

Lecture

PROBLEMS IN THE CLASSIFICATION OF FERNS

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MANY OF THE same problems of phylogenetic deduction and classification are found in all plant groups, but the *Filicineae* furnish an unusually good illustrative group. Fern classification is in a state of upheaval and has been since the time of F. O. Bower, but the disagreements—however inconvenient they may be to floristicians—do not make an entirely unhealthy state. They in fact provide valuable hypotheses that may be subjected to test. Christensen (1938), Ching (1940), Holttum (1946), Copeland (1947), Alston (1956), and Pichi-Sermolli (1958) have all contributed different systems. Christensen had one family with fifteen subfamilies where Holttum had five families with thirteen subfamilies; Copeland ten families, no subfamilies; and Ching holds the record with thirty-three families (no subfamilies). The old "*Polypodiaceae*" is of course the largest area of disagreement. Bower believed that parallel evolution was rampant among these plants and that similar structures could arise in different lines; this has since been repeatedly confirmed, and is one of the important reasons why many characters should be used in working out taxonomy, including "difficult" or technical ones. At the generic level there are many disagreements as well; for example, Copeland in the *Hymenophyllaceae* had 34 genera where Christensen had 2. At the species level the main questions at present deal with the so-called "biological species," i.e., plants which cannot form fertile hybrids with each other because of polyploid changes. The problems may be broken down as follows: (a) the data of comparison; (b) the methods of synthesizing the data; and (c) the application of categories. The latter two especially concern other plants as much as ferns.

For comparative purposes we have large gaps in our knowledge that will require much effort to fill in. New and simple techniques, like those of clearing and staining leaves and sori, of lactic acid or diaphane for spore studies, and the squash technique for chromosomes, are yielding information of major importance. The more laborious studies of gametophytes and young sporophytes, and the detailed ontogeny of organs are no less important, however. Taxonomists generally prefer to think in terms of key characters, the single or few characters that make for easy identification. The position and shape of the sorus is the time-honored key character in leptosporangiate ferns. It should be pointed out, however, that we really do not know what a single character is. How many genes are involved? Is a character in one part of the plant determined by another in another part? Assuming, though, that we *do* know what a "single character" is, then what is its value? The value is supposed to be measured by its constancy, i.e., reliability; what this means, I believe, is that it is reliable for identification or for keying purposes. Yet, as I have pointed out earlier, in *Pteris* with roughly 280 species

defined by a coenosorus, *P. lidgatii* has a dissected sorus; in *Athyrium* with 600 species with dorsal linear sori, *A. proliferum* has dennstaedtioid sori; and in *Elaphoglossum* with 400 paddle-leaved species, *E. cardenasii* has complex pedate fronds. In fact, between ferns with radically different key characters we may sometimes get hybrids; and the key characters are so different that they do not even combine or blend except by producing highly irregular morphology, as shown by the sori of the intermediates between *Aspidotis* and *Onychium*, the bulblets of the intermediates between *Cystopteris bulbifera* and *C. fragilis*, the leaves of *Tectaria* \times *Dictyoxiphium* or *Asplenium* \times *Camptosorus*, and many other examples.

The point is that single characters may be reliable and convenient for keys, but for phylogenetic research they must be used only in coordination with as many as possible other features. Reniform leaves have appeared by parallel evolution in wholly unrelated ferns. One form of *Cystopteris fragilis* has spores like the genus *Woodsia*. Even chromosome number is constant in some groups (for example, the "X" numbers of *Dryopteris*, *Asplenium*, and *Botrychium*) and variable in others (*Lindsaea*, *Hymenophyllum*, *Woodsia*, *Thelypteris*, and *Blechnum*). Much of the phylogenetic application of the "Telome Theory" has been without regard to other characters, a "disembodied phylogeny." The recent work of K. A. Wilson on the morphology of the leptosporangium exemplifies good coordination with other data; he did not evaluate relationships solely on the single feature he studied, but considered all the other facts together. Whether or not floristicians may prefer to think in only a few key characters, the problems of relationship can be solved only by working with large ensembles of data from all aspects of the plant.

Objective methods to synthesize the comparative facts may merely confirm the intuition of the good taxonomist, of course; but they may also greatly improve the reliability of our correlations. Basic ground plans of similarities underlie all phylogenetic groupings and this, to me, is the essence of systematic research. Various devices have been proposed recently for assessing relationships and evolutionary lines, but the visual ground plan correlation method I developed some time ago for teaching purposes and as an aid in research seems to be as simple as any of them, and based upon sound principles. A number of researchers (e.g., D. F. Brown on *Woodsia*; J. W. Hardin on *Aesculus*; R. L. Hauke on *Equisetum* Subg. *Hippochaete*; and R. F. Blasdell on *Cystopteris*) have adopted it as a useful tool. It involves three assumptions that would seem to apply to any natural and diverse group of plants: common ancestry—plants which have in common a majority of similar characteristics have the same common ancestry; evolutionary divergence—evolution proceeds normally in various directions, and different lines therefore change in different characters and different character-complexes; and inequality of evolutionary rates—evolution occurs at different rates at various times and in different lines. Some forms remain stereotyped and resemble the common ancestor, while others may change radically during the same time period. The ever-present pitfalls of reticulate and parallel evolution may be revealed only by general correlations of many characters. The more characters that are used, therefore, the more accurate are the conclusions.

To work out a phylogenetic problem three broad phases are involved: (a) systematic or comparative analysis of the plants in question to find and understand their contrasting characters; (b) determination of ground plans to

find the character states common to all or most of the plants in order to deduce the most probable ancestral or primitive states; and (c) phylogenetic synthesis to assemble the taxa according to their respective deviations from the basic ground plan and from each other. The detailed steps are as follows: (1) to compare and study all the variable characters among the taxa; (2) to determine the generalized or primitive conditions on the principle that characters found in most or all of a number of related taxa are inherited essentially unchanged from the common ancestor, using data also from related taxonomic groups of the same level. (If no obvious trend can be determined in a given character that character may be used only for grouping purposes.) (3) to assign for each character the value 0 for the generalized or primitive condition, and 1 for the specialized or secondary condition (the intermediate states being assigned the value 0.5); (4) to list in tabular form the taxa and for each give the divergence values from the ground plan, both for individual characters and in total; and (5) to determine the mutual character groupings between taxa and then arrange them in sequence according to these groupings on a concentric chart or graph, the radii and branchings to be determined by the mutual character complexes, and the distances by the divergence indices. So that the facts may be made readily visual, the secondary or advanced states of each character should be expressed by letters (intermediate conditions, lower case; fully developed changes, upper case). Taxa are connected to each other by their ensembles of common features, which are plotted as the points of separation, i.e., as the most probable common ancestors. Such a method as this (though certainly subject to improvement and refinement) helps to solve problems. We can find correlations that had been overlooked. We are forced to use all the available data and other workers can repeat our results with the same information. My method also shows at a glance the character groupings of the most probable common ancestors and thus outlines the pathways of phylogeny.

Authors have stated that one must know all the species of a genus in order to work out phylogeny, but how can this be so? The majority of species in any genus have probably disappeared from the earth anyway. If our methods have validity at all, it should be possible with considerable probability to assess relationships where large gaps exist—the fewer the lacunae, of course, the more valid our conclusions, but this does not mean that where they do exist our objective efforts are worthless. The idea that the paleobotanists alone hold the keys that can reveal the course of evolution seems to me to be a negativistic one, and essentially denies the worth of our methods of determining relationships. Phylogenetic relationships exist, of course, between times as well as at the same time. They may be considered, in fact, entirely independently of time, if by phylogeny we mean evolutionary changes and pathways. The primary aim of the phylogenist should be to determine the pathways of relationship, and it is immaterial whether the data come from plants which are living or fossil—both should be used. Ideally the phylogenist should embody all the data, from past and present, in his conclusions. The dating and correlation of phylogenetic pathways with geological horizons is secondary and must rest first on valid conclusions concerning relationships. All efforts should be bent, therefore, towards improving the objectivity of our determination of phylogenetic trends and relationships with the highest degree of probability; all other deductions are subsidiary to this.

Our biggest problem in fern taxonomy is a purely mechanical one which applies as well to other plant groups, and which I shall refer to as "hierarchical

inflation." It is my opinion that the "sub" categories are passing into disuse at all levels, a situation that not only tends to blur the subtleties of expression of relationship for which the categories were designed, but also leads to inflation. Harold Bold now has 25 phyla (divisions) for the plant kingdom. In monocots Bessey had 8 orders, Engler 10, but Hutchinson has 29. We all know the situation in the ferns. Two circumstances especially tend toward inflation: the group is extremely well studied, and the group has numerous members.

At the familial level, recent research and correlation of evidence has yielded numerous intriguing suggestions of relationships, such as the following: The gymnoگرامmeoid ferns may actually be much more separate from the *Dennstaedtia* group than we formerly assumed. A strong separation of the thelypteroid ferns from the aspidioid group may be questioned. The *Davallia-Oleandra* assemblage may be an epiphytic offshoot from the aspidioid groups; the *Blechnum* and *Elaphoglossum* groups are evidently also aspidioid. Whether *Dipteris* and *Cheiropleuria* are truly polypodioid ferns is dubious. The degree of taxonomic separation of the *Grammitis* group demands further evidence. However, as new differences are found, these must be balanced against the broad, traditional taxonomy of ferns. Rather than setting up whole new families without reference to the level of existing families, the following, possibly more accurate format is illustrated by hypothetical examples:

Fam. Aspidiaceae

Subf. Aspidioideae

Subf. Thelypteridoideae

Subf. Elaphoglossoidae

Subf. Davallioideae

Fam. Polypodiaceae s.s.

Subf. Polypodioidae

Subf. Grammitidoideae

Subf. Loxogrammeoidae

At the level of species, the problem of hierarchical inflation also threatens: very minor differences have been held to warrant species recognition. The separation of *Asplenium cryptolepis* from *A. ruta-muraria* is an example. This is a case where the concept of allopatric subspecies is ideally suited to the expression of relationships. The separation of the American *Phyllitis fernaldiana* from the Old World *P. scolopendria* as a distinct species is complicated by differences in polyploidy and physiology, but again the use of subspecies for their designation seems more reasonable and closer to the facts. The "aggregate species" comprising different levels of polyploidy (e.g., *Cystopteris fragilis*, *Asplenium trichomanes*, *Polypodium vulgare*) constitute a special theoretical problem. Different polyploid levels exist in plants which are otherwise nearly indistinguishable; is it possible that the pairing of chromosomes in these plants is determined by simple genetic factors rather than a multitude of differences in homology? Before we set up different "chromosome races" as separate species and upset our taxonomic traditions, more detailed knowledge of the factors that control chromosome pairing should be obtained.

In summary, many of our problems in fern classification may be brought nearer to solution by (a) obtaining new data, in many cases through the application of a variety of techniques, and avoiding, thereby, the snares of single- or few-character taxonomy; (b) using more objective methods for correlating phylogenetic data, such as the visual ground plan technique described above; and finally (c) working toward a reasonable application of the taxonomic categories that invoke the subtleties of the subcategories and conform as much as possible to the traditional standards.