

A CRITIQUE OF CRACRAFT'S CLASSIFICATION OF BIRDS

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ABSTRACT.—A recently proposed "phylogenetic" classification of birds (Cracraft 1981b) is not constructed according to cladistic principles and contains little information to support most of the taxa proposed in it. That which is presented is frequently misleading or erroneous. The nomenclature used is inconsistent and ungrammatical. In failing to provide synapomorphies to cluster taxa, in using data that are not presented in a primitive-derived sequence, in citing differences as evidence of nonrelationship, and using convergence to refute phylogenetic hypotheses, Cracraft commits the very methodological transgressions for which he has long criticized other systematists. *Received 4 January 1982, accepted 24 April 1982.*

In the past decade or so, there has been great controversy over methodology in systematics, occasioned by the rise of cladistics or "phylogenetic systematics." Most of this debate has taken place outside the field of ornithology, with the principal exception of a continuous series of papers and reviews by Cracraft (e.g. 1971, 1972, 1980, 1981a). Although these have primarily been discussions of methodology and criticisms of the work of others, Cracraft (1981b) has now put forth a classification of the entire Class Aves that permits an examination of how effectively he has applied his preferred methodology in actual practice.

CRACRAFT'S "DIVISIONS"

Because Cracraft (1981b: 681) considers that "most currently recognized orders and families [of birds] are probably monophyletic," his principal innovation would appear to be the segregation of the Class Aves into nine major categories, which he terms "Divisions." Indeed, it is clear from his abstract that this is to be regarded as the most important aspect of his classification. Yet these Divisions are not named formally, "because in a number of cases their status as monophyletic groups is not yet well documented" (Cracraft 1981b: 685). If no documentation is to be provided for the focal point of his classification, then we might fairly question from the outset why it was presented at all. Nevertheless, let us examine the basis for Cracraft's "Divisions," bearing in mind that the principal tenet of the cladist school is that "Taxa are clustered on the basis of synapomorphies (Hennig 1966), and the taxa so formed

are postulated to be strictly monophyletic" (Cracraft 1981b: 682).

Division 1.—This contains the orders Sphenisciformes, Gaviiformes (including the Podicipediformes and the Cretaceous toothed divers of the order Hesperornithiformes), Procellariiformes, and Pelecaniformes. Cracraft (1981b: 686) states that "These four orders have often been placed near one another, although a strong argument for their interrelationships has not yet been made." Not a single synapomorphy is advanced to justify "Division 1" as a monophyletic group.

Division 2.—This contains the paleognathous ratites and tinamous. An increasing amount of evidence, including new data from paleontology (Houde and Olson 1981), suggests that the few characters that can be used to define this group are primitive (plesiomorphous). Cracraft (1980, 1981b) has specifically admitted this possibility but rationalizes the consequences by saying that even if these characters "are primitive, that in itself does not constitute an argument against monophyly but merely signifies that the hypothesis of monophyly is not well corroborated" (Cracraft 1981b: 688). Not corroborated at all would be more accurate, because, in a cladistic phylogeny, monophyletic taxa are supposed to be defined by shared *derived* character states, without which there is no justification for Division 2. To cite neotenic features of ratites as shared derived characters, as Cracraft (1981b: 689) has done, is hardly likely to persuade nonornithologists of the monophyly of this group. By the same logic, all of the various neotenic species of salamanders

(belonging to each of the eight families of Urodela) would form a monophyletic group.

Division 3.—This category includes the Ciconiiformes and the Falconiformes, the latter including the Strigiformes. One will search in vain for a single synapomorphy that will define a group that contains both flamingos and owls as monophyletic within the Class Aves. Instead, we are told that "The placement of such disparate orders in the same Division may seem unwarranted, and, admittedly, there is no clear evidence for this . . . Their placement in Division 3 is tentative and boldly hypothetical" (Cracraft 1981b: 690). No synapomorphies are mentioned, and thus no evidence is presented that this weird taxon is monophyletic. It is decidedly misleading for Cracraft (1981b: 690) to cite Ligon (1967) as supporting the view that the Ciconiiformes and Falconiformes "may have a relationship." Ligon argued for a close relationship only between the Cathartidae and Ciconiidae, which he placed in their own order (Ciconiiformes) apart from herons (Ardeiformes) and hawks (Accipitriformes). This is completely contrary to Cracraft, who regards the Ciconiiformes and Falconiformes each to be monophyletic.

Division 4.—This contains the Galliformes and Anseriformes. Arguments against a close relationship between these two orders have been discussed elsewhere (Olson and Feduccia 1980a: 2). Practically the only morphological character that has been at all consistently cited as indicating a possible relationship between Anseriformes and Galliformes is the supposed similarity in the large, rounded "basipterygoid" processes. Olson and Feduccia (1980a: 5) documented that these structures are not really similar between the two groups, that they have a different developmental history, and that they are not homologous. But Cracraft (1981b: 696) simply ignores this and continues to cite basipterygoid morphology as possibly indicating a relationship between Anseriformes and Galliformes.

The fossil bird *Presbyornis*, which is known from thousands of specimens, has, in essence, the head of a duck and the body of a charadriiform. It provides strong evidence for a derivation of the Anseriformes from the Charadriiformes (Olson and Feduccia, 1980a). Cracraft, however, seems to regard *Presbyornis* as a hypothetical creature and finds "it disquieting for theoretical reasons . . . when two higher taxa

. . . are placed together because a fossil is *said* [emphasis added] to have a head only similar to one taxon and a postcranial skeleton only similar to the other taxon. The evidence of comparative morphology and systematics suggests that mosaic evolution does not work as absolutely as this" (Cracraft 1981b: 696). Thus, the concrete evidence offered by the fossils is dismissed, because preconceptions about how evolution works cannot accommodate it. Cracraft offers no alternative explanation for the relationships of *Presbyornis* and agrees with Olson and Feduccia that a relationship between Anseriformes and Galliformes "is not well documented" (Cracraft 1981b: 695).

Division 5.—In this category Cracraft includes the Gruiformes, Charadriiformes, and Columbiformes. He states that the interrelationships of these three orders "have not yet been resolved satisfactorily" but that "there is reason to maintain this association" because "it stands as a working hypothesis" and "because no alternative hypothesis of interordinal relationships seems better" (Cracraft 1981b: 697). Once again, no synapomorphies are advanced in support of monophyly of this group.

Division 6.—This includes only the order Psittaciformes, which most systematists consider to be composed of but a single family, Psittacidae. Never has it been doubted that the parrots constitute a natural group, and it should have been possible for Cracraft to provide synapomorphies here to demonstrate monophyly, but none is offered. Cracraft (1981b: 699) ignores the evidence that suggests a possible close relationship between the Psittaciformes and Columbiformes (Sibley and Ahlquist 1972) and, instead, says only that parrots "are so morphologically distinct from other birds that their relationships to other groups have remained unresolved." Considering that he criticizes other avian systematists for bestowing "high rank on taxa that are morphologically divergent compared to their closest relatives" (p. 683), would it not have been preferable to reflect uncertainty about the relationships of parrots by considering them *incertae sedis*, rather than raising the family Psittacidae to the same level as a taxon that contains penguins, loons, pelicans, grebes, and *Hesperornis*, among others?

Division 7.—This division also consists of a single order, the Cuculiformes. Cracraft's (1981b: 699) justification for this taxon is that "There is reasonably strong evidence for ac-

cepting a sister-group relationship between the turacos (Musophagidae) and cuculids, but the affinities of both families to other birds remain uncertain." What the "reasonably strong evidence" may be, or if it consists of synapomorphies, is never stated.

Division 8.—The Caprimulgiformes and Apodiformes are the constituents of this taxon. Although Cracraft explains why he believes the Caprimulgiformes to be related to the Apodidae and the Apodidae to the Trochilidae, he does not present any synapomorphies that are common to all members of this division and that would define it as monophyletic.

Division 9.—This is composed of the Piciiformes, Coliiformes, Coraciiformes, and Passeriformes—a group of taxa for which "a precise hypothesis of . . . interrelationships has not been supported" (Cracraft 1981b: 701). This is all that is said for the monophyly of Division 9.

SUBORDINATE TAXA

If Cracraft's "Divisions" are without substance, the same may be said of practically all of his subordinate taxonomic categories. Particularly egregious examples are the Gruiformes and Ciconiiformes. Apart from three families that are considered *incertae sedis*, Cracraft (1981b) divides the Gruiformes into two suborders: the Ralli, containing only the Rallidae and Heliornithidae, and the Grues, containing the remaining families of the order. He states (p. 697) that "The phylogenetic relationships of the suborder Grues have been documented elsewhere (Cracraft 1973, MS)." The contents of unpublished manuscripts [which Cracraft (1981b) cites on 12 occasions] cannot be assessed, of course, but the 1973 reference deals with a composition of the suborder Grues entirely different from that now advocated by Cracraft (1981b). His Grues of 1981 contains, among others, the families Cariamidae, Rhynochetidae, and Eurypygidae, which were *not* included in his Grues of 1973, whereas the Rallidae, which *were* included in his Grues of 1973, are placed in a different suborder in the 1981 classification. How can one concept of the suborder Grues be justified by citing a paper containing a completely different concept of that taxon? One of the criticisms made of Cracraft's 1973 paper (Olson 1974) was that characters were never provided to diagnose the suborder

Grues. This deficiency has still not been remedied, even though Cracraft (1981b) changed the composition of the taxon radically in the meantime. Nor will one find any mention of synapomorphies that define the suborder Ralli, the infraorders Arami or Psophii [sic], or the superfamilies Psophioidea or Rhynocheti [sic] as monophyletic.

Although at one point Cracraft (1981b: 691) promises to "note some of the data that are consistent with ciconiiform monophyly," nowhere do I find a discussion of the supposed "characters, shared hierarchically, that are consistent with ciconiiform monophyly" (p. 693). He states that flamingos, storks, and ibises constitute a taxon that is the sister group of herons and *Balaeniceps*, but the only supposed evidence for this is that "In terms of pure phenetic resemblance they all have very similar humeri, pelvis, and sterna. They all apparently have the iliotrochanteric medius muscle poorly separated (or not at all) from the iliotrochanteric anterior" (Cracraft 1981b: 692). But these are not presented as "an argument based on derived character sequences" such as Cracraft (1972: 387) would have others do. One need go no further than comparing the sternum of an ibis with that of *Balaeniceps* to demonstrate the erroneous nature of Cracraft's assertion that these and other bones of Ciconiiformes are "very similar." The iliotrochanteric medius is one of a number of muscles that show no significant variation within Ciconiiformes (Vanden Berge 1970), where its condition has not been shown to be different from that in other birds (see also Olson and Feduccia 1980b: 17).

Cracraft (1981b) repeatedly makes erroneous or misleading statements and ignores pertinent data in discussing the supposed sister-group relationship between flamingos and storks, one of few instances where he does provide some characters. He accuses Olson and Feduccia (1980b) of "overemphasizing differences" (Cracraft 1981: 692) between flamingos and Ciconiiformes, whereas in fact they consistently emphasized the many *similarities* between flamingos and Charadriiformes. Cracraft's (1981b: 692) statement that the hypotarsus of the fossil flamingo *Juncitarsus* "is totally unlike all known phoenicopterid genera, both fossil and Recent" is false, as it is actually very similar to the hypotarsus in fossil flamingos of the genus *Palaelodus*. This is an example of Cracraft himself

citing differences between taxa as evidence of nonrelationship, in contradiction to his own stated views (see below).

Olson and Feduccia (1980b: 42, fig. 18) discussed and illustrated the fact that the superficial similarities between storks and flamingos in the distal end of the tibiotarsus are not homologous. Cracraft omits any reference to this, however, and uses the deep intercondylar fossa of the tibiotarsus as a character linking flamingos and storks. He fails to mention that the four-headed gastrocnemius, in addition to being found in storks and flamingos, also occurs in the recurvirostrid *Cladorhynchus*, as clearly described and illustrated by Olson and Feduccia (1980b: 29, fig. 7a). Three more supposed morphological similarities between storks and flamingos that Cracraft cites are the lack of the peroneus brevis (= fibularis brevis), the presence of a "short and stout" iliacus (= iliofemoralis internus), and the narrow (or lack of) separation of the two heads of the puboischio-femoralis. He does this in disregard of the fact that Olson and Feduccia (1980b: 16, 24, 29) show that each of these conditions is present in *Cladorhynchus*. Thus, Cracraft has completely misrepresented the evidence, and not one of the characters he cites in any way refutes the charadriiform relationships for flamingos proposed by Olson and Feduccia (1980b).

THE INFORMATION CONTENT OF CRACRAFT'S CLASSIFICATION

Succinctly stated, the factual basis for Cracraft's (1981b) classification is nonexistent, as virtually no data are provided to justify the taxonomic categories used in it. Clearly, Cracraft's discussions of the information content of classifications (Cracraft 1981b: 682) are of little relevance to his own classification, as it is obviously impossible to retrieve information from a system into which no information was put in the first place.

One of the reasons that cladistic classifications should, in theory, lend themselves to information retrieval is that they are supposed to be based optimally on strictly dichotomous branching sequences, with sister groups receiving the same taxonomic rank. Thus, even though Cracraft does not present a cladogram of the phylogeny of birds, we should be able to derive one from his classification, if it were constructed according to cladistic principles. But

Cracraft's classification is not dichotomous nor sequenced in any way in which a phylogenetic tree could be consistently reconstructed from it.

The highest category in Cracraft's subclass Neornithes is the division; yet there are nine of these, so it would be impossible to arrange them dichotomously, even if categories between the division and the subclass were provided, which they are not. There is only one order in each of Divisions 2, 6, and 7, so in these cases an order is exactly equivalent to a division and is therefore redundant. Division 5 contains three orders, which, in the absence of sequencing, obviously cannot be arranged dichotomously while being maintained at equivalent rank. Division 9 contains four orders but with no taxa between the division and the order by which these four could be arranged in a dichotomous branching scheme. Furthermore, it would seem to be impossible to construct a dichotomous branching pattern that contains only two taxa each at the level of "cohort," "infrasuborder," and "infrasuperfamily," but at the same time contains 26 suborders and 33 infraorders. Thus, although Cracraft (1981b: 682) tells us that phylogenetic hypotheses are to be presented as cladograms, it is not difficult to discern why cladograms were omitted from his own paper. For Cracraft to represent his as a cladistic, "phylogenetic" classification is clearly unjustified.

CRACRAFT'S NOMENCLATURE

Even though Cracraft's classification is not dichotomous, it does contain the proliferation of higher taxa that such classifications necessitate. The names that are appended to these taxa present many problems. The endings used for orders, families, subfamilies, and tribes, are consistent, but among the superfamilies the name "Rhinocheti" should have been rendered as "Rhinochetioidea." For subordinal endings, Wetmore (1960) used the plural of the generic stem, with which the ending is supposed to conform in gender. Cracraft has evidently attempted to form the endings not only for suborders in this manner but for cohorts, infraorders, infrasuborders, and infrasuperfamilies as well, with the result that there is no way to distinguish one taxon from another by its ending. Furthermore, many of these endings do not agree in gender with the generic stem and

in some cases the generic stem itself is incorrect (e.g. "Scopiae," which would have to be derived from "Scopia" rather than *Scopus*). The names "Ciconii," "Psophii," "Caprimulges," "Upupes," "Pitti," "Muscicapi," "Bombycilli," "Sitti," and "Fringilli" are among others that are ungrammatically constructed. In several instances Cracraft has attempted to form two different names on the same stem in this manner, so at least one of the two names automatically has to be grammatically incorrect (e.g. Grues and Gruui, Arames and Arami, Alcedines and Alcedini). To make matters even more confusing, he has interjected the ending "-morpha" [sic], apparently as the fancy struck him, because it occurs once as a subordinal ending (Charadriomorpha) and twice among the infraorders (Tyrannomorpha, Passeromorpha). The carelessness of Cracraft's nomenclature alone is sufficient to make the adoption of his classification inadvisable.

ADDITIONAL SHORTCOMINGS

Cracraft has been very outspoken in his criticism of the role of biochemical studies in elucidating phylogenies because of their failure to resolve data into primitive-derived sequences and because "phylogenetic affinity can be based solely on a recognition of shared character-states that were inherited (i.e. derived) from the common ancestor" (Cracraft 1971: 158). His criticism of Sibley's research on egg-white proteins (Cracraft 1971) would seem to make his stand on this matter quite unequivocal. Although Cracraft's objections to the egg-white protein data were based on arguable philosophical grounds, Brush (1979) showed that problems with laboratory technique rendered the egg-white electrophoretic data of dubious systematic value, and Sibley himself now states that the egg-white analyses lead to what he now regards as erroneous conclusions (Sibley and Ahlquist 1980). Presumably, Cracraft has not forgotten his previous criticisms, and, because he cites Brush's (1979) paper, we may assume that he was aware of its implications. Yet he uses the same studies of egg-white proteins (Sibley and Ahlquist 1972) to support his phylogeny whenever it suits his purpose (Cracraft 1981b: 699, 700). In addition, Cracraft (1981b) cites as supporting his views a number of other papers that present biochemical, karyological, or other nonmorphological data that

have not been organized into primitive-derived sequences. If Cracraft does not take his own criticisms seriously, can others rightly be expected to do so?

Cracraft (e.g. 1972, 1981a,b) is reluctant to attribute a significant role to convergent evolution in the history of birds. He has been critical of those who have invoked the argument of convergence in postulating relationships and has repeatedly emphasized that differences between taxa do not constitute proof of nonrelationship. Notwithstanding Cracraft's views, convergent evolution is as prevalent among birds as it is in other groups of organisms and his classification may encompass as many or more instances of convergence as do the alternatives he seeks to supplant. Grebes would have to be convergent in their cervical myology with certain Gruiformes (Zusi and Storer 1969). Flamingos would have to be convergent on the Recurvirostridae in many aspects of their morphology and behavior (Olson and Feduccia 1980b). Ibises would have to be convergent with Charadriiformes and some Gruiformes in their schizorhinal nostrils, occipital fontanelles, four-notched sternum, and other osteological characters (Olson 1979). Herons would have to be convergent with the Mesoanatidae in their very distinctive pterylosis and tarsal morphology (Olson 1979). Parrots would be convergent with pigeons in the morphology of their humerus (Wetmore 1926) and with cuckoos and Piciformes in being zygodactyl. This list could be greatly extended. Cracraft has merely traded one set of convergences for another.

Although Cracraft (1972, 1981a) criticizes others for citing differences as evidence of nonrelationship and for invoking convergence to refute systematic hypotheses, he does the same himself. Take, for example, the flightless, two-toed running birds of the family Ergilornithidae that are known from Tertiary fossils from Asia. These have consistently been placed with the Gruiformes, yet they share clearly derived characters of the tarsometatarsus and toes with ostriches (Feduccia 1980). Cracraft (1973, 1981a), who also places the Ergilornithidae in the Gruiformes, attributes the similarities between the Ergilornithidae and ostriches to convergence. As evidence of this, however, he merely lists 10 differences between the tarsometatarsi of ergilornithids and *Struthio* (Cracraft 1973: 118), without discussing their phylogenetic significance. Is this not the very

approach that Cracraft (1972: 387) says "should be replaced by an argument based on derived character sequences"?

The similarities between the Shoebill (*Balaeniceps*) and Pelecaniformes (Cottam 1957) are attributed to convergence by Cracraft (1981b: 687, 693) because of the facts that "characters of the Shoebill do not fit into the hierarchical pattern of derived characters shown by the pelecaniforms but that they do within the ciconiiforms" (p. 687). Yet Cracraft does not present a "phylogenetic (primitive-derived sequence) analysis" (p. 687) for either the Pelecaniformes or the Ciconiiformes, and his classification is therefore as deficient in this respect as the one by Cottam (1957) that he criticizes. In another instance, Cracraft (1981b: 691) even projects the argument of convergence into the future: "I believe that the similarities between flamingos and *Cladorhynchus* will eventually be interpreted as convergences."

In the foregoing, we have seen that Cracraft (1) has not clustered taxa on the basis of synapomorphies, (2) has cited data that have not been resolved into primitive-derived sequences, (3) has used differences between taxa as evidence of nonrelationship, and (4) has resorted to the argument of convergence to refute phylogenetic hypotheses. In other words, he himself is guilty of exactly the things that he has spent over a decade harshly criticizing other systematists for doing.

CONCLUSION

The one unequivocal message that has emerged from recent arguments is that not all systematists are willing to accept one and the same methodology. Mayr and others (see Mayr 1981 and references cited therein) have presented counterarguments and alternatives to cladistics, for example. Dissent could continue indefinitely without a consensus being reached. Overlooked in the tumult is the basic fact that advances in avian systematics are the result of hard, often tedious work, whether it entails breaking up rocks and grinding out fossils, dissecting tiny muscles for hours under a microscope, skinning birds and counting feathers in pterylae, or other laborious procedures. Only through the accumulation of more and more data in this manner will our understanding of avian evolution be promoted. Unfortunately, the era of Hennig, Popper, and Croizat, which

has brought such controversy to systematics, has also created an environment in which unsubstantiated speculation is not only condoned but encouraged. Yet before we will ever have a phylogeny that reflects the probable evolutionary history of the Class Aves, someone will have to do the work upon which such a phylogeny must ultimately be based.

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LITERATURE CITED

- BRUSH, A. H. 1979. Comparison of egg-white proteins: effect of electrophoretic conditions. *Biochem. Syst. Evol.* 7: 155-165.
- COTTAM, P. A. 1957. The pelecaniform characters of the skeleton of the Shoe-bill Stork, *Balaeniceps rex*. *Bull. British Mus. Nat. Hist. (Zool.)* 5: 1-71.
- CRACRAFT, J. 1971. Review of "A comparative study of the egg-white proteins of passerine birds" by C. G. Sibley. *Bird-Banding* 42: 157-161.
- . 1972. The relationships of the higher taxa of birds: problems in phylogenetic reasoning. *Condor* 74: 379-392.
- . 1973. Systematics and evolution of the Gruiformes (Class Aves). 3. Phylogeny of the suborder Grues. *Bull. Amer. Mus. Nat. Hist.* 151: 1-128.
- . 1980. Phylogenetic theory and methodology in avian paleontology: a critical appraisal. *Contrib. Sci. Nat. Hist. Mus. Los Angeles Co.* 330: 9-16.
- . 1981a. Review of "The age of birds" by A. Feduccia. *Syst. Zool.* 30: 219-221.
- . 1981b. Toward a phylogenetic classification of the recent birds of the world (Class Aves). *Auk* 98: 681-714.
- FEDUCCIA, A. 1980. *The age of birds*. Cambridge, Massachusetts, Harvard Univ. Press.
- HENNIG, W. 1966. *Phylogenetic systematics*. Urbana, Illinois, Univ. Illinois Press.
- HOUDE, P., & S. L. OLSON. 1981. Paleognathous carinate birds from the early Tertiary of North America. *Science* 214: 1236-1237.
- LIGON, J. D. 1967. Relationships of the cathartid vultures. *Occ. Pap. Mus. Zool. Univ. Michigan* 651: 1-26.
- MAYR, E. 1981. Biological classification: toward a synthesis of opposing methodologies. *Science* 214: 510-516.
- OLSON, S. L. 1974. Review of "Systematics and evolution of the Gruiformes (Class Aves). 3. Phylogeny of the suborder Grues" by J. Cracraft. *Auk* 91: 862-865.

- . 1979. Multiple origins of the Ciconiiformes. Proc. Colonial Waterbird Group, 1978: 165–170.
- , & A. FEDUCCIA. 1980a. *Presbyornis* and the origin of the Anseriformes (Aves: Charadriomorphae). Smithsonian Contrib. Zool. 323: 1–24.
- , & ———. 1980b. Relationships and evolution of flamingos (Aves: Phoenicopteridae). Smithsonian Contrib. Zool. 316: 1–73.
- SIBLEY, C. G., & J. AHLQUIST. 1972. A comparative study of the egg-white proteins of non-passerine birds. Peabody Mus. Nat. Hist., Yale Univ., Bull. 39: 1–276.
- , & ———. 1980. The relationships of the "primitive insect eaters" (Aves: Passeriformes) as indicated by DNA × DNA hybridization. Proc. 17th Intern. Ornithol. Congr.: 1215–1220.
- VANDEN BERGE, J. C. 1970. A comparative study of the appendicular musculature of the order Ciconiiformes. Amer. Midl. Natur. 84: 289–364.
- WETMORE, A. 1926. Descriptions of additional fossil birds from the Miocene of Nebraska. Amer. Mus. Novitates 211: 1–5.
- . 1960. A classification for the birds of the world. Smithsonian Misc. Coll. 139: 1–37.
- ZUSI, R. L., & R. W. STORER. 1969. Osteology and myology of the head and neck of the Pied-billed Grebes (*Podilymbus*). Misc. Publ. Mus. Zool. Univ. Michigan 139: 1–49.