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MULTIPLE ORIGINS OF THE CICONIIFORMES

Storrs L. Olson

Department of Vertebrate Zoology
National Museum of Natural History
Smithsonian Institution
Washington, D. C. 20560

In the course of investigating the relationships of flamingos (Phoenicopteridae), it became increasingly apparent to me that the order Ciconiiformes is probably an entirely artificial assemblage consisting of various long-legged, long-necked, altricial waterbirds having little else in common. The charadriiform affinities of flamingos are being documented in some detail elsewhere (Olson and Feduccia, MS) and I shall attempt here only a summary of the evidence assembled so far in that regard. I would like to use this opportunity to put on record some preliminary ideas concerning the possible relationships of the remaining five families of Ciconiiformes (storks, Ciconiidae; shoebill stork, Balaenicipitidae; hammerhead, Scopidae; ibises and spoonbills, Threskiornithidae; herons, Ardeidae).

If, as I shall propose, the families of Ciconiiformes are derived from at least four different sources, what factor can be held to account for having masked their true affinities all this time? Entrenched tradition is by now much to blame, of course, but beyond that I suspect the trouble can be traced back to Huxley's (1867) attempt to classify birds according to palate types. Although the problems inherent in Huxley's classification have long been apparent (Newton, 1896; Sibley and Ahlquist, 1972), his paper nevertheless had a strong influence on subsequent avian systematists such as Fürbringer and Gadow, whose ideas of relationships have been passed on largely uncritically to form the basis for the system of avian classification in use today. All Ciconiiformes have been said to be desmognathous, that is the maxillo-palatine bones meet along the midline of the skull. This actually does not hold for some Ciconiiformes although the palatines are connected to each other in all the families. This condition has evolved repeatedly in birds, yet probably prevented earlier researchers from looking for relatives of Ciconiiformes among non-desmognathous birds. Combined with general limb and body proportions the desmognathous palate is probably responsible for the Ciconiiformes still being recognized as a separate order.

Let us first dispense with the Phoenicopteridae, a family for which there is now abundant evidence showing close relationships to birds other than Ciconiiformes. Long associated with the storks on account of their long legs and neck, flamingos have also been proposed as relatives of ducks and geese (Anseriformes) because of their webbed feet, filter feeding adaptations, and certain behavioral traits. All evidence has heretofore been interpreted with only these two alternatives in mind. On the basis of the osteology of modern forms and of early Eocene fossils (*Presbyornis*) thought to be related to flamingos, Feduccia (1976) first proposed that the Phoenicopteridae were derived from the shorebirds (Charadriiformes) and have no relationship with storks. Since then we have gathered evidence from osteology, paleontology, myology, pterylosis, behavior and life history (Olson and Feduccia, MS) showing a very close relationship between flamingos and the Recurvirostridae (avocets and stilts), particularly the Australian Banded Stilt, *Cladorhynchus leucocephalus*.

In commenting on Feduccia's (1976) hypothesis of a charadriiform relationship for flamingos, Parkes (1978:9) suggested that "the substantial amount of evidence gathered by earlier workers that indicates relationship of the flamingos to the Ciconiiformes" would first have to be disposed of. Consequently, we re-examined the earlier evidence as summarized by Sibley et al. (1969) in their paper on the relationships of flamingos. On critical examination, all of the morphological characters previously cited as showing a relationship between flamingos and storks proved to be merely non-anseriform characters that occur in several other orders, including the Charadriiformes. In addition, most of the

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morphological and behavioral characteristics regarded as being unique to flamingos (as opposed to storks or ducks) are also found in the Charadriiformes. In the final analysis, we encountered not a single substantial character of any sort that can be used to ally flamingos with storks.

The supposed anseriform characters of flamingos are also found in the Charadriiformes or are only superficially similar to ducks. For example, the filter feeding apparatus in the two groups is fundamentally different, the tongue in flamingos being accomodated by the lower jaw while that in the Anseriformes is unique among filter-feeding vertebrates in being housed in the upper jaw. The early Eocene fossil *Presbyornis* shows that the Anseriformes, like flamingos, evolved from a highly colonial charadriiform stock adapted to shallow saline or alkaline lakes, but the common ancestor of flamingos and ducks could have had few, if any, of the specialized features of either group (Olson and Feduccia, MS).

The following are some of the highlights of the evidence we have uncovered that demonstrates the charadriiform affinities of flamingos. First of all, as far as it is known, the ecology and behavior of the little-studied Australian Banded Stilt, *Cladorhynchus leucocephalus*, almost exactly duplicates that of flamingos. *Cladorhynchus* inhabits ephemeral, highly saline lakes and breeds at irregular intervals in extremely dense colonies in which territoriality is all but absent (see photographs in McGilp and Morgan, 1931). Unlike other Recurvirostridae, the young of *Cladorhynchus* do not leave the nest immediately after hatching. When they do leave, they gather in groups and receive at least some parental care (McGilp and Morgan, 1931; Kolichis, 1976). These are precisely the distinctive features of the breeding biology of flamingos that set them apart from other Ciconiiformes. In reviewing the literature, we found that virtually all behavior patterns of flamingos could also be found in the avocets and stilts, including even raising the eggs above the ground on mud or vegetation (Rooth, 1965:99-100; Makkink, 1936:35).

Unlike the young of any other shorebird, the young of *Cladorhynchus* are clothed in white, unpatterned down, as are the young of flamingos. Furthermore, we have found that there are two successive coats of nestling down in *Cladorhynchus*, a condition otherwise unknown in the Charadriiformes but which is characteristic of flamingos. Storks (but not herons or ibises) also have two coats of nestling down, a point which drew some emphasis from Sibley et al. (1969) in trying to defend their placement of flamingos in the Ciconiiformes, the condition of the down in *Cladorhynchus* being then unknown. Although ibises have also been said to have two coats of down (Palmer, 1962), this is not in fact the case (K. C. Parkes, *in litt*. 27 November 1978).

It is significant that in his detailed study of the musculature of the Ciconiiformes, Vanden Berge (1970) found no consistent pattern in the myology that could be used to unite the various families. However, he did describe a new thigh muscle unique to flamingos, the iliotibialis medialis (Vanden Berge, 1976). I found this same muscle to be present and well-developed in *Cladorhynchus* but not in other genera of Recurvirostridae. I found 21 additional characters in which the appendicular myology of flamingos agrees with *Cladorhynchus* and differs from all Ciconiiformes, plus 11 other myological characters shared between *Cladorhynchus*, flamingos, and one or more families of Ciconiiformes but not shared with storks.

The pterylosis of flamingos was said by Nitzsch (1867:132) to be "perfectly Stork-like" and he was quoted uncritically to this effect ever afterward. I found the pterylosis of flamingos to be utterly different from that of storks, whereas in the dense down and the dense, hard feathering of the pectoral and humeral tracts, flamingos are much more similar to *Cladorhynchus*, although the two are distinct in several other details of their pterylosis.

Similarities between the osteology of flamingos and shorebirds have been dealt with by Feduccia (1976) and are substantiated by our further studies. In this regard it is perhaps well to note that the osteology of *Cladorhynchus* does not differ in any major aspect from that of other Recurvirostridae, this being reflected by the fact that Strauch (1978), whose classification of the Charadriiformes was based almost entirely on osteological characters, accorded no special significance to *Cladorhynchus*.

Finally, a new fossil from the middle Eocene of Wyoming lends further support to the charadriiform nature of flamingos. This bird was intermediate in size between modern stilts and flamingos and combined the humerus and specialized cervical vertebrae of the Phoenicopteridae with the unfused thoracic vertebrae typical of shorebirds and a tarsometatarsus almost indistinguishable from that of stilts in the genus Himantopus. This is the oldest definite flamingo yet known, all of the supposed flamingos from the Cretaceous and Paleocene being based on equivocal or unverifiable fragments (Olson and Feduccia, MS). If flamingos were derived from storks, one would expect fossil forms to be more storklike than modern ones; this definitely is not the case.

It is our conclusion that the highly specialized feeding apparatus and certain postcranial osteological features, some of which are possibly correlated with increased size, entitle the flamingos to separate family rank. This family, however, cannot otherwise be separated from the suborder Charadrii, within which it should be placed immediately following the Recurvirostridae (Olson and Feduccia, MS).

Having seen that the flamingos have no business whatsoever in the Ciconiiformes, it is hoped that the reader might now regard the naturalness of the remainder of the order with some skepticism.

In making comparisons of flamingo skeletons with the Ciconiiformes it struck me that the ibises (Threskiornithidae) actually bear very little resemblance to storks. The bill in ibises is long, decurved, flexible, and equipped with sensory pits at the tip. This is quite unlike the hard, pointed bill of storks and herons. Analogy of ibises with curlews (Numenius, Charadriiformes) has often been made and just as often dismissed, doubtless on account of the supposedly desmognathous palate of the former. While the curlews themselves are probably not closely related to ibises, there are additional charadriiform characters of the Threskiornithidae, such as the four-notched sternum and the large retroarticular processes of the mandible, that are not found in other Ciconiiformes.

Ibises typically have paired apertures in the back of the skull above the foramen magnum, the occipital fontanelles. To my knowledge, these structures occur only in the Charadriiformes, flamingos and ducks (which evolved from the Charadrii), and in the derived gruiform families Gruidae and Aramidae (cranes and limpkins). Ibises have schizorhinal nostrils and supraorbital salt glands--conditions typical of almost all Charadriiformes and many Gruiformes, but absent in storks and herons. The proportions of the wing bones of ibises are unlike the much longer elements of other Ciconiiformes but are similar to certain Gruiformes. I have found that there is a particularly close resemblance between much of the postcranial skeleton of ibises and that of the sunbittern (Eurypygidae, Gruiformes). This has also been noted by Garrod (1876).

The Threskiornithidae deserve careful anatomical and behavioral study, for to me they appear to represent a more probable transitional group between the admittedly closely related orders Charadriiformes and Gruiformes, than any of the families heretofore suggested as bridging this gap. I can find nothing in any aspect of the morphology of recent Threskiornithidae that suggests an affinity with storks.

With two families eliminated from the Ciconiiformes, we turn next to the curious African Shoebill, Balaeniceps rex, which rightfully constitutes a monotypic family. Although the original describer regarded Balaeniceps rex as having pelecaniform affinities (Gould, 1852), the species soon came to be regarded as an aberrant stork. In a paper that should have been received as presenting a convincing, or at the least a provocative argument, Cottam (1957) discussed numerous salient features in the skeleton of Balaeniceps that indicate relationship to the Pelecaniformes. Her evidence, however, was dismissed offhand as being due to "convergence" and the status of Balaeniceps as a stork was preserved (e.g. Wetmore, 1960:10), despite the fact that the derivation of the storks themselves was an unresolved issue. The pelecaniform characters of Balaeniceps are actually quite pronounced and cannot be casually explained away. For example the grooved rostrum with a strongly hooked tip, the prominent coracoidal facets of the furcula, and the fusion of the furcula with the apex of the sternal carina are distinctly pelecaniform features. These characters, except for the last mentioned, are also present, though in a more modified state, in the Hammerhead, Scopus umbretta, itself a member of a monotypic family. In the Ciconiidae many of these features are absent, although the furcula still has a strong articulation with the sternum.

Feduccia (1977) has shown that Balaeniceps and the storks share a unique derived condition of the stapes. This condition is most closely approached in certain Pelecaniiformes (Feduccia, pers. comm.). The stapes is of the primitive avian type in flamingos, ibises, and herons, while that of Scopus is neither primitive nor like that of Balaeniceps and storks (Feduccia, pers. comm.). It may perhaps be of more than passing interest to note that Scopus has been observed to feed on the wing, quite successfully capturing prey from just beneath the surface of the water (Kahl, 1967), like a frigatebird or a gull.

From a preliminary assessment it appears possible that the Balaenicipitidae, Scopidae and Ciconiidae may represent a more or less natural assemblage having affinities with the Pelecaniformes. In this regard mention should be made of Ligon's (1967) hypothesis that the New World vultures (Cathartidae) are related to storks. This must now be entertained even more seriously because of the recently published, detailed anatomical studies of Jollie (1976-1977) showing the order Falconiformes also to be a totally artificial assemblage. Although Jollie did not specifically state to which orders the various "falconiform" families may be referred, he has established to my satisfaction that the Cathartidae bear no relationship to other diurnal raptors. Furthermore, in his paper it can be seen that the sternum in the extinct vulture Teratornis (Teratornithidae) is much more like that of a pelecaniform than is that of the Cathartidae. Future research should be directed towards confirming or refuting a hypothesis that the Pelecaniformes, Teratornithidae, Cathartidae, Balaenicipitidae, Scopidae, and Ciconiidae represent divergent members of a single natural assemblage.

Now where does this leave the Ardeidae? Herons have none of the pelecaniform features of the stork group nor any of the charadriiform characters of ibises. Cottam (1957), Ligon (1967), and Feduccia (1976) have each commented on the distinctive osteology of herons and considered them as unlikely relatives of storks. Certain peculiarities of herons permit an educated guess at their true affinities.

Nitzsch (1867) clearly showed that the pterylosis of herons is highly distinctive and totally unlike that of storks, the feathers being restricted to very narrow rows as in the gruiform sunbittern, Eurypyga. From the studies of Lowe (1924) it can be seen that the same is true of the peculiar Madagascan Gruiformes of the family Mesoenatidae. Nitzsch placed the herons and Eurypyga in a "family" Erodii, separate from the storks. Chandler (1916) stressed what he considered to be great similarity in the feather structure of herons and Eurypyga.

Even more distinctive are the patches of powderdown feathers of herons. There are typically three pairs of these patches in herons, with Cochlearius and some tiger herons having four, and bitterns having two. In Mesoenas there are five pairs of powderdown patches (Lowe, 1924) and these have exactly the appearance of those of herons (pers. observ.). There is a single pair in Eurypyga (Nitzsch, 1867), whereas in the New Caledonian Kagu (Rhynochetidae, Gruiformes) powderdowns are more generally distributed than in any of the preceding forms (Murie, 1871). The only "ciconiiform" besides herons that has powderdowns is Balaeniceps, in which there is a single dorsal patch. I have found, however, that the feathers here are more or less typical contour feathers with powderdown structure at their bases, whereas in herons and Mesoenas the powderdowns are densely packed and completely modified, contrasting markedly in color and texture with adjacent contour feathers.

The tarsometatarsus of herons is quite distinctive and easily recognized by the peculiar shape of the trochleae and their alignment in the same proximodistal plane. The tarsometatarsus of Mesoenas more closely resembles that of herons than does that of any other bird known to me. Although herons are "desmognathous", the overall architecture of the palate is much more similar to that of Eurypyga than to storks.

I suggest that the Ardeidae are the only currently successful group in an early radiation of primitive Gruiformes which includes the decidedly relictual families Mesoenatidae, Eurypygidae, and Rhynochetidae. This being the case, then the recently proposed sequence of genera of herons set forth by Payne and Risley (1976) should probably be nearly reversed. Solitary, ornately-plumaged (e.g. with barred wings), tropical, forest herons with a greater number of powderdown patches, such as the species of Tigriornithinae, or an aberrant form such as Zebrilus, would most likely be primitive, whereas the highly colonial, conspicuously plumaged day herons of the Ardeinae would be among the more derived forms of the family.

Although the relationships of the families of Ciconiiformes proposed here will require further documentation and analysis, it should be emphasized that the same constraints of proof should be imposed on those who advocate maintaining the Ciconiiformes as a natural, monophyletic group. By now, I feel fairly confident that there can be very little hope of making a strong case for the latter proposition.

The field biologist can play an important role in providing additional information by which to assess new theories of relationships and the questions raised here suggest ample opportunity for significant and interesting comparative behavioral studies. Imagine the challenge in studying the elusive and all but unknown Australian Banded Stilt---a living link between shorebirds and flamingos. Is there anything in the deportment of the poorly known Madagascan mesoenatids, the New Caledonian Kagu, or the Neotropical sunbittern that hints of what is known of the much-studied herons? What in the behavior of ibises---a neglected group in their own right---is reminiscent of Gruiformes or Charadriiformes? Can the evolution of behavioral patterns that are already well known be better understood and explained in light of the new theories of relationship proposed here? These and many other similar questions await resolution.

SUMMARY

The order Ciconiiformes appears to be a totally artificial assemblage of long-legged, desmognathous waterbirds having little else in common. Flamingos (Phoenicopteridae) are demonstrably closely related to avocets and stilts (Recurvirostridae) and belong in the suborder Charadrii of the Charadriiformes. Ibises (Threskiornithidae) appear to be a transitional group having similarities both to the Gruiformes and to the Charadriiformes. Shoebills, hammerheads, and storks (Balaenicipitidae, Scopidae, Ciconiidae) may be loosely interrelated and have affinities with the Pelecaniformes. Herons (Ardeidae) are quite probably part of an early radiation of Gruiformes and have their closest relationship with the relict families Mesoenatidae, Eurypygidae, and Rhynochetidae. Although more research is needed, there is little justification for continuing to recognize the Ciconiiformes as a natural order.

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