*Thinking of Biology*

# How to interpret botanical classifications—suggestions from history

The natural system—groupings of organisms that reflect those found in nature—was sketched out by the French botanist Antoine-Laurent de Jussieu in the 1770s and by his compatriot, the zoologist Georges Cuvier, in the 1790s. Since then, almost all systematists have described their classifications as "natural," although what nature was, other than God's creation, and how classifications related to this nature, has often been unclear. The form of classifications has changed little since the 1770s, aside from the addition of ranks in the hierarchy, such as tribe (which lies between family and genus); systematists still consult old works on an almost daily basis to see who was the first to describe a given genus or family. Most biologists believe that genera, families, and other, higher ranks have remained broadly the same over the last two centuries and that systematists have all been working toward the progressive perfection of the same natural system.

However, many of the authors of such classifications saw either classification or nature, or both, differently from the way we do now. I have recently examined the differing concepts of nature held by systematists of the period 1789–1859 and studied connections between these concepts and how these systematists saw relationships among groups and made classifications (Stevens 1994). In this article, I discuss what these systematists intended their classifications to represent and how these intentions relate to the use of classifications by twentieth century biologists. I focus on the work of two botanists: Antoine-Laurent de Jussieu (1748–1836) and George Bentham (1800–1884). Jussieu provided the first generally accepted natural classification of plants, and Bentham, with his collaborator Joseph Dalton Hooker, wrote a comparable study of plants that is still in use today. I conclude with some cautions about the comparison of taxa (groups at any rank of the taxonomic hierarchy) at the same hierarchical rank.

**by Peter F. Stevens**

Recent developments in phylogenetic systematics have clarified how to compare the relative biological diversity of different areas, the relative evolutionary success of different lineages, and the like. Bentham and Hooker, still less Jussieu, would never have imagined that their classifications would be used to answer such questions. However, many botanists, zoologists, ethnobiologists, and other scientists use ranks and groups of "natural" classifications, whatever their vintage, for comparative purposes, as if different genera (for example) were equivalent entities whose comparison might mean something in biological terms. Thus, for instance, the numbers of such genera in different areas is sometimes used as a measure of diversity. Similarly, the properties of curves of the size relationships of taxa at the same hierarchical rank may be examined (e.g., Burlando 1990, Minelli et al. 1991), perhaps showing patterns of evolution. Understanding the context in which classifications were produced will show how misleading such comparisons can be.

## Jussieu's subdivided reticulum

Jussieu's *Genera plantarum*, which was published in 1789 as the Bastille was falling, was the first generally accepted natural arrangement that included all plants. It was not a classification system in the sense that was understood at the time, such as the Linnaean sexual system, which was a divisive, analytic categorization of organisms using only a few characters selected on a priori grounds. Rather, Jussieu relied on a wider variety of features to form groups by first grouping species into genera, then grouping genera into families, and so on. His arrangement was "natural" in that he believed that many of the relationships he described existed in nature, although he conceded that some of his groupings above the level of family were made solely for the sake of convenience.

Indeed, Jussieu's belief in the continuity of nature guided his work. Infinitely graduated nuances linked plants in series. What was almost literally his last published phrase was one taken from Linnaeus, but which actually represented an idea of considerable antiquity: *natura non fecit saltus*—nature does not make leaps (Jussieu 1837). However, Jussieu did not go so far as to adopt the classical idea of a *scala naturae*, a unidirectional and unbranched series culminating in man, and ultimately in God. His continuity was more or less branched, although it had a strong linear element. Thus, his sequence of plants (discussed later in this article) represented increasing complexity. He also noted that the comparable sequence of animals was also largely linear (and parallel to that in plants). A corollary of this general belief in the continuity of nature is that the limits of groups are arbitrary, and as I show later, this is true of the groups recognized by Jussieu.

Jussieu placed all known plant genera (approximately 1850) in 100 families (which he called "ordines naturales"), although he was uncertain of the position of more than 130 genera. The families were divided among 15 unnamed classes, which were themselves grouped into acotyledons (everything from fungi to cycads), monocotyledons, and

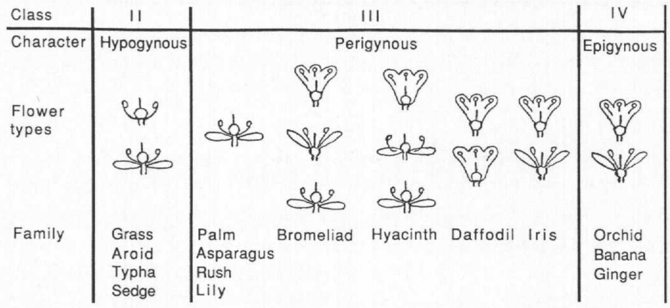


**Figure 1.** The relationship among features of the flower and group limits in Jussieu's third class. Cartoons of the flower show only perianth (free or fused; present or absent; borne on top of or below ovary), stamens (borne on perianth, or on top of or below ovary), ovary, and style. A "typical" hypogynous flower (in which perianth and stamens are attached separately below the ovary) is represented by the figure at the bottom left, and a "typical" epigynous flower (in which the stamens are attached to the top of the ovary) is shown at right. In a perigynous flower, the stamens are attached to the perianth (or the calyx in dicotyledonous plants). Only some of the variation that Jussieu described is shown. Because some of Jussieu's family names may be unfamiliar and many of his families have since been divided, common names for his families, or for genera in them, are used instead.

dicotyledons (including conifers). A major factor that constrained Jussieu's delimitation of groups was that of size: He decided that each must be composed of at least two, but preferably fewer than 100, members. Including at least two taxa in each group made it possible to "generalize" their common characters in the description of the higher-level taxon rather than repeating them in the description of each member of the group; Jussieu repeatedly mentioned the value of generalizing characters in this way. When he decided that *Marcgravia*, plus a couple of poorly known genera, were related to the Clusiaceae, he observed that "[p]erhaps it will eventually form a distinct and neighboring family, above all if further research adds new genera to this little group" (Jussieu 1809, pp. 408–409). His principles precluded recognizing *Marcgravia* as a family in 1809, because he knew only that genus well; no "generalization" of characters was possible then.

Jussieu was less explicit about the upper size limit of taxa, but he often mentioned size as a factor necessitating the subdivision of taxa with many members. In the *Genera plantarum*, he recognized exactly 100 families; none was monotypic, and none had more than 100 genera. The largest family, with 99 genera, was the Corymbiferae (which is now included in the Compositae; the three families into which Jussieu placed genera now included in the Compositae had 151 genera all together). The Leguminosae, at 98 genera, was the next largest family.

But size was not Jussieu's only criterion for establishing groups. He also found it necessary to identify characters, such as the presence of a corolla or its position relative to the ovary and stamens, to support the divisions he was making. Much of the Introduction to the *Genera plantarum* is a detailed enumeration of the characters he used; Jussieu also indicated where in the taxonomic hierarchy individual characters were most useful in delimiting groups. He repeatedly emphasized that characters used to delimit groups were constant within them, because he wanted his groups to be readily recognizable.

Despite Jussieu's efforts, the limits of characters and those of the taxa they are supposed to characterize—within both classes and families—were not the same (Stevens 1994). Rather, a character Jussieu identified as distinguishing a particular taxon is also found in adjacent taxa in the sequence, or it is absent in some of the members of the taxon it is supposed to characterize. Thus, Jussieu described the third of his 15 classes, a group of monocotyledonous families, as having stamens attached to the perianth (perigynous) and usually borne below the ovary. However, the first families in this class have stamens that are largely separate from the perianth (hypogynous), as in the second class, whereas in the last two families the perianth is borne on top of the ovary, as in the fourth class (Figure 1).

Similar character distributions occur in dicotyledonous groups. Thus, the sixth class is also described as being perigynous. However, the last three families mentioned as being members of this class—the Lauraceae, Polygonaceae, and Chenopodiaceae—are actually hypogynous, and they are immediately followed by the seventh class, itself characterized as hypogynous. Such a relationship between characters and groups is to be expected if nature is continuous and if Jussieu's groups divide it arbitrarily: Groups and characters have the same extent only incidentally (Figures 1, 2), and characters often have overlapping distributions.

Jussieu's use of size considerations to circumscribe taxa was entirely consistent with his view of nature as a continuum, as was the frequent failure of characters to define groups he recognized and his reliance on intermediates when establishing relationships. In other words, Jussieu's arrangement was not a natural classification or a system in the sense that we have come to understand these concepts, that is, as showing hierarchical relationships among more or less discrete groups that exist in nature. For Jussieu, there were no such groups, and the classificatory hierarchy was entirely the work of the botanist. As Figure 2 shows, nature can be divided or classified in many different ways when it is viewed as continuous. All classifications are equally unnatural, because nature itself is indivisible; thus, no classification can be interpreted as a hierarchy of groups existing in nature.

Jussieu's idea of nature and his approach to its subdivision was similar to that of his contemporaries Linnaeus, the Swiss philosopher Charles Bonnet, and the French biologist Jean Baptiste Lamarck. In the work of Linnaeus, we find the same catenalike distribution of characters as in that of Jussieu (Stevens and Cullen 1990). In his *Philosophie zoologique*, Lamarck distinguished clearly between a classification and an arrangement. A classification was needed in teaching and providing "points of rest for our imagination" (Lamarck 1984, p. 56), but the limits of taxa correspond to nothing real in nature. The arrangement, by contrast, was the indivisible, continuous series of relationships that comprised nature.

Jussieu's distinctive view of nature was linked to how he defined relationships and circumscribed groups and, hence, to many aspects of the "shape," or whole organization, of his system. The reader may object that this analysis of Jussieu's beliefs is solely of historical interest: Relationships among organisms do not form a seamless whole in this way. Indeed, although Jussieu expected future discoveries to fill in the gaps that existed among some of his groups, both Cuvier and the great Swiss botanist Augustin-Pyramus de Candolle noted early in the nineteenth century that these gaps were not being filled. Both men clearly understood some of the constraints of the Jussiaean arrangement; indeed, over the last 150 years explicit support for the idea of continuity in nature has been rare.

Unfortunately for nineteenth- and twentieth-century systematists, classifications have a strong element of historical inertia; classifications that are in general use are difficult to change. Joseph Dalton Hooker, Darwin's botanical confidant, noted sadly in a letter to Darwin in February 1858 "that to express [systematists'] views scientifically we must break up the whole nomenclature, & rather than do this excessively, we confine ourselves to stating our views without acting on them" (Burkhardt and Smith 1991, p. 25). New ideas of relationships were not being reflected in classifications, largely because horticulturists and other users of classifications would not have been interested in such relationships. Worse, most systematists have not understood that Jussieu's ideas about nature were fundamentally at odds with theirs, and that their taxonomic practice—in many ways, the same as his—was imbued with these ideas. Hooker recognized at least some of the problems systematists faced, and in 1882 he and the great systematist George Bentham completed their own *Genera plantarum*, on which they had been working for 25 years.

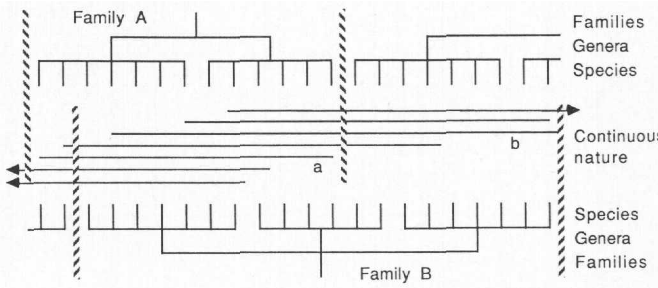


**Figure 2.** Alternative groupings of Jussiaean nature. Continuous nature is represented by the distributions of representative characters (horizontal lines); an arrow means that the character is found in taxa other than those in the diagram. The hatched vertical lines mark the limits of families A and B. Note that character a almost incidentally defines family A; family B is not so defined, and character b shows an overlapping distribution that is common in Jussieu's arrangement. Jussieu treated species as being separated by gaps, but it is immaterial for our purposes whether they are or not.

## Bentham's interpolated hierarchy

The spread of the natural system in Britain was due mainly to the influence of Robert Brown and his highly esteemed *Prodromus florae novae hollandiae* (Brown is the subject of an excellent recent biography [Mabberley 1985]). Brown recognized Jussieu's families, adding new families of his own; his systematic principles, insofar as they can be ascertained, are similar to those of Jussieu. Brown recognized that groups at the same rank were not necessarily equivalent. When he described new families related to the Malvaceae, he observed that "Malvaceae, Tiliaceae, Hermanniaceae, Butneriaceae, and Sterculiaceae, constitute one natural class; of which the orders [families] appear to me as nearly related as the different sections [subfamilies] of Rosaceae are to each other" (Brown 1818, p. 429).

Bentham also followed the natural system. However, he felt that Brown's approach glossed over a problem. Bentham explained his reservations in a short paper on genera (Bentham 1858) that he wrote to help Hooker with his work on the flora of India, which he was writing with Thomas Thomson. Bentham distinguished between the needs of language and those of science:

> In a purely scientific view it matters little if the orders are converted into classes or alliances, the genera into orders, and the sections and subsections into genera; their relative importance does not depend on the names given to them, but on their height in the scale of comprehensiveness; but for language, the great implement, without which science cannot work, it is of the greatest importance that the groups that give their substantive names to every species they include should remain large (Bentham 1858, p. 32).

Hooker, too, as we have seen in his letter to Darwin (quoted above), recognized a similar conflict between science and language.

Bentham believed that rank ("names") was of less importance than the kind and extent of relationships circumscribed by a taxon ("height in the scale of comprehensiveness"). Both he and Brown agreed that taxa at the same rank need not be equivalent. Indeed, a major goal for Bentham was simply to keep the number of families relatively small, approximately 200, so that "a botanist of ordinary capacity" would be able to memorize both the names of families and their characters; "double that number, and all is confusion." Similarly, genera would also have to be few in number (Bentham 1858, p. 32).

Soon after Bentham published his short paper on genera, he began work with Hooker on the three-volume *Genera plantarum*, of whose some 1,681,500 words he wrote the larger part. Hooker was director of the great botanic gardens at Kew and had many other responsibilities (Desmond 1995), although Bentham too was busy, having started writing his seven-volume *Flora australiensis*. The *Genera* is an enumeration of all of the genera and other, higher taxa of flowering plants and is still one of the most used of all systematic books, only recently having been replaced by *The Families and Genera of Vascular Plants* (Kubitzki 1990), the first volume of which appeared in 1990.

Bentham and Hooker saw the need for a comprehensive work based on uniform principles. Bentham discussed this point in his review of a volume of the great *Prodromus systematis naturalis regni vegetabilis*, a species-level treatment of all flowering plants edited first by Augustin-Pyramus de Candolle and then by his son, Alphonse. Bentham lamented that the large number of collaborators involved in the treatise had resulted in a lack of any unity in its systematic philosophy, and he noted "the usual tendency of partial monographists [people who work on parts of families] toward the multiplication of small genera" (Bentham 1864, p. 520). Bentham himself usually dismissed any idea of joint authorship, because it entailed joint responsibility, which in turn entailed having a systematic philosophy similar to that of the coauthor. In the case of the *Genera*, however, collaboration with Hooker was possible because Bentham believed that their systematic philosophies were compatible. Their *Genera* would have uniform principles and so could serve as a general comparative survey for botanists.

But what were these principles? The *Genera* has only the briefest of introductions, although it seems not to need one because it is structured by a conventional taxonomic hierarchy—in fact, the general arrangement in the *Genera* is little changed from that of earlier systems (Green 1914, Lawrence 1951). However, the question of guiding principles for this important book is relevant because Bentham was not an immediate convert to Darwinism, whereas Hooker was one of its earliest and strongest supporters. But although Hooker never wrote at length about the principles of classification at higher levels, his few remarks about groups and relationships suggest that evolution did not contribute to his classificatory ideas. Indeed, his and Darwin's thoughts about relationships seem scarcely compatible: Darwin saw relationships among organisms as being treelike, with the trunk and branches representing extinct organisms, whereas Hooker saw reticulating relationships, with connections largely between extant taxa (Stevens 1994).

Unlike Hooker and Darwin, Bentham's beliefs about evolution are not clear from his writings: all we have to go on are his short paper on genera (Bentham 1858) and a lengthier paper on species (Bentham 1861). However, the Royal Botanic Gardens, Kew, houses an extensive manuscript in Bentham's handwriting and with annotations by Hooker. Written in 1860 or thereabouts, the manuscript, which appears to be a draft of an introduction to the *Genera plantarum*, describes Bentham's classificatory principles (these principles are probably Hooker's as well, but I ascribe them to Bentham because he wrote the manuscript). The manuscript shows Bentham to be conscious of what he saw as an irreconcilable conflict: "However desirable it might be that orders [families] should be nearly of equal size, it is still more so that they should be nearly of equal value, and the one is incompatible with the other" (162 verso). He did not state explicitly what he meant by "value," but from this introduction and other writings, it seems to mean the morphological distinctness needed to maintain a taxon at a particular rank. Clearly, two taxa equally distinct from their nearest relatives can be very different in size.

Many of Bentham's principles dealt with the size of taxa:

> I Orders should be kept large
>
> II Genera should also be kept large
>
> III Orders and genera should be natural [not defined!]
>
> IV Intermediate [hierarchically] and subordinate groups should be numerous but may be more natural
>
> V Established combinations should be maintained where new ones present no very decided improvement (161 recto)

Bentham discussed these points over the following 22 pages of the manuscript. He noted that an ideally sized genus contained between 10 and 100 species. Monotypic orders were highly inconvenient, yet large groups should not be divided merely because they were large, even if large genera could end up with more than 100 species. He wrote that

> Summing up our ideas of what orders and genera ought to be, we have shown that taking the whole mass of known species to be between 80,000 and 100,000, it should so be divided and subdivided that there should never be more than ten or twelve, and seldom more than five or six groups of any grade under an immediately superordinate one (169 recto).

A further constraint was that the total number of families should be "well under two hundred, [since otherwise] it entails a useless burden on the memory" (161 verso). But with some 93,605 species (the total number in the *Genera*), each family would have approximately 470 species. So, even though the number of species had increased greatly since Linnaeus's time, Bentham wanted to keep the familiar Linnaean and Jussiaean familial and generic names; to ignore recently created and unfamiliar small taxa segregated from large and more familiar taxa, whether genera or families; and to recognize very small groups.

Bentham's solution to this apparently impossible task was simple: he interpolated informal groupings (in which the taxa were often not even named) among the major formal classificatory ranks to make taxa a convenient size. Thus, he divided the Ranunculaceae, with 30 genera, into five tribes; he further subdivided one of these tribes into three unnamed groups and another into two subtribes that he divided in turn into two and four unnamed groups. Ultimately, the 30 genera were divided into three groups of one genus each, six groups of two genera each, one group of three genera, and three groups of four genera (Bentham 1862). The advantage of such small groups was they could readily be compared and their distinguishing characters recalled.

Stability, the other and, in some ways, even more important goal for Bentham (and for Hooker), was also attained. Old names at all levels were maintained and new names ignored; indeed, Bentham believed that even poorly known taxa would be assignable to existing genera or families when they became better known (162 verso). Stability was critical, because the botanists at the Royal Botanical Gardens in Kew were involved in a monumental attempt to catalog the vegetable products of the British Empire, and Bentham and Hooker wanted to avoid the inconvenience of changing classifications and names.

The extent to which Bentham and Hooker structured their classification to produce groups of the desired size is remarkable. In Figure 3, the size of the taxa that they recognized—whether formal or informal—is graphed: More than 99% of the groupings have fewer than 12 immediately subordinate taxa, and more than 75% have 6 or fewer. Bentham's and Hooker's work in this respect is similar for both the monocots and dicots (Figure 4).

But this adjustment of the size of taxa is only half of the story. In fact, neither Bentham nor Hooker was confident about the circumscription of groups. Hooker thought that the limits of taxa were often arbitrary and indistinct. If a group was "natural" (by which he meant well separated), then, he suggested, only a few genera would link it to other families, but these genera would tend to be large. If there were only a single intermediate genus, most genera in the family might still be intermediate, because the family was linked to many others. Appropriately, Hooker went on to say that "the limits among many of the most natural groups of plants are purely arbitrary, as has been repeatedly shown" (Hooker 1856, pp. 182–183). This is a position he shared with Jussieu.

There is no evidence that either Bentham or Hooker believed that nature was a continuum; however, their taxonomic approach was compatible with such a belief. They not only subdivided taxa to recognize conveniently small groups, but also often found the limits of taxa notably indistinct; their respect for historically accepted taxa further complicated the issue. In papers on one of Bentham's favorite families, the Leguminosae (peas and their relatives), we can see how these factors interact and affect the interpretation of his classifications. Bentham revised the Dalbergieae, a tribe of the Leguminosae, in 1860, and recognized 23 genera. When looking at the geographic distributions of these plants, he realized that he should consider only "natural" genera, and he proceeded to merge 8 of these 23 genera; thus, he discussed the distributions of only 15 groups. Later, Bentham (1875a) placed *Pentaclethra* and *Parkia* alone in a tribe of the Mimoseae (Mimosoideae), but when he discussed geographical distributions he treated the two genera individually as equivalent with his other tribes. In short, for reasons of convention and utility, Bentham maintained genera, tribes, and other groupings that were not suitable for answering biological questions. Furthermore, as was the case for most botanists of his day, Bentham's acceptance of evolution did not affect his delimitations of taxa; his practice remained similar to that of Jussieu, however different his theory of the world might have been. The conflict among the various factors that influenced group circumscription meant that Bentham's taxa might be unnatural, even according to his own criteria.

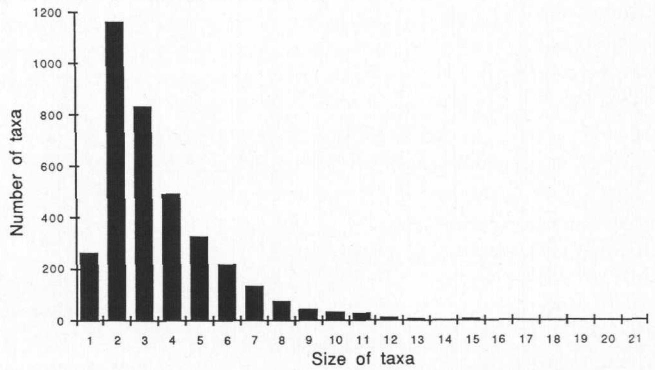


**Figure 3.** The size distribution of the numbers of taxa included in all immediately higher level taxa, whether formal or informal, above the level of genus. The graph summarizes Bentham's work in the *Genera* on dicotyledonous families.

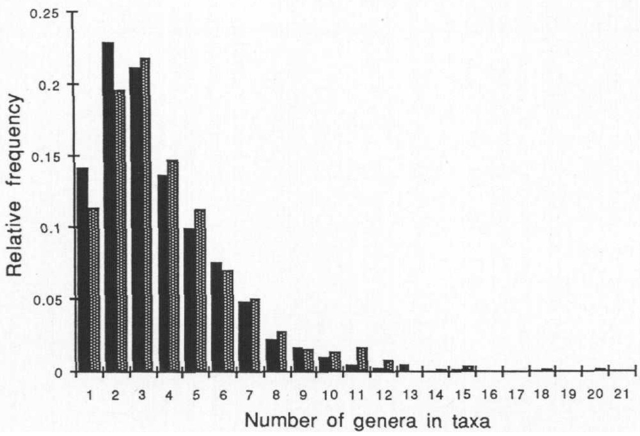


**Figure 4.** The size distribution of genera in the hierarchical level immediately above them, whether formal or informal. Classifications of Bentham (hatched bars) and Hooker (filled bars) in the *Genera* compared.

Toward the end of his life, Bentham claimed that all taxa, from variety to family and above, were similar in that all were the result of evolution: "[T]here is thus no difference but in degree between a variety...and order, [so] all disputes as to the precise grade to which a group really belongs are vain." (Bentham 1875b, p. 84; the "grade" of a group was its level in the taxonomic hierarchy). Although Bentham believed that all taxa were conceptually equivalent, that is, all had descended from a common parent, he did not believe that members of the same rank were equivalent. He even disliked uniform terminations ("-aceae") for families, because he feared that such terminations might encourage people to regard families as equivalent, whereas they were not (Stevens 1991). But if taxa within a rank were not equivalent, and if ranks did not exist in nature, then the only way to stabilize nomenclature would be to establish, as a matter of convention, their circumscription in one particular way. Thus, we return to one of the main reasons for the publication of Bentham and Hooker's *Genera plantarum.*

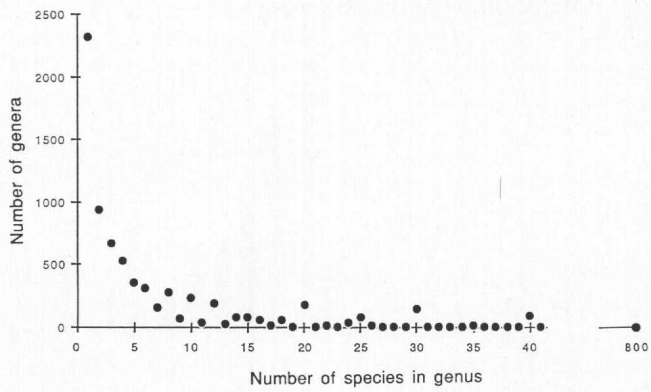


Figure 5. The size distribution of genera recognized by Bentham and Hooker in the *Genera*. The largest genus is *Senecio*, with 900 species. Bentham and Hooker rounded out the size of genera with 20 or more species, and they preferred even to odd numbers for describing the size of genera with between 5 and 15 species.

## A cognitive interpretation of classifications

The combination of Bentham's explicit appeal to convenience and memory when circumscribing groups, and the clear indications he gave as to what constituted the optimal size of a group, provide a clue for one interpretation of biological classifications: That is, they are in part memory devices. John McNeill (1979) emphasized this idea in his concept of "structural value," which is the simplest configuration possible for a group that would allow its subdivision into subgroups of a size that the memory could handle. McNeill thought that five was a convenient group size, with nine being an upper bound (see Miller 1956). Bentham's guidelines—groups should have 2–6 (to as many as 12) members—seem to have been created with exactly such ideas in mind; indeed, similar ideas are evident in memory systems developed from classical times onward (Yates 1966). Recent work shows that, with practice, the mind can effectively remember large quantities of information, so long as that information is committed to memory in chunks of five or fewer units (e.g., Ericsson and Polson 1988). Even Bentham's and Hooker's limitation of the number of families to 200 is similar to the number of folk generics (approximately 500) frequently found in ethnobiological classifications (Berlin 1992).

Many classifications (and not only of biological subjects) have small groups, as E. W. Holman (1992) has found. Only 19 of 306 taxa, formal and informal, in Jussieu's classification contain more than 12 members, and 157 contain between 2 and 5; McNeill (1979) found that there was an average of 5.86 genera in each immediately higher-order taxon. Interestingly, the French botanist Michel Adanson included on average almost 11 genera in the next highest taxon in his *Familles des plantes* (Adanson 1763). Adanson's work was largely ignored, partly because he did not follow Linnaean nomenclature (Lawrence 1964), but it seems possible that the size of his taxa might have contributed to the unpopularity of his system. Many of the idealistic classification systems that were popular in the first half of the nineteenth century were based on numerical regularities in classifications: Natural groups always had a defined number of members, typically two, three, four, or five (nearly always fewer than eight). This repeating number was evidence to the authors of such systems that they understood nature, but another attraction was that nature became easier to memorize, that is, to "learn." As G. T. Burnett (1830, p. 371) noted, "it would be very convenient as an assistant to the memory, if such a distribution [a low, repetitive number in groupings of organisms] could be naturally found out."

Bentham and Hooker's guidelines for recognizing taxa show that their classification was clearly—and successfully—constructed as a memory device. Thus, no matter how many genera were recognized in a family, those genera were always assembled into small groups. From this point of view, Figures 3 and 4 accurately reflect their classification. Familiar names for families and genera, whatever their size or "value," were retained, and the numbers of families, in particular, kept low so that a botanist would have a reasonable chance of remembering them all.

## Some caveats on the biological interpretation of classifications

As mentioned earlier, recent studies have examined the properties of curves of the size relationships of taxa at the same hierarchical rank. Such curves are explained, at least in part, in terms of the biology of the organisms involved. Earlier work of J. C. Willis (e.g., 1949) on the relationships among the age of taxa, the area where they live, and their size, showed numerous hollow curves, with an excess of very small, local taxa (e.g., genera), and a few very large taxa, rather as in Figure 5. Willis thought that the many small, localized genera had evolved recently, the few large, widespread genera being old. W. D. Clayton (1972), in a study of the sizes of angiosperm families and genera, explained similar curves as the "natural consequence of the evolutionary process" (Clayton 1974, p. 278), although he conceded that psychological factors (including the constraints of memory) helped to explain the very large numbers of monotypic taxa in twentieth-century classifications as systematists try to reduce large genera to a manageable size by splitting small genera off them. The issue is complicated by the fact that hollow curves (straight lines in log/log plots; Figure 5) result when such disparate subjects as the distribution of noncoding DNA sequences and the numbers of papers published by scientists in individual disciplines are graphed (Zipf's Law; Konopa and Martindale 1995, Zipf 1949).

In fact, the relative dearth of monotypes at the family level in Bentham's work (Figure 6), which Clayton remarked on, is due to the explicit constraints of memory and convenience. At least some of the numerical properties of the size dis-

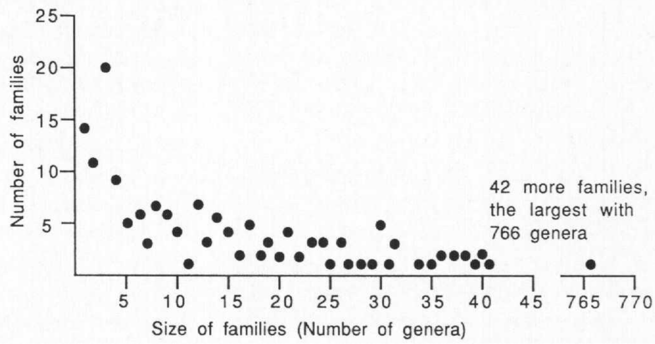


Figure 6. The size distribution of families recognized by Bentham and Hooker in the *Genera*.

tributions of taxa in the classifications of botanists such as Jussieu and Bentham can be related to their understanding of nature and of the purposes of classification. Their classifications cannot be interpreted as hierarchies in which members at the same rank are comparable. Twentieth-century evolutionary classifications are, in part, built on their Jussiaean and Benthamian predecessors. The framers of these later classifications have been unaware of Jussieu and Bentham's goals, instead assuming simply that the development of "the" natural system has remained a given in systematics. But Bentham would surely have questioned the use of general comparisons within a rank to tease out biological pattern. Even the complex hierarchical system of the *Genera* itself would be no basis for comparing groups or looking at the distribution of taxa. Nature and convenience—the two principles on which the work was based—were in irreconcilable conflict. Furthermore, Bentham and Hooker may have understood the reasons for their circumscription of all the taxa they recognized, but because they wrote all but one family account separately and gave few reasons for their decisions, any possibility of understanding the details of the hierarchy in the *Genera* was lost with the death of Bentham in 1884.

Indeed, the *Genera* can be analyzed to support very different understandings of nature. The shapes of the curves in Figures 3 and 6 suggest very different evolutionary interpretations, yet neither reflects Bentham and Hooker's ideas of nature. In Figure 3, most taxa have fewer than 12 members, but as already mentioned, group size was manipulated to attain this result. In Figure 6, families are the basic units; only 47% of the 201 families have 12 or fewer genera (and the Leguminosae has 399 genera and the Compositae 766 genera). Again, however, this situation does not reflect nature: Bentham and Hooker fixed the number of families at 200, and, at the same time, they recognized that the families were not equivalent.

Still another pattern—a hollow curve with a great excess of monotypes—is evident in the size distribution of genera (Figure 5). However, for Bentham, genera, like families, were not equivalent, and it would be rash to explain the hollow curve in biological terms. Clayton (1972, 1974) noted that the excess of monotypes has become more marked in recent classifications, as specialists subdivide the groups on which they are working with little thought of the consequences. Although Bentham thought that both monotypic taxa and the subdivision of large genera—with the creation of hundreds of new and unfamiliar names—burdened the memory, a tendency to split off small genera has long been evident. Even in Bentham's time, the names of many small genera were so deeply etched in the botanical consciousness that they could not be changed.

## Conclusion

Even if classifications function as memory devices, the "naturalness" of the groupings is not necessarily affected. A systematist can simply use gaps that exist in nature to form taxa of convenient size. However, until recently systematists have had difficulty articulating defensible grounds for favoring the use of a particular character in a classification or for preferring one circumscription of a taxon over another (see also Winsor 1991). Furthermore, genera included in Jussieu's families might not have the characters that he described those families as having, and some genera owed their familial assignment to Jussieu's belief in continuity. Much of Bentham's systematic practice was similar to that of Jussieu, although his descriptions were more precise. Add systemists' nomenclatural conservatism to the list of factors affecting the circumscriptions of groups, and the result in some cases was the recognition of taxa whose members had entirely independent evolutionary origins.

The various constraints that affect systematists' work, only some of which I have discussed here, clearly make the interpretation in evolutionary terms of the size properties of evolutionary classifications difficult. That taxa placed at one hierarchical rank are equivalent only by designation, as is commonly conceded (e.g., Cronquist 1988), is almost the least of the problems. However, Bentham's concern that people might misinterpret the uniformity of termination of names of taxa at the same rank for reality has been justified. It is easy to make curves that depict the sizes of taxa in particular ranks using monographs, floras, and faunas written over the last two centuries, but interpreting these curves is difficult; thus, finding a biological explanation is dubious. We must remember that there are still no generally accepted criteria for grouping or ranking in biological classifications, and no agreement as to what these classifications should represent. The situation is changing, however, and monophyly (the inclusion of all and only descendants of a common ancestor in a taxon) is now often a preferred grouping criterion, although for many comparisons, equivalence in the age of taxa is needed. Yet if there is still much to do in establishing monophyly as a generally accepted criterion for group recognition, previous classifications, especially those of the last century, are largely opaque as we seek to understand the diversity of life. Only by careful study can we hope to uncover the reasoning that led to their establishment and to understand the relationships between such classifications and the shape of nature as their authors saw it. It is already clear that these classifications cannot be easily understood in terms of patterns of diversification, and because of the way classifications have developed, comparable studies using twentieth-century evolutionary classifications is compromised.

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