusive clade, the EXSERTED-ANTHER and CAUDATA CLADES were united by large staminate receptacles (char. 49) as a clade, which in turn formed a trichotomy with the other two clades (FIGURE 2).

The BANDB analysis of most of these clades resulted in only one most parsimonious topology with a high consistency index (FIGURE 2). In cases with two or more equally parsimonious topologies, the equivocality developed because missing data could be assigned two or more feasible states by PAUP, not because homoplasious characters conflicted. The high number of equivalent topologies for EXSERTED-ANTHER + CAUDATA resulted from the lack of staminate characters in several closely related members of the *B. acanthocarpa* complex. Thus, the overall structure of all clades is well supported.

The BANDB analysis of the HTU's of the proximal clades (TUBERCULATE, EXSERTED-ANTHER + CAUDATA, NONFIBROUS, CAMPESTRIS, NON-OCREATE, and BALANOPHORA [i.e., OTU BAL]) resulted in a single most parsimonious tree with a high consistency index (FIGURE 2). The detailed composite cladogram (FIGURE 3) is built up from this basic structure by the insertion of the BANDB tree or strict consensus tree of BANDB trees of the constituent clades. Because weights and multiple states modify the length of a given character, the total length of the cladogram would be 606 steps if it were completely consistent (i.e., if CI = 1.0). However, the length was 1,502 steps and the consistency was much lower (CI = 0.447) than in the BANDB of proximal clades. This is expected because many characters were consistent among related species but homoplasious in the context of wider comparisons. Homoplasies were masked by the optimized HTU's as the BANDB analyses progressed but emerged in the Wagner-tree analysis of all 49 OTU's.

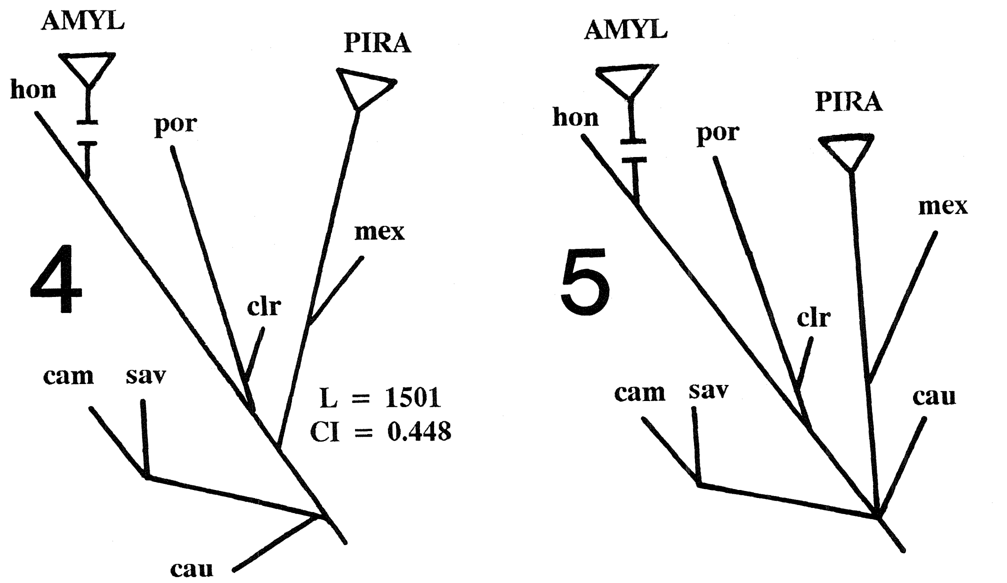
Only one tree was found that was shorter (by one step, <0.1% different, FIGURE 4). This differed only by the placing of CAUDATA with the CAMPESTRIS CLADE (synapomorphies: 74^0, pistil cylindric, C = 0.14; and 75^0, style branches free, C = 0.25). In the context of the whole genus, char. 49 (large staminate receptacles), which unites EXSERTED-ANTHER and CAUDATA, has a C of only 0.17. Hence, neither position of CAUDATA is very strongly supported, and the strict consensus tree, which places CAUDATA as a clade equivalent to EXSERTED-ANTHER and CAMPESTRIS, should be accepted for tentative taxonomic considerations (FIGURE 5).

The basic internal structure of *Bactris* (FIGURE 3, TABLE 3) can be viewed as consisting of four, roughly equivalent clades. Each of these is distinguishable by its autapomorphies (i.e., synapomorphies of the constituent OTU's), but the internodes separating the four clades contain few, mostly homoplasious, synapomorphies.

The first of the four, the BALANOPHORA CLADE, comprises the single species *B. balanophora,* which Burret placed in sect. *Bactris.* This is not surprising; all autapomorphies, except the basally broadened endocarp (102), occur in parallel elsewhere in the genus. However, its retention of the plesiomorphies—flattened, adnate endocarp fibers (96^0) and large stem diameter (1^2)—should have led Burret, who emphasized these so strongly in *Guilielma,* to place the two lineages in close proximity. It is surprising that Burret did not notice the endocarp character because he cited Spruce's material, which is probably the material from which Spruce (1871) described the mature drupes. This suggests that Burret did not consis-

←

FIGURE 3. Composite cladogram for all sampled OTU's in *Bactris,* showing details of clades that constitute FIGURE 2. See TABLE 1 and APPENDICES I and II for acronyms and number codes of characters. Clades along the main axis of the cladogram are indicated by angled brackets. Curved brackets mark the basal node of each of the additional clades mentioned in TABLE 3: A = ANTILLEAN, B = GUILIELMA (GUIL), C = NONFIBROUS, D = AMYLOCARPUS (AMYL), E = EXSERTED-ANTHER, F = PIRANGA (PIRA), G = CAMPESTRIS, H = CAUDATA, I = MILITARIS, J = SETULOSA, K = COROSSILLA, L = TURBINOCARPA, M = CONSTANCIAE, N = BIDENTATE, O = LONG-PROPHYLL, P = TUBIFLOROUS, Q = PILOSA. Dots indicate unique or parallel synapomorphies. Unless the changed character state is indicated by a superscript, the change is to the state 1. Circles indicate reversals to state 0 (unless other state is indicated). The unit consistency values (C) within *Bactris* are indicated as follows: 1) underlined numbers are unique occurrences within *Bactris* or unique reversals from the ancestral synapomorphy for *Bactris* (C = 1.00); 2) numbers not underlined are moderately homoplasious (C = 0.5 to 0.33); 3) characters not listed have C = 0.25 to 0.1. Patristic distance portrayed includes distances contributed by unlisted characters, i.e., those with C < 0.33. Correction in proof: 35 on K is a reversal.



Figures 4, 5. 4. Single shorter tree obtained by swapping branches of cladogram in Figure 3. Only the branch that differs from Figure 3 is illustrated. 5. Strict consensus tree for Figures 3 and 4.

tently examine non-guilielmas for the character. The BALANOPHORA CLADE is the sister group to the remaining three clades, which are united only by four homoplasious characters.

The NON-OCREATE CLADE, comprising GUIL and the antillean species of sect. *Bactris*, is strongly supported. These two groups share four unique synapomorphies (7^2, ocreae lost from adult leaves; 9, petiolar spines in three ranks; 48, staminate petals rounded; and 94, mesocarp thickly starchy) and several homoplasious ones (Figure 3, Table 3). On the other hand, the only apomorphy distinguishing GUIL from this more inclusive clade is the suppression of peduncular spines (char. 24, C = 0.17). Although the antillean species have developed nearly free endocarp fibers in parallel with the rest of genus, they still share with GUIL these unusual synapomorphies. The NON-OCREATE CLADE is the sister group to the two remaining clades of *Bactris*, which are united only by the two partially homoplasious characters, stem diameter moderate (1^1) and endocarp fibers completely free and terete (96^2).

The LATIBRACTEATE CLADE (Table 3) contains the NONFIBROUS, EXSERTED-ANTHER, CAMPESTRIS, and CAUDATA CLADES. It is the least well supported of the four major clades because the three defining synapomorphies suffer from homoplasy (26, reversing in a few OTU's, C = 0.33; 75, stigma recessed, C = 0.22; 98, outer mesocarp fibers few, C = 0.20).

The TUBERCULATE CLADE constitutes the last major lineage in *Bactris*. Its members share two unique synapomorphies (97, tuberculate endocarp; 106, asymmetry of endocarp pores). It encompasses a wide range of species from relatively plesiomorphic ones to those that are the most divergent in the genus.

Disposition of Burret's Groups

To provide the context for evaluating Burret's groups, one should consider the disposition of the four major clades already discussed. The classificatory philosophy adopted here is that for a taxon to be accepted, it must be monophyletic or at least not be shown to be non-monophyletic (i.e., para- or polyphyletic) when the phylogenetic status of the taxon is known. Because none of the major clades corresponds directly to the segregate genera and together form a monophyletic group, the most conservative view is to accept the traditional limits of *Bactris*, which includes all four clades. The alternative proposal of treating the clades as four genera (or of treating the clade LATIBRACTEATE + TUBERCULATE as a third genus) is undesirable. As noted earlier, the synapomorphies of NON-OCREATE + LATIBRACTEATE + TUBERCULATE and of LATIBRACTEATE + TUBERCULATE are few and homoplasious. In practical terms, the more plesiomorphic members of each clade resemble one another and are "typical" *Bactris* species. Thus, a more reasonable approach would be to treat each clade as a subgenus or section of *Bactris*.

Figure 6 illustrates that GUIL, PYRE, AIPH,

TABLE 3. Summary of known monophyletic groups in *Bactris* s.l., their delimiting characters, and their possible hierarchical levels as suggested by the cladistic structure of *Bactris* when treated as a single genus. Numbers in square brackets are the characters (APPENDIX II); unless indicated by a superscript, the number indicates the (first) apomorphic state, i.e., $7 = 7^1$. Each clade is characterized by the synapomorphies of its members. For clades in FIGURE 3 (i.e., nodes on the cladogram) that are not named and characterized, the synapomorphies are given under the constituent clades. For example, char. 63 is listed as an apomorphy of the TUBIFLOROUS, PILOSA, and PYRENOGLYPHIS CLADES, but it arises in the node below the TUBIFLOROUS CLADE. Likewise, char. 7 is given for *Bactris,* although it is a synapomorphy of both *Bactris* and *Desmoncus.* Reversals to apparently primitive states that serve as synapomorphies are indicated by "*". Character states that contrast a clade with equivalent clades are not typically listed either because they are simply implied plesiomorphies or because, in some cases, the clade is variable, having both apo- and plesiomorphies (refer to TABLE 2, APPENDICES II and III, and FIGURE 3). However, a few plesiomorphies that are of limited distribution and, hence, contribute to the clade's distinctiveness and diagnosis within *Bactris* are listed and indicated by underlining. "±" indicates more or less.

BACTRIS (Generic level)

At least juvenile (and usually adult) leaves with a membranous ocrea that becomes fibrous and often shredded at maturity, leaving an abscissionlike scar across the adaxial face of the petiole (i.e., leaf base) [7]; rachillae covered with bulbous or moniliform hairs [35]; triads in three or more ranks [39], which are usually longitudinally asymmetrically placed on the rachilla [43], female-sterile triads (i.e., staminate diads or monads) usually distributed among and below the female-fertile triads [40^2, 41].

BALANOPHORA CLADE (Subgeneric level):

Stems usually >6 cm in diam. [1^2]; spines fascicled [10]; rachillae lanate [36]; staminate petals connate [47]; filaments free [54]; pistillate calyx annulate [63], truncate [64]; pistillate corolla truncate [68], lanate [72]; stigma discoid [77]; fruit mesocarp oily [95]; endocarp ovoid [102], base expanded [104], *fibers stout, flattened and adnate* [96^0].

NON-OCREATE CLADE (Subgeneric level):

Stems usually >6 cm in diam. [1^2]; ocrea lacking on adult leaves [7^2]; petiolar/rachis spines in three ranks [9]; leaflet apex unequally bidentate with subapically terminating midrib [15^0*]; staminate flowers shorter than pistillate [44], petals rounded and not completely adnate to receptacle [48, 50]; mesocarp rich in mealy starch and oil [94, 95]. (Also leaf segments numerous, linear, in 3 to 6 ranks and clustered.)

ANTILLEAN CLADE (Sectional level):

Endocarp fibers few, proximally flattened and partially adnate, distally terete and spreading/declined [96].

TABLE 3. Continued.

GUILIELMA CLADE (Sectional level) = *Guilielma* sensu Burret:

Peduncular spines strongly reduced or lacking [24]; *endocarp fibers stout, flattened and adnate* [96^0].

LATIBRACTEATE CLADE (Subgeneric level):

Stems <6 cm in diam. [1]; inflorescence rachis-bracts (excluding mucro or awn) usually transversely oblong to linear [26]; endocarp fibers thin, terete and free or lacking [96^2]; outer mesocarp fibers few [98].

NONFIBROUS CLADE (Sectional level):

Staminate receptacle usually completely adnate to petals [50^0]; stigmatic surface usually marginal on lobes [76^0*]; endocarp fibers lacking [96^3].

SEVERAL PLESIOMORPHIC CLADES at subsectional level, including *B. hondurensis* and *B. coloradonis* complexes and unsampled ones.

AMYLOCARPUS CLADE (Subsectional level) = Sect. *Amylocarpus* sensu Burret:

Stems <1.3 cm in diam. [1^0]; peduncular bract apex acute [19]; rachillae few [28], rigid [33]; triads contiguous from base to near apex of rachilla [40^0*, 41^0*, 42]; pistillate corolla cylindric [66]; fruit pea-sized [85].

EXSERTED-ANTHER CLADE (Sectional level):

Staminate receptacle filling half of flower [49], not completely adnate to petals [50]; anthers small [60], exserted between petals [61]; pistillate corolla cylindric [66].

FEW PLESIOMORPHIC CLADES at subsectional level, including *B. mexicana* complex and, at least, the unsampled *B. oligoclada* complex.

PIRANGA CLADE (Subsectional level) = Sect. *Piranga* sensu Burret:

Rachillae usually >40 [30], filamentous compared to other spp. [34]; triads ±contiguous, often separated by only one or two nodes of staminate diads or monads [40^1*]; stamens free [54], usually central on receptacle [53]; pistillate corolla lepidote to setose [71].

CAMPESTRIS CLADE (Sectional level):

Spines strongly flattened [2], broad [3^2], and pale [6]; staminate sepals strongly connate [46^0]; staminate receptacle not completely adnate to petals [50]; stamens clearly free [54]; pistillate calyx annulate [63]; fruit pea-sized [85].

CAUDATA CLADE (Sectional level):

Petioles hollow upon drying [8]; staminate receptacle filling half of flower [49], *completely adnate to petals* [50^0], these strongly connate [47]. (Possibly a constituent of either the EXSERTED-ANTHER or CAMPESTRIS CLADE.)

TUBERCULATE CLADE (Subgeneric level):

Stems usually <6 cm in diam. [1]; endocarp fibers thin, free, terete with basal attachment forming tubercles on the endocarp [96^2, 97]; two of the three endocarp pores displaced together on one side of endocarp [106].

MILITARIS CLADE (Sectional level):

Leaf blade 4 or more times longer than broad [12];

TABLE 3. Continued.

peduncular spines strongly reduced or lacking [24]; pistillate calyx annulate [63]; *epicarp orange* [88^{0}]; endocarp pitted [103].

SETULOSA CLADE (Sectional level):
Stem usually >6 cm in diam. [1^{2}*]; spines slightly broadened near middle [3], fascicled [10]; anthers oblong-linear [58^{0}*]; pistillate corolla patelliform [67] and fimbriate [70]; *epicarp orange* [88^{0}].

COROSSILLA CLADE (Sectional level):
Spines fascicled [10]; peduncular bract densely covered with flexible setiform spinules [22]; rachillae glabrous or lepidote [35^{0}*]; anthers oblong-linear [58^{0}*]; *epicarp yellowish* [88^{0}]; fruit apex rostrate [92].

TURBINOCARPA CLADE (Sectional level):
Anthers oblong-linear [58^{0}*]; pistillate calyx deltate-lobed [65]; fruit ellipsoid [81^{0}*, 82]; epicarp ferruginous-lepidote [87] and *pale yellow-brown* [88^{0}]; fruit apex rostrate [92]; mesocarp consisting of juice sacs attached to endocarp fibers [93]; endocarp with fertile and sterile pores offset distally [100^{0}*] and base expanded [104].

CONSTANCIAE CLADE (Sectional level):
Anthers oblong-linear [58^{0}*]; epicarp rosy purple [89]; mesocarp consisting of juice sacs attached to endocarp fibers [93], these very fine, numerous, and basally attached to minute tubercles or papillae on the endocarp [97^{2}]; endocarp with fertile and sterile pores at same level distally [100^{0}*]. (Also epicarp splitting into acicular corky tubercles; character not added to analysis, which was nearly completed when authentic material became available.)

ATROPURPUREOUS CLADE (Sectional level):
Spines usually broadened slightly to greatly in middle [3]; anthers oblong-linear [58^{0}*]; epicarp dark purple-brown or blue-black [88]; mesocarp consisting of juice sacs attached to endocarp fibers [93], these very fine, numerous, and basally attached to minute tubercles or papillae on the endocarp [97^{2}]. (Some constituent clades, e.g., *B. tomentosa* complex, not sampled in study; these either may be equal to or are to be included in the following subsectional level clades.)

BIDENTATE CLADE (Subsectional level):
Shaft of spines pale [6]; leaflet apex with subapically terminating midrib [15^{0}*], usually equally bidentate, except in SET; peduncular spines strongly reduced or lacking [24]; staminate petals strongly connate [47].

LONG-PROPHYLL CLADE (Subsectional level):
Spines tapering from base [3^{0}*]; prophyll over half of length of peduncular bract [17], this densely covered with setose spinules [22]; in fruit, calyx about equal to corolla [78].

TUBIFLOROUS CLADE (Subsectional level):
Rachillae 15 or fewer [27]; pistillate calyx urceolate [62]; pistillate corolla lepidote [71], cylindric [66], *cuspidate or lobed* [68^{0}]; in fruit, calyx about equal to corolla [78].

PILOSA CLADE (Subsectional level):
Rachillae glabrous to lepidote [35^{0}*]; pistillate calyx urceolate [62]; pistillate corolla lepidote [71], *cupulate* [66^{0}], truncate [68]; in fruit, calyx about equal to corolla [78].

PYRENOGLYPHIS CLADE (Subsectional level) = *Pyrenoglyphis* sensu Burret:
Rachillae glabrous to lepidote [35^{0}*], alveolate [38]; pistillate calyx urceolate [62]; pistillate corolla lepidote [71], *cupulate* or cylindric [$66^{0 \text{ or } 1}$], truncate [68], internally with basally adnate staminodial ring [73]; in fruit, calyx about half the length of corolla [78^{0}*]; endocarp with fertile and sterile pores at same level distally [100^{0}*]. (All constituent complexes sampled. This clade exhibits the following divergent character trends, culminating in the most apomorphic taxa in *Bactris*: Inflorescence increasingly reduced in rachis length and number of rachillae (paniculate → digitate → spicate) [25, 27–29]; rachillae increasingly rigid, stout and short, and with increasingly close triads either by loss or refeminization of female-sterile triads [32, 33, 40^{0}*]; increasing connation of staminate petals, and flattening and adnation of filament bases [47, 55, 56^{0}*, 57^{0}*]; increasing elongation and attenuation of fruit and endocarp (obovoid-globose → ellipsoid → fusiform) [82, 101^{0}*, 104].)

AMYL, and PIRA (except for the inclusion of CNS) are each monophyletic. However, it also shows that Burret simply dumped the remaining, nondivergent taxa into BACT (sect. *Bactris*), which in reality is a paraphyletic assemblage of the more generalized species. The monophyly of the remaining groups is insufficient to support his taxonomic scheme.

Guilielma sensu Burret (GUIL) does not form a clade or entity divergent from the remainder of *Bactris* until it is grouped with the antillean species of BACT to form the NON-OCREATE CLADE. That is, segregating GUIL makes *Bactris* s. str. paraphyletic and GUIL cannot be treated as a genus without all equivalent clades being so treated. This would fragment *Bactris* into eight or more poorly defined genera. Treating GUIL as a subgenus, as was done by Drude (1887) and MacBride (1960), would likewise unduly inflate the number of subgenera and would obscure the strong support for the NON-OCREATE CLADE. If, however, the NON-OCREATE CLADE is treated as a subgenus, then GUIL may be treated as a section (TABLE 3).

The same holds true for *Pyrenoglyphis* sensu Burret (PYRE). However, it is even more deeply

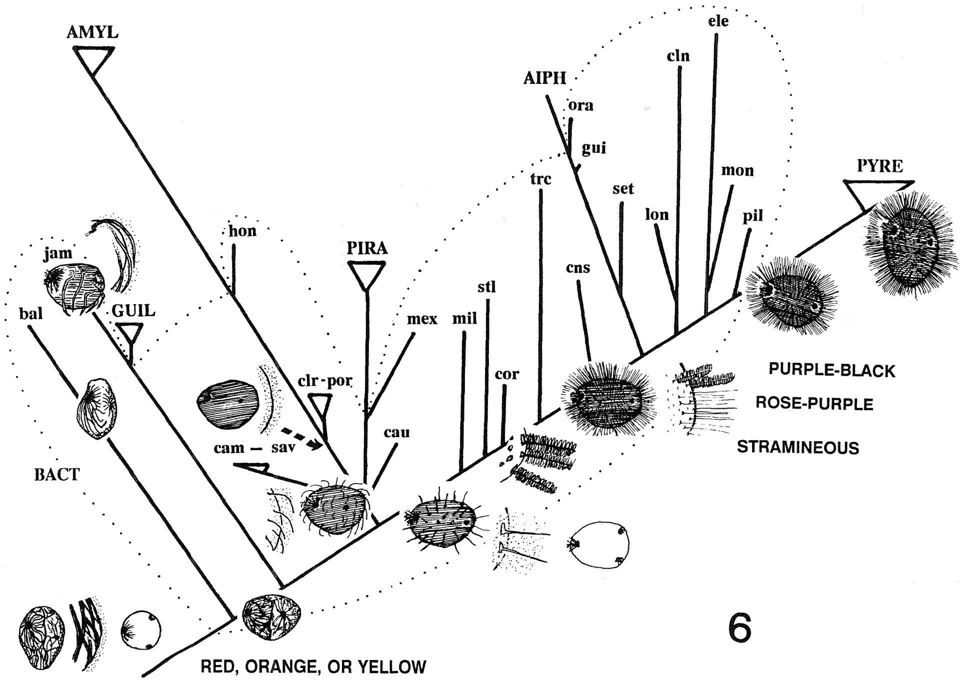


FIGURE 6. Disposition of Burret's (1933–1934) groups and illustration of trends in fruit characters in the context of the phylogeny of *Bactris*. Summarized monophyletic groups are indicated by triangles. Dotted line encompasses taxa included in BACT (sect. *Bactris* sensu Burret), which is paraphyletic. Drawings of whole spherical structures are fruits with epicarps removed in side view, oriented with distal end on top, not to scale. Partial illustrations are of enlarged endocarp surfaces and fibers; stippling indicates starchy mesocarp; pinnate structures are juice sacs attached to fibers. Outlines are endocarps in polar view showing relative radial position of germination pores with fertile pore to left. Colors are of the epicarp. Note sequential attainment of characters to build up the "pyrenoglyphis"-type fruit.

nested within the TUBERCULATE CLADE than GUIL is within the NON-OCREATE CLADE. Indeed, PYRE is divergent and apomorphic. However, the "generic" character of the staminodial ring (73) is simply a single, clear-cut synapomorphy that is one among several that have developed at different stages in the evolution of the TUBERCULATE CLADE. Indeed, the striking similarity between certain PYRE spp., e.g., *B. maraja,* and closely related species lacking the staminodial ring, e.g., *B. monticola,* will be noticed by anyone who tries to identify collections containing both. Thus, recognizing PYRE at either the generic or subgeneric level (Drude, 1887; MacBride, 1960) without treating equivalent clades similarly contradicts the phylogenetic evidence. PYRE would best be treated as a subsection or series within the TUBERCULATE CLADE (TABLE 3).

There are also problems with each of Burret's subgroups in *Bactris* s. str. Subgenus *Amylocarpus* sensu Burret comprises AMYL and PIRA. These two groups are monophyletic, but they do not form a more inclusive monophyletic group. Each arises on separate branches of the LATIBRACTEATE CLADE; this makes Burret's subgenus polyphyletic and completely untenable as a taxon. AMYL and PIRA are both several nodes from the base of the LATIBRACTEATE CLADE, which suggests that they should be recognized at the subsectional or series level (TABLE 3), rather than the sectional level as was done by Burret.

Furthermore, Burret partitioned sect. *Amylocarpus* into two subsections (not shown in FIGURE 1). Subsect. *Isochlamys* (Spruce) Burret sensu Burret has the pistillate calyx equalling the corolla. It corresponds directly with the *Bactris simplicifrons* complex (APPENDIX I) and is represented on the cladogram by the clade SIM + TEN (FIGURE 3). Subsection *Isochlamys,* thus, is monophyletic. However, subsect. *Brachycalyx* Burret, which is distinguished by annulate, inconspicuous pistillate calyces, is left as the paraphyletic remainder of AMYL. These taxa should not be maintained as equivalent groups as was done by Burret.

In subg. *Bactris* sensu Burret, the monotypic sect. *Aiphanoides* (i.e., *B. caryotifolia*; AIPH) is deeply nested within the TUBERCULATE CLADE

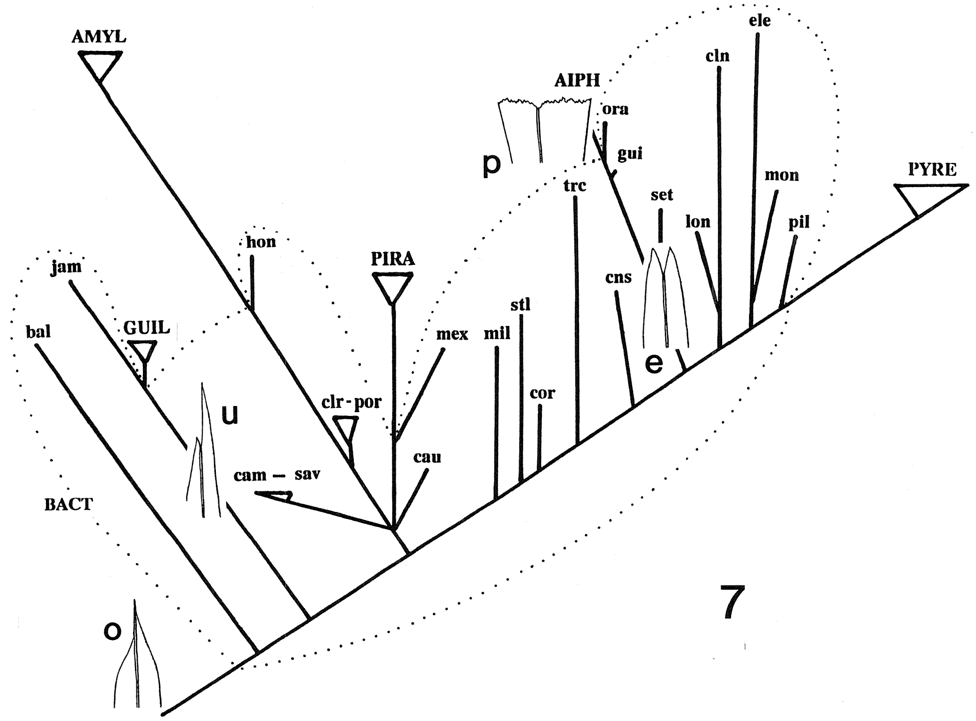


FIGURE 7. Evolution of character states of leaf-segment apices in *Bactris* suggested by parsimony analysis. Having oblique apices with the primary vein terminating apically (*o*, char. 15^1) is a synapomorphy for the species of *Bactris*. Having two strongly unequal apical teeth with the primary vein terminating subapically (*u*, char. 15^0) is a synapomorphy for the NON-OCREATE CLADE. Having two short equal teeth with the primary vein terminating subapically (*e*, char. 15^0) arose in the ancestor of the BIDENTATE CLADE (or clade distal to SET, which often has unequal teeth). The praemorse apex (*p*, char. 16^1) in AIPH is not fundamentally different to the rest of *Bactris*, but is simply a modification of the equally bident apex through distal broadening.

among species of BACT. To recognize this species as the sister group of all the typical species of *Bactris* hides its close relationship with the *B. guineensis* complex and the sequential evolution of its distinctive leaf form (FIGURE 7). Because BACT is paraphyletic and does not reflect relationships as they exist, section *Bactris* should not be maintained with Burret's circumscription.

The *modus operandi* of systematics in the time of Burret (1933–1934) was overall similarity. When viewed from this perspective, his terminal phenetic groups are usually consistent with the distributions of characters, attesting to his perceptivity. However, when evaluated by cladistic criteria, Burret's classification fails and should not be used.

Stability and Evolution of Taxonomic Characters

General evaluation. The process of selecting, observing, and analyzing characters is cyclic, being repeated at increasingly higher levels of generality. Thus, I agree with Neff (1986) that all characters that one proposes to observe and report should be viewed as hypotheses that are either accepted or rejected as the analyses proceed and as other workers try to use those characters. In this context, APPENDICES II and III detail the selection, use, and problems of each character. The discussion here focuses on generalizations made in the study and on the transformations of groups of characters that are important in the taxonomy of *Bactris*.

Most of the 106 characters were defined qualitatively. Because 33 characters lent themselves to quantification, they were defined to assess the variation more precisely. Only six of these (12, 18, 42, 43, 52, and 83: e.g., length-width ratio of peduncular bracts and number of stamens) broke into clearly discrete states. The other quantitatively defined characters yielded measurements with slight overlap or with overlap in only one or a few OTU's. This variational pattern is discussed for nine characters (1, 11, 27–31, 62, and 63) in APPENDIX II, but the remaining eighteen (17, 25, 32, 44, 46, 47, 49, 59, 60, 78–82, 84, 85, 92, and 101) also exhibit this pattern. In this study, the sample of specimens per OTU was small, such that the hypothesized gaps and/or modes must be verified in subsequent monographic studies in which meaningful statistics can be obtained.

Character analysis in *Bactris* illustrates that the hierarchical level at which one evaluates and uses a character is important. Across a large and species-rich genus, there are two major sources of homoplasy: 1) true parallelisms and reversals in characters with small genotypic/phenotypic differences between states; and 2) convergences, in which the subtle distinctions between characters are not readily perceived. However in a small, homogeneous group, such as the distal monophyletic groups analyzed by BANDB, numerous parallelisms/reversals and the occurrence of convergent characters are less likely. Comparisons of homoplasies at different levels draw one's attention to the characters which should be reinterpreted and/or reanalyzed. For example, the occurrence of bifid leaflet apices (char. 15^0) on two distant internal clades suggests that reexamination of this character should result in its redefinition as two distinct, nonhomologous characters (FIGURE 7).

A similar problem encountered in this study was that some characters, such as those associated with pistil and stigma structure, are interpreted with difficulty from rehydrated material. As new collections permit study of fresh or pickled material, a more accurate assessment of the distribution of these characters among taxa can be made.

It is generally agreed that different characters that are developmentally or functionally correlated, and presumably express the same genetic information, should be treated as a single cladistic character. The same effect would be achieved by dividing the normal weight of a character by the number of characters in the correlated complex. This prevents giving undue weight to any one character. However, the problem is to determine whether two or more characters are actually correlated, i.e., does one always occur where the other does? This may be hard to see in a large data set, such as this one. It is probably better to run an initial analysis and follow the two characters, which is easily done in PAUP with the CHGLIST option. For example, fruit shape (81) and endocarp shape (101) would seem to be under the same developmental constraints to form a highly correlated set of characters. They changed together at four nodes of the cladogram, yet fruit shape reversed five times independently of endocarp shape. Thus, what initially appeared to be redundant characters were only partially so.

Indeed, being able to pinpoint and compare clades in which the characters are dependent vs. ones in which they are independent may lead to important insights into the morphogenesis, adaptive ecology, and evolution of the respective taxa. In the case of fruit and endocarp shapes, both characters change concurrently to the apomorphic state in the ancestor of all *Bactris* spp. except the BALANOPHORA CLADE. Both then reverse concurrently to the plesiomorph in species (or clades with few species) of which the sister species retain the apomorph (1: in CLN, but not LON; 2: in MAJ [+other more distal PYRE], but not OTT or CRU; 3: in GAS + DAH, but not MAC). Additionally, in cases 2 and 3, the fruit shape diverges to state 81^2 in the next closest sister species (2: in MAR and in PIL; 3: in JAM). However, fruit shape reverses to 81^0 without a concomitant change in endocarp shape in two species while the sister species retains both apomorphs (4: in CAM, but not SAV; 5: in AUB, but not SIM + TEN). By knowing these sister-group relationships, one can make two-way comparisons of differences within sister groups and among dependent vs. independent classes (i.e., cases 1–3 vs. 4–5) to answer the following questions: What are the common and dissimilar features of fruit and endocarp development? How do fruit and endocarp ontogenies become decoupled? Are there any features in the ontogenies to suggest that the individual characters are not homologous among cases? What ecological parameters are similar or dissimilar among cases? Can the reproductive success of each species in its respective environment be related to its particular combination of states of these two characters? Because there are more than one case per class, congruent developmental or ecological patterns would strengthen one's conclusions.

Sequential evolution. The cladistic analysis reveals a striking case of sequential evolution of structures that are associated with derived morphologies. For example, if one thinks of *Pyrenoglyphis* as a specialized, distinct genus or subgenus, then there is the tendency also to think of its derived fruit type as a unique character complex in which the constituent characters evolved together in a correlated way only in this group. However, this is clearly not the case (FIGURES 3, 6). The characters of the group evolved stepwise in a series of ancestors leading up to PYRE. That is, increasingly closer sister groups retain increasing numbers of the "pyrenoglyphis"-like characters. Thus, the series of ancestors of PYRE are not expected to show all the basic PYRE characters, just as the fossil (and perhaps ancestral) angiosperms that paleobotanists hope to find need not possess all of the specializations of modern angiosperms (Doyle & Donoghue, 1986).

Character trends and reliable characters. Many vegetative characters are so highly plastic or inconsistent as to be unsuitable for cladistic analysis (APPENDIX 3). However, certain ones were completely or nearly consistent. In particular, the loss of the ocreae in the adult leaves, strongly unequally bidentate leaflets, and three-ranked petiolar spines defines the NON-OCREATE CLADE; the slightly broadened spines pervade the ATROPURPUREOUS CLADE; and the equally bidentate leaflets define the BIDENTATE CLADE (FIGURES 3, 7, TABLE 3). Other characters, e.g., fascicled spines, extremely broadened and flattened spines, and pale-colored spines, are useful in restricted groups but are homoplasious over the whole genus. Of special concern is Burret's character of massive stems (1^2). Even though outgroup comparison fails to polarize it, parsimony analysis suggests that it is plesiomorphic relative to both moderately thick and arundinaceous stems and that these latter two evolved in parallel in *Bactris* and *Desmoncus.*

Among general inflorescence features, the most important sources of characters are size differences and relative lengths and numbers of rachillae. Armature and indument of the inflorescence are often too variable to be used. Burret distinguished subg. *Amylocarpus* by the rachillae with contiguous triads; AMYL by rachillae 1 to 8, a few cm long, and with triads nearly to the distal end; and PIRA by rachillae 20 to 100, of normal length, and with triads only in the proximal half. These inflorescence characters do help to delimit AMYL and PIRA as monophyletic groups but are only partially reliable in cladistic terms. That is, the trend toward spicate inflorescences and contiguous triads is accomplished in various ways in several lineages, occurring in at least the NONFIBROUS, EXSERTED-ANTHER, TUBIFLOROUS, and PYRE CLADES. The *B. tomentosa* complex (APPENDIX I), if distinct from the TUBIFLOROUS CLADE, represents another parallel occurrence of the trend. Thus, Burret weighted these too heavily and relied on them to form major groups while excluding other more reliable characters.

The staminate flowers are extremely ephemeral in most species of *Bactris.* Because they were not available on many of the specimens that Burret studied, he did not use them in his classification. However, parsimony analysis suggests that they are important and that the ancestral staminate flower can be characterized as follows: as long as or longer than the pistillate; calyx lobes triangular; petals shortly connate, erect, and rhombic; stamens six, emerged around the margin of the receptable and possibly slightly adnate to the petals; and filaments flexuously folded in bud, thread-like, holding the ovate-oblong anthers within the corolla during and after anthesis. A few character changes are unique (e.g., the NON-OCREATE CLADE with rounded cucullate petals; the EXSERTED-ANTHER CLADE with anthers exserted between the petals; and CNC with completely connate, membranous petals and 12 stamens). Other changes (e.g., flower length, calyx lobe shape, stamen position and adnation, filament structure, and anther shape) are moderately homoplasious but appear to facilitate the delimiting of some major and many minor clades. The remaining characters (calyx lobe posture, moderate petal connation, and receptacle shape and adnation) are cladistically unreliable, but they may assist in defining species or minor clades in future studies.

Likewise, pistillate floral characters (other than the staminodial ring, which can be seen in fruit) played little part in Burret's scheme. The results here suggest that the ancestral pistillate flower had a cupulate, cuspidate calyx, and a shortly urceolate, cuspidate corolla that internally was beset with 6 triangular basally adnate staminodes. Most of the changes observed are unreliable for cladistic analysis except at the lowest levels. As noted above, this may be due in part to difficulty of interpreting the characters drawn from rehydrated material. Observations of pickled immature flowers suggest that some characters, such as the connation of style branches, may be under rather lax developmental controls. Certain of the characters (calyx lobing, calyx and corolla truncation, corolla indument), though homoplasious, may help to define major and minor clades. Curiously, the presence of triangular staminodes is extremely plastic in *Bactris,* varying intraspecifically, as well as among flowers of a single plant. This extreme plasticity was probably the case in ancestral species. However, the mutation for connate, truncate staminodes (the staminodial ring) became fixed in the ancestor of PYRE, the plasticity was lost, and the character became completely stable.

Fruits provide the most reliable characters at the genus level and are important in defining major clades and major evolutionary trends in the genus (FIGURE 6); why Burret did not profit from more of these characters is unknown. The results show that the ancestral type can be characterized as: elongate with a red, orange, or yellowish epicarp; mesocarp thinly starchy; and endocarp pale, covered with blackish, flattened adnate fibers that radiate and anastomose, with three germination pores latitudinally equidistant but longitudinally offset (sterile pair proximal to fertile one). In the BALANOPHORA CLADE, the endocarp became dilated proximally. In the ancestor to the remainder of the *Bactris,* the endocarp became oblate (fruit turbinate) with the pores not offset. In the ancestor of the clade LATIBRACTEATE + TUBERCULATE, the endocarp became blackened and the fibers became completely free and terete. Somewhat in parallel, the antillean species within the NON-OCREATE CLADE developed a darkened endocarp and partially free/terete endocarp fibers. It is not clear whether the tubercles evolved *de novo* in the ancestor of the TUBERCULATE CLADE with the LATIBRACTEATE CLADE having retained the previous condition, as suggested by the results. If char. 97 (presence and form of the tubercles) had been coded as a modification of 96^1 (fibers proximally flattened and adnate, distally terete and free) rather than a modification of 96^2 (fibers completely terete and free), then the tubercles would have arisen in the ancestor of both clades and subsequently would have been lost in the ancestor of the LATIBRACTEATE CLADE.

A further change within the LATIBRACTEATE CLADE is the complete loss of the endocarp fibers from the NONFIBROUS CLADE. Perhaps developmentally correlated with the small stature of AMYL is the reduction in fruit size, a character used by Burret.

In the ancestor of the TUBERCULATE CLADE, the two sterile germination pores became longitudinally distant from the fertile one. This is very pronounced in some lineages, e.g., the BIDENTATE CLADE. In the ancestor of the clade ATROPURPUREOUS + CNS + TRC, the mesocarp changed from starchy to the form of cellular juice-containing sacs attached to the endocarp fibers. In the ancestor of the clade ATROPURPUREOUS + CNS, the endocarp fibers became very fine and numerous, and the tubercles became reduced to papillae. In the ancestor of PYRE, the endocarp pores once again became latitudinally offset. Within this clade, there has been a marked apomorphic trend toward elongation and attenuation of the endocarp and whole fruit.

The cladistic results suggest a history of epicarp color that was not previously realized. Most species have either a dark purplish black fruit (presumably anthocyanin-based) or one that is orange-red to yellow (presumably carotene-based). Of the two, the latter is clearly plesiomorphous. TRC is unique in having a stramineous-yellow epicarp covered with ferruginous trichomes. At the outset of this analysis, this coloration was considered an odd modification of the plesiomorph in which it was included. CNS is also unique in having an epicarp that early in development becomes fissured into numerous aciculate corky projections. Soon after anthesis, the epicarp is a light green, then flesh colored, then gradually matures to a rich rosy purple. Because Burret included CNS in PIRA (APPENDIX II, char. 40), its coloration was coded as a unique character distinct from that found in the atropurpureous taxa. Rather surprisingly, the results show that atropurpureous epicarps evolved only once. Moreover, TRC and CNS are successive sister groups to the ATROPURPUREOUS CLADE; i.e., they are intermediate and form a bridge to the orange-colored ancestors. Thus, the stramineous, rose-purple, and purple-black epicarps may form a single transition series that clarifies the evolutionary development of the purple-black epicarps (FIGURE 6).

Because most fruit characters are cladistically reliable, future studies and classifications must rely on them. Especially useful would be developmental analyses to better determine the homologies of the tubercles at the bases of the endocarp fibers and of the allometric growth of the endocarp and epicarp.

CONCLUSIONS

Because the above characters are likely to be significant in future classifications, collectors should take special care to gather material that shows these characters. In addition to following the standard techniques for collecting palms (Dransfield, 1986), they should attempt to obtain the following: 1) immature, unopened inflorescences (as well as whole opened ones) that may be taken by shaving the subtending sheath away opposite the stem from the inflorescence, pulling away the whole leaf and leaf base, and wedging under the inflorescence until it snaps off at the point of attachment; 2) mature fruits, nearly mature fruits, or (if these are not available) old endocarps from the ground; 3) the leaf spear to show the young ocrea or at least a petiole showing the ocrea scar; and 4) a section of stem lacking sheaths.

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. However, because homoplasy in these characters is less pronounced in smaller, more homogeneous clades (FIGURE 2), they should not be discarded without more detailed numerical and developmental analyses at lower hierarchical levels where they may show absolute gaps or may be reinterpreted as distinct characters.

Given that Burret's classification should be abandoned, what should replace it? For several reasons, I believe it is premature to provide a new formal taxonomy based on the present cladistic analysis. First, the cladistic sampling is still incomplete, and the positions of several clades at the sectional, subsectional, and lower levels remain unresolved. Second, the limits of constituent species will remain uncertain until intraspecific variation is evaluated, such that discontinuities can be the basis of species limits and synonymy. Third, to lend support to clades based on homoplasious synapomorphies, explorations for novel characters and developmental studies of known characters are needed. For example, Tomlinson (1961) noted a number of interesting vegetative anatomical characters in *Bactris,* such as the distribution of fiber bundles in the leaf lamina, that deserve attention in future monographic or cladistic work. Fourth, current ecological, floristic, or agronomic articles rarely need to refer to an infrageneric classification. Thus, a new internal classification should be based on future monographic and cladistic studies.

However, several of the clades in TABLE 3 do have available names at the hierarchical level that I have suggested. If one is compelled to use infrageneric names, the earliest of these available names may be used for these clades in compliance with the International Code of Botanical Nomenclature (Greuter, 1988): NON-OCREATE CLADE = Subg. *Guilielma* (Mart.) Drude (type: *B. speciosa* (Mart.) Karst. = *B. gasipaes*); LATIBRACTEATE CLADE = Subg. *Trichobactris* Oerst. (type: *B. glandulosa*); NONFIBROUS CLADE = Sect. *Isochlamys* Spruce (type here designated: *B. negrensis* Spruce = *B. simplicifrons*); AMYL = Subsect. *Isochlamys* (Spruce) Burret; EXSERTED-ANTHER CLADE = Sect. *Macrophyllum* Drude (type here designated: *B. acanthocarpa*); TUBERCULATE CLADE = Subg. *Bactris* (type: *B. minor Jacq.* ≡ *B. guineensis*); ATROPURPUREOUS CLADE = Sect. *Bactris.*

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Appendix I. Representativeness of Taxa Sampled

Below are listed all the species referable to *Bactris* s.l. that are known to me. Specimens of the data sample (Table 2) were identified as elements of the species in boldface (OTU's, Table 1); the species in italics had no specimens identified with them, and hence, were not sampled. To confirm that the unsampled species are not the sole members of any subgeneric or sectional level clades that would have been discovered by the cladistic analysis, the unsampled species were associated with the OTU's in two ways. 1) All species were phenetically grouped into informal species complexes based on a perusal of the protologues, published plates of types (Dahlgren, 1959) and comments by Burret (1933–1934), Wessels Boer (1965), Croat (1978), Galeano and Bernal (1987), and De Nevers (1988). 2) The protologues of the unsampled species were searched for apomorphies, which were compared to the apomorphies of the OTU's to check the phenetic associations. There is a growing consensus among recent workers that some of these complexes are really only polymorphic species that comprise numerous synonyms.

On the other hand, this provisional assignment of species does *not* imply monophyly of the complexes. Rather, the complexes were associated with the clades (presented hierarchically as in Table 3) by the shared occurrence of OTU's. Complexes lacking OTU's were associated with known clades by appropriate apomorphies drawn from the literature. These apomorphies are indicated below, as are additional characters that help distinguish the unsampled complexes. Character notations are as in Table 3.

BALANOPHORA CLADE

1. balanophora complex: **B. balanophora.**

NON-OCREATE CLADE

ANTILLEAN CLADE

2. plumeriana complex: *B. cubensis* Burret, **B. jamaicana**, **B. plumeriana.**

GUILIELMA CLADE

3. gasipaes complex: *B. caribea* Karst., *B. ciliata* (R.&P.) Mart., **B. dahlgreniana** (≡*Guilielma microcarpa* Huber, non *B. microcarpa* Spruce), **B. gasipaes**, *B. insignis* (Mart.) Baill., **B. macana**, *B. speciosa* (Mart.) Karst., *B. utilis* (Oerst.) Hemsl.

LATIBRACTEATE CLADE

NONFIBROUS CLADE

4. ptariana complex: *B. ptariana* Steyerm.—no OTU, near base of clade (apomorphies 26, 45, 63, 96^3, 99; distinct in having 15^{0*} and 10).
5. coloradonis complex: **B. coloradonis**, *B. dianueura* Burret, **B. porschiana.**
6. hondurensis complex: **B. hondurensis**, *B. paula* L. H. Bailey, *B. pubescens* Burret, *B. standleyana* Burret, *B. wendlandiana* Burret.
7. chaetospatha complex: *B. armata* Barb. Rod., *B. chaetospatha* Mart.—no OTU, apparently on clade HON + AMYL; very similar to HON, but pistillate calyx urceolate (62) and longer than corolla.

AMYLOCARPUS CLADE

8. floccosa complex: *B. floccosa* Spruce—no OTU, near base of AMYL (plesiom. 36^0, 68^0, 71^0, 72^0; apom. 19, 21, 33, 40^{0*}, 42, 63; leaf segments several, sigmoid).
9. aubletiana complex: **B. aubletiana**, *B. kuhlmannii* Burret.
10. simplicifrons complex: *B. acanthocnemis* Mart., *B. amoena* Burret, **B. arenaria**, *B. brevifolia* Spruce, *B. carolinensis* Spruce, *B. dakamana* (L. H. Bailey) Glassman, *B. essequiboensis* (L. H. Bailey) Glassman, *B. gleasonii* (L. H. Bailey) Glassman, *B. huberiana* Burret (≡*Amylocarpus angustifolius* Huber), *B. inermis* Trail, *B. killipii* Burret, **B. leutzelburgii**, *B. maguirei* (L. H. Bailey) Steyerm., *B. microspatha* Barb. Rod., *B. paucisecta* Burret, *B. schultesii* (L. H. Bailey) Glassman, *B. simplex* Burret, **B. simplicifrons**, *B. soropanae* Steyerm., *B. stahelii* (L. H. Bailey) Glassman, **B. tenuis**, *B. tenuissimus* Barb. Rod., **B. trinitensis**, *B. uaupensis* (Trail) Spruce, *B. ulei* Burret, *B. xanthocarpa* Barb. Rod.
11. hirta complex: *B. atrox* Burret, *B. ericetina* Barb. Rod., **B. geonomoides**, **B. hirta**, *B. hoppii* Burret, *B. huebneri* Burret, *B. integrifolia* Wallace, *B. mollis* Dammer, *B. pulchra* Drude.
12. pectinata complex: *B. formosa* Barb. Rod., *B. hylophila* Spruce, *B. lakoi* Burret, *B. leptochaeta* Burret, *B. multiramosa* Burret, *B. microcarpa* Spruce, **B. pectinata**, *B. setipinnata* Barb. Rod., *B. syagroides* Barb. Rod. & Trail,

B. turbinata, *B. unaensis* Barb. Rod.; perhaps included in the hirta complex.

13. mitis complex: *B. cuspidata* Mart., *B. mitis* Mart.—no OTU, near clade GEO + HIR + PEC + TUR (apom. 19, 33, 35^{0}*, 40^{0}*, 42, 63; leaf segments few, wide, sigmoid).

EXSERTED-ANTHER CLADE

14. mexicana complex: *B. acuminata* Liebm., *B. aureodrupa* L. H. Bailey, *B. dasychaeta* Burret, *B. gracilior* Burret, **B. mexicana**, *B. trichophylla* Burret.
15. oligoclada complex: *B. oligoclada* Burret—no OTU, on clade PIRA + MEX (apom. 60, 61).

PIRANGA CLADE

16. acanthocarpa complex: **B. acanthocarpa**, **B. acanthocarpoides**, *B. aculeifera* Drude, **B. barronis**, *B. bradei* Burret, *B. devia* H. E. Moore, *B. exscapa* (Barb. Rod.) Barb. Rod., *B. fragae* Lindm., **B. humilis**, *B. interrupte-pinnata* Barb. Rod., *B. macrocalyx* Burret, *B. microcalyx* Burret, *B. mindellii* Barb. Rod., *B. pinnatisecta* Burret, **B. rhaphidacantha**, *B. tarumanensis* Barb. Rod.
17. cuesco complex: *B. cuesco* Engel, *B. trailiana* Barb. Rod.—no OTU; separated from acanthocarpa complex by simple leaves only. According to A. J. Henderson (pers. comm.), in the acanthocarpa complex leaves vary intrapopulationally from pinnate to simple.
18. glandulosa complex: **B. alleniana**, **B. glandulosa** (≡*B. bifida* Oerst.), *B. macrotricha* Burret, *B. oerstediana* Trail.

CAMPESTRIS CLADE

19. campestris complex: **B. campestris**, *B. lanceolata* Burret, *B. leptocarpa* ImThurn, **B. savannarum**.

CAUDATA CLADE

20. caudata complex: **B. caudata**.

TUBERCULATE CLADE

MILITARIS CLADE

21. militaris complex: **B. militaris**.

SETULOSA CLADE

22. setulosa complex: *B. circularis* L. H. Bailey, **B. cuesa**, *B. cuvaro* Karst., **B. setulosa**, *B. sworderiana* Becc.

COROSSILLA CLADE

21. corossilla complex: **B. corossilla**, **B. duplex**.
24. riparia complex: *B. coccinea* Barb. Rod. (≡ *Guilielma mattogrossensis* Barb. Rod., non *B. mattogrossensis* Barb. Rod), *B. ferruginea* Burret, *B. inundata* Mart., *B. riparia* Mart.—no OTU, near COROSSILLA or SETULOSA CLADE (apom. 97; but epicarps orange because lacks 88).

TURBINOCARPA CLADE

25. turbinocarpa complex: **B. turbinocarpa**.

CONSTANCIAE CLADE

26. constanciae complex: **B. constanciae**.

ATROPURPUREOUS CLADE

BIDENTATE CLADE

27. setosa complex: *B. cuyabaensis* Barb. Rod., *B. escragnollei* Burret, *B. lindmaniana* Lindm., **B. setosa**.
28. chloracantha complex: *B. chloracantha* Mart.—no OTU, near SET (plesiom. 62^{0}, 63^{0}; apom. 6, 15^{0}*, 24, 88; but lacks 81^{2}).
29. piritu complex: *B. piritu* (Karst.) H. Wendl. (=*Guilielma piritu* Karst.)—no OTU, near SET (apom. 15^{0}*, 81^{2}, 88, 93, 97^{2}).
30. guineensis complex: *B. anisitsii* Barb. Rod., *B. bidentula* Spruce, *B. glaucescens* Drude, **B. guineensis** (≡*B. minor* Jacq.), *B. horrida* Oerst., *B. nigrispina* Barb. Rod., **B. oraria**, *B. palustris* Barb. Rod., *B. polyclada* Burret, *B. rotunda* Stokes, *B. tucum* Burret.
31. caryotifolia complex: **B. caryotifolia**.

LONG-PROPHYLL CLADE

32. fusca complex: *B. fusca* Oerst., **B. longiseta**.
33. coloniata complex: **B. coloniata**.
34. vulgaris complex: *B. glazioviana* Drude, *B. vulgaris* Barb. Rod.—no OTU's, near LONG-PROPHYLL CLADE (plesiom. 2^{0}, $3^{0 \text{ or } 1}$, 6^{0}, 62^{0}; apom. 63, 81, 88, 93, 97^{2}; distinguished by 25, 27).
35. longifrons complex: *B. littoralis* Barb. Rod., *B. longifrons* Mart., *B. maraya-acu* Barb. Rod.—no OTU's, near LONG-PROPHYLL CLADE (as in vulgaris complex but with 27^{0} and 81^{2}).
36. granatensis complex: *B. granatensis* (Karst.) H. Wendl. (=*Guilielma granatensis* Karst.)—no OTU, near LONG-PROPHYLL CLADE (plesiom. $3^{0 \text{ or } 1}$, 62^{0}, 63^{0}, 73^{0} [as 6 distinct acuminate staminodial teeth]; apom. 6, 88, 93).

TUBIFLOROUS CLADE

37. monticola complex: **B. actinoneura**, *B. chaetochlamys* Burret, **B. diviscupula**, *B. elatior* Wallace?, *B. erostrata* Burret, *B. fuscospina* L. H. Bailey, *B. granariuscarpa* Barb. Rod., *B. gymnospatha* Burret, *B. kamarupa* Steyerm., *B. leptospadix* Burret, *B. leptotricha* Burret, *B. longicuspis* Burret, *B. longisecta* Burret, *B. macrocarpa* Wallace?, *B. microspadix* Burret, **B. monticola**, *B. paucijuga* Barb. Rod., *B. penicillata* Barb. Rod., *B. platyacantha* Burret, *B. sanctae-paulae* Engel?, **B. sigmoidea**, *B. sylvatica* Barb. Rod., *B. trichospatha* Trail, *B. umbraticola* Barb. Rod., *B. umbrosa* Barb. Rod., *B. vexans* Burret.
38. elegans complex: **B. elegans**, *B. elegantissima* Burret.
39. tomentosa complex: *B. capillacea* Drude, *B. pickelii* Burret, *B. tomentosa* Mart.—no OTU's, near LONG-PROPHYLL or TUBIFLOROUS CLADE (pleisom. 62^{0}; apom. 3, 6, 27, 71, 88, 93, 97^{2}; distinquished by 28, 29, 32, 33, 43^{3}, leaf-segments in 3 to 12 sigmoid pairs).
40. eumorpha complex: *B. arundinacea* (Trail) Burret, *B. bella* Burret, *B. bijugata* Burret, *B. capinensis* Huber, *B. chlorocarpa* Burret, *B.*

eumorpha Trail, *B. incommoda* Trail, *B. juruensis* Trail, *B. piranga* Trail, *B. pulchella* Burret—no OTU's, possibly included in the tomentosa complex but differs in having only 3 to 4 pairs of leaf segments, $6^{0\text{ or }1}$, $29^{0\text{ or }1}$, possibly 81^2.

41. sphaerocarpa complex: *B. angustifolia* Dammer, *B. longipes* Poeppig? (fruits described as dark purple, but Burret [1933–1934] placed it near *B. hirta*), *B. sphaerocarpa* Trail—no OTU, possibly included in the tomentosa complex but differs in having leaves bifid or with 2 pairs of segments, 6^0, 71^0, and possibly 81^2.
42. megistocarpa complex: *B. megistocarpa* Burret—no OTU, near TUBIFLOROUS CLADE (plesiom. 74^0, 81^0; apom. 27, 62, 88; leaf segments numerous, linear).
43. fissifrons complex: *B. fissifrons* Mart.—no OTU, near TUBIFLOROUS CLADE (plesiom. 71^0, 74^0; apom. 27–29, 62, 66; leaf segments few, sigmoid).

PILOSA CLADE

44. pilosa complex: *B. hirsuta* Burret, **B. pilosa**, *B. setiflora* Burret.
45. macroacantha complex: *B. acanthospatha* Drude, *B. confluens* Lind. & H. Wendl., *B. macroacantha* Mart.—no OTU's, near PILOSA or TUBIFLOROUS CLADE (plesiom. $3^{0\text{ or }1}$; apom. 6, 27, 62, 69, 71, 81, 88; rachillae hirsute).

PYRENOGLYPHIS CLADE

46. maraja complex: *B. brongnartii* Mart., *B. burretii* Glassman (≡*Pyrenoglyphis microcarpa* Burret non *B. microcarpa* Spruce), *B. leucantha* Lindm. & H. Wendl., **B. maraja**, *B. pallidispina* Mart., *B. piscatorum* Drude, *B. rivularis* Barb. Rod., *B. strictacantha* Burret, *B. tenera* (Karst.) H. Wendl. (=*Guilielma tenera* Karst.).
47. cruegeriana complex: **B. cruegeriana**, *B. megalocarpa* ImThurn.
48. ottostapfeana complex: **B. ottostapfeana**.
49. major complex: *B. albonotata* L. H. Bailey, **B. augustinea**, **B. balanoidea**, *B. beata* L. H. Bailey, *B. broadwayi* L. H. Bailey, *B. cateri* L. H. Bailey, *B. chaetorhachis* Mart., *B. chapadensis* Barb. Rod., *B. demerarana* L. H. Bailey, *B. ellipsoidalis* L. H. Bailey, *B. infesta* Mart., **B. major**, *B. mattogrossensis* Barb. Rod. (non *Guilielma mattogrossensis* Barb. Rod.), *B. minax* Miq., *B. obovoidea* L. H. Bailey, *B. ovata* Oerst., *B. planifolia* L. H. Bailey, *B. socialis* Mart., **B. superior**, *B. swabeyi* L. H. Bailey.
50. bicuspidata complex: *B. bicuspidata* Spruce, *B. curuena* Drude, *B. exaltata* Barb. Rod., **B. gaviona**, *B. pyrenoglyphoides* A. D. Hawkes (≡*Pyrenoglyphis hoppii* Burret), *B. nemorosa* Barb. Rod.
51. concinna complex: **B. concinna**.
52. bifida complex: **B. bifida**.
53. oligocarpa complex: *B. aristata* Mart.?, **B. gastoniana**, **B. oligocarpa**.

NAMES KNOWN FROM INADEQUATE MATERIAL (unlikely to represent a major, unrecognized clade):

B. baculifera Karw., *B. baileyana* H. E. Moore, *B. bergantina* Steyerm., *B. duidae* Steyerm., *B. falcata* J. R. Johnston, *B. faucium* Mart., *B. gracilis* Barb. Rod., *B. kalbreyeri* Burret, *B. platyspina* (Barb. Rod.) Burret, *B. venezuelensis* Steyerm.

APPENDIX II. CHARACTERS USED

Unless a character is indicated as being unordered, it is ordered, with 0 as the presumed ancestral state. As advocated by Pimentel and Riggins (1987), multistate characters, within which the transition of the states is evident, are coded in two ways. A linear series, in which one is the apomorphic precursor state to the one following, is coded as a simple multistate ordered character with the states indicated by sequential integers. A branched (i.e., partially ordered character) series, in which two states or two linear series of states had independent origins, is coded as a complex of two or more binary or ordered multistate variables. Characters 35 and 36, in which the transition of the states is unclear, were coded as a complex of additive binary variables (following Doyle & Donoghue, 1986). That is, it was unknown whether state 00 or 10 was the precursor state of a third state, which was coded as X1. Weights, as determined from C values in an initial analysis, are given in square brackets. C values obtained from the composite cladogram (FIGURE 3) are given in curved brackets.

STEM DIAMETER

1. 0 = usually <13 mm; 1 = 15–60 mm; 2 = usually >60 mm: unordered. [5] {0.33}

The states are not absolutely discrete, the character exhibits homoplasy, and systematic value may be compromised. However, the nondiscreteness may be variation induced by environmental stress.

The character could not be polarized because *Astrocaryum* possesses state 2 and *Desmoncus* is variable, having both states 0 and 1.

ARCHITECTURE AND COLOR OF GENERAL ARMATURE (spines of stem, leaf bases, petioles, leaf rachises, and peduncular bracts; excluding weak prickles or seta-like spinules, especially on softer tissues)

2. 0 = cross-section terete, elliptic, triangular, or oblong; 1 = linear (i.e., spine strongly flattened). [3] {0.33}

The states appear to be discrete. Some species of *Astrocaryum* have state 1, but this is considered a parallel derivation within the outgroup.

3. 0 = in longitudinal shape, tapering from base to apex; 1 = slightly broadened near middle; 2 = strongly broadened near middle. [2] {0.22}

Generally, strongly broadened spines are also strongly flattened, and undoubtedly the correlation is partially constrained developmentally. However, there is an incomplete correlation, as tapering spines may be either nearly terete or strongly flattened. Thus, characters 2 and 3 were maintained to study the degree to which they might be uncoupled.

State 2 is distinctive; the spines are many times wider in the middle than at the base. State 1 is easily overlooked on specimens because the distinction between it and state 0 is subtle (middle of shaft only about twice the width of its base).

4. 0 = pulvinus stramineous to white; 1 = black to gray or dark to medium brown. [1] {0.17}

Spines are radially spread or eventually reflexed by the swelling of a pulvinus, a mound of tissue in the axil of each. Hence, on immature growth the spines are not yet spread and the pulvini are hidden. The normal condition is to have pale pulvini for the mature life of the organ. On aging organs of a few specimens, the pulvini may eventually darken, although some light-colored ones persist. Bailey (1947) may have failed to appreciate the processes of pulvinus exposure and age-dependent color plasticity when he described different Trinidadian populations of *B. major* as eight new species, five "with spines white-bulbous at the base" and the others "with spines . . . not thickened and white at the base." It is important, therefore, that fully exposed pulvini are examined on mature, but not aging organs.

5–6. 00 = entire shaft of spine black or very dark brown to chestnut brown or gray; 10 = basal region of shaft (lower ⅕–⅓) stramineous; 01 = middle region stramineous; 11 = base and middle stramineous, though apex is usually dark. [5, 3] {1.00, 0.33}

These two characters are only partially correlated. Likewise, 6^1 is partially correlated with 3^2. Plants of CAM and SAV with gray spines are distinctive, but variation among organs and collections of these species verifies that gray spines intergrade into chestnut brown and nearly black ones. Species with state 11 are usually consistent for the stramineous color. *Bactris monticola* s.l. may be an exception. The species usually is characterized by state 11, but plants of *B. actinoneura,* which was placed in synonymy by Wessels Boer (1965), are characterized by state 00. Thus, these characters will require more careful analyses of variation in monographic studies.

Leaf base, petiole and leaf rachis

7. 0 = ocreae lacking; 1 = ocreae developed on all leaves; 2 = ocreae developed on juvenile leaves (of seedlings and sucker shoots) only. [10] {1.00}

An ocrea is a distal tubular extension of the leaf sheath above the point where the petiole diverges from the sheath. It is a synapomorphy of *Desmoncus* and *Bactris.* In *Desmoncus,* the ocreae are persistent, green and leaflike, and hence, are generally noticed and described in the literature. In *Bactris* they are ephemeral, membranous, and often shred into a fibrous mass; and they are rarely included in specimens of *Bactris.* Nevertheless, evidence of an ocrea (state 1) is available even on old leaves, if the correct portion of the petiole is included; the deteriorated ocrea leaves a scar (usually as an inverted "U" or "V") across the entire adaxial face of the petiole. Within single caespitose clumps of species of the NON-OCREATE CLADE can be found a few juvenile leaves with ocreae, fewer subadult leaves with partial ocreae, and numerous adult leaves lacking ocreae. Because ocreae are lacking from both adult and juvenile leaves in *Astrocaryum,* as well as *Aiphanes, Acrocomia,* and *Gastrococos,* absence in the adult leaf only (state 2) is interpreted as a derivation of state 1. Furthermore, herbarium specimens can be evaluated for state 2 because the sheath degrades to an auricle-like flap only on each margin (not a scar across the adaxial face) of the petiole of the adult leaves.

8. 0 = petiole firm or woody; 1 = ±hollow, crushable, and usually collapsing inward upon drying. [3] {0.25}

9–10. 00 = spines distributed ±evenly over the abaxial surface of the leaf base, petiole, or also leaf rachis; 10 = arranged in two marginal and one medial rank, which become especially discrete on the petiole and rachis; 01 = arranged in transverse lines or fascicles. [10, 3] {1.00, 0.25}

Among collections of GAS, some cultivated phenotypes have 9^1 modified either by having only two marginal ranks or by having only the medial rank.

Leaf-blade shape

11. 0 = slightly longer to 1.5 (averaging up to 1.4) times longer than rachis; 1 = at least 1.5 to several times longer. [5] {0.33}

The small amount of overlap in measurement of ranges was separated by means, midpoints and modes. Only the OTU TEN, which was scored as state 1, ranged from 1.45 to 1.55. It could be coded as unknown or as either state, but the topology of FIGURE 3 would not be changed. The character is partially correlated with bifid leaves, char. 13.

12. 0 = about 1–3 times longer than wide; 1 = about 4 or more times. [10] {0.50}

In the OTU's sampled, this was partially correlated with bifid leaves (char. 13); in the species with long bifid leaves, the veins diverge at a small angle and ascend rather than spreading outward as in the pinnatifid relatives.

13. 0 = pinnatifid; 1 = simple (i.e., bifid) or irregularly pinnatifid proximally with a large terminal bifid segment comprising at least the distal half of the blade. [5] {0.20}

The switch from pinnatifid to bifid may be developmentally and genetically simple. The apomorphic state across the whole genus is clearly homoplasious; it occurs in several diverse lineages and separates closely related species. Variability of the character within a species has been suggested for certain taxa (conspecific status of *B. hirta* and *B. pectinata* complexes, and of SIM and TEN; Wessels Boer, 1965; A. J. Henderson, pers. comm.; L. R. Noblick, pers. comm.). This variability is clearly documented for *B. duplex* (*Allen 3357,* BH). This needs much more careful attention in future monographic studies.

Leaf-blade indument

14. 0 = adaxial nerves glabrous; 1 = tomentose. [10] {1.00}

Taxa that are supposedly distinguished by the presence, density, and length of hairs on the nerves and laminar tissues were generally so variable that indument characters were useless cladistically. However, of these, this one character did appear to be consistent in distinguishing ELE. It may be useful in *a posteriori* placing the *B. tomentosa* complex near ELE.

STRUCTURE OF LEAF-SEGMENT APEX

15. 0 = midrib (primary vein) of segment bisects the distal portion of the segment into two equal or unequal teeth, and it either terminates subapically (*Astrocaryum* and *Bactris*) or extends to very tip (*Desmoncus*), not forming margin of either side of segment; 1 = midrib continues as inner margin of the longer side of the segment, usually terminating apically (thus, apex is oblique). [3] {0.50}

In state 1, one side of the segment is always shorter and decurrent onto the midrib. Either the outer margin of the longer side is decurrent onto an awnlike extension of the midrib or together the midrib and the longer side terminate in an acute point. Sometimes in state 1, the shorter side of the segment may pull away from the midrib, forming two unequal teeth; but the midrib still can be seen forming the inner margin of the longer side. In state 0, neither side of the segment is decurrent onto the midrib, and each usually forms a tooth. If one tooth is much longer, the condition may superficially resemble the apomorphy. I never observed any taxon with an intermediate condition.

The occurrences of state 0 in *Astrocaryum* and *Bactris* probably are not homologous. Furthermore, the conditions of state 0 (equal teeth in the BIDENTATE CLADE and very unequal teeth in the NON-OCREATE CLADE; FIGURE 7, TABLE 3) might be coded better as two separate modifications of state 1.

16. 0 = narrowed and entire or bidentate; 1 = broadened and praemorse. [10] {1.00} (See FIGURE 7.)

PROPHYLL

17. 0 = ½ or less as long as peduncular bract; 1 = ⅗ to nearly as long as peduncular bract. [3] {0.33}

PEDUNCULAR BRACT

18. 0 = 5–15 times longer than wide; 1 = >25 times longer than wide. [10] {1.00}

19. 0 = apex abruptly constricted and distally prolonged into a beak; 1 = ±acute and not prolonged into a beak [10] {1.00}

20. 0 = abaxial indument only scurfy, tomentose, lanate, or mixture thereof; 1 = predominantly lepidote or lepidote-setose. [10] {0}

State 1 is unique in *B. actinoneura* and *B. monticola* s. st. When these are combined with *B. diviscupula* and *B. sigmoidea,* the OTU MON becomes variable and is coded as "?". Thus, PAUP calculated the character as invariant.

21–22. 00 = armature moderately densely composed of spines and spinules; 10 = lacking; 01 = very densely composed of soft, flexible setiform spinules. [10, 3] {1.00, 0.33}

23. 0 = base and middle of shaft of spines/spinules black or dark brown (or lacking); 1 = light gray or stramineous. [2] {0.17}

This is only partially correlated with char. 6^1, as it occurs in several OTU's lacking that character state.

INFLORESCENCE AXIS

24. 0 = peduncle armed with spines or stout spinules; 1 = unarmed or with a few weak spinules. [3] {0.17}

The states are usually clear cut. A few species (HON, MON, and SET) are variable, having the intermediate condition in some collections.

25. 0 = rachis with well developed internodes, about ⅙ or more of the length of the peduncle; 1 = rachis abbreviated with poorly developed internodes; less than ⅐ of the length of the peduncle. [3] {0.25}

26. 0 = shape of rachis bracts (especially proximal ones) deltate, ovate, lanceolate, or oblong, with sides tapering to apical termination of nerve; 1 = tranversely oblong, terminal nerve may extend as mucronate, cuspidate, subulate, or caudate tip, but is weak and ephemeral; 2 = transversely linear (i.e., annulate flap subtending rachis branch), terminal vein usually extending only as a mucro or weak awn. [3] {0.33}

RACHILLAE

27–31. 00000 = numbering about 15 to 40; 10000 = about 5 to 15; 11000 = 3 to 5; 11100 = 1 or 2; 00010 = about 40 to 80; 00011 = about 100 or more. [3, 5, 10, 2, 10] {0.13, 0.33, 0.50, 0.33, 1.00}

In the context of the whole genus, the states are not sharply delineated and there is marked homoplasy. However, the discontinuities are clearer among closely related taxa. Scoring was complicated in some species by wide variation. For instance, *B. simplicifrons* s. str. has a single rachilla, but broadly delimited it has 1 to 4 rachillae. It was scored as state 11000, the more plesiomorphous of the two possibilities, on the assumption that this is the ancestral condition.

32. 0 = at anthesis, longer than 6 cm; 1 = 2–6 cm. [10] {0.50}

33–34. 00 = at anthesis, firm, either straight, curved, or flexuous; 10 = rigidly straight; 01 = filamentous and weak. [10, 10] {0.50, 1.00}

Rachilla diameter could not be used as an index of these characters; that is, diameter is only imperfectly correlated with them. The entire range of diameters in *Bactris* is only from about 0.3 to 3.0 mm, and there is often overlap in diameters between states 00 and 01.

35–36. 00 = glabrous, lepidote, or lepidote-mealy; 10 = scurfy or tomentose by means of bulbous or moniliform hairs; X1 = densely, thickly lanate by means of curly, slender hairs. [2, 5] {0.50, 0.50}

37–38. 00 = surface tuberculate or aciculate; 10 = lacunose; 01 = alveolate (with a thin, raised reticulum). [10, 10] {1.00, 0.50}

Typically, the rachilla in *Bactris* is somewhat grooved and ridged between intervening nodes because vascular and fiber bundles make up most of the internal structure. The pedicel scars and remnants are usually elevated and sometimes prolonged. The rachilla bracts are sometimes persistent, indurate and sharp. The whole appearance is one of an irregular and somewhat spirally twisted arrangement of alternating grooves and points along the length of the rachilla.

Both apomorphies appear to be independent responses to having pistillate flowers on adjacent nodes. Lacunose rachillae (state 10) are more cylindric than tuberculate ones (state 00) and do not reveal the underlying vascular traces as clearly. Each flower is actually impressed into a lacuna or depression of the rachilla, which is reminiscent of the structure of the (staminate) spikelet rachis in *Tripsacum* L. and related grasses. Unlike the tuberculate rachillae, the alveolate ones (state 01) have the grooves limited to the length of the insertion of the pistillate flowers, and the tissue between (part axis and part remnants of rachilla bracts) is raised into thin ridges; thus, a regular geometric pattern is formed.

39. 0 = phyllotactic spiral symmetrical; 1 = spiral asymmetric and nodes laterally offset from adaxial midline (or symmetrical if whole inflorescence is reduced to a single thickened spike). [10] {constant within *Bactris,* for which it is a synapomorphy}

ARRANGEMENT OF TRIADS (reduced cincinnus of two lateral staminate and one central pistillate flower)

40. 0 = on contiguous nodes; 1 = sometimes one or two diads/monads of staminate flowers separating triads, many of which are on contiguous nodes; 2 = nearly always separated by few to several nodes of diads/monads. [4] {0.40}

This was initially coded as binary for two states (0 and 2). However, several taxa in PIRA that were reported in the literature to possess state 0 actually had a few scattered diads/monads among the triads, and the character was divided into three states. It is not clear whether state 1 preceded state 2 in the evolution of the ancestor of *Bactris* or whether state 1 is simply a modification of state 2 in the ancestor of PIRA. State 0 (contiguous nodes) in *Bactris* was coded the same as contiguous nodes in the outgroups to see if parsimony analysis would suggest that AMYL and PIRA are primitive in *Bactris.* However, the analysis confirmed the opposite. Therefore, developmental studies would be useful to evaluate the homology among *Bactris, Desmoncus,* and *Astrocaryum.*

In positioning CNS in PIRA, Burret (1933–1934) implies that the species is characterized by state 0, a report that was repeated by Wessels Boer (1965). However, the material of CNS available clearly possessed state 2.

41. 0 = lacking nodes of diads/monads of staminate flowers proximal to nodes of triads; 1 = nodes bearing diads/monads proximal to triads. [5] {1.00}

Although this is partially correlated with char. 40, it was recognized to help distinguish PIRA from AMYL, in which state 1 is lacking. Developmental studies are needed to redefine these two interrelated characters.

42. 0 = triads only in the proximal ⅔ or less of rachilla length; 1 = extending the full length of the rachilla or nearly so. [10] {1.00}

43. 0 = on rachilla, triads distichous or helically subdistichous, distal diads/monads the same, or several ranked; 1 = triads and (when present) diads/monads 3 to 5 ranked; 2 = triads 3 to 5 ranked but diads/monads about 5 to 7 ranked; 3 = triads and diads/monads about 7 to 15 ranked. [10] {1.00}

STAMINATE FLOWERS—GENERAL STRUCTURE AND PERIANTH

44. 0 = staminate flowers longer than pistillate; 1 = shorter. [3] {0.33}

45. 0 = calyx rotate, i.e., lobes spreading; 1 = cupulate or campanulate, i.e., lobes erect or ascending: unordered. [1] {0.10}

46. 0 = calyx shallowly deltate-lobed or cuspidate, sepals connate more than ⅔ of length from base; 1 = calyx moderately triangular- or acuminate-lobed, sepals connate about ⅓ to ½; 2 = deeply subulate- or linear-lobed, sepals connate only ⅙ or less: unordered. [3] {0.33}

47. 0 = on average, petals connate for 0.1–0.4 of their length; 1 = on average, connate 0.45–0.6 of length; 2 = completely connate, apices sealed by thin membranous suture, possibly not opening normally at anthesis. [3] {0.33}

48. 0 = petals rhombic, trullate or triangular acuminate, flat or sharply inflexed apically; 1 = ovate, rounded, incurved and somewhat cucullate from the base. [10] {1.00}

The two components, petal shape and petal posture, are completely correlated and were combined as one character.

49. 0 = receptacle extending into flower no more than ⅓ the length of the petals; 1 = extending about ½ the length of the petals. [5] {0.17}

50. 0 = petals adnate to full length of the receptacle, so there is no clear separation between the two; 1 = not completely adnate, so there is a clear separation of receptacle and petal tissues above the insertion of the petals. [1] {0.14}

51. 0 = petals coriaceous; 1 = membranous. [10] {1.00}

ANDROECIUM

52. 0 = stamens 6; 1 = 12. [10] {1.00}

53. 0 = stamens marginal on the receptacle; 1 = ±central, clearly separate from the petals. [5] {0.33}

54–55. 00 = stamens barely adnate to petals for only a short distance above receptacle; 10 = completely free from petals; 01 = strongly adnate to petals [3, 3] {0.20, 0.33}

The states are usually clear cut. Characters 53 and 54 are partially correlated, but not all taxa having 54^1 also have 53^1.

56. 0 = filaments triangular-attenuate; 1 = filamentous or vermiform. [3] {0.50}

Because state 0 is found only in the outgroups and within derived lineages of the ATROPURPUREOUS CLADE, developmental studies are needed to evaluate homology of the character in the disparate groups.

57. 0 = filament erect and unfolded (except for inflexed insertion onto anther); 1 = tortuous or folded (sometimes becoming straight but persistently marked by fold lines). [3] {0.25}

58. 0 = anther rectangular-linear or oblong-linear; 1 = ovate or ovate-oblong. [2] {0.33}

59–60. 00 = anther about ⅕–¼ of corolla length; 10 = usually about ⅓ (to approaching ¼) of corolla length; 01 = about ⅙ or less of corolla length. [3, 5] {0.25, 0.50}

61. 0 = anthers included during all stages; 1 = exserted between corolla lobes at time of pollen release and persisting there as flowers deteriorate. [5] {1.00}

Pistillate flowers—perianth and staminodes

62–63. 00 = calyx broadly cylindric or cupulate, including any cusps, about ⅓–⅗ as long as corolla; 10 = urceolate (narrowed at mouth) or narrowly cylindric, including any cusps, about ¾ as long as or longer than corolla; 01 = annulate or flattened, including any cusps, about ⅒–¼ as long as corolla. [3, 2] {0.25, 0.14}

Because the calyx and corolla are often proximally pressed against the rachilla and dilated, the flower was removed from the rachilla for measurement. Short calyces have only a small distal portion visible from the side. Intra- and interspecific variation needs further study to verify gap coding.

64–65. 00 = calyx sinuate or shortly cuspidate, with sinuses large (relative to lobes or cusps) and rounded; 10 = truncate, completely without sinuses or cusps; 01 = lobed, with sinuses small, narrow and acute: 65, unordered. [10, 10] {0.50, 0.50}

66–67. 00 = corolla cupulate (broadly cylindric) or broadly urceolate; 10 = narrowly urceolate or narrowly cylindric; 01 = broadly campanulate-patelliform. [1, 10] {0.10, 1.00}

68–69. 00 = corolla ±lobed or evenly sinuate, if lobed, the lobes broadly deltate and the sinuses "V"-shaped or acute; 10 = truncate, completely without sinuses or cusps; 01 = cuspidate, the sinuses broad and rounded. [5, 1] {0.33, 0.11}

70. 0 = corolla margin not fimbriate; 1 = fimbriate. [3] {0.33}

71–72. 00 = corolla externally glabrous; 10 = lepidote to setose or scabrous; 01 = lanate. [2, 10] {0.17, 0.50}

73. 0 = staminodes absent or present only as 6 distinct toothlike appendages on corolla; 1 = connate, forming a cup and proximally adnate to base of corolla. [10] {1.00}

No intermediates are known. Because the presence of distinct toothlike staminodes is highly variable within species, it was not treated as an additional state.

Gynoecium

74. 0 = pistil ±cylindric, narrowly ovoid or oblongoid; 1 = ±globose or broadly ovate, often proximally tumid. [1] {0.14}

As indicated in the discussion section, all features of the gynoecium (74–77) need to be examined from fresh or liquid-preserved material for the patterns of variation to be clarified. The data in this study suggest that these characters will have greatest utility at the sectional level or below.

75. 0 = style branches free or only basally connate, entirely exposed, erect or recurved; 1 = branches completely connate along margins, either remaining ternate or rounding out into a blunt triangle or circle seated on apical surface of style, truncate across top, central convergence recessed into style (see char. 77); 2 = branches completely connate and completely submerged and recessed into center of style, indicated only by trilete mark on truncate apex of style: unordered. [1] {0.22}

Examination of developing flowers in TRC (*Bernal et al. 1103,* FTG) suggested to me that postgenital fusion of style branches can easily be modified. This may be the reason why the character is homoplastic above the level of species-complexes.

76. 0 = stigmatic surface marginal; 1 = covering entire surface: unordered. [3] {0.17}

77. 0 = stigma 3-lobed; 1 = unlobed. [2] {0.17}

Cupule (accrescent calyx and corolla in fruit)

78. 0 = corolla about 2 times or more the height of the calyx; 1 = about 1½ times or less the height of the calyx. [3] {0.33}

79–80. 00 = relative size of calyx and corolla remaining unchanged between anthesis and fruiting; 10 = calyx enlarges (relative to corolla) 1.5–1.8 times; 20 = calyx enlarges 2–4 or more times; 01 = calyx size relative to corolla reduced to 0.7 or less of original proportional size. [5, 3] {0.33, 0.14}

External characters of fruit

81–82. 00 = shape (excluding rostrum) globose, ovoid, obovoid (i.e., from base to apex, length about equalling to 1.2 times transverse diameter); 10 = distinctly depressed, i.e., oblate, broadly obovoid, or broadly obconic (length 0.9–0.8 times diameter); 20 = strongly depressed, transversely ellipsoid or oblongoid in side view (length 0.75 times diameter or less); 01 = ellipsoid (length 1.25–1.4 times diameter); 02 = narrowly ellipsoid (length 1.5–2.0 times diameter). [3, 10] {0.15, 0.50}

83. 0 = spherical in top view, all transverse diameters about equal; 1 = elliptical or oblong in top view, distinctly laterally compressed. [10] {1.00}

84–85. 00 = length + diameter, *including rostrum* = 21–35 mm; 10 = length + diameter = 40–80 mm; 01 = length + diameter = 20 mm or less. [3, 3] {0.17, 0.25}

This was used as an index of fruit size. Taken separately, both length and diameter lacked sufficient breaks in measurement ranges genus-wide to be coded as discrete states, whereas the combined measure yielded gaps.

86–87. 00 = glabrous; 10 = setose or scabrous; 01 = lepidote or scurfy; 02 = thinly tomentose or lanate. [5, 2] {0.40, 0.22}

88–90. 000 = mature epicarp red, orange, bright yellow, or stramineous; 100 = dark purplish brown, violet-black, or blue-black; 010 = deep rosy purple; 001 = red-orange with rapid necrosis to black. [10, 10, 10] {1.00, 1.00, 1.00}

For comments about 010, see discussion section.

Certain taxa of the *B. hirta* complex were originally described as having black fruits (char. 90^1); this was consistent with the label data on the listed sample studied here. However, my own field observations (made after the PAUP analysis was completed) suggested that this condition results from precocious necrosis of the epicarp. This tendency may be genetically based; but, because the collection time is critical to scoring, the state was deleted from the topology of the cladogram (FIGURE 3).

91. 0 = epicarp weakly striate or smooth; 1 = distinctly striate. [2] {0.20}

A logical basis for this character could be the presence or absence of stout bundles below the epicarp in the outer mesocarp (char. 99), but the results show that these two characters were not correlated.

92. 0 = apex rounded, mammillate or apiculate (i.e., any typical apical projection less than 15% of the length of body of fruit); 1 = clearly rostrate (typical rostrum longer than 15% of body of fruit). [2] {0.25}

MESOCARP AND ENDOCARP

93–95. 000 = mesocarp consisting of thinly mealy or starchy pulp; 100 = consisting of thin-walled juice sacs that are attached to endocarp fibers; 010 = consisting of thick or dense starch; 001 = containing copious amounts of oil that is easily pressed out of fresh or rehydrated material. [10, 10, 5] {1.00, 1.00, 0.33}

The discreteness of states 000 and 010 needs further analysis using fresh or liquid-preserved material.

96–97. 00 = endocarp fibers moderate in number, stout, flattened, apressed, and adnate to endocarp surface; 10 = moderate to few in number, firm and wiry, proximally somewhat flattened, appressed, adnate and often sunken in grooves, distally terete, diverging from endocarp surface and declined toward endocarp base; 20 = moderate to few in number, firm and wiry, completely terete, free from endocarp from point of insertion, diverging and declined through mesocarp; 21 = moderate in number, terete, firm and wiry to fine except at point of attachment where abruptly swollen into tubercular mound, radiating or only distally declined; 22 = extremely numerous, terete, very fine (entire mass almost cottony), attached by minute tubercles or papillae, radiating or only distally declined; 30 = varying from fibers lacking to very few, and if present, then terete, free, and declined. [10, 10] {0.50, 1.00} (See FIGURE 6.)

In most cases, scoring for states 21 and 22 was clear cut. The few transitional taxa (e.g., COR) were scored as state 21, the most plesiomorphous of the two states. Quantification of numbers is needed.

98. 0 = outer mesocarp fibers (periclinal and just internal to epicarp) relatively numerous, covering most of the circumference of mesocarp; 1 = relatively few, leaving noticeable sections of areas of mesocarp uncovered. [2] {0.20}

The differences are rather subjective; no quantitative basis was formulated for this study but is needed for future analyses.

99. 0 = outer mesocarp fibers regularly anastomosing over whole surface of mesocarp; 1 = parallel or with a few anastomoses at poles of mesocarp. [2] {0.13}

100. 0 = endocarp vertically oblique with fertile pore clearly more distal than the sterile pores; 1 = not oblique, fertile and sterile pores at about the same vertical position. [5] {0.20}

101. 0 = endocarp not depressed, length equalling or greater than diameter; 1 = depressed, broadly obconic, or oblate, diameter greater than length. [5] {0.25}

Although apparently connected with char. 81, it is in part not congruent with it. Furthermore, the measurement of endocarp length is not complicated by the presence of a rostrum as in the case of char. 81.

102. 0 = greatest diameter of endocarp medial or distal (hence, endocarp is globose, obconic, ellipsoid, etc.); 1 = proximal (hence, endocarp ovoid). [10] {1.00}

103. 0 = endocarp surface smooth, tuberculate, or weakly pitted only at base; 1 = sharply pitted medially and distally. [3] {0.25}

104. 0 = endocarp base normal, not expanded; 1 = expanded or elongate as evidenced by more widely separated fibers or tubercles. [10] {0.25}

The assumption is made that this represents an allometric difference, i.e., the rate or duration of elongation of the proximal half of the endocarp relative to the distal half. Because the results suggest that it is correlated with char. 101, developmental studies of the fruit may clarify the relationship and significance of these characters.

105–106. 00 = endocarp pores not equidistant (in polar view), not separated by equal angles; 10 = pores about 60° apart, equidistant; 01 = sterile pores strongly displaced to one side of endocarp. [10, 10] {1.00, 1.00}

The extremes of states 00 and 01 are readily distinguished subjectively although detailed quantitative characterization and analysis are needed to evaluate the actual gap among the three states.

APPENDIX III. REJECTED CHARACTERS

These characters were initially included in survey but were either widely variable within a species or species-complex, were unknown in too many taxa (marked by "*"), were uniform throughout the genus (written in bold), or had a unit consistency (C) less than 0.1 in the initial PAUP analysis (written in italic).

HABIT AND STEM. 1. Number of stems per cluster. 2. *Rhizome lengths relative to diameters as indicator of cluster densities. 3. *Number and size of basal adventitious roots. 4. *Stem height.* 5. Internode: a. *length, b. *zonation or banding, c. *armature, d. *indument. 6. *Width of node relative to internode below.

GENERAL FEATURES OF ARMATURE. 7. Modal length of: a. *longest spines,* b. *moderate spines,* c. shortest spines. 8. Orientation of spines. 9. **Presence of pulvinus-like swelling at insertion.** 10. Indument of: a. base, b. shaft. 11. **Color of apex.**

GENERAL FEATURES OF LEAVES. 12. Number in crown. 13. Orientation within crown.

LEAF SHEATH. 14. *Total length. 15. Apical free portion: a. *length, b. *texture, c. *shape. 16. Overall: a. striations, b. *armature,* c. structure of trichomes, d. indument color.

PETIOLE. 17. Dimensions: a. length, b. *diameter.* 18. *Adaxial features.* 19. Distribution of spinules. 20. Indument: a. structure of trichomes, b. color.

LEAF RACHIS. 21. *Length.* 22. Presence of terminal filamentous extension. 23. Adaxial indument: a. *structure of trichomes,* b. color. 24. Abaxial indument: a. *structure of trichomes,* b. color. 25. *Distribution of:* a. *spines,* b. *spinules.*

BLADE. 26. Dimensions: a. length, b. width, c. *length-width ratio when less than 3.* 27. Proportion of margins that are parallel. 28. Widest point along length. 29. Shape at base. 30. Angle of terminal bifurcation. 31. *Number of primary nerves.* 32. Texture. 33. Indument, adaxial surface of lamina: a. structure of trichomes, b. color. 34. Indument, adaxial surface of nerves: a. *structure of trichomes,* b. color. 35. Indument, abaxial surface of lamina: a. structure of trichomes, b. color. 36. Indument, abaxial surface of nerves: a. *structure of trichomes,* b. color. 37. Distribution of spines. 38. Distribution of spinules. 39. Number of secondary nerves per primary nerve. 40. Structure of transverse nerves.

BLADE SEGMENTS (LEAFLETS). 41. Modal number. 42. *Number of planes into which segments are oriented relative to rachis.* 43. *Spacing.* 44. Structure of insertion. 45. *Outline shape of apex.* 46. Curvilinear course: a. *basal region,* b. middle region, c. *apical region.* 47. Marginal bands: a. presence, b. general structure, c. width, d. *color.*

TERMINAL VS. NONTERMINAL SEGMENTS (characterization of each descriptor for each of segment types). 48. Dimensions: a. length, b. width, c. *length-width ratio.* 49. Length adnate to rachis. 50. Widest point along length. 51. Proportion of margins that are parallel. 52. Number of primary nerves. 53. Lateral connation.

INFLORESCENCE (GENERAL). 54. *Mode of emergence from leaf sheath.

PROPHYLL. 55. Width. 56. *Shape of apex. 57. Presence of armature. 58. Indument: a. structure of trichomes, b. color.

PEDUNCULAR BRACT. 59. Length. 60. Protraction of apex. 61. Adaxial (internal) surface: a. color, b. texture. 62. Abaxial (external) surface color.

PEDUNCLE. 63. Orientation. 64. Length. 65. **Cross-sectional shape**. 66. Diameter. 67. Indument: a. structure of trichomes, b. color, c. distribution.

RACHIS. 68. Length.

RACHIS BRACTS. 69. Length of: a. largest, b. *smallest.

RACHILLAE. 70. Armature distribution. 71. Indument: a. distribution, b. color.

STAMINATE FLOWERS. 72. Calyx length. 73. Corolla length. 74. Corolla indument: a. structure of trichomes, b. distribution. 75. Filament length. 76. **Anther insertion**. 77. Shape of anther base. 78. Pistillode: a. presence, b. length, c. shape.

PISTILLATE FLOWERS. 79. *Calyx length.* 80. Presence of annular flange inside calyx and adnate to its base.[1] 81. Corolla length. 82. Staminodes: a. *presence,* b. **degree of connation/adnation of basal portion**, c. shape when apical portion is free and distinct, d. length of adnate portion relative to corolla length. 83. Pistil indument type.

FRUITING CUPULE. 84. Calyx shape. 85. Corolla: a. shape, b. *splitting,* c. color, d. striations.

FRUIT. 86. Indument color. 87. Apical region sunken or not. 88. **Lack of mucilage in mesocarp**. 89. Endocarp length (no gaps for coding). 90. Structure of endocarp fibers radiating from fertile pore. 91. **Endosperm homogeneity**.

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[1] Karsten (1856, 1857) founded the monotypic genus *Pyrenoglyphis* on *B. major* and diagnosed it by the presence of a staminodial-like ring on the internal face of the pistillate calyx, in addition to the staminodial ring in the corolla (the character he used to define *Guilielma* Karst.). Burret (1933–1934) intimated that Karsten misinterpreted or erred in his observation because Burret himself was unable to locate any such structure on any of the material of *B. major* that he studied. With Burret's comment in mind, I began examining the material of *B. major.* To my surprise, the first specimen I examined (*Hull H-1,* FTG), which originated from near the type locality, clearly possessed this intracalycine ring; however, specimens that originated elsewhere were nearly identical but lacked the ring. This appears to be a geographically localized character within *B. major* that is of no taxonomic consequence although it may represent a case of homoeosis (Sattler, 1988).

Note added in proof—changes to APPENDIX I: Recent study suggests that *Bactris ferruginea* should be moved from the *riparia* complex (24) to the *longifrons* complex (35) and that *B. pickelii* should be moved from the *tomentosa* complex (39) to the *eumorpha* complex (40). A study by Wessels Boer (Palmas indigenas de Venezuela. Pittieria 17: 1–332. 1988) came to my attention in which he placed several inadequately known species in synonymy, as follows: *B. bergantina = B. setulosa, B. duidae = B. corosilla, B. falcata = B. setulosa, B. venezuelensis = B. corossilla.*