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Symposium 49
The Historical Impact of Ornithology on the Biological Sciences

Convenor: P.L. Farber

Introduction

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The study of birds, in addition to being interesting in its own right, has been of central importance in the development of what we now call the biological sciences. Ornithology has been a model and a pioneer in such areas as systematics, behavior, and evolutionary theory. The history of ornithology usually focuses on the internal development of the study of birds, or the broader context in which that study took place. Rarely has the significance of ornithology for the biological sciences been explored. The papers that follow explore some of the areas in which ornithology has played a key role.

Diagrammatic Classifications of Birds, 1819–1901: Views of the Natural System in 19th-century British Ornithology

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Abstract
Classifications of animals and plants have long been represented by hierarchical lists of taxa, but occasional authors have drawn diagrammatic versions of their classifications in an attempt to better depict the "natural relationships" of their organisms. Ornithologists in 19th-century Britain produced and pioneered many types of classificatory diagrams, and these fall into three groups: (a) the quinarian systems of Vigors and Swainson (1820s and 1830s); (b) the "maps" of Strickland and Wallace (1840s and 1850s); and (c) the evolutionary diagrams of the post-Darwin authors (1860 on). The quinarians distinguished between affinity and analogy and used both in their classifications, whereas Strickland rejected the quinarians' belief in numerical regularity and their use of analogy. Wallace's "maps" are easily given an evolutionary interpretation, and his approach was taken up and modified by later evolutionary anatomists. Sharpe returned to Strickland's methods and merely appended a superficial evolutionary interpretation. Contrary to common belief, systematics has a rich conceptual history, and many of the conceptual developments in 19th-century systematics were made by ornithologists.

Introduction

Throughout the history of systematics, classifications of animals and plants have most often been represented by hierarchical lists of names, those of Linnaeus's "Systema Naturae" being archetypal examples. Occasionally, however, systematists have drawn diagrammatic versions of their classifications in an attempt to better represent the "natural relationships" of their taxa. This paper is a review of such diagrams as they were used by ornithological systematists in England during the 19th century. I have divided the interval covered in this paper into three periods—the Quinarian (1819–1840); Mapmaking (1840–1859); and Evolutionary (1859–1901)—and will consider them sequentially. I end my analysis at 1901, the year of an important paper by P.C. Mitchell; after that date, interest in the higher classification of birds declined significantly, and microtaxonomy, the study of species, became the principal focus of systematic research.

Previous studies that discuss classification diagrams include Lam (1936), Wilson and Doner (1937), Voss (1952), Greene (1959), Stresemann (1975), Winsor (1976), Nelson and Platnick (1981), Stevens (1982, 1984b), and Gaffney (1984). General studies of the natural history or ornithology of the period may be found in Stresemann (1975), Farber (1982), Mayr (1982), Rehbock (1983), and Stevens (1984a). Systematics has been among the most neglected of the biological disciplines from the historian's point of view, partly because of a belief that its history is featureless. It has often been said, for example, that even the Darwinian revolution of 1859 had no effect on systematics (Simpson 1945; Mayr 1982). I hope to show here that contrary to common belief, systematics had a complex and conceptually rich development all through the 19th century, both before Darwin and after. Some of the developments in pre-Darwinian systematics may have been important in the emergence of evolutionary thinking, whereas the many post-Darwinian changes were based both on new ideas resulting from evolutionary thought and on reversions to certain earlier, pre-evolutionary conceptions.

Quinarian Period, 1819–1840

At the beginning of the 19th century, natural history was one of the most rapidly expanding fields of human knowledge, and voyages of exploration and colonization were bringing a wealth of new biological material to the museums of Europe (Farber 1982). This wealth of new material did more than enlarge museum catalogs, however; it provided, for those naturalists who looked beyond their workbenches, the impetus for a complete reassessment of the structure of natural creation. The extraordinary diversity of form, and the intricate similarities and differences that naturalists of the early 1800s saw, convinced them that living diversity could no longer be arranged in the simple, single chain of being that had been believed in throughout the Middle Ages and the Renaissance. The system of nature, they began to realize, must have a more complex structure.

We know today that this more complex structure is the structure of a tree, because natural diversity has been produced by a branching process of evolution. But in the pre-evolutionary period, trees were only one of a number of possible structures under consideration. Among the more popular systematic philosophies of the early 19th century was quinarianism, or circular classification, which was first proposed by the entomologist William Sharpe Macleay in 1819. Macleay's principal disciples were Vigors and Swainson, and it was Swainson's ornithological writings perhaps more than Macleay's original work that gave quinarianism its wide exposure.

Quinarianism takes its name from the emphasis it places on the number five: all taxa, the quinarians argued, are naturally divisible into five subgroups, each subgroup into five sub-subgroups, and so on. This can be seen in Fig. 1, which is one of Vigors's illustrations of his classification of birds. But numerical

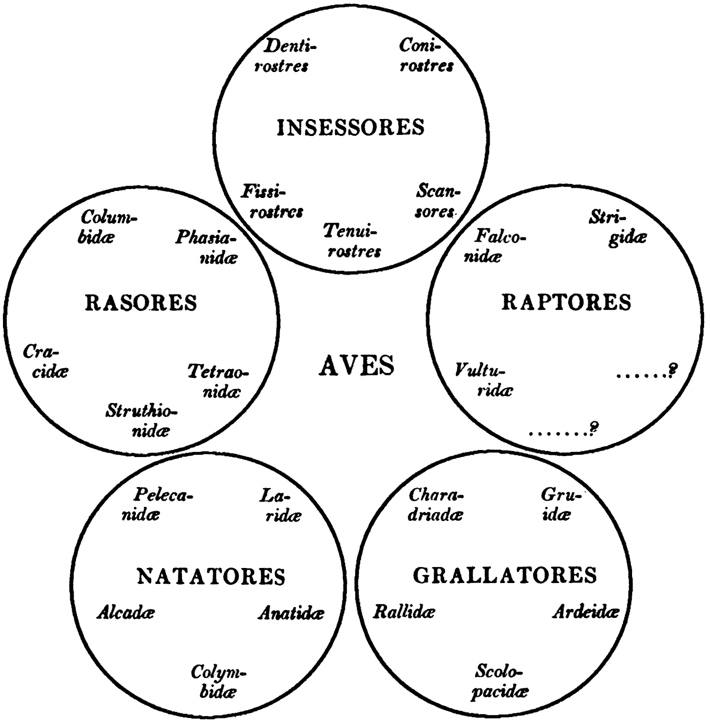

Figure 1. The circular affinities among the orders and families of birds according to Vigors (1824). Question marks indicate taxa that were believed to exist, but had not yet been discovered.

regularity was only one of a number of elements in the quinarian position, and it has received undue emphasis (e.g., Nelson and Platnick 1981). The central concept of quinarianism was the belief that two types of relationships may obtain among taxa: relationships of affinity, and relationships of analogy (Swainson 1835):

> It is evident that all natural objects possess two different sorts of relationship: one which is *immediate*, and another which is remote. The goatsucker and the swallow exemplify the first of these relations. These genera are intimately connected by structure, habits, and economy . . . but the goatsucker, besides this relation, has evidently another to the bats,—by flying at the same hour of the day, and by feeding in the same manner. The first relation is *intimate*—the latter *remote*. Hence arises the necessity, imposed upon all who wish to develope the natural system, of possessing clear perceptions of these two sorts of relations; and of becoming well acquainted with the difference between *affinity* and *analogy*. The first is exemplified by the swallow and the goatsucker; the latter by the goatsucker and the bat.

This distinction between affinity and analogy may have preceded quinarianism to some extent, but the followers of Macleay believed they were the first to develop it thoroughly (Vigors 1824).

Another notion central to the quinarian position was the belief that the affinities among taxa formed circular chains, so that if A showed affinity to B, and B to C, and C to D, and D to E, E would always show affinity back to A. This can be seen in Fig. 1 and Fig. 2, which is from Swainson (1836–1837). Figure 2 also shows the analogies among the taxa, by means of dotted lines. The quinarians claimed that analogies always subtended between taxa in the same positions in different circles of affinity, and that five "primary types of nature" were represented in every circle. The raptorial birds, for example, were clearly the cats of the avian class, just as the swimming birds (Natatores) were the analogs of the cetaceans. This "law of representation," that the five "primary types" were always represented analogically in every circle, was a great boon to the systematist, Swainson claimed, because it provided a test of any proposed circle of affinity: if the taxa in the circle did not show the proper analogies to taxa in other circles, their affinities had been incorrectly determined. "No law of the natural system is more calculated to keep in check the ardour of the imagination than this" (Swainson 1835).

Mapmaking Period, 1840–1859

Paradoxically, one of the greatest weaknesses of the quinarian position was that it had been very thoroughly presented. Macleay's original treatment was lengthy, and Swainson's elaborations filled a number of volumes. Critics therefore had a very clearly defined target, and the most carefully worked out attack on the quinarians came from Hugh Edwin Strickland. Strickland's 1841 paper, confidently titled "On the true method of discovering the natural system in zoology and botany," used the kingfishers and their allies to exemplify a new approach (Fig. 3) to the study of natural diversity, an approach that he claimed was purely inductive:

> The plan proposed is to take any species, A, and ask the question, What are its nearest affinities? If after examination of its points of resemblance to all other known species, it should appear that there are two other species, B and C, which closely approach it in structure, and that A is intermediate between them, the question is answered, and the formula BAC would express a portion of the natural system . . . . Then take C, and ask the same question. One of the affinities that of C to A, is already determined; and we will suppose that D is found to form its nearest affinity on the other side. Then BACD will represent four species, the relative affinities of which are determined. By repetition of this process . . . the whole of organized creation might be ultimately arranged in order of its affinities, and our survey of the natural system would then be finally effected.

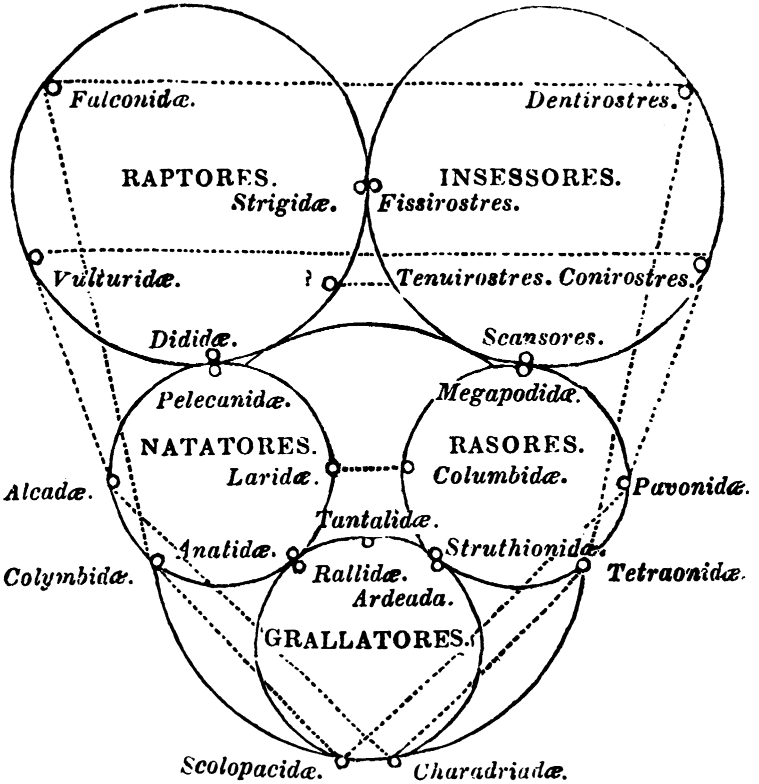

Figure 2. Affinities and analogies among the orders and families of birds, from Swainson (1836–1837). Nelson and Platnick (1981) interpret this diagram incorrectly; the taxa in each circle have affinity to one another, and the circles are connected by affinity at their points of contact, whereas the dotted lines indicate relationships of analogy.

This procedure, which Strickland elsewhere compared to the geographical surveying of an unmapped territory, may also uncover "lateral ramifications" of affinities, not just simple chains. Further, "these ramifications may occasionally anastomose and form a circle," and this was what led some to adopt the quinarian view; however, such circles are of irregular size and have none of the numerical symmetry the quinarians claimed they had. Strickland (1841) believed that the branches and loops of the natural system might be very complex, but how complex, he did not know:

> whether they are so simple as to admit of being correctly depicted on a plane surface, or whether, as is more probable, they assume the form of an irregular solid, it is premature to decide. They may even be of so complicated a nature that they cannot be correctly expressed by terms of space, but are like those algebraical formulae which are beyond the powers of the geometrician to depict.

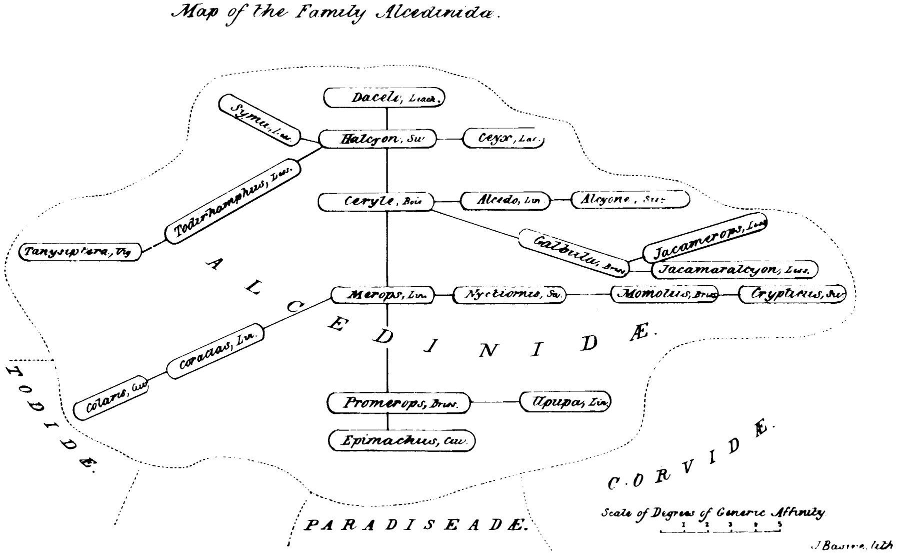

Figure 3. Strickland's (1841) "map" of the affinities of the kingfishers and their allies. The distances among the taxa can be measured by the "Scale of Degrees of Generic Affinity" seen in the lower right. Sharpe's (1868–1871) map (Fig. 7) is modeled directly on this figure.

Strickland rejected not only the two-dimensional, planar nature of quinarian classification, but also the notion that relationships of analogy have a place in systematics. Affinity, said Strickland (1841), determines "the place of a species in the natural system," whereas analogy is "in no way involved in the natural system."

After Strickland's death in 1853, his approach was explicitly taken up in an ornithological work by Alfred Russel Wallace. One of the two diagrams from this paper (Wallace 1856) is shown in Fig. 4. Like Strickland, Wallace rejected the use of "mere analogies" in systematics, but he ignored the possibilities of circular and multidimensional affinities, which Strickland had admitted, concentrating instead on branch structure. He also made an important modification, which makes an evolutionary interpretation of these figures easier: he began to remove taxa from the nodes of the diagrams and place them at the ends of branches (compare Fig. 3 with Fig. 4). The lengths of the branches he thought would be more appropriately occupied by extinct taxa, because "in very few cases is there a direct affinity between two groups, each being more or less distantly related to some common extinct group" (Wallace 1856). A year earlier, in his "Sarawak" paper (Wallace 1855), Wallace had argued that the results of species-level systematics accorded with an evolutionary view of nature. Here the implicit argument is that the results of higher classification also agree with evolution. All that Wallace needed was an evolutionary mechanism, natural selection, which he of course provided in another 2 years.

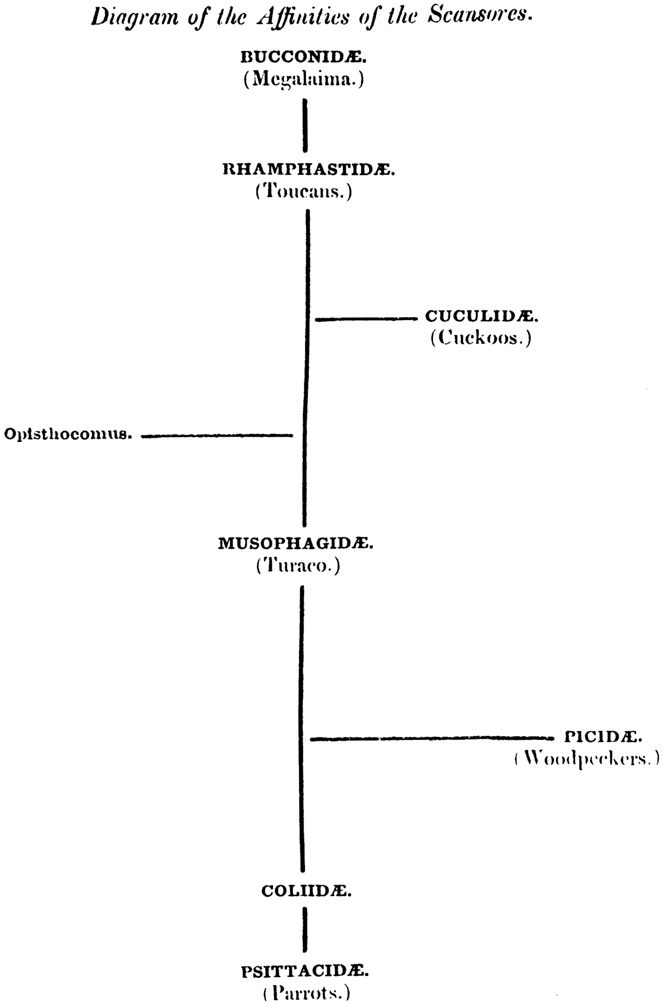

Figure 4. Wallace's (1856) diagram of the affinities of the scansorial birds. Wallace credits Strickland with being the first to use diagrams of this type, but Strickland's diagrams differ from Wallace's in having taxa at all nodes.

Evolutionary Period, 1859–1901

The conceptual development of systematics in the 40 yr following the publication of Darwin's "Origin" is very complex and cannot be treated adequately in a short space. All I will attempt to do here is outline two divergent paths taken by the major British workers during this period, one based on Strickland's original methods, and the other on Wallace's modifications of them. The latter path restructured the entire field of systematics and gave it a new purpose: reconstructing the history of life. The former, deriving directly from Strickland, retained intact his pre-evolutionary purpose for systematics—determining the "affinities" of taxa—and appended a relatively unimportant evolutionary

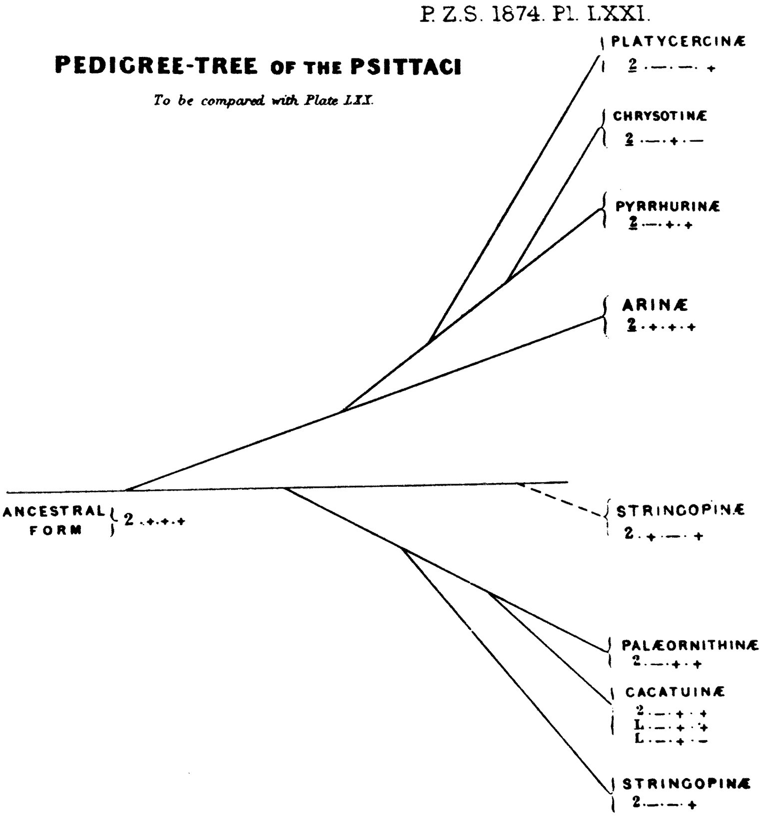

Figure 5. Garrod's (1874) "pedigree-tree" of the parrots. The lineages shown are not all cladistically monophyletic. Garrod was the first worker to show character distributions on his trees.

dimension that was clearly secondary to the primary goal of determining affinities.

Wallace's Approach Carried Through

The late 19th century was a golden age of comparative anatomy, and the center of anatomical research in England at the time was the Zoological Society of London. The Prosectors and other officers of the Society had the opportunity to dissect taxon after taxon never examined anatomically before, and the abundance of new anatomical variation they discovered, and the need to organize it in some way, led them to take a considerable interest in the methods of systematics. I will examine here the work of Arthur Henry Garrod, who was Prosector to the Society during the 1870s, and Peter Chalmers Mitchell, the Society's Secretary (a position first held by Vigors) near the turn of the century. Garrod and Mitchell devoted more time to the discussion of systematic methods than did any of their contemporaries, and so provide us with the greatest insight into the thinking of the day.

Garrod's most thorough exposition of his approach to systematics is contained in his 1874 paper on the anatomy and evolution of parrots. This paper contains two classification diagrams, one a tree and the other a nested set of circles. The tree is shown here as Fig. 5. Although this diagram superficially resembles a modern cladogram, it is not a cladogram, and considerable care must be taken to understand its production. Garrod's first step was to reconstruct a hypothetical parrot ancestor by examining the anatomical variation in parrots and related groups and then applying a somewhat vague mixture of the principles today called outgroup comparison, common-is-primitive, and Dollo parsimony. Once the characters of the ancestral parrot had thus been determined, Garrod identified the groups (Arinae and Palaeornithinae) that differed in the fewest respects from the ancestor and made them the two main branches of the tree. (I omit consideration of the Stringopinae, of whose position Garrod was uncertain.) The other groups then branch off from these according to their further deviations from the ancestor. Note that although the Arinae and Pyrrhurinae are shown as single lines, Garrod's set diagram, not reproduced here, makes it quite clear that they are in fact paraphyletic groups of genera. It is also clear that the branching order shown in the diagram, e.g., of the Platycercinae and Chrysotinae, is not meant to convey the relative sequence of events; all that is meant is that the Platycercinae and Chrysotinae are both derived from within the paraphyletic Pyrrhurinae.

Garrod's work was novel in that he specifically tried to reconstruct the characters of ancestral taxa and chart the course of character change through evolution. Indeed, Garrod's whole emphasis on characters and character change is relatively novel; previous workers had tended to speak of taxa being in their entirety "close to" or "far from" one another, rather than differing and being similar in particular respects.

The approach to character analysis begun by Garrod reached its culmination in the work of Peter Chalmers Mitchell 25 years later. Mitchell, in his 1901 paper on avian intestinal configurations, distinguished completely and precisely between what are now called primitive and derived states of characters (he called them archecentric and apocentric), and between uniquely derived (uniradially apocentric) and multiply derived or convergent (multiradially apocentric) characters. He recognized that the joint possession of primitive or archecentric characters is not an indication of relationship and cannot be used as evidence to unite branches of the evolutionary tree. Mitchell's paper contains many tree diagrams, one of which is shown here as Fig. 6. These diagrams, Mitchell emphasized, illustrate the history of character change and not necessarily the phylogeny of the taxa; they are what we would today call character-state trees. What Mitchell did not have, that we believe we have today in outgroup comparison, was a way of determining character polarity—the evolutionary direction of change.

The Return to Strickland

While Garrod, Mitchell, and the other anatomists of the Zoological Society of London were refining their techniques for reconstructing the history of life, Richard Bowdler Sharpe of the British Museum was taking systematics in another direction, continuing from where Strickland had left off in the 1840s.

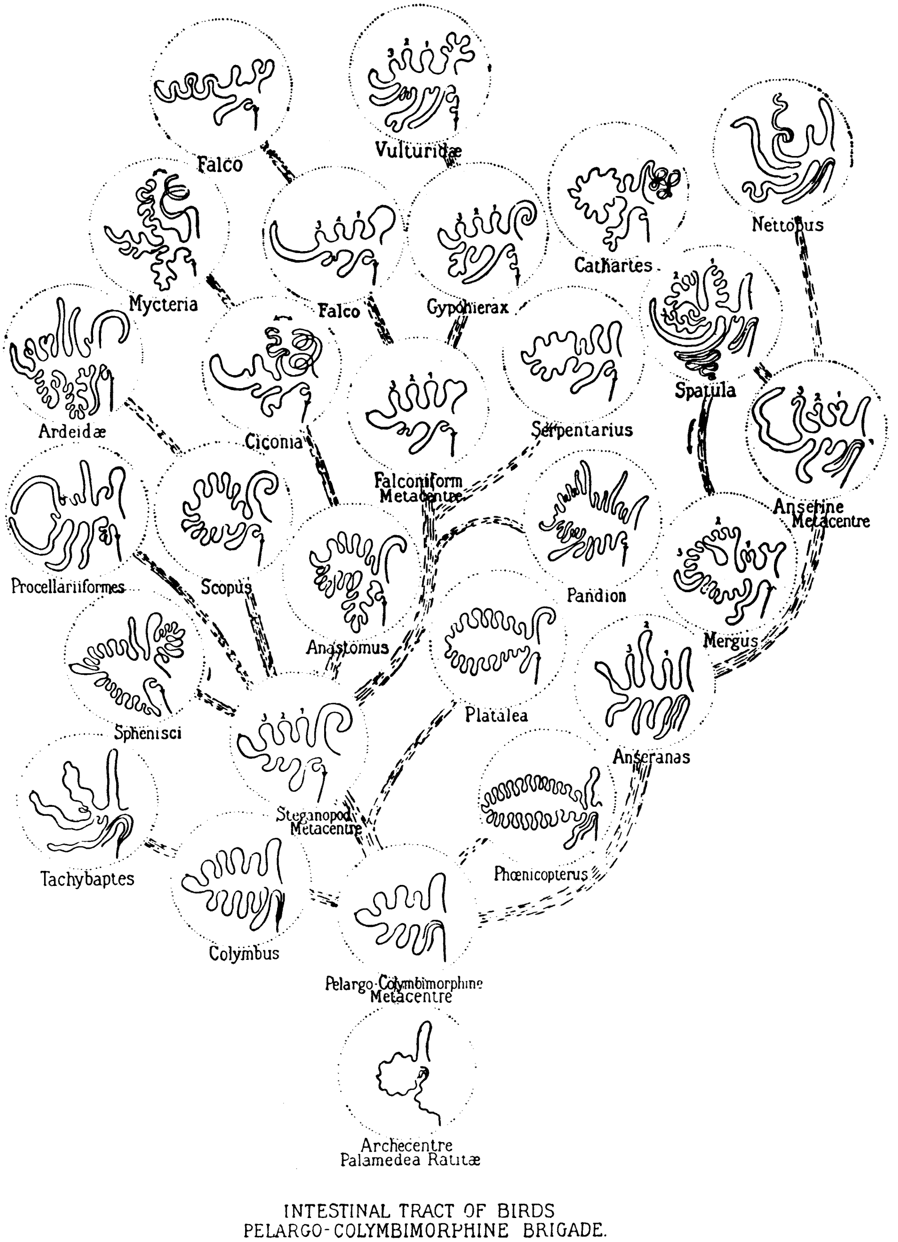

Figure 6. The evolution of the intestinal tract of the pelargo-colymbimorphine birds, from Mitchell (1901). Mitchell emphasized that this is what would now be called a character-state tree, and that it did not necessarily show the true evolutionary relationships of the taxa.

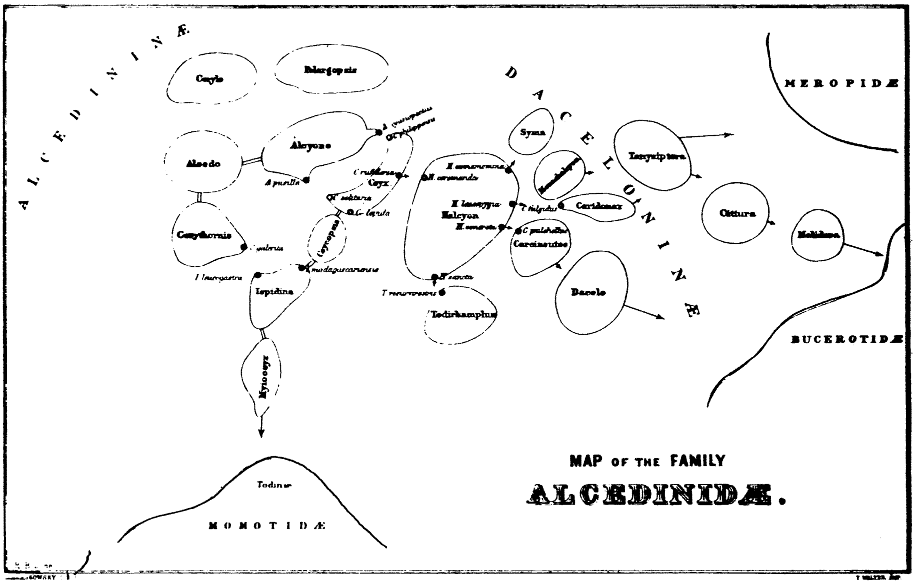

Figure 7. "Map of the Family Alcedinidae," from Sharpe (1868–1871). The original of this map is colored, the five genera in the upper left being pink, and the others green. This illustration is directly modeled on Strickland's map of the same group (Fig. 3). The evolutionary tree corresponding to this map is shown in Fig. 8.

Sharpe was one of the most prominent and most precocious museum ornithologists of his day, publishing his first major work, an illustrated monograph of the kingfishers (Sharpe 1868–1871), when he was in his twenties. Kingfishers were the birds Strickland had used to exemplify his "true method" in 1841, and it was quite natural for Sharpe to view his own monograph as a revision of Strickland's work. He therefore produced, as the frontispiece of his book, a "Map of the Family Alcedinidae," modeled on Strickland's map and reproduced here as Fig. 7. Sharpe's map, like Strickland's, shows the "relationships" or "affinities" of the kingfisher genera, but Sharpe was writing in the Darwinian era and so had to take evolution into account as well. Rather than "rooting" the map at some point, as we might expect him to do, Sharpe instead created, by completely unspecified means, an independent evolutionary tree (Fig. 8), which he suspended below the map.

Sharpe reaffirmed his faith in this approach to systematics in his review of bird classification read at the Second International Ornithological Congress in Budapest (Sharpe 1891). In this paper, Sharpe presented a map of the entire class (Fig. 9). From this map, Sharpe drew up a "phylogenetic scheme," not shown here, which was similar to the kingfisher phylum, only much wider. Like the kingfisher tree, it contained almost no branching structure. If one were to "take flight in an imaginary balloon," said Sharpe (1891), and look down on this avian evolutionary tree, the view seen would be that of the map (Fig. 9).

Although he was writing during the same years as Garrod and Mitchell, Sharpe was actually an ornithologist of a new breed: a species specialist. His

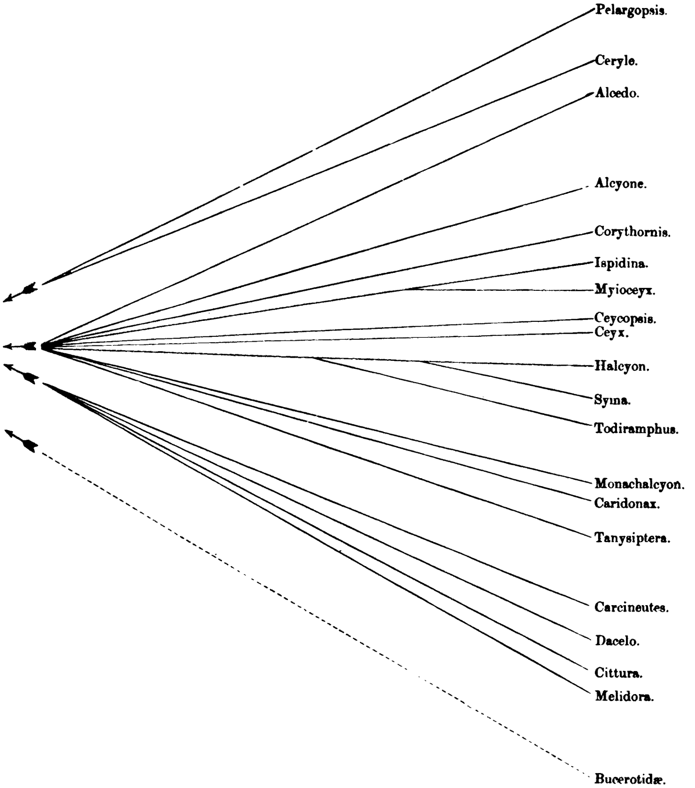

Figure 8. A "phylum" of the kingfishers, corresponding to the map shown in Fig. 7, from Sharpe (1868–1871). Observe that the tree has very little branching structure. The side branches that are shown (e.g., *Syma*) are for highly differentiated taxa whose recognition renders their parent genera (e.g., *Halcyon*) paraphyletic.

studies of the higher classification of birds were largely based on the published writings of others. From his work in the British Museum, he concluded that "a man can hope to acquire some practical knowledge of species and their literature by unswerving application to work for forty years! This will leave him but little leisure for either the study of comparative anatomy or osteology" (Sharpe 1891). As more and more ornithologists after 1900 became like Sharpe, students of species, less and less attention was paid not only to comparative anatomy, but to the methods and principles of higher classification in general. The systematics of the new century, thanks to men like Sharpe, was to be the systematics of species.

Conclusion

In addition to the many details of the various approaches to systematics outlined here, I hope that two general points will be taken. First, far from being featureless, the history of systematics is extraordinarily rich in changing ideas and

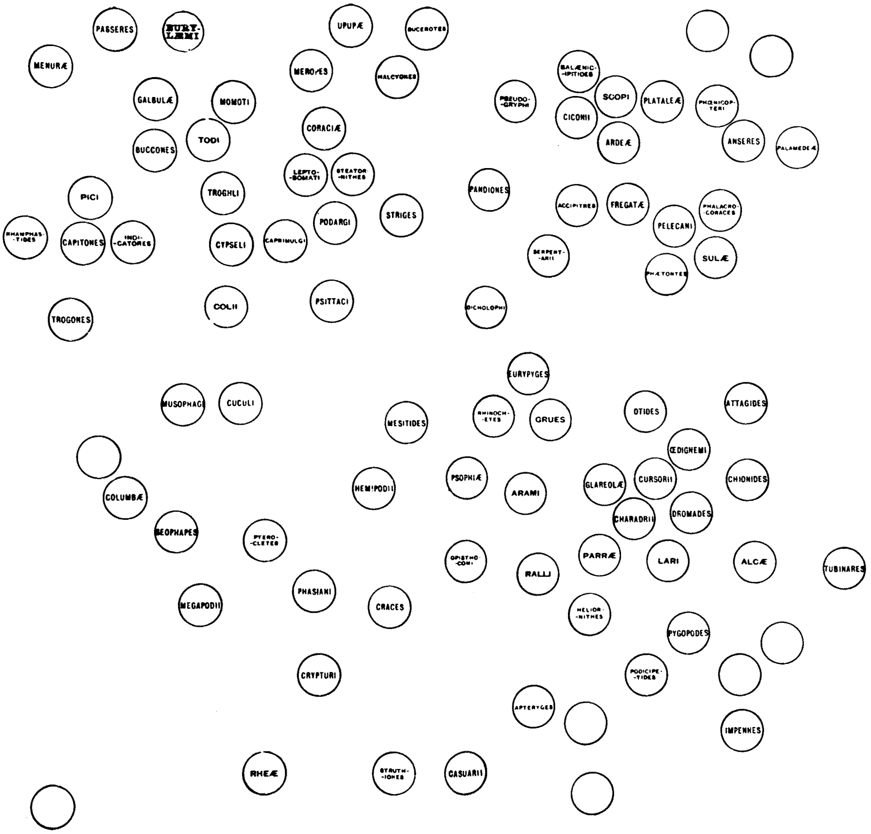

Figure 9. Map of the relationships of birds, from Sharpe (1891). This is the view one would see, said Sharpe, if one were to look down on the evolutionary tree of birds from above. The open circles represent taxa that are recently extinct.

concepts, and classification diagrams provide important insights into these changes. Second, although many of the workers discussed here studied other groups in addition to birds, it was their ornithological studies and examples that drove the development of theoretical systematics during the 19th century.

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