Selbyana 12: 91–101

PRELIMINARY CLASSIFICATORY STUDIES IN COCCOTHRINAX (PALMAE: CORYPHOIDEAE)

CLIFTON E. NAUMAN*

Fairchild Tropical Garden, 10901 Old Cutler Road,
Miami, Florida 33156

ROGER W. SANDERS

Fairchild Tropical Garden, 10901 Old Cutler Road,
Miami, Florida 33156; and Department of Biological Sciences,
Florida International University, Miami, Florida 33199

ABSTRACT. Published infrageneric classifications of *Coccothrinax* are based only on Cuban species. To provide an inclusive categorization of provisional infrageneric groupings for easy recognition in future field and herbarium studies, we compared all species in the genus with statistical, phenetic, and cladistic techniques. Statistical analyses indicated that 22 of 160 characters extracted from the published literature would be useful for phenetic and cladistic analyses. Phenetic analyses produced three distinct clusters of taxa. Cladistic analyses suggested that two of the phenetic clusters are paraphyletic and the third is monophyletic. The two paraphyletic clusters were also more plesiomorphic than the monophyletic cluster. Cladistic analyses further indicated that most of the 22 characters were highly homoplasious, and only the following were reliable for classificatory purposes at the infrageneric level: loss of transverse veins in the leaf, elongation of the leaf sheath strands, fusion of sheath strands into spine-like processes, and tan, corky fruits. The recognizable groups are as follows: Argentea Group (1 complex, 6 spp., paraphyletic); Argentata Group (2 complexes, 10 spp., probably paraphyletic)—*C. argentata* complex (8 spp., paraphyletic), *C. crinita* complex (2 spp., monophyletic); and Pauciramosa Group (4 complexes, 31 spp., probably monophyletic)—*C. miraguama* complex (11 spp., probably monophyletic), *C. pauciramosa* complex (11 spp., paraphyletic), *Haitiella* complex (2 spp., monophyletic), species *incertae sedis* (7 spp.).

As a result of recent name changes and an absence of detailed comments on species relationships, the taxonomy of *Coccothrinax* Sargent has become complex and poorly resolved. The number of recognized taxa in the genus is unstable and relatively large. The total number of species varies from 20 cited by Moore (1973) to 37 listed by Glassman (1972). Since 1966, numerous name changes have been proposed and 14 new taxa have been described (Borhidi & Muñiz, 1971, 1972, 1985; Borhidi et al., 1978; Muñiz & Borhidi, 1982a, 1982b; Quero, 1980; Read, 1966a, 1966b, 1980). Additionally, the only infrageneric classification (León, 1939) was based exclusively on Cuban taxa. León's (1939) scheme has been variously modified by Muñiz and Borhidi (1982b). These authors recognize two sections and four subsections, but do not elaborate on relationships among the groups, except as implied by the taxonomic rank of the groups. Species relationships within the groups are also not given, except as isolated comments noting affinities among two or three species. Muñiz and Borhidi's modifications of León's scheme are also based on an analysis of only the Cuban taxa.

The purpose of this study is to provide a hierarchial context for future detailed populational and species-level systematic studies, and to provide insight into the relationships within the genus. We examined the available literature data, augmented with field, herbarium, and garden studies, and developed an inclusive preliminary scheme that is hierarchially more complex than that of León ex Muñiz and Borhidi (1982b).

MATERIALS AND METHODS

Data set. Literature data, including previously published keys, descriptions, photographs, and drawings, were used to characterize the taxa for comparison. A list of recognized taxa is given in TABLE 1 and a list of literature consulted is cited in Nauman and Sanders (1991). The literature data were augmented with single or multiple specimen samples from 44 authenticated living accessions at Fairchild Tropical Garden (FTG), the herbarium, and field studies by one or both authors in Florida, Hispaniola, Mexico, and Trinidad (specimens cited in Nauman & Sanders (1991), APPENDICES I and II).

Character analysis. More than 160 characters used by previous authors to distinguish taxa and additional characters considered to be of potential value for indicating systematic relationships

---

* Present address: General Biology Program, 301 Hesler Biology Bldg., University of Tennessee, Knoxville, Tennessee 37996-1110.

Table 1. List of recognized taxa. Numbers refer to taxa in Figures 2 and 3, and Appendix II. Literature sources and synonymy are given in Nauman and Sanders (1990). Infraspecific taxa have been omitted at this time.

1. *C. acunana* León
2. *C. alexandri* León
3. *C. alta* (Cook) Beccari
4. *C. argentata* (Jacquin) Bailey
5. *C. argentea* (Lodd. ex J. A. & J. H. Schultes) Sargent ex K. Schum.
6. *C. baracoensis* Borhidi & Muñiz in Muñiz & Borhidi
7. *C. barbadensis* (Lodd. ex Martius) Beccari
8. *C. bermudezii* León
9. *C. borhidiana* Muñiz in Borhidi et al.
10. *C. camagueyana* Borhidi & Muñiz in Muñiz & Borhidi
11. *C. clarensis* León
12. *C. concolor* Burret
13. *C. crinita* (Griseb. & Wendl. ex Wright in Sauvalle) Beccari
14. *C. cupularis* (León) Borhidi & Muñiz
15. *C. ekmanii* Burret
16. *C. elegans* Muñiz & Borhidi
17. *C. fragrans* Burret
18. *C. garciana* León
19. *C. gracilis* Burret
20. *C. guantanamensis* (León) Muñiz & Borhidi
21. *C. gundlachii* León
22. *C. hioramii* León
23. *C. inaguensis* R. W. Read
24. *C. jamaicensis* R. W. Read
25. *C. leonis* Muñiz & Borhidi
26. *C. litoralis* León
27. *C. macroglossa* (León) Muñiz & Borhidi
28. *C. microphylla* Borhidi & Muñiz in Muñiz & Borhidi
29. *C. miraguama* (H.B.K.) León
30. *C. moaensis* (Borhidi & Muñiz) Muñiz in Muñiz & Borhidi
31. *C. montana* Burret
32. *C. munizii* Borhidi in Borhidi & Muñiz
33. *C. muricata* León
34. *C. nipensis* Borhidi & Muñiz in Muñiz & Borhidi
35. *C. orientalis* (León) Muñiz & Borhidi
36. *C. pauciramosa* Burret
37. *C. proctorii* R. W. Read
38. *C. pseudorigida* León
39. *C. readii* Quero
40. *C. rigida* (Griseb. & Wendl. ex Griseb.) Beccari
41. *C. salvatoris* León
42. *C. savannarum* (León) Borhidi & Muñiz in Muñiz & Borhidi
43. *C. saxicola* León
44. *C. spissa* Bailey
45. *C. victorinii* León
46. *C. yunquensis* Borhidi & Muñiz in Muñiz & Borhidi
47. *C. yuraguana* (A. Rich.) León

were surveyed for taxonomic utility. Patterns of character variation were analyzed, and coding procedures were determined from studies of four disjunct Floridian populations of *C. argentata* and living accessions of *C. argentea, C. argentata, C. miraguama, C. readii, C. yuraguana,* and *C. proctorii* at FTG (unpubl., data and results available upon request from C.E.N.). Herbarium material at FTG was used to supplement the studies of live material.

R-mode analyses, including multiple discriminant analysis, principal component analysis, and other statistical procedures, were applied to particular characters and garden populations to assess their usefulness for intertaxon discrimination. Several rejection criteria were used to evaluate each character. 1) The character had to exhibit some variation within or among the OTU's (operational taxonomic units, here considered equivalent to a named taxon, Table 1). This procedure emphasizes character differences among the OTU's. Additionally, where intra-OTU variation was greater than inter-OTU variation, i.e., where F-1 weighting (sensu Adams, 1975) would give zero weight to the character, differences among OTU's would not be detectable; these characters were eliminated. 2) The character had to be measurable on a large proportion of the available specimens. 3) The character had to exhibit measurement error smaller than the differences in that character among any two or more OTU's. Using these criteria and combining logically or empirically correlated characters into a character complex (e.g., tan corky fruits), the initial 160 characters were narrowed to 22 (Appendix I).

Character state coding for phenetic analyses was determined with statistical summaries, including a series of basic descriptive statistics. For most characters, modal states were considered representative due to their higher predictive value (cf. Nauman, 1982). This was especially important for characters exhibiting non-normal distributions. A character state distribution was considered non-normal if the third or fourth central moment statistics indicated significant skewness or kurtosis, $P < 0.05$. Modal states for continuous characters were obtained by partitioning the range into ten class intervals. In some instances, continuous characters were broken into classes delimited by natural breaks in the character state frequency distributions using a method similar to that of Almeida and Bisby (1984). Some characters were represented by maximal values for each taxon since these values were shown from analysis of field or garden populations to be discriminating only at the upper end of their ranges. Additionally, multivariate analysis indicated that the upper range limits for certain characters represent the only comparable developmental states. Basic statistical summaries were carried out with programs written by one of us (C.E.N.) on an IBM PC. The raw data matrix is given in APPENDIX II.

Phenetic analyses. The phenetic analyses consisted of: 1) generating the general similarity coefficient of Gower (1971) for all pairwise combinations of OTU's; 2) cluster analysis (CA) of the similarity matrix with four pair–group clustering methods, UPGMA—an unweighted method with arithmetic averages, WPGMA—a weighted method with arithmetic averages, weighted centroid, and unweighted centroid methods; and 3) Principal Coordinate Analysis (PCORD) on the similarity matrix with the method of Gower (1966). The WPGMA and centroid clustering were carried out with the Multivariate Statistical Package (W. L. Kovach, Indiana Univ.). Computation of the similarity matrices, UPGMA, and PCORD were carried out with a phenetic program package written by one of us (C.E.N.) on an IBM PC.

Cladistic analyses. For cladistic analyses, potential homology was estimated by similarities in positional and developmental relationships. Since such similarities can arise independently, congruence with the entire data set was considered the stronger test of homology. Polarities were assessed largely with the outgroup substitution approach of Donoghue and Cantino (1984). In most cases, *Thrinax* and *Zombia* were considered the immediate sister groups of *Coccothrinax* (cf. Uhl et al., 1990). When polarity assessment was conflicting, other more distantly related coryphoid genera were utilized. Where outgroup substitution was inappropriate for resolving polarities (e.g., when plesiomorphic states were ambiguous or non-existent in the outgroup) we used the "ontogenetic" criterion and compared seedlings of a number of taxa grown at FTG. Additional details of the polarity assessments are given in APPENDIX I. Computations were carried out on an IBM PC with PAUP (version 2.4.1) obtained from D. L. Swofford (Illinois Natural History Survey).

RESULTS

Phenetic analyses. The results of both CA (FIGURE 1) and PCORD (FIGURE 2) suggest three main phenetic clusters, here designated as the Argentata, Argentea, and Pauciramosa groups. Only the phenogram resulting from UPGMA clustering of 47 OTU's is presented (FIGURE 1) because the other three CA procedures were no more informative. In PCORD (FIGURE 2), positive scores on Axis 1 are associated with smaller leaves (segment length and number, and palman length, i.e., segment connation) and more open spacing of sheath strands. Positive scores on Axis 2 are associated with a lack of transverse veins, thicker sheath strands, and free strand tips formed by strand fusion (spine-like sheath tips). Positive scores on Axis 3 are associated with slender caudices.

The major discrepancy between the results of CA and PCORD is the placement of *C. acunana, C. gundlachii,* and *C. montana.* In CA, they arise at low levels of similarity, being clearly associated with none of the more distant clusters. In PCORD, they appear to be intermediate between the Argentata and Pauciramosa groups. These species recombine character states from these two groupings and the conflicting placement reflects how these two algorithms portray inter-OTU and inter-cluster relationships; CA tends to portray inter-OTU relationships more accurately, and PCORD tends to portray inter-cluster relationships more accurately.

Cladistic analyses. Approximately 100 minimal length trees were obtained with PAUP using the MULPARS option with global branch swapping and rooting by the Lundberg method. Since polarities were previously assigned by outgroup comparisons, we scored plesiomorphic states as 0 and apomorphic states as 1 or 2. Thus, the Lundberg rooting simulated the presence of a hypothetical ancestor possessing the plesiomorphic condition for all characters. The trees have a branch length of 69 and a Consistency Index of 0.41. A consensus tree of Adams for those 100 trees is given in FIGURE 3; it has a branch length of 70 and a Consistency Index of 0.40.

The character conflict in *C. acunana, C. gundlachii,* and *C. montana* is handled differently by cladistic procedures. Most of the conflicts in *C. acunana* and *C. montana* are in plesiomorphic character states; hence, the taxa are placed at the base of the tree. Those of *C. gundlachii* are primarily apomorphic in the context of its parsimoniously placed neighbors; hence, it is placed at the top of the tree.

The Argentea phenetic group remains coherent but is a paraphyletic assemblage whose common characters are plesiomorphic. The Argentata phenetic group similarly remains coherent and is also paraphyletic but intermediate in position, and no apomorphic character states unite the OTU's. The Pauciramosa phenetic group is an advanced monophyletic clade defined by characters of few segments and short palmans, both of which are homoplasious.

Only ten apomorphous character changes (2-1, 4-2, 6-2, 7-1, 8-1, 15-1, 17-1, 18-1 [-2], 20-1, and 22-1) of the possible 28 do not exhibit homoplasy. All of these except 6-2 and 17-1 are autapomorphies for species or closely related species pairs. Character state 6-2 (long sheath spines) unites nine taxa; 17-1 (no transverse veins) unites 39 taxa. Therefore, almost all of the hier-

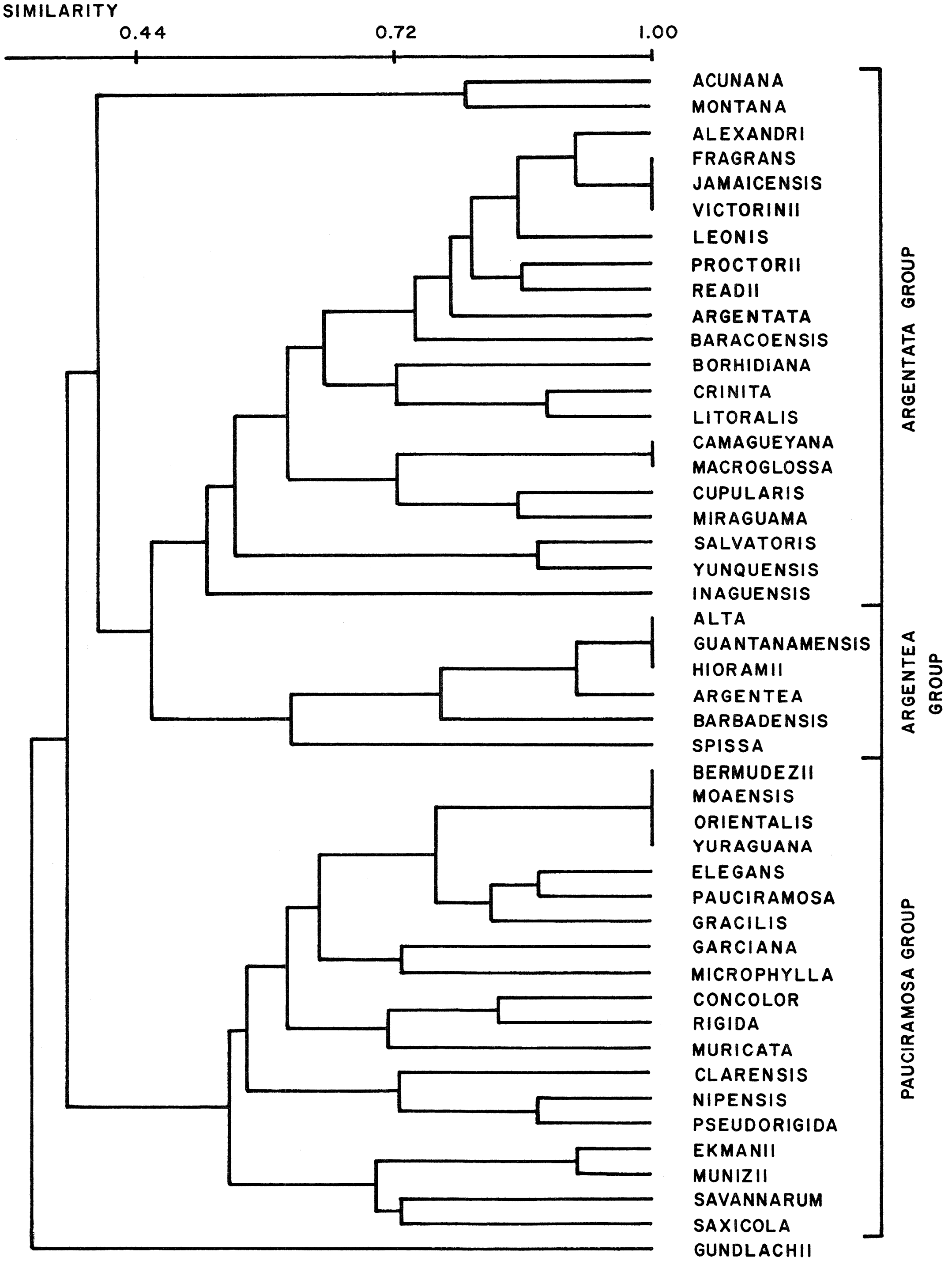

FIGURE 1. Phenogram resulting from UPGMA cluster analysis of 47 OTU's.

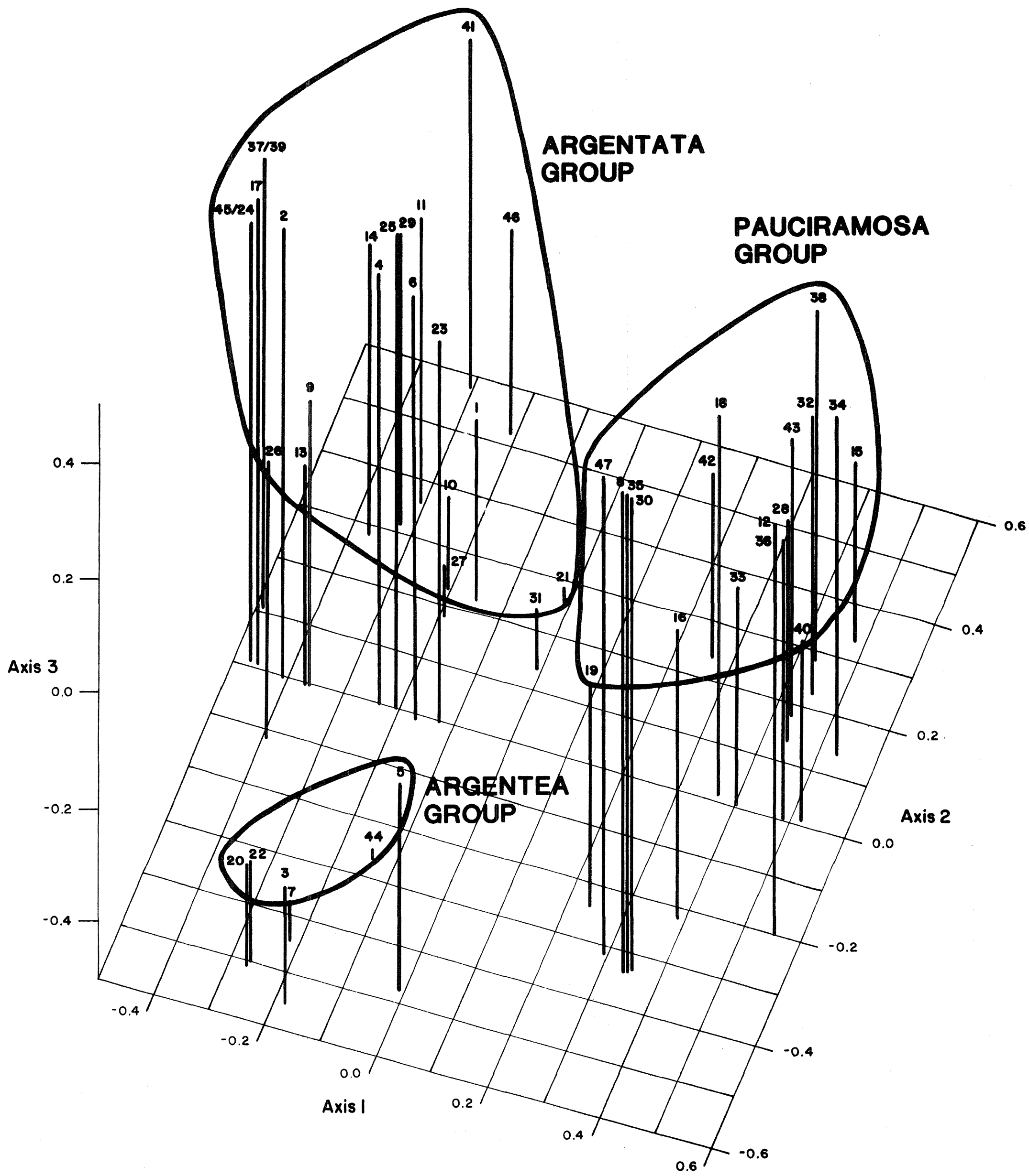

FIGURE 2. Three dimensional diagram of the results of Principal Coordinate Analysis of 47 OTU's (OTU numbers are given in TABLE 1).

archial structure of the tree is based on homoplasious characters with individual consistency values of 0.5 or less. If the tree structure is reduced to the two consistent apomorphies, we find 1) a clade of species lacking transverse veins arising from a primitive complex, and 2) within that clade, a secondary clade with long sheath spines.

DISCUSSION AND CONCLUSIONS

Limitations of the data. As one might expect, the data that can be obtained from species descriptions have limitations for broad comparisons and for numerical analyses. If the species are known only or primarily from type material, descrip-

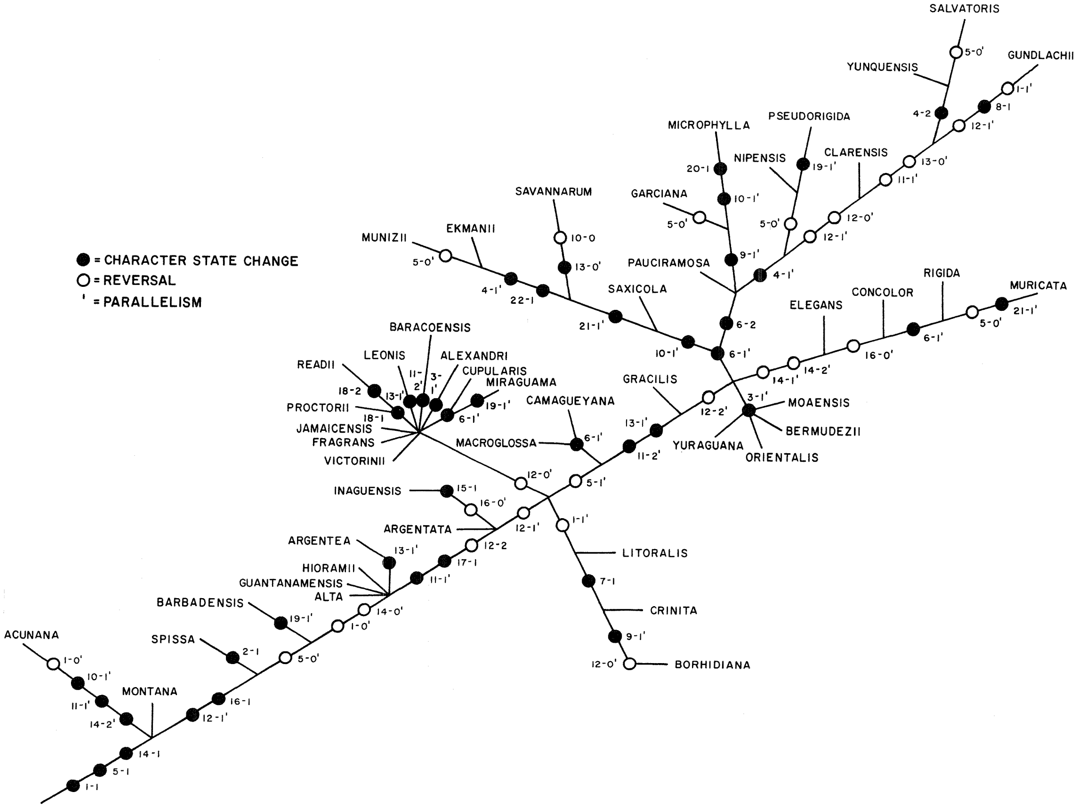

FIGURE 3. Consensus tree of Adams for 100 trees resulting from parsimony analysis of 47 OTU's. Numbers represent character state changes at each position, where the first number refers to the character and the second number refers to the resulting character state (see APPENDIX I).

tions tend to be incomplete. Thus, many of the 160 characters initially examined were not comparable across the genus. This is especially true for reproductive characters. (Note that only four reproductive characters are included in APPENDIX I and only one of these concerns the flower.) Vegetative characters are prone to parallelisms.

Most of the comparable vegetative characters from the literature are described quantitatively. When an attempt is made to convert the reported measures into discrete states, however, often only the extremes are distinguishable as morphological gaps. Hence, in our study, eight of the ten non-homoplasious characters were unique to a single species or species pair. As a result, the overall phenetic structure was derived from the quantitative vegetative characters. This is not problematic for most phenetic algorithms, but it does mean that the phenetic groups derived from such characters may not accurately reflect evolutionary relationships. In a cladistic context, these same characters exhibit relatively high degrees of homoplasy. P. F. Stevens (unpubl.) argues that the binary or ordinal coding of quantitative characters may not be valid unless the intraspecific variation is well documented and there are absolute gaps between the ranges of species scored for different character states. Because descriptions of new species often do not fulfill the first criterion, these types of data may be further limited for cladistic analysis.

We conclude that the clusters and hierarchy obtained from these data should not be directly taken at face value. Rather, they should be used as guides for direct observations of known as well as previously under-utilized characters. Furthermore, characters that were eliminated from consideration by one of the primary rejection criteria in the context of the entire genus take on a new significance in the context of individual groups resulting from the phenetic and cladistic analyses. Thus, we were led to re-evaluate the characters of a wider sample of specimens for absolute gaps rather than statistical differences. For example, the presence of transverse veins (character 17) in the Argentea phenetic grouping dif-

TABLE 2. Classification of Muñiz and Borhidi (1982b). Taxa indicated by numbers in TABLE 1. Asterisks indicate taxa outside Cuba and not treated by them.

Coccothrinax Sargent	
Section *Coccothrinax*	
Subsection *Coccothrinax*:	1, 2, 3*, 4*, 5*, 7*, 8, 14, 16, 17, 19*, 20, 22, 23*, 24*, 25–30, 31*, 33, 35, 37, 39, 41, 43, 44*, 45–47.
Subsection *Haitiella* (L. H. Bailey) Muñiz:	15*, 32.
Section *Longispadiceae* León ex Muñiz	
Subsection *Multiramosae* León ex Muñiz:	10, 13, 21.
Subsection *Pauciramosae* León ex Muñiz:	6, 9, 11, 12*, 18, 34, 36, 38, 40, 42.

fers dramatically from the absence of them in the other two phenetic groupings. (A minor exception is noted in Nauman and Sanders (1991) which may be due in part to garden hybridization.) The use of this character as a cladistic character is substantiated. On the other hand, direct observations of homoplastic or quantitatively varying characters show that personal interpretation more strongly influences the way previous authors described them or different workers score them. In this context, a comparison of our results with the published classifications provides additional insights.

Published classifications. The scheme of classification for the genus *Coccothrinax* published by Muñiz and Borhidi (1982b) (TABLE 2) recognizes two sections, section *Coccothrinax* and section *Longispadiceae*. Section *Coccothrinax* is characterized by short, cernuous to pendent inflorescences before fruit maturity, 1 to 6 primary inflorescence branches, and partly membranous external bracts. As circumscribed by Muñiz and Borhidi (1982b), the section contains two subsections, subsection *Coccothrinax* and subsection *Haitiella*. Subsection *Haitiella* (previously *Haitiella* Bailey) is distinguished by its densely muricate ovaries and fruits, by leaves that are less than ½ orbicular, by short (less than 4 dm long) segments, and by short (less than 2–2.5 dm long) petioles. These character states occur scattered in other subsections but are typical of members of subsection *Haitiella*. Subsection *Coccothrinax* is characterized by smooth ovaries and fruits.

Muñiz and Borhidi (1982b) characterized section *Longispadiceae* by elongated and ascending inflorescences with rigid external bracts and divided the section into two subsections, subsection *Pauciramosae* and subsection *Multiramosae*. Subsection *Pauciramosae* is characterized by small- to medium-sized plants with 1 to 7 primary inflorescence branches, and subsection *Multiramosae* is characterized by robust plants with 8 to 10 primary inflorescence branches.

Comparison of schemes. Section *Longispadiceae* corresponds to the Pauciramosa phenetic group, and section *Coccothrinax* corresponds to the Argentea and Argentata groups combined. The major exceptions are: 1) Muñiz and Borhidi (1982b) placed *C. borhidiana, C. crinita,* and *C. camagueyana* in section *Longispadiceae* because they possess long, horizontal to ascending inflorescences with rigid bracts; 2) because *C. ekmanii* and *C. munizii* have short, cernuous inflorescences with partly membranous bracts, they are placed in section *Coccothrinax* as subsection *Haitiella*; and 3) several species they excluded from subsection *Pauciramosae* fell in the Pauciramosa phenetic group. The need to segregate species of the Argentea group from section *Coccothrinax* would not have been obvious to Cuban authors because only two of the taxa occur in Cuba (TABLE 2).

Prior to our numerical analyses, we were unable to confirm the distinctions between rigid and partly membranous bracts and between ascending and cernuous inflorescences; these characters were therefore excluded from the numerical analyses. Although Muñiz and Borhidi (1982b) relied heavily on inflorescence characters, their scheme is remarkably similar to our results. We believe that in addition to their use of the inflorescence, they were intuitively influenced by the same characters used in our analyses. Indeed, when subsection *Haitiella* is placed within subsection *Pauciramosae*, the latter can be defined by free sheath strand tips (sheath spines) over 1 cm long (character state 6-1) as in FIGURE 3.

The reliance on inflorescence posture and length, however, appears to have created artificial associations. For example, Muñiz and Borhidi (1982b) recognized that *C. borhidiana* and *C. crinita* share the same type of unusual free strand tips. However, because the former has shorter inflorescences they were forced to place the two in different subsections, despite their obvious relatedness in other characters that are more conservative than inflorescence length. Furthermore, based on observations of seedlings, we believe that the free strand tips in *C. crinita* are

TABLE 3. Informal classification of *Coccothrinax,* deduced from the numerical and cladistic analyses (see TABLE 1). "±" indicates "more or less."

1. ARGENTEA GROUP: Most primitive, probably paraphyletic. Cuba to Trinidad, only 1 complex. A.
   - A. ARGENTEA COMPLEX: Stems ca. 10–30 cm or more in diameter; leaf sheath strands fine, hairlike, usually much less than 0.5 mm thick, tightly woven; leaf blade shallowly plicate in one plane, often with segments distally pendent; segments usually tapering gradually to tip; longitudinal veins widely spaced, interconnected by distinct transverse veins; inflorescence bracts ± tubular. Taxa: 3, 5, 7, 20, 22, 44.
2. ARGENTATA GROUP: Intermediate advancement, probably paraphyletic. Stem mostly 10–20 cm in diameter; leaf sheath strands fine, usually hairlike, usually less than 0.5 mm thick, usually tightly woven; leaf blade shallowly plicate, often broadly undulating or funnel shaped, often with segments distally pendent; segments usually tapering gradually to the tip; longitudinal veins numerous, closely spaced, not interconnected by distinct transverse veins; inflorescence bracts ± tubular. Northwestern Caribbean, 2 complexes.
   - A. ARGENTATA COMPLEX: Probably paraphyletic. No additional defining characters. Taxa: 4, 17, 23, 24, 26, 37, 39, 45.
   - B. CRINITA COMPLEX: Probably monophyletic. Free strand tips of leaf sheath due to elongation. Taxa: 9, 13.
3. PAUCIRAMOSA GROUP: Advanced, probably monophyletic. Stem usually 3–10 cm in diameter; leaf sheath strands coarse, usually woody, 1–4 mm or more thick (wiry and only 0.5 mm thick in a few taxa of the Miraguama complex); leaf blade deeply plicate in one plane, usually with segments distally held stiffly straight (hence, noticeably pinwheel shaped); segments usually abruptly contracted and producing shoulder-shaped acuminations distally; longitudinal veins numerous, closely spaced, not interconnected by distinct transverse veins; inflorescence bracts tubular to dilated. Cuba, with some taxa in Hispaniola, 3 or more complexes.
   - A. MIRAGUAMA COMPLEX: Monophyletic or paraphyletic. Leaf sheath strands in 3 layers (or occasional apparent reversal to 2 layers), ± tightly woven, free spiniform strand tips poorly developed to ca. 1 cm long or lacking; leaf segments variable in number, length, and connation. Taxa: 2, 6, 8, 10(?), 14, 25, 27, 29, 30, 35, 47.
   - B. PAUCIRAMOSA COMPLEX: Probably paraphyletic. Leaf sheath strands in 2 layers, ± loosely woven, free spiniform strand tips well developed (over 2 cm long); leaf segments usually fewer than 35, short, and weakly connate. Taxa: 11, 18, 21, 28, 33, 34, 36, 38, 41, 42, 46.
   - C. HAITIELLA COMPLEX: Monophyletic. Leaf sheath strands in 2 layers, ± tightly woven, free spiniform strand tips well-developed; leaves cuneate with segments fewer than 30, short, weakly connate; ovaries muricate, fruit tan, corky (autapomorphies in *Coccothrinax*). Taxa: 15, 32.
   - D. MISCELLANEOUS TAXA: Leaf sheath strands in 2 layers, ± loosely woven, free spiniform strand tips present or not; leaf segments variously but typically fewer than 35, short, and weakly connate. Taxa: 1, 12, 16, 31, 40, 43. (Included here is *C. scoparia,* once treated as a synonym of *C. argentea* by Bailey (1939). It was excluded when we conducted the numerical and cladistic analyses, but later study of authentic material showed it to be distinct and most related to *C. saxicola.*)

homologous with the fused strand tips in the Argentata group and not with the free spinelike strand tips in subsection *Pauciramosae.*

Of special interest are the taxa positioned in subsection *Coccothrinax* by Muñiz and Borhidi (1982b) and which clustered in the Pauciramosa group in our analyses. These taxa have sheath strands consistently more than 0.5 mm thick (wiry to woody in consistency), mostly loosely woven sheath strands, and leaf segments that are short, few per leaf, and only shortly connate. Also, the taxa centered around *C. yuraguana* share the apomorphy of three sheath layers. However, these same characters are variously recombined in the taxa centered around *C. miraguama* (*C. alexandri, C. cupularis, C. leonis,* and *C. macroglossa*). In contrast, these taxa are aligned with the Argentata phenetic grouping by both Muñiz and Borhidi (1982b) and our analyses.

With respect to these same characters, *C. miraguama* is sufficiently variable to be partitioned into subspecies. *Coccothrinax miraguama* subsp. *arenicola* approaches *C. yuraguana,* a species with wiry sheath strands in three layers, but differs from the latter in more numerous leaf segments that are more strongly connate. Subspecies *havanensis* and *roseocarpa* have thick, woody sheath strands in three layers as in *C. orientalis* but also have larger, more numerous, and more connate segments; subsp. *roseocarpa* is the more transitional of the two subspecies. Subspecies *miraguama* is nearly identical to subsp. *havanensis,* but has the sheath strands typically in two layers. However, in this subspecies the distinction between two and three sheath strand layers breaks down; three layers are often present proximally and two layers distally on the sheaths. Short, free strand tips about 1 cm long are usually present in *C. cupularis, C. macroglossa,* and some plants of *C. miraguama,* which suggests genetic similarity to other taxa in the Pauciramosa phenetic group. Thus, it appears that *C. miraguama* and associated taxa would be better placed in the

Pauciramosa group near *C. yuraguana.* Indeed, R. W. Read (pers. comm.) has opined that the two taxa may be conspecific. Such a move, in our opinion, makes the Argentata phenetic group more homogeneous and places in the Pauciramosa phenetic group all the taxa with similar character state combinations. This change would also reduce the homoplasy in certain characters, e.g., the number of sheath layers (character 3) and the presence of spinelike free sheath tips (character 6). The homoplasies that would remain, or become more homoplasious as a result of this action, are quantitative vegetative characters (leaf segment number (character 11), length (character 12), and fusion (character 13)).

Thus, it is clear that reliance on published data provides only a few significant classificatory characters, as well as numerous characters that are weak indicators of relationships. In our analyses, the latter tend to swamp out the former. However, by completing multiple analyses and by comparing the results with the published intuitive classifications and with living plants, we are able to draw two significant conclusions. First, the distinction between more reliable and less reliable characters is clarified. Second, additional morphological features that suggested patterns of affinities can be correlated with the reliable characters to produce eclectic, easily recognizable groups of intermediate size (TABLE 3). These eclectic groups are temporarily useful in assisting workers to focus efforts in field studies and on determining species limits. Future studies should concentrate on character data, both vegetative and reproductive, that can be compared among all species before meaningful hypothesis testing can begin. Our arrangement of taxa in TABLE 3 provides a framework for such studies as well as preliminary but readily testable hypotheses.

LITERATURE CITED

ADAMS, R. P. 1975. Statistical character weighting and similarity stability. Brittonia 27: 305–316.

ALMEIDA, M. T. AND F. A. BISBY. 1984. A simple method for establishing taxonomic characters from measurement data. Taxon 33: 405–409.

BAILEY, L. H. 1939. *Coccothrinax* in the southern Greater Antilles. Gentes Herb. 4: 247–259.

BORHIDI, A. AND O. MUÑIZ. 1971. Contributiones novae Florae Cubanae. I. Bot. Kölem. 58: 175–177.

——— AND ———. 1972. (1971). New plants in Cuba. II. Acta Bot. Acad. Sci. Hung. 17: 1–36.

——— AND ———. 1985. Adiciones al catalogo de las Palmas de Cuba. Acta Bot. Hung. 31: 225–230.

———, N. IMCHANITZKAYA, AND O. MUÑIZ. 1978. Dendrological novelties in the Flora of Cuba. Acta Agronom. Acad. Sci. Hung. 27: 428–437.

DONOGHUE, M. J. AND P. D. CANTINO. 1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Syst. Bot. 9: 192–202.

GLASSMAN, S. F. 1972. A revision of B. E. Dahlgren's index of American palms. Verlag von J. Cramer, Lehre, Germany. 294 pp.

GOWER, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53: 325–338.

———. 1971. A general similarity coefficient and some of its properties. Biometrics 27: 857–871.

LEÓN, H. 1939. Contribuçión al estudio de las palmas de Cuba: genero *Coccothrinax.* Mem. Soc. Cub. Hist. Nat. 13: 107–156.

MOORE, H. E. 1973. The major groups of palms and their distribution. Gentes Herb. 11: 27–141.

MUÑIZ, O. AND A. BORHIDI. 1982a. (1981). Palmas nuevos del genero *Coccothrinax* Sarg. en Cuba. Acta Bot. Acad. Sci. Hung. 27: 439–454.

——— AND ———. 1982b. Catalogo de las Palmas de Cuba. Acta Bot. Acad. Sci. Hung. 28: 309–345.

NAUMAN, C. E. 1982. Modal or mean character state values in plant descriptions? Taxon 31: 716–717.

——— AND R. W. SANDERS. 1991. An annotated key to the cultivated species of *Coccothrinax.* Principes 35: 27–45.

QUERO, H. J. 1980. *Coccothrinax readii,* a new species from the peninsula of Yucatan, Mexico. Principes 24: 118–124.

READ, R. W. 1966a. *Coccothrinax inaguensis*—a new species from the Bahamas. Principes 10: 29–35.

———. 1966b. *Coccothrinax jamaicensis.* The Jamaican silver thatch. Principes 10: 133–141.

———. 1980. Notes on Palmae, I. Phytologia 46: 285–287.

TOMLINSON, P. B. 1964. The vascular skeleton of coconut leaf base. Phytomorphology 14: 218–230.

UHL, N. W., J. DRANSFIELD, K. S. HANSEN, AND J. C. DOYLE. 1990. Phylogenetic analyses within the Coryphoideae (Palmae). Amer. J. Bot. 77 (Suppl. to no. 6): 160–161. (Abstract).

APPENDIX I. CHARACTERS AND CHARACTER STATE CODING. All character states coded as 0 are considered plesiomorphic; apomorphies are coded 1 or 2. The method of polarity assessment is given in parentheses following the character states.

1. Caudex maximum diameter (excluding persistent leaf sheaths and petiole bases). 0 = generally <2 dm; 1 = generally ≥2 dm. (outgroup).
2. Caudex up to 3 dm and ventricose. 0 = no; 1 = yes. (outgroup).
3. Sheath layers. The leaf sheath is composed of a network of enlarged fibrovascular bundles. These are the "sheath fibers" of other students of *Coccothrinax.* We here follow Tomlinson (1964) in calling them strands. The strands are arranged in layers where those within a layer are parallel to one another and more or less perpendicular to those of adjacent layers. Strands within a layer are held together by a reticulum of decidedly smaller cross-strands that branch at right angles to, and interconnect with, adjacent main strands. The number of layers was determined from mature sheaths near or at the apex of the sheath body, or base of the free tip if present. 0 = 2 or 2 with a 3rd indistinct layer; 1 = 3 layers. (outgroup).
4. Leaf sheath strand thickness, as the average width of the thicker strands in the body of the leaf sheath. 0 = up to 2 mm wide; 1 = 2.1–4.9 mm wide; 2 = 5 or more mm wide. (outgroup).
5. Leaf sheath strand spacing at the sheath body. 0 = tight (i.e., ≤1 × the strand thickness between strands); 1 = open. (outgroup).
6. Length of free leaf sheath strand tips (those due to fusion of bundles and lack of cross connections) at the sheath tip. 0 = <1 cm long; 1 = 1–2.9 cm long; 2 = ≥3 cm long. (ontogeny).
7. Length of free leaf sheath strands (those due to elongation of the sheath tip and fragmentation of the sheath, i.e., splitting of the strands from each other) greater than 10 cm. 0 = no; 1 = yes. (ontogeny).
8. Free leaf sheath strands with uncinate tips. 0 = no; 1 = yes. (ontogeny).

APPENDIX I. Continued.

9. Petiole length routinely less than 2 dm long. 0 = no; 1 = yes. (outgroup).
10. Lamina outline less than ½ orbicular. 0 = no; 1 = yes. (outgroup).
11. Segment number. 0 = 55 or more; 1 = 35 to 54; 2 = 34 or less. (outgroup).
12. Segment length. 0 = 4.1–6.9 dm; 1 = ≥7 dm; 2 = ≤4 dm. (outgroup).
13. Greater palman length. The palman is that portion of the leaf consisting of fused segments and excludes the free segment apices. Greater palman was measured as the length of the fused region between the central pair of segments. 0 = ≥1.3 dm; 1 = <1.3 dm. (outgroup).
14. Segments widest past the sinus. 0 = yes; 1 = intermediate or about at the sinus; 2 = no. (outgroup).
15. Lorica remnants generally present. 0 = no; 1 = yes. (outgroup).
16. Abaxial lamina indumentum color. 0 = concolorous; 1 = grayish, white, or silvery. (ontogeny).
17. Transverse veins obviously present. These are veins running perpendicular to the long axis of the segment. Such veins were considered present only if a well-developed reticulum is exhibited, i.e., one that can be easily seen with the unaided eye or a handlens. 0 = yes; 1 = no. (outgroup).
18. Adaxial hastula (ligule) apex bifid. 0 = no; 1 = sometimes; 2 = characteristically. (outgroup and ontogeny).
19. Rachilla length. 0 = <24 cm; 1 = ≥24 cm. (outgroup).
20. Anther length. 0 = <5 mm long; 1 = ≥5 mm long. (outgroup).
21. Ovary surface muricate. 0 = no; 1 = yes. (ontogeny).
22. Exocarp tan at maturity. 0 = no; 1 = yes. (outgroup and ontogeny).

APPENDIX II. RAW DATA MATRIX FOR PHENETIC AND CLADISTIC ANALYSES. OTU numbers are those listed in TABLE 1, character numbers are those listed in APPENDIX I. When character states for a given OTU were unknown or unavailable, the most parsimonious states were inserted by PAUP; these are indicated by underlining.

	Character																					
OTU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1.	0	0	$\underline{0}$	$\underline{0}$	1	0	0	0	0	1	1	0	0	2	0	0	1	0	0	0	0	$\underline{0}$
2.	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	$\underline{1}$	0	0	0	0	0
3.	0	0	$\underline{0}$	0	$\underline{0}$	0	0	0	0	0	0	1	$\underline{0}$	$\underline{0}$	$\underline{0}$	1	0	0	0	$\underline{0}$	0	0
4.	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1	1	0	0	0	0	0
5.	0	0	$\underline{0}$	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0
6.	0	0	0	0	0	0	0	0	0	0	2	0	0	$\underline{0}$	$\underline{0}$	1	1	0	$\underline{0}$	$\underline{0}$	0	0
7.	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0
8.	0	0	1	0	0	0	0	0	0	0	2	2	1	$\underline{0}$	$\underline{0}$	1	1	0	0	$\underline{0}$	0	0
9.	1	0	0	0	0	0	1	0	1	0	1	0	0	$\underline{0}$	0	1	1	0	0	$\underline{0}$	0	0
10.	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	$\underline{0}$	$\underline{0}$	0	0
11.	0	0	0	1	1	2	0	0	0	0	2	0	1	0	0	1	1	0	0	0	0	0
12.	0	0	$\underline{0}$	$\underline{0}$	$\underline{1}$	0	0	0	0	0	2	2	1	$\underline{2}$	$\underline{0}$	0	1	0	0	0	0	0
13.	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0
14.	0	0	$\underline{0}$	0	0	1	0	0	0	0	1	0	0	$\underline{0}$	$\underline{0}$	1	1	0	0	$\underline{0}$	0	$\underline{0}$
15.	0	0	0	1	1	1	0	0	0	1	2	2	1	0	0	1	1	0	0	0	1	1
16.	0	0	$\underline{0}$	0	1	0	0	0	0	0	2	2	1	$\underline{2}$	0	1	$\underline{1}$	0	0	0	0	0
17.	0	0	$\underline{0}$	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
18.	0	0	0	0	0	2	0	0	1	0	2	2	1	0	0	1	1	0	0	0	0	0
19.	0	0	$\underline{0}$	0	1	0	0	0	0	0	2	1	1	$\underline{0}$	$\underline{0}$	1	1	0	0	$\underline{0}$	0	0
20.	0	0	0	0	0	0	0	0	0	0	0	1	0	$\underline{0}$	$\underline{0}$	1	0	0	$\underline{0}$	$\underline{0}$	0	0
21.	1	0	0	1	1	2	0	1	0	0	1	1	0	$\underline{0}$	0	1	1	0	0	0	0	0
22.	0	0	0	0	0	0	0	0	0	0	0	1	0	$\underline{0}$	0	1	0	0	0	0	0	0
23.	0	0	0	0	0	0	0	0	0	0	1	2	0	0	1	0	1	0	0	0	0	0
24.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
25.	0	0	$\underline{0}$	0	0	0	0	0	0	0	1	0	1	$\underline{0}$	$\underline{0}$	1	1	0	$\underline{0}$	$\underline{0}$	0	0
26.	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0
27.	0	0	0	0	1	1	0	0	0	0	1	1	0	$\underline{0}$	$\underline{0}$	1	1	0	$\underline{0}$	0	0	0
28.	0	0	0	0	1	2	0	0	1	1	2	2	1	$\underline{0}$	$\underline{0}$	1	1	0	0	1	0	0
29.	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0
30.	0	0	1	0	0	0	0	0	0	0	2	2	1	$\underline{0}$	0	1	1	0	0	$\underline{0}$	0	$\underline{0}$
31.	$\underline{1}$	$\underline{0}$	$\underline{0}$	0	1	$\underline{0}$	$\underline{0}$	$\underline{0}$	0	0	$\underline{0}$	0	0	$\underline{1}$	$\underline{0}$	0	1	0	$\underline{0}$	$\underline{0}$	$\underline{1}$	1
32.	0	0	0	1	0	1	0	0	0	1	2	2	1	0	0	1	1	0	0	0	1	1
33.	0	0	0	0	0	1	0	0	0	0	2	$\underline{2}$	1	$\underline{2}$	0	0	$\underline{1}$	0	0	0	1	$\underline{0}$
34.	0	0	0	1	0	2	0	0	0	0	2	2	1	$\underline{0}$	$\underline{0}$	1	1	0	0	0	0	0
35.	0	0	1	0	0	0	0	0	0	0	2	2	1	$\underline{0}$	$\underline{0}$	1	1	0	$\underline{0}$	$\underline{0}$	0	0
36.	0	0	0	0	1	2	0	0	0	0	2	2	1	$\underline{0}$	$\underline{0}$	1	1	0	0	$\underline{0}$	0	0
37.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0
38.	0	0	0	1	0	2	0	0	0	0	2	2	1	0	0	1	1	0	1	0	0	0
39.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	2	0	0	0	0
40.	0	0	0	0	1	1	0	0	0	0	2	2	1	2	0	0	$\underline{1}$	0	$\underline{0}$	0	0	0
41.	0	0	0	2	0	2	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	$\underline{0}$
42.	0	0	0	0	1	1	0	0	0	0	2	2	0	0	0	1	1	0	0	$\underline{0}$	1	$\underline{0}$
43.	0	0	0	0	1	1	0	0	0	1	2	2	1	0	0	1	1	0	0	0	0	0
44.	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
45.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
46.	0	0	0	2	1	2	0	0	0	0	1	0	0	0	0	1	$\underline{1}$	0	0	$\underline{0}$	0	$\underline{0}$
47.	0	0	1	0	0	0	0	0	0	0	2	2	1	0	0	1	$\underline{1}$	0	0	$\underline{0}$	0	$\underline{0}$