To the Graduate Council:

I am submitting herewith a dissertation written by Clifton Edward Nauman entitled "A Systematic Revision of the Neotropical Species of Nephrolepis Schott." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

A. Murray Evans, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Vice Provost
and Dean of The Graduate School

A SYSTEMATIC REVISION OF THE NEOTROPICAL SPECIES OF *NEPHROLEPIS* SCHOTT

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Clifton Edward Nauman

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ABSTRACT

This study was a systematic revision of the neotropical species of Nephrolepis Schott. The genus has been plagued with chronic misapplication of epithets, misidentifications, and has not been critically revised since its recognition in 1834. This was the first detailed study of any portion of the genus utilizing modern taxonomic procedures. An initial classification was proposed from a study of morphological features using cluster analysis and principle coordinate analysis. These results were compared with species groups indicated by other categories of taxonomic evidence including palynology, gametophyte development and morphology, cytology, chemotaxonomy, phytogeography, and ecology. Artificial hybridization was also attempted in order to establish the hybrid origin of one taxon. Information from these additional data categories (except the gametophyte and hybridization studies) variously supported or conflicted with portions of the initial classification. Data from all of the categories were then integrated to produce a final phenetic classification. This final classification served as the basis for the taxonomic treatment. A conspectus of the entire genus was compiled as a preliminary step to future study and as a framework for indicating relationships of the neotropical species within the genus as a whole.

Relationships depicted by the initial morphological study were largely confirmed by data from palynology, cytology, chemotaxonomy, phytogeography, and ecology. Gametophyte and hybridization

studies did not reveal additional information of value in comparing species. Because the information from the other data categories largely supported the morphological relationships, the final classification was not radically different from the initial one.

Nine species were recognized in the final classification with the following relationships: Nephrolepis x averyi Nauman (an allotetraploid hybrid between N. biserrata (Swartz) Schott and N. exaltata (L.) Schott) and N. exaltata were the two most closely related species; N. rivularis (Vahl) Mett. ex Krug is most related to the former two species, but it is still a relatively distinct species; N. cordifolia (L.) Presl and N. occidentalis Kunze form a species pair most related to the preceding three species; N. pectinata (Willd.) Schott and N. pendula (Raddi) J. Smith form a species pair next most related to the preceding five species; and N. biserrata and N. multiflora (Roxb.) Jarret ex Morton form a distinct species pair well separated from the other species.

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CHAPTER I

INTRODUCTION

Nephrolepis Schott is a distinct group of about 30 species characterized primarily by vegetative features including the production of stolons and once pinnate fronds in which the pinnae are articulated to the rachis. Other features characterizing the genus include sori at the ends of free, forking veins; bilateral, monolete spores; indusiate soral structures ranging from discrete, circular, submedial sori [e.g., N. biserrata (Swartz) Schott] to nearly marginal coenosori [e.g. N. acutifolia (Desv.) Christ]; a base chromosome number of n = 41, and a pantropical distribution, with at least one species occurring extratropically in Japan and New Zealand.

Present difficulties in the genus center around interspecific relationships. The distinctness of the genus as a whole, coupled with its wide cultivation, has perhaps led workers to assume casually that the species are similarly distinct. This is evidenced by a chronic misapplication of epithets, misidentifications in both cultivars and wild species, and resulting taxonomic confusion. Christensen (1932, p. 74) referred to N. abrupta (Bory) Mett., N. cordifolia (L.) Presl, N. exaltata (L.) Schott, and N. biserrata as, "all very difficult to define, and probably all are aggregates." Copeland (1947, p. 91), in reference to species of Nephrolepis, wrote,

> Several reguarded [sic] as pantropic, are remarkably variable and ill definable; apparently they hybridize

> freely in nature. For this reason, N. exaltata, N. biserrata, and N. hirsutula, as names applied to specimens, are conventional rather than specific.

Alan R. Smith (1981, p. 153) wrote, in reference to Mexican populations of N. pectinata (Willd.) Schott, "Monographic study is badly needed." In addition to the species mentioned above, N. multiflora (Roxb.) Jarrett ex Morton is also part of this problematic group. Neotropical specimens of this species have been misidentified as N. biserrata and N. exaltata (Nauman, 1979a). Proctor, as recent as 1985, wrote as a preface to a key to the Jamaican species, "The species of Nephrolepis are often difficult to distinguish, especially if well-developed mature fronds are not available; thus, the following key cannot be guaranteed to work in every case." The problems are severe enough that little value can be attributed to literature data on any given species unless voucher specimens can be verified.

A number of factors appear to be contributing to the confusion. Incomplete or unclear taxonomies have certainly played a part, but are often a reflection of the absence of reliable data for their compilation. As an example, two supposedly reliable characters that distinguish between N. biserrata and N. exaltata are indusium shape and attachment. Typical plants can be separated with these characters but occasionally indusia characteristic of both species as well as intermediate indusia types can be found on a single plant. Similar situations can be found for many of the supposedly reliable characters.

Although the problems of species relationships are world-wide in scope, problems in the neotropics appear to be more acute. For

example, of the 30 or more species, chromosome counts have been reported for only 11 species and forms. These reports show deviations from the diploid condition of n = 41 in five taxa. Three of these five exceptions to the typical diploid condition were reported for neotropical species. Distributions are incompletely known. Only recently has it been determined that N. exaltata may be largely restricted to the Caribbean (Nauman, 1979a, 1981a; Stolze, 1981) and not pantropical in distribution as it has been traditionally construed. This was based in part on a more restricted application of the epithet. The native range of N. cordifolia remains uncertain (Nauman, 1979a, 1981a; Pichi Sermolli, 1969); this species is so widely cultivated that its occurrence in any given locality may or may not be the result of spore dispersal and establishment without human aid. Nephrolepis multiflora is still expanding its range in the neotropics as an escaped cultigen and the factors that may eventually limit its expansion are only recently becoming clear (Nauman, 1979a). Hybridization has been a source of confusion between N. biserrata and N. exaltata in Florida (Nauman 1979b). Whether hybridization occurs between these two species outside of Florida or occurs among any of the other neotropical species has not been investigated. Studies of gametophyte development and morphology have been carried out for only seven species; none of these studies have been done with material of definite neotropical origin. The flavonoid chemistry is completely unknown. Similarly, data on spore morphology is conspicuously scarce or absent for many of the neotropical species.

The present study is intended to provide a systematic revision of the neotropical species of Nephrolepis. Data on 110 morphological characters were gathered from 773 sample specimens from throughout the neotropics. A preliminary numerical analysis was performed on this data set to provide an initial classification. Data from palnyology, gametophyte development and morphology, flavonoid and xanthone surveys, cytology, phytogeography, and ecology were then gathered and compared to the initial classification. Attempts were also made to synthesize N. x averyi Nauman, the only suspected hybrid species, to establish more firmly its hybrid origin and parentage. The classification ultimately adopted resulted from a numerical analysis of the information from all data categories.

The results indicated which of the data categories might be the most useful in future studies of the genus. Studies of morphology revealed that details of the indument are more important than traditional treatments might suggest and that various features of the sorus are less important. Gametophyte development and morphology are relatively uniform in all of the species and therefore, they are of little value in species comparisons. Similarly, cytology did not provide useful differences among the species, with the exception of the hybrid. Palynology, flavonoid and xanthone surveys, phytogeography, and ecology showed trends more or less corresponding to those of morphology alone.

The final classification recognizes nine taxa within the neotropics. One, N. x averyi, is a tetraploid hybrid between N. biserrata and N. exaltata. Nephrolepis multiflora is an escaped

Asian species now pantropical in distribution. Nephrolepis biserrata and N. cordifolia are both pantropical in distribution. Nephrolepis exaltata, N. occidentalis Kunze, N. pectinata, N. pendula (Raddi) J. Smith, and N. rivularis (Vahl) Mett. ex Krug are all neotropical in distribution.

CHAPTER II

MORPHOLOGY

This chapter presents various observations on both macro- and micro-morphology of the neotropical species of Nephrolepis. In the present study morphology provided the data to formulate an inintial classification. This initial classification will be compared with data in subsequent chapters to establish a final classification. Most of the remaining information presented in this chapter has been summarized in the taxonomic descriptions in Chapter X. The comments below pertain to general observations on the neotropical species not presented by previous authors, describe tendencies of variation in each species that may not be obvious from the taxonomic descriptions, and serve to document character state expressions and interpretations used in other chapters. To simplify presentation of data, the entities eventually recognized as species are treated as such and referred to by their specific epithets here and in later chapters.

Materials and Methods

General Morphology

More than 3000 specimens (see Appendix) from 61 herbaria (see Acknowledgments) formed the bulk of the material for morphological studies. The herbarium material was augmented with field observations (Florida, Brazil, Suriname, Trinidad, and Tobago), earlier transplant

experiments (Nauman, 1979a), and greenhouse grown materials. Live plants were partly collected in the field (by me in Florida and by Dr. A. M. Evans in Puerto Rico), and partly obtained from the New York Botanical Garden (see Acknowledgments). Material for microscopic studies came from the same specimen sources.

For indument and sporangium studies materials were mounted in Diaphane or Euparal after air drying or immersion in 99% ethanol, or examined as part of epidermal preparations. Epidermal preparations were made by relaxing air dried material for 2-3 days in 5% sodium hydroxide, bleaching with 0.5% sodium hypochlorite (10% commercial bleach), and staining with the tannic acid-ferric chloride technique without counter staining (Foster, 1934). Drawings were made with a Bausch & Lomb microprojector or a drawing tube attached to a Nikon standard microscope. Drawings of macroscopic features (e.g., pinnae) were made from photographic or xerographic reproductions of both fresh and preserved materials.

Numerical Analysis

Measurements of 110 characters were made on specimens (see Appendix) representing all taxa throughout the neotropics. The characters were those used by previous authors to distinguish among the taxa and additional characters thought to be of potential value for indicating systematic relationships. The latter characters were chosen on the basis of preliminary studies, part of which are included in Nauman (1979a). Of the 773 specimens scored, 442 were variously pooled and used in the numerical analyses outlined below.

The OTU's (operational taxonomic units) employed in the numerical analysis consisted of single or multiple specimen samples of local populations, largely herbarium material. Though extensive data were obtained for some local populations (e.g., Florida), similarly intensive sampling was not feasible over the entire study area. Because of sampling limitations, single specimen samples from a given local area were assumed to be representative of the local population. Comparisons of specimens represented by several collections or duplicates, indicated that randomly chosen unicates fell within one or two standard deviations of the mean value for any randomly selected character. In the case of skewed character state distributions, the unicates were near the modal values computed for the duplicates as a whole. This is based on studies of Florida populations for which numerous collections were available and elsewhere on samples of duplicate collections available through herbarium loans. The ability of the unicates to represent the local populations may be partly due to the fact that what might be construed in most sampling procedures as a local population of Nephrolepis is often a colony formed through extensive asexual reproduction from a few individuals.

Samples were assembled by pooling data from subdivisions of the overall study area. For this purpose, the study area was divided into seven regions (see Figure 1) corresponding to the major phytogeographic regions represented in the neotropics [based on Cronquist's (1982) and Good's (1974) floristic regions].

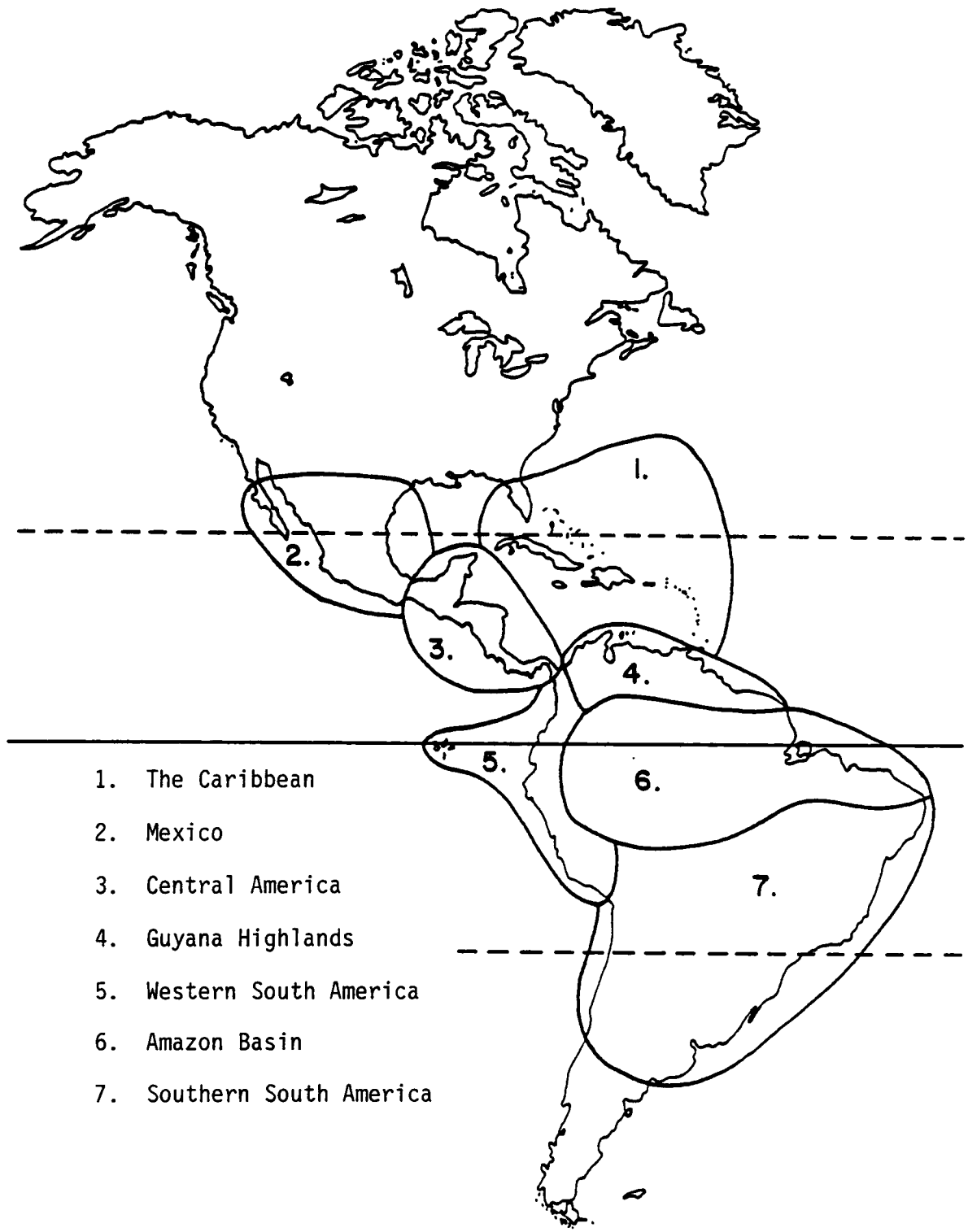


Figure 1. Phytogeographic regions recognized for the initial numerical analysis.

The OTU's used in the numerical analysis were pooled samples of local populations (represented by one to many specimens) of a given morphological group within one of the seven phytogeographic regions. Within each phytogeographic region individual specimens could be separated into nine morphological groups (e.g., those with tubers and those without tubers, etc.). Each morphological group in each region was treated as a separate OTU in subsequent numerical analysis. Not all of the 63 possible combinations of morphological group and phytogeographic region were available for analysis. Some of the morphological groups were not represented in every phytogeographic region (e.g., N. x averyi) and for others the data sets were not complete. As a result, a total of 43 OTU's were represented in the initial numerical analysis.

Not all of the characters evaluated in the preliminary analysis were suitable for subsequent numerical study and some were eliminated from the later phases of analysis. The criteria for retaining or rejecting a character for use in the analysis included the following: 1) The character had to exhibit some variation within or among OTU's. This procedure emphasizes character differences among OTU's. Additionally, in situations where intra-OTU variation was greater than inter-OTU variation [i.e., where F-1 weighting (sensu Adams, 1974) 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. For example, sterile frond characters were eliminated

because they were present on fewer than one-third of the overall sample of 442 specimens and present for fewer than 5% of some OTU's. 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 character complexes, the initial 110 characters were narrowed to 32. Of these 32, 24 (Table 1) were used for analysis. The eight characters not employed were largely size measurements combined as ratios in other characters.

Character states used in the raw data matrix are modal values computed from the OTU samples. Morphological measurements of the 24 characters in Table 1 were pooled for each OTU and a statistical summary compiled for each character. The statistical summary included the mean, standard deviation, variance, coefficient of variation, third and fourth central moment statistics, range, sample size, and standard errors for each statistic. Computations were carried out with a Texas Instruments TI 59 Programmable calculator with programs written by the author. The central moment statistics are indicators of skewness and kurtosis and if either statistic demonstrated significant differences ($p<0.05$) from that expected for a normal distribution, the distribution was considered non-normal. Modal values for non-normally distributed characters were computed from frequency distributions, also generated from the TI 59 but with different programs. Frequency distributions were constructed by partitioning the range into 10 class intervals. For normally

Table 1. List of characters used in the initial numerical analysis.

Character	Character States and Coding
1. Tubers	1 - present 0 - absent
2. Frond length/width ratio	
3. Stipe color	1 - stramineous 2 - brown 3 - castaneous (dark brown) 4 - black to purple-brown
4. Stipe scale density	1 - none or a few at the base 2 - moderate 3 - dense
5. Rachis/Stipe length ratio	
6. Rachis color	1 - stramineous 2 - brown 3 - castaneous (dark brown) 4 - black to purple-brown
7. Rachis scale density	1 - none or a few at the points of pinna attachment 2 - moderate 3 - dense
8. Interpinnal distance	Distance between adjacent pinnae on one side and in the central portion of the rachis in mm
9. Pinna length	Central pinnae in cm
10. Pinna length/width ratio	Central pinnae
11. Lower pinnae length/width ratio	Lowermost pinnae
12. Pinna margin type	1 - entire 2 - finely denticulate 3 - serrulate 4 - biserrate 5 - crenulate 6 - irregularly serrulate

Table 1 (Continued)

Character	Character States and Coding
13. Pinna shape	1 - oblong 2 - triangular 3 - elliptic-lanceolate to oblanceolate 4 - oblanceolate to obtriangular (widest near the apex)
14. Degree of "falcateness"	1 - not falcate 2 - slightly falcate 3 - distinctly falcate
15. Pinna attachment	0 - less than 1/2 of the distal pinnae basally attached 1 - more than 1/2 of the distal pinnae basally attached
16. Pinna base shape	1 - cuneate 2 - truncate 3 - cordate 4 - incised acroscopically and rounded to cordate basiscopically 5 - other
17. Pinna apex	1 - blunt 2 - deltoid to acute 3 - acuminate to abruptly so
18. Pinna pubescence density	1 - none 2 - few 3 - moderate 4 - dense
19. Pinna scale density	1 - none 2 - few (scattered along costa) 3 - moderate 4 - dense
20. Stellate scales	0 - absent 1 - present
21. Upper costa pubescence density	1 - none 2 - few 3 - dense

Table 1 (Continued)

Character	Character States and Coding
22. Acroscopic lobe shape	1 - none to obtuse 2 - deltoid to acute 3 - oblong
23. Sorus location	1 - supramedial 2 - intermediate 3 - medial (1/2 way between the costa and margin)
24. Indusium shape and attachment	1 - lunar to reniform and attached along the sinus 2 - hippocrepiform to circular and attached by a narrow point in the sinus 3 - circular and peltate

distributed characters the mean was used directly, since for such distributions the modal value is the mean value. For 2-state characters and multistate disordered characters modal values were calculated from the frequency distributions.

Once the preliminary statistical summaries and modal values were generated, those OTU's for which there were complete data sets were selected for numerical analysis.

The numerical analysis consisted of: 1) generating the similarity coefficient of Gower (Gower, 1971) for all possible pairwise combinations of OTU's, 2) cluster analysis (CA) of the OTU's using UPGMA (unweighted pair group method--using arithmetic averages) and construction of a phenogram, and 3) principle coordinate analysis (PCA) on the matrix of similarity values. The analysis was carried out on the University of Tennessee Computer System using programs written by Dr. E. E. Schilling (pers. comm.).

Though most of the taxa eventually recognized were readily separable entities, those which are included among the taxa traditionally recognized as N. cordifolia, N. pectinata, and N. pendula appeared problematic. Nephrolepis cordifolia has been considered conspecific with N. pendula by previous authors (Stolze, 1981; Tryon, 1964; Tryon and Tryon, 1982). To evaluate this hypothesis the same numerical analysis outlined above was performed with the following modifications. Individual specimens pooled for the initial analysis of N. cordifolia and N. pendula were employed as 34 separate, single-specimen OTU's. Forty specimens of N. pectinata from the initial

analysis were also included since some relationships to the other two taxa were indicated by the initial analysis. Nineteen of the 24 characters in Table 1 were used for the data matrix. The five excluded characters were those whose character states were constant across all 74 of these OTU's.

A summary of the initial analysis was also performed to simplify presentation and to emphasize the relationships among the species expressed by morphology. In this summary, the OTU's representing each species in the initial analysis were pooled to form nine OTU's. The character of stellate scales (no. 20 in Table 1) was combined with scale density (no. 19 in Table 1) on the basis of subsequent microscopic study. The CA and PCA procedures were otherwise the same as those of the initial analysis.

Results and Discussion

Plants

Plants of Nephrolepis consist of a short, more or less erect rhizome surrounded by a tuft of simply pinnate, erect to pendulous fronds. In addition to fronds, the rhizomes produce roots and lateral slender rhizomes (stolons). The plants may be terrestrial, epiphytic, or found growing in pockets of humus on rocks. Individual species can not be distinguished by growth habit (e.g., terrestrial or epiphytic) except in terms of general tendencies related in part to the size of the plants. Larger species (e.g., N. biserrata) are generally terrestrial but may also be epiphytic. Smaller species

(e.g., N. pectinata) may be terrestrial or epiphytic. Only N. occidentalis appears to be primarily restricted to terrestrial growth, but may also be found on mossy rocks or as an epiphyte. All species are perennial in growth, i.e., they produce fronds all year, except N. occidentalis, which exhibits a seasonal growth from tubers.

Rhizomes

The rhizome is erect to suberect, producing fronds, stolons, and roots on all sides. There is no dorsiventral orientation as in Davallia Smith. Vascularization is dictyostelic with leaf gaps and more than one trace per frond (Arbeleaz, 1928; Bower, 1928; Case, 1932; Espagnac, 1973; Holttum, 1949; Sporne, 1962; Richards et al., 1982). The protoxylem is mesarch (Sen and Sen, 1973). Leaf traces consist of a U-shaped bundle of several traces that fuse into a single trace in distal portions of the frond (Case, 1932; Holttum, 1954; Sen and Sen, 1973). Stolons emerge near the base of each frond, usually one per frond. Sahni (1915) and Case (1932) concluded that the stolon represents a specialized cauline structure. Other details of the vasculature have been described elsewhere (Bierhorst, 1977; McAlpin and White, 1974; Mahabale and Javalgekar, 1959; Sahni, 1915, 1916; Sen and Sen, 1973; Wagner, 1952).

The rhizome tends to be obconical in shape (the distal younger portions being wider) and may be covered with persistent leaf bases. The indument consists of peltate scales that are usually absent in older portions of the rhizome.

The rhizomes are relatively uniform in most characters with differences among the species occurring largely in overall size and indument features. Size of the rhizome is correlated to overall plant size, in particular frond length. The species can not be distinguished by rhizome size except for extremes, e.g., larger rhizomes (more than 15 cm long) are not found in typically small species (e.g., N. pectinata). The rhizome of N. occidentalis, because of its seasonal growth is generally small, poorly developed, and bears only a few fronds.

The rhizome indument consists entirely of scales. The various deciduous and glandular trichomes described by Sen and Sen (1973) for young scales of the rhizome have not been confirmed for the neotropical species. Glandular trichomes are present in young sporophytes of N. biserrata, N. cordifolia, N. exaltata, N. multiflora, and N. pendula on the stipes, rachises, and pinnae, but none were observed on the rhizome scales. Further observations are needed on scale development and the comments below pertain specifically to mature scales.

In the descriptions of the indument the terms papillate, ciliolate, and fibrillose are used to refer to marginal projections on the scales and are distinguished as: papillate--projections one to two times longer than wide, undivided, and distant from one another; ciliolate--projections more than two times longer than wide, divided one to two times or not, and separated from other projections by a distance greater than or equal to their length;

fibrillose--projections more than two times longer than wide, divided more than once or sinuous and close-set. The term "caudate" refers to scales in which the distal portion is conspicuously narrower than the proximal portion, i.e., "tail-like." Detailed descriptions of the indument for the entire plant are given for each species in the taxonomic descriptions in Chapter X. Illustrations of the indument are given for the rhizome scales, stolon scales (for one species), and pinna indument in the appropriate portions of this chapter.

Rhizome scales of N. cordifolia, N. exaltata, and N. occidentalis are similar. The rhizomes of these species are densely covered with light to dark brown or reddish brown, concolorous scales that extend to and intergrade with those of the stipe. The scales are loosely appressed to spreading except at the point of attachment. Shape of the scales ranges from narrowly triangular to lanceolate-attenuate (Figure 2). Basal portions of the scales (i.e., the end nearest the point of attachment) are generally the widest portion, are rounded in shape, and have margins ranging from papillate to ciliolate. The distal portions are entire to papillate. Tips of the scales may be uniseriate for 1/4 or more of the entire scale length.

In N. biserrata the rhizome scales are darker brown to black with a lustrous appearance. When young they are bicolorous (dark with a thin hyaline margin similar to N. multiflora) but become concolorous at maturity. The scales are similar in size to the

Figure 2. Rhizome scales of Nephrolepis cordifolia, N. exaltata, and N. occidentalis. (Bar = 2 mm; shading indicates the area of scale attachment.)

a. N. cordifolia.

b. N. exaltata.

c. N. occidentalis.

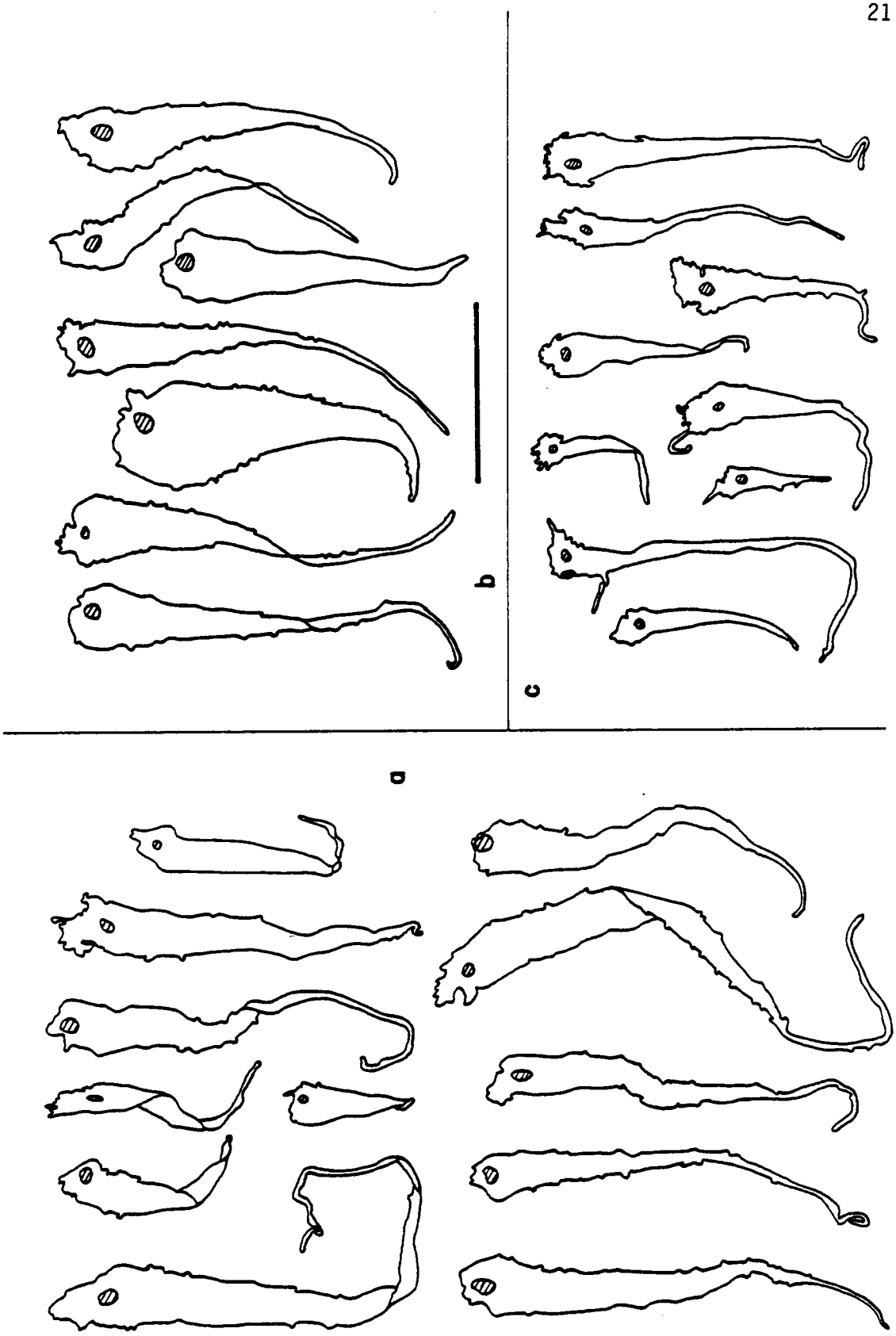


Figure 2

preceding three species but are more variable in margin and shape characters. Margins tend not to be entire, but are more often ciliolate with few papillae (Figure 3a). Shape is similar to the latter three species but there are circular, smaller scales present as in N. multiflora. The scales are loosely attached to the rhizome, ranging to barely appressed, but not as appressed as in N. multiflora and N. pendula. The scales are cauducous on stipe bases and croziers.

Nephrolepis x averyi has rhizome scales intermediate between N. exaltata and N. biserrata (Figure 3b).

Rhizome scales of N. rivularis are similar to those of N. cordifolia and N. exaltata in shape, but differ in other features. The color is a darker reddish-brown. The margins are indistinctly hyaline (i.e., bicolorous but not comparable to the condition in N. multiflora, and here considered essentially concolorous). The margins may be papillate but are more often ciliolate (Figure 3c). Scales may extend on to the stipe base as in N. exaltata and N. cordifolia.

Rhizome scales of N. multiflora differ from the other species in several ways. The scales are dark reddish-brown to (more often) black with a lustrous appearance, tend to be tightly appressed to the rhizome, and bicolorous with a hyaline margin. The margin generally lacks papillae and is ciliolate to fibrillose (Figure 4a). There is a progression in size and shape of the scales from small (0.3-0.5 mm wide), circular to elliptic scales to larger (0.6-3.0 mm long, 0.6-1.0 mm wide), oblong to elliptic-oblong scales (Figure 4a). If a uniseriate tip is present, it is short, i.e., not 1/4

Figure 3. Rhizome scales of *Nephrolepis biserrata*, *N.* x *averyi*, and *N. rivularis*. (Bar = 2 mm; shading indicates the area of scale attachment.)

a. *N. biserrata*.

b. *N.* x *averyi*.

c. *N. rivularis*.

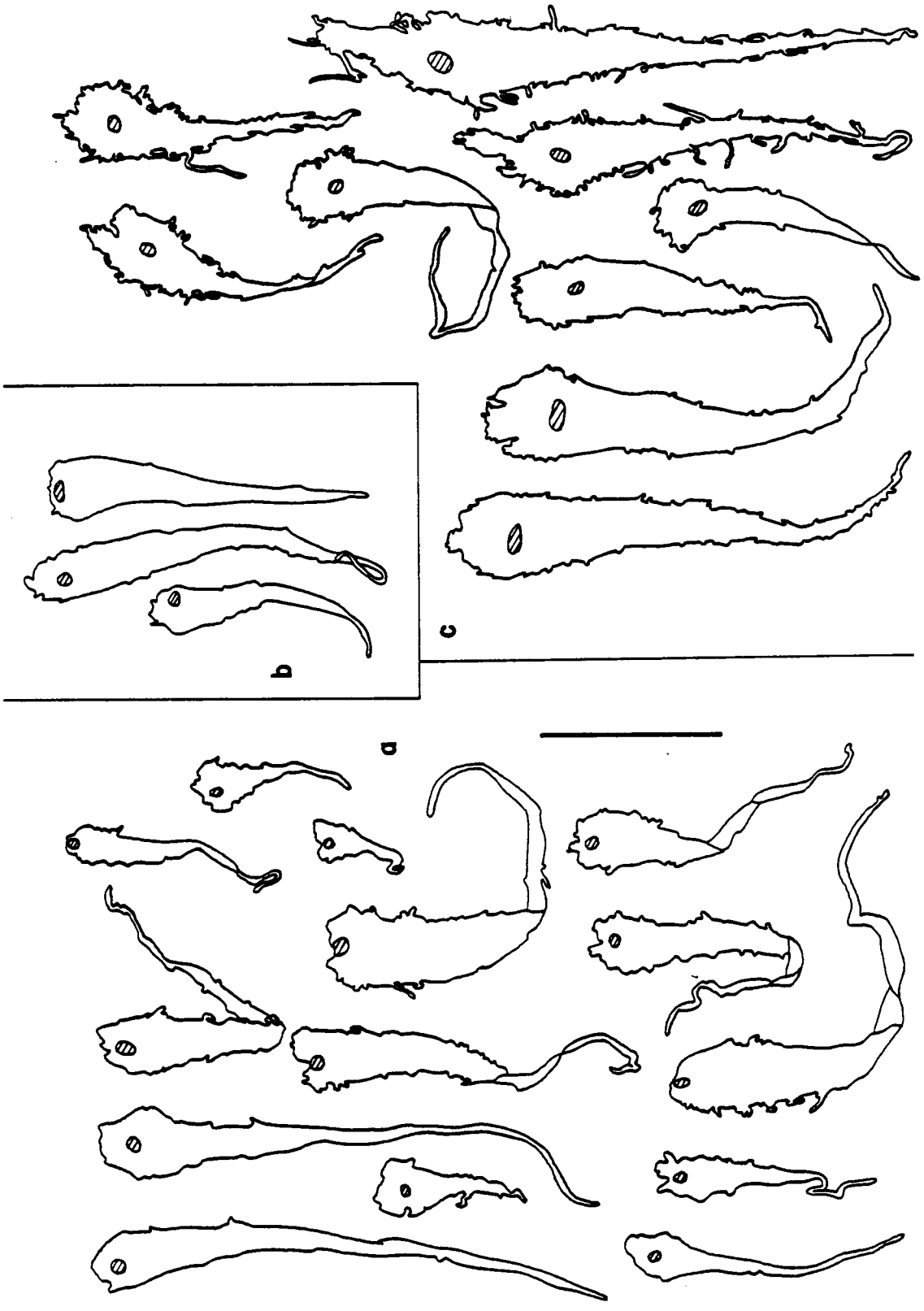


Figure 3

Figure 4. Rhizome scales of Nephrolepis multiflora, N. pectinata, and N. pendula, and stolon scales of N. cordifolia. (Bar = 2 mm; shading indicates the area of scale attachment.)

a. Rhizome scales of N. multiflora.

b. Rhizome scales of N. pectinata.

c. Rhizome scales of N. pendula.

d. Stolon scales of N. cordifolia.

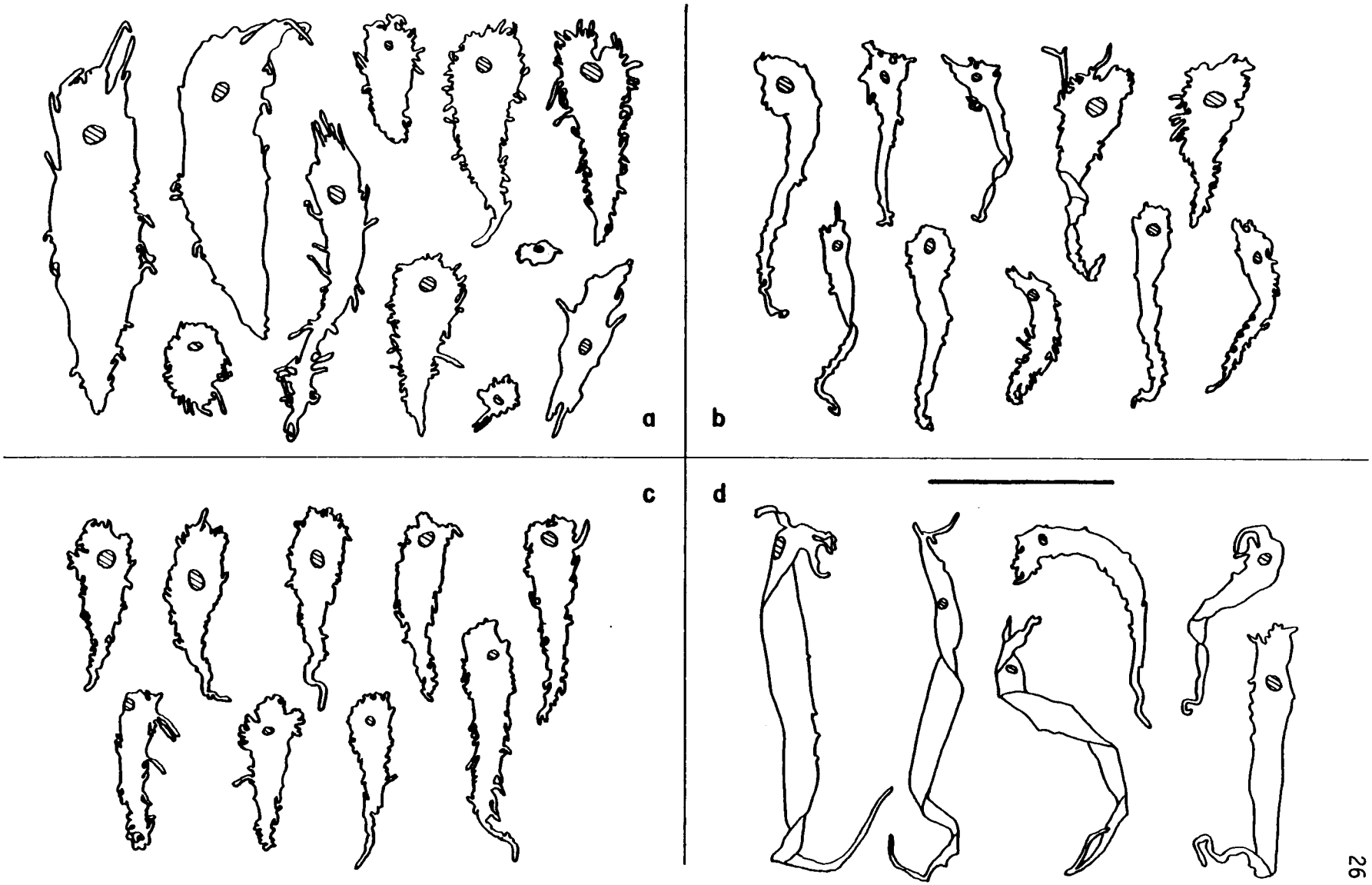


Figure 4

or more of the entire scale length. Scales extend on to and intergrade with those of the stipe.

Nephrolepis pectinata and N. pendula have similar scales, but show some differences. In both species the scales are small, dark brown to black, and differ from N. cordifolia (which they resemble in other features) by not becoming as reddish in color. Nephrolepis pendula possesses scales that are tightly appressed to the rhizome and are typically black and lustrous except for a form from the Galapagos Islands, Ecuador, and Central America that has slightly reddish scales. The scales of N. pectinata are seldom tightly appressed to the rhizome (most often being loose and spreading) and are rarely black and lustrous as are those of N. pendula. Shape of the scales in both species is narrowly triangular to lanceolate-attenuate (Figures 4b and 4c). Margins are typically ciliolate.

Stolons

Stolons are produced laterally from the rhizome in association with the leaves and are important in asexual reproduction and the production of tubers. Details of their internal anatomy have been described elsewhere (Arbeleaz, 1928; Bower, 1928; Case, 1932; Sahni, 1916; Sen and Sen, 1973).

Stolons bear new plants along their length, allowing the formation of sometimes extensive local colonies. Experimental studies by Espagnac (1973) with N. biserrata show that while still attached to the parental plant, a given stolon will undergo elongation, but once detached, young plants are formed (cf. also Richards et al.,

1982). Greenhouse and field observations indicate that plants may be produced while the stolon is still attached to the parental plant, but there is a minimum stolon length that must be obtained before new plants are produced.

With the exception of scale morphology and tuber production, the stolons provide essentially no major morphological distinctions among the neotropical species. Stolons of all the species vary from few to many per plant, generally one per frond. Color ranges from stramineous to dark brown in all species. Peltate scales are present in all species and resemble the rhizome scales in morphology. The only major differences from the rhizome scales are that the stolon scales are more medially attached and exhibit less ornamented margins (compare Figures 4d and 2a, page 20).

Tubers

Several species of Nephrolepis produce tubers (Arbeleaz, 1928; Copeland, 1947; Pichi Sermolli, 1969). The tubers are spherical to ellipsoidal or oblong in shape, covered with brown, peltate scales, and may reach several centimeters in length. Roots are produced irregularly over the entire tuber, but are concentrated near the ends. Tubers are most often produced along the stolons on short side branches, but may be borne by the rhizome directly in some species (Sahni, 1916). Vascularization is a system of dissected meristeles (Bower, 1928; Sahni, 1916) and there is a transition from the protostelic condition of the stolons to the dictyostelic condition of the tuber (Sahni, 1916). This same transition from

protostelic to dictyostelic exists at the junction of the stolon to the rhizome of offsets (Bower, 1928; Case, 1932). Further anatomical details may be found in Sahni (1916).

The tubers appear to act as storage organs. They have been reported to contain sugars and starch (Bower, 1928; Sahni, 1916), and may act as perenniating organs in regions with seasonally unfavorable growth conditions. It was proposed that the tubers were one of the reasons N. cordifolia has been able to extend its range farther north than other species in Florida (Nauman, 1979a).

In addition to a storage function, the tubers appear to play a role in asexual reproduction. Steil (1952) reported that tubers of N. cordifolia may produce one or more plants at either end when separated from the parental plant. Since an individual plant usually produces more than one tuber (Steil (1952) reported more than 200 per plant), the tubers may serve as a limited means of asexual reproduction.

Only two of the neotropical species produce tubers, N. cordifolia and N. occidentalis. Tubers in both species are borne on short side branches of the stolons. Nephrolepis occidentalis characteristically exhibits a seasonal growth from tubers produced in a preceding season. Stolon offsets produce tubers soon after establishment. Nephrolepis cordifolia, however, may or may not produce tubers. Whether tuber production in this species, or the lack of it, is controlled by environmental or genetic factors is at present uncertain. Field observations indicate that the tubers are restricted to plants

growing in humus. Tubers were not observed on epiphytic plants or plants growing in drier sites. These observations suggest some specific soil and moisture requirements for tuber production.

The tubers are densely covered with peltate scales. The scales are easily lost when the tubers are removed from the substrate or when substrate erosion exposes them. As a result, some collections may appear to have few scales. Tubers may also become green and presumably photosynthetic if exposed at the soil surface.

The tubers of N. cordifolia are spherical to ellipsoidal in shape, 1.0-3.5 cm long, 1-2 cm wide, and covered with concolorous, pale to reddish-brown scales. Tubers of N. occidentalis are more variable in shape and size than those of N. cordifolia. The tubers are usually elongate-ellipsoidal, but vary considerably with rare branching that results in a Y-shaped tuber. Length ranges from 1.0 to 3.5 cm and width from 0.4 to 2.0 cm. Tuber scales are less variable in shape than those of N. cordifolia and more distinctly caudate.

Fronds

Fronds in Nephrolepis are not articulated to the rhizomes and at the stipe base possess a variable number (1-11) of leaf traces that unite distally into a single strand in the rachis (Bower, 1928; Case, 1932; Espagnac, 1973; Sen and Sen, 1973). The fronds are typically once pinnate although divisions up to 4 or 5 times pinnate may occur in various cultivated forms.

Habit ranges from erect to pendulous and appears correlated to overall frond size and environmental conditions. Smaller fronds tend to be more erect in habit. More erect fronds are also found on plants growing in full sun or in otherwise drier conditions. Nephrolepis pendula typically has distinctly pendulous fronds, but shows enough variation that this feature is not entirely useful in distinguishing it from other species.

Texture ranges from almost membranous to coriaceous and is dependent on moisture availability; full sun and dry substrates result in fronds with a firmer texture.

Mature blades in all of the species are often found incompletely unfurled in the field and have been described as indeterminate (e.g., Wagner, 1952). Under greenhouse or relatively protected field conditions all of the species may produce a terminal portion. The terminal portions were not useful in distinguishing among the species.

Fertile pinnae are produced over the entire frond length in N. biserrata and N. multiflora. In N. exaltata and N. rivularis, only the distal 3/4 of the pinnae are fertile. Frequently sori on the proximal pinnae mature and fall off as distal portions of the blade are maturing; the blade appearing to have fertile pinnae only distally. This dropping of sori occurs in N. biserrata and N. multiflora, but is exhibited only on the lowermost pinnae. In N. cordifolia, N. occidentalis, N. pectinata, and N. pendula fertile pinnae are usually found on the distal 1/3 to 1/2 of the blade.

In N. x averyi fertile fronds are variable with 1/4 to 3/4 or more of the distal pinnae fertile.

Size measurements show various relationships among the species. Frond length ranges from 1.4 dm to 29.2 dm, far short of the 27 foot 3 inch (83.1 dm) mark given by Small (1918), or the 18 foot (54.9 dm) mark which he said (p. 132) was "not uncommon" for Florida plants. Three species can be grouped together as having small fronds, N. cordifolia, N. occidentalis, and N. pectinata (Figure 5 and Table 2). Though this might be useful for distinguishing species, there is still sufficient overlap with the other species to make the characters of frond length and width of little or no use at the lower end of the range of variation. There is a group of three species with relatively large fronds in terms of length; N. x averyi, N. biserrata, and N. pendula (Figure 5). Nephrolepis x averyi, though intermediate between its parental species (N. biserrata and N. exaltata) in many characters, here exceeds both in frond length. Frond width is within the range of its smaller parent, N. exaltata. Nephrolepis biserrata is the largest species in numerous morphological characters and is expected to have large fronds. Nephrolepis biserrata also has the widest fronds and exhibits considerable variation in this character compared to the other species. Nephrolepis pendula shows a range and pattern of variability similar to N. biserrata in frond length but is smaller in frond width.

The remaining species, N. exaltata, N. multiflora, and N. rivularis, make up a group with intermediate sized fronds (Figure 5).

Figure 5. Dice diagrams of frond length, width, and length/width ratio of the neotropical species of Nephrolepis. (Total bar length = range, black bar = one standard deviation above and below the mean, cross bar = mean; lengths and widths are given in dm.)

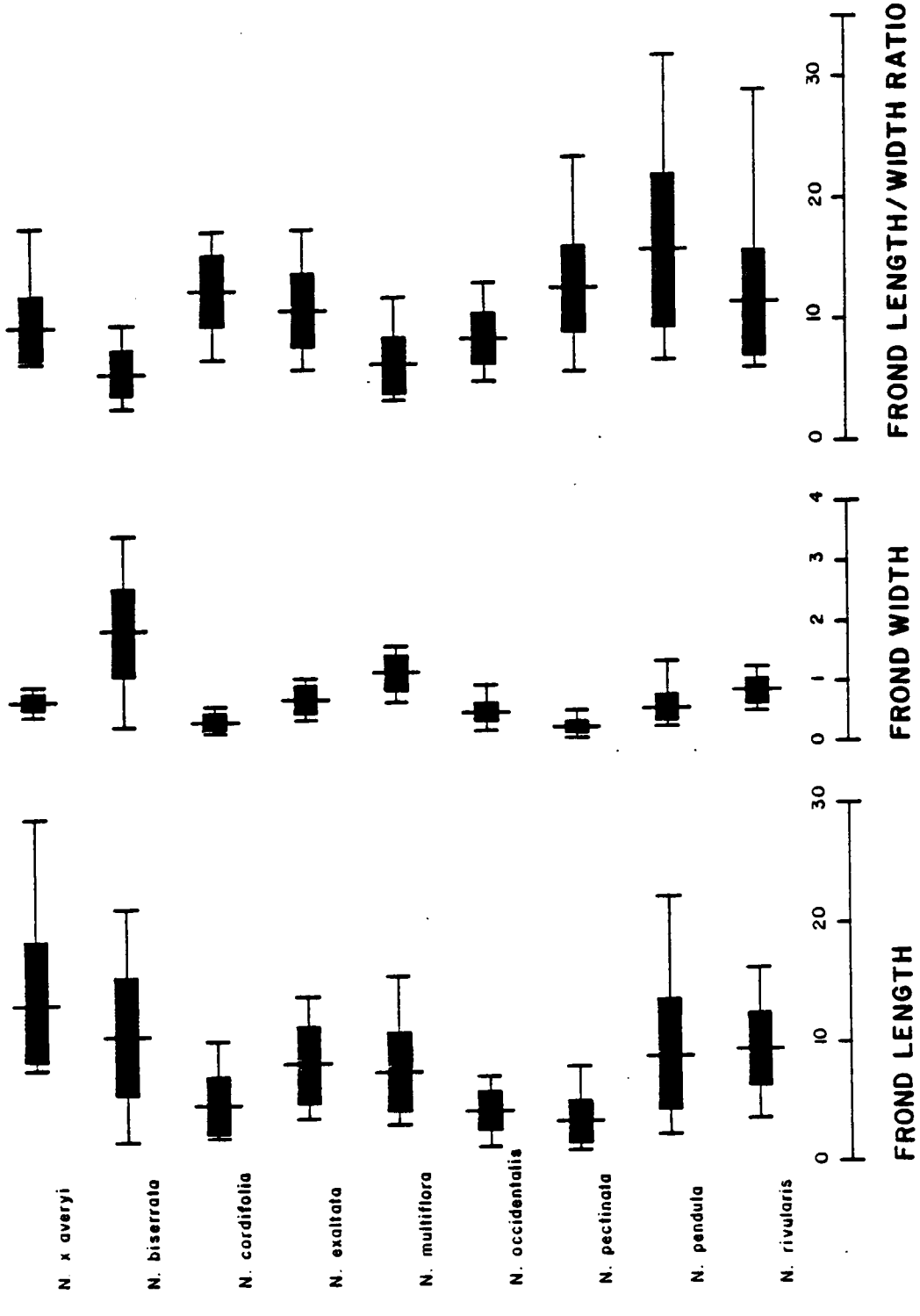

N x averyi
N. biserrata
N. cordifolia
N. exaltata
N. multiflora
N. occidentalis
N. pectinata
N. pendula
N. rivularis
FROND LENGTH
FROND WIDTH
FROND LENGTH/WIDTH RATIO
0
10
20
30
1
2
3
4

Figure 5

Table 2. Supporting data for Figure 5. Frond lengths, widths, and length/width ratios of the neotropical species of Nephrolepis. ($\bar{X}$ = mean, $S_{\bar{X}}$ = standard error of the mean.)

Species	$\bar{X}$	$S_{\bar{X}}$	Standard Deviation	Range
N. x averyi				
Length*	13.6	1.55	5.37	8.3 - 29.2
Width	0.8	0.04	0.15	0.5 - 1.0
Length/width	9.6	0.78	2.79	6.9 - 17.9
N. biserrata				
Length	11.0	0.71	4.89	2.2 - 21.6
Width	1.9	0.09	0.74	0.3 - 3.5
Length/width	5.8	0.26	1.76	3.0 - 9.9
N. cordifolia				
Length	5.3	0.62	2.38	2.5 - 10.7
Width	0.4	0.03	0.14	0.3 - 0.7
Length/width	12.9	0.76	2.93	7.1 - 17.7
N. exaltata				
Length	8.5	0.67	3.22	4.0 - 14.2
Width	0.8	0.04	0.21	0.5 - 1.2
Length/width	11.1	0.63	3.04	6.2 - 18.0
N. multiflora				
Length	7.9	0.68	3.24	3.5 - 15.9
Width	1.2	0.05	0.27	0.7 - 1.6
Length/width	6.6	0.47	2.24	3.7 - 12.0
N. occidentalis				
Length	4.6	0.23	1.51	1.8 - 7.4
Width	0.5	0.02	0.13	0.3 - 1.0
Length/width	8.6	0.36	2.13	5.0 - 13.2
N. pectinata				
Length	3.7	0.19	1.44	1.4 - 8.1
Width	0.3	0.01	0.08	0.1 - 0.6
Length/width	12.9	0.46	3.52	6.0 - 23.7
N. pendula				
Length	9.0	0.76	4.47	2.5 - 22.5
Width	0.6	0.03	0.21	0.3 - 1.4
Length/width	15.9	1.07	6.24	6.9 - 32.1

Table 2 (Continued)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. rivularis				
Length	9.6	0.50	3.04	3.9 - 16.5
Width	0.9	0.03	0.21	0.5 - 1.3
Length/width	11.6	0.70	4.28	6.3 - 29.1

*Lengths and widths are given in dm.

Frond width is similar among these species (slightly larger in N. multiflora) and lengths exhibit similar patterns of variation.

When the overall size factor is de-emphasized by combining length and width as a length/width ratio, slightly different species groupings are obtained. Nephrolepis biserrata and N. multiflora group together, exhibiting low length/width ratios within a relatively narrow range of variation. Fronds in these two species tend to be ovate to oblanceolate in shape. Nephrolepis cordifolia and N. exaltata possess narrower fronds with a linear to narrowly elliptic shape. Nephrolepis x averyi is intermediate between N. biserrata and N. exaltata. Nephrolepis occidentalis is intermediate between the N. biserrata-N. multiflora and N. cordifolia-N. exaltata groups. This species tends to have elliptic rather than linear elliptic fronds. Nephrolepis pectinata, N. pendula, and N. rivularis are characterized by larger length/width ratios and a greater range of variation. Nephrolepis rivularis has fronds with a shape as in N. cordifolia and N. exaltata, but is more variable. Nephrolepis pectinata and N. pendula have narrowly linear fronds; this is especially prominent in N. pendula.

Stipes and Rachises

Stipes and rachises of the neotropical species provide several characters important in analyzing relationships. Length measurements show the same relationships as general frond length. Interpinnal distance (greatest distance between adjacent points of pinna attachment on one side of the rachis measured in the central portion of

the rachis) is of use in extreme values. Stipe color and texture is of value in distinguishing N. pendula and some of its forms from other species. Rachis color is not of similar value. Indument features of both stipe and rachis, especially the former, are valuable in distinguishing among the species.

Stipe and rachis lengths express the same relationships as frond lengths. Three general size classes can be recognized: 1) small plants, including N. cordifolia, N. occidentalis, and N. pectinata, 2) intermediate plants, including N. exaltata, N. multiflora, and N. rivularis, and 3) large plants, including N. x averyi, N. biserrata, and N. pendula (Figure 6 and Table 3). Nephrolepis x averyi exceeds both of its parental species in overall frond length. Examination of stipe and rachis lengths separately shows that this is a reflection of a greater rachis length, with stipe lengths being intermediate between N. biserrata and N. exaltata (Figure 6). The larger frond lengths of N. pendula are also primarily a function of a larger rachis length; stipe length places this species in the intermediate size group.

Rachis/stipe length ratios, except for extreme values, are of little use in distinguishing species. Nephrolepis multiflora has generally short rachises relative to the stipe length and N. pendula generally has long rachises relative to the stipe length. Otherwise, the species show considerable range overlaps.

Interpinnal distance is distinctive for a few species. As with other size characters, there are three recognizable size classes.

Figure 6. Dice diagrams of stipe length, rachis length, rachis/stipe length ratio, and interpinnal distance of the neotropical species of Nephrolepis. (Total bar length = range, black bar = one standard deviation above and below the mean, cross bar = mean; stipe and rachis lengths are given in dm, interpinnal distances are given in mm.)

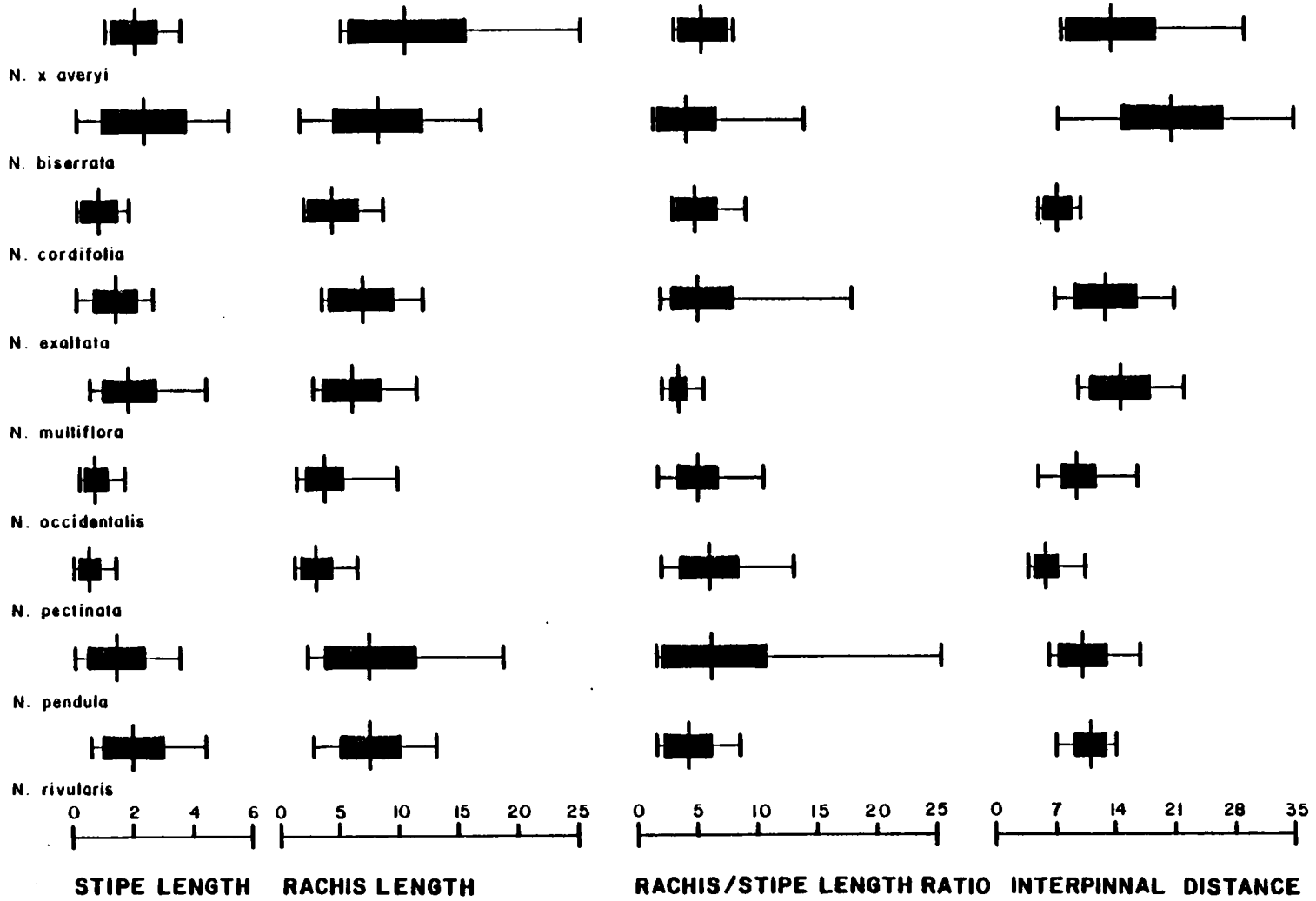

N. x averyi
N. biserrata
N. cordifolia
N. exaltata
N. multiflora
N. occidentalis
N. pectinata
N. pendula
N. rivularis
0 2 4 6
0 5 10 15 20 25
0 5 10 15 20 25
0 7 14 21 28 35
STIPE LENGTH
RACHIS LENGTH
RACHIS/STIPE LENGTH RATIO
INTERPINNAL DISTANCE

Figure 6

Table 3. Supporting data for Figure 6. Stipe lengths, rachis lengths, rachis/stipe length ratios, and interpinnal distances of the neotropical species of Nephrolepis. ($\bar{X}$ = mean, $S_{\bar{x}}$ = standard error of the mean.)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. x averyi				
Stipe length*	2.2	0.22	0.77	1.2 - 3.8
Rachis length	10.9	1.29	4.81	5.4 - 25.5
Rachis/stipe length	5.5	0.50	1.73	3.4 - 8.2
Interpinnal distance	16.7	0.82	3.40	9.0 - 24.5
N. biserrata				
Stipe length	2.5	0.20	1.39	0.2 - 5.4
Rachis length	8.5	0.52	3.75	1.8 - 17.1
Rachis/stipe length	4.3	0.36	2.47	1.8 - 14.1
Interpinnal distance	20.9	0.73	5.87	7.5 - 35.0
N. cordifolia				
Stipe length	1.0	0.13	0.50	0.3 - 1.9
Rachis length	4.5	0.53	2.10	2.2 - 9.0
Rachis/stipe length	5.0	0.44	1.70	3.2 - 9.3
Interpinnal distance	7.4	0.38	1.57	5.0 - 10.0
N. exaltata				
Stipe length	1.6	0.14	0.67	0.2 - 2.8
Rachis length	7.0	0.54	2.62	3.5 - 12.3
Rachis/stipe length	5.1	0.62	2.99	2.0 - 18.1
Interpinnal distance	13.0	0.70	3.45	7.3 - 21.0
N. multiflora				
Stipe length	1.9	0.18	0.88	0.6 - 4.4
Rachis length	6.0	0.51	2.45	2.7 - 11.5
Rachis/stipe length	3.4	0.16	0.58	1.3 - 5.5
Interpinnal distance	14.5	0.70	3.51	9.5 - 22.0
N. occidentalis				
Stipe length	0.8	0.06	0.36	0.3 - 1.8
Rachis length	3.9	0.24	1.57	1.5 - 9.9
Rachis/stipe length	5.0	0.28	1.86	1.8 - 10.6
Interpinnal distance	9.6	0.33	2.20	5.0 - 16.5
N. pectinata				
Stipe length	0.6	0.04	0.32	0.1 - 1.5
Rachis length	3.1	0.15	1.20	1.3 - 6.6
Rachis/stipe length	6.0	0.31	2.43	2.1 - 13.1
Interpinnal distance	5.9	0.16	1.25	4.0 - 10.5

Table 3 (Continued)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. pendula				
Stipe length	1.5	0.16	0.95	0.2 - 3.6
Rachis length	7.5	0.63	3.73	2.4 - 18.9
Rachis/stipe length	6.3	0.74	4.40	1.8 - 25.4
Interpinnal distance	10.2	0.42	2.68	6.3 - 17.0
N. rivularis				
Stipe length	2.1	0.16	0.99	0.6 - 4.5
Rachis length	7.7	0.39	2.41	3.0 - 13.2
Rachis/stipe length	4.4	0.31	1.89	1.7 - 8.5
Interpinnal distance	11.2	0.26	1.70	7.0 - 14.0

*Stipe and rachis lengths are given in dm, interpinnal distances are given in mm.

Nephrolepis pectinata and N. cordifolia exhibit relatively small interpinnal distances, with N. occidentalis showing the next largest interpinnal distances (Figure 6 and Table 3). All three of these species are small as judged by other frond measurements. The intermediate group consists of N. exaltata, N. multiflora, N. pendula, and N. rivularis (Figure 6). Larger interpinnal distances are exhibited by N. x averyi and N. biserrata (Figure 6). Nephrolepis pendula is not part of the larger size class as in previous characters (except stipe length). This species will be shown later to be separate in other size characters as well. Nephrolepis x averyi is similar to N. exaltata in interpinnal distance, but ranges beyond values typical of N. exaltata and approaches its other parent, N. biserrata.

The number of vascular bundles at the stipe base was considered constant enough by Tryon (1964) to be used as one of several key characters in distinguishing the Peruvian species. This character, however, is only weakly useful in distinguishing among the species. The number of vascular bundles varies from one to 11 and is associated with frond and rhizome sizes; larger plants (e.g., N. biserrata) tend to have a larger number of vascular bundles.

Stipe color and habit are useful in distinguishing certain species. Nephrolepis occidentalis shows a tendency toward lighter colored stipes, often stramineous or light brown. Nephrolepis pendula and N. rivularis have stipes ranging from dark brown to, more commonly, a purple-black color. All of the remaining species have medium

to dark brown stipes. Habit of the stipe (erectness) is correlated with frond size and stipe coloration. Larger fronds have proportionally larger stipe diameters and are more stiffly erect in habit. Darker colored stipes are associated with stiffer habits. In N. pendula the stipes are often stiff and wiry. Although they may be bent downward or arching, they are more brittle in texture. This feature of stiff, blackish stipes is distinctive for N. pendula when combined with other characters. Only two forms within N. pendula are different. One form from the Guyana Highlands is distinguished from N. cordifolia primarily by color, erectness, and indument of the stipe. The second form from the Galapagos Islands, Ecuador, and Central America approaches N. pectinata in stipe characters of color and indument distribution.

The stipe indument at maturity, if present at all, consists entirely of peltate scales in all of the species. The stipe scales are often similar to the rhizome scales in a given species and exhibit a morphological gradation from the rhizome to the stipe. A similar transition in scale morphology extends from the stipe to the rachis and from the rachis to the pinnae. The scales tend to become smaller, less numerous, and concolorous (if bicolorous on the stipe or rhizome) distally on the frond.

Stipe scales of N. exaltata and N. cordifolia are similar in morphology, color, size, and density. The scales are similar to those of the rhizome but more variable in size. The scales are generally persistent, but if cauducous, at least persistent near the stipe base.

The stipe scales of N. x averyi are intermediate in morphology between those of N. biserrata and N. exaltata.

Nephrolepis occidentalis has stipe scales similar to those of N. cordifolia and N. exaltata but with a slightly more caudate shape, fewer ciliolations, and smaller size.

Stipe scales of N. pectinata and N. pendula resemble the caudate rachis scales of N. exaltata but are more variable in size and shape. The scales of N. pendula are similar to those of N. pectinata in size and shape but more variable in margin types and darker in color.

Stipe scales of N. rivularis are similar to the rhizome scales and more uniform than in other species.

The stipe scales of N. biserrata are more variable in shape and size than the preceding species. The scales range from small (0.3 mm wide), circular to irregularly shaped scales to larger (1.5-8.4 mm long and 0.2-0.7 mm wide), narrowly triangular scales. Compared to the rhizome scales, those of the stipe are narrower, more caudate in shape, and more variable in size and coloration. On croziers and very young fronds, the scales are often hyaline-margined as in mature scales of N. multiflora but at maturity become concolorous or, in dry habitats, the margins are thinly hyaline and appear essentially concolorous.

In N. multiflora the scales are more distinctly hyaline-margined than those of the rhizome. They grade from small (0.3 mm wide), circular scales to larger (0.6-7.5 mm long and 0.4-1.3 mm wide),

elliptic to elliptic-lanceolate scales. The persistent, hyaline-margined, and appressed stipe scales of this species are distinctive enough to separate it from all other neotropical species on this basis alone.

The density and distribution of stipe scales are of some use in discriminating among some of the species. Nephrolepis exaltata, N. cordifolia, N. x averyi, and N. rivularis show a wide range of variation in the density and distribution of scales. The scales are loosely spreading and denser at the stipe base except in older fronds in which the scales may fall off the distal half of the stipe. In N. pectinata and N. occidentalis the scales are scattered, less dense than in the other species, and spreading in appearance. In N. pendula the scales are tightly appressed to the stipe surface and are seldom present except at the stipe base. In N. biserrata the scales are commonly as described for N. exaltata, N. cordifolia, N. x averyi, and N. rivularis, but in dry habitats the scales may be denser and more appressed to the stipe, approaching the condition in N. multiflora. In N. multiflora the scales are closely appressed to the stipe and tend to be persistent.

Nephrolepis cordifolia, N. pectinata, and N. pendula are usually distinguishable by the stipe indument and color when these features are used in combination with other characters, e.g., pinna attachment. The Galapagos form of N. pendula approaches N. pectinata in having loose stipe scales scattered on the proximal half of the stipe; this form must be separated with other characters. Stipes

of N. pendula are usually without scales or with scales only at the base, and these not as spreading or numerous as in N. cordifolia or N. pectinata. If the stipe scales of N. pendula are spreading or atypically numerous, it is only as much as in N. pectinata and they are blackish to reddish-black; in N. cordifolia they are orange to reddish-orange in color and larger. The Guyana form of N. pendula has a stipe indument resembling N. cordifolia, but may be distinguished by stipe color and erectness as well as other characters.

Rachis color shows an identical trend to that of stipe color with the rachis being lighter than, or the same color as, the stipe. Rachis habit was discussed under "Fronds" as frond habit (p. 31).

The rachis indument exhibits differences among the species similar to those exhibited by the stipe indument, but these are not as pronounced.

Rachis scales of N. biserrata are irregular in shape and size, generally linear or linear-triangular and caudate, fibrillose, pale brown, and concolorous. Trichomes may be present or absent on the rachis. Though no correlations are apparent with ecological conditions, trichomes are often found on young fronds and in those plants in which the trichome density is higher in other locations (e.g., pinnae). The trichomes are uniseriate, usually 5 (up to 6) cells in length, 0.3-0.6 mm long, septate, hyaline (sometimes with reddish septa) to pale brown, and overall resemble the "Ctenitis" trichome type described by Tindale (1965).

In N. multiflora the rachis scales are bicolorous, narrowly triangular to caudate, and fibrillose. There is considerable

variation in shape and size; bicolorous larger scales grade into concolorous smaller scales in the more distal portions of the rachis. Trichomes are often present on young fronds and early fronds of young plants. The trichomes are like those found on the upper costa surfaces.

The rachis scales of N. cordifolia are useful in distinguishing this species from others, especially in coloration. The scales are distinctly caudate, and pale to dark reddish-brown with distinctly darker points of attachment, giving the scales a bicolorous appearance.

Nephrolepis exaltata and N. rivularis exhibit rachis scales similar to those of N. cordifolia in shape but different in coloration. The scales of N. exaltata are light to medium brown and essentially concolorous, or, if bicolorous, then indistinctly so. These two species can be separated on this basis alone when other more obvious characters fail. The scales of N. rivularis are darker than those of N. exaltata and less distinctly bicolorous than those of N. cordifolia.

Rachis scales of N. x averyi are slightly shorter but otherwise more closely resemble those of N. exaltata than those of N. biserrata.

In N. occidentalis, N. pectinata, and N. pendula the rachis scales are similar to those of N. exaltata except in size and coloration. The rachises of N. occidentalis possess concolorous and generally hyaline scales, and may possess short (0.08 mm long) trichomes that are uniseriate and 1-2 cells in length. The trichomes occur in 1% or less of the specimens and were observed only on specimens

from Brazil. Nephrolepis pectinata and N. pendula have scales that tend to be more fibrillose than in N. exaltata and may become reddish to dark reddish-brown. In N. pectinata the scales may be bicolorous as in N. cordifolia but are less numerous. The rachis scales of N. cordifolia are usually dense, covering the surface of the rachis, while those of N. pectinata and N. pendula are concentrated near the points of pinna attachment, leaving most of the rachis surface exposed.

Rachis scales in all of the species are concentrated near the points of pinna attachment and species differences occur in the scale distribution elsewhere on the rachis. In N. pectinata the rachis scales occur almost exclusively at the points of pinna attachment, often appearing as small whitish mats on the rachis. The remaining species exhibit a condition in which the scales also occur on the adaxial surface of the rachis. This adaxial distribution of scales is rare in N. pendula (found only in the Guyana form) and distinguishes this species from N. cordifolia. In the Guyana form of N. pendula the rachis scales are similar to those of N. cordifolia only in density and distribution, but not in morphology. Nephrolepis occidentalis and N. pectinata may have few or no scales on the adaxial surface but are easily distinguished from N. pendula using other characters.

Pinnae

The pinnae of Nephrolepis are characteristically articulated to the rachis. Venation is open and pinnately branched one to several

times, with the veins ending in hydathodes near the margin (Case, 1932; Mahabale and Gorji, 1951; Pray, 1960; Sperry, 1983). Payne and Peterson (1973) reported an hypodermis as absent in N. biserrata and a cultivated form of N. exaltata, but as being present in other related genera (e.g., Oleandra Cav.). Sen and Sen (1973) reported a poorly developed mesophyll and intercellular spaces irregularly dispersed within the lamina. This has been confirmed for all of the neotropical species. Other features of the internal anatomy were not especially noteworthy.

The pinnae (except in rare abnormally developed fronds) are undivided in all of the naturally occurring species. Several cultivated forms show a large range of variation in pinna form, e.g., forking and divisions up to 4 or 5 times pinnate. The unusual pinna shapes and divisions are described for several cultigens that occur in the neotropics in Chapter X.

Numerous other pinna characters were of value in distinguishing among the species and are described below.

Veins arising from the costa in more distal portions of the pinna branch only once in smaller species (e.g., N. pectinata), and two or three times in larger species (e.g., N. biserrata); the extent of branching appears related to the pinna size and is of little value in distinguishing among the species.

Pinna lengths, widths, and length/width ratios allow the species to be grouped into size classes corresponding closely to those recognized with other characters (e.g., rachis and stipe lengths).

Nephrolepis biserrata, N. multiflora, and N. x averyi exhibit the longest and narrowest pinnae (Figure 7 and Table 4). Nephrolepis pectinata and N. cordifolia possess the smallest pinnae in terms of length and width (Figure 7). The remaining species show various intermediate pinna sizes. In Figure 7 a correlation can be seen between pinna length and width. Length/width ratios follow a similar pattern of variation; shorter pinnae tend to exhibit lower pinna length/width ratios. Nephrolepis pendula shows more variation in length/width ratios than other members of the intermediate size class (Figure 7). Of these three characters, pinna length is the most discriminating, but only in extreme values (e.g., plants with pinnae greater than 8 cm long are either N. biserrata or N. multiflora). Nephrolepis x averyi is intermediate in all three characters between N. biserrata and N. exaltata.

Length, width, and length/width ratios of the lowermost pinnae show similar but less pronounced differences among the species as central pinna length (Figure 8 and Table 5). When lowermost pinna length and width are combined into a ratio, only N. biserrata and N. multiflora show clear differences among the other species (Figure 8 and Table 5). Only N. x averyi shows a significant range overlap in this feature with these two species.

Pinna habit and texture show no major differences among the species. Large pinnae (those more than 5 cm long) may be arching or lax in habit. Shorter pinnae tend not to be arching except at the apices. In all of the species dry or exposed habitats result

Figure 7. Dice diagrams of central pinna length, width, and length/width ratio of the neotropical species of Nephrolepis. (Total bar length = range, black bar = one standard deviation above and below the mean, cross bar = mean; lengths and widths are given in cm.)

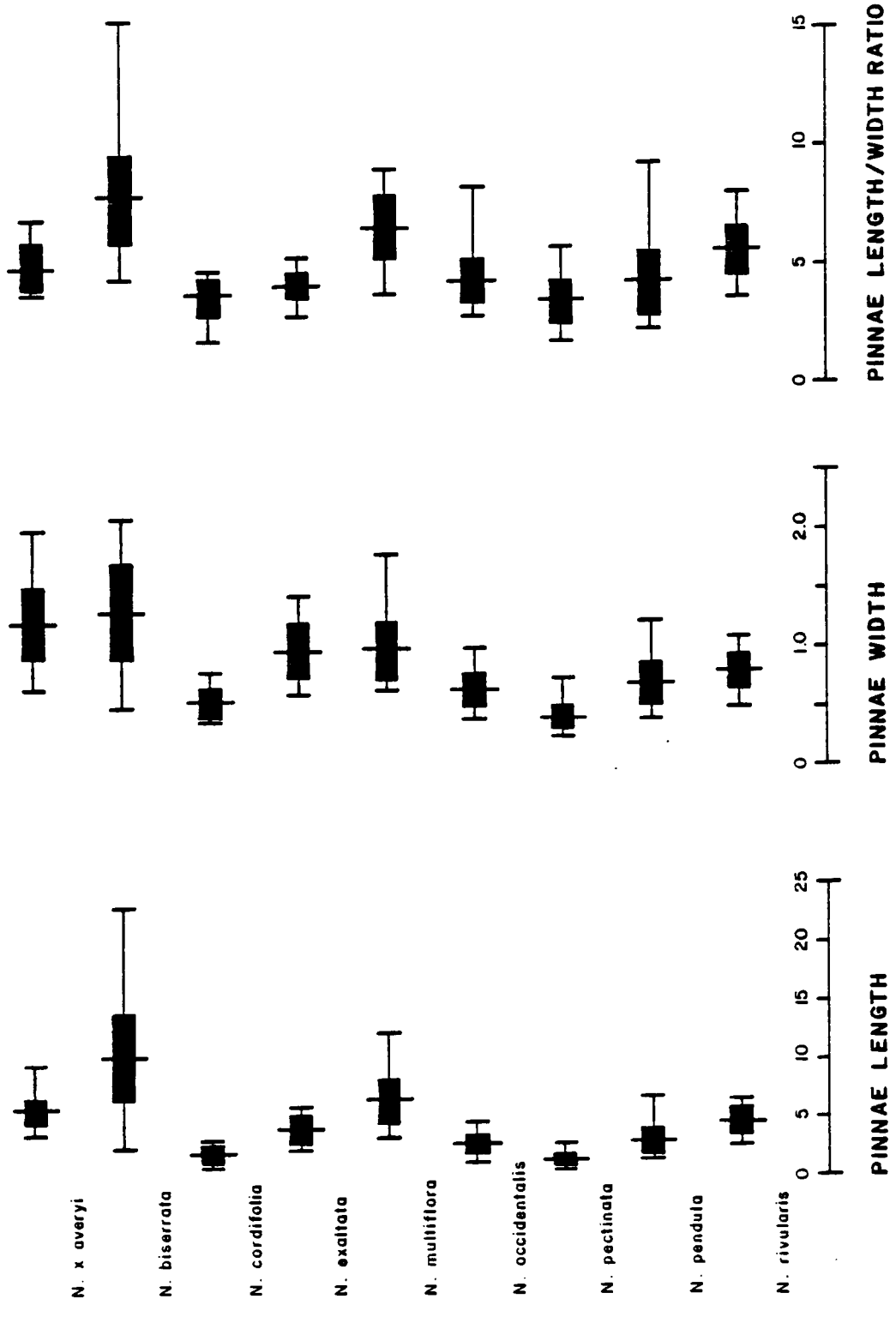

N. x averyi
N. bisarrata
N. cordifolia
N. exaltata
N. multiflora
N. occidentalis
N. pectinata
N. pendula
N. rivularis
PINNAE LENGTH
0
5
10
15
20
25
PINNAE WIDTH
0
1.0
2.0
PINNAE LENGTH/WIDTH RATIO
0
5
10
15

Figure 7

Table 4. Supporting data for Figure 7. Central pinna lengths, widths, and length/width ratios of the neotropical species of Nephrolepis. ($\bar{X}$ = mean, $S_{\bar{x}}$ = standard error of the mean.)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. x averyi				
Length*	5.9	0.33	1.36	3.6 - 9.0
Width	1.2	0.07	0.29	0.7 - 2.0
Length/width	4.9	0.20	0.84	3.8 - 6.8
N. biserrata				
Length	10.3	0.46	3.66	2.5 - 23.0
Width	1.3	0.05	0.40	0.5 - 2.1
Length/width	7.8	0.24	1.95	4.4 - 15.3
N. cordifolia				
Length	2.1	0.18	0.74	0.9 - 3.2
Width	0.6	0.03	0.12	0.4 - 0.8
Length/width	3.7	0.18	0.74	1.8 - 4.8
N. exaltata				
Length	4.0	0.21	1.09	2.3 - 5.9
Width	1.0	0.04	0.22	0.6 - 1.5
Length/width	4.0	0.11	0.55	2.8 - 5.3
N. multiflora				
Length	6.5	0.37	1.87	3.4 - 12.3
Width	1.0	0.05	0.25	0.7 - 1.8
Length/width	6.7	0.26	1.30	3.8 - 9.1
N. occidentalis				
Length	2.9	0.10	0.68	1.3 - 4.8
Width	0.7	0.02	0.13	0.4 - 1.0
Length/width	4.3	0.13	0.87	2.9 - 8.3
N. pectinata				
Length	1.5	0.05	0.40	0.7 - 2.9
Width	0.4	0.01	0.09	0.3 - 0.8
Length/width	3.5	0.11	0.85	1.8 - 5.8
N. pendula				
Length	3.0	0.17	1.05	1.6 - 6.8
Width	0.7	0.03	0.17	0.4 - 1.3
Length/width	4.3	0.21	1.31	2.3 - 9.3

Table 4 (Continued)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. rivularis				
Length	4.7	0.17	1.15	2.8 - 6.7
Width	0.8	0.02	0.13	0.5 - 1.1
Length/width	5.7	0.14	0.94	3.7 - 8.1

*Lengths and widths are given in cm.

Figure 8. Dice diagrams of lowermost pinna length, width, and length/width ratio of the neotropical species of Nephrolepis. (Total bar length = range, black bar = one standard deviation above and below the mean, cross bar = mean; lengths and widths are given in cm.)

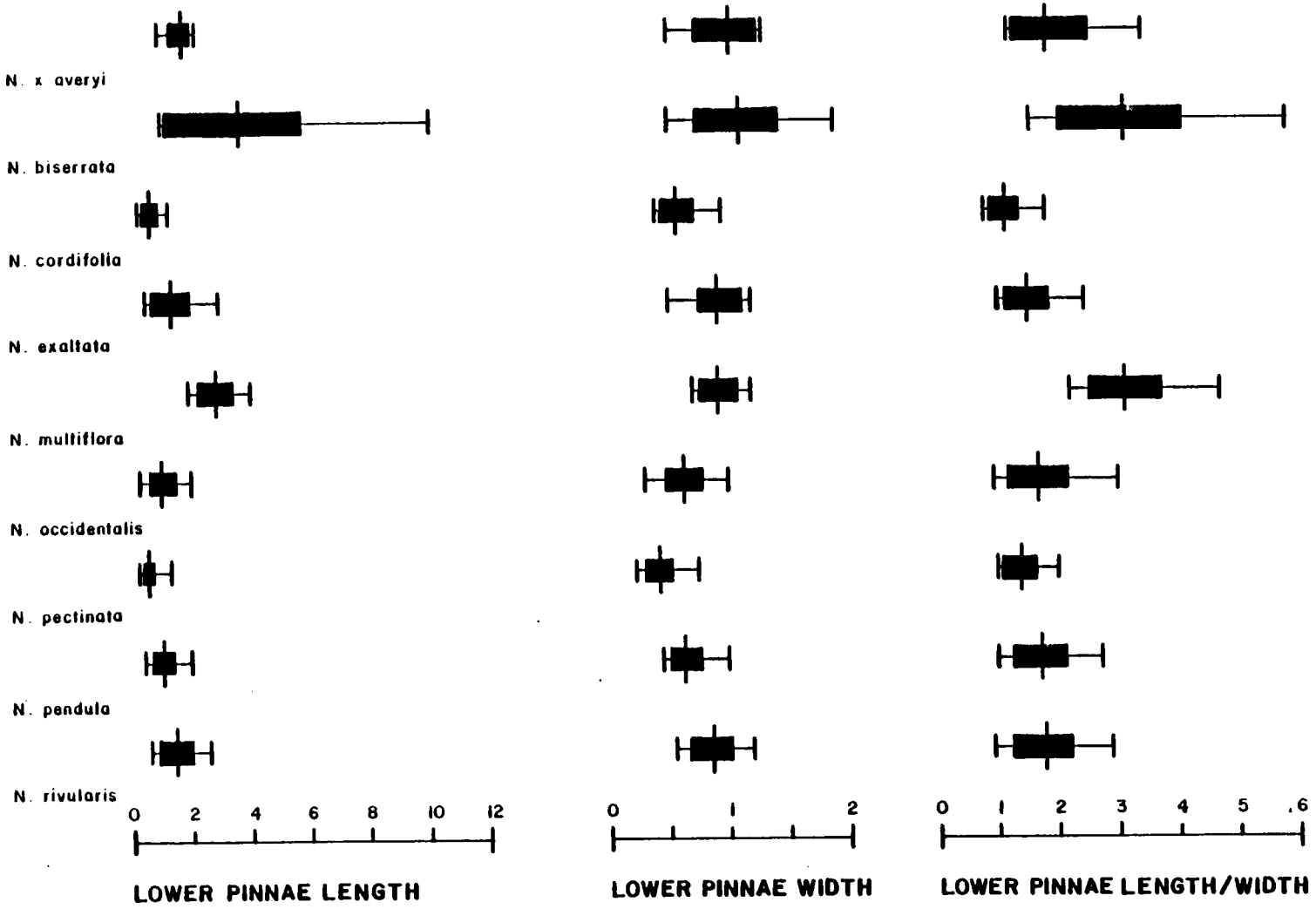

N. x averyi
N. biserrata
N. cordifolia
N. exaltata
N. multiflora
N. occidentalis
N. pectinata
N. pendula
N. rivularis
0 2 4 6 8 10 12
LOWER PINNAE LENGTH
0 1 2
LOWER PINNAE WIDTH
0 1 2 3 4 5 .6
LOWER PINNAE LENGTH/WIDTH

Figure 8

Table 5. Supporting data for Figure 8. Lowermost pinna lengths, widths, and length/width ratios of the neotropical species of Nephrolepis. ($\bar{X}$ = mean, $S_{\bar{x}}$ = standard error of the mean.)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. x averyi				
Length*	1.8	0.18	0.31	1.0 - 2.2
Width	1.0	0.16	0.28	0.5 - 1.3
Length/width	1.9	0.18	0.64	1.2 - 3.4
N. biserrata				
Length	3.7	0.19	1.06	1.6 - 5.8
Width	1.1	0.07	0.34	0.5 - 1.9
Length/width	3.1	0.19	1.06	1.6 - 5.8
N. cordifolia				
Length	0.7	0.08	0.27	0.8 - 1.8
Width	0.6	0.04	0.15	0.4 - 1.0
Length/width	1.2	0.08	0.29	0.8 - 1.8
N. exaltata				
Length	1.4	0.14	0.55	0.6 - 3.0
Width	0.9	0.05	0.18	0.5 - 1.2
Length/width	1.5	0.09	0.35	1.0 - 2.5
N. multiflora				
Length	2.9	0.12	0.54	2.0 - 4.0
Width	0.9	0.04	0.16	0.7 - 1.2
Length/width	3.2	0.14	0.62	2.2 - 4.7
N. occidentalis				
Length	1.1	0.07	0.40	0.3 - 2.0
Width	0.6	0.03	0.16	0.3 - 1.0
Length/width	1.7	0.09	0.52	0.9 - 3.0
N. pectinata				
Length	0.6	0.03	0.20	0.3 - 1.3
Width	0.4	0.02	0.11	0.2 - 0.8
Length/width	1.4	0.04	0.25	1.0 - 2.0
N. pendula				
Length	1.1	0.08	0.37	0.5 - 1.9
Width	0.6	0.03	0.14	0.5 - 1.0
Length/width	1.7	0.10	0.47	1.0 - 2.8

Table 5 (Continued)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. rivularis				
Length	1.5	0.10	0.54	0.7 - 2.6
Width	0.9	0.03	0.16	0.6 - 1.2
Length/width	1.8	0.08	0.48	0.9 - 2.9

*Lengths and widths are given in cm.

in a firmer pinna texture. Only N. occidentalis appears to have pinnae that are more membranous than is typical for the other species.

Overall pinna shape is variable in all nine species. Nephrolepis x averyi, N. exaltata, N. multiflora, N. occidentalis, N. rivularis, and N. cordifolia exhibit relatively uniform patterns of variation compared to the remaining species. Nephrolepis x averyi and N. exaltata have essentially identical pinna shapes, with N. x averyi differing only in having larger pinnae. The shape is linear-oblong to triangular and widest in the middle (a condition here referred to as elliptic) (Figures 9a and 9b). The pinnae in both species are generally falcate but may be non-falcate. In N. rivularis the overall pinna shape is linear-oblong to barely elliptic and typically falcate (rarely non-falcate) (Figure 9f). Nephrolepis occidentalis exhibits an overall pinna shape that is consistently traignular and falcate to slightly falcate (Figures 9c and 9d). Nephrolepis cordifolia exhibits an oblong-linear shape that barely narrows apically (Figure 9e), or in small plants and small pinnae, a more distinctly triangular shape. The pinnae of N. cordifolia are slightly or indistinctly falcate. Nephrolepis multiflora has linear-oblong to elliptic, non-falcate to slightly falcate, and relatively uniform pinnae (Figure 10a). This same pinna shape occurs in N. biserrata and is associated with dry habitats. Nephrolepis multiflora occurs almost exclusively in dry, exposed, or otherwise disturbed habitats (e.g., roadsides) and the pinna shape may vary to a wider more elliptic form in wetter or more protected locations. All six of these species

Figure 9. Pinna shapes of Nephrolepis x averyi, N. exaltata, two forms of N. occidentalis, N. cordifolia, and N. rivularis. (Bar = 5 cm.)

a. N. x averyi.

b. N. exaltata.

c. N. occidentalis - basally attached form.

d. N. occidentalis - submedially attached form.

e. N. cordifolia.

f. N. rivularis.

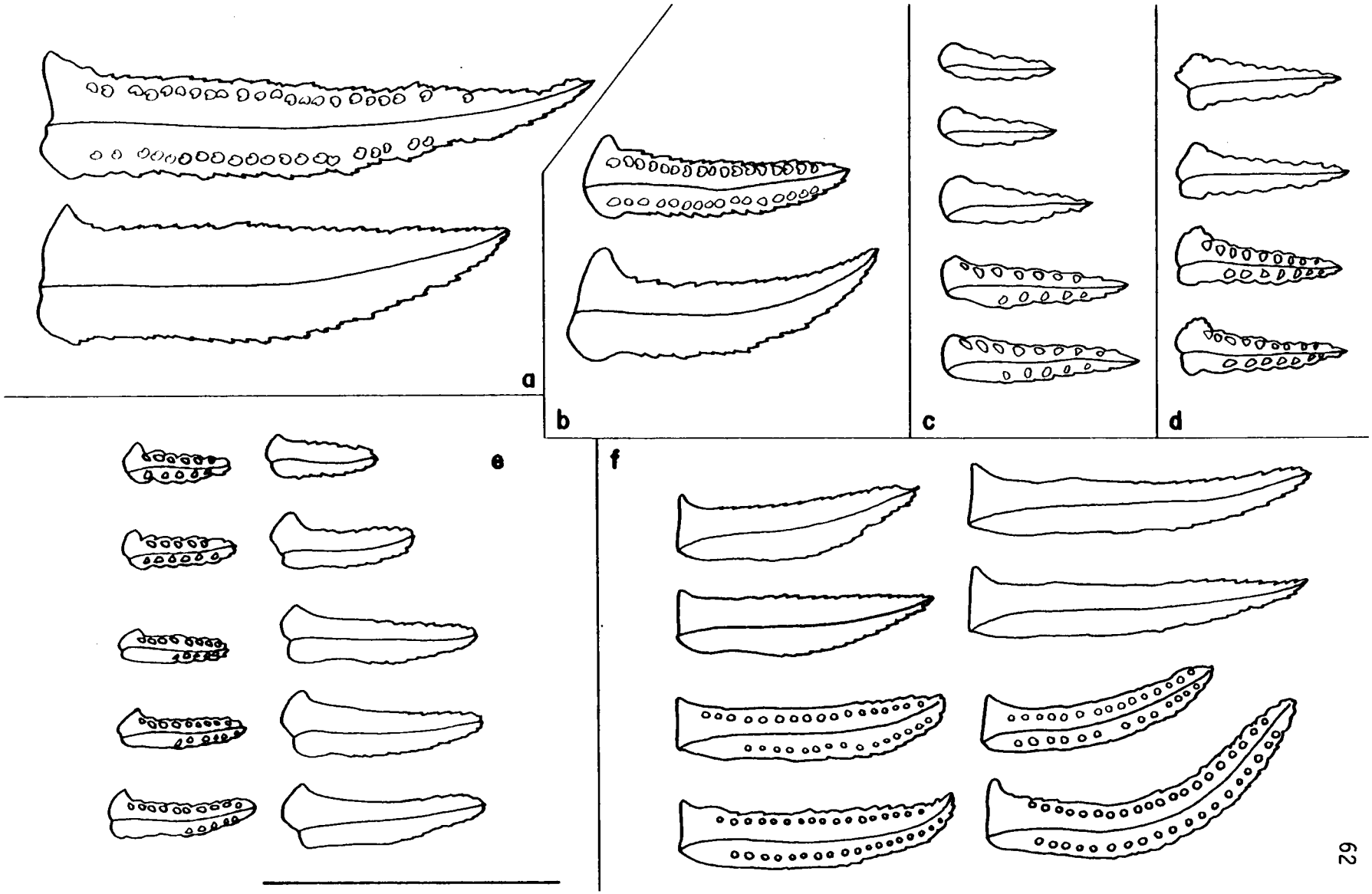


Figure 9

Figure 10. Pinna shapes of Nephrolepis multiflora, N. biserrata, and four forms of N. pectinata. (Bar = 5 cm.)

a. N. multiflora.

b. N. biserrata.

c. N. pectinata - typical form.

d. N. pectinata - oblanceolate form.

e. N. pectinata - deflexed form.

f. N. pectinata - Mexican form.

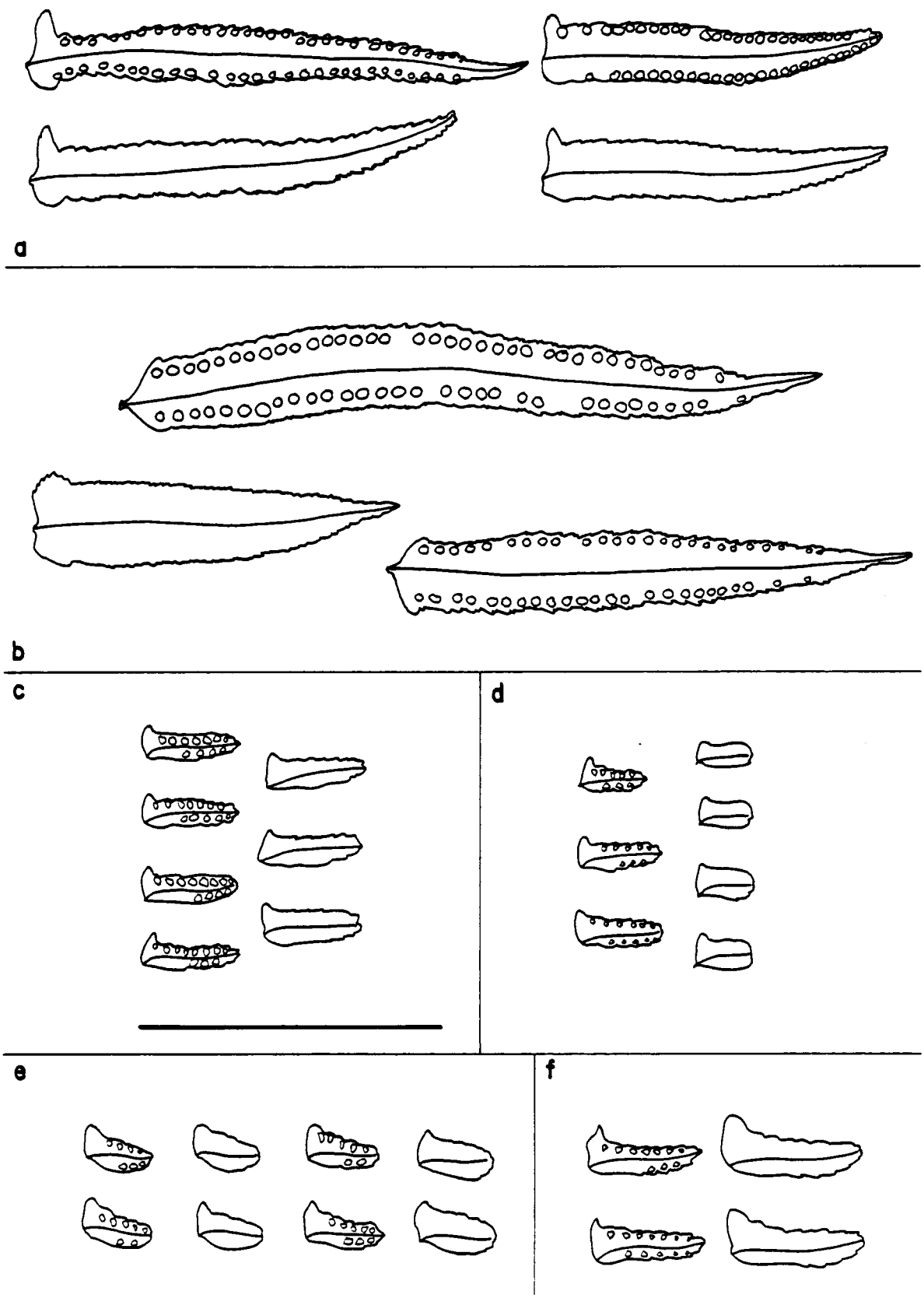


Figure 10

show little or no dimorphism between fertile and sterile pinnae. When dimorphism is exhibited, the fertile pinnae tend to be narrower and shorter than the sterile pinnae on the same frond; the fertile pinnae appear "contracted," if different at all from the sterile pinnae.

Nephrolepis biserrata shows two types of pinna shapes associated with environmental conditions, a dry form and a wet form. In shaded or moist habitats the pinnae are linear-oblong to elliptic (Figure 10b). In more exposed or dry habitats, the pinna shape is identical to that shown by N. multiflora (Figure 10a). Every intergradation between these two pinna forms can be found, and occasionally on a single frond. This similarity in pinna form between N. biserrata and N. multiflora, and a greater density of scales on all parts of the fronds in N. biserrata (also associated with dry habitats) are probably responsible for some misdeterminations.

Nephrolepis pectinata and N. pendula exhibit the greatest variation in pinna shapes. Both species possess forms that resemble each other enough to cause taxonomic confusion. All of the forms intergrade within each species, often one form grading into two or more other forms. Only two forms within N. pendula may, with sufficiently intense local study, prove to be deserving of formal taxonomic status as forms or varieties. None of the forms in either species, however, is here considered sufficiently distinct to warrant such formal recognition.

Four forms can be recognized for N. pectinata, here designated 1) typical, 2) oblanceolate, 3) deflexed, and 4) Mexican. The typical

form is the one most frequently found throughout the species' range. Fertile pinnae are oblong to barely triangular and non-falcate (Figure 10c) to distinctly falcate. Sterile pinnae are usually the same shape but may be indistinctly elliptic or oblanceolate. The oblanceolate form possesses fertile pinnae identical to the typical form but its sterile pinnae are distinctly oblong or oblanceolate (Figure 10d). The deflexed form possesses pinnae that are more triangular than oblong and its sterile pinnae are elliptic to oblanceolate. The basiscopic portion of the pinnae in the deflexed form are slightly wider than the acroscopic portion and give the pinnae a slightly falcate appearance (Figure 10e). The latter form also exhibits pinnae that are deflexed to varying degrees. The Mexican form is similar to the typical form but the pinnae are generally larger and resemble those of N. cordifolia (Figure 10f).

Five forms can be recognized for N. pendula, here designated 1) typical, 2) falcate, 3) Guyana, 4) brevis, and 5) Galapagos. The typical form is oblong to triangular-oblong or oblanceolate, slightly falcate or not, and the fertile pinnae are usually more triangular than the sterile pinnae (all forms are shown in Figure 11). This form is found throughout the species' range, and is the form most frequently encountered. The falcate form has longer, triangular to triangular-oblong, and distinctly falcate pinnae (Figure 11). In this form the fertile pinnae are crenate to crenulate and the sterile pinnae are barely crenulate to serrulate. The falcate form intergrades with the typical form through a more triangular, sometimes

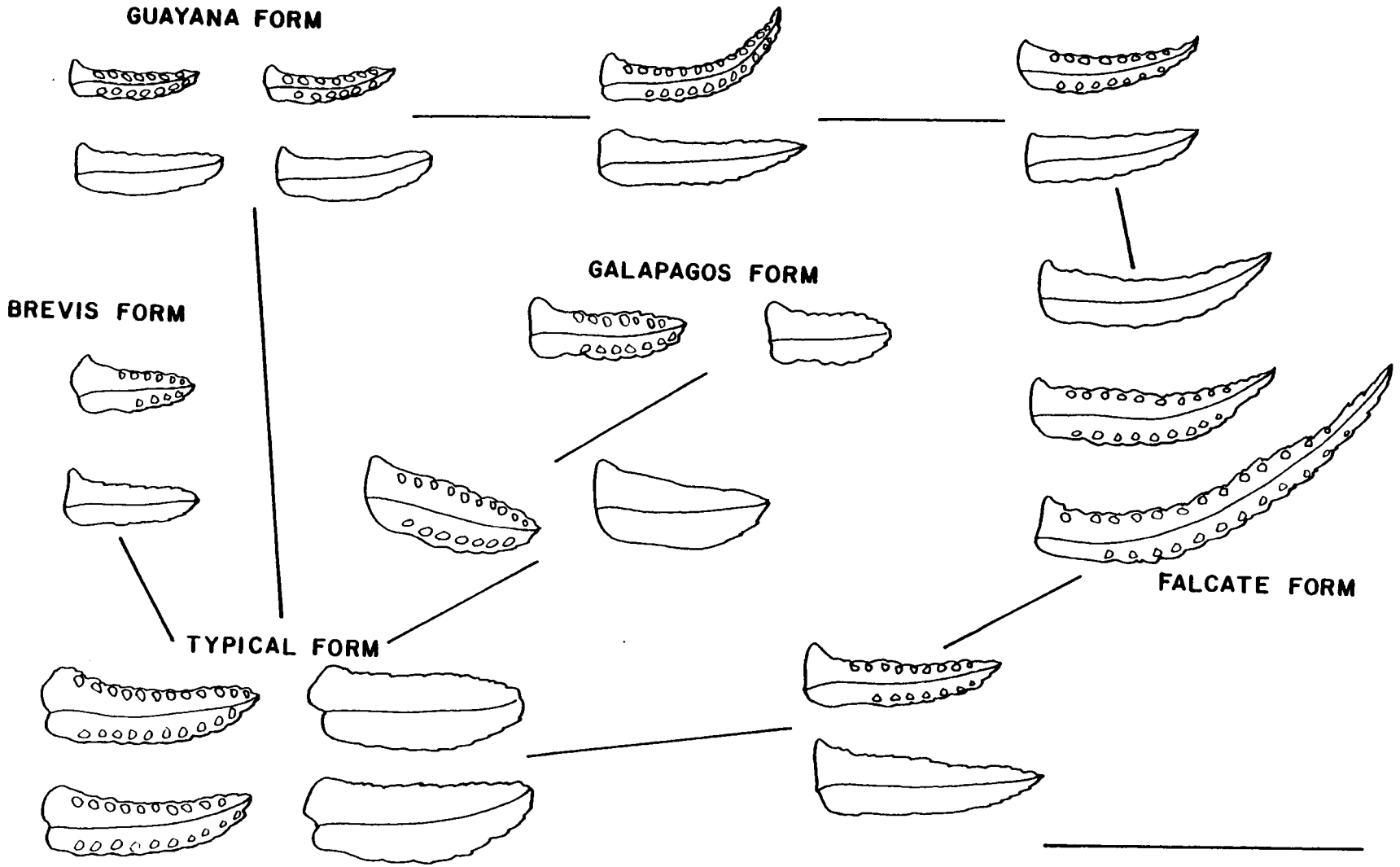


Figure 11. Pinna shapes of the forms of Nephrolepis pendula.

slightly deflexed form depicted in Figure 11. The Guyana form has pinnae that resemble those of N. cordifolia, are slightly to distinctly falcate, and grade into the falcate form (Figure 11). Fertile pinnae of the Guyana form are more crenate than the sterile pinnae. The brevis form represents a condition intermediate between the typical and Guyana forms and ranges toward the Galapagos form (Figure 11). The Galapagos form occurs as two intergrading types mostly occurring in Ecuador, the Galapagos Islands, and Central America. The first of these two types closely resembles the typical form and is often slightly deflexed. The second type is usually not deflexed or falcate. Pinnae in this form are usually oblanceolate and resemble the oblanceolate form of N. pectinata (Figure 10d). Sterile pinnae tend to be oblanceolate with serrulate margins, and fertile pinnae tend to be elliptic to oblong or oblanceolate with crenulate margins.

Pinna apices range from acute to narrowly acute or attenuate in N. x averyi, N. exaltata, N. multiflora, N. occidentalis, and N. rivularis (Figures 9a-9d, 9f, page 61, and 10a). Nephrolepis cordifolia exhibits acute to rounded or blunt pinna apices (Figure 9e). Nephrolepis biserrata exhibits acute to attenuate or abruptly attenuate pinna apices (Figure 10b). In N. pectinata the apex is as in N. cordifolia, except that in the oblanceolate form the apices are obtuse or rounded (Figures 10c-10f). In N. pendula the pinna apices are narrowly acute to attenuate (in the falcate form), or bluntly acute to obtusely rounded in the typical and Galapagos forms (Figure 11).

Pinna margins of N. x averyi, N. exaltata, and N. rivularis are typically serrulate to crenulate-serrulate (Figures 9a, 9b, and 9f, page 61). Margins of the sterile pinnae of N. cordifolia are entire to serrulate, and margins of the fertile pinnae are crenulate to crenate (Figure 9c). Pinna margins of N. occidentalis are crenulate to crenate in both the sterile and fertile pinnae and infrequently serrulate-crenulate in the sterile pinnae (Figures 9c and 9d). In N. multiflora and the dry form of N. biserrata the fertile pinna margins are "biserrate" (i.e., crenate with a small tooth on the distal side of each crenation) (Figure 10a, page 63). Sterile pinnae in N. multiflora and the dry form of N. biserrata are serrulate (Figure 10a). In the wet form of N. biserrata the pinnae are usually biserrate but may be irregularly serrulate or serrate (a rare condition).

The pinna margins of N. pectinata and N. pendula have been described along with pinna shape of their forms (pp. 65-68).

Base shape, shape of the acroscopic lobe, and pinna attachment are important features for distinguishing among several of the species, especially among similar forms of N. pectinata and N. pendula. Pinna in all of the species are sessile to subpetiolulate. Three types of attachment are here recognized, medial, submedial, and basal. Medial refers to a condition in which the point of pinna attachment on the pinna itself (where the costa joins the rachis) is midway between the acroscopic and basiscopic margins of the pinna base (e.g., Figures 9a, 9b, and 10f). Basal refers to a condition

in which the attachment point is at the basiscopic margin of the pinna base (e.g., Figure 9f, page 61). Submedial refers to a condition intermediate between the medial and basal forms of attachment.

In N. x averyi and N. exaltata the pinnae are truncate to truncate-auriculate. In the latter condition there is a triangular auricle (part of the acroscopic lobe) extending toward and often overlapping the rachis. The acroscopic lobe in both of these species is deltoid to narrowly deltoid (rarely obtuse) and pinna attachment is submedial to medial (Figures 9a and 9b).

The pinna base in N. biserrata is truncate to cuneate (rarely subcordate--see sterile pinna in Figure 10b, page 63) in the wet form, and rounded basiscopically and cordate or "incut" acroscopically in the dry form. The acroscopic lobe may be present or absent as a shallow, obtuse lobe or crenation in the wet form. In the dry form the acroscopic lobe is present as an oblong lobe roughly perpendicular to the long axis of the pinna (e.g., Figure 10a). Attachment is medial in this species. Pinnae of N. multiflora are as described for the dry form of N. biserrata.

Pinna base shape in N. cordifolia is shallowly but distinctly cordate, rarely approaching a truncate-rounded condition when the acroscopic lobe is not well developed (Figure 9e). The acroscopic lobe is narrowly to broadly deltoid and pinna attachment is submedial to medial.

Nephrolepis occidentalis shows two types of pinna bases. The first and most frequent, has a cordate base shape, medial attachment, and deltoid acroscopic lobe (Figure 9d). The second type

has an acroscopically rounded, asymmetrical base shape, basal attachment, and a shallow, obtuse to broadly deltoid acroscopic lobe (Figure 9c, page 61). Both types occur throughout the range of the species with the second type being typical of young or small plants and being replaced by the first type in later fronds.

Nephrolepis rivularis exhibits a truncate pinna base, acute to narrowly deltoid acroscopic lobe, and basal pinna attachment (Figure 9f). This basal attachment gives the pinnae a "cuneate" appearance.

Nephrolepis pectinata is variable in pinna base shape, ranging from a "cuneate" condition (see sterile pinnae in Figure 10c, page 63) to a condition in which the acroscopic portion of the base is rounded or truncate (see Figures 10d and 10e). The acroscopic lobe is shallow and obtuse to deltoid or acute. Attachment is basal in all pinnae of a given frond except in the Mexican pinna form. The Mexican form has basally attached pinnae for more than 3/4 of the distal portion of the fronds, i.e., only the lowermost pinnae are submedial to medial in attachment. This feature distinguishes the Mexican form of N. pectinata from the Galapagos form of N. pendula.

Three base shapes occur in N. pendula, shallowly but abruptly cordate, truncate-rounded, and truncate. The shallowly cordate type is typical, but there is a wide range of variation (Figure 11). The acroscopic lobe is usually shallow, rounded, and obtuse to nearly absent, but may be deltoid to narrowly deltoid, or nearly oblong and recurved in some forms. Attachment is medial in all

forms. In the Galapagos form, however, some plants exhibit basal attachment in less than 1/2 of the distal pinnae.

The presence or absence of a pinna indument, its type, location, and density were useful features for distinguishing among the species. The indument may consist of scales and or trichomes. Morphology of the scales is often similar to the rachis scales and grades into smaller more irregular scales that may be described as branched trichomes. Trichomes exhibit a relatively uniform morphology but differences in distribution and size occur among the species. Sen and Sen (1973) reported two scale types in N. exaltata and N. cordifolia, setiferous and glandular. The setiferous scales were described as terminating in a rigid and pointed trichome. Though the scales are often terminated by a uniseriate branch or trichome, this was seldom rigid and only rarely pointed. The glandular scales were described as having 2-celled glandular trichomes. None of the scales or trichomes on mature plants are glandular, although glandular trichomes are present on young sporophytes and on developing fronds. Discrepancies between the observations of Sen and Sen (1973) and mine may be, in part, because they were working with paleotropical material of N. cordifolia and only questionably with N. exaltata. They cited their N. exaltata material as originating from New Zealand. As far as can be determined, N. exaltata does not occur in New Zealand.

Nephrolepis biserrata possesses trichomes of variable density on all pinna surfaces. The trichomes are similar to those of the rachis, 3-7, usually 4 cells (0.3, ranging from 0.2 to 0.7 mm) long,

pale to light brown, septate, and erect (Figure 12a). Trichomes may or may not be present on the adaxial costa surface of the wet pinna form and are typically present in the dry pinna form; when present, the trichomes are dense and give the costa a tomentose appearance over most of its length. The abaxial lamina surface may be glabrous or have trichomes of variable density. The adaxial lamina surface is often without trichomes, and when present, they are of a lower density than on the abaxial surface. If trichomes are present adaxially, they are always present abaxially. The scales of N. biserrata are variable in both size and shape (Figure 12a). In the wet pinna form scales occur on both pinna surfaces and are few and scattered. In the dry pinna form, they are present abaxially and often form a dense mat; they are usually present adaxially as well but are less dense and concentrated near the costa.

Nephrolepis multiflora possesses both trichomes and scales. The trichomes have the same morphology as those of N. biserrata but are slightly shorter (0.1-0.3 mm) and have a different distribution. The trichomes are characteristically present and tomentose on the adaxial costa surface. The abaxial and adaxial lamina surfaces are usually glabrous except on young pinnae and early fronds of young plants. The pinna scales are similar to the rachis scales in morphology (Figure 12b), densely distributed over the abaxial surface, and sparsely to densely distributed over the adaxial surface.

The pinna indument of N. exaltata consists entirely of scales. The scales are irregular in shape and smaller scales grade into

Figure 12. Pinna induments of six species of Nephrolepis. (Bar = 2 mm; shading indicates the area of scale attachment.)

a. N. biserrata.

b. N. multiflora.

c. N. exaltata.

d. N. x averyi.

e. N. cordifolia.

f. N. rivularis.

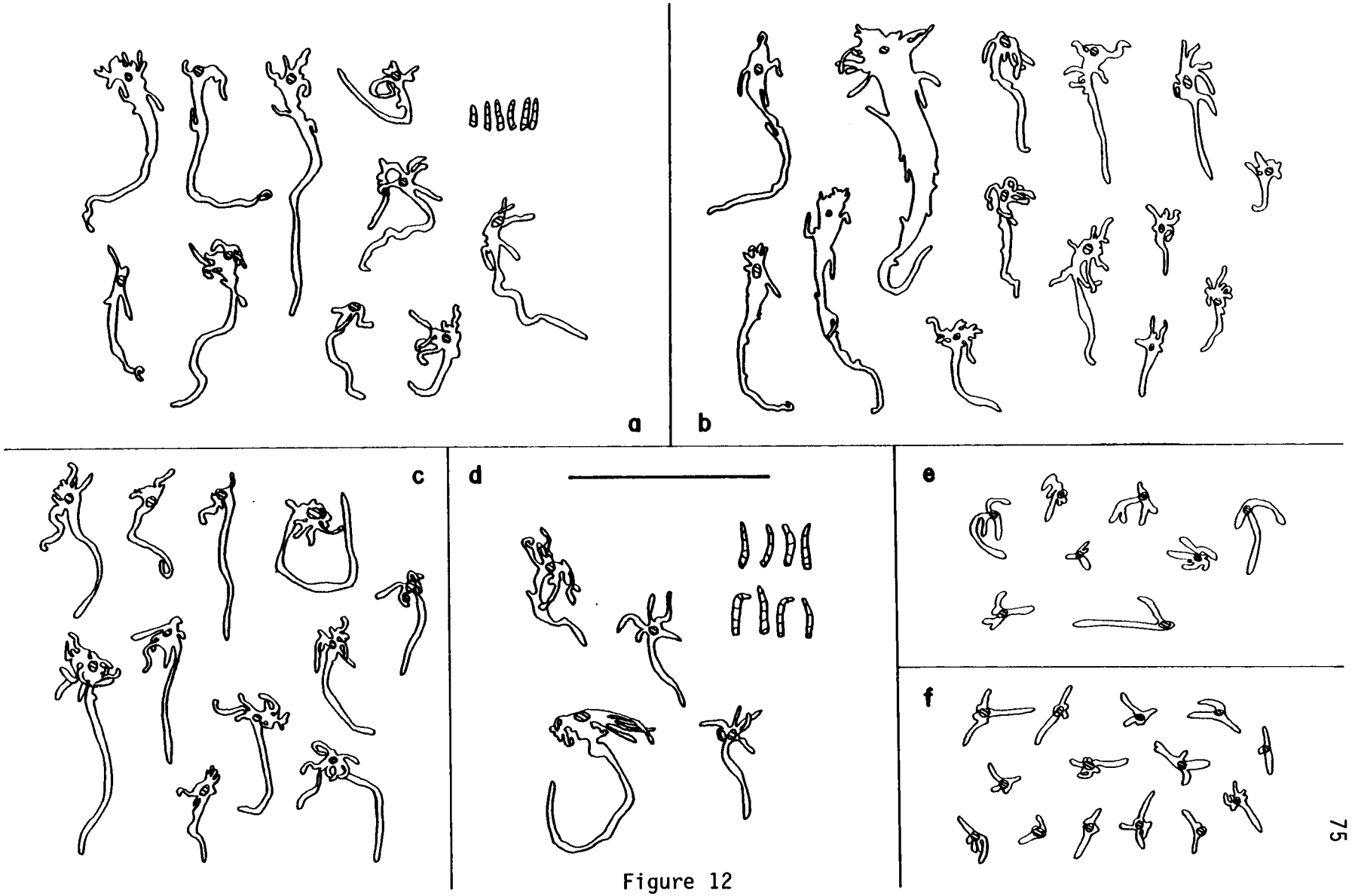


Figure 12

branched trichomes (Figure 12c). Scales in this species are sparsely distributed over both the abaxial and adaxial surfaces, usually concentrated near the costa proximally.

In N. x averyi trichomes are sparsely distributed on the adaxial costa surface, a condition intermediate between the tomentose condition in N. biserrata and the glabrous condition in N. exaltata. The trichomes are the same as those of N. biserrata but usually consist of 5 cells and are longer (0.47 mm) (Figure 12d). The scales are intermediate in size, shape, and variability between N. biserrata and N. exaltata (Figure 12d), and are distributed as in N. exaltata.

The pinna indument of N. rivularis consists of small (0.3-0.7 mm wide), irregular, peltate, and branched trichomes (Figure 12f). The trichomes are dark reddish-brown, uniformly scattered over the abaxial surface (occasionally on the adaxial surface), and are relatively obvious under 10x magnification. Uniseriate trichomes occur on less than 5% of the specimens. The trichomes are 2-3 cells (0.26-0.30 mm) long, and otherwise similar to those of N. biserrata.

Pinnae of N. occidentalis possess small, branched trichomes concentrated along the costa proximal to the pinna base both abaxially and adaxially. The trichomes resemble those of N. rivularis, but are pale in color (with or without reddish tips), and are few in number. This species also possesses small (0.09 mm long), uniseriate, pale, 3-cell long trichomes uniformly distributed over the lamina. These smaller trichomes are present or absent on plants throughout the species' range; plants with and without the trichomes are otherwise indistinguishable.

Nephrolepis cordifolia usually has no pinna indument at maturity. One plant was seen with small branched trichomes identical to those of N. rivularis (Figure 12e). Such trichomes were reported for young pinnae on otherwise mature fronds of N. cordifolia by Wagner (1952).

Nephrolepis pectinata and N. pendula lack any pinna indument at maturity.

The stomata of Nephrolepis have been described by Van Cotthem (1970a) as monocyclic, polocytic or staurocytic, and with a haplocheilic ontogeny. Stomatal ontogeny was reported by Sen and Sen (1973) to be syndetocheilic. Epidermal cell form was described by Van Cotthem (1970a) as anomorph on both the upper and lower surfaces, with the anticlinal walls ranging from sinuous to lobed. These observations are confirmed for the neotropical species with the exception that stomatal ontogeny was not studied. Terminology used below is that of Van Cotthem (1970a and 1970b). In all of the species the pinnae are hypostomatic. Differences among the species occur in both cell form and guard cell length.

Nephrolepis biserrata, N. multiflora, and N. x averyi exhibit strongly sinuous to deeply lobed epidermal cell forms (Figures 13a-13c). Nephrolepis exaltata (Figure 13e) represents a less deeply lobed transition to the type in N. cordifolia (Figure 13d) and N. rivularis (Figure 13f) in which the cell form is sinuous to lobed. In N. occidentalis the cell form ranges from merely sinuous to a degree of lobing equivalent to that in N. exaltata (see gradation in Figures 13g-13i). Nephrolepis pectinata exhibits cell forms equivalent

Figure 13. Upper and lower epidermal cell patterns of the neotropical species of Nephrolepis. (Bar = 0.1 mm; arrows indicate the locations of the apex (A), nearest margin (M), and nearest vein (V).)

a. N. biserrata.

b. N. multiflora.

c. N. x averyi.

d. N. cordifolia.

e. N. exaltata.

f. N. rivularis.

g. N. occidentalis - sinuous to lobed form.

h. N. occidentalis - intermediate form.

i. N. occidentalis - deeply lobed form.

j. N. pectinata - sinuous form.

k. N. pectinata - lobed form.

l. N. pendula.

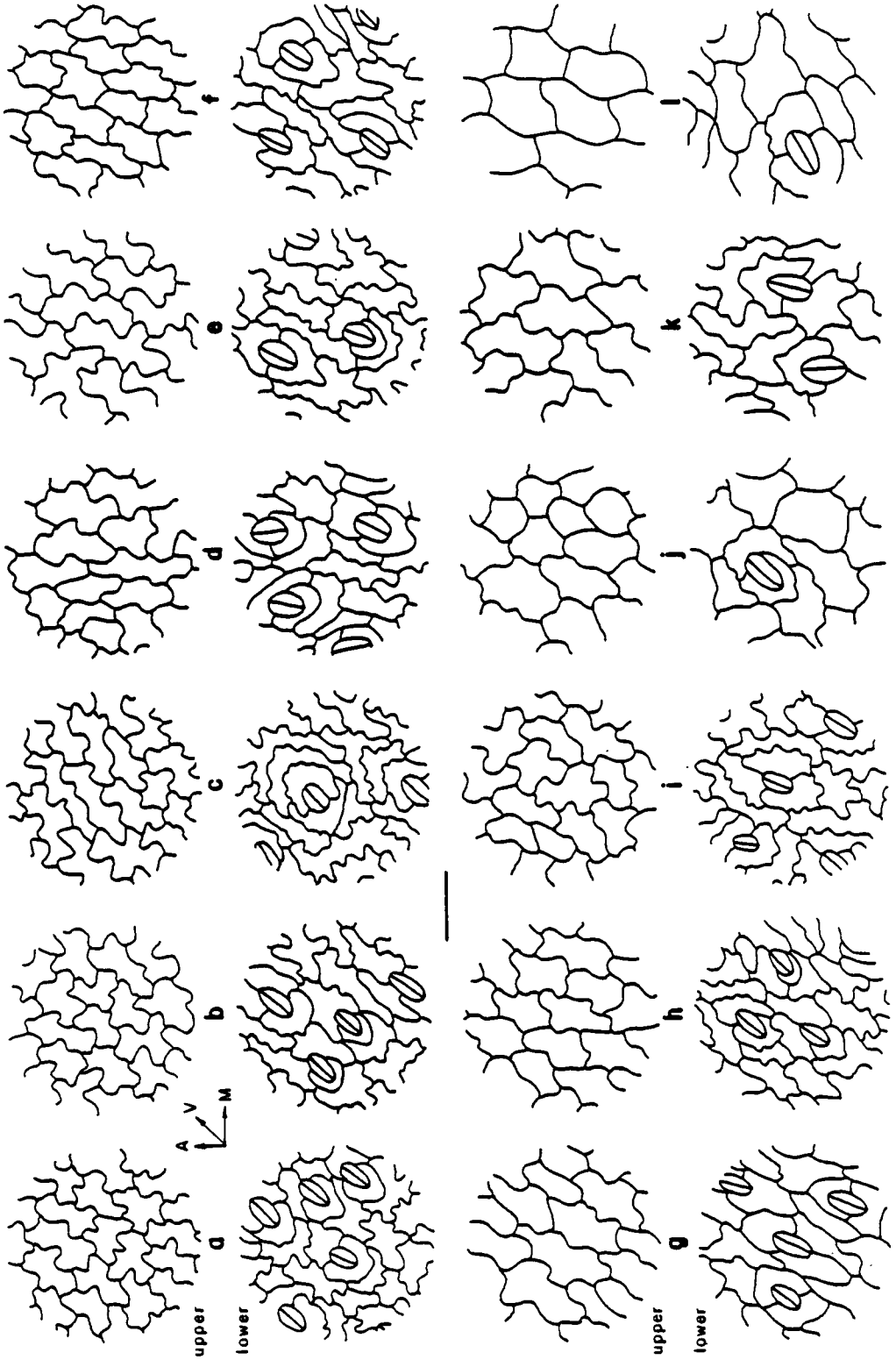


Figure 13

to the less lobed form of N. occidentalis (Figure 13j), but ranges to a condition central in the variational range of N. occidentalis (Figure 13k). Nephrolepis pendula exhibits a sinuous to nearly straight epidermal cell form (Figure 13l). The significance of these variations are difficult to assess since environmental conditions may variously affect the degree of cell wall undulation (c.f., Watson, 1942; Stace, 1965; and references in Van Cotthem, 1970a, 1970b).

Species groups based on guard cell lengths are, with a few exceptions, similar to those obtained with epidermal cell form. Nephrolepis biserrata and N. multiflora exhibit the smallest guard cell lengths and N. pendula the largest (Table 6). The other species represent various intermediate guard cell lengths (Table 6). Nephrolepis rivularis approaches N. biserrata and N. multiflora in guard cell length. Nephrolepis x averyi is intermediate between its parental species. Nephrolepis cordifolia and N. occidentalis are closest to one another and approach N. rivularis. Nephrolepis pectinata and N. pendula are closest to one another in guard cell length.

Nephrolepis x averyi is the only known polyploid species in this group, with the possible exception of some populations of N. pectinata (see Chapter V). Guard cell lengths in polyploids are often assumed to be larger than in related diploid species. This assumption has been supported and used by various authors to indicate ploidy levels in various groups (e.g., Blasdell, 1963;

Table 6. Guard cells lengths of the neotropical species of Nephrolepis. ($\bar{X}$ = mean, $S_{\bar{x}}$ = standard error of the mean, CV = coefficient of variation; all measurements are given in micrometers.)

Species	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range	CV
N. x averyi	51.7	0.43	5.24	41.6 - 65.0	10.1
N. biserrata	41.7	0.29	4.12	33.8 - 54.6	9.9
N. cordifolia	50.8	0.35	4.88	33.8 - 65.0	9.6
N. exaltata	56.1	0.25	3.48	46.8 - 65.0	6.2
N. multiflora	44.3	0.22	3.83	31.2 - 54.6	8.6
N. occidentalis	51.1	0.40	4.89	33.8 - 62.4	9.6
N. pectinata	60.1	0.60	7.34	41.6 - 78.0	12.1
N. pendula	63.0	0.69	6.86	44.2 - 78.0	10.9
N. rivularis	46.9	0.49	5.48	33.8 - 57.2	11.7

Evans, 1969; Mitui, 1966, 1967; Smith, 1971; Walker, 1962). This assumption can not be made blindly, however, it must be established for each group under consideration. Nephrolepis x averyi does not exhibit guard cell lengths that are statistically different ($p<0.05$) from N. occidentalis and N. cordifolia, both diploid species. Nephrolepis x averyi does exhibit statistically significant differences ($0.01<p<0.001$) from N. biserrata, N. multiflora, and N. rivularis, all three of which are diploid species with smaller guard cell lengths. There are also significant differences between N. x averyi and N. exaltata, N. pectinata, and N. pendula, also diploid species, but all with larger guard cell lengths. Guard cell lengths are, therefore, considered to be of no value in distinguishing among different ploidy levels.

Sori

Sori in Nephrolepis range from discrete submedial sori to marginal coenosori (Arbeleaz, 1928; Bower, 1928; Copeland, 1947; Holttum, 1949; Sporne, 1962; see also comments in Chapter IX). The neotropical species exhibit dorsal, discrete, medial to supramedial sori located over a vein ending. Developmental details can be found in Case (1932), Mahabale and Gorji (1951), and Sen and Sen (1973).

Location of the sorus with respect to the pinna margin is of some use in distinguishing among the species. In N. biserrata the sori range from midway between the costa and the pinna margin

(medial) to a slightly more marginal location (supramedial). The medial condition is typical for the wet pinna form, and a supramedial condition is typical for the dry pinna form (Figure 10b, page 63). Nephrolepis multiflora exhibits a supramedial condition (Figure 10a). Nephrolepis x averyi and N. exaltata exhibit a condition intermediate between medial and supramedial (Figures 9a and 9b, page 61). Nephrolepis cordifolia, N. occidentalis, and N. pectinata exhibit a medial condition (Figures 9c-9e and 10c-10f). Nephrolepis rivularis exhibits a supramedial to nearly medial sorus location and is relatively uniform in this feature (Figure 9f). Nephrolepis pendula exhibits a condition comparable to that of N. cordifolia, N. occidentalis, and N. pectinata, but the sori tend to be more supramedial (Figure 11, page 67). Although sorus location may be suitable in combination with other characters for distinguishing among the species, it is variable enough and the differences subtle enough that separation on this basis alone is difficult.

Indusium shape and attachment is represented by three basic types: 1) circular and peltate, 2) hippocrepiform to reniform and attached by a narrow sinus, and 3) reniform to lunar or triangular-rounded (± asymmetrical) and attached by a broad sinus. Indusia of the second or third types are flat to evenly conical and those of the first type are undulating to nearly plicate. Margins are entire in all but N. exaltata where one or two cells protrude and appear as papillae on the margin. This has been reported previously by Sen and Sen (1973). Young indusia of N. biserrata may possess

trichomes identical to those of the pinnae and rachises, but these fall off at maturity. Indusia lack an indument in all of the other species. Color of the indusium in all of the species ranges from light to dark brown with a lighter colored margin to concolorous and dark reddish brown.

Indusia of N. biserrata are 0.8-1.1 mm wide, and are most often of the first type, but range to the second type in the dry pinna form (Figure 14a). Indusia of N. multiflora are 1.1-1.3 mm wide and exhibit a condition intermediate between the first and second indusium types (Figure 14b). Nephrolepis rivularis possesses 0.6-1.2 mm wide indusia of the first type (Figure 14c). Nephrolepis x averyi and N. exaltata exhibit the second indusium type, with N. x averyi overlapping with the first type (Figures 14d and 14e). Indusia of N. x averyi are also narrower (0.9-1.1 mm) than those of N. exaltata (1.1-1.7 mm). Nephrolepis occidentalis, N. pendula, N. cordifolia, and N. pectinata exhibit the third indusium type with a range of indusium sizes on a single pinna (Figures 15a-15d). Indusia of N. pectinata and N. pendula are 0.9-1.5 mm wide, and those of N. cordifolia and N. occidentalis are 1.1-1.7 mm wide.

Small (1938) and Kepler (1975) have used sorus direction as a key character for distinguishing among some of the species. This feature refers to the direction in which the sorus opens when an imaginary line is drawn from the point of indusium attachment to a point midway along the distal free edge of the indusium. This character can not be evaluated on species with circular peltate

Figure 14. Indusia shapes of Nephrolepis biserrata, N. multiflora, N. rivularis, N. x averyi, and N. exaltata. (Bar = 2 mm; shading indicates the area of indusium attachment.)

a. N. biserrata.

b. N. multiflora.

c. N. rivularis.

d. N. x averyi.

e. N. exaltata.

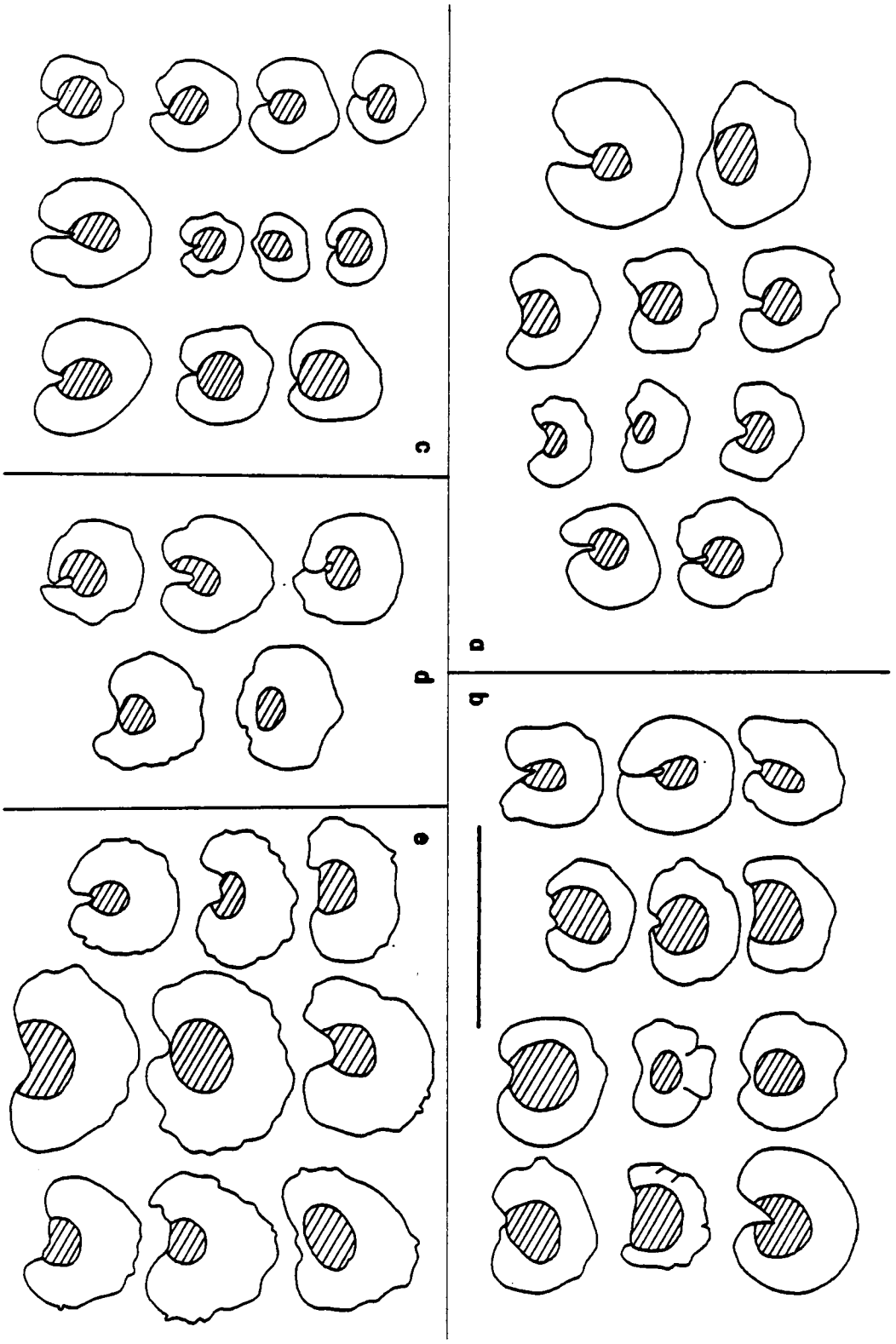


Figure 14

Figure 15. Indusia shapes of Nephrolepis occidentalis, N. pendula, N. cordifolia, and N. pectinata, and sporangia of N. biserrata and N. x averyi. (Bar in 25b = 2 mm and applies to 25a - d; shading indicates the area of indusium attachment; Bar for 25e and f = 200 µm.)

a. Indusia of N. occidentalis.

b. Indusia of N. pendula.

c. Indusia of N. cordifolia.

d. Indusia of N. pectinata.

e. Sporangia of N. biserrata - non-paraphysate.

f. Sporangia of N. x averyi - paraphysate.

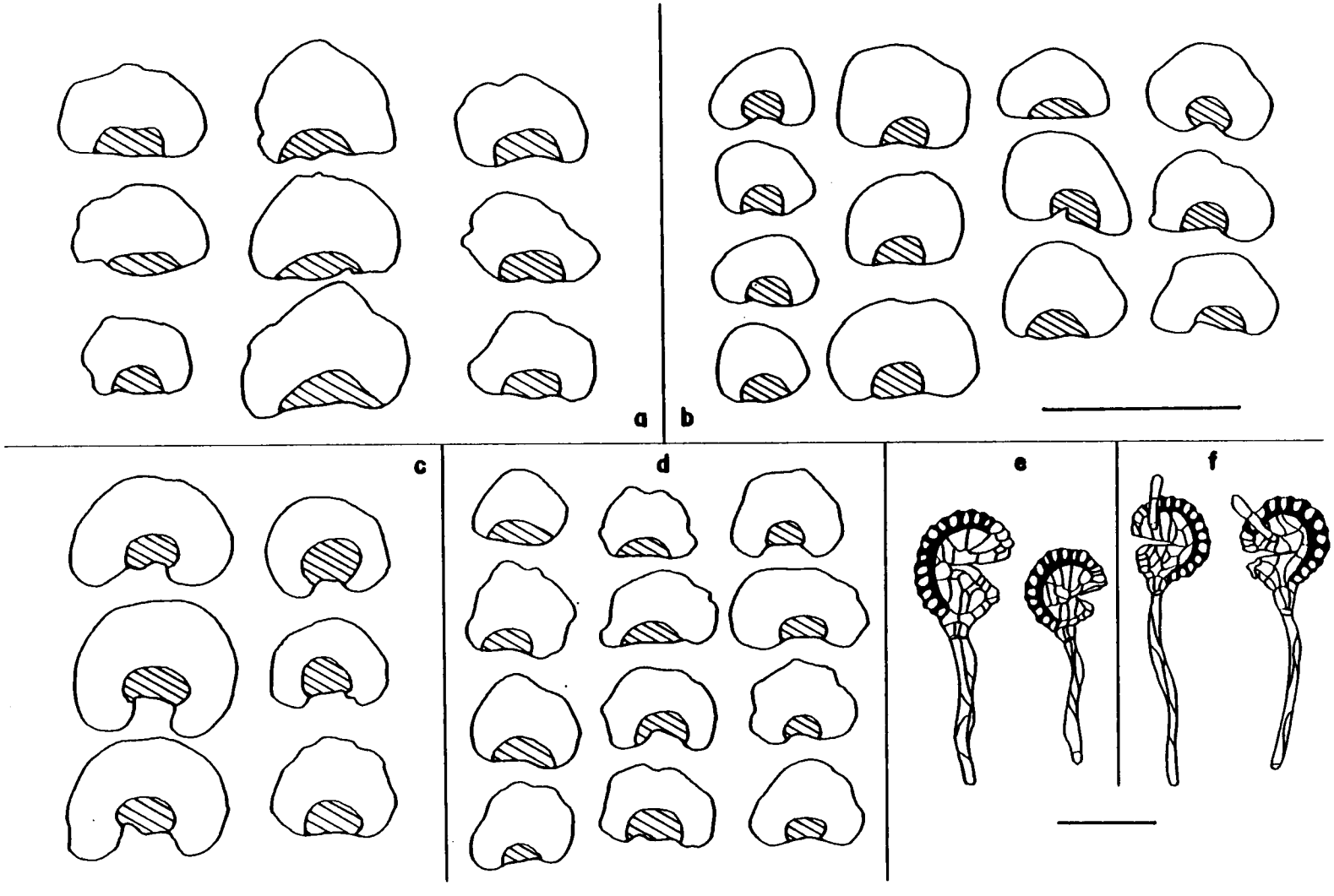


Figure 15

indusia (e.g., N. rivularis). In species where this character can be scored, the direction ranges from apical to nearly facing the margin, with an angled or intermediate condition being average. There is enough variation in this character, even on a single pinna, that it is of no value in distinguishing among the species.

Sporangia in Nephrolepis have been reported to exhibit initially a gradate-basipetal sequence of development that rapidly becomes and remains mixed (Case, 1932; Mahabale and Gorji, 1951). Sterile hairs have been reported as intermixed with young sporangia in N. exaltata, N. cordifolia, and N. radicans (Burm. f.) Kuhn (as N. volubilis J. Smith) by Mahabale and Gorji (1951), but I have seen no such hairs in the neotropical species. Paraphyses arising from the receptacle or indusium have been reported as absent in paleotropical material of N. exaltata, N. cordifolia, and N. biserrata (Case, 1932; Sen and Sen, 1973); this is the case for the neotropical populations of these species as well as for the other neotropical species.

Individual sporangial development is of the typical leptosporangiate type in all of the species. There is a three-rowed stalk and distinct stomium with an hypostomium and epistomium. Previous studies on mostly paleotropical taxa report 2-3 (5) cells in both the hypostomium and epistomium, 2 cells in the stomium, 13-16 indurated cells in the annulus, and 64 spores per sporangium (Case, 1932; Mahabale and Javalgekar, 1959; Sen and Sen, 1973). These observations have been confirmed for the neotropical species.

No discernible differences among the species were detected in these characters. Typical sporangia are illustrated in Figure 15e.

Only N. x averyi and N. occidentalis exhibit sporangial features distinguishing them from the other species. All species at maturity lack paraphyses on the individual sporangia. Young sporangia of N. x averyi and N. occidentalis, however, possess uniseriate, 2-celled paraphyses attached directly to the sporangial capsule (Figure 15f). The paraphyses occur only in young sporangia, and only on 10-20% of the sporangia in a given sorus. Only Case (1932) has reported hairs on the sporangia previously. Case (1932) reported this for N. cordifolia (plants of uncertain origin and identity); hairs were not observed on the neotropical populations of N. cordifolia. Nephrolepis x averyi is further distinguished by producing a large percentage of aborted sporangia.

Numerical Analysis

Three major analyses were performed: 1) classification of initial OTU samples, 2) assessment of the status of N. cordifolia, and 3) a summary of the initial analysis. The results of each of these analyses indicate that the neotropical material can be represented by nine morphological groups here referred to as species.

The initial CA (Figure 16) and PCA (Figure 17) indicate that, with one exception, all nine of the morphological groups form distinct clusters. The exception is a single OTU (no. 3) assignable to N. biserrata. This OTU clusters with N. x averyi and N. exaltata rather than with the bulk of OTU's representing N. biserrata. The discrepancy

Figure 16. Phenogram depicting the similarities among 43 OTU's representing the neotropical species of Nephrolepis. Clustering was performed on Gower's similarity coefficient using UPGMA. Each OTU is represented by two numbers separated by a dash, the first is the OTU number and the second codes for the geographic region according to the numbers given in Figure 1, page 8. Brackets indicate clusters for each species.

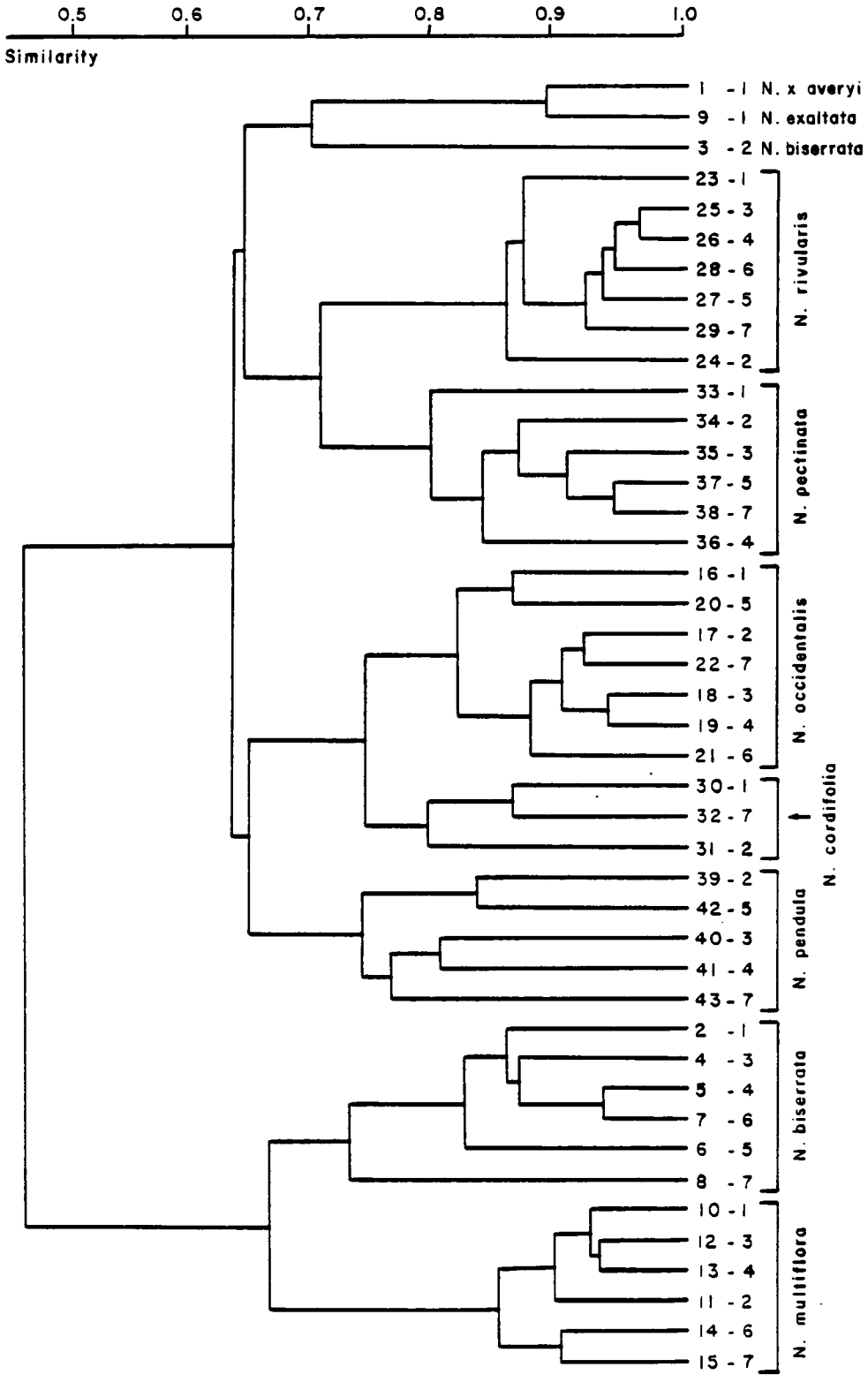

0.5
0.6
0.7
0.8
0.9
1.0
Similarity
1 - 1 N. x averyi
9 - 1 N. exaltata
3 - 2 N. biserrata
23 - 1
25 - 3
26 - 4
28 - 6
27 - 5
29 - 7
24 - 2
N. rivularis
33 - 1
34 - 2
35 - 3
37 - 5
38 - 7
36 - 4
N. pectinata
16 - 1
20 - 5
17 - 2
22 - 7
18 - 3
19 - 4
21 - 6
N. occidentalis
30 - 1
32 - 7
31 - 2
N. cordifolia
39 - 2
42 - 5
40 - 3
41 - 4
43 - 7
N. pendula
2 - 1
4 - 3
5 - 4
7 - 6
6 - 5
8 - 7
N. biserrata
10 - 1
12 - 3
13 - 4
11 - 2
14 - 6
15 - 7
N. multiflora

Figure 16

Figure 17. Three-dimensional diagram depicting the first three principle axes resulting from Principle Coordinate Analysis of 43 OTU's representing the neotropical species of Nephrolepis. Species clusters are circled on the diagram with the exception of N. x averyi and N. exaltata, each represented by a single OTU. Symbols for each species are as follows:

 = N. x averyi

 = N. biserrata

 = N. cordifolia

 = N. exaltata

 = N. multiflora

 = N. occidentalis

 = N. pectinata

 = N. pendula

 = N. rivularis

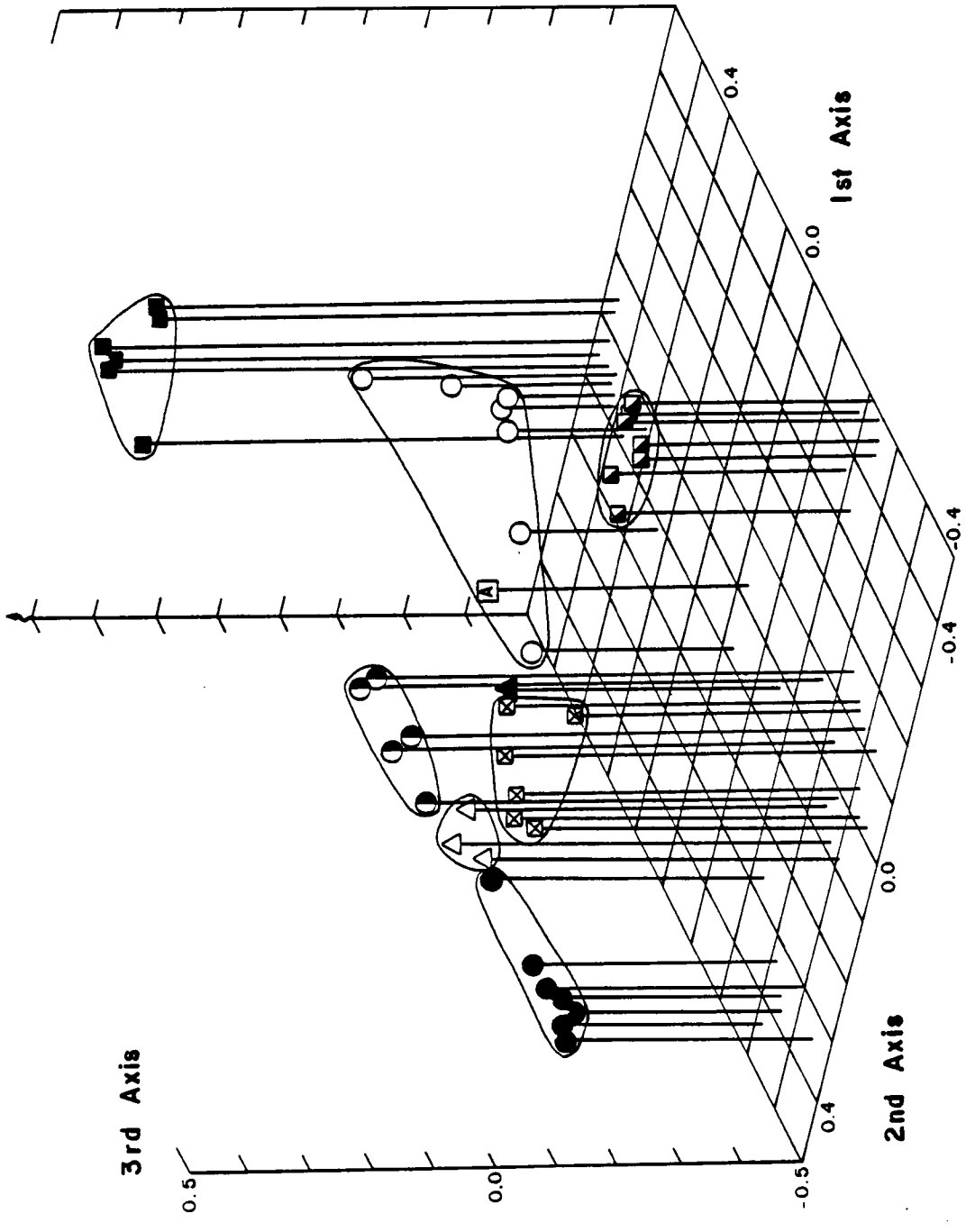


Figure 17

is not unexpected since N. x averyi is believed to be a hybrid between N. biserrata and N. exaltata (Nauman, 1979a, 1979b).

Two large clusters are obvious from the phenogram (Figure 16), one consisting of N. biserrata and N. multiflora, and another consisting of the remaining taxa. When morphological characters are examined, N. biserrata and N. multiflora show similarities in numerous features, especially in pinna characters and overall indument features. The similarities are further supported by other less obvious features of scale morphology and epidermal cell form. This clustering into two larger groups may also be correlated with different geographic origins. Nephrolepis multiflora is an Asian species (present in the neotropics as an escaped cultigen) and N. biserrata is pantropical in distribution. Members of the second cluster are largely neotropical in distribution. Nephrolepis cordifolia is the only species in the second cluster occurring in the paleotropics. Distribution of N. cordifolia, however, is difficult to interpret because the species is widely cultivated and frequently occurs as an escaped cultigen. The N. biserrata-N. multiflora cluster appears to reflect significant similarities between these two species and their distinctness from the other species.

Further emphasis on the distinctiveness of the N. biserrata-N. multiflora cluster can be seen in the PCA results (Figure 17). Though the species are not widely separated along the second principle axis, the first and third principle axes clearly depict them as distinct groups of OTU's. As a whole, the two species link up with

the others through N. x averyi and N. exaltata (Figure 17); this is not as apparent in the phenogram (Figure 16).

Several groups occur in the second larger cluster. The first consists of N. x averyi, N. exaltata, and OTU no. 3 of N. biserrata. The coherence of this group may be explained by hybridization and associated intermediacy. The next subordinate level of clustering depicts two main groups, however, PCA suggests slightly different relationships than those in Figure 16 by CA. The first of these two groups consists of N. pendula, N. cordifolia, and N. occidentalis, and the second of N. rivularis and N. pectinata. That N. cordifolia and N. occidentalis cluster closely is expected due to similarities in a number of characters (e.g., tuber production, pinna shape, etc.), but that N. pendula should cluster with these two species without N. pectinata is unexpected. Nephrolepis occidentalis is distinct from both N. cordifolia and N. pendula along the second and third principle axes in PCA (Figure 17). The coherence of this group in CA may be a reflection of the relatively large number of pinna characters used in the analysis; all three species are similar in several pinna characters. The N. rivularis-N. pectinata cluster can be separated from the previous cluster by pinna attachment alone and this appears to be an expression of the importance of pinna characters at this level of clustering for these five species. Nephrolepis rivularis is depicted as relatively distinct from other members of these two clusters in PCA (Figure 17). This species can be described as relatively uniform and distinctive in terms

of morphology. It is therefore expected to be distinct in PCA. The PCA further suggests closer relationships among N. cordifolia, N. pendula, and N. pectinata than is depicted by CA; these relationships are discussed below.

Nephrolepis pendula has been treated as conspecific with N. cordifolia by Tryon (1964), who (pp. 230 and 232) states,

> I have not been able to maintain the usually recognized N. pendula, being unable to find any character by which it might be clearly distinguished.

This treatment was followed in a later work by Tryon and Tryon (1982) and by Stolze (1981). Since the initial CA and PCA suggested a relationship between N. pectinata and these two species, all three were included in this analysis.

The hypothesis that N. cordifolia and N. pendula are conspecific is rejected. In both CA and PCA, N. cordifolia, N. pendula, and N. pectinata are represented by three distinct clusters (Figures 18 and 19). Differences between N. cordifolia and N. pendula occur in rhizome, stipe, and rachis induments, stipe color, length, and form, and in the presence or absence of tubers. All of these characters are relatively conservative. In CA (Figure 18) N. cordifolia shows greater similarity to N. pectinata than to N. pendula. This might suggest that all three taxa are conspecific, but when relationships in PCA are examined there is no overlap among the clusters (Figure 19). The species are distinct groups based on morphology. Other features (e.g., chemistry) further support this and will be pointed out in later chapters. Nephrolepis cordifolia is here treated

Figure 18. Phenogram depicting the similarities among 74 OTU's representing neotropical material of Nephrolepis cordifolia, N. pectinata, and N. pendula. Clustering was performed on Gower's similarity coefficient using UPGMA. Each OTU is represented by two numbers separated by a dash, the first is the OTU number and the second codes for the geographic region according to the numbers given in Figure 1, page 8. Brackets indicate clusters for each species.

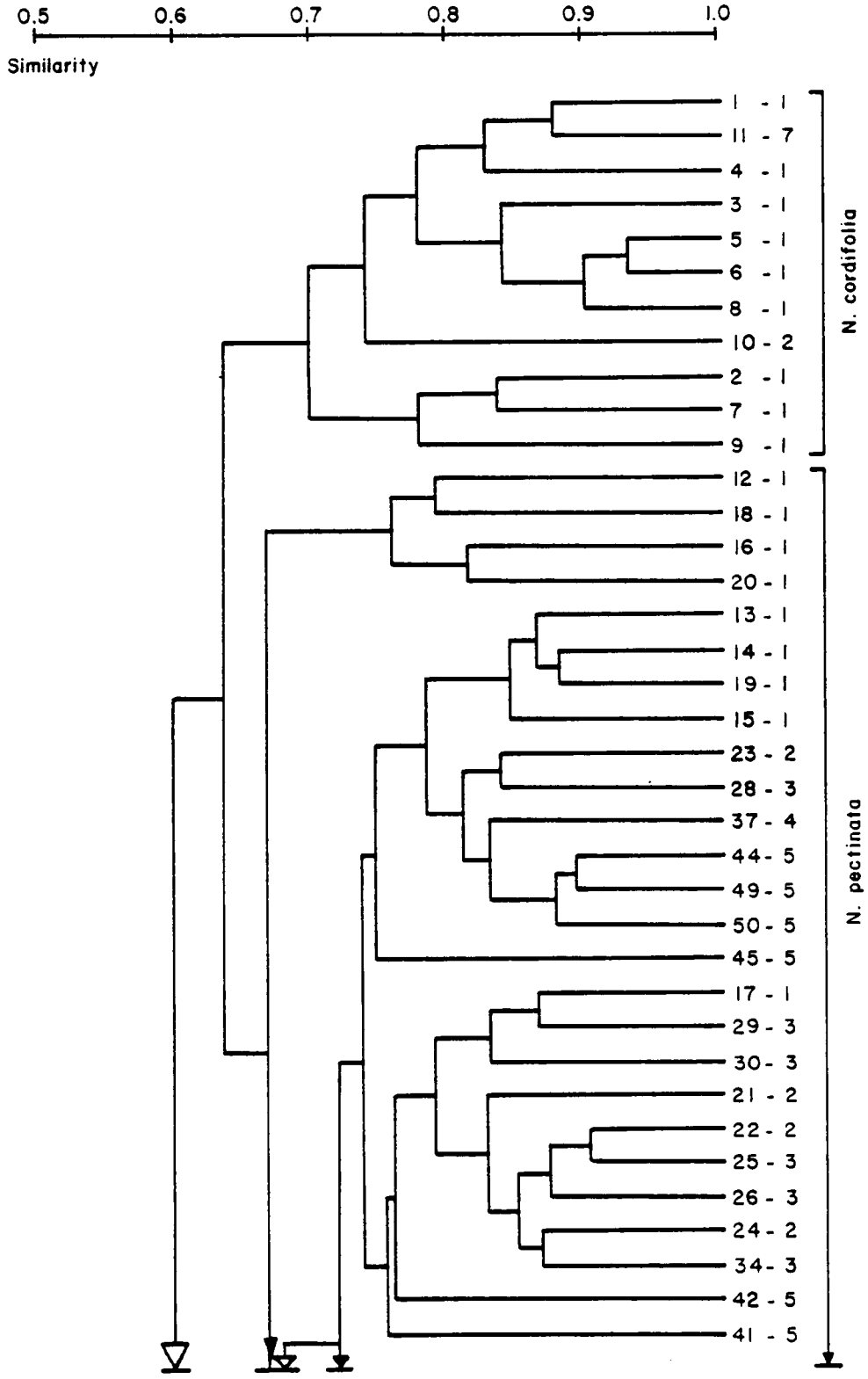

0.5
0.6
0.7
0.8
0.9
1.0
Similarity
1 - 1
11 - 7
4 - 1
3 - 1
5 - 1
6 - 1
8 - 1
10 - 2
2 - 1
7 - 1
9 - 1
12 - 1
18 - 1
16 - 1
20 - 1
13 - 1
14 - 1
19 - 1
15 - 1
23 - 2
28 - 3
37 - 4
44 - 5
49 - 5
50 - 5
45 - 5
17 - 1
29 - 3
30 - 3
21 - 2
22 - 2
25 - 3
26 - 3
24 - 2
34 - 3
42 - 5
41 - 5
N. cordifolia
N. pectinata

Figure 18

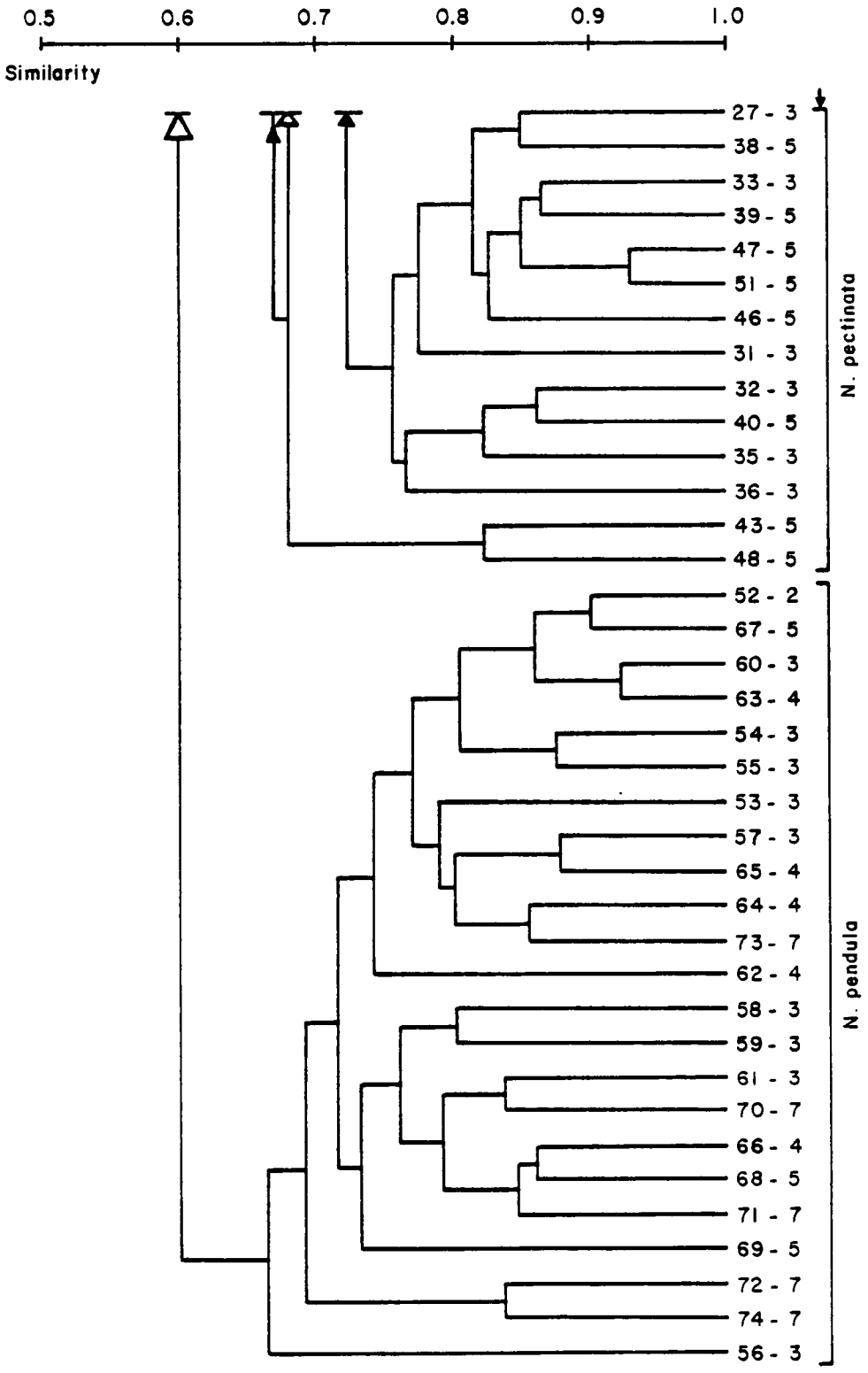

0.5
0.6
0.7
0.8
0.9
1.0
Similarity
27 - 3
38 - 5
33 - 3
39 - 5
47 - 5
51 - 5
46 - 5
31 - 3
32 - 3
40 - 5
35 - 3
36 - 3
43 - 5
48 - 5
N. pectinata
52 - 2
67 - 5
60 - 3
63 - 4
54 - 3
55 - 3
53 - 3
57 - 3
65 - 4
64 - 4
73 - 7
62 - 4
58 - 3
59 - 3
61 - 3
70 - 7
66 - 4
68 - 5
71 - 7
69 - 5
72 - 7
74 - 7
56 - 3
N. pendula

Figure 18

Figure 19. Three-dimensional diagram depicting the first three principle axes resulting from Principle Coordinate Analysis of 74 OTU's representing neotropical material of *Nephrolepis cordifolia*, *N. pectinata*, and *N. pendula*. (Solid squares = *N. pectinata*, open circles = *N. cordifolia*, and solid triangles = *N. pendula*.)

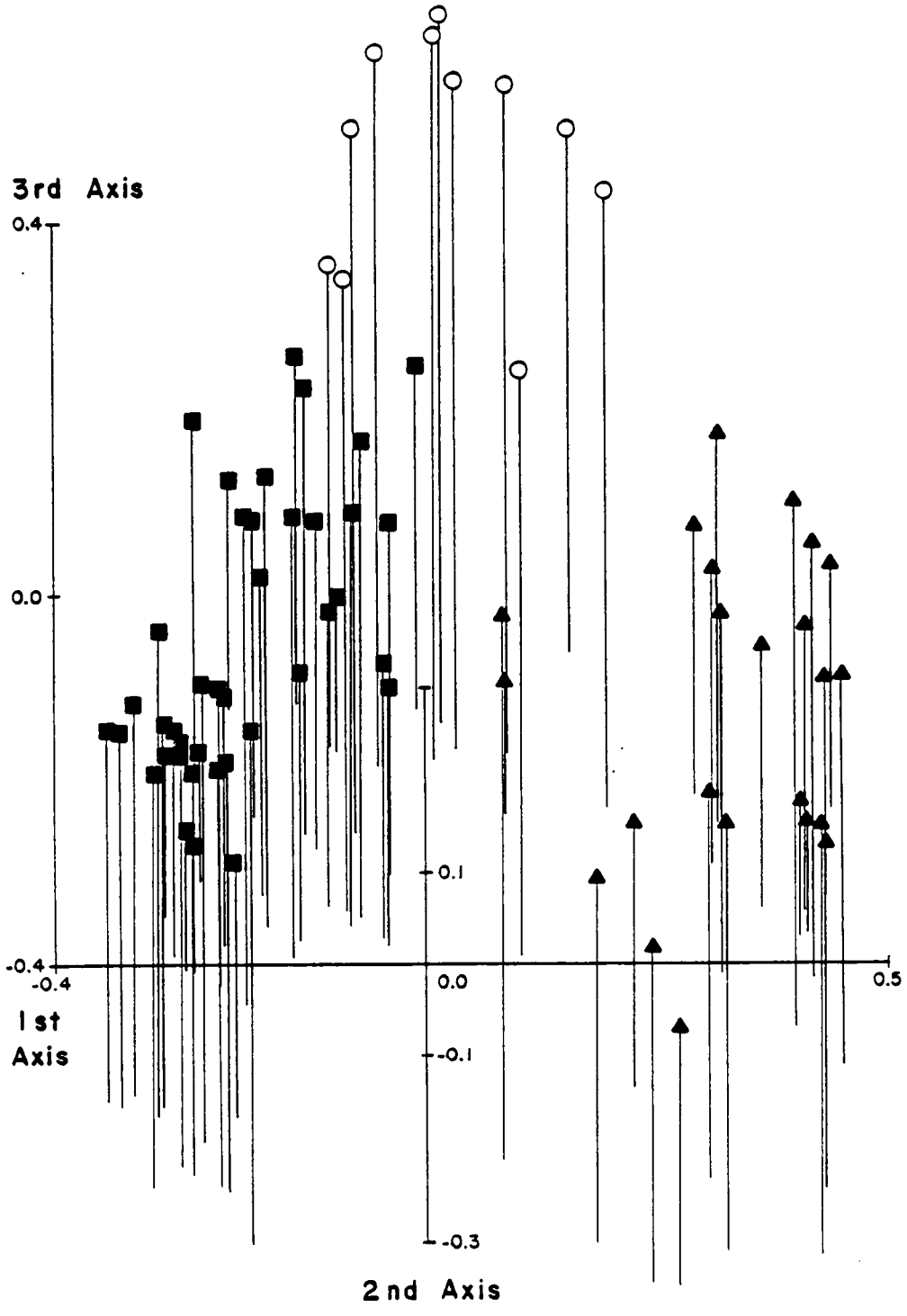


Figure 19

in a restricted sense and is not considered conspecific with N. pendula.

The pinna forms of N. pectinata and N. pendula did not form distinct groups in CA. The Mexican pinna form of N. pectinata is represented in Figure 18 by OTU's 21-24 and the remaining OTU's represent the typical forms. The forms of N. pendula are represented in Figure 18 as follows: OTU's 54-56 are the falcate form, 63-66 are the Guyana form, 67-69 are the Galapagos form, 73 and 74 are the brevis form, and all others are the typical form. No clear clusters representing the forms are apparent.

The results of the summary analysis are more in line with the PCA results of the initial analysis. Some discrepancies were noted between the results of CA and PCA in the initial analysis. These discrepancies reflect differences between the representation of relationships by each method. The CA tends to better represent relationships among individual OTU's within clusters and at lower levels of clustering, and PCA tends to better represent relationships at higher levels of clustering (Sneath and Sokal, 1973). The PCA then should provide a better picture of interspecific relationships than CA in the initial analysis. When OTU's of the initial analysis are pooled into a smaller number of OTU's, as done in this summary analysis, and the CA and PCA repeated, the results should provide a picture of interspecific relationships corresponding to PCA results of the initial analysis. This is indeed the case.

Two larger clusters are still apparent in both CA and PCA (Figures 20a and 20b). One cluster consisting of N. biserrata and

Figure 20. Summary of the phenetic relationships among the neotropical species of Nephrolepis.

a. Phenogram depicting similarities among the species. Clustering was performed on Gower's similarity coefficient using UPGMA.

b. Three-dimensional diagram depicting the first three principle axes resulting from Principle Coordinate Analysis of the species. Symbols for each species are as follows:

A = N. x averyi.

B = N. biserrata.

C = N. cordifolia.

E = N. exaltata.

M = N. multiflora.

O = N. occidentalis.

P = N. pectinata.

PEN = N. pendula.

R = N. rivularis.

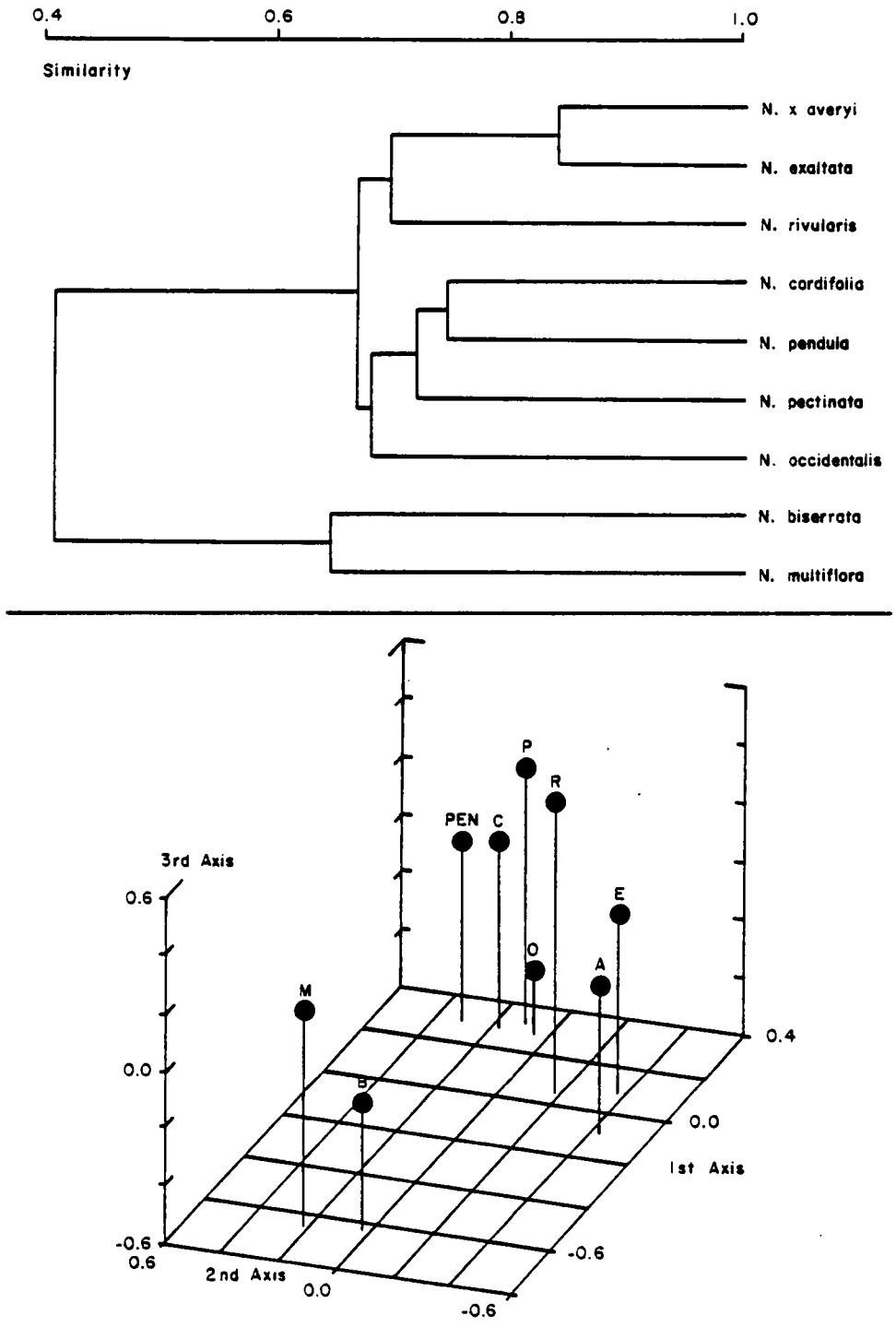

0.4
0.6
0.8
1.0
Similarity
N. x averyi
N. exaltata
N. rivularis
N. cordifolia
N. pendula
N. pectinata
N. occidentalis
N. biserrata
N. multiflora
3rd Axis
0.6
0.0
-0.6
0.6
2nd Axis
0.0
-0.6
P
R
PEN
C
E
O
A
M
B
0.4
0.0
1st Axis
-0.6

Figure 20

N. multiflora and the other of the remaining species. The N. biserrata-N. multiflora cluster is still clearly separated in PCA (Figure 20b).

Within the second cluster N. x averyi and N. exaltata are more similar to one another than to any other species (Figure 20a). This would be expected if N. x averyi arose as a hybrid with N. exaltata as one of its parents. Nephrolepis rivularis now clusters with the N. x averyi-N. exaltata cluster, indicating less emphasis on basally attached pinnae and more emphasis on size and shape of the pinnae and indusium features. Nephrolepis rivularis is still relatively distinct in PCA (Figure 20b). Nephrolepis pectinata clusters with N. rivularis in the initial analysis, but here clusters with N. cordifolia and N. pendula. The close clustering of these three species in CA and PCA is in line with the PCA results of the initial analysis and seems to reflect similarities in pinna size and indument. Nephrolepis occidentalis is depicted as being less similar to N. cordifolia than CA in the initial analysis indicates. Its placement here supports the PCA results of the initial analysis. Nephrolepis cordifolia and N. pendula cluster in close proximity in the summary analysis (Figure 20a), reflecting primarily similarities in pinna characters.

Summary

Macro- and micro-morphology provide a number of characters useful in distinguishing among the species. Of these characters,

42 (Table 7) were selected for use in the final numerical analysis (Chapter VIII).

Numerical analysis of morphology indicates nine distinct groups in CA and PCA (Figures 20a and 20b). Two larger clusters are apparent that seem to be correlated with geographic ranges. The neotropical species (including N. cordifolia) cluster separately from the paleotropical N. multiflora and the pantropical N. biserrata. Within the neotropical cluster two groups consistent with pinna and indument features are present; the first consists of N. x averyi, N. exaltata, and N. rivularis, and the second consists of N. cordifolia, N. occidentalis, N. pectinata, and N. pendula. Nephrolepis x averyi is shown to be more closely related to one of its parental species (N. exaltata) than any other species. Nephrolepis rivularis is shown to be relatively distinct in PCA and most closely related to N. x averyi and N. exaltata. Nephrolepis occidentalis is also a relatively distinct species, clustering with N. cordifolia, N. pectinata, and N. pendula; these latter three species form a distinct cluster. Within this cluster, N. cordifolia and N. pendula are closely related, but analysis of the taxa as single specimen OTU's indicates that N. cordifolia and N. pendula are not conspecific as suggested by previous authors.

Table 7. Morphological characters included in the final numerical analysis.

Character Number	Character
1.	Seasonality and rhizome development
2.	Rhizome scale habit
3.	Rhizome scale color at maturity
4.	Rhizome scale margin type
5.	Rhizome scale size
6.	Tubers
7.	Proportion of fertile/sterile pinnae per fertile frond
8.	Frond length
9.	Frond length/width ratio
10.	Stipe length
11.	Stipe color
12.	Stipe scale habit
13.	Stipe scale color at maturity
14.	Stipe scale margin type
15.	Stipe scale density
16.	Stipe scale size
17.	Rachis length
18.	Interpinnal distance
19.	Rachis pubescence
20.	Rachis scale color at maturity
21.	Rachis scale density
22.	Rachis scale size
23.	Pinna length
24.	Pinna length/width ratio
25.	Lower pinna length/width ratio
26.	Pinna "falcateness"
27.	Pinna shape
28.	Pinna tip shape
29.	Pinna margin type
30.	Pinna acroscopic lobe shape
31.	Pinna deflection
32.	Pinna base shape
33.	Pinna attachment
34.	Pinna pubescence - lamina
35.	Pinna pubescence - upper costa surface
36.	Pinna scale density
37.	Epidermal cell form
38.	Guard cell length
39.	Sorus location
40.	Indusium shape and attachment
41.	Indusium papillae
42.	Young sporangia paraphysate

CHAPTER III

PALYNOLOGY

Light microscope (LM) studies are an important source of systematic data (e.g., Wagner, 1974), and in recent years scanning (SEM) and transmission electron microscope studies have become standard tools in systematic research, SEM in particular (e.g., Gastony, 1974; Tryon and Tryon, 1982). In this investigation LM studies were used to evaluate spore size and SEM studies were used to evaluate spore sculpturing in the neotropical species. Size measurements and perine sculpturing were useful in distinguishing among the species and suggested relationships different from those suggested by morphology alone.

Materials and Methods

Spores for LM studies were obtained from air dried fresh material or herbarium specimens (Table 8). Three preparation types were employed: 1) spores partially cleared by heating for several hours in 85% lactic acid, 2) spores treated by the acetolysis procedure of Erdtman (1943) and mounted in glycerine jelly, and 3) spores mounted fresh in Diaphane or Euparal. The clearing effects of the lactic acid and acetolysis procedures demonstrated no advantages over the Diaphane or Euparal preparations, therefore, the Diaphane or Euparal preparations were used for the bulk of the LM studies. For SEM studies, spores from the same specimens used for

Table 8. Specimens employed for the palynological studies of the neotropical species of Nephrolepis.

Species	Vouchers
N. x averyi	FLORIDA: Cuthbert s.n. (FLAS); Durand 1, 49, 52, 71 (FAU); Nauman et al. 426, 427, 428, 433 (FAU); Scull s.n. (FLAS). CUBA: Shafer 7722 (NY).
N. biserrata	FLORIDA: Durand 60, 76, 84 (FAU); Evans s.n. (TENN); Nauman P2, 380, 318 (FAU); Nauman et al. 429, 431, 432 (FAU). CUBA: Brenckle 47-157 (NY); Howard 5831 (NY). CAYMAN ISLANDS: Millspaugh 1376 (F). JAMAICA: Evans 2540 - A (TENN). NICARAGUA: Proctor et al. 27312 (NY). COSTA RICA: Evans & Bowers 3335 (TENN). PANAMA: Gentry & Nee 8676 (NY). VENEZUELA: Stevermark 88868 (NY). PERU: Croat 20059 (TENN); Schunke 4046 (F). BRAZIL: Amapa - Egler & Irwin 45987 (NY). Bahia - Boom & Mori 899 (NY).
N. cordifolia	FLORIDA: Austin et al. 6469 (FAU); Nauman 410 (FAU); Nauman et al. 218, 399 (FAU). CUBA: Wright 1803 (NY). JAMAICA: Maxon & Killip 654 (NY). DOMINICA: Fuertes 1545 (F). GUATEMALA: Brenckle 47-158 (NY). BRITISH GUYANA: Jenman s.n. (NY). BRAZIL: Rio Grande do Sul - Frengero 99 (NY).
N. exaltata	BERMUDA: Howe s.n. (NY). FLORIDA: Austin et al. 6764 (FAU); Nauman P5, 264, 271, 451, 702 (FAU); Staples 139 (FAU). CUBA: Leon & Gustavo 3862 (NY). HAITI: Nash 115 (NY). JAMAICA: Underwood 2671 (NY).
N. multiflora	FLORIDA: Nauman 192, 203, 204, 205, 312 (FAU); Nauman & Austin 181 (FAU). BAHAMAS: Correll & Meyer 44594 (NY). DOMINICAN REPUBLIC: Jones & Norris 1140 (NY). JAMAICA: Hespenheide 1014 (NY). DOMINICA: Robinson s.n. (TENN). MEXICO: Martinez 1851 (NY). GUATEMALA: Contreras 5643 (NY). COSTA RICA: Evans & Bowers 2880 (TENN).

Table 8 (Continued)

Species	Vouchers
N. multiflora (continued)	COLOMBIA: Forrero et al. 2136 (NY). BRAZIL: Amapa - Austin et al. 7161 (MG); Prance & Mello 17621 (NY). Bahia - Boom & Mori 841 (NY).
N. occidentalis	HAITI: Leonard 7923 (NY). MEXICO: Pringle 1835 (NY); Sharp 52168 (TENN); Sharp et al. 50158 (TENN). COSTA RICA: Cruz 107 (FLAS); Evans et al. 23 (TENN). COLOMBIA: Smith 2563 (NY). ECUADOR: Holm-Nielson et al. 3103 (NY). BRAZIL: Para - Plowman et al. 8568 (NY). Goias - Irwin et al. 21683 (F); Plowman et al. 8238 (NY).
N. pectinata	JAMAICA: Underwood 89, 2688 (NY). MEXICO: Dressler 1642 (NY). GUATEMALA: Molina & Molina 12025 (NY). COSTA RICA: Evans & Bowers 2719 (TENN); Mickel 2255 (NY). ECUADOR: Hitchcock 20479 (NY). PERU: Schunke 793 (F), 3788 (NY); Stock & Horton 9429 (F). BOLIVIA: Williams 1107 (NY).
N. pendula	CUBA: Carabia 3738 (NY); Shafer & Leon 13553 (NY). DOMINICAN REPUBLIC: Valeur 625 (F). MEXICO: Breedlove 33140 (NY). NICARAGUA: Hall & Bockus 7554 (FLAS) COSTA RICA: Evans & Bowers 3249 (TENN); Woodruff s.n. (FLAS). PANAMA: Seibert 642 (NY). COLOMBIA: Barkley & Gutierrez 1477 (NY). BRITISH GUYANA: Maguire & Maguire 35401 (NY). VENEZUELA: Maguire & Wurdack 33963 (NY); Manara s.n. (NY). ECUADOR: Wiggins 11063 (NY). PERU: Fosberg 27787 (NY); Tryon & Tryon 5452 (F). BRAZIL: Minas Gerais - Anderson et al. 36023 (NY). BOLIVIA: Brooke 6535 (NY).
N. rivularis	PUERTO RICO: Staples 71 (FAU). CUBA: Howard 6152 (NY). DOMINICA: Long & Norstog 3397 (TENN). COSTA RICA: Mickel 2926 (NY). PANAMA: Porter et al. 4435 (NY).

Table 8 (Continued)

Species	Vouchers
N. rivularis (continued)	SURINAME: Boer 1291 (TENN); Maguire et al. 39112 (NY). VENEZUELA: Steyermark 89148 (NY). PERU: Klug 176 (F); Schunke 219 (NY). BRAZIL: Roraima - Prance et al. 9433 (NY); Acre - Prance et al. 12179 (NY).

the LM studies (Table 8) were mounted on studs with double-sticky tape and gold coated in Denton model 515 vacuum-coater with a randomly rotating head.

Analysis for the LM studies were made on both standard Nikon and Leitz compound microscopes. The SEM studies were carried out on an ETEC Autoscan model U-1. Photomicrographs for the SEM studies were made with Polaroid positive/negative type 55 film.

Several characters were measured in the LM studies: length of the spore in micrometers (μm) along the polar, longitudinal, and equatorial axes; laesura length; and a P/E ratio (polar/equatorial axis length x 100) was calculated. Statistical summaries were compiled for each character as outlined for the characters of morphology (p. 11). For each of the axes and laesura lengths, a minimum of 100 measurements were made.

Terminology follows the more conservative system of Harris (1955) with the exception that "perine" is used in the sense of Lugardon (1972, 1974) rather than the traditional sense in which the term is only applied to extensive perines as in the dryopteroid and asplenioid ferns. The remaining layers of sporoderm (those exclusive of the perine) were not distinguishable as multiple layers by LM or SEM methods and here referred to inclusively as "exine." Additional terms are defined when they are first used below.

Results and Discussion

Several features are common to all of the neotropical species. The spores are (except for N. x averyi) free, bilateral, anisopolar,

and monolete. In profile view the shape is plano- to concavo-convex, with the proximal wall flat to concave. In cross-sectional view the shape is circular, with the proximal wall rounded or V-shaped. In polar view the shape is oblong to elliptic-oblong. Since the species can not be distinguished on the basis of these features, none of these were included in the final numerical analysis.

Measurements of the polar, longitudinal, and equatorial axes, and laesura are of little use in distinguishing among the species. Statistical summaries show sufficient overlap of ranges among the species to preclude these features from use as taxonomic discriminators (Figure 21 and Table 9). Only N. exaltata exhibits differences from the other species; being larger in all four characters (Figure 21). Length differences are greatest between N. exaltata and N. cordifolia, especially in equatorial axis length and in laesura length. The P/E ratios show similar statistical distributions (Table 9). Of the length measurements, only equatorial axis length was chosen for the final numerical analysis.

Literature data for some of the species are summarized in Table 10. Though there are some apparent differences, comparisons and interpretations are confounded by large differences in the geographic sources of the samples, differences in the methods of spore preparation, and the possibility of misidentifications. In addition to the data differences in Table 10, Case (1932) reported two spore sizes in N. biserrata, both oval in shape with the smaller more concave on one side. Though there is considerable variation in this species I did not observe two distinct size or shape classes.

Figure 21. Dice diagrams of spore data of the neotropical species of Nephrolepis. (Total bar length = range, black bar = one standard deviation above and below the mean, cross bar = mean; lengths are given in µm.)

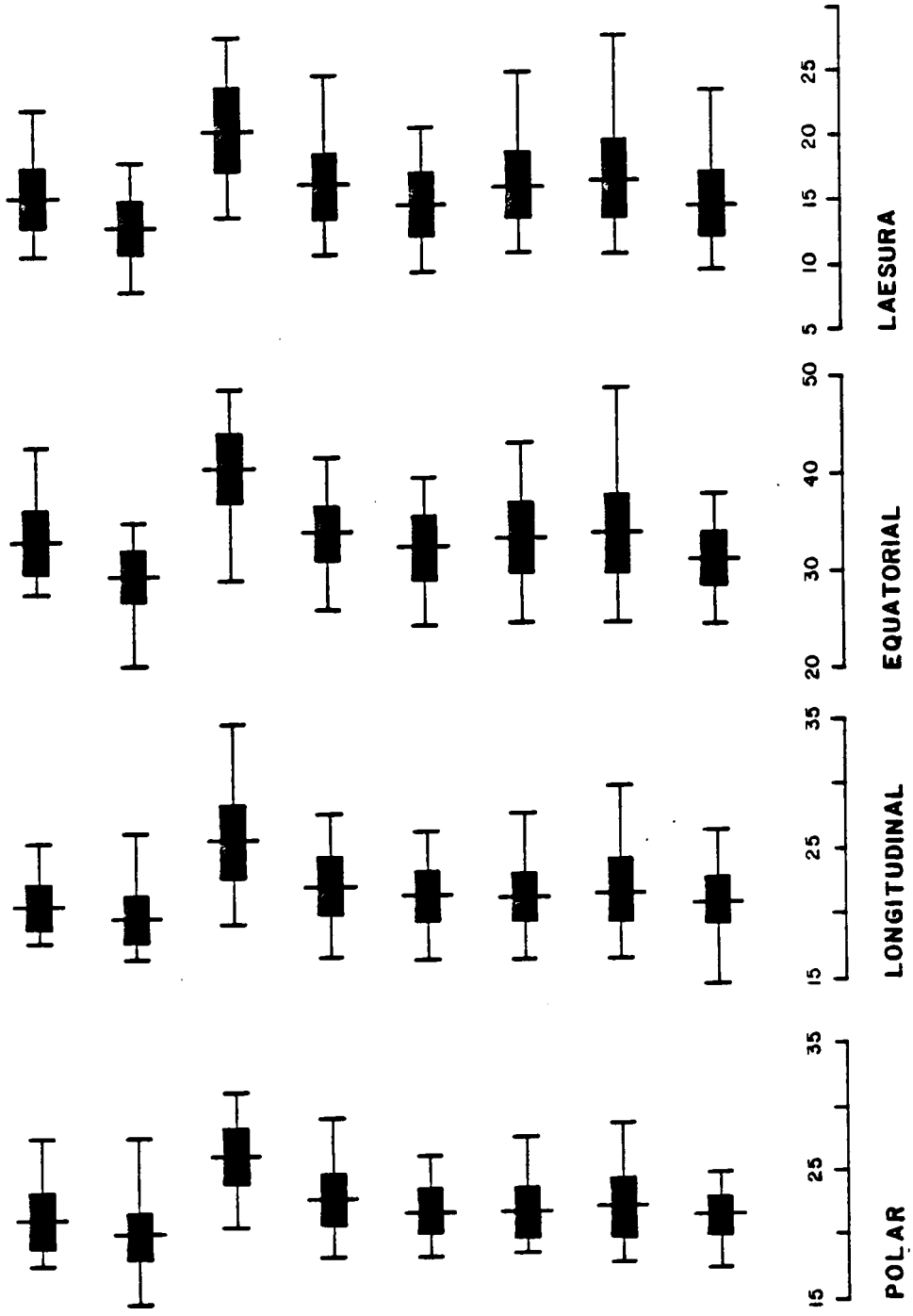

N. biserrata
N. cordifolia
N. exaltata
N. multiflora
N. occidentalis
N. pectinata
N. pendula
N. rivularis
POLAR
15 25 35
LONGITUDINAL
15 25 35
EQUATORIAL
20 30 40 50
LAESURA
5 10 15 20 25

Figure 21

Table 9. Supporting data for Figure 21. Selected statistics of spore data for the neotropical species of Nephrolepis. ($\bar{X}$ = mean, $S_{\bar{X}}$ = standard error of the mean.)

Species & Character	$\bar{X}$	$S_{\bar{X}}$	Standard Deviation	Range
N. biserrata				
Polar length*	21.6	0.20	2.02	18.2 - 28.0
Longitudinal length	21.0	0.16	1.62	18.2 - 25.9
Equatorial length	33.8	0.32	3.22	28.0 - 43.4
Laesura length	15.6	0.22	2.22	11.2 - 22.4
P/E ratio	64.1	0.39	3.94	56.0 - 73.9
N. cordifolia				
Polar length	20.5	0.19	1.93	15.4 - 28.0
Longitudinal length	20.1	0.28	2.78	16.8 - 26.6
Equatorial length	29.9	0.28	2.78	21.0 - 35.7
Laesura length	13.2	0.20	1.99	8.4 - 18.2
P/E ratio	68.7	0.55	5.54	56.0 - 73.9
N. exaltata				
Polar length	26.5	0.22	2.16	21.0 - 31.5
Longitudinal length	26.0	0.28	2.84	19.6 - 35.0
Equatorial length	41.0	0.38	3.77	29.4 - 49.0
Laesura length	20.7	0.32	3.24	14.0 - 28.0
P/E ratio	64.9	0.39	3.90	54.4 - 78.6
N. multiflora				
Polar length	23.0	0.19	1.90	18.9 - 29.4
Longitudinal length	22.4	0.21	2.12	16.8 - 28.0
Equatorial length	34.4	0.29	2.86	26.6 - 42.0
Laesura length	16.6	0.25	2.48	11.2 - 25.0
P/E ratio	67.1	0.39	3.92	57.4 - 84.1
N. occidentalis				
Polar length	22.2	0.19	1.86	16.8 - 26.6
Longitudinal length	21.9	0.19	1.85	16.8 - 26.6
Equatorial length	33.0	0.32	3.20	25.2 - 40.6
Laesura length	15.0	0.24	2.41	9.8 - 21.0
P/E ratio	67.5	0.36	3.56	57.1 - 78.9
N. pectinata				
Polar length	22.1	0.19	1.85	18.9 - 28.0
Longitudinal length	21.5	0.18	1.83	16.8 - 28.0
Equatorial length	33.6	0.34	3.37	25.2 - 43.4
Laesura length	16.2	0.27	2.70	11.2 - 25.2
P/E ratio	64.8	0.54	5.44	53.7 - 88.9

Table 9 (Continued)

Species & Character	$\bar{X}$	$S_{\bar{x}}$	Standard Deviation	Range
N. pendula				
Polar length	22.4	0.23	2.31	18.2 - 30.1
Longitudinal length	21.9	0.24	2.36	16.8 - 30.1
Equatorial length	34.0	0.40	3.97	25.2 - 49.0
Laesura length	16.8	0.31	3.09	11.2 - 28.0
P/E ratio	66.1	0.47	4.70	54.8 - 77.1
N. rivularis				
Polar length	21.3	0.14	1.37	17.5 - 25.2
Longitudinal length	21.2	0.18	1.77	14.7 - 26.6
Equatorial length	31.4	0.24	2.41	25.2 - 38.5
Laesura length	14.8	0.25	2.53	9.8 - 23.8
P/E ratio	68.3	0.41	4.13	54.6 - 78.1

*Lengths are given in µm.

Table 10. Comparative spore literature data for three species of Nephrolepis (measurements are in micrometers).

Source	Polar	Longi-tudinal	Equa-torial	Laesura	Reference*
N. biserrata					
Ceylon	23	26	39	14	3
Africa	---	22	35	17	2
Africa	22	21	32	17	7
Guatemala	---	14-18	25-27	18	1
Florida	13(21)30	13(21)27	26(33)38	11(17)24	6
N. cordifolia					
N. Zealand	11(16)21	---	18(25)32	1/2 long.	4
Hong Kong	27	26	38	19	3
Guatemala	---	14-16	23-26	16	1
Venezuela	---	18-23	29-36	2/3 long.	9
---	---	15(20)24	28(34)36	12	2
Florida	17(23)29	16(22)28	25(32)38	8(13)19	6
N. exaltata					
India	12-15	25	---	---	5
India	---	18	30	12	2
Hawaii	24-28	---	41-50	---	8
West Indies	22	23	37	21	3
Cuba	---	20-25	33-38	24	1
Florida	21(27)30	25(27)32	32(41)50	9(15)25	6

*References: 1. Braggio (1966); 2. Devi and Nayar (1971); 3. Erdtman and Sorsa (1971); 4. Harris (1955); 5. Mahabale and Gorji (1951); 6. Nauman (1981b); 7. Nayar et al. (1964); 8. Selling (1946); 9. Tschudy and Tschudy (1965).

A perine is present in all of the neotropical species. The perine is closely adherent to the exine, which accounts, in part, for previous authors describing the perine as absent or having been non-committal (Braggio, 1966; Harris, 1955; Erdtman and Sorsa, 1971; Nauman, 1981b; Selling, 1946). Lugardon (1972) has defined the perine, in part, as an outer, acetolysis-resistant layer, and this is the case for mature spores of the neotropical species. However, in younger spores the perine is at least partially labile to acetolysis. Acetolysis of younger spores generally results in spores without a perine, or with only fragments of perine remaining. In both cases fragments of perinous material are present in the slide preparations. If the spores are at a sufficiently early stage of development, the fragmentation and separation of the perine is also seen in the lactic acid and the Diaphane and Euparal preparations. The perine is particularly evident in SEM preparations (Figure 22a). Irregular perine deposition is associated with abnormal spore development in N. x averyi. The observation that a perine is present confirms the report of Tryon and Tryon (1982) for the neotropical species and reports for various paleotropical species by Liew (1977), Nayar et al. (1964), and Devi and Nayar (1971).

Surface sculpturing of the perine is useful for distinguishing among the species. Tryon and Tryon (1982) presented the only previous SEM photomicrographs of spores of the neotropical species. My own studies confirm their observations with the following exception. Their figure of N. exaltata (page 661, Figure 102.10) more closely

Figure 22. SEM photomicrographs of spores of Nephrolepis biserrata and N. cordifolia.

a. N. cordifolia, arrow indicates the perine layer (Brenckle 47-158 (NY) Guatemala, 4800x).

b. N. biserrata, (Evans & Bowers 3335 (TENN) Costa Rica, 1350x).

c. N. biserrata. (Evans & Bowers 3335 (TENN) Costa Rica, 2600x).

d. N. cordifolia, (Maxon & Killip 654 (NY) Jamaica, 1500x).

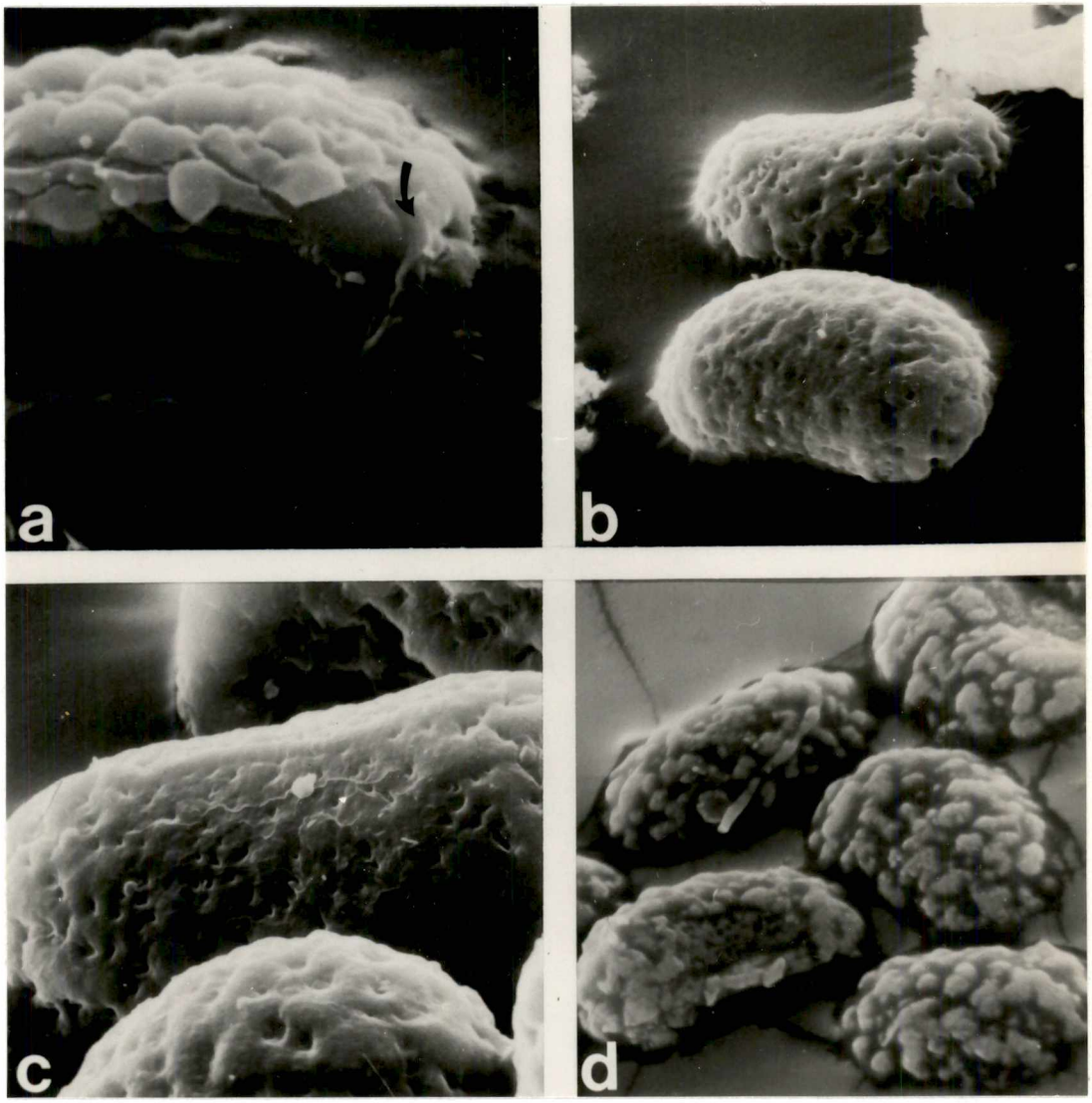


Figure 22

resembles N. multiflora than N. exaltata. This discrepancy may be due to a misidentification, but has not been confirmed. Their illustrations for N. rivularis, N. biserrata, and N. occidentalis agree with my findings. Tryon and Tryon (1982) describe the spores as "rugose" to "tuberculate," terms corresponding to my "rugose" and "verrucate," respectively. Rugose is here used to describe the typical condition of N. biserrata (Figure 22b) where the perine is more or less evenly deposited and possesses numerous pore-like pits (Figure 22c). The verrucate condition is exemplified by N. cordifolia (Figure 22d) where the perine is a thin uniform layer ornamented with irregularly rounded to spheroid projections of variable sizes (verrucae). The rugose condition seems to represent a situation in which the verrucae have coalesced and left small gaps and pits between more widely separated verrucae. Intermediate conditions as in N. occidentalis (Figure 23a) further suggest this connection between the rugose and verrucate conditions. Intermediate conditions are designated by hyphenating the terms.

Various species and species groups can be distinguished by perine sculpturing. Nephrolepis biserrata, N. pectinata, and N. pendula exhibit a rugose perine, ranging from rugose to rugose-verrucate (e.g., Figures 22b and 22c). Nephrolepis exaltata, N. occidentalis, and N. rivularis exhibit a rugose-verrucate perine, ranging to verrucate (e.g., Figures 23a and 23c). Nephrolepis cordifolia exhibits a verrucate to verrucate-rugose perine (Figures 22a and 22d). Nephrolepis multiflora exhibits a granular perine (Figure 23b); the granulae were shown by SEM to be small verrucae.

Figure 23. SEM photomicrographs of spores of Nephrolepis occidentalis, N. multiflora, N. exaltata, and N. x averyi.

a. N. occidentalis, (Sharp 52168 (TENN) Mexico, 1300x).

b. N. multiflora.
(Robinson s.n. (TENN) Jamaica, 1600x).

c. N. exaltata, (Underwood 2671 (NY) Jamaica, 1600x).

d. N. x averyi, spherical spore (Shafer 7722 (NY) Cuba, 1500x).

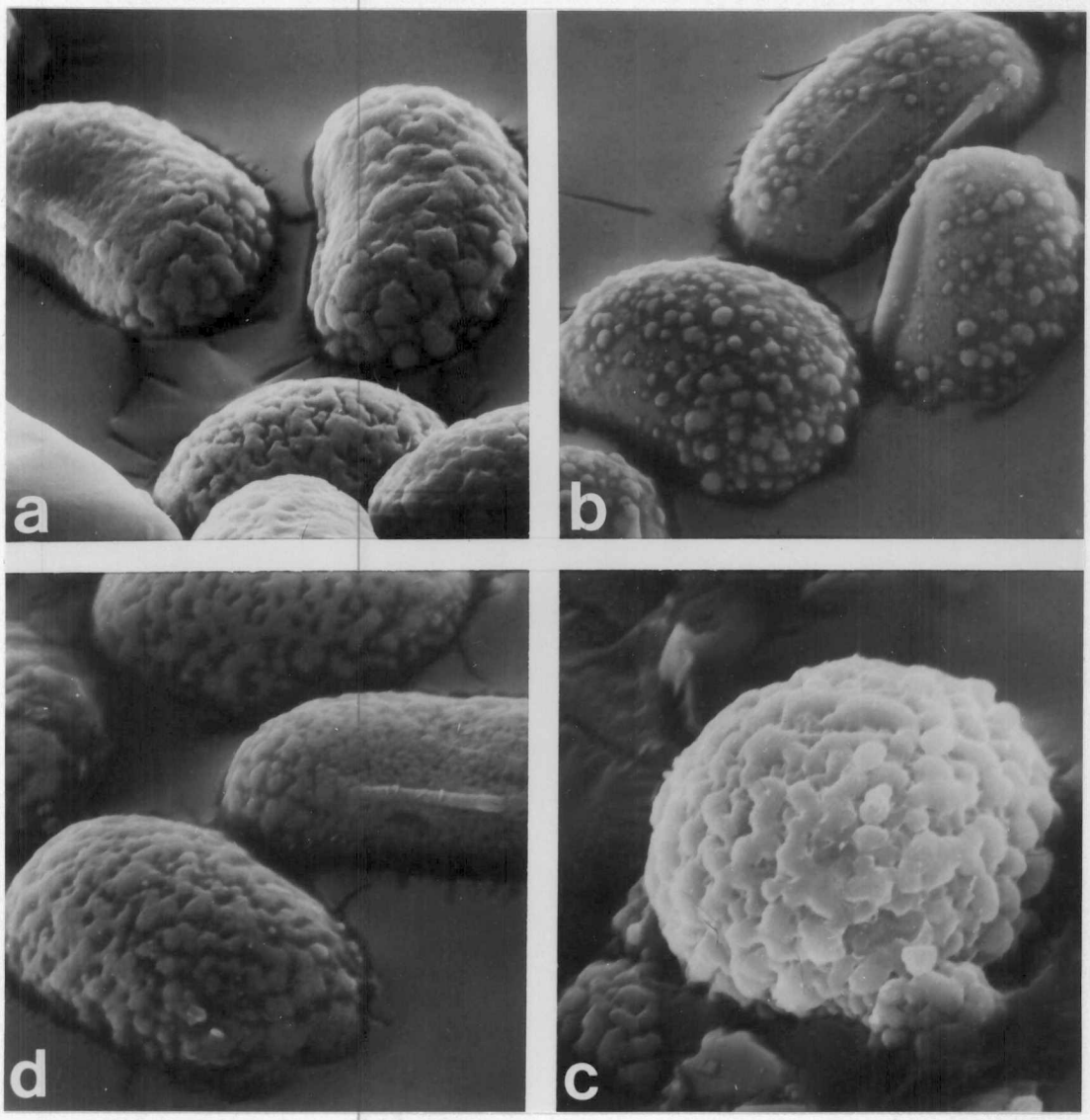


Figure 23

Spore morphology of N. x averyi is distinct from the other species. The spores are irregular, alete, spherical (Figure 23d), and exhibit features described for Polystichum Roth. hybrids (Morzenti, 1962). Preparations contain a large number of aborted spores, aborted tetrads, globules of perinous material, and rarely (< 2%) spores with a normal reniform shape. Frequency distributions of maximum spore length are platykurtic when compared to N. biserrata and N. exaltata, the putative parent species (see Figure 3 in Nauman, 1979b). Platykurtic distributions such as this appear to be significant features of fern hybrids (Diagobo, 1967; Kanamori, 1969, 1971; Wagner and Chen, 1965). The spherical spores average 32.6 µm in diameter and exhibit a perine sculpturing intermediate between the parent species.

Summary

Palynological studies of the neotropical species revealed two characters useful in distinguishing among the species, and that these characters suggest slightly different species relationships than morphology alone. Nephrolepis pectinata and N. pendula are closely related according to morphology alone, but palynology places them close to N. biserrata. Nephrolepis biserrata is placed close to N. multiflora by morphology, yet palynology suggests a wide separation of N. multiflora from all of the other species. Morphology places N. occidentalis closer to N. cordifolia than to N. exaltata, but palynology places N. occidentalis closer to N. exaltata and N. rivularis. Nephrolepis exaltata occupies a central position

in the variational spectrum for both morphology and palynology. Morphology alone places N. rivularis near N. pectinata and N. pendula, but palynology places the species nearer N. exaltata.

Characters of equatorial axis length and perine sculpturing were chosen to represent palynology in the final numerical analysis.

CHAPTER IV

GAMETOPHYTE AND HYBRIDIZATION STUDIES

Development and morphology of fern gametophytes have been the subjects of continuing research in recent years (e.g., Dyer, 1979). Though the gametophyte generation tends to provide characters of greater use at familial and generic levels of classification (cf. Atkinson and Stokey, 1964; Stokey, 1951), its potential at the species level should not be overlooked. Gametophyte development and morphology were investigated in the present study in an effort to discover additional characters of value in evaluating systematic relationships among the neotropical species. These studies indicated no characters of value in distinguishing among the species. Hybridization attempts were also made to establish the parentage of N. x averyi; these attempts failed.

Materials and Methods

A preliminary investigation was carried out to determine which of three readily available culture media and which of two temperature/light regimes would provide optimal growth. Optimal growth is here interpreted to mean the most rapid growth and development.

Three spore samples were employed in the preliminary study (Table 11). Spores for this and all other phases of study were collected from air dried leaves or herbarium material and stored

Table 11. Spore sources for gametophyte and hybridization studies.

Species	Voucher
N. x averyi	FLORIDA: Nauman 1549 (TENN).
N. biserrata	FLORIDA: Nauman 1557[h], 1558[h], 1589 (TENN).
N. cordifolia	FLORIDA: Nauman et al. 466 (TENN).
N. exaltata	FLORIDA: Nauman 1539*, 1541[h], 1543[h] (TENN).
N. multiflora	FLORIDA: Nauman 1519*, 1522, 1523 (TENN).
N. occidentalis	ORIGIN UNKNOWN: New York Botanical Garden (no. 625/71).
N. pendula	COLOMBIA: New York Botanical Garden (no. 383/77).

[h]Samples used for hybridization study.

*Samples used for preliminary study.

in vials under refrigeration. Spores were sown aseptically on sterile culture medium in 100 x 15 mm petri dishes following a sterilization pretreatment described below:

1. Spores added to a sterile centrifuge tube and ca. 3-4 ml of a fresh Tween solution added (12 drops of 20% Tween in 100 ml of distilled water).
2. Tubes swirled and centrifuged for 2 minutes at 2000 rpm.
3. Tween solution removed and 3-5 ml of tap water added.
4. Tubes allowed to stand overnight in darkness. (This step allows germination of potential contaminants without stimulating the germination of the spores and therefore provides a more efficient killing of the contaminants in subsequent steps).
5. Tubes swirled and centrifuged as in step 2.
6. Tap water removed and 3-4 ml of a fresh sterilizing solution added (1:5, commercial bleach:distilled water). (Spores should not be exposed to the sterilizing solution for more than 3 minutes.)
7. Tubes swirled and centrifuged as in step 2.
8. Sterilizing solution is removed and 3-5 ml of sterile distilled water added.
9. Tubes swirled and centrifuged as in step 2.
10. Water is removed and 1 ml of sterile distilled water added.
11. Spores sown aseptically.

Two replicate plates were sown for each spore stock on Knop's medium, Knudson's medium (both as modified by Steeves et al., 1955), and Thompson's medium (Parker's macronutrients and Thompson's micronutrients--see Klekowski, 1969). Replicates were placed under continuous lighting at 25° C with two 34 watt Sylvania Cool White fluorescent lamps suspended 4.6 dm above the plates at an intensity of 14-17 watts/m^2, and at 32° C with six 34 watt Sylvania Cool White fluorescent lamps and four 25 watt General Electric incandescent lamps suspended 7.1 dm above the plates at an intensity of 3-10 watts/m^2.

The following growth conditions were determined to be optimal and employed throughout the study; Knop's medium at 25° C with continuous lighting from a bank of two 34 watt Sylvania Cool White fluorescent lamps suspended 4.6 dm above the plates at an intensity of 14-17 watts/m^2.

Development and morphology of each spore stock (Table 11) were studied from live plants, plants mounted in a mixture of 0.5% acetocarmine and Hoyer's medium (Beeks, 1955), or plants fixed in FAA (Berlyn and Miksche, 1976) and then stained in Fast Green (0.5% in 70% ethanol) or in Safranin (1% in 70% ethanol), and mounted in Diaphane.

Plants were watered once per week after reaching sexual maturity to facilitate fertilization and resulting sporophytes were reared to maturity as sources of material for morphological, cytological, palynological, and chemical studies.

Reciprocal crosses (20 replicates per cross) were attempted among four spore stocks of N. biserrata and N. exaltata (Table 11). Individuals to serve as females were isolated on 60 x 15 mm petri dishes before becoming sexual. Plants to serve as males were grown in crowded culture on 100 x 15 mm petri dishes sown 20-30 days after sowing of the female stocks. Crossing was attempted when both male and female stocks were at the appropriate sexual stages. The male cultures were flooded with sterile distilled water. When sperm became visible under a dissecting microscope the water was poured off and the appropriate females flooded with the sperm broth. Unsuccessful crosses were repeated after one week, and if a second cross was also unsuccessful, the females were watered with sterile distilled water to encourage self fertilization.

Results and Discussion

Preliminary Study

The following observations and conclusions were made as a result of the preliminary study.

1. Germination occurred in 4-10 days at 25° C and 14 days at 32° C; there were no differences among media with regard to germination times within each spore stock.
2. Appearance of two-dimensional growth and subsequent phases of development were faster at 25° C in all media types and spore stocks.
3. Growth and development (with either temperature/light regime) were faster on Knop's medium than on Knudson's

or Thompson's for all spore stocks; the latter two media produced similar growth and development rates.

Development and Morphology

All seven of the species examined exhibited the same morphological and developmental pattern, a pattern typical of leptosporangiate ferns in general and confirm observations of other species and populations by Lloyd (1974a, 1974b), Mahabale and Javalgekar (1959), Sen and Sen (1973), and Wagner (1952). There were no differences among the species.

Sterile, male, female, and hermaphroditic plants occurred intermixed in culture. There was no evidence of an antheridogen system, though N. cordifolia and N. hirsutula (Forst.) Presl have been reported to respond positively to Pteridium Scop. antheridogens (Näf, 1960; Näf et al., 1975; Voeller, 1964). This developmental sequence was also reported for Hawaiian populations of N. exaltata by Lloyd (1974a, 1974b).

Vegetative reproduction of the gametophyte was frequent in all species, occurring through small outgrowths. By day 90 some outgrowths had become male and were presumably capable of becoming hermaphroditic, but archegonia were not observed up to termination of observations at day 120. The outgrowths occasionally became numerous, up to 30 per plant by day 80.

Callous growths, vascular patches, and apogamous roots were observed for several species. These features have been described for a number of fern species and are variable in occurrence and

causes (cf. Miller, 1968; Sulklyan and Mehra, 1977; Steil, 1939, 1951; Whittier, 1962). These features may be of value in studies of gametophyte development in general, but were of no value in the present study for comparing species.

Though apogamous sporophyte production was reported by Lloyd (1974a) for N. exaltata in Hawaii, no apogamous sporophytes were produced by any species in this study. Gametophytes isolated before becoming sexual produced sporophytes, but all of these were sexual in origin as evidenced by the presence of a foot at the point of attachment to the gametophyte.

Some species differed in germination percentages, but the differences are not considered significant. Nephrolepis x averyi, N. biserrata, and N. occidentalis exhibited low germination rates (1% by day 8). Germination in N. x averyi occurred only in the "normal" spores. The larger, spherical, presumably unreduced spores did not germinate. Nephrolepis exaltata and N. cordifolia exhibited intermediate germination rates, ca. 45% by day 8. Nephrolepis multiflora and N. pendula exhibited the highest germination rates, 98% and 80% by day 8, respectively.

Approximately 70% of the plants on a given plate produced sporophytes in all of the species except N. x averyi. This species produced gametophytes that were "normal" in appearance, but only one sporophyte was produced. This sporophyte was reared to maturity to confirm that it was N. x averyi.

Literature Data

Previous literature on the gametophytes of Nephrolepis is scattered and incomplete. The literature data available is mostly concerned with various aspects of gametophyte development in general and seldom with species relationships. As a result, comparative information can only be obtained in small amounts from widely different sources. The earlier literature includes information for N. acuminata (Houtt.) Kuhn (as N. davallioides (Swartz) Kunze), N. acutifolia, N. auriculata (L.) Trimen (as N. paucifrondosa d'Almeda), N. biserrata (often as N. acuta (Schkuhr) Presl), N. cordifolia (sometimes as N. tuberosa (Bory ex Willd.) Presl), N. exaltata, and N. hirsutula (Burgerstein, 1901; Hurel-Py, 1943; Javalgekar and Mahabale, 1959; Lloyd, 1974a, 1974b; Mahabale and Javalgekar, 1949, 1959; Näf, 1960; Näf, et al., 1975; Nagai, 1941; Sen and Sen, 1973; Sulklyan and Mehra, 1977; Voeller, 1964; Wagner, 1952; Weinburg and Voeller, 1969). General observations not citing specific species include Atkinson and Stokey (1964) and Nayar and Kaur (1968). In all of these studies the source material was paleotropical or horticultural in origin; there were no studies of material with a definite neotropical origin. Given the uncertain origins of the materials, scattered nature of the information, as well as problems of misidentification and misapplication of epithets, the previous literature provided little useful information.

Hybridization

Two spore stocks each of N. exaltata and N. biserrata were used in the hybridization attempts (Table 11, page 129). Of the

160 individual crosses, each performed twice, no sporophytes were produced. Failure of these attempts, however, does not provide convincing evidence against N. biserrata and N. exaltata being the parents of N. x averyi.

One way to determine if the failure of the crosses was due to an inability of N. biserrata and N. exaltata to produce hybrids, is to compare these results to those from intraspecific crosses involving both intergametophytic and intragametophytic selfing within each stock and between stocks within a species. There were difficulties, however, in making such comparisons. Plants from which the spore stocks were obtained for a given species only exhibited character differences attributable to environmental factors or showing enough variation that differences between stocks could not be reliably detected (i.e., there were no genetic markers). Because the gametophytes are hermaphroditic when archegonia are produced, and because of a lack of genetic markers, even if sporophytes were produced they would be indistinguishable from plants resulting from interstock crosses or intragametophytic selfings. Therefore, only intragametophytic selfings could be effectively compared to the results from the intersepcific crossing attempts.

Comparisons of the selfing results with the crossing results is also confounded. Low numbers of sporophytes indicate problems apart from an inability of N. biserrata and N. exaltata to form hybrids. Sporophytes occurred in only 10% of the 160 plants employed in the selfing attempts. This low percentage might indicate sporophyte

abortion or malformation, or low numbers of antheridia, functional sperm or functional archegonia. Visual inspection did not reveal aborted or malformed sporophytes, and antheridia and archegonia were indistinguishable between plants that did and plants that did not produce sporophytes. Since the numbers of sperm were considerably higher during the interspecific crossing attempts than during selfing of these same plants, failure of the interspecific crosses can not be attributed to this factor, though this may account for the low numbers of sporophytes produced during the selfing attempts.

Genetic load may cause low numbers of sporophytes in the selfing procedures. Yet, Lloyd (1974a, 1974b) reported 0.0% genetic load for populations of N. exaltata in Hawaii. In his studies, Lloyd associated the low genetic load with other aspects of the species' biology, e.g., morphological variability, gametangial ontogeny, gametophyte longevity, and habitat. Since the features he associated with a low genetic load were exhibited by the plants from which the spore stocks were obtained, a high genetic load was unlikely. It is difficult to determine the extent to which genetic load might reduce the number of sporophytes produced without performing more specific tests such as the pairs/isolates test of Klekowski (1971). Genetic load was probably not a major factor in producing low numbers of sporophytes in the intragametophytic selfings.

The most likely reason for the low numbers of sporophytes produced in the selfing attempts and the failure of interspecific crosses is the technique itself. Since sporophytes were readily

produced in crowded culture (ca. 70% of the plants from these same spore stocks), isolation of the gametophyte appears to lower the number of sporophytes produced. This may be due to lower numbers of sperm available or due to some undetermined factor of the cultural conditions (e.g., depletion of nutrients, hormone accumulation, etc.). The specific factors that may have been involved were not determined.

Genetic incompatibility between N. biserrata and N. exaltata may still have been one of the reasons for the failure of the interspecific crosses. However, given the potential for failure of the crosses due to one or more of the factors above, incompatibility between these two species can not be assessed. Only sporophyte production and subsequent morphological and cytological study are useful indicators of parentage for N. x averyi. Since no sporophytes were produced, no conclusions from artificial hybridization can be made at this time.

Summary

Gametophyte development and morphology in the neotropical species provided no characters of value for species comparisons. All seven of the species studied exhibited a typical leptosporangiate pattern of development and morphology. Because differences were not exhibited among the species, characters of the gametophyte generation were not included in the final numerical analysis.

Hybridization attempts failed and firm conclusions on the parentage of N. x averyi can not be made at this time.

CHAPTER V

CYTOLOGY

Previous chromosome counts indicate a base gametic number of n=41 for Nephrolepis. Seven of the neotropical species were available for chromosome counts in this study. With the exception of N. x averyi, a gametic number of n=41 was confirmed for all specimens counted, including N. multiflora and N. rivularis (reported here for the first time). Nephrolepis x averyi exhibits n=82 with irregular and variable pairing. This uniformity in chromosome number did not provide additional information on interspecific relationships except in the case of N. x averyi.

Materials and Methods

Young sporangia were fixed for 1 to 24 hours in ethanol:acetic acid (3:1) or prepared without fixation. In all cases sporangia were prepared according to the standard squash technique and stained in aceto-carmine, aceto-orcein/HCl, lacto-propionic orcein, or a combination of two or more of these stains. Chromosome figures were drawn with a drawing tube attached to a standard Nikon microscope or photographed with an Olympus Vanox equipped with a PM-10-A photomicrographic system with Kodak Panatomic-X film developed in the standard manner. Attempts were made to permanize some preparations using the Conger dry-ice method or by floating off the coverslip in 45% acetic acid, dehydrating in 99% ethanol, and mounting in

Diaphane; these attempts failed to preserve the figures. Subsequent preparations were made semi-permanent by sealing with Hoyer's medium (Beeks, 1955).

Results and Discussion

All counts except those for N. x averyi exhibit n=41 with regular pairing (Table 12). Nephrolepis multiflora and N. rivularis are here reported for the first time with n=41 and regular pairing. Nephrolepis x averyi is a tetraploid with n=82 and exhibits variable and irregular pairing. The pairing ranges from $67_{II} + 30_{I}$ and $69_{II} + 26_{I}$ to 82_{II}; the latter seen in only one figure.

Five previous counts show deviations from n=41 (Table 13). Nephrolepis hirsutula was reported to show 2n=164 (Table 13). Nephrolepis pectinata was reported to show n=41 and n=82. Nephrolepis pendula (as N. pendula var. deflexa Jarrett in Jarrett et al.) was reported to show n=ca. 40, 2n=82, and irregular pairing. Nephrolepis occidentalis was reported to show n=ca. 45. All other previous counts report n=41 and/or 2n=82.

Nephrolepis occidentalis counted in this study shows n=41. A higher gametic number (e.g., n=ca. 45) was not substantiated.

Nephrolepis pectinata appears to exhibit two cytotypes. Tetraploids were reported for Jamaica and diploids for Mexico (Table 13). I have seen the voucher cited by Smith and Mickel (1977) for the diploids, and it is the Mexican pinna form. I have not seen the voucher for the Jamaican tetraploids, but none of the plants I have seen from Jamaica are of the Mexican pinna form. If Walker's

Table 12. New chromosome counts for the neotropical species of Nephrolepis.

Species	n	Location and Voucher
N. x averyi	$67_{II}+30_{I}$	FLORIDA: Nauman 1545 (TENN)
	$69_{II}+26_{I}$	FLORIDA: Nauman 1546 (TENN)
	82_{II}	
N. biserrata	41_{II}	FLORIDA: Nauman 1589 (TENN)
N. cordifolia	41_{II}	FLORIDA: Nauman et al. 466 (FAU, TENN)
N. multiflora	41_{II}	FLORIDA: Nauman 1527 (TENN)
	41_{II}	PUERTO RICO: Evans et al. 4414 (TENN)
N. occidentalis	41_{II}	"ORIGIN UNKNOWN": New York Botanical Garden No. 625/71
N. pendula	41_{II}	COLOMBIA: New York Botanical Garden No. 383/77
N. rivularis	41_{II}	PUERTO RICO: Evans et al. 4425 (TENN)

Table 13. Summary of previous chromosome counts for the genus Nephrolepis.

Taxon	Source	n	2n	Reference
N. biserrata	India	41		Ghatak, 1962, 1963
	India	41		Mehra, 1961
	Africa	41		Manton in Alston, 1959
(as N. saligna)	New Guinea		82	Holttum & Roy, 1965
	Jamaica	41		Walker, 1966
	Puerto Rico	41		Sorsa, 1964 (fide Fabbri, 1965)
N. cordifolia	India	41		Manton & Sledge, 1954
	India	41		Mehra, 1961
	India	41		Mehra & Khanna, 1959
	India	41		Abraham, et al., 1962
(as N. cordifolia & N. tuberosa)	India	41	82	Roy, et al., 1971
	India		82	Roy & Pandez, 1963 (fide Löve, et al., 1977)
N. cordifolia cv. Duffi	?		82	Abraham, et al., 1962
N. exaltata (?)	India		82	Abraham, et al., 1962
	India		82	Roy & Pandez, 1963 (fide Löve, et al., 1977)
N. exaltata	Jamaica	41		Walker, 1966
N. exaltata cultivars	?	38	c. 76	Conley, 1945
N. falcata f. furcans	India (cult.)		82	Abraham, et al., 1962

Table 13 (Continued)

Taxon	Source	n	2n	Reference
N. hirsutula	India	41		Manton & Sledge, 1954
	?		164	Kuriachan (fide Fabbri, 1965)
N. hirsutula var. mayi (?)	India	41		Abraham, et al., 1962
N. lauterbachi	New Guinea	c. 40		Holttum & Roy, 1965
N. occidentalis	Mexico	c. 45		Mickel, et al., 1966
N. pectinata	Jamaica	82		Walker, 1966
	Mexico	41		Smith & Mickel, 1977
N. pendula var. deflexa	Galapagos	c. 40	82	Jarrett, et al., 1968
N. pumicola	Africa	41		Manton in Alston, 1959
N. undulata	Africa	41		Manton in Alston, 1959

(1966) identification is correct, and considering the morphology of the materials I have seen from Jamaica, the tetraploid is most likely of the typical pinna form. Since the typical pinna form also occurs in Mexico, different ploidy levels may account for the report of two morphological types of N. pectinata in Mexico by Smith (1981). The possibility of more than one ploidy level suggests that further cytological study would be promising, particularly if there is a correlation between morphology and ploidy levels. Live material of N. pectinata was not available for this study, therefore, information concerning correlations between chromosome number and morphology is still needed.

Colombian populations of N. pendula exhibit n=41 with regular pairing. The only previous count (Table 13), for Galapagos plants, indicates the same chromosome number but irregular pairing. Because the Galapagos pinna form is the most common type on the islands, the report is probably for that pinna form. Further study is needed on the mainland populations of the Galapagos pinna form, as well as other morphological types within the species before conclusions can be drawn; cytological irregularity may only be associated with the insular populations rather than with morphology.

Nephrolepis x averyi represents a complex cytological situation. The taxon is a tetraploid with irregular pairing, a situation with several alternative explanations.

1. The 4n hybrid resulted from an early somatic doubling of an F_1 generation.

2. An initial 2n F_1 hybrid produced 2n gametophytes and these underwent selfing (or crossing with other 2n F_1 hybrids) to produce a 4n F_2 hybrid.
3. One or both parental species produce 2n gametophytes and,
   a) the 2n gametophytes crossed to produce a 4n F_1 hybrid.
   b) the 2n gametophytes of one parent backcrossed with that parent to produce a 3n parent plant that crossed with a 1n gametophyte of the other parent to produce a 4n F_1 hybrid.
   c) the 2n gametophytes of one parent crossed with a 1n gametophyte of the second parent to produce a 3n F_1 hybrid that backcrossed with a 1n gametophyte of either parent to produce a 4n F_2 hybrid.

The third alternative and its variations require the presence of a 3n parent or hybrid, 4n parental plants, and potentially other ploidy levels. The second alternative predicts the presence of 2n parental plants and of both 2n and 4n hybrid plants. Only 2n parental plants and 4n hybrids are predicted by the first alternative. Although only the first alternative is supported by the presently available data, the second and third alternatives are not ruled out (i.e., they are not refuted by the current data).

One complication arising from acceptance of the first alternative is that a hybrid arising by somatic doubling should exhibit regular pairing. Nephrolepis x averyi rarely exhibits regular pairing

and this may be seen as evidence for version c) of the third alternative. However, until 3n plants are documented (and applying Occam's razor) the best explanation for the origin of N. x averyi is the first alternative.

The pairing in N. x averyi occasionally results in 82_{II}. This full pairing may be what results in the low percentage of "normal" looking spores produced by this species. Only these "normal" spores gave rise to gametophytes in culture (see Chapter IV).

Current information suggests that N. x averyi represents an allotetraploid hybrid between N. biserrata and N. exaltata. I was able to obtain a single sporophyte (from either intragametophytic or intergametophytic selfing) of N. x averyi. This plant exhibits various irregularities in morphology. The plant is shorter than would be expected for N. x averyi, 4 dm tall compared to more than 1 m in wild plants. The pinnae are smaller, have a thicker texture, are yellowish-green, and have irregularly lobed or dissected pinnae margins. The plant has remained sterile for at least 18 months. Indument features are comparable to those of N. x averyi, the plant possessing the characteristically pubescent upper costa surface. Since N. x averyi is only known to occur in the field in association with mixed populations of the two parent species, it may not be reproducing sexually to any significant extent. The plants do reproduce asexually by stolons and may persist in local areas as relatively large colonies.

Summary

Chromosome counts indicate that only N. x averyi and N. pectinata deviate from a gametic number of n=41 and 2n=82. Nephrolepis pectinata exhibits two ploidy levels, diploid and tetraploid. Furthermore, these two ploidy levels may be associated with different morphological types, but this requires additional study. Nephrolepis x averyi is a tetraploid hybrid between N. biserrata and N. exaltata.

The relative uniformity in chromosome number does not provide additionial information on the interspecific relationships among the neotropical species except for the hybrid N. x averyi.

CHAPTER VI

CHEMOTAXONOMY

Secondary plant products are an important source of taxonomic characters in a wide variety of plant groups (e.g., Giannasi, 1978). Flavonoids are one of the prominent classes of compounds of use in fern systematics (Cooper-Driver, 1980; Giannasi, 1974; Swain, 1980) and more recently studies of C-glycosylxanthones are becoming important in various groups (Markham and Wallace, 1980; Richardson, 1982, 1983, 1984; Richardson and Lorenz-Liburnau, 1982; Richardson and Palta, 1983; Smith and Harborne, 1971; Wallace et al., 1982). In the present study surveys were made to determine the flavonoid and xanthone profiles for each of the neotropical species. Flavonoid and xanthone profiles provided additional characters for comparing the species and largely substantiated the relationships suggested by morphology alone.

Materials and Methods

Characterization of flavonoid and xanthone profiles and identification of the compounds followed the procedures of Mabry et al. (1970) and Markham (1982) with little modification.

For population samples, 0.2 to 0.5 g quantities of air dried or herbarium material consisting of whole pinnae (Table 14) were crushed and successively extracted in 85% MeOH (methanol) for 24 hours and 100% MeOH for 48 hours. Fractions were combined and drawn

Table 14. *Nephrolepis* populations sampled for flavonoids and xanthones.

Species	Population Number	Voucher
N. x *averyi*	A-1	FLORIDA: Nauman 1548 (TENN).
	A-2	FLORIDA: Nauman 1549 (TENN).
	A-3	FLORIDA: Nauman 1570 (TENN).
	A-4	CUBA: Shafer 7722 (NY).
N. biserrata	B-1	FLORIDA: Nauman 1552 (TENN).
	B-2	FLORIDA: Nauman 1555 (TENN).
	B-3	FLORIDA: Nauman 1557 (TENN).
	B-4	FLORIDA: Nauman 1558 (TENN).
	B-5	FLORIDA: Nauman 1596 (TENN).
	B-6	JAMAICA: Evans 2540-A (TENN).
	B-7	COSTA RICA: Evans & Bowers 3335 (TENN).
	B-8	PERU: Croat 20059 (TENN).
	B-9	BRAZIL: Egler & Irwin 45987 (NY).
	B-10	BRAZIL: Boom et al. 899 (NY).
N. cordifolia	C-1	FLORIDA: Nauman et al. 466 (TENN).
N. exaltata	E-1	FLORIDA: Nauman 1533 (TENN).
	E-2	FLORIDA: Nauman 1534 (TENN).
	E-3	FLORIDA: Nauman 1535 (TENN).
	E-4	FLORIDA: Nauman 1536 (TENN).
	E-5	FLORIDA: Nauman 1538 (TENN).
	E-6	FLORIDA: Nauman 1539 (TENN).
	E-7	FLORIDA: Nauman 1541 (TENN).
	E-8	FLORIDA: Nauman 1543 (TENN).
	E-9	FLORIDA: Nauman 1582 (TENN).
N. multiflora	M-1	FLORIDA: Nauman 1517 (TENN).
	M-2	FLORIDA: Nauman 1518 (TENN).
	M-3	FLORIDA: Nauman 1519 (TENN).
	M-4	FLORIDA: Nauman 1520 (TENN).
	M-5	FLORIDA: Nauman 1522 (TENN).
	M-6	FLORIDA: Nauman 1523 (TENN).
	M-7	DOMINICA: Robinson s.n. (TENN).
	M-8	MEXICO: Martinez 1851 (NY).
	M-9	COSTA RICA: Evans & Bowers 2880 (TENN).
	M-10	COLOMBIA: Forrero et al. 2136 (NY).
	M-11	BRAZIL: Prance & Mello 17621 (NY).
	M-12	BRAZIL: Boom & Mori 841 (NY).

Table 14 (Continued)

Species	Population Number	Voucher
N. occidentalis	O-1	HAITI: *Leonard 7923* (NY).
	O-2	MEXICO: *Sharp et al. 50158* (TENN).
	O-3	MEXICO: *Sharp 52168* (TENN).
	O-4	COSTA RICA: *Evans et al. 23* (TENN).
	O-5	COLOMBIA: *Smith 2563* (NY).
	O-6	ECUADOR: *Holm-Nielson et al. 3103* (NY).
N. pectinata	P-1	JAMAICA: *Watt s.n.* (TENN).
	P-2	MEXICO: *Dressler 1642* (NY).
	P-3	COSTA RICA: *Evans & Bowers 2719* (TENN).
	P-4	PERU: *Schunke 3788* (NY).
N. pendula	PEN-1	CUBA: *Carabia 3738* (NY).
	PEN-2	MEXICO: *Breedlove 33140* (NY).
	PEN-3	COSTA RICA: *Evans & Bowers 3249* (TENN).
	PEN-4	VENEZUELA: *Manara s.n.* (NY).
	PEN-5	ECUADOR: *Mowbray 699107* (TENN).
	PEN-6	BOLIVIA: *Brooke 6535* (NY).
N. rivularis	R-1	DOMINICA: *Long & Norstog 3397* (TENN).
	R-2	PANAMA: *Kennedy et al. 2094* (TENN).
	R-3	SURINAME: *Boer 1291* (TENN).
	R-4	PERU: *Schunke 219* (NY).
	R-5	BRAZIL: *Prance et al. P26554* (NY).

to dryness on a rotary flash evaporator. The resulting crude extract was redissolved in 100% MeOH and spotted on Whatmann 3MM chromatography paper, which was developed as a two-dimensional descending chromatogram (2-D PC) in TBA (tertiary butanol:acetic acid:water, 3:1:1) and 15% HOAc (acetic acid). The chromatograms were then viewed under UV (ultraviolet light) and UV/NH_3 (UV in the presence of ammonia vapors).

For identification of the individual compounds 10 g quantities of air dried material were extracted in the manner described for the population samples. Crude extracts were streaked on Whatman 3MM chromatography paper and developed as one-dimensional descending chromatograms (1-D PC) in 15% HOAc. The resulting bands were eluted with 85% or 100% MeOH. Compounds in each band were isolated by column chromatography with 85% or 100% MeOH on Sephadex LH-20. Individual compounds from different samples were compared by thin layer chromatography (TLC) in four solvents on cellulose sheets (Eastman Kodak Chromagrams, without fluorescent indicator). Those compounds that had similar R_f values in all four solvents were treated as being identical and combined to obtain sufficient quantities for identification. Solvents used for TLC were TBA, 40% HOAc, water, and 15% HOAc or Forrestal's (acetic acid:hydrochloric acid:water, 30:3:10).

Several criteria were used to identify each compound including: spot color on 2-D PC in UV and UV/NH_3, R_f values, UV absorption spectra, and cochromatography with standards. The UV spectra were

determined according to the procedures of Mabry et al. (1970) except that "fused NaOAc" was used for the NaOAc spectra. Aglycone and sugar components of the O-glycosides were separated with acid hydrolysis (6% hydrochloric acid for up to 60 minutes on a steam bath). The aglycones were identified by color in UV and UV/NH_3, R_f values, UV spectra, and cochromatography with standards on cellulose TLC. Sugars were identified by cochromatography with standards on cellulose TLC (Analtech, Inc.--MN 300 cellulose normal, 250 μm thick plates) in pyridine:ethyl acetate:acetic acid:water (36:36:7:21). Sugar plates were sprayed with aniline phthalate spray reagent (E. Merck, Cat. No. 1266) and heated at 65° C until the spots were observable. Standards of quercetin, kaempferol, 3-O-glucosides of the latter two aglycones, and sugars were kindly supplied by Dr. E. E. Schilling. Mangiferin and isomangiferin standards were obtained from Asplenium montanum Willd. (Evans et al. 40980, Cumberland Co., Tenn., 14 Oct. 1966 (TENN)) as suggested by P. M. Richardson (pers. comm.) using the same extraction and isolation procedures.

Results and Discussion

Compounds

A preliminary study revealed no detectable differences in chromatographic profiles between sterile and fertile pinnae. Because fertile pinnae were more available than sterile pinnae, they were used in all other phases of this study. A survey was also made for surface compounds. Whole, unbroken pinnae were dipped in chloroform

and the extract dried. The extracts were run on 2-D PC in TBA and 15% HOAc. No flavonoid or xanthone compounds were detected on the sheets. Further study of surface compounds was not made.

Fifteen compounds were isolated for identification and systematic study. The identities, chromatographic properties, and selected UV spectra are given in Tables 15 and 16. Chemical structures for four of the compounds and a composite 2-D PC profile for all of the species are given in Figure 24.

Compounds 5, 6, 9, and 10 were the only compounds identified with some confidence. Compounds 9 and 10 were identified as the 3-O-glucosides of quercetin and kaempferol, respectively (see Figure 24a). Compounds 5 and 6 were identified as isomangiferin and mangiferin (Figure 24a), respectively. The UV spectra, color in UV and UV/NH_3, and R_f values correspond to the standards isolated from Asplenium montanum.

The UV spectra, color in UV and UV/NH_3, and R_f values for compounds 7, 8, 11, and 12 suggest that these are flavonoids, but they were not present in sufficient quantities to be adequately characterized. All four compounds are purple in UV, 7, 8, and 11 are green in UV/NH_3, and 12 is purple in UV/NH_3. Only compound 7 was present in sufficient quantities to permit the determination of UV spectra.

Compounds 1, 2, 3, 4, 13, 14, and 15 exhibit UV spectra and/or colors and R_f values notably different from flavonoids and xanthones and no effort was made to carry their identification further.

Table 15. Identity and chromatographic properties of the compounds examined in the neotropical species of Nephrolepis.

	Compound	Color*		R_f	
		UV	UV/NH_3	TBA	15% HOAc
1.	Unknown	Y*	R	0.06	0.00
2.	Unknown	LB	LB	0.21	0.10
3.	Unknown	LBG	LB	0.67	0.16
4.	Unknown	LB	LB	0.43	0.24
5.	Isomangiferin	RO	Y	0.39	0.32
6.	Mangiferin	RO	Y	0.51	0.53
7.	Unknown	P	G	0.63	0.48
8.	Unknown	P	G	0.63	0.29
9.	Quercetin-3-O-glucoside	P	G	0.65	0.69
10.	Kaempferol-3-O-glucoside	P	G	0.72	0.65
11.	Unknown	P	P	0.16	0.34
12.	Unknown	P	P	0.38	0.43
13.	Unknown	Pi	Pi	0.41	0.69
14.	Unknown	Y	Y	0.39	0.19
15.	Unknown	Y	Y	0.23	0.10

*Y = yellow, R = red, O = orange, LB = light blue, P = purple, G = green, PI = pink.

Table 16. Selected UV absorption spectra for the compounds examined in the neotropical species of Nephrolepis.

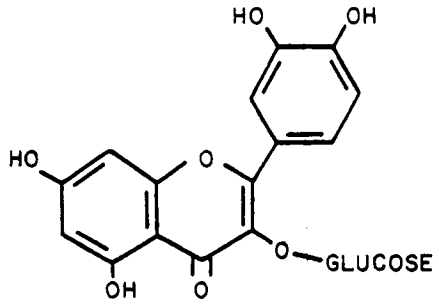
Compound	MeOH	NaOMe	$AlCl_3$	$AlCl_3$/HCl	NaOAc	NaOAc/H_3BO_3
1.	---	334sh*, 345	358sh	356sh	---	---
2.	275sh	275sh, 340sh	272sh, 350sh	272sh, 366sh	278sh, 353sh	276sh
3.	273sh	276sh, 346sh	273sh	270sh	270sh	270sh
4.	277sh	272sh	276sh	270sh, 360sh	277sh	276sh
7.	254sh, 352	279, 240sh, 418	271, 298sh, 335sh, 357sh 405	268, 300sh, 361, 399	257sh, 363	263,377

*sh = shoulder.

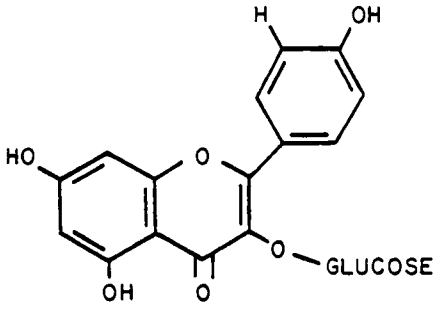
Figure 24. Chemical structures of four of the compounds and a composite two-dimensional chromatographic profile of compounds examined in the neotropical species of Nephrolepis.

a. Chemical structures of four of the compounds examined.

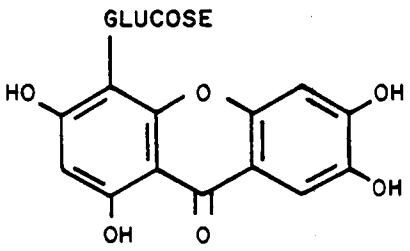
b. Composite two-dimensional chromatographic profile of the compounds examined. Spot numbers correspond to compound numbers given in Table 15.



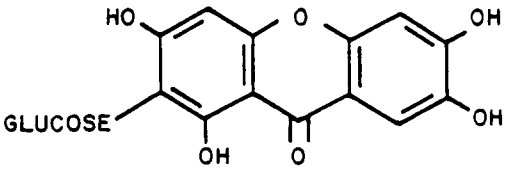
QUERCETIN-3-O-GLUCOSIDE



KAEMPFEROL-3-O-GLUCOSIDE



MANGIFERIN



ISOMANGIFERIN

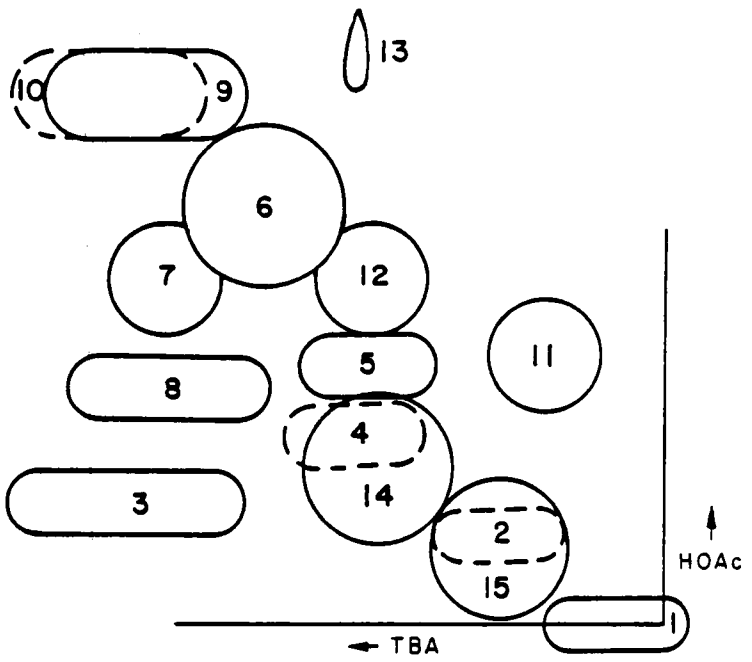


Figure 24

Compound 1 is present in all samples and therefore does not exhibit enough variation to be of systematic value. Compounds 2, 3, and 4 are variable in occurrence, but show sufficient variation in concentrations and associated spot intensities to make their scoring unreliable. Compound 13 is pink in both UV and UV/NH_3, and compounds 14 and 15 are yellow to fluorescent yellow in UV and UV/NH_3. These three compounds might be degradation products resulting from the age of the specimens (all three only occurred in herbarium specimens), or resulting from the procedure itself. Both of these alternatives are unlikely. If the compounds are the result of degradation over time, they should occur in other samples of similar age; they did not. Since all samples were treated in an identical manner and the same vessels were used for extractions and storage of samples, if the compounds are an artifact of the procedure, they should have appeared in other samples of any age; they did not. Whatever their source, compounds 13, 14, and 15 were scored for in population samples and used for interspecific comparisons. These three compounds were present in only two species for which large quantities of material were not available and therefore sufficient quantities of the compounds were not available for characterization.

The first four compounds appear to be present in all of the species with the possible exception of compound 4, which is absent in N. pendula and N. occidentalis (Table 17). In these two species compound 4 may be masked by compounds 14 and 15 when the latter are present. The occurrence of these compounds is variable in all

Table 17. Distribution of phenolic compounds in neotropical populations of Nephrolepis.

Species, Location & Population No.*	Compounds**														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
N. x averyi															
FLORIDA - A1	+		+	+	+	+			+						
FLORIDA - A2	+	+	+	+	+	+									
FLORIDA - A3	+		+	+	+	+			+						
CUBA - A4	+	+	+		+	+		+	+						
N. biserrata															
FLORIDA - B1	+		+	+	+	+	+		+						
FLORIDA - B2	+		+	+	+	+	+		+						
FLORIDA - B3	+		+	+	+	+	+		+						
FLORIDA - B4	+	+	+	+	+	+	+		+		+				
FLORIDA - B5	+			+	+	+									
JAMAICA - B6	+	+	+	+	+	+			+						
COSTA RICA - B7	+	+	+	+	+	+			+						
PERU - B8	+	+	+	+	+	+			+						
BRAZIL - B9	+				tr	+									
BRAZIL - B10	+		+		+	+									
N. cordifolia															
FLORIDA - C1	+	+	+	+	tr	+	+		+						
N. exaltata															
FLORIDA - E1	+	+	+	+	+	+	+		+						
FLORIDA - E2	+	+	+	+	+	+	+		+						
FLORIDA - E3	+	+	+	+	+	+	+		+						
FLORIDA - E4	+	+	+	+	+	+			+						

Table 17 (Continued)

Species, Location & Population No.*	Compounds** 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
(N. exaltata)															
FLORIDA - E5	+	+	+	+	+	+			+						
FLORIDA - E6	+	+	+	+	+	+			+						
FLORIDA - E7	+	+	+	+	+	+	+		+	+					
FLORIDA - E8	+	+	+	+	+	+			+						
FLORIDA - E9	+		+	+	+	+			+						
N. multiflora															
FLORIDA - M1	+	+	+	+	+	+	+								
FLORIDA - M2	+	+	+	+	+	+	+								
FLORIDA - M3	+	+	+	+	+	+	+								
FLORIDA - M4	+	+	+	+	+	+	+								
FLORIDA - M5	+	+	+	+	+	+	+								
FLORIDA - M6	+	+	+	+	+	+	+								
DOMINICA - M7	+	+	+	+	+	+	+	+			+				
MEXICO - M8	+		+		+	+			?+						
COSTA RICA - M9	+		+	+	+	+	+								
COLOMBIA - M10	+				tr	tr									
BRAZIL - M11	+				+	+									
BRAZIL - M12	+				+	+									
N. occidentalis															
HAITI - 01	+	+	+						+		+			?+	?+
MEXICO - 02	+				+	+			+						
MEXICO - 03	+				+	+			+						
COSTA RICA - 04	+				+	+		+	+	+				+	+
COLOMBIA - 05	+								+						
ECUADOR - 06	+		+					?+	+		?+				

Table 17 (Continued)

Species, Location & Population No.*	Compounds**														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
N. pectinata															
JAMAICA - P1	+	+	+	+											
MEXICO - P2	+														
COSTA RICA - P3	+											+			
PERU - P4	+		+						+						
N. pendula															
CUBA - PEN1	+	+	+						+						
MEXICO - PEN2	+														
COSTA RICA - PEN3	+	+	+										+	+	+
VENEZUELA - PEN4	+														
ECUADOR - PEN5	+	+	+												
BOLIVIA - PEN6	+	+							+						
N. rivularis															
DOMINICA - R1	+	+	+	+								+	+		
PANAMA - R2	+	+	+	+								+			
SURINAME - R3	+	+		+											
PERU - R4	+														
BRAZIL - R5	+											+			

*Population numbers refer to those given in Table 14.

**Compound numbers refer to those given in Table 15: + = compound present, ?+ = a compound is present but is questionably the one indicated, and tr = trace amounts.

of the species, except for compound 1. This variability may be misleading. Compounds 2, 4, 7, and 8 are weak in appearance on 2-D PC's and decidedly more variable when the population samples are taken from herbarium sheets of varying ages. It is possible that they exhibit some form of degradation over time. All fresh samples collected by me in Florida, with only a few exceptions, show these compounds as present more often than in other samples (Table 17).

Compounds 5 and 6, isomangiferin and mangiferin, are distinctly present or absent in the population samples and always occur together. For species comparisons these compounds were scored as a single compound class.

Compounds 9 and 10, quercetin and kaempferol glucosides, were best scored as a single class of compounds. Of the 57 population samples, only one population of N. exaltata (E7) and one population of N. occidentalis (04) exhibit the clear presence of two compounds in 2-D PC surveys. Bulk extraction and analysis carried out for some populations of N. x averyi, N. biserrata, and N. exaltata indicate that both compounds are present in what was scored as "spot no 9." Since bulk extraction could not be carried out on all population samples, only the class of flavonol glucosides was considered for species comparisons.

Compound 11 occurs in three species and is represented by faint spots. Compounds 12, 13, 14, and 15 occur in only two species each. Compounds 14 and 15 always occur together and were scored as a single compound class.

Species Comparisons

When the compound distributions (as present or absent) for each species are examined (Table 18), several species groups become apparent. Nephrolepis x averyi, N. cordifolia, and N. exaltata are identical in 2-D PC profiles; possessing xanthones and flavonol glucosides. Nephrolepis biserrata, N. occidentalis, and N. multiflora are similar except that N. occidentalis possesses compounds 14 and 15 and N. multiflora lacks the flavonol glucosides. Nephrolepis pectinata, N. pendula, and N. rivularis form a group that is chemically dissimilar from the other species. All three species lack the xanthones and compound 11. The flavonol glucosides are rare or infrequent in N. pectinata and N. pendula, and absent in N. rivularis. Compounds 12 and 13 are restricted to these three species.

When species groups based on 2-D PC profiles are compared to groups based on morphology alone, there are similarities and differences. Nephrolepis x averyi and N. exaltata are identical in 2-D PC profiles and differ from N. biserrata only in the absence of compound 11. Since compound 11 is rare in N. biserrata, these three species appear closely related. This supports the morphological relationships. Morphology places N. multiflora nearest N. biserrata and the 2-D PC profiles substantiate this. Morphology places N. cordifolia and N. pendula in close proximity, but chemistry clearly separates these two species. This is additional evidence in favor of rejecting the hypothesis that N. cordifolia and N. pendula are conspecific. Nephrolepis rivularis and N. pectinata are chemically

Table 18. Distribution of phenolic compounds used for interspecific comparisons of the neotropical species of Nephrolepis.

Species	Compounds*					
	5 & 6	9 & 10	11	12	13	14 & 15
N. x averyi	1.00*	0.75				
N. biserrata	1.00	0.70	0.10			
N. cordifolia	1.00	1.00				
N. exaltata	1.00	1.00				
N. multiflora	1.00		0.08			
N. occidentalis	0.50	1.00	0.33			0.33
N. pectinata		0.25		0.25		
N. pendula		0.33			0.17	0.17
N. rivularis				0.60	0.20	

*Compound numbers refer to those given in Table 15.

**Values given are the proportion of the populations exhibiting the compound; blank spaces indicate 0.00% for that species and compound.

distinct by the possession of compound 12. Nephrolepis pectinata exhibits compound 12 and the flavonol glucosides, the former compound elsewhere found only in N. rivularis. Nephrolepis rivularis is related to the other species through N. pectinata by the presence of compound 12 and through N. pendula by the presence of compound 13. Nephrolepis rivularis is a distinct species on the basis of 2-D PC profiles and this supports the morphological placement of this species.

No previous studies have reported flavonols in Nephrolepis and they are here reported for the first time. The presence of these compounds is not especially noteworthy since they have been described as nearly ubiquitous in ferns (e.g., Cooper-Driver, 1980).

The only previous studies of xanthones in Nephrolepis have been by Wallace et al. (1982) and Richardson (1983). Wallace et al. (1982) reported xanthones as absent in N. occidentalis and Richardson (1983) reported them as present in this species. This is consistent with the variability observed for N. occidentalis in this study. Richardson (1983) reported mangiferin and isomangiferin as occurring together in N. acuminata, N. biserrata, N. exaltata, N. occidentalis, and N. waimea hort. He reported the presence of only mangiferin in N. dryeri hort. and N. rufescens Wawra (identity of the latter is uncertain since this name has been applied to a number of species). He reported both compounds as absent in N. cordifolia, N. pectinata, N. pendula, and N. rivularis. All of

this is consistent with my findings except that both mangiferin and isomangiferin occur in N. cordifolia. It is possible that N. cordifolia exhibits interpopulational variability similar to that exhibited by N. occidentalis.

Richardson (1983) also reported the presence of two compounds in N. acuminata whose colors and crude R_f values in 15% HOAc indicate they are O-glycosides of mangiferin and isomangiferin. Similar compounds were not detected in this study.

Summary

A chemotaxonomic survey was conducted on 57 populations representing the neotropical species. Of 15 compounds examined, nine (grouped into six compounds and compound classes) were used for interspecific comparisons. Of the six compounds and compound classes each was included in the final numerical analysis.

Interspecific comparisons based on the six compounds and compound classes resulted in species groups corresponding to a large extent with species groups based on morphology alone. Nephrolepis x averyi, N. biserrata, N. cordifolia, and N. exaltata form one group based on the common possession of quercetin and kaempferol glucosides, mangiferin and isomangiferin. The species most closely related to this group is N. multiflora. This species is more closely related to N. biserrata than to the other species. Nephrolepis occidentalis is the next most closely related species, differing by a variable occurrence of xanthones and by possessing compounds

14 and 15. Nephrolepis pectinata, N. pendula, and N. rivularis form a group based on the absence of xanthones and the presence of compounds 12 and 13. Within this group, N. pectinata and N. pendula are more closely related to each other than to N. rivularis. Nephrolepis pectinata and N. pendula possess flavonol glucosides, a feature they share with the first group. Nephrolepis pendula possesses compounds 14 and 15 which link it to N. occidentalis. Nephrolepis rivularis represents the most chemically distinct species. It shares a different and single compound with both N. pectinata and N. pendula; in both cases a compound restricted to these three species (compound 12 or 13).

The chemical relationships mostly correspond to the morphological relationships, with a single exception. Nephrolepis cordifolia is represented as chemically identical to N. exaltata and N. x averyi, but morphology places the species closer to N. pectinata and N. pendula.

CHAPTER VII

DISTRIBUTION AND ECOLOGY

The genus Nephrolepis is pantropical in distribution (Copeland, 1947), with two species reported in Japan and New Zealand (the latter is dubious, see Brownsey, 1981). Among the neotropical species, individual species can be characterized by their particular ecological tolerances and geographic ranges. In most cases, the differences among the species are subtle and reflect general tendencies rather than discrete interspecific differences. The differences do, however, appear to represent real morphological and physiological adaptations. Some of these differences were summarized into three distributional and ecological characters and included in the final numerical analysis.

Materials and Methods

Distributional and ecological information for each species were compiled from personal field observations, communication with other collectors, greenhouse studies, specimen label data, and published literature.

Distribution maps are used to indicate the generalized geographic distribution for each species. Specific locations used to derive the generalized distributions are indicated by individual map symbols where: solid symbols indicate locations determined within the levels of accuracy and precision allowable for the map scale and symbol size, and open symbols indicate locations based

on incomplete specimen label data. When a given collection was determined to be from a cultivated population, it was not plotted. When it could not be determined if a collection represented a wild or adventive population, the collection was assumed to be of a wild population for purposes of plotting distributions. If a location was sufficiently disjunct from the main distributional range of a species, or based on few collections, it was plotted but not included in estimating the generalized distribution. These situations were few in number and are readily apparent on the maps. Generalized distributions are not given for the two largely adventive species, N. cordifolia and N. multiflora. The map symbols do not represent frequency of occurrence for a given species. In most cases, the frequency of map symbols reflects the extent of collecting for the region as well as the bias introduced by specimen acquisition in the institutions that sent loans for examination. Loans were requested from a large number of herbaria over as wide a geographic range as practical to reduce the acquisition bias (see list of herbaria in the Acknowledgments).

Results and Discussion

General Ecology

All of the species may be terrestrial, epiphytic, or epipetric in a broad range of mesic to hydric habitats. The species largely occur in forested habitats, but may be found in relatively open location, e.g., roadsides. They are mostly absent from characteristically xeric habitats such as deserts and savannas, except in

locally protected and moist conditions. Substrate types range from water-logged, organic soils typical of swamps to various well-drained, sandy soils. The soil parent materials are also various, ranging from acid volcanic and sandstone deposits to alkaline limestone formations.

Each of the species may form extensive local colonies by vegetative reproduction from stolons. Extensive colonies are seldom formed under relatively dense cover.

There are no readily apparent seasonal growth events except in N. occidentalis. This species becomes dormant during seasonally dry periods throughout its range. With the return of wetter conditions, growth is resumed from subterranean tubers, but not from the rhizomes of the preceding season. When the species occurs in perennially wet conditions, e.g., near waterfalls, it may bypass the usual dormant phase.

Plants may be fertile all year throughout their ranges, but require higher light intensities to produce fertile fronds than required to maintain vigorous vegetative colonies. This may be either a light requirement or a response to drier conditions resulting from habitat disturbances that allow higher light intensities. Only N. biserrata seems to become fertile under a wide range of ambient light levels. Nephrolepis x averyi is also an exception, in that it produces fewer fertile fronds, relative to the number of sterile fronds, even in full sun.

In all but one of the species it is possible to distinguish morphological forms corresponding to "dry" and "wet" environmental

conditions. In relatively dry, open habitats, fronds are generally smaller and more erect in habit, the pinnae are smaller, stiffer in texture, and may possess a denser indument than if the plants were in a relatively wet (or shaded) habitat. These distinctions between dry and wet forms may be easily seen in some species and less dramatic in others.

The particular range and type of response to dry and wet environmental conditions allows each species to be placed into one of five groups:

1. Nephrolepis occidentalis--exhibiting no discernible differences.
2. Nephrolepis x averyi, N. exaltata, and N. rivularis--exhibiting relatively small differences between dry and wet forms.
3. Nephrolepis cordifolia--exhibiting a moderate degree of difference between dry and wet forms.
4. Nephrolepis biserrata and N. multiflora--exhibiting a greater degree of difference between dry and wet forms than the preceding groups, and exhibiting similar dry forms.
5. Nephrolepis pectinata and N. pendula--exhibiting a wide range of forms.

These groups correspond favorably with the relationships expressed by morphology alone. The only major deviation is that N. cordifolia is more distinct from N. pectinata and N. pendula than would be

expected on the basis of morphology alone. This provides further evidence in favor of rejecting the hypothesis that N. cordifolia and N. pendula are conspecific.

Individual Species

The nine species recognized in this study include six that are distinctly neotropical in distribution, one that is truly pantropical, one that is adventive in the neotropics, and one that is both adventive and native to the neotropics.

Among the neotropical species, N. x averyi and N. exaltata represent Caribbean components. The first of these, N. x averyi, occurs in forested areas, often moist habitats in or near bodies of water, e.g., swamps and streams, but it may also occur in relatively dry or disturbed habitats. Though it may be epiphytic or epipetric (rarely), this species is most often terrestrial. In Florida it is known to occur only with its parent species, N. biserrata and N. exaltata, in mixed colonies. Whether it occurs only in association with the parents in other parts of its range is uncertain, partly because associates are often not reported on herbarium labels, and partly because it is easily confused with either parent and may not be collected. This species is usually more aggressive than either parent and frequently forms large local colonies. The species occurs from sea level to 520 m in elevation.

Nephrolepis x averyi occurs in Cuba, Florida, Jamaica, Puerto Rico, and Mexico (Figure 25). The species is apparently rare in Mexico and Puerto Rico, of uncertain frequency in Cuba and Jamaica,

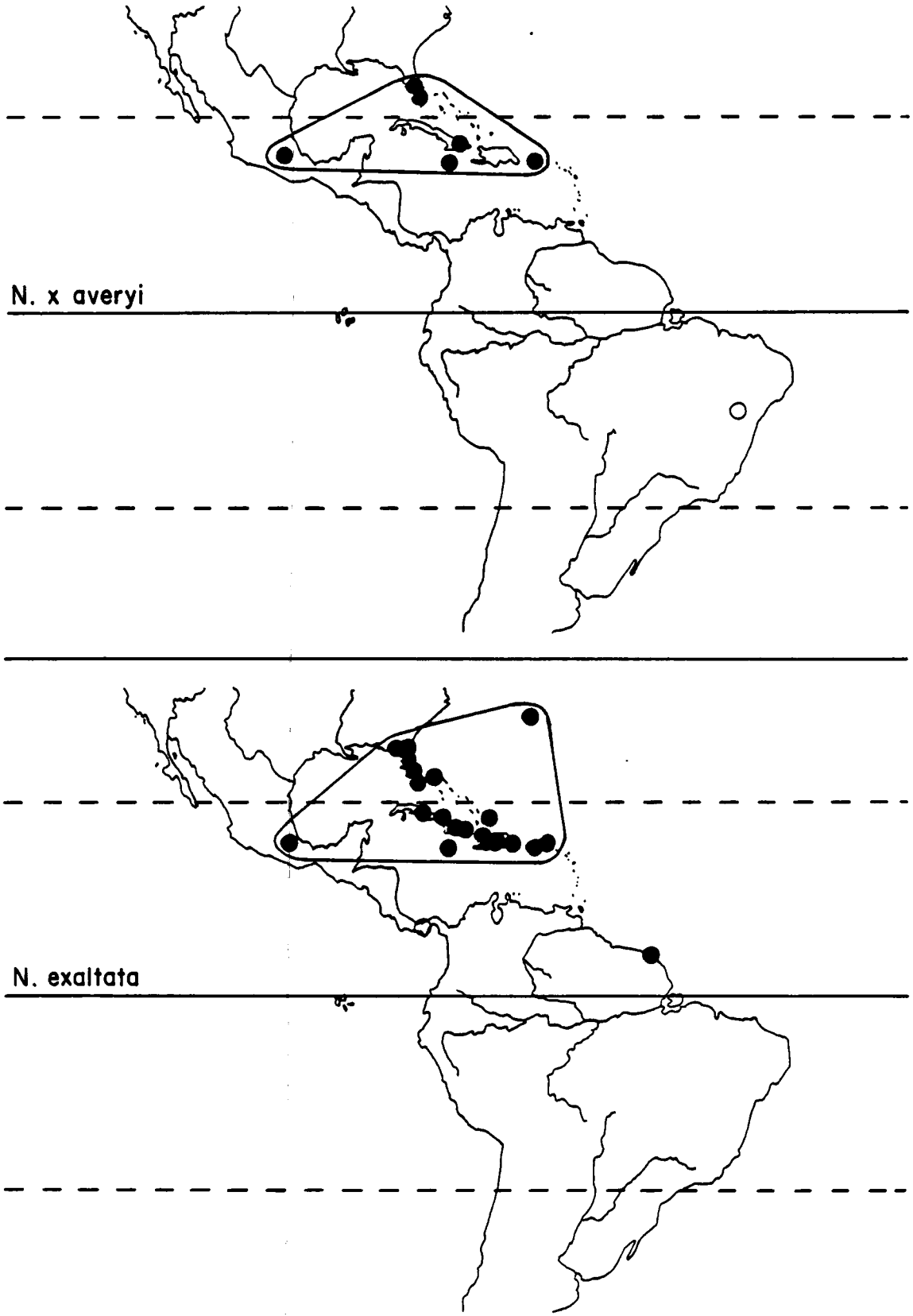


Figure 25. Distributions of Nephrolepis x averyi and N. exaltata.

and moderately common to occasional in Florida. The general distribution of this species corresponds closely to the region of overlap between the ranges of its two parents. This includes most of the range of N. exaltata, but only a small portion of the range of N. biserrata. Nephrolepis biserrata, for example, reaches its northern limits in Florida near the central portion of the peninsula, while N. exaltata extends farther north into the Florida panhandle. Nephrolepis x averyi reaches its northern limits in Florida at the same relative latitude as N. biserrata, and does not extend beyond the range of N. exaltata southward or westward. One specimen was seen from Bahia, Brazil, but this record is suspect. The Brazil location is well out of the normal range for N. x averyi and N. exaltata. Since N. x averyi is easily confused with N. exaltata, which is cultivated in Brazil, it is possible that the N. x averyi specimen also originated from cultivation.

Nephrolepis x averyi's restriction to the Caribbean is best explained as a result of the limited distribution of one of its parents, N. exaltata, and as a result of N. x averyi's inability to colonize areas outside the region of parental species overlap. Dispersal ability resulting from the use of spores as dispersal agents is, itself, unlikely to prohibit N. x averyi from spreading beyond its present range (Tryon, 1970, 1972; Smith, 1972). Since N. x averyi demonstrates a low percentage of spore germination and of sporophyte production from gametophytes (see Chapter IV), it is likely that N. x averyi is unable to colonize new habitats in general. Since N. x averyi only occurs in mixed populations of

the parental species in hybridized habitats, local populations may be formed primarily by *in situ* hybridization. This would exclude the species from areas where the parental species do not co-occur. *Nephrolepis* x *averyi* does not occur in Panama and French Guyana, regions otherwise occupied by both parental species. Since *N. exaltata* appears to be rare in both of these areas, it may be that the necessary conditions favoring co-occurrence of the parental species are rare. This would decrease the probability of there being habitats favorable for colonization by *N.* x *averyi* as well as conditions favorable for *in situ* hybridization. Where *N.* x *averyi* and *N. exaltata* occur together, *N. exaltata* is more common, suggesting further that if *N.* x *averyi* is in Panama or French Guyana, it is likely to be less frequent than *N. exaltata*, which is known from these areas only from a few specimens.

The second Caribbean component, *N. exaltata*, occurs in a variety of habitats with about equal frequency as an epiphyte or terrestrial, less often epipetric. Maxon (1926) reported the species to occur at low to middle elevations, and my observations indicate a range from sea level to 1170 m. It occurs in Florida, the Bahamas, Turks and Caicos, Cuba, Hispaniola, Puerto Rico, Jamaica, Mexico (Vera Cruz only), Bermuda, Panama (few collections), and French Guyana (one specimen seen) (Figure 25). Of the three species of *Nephrolepis* that occur in Bermuda, this is the most common. The species is rare in the Bahamas, and absent from the Lesser Antilles as reported by Maxon (1926) and Proctor (1977). It is usually

reported elsewhere in the neotropics only as escaped from cultivation or as cultivated (e.g., Smith, 1981; Stolze, 1981; Tryon, 1964). These reports refer to one or more of the numerous cultivated forms. The wild form of the species is seldom cultivated, but it is known to be cultivated in Florida and Brazil.

Nephrolepis exaltata has been traditionally construed as pantropic, but it is here considered to have a more restricted distribution. The previous concept was based on misapplication of the epithet and misidentifications. The currently recognized distributional pattern was first suggested by Maxon (1926) who pointed out that reports of this species from the Lesser Antilles were based on specimens of N. rivularis, and reports from Central and South America were based on specimens of N. pendula. Both of these species are frequently misidentified as N. exaltata.

Nephrolepis exaltata exhibits an insular distributional pattern distinguishing it and N. x averyi from the other species. As a whole, the region in which N. exaltata occurs, the Greater Antilles, is regarded as insular rather than continental (Good, 1974; Tryon, 1972). The islands of the Caribbean are peaks of a mountain chain that extends from Honduras east and south to Trinidad. Portions of Cuba that are not part of this chain are part of another mountain chain including Florida and the Yucatan. The remaining islands of the Caribbean have a different and younger geological origin and are considered less insular in character (Freeland and Deitz, 1971; Good, 1974; Schuchert, 1935). Since N. exaltata is rare or

absent from these younger regions of the Caribbean, its distribution is considered insular. Where N. exaltata occurs on continental land masses (excluding Florida which is here considered part of the Greater Antilles), it is on the fringes of the major continental distribution centers for neotropical ferns as recognized by Tryon (1972).

The third neotropical species, N. pectinata, is the only species comprising an Andean/Central American component. This species occurs in a variety of habitats from dense forests to open sites, frequently on or among rocks. Stolze (1981) reports N. pectinata to occur from 800 to 1600 m, and Tryon (1964) reports it from 200 to 2900 m in elevation. My observations show the species occurring from sea level to 2470 m, though largely at middle to high elevations, with less than 20% of the specimens reporting elevation data from below 500 m, 71% between 500 and 1500 m, and the remainder above 1500 m. The Mexican form of this species is indistinguishable from the typical form in terms of habitats and elevational distribution.

Nephrolepis pectinata occurs in Cuba, Hispaniola, Jamaica, throughout Central America, in portions of southern Mexico, and in western South America south to Peru (Figure 26). One specimen was seen from Bolivia and one from Brazil; the latter location was so vague that it was not plotted in Figure 26. The species has also been reported to occur in Florida by Wherry (1964), but this was based on a misdetermination (Darling, 1982). The Mexican form occurs largely in Mexico (Chiapas, Oaxaca, Puebla, and Vera Cruz),

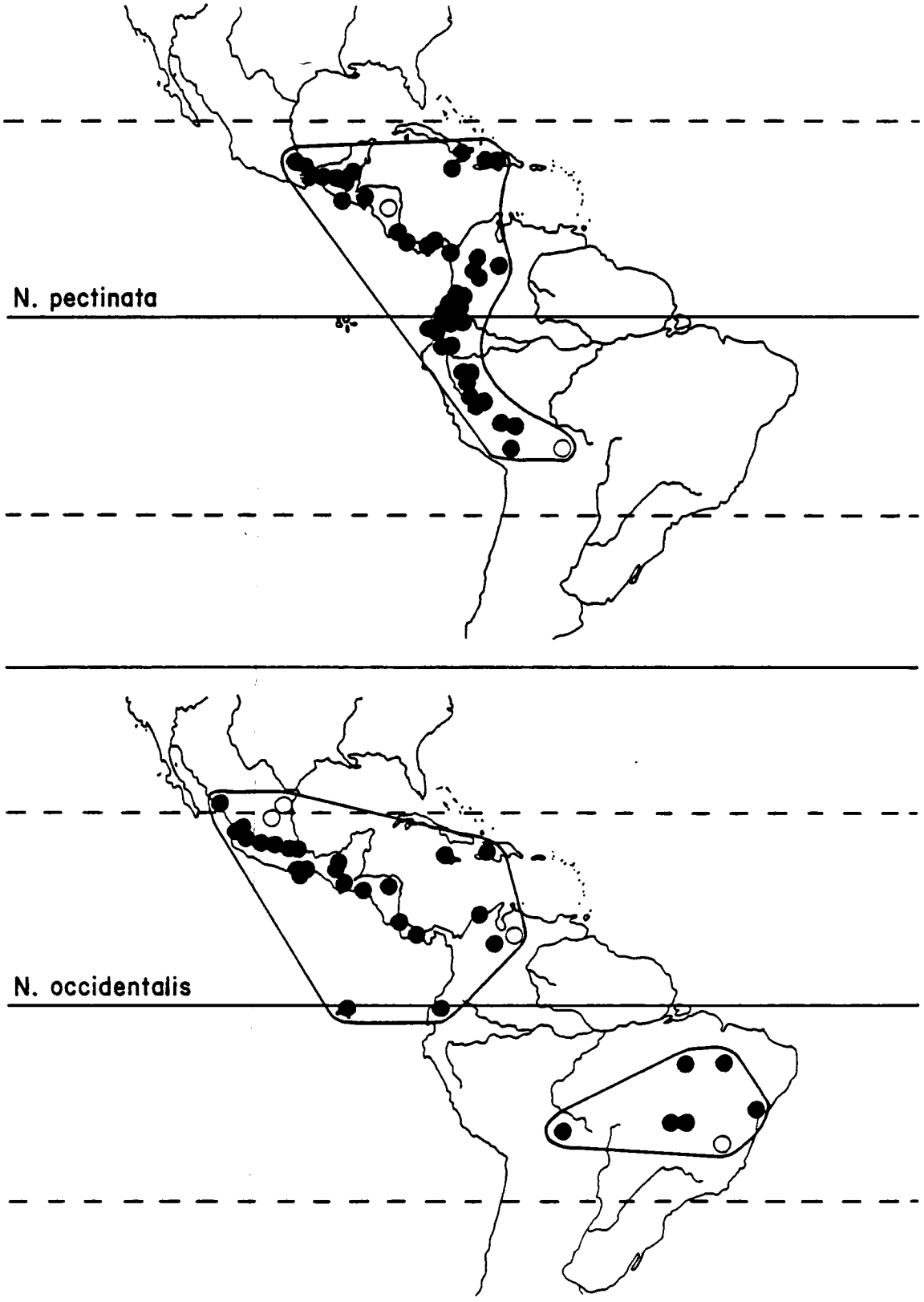


Figure 26. Distributions of Nephrolepis pectinata and N. occidentalis.

but also occurs in Honduras and Colombia. Smith (1981) reported N. pectinata to be the most common species of Nephrolepis in Chiapas, Mexico. From his description (p. 153), it appears that most of the specimens he examined were of the Mexican form. I have, however, seen specimens of the typical form from Chiapas, as well as Oaxaca, and Puebla, Mexico. The species is cultivated in and escaped in Puebla, Mexico, but it is not known to be cultivated elsewhere in its range.

The distributional pattern of N. pectinata is here considered to be primarily continental and centered on the Andean and Central American regions (Tryon, 1972). In the Caribbean portion of the species' range, it is restricted to the geologically older regions (see discussion of the regions under N. exaltata). Outside the Caribbean, the species occurs in three of the regional distribution centers described by Tryon (1972), the Central American, the Andean, and a portion of the Mexican region. Since N. pectinata is found throughout only two of these regions, the Andean and the Central American, its distribution is here referred to as Andean/Central American. It is absent from Tryon's Guayanan and Brazilian regions. This pattern of distribution is considered distinct from other neotropical species. Nephrolepis x averyi and N. exaltata are distinctly Caribbean in distribution and the other neotropical species, though possessing ranges that overlap with N. pectinata, also occur over a significantly broader region characterized by different geological histories.

The remaining neotropical species exhibit broad distribution patterns (being absent or rare in only one of the seven geographic regions each). They have been lumped together because of the commonly broad distributions. Despite similarly wide ranges, each species exhibits its own distributional characteristics.

Nephrolepis occidentalis occurs on or among rocks, ledges, lava flows, or wet cliffs in a variety of habitats, is occasionally epiphytic on palms and mossy tree trunks or is terrestrial. The species occurs from 350 to 2134 m, generally at middle to high elevations. Less than 8% of the specimens reporting elevations were from below 500 m.

The distribution of N. occidentalis is broken into two major portions. The first, ranges from Haiti and Jamaica to central Mexico and southward through Central America to Colombia, Venezuela, and Ecuador (including the Galapagos Islands). The second portion is in southeastern Brazil and part of Bolivia (Figure 26). The species is either not common, or has not been collected in the Caribbean. It is known to me from three collections in Haiti in 1919 and 1925, and from one collection in Jamaica in 1960. Like the previous three species, it does not occur in the geologically younger portions of the Caribbean. I am not considering the Caribbean to be a major portion of this species' range. The major portions of its range are in Mexico, Central America, and southeastern Brazil. All three are regional distribution centers according to Tryon (1972). In the two regions considered to be major centers by Tryon (1972),

Mexico and southeastern Brazil, the species shows a decidedly larger number of collections from volcanic and sandstone areas, often occurring directly on the volcanic or sandstone outcroppings in pockets of humus or moss. This distribution pattern is similar to, and intermediate between, the patterns given for Jamesonia Hook. et Grev. and the Sphaeropteris horrida group by Tryon (1972). The major difference is an absence of N. occidentalis from Peru southward and eastward. Tryon (1964) reported a single specimen of this species (Bryan 415 (F, GH)) from Huánuco, Peru, on a "Rocky mountain side" (p. 233). The location is apparently part of what he called the Sierra Steppe and Scrub, a generally xeric area mostly above 3400 m. He described the area as characteristically possessing various xerically adapted species of Notholaena R. Brown, Cheilanthes Swartz, and Pellaea Link, genera he later (1972) cited as also characteristic of the Mexican distribution center. This similarity suggests that N. occidentalis may occur in Peru, but it is rare. The species is absent from the Amazon basin.

Nephrolepis pendula occurs most frequently as an epiphyte, but may also be terrestrial or epipetric. It occurs in generally moist habitats such as cloud forests, and occasionally on roadsides or very open habitats. The species occurs from sea level to 4267 m and is more or less evenly distributed to about 2000 m. Of the specimens reporting elevations, the percentages are 25.9% at 0-500 m, 23.8% at 500-1000 m, 16.1% at 1000-1500 m, 22.3% at 1500-2000 m, 9.3% at 2000-2500 m, and 2.6% above 2500 m. The Guyana and Galapagos

forms show a more frequent occurrence in drier habitat types such as the Roraima sandstones of the Guyanas and the Campo Limpo flora of the sandstones of Minas Gerais, Brazil (see descriptions in Maguire, 1969, 1970; Steyermark, 1951-1957; Smith, 1962; Sugden, 1982). The Galapagos and Guyana forms are mostly terrestrial in generally open habitats. The Galapagos form occurs at elevations of 46-4267 m, and the Guyana form at elevations of 400-2800 m (generally 1200-2800 m in the Guyanas). Both forms appear to be represented only in particular habitat types within the overall range of N. pendula, but it has not been determined whether they are distinct taxa with different ecological adaptations, or morphological responses to distinct ecological conditions by a single taxon. The two forms differ from the typical forms in the same manner that dry forms differ from wet forms in other species, and are known from drier than is typical habitats. They are assumed to be morphological responses by a single taxon to different ecological conditions. There is no evidence to suggest they are distinct taxa. Greenhouse and transplant studies would provide valuable information on this problem, but live material was not available of either form.

Nephrolepis pendula occurs throughout the neotropics from Cuba south to Santa Catarina, Brazil (Figure 27). It is rare, however, in Bermuda, the Amazon basin, the Lesser Antilles, and was reported as uncommon in Chiapas, Mexico by Smith (1981). It was reported as absent in the Lesser Antilles by Proctor (1977), but I have seen one specimen from Monserrat. Nephrolepis pendula is generally not

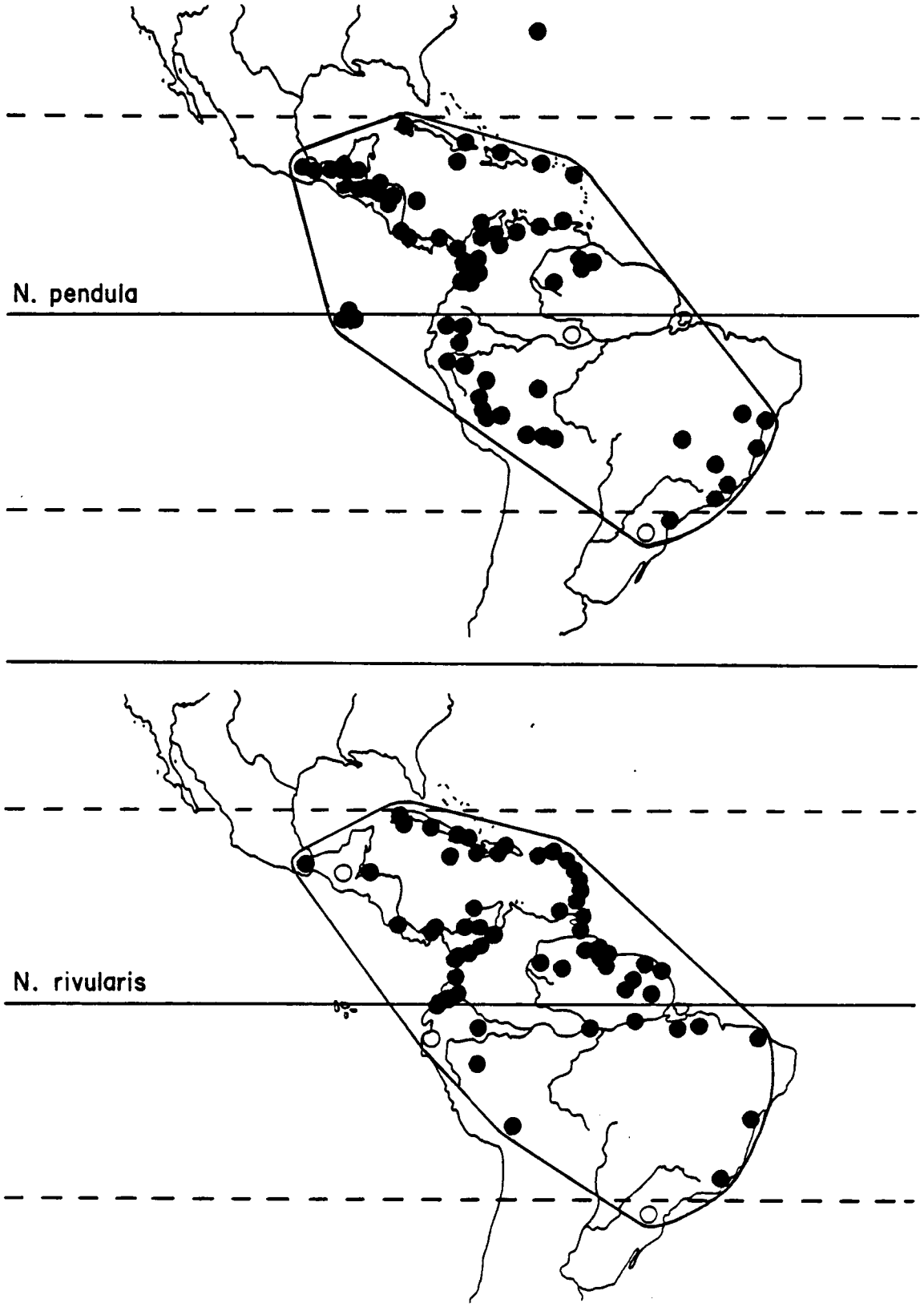


Figure 27. Distributions of Nephrolepis pendula and N. rivularis.

known from cultivation, but I have seen it cultivated twice in Florida. The Guyana form ranges from Guatemala south to Bolivia and east to Venezuela and southeastern Brazil. It is most commonly collected in Colombia, Venezuela, Peru, and the States of Goias and Minas Gerais, Brazil. The Galapagos form is common on the Galapagos Islands, but it is known also from Ecuador with intergrading forms occurring in Bolivia, Mexico, and Guatemala.

Nephrolepis rivularis is the last of the neotropical elements. It occurs in forested, often moist habitats, and is commonly terrestrial or epiphytic. My observations indicate that it is a species of low to middle elevations, though Maxon (1926) described it as occurring at middle to high elevations. Stolze (1981) reports N. rivularis at 50-350 m, and Tryon (1964) reports it at 100-1000 m, I have seen specimens from 5 to 2200 m, with 36.3% of the specimens reporting elevations below 500 m, 50.4% at 500-1000 m, 10.6% at 1000-1500 m, and the remaining 2.7% above 1500 m.

Nephrolepis rivularis is distributed throughout the neotropics from Cuba and southern Mexico south to Bolivia and east to the Lesser Antilles, and Panraña, Brazil (Figure 27). The species is relatively uncommon to rare in the Mexican, southern Andean, and southeastern Brazilian regions. It is relatively more common in the Amazon basin, and the Lesser Antilles (Proctor, 1977). Though occurring over essentially the same geographic range as N. pendula, it appears to show an opposite trend in frequency, i.e., where N. rivularis is common, N. pendula is not.

Nephrolepis biserrata is the only truly pantropical species occurring in the neotropics. The species is most frequently terrestrial or epiphytic in forested, relatively wet locations, e.g., swamp associations, but may also occur on steep banks and roadsides, occasionally clearings or thickets. It may occur on limestone or other rock formations, occasionally on moist sands, in drier parts of mangrove swamps (Cayman Islands), or form large coastal brakes (Galapagos Islands). Nephrolepis biserrata ranges in elevation from sea level to 1400 m. The species was reported at low to middle elevations by Maxon (1926) and Proctor (1977), 0-400 m by Stolze (1981), 100-900 m by Tryon (1964), and at 350 m by Smith (1981). Of the specimens reporting elevations, ca. 80% were below 700 m. Throughout its range, N. biserrata is more frequent in wetter or more protected habitats than other species. Kornás (1979) described it as occurring in swampy, water-logged areas of Zambia, Africa, and Holttum (1954) said it occurs in Malasia in areas that are not too dry or exposed.

Nephrolepis biserrata occurs throughout the neotropics (Figure 28) and is widely scattered in the paleotropics. The species is mostly absent or rare in the major sandstone floras of the Guyanas and southeastern Brazil, and drier areas of Mexico (Figure 28). The species is also rare in Bermuda. The species is seldom cultivated because of its size, but it is known from cultivation in Florida, Brazil, and Suriname.

Nephrolepis multiflora occurs in generally drier and more open sites than those occupied by the other species. It occurs

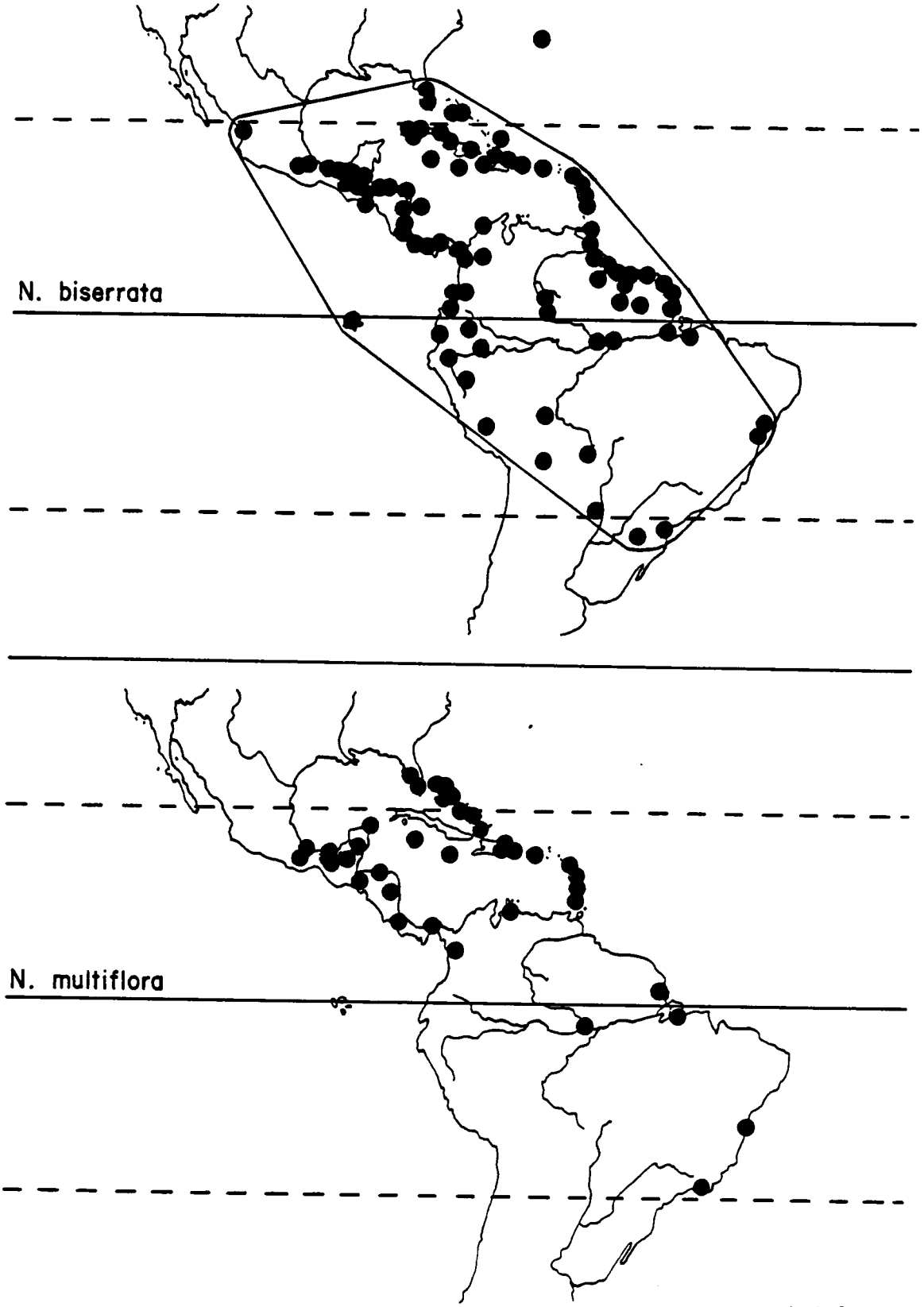


Figure 28. Distributions of Nephrolepis biserrata and N. multiflora.

on roadsides, in thickets, on old masonry, rocks, ledges, etc., mostly in disturbed areas. The species ranges in elevation from sea level to 1650 m; 65.8% below 500 m, 30.6% between 500 and 1000 m. Stolze (1981) cites 50-600 m as the elevational range for this species, Smith (1981) cites 350-450 m, and Proctor (1977) cites low to middle elevations.

Nephrolepis multiflora is widely naturalized in the neotropics as an escaped cultigen. Collection dates are relatively recent when compared to the other species. The earliest collection was in 1907 from the "Upper Rio Negro." The next earliest collections are 1937 from Jamaica, and 1945 from the Amazon region of Brazil. The species was apparently introduced in the early 1900's. It is known to be cultivated in Brazil, Florida, Dominican Republic, and possibly Jamaica.

This species is native to the paleotropics where it is often confused with N. biserrata and the closely related N. hirsutula. The confusion with these two species is so widespread that it is not possible at this time to cite a specific range for N. multiflora in the paleotropics based on literature information. In the neotropics the species is widespread through the Caribbean, southern Mexico, Central America, the Amazon basin, and southeastern Brazil (Figure 28). It appears to be absent from Cuba (Figure 28), but this is probably due to a lack of recent collection information from the area rather than an absence of the species.

Nephrolepis cordifolia occurs in wet shady places, limestone ledges, cliffs, rocks, roadsides, and often in old homesites or

dumps. It occurs at elevations from sea level to 2200 m, with most of the collections at middle to high elevations. In most of its range it appears to be present only as an escaped cultigen. In Florida, for example, it is widespread, but found only where it is most likely persistent or escaped from cultivation. I know of only one site where it has become established without human aid (Nauman, 1979a). Many locations given may or may not be situations where it is only escaped from cultivation.

The species is known in the neotropics from northern Florida and central Mexico southward into the Caribbean and Central America, eastward to Colombia and portions of the Guyana region, and farther southward to central and southern Brazil (Figure 29). The species is absent from the Amazon basin and western South America. Nephrolepis cordifolia seems to be represented by wild, apparently native populations in Cuba, Hispaniola, Jamaica, Puerto Rico, Barbados, Colombia, Venezuela, Nicaragua, Mexico, and Guatemala. Populations in these areas are at slightly higher elevations than for the species as a whole. Of the specimens reporting elevations, 7.9% were at 0-500 m, 28.9% at 500-1000 m, 50.0% at 1000-1500 m, and 13.2% above 1500 m. Maxon (1926) reported the species as occurring at higher elevations as well. Stolze (1981) and Tryon (1964) reported elevational data, but they were treating N. pendula and N. cordifolia as conspecific and I was unable to sort out the data for either species from their descriptions.

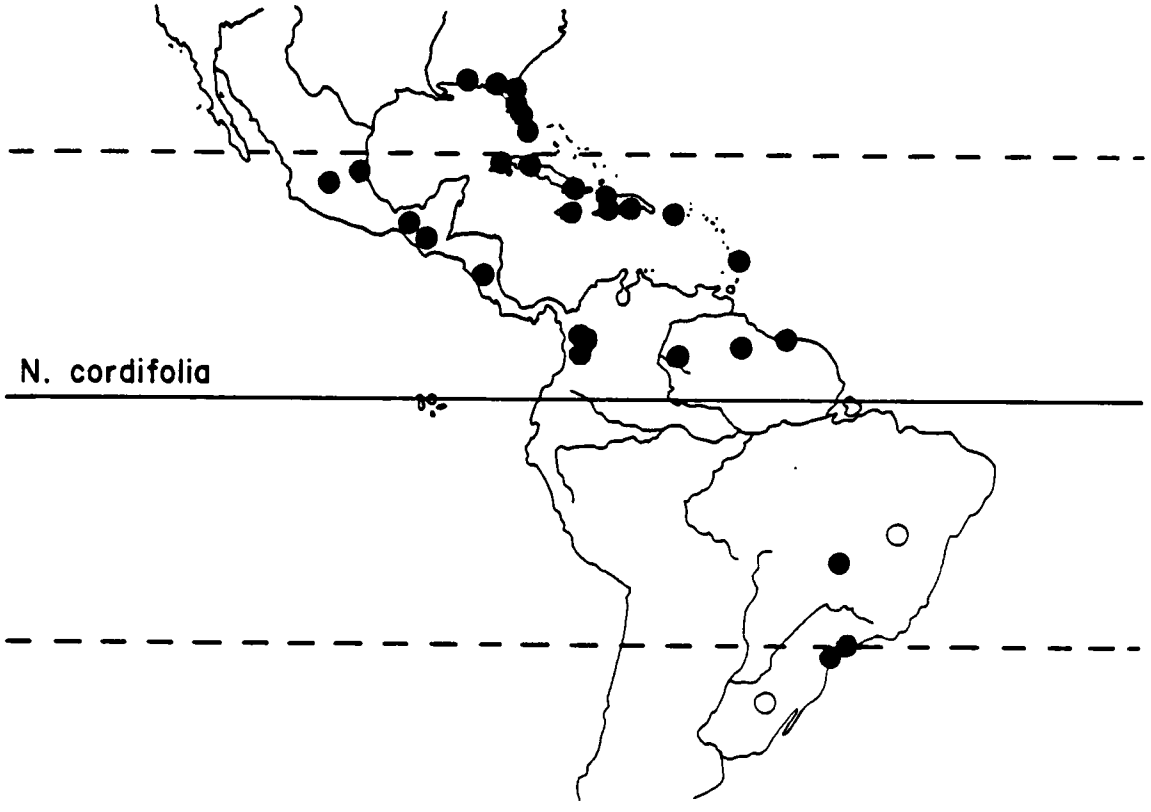


Figure 29. Distribution of Nephrolepis cordifolia.

Summary

Nephrolepis occurs throughout the neotropics in a broad range of mesic to hydric habitats at elevations from sea level to over 4000 m. The species may be terrestrial, epiphytic, or epipetric and may form large local colonies. All of the species can be placed into one of five groups based on the type and range of morphological response to dry and wet conditions that mostly correspond to the relationships indicated by morphology alone.

Each of the species could also be grouped according to their elevational distributions. *Nephrolepis* x *averyi*, *N. exaltata*, *N. biserrata*, *N. rivularis*, and *N. multiflora* occur at low to middle elevations. *Nephrolepis cordifolia*, *N. pectinata*, and *N. occidentalis* occur at middle to high elevations. *Nephrolepis pendula* occurs across a broad elevational range.

Each of the species can be characterized by particular distributional patterns. Six of the species are restricted to the neotropics and are represented by two Caribbean elements, one Andean/Central American element, and three broadly distributed elements. Two of the species are pantropical in distribution; one of these is native to the paleotropics and is naturalized in the neotropics as an escaped cultigen. The last species is possibly native, but largely escaped or persistent from cultivation in the neotropics.

The distributional, morphological, and elevational patterns were included in the final numerical analysis.

CHAPTER VIII

FINAL NUMERICAL ANALYSIS

Information from each of the data categories presented in Chapters II through VII was utilized to produce a final phenetic analysis of the neotropical species. A total of 54 characters described in the previous chapters was compiled and each of the nine species scored. Comparisons were made through cluster analysis and principle coordinate analysis on a matrix of similarity coefficients. The analysis indicated the following species groups: N. biserrata and N. multiflora; N. x averyi, N. exaltata, and N. rivularis; N. cordifolia and N. occidentalis; and N. pectinata and N. pendula. These groups correspond to those based on morphology alone with a few exceptions.

Materials and Methods

A series of 54 characters (Table 19) from all of the previous chapters (except Chapter IV--Gametophyte and Hybridization Studies), were used for the numerical analysis. All nine species were scored and the resulting data matrix was submitted to the same numerical analysis described in Chapter II (p. 15).

Results and Discussion

The results of CA and PCA show similarities and differences between the relationships indicated by morphology alone and by this analysis (Figure 30).

Table 19. Characters and character state coding used for the final numerical analysis of the neotropical species of Nephrolepis.

Character	Character State Coding
1. Seasonality and rhizome development	0 - growth seasonal; rhizome poorly developed 1 - growth perennial; rhizome well developed
2. Rhizome scale habit	1 - spreading 2 - intermediate 3 - appressed
3. Rhizome scale color at maturity	0 - concolorous 1 - distinctly bicolorous
4. Rhizome scale margin type	1 - entire to papillate 2 - ciliolate 3 - fibrillose
5. Maximum rhizome scale length	continuous, in mm
6. Tubers	0 - absent 1 - present
7. Proportion of fertile to sterile pinnae per fertile frond	1 - < 1/2 of the distal pinnae 2 - 1/2 to 3/4 of the distal pinnae 3 - > 3/4 of the distal pinnae
8. Frond length	continuous, in dm
9. Frond length/width ratio	continuous
10. Stipe length	continuous, in dm
11. Stipe color	1 - stramineous 2 - brown 3 - purple-black
12. Stipe scale habit	1 - spreading 2 - intermediate 3 - appressed
13. Stipe scale color at maturity	0 - concolorous 1 - distinctly bicolorous

Table 19 (Continued)

Character		Character State Coding
14.	Stipe scale margin type	1 - entire to papillate 2 - ciliolate 3 - fibrillose
15.	Stipe scale density	1 - none, or few scales at the stipe base 2 - intermediate 3 - dense
16.	Maximum stipe scale length	continuous, in mm
17.	Rachis length	continuous, in dm
18.	Interpinnal distance	continuous, in mm
19.	Rachis pubescence	0 - absent 0.5 - rare or infrequent 1 - present
20.	Rachis scale color at maturity	0 - concolorous 1 - distinctly bicolorous
21.	Rachis scale density	1 - none, or few at the points of pinna attachment 2 - intermediate 3 - dense (especially adaxially)
22.	Maximum rachis scale length	continuous, in mm
23.	Pinna length	continuous, in cm
24.	Pinna length/width ratio	continuous
25.	Lower pinna length/width ratio	continuous
26.	Pinna "falcateness"	1 - not falcate 2 - slightly falcate 3 - strongly falcate
27.	Pinna shape	1 - oblong 2 - oblong-triangular 3 - triangular 4 - linear-elliptic

Table 19 (Continued)

Character	Character State Coding
28. Pinna tip shape	1 - blunt 2 - deltoid to acute 3 - acuminate to abruptly so
29. Fertile pinna margin type	1 - serrulate 2 - biserrate 3 - crenulate
30. Acroscopic lobe shape	1 - none to deltoid 2 - deltoid to acute 3 - oblong
31. Pinna deflection	0 - not deflexed 1 - deflexed, even if rare
32. Pinna base shape	1 - cuneate-truncate 2 - truncate 3 - truncate-auriculate 4 - cordate 5 - shallowly cordate acroscopically and deeply so basiscopically
33. Pinna attachment	1 - medial to submedial 2 - both states (1 & 3) may occur 3 - basal for more than 1/2 of the distal pinnae
34. Pinna pubescence - lamina	1 - none 2 - few 3 - dense
35. Pinna pubescence - upper costa surface	1 - none 2 - few 3 - dense
36. Pinna scale density	1 - none 2 - few 3 - dense
37. Epidermal cell form	1 - deeply lobed 2 - sinuous to lobed 3 - straight to sinuous

Table 19 (Continued)

Character		Character State Coding
38.	Guard cell length	continuous, in μm
39.	Sorus location	1 - supramedial 2 - intermediate 3 - medial (1/2 way between the costa and margin)
40.	Indusium shape and attachment	1 - circular and peltate 2 - hippocrepiform to reniform and attached by a narrow sinus 3 - reniform to lunar or triangular-rounded and attached by a broad sinus
41.	Indusium margin papillate	0 - no 1 - yes
42.	Young sporangia paraphysate	0 - no 1 - yes
43.	Spore - equatorial axis length	continuous, in μm
44.	Spore - perine sculpturing	1 - rugose 2 - rugose-verrucate 3 - verrucate 4 - granular-verrucate
45.	Chromosome number	0 - n = 41 1 - n = 82
46.	Flavonol-3-O-glucosides	0 - absent 1 - present
47.	Xanthones	0 - absent 1 - present
48.	Compound no. 11	0 - absent 1 - present
49.	Compound no. 12	0 - absent 1 - present
50.	Compound no. 13	0 - absent 1 - present

Table 19 (Continued)

Character	Character State Coding
51. Morphological response to dry and to wet ecological conditions	1 - essentially none 2 - slight morphological response 3 - moderate morphological response 4 - large morphological response 5 - large morphological response and multiple forms
53. Elevational distribution	0 - low to middle elevations (mostly below 1000 m) 0.5 - evenly at all elevations 1 - middle to high elevations (mostly above 1000 m)
54. Distributional pattern	1 - neotropical - Caribbean 2 - neotropical - Andean/ Central American 3 - neotropical - broadly 4 - pantropical 5 - adventive

Figure 30. Summary of the results of the final numerical analysis of the neotropical species of Nephrolepis.

a. Phenogram depicting the similarities among the species. Clustering was performed on Gower's similarity coefficient using UPGMA.

b. Three-dimensional diagram depicting the first three principle axes resulting from Principle Coordinate Analysis of the species. Symbols for each species are as follows:

A = N. x averyi.

B = N. biserrata.

C = N. cordifolia.

E = N. exaltata.

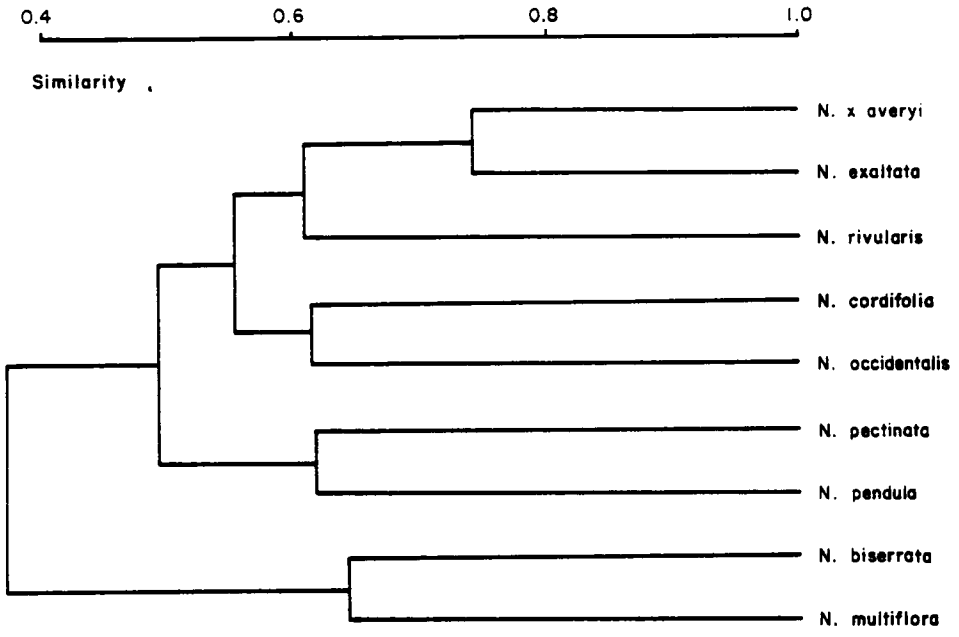
M = N. multiflora.

O = N. occidentalis.

P = N. pectinata.

PEN = N. pendula.

R = N. rivularis.


0.4
0.6
0.8
1.0
Similarity
N. x averyi
N. exaltata
N. rivularis
N. cordifolia
N. occidentalis
N. pectinata
N. pendula
N. biserrata
N. multiflora

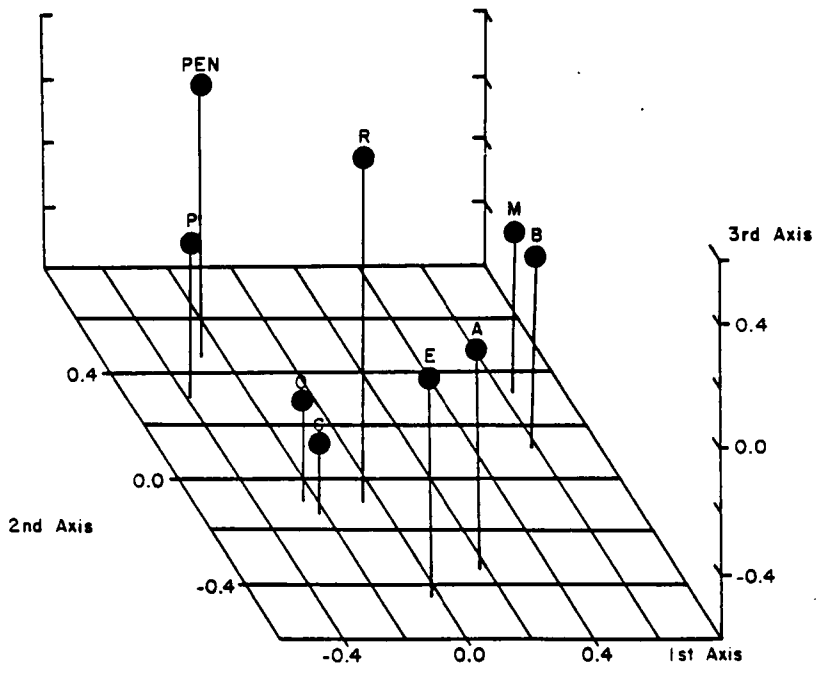

PEN
R
P
M
B
A
E
C
3rd Axis
0.4
0.0
-0.4
2nd Axis
0.4
0.0
-0.4
-0.4
0.0
0.4
1st Axis

Figure 30

When these results are compared to the summary analysis (pp. 103-106), similarities between the two phenograms become apparent. Nephrolepis biserrata and N. multiflora cluster first with each other and form a distinct group. Nephrolepis x averyi and N. exaltata cluster at a lower level than any other species pair; presumably due to the hybrid origin of N. x averyi. Nephrolepis rivularis clusters first with the latter two species. In these respects the addition of information from other data categories has not dramatically altered the scheme based on morphology alone.

Clustering of the last four species indicates relationships different from those suggested by morphology. Nephrolepis pectinata and N. pendula are still depicted as closely related, but in the analysis of morphology N. cordifolia was placed in their cluster and depicted as more related to N. pendula than N. pectinata is to N. pendula. Nephrolepis cordifolia is shown here to be less related to either N. pectinata or N. pendula than in the analysis of morphology. This is further evidence that N. cordifolia and N. pendula are not conspecific. Nephrolepis occidentalis is shown in this analysis to be related to the latter three species as in the analysis of morphology. Yet, here it is placed closer to N. cordifolia than to N. pectinata and N. pendula.

At higher clustering levels, N. biserrata and N. multiflora are still depicted as a group distinct from the other species. Nephrolepis cordifolia and N. occidentalis cluster with N. pectinata and N. pendula in the analysis of morphology, but are here indicated

as more closely related to the N. x averyi-N. exaltata-N. rivularis cluster. Relationships among these clusters is further emphasized in the PCA results (Figure 30b).

Summary

When all nine species are compared in CA and PCA using 54 characters from all of the data categories (except gametophyte development and morphology), the following relationships are indicated:

1. Nephrolepis x averyi and N. exaltata are the two most closely related species, possibly a result of N. x averyi's hybrid origin with N. exaltata as one of its parents.
2. Nephrolepis rivularis is most closely related to N. exaltata and N. x averyi, yet is still a relatively distinct species.
3. Nephrolepis cordifolia and N. occidentalis form a cluster more related to the N. x averyi-N. exaltata-N. rivularis cluster than to any other cluster.
4. Nephrolepis pectinata and N. pendula form a cluster that is the next most related to the five preceding species.
5. Nephrolepis biserrata and N. multiflora form a distinct cluster that is well separated from the other clusters.

These relationships, though similar to those expressed by morphology alone, indicate that the use of information from other data categories may alter details of the expressed relationships. The relationships indicated in Figure 30 are here considered final pending a full monograph of the genus. A preliminary study of the relationships

within the genus as a whole is presented in Chapter IX and suggests that a genus wide study would yield a different picture of inter-specific relationships for these taxa.

CHAPTER IX

CONSPECTUS OF THE GENUS

Types and general materials became available for some of the paleotropical species while examining materials for a type study of the neotropical species. This additional material allowed me to fix the application of many names to paleotropical species and to produce a tentative list of species for the entire genus. Discussions of the historical treatment, generic relationships, and cultivation of Nephrolepis are presented along with an enumeration of the species and an assessment of their possible relationships with phenetic and phylogenetic analyses.

The 25 species of Nephrolepis that I am currently recognizing are listed alphabetically with general comments on each. Synonomies are still under study and have not been included in this list; synonomies for the neotropical species are given in the taxonomic treatment (Chapter X). The enumeration is followed by comments on species relationships and groupings. Because insufficient material was avaialble for study of many of the taxa, the inferred relationships are to be considered highly tentative.

Historical Treatment

The genus Nephrolepis was originally proposed (Schott, 1834) to accommodate three species, N. exaltata, N. biserrata, and N. pectinata. These species had formerly been associated with genera

such as Aspidium Swartz and Nephrodium Richard largely on the basis of soral structure; all three having discrete dorsal sori with circular to lunar or reniform indusia. The later transfer of species with different soral structures to Nephrolepis suggests that subsequent authors (e.g., Mettenius, 1856) realized the importance of vegetative features in delimiting the genus. The diversity of soral features is considerable. Nephrolepis abrupta has sori on marginal teeth. Nephrolepis dicksonioides Christ has small coenosori in marginal lobes. Further progression is found in N. acutifolia with an interrupted to continuous coenosorus along the length of the pinna.

The diversity in soral structure has led to several treatments at the generic level. Leptopleuria Presl (1836) was created to accommodate N. abrupta. In 1842, J. Smith included N. acutifolia (as I. languinosa J. Smith) in his genus Isoloma on the basis of its similarity in soral structure and superficial resemblance to the only other member and type of the genus, I. divergens J. Smith (a species releated to and often treated as a member of Schizoloma sensu Copeland (1947) of the Lindsaeaceae). Lepidoneuron Fée was proposed in 1852 to accommodate those species with peltate indusia and discrete sori (N. biserrata and 12 other taxa). Recent authors (Copeland, 1947; Pichi Sermolli, 1977, 1978) are of the opinion that recognition of these groups at the generic level is unjustified due to the intermediacy and intergradation of the soral features.

Several treatments have also been proposed at the infrageneric level. Mettenius (1856) recognized, but did not name, four groups

based on soral position and the indusium. Moore (1857) created two sections on the basis of the shape and insertion of the indusium, Nephrolepis and Cardiostegia. Christ (1897) split the genus into five groups on the basis of soral position, structure, and vascular supply, Aspidioideae, Davallioideae, Dicksonioideae, Lindsayoideae, and Ramosae (endings are Christ's), the latter is now included in Arthropteris J. Smith. The first four of Christ's groups were treated as subgenera by Christensen (1906). Without formally naming them, Pichi Sermolli (1978) divided the genus into three subgenera, subg. Nephrolepis with two sections (Nephrolepis and Cardiostegia), subg. Leptopleuria with two sections (without names), and subg. Lindsayoides. Adequate information is still lacking in several potentially useful areas of investigation so that formal recognition of infrageneric taxa remains speculative.

Generic Relationships

The Davalliaceae can be broken into three groups: the first consists of Davallia, Humata Cav., Leucostegia Presl, and related genera; the second consists of Nephrolepis, Arthropteris, and Psammiosorus C. Chr.; and the third consists of Oleandra. The taxonomic treatment of these groups has been varied. Christensen (1938) placed all three groups in the Davallioideae of the Polypodiaceae. Ching (1940) placed the first and second groups in the Davalliaceae, separating them as subfamilies, and recognized the third group as a separate family. Holttum (1947) placed the second and third groups

together, including the genus Diellia Brackenridge, in the Oleandroideae of the Dennstaedtiaceae, and recognized the first group as a separate subfamily, the Davallioideae. Copeland (1947) and Alston (1956) included all three groups in the Davalliaceae. Pichi Sermolli (1977) recognized each group as a separate family. Lovis (1977) placed all three in a single family and merged the second and third groups into a single subfamily.

Despite the varied treatment, there are at least two common interpretations of the relationships among these groups. First, that the Davalliaceae (sensu latu) consists of three separate, but related evolutionary lines: 1) Davallia, Humata, Leucostegia, and related genera, 2) Nephrolepis, Arthropteris, and Psammiosorus, and 3) Oleandra. Second that the third group is more closely related to the second group than to the first group. Support is found, for exammple, in cytological studies (e.g., Abraham et al., 1962; Manton and Sledge, 1954; Manton in Alston, 1959). The base chromosome number for the Nephrolepidoid genera and Oleandra is n=41, but for most of the Davallioid genera n=40. Van Cotthem (1970a, 1970b) indicated a basic split between the Davalloid genera and the others based on cell form of the upper and lower epidermis. Morphological features were used by Sen and Sen (1973) to illustrate a split between the Davallioid genera and the others. Payne and Peterson (1973) reported a hypodermis to be present in one species of Oleandra and three species of Davallia, but absent in two species of Nephrolepis. Pichi Sermolli (1977) cited phytochemical evidence by Voirin (1970)

that supported the separation of the Davallioid and other genera. Yet, additional phytochemical evidence seems to argue against a division of the groups. Richardson (1983, 1984) reported xanthones to be present in 7 of 11 species of Nephrolepis (10 of 13 when the data from this study are added), 4 of 27 species of Humata, 6 of 10 species of Davallia, but as absent in one species each of Oleandra, Scyphularia Fée, Davalliodes Copel., and Araiostegia Copel. Until more information becomes available on all genera, the family level treatment of the groups will probably remain unstable. I find Pichi Sermolli's (1977) treatment at present the most reasonable but take exception to the rank at which he places the groups. The Davalliaceae (sensu Pichi Sermolli, 1977) is a satisfactory treatment, but I favor uniting his Oleandraceae and Nephrolepidaceae into a single family, Oleandraceae; recognizing Oleandra as a separate subfamily, Oleandroideae, and Nephrolepis, Arthropteris, and Psammiosorus as a second subfamily, Nephrolepidioideae.

Holttum (1947, 1949) and Copeland (1947) suggested a Dicksonioid ancestor for the Davalliaceae (sensu latu). More recent works (e.g., Braggio, 1966; Nayar, 1970; Pichi Sermolli, 1977) have suggested a relationship with the Aspidiaceous ferns, with which I agree. Similarities between Nephrolepis and some Aspidiaceous genera in certain features are too great to ignore. These include base chromosome numbers, staurocytic stomata, the presence of "Ctenitis hairs" (sensu Tindale, 1965), grooved rachises, indusiate sori terminal on vein endings (except in Psammiosorus), and bilateral, monolete

spores. In the gametophyte and hybridization studies of this investigation, Thelypteris kunthii (Desv.) Morton (an Aspidiaceous fern) was a frequent contaminant in the cultures. It is worth noting that the gametophytes of this species were indistinguishable from those of Nephrolepis until sporophytes were produced. Yet, there are considerable differences between the Davallioid and Aspidioid genera, suggesting that the relationship is remote. Pichi Sermolli (1977) stated that the Davallioid and Aspidioid ferns may have had a common ancestor; I am of the same opinion.

Cultivation

Species of Nephrolepis are frequent in cultivation and popularly known as the "Boston Ferns," a name more strictly applied to N. exaltata, but often misapplied to any cultivated form or species in the genus. Those taxa in cultivation include N. biserrata, N. cordifolia, N. exaltata and its forms, N. falcata f. furcans (Moore in Nicholson) Proctor, and others. Among these, the most popular are the nearly 200 named mutant forms arising from N. exaltata cv. bostoniensis Davenport or its derivatives. The mutations occur in a number of characters including the degree of blade dissection, forking of the pinnae, dwarfing, and changes in frond texture. For detailed information of the origins and characteristics of the cultivars the reader is referred to R. C. Benedict (1915, 1916a, 1916b, 1922a, 1922b, 1922c, 1923a, 1923b, 1924a, 1924b), Morton (1958) and Sessions (1978, unpublished).

Enumeration of the Species

1. Nephrolepis abrupta (Bory) Mett.

This is a medium-sized species with a distinctive soral arrangement. Individual sori are located in short, "tooth-like," marginal lobes. Each lobe is about as long and as wide as the sorus itself. Each sorus is subtended by a single vein, suggesting that this condition arose from a single sorus in a marginal lobe (e.g., N. acuminata) as contrasted with the condition in N. dicksonioides. Nephrolepis abrupta appears to be most related to N. acuminata and N. floccigera (Blume) Moore (see comments under N. acuminata). The species is known from Madagascar, the Mascarenes, Mauritius, and Reunion.

2. Nephrolepis acuminata (Houtt.) Kuhn

The combination N. acuminata (Houtt.) Kuhn is predated by the same combination, as N. acuminata (Willd.) Presl (a synonym of N. biserrata), therefore the combination made by Kuhn is superfluous. Since I have not seen the type for the Kuhn combination (Ophioglossum acuminatum Houtt.), I feel that it would be premature to propose a nomen novum at this time, particularly since not all of the earlier names may have been located. I am here using the name N. acuminata in the sense of Holttum (1954). Nephrolepis davallioides (Swartz) Kunze may eventually prove to be the earliest available epithet.

The species is most related to N. abrupta, N. floccigera, and possibly N. dicksonioides. Nephrolepis acuminata has sori in lobes ranging from broad-based and triangular to oblong and about as wide as the sorus, but longer than wide. The marginal lobes

of N. abrupta are as wide as the sorus, but short and "tooth-like." The lobes in N. floccigera are broad-based and triangular. All of the species have one vein subtending each soral structure, except N. dicksonioides, which may have several veins subtending each soral structure. Nephrolepis dicksonioides also differs from N. acuminata in perine sculpturing, and by having a broad-based indusium (even when the soral structure is composed of a single sorus), while those of N. acuminata are hippocrepiform with a narrow sinus. These two species are otherwise similar in other features of gross morphology.

Nephrolepis acuminata occurs in Perak, Malesia, and is relatively common from Sumatra to the Celebes, and probably other regions of the Asian tropics.

3. Nephrolepis acutifolia (Desv.) Christ

This species possesses a nearly marginal, continuous to interrupted coenosorus that makes it one of the most distinctive species of Nephrolepis. Only one other coenosoric species is known, N. marginalis Copeland, but the status of this taxon is questionable (see discussion under N. marginalis). Nephrolepis acutifolia appears to be related to N. dicksonioides. The sori in N. dicksonioides occur individually in the marginal lobes, or as two to three sori fused into a coenosorus in each lobe. If the sori in N. dicksonioides were not in lobes, they would resemble the interrupted coenosorus occasionally seen in N. acutifolia. Nephrolepis acutifolia also resembles N. davalliae v.Ald.v.Ros and N. abrupta. The coenosoric condition could have arisen by fusion of the marginal lobes in N. abrupta or of the nearly marginal sori in N. davalliae. Given a

greater similarity in other features of gross morphology between N. abrupta and N. acutifolia, the former seems more likely.

Nephrolepis acutifolia is widely distributed in the paleotropics; the Mascarenes, Marquesas, Singapore, New Guinea, tropical Africa, Australia, and southeastern Asia to Polynesia.

4. Nephrolepis auriculata (L.) Trimen

This is a small species exhibiting seasonal growth from tubers, and is related to the N. occidentalis-N. undulata group. The nomenclature associated with the species is problematic, the type consists of a small portion of a sterile frond. Without a rhizome, it can not be determined if this name should be applied to the tuber-bearing species to which the name is normally applied (e.g., Walker, 1976). I am here adopting the name in a broad sense to include N. delicatula (Decne in Jacquem.) Pichi Sermolli and N. paucifrondosa d'Almeda. The species ranges over a broad geographic area including: India, Assam, China (Yunan), Thailand, Burma, Sudan, Congo, Tanzania, Zambia, Rhodesia, Angola, Commeroon, Ghana, Guinea, Fernando Po (Pichi Sermolli, 1969, as N. delicatula), Okinawa, and the Ruyukyu Islands (Walker, 1976).

5. Nephrolepis x averyi Nauman

This species is an allotetraploid hybrid between N. exaltata and N. biserrata, restricted to the Caribbean. The species is most related to N. exaltata and may actually represent a backcross to that parent, but the current information is inconclusive. The cytology of this species needs more study.

6. Nephrolepis biserrata (Swartz) Schott

This is a variable species characterized by medial sori with indusia that range from peltate and circular to hippocrepiform and attached by a narrow sinus, a large size, and biserrate pinna margins. A full description of the neotropical material is given in the taxonomic treatment in Chapter X. The paleotropical material shows a nearly identical range of variation in gross morphology. The relationships of the species are not clear, but appear to be with N. falcata (Cav.) C. Chr. and with the N. hirsutula-N. multiflora complex. Nephrolepis biserrata is pantropical.

7. Nephrolepis cordifolia (L.) Presl

This species' closest relationships are with the N. occidentalis-N. undulata group. Scale morphology and distribution suggest a relationship with N. rivularis and related species, but the production of tubers link this species with the former group. Within the tuber-bearing group of species, N. cordifolia is the only species that is not seasonal in growth and may occasionally not produce tubers. The species in general, is a mixture of traits otherwise associated with different species groups, and its relationships remain obscure.

The distribution of the species is reported to be pantropical, but it is so often escaped from cultivation on a world wide basis that its native range is presently unknown. It has been reported to occur extratropically in Japan and New Zealand, but reports from New Zealand are suspect (see Brownsey, 1981).

8. Nephrolepis davalliae v.Ald.v.Ros.

This appears to be a valid species, though I have not seen it mentioned in the literature except for the protologue. The type specimens superficially resemble some forms of N. pendula, but have more marginal sori with indusia attached by a broad, triangular base, and the indument approaches that of N. rivularis. The species is known from New Guinea.

9. Nephrolepis dicksonioides Christ

General characteristics of this species have been mentioned under N. abrupta, N. acuminata, and N. acutifolia. Its relationships are unclear, but it is closest to N. acuminata in gross morphology and may be a coenosoric form of that species. Some populations do not always produce the fused, small coenosori, but may exhibit single sori in each lobe (as reported by Holttum, 1954). If this turns out to be the modal state for this character, then N. dicksonioides would differ from N. acuminata primarily in the shape and attachment of the indusium. I have reported previously (Nauman, 1979a, 1979b, 1981a) that the shape and attachment of the indusia can be a variable character, and suspect that some populations of N. acuminata may occasionally produce "small coenosori." If this is true, then the relationships of N. dicksonioides would be with N. acuminata and not with N. acutifolia, and that coenosori have arisen at least twice within the genus, once in N. dicksonioides and once in N. acutifolia. This is not an untenable hypothesis, since both of these species are part of a larger group of related

taxa. Nephrolepis dicksonioides is known from Malesia, Celebes, Borneo, and New Guinea.

10. Nephrolepis exaltata (L.) Schott

This species occurs in the Caribbean, scattered parts of Central and South America, and in Hawaii (?). A full description is given in the taxonomic treatment (Chapter X). The relationships of the species are obscure, but appear to be with N. biserrata, N. rivularis, and N. falcata.

11. Nephrolepis falcata (Cav.) C. Chr.

This species is closely related to N. biserrata. It differs from the latter species in having pinnae that are distinctly and abruptly falcate, more medial sori than is typical for N. biserrata, lacks trichomes, and has fewer scales on all portions of the frond. Nephrolepis falcata occurs in Malaya north to Siam and Indo-China (Holttum, 1954), India, and the Philippines (Luzon, Sorssogon, and Marianis).

12. Nephrolepis floccigera (Blume) Moore

This species is related to N. abrupta and bridges the gaps to N. acuminata and N. dicksonioides. The sori are in triangular, broad-based lobes barely or not at all extending past the margin, and in this character differs from the latter three species. It is known from Java and the Celebes.

13. Nephrolepis hirsutula (Forst.) Presl

This species is questionably distinct from N. multiflora, if not, then this name has priority. This species differs from

N. multiflora in having a glabrous upper costa surface and a denser covering of more reddish-orange scales on the rachis and pinnae. Some authors (e.g., Smith, 1981) have regarded these two species as conspecific. Since the neotropical populations of N. multiflora consistently have a tomentose upper costa surface, and the type of N. hirsutula as well as various paleotropical specimens that I have seen have glabrous upper costa surfaces and a denser, differently colored indument, it seems best to maintain these as two distinct species pending further study.

Distribution of N. hirsutula is paleotropical, but because it has been so thoroughly confused with N. multiflora and with other species, its distribution can not be determined from the literature. It is not known from the neotropics except in cultivation.

14. Nephrolepis iridescens v.Ald.v.Ros.

This species is known to me only from a photograph of the type. It most closely resembles N. cordifolia, differing from the latter primarily in having slightly longer stipes, more widely spaced and more truncate pinnae (it may or may not produce tubers, this can not be determined from the photograph). It is known from "Ins. Kei."

15. Nephrolepis lauterbachii (Christ in Schum. et Lauterb.) Christ in Schum. et Lauterb.

I have seen only a handful of specimens of this species and can not distinguish it from N. pectinata except that it has darker and smaller scales on the stipe and rachis than N. pectinata. It is known from New Guinea.

16. Nephrolepis marginalis Copeland

This species is questionably distinct from N. acutifolia. I have seen only a fragment of the type (one fertile pinna), and the protologue does not distinguish it from N. acutifolia. It is here maintained on a provisional basis. The species is known from North Borneo.

17. Nephrolepis multiflora (Roxb.) Jarrett ex Morton

This species is native to the paleotropics and has escaped from cultivation and become widely naturalized in the neotropics. A full description is given in the taxonomic treatment (Chapter X). It is most closely related to N. hirsutula (see discussion under N. hirsutula).

18. Nephrolepis occidentalis Kunze

This is a neotropical species distinguished primarily by the production of tubers and a seasonal growth pattern. It is most related to N. undulata and N. auriculata. These three species form an apparently natural group based on morphology. A full description is given in the taxonomic treatment (Chapter X).

19. Nephrolepis pectinata (Willd.) Schott

This is a neotropical species distinguished by its basally attached pinnae and indument features. It is most related to N. lauterbachii (see discussion under N. lauterbachii). A full description is given in the taxonomic treatment (Chapter X).

20. Nephrolepis pendula (Raddi) J. Smith

This is a neotropical species represented by three more or less distinct forms. It appears to be most related to N. pumicola,

and through that species to N. pectinata and N. lauterbachii. These species appear to represent a group derived from the N. occidentalis-N. undulata group. A full description is given in the taxonomic treatment (Chapter X).

21. Nephrolepis pumicola Ballard

This species is known only from San Thome, Mount Cameroun. It is a fern of lava flows and open habitats and in several features resembles the insular Galapagos form of N. pendula. It differs most in having numerous pinnae oriented in a horizontal plane.

22. Nephrolepis radicans (Burm. f.) Kuhn

This is a distinctive species characterized by a scandent main rhizome, linear oblong pinnae, medial sori, and circular and peltate indusia. The species does not appear closely related to any other species in the genus. It is a mixture of character states from several other species groups. Nephrolepis radicans is known from Burma and Indo-China south to Malaya and the Philippines.

23. Nephrolepis rivularis (Vahl) Mett. ex Krug

This is a distinct neotropical species whose affinities are unclear. It has distinctly medial sori with circular and peltate indusia, but it is not clearly related to other taxa with these features. Its basally attached pinnae and flavonoid chemistry suggest a relationship with N. pectinata and N. pendula, but other features of gross morphology contradict this. A full description is given in the taxonomic treatment (Chapter X).

24. Nephrolepis thomsonii v.Ald.v.Ros.

This species, like N. radicans, has questionable affinities. It is known to me only from the type specimen, but this specimen is distinct enough to warrant recognition of the taxon. The species has long, pendulous frond, pinnae that are small to medium-sized (ca. 3 cm long), delicate, and falcate, and has nearly medial sori with circular and peltate indusia. It is known from New Guinea.

25. Nephrolepis undulata (Afz. ex Swartz) J. Smith

This species is related to N. occidentalis, differing in having more widely auricled pinna bases, more abruptly tapering, more imbricate and firmer textured pinnae and firmer textured rachises. It is so similar to N. occidentalis, that only further study will indicate if it is useful to recognize it as a separate taxon. The species is widely distributed in tropical Africa and Madagascar. It has also been reported to occur in Malgassia, India, and Thailand (Pichi Sermolli, 1969), but I have not seen specimens from these areas nor other reports of the species for these areas.

Interspecific Relationships

Because the relationships of several of the species are obscured by complex mixtures of character states, two operations were performed to express and simplify the interspecific relationships, a phenetic and a phylogenetic analysis. Again, it should be pointed out that the relationships expressed here are based on incomplete information for many of the taxa and are to be considered tentative.

Phenetic Analysis

The phenetic analysis employed 25 characters (Table 20) and followed the same numerical procedures of CA and PCA described in Chapter II. Several species are of dubious status and are provisionally recognized, in particular, N. auriculata, N. marginalis, N. iridescens, and N. lauterbachii. The numerical analysis was performed with and without these taxa and the same species groups were obtained. The only differences between the results obtained with and without these taxa occurred in the levels of similarity at which the clusters formed. Only the results including all 25 taxa are presented.

There are four major phenetic groups. Each group is labeled with a Roman numeral (I-IV) and set off by brackets in Figure 31, and by circles in Figure 32. Group I consists of N. abrupta, N. acuminata, N. dicksonioides, and N. floccigera. Group II consists of N. x averyi, N. exaltata, N. biserrata, N. rivularis, and N. falcata. Group III consists of N. acutifolia, N. marginalis, N. davalliae, N. radicans, N. thomsonii, N. multiflora, and N. hirsutula. Group IV can be split into two subgroups, labeled IVA and IVB. Subgroup IVA consists of N. auriculata, N. occidentalis, N. undulata, N. cordifolia, and N. iridescens, and subgroup IVB consists of N. lauterbachii, N. pectinata, N. pumicola, and N. pendula.

Group I consists of species characterized by medium to large-sized fronds, sori in marginal lobes, and sparsely to moderately dense, concolorous pinna scales. The group is relatively coherent, with N. abrupta as the most discordant element.

Table 20. Characters and character state coding used for the phenetic analysis of the species of Nephrolepis.

Character	Character Coding
1. Neotropical in distribution	1 = yes 0 = no
2. African in distribution	1 = yes 0 = no
3. Asian in distribution	1 = yes 0 = no
4. Seasonal growth (annual)	1 = yes 0 = no
5. Tubers	1 = present 0 = absent
6. Main rhizome radicant	1 = yes 0 = no
7. Rhizome with appressed scales	1 = yes 0 = no
8. Typical frond size	0 = large (more than 1.5 m long) 0.5 = medium (0.5 - 1.5 m long) 1 = small (less than 0.5 m long)
9. Stipe atropurpureous	1 = yes 0 = no
10. Stipe with appressed scales	1 = yes 0 = no
11. Rachis scales	0 = dense and spreading 0.5 = dense but "cob webby" 1 = sparse to absent
12. Fertile and sterile pinnae dimorphic	0 = no 0.5 = indistinctly 1 = distinctly
13. Pinna texture delicate	1 = yes 0 = no
14. More than 1/2 of distal pinnae basally attached	1 = yes 0 = no

Table 20 (Continued)

Character	Character Coding
15. Pinna length	0 = large (more than 8 cm) 0.5 = medium (2.5 - 8 cm) 1 = small (less than 2.5 cm)
16. Falcateness	0 = not falcate 0.5 = slightly to moderately falcate 1 = distinctly and abruptly falcate
17. Pinna base shape	1 = cuneate to truncate 2 = truncate-auriculate 3 = cordate
18. Acroscopic lobe shape	1 = none to obtuse 2 = deltoid to acute 3 = acute to oblong
19. Fertile margin type	1 = entire to serrulate 2 = serrulate-crenulate to crenulate 3 = biserrate 4 = other
20. Upper costa pubescence density	0 = glabrous 0.5 = sparse 1 = dense
21. Trichomes on lamina	1 = present 0 = absent
22. Scales on lamina	0 = present and dense 0.5 = present and sparse 1 = absent
23. Soral form	1 = coenosoric 2 = coenosori in lobes 3 = discrete in oblong lobes 4 = discrete in abrupt teeth 5 = discrete in crenations or near margin 6 = discrete in submedial to medial sori (1/2 way to costa)

Table 20 (Continued)

Character	Character Coding
24. Indusium shape and attachment	1 = broad-based to triangular (includes coenosori) 2 = reniform to hippocrepiform, attached by a narrow sinus 3 = hippocrepiform to circular and peltate
25. Spore sculpturing	1 = granular 2 = rugose-verrucate 3 = verrucate 4 = with long equatorial ridges

Figure 31. Phenogram depicting the similarities among the species of Nephrolepis. Clustering was performed on Gower's similarity coefficient using UPGMA. Brackets with Roman numerals indicate particular species groups as they are discussed in the text.

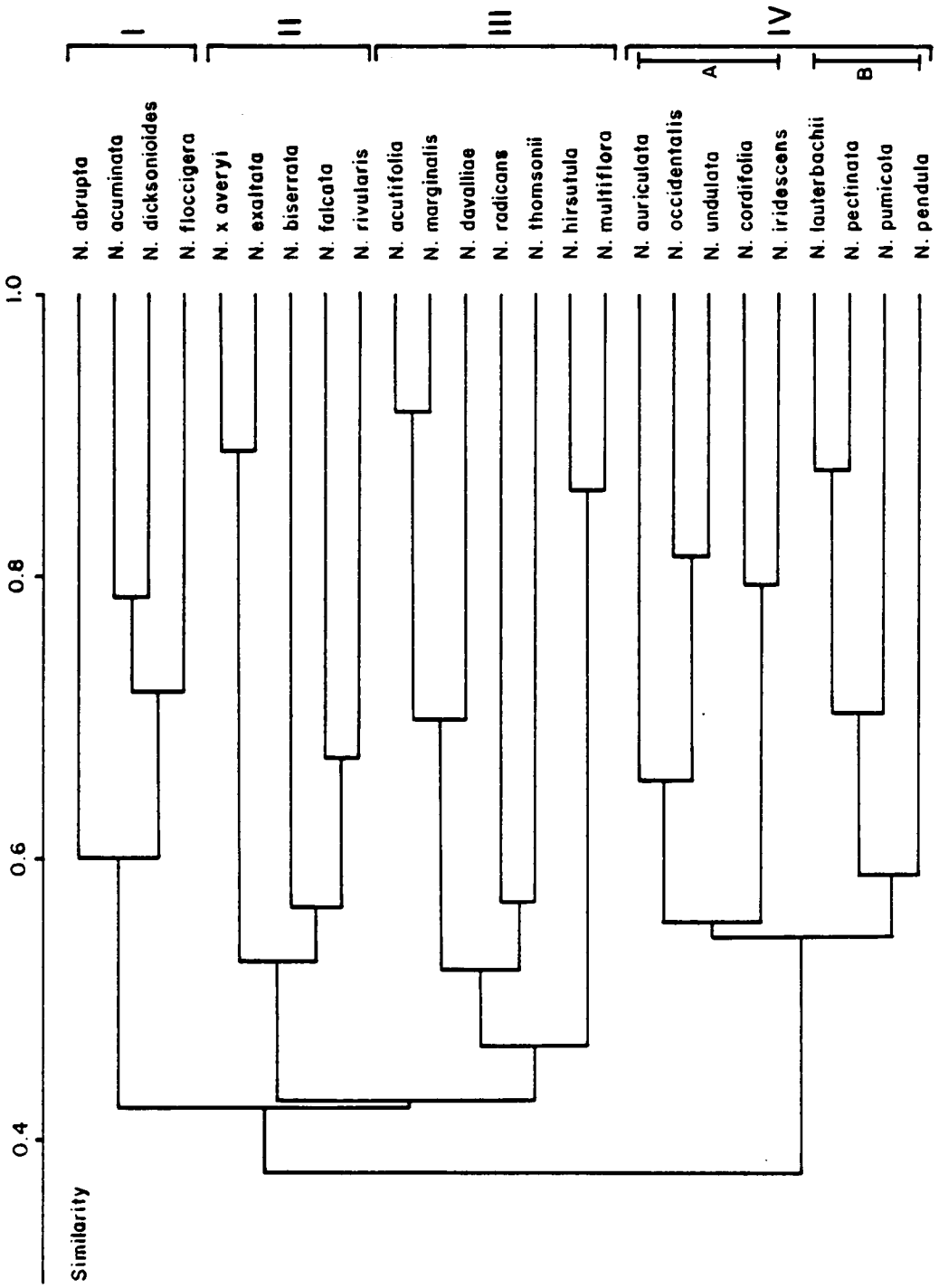

I
II
III
IV
A
B
N. abrupta
N. acuminata
N. dicksonioides
N. floccigera
N. x averyi
N. exaltata
N. biserrata
N. falcata
N. rivularis
N. acutifolia
N. marginalis
N. davallioe
N. radicans
N. thomsonii
N. hirsutula
N. multiflora
N. auriculata
N. occidentalis
N. undulata
N. cordifolia
N. iridescens
N. lauterbachii
N. pectinata
N. pumicola
N. pendula
1.0
0.8
0.6
0.4
Similarity

Figure 31

Figure 32. Three dimensional diagram depicting the first three principle axes resulting from Principle Coordinate Analysis of the species of Nephrolepis. Circles with Roman numerals indicate particular species groups as they are discussed in the text. Individual species are indicated by numbers as follows:

1 - N. abrupta
2 - N. acuminata
3 - N. acutifolia
4 - N. auriculata
5 - N. x averyi
6 - N. biserrata
7 - N. cordifolia
8 - N. davalliae
9 - N. dicksonioides
10 - N. exaltata
11 - N. falcata
12 - N. floccigera
13 - N. hirsutula
14 - N. iridescens
15 - N. lauterbachii
16 - N. marginalis
17 - N. multiflora
18 - N. occidentalis
19 - N. pectinata
20 - N. pendula
21 - N. pumicola
22 - N. radicans
23 - N. rivularis
24 - N. thomsonii
25 - N. undulata

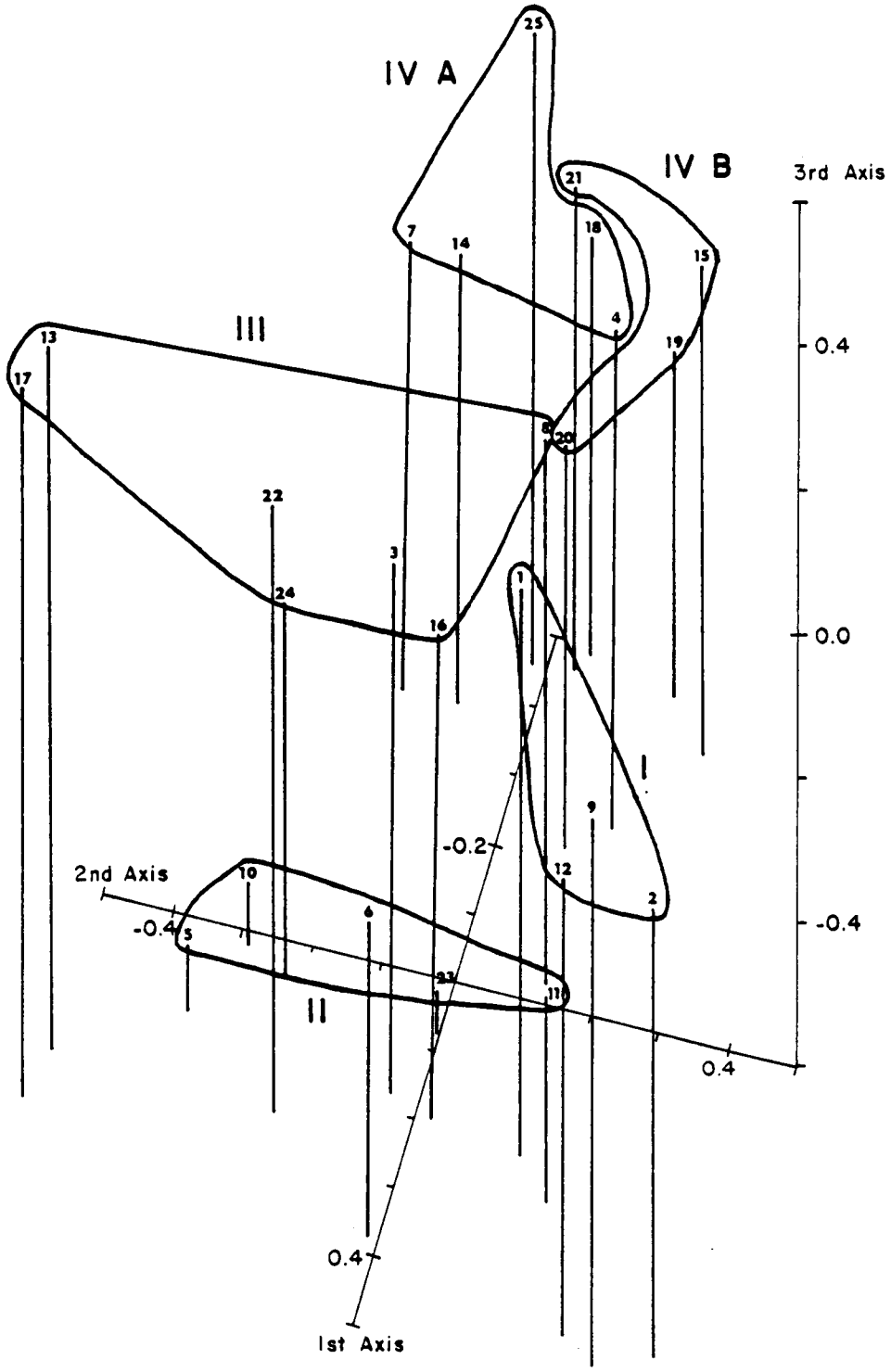

IV A
IV B
III
II
I
3rd Axis
0.4
0.0
-0.4
2nd Axis
-0.4
-0.2
0.4
0.4
1st Axis
25
21
18
7
14
15
4
19
13
17
8
20
22
3
24
16
1
9
12
2
10
5
6
23
11

Figure 32

Group II, though distinct, shows relationships with each of the other groups. That N. biserrata, N. exaltata, and N. x averyi are included in one group, is consistent with the hybrid origin of N. x averyi. Nephrolepis falcata is closely related to N. biserrata and this is suggested by the phenogram (Figure 31); few characters separate these species. The placement of N. rivularis in this group requires further study. This species shows relationships with N. cordifolia (of Group IVA) in indument features, and with N. pectinata (of Group IVB) through the form of pinna attachment, flavonoid, and xanthone characters. The dry form of N. biserrata suggests a close relationship with N. multiflora and N. hirsutula (both of Group III), and in features other than soral form, N. exaltata superficially resembles N. abrupta (of Group I). The relationships with each of the other groups suggests that members of Group II may be reassigned when more is known about members of all of the groups.

Group III is a mixture of doubtfully related species, often possessing mixtures of character states from other less related species. Nephrolepis multiflora and N. hirsutula show a number of similarities with N. biserrata (of Group II) and appear aberrant when compared to other species of Group III. Nephrolepis acutifolia and N. marginalis cluster with N. davalliae largely on the basis of marginal, broad-based indusia, and truncate, medially attached pinnae with an obtuse to nearly absent acroscopic lobe. The superficial resemblances and indument features suggest that these species are only distantly related. Nephrolepis radicans and N. thomsonii

also appear discordant and only distantly related to each other. As a whole, Group III consists of taxa with a number of unique features or combinations of features not clearly related to other groups. The most related group is Group II, which is consistent with the proposed relationships between N. multiflora and N. hirsutula (of Group III) and N. biserrata (of Group II), as well as superficial resemblances among N. acutifolia and N. marginalis (of Group III) and N. exaltata (of Group II) and N. abrupta (of Group I).

Group IV is the most coherent, and appears to represent a natural group of species. The first subgroup (IVA) are the "tuber-bearing" taxa. All members of this subgroup (with the possible exception of N. iridescens) possess tubers. There is also a distinction between plants that are seasonal from tubers (N. auriculata, N. occidentalis, and N. undulata) and plants that are perennial and may or may not produce tubers (N. cordifolia and (?) N. iridescens). Besides tubers, these species also share a general absence of trichomes and lamina indument, small fronds and pinnae, similar variation in the form of pinna attachment, similar variation in flavonoid and xanthone chemistry, and other characters. Group IVB consists of species that share a number of features in, scale morphology, pinna indument, spore morphology, flavonoid and xanthone chemistry, variation in pinna forms, and epidermal cell forms. Group IV as a whole, appears to be a relatively natural group compared to the first three groups.

Future studies of Groups I-III will probably result in substantial rearrangements of not only group contents, but of intergroup

relationships. Additional studies of Group IV, however, will probably not result in similarly significant changes in group content or interspecific relationships.

Phylogenetic Analysis

Phylogenetic analysis consisted of manually constructing a Wagner tree (directed Wagner network) following the procedures of Farris (1970). Twelve characters (Table 21) and 19 of the 25 species were used to construct the Wagner tree. Rationale for the choice of character polarities, and for the omission of six of the species are described below.

A variety of criteria have been proposed to determine polarity of character trends (e.g., Crisci and Stuessy, 1980). Because little information is available for many of the species in this study, only a few of these criteria were applicable, in particular, common = primitive (a form of ingroup comparison), outgroup comparisons, and ontogenetic studies. Ontogenetic studies are based on observations of young sporophytes of the seven species examined in the gametophyte studies (Chapter IV). The outgroup comparisons are tentative at best because the affinities of Nephrolepis are not well understood. The Davalliaceae (sensu strictu), Oleandra, Arthropteris, and Psammiosorus are the most likely candidates as outgroups. As demonstrated in other studies (e.g., Sen and Sen, 1973), the Davalliaceae is the least likely of the four alternatives to be closely related to Nephrolepis. Psammiosorus is relatively unknown and combines features of several genera among the Davallioid

Table 21. Characters and character state coding used to construct a Wagner tree for the species of Nephrolepis.

Character	Character Coding
1. Seasonality	0 = perennial* 1 = seasonal (annual)
2. Tubers	0 = absent 1 = present
3. Radicant Main Rhizome	0 = present 1 = absent
4. Rhizome Scales	0 = appressed 1 = spreading
5. Pinna Attachment	0 = medial to submedial 1 = basal in more than 1/2 of the distal pinnae
6. Pinna Falcateness	0 = not falcate 0.5 = slightly falcate 1 = distinctly and abruptly falcate
7. Pinna Base Shape	0 = cuneate-truncate 0.5 = truncate-auriculate 1 = cordate
8. Laminar Scales	0 = present, sparse or rare 1 = absent -1 = present, moderate to dense
9. Sorus Location	0 = medial 0.5 = intermediate 1 = supramedial
10. Indusium Shape and Attachment	0 = reniform to hippocrepiform, attached by a narrow sinus 1 = triangular to rounded, attached by a broad base -1 = circular, peltate
11. Coenosori	0 = absent 1 = present

Table 21 (Continued)

Character	Character Coding
12. Perine Sculpturing	0 = rugose-verrucate 0.5 = verrucate 1 = with elongate ridges -1 = granular

*Character state coded as 0 are considered pleisiomorphic, 0.5 as intermediate, 1 or -1 are considered apomorphic.

ferns. Because so little information was available, Psammiosorus was not considered a suitable outgroup. The last two genera, Oleandra and Arthropteris, seem to be the closest relatives to Nephrolepis among the Davallioid ferns; these two were used for the outgroup comparisons. Since both Oleandra and Arthropteris show the same apomorphies for the characters chosen for analysis, they were treated as a single outgroup.

The characters chosen were assigned polarities as follows:

1. Seasonality--The annual habit is considered apomorphic over the perennial habit based on common = primitive and outgroup comparisons.
2. Tubers--The presence of tubers is considered apomorphic over the absence of tubers for the same reasons in 1 above.
3. Radicant Main Rhizome--The possession of a radicant main rhizome is here considered pleisiomorphic. A radicant main rhizome would be considered an apomorphy based on common = primitive (only one species exhibits this feature). Outgroup comparisons indicate this to be pleisiomorphic, however, and the outgroup comparisons were given greater weight.
4. Rhizome Scales--Appressed rhizome scales is considered pleisiomorphic based on outgroup comparisons, but it is an apomorphic condition based on common = primitive. As with character 3, outgroup comparisons were given greater weight, and appressed scales are considered pleisiomorphic.

5. Pinna Attachment--The character state of more than 1/2 of the distal pinnae being basal in attachment is considered apomorphic based on common = primitive and outgroup comparisons.

6. Pinna Falcateness--Falcate pinnae are considered apomorphic for the same reasons given in 5 above and on the basis of ontogenetic studies.

7. Pinna Base Shape--Cuneate-truncate is pleisiomorphic based on common = primitive, outgroup comparisons, and ontogenetic studies. The apomorphic alternative is cordate, and there is a transitional state of truncate-auriculate.

8. Laminar Scales--The presence of a few scales on the lamina is considered pleisiomorphic based on common = primitive and outgroup comparisons.

9. Sorus Location--Outgroup comparisons show supramedial or submarginal sori (in lobes, crenations, or not) to be apomorphic over medial sori.

10. Indusium Shape and Attachment--Based on outgroup comparisons, triangular to rounded indusia attached by a broad sinus (including the coenosori) and circular and peltate indusia are apomorphic states. Reniform to hippocrepiform indusia attached by a narrow sinus represent the pleisiomorphic condition.

11. Coenosori--Based on common = primitive and outgroup comparisons, coenosori are apomorphic over discrete sori. This character may have to be re-evaluated in future studies since coenosori may have arisen twice.

12. Perine Sculpturing--This character exhibits alternate apomorphic conditions. The pleisiomorphic condition is rugose-verrucate and appears to have given rise to elongate ridges with a verrucate condition intermediate to rugose-verrucate. This is based on common = primitive; both outgroups do not exhibit a comparable perine sculpturing. This character may also need to be re-evaluated in future studies.

Six of the 25 taxa were omitted during the construction of the Wagner tree. Nephrolepis x averyi was excluded because it is a hybrid, and it was later inserted between its putative parent species. Insufficient information was available for N. marginalis and N. iridescens to score for the character employed in this analysis and these taxa were excluded. They were later inserted next to their nearest presumed relatives, N. acutifolia and N. cordifolia, respectively. Nephrolepis lauterbachii, N. hirsutula, and N. undulata did not differ from their nearest presumed relatives (N. pectinata, N. multiflora, and N. occidentalis, respectively) in any of the characters chosen for this analysis. These three taxa were omitted during construction of the Wagner tree and later inserted next to their nearest presumed relatives.

There are both similarities and differences between the results of the phenetic analysis (Figure 31, page 222; Figure 32, page 224) and the phylogenetic analysis (Figure 33). Group I is shown to be paraphyletic, with N. floccigera and N. dicksonioides excluded and now placed with Group II and Group III, respectively (Figure 33).

Figure 33. Wagner tree depicting the proposed relationships among the species of Nephrolepis. Entities indicated by letters are hypothetical taxonomic units. Species are referred to by their species epithet (except for the ancestor, which is a special case of an hypothetical taxonomic unit). Species in parentheses were excluded during construction of the tree and later inserted next to their presumed nearest relatives. Numbers next to each internode indicate the internode length. Circles with Roman numerals indicate particular species groups as they are discussed in the text.

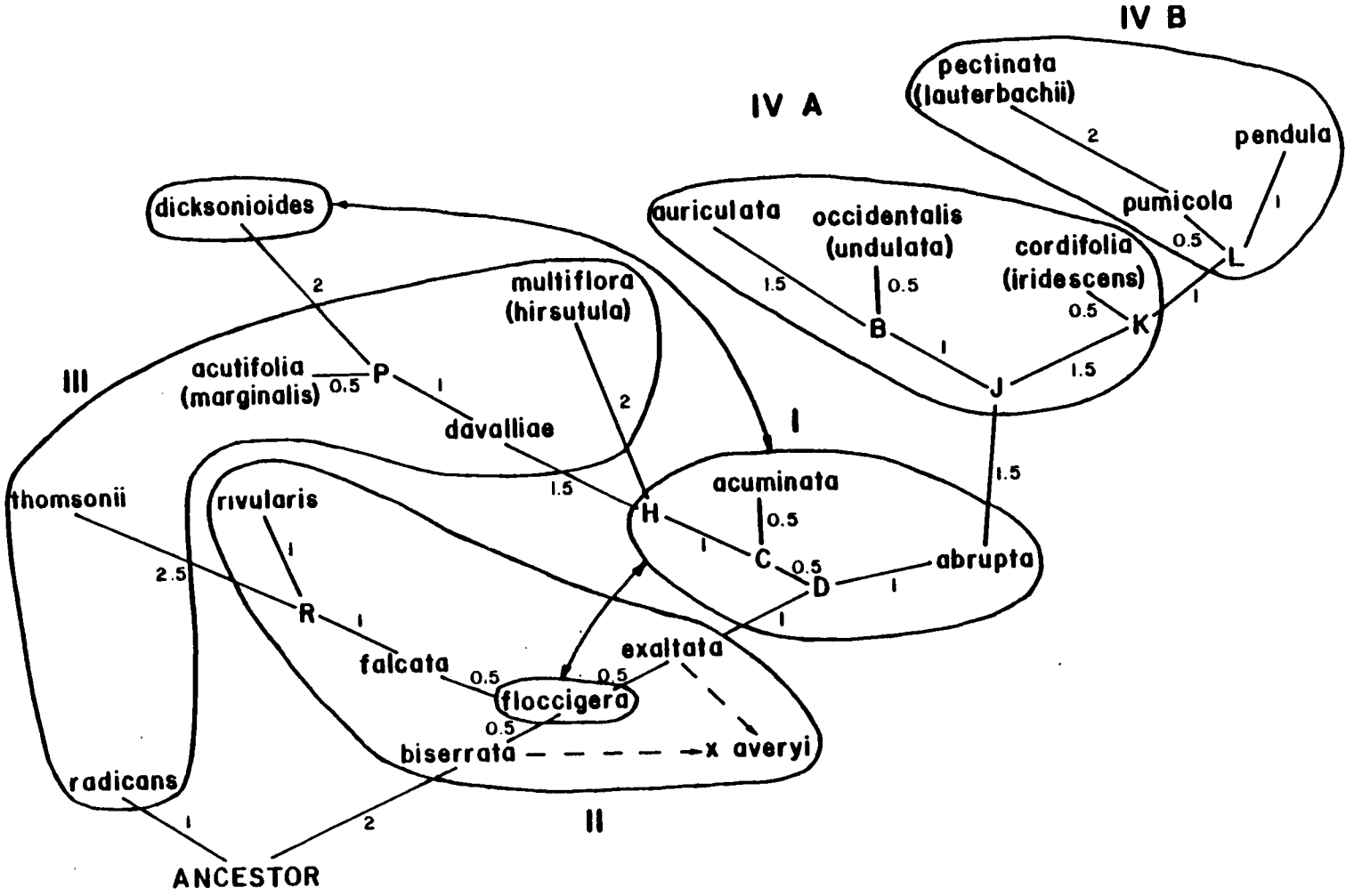

IV B
IV A
pectinata
(lauterbachii)
pendula
pumicola
dicksonioides
auriculata
occidentalis
(undulata)
cordifolia
(iridescens)
multiflora
(hirsutula)
L
B
K
J
III
acutifolia
(marginalis)
P
davalliae
I
thomsonii
rivularis
acuminata
H
C
D
abrupta
R
falcata
exaltata
floccigera
biserrata
x averyi
radicans
II
ANCESTOR
2
1.5
0.5
1
2.5

Figure 33

Group III is also shown to be paraphyletic. Group II is the same as in the phenetic analysis except that it now includes N. floccigera. Group IV is shown to be monophyletic. Within each subgroup the species relationships are the same as those indicated by the phenetic analysis.

Species that appear to be related phenetically are shown in the Wagner tree to be more distantly related. Due to a lack of information, the only base of comparison by which the tree can be judged is by its correspondence with the phenogram. The discrepancies that occur when the phenogram (Figure 31, page 222) and the tree (Figure 33) are compared suggest that a great deal of further study is needed, especially of the members of the first three groups.

Summary

A world wide conspectus is presented for Nephrolepis. The conspectus includes discussions of the historical treatment, generic relationships, and cultivation of the genus, as well as an enumeration of the species, and an assessment of their probable relationships using phenetic and phylogenetic analyses.

Phenetic analysis of the 25 recognized taxa indicated four main groups of species (Groups I-IV). Phylogenetic analysis suggests that only Group IV may be monophyletic; the other groups are in need of more study. In particular, the analyses point to the following as requiring the immediate attention of researchers.

1. Relationships among N. abrupta, N. acuminata, N. biserrata, N. dicksonioides, N. floccigera, N. hirsutula, and N. multiflora. These species are similar in indument and gross morphology, but show major differences in soral form. There is enough variation in indument, spore sculpturing, flavonoids, xanthones, and soral form that these would be promising areas of study.

2. The existence of species such as N. radicans, N. davalliae, and N. thomsonii, which are very different from most of the species, indicates that searches for additional new species may be promising. There may be additional taxa that would close the morphological gaps among these taxa and others within the genus, particularly in the paleotropics. So little information is available for these taxa that a close study of their biology may reveal generic level features currently unknown for Nephrolepis. This information would be valuable in assessing generic and familial level relationships for the genus. Until such information becomes available, the species relationships within the genus will remain speculative.

3. Several pairs of taxa warrant species level systematic study, N. cordifolia and N. iridescens; N. pectinata and N. lauterbachii; N. multiflora and N. hirsutula; N. acutifolia and N. marginalis; and N. occidentalis and N. undulata. Each of these pairs consists of taxa that are differentiated by only a few characters, and frequently one of the species in the pair is poorly known. The ranges and patterns of variation in the taxa must be evaluated fully to determine the status of each member of the pairs.

CHAPTER X

TAXONOMIC TREATMENT

The following taxonomic treatment includes three main sections, a treatment of the neotropical species, a list of cultivars, and a list of excluded names. The taxonomic treatment includes an artificial key to the neotropical species, followed by synonomies, descriptions, distributions, ecologies, and comments for each species. The synonomies include names applied to neotropical and paleotropical materials so far as the material for fixing epithets was available. Paleotropical names were included to initiate the correction of misapplications of these names. Some names applied to neotropical species were not possible to place with certainty due to missing, destroyed, or otherwise unavailable types, or inadequate protologues. These have been listed in the Excluded Names section. Data for the descriptions were taken largely from the preceding chapters. Terms describing the following were defined earlier: scale morphology (Chapter II, pp. 18-19), interpinnal distance (Chapter II, pp. 37-38), pinna attachment (Chapter II, pp. 69-70), indusium shape and attachment (Chapter II, p. 83), and pinna sculpturing (Chapter III, p. 123). Ranges given for character states are based on the larger sample of 773 specimens (see Chapter II, p. 7) rather than the smaller sample used for the initial numerical analysis. Distributions and ecology are summarized from Chapter VII. Representative specimens are listed in the Appendix. The list of cultivars is tentative and incomplete. I have listed those taxa known from herbarium collections regardless of the specimen's origin. This was done because it could not be determined if some of the specimens were collected as an escaped plant or directly from cultivation.

An Artificial Key to the Neotropical Species of Nephrolepis

1. Adaxial costa surface of medial pinnae sparsely to densely covered with short, erect trichomes (often also with scales)..... 2.
   2. Basal portions of mature stipes covered with dark brown, appressed scales with pale margins; perine sculpturing granular.....N. multiflora.
   2. Basal portions of mature stipe not covered with dark brown, appressed scales with pale margins, but often with a few loose, reddish to light brown scales or none; perine sculpturing rugose-verrucate to verrucate.....3.
      3. Adaxial costa surface sparsely pubescent, the trichomes ca. 0.5 mm long; pinnae mostly falcate; frond length/width ratio 6.9-19.9 (mean = 9.6); spores mostly aborted or deformed.....N. x averyi.
      3. Adaxial costa surface densely pubescent to tomentose (if glabrous, see couplet 8), trichomes ca. 0.4 mm long; pinnae not falcate to slightly so; frond length/width ratio 3.0-9.0 (mean = 5.8); spores normal (or very few aborted).....N. biserrata.
1. Adaxial costa surface of medial pinnae glabrous (sometimes with a few scales).....4.
   4. Base of at least 1/2 of the distal pinnae distinctly basal in attachment (i.e., unequal with little or no lamina tissue on the basiscopic side of the pinna base), the pinnae appearing truncate or cuneate.....5.

5. Indusium circular, peltate, medial, dark reddish brown, concolorous; pinnae falcate to slightly so, bearing small (0.3-0.7 mm wide), stellate, peltate, dark reddish brown scales abaxially.....N. rivularis.

5. Indusium lunate or triangular-rounded to reniform and attached along a broad sinus, supramedial, pale to dark brown with a pale margin or concolorous; pinnae falcate or not, not bearing scales as described above (in N. occidentalis there are light brown scales or branched trichomes).....6.

6. Plants bearing tubers, seasonal in growth; main rhizomes poorly-developed with few fronds; pinnae mostly medial or submedial in attachment with a cordate base, usually with a few small scales or branched trichomes near the costa abaxially and proximally, lamina usually thin, veins evident.....N. occidentalis.

6. Plants without tubers, perennial; main rhizomes small but well-developed with several to many fronds; pinnae basal in attachment, without scales or trichomes; lamina thin to thick, veins evident or not.....N. pectinata.

4. Base of at least 1/2 of the distal pinnae medial to submedial in attachment and rounded to cordate or truncate on the basiscopic side, not appearing cuneate, or if cuneate, then medial in attachment.....7.

7. Indusium circular to hippocrepiform and peltate or attached by a narrow sinus, the largest ca. 1.0 mm wide; plants

generally large; interpinnal distance 20.9 (7.5-35.0) mm; pinnae usually more than 5.1 cm long, often with 0.3-0.4 mm long, relatively conspicuous trichomes on the lamina surface.....N. biserrata.

7. Indusium reniform, hippocrepiform or lunate to triangular-rounded and attached by a narrow or broad sinus, the largest ca. 1.2 mm wide or wider; plants generally small to medium; interpinnal distance 10.1 (5.0-21.0) mm; pinnae usually less than 5.1 cm long, without trichomes or the trichomes less than 0.3 mm long and relatively inconspicuous.....8.

8. Plants bearing tubers; seasonal in growth; main rhizomes poorly-developed and often bearing few fronds; pinna bases cordate and medial to submedial in attachment (or if basally attached and rounded-truncate, see couplet 6), lamina thin, veins evident.....N. occidentalis.

8. Plants with or without tubers; perennial in growth (at least not characteristically seasonal); main rhizomes well-developed and bearing several to many fronds; pinna bases cordate, truncate, or truncate-auriculate, not or very rarely basal in attachment, lamina thin to thick in texture, veins evident or not.....9.

9. Plants never bearing tubers; rhizomes with appressed, blackish, lustrous scales; frond length/width ratio 15.9 (6.9-32.1); stipes purple-black, without scales or with a few appressed scales extending from the rhizome to the stipe base (rarely with a few black scales no more than 1/2 way to the lamina in the Galapagos

form); rachis/stipe length ratio 6.8 (1.8-25.4); rachis with few or no scales adaxially and with others appressed and concentrated around the points of pinna attachment; pinna indument absent, acroscopic lobe usually broadly obtuse to absent .....N. pendula.

9. Plants with or without tubers; rhizomes with spreading, light to dark, reddish, or orange brown scales; frond length/width ratio 12.0 (6.2-18.0); stipes usually light to dark brown, seldom purple-black; densely to moderately covered with spreading scales for more than 1/3 of the proximal portion of the stipe (usually all of the stipe); rachis/stipe length ratio 5.1 (2.0-18.1); rachis moderately to more often densely covered with scales adaxially and around the points of pinna attachment; pinnae with or without scales, acroscopic lobe usually deltoid to deltoid-acute.....10.

10. Plants with or without tubers; adaxial rachis scales distinctly bicolorous (pale with a darker point of attachment), often dense; interpinnal distance 7.4 (5.0-10.0) mm; pinnae without indument; indusia lunar to triangular-rounded or reniform, attached by a broad base.....N. cordifolia.

10. Plants never bearing tubers; adaxial rachis scales concolorous or indistinctly bicolorous, dense to sparse; interpinnal distance 13.0 (7.3-21.0) mm; pinnae with a few scales near the costa and proximally; indusia usually reniform to hippocrepiform, attached by a narrow sinus.....N. exaltata.

Nephrolepis x averyi Nauman, Amer. Fern J. 69(3): 69. 1979.

HOLOTYPE: Florida, Collier Co., Fakahatchee Strand, off West Grade, 50 feet E of Indian Mound Slough Bridge. 29 Jan. 1979. Nauman et al. 635 (US !). ISOTYPES: FAU !, GH !, MSC !, FLAS !, NY !. PARATYPES: Florida, Broward Co., Cypress Creek Hammock, Durand 65 (UC !); Durand 71 (FSU !); Nauman 434 (TENN !); Nauman 436 (USF !).

Plants medium to large sized; perennial. Rhizomes erect to ascending, well-developed; covered with 1.0-6.1 mm long, 0.3-1.1 mm wide, loosely appressed to spreading, lanceolate-attenuate, ciliolate-papillate, medium to dark brown, essentially concolorous, relatively uniform scales. Tubers absent. Stolons pale to dark brown; moderately paleate with 1.7-7.5 mm long, 0.4-0.7 mm wide, narrowly triangular to narrowly oblong, proximally ciliolate, papillate, pale to dark brown, indistinctly bicolorous scales. Fronds arching to arching-pendent; 13.6 (8.3-29.2) dm long, 0.8 (0.5-1.3) dm wide, 9.6 (6.9-17.9) times longer than wide; narrowly elliptic-lanceolate. Stipes 2.2 (1.2-5.0) dm long; medium to dark brown; usually 3 or 4 (to 10) leaf traces at the base; moderately to densely paleate with 1.3-5.0 mm long, 0.2-1.5 mm wide scales like those of the rhizome. Rachises 0.9 (5.4-25.5) dm long, 5.5 (3.4-8.2) times longer than the stipe, interpinnal distance 16.7 (9.0-24.5) mm; stramineous to dark brown; glabrous; moderately paleate around points of pinna attachment and adaxially with 1.5-3.2 mm long, 0.1-0.2 mm wide, iregular, linear-caudate, fibrillose, brown, concolorous scales.

Pinnae sessile to barely subpetiolulate; median pinnae 5.9 (3.6-9.0) cm long, 1.2 (0.7-2.0) cm wide, 4.9 (3.8-6.8) times longer than wide; narrowly triangular to oblong triangular; narrowly acute to attenuate and falcate to slightly so at apex; medial to submedial in attachment, truncate, sometimes barely auriculate acroscopically and rounded basiscopically; acroscopic lobe obtuse to acute; serrulate; veins 2- or 3-forked in central portion of pinna, mostly evident; adaxial costa surface sparsely pubescent with trichomes like those of N. biserrata but slightly longer (0.5 mm); blade glabrous adaxially and glabrous to occasionally pubsecent abaxially with trichomes like those of N. biserrata; moderately paleate with scales like those of N. exaltata; lowermost pinnae 1.8 (1.0-2.4) cm long, 1.0 (0.5-1.3) cm wide, 1.9 (1.2-3.4) times longer than wide, oblong deltoid; guard cells 51.7 (41.6-65.0) µm long, epidermal cell walls sinuous to deeply lobed. Sori supramedial. Indusia hippocrepiform to circular, attached by a narrow sinus or peltate; 0.9-1.1 mm wide; margins occasionally minutely papillate; pale to dark brown, mostly concolorous. Sporangia paraphysate when young. Spores aborted or spherical and alete; orbicular to ovoid to plano-convex, often collapsed; spherical spores 32.6 µm in diameter; laesura (when present) 21.8-24.5 µm long; perine verrucate to irregularly ridged. (n=82, pairing irregular and variable)

DISTRIBUTION AND ECOLOGY: Largely Caribbean, in Cuba, Florida, Jamaica, Puerto Rico, and Mexico (Figure 25, p. 173); forested areas, often moist habitats, e.g., swamps, on streambanks, or dry relatively disturbed habitats; at low to middle elevations (0-520 m).

COMMENTS: An allotetraploid (based on counts from one collection) hybrid between N. biserrata and N. exaltata, only known to occur in mixed populations of both parent species. The species superficially resembles N. exaltata but it is easily distinguished by the sparsely pubescent adaxial costa surface, larger size, and aborted spores. Because N. x averyi is relatively common in Florida (Nauman, 1979a, 1981a), capable of sexual reproduction (?), and is distinct from the other species morphologically, chemically, and cytologically, I am maintaining it at the status of species over treatment as a more transient hybrid entity.

Nephrolepis biserrata (Swartz) Schott, Gen. Fil. text to Pl. 3. 1834.

Aspidium biserratum Swartz, J. Bot. Schrad. 1800(2): 32. 1802.

HOLOTYPE: Mauritius, Grondat (Hb. Swartz S-PA ! (Nauman photos 551, 552, 680, 683, at FAU !)).

Nephrodium biserratum (Swartz) Presl, Rel. Haenk. 1: 31. 1825.

Hypopeltis biserrata (Swartz) Bory, Bel. Voy. Bot. 2: 65. 1833.

Lepidoneuron biserratum (Swartz) Fée, Mem. Fam. Foug. 5: 301. 1852.

Nephrolepis exaltata var. biserrata (Swartz) Baker, Mart., Fl. Bras. 1(2): 493. 1870.

Nephrolepis hirsutula δ biserrata (Swartz) O. Ktze., Rev. Gen. 2: 816. 1891.

Tectaria fraxinea Cav., Descr. 250. 1802.

HOLOTYPE: Peru, Obragillo, Nee (MA - 2 sheets - photos !).

Polypodium punctulatum Poiret in Lam., Encycl. Meth. Bot. 5: 533. 1804. [non Hooker, 1845].

LECTOTYPE: East Indies, Martinique, Sommerat (P-LA--photo (Morton neg. no. 2666) at BM !, C !, G !, and US). Morton, in a label with the BM photo said this should be the lectotype, since the species was based on both the specimen and literature citations.

Aspidium punctulatum (Poiret in Lam.) Swartz, Syn. Fil. 46. 1806.

Nephrodium punctulatum (Poiret in Lam.) Desv., Prodrome 2: 253. 1827.

Nephrolepis punctulata (Poiret in Lam.) Presl, Tent. Pterid. 79. 1836.

Lepidoneuron punctulatum (Poiret in Lam.) Fée, Mem. Fam. Foug. 5: 301. 1852.

Nephrolepis biserrata subsp. punctulata (Poiret in Lam.) Bonaparte, Bonap. Notes Pterid. Fasc. I, 165. 1915.

Aspidium acutum Schkuhr, Krypt. Gew. 1: 32. t. 31. 1806.

LECTOTYPE: The plate cited above (t. 31) is here designated as the lectotype. The location and origin of the specimen from which the plate was drawn is unknown.

Nephrodium acutum (Schkuhr) Presl, Rel. Haenk. 1: 31. 1825. [non Hooker, 1862].

Nephrolepis acuta (Schkuhr) Presl, Tent. Pterid. 79. 1836.

Nephrolepis hirsutula α acuta (Schkuhr) O. Ktze., Rev. Gen. 2: 816. 1891.

Aspidium ensifolium Schkuhr, Krypt. Gew. 1: 32. t. 32. 1806.

TYPE: A sheet, "A. ensifolium Sck 4 32" (G - Hb. Delessert !), is presumed to be the type material seen by Schkuhr.

Lindsaya ensifolia (Schkuhr) Desv., Prodrome 2: 317. 1827. [non Swartz, 1801].

Nephrolepis ensifolia (Schkuhr) Presl, Tent. Pterid. 79. 1836.

Nephrolepis hirsutula β ensifolia (Schkuhr) O. Ktze., Rev. Gen. 2: 816. 1891.

Aspidium acuminatum Willd., Sp. Pl. 5: 221. 1810.

HOLOTYPE: "Habit in America," Flugge (B - Hb. Willd. No. 19741, 2 sheets - photos !). Sheet 2 has "America" crossed out on the label and replaced with "Insula Mauritii" in the same hand as the original label.

Nephrodium acuminatum (Willd.) Presl, Rel. Haenk, 1: 31. 1825.

Nephrolepis acuminata (Willd.) Presl, Tent. Pterid. 79. 1836.

Nephrolepis biserrata var. acuminata (Willd.) Hieron., in ed. Made on the type for Aspidium acuminatum Willd.

Lepidoneuron acuminatum (Willd.) Fée, Mem. Fam. Foug. 5: 310. 1852.

Aspidium paraense Willd., Sp. Pl. 5: 228. 1810.

HOLOTYPE: Brazil, Pará, Hoffmannsegg (B - Hb. Willd. No. 19752 - photo !).

Nephrolepis paraense (Willd.) Presl, Tent. Pterid. 79. 1836.

Nephrolepis biserrata var. paraense (Willd.) Hieron., in ed. Made on the type for Aspidium paraense Willd.

Aspidium gibbosum Willd., Sp. Pl. 5: 222. 1810.

HOLOTYPE: Philippines and Marianis (B - Hb. Willd. No. 19743, 2 sheets - photos !). Note: Sheet "1a" is a mixed collection, the left hand frond is A. gibbosum, the right hand frond is a Blechnum sp.; sheet "1b" is A. gibbosum only.

Nephrodium gibbosum (Willd.) Gaud., Trezc. Voy. Bot. 338. 1828.

Nephrolepis gibbosa (Willd.) Presl, Tent. Pterid. 79. 1836.

Nephrolepis biserrata var. gibbosa (Willd.) Hieron., in ed.

Made on the type for A. gibbosum Willd.

Aspidium splendens Willd., Sp. Pl. 5: 220. 1810. [non Ham.; Wall. list no. 2241. 1829; non Christ, 1897].

HOLOTYPE: Ceylon, D. Klein (B - Hb. Willd. No. 19740, 2 sheets - photos !).

Nephrodium splendens (Willd.) Desv., Prodrome 2: 253. 1827. [non Hooker, 1862, excl. var.].

Nephrolepis splendens (Willd.) Presl, Tent. Pterid. 79. 1836.

Nephrolepis biserrata var. splendens (Willd.) Hieron., in ed. Made on the type for Aspidium splendens Willd.

Aspidium mauritianum Desv., Berl. Mag. 5: 320. 1811. [non Kuhn, 1868].

HOLOTYPE: Isle de France (Mauritius), Hb. Commerson (P - Hb. Juss. Cat. No. 1151 - photo BM (Morton neg. no. 2984) ! and at US).

Nephrodium mauritianum (Desv.) Desv., Prodrome 2: 252. 1827.

Nephrolepis mauritiana (Desv.) Moore, Ind. Fil. 96. 1858.

Nephrodium rufescens Schrad., Goett. g. Unzeigen. 896. 1824.

TYPE: No specimens were cited by Schrader but a collection at BR (BM - 2 photos !) is presumably the type. Schrader (loc. cit.) says, "mit N. sesquipedale werwandt," along with a description on the specime is "Affine N. sesquipedale." No locality is given. The specimen is labeled "TYPUS" and is part of Herb. Mart. A label in a packet says, "Filix hanging from trees in Serra de Inuá Neuwies (Engl.) 11.19 Reese I, 1.49 . . . Lagoa lianca [ahbefor Cabo Frio]," presumably a New World location. Note: Copeland (1958) says, "(Sorsogon, the type)"; and I am not sure where he got this information.

Asidium rufescens (Schrad.) Kunze, Flora Bleibl. 34. 1839. [non Bl., 1828].

Nephrolepis biserrata var. rufescens (Schrad.) Kunze, Linnaea 21: 230. 1848.

Nephrolepis biserrata var. rufescens (Schrad.) Luetzelburg, Estudo Bot Nordéste Brazil 3: 246. 1923.

Lepidoneuron rufescens (Schrad.) Fée, Mem. Fam. Foug. 5: 301. 1852.

Nephrolepis rufescens (Schrad.) Wawra, Maxim. Reise 200. t. 101. 1866.

Nephrolepis punctulata var. rufescens (Schrad.) Hieron., Engler's Bot. Jahrb. 34: 454. 1904.

Nephrolepis hirsutula var. rufescens (Schrad.) Wawra ex Bonaparte, in ed. Made on the type for Nephrolepis dayakorum in Bonaparte's hand.

Aspidium rufescens var. minor O. Ktze., in ed.

Nephrodium bidentatum Presl, Rel. Haenk. 1: 32. 1825.

HOLOTYPE: "In insulis marianis," Henke (PRC - photo K (neg. no. 9799), dup. at BM !).

Aspidium bidentatum (Presl) Sprengel, Syst. ed. 16. 1827.

Lepidoneuron bidentatum (Presl) Fée, Mem. Fam. Foug. 5: 301. 1852.

Nephrolepis bidentata (Presl) Presl, Tent. Pterid. 79. 1836.

Aspidium paludosum Raddi, Pl. Bras. 1: 29. t. 44. 1825. [non Bl., 1828; non Mett., 1858].

HOLOTYPE: (?) Brazil, Raddi, as Aspidium paludosum (K; photo at UC !). Annotated as the type for Nephrolepis exaltata var. hirsutula as cited by Baker in Mart., Fl. Bras. 1870.

Nephrolepis paludosa (Raddi) Sehnem, in Reitz, Fl. Illustr. Catar. fasc. DAVA: 16. 1979.

Aspidium guineense Schumack in Kongel, Dansk. Vid. Selsk. Afh. 4: 229. 1829. (1827 fide Christensen (1906)).

HOLOTYPE: Africa (C, 2 sheets !, photos (3) at BM !).

Hypopeltis palmoides Bory, Bel. Voy. Bot. 2: 65. 1833.

ISOSYNTYPES: Mauritius, Bory (L !, photos (Morton neg. no. 1682) at C ! and US); there is a second sheet at L - photo (Morton neg. no. 1685) at G !). Notes by Morton on the photos point out that this is a superfluous name change and therefore illegitimate.

Nephrodium palmoides (Bory) Rich., Sert. Astrol. xxxix. 1834.

Nephrolepis subcordata Presl, Tent. Pterid. 79. 1836.

HOLOTYPE: Aspidium subcordatum "Sieb. fl. mart. n 60 partim." (PRC - photo at K (neg. no. 9794), dup. at BM !).

Nephrolepis seiberi Presl, Tent. Pterid. 79. 1836.

LECTOTYPE: A sheet labeled "Aspidium seiberi" and "Nephrolepis seiberi" from "Isle de Bourbon" (G !).

SYNTYPE: A sheet labeled "Synopsis Filicum No. 35" and as "A. biserratum v. pubescens Mr. Seiber 1825 insula Mauritii" (G !).

Aspidium flagelliferum Roxb.; Wall., List No. 2234. 1829. nom. nud.

Polypodium flagelliferum Roxb., Calcutta J. Nat. Hist. 4: 487. t. xxxi. 1844.

LECTOTYPE (selected by Morton (1974)): A specimen at BR with the name in Roxburgh's hand (Morton photo 19930a). There is a possible isolectotype at BM (!) annotated as such by Morton in 1971. This sheet is also from India; a label (in a packet) says, "East Indies Roxb.," and another says, "Polypodium marginale."

Polypodium marginale Roxb., in ed.

Nephrolepis macrophylla Presl, Epim. 43. 1849.

ISOTYPES: Ins. Philippines, Cuming 22 (PRC, 3 sheets - at BM !, dup. of photos at K (neg. nos. 9796 - 9798), 1 sheet at W !, 2 sheets at G !, and 2 sheets at RO (1 in Hb. Cesatianum and 1 in general herb.) !). A lectotype should probably be chosen from the sheets at PRC, but I have not seen these and can not otherwise determine which of the duplicates should serve as lectotype.

Nephrolepis biaurita Presl, Epim. 403. 1849.

HOLOTYPE: Insula Mauritii, "Flora mixta No. 297" (PRC - photo at K (neg. no. 9792), dup. at BM !, ISOTYPES: 3 sheets at G !.

Lepidoneuron biauritum (Presl) Fée, Mem. Fam. Foug. 5: 301. 1852.

Nephrolepis saligna Carruth. in Seem., Fl. Vit. 361. 1873. [Polypodium salignum Sol., mscr. in ed.].

LECTOTYPE (chosen by Jarrett, in herb., 1974): Banks and Solander, Cook's first voyage, "Otaheite" 1769 (BM !). SYNTYPES: "Viti" Islands, B. Seeman 743, 1860 (BM !), Fiji Mauis. Sir E. Howe Bt. 1853 (BM !, photo (Morton neg. no. 6873) at G !).

Nephrolepis periscifolia Christ, Nova Guinea 8: 159. 1909.

HOLOTYPE: New Guinea, Versteeg 1017 (P - photo, drawing, and fragment at BM !, ISOTYPES: L (Hb. Ludg. Bat. No. 910,211,273 ! and No. 910,211,274 !); Morton photo (neg. no. 1709) at BM !, G !, and US).

Nephrolepis caudata Christ, Ann. Mus. Cong., Bot. Ser. 5, 3: 27. 1909.

HOLOTYPE: Congo, 2 sheets, one with "1027" and one with "1/2/07" part of Hb. Christ (BR, 2 sheets - photos at BM !).

Nephrolepis dayakorum Bonap., Bonapatre Notes Pterid. 7: 399. 1918.

HOLOTYPE: Borneo, Mt. Santuburg # 70, 13 Mar. 1914 (mixed coll., left hand frond is the type) (C !, frag. at BM labeled "Mt. Larrisburg," and "N. hirsutula x N. pilosula" !).

Nephrolepis mollis Rosenst., Fedde Rep. Spec. Nov. 22: 13. 1925.

LECTOTYPE: Costa Rica, Hundriesser, VIII. 1090. Brade 141, Rosenst. exsicc. 289. litorale atlanticum (NY ! (Nauman photos 2855, 2858, 2860 at FAU !)), ISOTYPES: UC and S.

Nephrolepis biserrata var. auriculata Ching, Flora Reip. Pop. Sinicae II: 378. (317). 1959.

HOLOTYPE: China, Haina, Ling Shui, Hsien, Lung Tau Tso; H. Fung 20043. 26-29 IV 1932. Note: I have not

seen the type but the protologue description suggests that this does not warrant recognition; it has merely a pronounced auricle. Further study is needed.

Plants large sized; perennial. Rhizomes erect to ascending, well-developed; covered with 0.5-6.8 mm long, 0.3-1.1 mm wide, loosely appressed to spreading, orbicular to lanceolate-attenuate, ciliolate-papillate, brown to castaneous, sometimes lustrous scales with or without a pale margin. Tubers absent. Stolons pale to dark brown; sparsely to moderately paleate with 0.8-6.3 mm long, 0.2-1.0 mm wide, spreading, triangular to narrowly oblong, attenuate, ciliolate, pale to dark brown, indistinctly bicolorous scales. Fronds erect to pendulous; 11.0 (2.2-21.6) dm long, 1.9 (0.3-3.5) dm wide, 5.8 (3.0-9.9) times longer than wide; elliptic-lanceolate. Stipes 2.5 (0.2-5.4) dm long, medium to dark brown; up to 11 leaf traces at the base; sparsely to moderately paleate with variable small, 0.3-0.4 mm wide, irregular to circular scales, and larger, 1.5-8.4 mm long, 0.2-0.7 mm wide, narrowly triangular scales like those of the rhizome that may be cauducous on all the proximal portions of the stipe. Rachises 8.5 (1.8-17.1) dm long, 4.3 (1.8-14.1) times longer than the stipe, interpinnal distance 20.9 (7.5-35.0) mm; medium to dark brown; glabrous to pubescent in the adaxial groove with 0.3-0.6 mm long, articulated, uniseriate trichomes usually with reddish septa; paleate mostly around the points of pinna attachment with 1.1-7.7 mm long, 0.1-0.6 mm wide, irregular, linear-triangular, caudate, fibrillose, pale brown, essentially concolorous scales.

Pinnae sessile to subpetiolulate; median pinnae 10.3 (2.5-23.0) cm long, 1.3 (0.5-2.1) cm wide, 7.8 (4.4-15.3) times longer than wide; narrowly triangular to narrowly elliptic-lanceolate; attenuate to abruptly so at apex; medial to submedial in attachment, cuneate, truncate to auriculate-cordate acroscopically and rounded basciscopically; acroscopic lobe absent or a small oblong lobe; biserrate (i.e., alternately crenate and serrate) to serrulate, the latter especially on lower pinnae; veins to 4-forked in central portion of pinna, mostly evident; upper costa surface densely pubescent to tomentose with 0.3 mm long, erect pale trichomes like those of the rachis, or glabrous; blade glabrous to pubescent (mostly on the veins), mostly abaxially, with pale to light brown, uniseriate, 0.3 (0.2-0.7) mm long, septate trichomes; sparsely to densely paleate adaxially and abaxially with 0.9-2.0 mm long, 0.06-0.15 mm wide, caudate, filiform, fibrillose, pale brown scales; lowermost pinnae 3.7 (1.1-5.6) cm long, 1.1 (0.5-1.9) cm wide, 3.1 (1.6-5.8) times longer than wide, usually oblong; guard cells 41.7 (33.8-54.6) µm long, epidermal cells sinuous to deeply lobed. Sori supramedial to medial, mostly supramedial and distant from the margin by at least their width. Indusia circular to hippocrepiform, pelate or attached by a narrow sinus; 0.8-1.1 mm wide; margins entire; pale to medium brown, concolorous or with a pale margin. Sporangia non-paraphysate. Spores polar length 21.6 (18.2-28.0) µm; longitudinal length 21.0 (18.2-25.9) µm; equatorial length 33.8 (28.0-43.4) µm; laesura length 15.6 (11.2-22.4) µm; P/E ratio 64.1 (56.0-73.9); perine rugose to rugose verrucate. (n=41; 2n=82).

DISTRIBUTION AND ECOLOGY: Pantropical and distributed throughout the neotropics (Figure 28, p. 186); in forested, relatively wet habitats, e.g., swamps, but occasionally thickets, roadsides or clearings; at low to middle elevations (0-1400 m).

COMMENTS: The only species with which N. biserrata is likely to be confused in the neotropics is N. multiflora. Nephrolepis biserrata, in its dry form, closely resembles N. multiflora in pinna shape and indument, but lacks the distinctly hyaline-margined (i.e., bicolorous) and persistent stipe scales of the latter species. Nephrolepis multiflora may also be distinguished by the presence of more appressed and darker colored rhizome scales and a granular rather than rugose to rugose-verrucate perine.

Nephrolepis cordifolia (L.) Presl, Tent. Pterid. 79. 1836.

Polypodium cordifolium L., Sp. Pl. 1089. 1753. [non Mart. et Gal., 1842].

TYPE: Petiver, Pterigraph Amer. t. 1. f. 11. 1712 (!). Supposedly a copy of Plumier's t. 71 (1705) (!). The Plumier plate is a poor drawing of what might be a species of Nephrolepis and the Petiver drawing is a poor copy of this. As a result, it is difficult to fix the name precisely. Since the Plumier plate is based on plants from the Dominican Republic, I am applying the name in a manner consistent with the plants I have seen from the Dominican Republic.

Aspidium cordifolium (L.) Swartz, J. Bot. Schrad. 1800(2): 32. 1802.

Aspidium tuberosum Bory ex Willd., Sp. Pl. 5: 234. 1810. HOLOTYPE: Burbon sur les arbes, no. 111, Bory de St. Vincent (B - Hb. Willd. No. 19759 - photo !, photos also at GH ! and FAU !). ISOTYPES: P (photo !, dup. at FAU !); FI.

Nephrodium tuberosum (Bory ex Willd.) Desv., Prodrome 2: 252. 1827.

Nephrolepis tuberosa (Bory ex Willd.) Presl, Tent. Pterid. 79. 1836.

Nephrolepis cordifolia var. tuberosa (Bory ex Willd.) Baker, Mart. Fl. Bras. 1(2): 491. 1870.

Nephrolepis exaltata β tuberosa (Bory ex Willd.) O. Ktze., Rev. Gen. 2: 816. 1891.

Aspidium imbricatum Kaulf. ex Sprengel, Syst. Veg. 4: 97. 1827. [non Fourn., 1872].

LECTOTYPE: Ins. Mauritii, Seiber 41, Syn Fil. 41 (B, 3 sheets !; Nauman photos 697, 700, 703, 707, 710, 713, 717, 720 at FAU !; photos at K ! and P !). Sheet 1 (with 5 fronds) is the lectotype, sheets 2 and 3 (with two fronds each) are isotypes.

Nephrolepis imbricata (Kaulf. ex Sprengel) Presl, Tent. Pterid. 79. 1836.

Nephrodium imbricatum (Kaulf. ex Sprengel) Boj., Hort. Maur. 392. 1837.

Plants small to medium sized; perennial. Rhizomes erect to ascending, well-developed; covered with 2.0-9.0 mm long, 0.4-1.3 mm wide, spreading, triangular to lanceolate-attenuate, entire to papillate, pale to dark brown, reddish or orange, essentially concolorous scales. Tubers present or absent; 1.0-3.5 cm long, 1.0-2.0 cm wide, spherical to ellipsoidal; covered with 2.2-5.8 mm long, 0.2-0.7 mm wide, triangular to narrowly linear-oblong, papillate, pale to dark or reddish brown, indistinctly bicolorous scales. Stolons pale to dark brown; sparsely to moderately paleate with scales as on the tubers. Fronds stiffly erect to arching; 5.3 (2.5-10.7) dm long, 0.4 (0.3-0.7) dm wide, 12.9 (5.1-17.8) times longer than wide; linear-elliptic. Stipes 1.0 (0.3-1.9) dm long; stramineous to medium brown; usually 1 (to 3) leaf traces at the base; moderately to densely paleate with 3.0-8.5 mm long, 0.3-1.6 mm wide scales essentially like those of the rhizome that may be cauducous on all but the proximal portions of the stipe. Rachises 4.5 (2.2-9.0) dm long, 5.0 (3.2-9.3) times longer than the stipe, interpinnal distance 7.4 (5.0-12.0) mm; medium to dark brown; glabrous; moderately to densely paleate around the points of pinna attachment and adaxially with 1.8-5.4 mm long, 0.1-0.5 mm wide, linear-caudate, ciliolate-fibrillose, pale to dark brown scales with a distinctly darker point of attachment, making the scales appear bicolorous. Pinnae sessile; median pinnae 2.1 (0.9-4.8) cm long, 0.6 (0.4-0.9) cm wide, 3.7 (1.8-4.8) times longer than wide; oblong to lanceolate-oblong, straight to slightly falcate; acute to bluntly rounded at

apex; submedial to medial (sometimes nearly basal) in attachment, auriculate-cordate, acroscopically overlapping the rachis; acroscopic lobe consistently deltoid and usually overlapping the basiscopic portion of the next distal pinna; entire to serrulate, fertile pinnae occasionally with a smoothly crenate margin; veins 1-forked (to 2-forked) in central portion of pinna, sometimes obscure; upper costa surface glabrous; blade glabrous (rarely with a few branched trichomes like those of N. rivularis abaxially); non-paleate; lowermost pinnae 0.7 (0.6-1.8) cm long, 0.6 (0.4-1.0) cm wide, 1.2 (0.8-1.2) times longer than wide, deltoid; guard cells 50.8 (33.8-65.0) µm long, epidermal cell walls sinuous to lobed. Sori supramedial to medial. Indusia reniform to lunar or triangular-rounded, attached along a broad sinus; 1.1-1.7 mm wide; margins entire; pale to dark brown, usually with a pale margin. Sporangia non-paraphysate. Spores polar length 20.5 (15.4-28.0) µm; longitudinal length 20.1 (16.8-26.6) µm; equatorial length 29.9 (21.0-35.7) µm; laesura length 13.2 (8.5-18.2) µm; P/E ratio 68.7 (56.0-73.9); perine verrucate to verrucate-rugose. (n=41; 2n=82)

DISTRIBUTION AND ECOLOGY: Pantropical but widely escaped from cultivation and only questionably native to any particular region, in the neotropics from northern Florida and central Mexico southward to the Caribbean and Central America, eastward to Colombia and portions of the Guyana region, and further southward to central and southern Brazil (Figure 29, p. 189); in wet, shady places, limestone ledges, cliffs, rocks, roadsides, and often old homesites or dumps; at middle to higher elevations (0 - over 1500 m).

COMMENTS: When tubers are present, this is a distinctive species. Only N. occidentalis also produces tubers, but is easily separated by its poorly-developed rhizome. The only other species with which N. cordifolia is likely to be confused (when tubers are absent) are N. exaltata, N. pectinata, and N. pendula. Nephrolepis exaltata is usually confused with N. cordifolia when sterile; N. cordifolia can be separated by its distinctly bicolorous adaxial rachis scales. Nephrolepis pectinata differs from N. cordifolia largely in having more basally attached pinnae, fewer scales on the stipes and rachises, and black or dark brownish scales compared to the orange or reddish to light brown scales of N. cordifolia. Nephrolepis pendula can be separated by its purple-black, usually naked stipes, longer interpinnal distance, larger pinnae and fronds, and appressed, black and lustrous rhizome scales. The Guyana form of N. pendula is superficially similar to N. cordifolia in size and indument density, but differs in the color of the indument, in having darker and longer stipes (relative to the rachis), and in having truncate pinnae with an obtuse or absent acroscopic lobe.

Nephrolepis exaltata (L.) Schott, Gen. Fil. Pl. 3. 1834.

Polypodium exaltatum L., Syst. Nat. 10: 1326. 1759.

TYPE: Plate; Sloane Jam. t. 31 (based on a specimen in the Sloane Hb., 1: 52 at BM - photo !, dup. at FAU !).

Aspidium exaltatum (L.) Swartz, J. Bot. Schrad. 1800(2): 32. 1802.

Nephrodium exaltatum (L.) R. Brown, Prodrome 1: 148. 1810.

Hypopeltis exaltata (L.) Bory, Bel. Voy. Bot. 2: 66. 1833.

Nephrolepis neglecta Kunze, Linnaea 13: 148. 1833.

NEOTYPE: According to the protologue, "In rupibus hacienda de la Laguna (cueva grande) Aug. leg. Schiede" (probably at LZ - destroyed). There is a photo of two sheets at BM (!) and the left hand sheet says "Nephrolepis neglecta mihi," and "Addit. ad. fil Mexico. No. 766$^{a}_{=}$," "in Berol. nom exaltati," collected by Kunze - this sheet is here designated as a neotype until the Schiede collection is located. There is a duplicate (isoneotype) of Kunze 766$^{a}_{=}$ at BM !). The right hand sheet of the BM photo is only authentic material.

Nephrolepis cultrifolia Presl, Tent. Pterid. 79. 1836.

HOLOTYPE: "In insula OuWahu Sandwichianum," in herb. Meyen, Meyen 1835 (PRC - photo at K (neg. no. 9791), dup. of photo at BM !).

Plants medium sized; perennial. Rhizomes erect to ascending, well-developed; covered with 2.0-9.0 mm long, 0.4-1.3 mm wide, spreading, lanceolate to narrowly triangular, attenuate, entire to papillate, pale to dark brown, sometimes reddish, essentially concolorous scales. Tubers absent. Stolons pale to dark brown; sparsely to moderately paleate with 2.2-5.8 mm long, 0.2-0.7 mm wide, triangular to narrowly linear-oblong, papillate, pale to dark brown, concolorous or indistinctly bicolorous scales. Fronds erect to arching-pendent; 8.5 (4.0-14.2) dm long, 0.8 (0.5-1.2) dm wide, 11.1 (6.2-18.0) times

longer than wide; narrowly linear-elliptic. Stipes 1.6 (0.2-3.9) dm long; stramineous to medium brown; 1 to several leaf traces at the base; sparsely to moderately paleate with 2.6-8.4 mm long, 0.2-0.8 mm wide scales essentially like those of the rhizome that may be cauducous on all but the proximal portions of the stipe. Rachises 7.0 (2.4-16.3) dm long, 5.1 (1.8-18.1) times longer than the stipe, interpinnal distance 13.0 (7.3-21.0) mm; medium to dark brown; glabrous; moderately paleate around the points of pinna attachment and adaxially with 1.5-5.0 mm long, 0.1-0.3 mm wide, linear-caudate, ciliolate-fibrillose, pale to dark brown scales in which the point of attachment is indistinctly darker, the scales appearing essentially concolorous. Pinnae sessile to barely subpetiolulate; median pinnae 4.0 (2.3-7.4) cm long, 1.0 (0.6-1.8) cm wide, 4.0 (2.8-5.3) times longer than wide; triangular-oblong, slightly to distinctly falcate; acute to deltoid apices; medial to submedial in attachment, truncate to truncate-auriculate or auriculate, occasionally overlapping the rachis; acroscopic lobe deltoid to acute; serrulate; veins 2-forked (to 3-forked) in central portion of pinna, sometimes obscure; upper costa surface glabrous; lamina glabrous; sparsely to moderately paleate adaxially and abaxially near the costa proximally with 0.8-2.0 mm long, 0.06-0.23 mm wide, proximally fibrillose, caudate, pale brown scales; lowermost pinnae 1.4 (0.6-3.0) cm long, 0.9 (0.5-1.2) cm wide, 1.5 (1.0-2.5) times longer than wide, deltoid; guard cells 56.1 (46.8-65.0) µm long, epidermal cell walls sinuous to lobed. Sori supramedial to medial, position variable. Indusia reniform to hippocrepiform,

attached by a narrow or broad sinus; 1.1-1.7 mm wide; margins minutely papillate; pale to dark brown, concolorous or with a pale margin. Sporangia non-paraphysate. Spores polar length 26.5 (21.0-31.5) µm; longitudinal length 26.0 (19.6-35.0) µm; equatorial length 41.0 (29.4-49.0) µm; laesura length 20.7 (14.0-28.0) µm; P/E ratio 64.9 (54.4-78.6); perine rugose-verrucate to verrucate. (n=41)

DISTRIBUTION AND ECOLOGY: Largely Caribbean, Florida, Bahamas, Turks and Caicos, Cuba, Hispaniola, Puerto Rico, Jamaica, Mexico (Vera Cruz), Bermuda, Panama (few collections), and French Guyana (one specimen) (Figure 25, p. 173); in forested to open areas often as an epiphyte; at low to middle elevations (0 - 1170 m).

COMMENTS: Only N. x averyi and N. cordifolia are likely to be confused with N. exaltata, especially when the plants are sterile. Distinguishing characters are given in the comments sections for N. x averyi (p. 246) and N. cordifolia (p. 261).

Nephrolepis multiflora (Roxb.) Jarrett ex Morton, Contrib. U.S. Nat. Herb. 38(7): 309. 1974.

Davallia multiflora Roxb., Calcutta J. Nat. Hist. 4: 515, t. xxxi. left hand. 1844.

LECTOTYPE (chosen by Morton (1974)): BR - not found fide Lawalree (in litt.) - frag. at US !.

Nephrolepis acutangula Presl, Tent. Pterid. 79. 1836. nom. nud., Epim. Bot. 403. 1849.

HOLOTYPE: "Habitat as Cantonem Chinae (Meyen)," (Herb. Meyen at PRC - photo at K (neg. no. 9793), dup. of photo at BM !).

Nephrolepis tomentosa v.Ald.v.Ros., Bull. Jard. Bot. Buit. II no. I. 11. 1911.

HOLOTYPE (?): Java, Probalingga, S. H. Koorders 24095 B (L - Hb. Ludg. Bat. No. 923,362,277 ! - photo at BM !).

Nephrolepis hirsutula var. rotundipinnata Bonaparte, in ed.

Plants medium sized; perennial. Rhizomes erect to ascending, well-developed; covered with small, 0.3-0.5 mm wide, circular to elliptic scales and 0.6-3.0 mm long, 0.6-1.0 mm wide, oblong to elliptic-oblong, appressed, ciliolate-fibrillose, dark brown to black, lustrous, hyaline-margined scales. Tubers absent. Stolons pale to dark brown; moderately paleate with 0.7-3.3 mm long, 0.3-1.0 mm wide, small circular or linear-oblong to lanceolate-oblong, ciliolate-papillate, dark brown to black, ± lustrous, hyaline-margined scales. Fronds erect to ascending; 7.9 (3.4-24.4) dm long, 1.2 (0.3-1.6) dm wide, 6.6 (3.1-12.0) times longer than wide; elliptic to narrowly elliptic. Stipes 1.9 (0.4-4.4) dm long; pale to dark brown; usually 2 or 3 leaf traces at the base; moderately to densely paleate with variable, small, 0.3-0.4 mm wide, circular scales and larger, 0.6-7.5 mm long, 0.4-1.3 mm wide, persistent, bicolorous scales otherwise like those of the rhizome. Rachises 6.0 (2.7-20.4) dm long, 3.4 (1.3-9.0) times longer than the stipe, interpinnal distance 14.5 (8.0-24.0) mm; pale to dark brown; glabrous at maturity but rarely pubescent with trichomes like those of N. biserrata; moderately to densely paleate around the points of pinna attachment and adaxially with 0.6-3.4 mm long, 0.1-0.6 mm wide scales like those of the stipe,

becoming smaller and more sparse distally as well as more concolorous and hyaline. Pinnae sessile to barely subpetiolulate; median pinnae 6.5 (3.4-12.3) cm long, 1.0 (0.6-1.8) cm wide, 6.7 (3.5-9.5) times longer than wide; narrowly triangular, sometimes elliptic, attenuate and occasionally slightly falcate at apex; medial to submedial in attachment, rounded basiscopically and slightly auriculate to truncate acroscopically (the latter more predominant in sterile pinnae); acroscopic lobe acute to oblong, occasionally overlapping the rachis and the next distal pinna; biserrate to irregularly serrate fertile pinnae and finely serrate sterile pinnae; veins 2-forked (to 3-forked) in central portion of pinna, mostly evident; upper costa surface densely pubescent with 0.1-0.3 mm long trichomes like those in N. biserrata; blade glabrous adaxially, occasionally sparsely to moderately pubescent abaxially with trichomes like those of the upper costa surface; paleate adaxially and abaxially with 0.6-2.1 mm long, 0.08-1.1 mm wide scales otherwise like those of N. biserrata; lowermost pinnae 2.9 (2.0-4.0) cm long, 0.9 (0.7-1.2) cm wide, 3.2 (2.2-6.0) times longer than wide, oblong-deltoid to oblong; guard cells 44.3 (31.2-54.6) µm long, epidermal cell walls sinuous to deeply lobed. Sori supramedial. Indusia circular to hippocrepiform, peltate or attached by a narrow sinus; 1.1-1.3 mm wide; margins entire; pale to dark brown, mostly with pale margins, occasionally concolorous. Sporangia non-paraphysate. Spores polar length 23.0 (18.9-29.4) µm; longitudinal length 22.4 (16.8-28.0) µm; equatorial length 34.4 (26.6-42.0) µm; laesura length 16.6 (11.2-25.0) µm; P/E ratio 67.1 (57.4-84.1); perine granular. (n=41)

DISTRIBUTION AND ECOLOGY: Native to the paleotropics but widely scattered and naturalized in the neotropics as an escaped cultigen, in the Caribbean, southern Mexico, Central America, the Amazon Basin, and southeastern Brazil (Figure 28, p. 186).

COMMENTS: This is a distinctive species only likely to be confused with the dry form of N. biserrata. It can be distinguished from all of the other neotropical species by the distinctly bicolorous stipe scales.

Nephrolepis occidentalis Kunze, Linnaea 18: 343. 1844.

HOLOTYPE: Mexico, Leibold 27 (B - destroyed). Note: As pointed out by Pichi Sermolli (1969), Kunze apparently studied two specimens, one at LZ (now destroyed) and one in Roemer's Herb. at BM. The specimen at BM has not been found. Tryon (1964) mentions that Leibold 127 (B) is this species. Perhaps "No. 27" in Kunze (1844) was meant to be "No. 127," but Leibold 127 is given under Diplazium lonchophyllum by Kunze (p. 333). I have not designated a neotype pending a more thorough search at BM for the Roemer's specimen.

Nephrolepis cordifolia var. occidentalis (Kunze) Kuhn ex Krug, Engler's Bot. Jahrb. 24: 121. 1897.

Nephrolepis pectinata var. occidentalis (Kunze) Urban, Symb. Ant. 9: 316. 1925.

Nephrolepis intermedia Fée, Mem. Fam. Foug. 9: 32. 1857. [non Sodiro, 1883].

TYPE: Mexico, Vera Cruz, "Orizaba," Schaffner 447 (isotype at K fide Smith, 1981).

Plants small to medium sized; annual or seasonal. Rhizomes erect, poorly-developed, bearing only a few fronds; covered with 1.3-5.0 mm long, 0.2-0.6 mm wide, triangular to lanceolate-attenuate, entire to papillate, pale to dark brown, essentially concolorous scales. Tubers present; 1.0-3.5 cm long, 0.4-2.0 cm wide, elongate-ellipsoidal to cylindrical; covered with 2.2-4.0 mm long, 0.1-0.8 mm wide, narrowly deltoid to triangular, often caudate, pale to dark brown, concolorous scales. Stolons pale to medium brown; sparsely to moderately paleate with 1.4-3.4 mm long, 0.1-0.4 mm wide, triangular to lanceolate-attenuate, entire to papillate, pale to dark brown, essentially concolorous scales. Fronds erect to arching; 4.6 (1.8-7.4) dm long, 0.5 (0.3-1.0) dm wide, 8.6 (5.0-13.2) times longer than wide; narrowly elliptic to narrowly elliptic-lanceolate. Stipes 0.8 (0.3-1.8) dm long; stramineous to dark brown; usually 1 (to 2) leaf traces at the base; sparsely paleate with 2.1-5.0 mm long, 0.2-0.6 mm wide, persistent scales like those of the rhizome. Rachises 3.9 (1.5-9.9) dm long; 5.0 (1.8-10.6) times longer than the stipe; interpinnal distance 9.6 (5.0-16.5) mm; stramineous to dark brown; usually glabrous at maturity, but rarely (less than 1%) with small (80 μm long) uniseriate trichomes; moderately to sparsely paleate mostly around the points of pinna attachment with 0.8-2.5 mm long, 0.1-0.6 mm wide, irregular, caudate, hyaline to pale brown, concolorous scales. Pinnae sessile; median pinnae 2.9

(1.3-4.8) cm long, 0.7 (0.4-1.0) cm wide, 4.3 (2.9-8.3) times longer than wide; triangular, falcate to non-falcate, mostly slightly falcate; acute to attenuate at apex; medial to submedial or basal in attachment (the latter more often in younger plants), cordate-auriculate, acroscopically overlapping the rachis; acroscopic lobe broadly deltoid ranging from acute to obtuse; serrulate to crenulate or crenulate-serrulate in fertile pinnae; veins 1- to 2-forked in central portion of pinna, evident; upper costa surface glabrous; lamina with few 0.3-0.7 mm wide, branched, pale trichomes adaxially and abaxially near the costa proximally (rarely with 90 µm long, 3-celled, uniseriate trichomes on the lamina surfaces); lowermost pinnae 1.1 (0.3-2.0) cm long, 0.6 (0.3-1.0) cm wide, 1.7 (0.9-3.0) times longer than wide, deltoid to occasionally triangular-oblong; guard cells 51.1 (33.8-62.4) µm long, epidermal cell walls variable from nearly straight to deeply lobed. Sori supramedial to medial. Indusia reniform to lunar or triangular-rounded, attached along a broad sinus; 1.1-1.7 mm wide; margins entire; mostly medium brown, concolorous or with a pale margin. Sporangia paraphysate when young. Spores polar length 22.2 (16.8-26.6) µm; longitudinal length 21.9 (16.8-26.6) µm; equatorial length 33.0 (25.2-40.6) µm; laesura length 15.0 (9.8-21.0) µm; P/E ratio 67.5 (57.1-78.9); perine rugose-verrucate to verrucate. (n=41)

DISTRIBUTION AND ECOLOGY: Widespread in the neotropics in two major areas, the first from Haiti and Jamaica to central Mexico and southward through Central America to Colombia, Venezuela, and

Ecuador (including the Galapagos Islands), the second in southeastern Brazil and parts of Bolivia (Figure 26, p. 178); on or among rocks, ledges, lava flows, or wet cliffs in a variety of habitats and occasionally epiphytic on palms and mossy tree trunks, or terrestrial; at middle to higher elevations (350-2134 m).

COMMENTS: A distinctive species characterized by the presence of tubers and a poorly developed rhizome. Plants may rarely exhibit pinnatisect pinnae.

Nephrolepis pectinata (Willd.) Schott, Gen. Fil. text to Pl. 3. 1834.

Aspidium pectinatum Willd., Sp. Pl. 5: 223. 1810.

HOLOTYPE: B - Hb. Willd. No. 19753 - photo !, dup. of photo at FAU !, GH !, and IJ !.

Nephrodium pectinatum (Willd.) Sweet, Hort. Brit. 462. 1827. [non Hieron., 1899].

Nephrodium pectinatum (Willd.) Link, Hort. Berol. 2: 125. 1833.

Nephrolepis cordifolia β pectinata (Willd.) Baker, Syn. Fil. 301. 1867.

Nephrolepis cordifolia var. pectinata (Willd.) Baker, Mart. Fl. Bras. 1(2): 493. 1870.

Nephrolepis exaltata γ pectinata (Willd.) O. Ktze., Rev. Gen. 2: 816. 1891.

Nephrolepis schkuhrii var. minor Fée, Mem. Fam. Foug. 5: 319. 1852.

HOLOTYPE: Cuba, Linden 1881 (G !).

Plants small to medium sized; perennial. Rhizomes erect, small but well-developed; covered with 1.0-3.2 mm long, 0.2-0.7 mm wide, spreading, narrowly triangular to lanceolate-attenuate, ciliolate, pale to dark brown (sometimes black), concolorous scales. Tubers absent. Stolons pale to medium brown; sparsely to moderately paleate with 1.3-3.6 mm long, 0.1-0.4 mm wide, triangular to lanceolate-attenuate, ciliolate-papillate, pale to dark brown, concolorous scales. Fronds erect to arching; 3.7 (1.4-8.1) dm long, 0.3 (0.1-0.6) dm wide, 12.9 (1.5-23.7) times longer than wide; linear-elliptic to narrowly linear-elliptic. Stipes 0.6 (0.1-1.5) dm long; stramineous to dark brown; usually 1 (to 3) leaf traces at the base; sparsely paleate with 1.2-4.3 mm long, 0.2-0.7 mm wide, papillate to fibrillose, narrowly triangular to caudate, light to dark brown (rarely black) scales. Rachises 3.1 (1.3-6.6) dm long, 6.0 (2.1-13.1) times longer than the stipe, interpinnal distance 5.9 (4.0-10.5) mm; stramineous to dark brown; glabrous; sparsely to moderately paleate mostly around the points of pinna attachment with 1.0-3.2 mm long, 0.1-0.5 mm wide, linear-caudate, light brown, bicolorous or concolorous scales resembling those of N. cordifolia but less dense. Pinnae sessile; median pinnae 1.5 (0.7-3.4) cm long, 0.4 (0.3-0.8) cm wide, 3.5 (1.8-6.8) times longer than wide; triangular to triangular-oblong to occasionally oblong, non-falcate to slightly falcate, rarely distinctly falcate; obtusely rounded to deltoid or acute at apex; more than 1/2 of the distal pinnae, or all pinnae basal in attachment, truncate to cuneate or the acroscopic side rounded to auriculate

and overlapping the rachis; acroscopic lobe obtuse to deltoid-acute; serrulate to crenulate on fertile pinnae, almost entire on sterile pinnae; veins 1-forked in central portion of pinna, sometimes obscure; upper costa surface glabrous; lamina glabrous; non-paleate; lowermost pinnae 0.6 (0.3-1.3) cm long, 0.4 (0.2-0.8) cm wide, 1.4 (1.0-2.1) times longer than wide, deltoid to nearly circular; guard cells 60.1 (41.6-78.0) µm long, epidermal cell walls nearly straight to sinuous. Sori supramedial to medial. Indusia reniform to lunar or triangular-rounded, attached along a broad sinus; 0.9-1.5 mm wide; margins entire; pale to dark brown, concolorous or with pale margins. Sporangia non-paraphysate. Spores polar length 22.1 (18.9-28.0) µm; longitudinal length 21.5 (16.8-28.0) µm; equatorial length 33.6 (25.2-43.4) µm; laesura length 16.2 (11.2-25.2) µm; P/E ratio 64.8 (53.7-88.9); perine rugose to rugose-verrucate. (n=41, 82).

DISTRIBUTION AND ECOLOGY: Andean/Central American, in Cuba, Hispaniola, Jamaica, throughout Central America, in portions of southern Mexico and in western South America south to Peru (one specimen each seen from Bolivia and Brazil) (Figure 26, p. 178); in a variety of habitats from dense forest to open sites, often on or among rocks; at middle to higher elevations (0-2470 m).

COMMENTS: This is a species represented by two morphological types, a typical form and a Mexican form. The Mexican form is diploid, and occurs in Mexico (Chiapas, Oaxaca, Puebla, and Vera Cruz), Honduras, and Colombia. The typical form is apparently a tetraploid (more study is needed on the cytology of this species),

and occurs throughout the species' range, though it is apparently rare in Chiapas, Mexico (see Smith, 1981 and comments in Chapter VII, pp. 140 and 144). The Mexican form is distinguished by its larger overall size, the pinnae often being twice as long as in the typical form and less distinctly basal in attachment (compare Figures 10c, d, and e with 10f, p. 63). Because of its larger size, the Mexican form might be confused with N. cordifolia, but can be separated by the absence of a dense covering of scales on the adaxial rachis surface and stipe, by its smaller, less reddish-orange and more blackish to brown scales, in the absence of tubers, and in having more than 1/2 of the distal pinnae basal in attachment.

Nephrolepis pendula (Raddi) J. Smith, Hooker's J. Bot. 4: 197. 1841.

Aspidium pendulum Raddi, Opusc. Sci. Bolog. 3: 289. 1819. [non Splitgb., 1840].

HOLOTYPE: "Brasil: Mandiocca." Raddi (FI; isotype frag. at US (# 2423754) !, ISOTYPE: K (fide Smith (1981)).

Nephrodium pendulum (Raddi) Desv., Prodrome 2: 252. 1827.

Nephrolepis tuberosa var. pendula (Raddi) Hooker, Sp. Fil. 4: 151. 1862.

Nephrolepis cordifolia var. pendula (Raddi) Baker, Mart., Fl. Bras. 1(2): 492. 1870. [Note: The combination is here wrongly attributed to Hooker by Baker, and he may have unintentionally made the combination.]

Nephrolepis pectinata subsp. pendula (Raddi) Jenman, Bull. Bot. Dept. Jam. 3: 261. 1896.

Nephrodium crenatum Desv., Prodrome 2: 252. 1827. [Note: Desvaux cites Desv., Fl. Ind. Occ. Hamilis, and this may predate this name.] [non Keys, 1873; non Baker, 1877].

HOLOTYPE: Habitat in America Aequinoxiali (P - photo at BM !, UC !).

Nephrolepis crenata (Desv.) Fée, Mem. Fam. Foug. 1: 14. t. 1. f. 19. 1844.

Nephrolepis pendula f. abbreviata Rosenst. in Leutzelburg, Bot. Nordéste Bras. 3: 246, 260. 1923. nom. nud.

Plants medium to large sized; perennial. Rhizomes erect, well-developed; covered with 0.6-4.0 mm long, 0.1-0.8 mm wide, appressed, narrowly triangular to lanceolate-attenuate, ciliolate, black, lustrous, concolorous scales. Tubers absent. Stolons medium to dark brown, black or purple-black, wiry; sparsely paleate with 1.0-4.0 mm long, 0.2-0.8 mm wide, triangular to lanceolate-attenuate, ciliolate-papillate, dark brown, concolorous scales. Fronds mostly pendent but varying to erect in smaller fronds; 9.0 (2.5-22.5) dm long, 0.6 (0.2-1.4) dm wide, 15.9 (1.6-32.1) times longer than wide; narrowly linear to narrowly linear-elliptic. Stipes 1.5 (0.2-3.6) dm long; dark brown to most often purple-black and wiry; usually 1 (to 4) leaf traces at the base; non-paleate to sparsely paleate at the base with 1.2-4.3 mm long, 0.2-0.7 mm wide, appressed scales like those of the rhizome (in the Galapagos form these are sparse, black, and resemble the scales of N. pectinata, and in the Guyana

form these are denser, dark reddish brown and resemble the scales of N. cordifolia but are shorter, less than 5 mm long). Rachises 7.5 (2.1-18.9) dm long, 6.3 (1.8-25.4) times longer than the stipe, interpinnal distance 10.2 (6.0-17.0) mm; dark brown to purple-black; glabrous; sparsely paleate mostly around the points of pinna attachment with 1.0-3.2 mm long, 0.1-0.5 mm wide, linear-caudate, hyaline to pale brown scales (the scales resemble those of N. cordifolia in color and density in the Guyana form, but differ in shape and size). Pinnae sessile; median pinnae 3.0 (1.6-6.8) cm long, 0.7 (0.4-1.3) cm wide, 4.3 (2.3-9.3) times longer than wide; oblong, oblong-elliptic to oblong-triangular or triangular, fertile pinnae mostly triangular, slightly falcate to distinctly falcate (occasionally non-falcate); mostly acute but ranging from obtusely rounded to acute-attenuate apices; medial to submedial in attachment, base variable from shallowly but abruptly cordate to auriculate or truncate, occasionally overlapping the rachis; acroscopic lobe absent or obtuse (acute to oblong in the Galapagos form); serrulate to serrulate-crenulate or nearly entire, fertile pinnae often more crenulate; veins 1-forked in central portion of pinna, evident to obscure; upper costa surface glabrous; lamina glabrous; non-paleate; lowermost pinnae 1.1 (0.5-1.9) cm long, 0.6 (0.5-1.0) cm wide, 1.7 (1.0-2.8) times longer than wide; guard cells 63.0 (44.2-78.0) µm long, epidermal cell walls nearly straight to sinuous. Sori supramedial. Indusia reniform to lunar or triangular-rounded; attached along a broad sinus; 0.9-1.5 mm wide; margins entire; pale to dark brown, concolorous

or with pale margins. Sporangia non-paraphysate. Spores polar length 22.4 (18.2-30.1) µm; longitudinal length 21.9 (16.8-30.1) µm; equatorial length 34.0 (25.2-49.0) µm; laesura length 16.8 (11.2-28.0) µm; P/E ratio 66.1 (54.8-77.1); perine rugose to rugose-verrucate. (n=41; 2n=82)

DISTRIBUTION AND ECOLOGY: Widespread in the neotropics, from Cuba southward to Santa Catarina, Brazil, but rare in Bermuda, the Amazon Basin, Lesser Antilles, and uncommon in southern Mexico (Figure 27, p. 183); most often as an epiphyte but also terrestrial or epipetric in generally moist habitats, cloud forests, occasionally roadsides or other open areas; more or less evenly distributed at all elevations (0-4267 m).

COMMENTS: Three major morphological forms can be recognized within N. pendula, typical, Galapagos, and Guyana. Both the Guyana and Galapagos forms show a more frequent occurrence in drier habitats, e.g., the Roraima sandstones of the Guyanas and the Campo Limpo Flora and sandstones of Minas Gerais, Brazil. Whether these two forms represent distinct taxa with different ecological adaptations or are responses to different environments by a single taxon is still uncertain. Both of these forms are also generally terrestrial and have shorter fronds than is typical for the species as a whole. The Guyana form ranges from Guatemala southward to Bolivia and eastward to southeastern Brazil. The Galapagos form occurs in Ecuador and the Galapagos Islands but is represented by intergrading forms in Bolivia, Mexico, and Guatemala. The Guyana form most resembles

N. cordifolia in size, habit, and indument density and distribution, but its pinnae are truncate, often without an acroscopic lobe, and the scales are of a different size and shape. This form differs from the typical form primarily in pinna shape (see Figure 11, p. 67). The Galapagos form similarly differs from the typical form primarily in pinna characters and resembles N. pectinata in stipe and rachis indument.

Nephrolepis rivularis (Vahl) Mett. ex Krug, Engler's Bot. Jahrb. 24: 122. 1897.

Polypodium rivulare Vahl, Eclog. Amer. 3: 51. 1807.

HOLOTYPE: W. Indies, Montserrat, Ryan (3 sheets at C ! - photo at IJ !).

Nephrolepis exaltata var. rivularis (Vahl) Hieron., Engler's Bot. Jahrb. 34: 454. 1904.

Aspidium sesquipedale Willd., Sp. Pl. 5: 230. 1810.

HOLOTYPE: Brazil, Hoffmannsegg (B - Hb. Willd. No. 19755 - photo !; photos (2) at BM !; photo at IJ !).

Nephrolepis sesquipedale (Willd.) Presl, Tent. Pterid. 79. 1836.

Lepidoneuron sesquipedale (Willd.) Fée, Crypt. Vasc. 1: 148. 1849.

Nephrolepis hirsutula γ sesquipedale (Willd.) O. Ktze., Rev. Gen. 2: 816. 1891.

Aspidium eminens Wickstr., Vet. Akad. Handl. 1825: 436. 1826. [non Beddome, 1888].

HOLOTYPE: Guadeloupe, Forsström (S-PA !; photos (2) at BM !).

Nephrolepis valida Kunze, Linnaea 21: 229. 1848.

LECTOTYPE: Suriname, "Ad arbor. truncos in syvis pr. Marriepaston," Kegel 1379 May 1846 (GOET - photo !).

Nephrolepis intermedia Sodiro, Sodiro, Crypt. Vasc. Quitenses, 57. 1883. [non Fée, 1857].

LECTOTYPE: Ecuador, "in sylv. tropical," Sodiro, Oct. 1882 (K - photo (neg. no. 18479), dup. of photo at FAU !; ISOTYPE: US (# 1196807) !). SYNTYPES: 2 sheets at K - photos (neg. nos. 18480 and 18481) !.

Plants medium sized; perennial. Rhizomes erect to ascending, well-developed; covered with 2.0-6.5 mm long, 0.4-1.1 mm wide, narrowly triangular to lanceolate-attenuate, papillate, medium to dark reddish brown, essentially concolorous scales. Tubers absent. Stolons medium to dark brown; moderately to sparsely paleate with 2.0-5.2 mm long, 0.2-0.9 mm wide, triangular to linear-oblong, papillate-ciliolate, light to dark brown, indistinctly bicolorous scales. Fronds erect-arching to pendent; 9.6 (3.9-16.5) dm long, 0.9 (0.5-1.3) dm wide, 11.6 (6.3-29.1) times longer than wide; narrowly linear-elliptic. Stipes 2.1 (0.6-4.5) dm long; light to purple-brown (not wiry as in N. pendula); usually 2 to 3 leaf traces at the base; sparsely to densely paleate with 1.8-7.0 mm long, 0.2-1.3 mm wide, narrowly triangular to caudate, entire to ciliolate, light to dark brown or reddish brown scales otherwise resembling those of the

rhizome. Rachises 7.7 (3.0-13.2) dm long, 4.4 (1.7-8.5) times longer than the stipe, interpinnal distance 11.2 (7.0-14.0) mm; light to dark brown; glabrous; moderately to densely paleate around the points of pinna attachment and adaxially with 0.8-4.8 mm long, 0.1-0.9 mm wide, irregular, caudate, fibrillose-ciliolate, light to dark brown, occasionally bicolorous scales. Pinnae sessile to barely subpetiolulate; median pinnae 4.7 (2.8-6.7) cm long, 0.8 (0.5-1.1) cm wide, 5.7 (3.7-8.1) times longer than wide; narrowly triangular to narrowly triangular-oblong, distinctly falcate, sometimes slightly so; apices acute to attenuate; basal in attachment (often appearing cuneate), the acroscopic side may be cuneate-truncate to rounded-auriculate, occasionally overlapping the rachis, usually truncate and not overlapping the rachis; acroscopic lobe deltoid to acute (rarely oblong); serrulate; veins 1- to 2-forked in central portion of pinna, mostly evident; upper costa surface glabrous; lamina with scattered, small (0.3-0.7 mm wide), dark reddish brown, branched trichomes (? scales) that may be cauducous and appear as punctuations; lowermost pinnae 1.5 (0.7-2.6) cm long, 0.9 (0.6-1.2) cm wide, 1.8 (0.9-2.9) times longer than wide, oblong to triangular-oblong; guard cells 46.9 (33.8-57.2) µm long, epidermal cell walls sinuous to lobed. Sori supramedial to more often medial. Indusia circular to hippocrepiform, peltate or attached by a narrow, indistinct sinus; 0.6-1.2 mm wide; margins entire; dark reddish brown, concolorous. Sporangia non-paraphysate. Spores polar length 21.3 (17.5-25.2) µm; longitudinal length 21.2 (14.7-26.6) µm; equatorial

length 31.4 (25.2-38.5) µm; laesura length 14.8 (9.8-23.8) µm; P/E ratio 68.3 (54.6-78.1); perine rugose-verrucate to verrucate. (n=41)

DISTRIBUTION AND ECOLOGY: Widespread in the neotropics from Cuba and southern Mexico southward to Bolivia and Paraña, Brazil (Figure 27, p. 183); in forested, often moist habitats; at low to middle elevations (5-2200 m).

COMMENTS: This is a distinctive species that is seldom confused with others, it is characterized by basally attached pinnae; punctate lamina scales, mostly medial sori, and circular, peltate and largely concolorous indusia.

Excluded Names

Lepidoneuron distans Fée, Mem. Fam. Foug. 5: 302. 1852.

Type: "Santo Domingo (De Tussac)."

Lepidoneuron obtusatum Fée, Mem. Fam. Foug. 5: 301. 1852.

Type: "Habitat in Brasilis (Blanchet, sub nomine Aspidii exaltati donavit) Santo Domingo (De Tussac)."

Lepidoneuron rufescens var. β Moore, ? Ind. Fil. [fide Fée, 1869'.

Type: Mart. Hb. Bras. no. 322, Blanchet la Jacobine; Rio de Janiero. Glaziou 2353.

Nephrodium brownii Desv., Prodrome 2: 252. 1827.

? a nomen novum for N. exaltata.

Nephrodium exaltatum α Presl, Rel. Haenk. 1: 33. 1825.

Type: "Hab. α in Mexico (Haenke)."

Nephrodium exaltatum β Presl, Rel. Haenk. 1: 33. 1825.

Type: "β in Antillis (Plumier, Kohaut) in Brasilia and Rio Janiero (Pohl)."

Nephrolepis cisneriana Glaziou ex Sampaio, Mus. Nac. Rio Janiero Publ. No. 5: 33. 1924. nom. nud.

Type: "Fr. Allemão e Cysneiros; Ceará."

Nephrolepis cordifolia fa. eucordifolia V. Vareschi, Fl. Venez. vol. I, tome I. p. 279. t. 57. 4 & 5, photo no. 4. 1969. "Here Vareschi erects (perhaps unintentionally) the nomenclatural equivalent to the autonymic form without a full author citation or references.]

Nephrolepis cordifolia f. minor Chirst ex Krug, Engler's Bot. Jahrb. 24: 121. 1897.

Type: "Habitat in Cuba: Eggers n. 5111."

Nephrolepis cordifolia β obtusata Sodiro, Sodiro, Crypt. Vasc. Quitenses. 276. 1894. [Ann. Univ. Quito 10(67): 133. 1894].

Type: Equador, "Crese en Niebli Quisaya, Canzacoto, etc."

Nephrolepis ensifolia var. β Moore, ? Ind. Fil. [fide Fée, 1869, under Lepidoneuron rufescens].

Type: "Blanchet, la Jacobine; Rio -Janiero, Glaziou nº 2353."

Nephrolepis exaltata f. fallax Domin, Mem. Roy. Czech. Soc. Sci. Nat. Hist. & Math. n.s. no. 2: 235. 1929.

Type: Bermuda.

Nephrolepis exaltata α normalis O. Ktze., Rev. Gen. 2: 816. 1891.

Type: Panama: Monkhill, Costarica: Turrialva.

Nephrolepis pendula var. deflexa Jarrett in Jarrett, Manton, and Roy, Kew Bull. 22: 478. 1968. nom. illeg.

Nephrolepis pickelii Rosenst. ex Sampaio, Arch. Mus. Nac. Rio Janiero 1932: 36. 1930. [without Latin diagnosis].

Type: Brazil, Pernambuco and Pará, A. Sampaio 4888.

Nephrolepis punctulata f. genuina Hieron., Hedwigia 47: 206. 1908.

Type: "Brasilia crescit in sylvis prope urbem Para (n. 1138)."

Nephrolepis rivularis var. dominicensis Domin, Mem. Roy. Czech. Soc. Sci. Nat. Hist. & Math. n.s. no. 2: 237. 1929.

Type: Dominica.

Cultivated Taxa

Nephrolepis cordifolia f. duffi (Moore) Proctor

This form is typified by small (ca. 1 cm wide), circular pinnae that are widely spaced on the rachis. I have not seen it with tubers. The taxon occurs in Barbados, British Guyana, Dominican Republic, Guatemala, Jamaica, ? Mexico, Peru, Puerto Rico, St. Croix, and Florida. Stolze (1981) reports the taxon to be cultivated all over Central America, but that he has not seen it escaped. Proctor (1977) reports the plant for the Lesser Antilles. This form has also been referred to under the names N. cordifolia cv. "Duffi," N. duffi Moore, N. cordifolia "lus" nummularifolius by Vareschi (1969).

Nephrolepis cordifolia - Un-named form

I have seen only one specimen for this form from the neotropics (Mexico, Distr. Federal, R. Fernandez N. 2, 4 July 1978 (ENCB)). This form is typical of N. cordifolia except that the fronds are

twice-pinnate. The specimen is without a rhizome or stolons and it could not be determined if tubers are produced or not. Similar plants are known to me from cultivation in Knoxville, Tennessee under the name of N. exaltata cv. 'Bostoniensis' and are apparently in cultivation in California (Hoshizaki, pers. comm.). This form occurs in Venezuela as well (I have not seen specimens) (see Vareschi (1969) who refers to this as N. cordifolia "lus" composita).

Nephrolepis exaltata cultivars

Numerous forms of N. exaltata cv. 'Bostoniensis' and its derivatives are cultivated throughout the neotropics. These various forms are often difficult to distinguish and the nomenclature is especially problematic. The following are known to me from specimens in the neotropics:

N. exaltata cv. 'Bostoniensis' - Mexico (Chiapas), Florida, and the Lesser Antilles (Proctor, 1977).

N. exaltata cv. 'Elegantissima' Complex - Florida.

N. exaltata cv. 'Florida Ruffles' - Florida.

N. exaltata cv. 'M. P. Mills' - Florida.

N. exaltata cv. 'Piersonii' Complex - Guadeloupe, Guatemala, Jamaica, Mexico (Vera Cruz), Peru, and St. Croix.

N. exaltata cv. 'Whitmanii' Complex - Mexico (Chiapas, Vera Cruz).

Nephrolepis falcata f. furcans (Moore in Nicholson) Proctor

This form resembles N. biserrata in size, pinna shape, and sori, but characteristically exhibits forking (furcate) pinnae and

rachises. It is widely cultivated and persists when escaped, but it is not known to be spreading from spores. The form is known from Brazil (Pará), Cuba, Dominica, Florida, Guatemala, Jamaica, Mexico (Guerrero, Chiapas), Paraguay, Venezuela, and Proctor (1977) reports it from the Lesser Antilles. It is known in the literature under the following names: Aspidium biserratum var. furcans (Moore in Nicholson) (?) Farwell, Nephrolepis biserrata var. furcans (Moore in Nicholson) Hort. ex Bailey, Nephrolepis cordifolia "lus" furcata (see Vareschi, 1969), and Nephrolepis davallioides furcans Moore in Nicholson.

Nephrolepis hirsutula

One specimen was seen from Puerto Rico (Spetzman & Diaz (FTG)), and the species was reported for the Lesser Antilles by Proctor (1977).

Nephrolepis hirsutula cv. 'Superba.'

This form has irregularly pinnatisect, elliptic pinnae, and is densely covered over most of the frond surface by reddish-orange scales. It occurs in British Guyana, Dominica, Florida, Jamaica, Mexico (Chiapas), and St. Vincent.

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APPENDIX

APPENDIX

Specimens seen are listed below for each species. The specimens are listed alphabetically by country, state (or other major geopolitical subdivision), collector, and collector number; specimens of unknown or uncertain collector or location are listed last for each species. Specimens used in the numerical analysis in Chapter II are indicated by an asterisk (*) over either the collector number or the herbarium acronym, whichever more clearly indicates the duplicate employed for analysis.

Nephrolepis x averyi

BRAZIL: Bahia: Blanckok 534 (NY). CUBA: Oriente: Shafer 7722 (NY*). ?: Leon 1050 (MICH). JAMAICA: St. Ann: Stern 710 (IJ). St. Catharine: Proctor 6176 (IJ). St. Thomas: St. John 1975 (FLAS). MEXICO: Puebla: Venture 576 (MICH). PUERTO RICO: Aquadilla: Quick s.n. (MICH - 2 sheets). UNITED STATES: Florida: Broward Co. - Durand 1*, 4*, 49*, 52*, 56, 57, 65*, 66, 67, 68, 69, 70, 71* (FAU); Lohr s.n. (FAU*); Nauman 318*, 434 (FAU); Nauman et al. 645, 646, 647 (FAU). Collier Co. - Beck 2027* (FSU); Field & Lazon s.n. (US); Fischer 8 (US*); Howell 855 (US); Nauman 1570 (TENN); Nauman et al. 426, 427, 428, 433, 629, 631, 632, 636 (FAU); Scull s.n. (FLAS - 2 sheets); Tatje et al. 426, 427, 428, 433 (FAU). Dade Co. - Curtiss 5460 (FLAS - 2 sheets*, MSU, UC*, US*); Davis s.n. (MICH - 2 sheets); Diddle s.n. (FLAS - 2 sheets); Eaton 991 (F); Garber s.n. (F - 2 sheets, FLAS*, PH - 2 sheets); Hardy 10 (PH); Lakela 31449 (USF); Small 7384 (NY); Tatnall 805 (PH). Manatee Co. - Cuthbert s.n. (FLAS*). Monroe Co. - Nauman 1545, 1546, 1548, 1549 (TENN). Palm Beach Co. - Atwood s.n. (MICH); Stevens s.n. (FAU*). Pinellas Co. - Bebb s.n. (F). Polk Co. - White s.n. (FLAS - 2 sheets).

Nephrolepis biserrata

BAHAMAS: Caicos: Millspaugh & Millspaugh 9095 (NY), 9097 (CAS, NY - 2 sheets). Cat Isd: Correll & Sauleda 50453 (NY). N. Andros: Correll et al. 49673-A (IJ). BELIZE: El Cayo: Bartlett 13027 (MICH, UC); Gentle 2571 (MEXU, MICH), 9115 (IJ). Stann Creek: Proctor 36590 (IJ - 2 sheets); Schipp 394 (NY, UC). Toledo: Gentle

3733 (MICH, NY), 6697 (IJ). ?: Gentle 1472 (MICH, NY, UC); Whiteford 1294 (IJ). BERMUDA: Andrews 1426 (NY). BOLIVIA: Beni: Rolleri 47 (LP). Sara: Steinbach 5406, 5544 (NY). Pando: Prance et al. 5789 (MG, NY*). BRAZIL: Amapá: Austin et al. 7129 (MICH, MG, NY); Egler & Irwin 45987 (NY, UB, UC); Westra 47304 (NY*). Amazonas: Coelho 6294 (MG); Prance et al. 5057 (MG, NY*), 15680 (MICH, NY*), 16842 (MG, NY - 2 sheets*); Tate 12 (NY). Bahia: Belem & Pinheiro 2958 (UB); Boom et al. 899 (NY*); Salzmann s.n. (NY - 2 sheets). Mato Grosso: Prance et al. 26122 (NY). Pará: Egler & Irwin 45987 (MG); Mexia 5917 (NY); Oliveira 6340 (MG); de la Sota 2441 (LP). Paraña: Dusen 14645 (PH), 15247 (NY*, PH), 17133 (NY, PH); Westra 47304 (MG). Rio de Janeiro: Webb s.n. (MICH). São Paulo: Brade 7125 (UC); Wacket 206 (NY*). ?: Luetzelburg 21263 (MICH, NY). BRITISH GUYANA: E. Demerara: Davis 193 (NY); Hitchcock 16886 (NY). Mazaruni Potaro: de la Cruz 1893 (NY*); Gleason 132, 668 (NY); Schomburgk s.n. (NY). Northwest: de la Cruz 1139, 3854 (NY*, PH). Pomeroon: de la Cruz 1203 (NY). W. Demerara: Wagner s.n. (PH*). ?: "Forest Dept." WB11 (BRG - 2 sheets, NY); Harrison 1249 (BRG); Jenman s.n. (BRG); Shomburgk 1667 (UC). CAYMAN ISLANDS: Grand Caymen: Brunt 1864, 2034 (IJ); Millspaugh 1376 (F). COLOMBIA: Antioquia: Pennell & Rusby 52 (NY). Chocó: Forero et al. 1971 (ENCB); Lellinger & de la Sota 617 (LP). El Valle: Killip & Cuatarecasas 39032 (UC). Nariño: Taylor 1234, 1235 (MICH). Isla de Providencia: Proctor 3460 (PH). Santa Marta: Smith 2644 (NY - 4 sheets*). Santander: Haught 1499 (MICH, UC). ?: "Eleanor Creek" Rusby & Squires 386 (PH). COSTA RICA: Alajuela: Molina et al. 17201 (NY*). Cartago: Mickel 2601 (NY). Guanacaste: Jimenez 2691 (NY). Heredia: Burger & Stolze 5890 (NY*); Evans & Bowers 3335 (TENN); Mickel 3487 (NY*); de la Sota 5271 (LP); Stork 4765 (NY*, UC). Limon: Stork 2254 (MICH, UC), 3205, 3208 (UC); Weber 6215 (NY*). San José: Alfaro 150 (MICH). "Cocos Isd.": Gomez 3352 (NY); Jimenez 3142 (NY); Klawe s.n. (UC); Pittier 12361 (UCWI); Schmitt 133 (UC). ?: Smith 6909, 6910 (NY); Lankester s.n. (UC); Pittier 10262 (NY). CUBA: Camaguey: Shafer 482, 1071 (NY). Habana: Wilson 2326 (NY). Isle of Pines: Britton et al. 15448*, 15722 (NY); Curtiss 289 (NY); Jennings 132 (MICH, NY); Killip 43559 (IJ, UC). Oriente: Ekman 5935 (NY); Howard 5831 (NY - 2 sheets); Leon & Gustavo 3884 (NY); Shafer 1706, 4423, 7978* (NY); Underwood & Earle 268*, 1294 (NY); Wright 1011 (NY - 2 sheets*, PH, UC). Pinar del Rio: Palmer & Riley 79 (NY); Shafer 387 (NY*). Santiago: Pollard et al. 74 (MICH, NY, PH). Santa Clara: Feruaudo 525 (NY); Leon & Lonstalot 9501 (NY*). ?: Britton et al. 783 (NY); Rugel 25 (NY); Shafer 4220 (NY). DOMINICA: Hodge 2477 (NY). DOMINICAN REPUBLIC: El Seibo: Jones & Norris 1191 - 2 sheets, 1198 (NY). La Vega: Augusto 687 (NY); Valeur 392 (NY). Puerto Plata: Ekman 14581 (NY). Samana: Taylor 99 (NY). ECUADOR: Galapagos Islands: Foster 4152 (CAS); Howell 9477 (CAS); Itow 31300-6 (DS); Snodgrass & Heller 779, 953 (DS); Stewart 234, 235, 236, 237, 238, 916, 917, 918, 919, 920 (CAS), 921 (CAS, NY); Weber 1043/A (DS); van der Werff 1243 (CAS, NY). Guayas: Hitchcock 20529 (NY*). ?: Sodiro s.n.

(BA, MICH, UC). EL SALVADOR: La Libertad: Seiler 1046 (NY). San Salvador: Garcia 93 (UC). FRENCH GUYANA: Cayenne: Broadway 716 (NY). ?: Walker-Arnott s.n. (NY). GRENADA: Sherring 219 (NY). GUADELOUPE: Allorge B27 (IJ); Duss 4161, 4162* (NY); Feldman s.n. (IJ); Proctor 20203 (IJ, MICH); Stehle 301 (IJ). GUATEMALA: Alta Verapaz: Tuckerheim 8341 (NY). Izabel: Brenkle 47-157 (CAS, NY, UC); Maxon & Hay 3053 (NY*); Rowland B-57 (FLAS - 2 sheets); Tun Ortiz 2296 (NY). Petén: Contreras 3057 (IJ, MICH); Lundell 2952, 3320 - 2 sheets, 3890 (MICH). ? - Deam s.n. (MICH), 478 (MICH, NY); Harmon & Dwyer 4012 (NY); Perris 35 (NY); Weatherwax 192, 204 (UC). HAITI: Nord: Leonard 9200 (NY, UC); Nash 118 (NY*). Nord-Ouest: Ekman 3788 (IJ). Sud: Nash & Taylor 1030 (NY*). ?: Ekman 4282 (IJ); Nash 413 (NY). HISPANIOLA: Augusto 259, 389, 400 (NY). HONDURAS: Atlantida: Williams & Molina 13076 (IJ); Yuncker 4764 (MICH); Yuncker et al. 8324 (MICH, NY). Colón: Saunders 845, 882 - 2 sheets (NY), 1025 (MEXU). ?: "La Mosquita" - Clewell 3630 (NY*). ? - Steeves & Ray 374 (UC), 396 (MICH, UC); Thieme 5 (UC); Wilson 63 (NY). JAMAICA: Hanover: Proctor 7166, 37516, 37350, 37531 (IJ); Sinha 772 (IJ). Manchester: Crawford 795 (PH). Portland: Armour 1000 (NY); Clute 57 (NY - 2 sheets, PH), 269 (NY*); Evans 2540-A, 2540-B* (TENN); Fischer 136 (NY); Hart 449 (UCWI - 2 sheets); Maxon 2528, Proctor 5018 (IJ); Underwood 2984 (NY - 2 sheets). St. Ann: Britton 729 (NY - 3 sheets); Chrysler 2068 (MICH, PH); Crosby et al. 557 (F, IJ, MICH - 2 sheets, NY - 2 sheets, UC); Howard & Proctor 13415, 14014 (IJ); Mueller 3 (FAU); Orcutt 6082 (UC); Proctor 27872 (IJ); Yuncker 18231 (MICH). St. Catharine: Proctor 5126 (IJ). St. Elizabeth: von der Porter s.n. (IJ); Proctor 37638 (IJ - 3 sheets). St. Mary: Papenfuss s.n. (MICH); Proctor 5387 (IJ); Yuncker 18445 (MICH). St. Thomas: Maxon 2372 (NY*); Underwood 2827 (NY - 3 sheets). Westmoreland: Britton 512 (NY*); Orcutt 7357 (FLAS, MICH, UC); Proctor 4834, 34685 (IJ). ?: Maxon & Killip 1545 (NY); Moore 302 (UCWI - 3 sheets); Wolle 7874 (NY*, PH, USF - 2 sheets); Alexander s.n. (UC); Jenman s.n. (NY - 4 sheets*, OXF). MARTINIQUE: Duss 1575 (NY); Plei s.n. (NY). MEXICO: Chiapas: Breedlove 33220 (DS). Nayarit: Ortega 6273 (PH). Puebla: Ventura 576 (NY*). Sinaloa: Ortega 73 (MEXU). Tabasco: Matuda s.n. (MICH), 3021 (MEXU); Rovirosa 238 (NY, PH). Vera Cruz: Fink 129 (NY - 2 sheets); Smith 2112 (MEXU, NY, UC). MONTSERRAT: Shafer 577 (NY - 2 sheets). NICARAUGUA: Bluefields: Proctor et al. 27312 (NY - 5 sheets). Rio San Juan: Atwood & Hamblett 2019 (NY, UC). Zelaya: Proctor et al. 27313 (IJ - 2 sheets); Seymour 5064 (NY). PANAMA: Bocas del Toro: Croat 38093 (NY); Wedel 857, 2437 (UC); Woodson et al. 1833 (LP, NY). Canal Zone: Cowell 219 (NY); Croat 4970 (NY), 5437 (UC); Gentry & Nee 8676 (IJ, NY*); Pittier 2310 (NY). Liesner 328 (CAS, ENCB, USF*). Colón: Croat 9847 (NY); Lewis et al. 3216 (UC); Maxon 5819 (NY). Panama: Seibert 639 (NY - 2 sheets, PH). ?: Cornman & Killip 586 (MICH - 2 sheets, UC); Crawford 534a, 547 (PH); Fendler 420 (UC); Hayes 15 (NY*), 16 (PH); Knight s.n. (FLAS); Williams 428 (NY*). PARAGUAY: ?: Frieburg 5062 (MICH);

Hassler 10550 (MICH). PERU: Azacucho: Killip & Smith 22856 (NY). Cajamarca: Ferreyra & Sanchez 19646 (USM). Huánuco: Schunke 1735 (F). Loreto: Croat 20059 (NY*, TENN); Lopez 4337 (LP); Mexia 6489 (CAS, MICH - 2 sheets, NY*, PH*, UC); Rimachi 4506 (NY*); Simpson & Schunke 680 (NY); Tessmann 3544 (NY). San Martin: Schunke 4046 (F), 8527 (NY); Woytkowski 35136, 35230 (UC). PUERTO RICO: Aguadilla: Jenman 5962 (NY); Quick s.n. (MICH); Sargent B162 (DS); Sintensis 431 (UCWI), 5962 (NY). Arecibo: Blomquist 12255 (UC); Underwood & Griggs 3, 960 - 2 sheets* (NY). Bayamon: Britton et al. 2856 (MICH, NY). Guayama: Britton et al. 8405 (NY); Jackson 1082 (IJ); Kuntze 318 (NY); Scamman 8128 (MEXU). Huanucao: Britton & Brumer 7572 (NY); Heller & Heller 1040 (NY*); "Kuhn 1766[a]" (NY); Shafer 3397 (NY); Thorp s.n. (PH). Mayaguez: Britton & Marble 587 (NY - 2 sheets). Ponce: Underwood & Griggs x (NY*). San Juan: Heller 6381 (NY, PH); Heller & Heller 1265 (F, NY*); Hioram s.n. (IJ); Liogier et al. 29969 (NY); Otero 59 (NY). ?: Britton & Britton 8794 (NY); Britton & Shafer 1683 (NY); Griffith s.n. (PH); Hioram s.n. (MEXU - 2 sheets). ST. LUCIA: Box 1703 (IJ - 2 sheets); Howard 11584 (IJ). SURINAME: Paramaribo: Kramer & Hekking 2312 (IJ); Tryon & Kramer 5594, 5603 (MICH, NY). ?: Lanjow & Lindeman 1449 (IJ); Hostmann s.n. (UC). TRINIDAD: Britton et al. 101, 1025 (NY*); Broadway 5250, 6124 (UC); Eggers 1108 (UC); Fendler s.n. (CAS, UC), 55 (MICH, NY - 6 sheets*, UC); Jenman s.n. (NY - 2 sheets); St. John 2360 (FLAS); Webb 4565 (MICH). UNITED STATES: Florida: Broward Co. - Diddle s.n. (FLAS); Durand 58, 59, 60, 61, 62, 63, 64, 72, 74, 75, 76 (FAU); Leeds 342 (NY*, PH - 2 sheets); Moldenke 483 (NY, PH, US); Nauman P1, P2, P3, 463 (FAU); Nauman & Nauman 380, 318 (FAU); St. John 175I (FLAS - 2 sheets). Collier Co. - Correll 6081 (FLAS); Diddle 698 (FLAS); Evans s.n. (TENN); Lakela et al. 27996, 31825 (FLAS*); Nauman 1589, 1596 (TENN); Nauman & Austin 555, 558, 559, 560 (FAU); Nauman et al. 429, 431, 432, 633, 634 (FAU); Scull s.n. (FLAS); Tatje et al. 429, 430, 431, 432 (FAU). Dade Co. - Avery & Loope 1918 (FAU); Bessey s.n. (MSU - 3 sheets); Britton 428 (F, NY); Buswell s.n. (FAU); Carter 204 (PH); Correll 5987 (GH, US); Correll & Popenoe 49481 (IJ, NY*); Darling s.n. (US - 2 sheets); Davis, B. s.n. (MICH - 2 sheets); Davis, J. s.n. (FLAS); Eaton s.n. (F), 132 (MICH); Evans s.n. (TENN); Long et al. 1941 (NY*, USF); Meredith s.n. (PH); Munroe s.n. (GH, NY - 2 sheets*, UC*); Safford & Mosier 105 (US); Scull s.n. (FLAS); Small & Carter s.n. (FLAS, US), 785 (PH), 2385 (NY, US); Small & Lowe s.n. (NY*); Small & Mosier 5890 (NY, US); Small & Nash 152 (NY*); Small & Small 4535 (NY); Small et al. 5651 (NY); Tatnall 804 (PH); Taylor s.n. (BA); ? 488 (NY). Highlands Co. - Garrett 60 (FLAS); Garrett & Ray 194624 (FLAS); McFarland 10714 (GH). Monroe Co. - Delchamps & Wherry s.n. (PH); Lakela & Almeda 30526 (USF); Nauman 1552, 1555, 1557, 1558 (TENN). Orange Co. - Lewis s.n. (FLAS). Palm Beach Co. - Durand 7, 25, 28, 30, 80, 83, 84 (FAU); Hill 152 (NY*); McJunkin s.n. (FAU - 2 sheets*); Schumaker A, B (FAU). ? Co. - Knobloch 1488 (MSU); Stifler 1526 (MSU). VENEZUELA: Amazonas: Broadway 666, 713* (NY). Bolivar:

Steyermark 88047, 88868 (IJ, NY); Trujillo & Fernandez 16210 (MY). ?: "Lower Orinoco" Rusby & Squires 386 (NY).

Nephrolepis cordifolia

ARGENTINA: Buenos Aires: Fernandez 5 (LP); Rodrigo 2057 (LP). Cordoba: Ariza 2865 (CORD - 2 sheets); Kurtz s.n. (CORD). BARBADOS: Proctor 26209 (IJ). BERMUDA: Mackenzie s.n. (PENN - 2 sheets). BRAZIL: Goiás: Irwin et al. 15545 (IPEAN). Rio de Janeiro: Carauta 643 (LP). Rio Grande do Sul: "Frñgeno n. Gg." (NY*). São Paulo: Wacket s.n. (Rosentt ex. no. 91) (MICH - 2 sheets, NY*), 62 (UC). BRITISH GUYANA: Mazaruni Potari: Jenman s.n. (NY*). ?: Jenman s.n. (BRG, NY - 2 sheets*). COLOMBIA: Antioquia: Barkely & Gutierrez 1477 (PH). Cauca: Killip & Smith 15084 (NY); Hb. Lehmannianum 4421 (PH). Chocó: Pennell 5893 (NY). Cundinamarca: Murillo et al. 372 (NY). CUBA: Oriente: Ekman 3115 (NY*); Leon 11141 (NY*); Leon et al. 10529 (NY); Shafer 9006 (NY); Taylor 509 (NY*); Wright 1803 (NY - 2 sheets*). Pinar del Rio: Britton et al. 7456 (NY); Proctor 16359 (IJ); Shafer 12034, 13809* - 2 sheets (NY); Shafer & Leon 13553 (NY*). Santa Clara: Howard 5730, 6509 (NY); Jack 7258 (DS, NY), 7464, 8325 (NY); Leon & Clement 6506 (NY); Leon & Roca 7990 (NY); Luna 97 (NY). ?: Hioram s.n. (FLAS). DOMINICAN REPUBLIC: Barahona: Fuertes s.n. (UC). Santo Domingo: Tuckerheim 3490 (NY*). EL SALVADOR: San Salvador: Seiler 509 (NY). GUATEMALA: Alta Verapaz: Schauensee s.n. (PH); Tuckerheim 2210 (NY). Izabel: Brenkle 47-158 (NY, UC). ?: Brenkle 47-88 (UG); Dept. Quiche Leeds s.n. (PH*). HAITI: Haiti: Leonard 3692 (UC). Nord Ouest: Leonard & Leonard 15047 (NY*); Ouest: Buch 1957 (IJ); Picarda P680 (IJ). ?: (?) Haigar s.n. (MICH). HISPANIOLA: Smith 25 (NY). JAMAICA: St. Andrew: Carhart s.n. (NY); Clute 185 (NY*); Chrysler s.n. (MICH), 4539 (UC); Davis s.n. (MICH); Farr s.n. (NY); Harris 12459 (NY, UCWI); Maxon 8653 (NY*); Maxon & Killip 654 (F, NY*); Underwood 1121, x (NY), 3108 (MICH, NY). St. Thomas: Maxon 9682 (NY); Proctor 5554 (IJ). ?: "Abbey Green" - Maxon 10055 (PENN*); Orcutt 3217 (UC). ? - Atwater s.n. (MICH); Fraser s.n. (IJ); Jenman s.n. (NY - 3 sheets, OXF); Wolle s.n. (PH); ? (NY*). MEXICO: Chiapas: Breedlove 16064 (DS), 34563 (NY); Breedlove & McClintock 23670 (DS). Michoacán: Arscom 6670 (MEXU). Puebla: Rzedowski 1200 (IJ), 29996 (ENCB, LP, NY). Vera Cruz: Ventura 884 (ENCB, NY*). ?: "Distr. Choapam" - Mexia 9274 (NY). NICARAGUA: "Dept. Grenada" - Hall & Bockus 7554 (NY). PERU (?): Miller s.n. (PENN). PUERTO RICO: Bayamon: Britton et al. 5616 (NY). SURINAME: Paramaribo: Samuels 429 (NY). UNITED STATES: Alabama: Mobile Co. - Dukes s.n. (NY). Florida: Brevard Co. - Hollister s.n. (US); Shuey M1084 (USF). Broward Co. - DeCarlo s.n. (FAU); McCart & Snyder 9523 (FAU); Nauman 825 (FAU). Citrus Co. - St. John, E. et al. s.n. (NY); St. John, R. 197 (FLAS); Scull s.n. (FLAS). Dade Co. - Evans s.n. (TENN - 2 sheets); Hardy 5 (PH); Moldenke 436 (PENN). Duval Co. - Darling s.n. (US); Diddle 915 (FLAS); Rhea s.n. (NY).

Escambia Co. - Burkhalter 5919 (UWF - 3 sheets). Hernando Co. - Cooley 861 (USF); Cooley et al. 8307 (GH, USF); Mickel et al. 1782 (UC); Moldenke & Moldenke 29488 (US). Highlands Co. - McFarland 8957 (FLAS). Hillsborough Co. - Evans 2303 (TENN); Mickel et al. 1789 (US); Scudder 441 (FAU). Leon Co. - Hume s.n. (FLAS - 2 sheets). Marion Co. - Mickel et al. 1742 (UC). Martin Co. - Austin et al. 6469 (FAU); Nauman & Austin 186 (FAU); Popenoe 797 (FTG); Tatje s.n. (FAU). Orange Co. - Medgeser s.n. (UC). Palm Beach Co. - Austin s.n. (FAU); Baker s.n. (FAU); Cassen 89 (USF), 601, 642 (FLAS); Hill 149 (NY); Mueller s.n. (FAU); Nauman 219, 410, 486 (FAU); Nauman et al. 218, 398, 399, 402, 407, 408, 410 (FAU), 466 (NY); Wilhelm 121 (FAU). Pasco Co. - Carpenter s.n. (GH). Pinellas Co. - Genelle & Fleming 2508 (USF); Scudder 436 (FAU). Polk Co. - Buswell s.n. (USF); Cooley 11783 (USF). St. Lucie Co. - Nauman & Tatje 518 (FAU); Nauman et al. 255 (FAU). Sarasota Co. - Wherry s.n. (PH). Sumter Co. - St. John s.n. (FLAS*). Volusia Co. - Lakela 31864 (USF). ? Co. - Curtiss s.n. (NY, TENN); Miller s.n. (NY); Molcott s.n. (NY); Robinson s.n. (NY*); Stifler 1527 (MSU). VENEZUELA: Amazonas: Tate 892 (NY). ?: Michelangeli & Clavijo 54 (MY).

Nephrolepis cordifolia cv. 'Duffi'

BARBADOS: Dash 636 (NY). BRITISH GUYANA: Rupununi: de la Cruz 1680 (NY), 2606 (NY, PH). DOMINICAN REPUBLIC: Banao: Valeur 402 (NY). GUATEMALA: "Finca El Naranjo - Chicacao" - Brenkle 47-159 (UC). JAMAICA: Clarendon: Proctor 34560 (IJ). St. Ann: Yuncker 18420 (MICH). St. Mary: Ahung s.n. (PH); Yuncker 17274 (MICH). MEXICO: (?) Vera Cruz: Nevling & Gomez-Pompa 260 (MEXU). PERU: Loreto: Williams 1825, 3578 (F). PUERTO RICO: Guayama: Taylor 2129 (MICH). Humacao: (?) Liogier 31030 (NY). ST. CROIX: King s.n. (UC). UNITED STATES: Florida: Dade Co. - Will s.n. (FLAS).

Nephrolepis exaltata

BAHAMAS: Caicos: Millspaugh & Millspaugh 9094 (F), 9095 (NY). Grand Bahama: Correll & Worsford 50375 (IJ, MICH, NY*). BERMUDA: Brown & Britton 85 (NY, PENN, PH, UC), 878 (NY, PH); Collins 125, 356 (NY); Degener 17604 (NY); Harsburger s.n. (NY, PENN, PH); Howe s.n. (NY - 3 sheets); Kemp s.n. (NY); Millspaugh 59 (F); Taylor 1098, 1164 (MICH - 2 sheets). BRAZIL: Rio de Janiero: Henigen 1271 (NY). ?: Miller s.n. (PENN). CUBA: Camguez: Maxon 3959 (NY); Shafer 31 (NY). Oriente: Ekman 1578 (NY); Grave 1406 (MICH); Hioram & Btiste 1466 (NY); Leon & Gustava 3862 (NY*); Leon et al. 9862, 10529 (NY); Morton & Acuna 3155 (NY, UC); Shafer 1706, 8588, 8707 (NY); Underwood & Earle 269 (NY); Wright 826 (NY, PH*). Pinar del Rio: Wilson & Leon 11552 (MICH, NY). Santa Clara: Britton & Wilson 5375 (NY). ?: Eggers 4897, 5331[a] (NY); Leon & Wilson 3369 (NY*); Linden 1860 (NY). DOMINICAN REPUBLIC: Barahona: Fuertes 812 (UC); Poiteau s.n. (PH). El Seibo: Jones & Norris 1197 (NY*,

TENN). La Vega: Jones & Norris 1079 (NY), 1087 (NY, TENN). FRENCH GUIANA: Cayanne: Lepieur s.n. (NY). HAITI: l'Artibonite: Holdridge 2023 (MICH, NY); Leonard 7875 (IJ, NY). Nord: Leonard 8294 (UC); Leonard & Leonard 14232 (NY); Nash 115 (NY*). Ouest: Buch 869, 1762 (IJ). JAMAICA: Clarendon: Maxon & Killip 1547 (NY); Proctor 37845 (IJ - 2 sheets). Hanover: Harris 9293 (UCWI - 2 sheets). Manchester: Crawford 801 (PH); "Hervard" 30 (NY); Maxon 2558 (NY); Proctor 34891 (IJ). Portland: Fredholm 3297 (NY); Millspaugh 916 (NY*); Orcutt 4784 (UC). St. Ann: Chrysler 2069 (PH*); Davis s.n. (MICH); Harris 8499 (NY, UCWI); Howard & Proctor 14013 (IJ); Maxon 2304 (NY*); Underwood 1768 (NY - 2 sheets). St. Andrew: Davis s.n. (MICH); Balch s.n. (NY); Fisher 9 (NY); Harris 7330 (IJ - 2 sheets); Maxon 8566 (NY, PENN); Proctor 7005 (IJ). St. Catharine: Proctor 5125 (IJ). St. Elizabeth: Orcutt 600, 2319 (UC). St. Thomas: Orcutt 2059 (UC), 3102 (NY*); Underwood 2672 (NY - 2 sheets). ?: Moody's Gap - Clute 171 (NY - 2 sheets*, PH). Dolphin Beach - Harris 9293 (NY - 2 sheets). Abbey Green - Maxon 10049 (NY, PENN*). Farm Hill - Orcutt 3747 (FLAS, UC). Moy Hall - Orcutt 6883 (UC). Ceadarhurst - Underwood 1559 (NY). ? - Alexander s.n. (UC); Fraser s.n. (IJ); Jenman s.n. (NY - 3 sheets, OXF); Moore (?) 488 (UCWI); Parkhurst 37 (UC); Wolle s.n. (PH, USF*). MEXICO: Vera Cruz: Müller 441 (NY); Purpus 3812 (MICH, NY, UC). PANAMA: "Matachui to Las Cascadas" Cowell 354 (NY). PUERTO RICO: Aguadilla: Britton 3921, 3929 (NY); Britton et al. 4488 (NY); Quick s.n. (MICH); Sintensis 412 (UCWI); Thorp s.n. (PH*). Arecibo: Britton & Marble 1062 (NY); Thorp s.n. (PH); Underwood & Griggs 773, 774 (NY). Guayama: Britton et al. 8403 (NY); Kuntze 386 (NY). Hunacao: Blomquist 11904 (UC); Shafer 3537 (NY). Mayaguez: Britton & Britton 7386 (NY); Heller 4453 (NY). Ponce: Britton & Brown 6231 (NY); Britton & Marble 767 (NY); Britton & Shafer 2093 (NY); Britton et al. 6377 (NY); Underwood & Griggs 103 (NY). San Juan: Otero 57 (NY). ?: ex hb. Hillebrand (NY); Hioram s.n. (UC), 200 (MEXU); Stimson 1466 (MICH). ST. THOMAS: Brentel 10744 (UC); Britton & Marble 1429 (NY*); Eggers s.n. (NY). TORTOLA: Britton & Shafer 837[a] (NY); D'Arcy 2089 (FLAS*). UNITED STATES: Florida: Brevard Co. - Baldwin 83 (PENN, PH); Burgess 697 (F, NY); Long et al. 4038 (USF); Schallert 350 (FLAS, USF); Small et al. 10802 (NY). Broward Co. - Abbott s.n. (FAU); Durand 13, 15, 73 (FAU); Geisgiana 12550 (PH); Hopkins 31 (FAU); Janda 29 (FAU); Lawson 30 (FAU); Leeds 343 (PH - 2 sheets); Nauman 464 (NY), 826 (FAU); Nauman & Nauman P4, P5, P6 (FAU); Peterson s.n. (FLAS); Sandler s.n. (FAU); Schneider s.n. (FAU); Smith et al. 829 (FLAS). Charlotte Co. - Ward et al. A-69 (FLAS). Citrus Co. - St. John s.n. (FLAS). Collier Co. - Austin & Austin 6669 (FAU); Austin et al. 6763, 6764 (FAU); Clewell 286 (FSU); Cooley 786 (USF); Cooley et al. 9149 (USF); Duca s.n. (USF); Evans s.n., 4131 (TENN); Eyles & Eyles 8235 (GH); Gillis 10481 (MSU); Hitchcock s.n. (F); Knobloch s.n. (MSU); Lakela & Almeda 29941, 29996 (USF); Lakela & DeBoer 29867 (USF); Lemaine 456 (FSU); Long et al. 2393 (USF); Nauman 1582 (TENN); Nauman et al. 328, 333, 338 (FAU); St. John 369, 1710 (FLAS); Scull s.n. (FLAS*); Sturtevant 44 (FLAS, US); Wiggins 20095 (FLAS). Dade Co. - Atkinson s.n. (PENN);

Bessey s.n. (MSU - 2 sheets); Curtiss 5460 (NY); Evans s.n. (TENN - 2 sheets); Garber s.n. (F - 2 sheets, NY - 2 sheets); Hill 3079 (FTG); Moldenke 434 (US), 436, 3761 (NY), 437 (NY, PENN); Nagy 13 (FAU); Price s.n. (NY); Scull s.n. (FLAS, NY); Small 7384 (NY, TENN - 2 sheets), 7390, 8324 (NY); Small & Carter s.n. (US), 522 (PH), 2395 (NY*); Small & Mosier 5887 (F, NY*); Tracy 9135 (F, MSU, NY, PENN, US); Wherry s.n. (PENN, PH). Duval Co. - Calkine s.n. (F). Glades Co. - Ward et al. 1-10 (FLAS, USF). Hardee Co. - Kirk s.n. (FLAS). Hendry Co. - Davis s.n. (FLAS); Jennings s.n. (USF); Ward et al. 2396 (FLAS, FSU). Hernando Co. - St. John s.n. (FLAS). Highlands Co. - Evans 2292 (TENN); Lakela 26793 (USF); Mickel et al. 1815 (FSU, UC); Nauman 90 (FAU); Porter & Porter 10618 (NY, UC); Sargent 7144 (FSU); Wilbur & Webster 2610 (GH, MICH, NY*, US - 2 sheets). Hillsborough Co. - Curtiss 3764 (PH); Fleming et al. s.n. (FLAS); Mickel et al. 1789 (UC). Indian River Co. - Small 8849 (NY). Lake Co. - Haas s.n. (TENN); Nash 1288 (F, GH, MICH, NY, PH, UC, US); Underwood s.n. (F, GH), 274 (US), 1519, 1904 (NY). Lee Co. - Brumbach 5348 (FAU, FLAS); Correll 5919 (GH); Hitchcock 542 (F, GH, US); Standley 124 (F, GH, NY), 12990 (US). Leon Co. - Jackson s.n. (FSU). Manatee Co. - Churchill s.n. (MSU); Simpson s.n. (NY). Martin Co. - Nauman 264, 271, 522, 527 (FAU); Nauman & Tatje 262, 265, 266, 270, 272, 274, 278, 279, 520 (FAU); Popenoe & Popenoe 688 (FTG); Will s.n. (FLAS*). Monroe Co. - Long et al. 1703 (USF); Nauman 1533, 1534, 1535, 1536, 1538, 1539, 1541, 1543 (TENN); Scull s.n. (FLAS). Okeechobee Co. - McCart 10287 (FAU). Orange Co. - Rapp s.n. (PH). Osceola Co. - Mearns 31 (US). Palm Beach Co. - Atwood s.n. (MICH); Austin 6636 (FAU); Cooley et al. 4877 (GH, USF); Deam 1667 (PH); Durand 10, 77, 78, 79, 81, 82, 87, 89 (FAU); Hitchcock 2402 (F); Kral 5680 (FSU); Meagher 895 (FTG); Misner s.n. (FAU); Mixon s.n. (FAU); Nauman 702 (FAU); Nauman & Austin 182, 183 (FAU); Nauman et al. 415 (FAU); O'Neil s.n. (NY); Randolph 140 (GH); Richardson s.n. (FAU); Seifert s.n. (FAU); Small 8262 (NY*); Small & Small 4452 (NY*); Staples 139 (FAU); Tyson 117 (FAU); Underwood 2219 (NY); Webber 218 (F); Yates s.n. (FAU). Pasco Co. - Odenwelder 10 (TENN); Underwood 1931 (NY). Pinnellas Co. - Curtiss 3764 (F, NY, UC); Gennelle & Fleming 1640, 1693 (USF), 2565 (TENN); Rolfs 750, 834 (F, FLAS); Scudder 104 (FAU); Taylor & Taylor s.n. (FLAS); Thorne 10315 (UC); Williamson s.n. (PH). Polk Co. - Conard s.n. (FLAS*); Jennings & Jennings s.n. (USF); McFarland s.n. (FLAS), 3902 (MICH); Smith s.n. (US); Wherry s.n. (PH). St. Lucie Co. - Austin et al. 6436, 6454 (FAU); Leeds 344 (PH); O'Neil s.n. (FLAS, US); Small & Matthaus 9640 (NY). Sarasota Co. - Smith s.n. (PH). Seminole Co. - Lambert 18 (PH); Nauman et al. 293, 294 (FAU); Rapp s.n. (FLAS); Ward & Ward 4391 (FLAS). Sumter Co. - St. John s.n. (FLAS, NY - 2 sheets); Smith s.n. (US). Suwannee Co. - Leonard 6667 (FSU). ? Co. - Austin, C. s.n. (NY); Curtiss 3764 "Indian River" (F - 3 sheets, FLAS - 2 sheets, MICH, NY - 4 sheets, US); Darling s.n. (USF); Eaton s.n. (UC); Myekke 7069 (NY); Reynolds s.n. (GH, NY - 2 sheets*, PENN), 1906 (MICH); Stifler 1528 (MSU).

Nephrolepis exaltata cv. 'Bostoniensis'

MEXICO: Chiapas: Breedlove & McClintock 23496 (DS). UNITED STATES: Florida: Broward Co. - Nauman 450, 451, 456 (FAU).

Nephrolepis exaltata cv. 'elegantissima' complex

PERU: Loreto: Williams 3597 (F). UNITED STATES: Florida: Highlands Co. - McFarland 8969, 8974, 9176 (FLAS). Pasco Co. - Scudder 129 (FAU).

Nephrolepis exaltata cv. 'Florida Ruffles'

UNITED STATES: Florida: Palm Beach Co. - Nauman 438, 439 (FAU).

Nephrolepis exaltata cv. 'M. P. Mills'

UNITED STATES: Florida: Lee Co. - Standly s.n. (US).

Nephrolepis exaltata cv. 'Piersonii' complex

GUADELOUPE: Scamman 8162, 8163 (MEXU). GUATEMALA: "Finca Chocola" - Brenkle 47-89, 47-90 (UC). JAMAICA: Manchester: Proctor 24070 (IJ - 3 sheets). MEXICO: Vera Cruz: Nevling & Gomez-Pompa 213 (MEXU). PERU: Loreto: Williams 4053 (F). ST. CROIX: King s.n. (UC - 5 sheets).

Nephrolepis exaltata cv 'Whitmanii' complex

MEXICO: Chiapas: Breedlove 16061 (DS), 22862 (DS, MEXU). Vera Cruz: Martinez 405 (MEXU).

Nephrolepis falcata f. furcans

BRAZIL: Pará: Cavalcante 1081 (MG); Hernandez s.n. (MICH). CUBA: "La Havane Vedado" - Leon s.n. (UC). DOMINICA: Lellinger 464 (IJ). GUATEMALA: Izabel: Brenkle 47-156 (UC). JAMAICA: St. Thomas: Orcutt 3072 (MICH, UC). ?: "Carisbrook" - Orcutt 2119 (UC). MEXICO: Chiapas: Matuda 18762 (MEXU). Guerrero: Bonilla s.n. (ENCB - 2 sheets). PARAGUAY: "Anuncion" - Schinini 13485 (LP - 2 sheets). UNITED STATES: Florida: Alachua Co. Weber & West s.n. (FLAS). Broward Co. - Nauman 446, 447, 458, 459 (FAU); Sturtevant 120 (US). Dade Co. - Beckner 871 (FLAS); Evans s.n. (TENN - 5 sheets). Duval Co. - Kearsley s.n. (NY - 2 sheets). Hendry Co. - Timmez 28 (FAU). Highlands Co. - McFarland 8969 (FLAS). Hillsborough Co. - Mickel et al. 1790 (NY). Lee Co. - Brumbach 8103 (FLAS), 9179 (FLAS, NY); Lakela et al. 30556 (FLAS, USF). Martin Co. - Albertson s.n. (FAU). Palm Beach Co. - Baker s.n. (FAU); Cassen 602 (FLAS - 2 sheets); Nauman et al. 391, 392 (FAU). VENEZUELA: Zulia: Morriguez 87 (MY).

Nephrolepis hirsutula

PUERTO RICO: Mayaguez: Spetzman & Diaz s.n. (FTG).

Nephrolepis hirsutula cv. 'Superba'

BRITISH GUYANA: W. Demerara: de la Cruz 2605 (NY). DOMINICA: Lellinger 351 (IJ, MICH, UC). JAMAICA: Manchester: Proctor 23615 (IJ). St. Ann: Proctor 27873 (IJ). St. Thomas: Proctor 23948 (IJ); Orcutt 5114 (UC). MEXICO: Chiapas: Breedlove 16031 (DS). ST. VINCENT: Cooley 8312 (IJ). UNITED STATES: Florida: Dade Co. - Evans s.n. (TENN); Hardy 3 (PH); Nagy 7 (FAU).

Nephrolepis multiflora

BAHAMAS: Abaco: Gillis 7329 (FTG); Correll & Meyer 44594 (FTG, NY*). Crooked Island: Correll 44404 (FTG, NY); Proctor & Correll 37024 (IJ). Grand Bahama: Beckner 798 (FLAS); Correll 40549 (FTG); Correll & Kral 42848 (FTG); Gillis 7833 (FTG, IJ). Great Exuma: Correll 40857 (FTG); Correll & Correll 46885, 47978 (FTG). Inagua: Proctor & Gillis 33892 (IJ). Little Inagua: Buden 2 (IJ). Long Island: Correll 44902, 44943 (FTG); Hill 2373 (FTG, NY). N. Andros: Correll & Proctor 47852 (FTG, IJ, NY); Correll et al. 49673-A (NY). N. Eleuthra: Correll 41232 (FTG). BRAZIL: Amapá: Ribeiro 1598 (MG, NY). Amazonas: Bautista 117 (MG); Chagas 447 (MG); Conant 896 (NY); Eiten et al. 5278 (UB); Maas & Maas 485 (IJ); Prance & Mello 17621 (MG, NY - 2 sheets*); Prance et al. 3052 (F, MG, NY), 15680 (MG), 18016 (MG, NY - 2 sheets*); Rodrigues 511 (MG). Bahia: Belem & Pinheiro 2148 (UB); Boom & Mori 841 (NY*); Mori 11520 (NY*); Santos 1035 (NY*); Silva et al. 1340 (NY*). Pará: Pires & Black 540 (MICH). Rio de Janeiro: Sobro 502 (LP). ?: "Upper Rio Negro" - Weiss & Schmidt s.n. (NY). CAYMAN ISLANDS: Cayman Brac: Proctor 29364 (IJ). Grand Cayman: Brunt 1854 (IJ); Proctor 15285 (IJ). COLOMBIA: Chocó: Forero et al. 2136 (ENCB, NY*). COSTA RICA: Cartago: Lankester s.n. (UC), II-55 (MEXU). Guanacaste: Evans & Bowers 2880 (TENN*). Herida: Mickel 3512 (NY). Puntarenas: Evans & Bowers s.n. (TENN). DOMINICA: Chambers 2666 (MICH, UC); Lellinger 621 (IJ, LP); Long & Norstog 3399 (USF*); Robinson s.n. (TENN); Taylor s.n. (MICH); Wilbur et al. 7729 (MICH). DOMINICAN REPUBLIC: Barahona: Howard & Howard 8473 (NY); Jones & Norris 1140 (NY - 2 sheets). El Seibo: Jones & Norris 1191 (TENN), 1193 (TENN, NY); Mejia et al. 10144 (JSBD). La Altagracia: Zanoni et al. 12061 (JSBD). La Vega: Jones & Norris 1012 (NY); Mejia & Zanoni 9597 (JSBD); Zanoni et al. 12940 (JSBD). Distr. Nacional: Zanoni 9332 (JSBD); Zanoni et al. 11565 (JSBD). Peravia: Mejia 29 (JSBD); Mejia & Pimentel 9972 (JSBD); Mejia & Zanoni 6850 (JSBD). Puerto Plata: Liogier & Liogier 23131 (JSBD); Jones & Norris 1148 (TENN). Sanchez Ramirez: Mason 3428 (JSBD). Santo Domingo: Augusto 315 (NY). EL SALVADOR: Seiler 945, 1044, 1088a*(NY). GRENADA:

Proctor 17117 (IJ). GUATEMALA: Izabel: Harmon 1880 (ENCB); Jones & Tracy 3368 (IJ - 2 sheets, MICH, NY); Snedaker D-72 (FLAS); Williams et al. 41808 (NY). Petén: Contreras 5643 (NY*), 6194 (IJ); Molina 15572 (NY*). HAITI: Havassa Island - Proctor 15466 (IJ). HONDURAS: Atlantida: Webster et al. 12594 (MICH). Dept. Colón: Saunders & Midence 1025 (NY). Dept. Copán: Molina 30760 (ENCB). Dept. Cortez: Clewell 3186 (NY*). Dept. Lempira: Nelson et al. 299 (NY*). JAMAICA: Clarendon: Proctor 4500, 15901, 37846 (IJ). Hanover: Proctor 4893, 7197, 33047 (IJ). Manchester: Bengry s.n. (IJ); Porter s.n. (IJ); Proctor 4991, 6048, 6299, 24089 (IJ). Portland: Bengry s.n. (IJ - 2 sheets); Knight s.n. (FLAS); Riba et al. 162 (MEXU). St. Ann: Crosby et al. 137 (F, UC), 720 (MICH, UC); Hespenheide 882, 1014 (MICH, NY*); Proctor 4471 (IJ). St. Andrew: Barry s.n. (IJ); Crosby et al. 149, 177 (MICH, NY*); Proctor 5848 (IJ); Yuncker 17602 (F, MICH). St. Catharine: Bengry s.n. (IJ); Proctor 5958, 6950 (IJ). St. Elizabeth: Howard & Proctor 13899 (IJ); Proctor 7742 (IJ). St. Mary: Barry s.n. (IJ); Proctor 5088, 5768, 6635 (IJ). St. Thomas: Yuncker 17515 (MICH). Trelawny: Peirce 4 (IJ); Proctor 3951, 4158, 4697, 15617 (IJ). Westmoreland: Proctor 4842 (IJ); Sinha 382 (IJ). MARIE GALANTE: Proctor 20977-a (IJ). MARTINIQUE: Egler 39-121 (NY); Proctor 21801 (IJ). MEXICO: Chiapas: Breedlove 26449 (DS, MEXU, NY*), 34482 (DS, ENCB, MEXU, NY*), 45918 (CAS); Roe et al. 1431 (TENN). Oaxaca: Hellwig 345, 455 (NY); Martinez 767 (CAS, MEXU), 848 (CAS, MEXU, NY); Mickel 1461 (ENCB, MICH, NY). Quintano Roo: Cabrera & Ibarra 121 (CAS); Chater et al. 64 (MEXU). Tabasco: Haynes 5612 (NY). Vera Cruz: Lira 15 (ENCB); Martinez 1851, 2115 (CAS, ENCB, NY*). MONTSERRAT: Proctor 19129 (IJ). NICARAGUA: Dept. Zelaya: Atwood & Seymour 3108 (FLAS, MICH). Madregana - Seymour 5064 (UC). PANAMA: Bocas del Toro: Kirkbride & Duke 520 (MEXU, NY). PUERTO RICO: Huanucao: D'Arcy 1848, 1870 (FLAS); Spetzman 656 (FTG - 2 sheets). Mayaguez: Staples 4, 7, 89 (FAU); Stimson 3394 (MICH). ?: Spetzman 558 (FTG - 2 sheets); Vivaldi 71-47 (FTG). ST. LUCIA: Proctor 18222 (IJ). ST. VINCENT: Beard 1393 (F); Morton 5208 (LP); Proctor 26104 (IJ). UNITED STATES: Florida: Broward Co. - Avery & McPherson 1327 (USF); Lakela & Long 1598, 29690 (USF). Collier Co. - Austin et al. 6767 (FAU); Correll et al. 47290 (FTG); Evans s.n.., 4097, 4130 (TENN); Lakela 29471 (USF); Lakela & Almeda 29988 (GH, USF), 29991 (US, USF); Lassiter et al. 9 (USF). Dade Co. - Avery 1046 (FLAS); Avery & McPherson 1327, 1328, 1330 (FLAS), 1329 (FLAS, USF); Evans s.n. (TENN); Gillis 10856 (FTG, IJ); Nauman 1517, 1518, 1519, 1520, 1522, 1523, 1527 (TENN). Hillsborough Co. - Long et al. 2942 (USF); Scudder 439, 440 (FAU); Shuey s.n. (USF). Lee Co. - Austin 6625 (FAU); Brumbach 5349 (FLAS), 8743 (MICH, NY, US); Cooley s.n. (USF), 2548 (FLAS, GH, NY*, US), 2551 (USF). Martin Co. - McCart 10406 (FAU, FLAS); Nauman & Tatje 258, 259, 260 (FAU); Nauman et al. 200 (FAU). Monroe Co. - Avery s.n. (FLAS). Palm Beach Co. - Brawner s.n. (FAU); Durand 5, 85, 86, 88, 90 (FAU); Nauman 192, 203, 204, 205, 312 - 2 sheets (FAU), 465 (NY); Nauman & Austin 181, 185, 192, 193 (FAU);

Nauman et al. 206, 207, 250, 251, 393, 394, 395, 396, 400, 401 (FAU). VENEZUELA: Falcon: "(H.W.R.W.)" 121 (FAU); van der Werff 3319 (FAU).

Nephrolepis occidentalis

BOLIVIA: Santa Cruz: Krapovickas & Schinini 32196 (LP). BRAZIL: Bahia: Webb s.n. (NY). Goiás: Anderson 6399, 10315 (NY*, UB), 10150a (NY, UB); Chase 11498 (NY*); "Hiruigr" 12017 (UB); Irwin et al. 21477 (NY*, UB), 21683 (F, NY*, UB), 21770, 34300 (NY*, UB, UC); Plowman et al. 8238 (NY*). Maranhão: Eiten & Eiten 4697 (NY), 10711 (UB). Mato Grosso: Rotter & Santos Neto 4168 (UB). Minas Gerais: Emygdio et al. 3564 (NY*); Regnell 1475 (LP). Pará: Plowman et al. 8568 (MICH, NY*). ?: "Hill" 2253 (NY*). COLOMBIA: Santa Marta: Smith 2563 (CAS, ENCB, IJ, NY - 2 sheets*, PH - 2 sheets*, UC), 2712 (NY - 2 sheets*). ?: Smith 1032 (NY). COSTA RICA: Alajuela: Brenes s.n., 4951* (NY). San José: Brade 167 (UC); de la Cruz 107 (FLAS*); Evans et al. 23 (TENN); Steele s.n. (NY). DOMINICAN REPUBLIC: ?: "Las Cauitas" - Fuertes 1881 (NY). ECUADOR: Bolivar: Holm-Neilson et al. 3103 (F, NY*). Galapagos Islands: Dawson D-24 (DS); Weber 769/A (DS); van der Werff 1344 (CAS), 2329 (CAS, NY). EL SALVADOR: Garcia 92 (UC); Seiler 44*, 1215 (NY). GUATEMALA: Dept. Santa Rosa - Heyde & Lux 4098 (NY*, PH*). HAITI: l'Artibonite: Leonard 7923 (IJ, MICH, NY*, UC). Ouest: Buch 1711 (IJ). ?: Ekman 6146 (IJ). HONDURAS: Dept. Morazan - Molina 23411 (DS, NY); Molina & Williams 31188 (ENCB). Dept. Ocotopeque - Molina 22199 (NY), 30973 (ENCB). JAMAICA: Westmoreland: Proctor 21464 (IJ). MEXICO: Chiapas: Alava 1345 (DS, MEXU, MICH, NY, UC); Breedlove 28698, 38604 (DS), 40113 (DS, MEXU), 52137 (CAS); Breedlove & Almeda 44956 (CAS); Breedlove & Davidse 53922 (CAS); Ghiesbreght 309 (NY); Münch s.n., 25 (DS); Purpus 6866 (UC). Guerro: Rowell 3108 (MICH). Jalisco: Gonzalez 295 (ENCB); Luna 5406 (ENCB); McVaugh 16025 (MEXU, MICH), 18127 (MICH), 20218 (MICH); Palafox 5406 (NY, UC); Pringle 1835 (DS, MICH, NY - 3 sheets*, PH*, UC), 2771 (DS, MEXU, MICH - 2 sheets, UC), 5403 (DS, MICH); Tamayo 295 (MICH). México: Matuda 26991 (MEXU); Roe et al. 1579 (ENCB, MICH), 1671 (ENCB, MICH - 2 sheets); Rzedowski 20663 (DS, ENCB, LP, MICH). Michoacán: Davidse & Davidse 9880 (MEXU); Hinton et al. 15491 (NY, PH*); Langlasse 327 (MEXU); Leavenworth 555 (MICH, NY); Luna 7510 (ENCB, UC); Sanchez 2678 (ENCB); Ventura 2461 (ENCB, MICH). Morelos: Pringle 11783 (CAS, MICH, TENN*, UC), 15717 (CAS, MICH, PH*, UC). Nayarit: Kral 25646 (ENCB, MICH); McVaugh 16550 (MEXU, MICH, NY); Mexia 707 (CAS, DS, NY*, UC). Oaxava: Mickel 1108 (ENCB, MEXU, MICH); Mickel & Hellwig 3981, 4026 (ENCB); Mickel & Leonard 4727, 5089 (ENCB), 5067 (NY*); Mickel & Pardue 6965 (NY*), 6998 (ENCB). San Louis Potosi: (?) Hinton 130 (MEXU). Sinaloa: Pennell 20138 (PH*); (?) Hinton 37 (MEXU). Tamaulipas: Sharp 52168 (TENN*); Sharp et al. 50158 (TENN*). Vera Cruz: Botteri 67 (CGE); Bourgeau 1938, 3066 - 3 sheets (NY*); Harshberger 356 (PH - 2 sheets*); Hinton 1641* (NY, PH), 1805 - 2 sheets (MEXU, NY*); ex Hb. LeRoy s.n. (NY);

Riba et al. 397 (MEXU, NY); Seaton 98 (NY - 2 sheets). ?: "Manchon" - Hinton et al. 9341 (NY, PH), 9483 (NY - 2 sheets, PH). "Vallecitos" - Hinton et al. 11382 (MEXU, NY*, PH*), 11389 (MEXU, NY - 2 sheets*, PH*). ? - Müller s.n., 52 (NY). PANAMA: Chiriqui: Armond 197 (CAS). VENEZUELA: Merida: Fendler 161 (PH*).

Nephrolepis pectinata

BOLIVIA: ?: Williams 1107 (NY*). BRAZIL (?): Hostmann s.n. (UC). COLOMBIA: Antioquia: Gutierrez 35563 (UC). Cundinamarca: Luteyn et al. 4829 (NY*). El Valle: de la Sota & Morillo 6316 (LP). Huila: Mason 13935 (UC). Nariño: Ewan 16853 (IJ). Putumayo: Etienne 68-60 (CAS); Ewan 16273 (IJ, UC). Santander: Haught 1934 (MICH, UC). Sucré: Luzefrczuk 6545 (MICH, UC). COSTA RICA: Alajuela: Brade s.n. (UC); Brenes 5673, 11337*, 11460, 11673, 16128 (NY); Burger & Stolze 4932 (NY); Maxon 403 (NY*); Molina et al. 17206 (NY*); Taylor & Taylor 11635 (NY); Williams et al. 28961 (NY*). Cartago: Burger & Liesner 6854 (NY); Burger & Stolze 5639 (NY); Hauke 417 (NY); Mickel 1867, 2315, 2316 (NY); Stolze 1499 (NY*, UC); Stork 4821 (MICH, NY, UC). Guanacaste: Evans & Bowers 2881 (TENN*); Mickel 2896 (NY). Puntarenas: Evans & Bowers 2719, 3084 (TENN*); Mickel 2815*, 3102, 3170* (NY). San José: Brade 189 (NY); Chrysler & Roever 5259 (MICH, UC); Jimenez 632 (NY); Mickel 2214, 2255*, 2532* (NY); Skutch 2650 (MICH, NY); Stolze 1441 (NY, UC). CUBA: Oriente: Ekman 3935 (NY); Leon 3810, 10930* (NY); Morton & Acuna 3523 (UC); Shafer 3887 (NY); Wright 1803 (NY - 2 sheets, PH*). ?: Jenman s.n. "St. Yago Mt. Liban" (NY). DOMINICAN REPUBLIC: Barahona: Fuertes s.n. (NY, UC). La Vega: Jimenez 6132 (JSBD). ECUADOR: Carichi: Holm-Nielsen et al. 6090 (NY). BOLIVAR: Holm-Nielsen 3034 (NY*). El Oro: Wiggins 10928 (DS, NY*), 10941 (DS, NY). Guayas: Hitchcock 20479 (NY*). Napo-Pastaza: Asplund 18773 (NY*); Fuller 91 (DS*); Grubb et al. 1262 (NY); MacBryde 1479 (NY); Mexia 6858, 6917 (UC), 7239 (MICH, NY, UC); Prescott 432 (DS); Proctor 38705 (IJ); Schimpff 712 (UC). Pichincha: Asplund 16399 (NY); Cazalt & Pennington 5262 (NY*, UC); Dodson et al. 8605 (ENN*). Santiago-Zamora: Gazalt & Pennington 7798 (NY*, UC). Tunguraha: Mexia 7054 (MICH, UC). ?: "Rio Paloga" - Reinbach 71 (PH*). ? - Spruce 4082 (MICH). GUATEMALA: Alta Verapaz: Maxon & Hay 3231 (NY*); Molina & Molina 12025 (NY*); Standley 89657 (UC); Tuckerheim 2210 (NY*). Petén: Contreras 2572 (IJ, MICH). HAITI: Haiti: Leonard 3891 (NY*). ?: "Les Payes" - Ekman 5232 (IJ). "Savanna Zambi" - Holdridge 2065 (MICH). HONDURAS: Dept. Comayagua: Yuncker et al. 5893 (MICH, NY*, UC), 6119 (MICH, NY*). Santa Cruz: Edwards P-705 (NY). JAMAICA: Clarendon: Proctor 6531, 33716 (IJ); Underwood 2138 (NY - 2 sheets*). Manchester: Day 30, 91 - 3 sheets (NY); Proctor 37596 (IJ). Portland: Barry s.n. (IJ); Crosby et al. 996 (MICH); Davis s.n. (MICH); Hawkes 7167 (IJ); Hespenheide et al. 778 (NY); Knight s.n. (FLAS); Laessle s.n. (FLAS); Maxon & Killip 151, 241* (NY); Orcutt 3799 (UC); Proctor 4588, 5227, 5591, 5741, 36420 (IJ), 22521 (IJ, MICH), 28255 (F, IJ); St. John 1966 (FLAS);

Sibley s.n. (IJ); Yuncker 18559 (MICH). St. Ann: Alexander s.n. (PH*); Howard & Proctor 14311 (IJ); Hunnewell & Griscom 14266 (IJ); Maxon 1881, 2267 (NY*), 10407 (NY*, PENN); Wilson & Webster 493 (IJ, MICH); Yuncker 18230 (MICH). St. Andrew: Balch s.n. (NY*); Bengry s.n. (IJ, USF*); Fisher 145 (NY); Harris 7506 (NY), 9006 (UCWI); Maxon 8569 (NY, PH), 10307 (NY, PENN*); Proctor 4560 (FLAS, IJ), 4974, 5477, 20825 (IJ); Taylor 26310 (MICH - 2 sheets); Underwood 1201 (NY). St. Catharine: Crosby et al. 609 (MICH, NY*, UC); Hespenheide 1317 (MICH, NY); Maxon 10439 (PENN); Maxon & Killip 432 (NY*); Proctor 22774 (IJ). St. Elizabeth: Proctor 20859 (IJ). St. Mary: Underwood 89 (NY*). St. Thomas: Bengry s.n. (IJ); Fredholm 3223 (NY); Maxon 8917 (PENN*), 8940 (NY), 9458 (NY, PENN); Orcutt 2046 (UC); Stokey C.9 (IJ); Underwood 2688 (NY*); Yuncker 18069 (F, MICH). ?: Alexander 3 (UC); Chrysler 1944 (MICH), 4571 (UC); Hartweg 1508 (NY); Jenman s.n. - 6 sheets (NY), 69 (UC); Johnson s.n. (NY), 1142 (MICH); MacFayden s.n. (NY); Underwood 1582 (NY - 2 sheets); Watt s.n. (TENN*), 108 (UC); Wilson s.n. (NY). MEXICO: Chiapas: Breedlove 10364 (DS, IJ, MICH), 24881 (DS*, MEXU, NY), 25123 (DS*), 32908 (DS), 34563 (DS, ENCB, MEXU, MICH); Breedlove & Smith 21804 (DS*, MEXU), 22357 (DS*, MEXU, MICH, NY*), 31427*, 31498, 32129, 32454 (DS); Breedlove & Thorne 21052 (DS, MEXU, NY*); Dressler 1642 (MEXU, MICH, NY*); Münch 153 (DS); Rzedowski 687 (ENCB, LP), 33135 (ENCB); Schultes & Reko 926 (MEXU). Oaxaca: Gonzalez & Conzatti 719 (CAS); Hallberg 1708 (NY); Martinez 502 (CAS*, MEXU, NY): Mexia 9274 (CAS, MICH, UC); Mickel 1074, 7137 - 2 sheets (NY), 1580 (ENCB, MICH, NY*), 6473 (ENCB, NY), 7256 (ENCB, NY*); Mickel & Leonard 4801 (ENCB, NY*). Puebla: Riba et al. 955 (ENCB); Santos 3354 (MICH). Vera Cruz: Bourgeau 1938 (MICH, NY); Fink s.n. (NY), 73 (MEXU); Ventura 8038 (ENCB, IJ, MEXU, MICH, NY*), 12225 (ENCB), 12653 (ENCB). NICARAGUA: "Volcan Mombacho" - Hall & Bockus 7554 (UC). PANAMA: Chiriqui: Croat 15848 (MEXU). Cocle: Allen 1208 (NY*); Lewis et al. 2648 (UC). Darien: Bristan 1240(2) (NY*); Kirkbride & Duke 1233 (NY). Veraguas: Croat 23096 (MEXU). ?: Cornman 1305 (MICH, UC); Dwyer & Hayden 8098 (UC); Porter et al. 4922 (USF*), 4924 (UC); Williams 481 (NY). PERU: Huánuco: Boeke 1234 (NY*); Mexia 8135 (CAS, MICH, NY*, UC), 8324 (MICH - 2 sheets, NY*, UC); Stork & Horton 9429 (F, UC), 9870 (UC). Junín: Hutchinson 1203 (NY, UC); Killip & Smith 24613*, 25325, 25506, 25859 (NY); Leon 274 (USM - unmounted); Schunke 793 (F). Loreto: Klug 3246 (NY*); Mexia 6219 (CAS, MICH, NY*, PH*, UC). Paucartambo: Vargas 10217 (UC); West 7125 (MICH, UC). Puno: McCarroll 61 (MICH). San Martin: Belshaw 3441 (MICH, NY*, UC); Schunke 3788 (NY*), 6106 (CAS, LP); Woytkowski 32245 - 2 sheets, 35331 (UC). ?: Couthouy 58 (PH*); Asplund 16399 (NY*); Mexia 7239 (NY*); Pöffing s.n. (UC). VENEZUELA: Ruiz-Ferar & Lopez-Polacios 10977 (NY*).

Nephrolepis pendula

BELIZE: El Cayo: Bartlett 13026 (MICH, UC); Gentle 2353 (MEXU, MICH); Lundell 6305 (MICH, NY*); Proctor 29861 (IJ). ?:

Lundell 460 "Roaring Creek" (DS, UC*). BERMUDA: Howe s.n. (NY). BOLIVIA: Beni: Rusby & White 383 (NY). Cochabamba: Cardenas & Cutler 7375 (IJ, NY - 2 sheets*, UC); Steinbach 8837 (NY*, PH), 8874 (NY - 2 sheets*, PH). La Paz: Bridarolli 4374, 4478 (LP); Brooke 6497, 6535* (NY); Buchtein s.n. (MICH, UC*); Buckhiem 4236 (NY*); Krukoff 10464 (LP, MICH - 2 sheets, NY); Tate 754 (NY). Santa Cruz: Steinbach 5408 (NY, PH*), 5409 (NY). ?: "Yungas" - Bang 291 (MICH - 2 sheets, NY, PH - 2 sheets, UC); Britton & Rusby 291 (NY); Rusby 411 (MICH - 2 sheets, NY - 3 sheets*, PH). "Bopi River Valley" - Rusby 323, 560 - 2 sheets (NY). ? - Buchtein 1003 (NY); Tate 507 (NY); Williams 1105, 1106 (NY). BRAZIL: Acre: Prance et al. 7296 (MG, NY). Amazonas: Prance et al. 18016 (NY). Bahia: Almeida & Santos 201 (NY*); Belem & Magolhaes 1142 (UB); Blanchet 6015 (MG); Mori 12910 (NY); Mori et al. 12677 (NY*); Rose & Russell 20141 (NY*); Vinha 94 (NY); Webb s.n. (NY); ? 2237 (MG). Goiás: Irwin et al. 15545 (NY*, UB). Minas Gerais: Anderson et al. 36023 (NY*, UB, UC*); Foster 712 (DS); Hatschbach et al. 36446 (NY, UC*); Irwin et al. 29116 (NY*, UB, UC*); Mexia 4246 (CAS, IPEAN, MICH, NY*, PH, UC*), 5008-a (UC). Paraña: Hatschbach 10187 (NY). Rio de Janeiro: Dusen 718 (MG, UC); Luetzelburg 6037 (W, UC); Pereira & Pabst 8463 (NY - 2 sheets); Pohl s.n. (W); Rose & Russell 20753 (NY*); Smith 1627 (NY, UC); Webb s.n. (MICH). Roraima: Prance et al. 9991 (NY*). Santa Catarina: Wacket 178 (NY). São Paulo: Brade 6622, 8225 (NY*, UC), 8345 (IJ). ?: Brade 20740 (NY*), Riegel s.n. (MICH). BRITISH GUYANA: Mazaruni Potari: Jenman s.n. (NY*); Maguire & Fanshawe 23137*, 23143 (NY); Tate 356 (NY); Tillett & Tillett 45595 (NY). "Amazonas" - Maguire & Maguire 35401 (NY*). ? - Schomburgk (UC). COLOMBIA: Antioquia: Barkely & Gutierrez 1477 (MEXU, MICH, NY, UC); Barkely et al. 1585 (UC); Feddema 2020 (MICH, NY*); Pena et al. 17 (MICH). Bolivar: Pennell 4559 (NY*). Caldas: Acosta-Artega 638 (NY*); Killip & Hazen 8820* (NY, PH); Sneidern 5513 (MICH). Chocó: Lellinger & de la Sota 528 (LP). Cundinamarca: Acosta-Artega 150, 796 (NY); Forero & Jaramillo 425 (NY); Holton 679 (NY*); Luteyn et al. 4829 (UC); Murillo & Murillo 210 (NY - 2 sheets*); Murillo et al. 372 (NY). Huila: Idrobo et al. 2917 (NY); Rusby & Pennell 936 (NY*). Isla de Providencia: Proctor 3439 (PH). Santa Marta: Smith 1032 (MICH). Nariño: Ewan 16032 (UC). Santander: Killip & Smith 14754, 15084*, 15204 (NY); Langenheim 3326 (UC*). Valle del Cauca: Murilla 1038 (NY); Pennell & Killip 5893, 6371 (NY, PH). ?: Hartweg 1508 (NY); Mutis 3096 (NY). COSTA RICA: Alajuela: Brenes 14643a (NY*); Smith 1087 (NY*). Cartago: Carlson 3232 (NY); Holm & Iltis 61 (NY*); Jimenez 1625 (NY); Kuntze 2213 (NY); Mickel 1866*, 2316*, 3338 (NY); Stork 486, 3243 (UC), 1461 (MICH - 2 sheets, UC), 1718, 2452 (MICH, UC), 4763 (MICH, IPEAN, NY, UC); Taylor 18017 (NY*); Woodruff s.n. (FLAS*). Guanacaste: Mickel 2896 (LP, NY* - 2 sheets). Heredia: Chrysler & Roever 4889 (MICH); Lent 2845 (NY). Limon: Stork 1692 (UC). Puntarenas: Elmore F4 (DS, MICH, PH); Koptur 164, 212 (UC*); Lens & Shoemaker s.n. (TENN); Mickel 1969, 2034 (NY); Perez & Fraile

48 (ENCB); Webster et al. 12405 (IJ, MICH), Williams et al. 28791 (NY). San José: Burger & Stolze 5332 (NY*); Evans & Bowers 3249 (TENN); Lellinger & White 1389 (MICH); Mickel 2254, 2531, 3281* (NY); Palmer s.n. (NY); Skutch 2299 (NY); Taylor 11294 (NY). ?: Horich s.n. (UC); Jimenez 2924 (NY*). CUBA: Oriente: Carabia 3738 (NY); Ekman 3115 (NY); Morton & Acuna 3053 (CAS, NY, UC). Pinar del Rio: Shafer & Leon 13553 (NY*). DOMINICAN REPUBLIC: Distr. Nacional: Ekman 12882 (NY). Santiago: Valeur 20 (F, NY). ECUADOR: Chimborazo: Camp E-3401 (NY*, UC); Holm-Neilson 2828 (NY); Sodiro s.n. (MICH); Wiggins 11063 (DS, NY*, UC). Cotopaxi: Etienne 68-133 (CAS). El Oro: Escobar 854 (NY). Galapagos Islands: Bowman 86 (CAS); Colinvaux 351 (DS); Dawson D-4, D-10, D-12 (DS); Howell 9207 (CAS*); Itow 86*, 22300-6, 32304-6, 40800-24, 41100-10, 41100-12, 50600-5* (DS); Schimpff 156 (CAS, NY); Stewart 922, 925*, 926, 927, 928, 929* (CAS), 923 (CAS, NY), 924* (CAS, DS), 7367-7375 (DS - 2 sheets); Taylor 962 (NY); Weber 660/A, 673/A (DS); van der Werff 1318 (CAS*, NY); Wiggins 18537*, 18544, 18614 (DS). Napo-Pastaza: Asplund 9464 (CAS, NY); Balslev & Madsen 10332 (NY); Etienne 68-160 (CAS); Mowbray 699107 (TENN); Øllaard & Balslev 10209 (NY*). Pichincha: Cazalt & Pennington 5223 (NY, UC); Pennington 61 (NY). Tungurahua: Mexia 7042 (MICH, UC). ?: Andre 836*, 2330 (NY); Sodiro s.n. (NY*, UC - 2 sheets*), 57795 (mus. no.) (BA). GUATEMALA: Alta Verapaz: Hatch & Wilson 205 (UC); Schauensee s.n. (PH - 2 sheets); Tuckerheim 8037 (NY); Williams et al. 40074, 40158 (NY). Izabel: Standley 24462 (NY); Weatherwax 190a (UC). Petén: Contreras 1767 (IJ, MICH), 3819 (IJ); Lundell 2258 (CAS, MICH), 2752, 2758, 2816, 2915 (MICH). ?: Morton 199, 200*, 201, 239 (NY). HONDURAS: Dept. Colón: Saunders 350 (NY). Cortez: Steeves & Ray 471 (MICH); Yuncker 4834 (MICH, UC). El Cayo: Lundell 6305 (NY*). El Paraise: Molina 11420 (NY). Olancho: Nelson & Clewell 659 (NY). Puerto Sierra: Wilson 415 (NY). Santa Barbara: Thieme 23 (UC), 5665 (MICH, NY). Toledo: Peck 538 (NY). Yoro: Yuncker et al. 8164 (MICH, NY*, UC*). ?: Dyer s.n. (NY); Campbell 3 (NY). JAMAICA: Portland: Chrysler 1545 (PH). ?: Jenman s.n. (OXF). MEXICO: Chiapas: Breedlove 24035 (DS, MEXU, MICH, NY*), 32801 (DS*, MEXU, MICH), 33140 (DS, MEXU, NY), 33944 (DS, MEXU), 34481 (DS, MEXU, MICH, NY); Breedlove & Almeda 48362*, 57600 (CAS); Breedlove & McClintock 34272 (DS); Chater et al. 178 (MEXU); Sohns 1663 (MEXU). Oaxaca: Mickel 6460 (NY). Tabasco: Gilley & Hernandez 66 (MICH); Matuda 3332 (MEXU, MICH, NY); Rovirosa 237 (NY, PH), 576 (NY - 2 sheets, PH). Vera Cruz: Dorantes 2733 (MEXU), 2768 (MEXU, UC); Vazquez 699 (ENCB, MEXU). MONTSERRAT: Shafer s.n. (NY). NICARAGUA: near Jalapa: Atwood et al. 6828 (FLAS, MICH, NY, UC). ?: Hall & Bockus 7554 (FLAS*). PANAMA: Bocas del Toro: Woodson et al. 1896 (NY). Canal Zone: Cowell 293, 294 (NY); Croat 5054 (NY*); Miller 1762 (MICH); St. John 2427 (FLAS); Spellman et al. 537 (NY*); Taylor 1131, 1339 (MICH); Wetmore & Woodworth 142 (NY). Chiriqui: Croat 15816, 15938 (MEXU); Dwyer et al. 483 (UC); Proctor 31963 (IJ); Stern et al. 1013 (UC); Woodson et al. 980 (NY*). Darien: Duke 10053(2) (NY*).

Panama: Seibert 642* (NY - 2 sheets, PH). ?: Cornman 595 (MICH, UC); Hays 14 (NY); Knight s.n. (FLAS); Killip 2821 (IJ); Kuntze 1866 (NY - 2 sheets); Parry s.n. (NY); Williams 903 (NY*). PERU: Amazonas: Wurdack 883 (NY - 2 sheets*). Ayacucho: Killip & Smith 22674 (NY*). Cajamarca: Fosberg 27787 (NY*); Lorckur & Carmova 5079 (LP). Huánuco: Coronado 71 (UC*); Ridoutt s.n. (USM - 3 sheets); Schunke 2940 (F, NY); Stork & Horton 9877 (UC). Junín: Cerrate 2886 (USM); Constance & Tovar 2257 (UC); Coronado 245, 258 (UC); Killip & Smith 23707 (NY); Tryon & Tryon 5452 (F); Woytkowski 35481, 35500 (UC). Loreto: Mexia 6163 (CAS, MICH, NY, PH*, UC). Pasco: Leon et al. 312 (USM). San Martin: Klug 3736 (CAS, NY*); Schunke 3680, 4337 (NY), 5975 (CAS, NY). Urubamba: Hutchinson 1761 (MICH, NY*, UC*). PUERTO RICO: Aguadilla: Britton et al. 2610 (NY). ?: Hess 2581 (NY). VENEZUELA: Amazonas: Maguire & Maguire 35401 (IJ); Phelps & Hitchcock 63 (NY); Steyermark 105953 (NY*); Tate 707 (NY). Anzóategui: Steyermark 61278 (NY). Bolivar: Bunting 3047 (NY); Maguire & Wurdack 33963 (MICH, NY); Moore et al. 9785 (MICH, NY); Steyermark 58705 (NY); Steyermark & Wurdack 561 (NY*); Tate 1266 (NY). Distr. Federal: Kuntze 1282 (NY - 2 sheets); Truijillo 1160 (MY). Isla de Margarita: Johnston 149 (NY). Mérida: Bautista 3846 (LP - 6 sheets); Fendler 162 (PH*). Portuguesa: Manara s.n. (NY). Sucre: Steyermark 62674 (NY). Trujillo: Box 3994 (NY). Zulia: Steyermark & Fernandez 99793 (NY). ?: Fendler 112 B, 162 (NY).

Nephrolepis rivularis

BOLIVIA: La Paz: Buchtein 1008 (NY). BRAZIL: Acre: Prance et al. 12179 (F, MICH, MG, NY). Amapá: Egler & Irwin 46692 (MG, UB). Amazonas: Prance et al. 20640 (NY). Bahia: Belem 1645 (UB); Belem & Pinheiro 3114 (UB); Blanchet 3142 (MG); Rose & Russell 19636 (NY*); Salzman s.n. (NY). Ceará: Ducke 1666 (MG). Pará: Ducke 12165 (MG); Mexia 5917 (UC); Prance et al. p26554 (NY*); Rose & Lira 2352 (MG, NY). Paraña: Hatschbach 19612 (UC). Rio de Janeiro: Porasil 317 (NY). Roraima: Prance et al. 9433 (MG, NY*), 9829 (MG, NY). BRITISH GUYANA: E. Berbice: de la Cruz 2994, 3117 (NY*, PH); Hohenkerk s.n. (BRG). Mazaruni Potari: de la Cruz 2166 (NY); Gleason 128, 581* (NY); Harrison 1638 (BRG). Northwest: de la Cruz 1351 (NY*, PH), 3416 (NY, PH). W. Demerara: de la Cruz 1656 (NY); Wagner s.n. (PENN). ?: Fanshawe M320 (IJ); Gleason 711 (NY*); Jenman s.n. (BRG, NY - 3 sheets); Schomburgk (244 or 285 ?) (UC). COLOMBIA: Antioquia: Haught 1517 (MICH, UC); Lellinger & de la Sota 957 (LP). Bolivar: Pennell 4476*, 4788 (NY). Caldas: Sneider 5262 (UC). Chocó: Forero et al. 1416 (NY); Lellinger & de la Sota 363, 438, 725 (LP). Cordoba: Killip 5099 (PH), 5327 (NY, PH). Magdalena: Smith 1032 (NY - 2 sheets*), 2643 (LP, NY - 2 sheets, PH, USF*). Putumayo: Ewan 16708 (UC). COSTA RICA: Alajuela: Brenes 5779c (NY); Mickel 2926 (NY*). Cartago: Mickel 3444 (NY*). Heredia: Woodruff s.n. (FLAS). Puntarenas: Evans & Bowers 2823 (TENN); Mickel 2837 (NY*). CUBA: Isle de Pines: Britton et al.

14763 (NY); Howard 6152 (NY*); Leon 10977 (NY); Morton & Acuna 3354 (UC); Shafer 3248 (NY); Taylor 261 (NY); Underwood & Earle 970 (NY); Wright 826 (NY, UC), 1803 (NY). Pinar del Rio: Leon 5163 (NY*). Santa Clara: Britton & Britton 4991 (NY); Feruaudo 593 (NY); Leon & Roca 7886 (NY). ?: Eggers 5235 (NY). DOMINICA: Chambers 2528 (IJ, LP, MICH); Cooper 105 (F, NY); Farr 1724 (IJ); Fosberg 48296 (MICH); Fuertes 1545 (F): Hodge 133 (NY*); Hodge & Hodge 1055 (CAS), Lellinger s.n., 588* (TENN), 426 (IJ); Lloyd 648 (NY); Long & Norstog 3390, 3396 (USF*), 3397 (TENN*, USF); Wilbur et al. 7416 (MICH, UC). DOMINICAN REPUBLIC: Barahona: Loigier & Loigier 25792, 26167 (JSBD). Duarte: Abbott 2040 (IJ). La Vega: Zanoni et al. 12855 (JSBD). ECUADOR: Carichi: Holm-Neilson et al. 6102 (NY). El Oro: Escobar 1384 (NY); Wiggins 10923 (DS). Pichincha: Cazalt & Pennington 5124 (NY, UC). ?: Sodiro s.n. (NY - 3 sheets*). FRENCH GUIANA: Cayenne: Granville 1735-A (NY); Leprieur s.n. (NY). GRENADA: Beard 1315 (UC); Broadway s.n. (NY); Jenman s.n. (NY*); Proctor 17066 (IJ); Sherring 93 (IJ, NY). GUADELOUPE: Duss 4163 (NY, PH*); Grisebach s.n. (NY); Scamman 8164 (MEXU). GUATEMALA: Alta Verapaz: Tuckerheim 8055 (NY). HAITI: Sud: Ekman 10396 (IJ). HONDURAS: "Puerto Sierra": Wilson 223 (NY). JAMAICA: Manchester: Day 391 (NY). Portland: Evans 2539 (TENN*); Proctor 5206, 5718 (IJ). St. Thomas: Maxon 9409 (NY); Proctor 5510 (FLAS, IJ). ?: Jenman s.n. (NY - 2 sheets). MARIE GALANTE: Proctor 20977 (IJ). MARTINIQUE: Duss 1576 (NY - 2 sheets); Hahn 45 (UC); Stehle 3298 (MICH). MEXICO: Oaxaca: Hollberg 1313, 1589* (NY); Mickel 6460 (ENCB), 7162 (NY); Santos 3423 (ENCB, MICH). ?: Schlechtendal s.n. (NY). MONTSERRAT: Shafer 285 (NY), 747 (F, NY). NEVIS: Proctor 19337 (IJ). PANAMA: Cocle: Armond 412 (CAS); Croat 13394 (MEXU); Dwyer & Correa 7952, 8017 (UC); Kennedy et al. 2094 (TENN*); Liesner 751 (ENCB, MEXU, TENN*, USF*); Porter et al. 4435 (NY*). Panama: Armond 333 (CAS); Croat 22677 (NY*), 22839 (MEXU). Veraguas: Nee 11190 (IJ, MEXU, NY). ?: "Cerro Colorado" - Croat 33218 (NY). PERU: Loreto: Ducke 7525 (MG); Klug 176 (F, NY*); Schunke 219 (NY, UC, USM). PUERTO RICO: Aguadilla: ex herb. Krug & Urban 5660 (NY). Arecibo: Thorpe s.n. (PH). Guyama: Alain et al. 29944 (NY); Britton et al. 6883 (NY); Quick s.n. (MICH); Wagner s.n. (PENN). Humacao: Britton & Cowell 3822 (NY); Chrysler 6520 (PENN); Evans et al. 4425, 4470 (TENN); Fosberg 44196 (NY); Ofer 27 (NY); Sargent 324 (DS); Shuffl 277 (NY); Sintensis 1766 (UCWI); Urban 1466 (NY); Wilson 256 (NY). Mayaguez: Staples 48, 67, 71 (FAU). San Juan: Wolcott 2822 (NY). ?: Hb. Luerssen no. 870 (UC); Stevens 4778 (NY). SABA: Baldwin 1802 (NY). ST. KITTS: Britton & Cowell 309, 382, 409 (NY); Howard 11385 (MICH); Proctor 19608 (IJ). ST. LUCIA: Box 430 (IJ); Howard 11385 (IJ, NY - 2 sheets*); Proctor 17908 (IJ). ST. VINCENT: Beard 1353 (UC); Cooley 8609 (USF*); Morton 5349, 5392 (IJ); Nuttall s.n. (PH); Smith & Smith 238 (UCWI - 2 sheets). SURINAME: Marowijne: Boer 1291 (TENN); Maguire et al. 39112 (NY*); Tryon 5666 (IJ, MICH, NY). Nickerie: Irwin et al. (F, NY). ?: Daniels & Jonker 914 (IJ). TORTOLA: Britton & Shafer 837 (NY);

Fishlock s.n. (PH), 384 (NY). TRINIDAD: Britton et al. 609, 1259 (NY*); Broadway 3641 (NY), 5756 (PH, UC - 2 sheets), 9931 (NY); Fendler 55 (UC), 70 (NY - 6 sheets*, UC). VENEZUELA: Amazonas: Maguire & Politi 27730 (IJ, NY); Steyermark 107147 (NY). Bolivar: Steyermark 89148 (NY*); Wurdack 34443 (NY*). Delta Amacuro: Steyermark 87512 (IJ, NY). Isle Margarita: Johnston 163 (NY*); Miller & Johnston 167 (NY). Merida: Fendler 370 (PH*). ?: Rusby & Squires 368 (NY - 2 sheets).

VITA

Clifton Edward Nauman was born January 6, 1954, in Miami, Florida. He completed his primary and secondary educations in southern Florida. In 1977 he received a Bachelor of Science with a major in the Biological Sciences from Florida Atlantic University, and received a Master of Science degree with a major in the Biological Sciences from this same institution in 1979. For the next two and one half years, he worked as a research assistant on several Department of Interior Contracts to evaluate the rare and endangered status of a number of plant species in southern Florida, published a number of scientific articles, and participated in an expedition to the Territory of Amapá, Brazil. He entered the Doctoral program in the Department of Botany in January of 1982 and received a Ph.D. with a major in Botany in August of 1985. In late August of 1985 he began a two year postdoctoral position as a plant systematist at Fairchild Tropical Garden in Miami, Florida.