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What Systematic Method Will Ornithology Adopt?—A Reply to Olson (1982)

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The question posed by the title of this response—What Systematic Method will Ornithology Adopt?—is at the heart of the differences between Olson (1982) and myself (1981a) and is far more significant for ornithology than any contention about the relationships of a particular group. In his scientific papers, including his critique (1982) of my paper, Olson has exhibited an apparent disinterest in discussions about systematic theory and methodology, preferring instead to believe that a persistent pursuit of new "facts" or data will eventually give rise to statements or conclusions of greater generality. In contrast, I have suggested that a major problem in systematic ornithology has been the lack of an effective comparative method: all observations ("facts") are theory-laden and make sense only within the context of some organizing principle, be it a theory, hypothesis, or a specific comparative method. Without question, the systematic community at large is increasingly adopting phylogenetic systematics (cladistics) as its method of choice.

In my paper, virtually all the commentary on the papers of Olson and his colleagues focused on their inadequacies in phylogenetic argumentation; other ornithologists have raised similar criticisms of that work (Clark 1981, Raikow 1981). Olson's only response to cladistics is to cite Mayr (1981) in support of the proposition that not everyone is willing to accept the same methodology, but an appeal to authority does not substitute for a cogently reasoned rationale of one's own scientific methods. In fact, one searches in vain through Olson's papers for a statement describing and rationalizing a comparative method of any kind.

A major purpose of my paper was to delineate in detail—for the first time in the ornithological literature—the importance of pursuing cladistic classifica-

tions in place of the "eclectic" approach that has been our tradition. In his critique, Olson fails to state why cladistic classification is not a desirable goal for ornithology. Such a classification promotes the recognition of natural groups, i.e. those postulated to represent strictly monophyletic taxa. If Olson agrees with this goal, then it is difficult to understand why he did not exhibit some charity toward my paper instead of the sustained invective he directed at it. If he does not agree with this goal, then perhaps he can apprise ornithologists why we should instead be classifying unrelated groups together.

Philosophical matters aside, Olson promotes two major arguments, both strawmen and without validity. His first claim is that my arrangement of orders into "divisions" was the most important focus of my paper; he then proceeds to point out the dicey nature of those groups. It is clear, however, that I viewed (1981a: 685–686) the category of division as *the most tentative* of all systematic groupings—that is why I did not formally name those hypothesized taxa, even when several referees strongly recommended that I do so. Olson's second line of argumentation was to choose a liberal number of my admissions of uncertainty and display them as if they constituted the entire content of my paper. Without belaboring the point, I call the reader's attention to p. 685 of my paper where I state, unequivocally, that there are still many uncertainties in our knowledge and that these will be openly admitted. The paper was titled "*Toward a phylogenetic classification . . .*" intentionally, and I made no claim that I could provide supporting data for each taxonomic group. If a reader wishes to criticize my efforts on the grounds of prematurity, all well and good, but surely that same criticism must then be applied to all previous classifications and, because knowledge is always uncertain, to all those that will follow.

Another major purpose of my paper was to hypothesize natural groups for the higher taxa *within orders* to the extent that present knowledge permits. A comparison between the classic papers of Mayr

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and Amadon (1951) and Wetmore (1960) and my classification will show significant differences in the arrangement *within* orders. Although many of these groups remain poorly corroborated, the classification is better documented than previous ones. Obviously, I am not satisfied with the amount of evidence for many proposed relationships, and, had I not been constrained by (understandable) policies on manuscript length, it would have been possible to provide much more specific documentation. Olson is familiar with having to summarize complicated systematic data in a paper of restricted length and the consequent necessity of having to cite unpublished work (e.g. Olson 1979); therefore, I am perplexed as to why he found this altogether objectionable.

Olson claims my classification is not cladistic because it is not constructed according to cladistic principles, which he suggests include (1) that classifications must be strictly dichotomous, and (2) that they must be constructed so that a tree (or cladogram) can be "consistently reconstructed from it." His argument is false; a passing familiarity with the recent literature on cladistics (e.g. Eldredge and Cracraft 1980, Nelson and Platnick 1981, Wiley 1981) should have convinced him that strict dichotomy is simply no longer an issue with cladists [Bock and Farrand (1980) and Mayr (1981, 1982: 229) perpetuate the same misconception]: *one can only resolve relationships to the extent allowed by the available data*. To be sure, a dichotomous hypothesis expresses more information than a less resolved hypothesis, and this is a desirable goal, but dichotomy is not a prerequisite for cladistic classifications.

Much more difficult to understand is Olson's claim that one cannot reconstruct a tree (or cladogram) from my classification. As cladists have stressed time and time again, one can represent *any* classification in terms of a branching diagram, and the two can be made completely isomorphic with respect to their information content about group membership. I did not publish cladograms because they would have been redundant.

Yet another misunderstanding about cladistics is found in Olson's criticism of some of my evidence for monophyly. For example, in discussing my reasons for uniting the Caprimulgiformes and Apodiformes, he states that I do not "present any synapomorphies common to all members of this division and that would define it as monophyletic." This is either a deliberate attempt to imply I did not list defining characters, or else Olson makes an elementary error of character-analysis. In fact, I proposed three well-marked synapomorphies for this division (p. 700), but I did note that they apparently had become further modified in some of the included families (but not all, of course). Olson seems to imply, therefore, that *all* taxa of a group must share a character before it can be used to define the group. This is simply not true, of course, for if it were, then Ol-

son might as well suggest that snakes should be excluded from the Tetrapoda because they lack legs (see also Raikow and Cracraft 1983).

In the remaining space available to me, I want to cite just a few examples of the ways in which Olson misrepresents much of my paper.

1. *Palaeognath monophyly*.—While admitting that some postulated defining characters of palaeognaths might be primitive, we still must acknowledge that any hypothesis of synapomorphy is only as reliable as the evidence provided by the congruence of other characters. If, in fact, characters support an alternative hypothesis, then the original hypothesis of synapomorphy is weakened [to imply, as Olson does (p. 737), that I think convergence might not be common is not only silly but irrelevant: all I claim is that, if relationships are postulated using cladistic analysis, then examples of convergence will be less common than traditionally thought, merely because parsimony demands the minimization of character conflicts and other *ad hoc* assumptions (see Farris in press)]. With respect to palaeognath monophyly, no one has yet provided convincing evidence for an alternative hypothesis [e.g. there is absolutely nothing in Feduccia (1980) or Houde and Olson (1981) to preclude palaeognath monophyly]. At this time, then, the monophyly of the palaeognaths is corroborated by postulated synapomorphies.

In addition, I *did not* use neoteny to support ratite monophyly. Instead, I stated (p. 689) that, *if* one posits some characters of ratites to be neotenus, then *by definition* those characters must be derived.

2. *Galliformes-Anseriformes*.—Rather than "ignore" the conclusions of Olson and Feduccia (1980), I simply chose to disagree for the reasons already stated (1981a: 694–696). Unlike Olson, I do not believe it possible to "document" homology or to use fossils as if they are revelatory of, or provide "concrete evidence" (= truth?) for, relationships. Instead, homology is a hypothesis, always susceptible to rejection if the evidence warrants, and the characters of fossils must be analyzed in the same way as those of Recent taxa (see Cracraft 1980, 1981a, b; Raikow 1981).

3. *Psittaciformes*.—Olson chastizes me for maintaining the parrots in a separate division and then accuses me of giving this taxon high rank compared to its closest relatives. Because I was agnostic about their relationships, however, I merely followed a long tradition within ornithology of classifying parrots by themselves. Moreover, how could I have given them high rank "compared to their close relatives" when I did not postulate any such relationship?

4. *Gruiformes*.—If one examines my earlier classification of some gruiforms (1973: 124), it will be seen that it differs from the arrangement in Cracraft (1981a) in two significant ways: (1) the Ralli and Grues (= the "Gru" of 1973) are now ranked as suborders instead of infraorders, and (2) the Heliornithidae,

Rhynchoetidae, Eurypygidae, and Cariamidae have been interpolated into the classification. Thus, the *relative* phylogenetic relationships of the taxa of the 1973 paper have *not* been changed. Altering the ranks does not modify the information content of the classification, but, even if I had changed my mind, why would that be a transgression in Olson's eyes? A paper discussing gruiform relationships has been published elsewhere (Cracraft 1982). Olson apparently accepts Feduccia's hypothesis (1980: 126–127) that the fossil group Ergilornithidae is the sister-taxon of the ostriches. *Contra* Olson, Feduccia notes only one character—reduction of the inner trochlea of the tarsometatarsus—in support, whereas Wetmore (1934), Cracraft (1973), and Kurochkin (1976) provide numerous reasons for their gruiform affinities.

5. *Ciconiiformes*.—Once again, I did not "ignore" the papers of Olson and Feduccia. I question their conclusions for the reasons already stated (Cracraft 1981a, b; Raikow 1981). A consideration of ciconiiform relationships is in preparation.

6. *Nomenclature*.—I confess to a grievous deficiency in Latin, and these errors will be corrected in subsequent papers. That my endings for some supra-specific names were not consistent within ranks is relatively unimportant, however, as systematists have noted that such consistency can cause numerous problems (e.g. Mayr 1969: 358).

7. *Egg-white protein data*.—Olson raises my previous criticisms of egg-white protein comparisons in questioning why I used some of those data, "when-ever it suits his purpose" as he put it. I earlier professed misgivings about the interpretation of egg-white data because it was based—much like the work of Olson itself (Raikow and Cracraft 1983)—primarily on phenetic (general overall) similarity. Naturally, this does not imply that an alternative method of comparison cannot extract valuable systematic conclusions from those data. Thus, in the case of some charadriiforms and caprimulgiforms, an examination of the data suggests that certain egg-white patterns are unique (i.e. *derived*) within birds, and therefore they provide valid systematic data. Olson fails to mention how I interpreted these data, choosing instead to imply that I was "inconsistent." But this is a common pattern in his critique: Why did he not mention, for example, that, whenever I cited biochemical, karyological, or other data that were not expressed in terms of primitive or derived characters, I specifically made mention of this? The supposed "inconsistency" that Olson tries to create in the reader's mind about my paper is a strawman of his own manufacture.

In conclusion, I have attempted to show that a root cause for Olson's criticism of my paper lies with his poorly formulated ideas about systematic theory and methodology. This, I suggest, often leads him to alternative views about avian relationships. It is perhaps too early to judge which hypotheses are to be

preferred, but such a judgment may not be possible until the alternative hypotheses are precisely formulated and evaluated by properly analyzed comparative data.

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Evidence for Hybrid Murre Reconsidered

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In accordance with a recent editorial (Wiens 1981), which expressed the view that scientists should read published papers critically and not hesitate to note in print certain flaws discovered in the articles in question, I would like to make some comments on a paper by Cairns and deYoung (1981).

Cairns and deYoung (1981) described a breeding pair of murres from Newfoundland, one member of which was a Common Murre (*Uria aalge*) and its partner an apparent hybrid between *U. aalge* and the Thick-billed Murre (*U. lomvia*). Indications of the hybrid nature of the latter bird were the white gape mark that was "similar to that of *lomvia* in position, length, and pigment density, but about one half as wide," the intermediate appearance of the inverted white V-form on the throat, and the intermediate color of the upperparts. Neither color (variable in both species and dependent on conditions of observation) nor shape of the point of the breast plumage on the neck was considered decisive evidence for the hybrid origin of the bird. Consequently, the entire argument hinges on the presence of a white gape mark in the bird in question. This feature, however, is unreliable in identifying possible hybrid birds, whereas other distinguishing features were ignored by Cairns and deYoung.

Possible hybrid murres with narrow white gape marks were recorded for the first time from northern Norway (Tschanz and Wehrlin 1968). These authors observed an actual case of hybridization between a mixed breeding pair of *lomvia* × *aalge*, which raised a chick that lived at least 10–12 days. Unfortunately, from the photograph they published of the parents and their young, one cannot see properly whether the juvenile bird was similar to *aalge* or to *lomvia*. It looks as if the young bird lacks the white feathers

behind the eye and across the hind neck and the white patches at the side of the neck with a narrowing brown line running backwards from the eye, which are characteristic for chicks of *aalge* (Sluys MS). In the same breeding colony Tschanz and Wehrlin (1968) observed several birds with narrower white gape marks than normal *lomvia* specimens. They stated, cautiously, that this might be the result of hybridization. Tschanz and Wehrlin were quite correct in their critical approach, because a narrow white gape mark is insufficient evidence for a hybrid murre. Pale, horn-colored gape marks are present occasionally in the Common Murre, although they are never as broad as in *lomvia* (cf. Yadon 1970, Smith 1981, de Wijs 1981). According to Cairns and deYoung, their apparent hybrid showed a rather narrow, but still distinctly lanceolate, white gape mark. If the authors were able to observe that the gape mark was "distinctly lanceolate in shape," then it cannot have been all that narrow.

Moreover, in murres the sheath of the bill is shed in bits and pieces, which could explain the temporary narrow appearance of the white gape mark. The timing of this shedding is not well known, but it is probably paralleled by the post-breeding body molt, which lasts from the end of July to late September. The shedding of the bill sheath results in the gape mark of *lomvia* being yellow-brown in winter (Sluys MS).

Thus, cases of possible hybrid murres should be substantiated by stronger evidence. As it may be expected that hybrids are intermediate between their parents in several characters, notice should be taken of a number of features. For example, the shape of the bill should be taken into consideration. Common and Thick-billed Murres differ considerably in the length and depth of the bill, although some overlap exists. In *lomvia* the angle of gonys is generally much more prominent. Cairns and deYoung made no mention at all of the shape of the bill. The Thick-billed

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