Hyospathe

ANDREW HENDERSON New York Botanical Garden Bronx, New York 10458 USA



1. *Hyospathe macrorachis* in Ecuador - note the elongate inflorescence borne amongst the leaves, and red flowers.

Statistical analysis of characters displayed by herbarium specimens of a palm genus allows botanists to develop a more objective method of deciding how many species there really are in the genus, instead of relying on more subjective, intuitive approaches. Here this more objective approach is applied to *Hyospathe*.

By 1964, the year the eminent German palm taxonomist Max Burret died in Berlin, there were 18 recognized species of *Hyospathe*, eight of them described by Burret himself. Twenty-five years later, only two remained (Skov & Balslev 1989). What, you may ask, happened to the other 16? Did they die too? Recently, I became interested in *Hyospathe*, inspired by some unusual specimens collected in Panama. I asked the same question as earlier taxonomists – how many species? – but I changed the way it was asked. How might we know, in a scientific way, how many species there are?

Traditional herbarium taxonomy, as practiced by most palm taxonomists, has produced widely differing estimates of the number of species per genus, not just in *Hyospathe*. The reasons for this are complex, but rest on one basic fact. There is no scientific method in herbarium taxonomy. The process by which taxonomists place specimens in species is not repeatable, quantitative, nor explicit. Rather it is based on intuition and subjectivity. When different taxonomists look at the same specimens, they come up with different numbers of species, with all the associated confusion in names. Furthermore, different taxonomists have different concepts of exactly what constitutes a species.

It was against this background that I began a study of *Hyospathe*. I wanted to carry out a logical sequence of steps that would lead to a scientific taxonomy of the genus, at the same time avoiding the pitfalls of earlier workers. I wanted to avoid, at least in the early stages of the work, 'species' altogether, and just analyze morphological variation of the specimens. The work is now published (Henderson 2004), and here I give a brief outline of the methods and results.

First, I assembled a sample of 538 specimens, borrowed from various herbaria in the United States. The first thing I noticed was the poor quality of many specimens, and I excluded 110



2. Inflorescence of *Hyospathe pittieri* from Colombia – note the inflorescences borne below the leaves and red flowers.



3. *Hyospathe elegans* subsp. *elegans* in the central Amazon – note small size of the plant, leaves with only a few, multi-fold leaflets, inflorescence borne below the leaves and yellow flowers.

(about 20%) from further analysis. I then looked through the specimens and searched for characters. These are any measurable attribute, qualitative or quantitative, of the specimens. An example of a qualitative character is the position of the inflorescence – borne among the leaves or below the leaves. In this case the character has two states (among or below), and each specimen has only one state. An example of a quantitative character is how many flowering branches there are on an inflorescence. In *Hyospathe* this ranges from two to 51. Having chosen a list of 33 characters, I then made a data matrix and scored

each specimen for each character. Also included in the matrix were geographic data (latitude, longitude and elevation) taken from specimen labels.

When the data matrix was complete, I began the analysis. The first stage was to use qualitative characters to place specimens in groups, each group being defined by a unique combination of character states. This process is achieved using Cluster Analysis, and the results are unequivocal. I discovered six groups, each with a unique combination of states. The next stage in the



analysis was to study each of these groups in turn, using both quantitative characters and geographic distributions. In this way, sub-groups may be found which differ statistically in one or more characters and are geographically isolated from other sub-groups.

The final stage in the process is to apply a species concept and names to the groups discovered. In this study I used what is known as the Phylogenetic Species Concept of Nixon and Wheeler (1990), where species are defined as: "the smallest aggregation of populations....diagnosable by a unique combination of character states in comparable individuals." The great advantage of the Phylogenetic Species Concept is that it is 'operational.' It not only gives a definition but also an operation for delimiting species. There are many other species concepts, but few can be applied by the herbarium taxonomist. Because I found six unique character groups, I applied the Phylogenetic Species Concept to these and so recognized six species. Within some of these species I also found geographic and quantitative variation, and I applied a sub-species concept to these sub-groups. The final stage, application of names, is easy. Type specimens were included in the analysis, and the oldest named type specimen in each group of specimens determined the name of the species. If a group had no type specimen included, it then automatically became a new species and was described according to the wellestablished rules of naming new species.

Briefly, I will now describe the six species. The first is *Hyospathe macrorachis* (Fig. 1). This is very distinctive because it is the only species with an inflorescence borne amongst the leaves. It is also notable for its elongate inflorescence and male and female flowers that are borne on short stalks. The species occurs on eastern Andean slopes in Ecuador and Peru, at a mean elevation of 1630 m.

Very similar to *Hyospathe macrorachis*, but differing in its inflorescence borne below the leaves, is a new species, *H. peruviana*. This also occurs on eastern Andean slopes in Peru, at a similar mean elevation (1640 m).

Hyospathe wendlandiana is known only from the Central Cordillera of the Andes, in the department of Antioquia, Colombia, at a mean elevation of

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4. Tall, clustered stems of *Hyospathe elegans* subsp. *costaricensis* from Costa Rica – note large, regularly divided leaves with many, single-fold leaflets.

1600 m. It differs in its tubular sepals of the female flowers.

Hyospathe frontinensis, another new species, is also from the Colombian Andes, but from the western Cordillera. It occurs at a mean elevation of 1370 m. It is distinctive in its mostly simple leaves and inflorescences with few flowering branches.

All the four species discussed so far come from small areas at higher elevations in the Andes. They have also been collected only a few times, and there are very few specimens in herbaria. The last two species are more widespread and much more commonly collected. *Hyospathe pittieri* (Fig. 2) is larger in size than the other species, with stems reaching a mean of almost 5 m in height. It also has regularly divided pinnate leaves and inflorescences borne below the leaves. It is widely distributed in montane areas in northern Venezuela and Andean Colombia, and just reaches Panama. Populations are scattered and the species does not appear common in any part of its range.

Finally, we come to the most widespread species, *Hyospathe elegans* (Fig. 3). This occurs in two areas; west of the Andes in Costa Rica, Panama and the Pacific coast of Colombia and Ecuador, and east of the Andes throughout the Amazon basin. In the western Andean region, I found that the range of the species is not continuous but is split into several discrete areas. When I compared quantitative variables of specimens from each area, I discovered that there were significant differences in several characters amongst the different areas. Because of these geographic and morphological differences, I recognized specimens from these areas as separate subspecies. So, for example, the subspecies from Costa Rica, subsp. costaricensis (Fig. 4), has tall stems over 4 m tall and 1.6 cm diameter, a leaf rachis 82 cm long with 22 leaflets per side (all figures here are means). In contrast, subsp. tacarcunensis, from higher elevations (1300–1400 m) on Cerro Tacarcuna, along the border between Panama and Colombia, has small stems only 2 m tall and 0.5 cm diameter, a leaf rachis only 8 cm long and simple leaves.

The subspecies from east of the Andes, subsp. elegans, is particularly variable, especially along the eastern Andean slopes in southern Colombia, Ecuador and Peru. However, separate groups cannot be distinguished. Variation in quantitative variables here was so great that I suggested that there might be a hybrid zone along the eastern Andean slopes, between the lowland Amazon plants of subsp. *elegans* and the higher elevation species *H. pittieri*. However, with only herbarium specimens as the data source, there was no way to test this hypothesis. Multivariate analysis is a very powerful tool for taxonomists. Not only does it give insights that could not be made using traditional, intuitive taxonomy, but it also produces scientific results, i.e., ones that are based on an explicit methodology, are repeatable and lead to testable hypotheses. The method is certainly not without problems, the biggest of which are the poor quality of palm specimens in general and the few collections from some areas. This problem leads to missing data in the matrix, and missing data are the bane of multivariate analyses. There are also some kinds of variation where the method fails to resolve a taxonomic problem. We have seen one in *Hyospathe*, where we suspect that a hybrid zone occurs between two species, but we cannot analyze this using multivariate analysis of herbarium specimens. Another example of where the method fails is in species complexes. However, the advantages of multivariate analysis far outweigh the drawbacks.

The two-stage approach to herbarium taxonomy that I used in the study of *Hyospathe* – multivariate statistical analysis to delimit specimen groups and subsequent application of a specific species concept – has important implications for palms.

This approach leads to a more realistic and certainly more scientific estimate of taxonomic diversity in the palm family than do traditional herbarium methods. It also appears to lead to a higher number of taxa. Using similar methods to those used in *Hyospathe*, I recognize 18 species of *Calyptrogyne* (Henderson, in preparation), whereas de Nevers (1995) recognized eight. Here I recognize six species of *Hyospathe*, whereas Skov and Balslev (1989) recognized two. Based on these few studies, the number of palm species may be more than double the currently accepted number of 2300!

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