Charles Darwin’s Views of Classification in Theory and Practice

KEVIN PADIAN

Department of Integrative Biology and Museum of Paleontology, 1101 VLSB, University of California, Berkeley, California 94720, USA; E-mail: kpadian@socrates.berkeley.edu

Abstract.—It has long been argued that Charles Darwin was the founder of the school of “evolutionary taxonomy” of the Modern Synthesis and, accordingly, that he recognized genealogy and similarity as dual, synergistic criteria for classification. This view is based on three questionable interpretations: first, of isolated passages in the 13th chapter of the Origin of Species; second, of one phrase in a letter that Darwin wrote about the work of an author he had partly misunderstood; and third, of his taxonomic practice in the barnacle monographs, which only implicitly embody his philosophy of classification, if at all. These works, seen in fuller context and with the perspective of extensive correspondence, are consistent with the view that Darwin advocated only genealogy as the basis of classification, and that similarity was merely a tool for discovering evolutionary relationships. Darwin was neither a Mayrian taxonomist nor a cladist, and he did not approach systematic issues in the same terms that we do in the late 20th century. [Cladistics; classification; Darwin; systematics.]

What criteria did Charles Darwin regard as the best basis for classification of organic beings? And did he follow his own philosophy in practice? Darwin’s views on classification have been extensively researched and debated, especially in the decades following the rise of the competing “evolutionary,” “phenetic,” and “cladistic” schools of systematics (e.g., Ghiselin and Jaffe, 1973; Nelson, 1974; Mayr, 1982, 1995; Ghiselin, 1985). Some scholars have advanced the view that “Darwinian” classification (in theory, in practice, or both) involved dual criteria of genealogy and degree of similarity, at least to some extent (e.g., Ghiselin and Jaffe, 1974; Mayr, 1982, 1994a, 1994b, 1995). Others (e.g., Nelson, 1974; Ghiselin, 1985; Desmond and Moore, 1991; Padian, 1994) have stressed Darwin’s insistence on genealogy alone. Most scholars agree that Darwin cannot be regarded simply as an “evolutionary taxonomist” or a cladist, or as a patron saint to any current school. However, issues and terms have shifted so much over the years that it has become both difficult and inappropriate to shoehorn the ideas and language of Victorian science into current debates. Nevertheless, Darwin’s ideas about classification are interesting and important for their own sake—for what they tell us about the changing climate of thought during the era when he wrote, and for the relationship that they bear to his other ideas about evolution (e.g., Desmond and Moore, 1991).

New publications of Darwin’s letters and recent advances in scholarship have provided some fresh insights into Darwin’s thought in the context of his times (Desmond and Moore, 1991; Browne, 1995; and notably the series, Correspondence of Charles Darwin, edited by Burkhart and Smith [1985, 1988, 1990, 1991, 1993], denoted here as CCD with appropriate volume and page numbers). Current historiographical methods aim to set texts and authors in their appropriate cultural place and time, acknowledging that the meanings of words as well as the grounds of basic issues and even philosophical standards have changed. To understand what Darwin actually said and thought, it is important first to read his passages in context, not in isolation (Ghiselin and Jaffe, 1973). Darwin often developed his ideas over series of pages, and an isolated quotation can be misleading. Second, it is important to know when Darwin is stating his own views and when he is summarizing, however sympathetically, the views of others with whom he disagreed (Ghiselin, 1985:460). Darwin was extremely deferential to the views of others, particularly when he was about to advance an alternative, and he tried scrupulously to be fair about representing established views. He also went out of his way to consider the views of those who he thought
would be most likely to object to his own, regardless of whether he thought their criticisms relevant or justified (his self-styled “trucking passages”). Frequently, Darwin’s letters to his friends contain franker and more elaborate statements of his views, and these have been effectively analyzed and compared in understanding the development of his ideas (e.g., Ghiselin and Jaffe, 1973; Osypovat, 1981; Desmond and Moore, 1991; Browne, 1995). Third, it is important to read what Darwin himself read. Often in his published writings as well as his letters, his language reflected arguments and terms of others that were current at the time; for example, the Quinarian classification scheme of W. S. MacLeay, which intrigued many biologists in the 1820s and 1830s (Osypovat, 1981:110–114) but is largely forgotten today. Finally, one must take into account that the meanings of some crucial words have changed since the 1840s. Darwin, for example, had to ask G. R. Waterhouse in 1843 what he meant in his letters by “relationship” in classifying organisms (CCD 2:378). Waterhouse replied “by relationship I mean merely resemblance—I use it in a most vague way”—and he differentiated a relationship of affinity (similarity shared by members of a “natural” group) from one of analogy (convergent similarity). For Waterhouse, relationship was purely a question of degree of “resemblance” (CCD 2:381–382), a meaning that 20th century systematists would not accept because it does not strictly presume a genetic basis. This is another hazard of taking Victorian vocabulary out of context.

In this essay I make three points about Darwin’s views of classification. First, Darwin advocated and insisted on genealogy as the criterion for classification. He did not connect or correlate it with any other criterion, though he recognized factors such as degree of similarity and correlations in embryological stages as important in revealing genealogy (and this is a crucial distinction). He maintained this position in letters from 1843 until after the initial publication of the Origin of Species (1859) and through every later edition, as well as in The Descent of Man (1871). Second, the argument that Darwin advocated dual criteria of genealogy and degree of similarity is not supported by his writings on how classification should be done, but is rather an interpretation that hinges on a single statement, taken out of context, that Darwin wrote about another author’s work—one that he himself does not seem to have fully understood. In fact, on several occasions Darwin denied explicitly that similarity should be the basis for classification. Third, in his work on living and fossil barnacles, Darwin apparently did not follow his own stated theoretical precepts, in the sense that he did not make genealogy a focus of discussion as the basis of classification, and in fact barely referred to it. Nor did he develop in these works any philosophy of classification. However, I suggest that his practical taxonomic work did indeed support his view that classification should be based on genealogy. The difficulty of his taxonomic subjects simply prevented him from achieving his ideal and has prevented us from understanding why.

**Darwin’s Emphasis on Genealogy**

Mayr (1982:209) regarded Darwin as “the founder of the whole field of evolutionary taxonomy,” and quoted Simpson (1961): “Evolutionary taxonomy stems explicitly and almost exclusively from Darwin.” Mayr’s (1982) Chapter 5, reiterated in part more recently (1994a, 1994b), summarizes his view of taxonomy and of Darwin’s role in the development of taxonomy. After quoting Simpson with approval, Mayr quoted some famous passages from the 13th chapter of Darwin’s Origin of Species (1859:411–413) to the effect that classification is not arbitrary, like the groupings of stars into constellations, but attempts to follow a “Natural System.” Darwin said that what naturalists then called the “Natural System” took several forms (Ghiselin, 1969): It was variously a scheme for separating and grouping unlike and like “living objects” (why did Darwin not use the term “organic beings,” as he did throughout the Origin?) according to resemblances, key characters, embryology, or other factors; or it was an attempt to understand the plan of the Creator (as Natural
Theology did), for which no natural rules had been adduced; or it was a combination of these factors (which could be said to have been the goal of Linnaeus, among others including Owen, Sedgwick, and even Lyell).

For Darwin, the only real difference between these traditional systems and what he regarded as the proper basis of classification was that descent with modification replaced divine plan or other philosophical considerations. But he still needed a practical way to discover genealogical relationships. He recognized that many of the traditional criteria, such as degree of similarity, embryological resemblances, and so on, reflected genealogical proximity. In these respects, he appreciated that traditional taxonomy had probably been replicating more or less faithfully the pathways of diverging parentage. In one sense evolutionary taxonomy follows Darwin’s view, in that it accepts genealogy as the underpinning of most similarity, and only inherited similarity can be a basis for taxonomy. The founders of evolutionary taxonomy explicitly traced this rationale to Darwin’s doorstep. It could even be argued that Darwin condensed paraphyletic taxa (Ghiselin and Jaffe, 1973), a sticking point between the “evolutionary” school and the cladistic school, inasmuch as some of his barnacle taxonomy admitted them. But in the full compass of his writings, Darwin regarded such groups as necessary evils only because the complete genealogy was not known (thanks to differential extinction). Without these gaps, classification would be purely genealogical.

Mayr (1982) was correct that Darwin was contemptuous of the Natural System. Darwin (1859) traced this system, in its various forms, to Linnaeus and other authors of the 18th and 19th centuries, noting that, at least in its mature form in mid-Victorian England, it incorporated both similarity and Divine Plan. However, the various versions of the “Natural System” were sufficiently confusing that he had to apologize profusely to Richard Owen for including him with the special creationists in the first edition of the Origin.

Let us first see what Darwin thought about the Natural System and why. In 1843 G. R. Waterhouse wrote to him to ask his advice on the ranks of classification in the Natural System. Darwin characterized the “Natural System” as follows in his response (CCD 2:375–376; emphasis in original):

Most authors say it is an endeavour to discover the laws according to which the Creator has willed to produce organized beings—But what empty high-sounding sentences these are—it does not mean order in time of creation, nor propinquity to any one type, as man—in fact it means just nothing.

According to my opinion, (which I give everyone to hoot at . . .) classification consists in grouping beings according to their actual relationship, i.e., their consanguinity, or descent from common stock.

Darwin paraphrased this passage, somewhat toned down, 16 years later, on page 413 of the Origin of Species, which suggests that his views did not change in the ensuing years, and that he felt that this was a sufficiently clear statement of them. But some following passages in his letter to Waterhouse (CCD 2:376) are equally revealing:

To me, of course, the difficulty of ascertaining true relationship [i.e., a natural classification[,] remains just the same, though I know what I am looking for . . . we ought to look at classification as a simple logical process, i.e.[,] a means of conveying much information through single words—now the laws of classification tried by this rule—it is clear that neither number of species—or grade of organization ought to come in, as an element. . . the only cheque to the splitting of groups, appears to be convenience; . . . I repeat, that until you can define your object in classifying, you have no right to introduce number of species or (arbitrary) grades of organization, but are bound to follow simple amount of differences of organization [as, he notes, botanists do]. . . . This is clearly the rule, on the view of classification, being a genealogical process, exhibiting literal or actual relationship.

In this passage, Darwin links genealogy and amount of differences, but he is not saying that they are dual criteria for classification. He says in both passages that classification should be strictly genealogical, and that numbers of species or arbitrary grades of organization (for example, whether a barnacle is stalked or not) should not characterize major groups. The reason he advocates following “simple amount of differences of organization” in classification is that progressive differences suggest progressive divergence, reflecting the gradual process of evolution by which genealogy can be traced, given a
sufficient series of forms. In another letter to Waterhouse a few days later (CCD 2:377–379, in which he also protested against number or grades of organization being used in classification), he emphatically stated “that all rules for a natural classification are futile until you can clearly explain, what you are aiming at” (emphasis in original). Darwin’s underpinning idea of the consanguinity of all creatures was clearly what he was aiming at, but that idea was not generally accepted in 1843, or he would not have risked shocking Waterhouse by his views (he ended his earlier letter, “Have you had patience to read thus far.”). This letter, again, says nothing about “degree of similarity”; it speaks only of relationship by descent.

These views of Darwin’s were neither hastily composed nor temporarily held. Fourteen years later, Darwin carried on a similar correspondence with Huxley. Two letters, from 26 September and 3 October 1857, reiterate his views on the Natural System and on genealogy in classification (CCD 6:456):

In regard to Classification, & all the endless disputes about the “Natural System[.]” which no two authors define in same way, I believe it ought, in accordance to my heterodox notions, to be simply genealogical.—But as we have no written pedigrees, you will, perhaps, say this will not help much; but I think it ultimately will, whenever heterodoxy becomes orthodoxy, for it will clear away an immense amount of rubbish about the value of characters &—will make the difference between analogy & homology, clear.—The time will come I believe, though I shall not live to see it, when we shall have very fairly true genealogical trees of each great kingdom of nature.—

Darwin regarded the lack of intermediate forms in both the living world and the fossil record as the main impediment to achieving a fully genealogical classification (e.g., CCD 2:376, 415). Huxley wrote back to Darwin (CCD 6:461) that “Cuvier’s definition of the object of Classification seems to me to embody all that is really wanted in Science—it is to throw the facts of structure into the fewest possible general propositions”—(emphasis in original) Darwin replied,

I knew, of course, of the Cuvierian view of Classification, but I think that most naturalists look for something further, & search for ‘the natural system’,—‘for the plan on which the Creator has worked’ &c &c.—It is this further element which I believe to be simply genealogical.

And he went on to give Huxley an extended example of his view (emphasis in original) that it would be possible to make classifications purely genealogical if missing intermediates were known (CCD 6:463):

Grant all races of man descended from one race; grant that all structure of each race of man were perfectly known—grant that a perfect table of descent of each race was perfectly known.—grant all this, & then do you not think that most would prefer as the best classification, a genealogical one, even if it did occasionally put one race not quite so near to another, as it would have stood, if allocated by structure alone. Generally, we may safely presume, that the resemblance of races & their pedigrees would go together.

He ended his letter to Huxley, who had pushed development as a prime cog in the nascent machine of “a Scientific & logical Zoology & Botany” (CCD 6:461), with the following postscript: “It might be asked why, development so all-potent in classification, as I fully admit it is; I believe it is, because it depends on, & best betrays, genealogical descent; but this is too large a point to enter on.” Huxley completely missed the point, writing back, “Your pedigree business is a part of Physiology—no more to do with pure Zoology—than human pedigrees has with the Census.—Zoological classification is a Census of the animal world” (CCD 6:462).

Darwin’s own words, cited above, indicate his frustration with the Natural System (which he put in quotation marks) as it was practiced in his day, and his strong advocacy of genealogy as the central and only criterion for classification. They also illustrate his frustration with the gaps that exist between living forms and in the fossil record, without which the establishment of a classification by genealogy would be much easier. The “Natural System,” to him, could not be truly natural unless genealogy were its basis, and this is why he viewed the “Natural Systems” of his time with frustration and cynicism.

The most crucial passage on classification in the Origin of Species (Chapter 13, p. 420) has been widely cited, but often interpreted out of context. As this passage begins, Dar-
win has just finished discussing the ideas of various authors (not his own) on criteria for developing classifications (adaptive, inadaptive, reproductive, rudimentary, and embryological characters), and how mutually conflicting these characters can be. He then advances his own view that all of these features can be explained by descent with modification; and hence, if one were to accept this view, “the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, and, in so far, all true classification is genealogical.” Note that he is not saying that this is how taxonomy was practiced or understood in his day (it was not); rather, he is saying that if the patterns of variation can be explained by descent with modification, then a true classification would be strictly genealogical.

Moreover, for Darwin the resemblances that naturalists have been using all along are really genealogical. He immediately continues in the same vein (emphasis added): “that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike.” Darwin’s statement here reveals that similarity is not in itself a criterion for classification, but a means to understand genealogy. In that final phrase, in fact, he could be read as throwing cold water on the idea that degree of difference should have an intrinsically important role. Rather, he used similarities in (what we would call) both labile and conservative features, as well as in all stages of embryology, to try to understand genealogical relationships.

Ghiselin has long argued that genealogy was the only criterion of Darwin’s philosophy of classification, though some of his earlier work (Ghiselin and Jaffe, 1973) regarded Darwin’s view as closer to Mayr’s than to Hennig’s. In his 1969 book, The Triumph of the Darwinian Method, Ghiselin stated simply (1969:89): “It has already been demonstrated that Darwin considered ‘propinquity of descent’ the basis of natural classification. His motives have been explained as the consequence of a particular kind of nominalism: a taxon is a genealogical entity, not a class of morphologically similar organisms.” Ghiselin (1985) clarified this apparent paradox. He noted that Darwin’s view of the “Natural System” in use at his time “only roughly corresponds to the genealogical nexus. Since the amount of difference is expressed, it had to be done by means of categorical rank. However, [Darwin] did not endorse that step, but only enunciated what could better be read as a conditional statement.”

Ghiselin, like Nelson (1974), detailed Darwin’s treatment of the classification of humans in The Descent of Man as an example of how he subjugated ideas about degree of difference to those of genealogy, where it could be known (Darwin, 1871:181):

[N]aturalists have long felt a profound conviction that there is a natural system. This system, it is now generally admitted, must be, as far as possible, genealogical in arrangement—that is the co-descendants of the same form must be kept together in one group, apart from the co-descendants of another form; but if the parent forms are related, so will their descendants, and the two groups together will form a larger group.

Darwin argued in the following pages that humans have separated themselves from other animals largely by their degree of difference. “If man had not been his own classifier, he would never have thought of founding a separate order for his own reception...” (p. 188)... under a genealogical point of view, it appears that this rank is too high, and that man ought to form merely a Family, or possibly even only a Sub-family [p. 187]. Darwin recognized that man is “unequivocably” an offshoot of the Catarrhines (“Old World monkeys”), “and that, under a genealogical point of view he must be classed with [them].” (p. 189) Classification should not, to Darwin, be based on amount of difference, no matter how important the differences, but rather should be rooted strictly by the recognition of closest divergence from a common ancestral stock. When this point is known, the taxonomic rank will follow, as his examples above suggest.

Peter Stevens, in reviewing an earlier draft of this paper, astutely pointed out the im-
portance of distinguishing among Darwin’s uses of the words *genealogy*, *arrangement*, and *classification* (as for example in Chapter 13 of the *Origin*, discussed above). I had over-looked arrangement as a weak synonym of other terms, and agree that this should be regarded as a separate intellectual activity for Darwin. Some kinds of arrangements (i.e., genealogies with all intermediates present) could not be represented as classifications, and this was a problem that worried Darwin (see below). A set of related species can be arranged according to given criteria of characters and an idea of the rationale for this activity (“what you are aiming at” in Darwin’s words); a classification can be drawn from the results. These three terms are as different as are *systematics*, *taxonomy*, and *classification* (pace Simpson, 1961; Mayr, 1982). *Systematics* can be seen as the philosophy of organizing nature; *taxonomy* as the use of sets of organic data guided by systematic principles, which sort of sets will differ among taxa (teeth for fossil mammals, genitalia for flowering plants); and *classification* as the tabular or hierarchical end result of this activity. Darwin regarded *genealogy* as the overriding principle by which organisms should be ordered; he saw the *arrangement* of organisms as basically genealogical but varying in placement according to the evolutionary differentiation of features and the work of extinction in eliminating intermediate forms (see below); and *classification* as an expression of genealogy, ironically made possible in part because extinction had created visible divisions in the natural genealogical flow.

**Darwin’s Dual Criteria? Genealogy versus Similarity**

Up to this point, I have concentrated on clarifying Darwin’s disregard for the “Natural System” of his times, and how, in the *Origin of Species* and *The Descent of Man*, Darwin’s statements on classification advocate genealogy as its unique criterion (Nelson, 1974; Ghiselin, 1985). In contrast, Mayr (1982, 1994a, 1994b) has long championed the view that Darwin advocated the two criteria of genealogy and degree of similarity in classification. Much of the basis of this interpretation by Mayr and others (e.g., Ghiselin and Jaffe, 1973) has traditionally come from a passage in Chapter 13 (p. 413) of the *Origin of Species*:

> I believe that something more is included [in our classification], than mere resemblance; and that propinquity of descent—the only known cause of the similarity of organic beings—is the bond, hidden as it is by various degrees of modification which is partially revealed to us by our classifications.

It would be possible to infer from this isolated passage that Darwin was saying that resemblance should be involved in classification, but that another element, propinquity of descent, is what is really important. But Darwin is making a deeper point. In his other writings Darwin clearly says that the reason that we are able to rely as much on resemblances in our classification as we do is that common descent is what actually causes these resemblances, and that is why traditional classifications (unintentionally) reflect genealogy so well. In a passage on pages following the one quoted above (p. 420), Darwin attempts to explain his meaning more fully (emphasis in original):

> I believe that the arrangement of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical; but that the amount of difference in the several branches of groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders.

Mayr (1982, 1994a, 1994b) regards this as two criteria, but this interpretation is undermined by the plain difference between the “must be” of strict genealogy and the “may” of the amount of difference. Darwin chose his verbs carefully. As in the previous passage, Darwin is clearly saying here that the arrangement, and hence the classification, must be genealogical, even though differences among descendant taxa may vary widely. (He goes on to explain that differential extinction has forged these variable distinctions among taxa, whose ranks simply reflect the current absence of now extinct, transitional forms descended from
common ancestors.) The third verb in this passage expresses the fact that in current practice (in his day), this degree of modification is expressed by degrees of ranking, which may reflect the intermediate gaps, but he is not advocating this ranking practice for classification (i.e., the practical outcome of the arrangement of groups with respect to other groups). His following discussions explain his illustration of what might be called a genealogical arrangement, the only illustration in the book; and his analogy to the classification of languages that follows (p. 422–423) is strictly genealogical without any criterion of degree of similarity or difference entailed. Ghiselin (1985:460) has cited this passage, emphasizing Darwin’s (1859:422–423) acknowledgment that differences among languages “would have to be expressed by groups subordinate to groups; but the proper or even only possible arrangement would still be genealogical; and this would be strictly natural, as it would connect together all languages, ancient and modern, by the closest affinities”. “[I]f we had a real pedigree,” Darwin continued, “a genealogical classification would be universally preferred”. This point is clearly borne out in the passages on classification of humans cited above. So in these passages Darwin does not seem to be advocating “dual criteria” of genealogy and similarity.

Mayr (1982:210) has forcefully stated his view that, “In the Origin, and in his correspondence, Darwin stresses again and again that ‘all true classification is genealogical’ (p. 420), but ‘genealogy by itself does not give classification’ (L.L.D., II:247).” From this, Mayr (1994a) developed his concept that Darwin prescribed dual criteria for classification, which differentiate it from the “Hennigian” system (emphasis is added):

There are now two systems of ordering organisms in use—Darwinian classification, by which organisms are grouped according to both similarity and genetic relationship, and Hennigian ordering, by which organisms are grouped according to the branch of the phylogenetic tree on which they occur.

Mayr (1994b) reiterated this claim with respect to the Origin—though note a subtle change in wording:

Darwin showed that all classifications must be genealogical in order to reflect his theory of common descent. Furthermore, Darwin strongly emphasized that a second criterion was needed to achieve a sound classification, that of representing degree of similarity [1859:420]. Again and again Darwin stated, “Genealogy alone does not give a classification.” Darwin’s advice to base classifications on two criteria, genealogical relationship and degree of similarity, was more or less followed by all good taxonomists in the next 90 years. There was no need to designate this method as Darwinian because it was the only properly presented method of classifying.

In the passage quoted previously, Mayr has Darwin saying “again and again” that all true classification is genealogical, which I have emphasized with Nelson and Ghiselin is a correct statement. But in the passage just quoted, Mayr (1982:210; 1994a) also has Darwin saying “again and again” that “genealogy alone does not give a classification,” which I think is demonstrably false and which removes the underpinnings from Mayr’s “dual criteria” argument. Darwin never said anything like this in the Origin of Species. The Concordance to the Origin (Barrett et al., 1981) shows no use of the word “degree” in the book in association with the words “of similarity” or “of difference” in the context of classification, and no similar construction associated with any other word in this phrase. Darwin also never said the words “again and again.” He used the words “genealogies” and “genealogical” sixteen times in the Origin, and when he did so in the context of classification, it is clearly the only criterion under discussion. Mayr (1982:210) was originally correct in saying, “In the Origin, and in his correspondence, Darwin stresses again and again that ‘all true classification is genealogical’ (p. 420),” in contrast to his 1994a statement. But Mayr (1982:210) I think, was not correct in linking this fact to the conditional statement, “but ‘genealogy alone does not give classification.’” The latter phrase is a comment Darwin made in a December 1859 letter to Joseph Hooker, his friend and close correspondent, about the French botanist C. V. Naudin. But Mayr has taken it out of context, and its origins are both complex and revealing.

In the months following the publication of the first edition of the Origin of Species,
the flush of criticism from people who misunderstood and wanted to pillory Darwin for his ideas was bizarrely complemented by others who wanted to take credit for them (see, e.g., Hull, 1983; Desmond and Moore, 1991). Naudin’s colleague Joseph Decaisne, an editor of the *Revue Horticole*, had represented to Hooker that Naudin had already published many of Darwin’s ideas in that journal in 1852. Darwin replied to Hooker, who had sent him Naudin’s article. Darwin was mostly concerned with his own priority for the idea of Natural Selection, but he directed a few comments at Naudin’s statements on classification in the last long sentence of this passage (CCD 7:443–444):

I am surprised that Decaisne should say it was same as mine. Naudin gives artificial selection as well as a score of English writers; & when he says species were formed in same manner I thought the paper would certainly prove exactly the same as mine. But I cannot find one word like the Struggle for existence & Natural Selection. … He assumes (like old geologists assumed the forces of nature were formerly greater) that species were at first more plastic. His simile of tree & classification is like mine (others), but he cannot, I think, have reflected much on subject, otherwise he would see that genealogy by itself does not give classification. I declare I cannot see much closer approach to Wallace & me in Naudin than in Lamarck—we all agree in modification and descent.

What did Naudin really say? The long passage from Naudin that concerns us here (1852:105–106) begins with the recognition that species are simply varieties that have been separated for a much longer period of time. Taken a step farther, all of nature shares a consanguinity that reflects a commonality of origin, and in turn is reflected by a commonality of organization that is classification. Exactly as Darwin did in the *Origin*, Naudin went on to criticize the contemporary system in which resemblances were thought to be fortuitous, merely adaptive, or independently created. To the contrary, these resemblances are the consequence of a real parentage and inheritance from a common ancestor. Hence, Naudin said (1852:105–106; my translation; emphasis in original),

In our system, by contrast, these resemblances are at the same time the consequence and the proof of a parentage, no longer metaphorical, but real, that they inherit from a common ancestor, from which they have descended over more or less remote epochs and through a more or less numerous series of intermediates; such that we would explain the true relationships among species by saying that the sum of their reciprocal analogies [similarities] is the expression of their degree of common parentage, as the sum of their differences is that of their separation from the common stock from which they originated.

Seen from this point of view, the vegetable kingdom would no longer present itself as a linear series whose ends would run along lines of increasing or decreasing complexity of organization, whether one examined it beginning at one end or the other; it would no longer be a disorganized tangle of intercrossed lineages, nor even a geographic map whose regions, different in shape and extent, would be connected by a greater or lesser number of points; it would be a tree whose roots, mysteriously hidden in the depths of cosmic time, would have given rise to a limited number of stems that successively divided and subdivided. These first stems would represent the primordial types of the kingdom; their last branches would be the living species.

It follows from this that a perfect and rigorous classification of organic beings of the same kingdom, order, and family would be nothing but the genealogical tree of these species itself, showing the relative age of each one, its degree of spécificité [he means by this something incorporating both degree of divergence and also the integrity of the phenotype of a species] and the ancestral lines from which it descended. But how this would be represented, in a somewhat palpable and material way, the different degrees of common ancestry among species, as well as those of groups of diverse degrees, going all the way back to the primordial types. Such a classification, summarized in a written table, would be perceived with equal ease by the mind as well as the eyes, and would present the best application of the principle generally admitted by naturalists: that nature is miserly with its causes and prodigal with its effects.

It is clear from the first paragraph that Naudin fully accepts descent with modification and goes on to say that classification should reflect this. But he never said that genealogy gave classification in practice; like Darwin, he said that it should do so, in contrast to the system in use in their time, and perfectly in agreement with Darwin’s views. In fact, Darwin could almost have written Naudin’s last paragraph himself.

How did the confusion arise? One interpretation is that Darwin appears not to have recognized that Naudin was writing in the conditional tense, manifest in every verb in this passage (résulterait instead of resulte; seraient instead of sont). In other words, everything that Naudin was saying repre-
sented an ideal, not reality. Could Darwin have misinterpreted Naudin? The phrase in question is only one point of several that Darwin treated in his hasty letter to Hooker (Darwin’s haste is evidenced in his run-on sentences, abrupt transitions of topic, and omissions of articles that were typical of his quick notes to his friend). By all accounts, Darwin’s French was less than fluent, and he may have read Naudin’s passage quickly. Darwin was far more interested in Naudin’s treatment (or omission of) artificial selection, natural selection, the struggle for existence, and decreasing variability through time, than in the treelike approach to classification. In 1860, when he determined to add an “historical sketch” of Natural Selection and related ideas to the second edition of the Origin of Species, Darwin wrote to Hooker (CCD 8:60) asking for a sentence from Naudin’s paper dealing with the principle of finality. In his sketch he treated Naudin’s views on selection and the formation of species with his usual polite circumlocution, but he could not resist a jab about Naudin’s underlying explanation of “finality.” He did not mention Naudin’s views on classification and never seems to have thought of them again.

Regardless of Darwin’s reading of him, Naudin’s meaning is clear. But more important for our purposes is what Darwin was talking about in his letter to Hooker. Darwin did not mean should when he said “genealogy alone does not give classification.” In other words, he meant that in practice it does not, and he could not see how Naudin (as he thought) could say that it did. But in all other statements on the subject, as shown above, Darwin firmly believed that ideally, genealogy should give classification.

This statement of Darwin’s concerning Naudin’s views is essential to the argument that Darwin felt that classification should not be based on genealogy alone (Mayr, 1982, 1994b, 1995). Because it is plain that Darwin misinterpreted Naudin’s views, the phrase in question provides no support for that argument. The contradiction between this statement of Darwin’s and his other views on classification did not escape Os-
cially in the light of more recent discoveries, interpretations, and classifications.

The barnacle papers are in most respects characteristic of taxonomic monographs from Darwin’s day to this, in that evolution and genealogy are topics subjugated to enumerating, describing, distinguishing, and evaluating characters and taxa, and such judgments have their own reasonable subjectivity and logic. In fact, in the barnacle monographs, there is hardly any attempt to document evolution; there is no statement of systematic philosophy; and virtually the only attempt to put any kind of evolutionary perspective to the classification is Darwin’s inference that sessile barnacles evolved from stalked ones, because the latter are geologically older. Ghiselin (1969) masterfully showed how much Darwin transcended most systematic work of his day by introducing considerations of correspondence in larval form, sexual dimorphism, and adaptive modifications to taxonomy, in an effort to reflect evolutionary change; but these considerations were largely inferential and implicit, not explicit. That is, we can read them now if we look for them, but few in Darwin’s time would have grasped these subtleties. Ghiselin (1969:105) acknowledged that Darwin nowhere discussed the relationship between evolutionary theory and systematics and nowhere laid out a philosophy of classification.

One can, of course, search the monographs for evidence that Darwin followed one or another practice of recent schools of thought. He eliminated some polyphyletic taxa, and he reduced some paraphyly: “For example, he could have used the ‘amount of difference’ to separate the Cirripedia from the Crustacea, but he did not” (Ghiselin, 1985; see also Ghiselin and Jaffe, 1973). On the other hand, he chose not to group the 11 genera of Lepadidae into subfamilies (1851b:64), even though he recognized their long history and considerable (overlapping) divergence. But he was not wrestling with our problems. His first problem was to determine the point at which cirripedes could be separated from other crustaceans, and so reveal their taxonomic rank. This was difficult, as he showed (1854b:17–18), because authorities of the time conferred degree of rank based on factors such as species diversity, degree of difference, or “perfection of organs” as being “high” or “low” in relation to a standard type (letters from Darwin to Waterhouse in 1843 [CDD 2:378] express his frustration with this). Darwin wrestled with all these, hoping to offend no one, and finally sided with Dana and against Milne-Edwards (to whom the work was dedicated in recognizing Cirripedia as a subclass of Crustacea, rather than a subgroup of entomostracan crustaceans. Genealogy, at this point, never explicitly entered the question. Darwin does not say that the differences that separate barnacles from other crustaceans reflect their deep genealogical divergence, he simply contrasts their similarities and differences. Yet even a decade earlier he was vehemently stressing to Waterhouse that classification should be based on genealogy alone, and he was still doing it in *The Descent of Man* in 1871. This is the real paradox of the barnacle monographs.

Among the characters Darwin considered, he tried to look for unusual or unique resemblances, and some of these are clearly what cladists would call “derived.” But it cannot be said that Darwin methodically searched for what we would call synapomorphies. He gave considerable attention to weighting embryological and other “conservative” characters traditionally considered important in taxonomy (Ghiselin and Jaffe [1973] and Newman [1993] provided well-detailed examples). For example, he chose to evaluate the unusual cirripede *Cryptophialus* on the basis of its conservative female morph, not on the complementary male form. But at the same time, he was tempted to group *Cryptophialus*, to which he gave its own order, with *Alcippe* on the basis of what we would call uniquely shared features (1854b:564–566).

On the other hand, Darwin seemed to use both general “affinity” and “degree of similarity” to classify some barnacles. His erection of the lepadid genus *Oxynaspis* (1851b:133), for example, reflected its similarities in various features to those of *Lepas*, *Paecilasma*, and *Scalpellum* without being able to place it in any of these. This would
seem to support Mayr’s view that Darwin used both genealogy and similarity as taxonomic criteria. But Darwin was not being precise about genealogy here (Ghiselin and Jaffe, 1973:Fig. 1); in fact, genealogy was shrouded by the intricate and parallel adaptive modifications of these taxa. Rather, Darwin understood that at some level all these forms, and doubtless others, had evolved from a single common ancestor. In the course of their divergence they retained and elaborated some characteristics of that lepida-did ancestor, while differentiating in other ways; “and this is what might have been expected,” Darwin concluded, “for it is the most ancient family, and extinction has done its work, separating genera which, in accordance to analogy, we may suppose were once more nearly connected by intermediate forms” (Darwin, 1854b:32; emphasis added).

In other words, Darwin was trying to solve the same problem over and over. Visualize an evolving lineage growing upward, and separating as it grows into various branches; now transect the tree’s upper reaches with a horizontal plane. The plane represents our current slice of time. From this slice, the problem is to trace the divergence of the branches, using only present forms, given that extinction has removed the intermediates. This is how genealogy would have to be discovered. Darwin did not explicitly search for synapomorphies; he searched for any similarities that would reveal genealogy, as taxonomists still do—on the basis of what seem to be valuable characters.

As Ghiselin and Jaffe (1973) noted, Darwin “was formulating a system for his times, and the times were not yet ripe for a strictly genealogical arrangement”—at least one that would have had to be argued as strongly as cladists have argued their philosophy since the 1970s. It is unlikely that Darwin wished to take up that particular cudgel at the time (or could have), given his larger plan. I think, with Ghiselin (1985), that it is a mistake to read too much systematic philosophy into these monographs. For one thing, Darwin never classified any barnacle on the basis of genealogy, which is indisputably regarded as his central criterion—even though, by the 1850s, it clearly underlay his ideas (as his 1843 letters to Waterhouse show). To argue on the basis of the barnacle monographs that Darwin regarded similarity as an equally important criterion, merely because he uses similarities in his taxonomy, makes no sense, because the entire concept of genealogy is suppressed.

Why didn’t Darwin bring genealogy more strongly into his barnacle monographs? The simplest explanation, though circumstantial, is consistent with Darwin’s long secrecy on many of his views. To establish genealogy as the basis of classification for barnacles, he would have had to establish the evidence for the common origin and descent of all living things at the same time. With his great book in a premature stage of gestation, he obviously did not want to let the cat out of the bag too early (Desmond and Moore, 1991). Accordingly, he produced a conventional taxonomy that addressed the issues of his day. Recall that he undertook the whole exercise to begin with because of a stray remark in a letter from Hooker (regarding Gérard’s views on species: CCD 3:250–256), who seemed to suggest that Darwin’s own theories might not be taken seriously unless he had himself labored in the taxonomic vineyards. Darwin used similarities not to construct classifications, but to reveal common ancestry on which classifications should be based. His greatest impediments to this were the gaps among living forms and between living and fossil forms. He used neither primitive nor derived character states on principle; he did not mind what we would call “paraphyletic” taxa if he could not resolve their membership more definitively; and he did not advertise his view that classification should be based on genealogy.

**CONCLUSION**

In his book on the fertilization of orchids (1862:330–331), Darwin wrote,

To make a perfect gradation, all the extinct forms which have ever existed, along many lines of descent converging to the common progenitor of the order, would have to be called into life. It is due to their absence, and to the consequent wide gaps in the series, that we are enabled to divide the existing species into definable groups . . . . If there had been no extinction,
there would still have been great lines, or branches, of special development,—... but ancient and intermediate forms, very different probably from their present descendants, would have rendered it utterly impossible to separate by distinct characters ... one great body from another.

Because living things have suffered differential extinction, we have only incomplete series of related forms; because we cannot seriate their entire genealogies, we must rely on their shared similarities to reconstruct that genealogy. This seems to me the closest approach that we can make to Darwin's view of classification.

The preponderance of available evidence indicates that Darwin's only criterion for classification was genealogy, a point he summarized in the last chapter (p. 486) of the *Origin of Species*, when he was describing the effects that will accrue (again, in a conditional future) to natural history if and when common descent is recognized as the central underlying principle of biological phenomena: “Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation. The rules for classifying will no doubt become simpler when we have a definite object in view.” This last sentence, as the reader will see, recurs to the phrase in the letter he wrote long before to Waterhouse, quoted above. Hence, I conclude, it is difficult to accept Mayr’s case for “dual criteria” of genealogy and similarity in Darwin’s views on classification. There is certainly enough ambiguity to allow room for interpretation in many of his passages, taken by themselves, but in larger context the argument does not hold up very well. The interpretation that Darwin used similarities to get at genealogy seems to explain more of the available evidence. Moreover, Darwin in taxonomic practice was not particular about what we would call “primitive” and “derived” similarities, nor about paraphyletic groups when strict genealogy could not be discovered. It is not relevant to force Victorian sensibilities into 20th century modes. Just as Darwin was neither a cladist nor a Linnean, it is not historically faithful to graft the taxonomic philosophies of the Modern Synthesis or those of phylogenetic systematics onto his ideas and practices.

**ACKNOWLEDGEMENTS**

I thank Stan Rachootin, Adrian Desmond, Kevin de Queroz, David Cannatella, David Lindberg, Wendy Olson, M. P. Winsor, Keith Benson, Mickey Rowe, and Jeremy Ahouse for comments and helpful conversations, while holding them blameless for any errors on my part. I am particularly grateful to Michael Ghiselin for his patience and generosity with ideas, and to Peter Stevens for his trenchant insight on the difference between classification and arrangement. Special thanks to Peter-John Leone and Robin Smith for providing copies of Darwin’s edited correspondence, and to Jim Valentine for the long loan of rare Darwiniana. This is University of California Museum of Paleontology Contribution No. 1685.

**REFERENCES**


**Darwin, C.** 1851b. A monograph on the sub-class Cirripedia, with figures of all the species: The Lepadidae, or pedunculated cirripedes. Ray Society, London.


**Darwin, C.** 1854b. A monograph on the sub-class Cirripedia, with figures of all the species: The Balanidae (or sessile Cirripedes); the Verrucae, etc., etc., etc. Ray Society, London.


**Darwin, C.** 1862. On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. John Murray, London.

Received 21 August 1998; accepted 11 November 1998
Associate Editor: R. Olmstead