



Relationships and Evolution
of Flamingos
(Aves: Phoenicopteridae)

STORRS L. OLSON
and
ALAN FEDUCCIA

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ABSTRACT

Olson, Storrs L., and Alan Feduccia. Relationships and Evolution of Flamingos (Aves: Phoenicopteridae). *Smithsonian Contributions to Zoology*, number 316, 73 pages, 40 figures, 2 tables, 1980.—Previous evidence supposedly showing a relationship between flamingos and either storks (Ciconiiformes) or ducks (Anseriformes) is re-examined in light of the recent hypothesis deriving flamingos from shorebirds of the order Charadriiformes. Anatomical characters used to indicate relationship between flamingos and storks are shown to consist entirely of primitive “non-anseriform” traits found in several other orders, including Charadriiformes. Most of the presumed anseriform characters of flamingos also occur in the Charadriiformes, as do all of the characters of flamingos that do not occur in either Ciconiiformes or Anseriformes. The distinctive life history and behavior of flamingos is demonstrated as being very similar to that of the Recurvirostridae (Charadriiformes), particularly the Australian Banded Stilt (*Cladorhynchus leucocephalus*), but is unlike that of storks or ducks. The appendicular myology of *Cladorhynchus* is described and is found to be quite similar to that of flamingos, whereas neither is close to storks. The thigh muscle M. iliotibialis medialis, heretofore considered unique to flamingos, was discovered in *Cladorhynchus* but not in other Recurvirostridae. Evidence from osteology, natal down, oology, and internal parasites strongly supports a charadriiform derivation of flamingos; pterylosis does not contradict such a relationship; and knowledge of the early evolution of flamingos and Anseriformes offers a logical explanation for their sharing similar mallophagan parasites. The earliest certain flamingo, from the early Middle Eocene of Wyoming, is described herein as a new monotypic genus and species that was intermediate in size and morphology between the Recurvirostridae and modern flamingos. Other aspects of paleontology of flamingos are discussed. Evolutionary steps in the development of filter feeding in birds are outlined. The structure of the feeding apparatus of flamingos is shown to be entirely different from that of the Anseriformes, but is strikingly convergent towards that of baleen whales. Morphological and behavioral precursors for filter feeding are shown to occur in the Charadriiformes but not in the Ciconiiformes. Flamingos (Phoenicopteridae) clearly belong in the order Charadriiformes, suborder Charadrii, immediately following the Recurvirostridae.

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Contents

	<i>Page</i>
Introduction	1
Acknowledgments	3
Review of Previous Anatomical Information	3
Life History and Behavior	9
Myology	15
Appendicular Myology of <i>Cladorhynchus</i>	17
Pterylosis	31
Natal Down	34
Oology	34
Parasitology	36
Biochemistry	39
Osteology	39
Skull	39
Postcranial Skeleton	40
Paleontology	43
A New Stilt-like Flamingo from the Middle Eocene of Wyoming	47
Order CHARADRIIFORMES Huxley, 1867	48
Suborder CHARADRII Huxley, 1867	48
Family PHOENICOPTERIDAE Bonaparte, 1831	48
<i>Juncitarsus</i> , new genus	48
<i>Juncitarsus gracillimus</i> , new species	48
Aspects of Evolution of Filter Feeding	58
Conclusions	66
Literature Cited	69

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Introduction

The living flamingos (Phoenicopteridae) constitute a small and easily recognized group of four to six species of large, brightly colored waterbirds with extremely long legs and neck and a uniquely shaped bill adapted for filter-feeding. They are colonial and characteristically inhabit highly saline bodies of shallow water. The existing species are placed in three genera that are separable into two groups on bill morphology: (1) *Phoenicopterus*, which has a more primitive filtering apparatus, and (2) *Phoenicoparrus* and *Phoeniconaias*, which are more specialized (Jenkin, 1957). The last two genera are separated from each other only by the presence or absence of the hind toe, which is very reduced in flamingos in any case, so that continued recognition of the genus *Phoeniconaias* is probably unwarranted. We have not detected characters of generic value in the postcranial skeleton that will separate the two groups differing in feeding adaptations. For purposes of extrafamilial comparisons, modern flamingos can be regarded as essentially monogeneric, although we have

made no innovations in generic usage in the present paper.

The proper phylogenetic position of the Phoenicopteridae has long been a perplexing problem in avian systematics. Because of the conflicting nature of the taxonomic evidence presented so far, the relationships of these birds have never been satisfactorily resolved. Flamingos are most often placed with storks, herons, and ibises in the order Ciconiiformes. This assemblage consists of large, long-legged waterbirds having a long neck, "desmognathous" palate, and usually altricial young. Olson (1979) has recently suggested that the order may be an entirely artificial collection of unrelated families. The association of flamingos with storks and their supposed allies was probably made originally solely on the basis of their large size and general proportions. This allocation was later "supported" by a body of evidence that we shall show to be altogether fallacious.

Other workers noted that the lamellate bill, webbed feet, mallophagan parasites, and some general aspects of the behavior of flamingos seemed to point toward a relationship with ducks and geese (Anseriformes). Controversy has subsequently centered on whether flamingos are more closely related to the storks or to the ducks.

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Continual equivocation has resulted in some authors elevating the flamingos to an order of their own (Phoenicopteriformes), an action that merely avoids the question of relationships.

All comparisons of flamingos have traditionally been made with Ciconiiformes on one hand and Anseriformes on the other, but as we shall see, most of the characters cited as showing relationship also occur outside those two groups. Many of the supposed ciconiiform characters of flamingos are really only negative characters that are simply "non-anseriform" in nature and not really indicative of relationship to storks. Characters of flamingos that are shared with both Anseriformes and Ciconiiformes have even been cited by some authors as evidence of a common origin of all three groups, despite the fact that these characters are likewise found in birds of several other orders.

The first alternative to the ciconiiform-anseriform hypothesis of flamingo relationships was advanced by Feduccia (1976), who proposed that flamingos are related to shorebirds (Charadriiformes) and have no affinity with the Ciconiiformes. This idea came about through studies of the fossil bird *Presbyornis* (McGrew and Feduccia, 1973; Feduccia and McGrew, 1974; Feduccia, 1976, 1977a, 1977b, 1978, in press). Bones of *Presbyornis* occur in great concentrations in early Eocene deposits of the western United States and the birds were evidently highly colonial, as are modern flamingos. For this reason and because *Presbyornis* had originally been described by Wetmore (1926) as a new family of Charadriiformes related to the Recurvirostridae, Feduccia (1976) made comparisons with shorebirds. He found both *Presbyornis* and the Phoenicopteridae to be most similar in their postcranial osteology to the Charadriiformes and very different from storks and herons. We now know, however, that the skull of *Presbyornis* is duck-like (Feduccia, 1978; Olson and Feduccia, in press) and, apart from a rather close similarity in the naso-frontal area, is quite different from that of flamingos. *Presbyornis* provides evidence for a charadriiform origin of the Anseriformes (Olson and Feduccia, in press), but similarities between *Presbyornis* and flamingos

may be attributable to both having been derived from the Charadriiformes, rather than indicating that they are closely related to each other. Nevertheless, *Presbyornis* coincidentally pointed the way towards the proper association of flamingos with the Charadriiformes.

In the course of our investigations we found that all the evidence relating to the systematics of flamingos could be best explained by their having a charadriiform origin. Furthermore, it soon became apparent not just that flamingos were derived from the Charadriiformes but that they were derived from a particular family, the Recurvirostridae. In this connection we have made repeated comparisons with the Australian Banded Stilt, *Cladorhynchus leucocephalus*, an extraordinary bird that shares a number of unique traits with flamingos and which can in many respects be regarded as forming an intermediate between the Recurvirostridae and the Phoenicopteridae.

In view of our findings, we take satisfaction in noting that in Willughby's *Ornithology* (Ray, 1678), which is regarded as the foundation of the scientific study of birds, the flamingo appears in Book III, Part II, with "birds of a middle nature between swimmers and waders, or that do both swim and wade" (page 312), in a separate section, the "whole-footed [webbed] long-legged birds" (page 320), that otherwise includes only the avocet (*Recurvirostra*, Charadriiformes). These two were far removed from the "cloven-footed waterfowl" in which were placed the storks and herons.

In his *Systema Naturae*, Linnaeus (1758) generally followed the classification of Willughby and Ray for birds, "and where he departed from his model he seldom improved upon it" (Newton, 1896:8 [intro.]). Linnaeus led off his order Grallae with the flamingos, followed immediately by spoonbills (Threskiornithidae), certain storks (Ciconiidae), and the species he included in *Ardea*, which was composed mainly of herons, storks, and cranes. These were succeeded by shorebirds and various gruiforms. The association of flamingos with storks and herons, thus begun, has continued up to the present and has quite successfully obscured the true relationships of flamingos.

Sibley, Corbin, and Haavie (1969:176) provided a comprehensive review of the classification and relationships of flamingos, citing previous evidence from paleontology, anatomy, parasites, behavior, and new evidence from biochemistry, from which they concluded that the flamingos should be "treated as a suborder, Phoenicopteriformes, in the Order Ciconiiformes and that, in a linear list, the Anseriformes and Ciconiiformes be placed adjacent to one another." Because their study has come to be regarded as a standard reference on the systematics of flamingos and has been cited as showing proof of ciconiiform affinities (e.g., Parkes, 1978), we have analyzed the evidence they presented in critical detail, augmenting this with new data and evaluating the whole in light of the charadriiform affinities first proposed by Feduccia (1976).

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Review of Previous Anatomical Information

Sibley et al. (1969) have most recently been cited by Parkes (1978:9) in connection with the supposed "substantial amount of evidence . . . gathered by earlier workers that indicates relationship of the flamingos to the Ciconiiformes" that "would have to be disposed of satisfactorily before serious consideration can be given to Feduccia's proposed phylogeny for flamingos that involves no relationship at all to Ciconiiformes." In their discussion of anatomical evidence, Sibley et al. (1969:159, table 3) present a summary of most of the characters cited in the earlier literature on flamingo systematics (reproduced here as Table 1). In accordance with Parkes' admonitions, we have analyzed each of these.

"Characters Shared with the Ciconiiformes"

1. "(partly) nidifugous": The intention is not clear, particularly since "nidifugous" is given later as a character (19) shared with Anseriformes. According to the terminology of Nice (1962), all Ciconiiformes except flamingos are semi-altricial (unable to leave nest, down covered, fed by parents); Anseriformes are type 2 precocials (leave nest first day or two, down covered, follow parents but feed themselves); flamingos are semi-precocial (stay at nest though able to walk, down covered, fed by parents). Charadriiformes may be either precocial (e.g., shorebirds) or semi-precocial (e.g., gulls). Downy flamingo chicks leave the nest within three or four days and so seem much

TABLE 1.—Summary of anatomical characters of flamingos reproduced exactly as in Sibley et al. (1969, table 3) except with characters numbered to facilitate reference to the text

<i>Characters shared with Ciconiiformes</i>	<i>Characters shared with Anseriformes</i>	<i>Characters shared with both orders</i>	<i>Characters shared with neither order</i>
Developmental:	Developmental:	Integumental:	Integumental:
1 (partly) nidifugous	18 thick down on young	32 tufted oil gland present	42 reduced hallux
2 two coats of down	19 nidifugous	33 11 primaries	43 inverted bill
Integumental:	Integumental:	34 diastataxic	44 filter apparatus
3 down structure	20 feather structure	Skeletal:	Muscular:
4 pterylosis	21 waterproof plumage	35 carinate	45 flexor tendons type IV
5 aftershaft present	22 webbed feet	36 desmognathous	46 1 pair syrinx muscles
Skeletal:	23 lamellate bill	37 holorhinal	47 small femoral-caudal
6 basipterygoid process present	Skeletal:	38 pervious nares	48 BXY + muscle formula
7 palatine and vomer	24 nasal aperture	39 no ectocondylar process	Other:
8 rostrum	25 supraorbital depression	40 16–25 cervical vertebrae	49 type of air cells in lung
9 pelvis	26 lachrymals	Muscular:	
10 number ribs	27 quadrate	41 ambiens present	
Muscular:	28 mandibular angle		
11 flight muscle attachment	29 pectoral girdle		
12 gastrocnemius	Others:		
Others:	30 caeca		
13 carotid artery arrangement	31 tongue shape		
14 cervical air sacs divided			
15 intestinal convolutions			
16 penis rudimentary			
17 abdominal air sacs large			

more like the young of shorebirds or ducks than the helpless young of Ciconiiformes. Among the Charadrii, the young of *Cladorhynchus* do not leave the nest immediately after hatching, as do those of all other Recurvirostridae, but the degree of parental attendance is not yet known.

2. “two coats of down”: Sibley et al. (1969) stress the fact that in young flamingos there are two successive coats of natal down, a condition they represent as characteristic of the Ciconiiformes but absent in the Anseriformes. The situation is more complicated than they indicate, and is discussed beyond (page 34), where we show that the condition of the natal down in *Cladorhynchus* is unique in the Charadriiformes in being like that of flamingos.

3. “down structure”: Sibley et al. (1969) cite Reichenow (1877) as noting that flamingos

have simple, unbranched down like that of Ciconiiformes and unlike the branched rhachidial down of Anseriformes. The down of flamingos, however, does not differ in this respect from the non-rhachidial down of the Charadriiformes or that of most other precocial birds.

4. “pterylosis”: This comes ultimately from Nitzsch’s (1867:132) statement that the pterylosis of *Phoenicopterus* is “perfectly Stork-like.” This came about through contrasting the pterylosis of flamingos and storks with the highly divergent pterylosis of herons. There is actually little similarity between the pterylosis of flamingos and storks (see page 31).

5. “aftershaft present”: The aftershaft is absent or rudimentary in the Anseriformes and it is present in flamingos and Ciconiiformes. It is also present in the Charadriiformes and many other

orders of birds (Beddard, 1898).

6. “basipterygoid process present [sic]”: This would be interpreted as a lapsus calami if Sibley et al. (1969:161) had not repeated that the “presence of a basi-ptyerygoid process” is a shared character uniting flamingos with Ciconiiformes. This statement may derive from Beddard’s (1898:441) erroneous assertion that the skull in *Phoenicopterus* has “basipterygoid processes, to which the anterior ends of the pterygoids are attached.” In fact, the basipterygoid processes are invariably absent in the Ciconiiformes and are absent or only very rudimentary in flamingos, whereas in the Anseriformes the so-called basipterygoid processes are particularly large and well developed. These processes may well not be homologous from one group of birds to another. The basipterygoid processes are quite variable in the Charadriiformes, being absent in some groups and present in others. This character is certainly not useful for determining the relationships of flamingos.

7. “palatine and vomer”: See character 8 below.

8. “rostrum”: The supposed similarity of the palatine, vomer, and rostrum of flamingos to those of storks seems to have been taken by Sibley et al. from uncritical comments of Reichenow (1877) and Gadow (1877) and may also stem in part from Huxley’s (1867:461) erroneous and unsubstantiated statement that in flamingos “the general structure of the rostrum is quite similar to that found in the Storks and Herons.” Quite to the contrary, the general structure of the rostrum of adult flamingos is not like that of any other bird. Reichenow’s (1877) paper concerns only the Ciconiiformes, to which he had already assumed the flamingos belonged, and he saw similarities where none existed. Although distinctive, the palate in flamingos is actually more similar to that of shorebirds (as exemplified by the Recurvirostridae) than that of storks (pages 39–40).

9. “pelvis”: This seems to stem from a single sentence in Gadow (1877:386), stating that the pelvis in flamingos is purely stork-like and hardly similar to that of ducks at all, particularly in the features of the pubis. This is partly true, although

further comparison shows the pelvis of flamingos to be even more similar to that in the Recurvirostridae than to storks (page 41).

10. “number ribs”: We have not located a prior reference to this character but it may derive from some of the statements of Gadow (1877), who later stated that “from a taxonomic point of view Ribs are valueless” (Gadow, in Newton, 1896:789). We found that flamingos may have either 5 or 6 ribs attached to the sternum. The same number may be found in the Charadriiformes, in some Ciconiiformes and Anseriformes, and in many other orders as well (Fürbringer, 1888).

11. “flight muscle attachment”: This comes from the observations of Weldon (1883:647).

In Storks it is well known that the pectoralis major is divided into two or more layers, easily separable from one another, and that its attachment to the humerus forms a tendinous arch beneath which the brachial muscles pass from the coracoid to the arm. In *Phoenicopterus*, Gadow has shown that these features are exactly repeated; . . . I need hardly point out that this condition is absolutely unknown among Lamellirotres [= Anseriformes].

The “pectoralis major” (= *M. pectoralis*) is known to be divided into two or three layers in the Gruidae, Cathartidae, Procellariiformes, Pelicaniformes, and Scopidae, in addition to storks (George and Berger, 1966:307–308). Hudson et al. (1969) describe this muscle as being divided in the Laridae and Alcidae. We dissected specimens of *Cladorhynchus leucocephalus* and *Himantopus mexicanus* (Recurvirostridae) and found this muscle to be distinctly divided into two sections, which are partially coalesced along the dorsolateral margin (page 19). The general configuration is as described and illustrated by Weldon (1883) for *Phoenicopterus* and is indeed quite distinct from the condition we observed in a specimen of duck, *Anas poecilorhynchus*. The division of this muscle in certain storks (*Leptotilos*) is actually quite different from that of flamingos (Vanden Berge, 1970). This appears to be another character that separates flamingos from the Anseriformes but that is shared with numerous other orders, including the Charadriiformes.

12. “gastrocnemius”: Weldon (1883) is again

cited for noting that flamingos supposedly differ from the Anatidae in having the gastrocnemius arising by three heads instead of two and in having the accessory semitendinosus muscle (= *M. flexor cruris lateralis pars accessoria*) present. He did not mention that in the last character flamingos differ just as much from storks, in which the accessory semitendinosus is also absent. Furthermore, the gastrocnemius in at least some Anatidae arises by three heads (Raikow, 1970: 34). The three-headed gastrocnemius and the accessory semitendinosus occur in many birds, including the Charadrii (George and Berger, 1966). Actually, the gastrocnemius in flamingos has four heads (Vanden Berge, 1970), as does that of *Cladorhynchus* (Figure 7a).

13. "carotid artery arrangement": Sibley et al. regard Glenny's (1955) findings on the carotid arteries as only questionably indicating a relationship between flamingos and the Ciconiiformes. Flamingos have type B-2-s carotid arteries. Anseriformes, Charadriiformes, all Ciconiidae and Threskiornithidae, and most Ardeidae have type A-1 carotids. A few of the Ardeidae have type B-1 carotids, *Ardeola speciosa* has type B-2-s, and *Botaurus lentiginosus* may have either type B-1 or B-2-s. The B-2-s condition was evidently derived independently from the A-1 condition at least twice within the Ardeidae. The B-2-s condition in flamingos had to have been derived independently of that in *Botaurus lentiginosus* and *Ardeola speciosa* and it could as easily have come from the A-1 condition in shorebirds or ducks as from the A-1 condition in Ciconiiformes, a point later specifically admitted by Sibley and Ahlquist (1972).

14. "cervical air sacs divided": This character, along with character 17 ("abdominal air sacs large"), stems from Weldon's (1883) observations that the air sacs in flamingos are in these respects more like those of storks than ducks. In a modern account of the air sac system of birds (Duncker, 1971), no mention is made of any peculiarities of flamingos. The cervical air sacs are paired in most birds and are unusually large in the Spheniscidae, Anatidae, Falconidae, and Accipitridae (Duncker, 1971:49), so it would appear that this

is but another character in which flamingos differ from ducks but resemble many other birds. The same is true of the large abdominal air sacs, which are typical of most birds. According to Duncker (1971:62) storks differ from all other birds in having the posterior thoracic air sac divided into medial and posterior sacs. If any conclusion can be drawn from this it is that the air sacs of flamingos do not seem to agree with those of either storks or ducks.

15. "intestinal convolutions": Beddard (1898: 441) stated only that in flamingos "the intestines are not duck-like," which carries no information about affinities with other groups. We note from the table in Gadow (1889) that the general intestinal pattern in flamingos is found in the Charadrii as well as in storks, although Gadow's attempts to use the varying patterns of intestinal convolutions in birds as taxonomic characters have been largely discredited (see Sibley and Ahlquist, 1972:21-22).

16. "penis rudimentary": This feature is of importance only in contrast to ducks, which have a well-developed penis. The penis is rudimentary or lacking in most birds, including flamingos and shorebirds, although it might be noted that Beddard (1898:37) states that a penis exists in the Ciconiiformes (he does not say in which forms) and in *Burhinus* (Charadriiformes), in addition to ratites, tinamous, cracids, and ducks.

17. "abdominal air sacs large": See character 14 above.

"Characters Shared with Anseriformes"

18. "thick down on young": Thick down is also present in the young of Charadriiformes and other precocial birds.

19. "nidifugous": See character 1 above.

20. "feather structure": See character 21 below.

21. "waterproof plumage": To Chandler (1916) the feather structure of flamingos was much more similar to that of Anseriformes than Ciconiiformes, but he did not specifically compare flamingos with Charadriiformes. Sibley et al. (1969:160) felt that the "close, hard, waterproof nature of the plumage as a whole, shared

by flamingos and geese, could easily be the result of convergence.” They cite Rutschke (1960) as showing that “water birds in different orders are more alike in feather structure than non-aquatic birds even within the same order.” Nonetheless, it is worth observing that the feathers in the *Recurvirostridae* are notably close, hard, and dense; photographs of *Recurvirostra americana* engaged in feeding show the plumage to be quite waterproof as well (Tremaine, 1975:75).

22. “webbed feet”: Species of birds with webbed feet occur in a variety of orders other than *Anseriformes*, including the *Charadriiformes*. Within the *Recurvirostridae*, *Recurvirostra* and *Cladorhynchus* have webbed feet, while *Himantopus* has only vestigial webs.

23. “lamellate bill”: As detailed later (pages 59–60), the structure of the bill and lamellae in flamingos and ducks is fundamentally different and is not indicative of relationship.

24. “nasal aperture”: This character and the following three appear to have been based mainly on the authority of Shufeldt (1901:305), who stated that

in its external narial apertures; in the possession of supraorbital glandular depressions; to a small degree in its lachrymal bones; . . . in its quadrates; in the possession of large recurved processes at the mandibular angles—the skull of the Flamingo is more or less anserine in character.

The nasal region in flamingos actually differs considerably from that of ducks, particularly in lacking the large internal narial opening in the rostrum characteristic of the *Anseriformes*.

25. “supraorbital depression”: These depressions accommodate salt glands and are found in a supraorbital position in the *Charadriiformes* and most other water birds, including even *Hesperornis*. In the *Pelecaniformes* the salt glands are located within the orbit, as they are in storks and herons, but not in the *Threskiornithidae*. The condition of this character in flamingos is as much like that of shorebirds as that of ducks.

26. “lachrymals”: In addition to Shufeldt’s comment above, Beddard (1898:441) also made the misleading statement that the “lachrymals are large and rather duck-like.” The lachrymals in ducks are thin, antero-posteriorly elongated

bones that are broadly fused with the skull (except in *Anseranas*) and that do not nearly reach the jugal bar. In flamingos the lachrymals are entirely different, being unfused, thickened, pneumatized bones that reach to the jugal bar but have a much narrower contact with the skull.

27. “quadrate”: Despite the remarks of Shufeldt (1901), the quadrates of flamingos are very different from those of ducks in every aspect, particularly in the nature of the articulation with the lower jaw.

28. “mandibular angle”: This refers to the long, recurved, bladelike retroarticular processes of the mandible, which are superficially very similar in ducks and flamingos. Nevertheless there are differences in the development of these structures between the two groups and the similarities probably are the result of similar needs for increased attachment for *M. depressor mandibulae* (page 64).

29. “pectoral girdle”: Evidently Shufeldt’s (1901:313) observations have been used by Sibley et al. for this character. Sibley and Ahlquist (1972:7) have remarked that Shufeldt “worked in a rather haphazard fashion, simply describing and comparing what he happened to have before him,” and it is widely recognized that his writings on osteology and paleontology are unreliable. We find little similarity between flamingos and ducks in the bones of the shoulder girdle.

30. “caeca”: The caeca are well-developed in both flamingos and *Anseriformes* but are rudimentary in *Ciconiiformes*. Beddard (1898:336) states that in the *Charadrii* the caeca are “nearly always large.” Large caeca are also present in other orders of birds, such as *Gruiformes*.

31. “tongue shape”: Although flamingos and ducks have large fleshy tongues used in filter-feeding, the morphology and placement is entirely different in the two groups, as is the structure of the bony hyoid apparatus (page 60).

“Characters Shared with Both Orders”

32. “tufted oil gland present”: A tufted oil gland occurs in the *Charadriiformes* and in the majority of other orders of birds.

33. “11 primaries”: This character is mis-

placed by Sibley et al. (1969) and should be listed as shared with the Ciconiiformes (storks only): Ducks, shorebirds, and Ciconiiformes except storks have 10 functional primaries, whereas in flamingos, Ciconiidae, and Podicipedidae (grebes) there are 11 (W. D. Miller, 1924). The extra primary in flamingos probably evolved with a lengthening of the wing, as the number of secondaries in flamingos is considerably greater than in storks (page 34). The taxonomic distribution of this character strongly suggests independent derivation in all three instances.

34. "diastataxic": The diastataxic condition of the secondaries is found in many orders of birds, including all the Charadriiformes.

35. "carinate": An entirely useless character in this instance, as all birds except the "ratites" are "carinate."

36. "desmognathous": The so-called desmognathous condition of the palate is found in other orders and must have evolved numerous times from the schizognathous condition. The fossil bird *Presbyornis* shows that the desmognathous palate of ducks must have evolved from the schizognathous palate of shorebirds (Olson and Feduccia, in press) and the same is likely true of flamingos.

37. "holorhinal": As with the preceding, the holorhinal nostril occurs in many orders, including certain Charadriiformes (e.g., *Burhinus*, *Pluvianus*). This character varies within the Ciconiiformes (as presently constituted) in that the Threskiornithidae are schizorhinal, except for spoonbills (*Platalea*), which are sometimes secondarily holorhinal, thus demonstrating the probable ease with which the holorhinal condition can arise.

38. "pervious nares": A condition found in most birds, including Charadriiformes.

39. "no ectocondylar process": This refers presumably to the ectepicondylar prominence at the distal end of the humerus, though it is not evident why this should have been mentioned in any discussion of flamingos. The ectepicondylar prominence is developed into a large spur in Procellariiformes and most Charadriiformes but is usually reduced in most other birds, including

flamingos. The spur, however, is absent in the Jacanidae and Burhinidae, smaller in the Recurvirostridae and Rostratulidae than in most Charadrii, and has been secondarily lost or reduced in other Charadriiformes (e.g., *Scolopax minor*) and their derivatives.

40. "16-25 cervical vertebrae": The number of cervical vertebrae in birds may vary at almost any taxonomic level. According to Fürbringer (1888, volume 2, table 41), flamingos have 18 or 19 cervicals, the Ciconiiformes have 16 or 17, with only the Ardeidae having 18 or 19. The Charadriiformes usually have 15, or 16 in the case of the Burhinidae and Jacanidae. In the Anatidae, the cervicals range in number from 16 to 25, with the high numbers occurring in the long-necked swans. Obviously, this is a highly adaptive character. The greater number of cervical vertebrae in flamingos than in shorebirds is probably correlated with the evolution of a long neck associated with the exceptional feeding apparatus.

41. "ambiens present": The ambiens muscle is also present in the Charadriiformes and many other orders of birds. In Ciconiiformes, however, it is present only in some ibises and some storks (Vanden Berge, 1970).

"Characters Shared with Neither Order"

42. "reduced hallux": The hallux is reduced or absent in modern flamingos. Although thought not to be of taxonomic consequence, the hallux is nevertheless always present and rather well developed in the Ciconiiformes and Anseriformes. In the Charadriiformes, on the other hand, the hallux has been reduced or lost repeatedly. For example, in the Recurvirostridae, the hallux is present in *Recurvirostra* and absent in *Himantopus* and *Cladorhynchus*. Sibley et al. (1969:160) note that the short toes of flamingos are different from either the Ciconiiformes or Anseriformes. The toes are quite short in many Charadrii and notably so in the Recurvirostridae.

43. "inverted bill": See character 44.

44. "filter apparatus": These characters are unique to flamingos and provide one of the very few major points of separation of the Phoenicop-

teridae from other Charadriiformes.

45. "flexor tendons type IV": Of the various patterns of the deep flexor tendons (see George and Berger, 1966:446-449), the Ciconiiformes and most Charadriiformes have the type I configuration, and the Anseriformes have the type II configuration. Flamingos differ in having type IV deep flexor tendons, a condition that occurs in several groups in which the hallux is reduced or lost, including the Recurvirostridae (page 30).

46. "1 pair syrinx muscles": A condition also found in the Charadriiformes (including *Cladorhynchus*, pers. obs.) and other orders (Beddard, 1898).

47. "small femoral-caudal [sic]": This is the femorocaudal of Garrod (1874), designated "A" in his thigh muscle formulae, which forms part of the caudo-iliofemoralis of modern usage. We do not know why Sibley et al. (1969) list this as "small" because it is actually lacking in flamingos (Vanden Berge, 1970), as the following character signifies.

48. "BXY+ muscle formula": This represents only part of the expanded thigh muscle formulae used by some modern authors (see George and Berger, 1966:233). The formula in most shorebirds is ABXY+, since the caudo-femoral part of *M. caudo-iliofemoralis* ("A") is usually present. This muscle is now known to be lacking in certain genera of Charadrii (page 27), as well as in flamingos. In storks and in herons it is present in some genera and absent in others (Vanden Berge, 1970), and thus appears to be easily lost and probably of little taxonomic use.

49. "type of air cells in lung": This evidently derives from a misreading of Weldon's (1883:639) statement that in flamingos "the lungs present nothing remarkable, but the air-cells and their associated septa are strikingly characteristic." Further reading reveals that by "air-cells" Weldon was referring to the air sac system (see character 14 above). Nothing in his paper indicates that anything inside the lungs of flamingos is distinctive.

The foregoing analysis should be sufficient to

reveal the glaring inadequacy of the anatomical "evidence" that has been used previously in attempting to determine the relationships of flamingos. The characters supposedly demonstrating affinity with the Ciconiiformes we have shown to be of wide occurrence in other orders of birds, including the Charadriiformes, and are useful only in showing lack of affinity with the Anseriformes. Advocates of a ciconiiform relationship for flamingos are now faced with the fact that there is not a single convincing anatomical character supportive of such a hypothesis.

Anatomical evidence for a relationship between flamingos and Anseriformes is equally deficient. Some of the characters, such as webbed feet and large caeca, are shared with the Charadriiformes as well. Others, particularly feather structure, cannot be evaluated without proper comparison with Charadriiformes. Still other apparent similarities to Anseriformes, such as the feeding apparatus, are not really similarities at all and are actually completely different in the two groups. Flamingos simply possess none of the derived characters of osteology and myology that distinguish the well-defined monophyletic order Anseriformes, so their ancestry must be sought elsewhere.

Apart from features that are unique, almost every one of the characters of flamingos cited by Sibley et al. (1969) may be found in the Charadriiformes, including all of those that do not occur in either the Ciconiiformes or the Anseriformes. Thus, even without the additional information supplied beyond, the evidence thus far presented is much better explained by a charadriiform origin of flamingos.

Life History and Behavior

Various aspects of general life history and behavior have been summarized and discussed by Sibley et al. (1969:163), who concluded that many of the distinctive characteristics of flamingos are probably related to their extreme gregariousness, which, like the feeding apparatus, is part of their adaptation to a "narrow ecological niche" in "barren isolated areas." They interpreted the

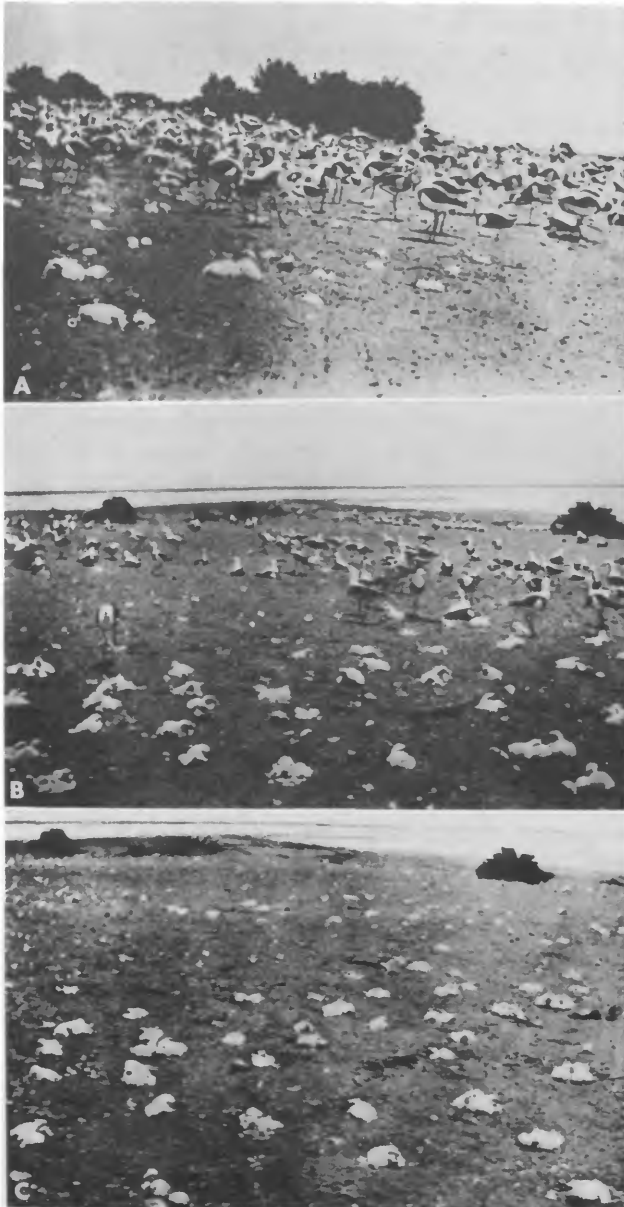
behavioral evidence as indicating that "approximately equal numbers of behavioral elements are shared by flamingos with the Anseriformes and with the Ciconiiformes," and they considered it "unlikely that any valid conclusions about relationship can be drawn from these data" (page 168). We were at first inclined to agree, but upon reading Hamilton's (1975) accounts of behavior in North American Recurvirostridae we were impressed with the apparent similarities to flamingos. This led us to the literature on the Australian Banded Stilt, *Cladorhynchus leucocephalus*, where we discovered that the life history of this species very closely approximates that of flamingos.

Flamingos are highly social birds living in large flocks in remote, barren areas of shallow saline lagoons or alkaline lakes. They feed mainly on small crustaceans and insect larvae, or in the case of the more specialized species, on microorganisms such as diatoms. Because of the isolation of breeding colonies, even the correct sitting posture of incubating flamingos was not known until 1880 (Allen, 1956); the nest and eggs of the abundant *Phoeniconaias minor* were not discovered until 1954 (Brown, 1959), and those of *Phoenicoparrus jamesi* were discovered only in 1957 (Johnson, et al., 1958). For a given flock, both the timing and site of breeding may vary irregularly. Nesting colonies are usually large and very densely packed; territoriality is virtually absent, as is response to terrestrial predators. A single, chalky white egg, large in proportion to the bird, is usually, but not always, deposited on a raised cone of mud. Young are covered with white or grayish unpatterned down and remain in the nest for several days before departing and gathering in large groups attended by adults, at which time they often swim. The parents feed the young for extended periods. This general pattern of life history is not duplicated among any of the Ciconiiformes or Anseriformes.

We will briefly compare the above with what little is known of the overall life history of *Cladorhynchus leucocephalus* and then compare aspects of the behavior of flamingos with that of some of the better-known Recurvirostridae. Most of the significant information relating to the life

FIGURE 1.—The 1930 nesting colony of the Australian Banded Stilt, *Cladorhynchus leucocephalus*, at Lake Callabonna, South Australia: *a*, part of the colony showing the extremely close spacing of nests; *b*, portion of the colony with adult birds sitting on nests; *c*, adults rising from nests. (Photographs from McGilp and Morgan, 1931.)

FIGURE 2.—The 1930 nesting colony of the Australian Banded Stilt, *Cladorhynchus leucocephalus*, at Lake Callabonna, South Australia: *a*, closer view of adults at nests; *b*, adults with newly hatched young; *c*, young birds remaining in nest after adults have temporarily departed. (Photographs from McGilp and Morgan, 1931.)



history of *Cladorhynchus* may be found in the publications of Glauert and Jenkins (1931), McGilp and Morgan (1931), Howe and Ross (1931), Jones (1945; a summary of all previous literature on the species), Carnaby (1946), Beruldsen (1972), Jenkins (1975), and Kolichis (1976). In addition, we were fortunate to be supplied by J. A. McNamara (1976) with a copy of his unpublished paper on the feeding ecology of *Cladorhynchus*.

Cladorhynchus lives in remote areas in the southern half of Australia, where it occurs in great flocks that frequent very saline temporary lakes in which may be found enormous quantities of small crustaceans, upon which the birds feed (Jones, 1945). McNamara (1976), who examined gut contents of *Cladorhynchus*, found a variety of food items, but principally brine shrimp (*Parartemia*) and brine flies (Ephydriidae). In connection with the heavy fat deposits mentioned by Sibley et al. (1969) as being characteristic of flamingos, it should be noted that McNamara's specimens of *Cladorhynchus* had extremely heavy subcutaneous fat deposits, whereas specimens of *Himantopus* and *Recurvirostra* taken at the same time and place did not.

The breeding habits of *Cladorhynchus* remained unknown until 1930 (Glauert and Jenkins, 1931), a mystery not without parallel among flamingos. It was then discovered that *Cladorhynchus* breeds in great, densely packed colonies on islands and sandbars. McGilp and Morgan (1931) estimated nearly 27,000 pairs in a colony at Lake Callabonna (Figures 1, 2). Nests consist of depressions in the ground and are regularly spaced about 30 cm apart (Figure 1a). Nests in the Callabonna colony had from 1 to 5 eggs, with most nests having 3 eggs; clutches of 2 eggs appeared to be complete (McGilp and Morgan, 1931; Kolichis, 1976). Adult and young birds in a colony are practically fearless, with no apparent predator response. The timing and place of breeding of *Cladorhynchus* appear to be extremely irregular and are correlated with variable local conditions. For example, the great colony found on Lake Callabonna in 1930–1931 is the only known nesting record for South Australia; all others are from Western Australia (J. A. McNamara, in litt., to

Olson, 30 May 1978).

There appears to be a nearly complete lack of aggression or territoriality in *Cladorhynchus*, as is true of flamingos. McNamara (in litt. to Olson, 30 May 1978) reports that

only once in about 110 hours observation over 8 months did I see anything like display (courtship or otherwise). This took place on a bank in the salt fields with dry powdery ground; one bird knelt on the ground with wings out and the other standing while both fenced with bills. Also at this time one bird chased another for a short distance (10") [25 cm] then both stopped and assumed an "aggressive" posture with head down, bill pointed at [the] other and back feathers raised.

This could correspond to the bill-fighting and bowing reported in *Phoenicopterus* by Rooth (1965).

Furthermore, McNamara quotes Mr. Tom Spence, Director, Perth Zoological Gardens, as noting that

the display of the Banded Stilt is quite spectacular and very reminiscent of that of the Lesser Flamingo. They parade in a tight little pack with their long mantle feathers raised (just like a Flamingo) and synchronise their movements pretty closely. I have also seen this in the wild.

This behavior may be the exact equivalent of the marching display of flamingos (Kahl, 1975). Raising the "back" feathers is a characteristic feature of flamingo displays, and in the breeding plumage of *Cladorhynchus* the tertials are greatly elongated, much more so than in other *Recurvirostridae*.

The eggs of *Cladorhynchus* are exceptional among the *Charadriiformes* for their large size and white ground color (Howe and Ross, 1931), both of which recall the eggs of flamingos. Although most eggs of *Cladorhynchus* are marked with dark lines and blotches, as typical of other *Charadriiformes*, the markings are quite variable, and McGilp and Morgan (1931:45) reported that a "fair proportion" were nearly immaculate and at least one was found that was pure white (Figure 12).

Most remarkably, the young of *Cladorhynchus* are clothed in *white, unpatterned* down (Figure 3), a combination not met with anywhere in the remainder of the *Charadrii* (Jehl, 1968), but



FIGURE 3.—Chick of the Australian Banded Stilt, *Cladorhynchus leucocephalus*, showing the dense, unpatterned, white down, unlike that of any other *Charadrii*, but similar to flamingos.

which is typical of flamingos. A most important point of similarity with flamingos is that *Cladorhynchus* has two coats of nestling down, a character not found in any other known shorebird (page 34).

It is not known when the young leave the nest or whether the adults feed the young, but McGilp and Morgan (1931:43) report that disturbed young "kept scampering back towards the nests" and their photographs show many young birds remaining in nests after the temporary departure of adults (Figure 2c). This is in contrast to North American *Recurvirostridae* as observed by Hamilton (1975:89): "Even before chicks are dry, they begin to toddle away from the nest, and soon after the brood has hatched, the young can no longer be found in the vicinity of the nest."

The accounts of *Cladorhynchus* emphasize the rapidity of breeding and the simultaneous hatch-

ing of young in a colony. The young aggregate and are attended by adults, which is probably not different from the so-called "creche" behavior of flamingos. McGilp and Morgan (1931) mention "three old birds leading perhaps 60 young ones into the water" and they include a photograph of a flock of chicks swimming off into the lake in the manner of young flamingos. At Lake Marmion, Western Australia, Kolichis (1976:116) "saw Banded Stilts on the water in small groups varying from three young with two adults to about 40 young with six to nine adults."

Cladorhynchus provides a nearly perfect intermediate in its life history and development between flamingos and the more typical Recurvirostridae and thus supplies evidence not only that flamingos are derived from the Charadrii, but more particularly from the Recurvirostridae. There could hardly be a more rewarding endeavor for a field ornithologist than a detailed comparative ethological study of *Cladorhynchus* and flamingos.

In analyzing the ecological requirements of the Recurvirostridae, Hamilton (1975:14) found that although *Himantopus* generally resorts to fresh water, "avocets [*Recurvirostra*] prefer alkaline or saline habitats." They feed mainly upon brine shrimp, *Artemia*, and adults and larvae of brine-flies, *Ephydra* (Hamilton, 1975; Wetmore, 1925:14). We have already noted the similar food habits of *Cladorhynchus*. On Bonaire the "staple diet" of flamingos is the larvae and chrysalids of *Ephydra* (Rooth, 1965:51).

Sibley et al. (1969:164) maintained that adult flamingos do not voluntarily swim, and interpreted this as being contrary to an anseriform derivation, thereby implying similarity to Ciconiiformes. Rooth (1965) records *Phoenicopterus ruber* on Bonaire as swimming while feeding. Brown (1975:42), in countering Sibley et al., stated that *Phoeniconaias minor* in Africa feeds from near the surface of the water away from the shoreline and "habitually swim; in fact they could not have reached their present numbers if they did not swim" (see Figure 4).

While swimming, flamingos may feed by tipping up in manner reminiscent of swans and

dabbling ducks, which has been interpreted as an indication of relationship. Rooth (1965:43) describes this behavior in *Phoenicopterus ruber* as follows:

The head, neck and the rostral part of the body are totally immersed, more or less straight down. The rear part of the body then sticks up out of the water, so that the legs have to carry out all possible movements to preserve the balance of this position. . . . This unsteady position necessitates that the movements of the feet can take place in the surface water only. It can be seen that the tibiotarsus is directed at an angle upwards and that only one half or three quarters of the tarso-metatarsus is in the water.

Avocets and *Cladorhynchus* likewise do a considerable amount of feeding while swimming and also tip up in order to obtain food (Ross, 1924; Hamilton, 1975; McNamara, 1976; Dinsmore, 1977). Compare the following description for *Recurvirostra americana* as given by Hamilton (1975: 52) with that of *Phoenicopterus ruber* above.

The feeding bird immerses its head and breast into the water by tipping on the transverse axis from a swimming or breast-wading position and brings the bill to the bottom. The upended position of the bird is maintained by a backward kick of the feet; the tibiotarsi often break the surface. . . .

Flamingos vocalize in flight and the calls of some are reminiscent of gooselike honkings, which has also been cited as favoring anseriform affinities. The notes of *Phoeniconaias minor* are higher pitched than in *Phoenicopterus ruber* and have been likened to a "yelping" (Cramp and Simmons, 1977:367). Proper comparisons are wanting, but it should be noted that the Recurvirostridae are notorious for vocalizing in flight and "yelping" is a term commonly employed to describe the sound of their nearly incessant calls when disturbed on the breeding grounds.

The use of neck postures in the threat displays of flamingos was likened to that in the Anatidae by Sibley et al. (1969), whereas the raising of the scapular and the back feathers in threats was said to be more characteristic of the Ciconiiformes. Both of these behavioral components are found in the Recurvirostridae (Hamilton, 1975, fig. 15). Bill-dipping or displacement drinking, which is performed by flamingos and ducks but not Ciconiiformes (Sibley et al., 1969), is also part of the



FIGURE 4.—Lesser Flamingos, *Phoeniconaias minor*, at Lake Hannington, Kenya, showing numbers of birds swimming in the middle of the lake. (Photograph by Alan Feduccia.)

normal precopulatory display in the *Recurvirostridae* (Hamilton, 1975:73). The near absence of specialized pairing displays and the seasonal pair bonds of flamingos are likewise characteristic of the *Recurvirostridae*. In both flamingos and *recurvirostrids*, in such courtship as exists, there is a similar heavy reliance on ritualized preening, bill-dipping, head shaking and splashing of water. The “bowing” display in *Phoenicopterus* (Rooth, 1965:88, fig. 14) might be equivalent to the posture assumed in the “Group Circle” display of *Recurvirostra americana* (Hamilton, 1975:68, fig. 16a). In flamingos, the “attraction function of courtship display to other members of the species” was cited by Sibley et al. (1969:167) as resembling the *Ciconiiformes*. However, Hamilton (1975:68) observed that the ritualized special postures used in highly social group interactions in the *Recur-*

virostridae “seem to attract conspecifics from near and far.”

Copulation in flamingos takes place away from the nest and usually in water, unlike *Ciconiiformes* but similar to most *Anseriformes* (Sibley et al. 1969). The same is true, however, in the *Recurvirostridae*. The reader is invited to note the similarity in the copulatory posture of *Phoenicopterus* (Rooth, 1965; fig. 16) and that of *Recurvirostra americana* (Hamilton, 1975, fig. 17e).

Although under certain circumstances flamingos will lay their eggs in a depression in the ground, as do most shorebirds, they usually construct a characteristic truncated cone of mud, upon which to deposit the egg. According to Rooth (1965:99–100), “the function of these high constructions is clear at high water although the literature often reports the flooding of colonies,

despite the high nests." He then adds, "It is typical that the wader *Himantopus himantopus* [Recurvirostridae] which breeds along the shores of the salinas [on Bonaire] also makes such high nests!" The exclamation point is his; we can only regret in light of the present discussion that this statement was not elaborated upon. Nests of avocets and stilts usually consist of a depression in the ground lined with any available material, including mud chips (Hamilton, 1975:82). In a number of references cited by Hamilton (1975:83), avocets and stilts are reported as adding material to their nests during floods to raise the eggs up on a platform. All 15 nests in a colony of *Recurvirostra avosetta* were adjusted in this manner during a night of heavy rains (Makkink, 1936:35). Certainly it is not difficult to envision that this behavior could be modified to produce that of flamingos, whereas the nest-building habits of Ciconiiformes, which generally construct arboreal platforms of sticks, does not seem at all appropriate as a precursor of the phoenicopterid method.

Although none of the other Recurvirostridae are as highly colonial as *Cladorhynchus*, all are gregarious and their nesting sites are composed of loose aggregations to which the term "colony" is consistently applied in the literature. As with flamingos there is no site fidelity and colonies tend to shift location from one year to the next (Hamilton, 1975:79).

In contrast to the Ciconiiformes, with their elaborate nest-relief ceremonies during incubation, flamingos have almost none—one bird walks up and its partner walks away, sometimes indulging in displacement feeding (Rooth, 1965:107). Much the same behavior is recorded for the Recurvirostridae, although Hamilton (1975:85) interpreted the displacement "feeding" as displacement nest building, in which objects are picked up and tossed about.

Apparently the only unique etho-ecological adaptations of flamingos not found in recurvirostrids are the parental feeding of the young (possibly present in *Cladorhynchus*) and the single egg clutch. Both of these must be directly correlated with the highly specialized feeding apparatus of adult flamingos. Because this structure does not

develop until late in ontogeny, some parental feeding of young would be a necessity. The single egg clutch probably evolved as a result of this increased parental responsibility.

The foregoing is only a brief sketch, but should serve to illustrate the similarities in the life history and behavior of flamingos and the Recurvirostridae. Not only can all the supposed ciconiiform and anseriform behavioral traits of flamingos be accounted for by having flamingos derived from the Charadrii, but also the seemingly unique characteristics of the Phoenicopteridae that are irreconcilable with either storks or ducks can be explained as well.

Myology

Vanden Berge (1970) conducted a broad, comparative study of the appendicular myology of the Ciconiiformes, including the Phoenicopteridae. We regard it as significant that he found "no consistent pattern in the appendicular musculature of the Ciconiiformes [that] contributes significantly to a taxonomic clarification of this large, loosely applied assemblage of long-legged, long-necked, wading type birds" (page 361). Such a conclusion would be expected if the Ciconiiformes were entirely an artificial group (Olson, 1979). In the following comparisons we use "Ciconiiformes" for the families traditionally included in the order, but excluding flamingos.

One of Vanden Berge's most interesting discoveries was a previously unknown thigh muscle, unique to flamingos, to which he later applied the name *M. iliotibialis medialis* (Vanden Berge, 1976). In preliminary dissections we discovered this muscle in *Cladorhynchus*, whereas it was absent in *Recurvirostra* and *Himantopus*. This highly important discovery led us to examine the rest of the appendicular myology of *Cladorhynchus* to make further comparisons with flamingos. Details are presented in the following section. The tabulations below summarize myological comparisons between flamingos, *Cladorhynchus*, and Ciconiiformes, especially storks. Naturally, not all of these characters are of equal value.

A. Unique Character in Which Flamingos and *Cladorhynchus* Differ from All Known Birds

1. Presence of *M. iliotibialis medialis*.

B. Characters Shared by Flamingos and *Cladorhynchus* That Differ from All Ciconiiformes

1. Origin of *M. latissimus dorsi* pars cranialis not partly from cervical vertebrae.
2. Origin of *M. latissimus dorsi* pars metapatagialis partly from synsacrum.
3. Far caudal origin of *M. serratus superficialis* pars caudalis.
4. More distal origin of *M. scapulohumeralis* caudalis.
5. *M. pectoralis* pars subcutanea thoracica and pars subcutanea abdominalis present and well-developed.
6. *M. tensor propatagialis* pars brevis with two separate tendons.
7. Greater fusion of tendons of *M. extensor metacarpi radialis*.
8. Distal head of *M. extensor longus digiti majoris* vestigial.
9. Both origin and insertion of *M. adductor alulae* fleshy.
10. Nature of origin of *M. interosseus ventralis* (particularly different from storks).
11. Combination of *M. iliofemoralis internus* being short and stout and inserting caudal to origin of *M. femorotibialis internus*.
12. *Ambiens* present and inserting directly on belly of *M. flexor perforatus digiti II*.
13. Nature of *flexor cruris lateralis* complex.
14. Greater proximal width of *flexor cruris medialis*.
15. None of the digital flexors with a fleshy origin from shaft of fibula.
16. *M. flexor perforans et perforatus digiti II* with two heads.
17. *M. flexor perforans et perforatus digit III* with two heads.
18. Insertion of *M. popliteus* distal to origin.
19. Deep flexor tendons type IV.
20. *M. extensor hallucis* absent.
21. *M. flexor hallucis brevis* vestigial.

C. Characters Shared by Flamingos, *Cladorhynchus*, and One or More Ciconiiformes but Differing from Storks

1. Propatagial slip of *M. biceps brachii* present and well-developed.
2. *M. iliofemoralis* ("B") present.
3. Scapular origin of *M. triceps brachii* entirely fleshy.
4. Origin of *M. latissimus dorsi* caudalis from last free vertebra, synsacrum, and fasciae.
5. *M. scapulohumeralis* cranialis present.
6. Origin of *M. coracobrachialis* cranialis tendinous.
7. Ventral head of *M. deltoideus minor* present and reasonably well-developed.

8. Postacetabular portion of *M. iliotibialis lateralis* present.
9. Pars accessoria, *M. flexor cruris lateralis*, present.
10. Extensive fleshy insertion of *M. pubo-ischiofemoralis*.
11. More proximal origin of *M. adductor digiti II*.
12. Insertion of *M. iliofemoralis internus* caudal to origin of *M. femorotibialis internus*.

D. Characters in Which Flamingos and Storks Differ from Other Ciconiiformes but Also Agree with *Cladorhynchus*

1. *M. fibularis brevis* absent.
2. Nature of origin of *M. serratus profundus*.
3. More tendinous origin of *M. rhomboideus superficialis* pars scapularis.
4. *M. iliofemoralis* short and stout.

E. Characters in Which *Cladorhynchus* Differs from Flamingos

1. *M. iliotibialis medialis* inserts on patellar tendon.
2. More fusion in elements of *tensor propatagialis* complex.
3. *M. flexor hallucis brevis* arises more proximally.
4. *M. subcoracoideus* with two distinct heads.
5. Origin of *M. humerotriceps*.
6. Lateral head of *M. subscapularis* smaller and more dorsolaterally situated.
7. Nature of *M. pectoralis propatagialis*.
8. Nature of insertion of *M. coracobrachialis* cranialis.
9. Belly of *M. ulnometacarpalis ventralis* longer.
10. Total lack of fusion in the parts of *M. femorotibialis*.
11. Heads of *M. gastrocnemius* with less distal fusion.
12. *M. serratus superficialis* pars metapatagialis from two distinct slips.
13. *M. caudofemoralis* ("A") present.
14. Belly of *M. flexor digitorum profundus* notched by insertion of *M. brachialis*.
15. *M. pronator profundus* fused with *M. extensor longus digiti majoris*.
16. Origin of *M. fibularis longus* not fleshy.

The appendicular myology of flamingos in no way supports a relationship with the Ciconiiformes. The preceding tabulation lists 22 characters in which flamingos differ from all Ciconiiformes and 34 in which they differ from the Ciconiidae in particular. In all of these characters flamingos agree with *Cladorhynchus*, even to the possession of *M. iliotibialis medialis*, a muscle not known to occur in any other birds.

Differences between *Cladorhynchus* and flamingos are summarized in tabulation E. Of these, characters 1 through 3 are but modifications of flamingo-like conditions not found in any ciconiiform. Characters 4 through 8, and possibly 9,

probably represent a single functional complex associated with changes in pneumatization of the humerus and consequent modification of the shoulder. Characters 10 through 13 involve only fusion of muscles to derive a flamingo-like state and may be size-related. Character 13 has no taxonomic value even at the family level. The significance of characters 14 through 16 is not apparent, but all of them are variable within the Ciconiiformes, as currently constituted.

The differences between flamingos and *Cladorhynchus* are both fewer in number and less in significance than those between flamingos and Ciconiiformes. Appendicular myology provides strong evidence in favor of a relationship between flamingos and Charadriiformes, particularly *Cladorhynchus*, whereas there is almost no similarity between flamingos and storks.

APPENDICULAR MYOLOGY OF *Cladorhynchus*

We dissected the appendicular musculature in a single adult female of *Cladorhynchus leucocephalus* (SAM B30446), making comparisons chiefly with the descriptions of ciconiiform myology in Vanden Berge (1970). Beyond checking for the presence of *M. iliobtibialis medialis* in various Recurvirostridae, we have made no attempt to compare *Cladorhynchus* with other shorebirds, nor have we repeated Vanden Berge's dissections of flamingos except to check a few specific muscles in two rather emaciated specimens of *Phoeniconaias minor*, the only fluid-preserved flamingos immediately available to us. Vanden Berge (1970) did not examine this species but dissected specimens of *Phoenicopterus ruber*, *P. chilensis*, and *Phoenicoparrus jamesi*. It is not our purpose to provide a detailed description of the myology of *Cladorhynchus*, but mainly to present a comparative assessment of its similarities and differences with regard to flamingos.

We have adopted the myological nomenclature of the *Nomina Anatomica Avium* (Baumel et al., 1979), using the sequence of Vanden Berge's (1970) original paper for facility of comparison and quoting his nomenclature in parentheses when it differs substantially from that of the *NAA*.

For certain muscles, Vanden Berge (1970) found little or no significant variation within the Ciconiiformes. Of these, those in *Cladorhynchus* that did not differ from his descriptions are listed as follows and are not discussed further: *M. brachialis*, *M. supinator*, *M. flexor digitorum superficialis* ("sublimus"), *M. extensor digitorum communis*, *M. extensor metacarpi ulnaris*, *M. ectepicondylo-ulnaris* ("anconeus"), *M. flexor alulae* ("flexor pollicis"), *M. extensor brevis alulae* ("extensor pollicis brevis"), *M. abductor digiti majoris* ("abductor indicis"), *M. ilirotrochantericus cranialis*, *M. ilirotrochantericus medius*, *M. iliofibularis* ("biceps femoris"), *M. tibialis cranialis*, *M. extensor digitorum longus*, *M. plantaris*.

M. latissimus dorsi pars cranialis ("anterior")

This is a broad, very thin muscle arising as a thin tendinous sheet from the spinous processes of the second through fourth thoracic vertebrae. The insertion is fleshy on the cranial surface of the proximal third of the humerus.

Vanden Berge (1970) found that this muscle in flamingos originated from the first through third thoracics, whereas in all other Ciconiiformes the origin involved one or more cervical vertebrae. Despite the fact that in one skeleton of *Cladorhynchus* we examined, the first thoracic rib had no sternal component and would therefore have to be considered as a "cervical," our evidence suggests that the origin of *M. latissimus dorsi cranialis* is from the same series of vertebrae as in flamingos. In neither flamingos nor *Cladorhynchus* is the origin in part from the true cervical series as it is in Ciconiiformes.

M. latissimus dorsi pars caudalis ("posterior")

The origin is tendinous mainly from the cranial margin of the ilium and also from the last free vertebra and surrounding fasciae. This is as described by Vanden Berge (1970) for flamingos and ibises and differs from that of herons (dorsal vertebrae only), *Balaeniceps* (last 2-3 free vertebrae and synsacrum) and storks (origin not involving fasciae).

M. latissimus dorsi pars metapatagialis

This slender but well-developed muscle originates from the cranial tip of the synsacrum and partly from the last free thoracic vertebra. The insertion subtends the humeral feather tract. Flamingos agree with *Cladorhynchus* in having the origin partly from the synsacrum whereas in the Ciconiiformes it is entirely from the vertebrae.

M. rhomboideus superficialis

PARS CLAVICULARIS.—The origin is a thin tendinous sheet from the last cervical and first thoracic vertebrae and the insertion is fleshy along the cranial portion of the dorsal (vertebral) margin of the scapula extending ventrad on the adjacent dorsal projection of the clavicle, ventral to the origin of *M. tensor propatagialis*.

PARS SCAPULARIS.—The origin is a tendinous sheet extending from the second thoracic vertebra to the last free thoracic. The insertion is fleshy on the dorso-medial margin of the cranial three-fourths of the scapular blade, extending as far caudally as the bend in the blade.

According to Vanden Berge (1970) a more extensively tendinous pars scapularis differentiates flamingos and storks from other Ciconiiformes; *Cladorhynchus* fits this pattern, though the origin is longer than reported for those forms.

M. rhomboideus profundus

This deep muscle arises as a broad, thin, tendinous sheet from the spinal processes of the first through the fourth thoracic vertebrae. The insertion is fleshy along the costal aspect of the caudal four-fifths of the scapula. This condition agrees generally with that of most Ciconiiformes except *Balaeniceps* (Vanden Berge, 1970).

M. serratus profundus

This muscle consists of three distinct slips arising fleshy from the last cervical and first two thoracic ribs; these insert fleshy on the costal surface of the cranial half of the scapula.

Flamingos and storks both agree with the conformation in *Cladorhynchus*. These differ, on the one hand from herons, in which the muscle arises only from cervical vertebrae (four fleshy slips) or

from cervical vertebrae and the first thoracic (five slips), and on the other hand from ibises and *Balaeniceps*, in which the three slips arise from the last two cervical and first thoracic vertebrae.

M. serratus superficialis pars cranialis
and *pars caudalis*

These are entirely separate muscles in *Cladorhynchus*. Pars cranialis arises fleshy from the last cervical and first thoracic ribs, with a thin tendinous sheet spreading to the penultimate cervical. The insertion is by a thin tendinous sheet attaching to the cranial sixth of the ventral margin of the scapula. Pars caudalis originates from a thin sheet of tendon on the third through sixth thoracic ribs and inserts by a thin tendinous sheet on the ventral margin of the caudal third of the scapula. In the far caudal origin of *M. serratus superficialis caudalis*, flamingos differ from Ciconiiformes and agree with *Cladorhynchus*. In his one specimen of *Phoenicopterus chilensis*, Vanden Berge (1970:303) found the origin to be on thoracics 2 through 4, as in storks and some ibises. *Phoenicoparrus jamesi* and *Phoenicopterus ruber* were shown to be unique in the Ciconiiformes in having the origin from thoracics 2 through 5, and in the latter species "the origin extended posteriorly almost to the sixth thoracic," the condition met with in *Cladorhynchus*.

M. serratus superficialis
pars metapatagialis

This well-developed muscle consists of two distinct slips, one arising fleshy from thoracic ribs 4 and 5 and the other arising tendinously from the sixth thoracic. The insertion is on the humeral feather tract—we did not notice that it fused with *M. latissimus dorsi metapatagialis* or that there was a tendinous slip to the scapula as described for flamingos and herons (Vanden Berge, 1970), but either condition may have been obscured by specimen damage.

Cladorhynchus appears to differ from flamingos in that separate slips are not mentioned by Vanden Berge (1970). The more caudal origin in *Cladorhynchus* agrees with *Phoenicopterus ruber* but the origin in *P. chilensis* and *Phoenicoparrus* is re-

ported to be from thoracics 3 to 5 as in storks and ibises (Vanden Berge, 1970).

M. scapulohumeralis cranialis

This is a very small, entirely fleshy muscle, only a few fibers wide. The origin is from the ventral surface of the glenoid facet of the scapula; at its midpoint it is partly attached to *M. scapulohumeralis caudalis*. The insertion is just distal to the ridge dividing the tricipital fossa, between the humeral heads of *M. triceps brachii*.

Vanden Berge (1970) found this muscle only in herons and two species of flamingos, but not in *Phoenicopterus ruber* or any other Ciconiiformes. It was well-developed in the fossil flamingos *Palaeolodus* and *Juncitarsus* and its reduction or loss in modern species may be correlated with increased pneumatization of the humerus and the consequent loss of area for insertion.

M. scapulohumeralis caudalis

The origin is fleshy from the full length of the dorsal and lateral surfaces of the scapula except for that part occupied by *M. subscapularis caput laterale* ("pars externa"). The insertion is both tendinous and fleshy on the distal end of the ventral rim of the tricipital fossa. The more posterior origin is apparently similar to that of flamingos and differs from herons and storks (Vanden Berge, 1970).

M. pectoralis

The origins of this great muscle are both fleshy and tendinous from the postero-lateral process of the sternum and adjacent ribs, fleshy from the ventral rim of the carina and from the lateral surface of the clavicle and *Membrana sternocoracoclavicularis*. The insertion is partly by a tendinous connection to the bicipital surface of the humerus but with the principal tendon attaching on the ventral margin of the deltoid crest. *M. pectoralis* is partially divided into two distinct layers; a larger external one with a tendinous sheet on its antero-medial surface separating it from a smaller medial muscle layer. These layers fuse only in the posterior fourth of the whole muscle mass.

As discussed previously, much was made in the earlier literature of the layering of this muscle in flamingos, but as we have seen, this serves only to separate them from ducks and will not distinguish them from a variety of other birds, including shorebirds such as *Cladorhynchus*.

M. pectoralis pars propatagialis

This subcutaneous slip of the pectoralis is only weakly differentiated in *Cladorhynchus*, being represented by the separation of fibers attaching along a raphe that also forms the origin of *M. tensor propatagialis*. Vanden Berge (1970) indicates this muscle to be best developed in herons and flamingos within the Ciconiiformes, but such would not appear to be the case in *Cladorhynchus*.

*M. pectoralis pars subcutanea thoracica
and abdominalis*

Pars subcutanea thoracica and *Pars subcutanea abdominalis* are present and constitute a broad, well-developed sheet on the skin of the breast and flank, attaching to the lateral abdominal wall and to the pubis. Vanden Berge (1970) found both slips to be well-developed in flamingos. In herons, *pars subcutanea abdominalis* is present or absent; *pars subcutanea thoracica* is present but very narrow. Both slips are absent in storks, ibises, and *Balaeniceps*. Thus, flamingos agree much better with *Cladorhynchus* in this respect than with any Ciconiiformes.

M. supracoracoideus

The origin is fleshy from the dorsolateral surface of the carina and the medial portion of the body of the sternum; although the belly lies over the sternocoracoclavicular membrane, it does not seem to attach to it. The muscle tapers to a tendon that passes through the triosseal canal to insert dorsally on the dorsal tubercle ("external tuberosity") of the humerus. Vanden Berge (1970) does not specifically mention the condition of this muscle in flamingos.

M. coracobrachialis cranialis

This is very well developed in *Cladorhynchus*, arising tendinously from the lateral surface of the

head of the coracoid and the glenoid joint capsule. The insertion is very strong both by tendons in the ligamental furrow and to the prominence between the ligamental furrow and the bicipital furrow (*impressio m. coracobrachialis cranialis*) and by fleshy fibers on most of the bicipital surface. Distally it forms a sheet of tendon that is continuous with the origin of the dorsal (coracoid) head of *M. biceps brachii*. The tendinous origin agrees with flamingos, herons, and *Balaeniceps* and differs from storks and ibises, but the insertion in *Cladorhynchus* is quite different from that described for flamingos or any of the Ciconiiformes by Vanden Berge (1970), and is probably typical for the Charadriiformes, to judge by the conformation of their humeri.

M. coracobrachialis caudalis

The origin is fleshy from the lateral process of the sternal end of the coracoid and the adjacent portion of the sternum, with a tendinous connection to the tip of the cranio-lateral (sternocoracoid) process of the sternum. The insertion is by a tendon to the tip of the ventral tubercle ("internal tuberosity") of the humerus. The origin partly from the sternum agrees with flamingos, two species of herons, and two genera each of storks and ibises studied by Vanden Berge (1970), whereas in all other forms the origin was found to be confined to the coracoid.

M. sternocoracoideus

The origin is mixed fleshy and tendinous from the ventral surface of the cranio-lateral process of the sternum and the first two sternal ribs. The insertion is fleshy in the sternocoracoid impression and process of the coracoid. We did not detect any layering in this muscle as described by Vanden Berge (1970) for flamingos and storks.

M. subcoracoideus

This is a large, bulging, rounded muscle mass with two distinct heads. The dorsal head arises fleshy from the medial surface of the dorsal part of the clavicle, while the larger ventral head arises fleshy entirely from the medial surface of the sternocoracoclavicular membrane. These heads

become extensively commingled with *M. subscapularis* and contribute to a common tendinous insertion with that muscle.

M. subcoracoideus is weakly developed in herons and *Balaeniceps* and is more extensive in other Ciconiiformes and flamingos. *Cladorhynchus* differs from all of them in having two separate heads, a condition that is typical of many other birds, however (George and Berger, 1966).

M. subscapularis

This muscle arises from two distinct heads lying on opposite sides of the scapula. The lateral (external) head originates fleshy from the dorsolateral surface of the cranial fifth of the scapula, behind the glenoid. The medial (internal) head originates fleshy from most of the costal or ventral surface of the scapula, with a long, narrow, tapering extension running the full length of the ventral margin. The insertion is a common tendon with *M. subcoracoideus* on the ventral tubercle of the humerus. In the clearly dorso-lateral position and short length of the lateral head, *Cladorhynchus* differs from the condition described for flamingos and the Ciconiiformes, in all of which except herons the external head is described as being as large as, or larger than, the internal head (Vanden Berge, 1970).

M. tensor propatagialis

Pars longa has a partly fleshy attachment on the proximal end of the deltoid crest and a broad tendinous attachment to the propatagial slip from *M. pectoralis*. In addition, the belly extends proximally over the shoulder and has a common origin with *pars brevis* from the dorsal portion of the clavicle.

Par brevis terminates as two separate tendons (Figure 5a), the proximal tendon inserting directly on dense fasciae over the tendon of origin of *M. extensor metacarpi radialis*. The distal tendon is closely bound to that of *pars longa* proximally; at the level of the propatagial elastic ligament, it diverges to insert on the proximal forearm as a bifurcated tendon. The distal ramus of this bifurcation is wider and receives an inelastic tendinous slip from the elastic ligament itself.

The elastic ligament of the propatagium is directly continuous with the tendon of pars longa and, at the same level, receives the propatagial slip from *M. biceps brachii*. The elastic ligament then trifurcates in a complicated manner, the three rami merging distally to form a distal inelastic tendon that is buried in a sheath in the leading edge of the propatagium. This inelastic tendon encloses a tough fibrous dilation imbedded in the skin opposite the insertion on the carpal joint. In addition to the inelastic tendinous slip that unites with the bifurcated tendon of pars brevis, previously mentioned, there is also a very narrow tendon from the leading elastic ramus; it terminates on the retinaculum that restrains the tendon of the superficial digital flexor.

Vanden Berge (1970) reports that flamingos differ from all Ciconiiformes in possessing two separate tendons of pars brevis. This, in fact, appears to be a feature characteristic of Charadriiformes, as Fürbringer (1902, pl. 21: figs. 218-

219) illustrates a similar condition in *Larus* (Laridae) and *Parra* (= *Jacana*, Jacanidae). In the specimen of *Phoeniconaias* we examined (Figure 5b), *M. tensor propatagialis* was similar to that of *Cladorhynchus* except that there was no fusion of the distal tendon of pars brevis with the tendon of pars longa proximally; the smaller propatagial slip of the biceps, instead of fusing to this combined tendon gives rise to a small, partially elastic, separate tendon that inserts far distally on the tendon of pars longa, near the distal end of the radius. Most of the differences exhibited by *Cladorhynchus* could probably be accounted for by fusion of elements present in flamingos. *M. tensor propatagialis* in flamingos and *Cladorhynchus* is very different from that of storks (see Fürbringer, 1902, pl. 21: fig. 222).

M. deltoideus major

This arises fleshy from the dorsal portion of the scapula between the acromion and the glenoid

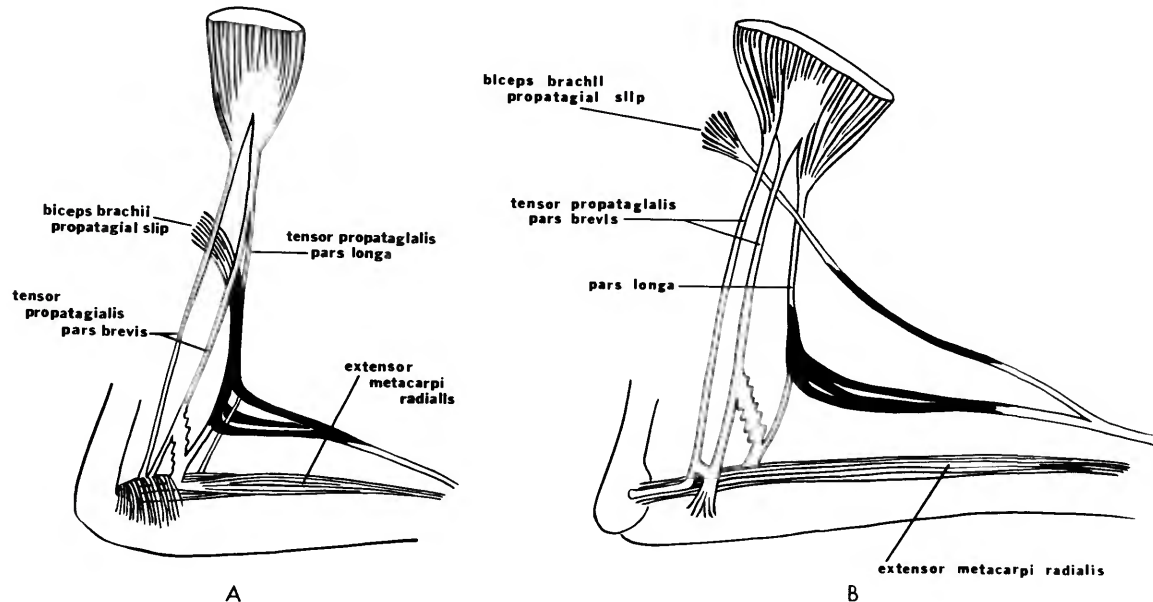


FIGURE 5.—Dorsal view of right wing to show configuration of *M. tensor propatagialis* in *Cladorhynchus leucocephalus* (a) and *Phoeniconaias minor* (b). The double tendon of pars brevis appears to be a fairly typical charadriiform character that is absent in storks. The biceps slip is also typical of Charadriiformes and occurs in "Ciconiiformes" only in the Threskiornithidae. Blackened portions indicate elastic tendons. (Not to scale.)

facet and also from the strong coraco-scapular ligament. The belly lies on the dorsal surface of the deltoid crest and has a fleshy attachment on the edge of the crest and along a line tapering distally on the shaft for one-third the length of the humerus, becoming tendinous towards the distal end.

The fleshy origin of this muscle is as described for flamingos, *Ciconia*, *Eudocimus*, and *Plegadis* and differs from other genera of Ciconiiformes, in which the origin may be partly tendinous or more lateral (Vanden Berge, 1970).

M. deltoideus minor

This muscle consists of two distinct heads originating in the triosseal canal and passing out over the insertion of *M. supracoracoideus*. They are entirely separate, at least after emerging from the triosseal canal, with the larger dorsal head completely overlying the ventral head. The dorsal head originates fleshy, partly from the acromion of the scapula but mostly from the procoracoid process of the coracoid. The insertion is fleshy on the proximal end of the deltoid crest just distal to the dorsal tubercle. The origin of the ventral head was not traced, having come away with the removal of *M. supracoracoideus*. The belly becomes tendinous at the level of the dorsal tubercle of the humerus and inserts in tissue in the ligamental furrow on the ventral side of the humerus. The ventral head is either very weak or absent in storks and *Balaeniceps*, better developed in flamingos, ibises, and certain herons, and best developed in other herons (Vanden Berge, 1970); flamingos thus agree with *Cladorhynchus* and differ from storks in this respect.

M. triceps brachii

The scapular head (*M. scapulotriceps*) arises both fleshy and tendinous from the lateral side of the scapula just caudal to the glenoid facet, and also by a short adjacent retinaculum to the edge of the scapula slightly more caudally. There is a tendinous retinaculum to the humerus in common with the insertion of *M. latissimus dorsi pars caudalis*. The belly continues along the entire shaft of the humerus to insert on the proximal

end of the ulna.

The humeral head (*M. humerotriceps*) arises fleshy from two portions bisected by the insertion of *M. scapulohumeralis caudalis*. These two portions fuse on a median raphe and have fleshy origins from the entire caudal surface of the shaft of the humerus, occupying the double, non-pneumatic fossa characteristic of most Charadrii and differing from all Ciconiiformes and flamingos. The common tendon of these two parts inserts both fleshy and tendinous on the olecranon.

Flamingos agree with *Cladorhynchus* and ibises, except *Ajaia*, in having the scapular origin entirely fleshy, whereas in other Ciconiiformes it is at least partly tendinous and in storks there are two distinct tendons of origin (Vanden Berge, 1970).

M. biceps brachii

This muscle arises from two heads; the more ventral humeral head originates by a short tendon from the ventro-distal edge of the bicapital crest. The smaller dorsal or coracoidal head arises from the broad, strong, distal tendon of *M. coracobrachialis cranialis*. This head gives rise to the strong slip to *M. tensor propatagialis*. The two heads give rise to entirely separate tendons, the more ventral one inserting on the proximal end of the radius, and the dorsal one inserting at the proximal end of the "brachialis" scar of the ulna.

In the Ciconiiformes, the biceps slip is well-developed only in flamingos and ibises. It is vestigial in herons and absent in storks and *Balaeniceps*. In the more distinct division of the belly of the biceps, *Cladorhynchus* appears to differ somewhat from the forms described by Vanden Berge (1970), in all of which the belly is essentially undivided proximally.

M. expansor secundariorum

This is a small, diffuse muscle inserting on the bases of 3 or 4 secondaries at the proximal end of the ulna and from fasciae over the dorsal surface of the elbow joint. The very slender tendon extends proximad and enters the axilla. We did not trace the delicate origins, but encountered one of them that emerged from connective tissue in the

axilla and attached to the dorsal surface of the sternocoracoidal ligament. The belly is not weakly developed as in herons and is therefore in agreement with flamingos, storks, and ibises.

M. pronator superficialis

The origin is both tendinous and fleshy from the cranioventral corner of the distal end of the humerus ("attachment of anterior articular ligament" of Howard, 1929). The insertion is by a tendinous sheet opposite the insertion of *M. supinator* on the cranioventral edge of the proximal third of the radius. There is an indication of a division in the belly. The origin is apparently entirely tendinous in flamingos and Ciconiiformes except *Eudocimus* and *Ajaia* (Vanden Berge, 1970).

M. pronator profundus

This arises tendinously from the ventral epicondyle (entepicondyle) of the humerus and inserts fleshy along the ventral surface of the proximal half of the radius, including the proximal sixth or so. It fuses distally with *M. extensor longus digiti majoris* ("extensor indicis longus"). This is like the condition described for ibises and most herons and differs from flamingos, storks and *Balaeniceps* in which the muscle becomes tendinous distally and does not fuse with *M. extensor longus digiti majoris* (Vanden Berge, 1970).

M. flexor carpi ulnaris

This is the most caudal of the ventral muscles of the ulna and arises as a strong tendon from the flexor process at the distal end of the humerus. There is a proximal division of the belly, the combined fibers of which run the full length of the ulna. The insertion is tendinous on the ulna. Vanden Berge (1970) does not mention any distinctive condition in this muscle in flamingos.

M. flexor digitorum profundus

The origin is from two slips on the ventral surface of the proximal end of the ulna that are separated by the insertion of *M. brachialis*. The tendon forms about midway along the ulna, runs over the pisiform process, under *M. flexor alulae*, and extends along the cranial edge of the carpo-

metacarpus to insert at the base of the distal phalanx of the major digit. The belly is also notched by *M. brachialis* in ibises, herons, and *Balaeniceps* but evidently not in flamingos and storks (Vanden Berge, 1970).

M. ulnometacarpalis ventralis

This differs from flamingos and Ciconiiformes in that the belly is longer, tapering over the distal three-fourths of the ulna.

M. extensor metacarpi radialis

This muscle is clearly divided into two bellies, the larger ventral one arising fleshy from the ectepicondylar spur of the humerus and the dorsal one from a superficial tendon in common with the insertions of *M. tensor propatagialis brevis*. About three-fourths distally the length of the radius they form a common tendon that runs along the leading edge of the wing through a groove in the radius, over the carpal joint, to insert on the extensor process of the alular metacarpal, there partly fusing with the underlying tendon of *M. extensor longus alulae* ("pollicis longus").

In flamingos the two bellies fuse distally and produce a common tendon, whereas in all Ciconiiformes the bellies are separate and the tendons do not fuse except at the distal end of the radius. *Cladorhynchus* approaches the condition in flamingos in that the fusion of the tendons is farther proximad, although the bellies are nevertheless completely separate.

M. extensor longus alulae
("pollicis longus")

This is about as described for flamingos and Ciconiiformes except that we could not detect that there were two heads as reported by Vanden Berge (1970).

M. extensor longus digiti majoris
("indicus longus")

This muscle is as described for flamingos by Vanden Berge (1970). The distal head is extremely small, only about 3 to 4 mm long and less than 1 mm in width. It is better developed in

Ciconiiformes but in flamingos it occurs only as a few fleshy fibers in *Phoenicopterus chilensis* and it is absent in *P. ruber* and *Phoenicoparrus jamesi* (Vanden Berge, 1970).

M. ulnometacarpalis dorsalis

This muscle appears to be similar to the typical form in flamingos and Ciconiiformes in general; there are two bellies, in contrast to the single belly reported for *Leptoptilos* (Vanden Berge, 1970).

M. abductor alulae ("pollicis")

There is no suggestion of a division as reported for *Phoenicopterus ruber* but not other flamingos (Vanden Berge, 1970).

M. adductor alulae ("pollicis")

Both the origin and the insertion are fleshy; the insertion is on the alular bone and not on feathers. The same is true for flamingos, whereas in all Ciconiiformes except *Balaeniceps* the origin is tendinous distally and the insertion is mainly on feathers, except in ibises.

M. interosseus dorsalis

The origin is as described for Ciconiiformes. The tendon bifurcates after the metacarpophalangeal joint and sends a short tendon to the dorsal surface on the proximal half of the proximal phalanx of the major digit. The other ramus continues distally and inserts as a broad band on the proximo-dorsal edge of the distal phalanx, with a weaker extension going out to the tip of the phalanx and the bases of the distal primaries. No ramus to the proximal phalanx is mentioned by Vanden Berge (1970) for the Ciconiiformes or flamingos.

M. interosseus ventralis ("volaris")

The origin within the metacarpal space is from the entire margin of the major metacarpal ("II") and all but the distal fifth of the minor metacarpal ("III"). This is as in flamingos and *Balaeniceps* except that in those forms the attachment to the minor is less extensive and is confined to the proximal half of the bone. In storks there is no attachment to the minor, whereas in herons and

ibises the origin runs the entire length of the minor metacarpal.

M. flexor digiti minoris ("IIP")

The origin is fleshy, begins at the insertion of *M. ulnometacarpalis dorsalis*, and extends along the remainder of the caudal margin of the minor metacarpal ("III"), with the longest fibers arising in the distal third of the belly. This is in agreement with flamingos, storks, and *Balaeniceps*, whereas in herons and ibises the main fleshy fibers are more proximally situated.

M. ilirotrochantericus caudalis

This muscle originates fleshy from almost the entire preacetabular ilium, the origin being somewhat more aponeurotic posteriorly. The insertion is a broad tendon along the craniolateral surface of the trochanter, extending proximally deep to *M. iliofemoralis externus* ("glutaeus medius et minimus"). Vanden Berge (1970) notes that in the stork *Leptoptilos* this muscle is covered only by the very extensive aponeurosis of *M. ilirotibialis lateralis*, whereas in the Phoenicopteridae, as in *Cladorhynchus*, it is covered by the fleshy bellies of the ilirotibialis complex.

M. iliofemoralis externus
("glutaeus medius et minimus")

The origin is fleshy from the edge of the ilium above the acetabulum, becoming aponeurotic caudally. The insertion is by a fairly long tendon attaching in the middle of the lateral aspect of the proximal end of the femur. As in the Phoenicopteridae, Ciconiidae, and Threskiornithidae, the insertion is cranial to that of *M. ischiofemoralis*, in contrast to *Balaeniceps* and the Ardeidae, in which it is caudal (Vanden Berge, 1970).

M. iliofemoralis internus ("iliacus")

This is a short, diagonal muscle originating fleshy from the ventral border of the preacetabular ilium and inserting fleshy on the medial surface of the femur, below the head, proximal and caudal to the origin of *M. femorotibialis internus*. The insertion is in agreement with both flamingos and ibises and differs from storks, in

which the insertion is cranial to the origin of *M. femorotibialis internus* (Vanden Berge, 1970). *Cladorhynchus* agrees with both flamingos and storks in that this muscle is short and stout, whereas in other Ciconiiformes it is long and narrow.

M. ambiens

The *ambiens* is present in *Cladorhynchus* and arises from a fairly long tendon from the pectineal process of the pelvis. Its long, thin tendon of insertion runs through the patellar tendon and then deep to the insertion of *M. iliofibularis* to insert mainly on the belly of *M. flexor perforatus digiti II*, but also with a tenuous extension to *M. flexor perforatus digiti III*. The *ambiens* is absent in herons and *Balaeniceps*, and possibly in *Scopus* and some storks (see references cited by Vanden Berge, 1970:333). In those Ciconiiformes in which the *ambiens* is present, the insertion "is directly continuous with a small medial head" of *M. flexor perforatus digiti II*, except in flamingos, in which the insertion is on the belly of that muscle (Vanden Berge, 1970:333). In this respect then, flamingos are more similar to *Cladorhynchus* than to any of the Ciconiiformes.

M. iliotibialis lateralis

This is a broad, thin sheet originating as an aponeurosis from the dorsal crest of the ilium and cranially from the dorsal crest of the synsacrum. It covers much of the lateral surface of the thigh, including a portion of *M. iliofibularis* ("biceps femoris") caudally and *Mm. ilirotrochanterici* cranially. The postacetabular and preacetabular portions are continuous and not separated proximally by a tendinous sheet as in flamingos, but distally they are separated by an aponeurosis (Figure 6b) that fuses with the underlying *M. femorotibialis* and inserts on the patellar tendon. Flamingos differ from *Cladorhynchus* in having the two heads of this muscle "separated by a thin tendinous sheet covering the *Il. troc. post.* [caud.]" (Vanden Berge, 1970:335), but they are more similar to *Cladorhynchus* than to the Ciconiidae or *Scopus*, in which the postacetabular portion is absent and *M. iliofibularis* is exposed.

M. iliotibialis medialis and *M. iliotibialis cranialis* ("sartorius")

In *Cladorhynchus* these two muscles (Figure 6b) originate from a common aponeurosis on the most cranial portion of the dorsal crest of the synsacrum. *M. iliotibialis medialis* is a broad (8.5 mm), thin strap underlying the *M. iliotibialis cranialis*, which is considerably narrower (4.5 mm at midpoint). The caudal portion of *M. iliotibialis medialis* is covered by *M. iliotibialis lateralis*. Both *Mm. iliotibialis medialis* and *cranialis* insert on the patellar tendon, the former being more medial to the latter. Vanden Berge (1976) reports that *M. iliotibialis medialis* inserts at the base of the inner cnemial crest of the tibiotarsus in flamingos; thus in *Cladorhynchus* the insertion on the patellar tendon probably represents a slightly more primitive state. *M. iliotibialis medialis* was present and developed to the same degree on both sides of the specimen of *Cladorhynchus* dissected in this study.

We examined specimens of *Recurvirostra americana* (Figure 6a) and *Himantopus mexicanus*, in neither of which was *M. iliotibialis medialis* present. The occurrence of this muscle in *Cladorhynchus* and flamingos and no other known birds, is very strong evidence of relationship. In view of the amount of concurring data, it seems incontrovertible.

M. femorotibialis

M. FEMOROTIBIALIS INTERNUS.—This is a separate muscle originating fleshy along the entire medial face of the femur distal to the insertion of *M. iliofemoralis internus* ("iliacus"). It inserts partly by a strong tendon on the medial side of the tibial head just behind the inner cnemial crest and contributes weakly to the medial portion of the patellar tendon, covering much of the medial surface of the distal end of the femur. This tendon does not cover the tendon of insertion of *M. iliotibialis medialis* as reported for *Phoenicopterus* (Vanden Berge, 1970).

M. FEMOROTIBIALIS MEDIUS.—The origin is fleshy from the caudolateral surface of the shaft of the femur, beginning at the level of the tro-

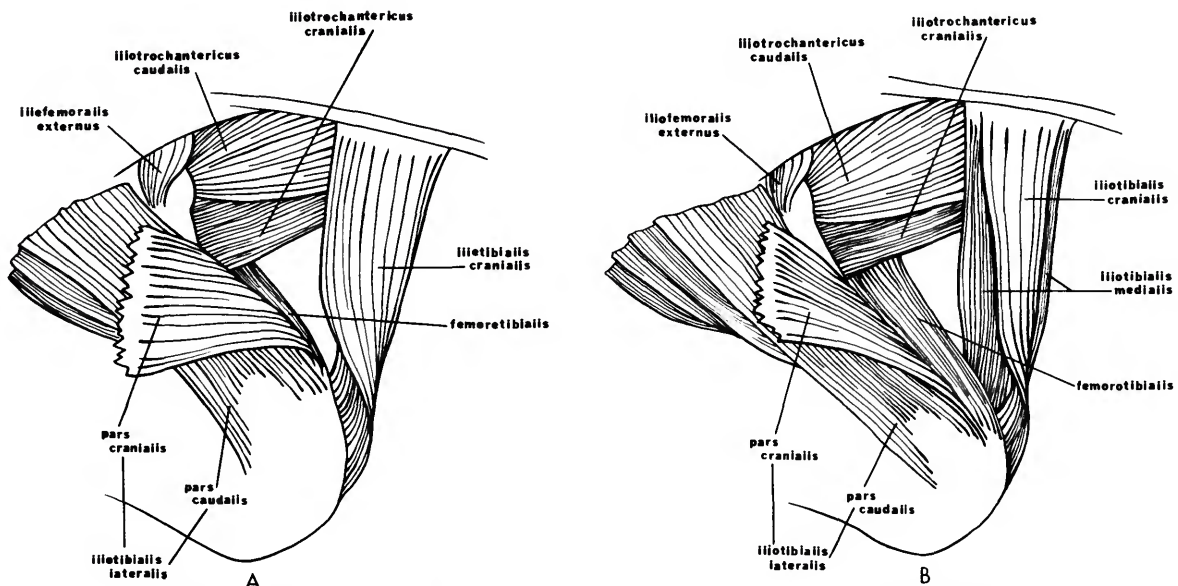


FIGURE 6.—Lateral view of right thigh of *Recurvirostra americana* (a) and *Cladorhynchus leucocephalus* (b) with *M. ilioprochantericus lateralis* reflected from origin. *M. ilioprochantericus medialis* is absent in *Recurvirostra* but present in *Cladorhynchus*. This muscle occurs elsewhere only in flamingos.

chanter. It barely overlaps the insertion of *M. ilioprochantericus cranialis* and continues on around to the cranial surface of the shaft at the level of the distal extent of the trochanter. The insertion forms much of the patellar tendon, which, as mentioned, is partly fused with the superficial aponeurosis of *M. ilioprochantericus lateralis*.

M. femorotibialis externus.—This is also an entirely separate entity, not fusing with *femorotibialis medius*. It arises fleshy from the caudolateral distal three-fifths of the femur. It overlies the iliofibular (“biceps”) loop and inserts as a fairly broad tendon on the patellar tendon, distal to most of the insertion of *femorotibialis medius*.

Cladorhynchus differs from flamingos, storks, and *Balaeniceps* in the lack of fusion of *Mm. femorotibialis medius* and *externus*. In the *Ciconiiformes* the external muscle was reported as most clearly developed in herons and ibises.

M. caudo-iliofemorialis (“*piriformis*”)

M. iliofemorialis.—This muscle arises mainly fleshy (tendinous caudally) from the ventral edge of the postero-lateral corner of the ilium and

extends as a thin triangular sheet, encompassing a small tendinous area in the middle of the dorsal edge, to insert via a short tendon (fusing with that of *M. caudofemoralis*) on the caudolateral face of the shaft of the femur about one-third the way distally.

M. CAUDOFEMORALIS.—This is present in *Cladorhynchus* and arises from a long, thin tendon on the ventral surface of the caudal bulb and extends as a narrow strap across the thigh deep to *M. flexor cruris lateralis* and dorsal to *M. flexor cruris medialis*, having a common insertion with *M. iliofemorialis* by a fairly long tendon.

These are two of the “Garrod formula” thigh muscles that have figured so prominently in much of the past taxonomic literature. *M. caudofemoralis* (“A” of Garrod, 1874) is absent in flamingos (including *Phoeniconaias*, this study) but is present in *Cladorhynchus*. The same variation occurs within the *Ciconiidae* and the *Ardeidae*, in which this muscle is present in some genera but absent in others (Vanden Berge, 1970). Fisher and Goodman (1955) found *M. caudofemoralis* in two specimens of *Grus americana* but it was absent in a

third. Within the Charadriiformes it has been reported as absent in *Burhinus* (George and Berger, 1966). The late George Hudson (unpublished MS, fide Vanden Berge) found it to be present in *Burhinus bistratus*, however, but absent in several genera of Scolopacidae and in *Steganopus* and *Lobipes* (Phalaropodidae).

M. iliofemorales ("B" of Garrod) is present in *Cladorhynchus*, flamingos, and ibises, but is uniformly absent in other Ciconiiformes.

M. flexor cruris lateralis
("semitendinosus")

Both parts of the muscle present somewhat of an anomalous condition in *Cladorhynchus* (Figure 7a). Pars pelvica arises from a broad aponeurosis on the caudo-lateral corner of the ilium, being partly fused with the aponeurosis of origin of *M. transversus cloacae*. It passes distally as a narrow strap to insert on a very short, nearly vertical raphe shared with pars accessoria, the fibers of which fuse with the slender belly of *M. gastrocnemius pars intermedia* to insert fleshy in the popliteal fossa of the femur, some of the fibers fusing medially with *M. pubo-ischiofemorales pars lateralis*. There is no medial tendon from the raphe to the underlying *M. flexor cruris medialis*.

Vanden Berge (1970:338) states that in herons, *Balaeniceps*, and flamingos pars accessoria is

clearly separable from *M. gastrocnemius pars intermedia* and that in the Phoenicopteridae "the fleshy insertion extends over the distal three-fifths of the femoral shaft." He did not examine *Phoeniconaias*, however, and the two specimens we dissected differed greatly from his description for the other genera of flamingos. In lateral view (Figure 7b), the arrangement in *Phoeniconaias* is quite similar to that seen in *Cladorhynchus* except that the raphe between pars pelvica and pars accessoria extends as a long diagonal intersection that is continuous with *M. gastrocnemius pars intermedia*. Therefore, pars accessoria in *Phoeniconaias* is not separable and attaches to a shorter area on the distal end of the femur, far less than three-fifths of the femoral shaft. In medial view (Figure 8) the raphe is more distinct and gives off a tendinous slip to the tendon of insertion of *M. flexor cruris medialis*, unlike *Cladorhynchus*.

In most birds possessing both parts of the lateral flexor, the fibers meet at a greater angle than in *Cladorhynchus* and *Phoeniconaias*. It is difficult to reconcile what we observed in *Phoeniconaias* with Vanden-Berge's description of flamingos based on *Phoenicopterus* and *Phoenicoparrus*. The similarity between *Cladorhynchus* and *Phoeniconaias* is nevertheless considerable and these genera differ from the Ciconiiformes in general and the storks in particular, as in that group the accessory part is

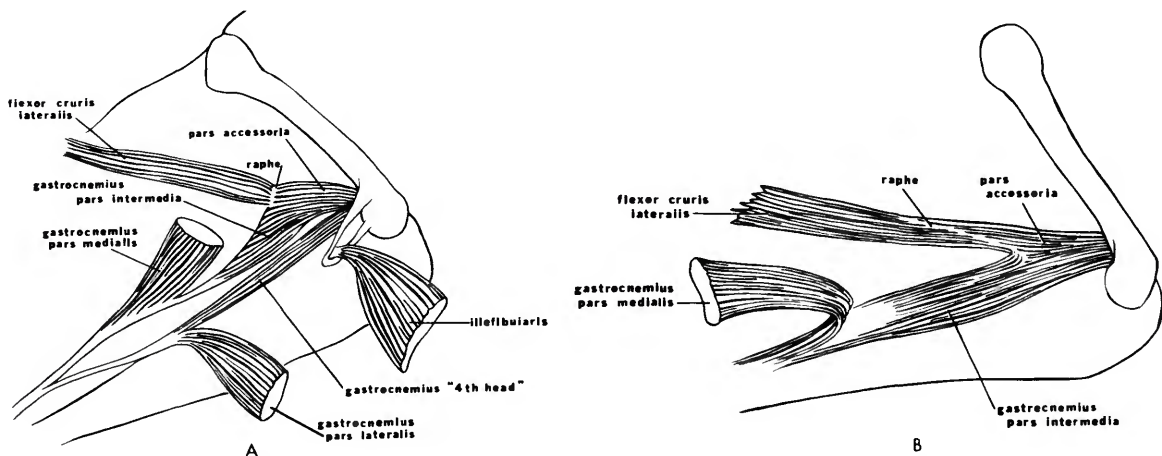


FIGURE 7.—Lateral view of right hindlimb showing the disposition of the *M. flexor cruris lateralis* complex in *Cladorhynchus leucocephalus* (a) and *Phoeniconaias minor* (b).

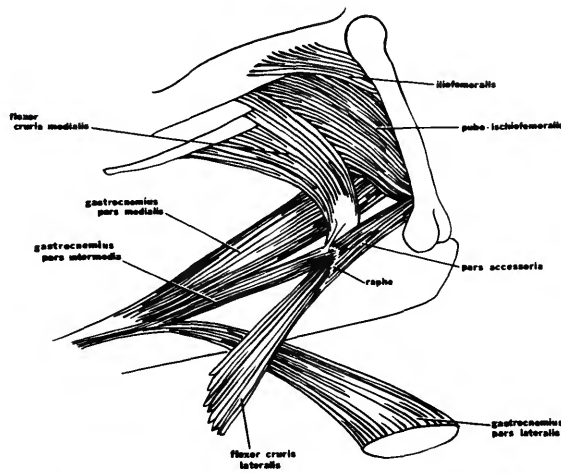


FIGURE 8.—Right hindlimb of *Phoenicaias minor* with *M. flexor cruris lateralis* reflected outward to reveal its medial surface and the connection with *M. flexor cruris medialis*. This connection is absent in *Cladorhynchus*.

only a vestigial bundle of fibers that does not insert on the femur at all (Vanden Berge, 1970). In the condition of the raphe and the loss of the connection with the medial flexor, *Cladorhynchus* seems more specialized than any of the flamingos, Ciconiiformes, or more typical shorebirds.

M. flexor cruris medialis
("semimembranosus")

This muscle arises fleshy from the ventral (pubic) margin of the ischium, overlying the pubis behind the obturator foramen. It is a broad tapering strap that inserts by a tendon on a short ridge on the medial surface of the shaft of the tibiotarsus, about 1 cm distal to the medial articular facet. Vanden Berge (1970) notes that in flamingos the medial flexor is extremely wide proximally compared with other Ciconiiformes. Without seeing these forms ourselves it is difficult to evaluate the condition in *Cladorhynchus*, but the muscle is nevertheless quite wide proximally.

M. ischiofemorals

This arises fleshy from most of the concavity caudal to the acetabulum, including the membrane of the ilioischiatric fenestra. It inserts both tendinous and fleshy on the caudo-lateral surface

of the trochanter, caudal to the insertion of *M. iliofemorals externus*. In agreement with flamingos, storks, and ibises, and in contrast to herons and *Balaeniceps*, it lies cranial to *M. flexor cruris medialis*.

M. obturatorius medialis et lateralis
("obturator internus et externus")

In *Cladorhynchus*, as in all the families examined by Vanden Berge (1970) except the Ardeidae, the two muscles are fused and cannot be separated. The major part forms an elongate oval arising on the medial side of the pelvis from the margins of the ischio-pubic fenestra. It passes through the obturator foramen and inserts fleshy on the caudal aspect of the trochanter.

M. pubo-ischiofemorals
("adductor longus et brevis")

Pars lateralis and pars medialis are fused proximally so as to be indistinguishable; they originate from a broad tendon on the cranio-ventral portion of the ischium, covering the ischio-pubic fenestra and the corresponding portion of the pubis. The insertion is fleshy on the caudomedial surface of the shaft of the femur above the popliteal fossa, the fibers coalescing distally with the combined flexor cruris lateralis pars accessoria and gastrocnemius pars intermedia, which inserts farther distally. The fused heads are found in flamingos and all Ciconiiformes except herons, whereas the fleshy insertion in *Cladorhynchus* is most similar to that described for flamingos (Vanden Berge, 1970).

M. fibularis [peroneus] longus

This muscle arises from a broad aponeurosis over the entire tibial head and underlying musculature, but is most strongly attached to the rim of the inner, and tip of the outer, cnemial crests. Distally the belly is divided by a long tendinous area. The tendon extends down the lateral surface of the tibial shaft, sends off an aponeurotic attachment to the posterior rim of the internal condyle and continues diagonally over the lateral surface of the intertarsal joint and lateral to the hypotarsus to insert just distal to the hypotarsus on the tendon of *M. flexor perforatus digiti III*.

Vanden Berge (1970) indicates that in flamingos and Ciconiiformes other than herons, the origin from the tibial crest and most of the fibula is fleshy, which is not true of *Cladorhynchus*.

M. fibularis [peroneus] brevis

Absent in *Cladorhynchus*. This muscle is present in all Ciconiiformes except storks and flamingos, a fact that has often been mentioned in the literature (see references in Vanden Berge, 1970: 343). Its absence in *Cladorhynchus*, and also in *Recurvirostra* (George and Berger, 1966), negates one more supposed storklike character of flamingos. Hudson's manuscript notes (fide Vanden Berge) indicate this muscle to be unilaterally present in *Recurvirostra americana*, and absent in *R. novaehollandiae*, *Himantopus*, and certain other Charadrii.

M. gastrocnemius

In *Cladorhynchus* this muscle arises from four entirely separate heads (Figure 7a). The common tendon of the four heads is the most superficial on the caudal surface of the shank and inserts on the hypotarsus.

PARS MEDIALIS ("INTERNA").—This originates fleshy from the entire medial surface of the inner cnemial crest, extending over onto the patellar tendon so as to obscure the insertions of *M. iliotibialis cranialis* and *medialis*.

PARS INTERMEDIA ("MEDIA").—This originates fleshy from the popliteal fossa in common with the fused accessory part of the lateral crural flexor. It becomes tendinous and inserts on the distal margin of *pars medialis* about three-fourths the length of the latter.

PARS LATERALIS ("EXTERNA").—This arises fleshy from the lateral supracondylar crest of the femur, being overlain by *M. femorotibialis externus* and overlying the iliofibular loop. It fuses with the fourth head to form a tendon that in turn fuses midway down the shank with the tendon of *pars medialis*.

"FOURTH HEAD."—This slender muscle arises in the popliteal fossa from a long, narrow tendon separate from, and distal to, the origin of the combined *pars intermedia* and accessory lateral

crural flexor. It inserts distally on *pars lateralis* about 6 mm before the latter becomes tendinous.

The four-headed gastrocnemius is also reported from storks, ibises, and flamingos, but does not occur in herons or *Balaeniceps* (Vanden Berge, 1970). In flamingos the *pars medialis* covers the anterior surface of the knee and the entire patellar tendon and meets the proximal edge of *pars lateralis* laterally. This is not true of *Cladorhynchus* but may well be a size-related factor. We noted also that in *Phoeniconaias* there was considerably more distal fusion of the heads of the gastrocnemius, these being less easily separated and distinguished than in *Cladorhynchus*.

Digital Flexors

Vanden Berge (1970) notes that at least some of the various flexor muscles of the toes have fleshy origins from the shaft of the fibula in all of the Ciconiiformes but not in the Phoenicopteridae. In *Cladorhynchus*, as in flamingos, there is no fleshy attachment between any of the flexors and the shaft of the fibula.

M. flexor perforans et perforatus digiti II

This muscle arises from two distinct heads, one originating by a short tendon on the articular capsule opposite the lateral condyle of the femur and the other head from a broad, thin aponeurotic sheet partly coextensive with the patellar tendon and partly covering the origin of *M. fibularis longus*. Some of the deep fibers along the midline fuse with those of the underlying *M. flexor perforans et perforatus digiti III*. The tendon runs through the deepest, most medial, groove of the hypotarsus and the insertion is similar to that in flamingos and ciconiiforms.

Flamingos agree with *Cladorhynchus* and differ from all Ciconiiformes in having this muscle double-headed instead of single-headed.

M. flexor perforans et perforatus digiti III

This can also be considered as having two heads, though these are more intimately connected than in the preceding muscle. The caudal head is fleshy and arises from the head of the

fibula and possibly from the lateral collateral ligament between the fibula and the distal end of the femur. The cranial head arises partly from the disto-lateral surface of the patellar tendon, overlying that portion contributed mainly by *M. femorotibialis externus*, and is most strongly attached to the tip of the lateral cnemial crest. There is a weak vinculum with *M. flexor perforatus digiti III* about 1 cm above the trochlea and the insertion is typical. Again, flamingos agree with *Cladorhynchus* and differ from Ciconiiformes, in all of which this muscle has but a single head.

Mm. flexores perforati

Of the three perforated flexors, that for digit IV is the most superficial and that for digit II is the deepest. These three muscles are fused proximally and are all essentially double-headed, with the heads diverging around the insertion of *M. iliofibularis*. The superficial or lateral heads of IV and II take a common origin tendinously from the head of the fibula. The lateral portion of III attaches to the belly of II. The three fused deep or medial heads take their origin fleshy from the depths of the popliteal fossa, distal to the insertions of the accessory lateral crural flexor and the intermediate and fourth heads of the gastrocnemius. The deep surface of *M. flexor perforatus digiti II* fuses partly with the belly of the much smaller *M. flexor hallucis longus*. The tendon of IV becomes thickened at the level of the trochlea and is perforated at the level of the base of the toe; it gives rise to paired insertions at the distal ends of each phalanx. The tendon of III receives the tendon of *M. peroneus longus* and continues on to receive another, but weaker, vinculum from *M. flexor perforans et perforatus digiti III* about 0.5 cm above the trochlea. This vinculum is also present in flamingos and all ciconiiforms except the Ardeidae. The tendon of III is perforated in the middle of the basal phalanx and bifurcates to insert on the ventral corners of the base of phalanx 2. The tendon of II inserts as a thickened capsule at the base of phalanx 1 digit II.

M. flexor hallucis longus

Although the hallux is absent, its flexor is present and has a partly fleshy origin medial to

the distal attachment of the iliofibular loop. There is a short tendinous attachment to the most caudolateral protruberance of the lateral condyle of the femur and the origin is fleshy medial to this; the fleshy origin continues from a raphe extending distally on the deep surface of *M. flexor perforatus digiti II*. The belly is very short, flat, and triangular. The slender tendon runs through the lateral side of the tibial cartilage and through a groove in the lateral crest of the hypotarsus. About 1 cm or less distal to the hypotarsus it fuses with the tendon of *M. flexor digitorum longus*. This corresponds to the type IV condition of the deep flexor tendons, according to the terminology of Gadow (1896). This condition is found in a number of often unrelated birds in which the hallux is absent or greatly reduced. It occurs in flamingos but in none of the Ciconiiformes.

M. flexor digitorum longus

This is the deepest muscle on the caudal aspect of the shaft of the tibiotarsus. One head arises fleshy from the head of the fibula and the proximal third of its shaft. The other head extends medially on the shaft of the tibiotarsus alongside the origin of *M. plantaris*. The tendon is the deepest one passing through the sulcus between the two crests of the hypotarsus; it receives the tendon of *M. flexor hallucis longus* just distal to the hypotarsus. At the distal end of the tarsometatarsus it trifurcates and inserts on the three digits. The significance of the deep flexor tendons is discussed above.

M. popliteus

This small muscle arises from the head of the fibula deep to all other muscles. It runs diagonally to attach disto-medially on a small protruberance on the caudal face of the proximal end of the shaft of the tibiotarsus. Flamingos agree with *Cladorhynchus* and differ from all Ciconiiformes in having the insertion of *M. popliteus* distal to the origin (cf. Vanden Berge, 1970).

Intrinsic Muscles of the Tarsometatarsus

Because of the extremely slender shaft and the absence of the hallux, the muscles originating on

the tarsometatarsus in *Cladorhynchus* are greatly reduced or absent (true also of flamingos), whereas most of these muscles are much better developed in all Ciconiiformes. As in the case of the deep flexor tendons, it would be easy to argue that similarities in these respects between *Cladorhynchus* and flamingos could be due to independent reduction of the hallux, yet it must be remembered that this has never occurred in the Ciconiiformes. In some cases we have not made comparisons when Vanden Berge (1970) has not specifically described the condition in flamingos.

M. extensor hallucis longus

Absent in *Cladorhynchus* and flamingos except *Phoenicopterus*, where it is stated to be present but vestigial (Vanden Berge, 1970). It is well-developed in Ciconiiformes.

Mm. extensores brevis

M. extensor brevis digiti III and *M. extensor brevis* digiti IV arise from a bundle of connective tissue just distal to the lateral cotyla on the dorsal face of the tarsometatarsus. They appear to have very few muscle fibers associated with them. That for digit IV is the most lateral but its long tendon then runs deep to that of digit III and is closely bound to the face of the shaft of the tarsometatarsus; where it enters the distal foramen it is covered by the expanded sheath of the tendon of III. The long tendon of *M. extensor brevis* digiti III runs deep to that of *M. extensor digitorum longus*; above the distal foramen it fans out into a broad sheath covering most of trochleae III and IV and having its insertion at the bases of their phalanges. Vanden Berge (1970) does not give many details of these muscles in flamingos but it is evident that they are better developed in Ciconiiformes.

M. abductor digiti II

This is a fleshy muscle on the medial aspect of the distal fifth of the tarsometatarsus. It inserts on the base of phalanx 1 digit II.

M. flexor hallucis brevis

This tiny muscle arises as a wisp of fibers descending from the ligamentous distal extension

of the medial crest of the hypotarsus. The belly is about 8 mm long and the exceedingly slender thread of a tendon extends distally on the medial margin of the shaft of the tarsometatarsus and appears to lose itself in the belly of *M. abductor digiti II*. This muscle is also vestigial in flamingos, in which, however, it appears to arise farther distally. It is better developed in all Ciconiiformes.

M. adductor digiti II

This arises lateral to *M. flexor hallucis brevis* from the distal end of the lateral crest of the hypotarsus and adjacent surface of the tarsometatarsus, tapering for 13 mm before becoming tendinous. The long tendon inserts on the medial side of the base of phalanx 1 digit II. This muscle also arises proximally in flamingos and ibises, whereas in Ciconiiformes it is more distally located.

M. lumbricalis

Not detected in *Cladorhynchus* and quite vestigial in flamingos and in Ciconiiformes, except herons (Vanden Berge, 1970).

M. abductor digiti IV

The tendon of insertion attaches on the lateral corner of the plantar aspect of phalanx 1 digit IV and runs the length of this short tapering muscle. The fibers are oriented obliquely from this tendon to the distal fifth of the lateral side of the plantar face of the tarsometatarsus. This is about as described for flamingos and storks and differs from the condition in herons (Vanden Berge, 1970).

Pterylosis

To Nitzsch (1867:132), the pterylosis of flamingos was "perfectly Stork-like," a statement with which Gadow (1877) agreed and which has been repeated without corroboration ever since. On the contrary, we found the pterylosis of flamingos to be quite different from that of storks.

Nitzsch's great opus, which was published posthumously, is the original and only class-wide study of comparative pterylosis. Unfortunately, it has never been superseded by a more modern

and comprehensive analysis. Nitzsch first contrasted his family Pelargi (Ciconiidae and Scopidae) with the Erodii (Ardeidae) and showed the rather generalized pterylosis of storks to be quite different from the peculiar pterylosis of herons. He then discussed the "Odontoglossae" (= Phoenicopteridae) and found the pterylosis of flamingos to be of a more usual pattern and therefore "perfectly Stork-like" (as compared to herons, one may assume).

Mary H. Clench (in litt. to Olson, 8 December 1978) states that "the only valid approach to pterylography is a study of the tract *patterns*—how the feathers are arranged in rows, the relationship of the rows to each other, the numbers and lengths of rows (to a lesser extent)—in other words, what one can see *within* a tract, not just its general outlines (and resulting apteria)." Neither our brief inquiry into pterylosis, nor the studies of Nitzsch for that matter, meet these requirements. Our observations and illustrations (Figure 9) are intended solely to show that there is little reason to regard the pterylosis of flamingos as being storklike. We emphasize that the following is not intended as a proper pterylographic analysis.

To investigate pterylosis, we examined fluid-preserved specimens of *Phoeniconaias minor*, *Ciconia abdimii*, and *Cladorhynchus leucocephalus*, from which we had clipped the feathers. All of these specimens had been partially dissected, obscuring the configuration of the feather tracts in certain areas, particularly the abdomen in the flamingo and stork, and the neck and ventral midline in *Cladorhynchus*. Terminology follows that of Lucas and Stettenheim (1972).

The great density both of contour feathers and down in *Phoeniconaias* and *Cladorhynchus* (Figure 9) contrasts markedly with the sparse feathering and reduced down of *Ciconia*. In *Ciconia* the neck is feathered in two lateral bands separated by wide ventral and dorsal apteria; the latter is an anterior extension of the interscapular apterium. The two cervical apteria extend two-thirds the length of the neck, the remainder of which appears to be nearly continuously feathered all around. *Phoeniconaias* and *Cladorhynchus* have the neck much

more densely clothed in feathers and down than in *Ciconia*. There appears to be no dorsal cervical apterium or ventral cervical apterium in *Cladorhynchus*. Only the latter is present in *Phoeniconaias*; it is much smaller than in *Ciconia* and extends for less than one-fourth the length of the neck. In *Cladorhynchus*, a small lateral cervical apterium lies on each side of the base of the neck. These are absent in *Phoeniconaias* and *Ciconia*.

Ciconia has a rather wide sternal apterium; this is narrower in *Phoeniconaias* and we could not detect it in our specimen of *Cladorhynchus*, which, however, had previously been cut down the midline. The pectoral tract in *Ciconia* is broad and clothed with regularly spaced, sparse, weak feathers. *Phoeniconaias* and *Cladorhynchus* are much more densely feathered and have several rows of closely spaced, large, stiff-shafted feathers in the dorsal portions of the tract. *Cladorhynchus* differs from *Phoeniconaias* in having pectoral apteria that delimit a median tract, in which, as mentioned, the sternal apterium of our specimen was absent or destroyed.

In *Cladorhynchus* and *Phoeniconaias*, the femoral, crural, and dorsal caudal tracts are nearly continuously and rather densely feathered, and several longitudinal rows of stiffer feathers occur along the ventral margin of the pelvis above the crus. This differs from *Ciconia*, in which the dorsal caudal tract consists of a few rows of sparse feathers separated from the femoral tracts by lateral pelvic apteria. *Ciconia* also has crural apteria, which appear to be lacking in *Cladorhynchus* and *Phoeniconaias*. The uropygial gland is distinctly tufted in *Phoeniconaias* and *Cladorhynchus* and nearly bare in *Ciconia*. David W. Johnston, (in litt. to Olson, 17 October 1978) found this gland in *Phoenicoparrus* to be more similar to that of *Himantopus* than to that of either *Mycteria* (Ciconiidae) or *Anas* (Anatidae).

In dorsal view (Figure 9), the humeral tracts in *Cladorhynchus* and *Phoeniconaias* are broad, elongate patches of extremely densely packed and very stiff feathers; in contrast, this tract in *Ciconia* is smaller and consists posteriorly of a few very large feathers and anteriorly of sparse, weak feathers.

As previously noted, there are 11 primaries in

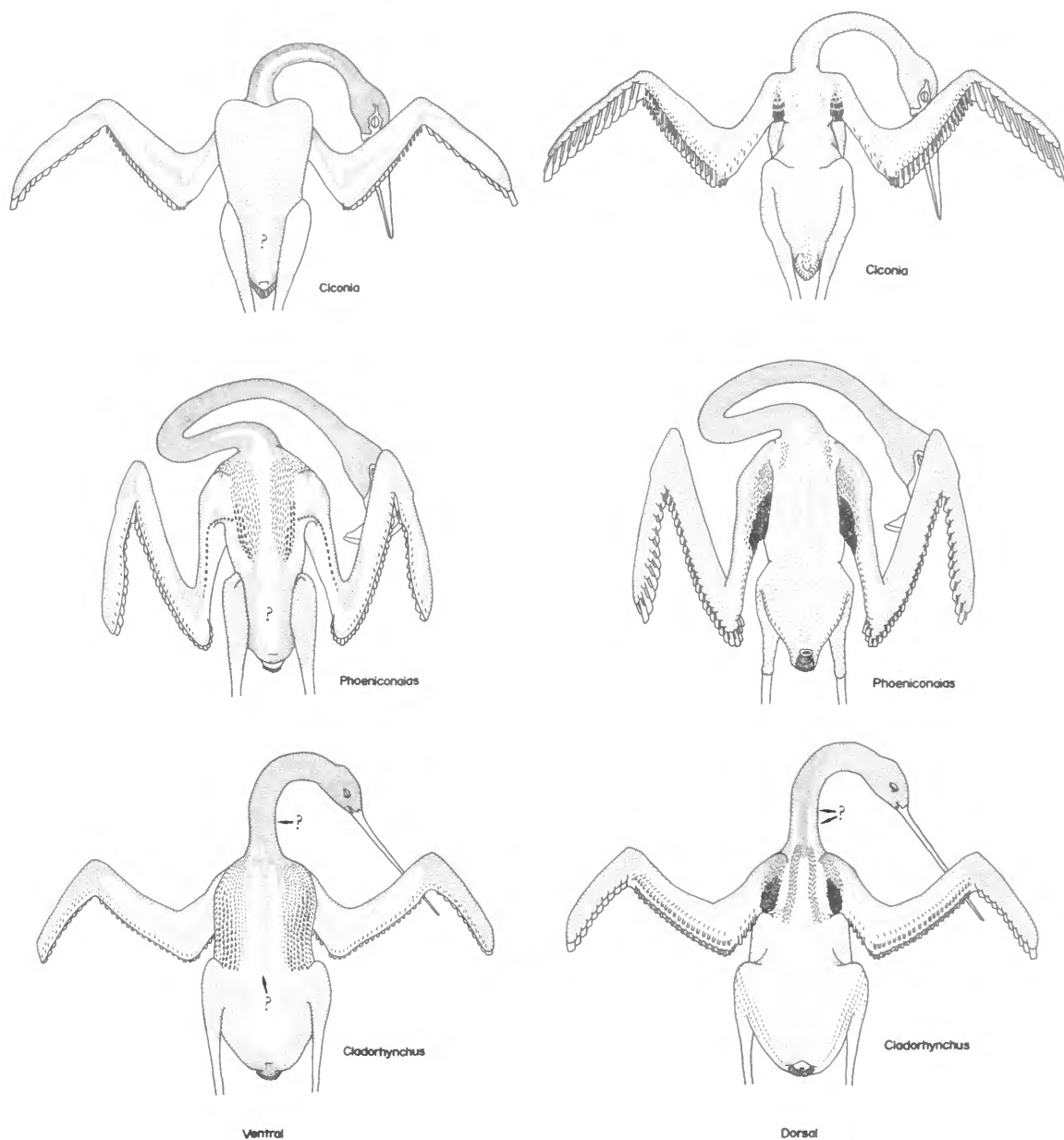


FIGURE 9.—Semidiagrammatic views contrasting the pterylographic patterns of a stork (*Ciconia abdimii*), flamingo (*Phoeniconaias minor*), and the Australian Banded Stilt (*Cladorhynchus leuccephalus*). (Question marks indicate those areas in our specimens that were destroyed by previous dissections. These drawings are intended only to show basic patterns and do not accurately represent the distribution of feathers within tracts.)

storks and flamingos. *Cladorhynchus* has 10. Of secondaries (counting tertials) there are 19 in *Cladorhynchus*, 20 in *Ciconia*, and 25 in *Phoeniconaias*. This, along with the general proportions of the wing, suggests that the entire wing in flamingos has become elongated, which could account for the greater number of secondaries and the addition of a primary. This has coincidentally resulted in flamingos having the same number of primaries as storks, whereas the number of secondaries is considerably greater.

There are substantial differences in pterylosis between all three of the forms we examined. There is at least some similarity between *Cladorhynchus* and *Phoeniconaias* in the density of feathering, particularly of the neck and pectoral and humeral tracts. This could represent an independently evolved response to the caustic habitat in which each lives. We conclude only that the pterylosis of flamingos cannot be said to be stork-like.

Natal Down

The literature on natal down contains considerable misleading information. The subject is of importance here because the natal down of flamingos has been said to be like that of storks. The following summary is largely an outgrowth of correspondence with Kenneth C. Parkes, to whom we are indebted for supplying unpublished observations.

In the young of certain birds there may appear to be two successive coats of down, i.e., two sets of downy growth emerging sequentially from the same set of feather follicles. This is strictly true only of a limited number of taxa such as Procellariiformes, Gaviiformes, and Sphenisciformes. In most other such birds the second coat of down is actually the very plumulaceous tips of the emerging juvenal plumage.

The Anseriformes and Charadriiformes have a single coat of natal down, whereas the Ciconiiformes and flamingos, are thought to have two, although it is known that herons have but one (Palmer, 1962). The condition in the Scopidae

and Balaenicipitidae is unknown to us. Although ibises (Threskiornithidae) are said to have two coats of down (Palmer, 1962), the supposed second coat is body down that grows from different follicles (Parkes, in litt. to Olson, 27 November 1978). Storks and flamingos have a second coat of down formed by the tips of the juvenal plumage. Sibley et al. (1969) gave considerable emphasis to this character in attempting to show ciconiiform affinities for flamingos.

In two fluid-preserved specimens of downy chicks of *Cladorhynchus*, we found clear evidence of two successive stages of down, the first of which could still be seen attached to the second (Figure 10). Feather growth in these specimens was insufficient to ascertain whether the second set of down was actually the tips of the juvenal plumage, however we assume this to be the case. No other member of the Charadrii is known to have two coats of natal down. The white coloration and lack of markings in the downy young of *Cladorhynchus* are likewise unique in the Charadrii (page 11). In view of all the other flamingo-like attributes of *Cladorhynchus*, the nature of its natal down assumes considerable significance. The condition of the natal down in flamingos, therefore, is at least as similar to that of *Cladorhynchus* as it is to that of storks.

Oology

The eggs of flamingos are large relative to the size of the bird and this is likewise one of the striking features of the eggs of *Cladorhynchus*. Although *Cladorhynchus leucocephalus* is somewhat smaller than *Recurvirostra americana*, its eggs are much larger (Figure 11). The weight of the egg of *C. leucocephalus* taken as a percentage of body weight is twice that of *R. americana* (Table 2). The same is true of the flamingo *Phoenicopterus ruber*, versus the stork *Mycteria americana*; both of these birds are about the same size, yet the relative egg size of the flamingo is twice that of the stork (Table 2). Naturally, because of allometric effects, the relative size of the eggs is smaller in the larger birds (the body weight of the flamingo is ten



FIGURE 10.—Feather from a chick of the Australian Banded Stilt, *Cladorhynchus leucocephalus*, showing (a) the “two coats of down,” the upper portion being true down and the lower probably being the plumulaceous tip of the juvenal feather, as in flamingos, and (b) further enlarged view of same to show the juncture of the first and second coat of down.

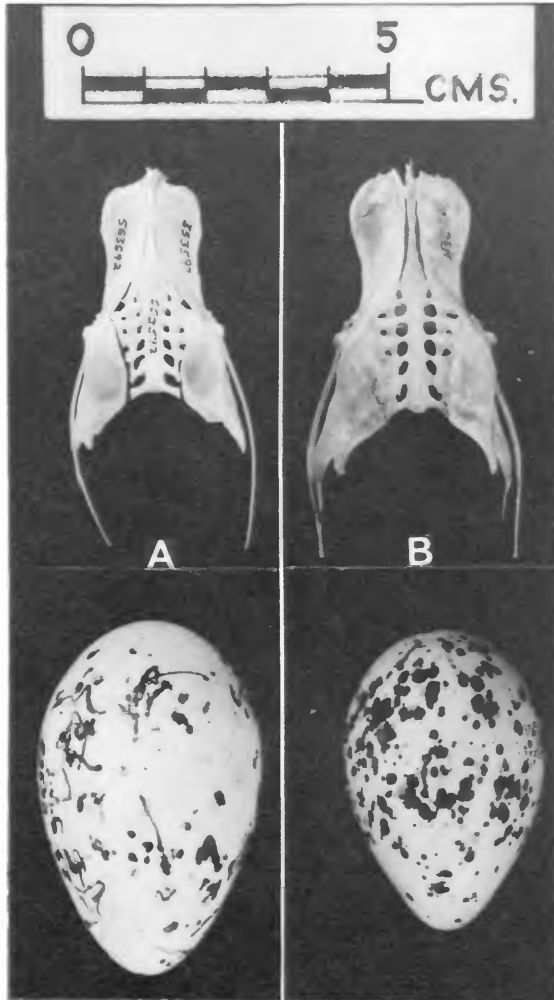


FIGURE 11.—Comparison of the pelvises (top) and eggs (bottom) of the Australian Banded Stilt, *Cladorhynchus leucocephalus* (a), and American Avocet, *Recurvirostra americana* (b), to show the disproportionately large size and light color of the egg of *Cladorhynchus*.

times that of *Cladorhynchus* and its egg weight obviously could not increase by a like proportion). The large egg size in *Cladorhynchus* and flamingos is probably correlated with the need to produce large well-developed young that are better able to survive in a harsh and often ephemeral habitat.

Flamingo eggs are white, unmarked, and covered with a rather thick chalky coat that is absent

TABLE 2.—Relative egg weights of two recurvirostrids, a flamingo, and a stork (all weights in grams; averages of egg weights obtained from water filled egg-shells (n = 3, except *Cladorhynchus*, n = 2); body weights are averages: *Recurvirostra*, 17 females (Hamilton, 1975); *Cladorhynchus*, 2 unsexed (McNamara, 1976); *Phoenicopterus*, 3 males and 2 females (Rooth, 1965); *Mycteria*, 2 males (Palmer, 1962))

Species	Body weight	Egg weight	Egg weight as % of body weight
<i>Recurvirostra americana</i>	310	30	9.7
<i>Cladorhynchus leucocephalus</i>	238	44	18.5
<i>Phoenicopterus ruber</i>	3050	160	5.2
<i>Mycteria americana</i>	3171	86	2.7

in storks and shorebirds. As mentioned, the ground color of the eggs of *Cladorhynchus* is peculiar among the Charadrii in being white, and markings may occasionally be absent (Figure 12). Although McGilp and Morgan (1931:44) describe the texture as "chalky," there is no powdery coating as in flamingos.

We examined the surface structure of the egg-shell of *Recurvirostra*, *Cladorhynchus*, *Phoenicopterus*, and *Ciconia* with a scanning electron microscope, first removing the powdery layer from the flamingo egg with a small buffing wheel. The two recurvirostrids and the flamingo exhibit a rather uniform granular structure that is significantly different from that of *Ciconia*, in which the surface of the shell is regularly pitted with distinct pores (Figure 13), a condition long recognized as being typical of storks (Des Murs, 1860). We conclude from this only that the eggs of storks bear no resemblance to those of flamingos.

Even if the distinctive attributes of the eggs of *Cladorhynchus* evolved independently of those of the Phoenicopteridae, this at least demonstrates that a flamingo-like condition can be derived from that of the Charadrii.

Parasitology

Sibley et al. (1969:162) reviewed the literature on the parasites of flamingos but concluded only that this evidence was "as conflicting and difficult to interpret as is that from morphology."

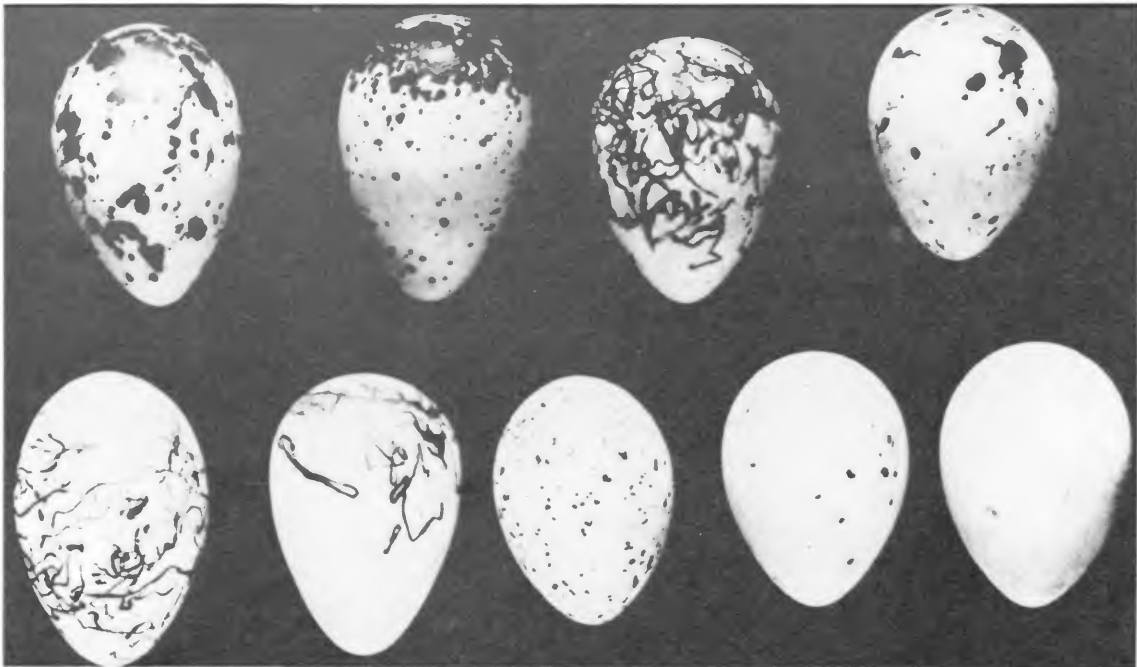


FIGURE 12.—Eggs of the Australian Banded Stilt, *Cladorhynchus leucocephalus*, to show variation in markings, which may occasionally be absent. (Photograph from McGilp and Morgan, 1931.)

Concerning the cestode parasites, the remarks of Baer (1957:274) are of considerable interest: "One finds in flamingos four monotypic, endemic genera (*Amabilia*, *Cladogynia*, *Gynandrotaenia*, *Leptotaenia*). The last two, very specialized overall, are derived from a family of cestodes characteristic of the Charadrii" (our translation). Baer (1951, 1957) has argued that the high degree of host specificity of cestodes renders them useful for assessing phylogenetic relationships of hosts. The evidence in this case is neither conflicting nor difficult to interpret, as it agrees with the hypothesis of charadriiform origins of flamingos.

The mallophagan ectoparasites of flamingos, however, present a different picture. Hopkins (1942:102) reported that flamingos are parasitized by three genera of feather lice that occur elsewhere only on the Anseriformes. He regarded this "as complete proof that the Flamingos are Anseriformes, and even that their divergence from the stock that gave rise to the Anatidae took place at no very remote period of time." However,

K. C. Emerson (pers. comm.) has indicated to us that the species of *Anatoecus*, *Anaticola*, and *Triniton* found on flamingos differ from those found on the Anatidae to a degree that would suggest their divergence did not occur recently.

Some authors have considered host transfer of Mallophaga to be frequent (Mayr, 1957; Stresemann, 1959), suggesting that flamingos "have acquired their feather lice from the Anatidae since they have lived in the same environment . . ." (Sibley et al., 1969:162). This seems oversimplified and were this often the case, one would expect most waterbirds to have the same kinds of Mallophaga.

The evolutionary history of flamingos and the Anseriformes suggests a logical possibility for transfer of Mallophaga that transcends mere chance. Modern flamingos nest in dense colonies in harsh, saline environments, and therefore, when breeding, are actually relatively isolated from other birds. The available evidence indicates that the same was probably true of early flamin-

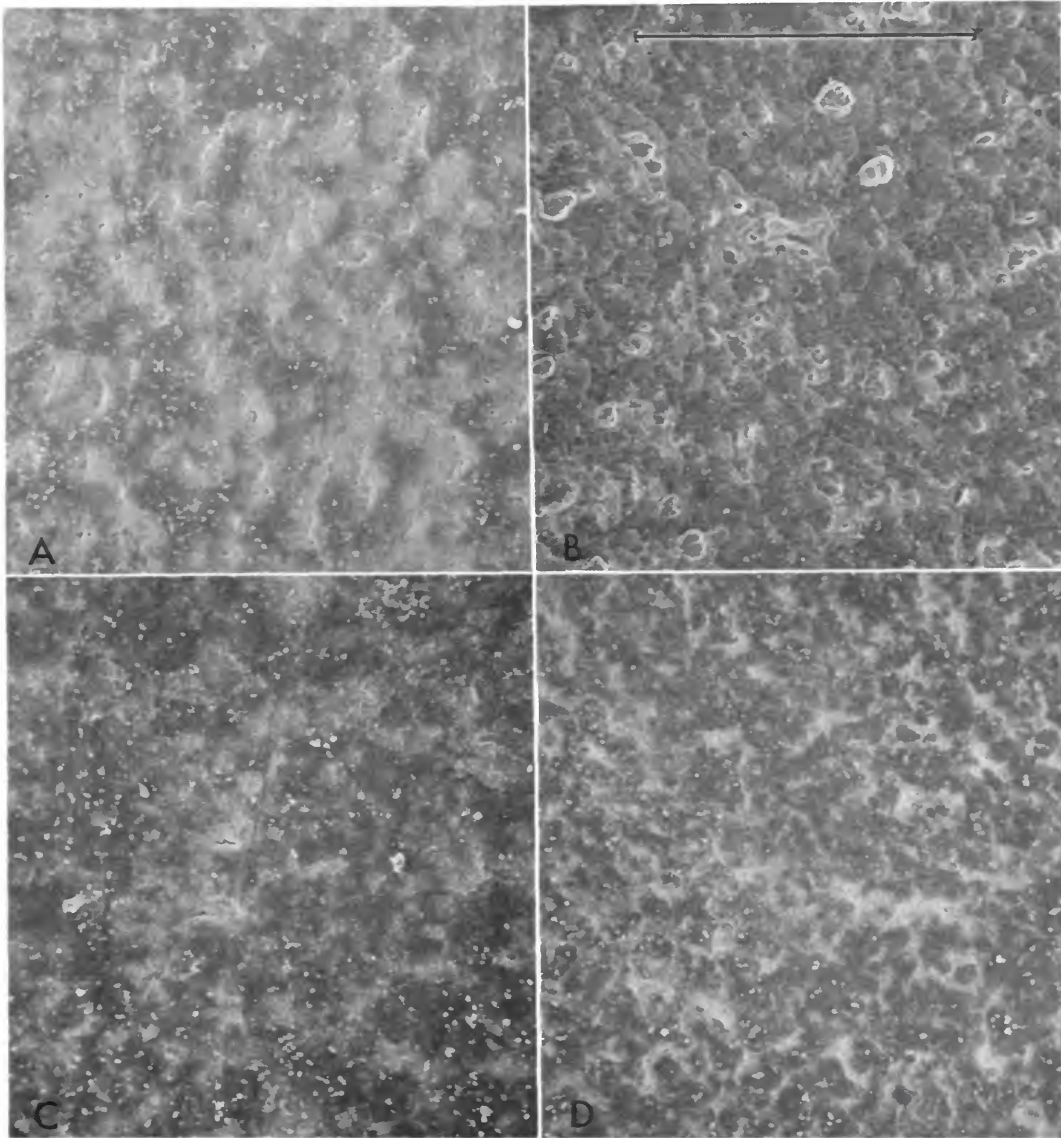


FIGURE 13.—Scanning electron micrographs of eggshell surface: *a*, stork, *Ciconia nigra*; *b*, flamingo, *Phoenicopterus ruber*; *c*, Australian Banded Stilt, *Cladorhynchus leucocephalus*; *d*, avocet, *Recurvirostra americana*. Note the distinctly pitted surface in the stork as opposed to the unpitted, granular surface in the others. (Scale = 1 mm. Photographs by Mary Jacque Mann.)

gos (page 48). As represented by *Presbyornis*, the ancestors of the Anseriformes were likewise extremely colonial shorebirds that lived in the same kinds of habitat (Olson and Feduccia, in press). For at least part of their history, flamingos were

probably contemporaneous with *Presbyornis*. Opportunity for transfer of Mallophaga from outside sources would presumably have been reduced due to the lack of other species of birds adapted to such a harsh environment. On the other hand,

one may readily imagine that the often ephemeral nature of suitable breeding sites might at times have caused colonies of flamingos and *Presbyornis* to be situated adjacent to one another, or they may even have bred in mixed colonies. Densely packed, mixed flocks of flightless downy young could have resulted from such a juxtaposition, and would have provided ample opportunity for transfer of ectoparasites. Thus, the similarity of anseriform and phoenicopterid Mallophaga is not necessarily due to a close relationship of the hosts, but to the fact that the ancestors of these two groups shared similar specialized habits and habitat and were in intimate contact with each other as a consequence.

Specimens of Mallophaga from *Cladorhynchus* were kindly forwarded to us by Shane Parker of the South Australian Museum. They were identified as belonging to the genera *Actornithophilus*, *Austromenopon*, and *Quadriceps*, which are characteristic of the Charadriiformes (K. C. Emerson, pers. comm.). Thus, the Mallophaga of flamingos must have been acquired subsequent to their divergence from the Recurvirostridae.

A charadriiform origin of flamingos provides a concordant explanation for the parasites they harbor, whereas parasitology provides no evidence in favor of a relationship between flamingos and the Ciconiiformes.

Biochemistry

Biochemical information from several sources has been used in attempts to determine the relationships of flamingos. Mainardi (1962) investigated red-cell antigens; Sibley (1960) used paper electrophoresis to compare egg-white proteins; and Sibley et al. (1969) studied starch-gel electrophoresis of egg-white proteins and hemoglobins, tryptic peptides of hemoglobins, and thin-layer electrophoresis of tryptic peptides of ovalbumin. Sibley and Ahlquist (1972) reviewed the egg-white protein evidence for non-passerine birds, including flamingos. These investigations antedated the use of the isoelectric focussing technique (see Sibley and Frelin, 1972), which results in more detailed patterns somewhat more suscepti-

ble to evaluation by the uninitiated. Brush (1979) has recently shown that there were serious procedural difficulties inherent in Sibley's electrophoretic methodology that render dubious the results obtained.

Regardless, these biochemical investigations are unfortunately uninformative for interpreting the relationships of flamingos because all comparisons were conducted with the traditional idea in mind that flamingos must be related either to storks or to ducks. Sibley et al. (1969) concluded that the biochemical evidence showed flamingos to have more in common with Ciconiiformes than Anseriformes, but in the absence of any meaningful comparisons with Charadriiformes, particularly the Recurvirostridae, such a conclusion has little significance. As long as biochemistry is used in avian systematics merely to legitimize preconceptions based on the incomplete anatomical studies of the nineteenth century, its usefulness as a taxonomic tool is bound to remain severely limited.

Osteology

Feduccia (1976) discussed and illustrated osteological features of flamingos that indicate relationships to the Charadriiformes rather than Ciconiiformes. These observations are augmented below. Because even with the removal of the Phoenicopteridae from the Ciconiiformes, the order is still probably hopelessly unnatural (Olson, 1979), and because storks in particular have most often been mentioned as relatives of flamingos, we have confined our comparisons to the Ciconiidae. Terminology generally follows Howard (1929).

SKULL

Despite the great modification of the skull in flamingos, the architecture of the palate is decidedly not like that of a stork (Figure 14). The palatines of flamingos are longer and narrower and the pterygoids shorter and more expanded anteriorly than those of storks, thus resembling shorebirds. The choanal aperture extends posteriorly to the palatine-ptyergoid articulation in flamingos and shorebirds, whereas it ends consid-

erably anterior to this in storks. The posterior margin of the palatine curves gently into the articulation with the pterygoid in flamingos and shorebirds, whereas in storks it is sharply truncate and the palatines become much narrower before articulating with the pterygoid (Figure 14). The fact that the palatines in flamingos have fused along the midline ("desmognathy"), as in storks, seems of relatively minor importance compared with the otherwise great differences in the palates of these birds.

In his studies of the middle ear region of the skull, Saiff (1978) found that the Phoenicopteridae differed significantly from other families of "Ciconiiformes," though he made no comparisons with the Charadrii.

A character in the skull of flamingos that is probably of greater taxonomic significance than previously thought is the presence of distinct paired occipital fontanelles above the foramen magnum. These are characteristic of most Charadrii and certain Alcidae; they are present in most Anseriformes, which were in turn derived from the Charadriiformes (Olson and Feduccia, in press). In the Gruiformes, occipital fontanelles occur solely in the closely related Aramidae and Gruidae, which may be among the more derived members of the order. Elsewhere, these apertures are found only in the ibises, Threskiornithidae, which are probably a transitional group between

Gruiformes and Charadriiformes (Olson, 1979). The presence of occipital fontanelles in flamingos is best interpreted as a derived character shared with the Charadrii.

POSTCRANIAL SKELETON

In the following characters of the postcranial skeleton, flamingos agree with Recurvirostridae and differ from the Ciconiidae.

CORACOID.—(1) Shaft much shorter and stouter; (2) procoracoid larger, projecting farther medially, perforate (except in *Cladorhynchus*); (3) acrocoracoid narrower and much more elevated above the glenoid facet; (4) furcular facet a distinct, flat, rectangular surface; (5) sternal margin curved, not straight; (6) sternal facet much longer, not confined to medial half of sternal end; (7) sterno-coracoidal process deeper and more truncate. In most shorebirds, the brachial tuberosity and furcular facet are more extensive than in flamingos (Figure 15); this area has been noted by Strauch (1978:309, fig. 21) to be variable in the Charadriiformes. Its reduction in flamingos may well be correlated with the changes in the proximal end of the humerus and the associated modification of the shoulder musculature.

SCAPULA.—(1) Acromion long and pointed, not square and blunt; (2) shaft narrower proximally.

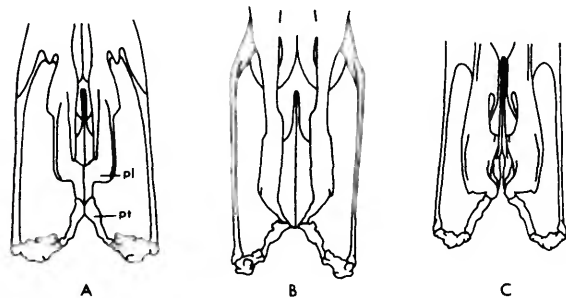


FIGURE 14.—Semidiagrammatic ventral view of palate: a, stork, *Ciconia episcopus*; b, flamingo, *Phoenicopterus ruber*; c, recurvirostrid, *Cladorhynchus leucocephalus*. The flamingo, as would be expected from the unique feeding apparatus, differs from either of the others, but is less similar to the stork. Note particularly the distinctive constriction of the palatines (pl) before they contact the pterygoids (pt) in the stork.

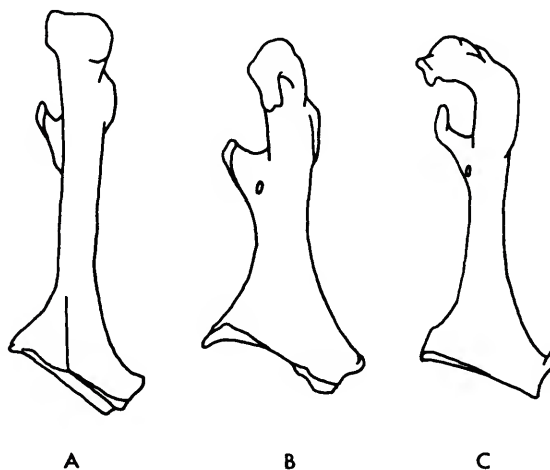


FIGURE 15.—Ventral view of left coracoid: a, stork, *Ciconia abdimii*; b, flamingo, *Phoenicopterus ruber*; c, recurvirostrid, *Recurvirostra americana*.

FURCULA.—(1) Narrow, U-shaped, with clavicles parallel, not diverging dorsally; (2) scapular tuberosity longer, narrower, and more pointed; (3) hypocleidium very small, not approaching carina (in storks the hypocleidium is very large and articulates by a large facet at the anterior end of the sternal carina; see Figure 16c).

STERNUM.—(1) Longer and narrower; (2) carina does not project anteriorly beyond the manubrium; (3) manubrium a deep blade, not a simple peg-like process (Figure 16; see also Feduccia, 1976, fig. 6).

HUMERUS.—(1) Bicipital crest long, tapering gently into shaft, not jutting out abruptly; (2) scar for attachment of *M. pectoralis* not lying mainly distal to deltoid crest; (3) entepicondylar prominence poorly developed; (4) olecranal fossa narrow and distinct; (5) scar for *M. latissimus dorsi posterioris* lying ventral to midline of shaft, not dorsal as in storks; (6) distal end relatively

narrower.

CARPOMETACARPUS.—(1) Metacarpal I more proximally directed, less vertical; (2) ventromedial rim of carpal trochlea less prominent; (3) proximal metacarpal symphysis much shorter; (4) metacarpal III straight, not bowed ventrally; (5) distal metacarpal symphysis relatively longer.

PELVIS.—(1) Anterior iliac shield not markedly expanded anteriorly; (2) postacetabular ilium not fused to synsacrum; (3) obturator foramen relatively smaller.

FEMUR.—(1) Proportionately shorter and stouter; (2) anterior and proximal extent of trochanter greater; (3) configuration of muscle scars on proximo-lateral surface similar in flamingos and recurvirostrids and quite distinct from that of storks; (4) anterior rim of internal condyle extends farther anteriorly and proximally; (5) internal condyle in medial view more pointed; (6) rotular groove deeper. It should be noted that the femur in *Cladorhynchus* is stouter and more flamingo-like than in *Recurvirostra* or *Himantopus*.

TIBIOTARSUS.—(1) Inner cnemial crest much more extensive anteriorly, appearing squared in medial view (see Feduccia, 1976, fig. 2); (2) inner cnemial crest extends proximally far above level of outer cnemial crest, whereas in storks the crests are at about the same level (Figure 17); (3) notch

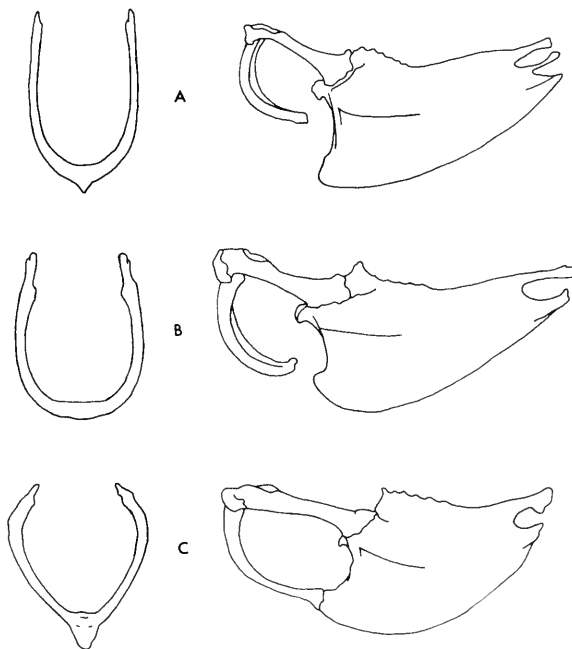


FIGURE 16.—Outline of furcula in anterior view (left column) and left lateral view of sternum, coracoid, and furcula (right column): a, recurvirostrid, *Cladorhynchus leucocephalus*; b, flamingo, *Phoenicopterus ruber*; c, stork, *Ciconia episcopus*. Note the large hypocleidium of the furcula in the stork and its solid articulation with the apex of the carina.

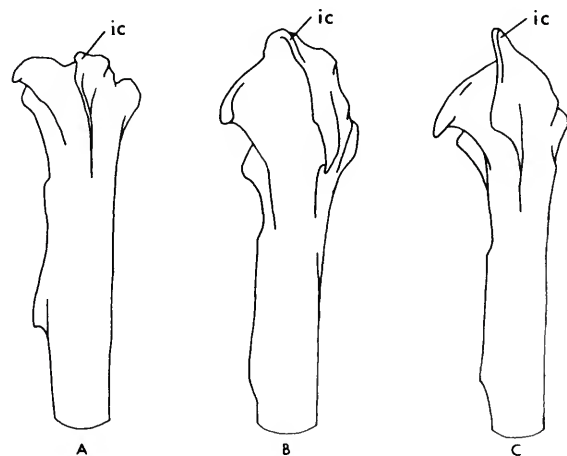


FIGURE 17.—Proximal end of right tibiotarsus in anterior view: a, stork, *Ciconia abdimii*; b, flamingo, *Phoeniconaias minor*; c, recurvirostrid, *Cladorhynchus leucocephalus*. Note the much reduced inner cnemial crest (*ic*) in the stork.

present in distal rim of internal condyle; (4) anterior intercondylar fossa expanded proximally, not almost round as in storks (Figure 18); (5) distal end more expanded, particularly medially, with the internal ligamental prominence larger; (6) internal condyle in medial view longer and narrower (particularly true of *Cladorhynchus*, which is most similar to the extinct genus *Palaeolodus* in this respect); (7) posterior articular surface does not extend as far proximally.

TARSOMETATARSUS.—(1) Intercotylar knob much broader and more rounded, not notched laterally (Figure 24); (2) shaft much more laterally compressed; (3) distal foramen smaller; (4) inner trochlea much higher and more posteriorly rotated (Figure 24; also Feduccia 1976, figs. 3 and 4); (5) scar for hallux reduced or absent.

PHALANGES.—(1) All phalanges, including unguals, much shorter, wider, and deeper, whereas in storks the phalanges, including the well-developed hallux, are long and slender.

The vertebral count and the structure of the cervical vertebrae of flamingos differ from both shorebirds and storks, but these modifications are almost certainly correlated with the feeding adaptations. The first three or four anterior thoracic vertebrae are fused into a notorium in modern flamingos, a condition absent in shorebirds and storks but which evidently has evolved in flamingos since the early Eocene (page 57). The first thoracic vertebra in flamingos bears a large hemapophysis, which is true of the *Recurvirostridae* but not storks, in which this process is absent.

There is a superficial resemblance between flamingos and storks in the distal end of the tibiotarsus, in both of which there is a deep, distinct anterior intercondylar fossa and a tubercle on the tendinal bridge. The shape of this fossa, however, is nearly round in storks, whereas it is expanded proximally in flamingos, particularly on the lateral side, where it incises the external condyle (Figure 18). Furthermore, the tubercle on the tendinal bridge of flamingos is nearly continuous with another tubercle directly proximal to it,

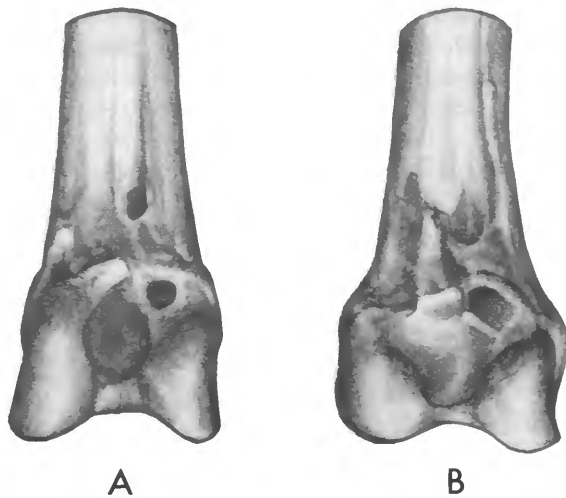


FIGURE 18.—Distal end of right tibiotarsus: a, stork, *Ciconia abdimii*; b, flamingo, *Phoeniconaias minor*. Although in both families there is a deep intercondylar fossa, its shape, as well as that of the rest of the element and the placement of the tubercles is entirely different.

whereas in storks the second tubercle is separate and lies entirely lateral to the first.

The sterna of flamingos and storks have but two posterior notches. Most *Charadrii* typically have a four-notched sternum but only two notches occur in the *Jacaniidae*, *Rostratulidae*, *Thinocoridae*, and some individuals of *Burhinidae*. It is likely that the loss of the medial notches in flamingos is a secondary development.

The proportions of the hindlimb elements of flamingos are quite different from those of storks and are more similar to those in the *Recurvirostridae*. As an example, the absolute length of the femur in *Phoenicopterus ruber* is less than that in *Ciconia nigra*, whereas the tarsometatarsus of the flamingo is much longer than that of the stork.

Because of the number of unique non-skeletal features shared by flamingos and *Cladorhynchus*, it should be noted that the osteology of *Cladorhynchus* does not differ appreciably from that of the other members of the *Recurvirostridae* (Strauch, 1978; this study) and it lacks the skeletal peculiarities diagnostic of the *Phoenicopteridae*.

Significant osteological differences between flamingos and shorebirds are seen, of course, in the modification of the feeding apparatus and cervical vertebrae. These specializations are unique to flamingos and hence cannot show relationships, but as discussed later, they are more easily derived from the charadriiform condition than that in Ciconiiformes, particularly storks.

Apart from the feeding specializations, the greatest differences between flamingos and typical Charadrii are seen in the humerus and the shoulder joint. Many of these differences are probably due to the pneumatization of the proximal end of the humerus. This is almost certainly a size-related phenomenon, because in almost all birds the size of extant flamingos the humerus is pneumatized. Comparison of the fossil frigatebird *Limnofregata* (Pelcaniformes: Fregatidae) with Recent species in the same family, shows the great extent to which the humerus may be modified with increasing pneumatization (Olson, 1977:23). Adaptations paralleling those of flamingos, such as the reduction of the ectepicondylar spur of the humerus and the brachial tuberosity of the coracoid, are also found in the charadriiform species *Scolopax minor*, whereas they are absent in other members of the genus (Olson, 1976). The humerus is not pneumatic in *S. minor*, however, and the modifications of the wing probably evolved in connection with sound production during mating displays. Nevertheless, this shows that adaptations similar to some of those in the wing and shoulder of flamingos have evolved within a single genus of Charadriiformes.

With the exceptions noted above, the osteology of the Phoenicopteridae conforms very well with that of the Charadrii. On the other hand, nothing in their skeletal structure can be used to support a relationship with the Ciconiiformes.

Paleontology

The fossil record of flamingos has been inventoried by Brodkorb (1963a) and briefly discussed by Sibley et al. (1969). We shall review the importance (or lack thereof) of the various fossils

attributed to flamingos, adding a description of a significant new genus from the middle Eocene of Wyoming.

A few fragments of Cretaceous bones have been said, on very insufficient grounds, to belong to birds related to flamingos. The earliest of these, and one of the earliest birds known, is *Gallornis straeleni*, described by Lambrecht (1931) as a new genus of Anatidae from the Lower Cretaceous (Neocomian) of France. This was based on "the proximal portion of a femur and a scrap of humerus, the latter of no comparative value" (Brodkorb, 1963b:63). Using only Lambrecht's illustrations for comparison, Brodkorb (1963b) decided that *Gallornis* was definitely not anseriform and he referred it to the neighborhood of flamingos, placing it in the extinct family Scaniornithidae. We regard it as impossible to determine the affinities of Mesozoic birds with such undiagnostic fragments; in fact, it is difficult enough and usually impossible to determine the nature even of early Tertiary birds from such material (see Olson, 1977:31).

The same applies, though even more emphatically, to a single vertebra from the late Cretaceous (Campanian) of Sweden that Lambrecht (1933:335) optimistically described as a flamingo under the name *Parascaniornis stensioi*.

The avifauna of the late Cretaceous (Maestrichtian) Lance Formation, analyzed by Brodkorb (1963b), contains what was described as a new genus and species of flamingo, *Torotix clemensi*, based on the distal end of a humerus (not a "head" as stated by Sibley et al., 1969:158). Brodkorb placed this in a new family Torotigidae, to which he arbitrarily assigned *Gallornis* and *Parascaniornis*.

Brodkorb (1963b) identified two other families of birds from the Lance Formation: the Cimolopterygidae, an extinct family of Charadriiformes known only from coracoids, and the Lonchodytidae, a family consisting of two species supposed to belong to the Gaviiformes, and known from a fairly diagnostic distal end of a tarsometatarsus, as well as a fragment of carpometacarpus that we regard as indeterminate.

After preliminary examination of much of this material, we consider it quite possible that all of the birds so far known from the Lance Formation may be referable to the Charadriiformes. As evidenced by the following, the holotype tarsometatarsus of *Lonchodytes estesi* is more similar to the Charadrii than to the Gaviidae: (1) lesser lateral compression of the shaft; (2) greater elevation of the outer trochlea relative to the middle trochlea; (3) lesser retraction of the inner trochlea. Professor Brodkorb (pers. comm.) now concurs with us at least that *L. estesi* is not gaviiform; we consider it to be closest to the Charadriiformes.

The holotype of *Torotix clemensi* lacks the large ectepicondylar spur typical of most Charadriiformes and thus resembles both the Phoenicopteridae and the Presbyornithidae, a charadriiform family near the ancestry of ducks. This humerus could well belong to one of the species of *Cimolopteryx*, known only from coracoids, while the type of *Lonchodytes estesi* may be referable to one of the larger species of Cimolopterygidae. Without better material it probably is not possible to determine whether the Lance avifauna contains flamingo-like or presbyornithid-like Charadriiformes, or neither.

Scanionis lundgreni Dames (1890), from the lower Paleocene of Sweden, is based on a humerus, scapula, and coracoid. Dames' rather indifferent illustration shows these to be poorly preserved, mostly as impressions in a slab. Although nothing in his illustration rules out the possibility that the species was a flamingo, neither is there anything diagnostic to be seen. Until the specimen is reprepared and restudied, its affinities must be regarded as uncertain. The family Scanionithidae proposed by Lambrecht (1933) is unjustified and undiagnosable on the basis of available information.

The genus *Telmabates* from the lower Eocene of Patagonia, was regarded by Howard (1955) as forming a new family, Telmabatidae, having some affinities with flamingos. Feduccia and McGrew (1974) showed that *Telmabates* and Telmabatidae are junior synonyms of *Presbyornis* and Presbyornithidae, respectively, known from con-

temporaneous deposits in the western United States. Most, if not all, of the flamingo-like characters of these birds are actually charadriiform in nature. We treat these charadriiform-anseriform mosaics in another paper dealing with the origin of the Anseriformes (Olson and Feduccia, in press).

The genus *Agnopterus* was founded by Milne-Edwards (1868) for his species *A. laurillardii*, based on the distal portion of a tibiotarsus lacking most of the diagnostic features. His illustration does not serve to confirm or deny his placement of the genus with the flamingos. Lambrecht's (1933) elevation of it to family rank cannot be justified on the basis of such a specimen.

Agnopterus turgaiensis Tugarinov (1940), from the upper Oligocene of Kazakhstan, is based on a well preserved distal end of a tibiotarsus that seems, on the basis of the original illustrations, to be correctly called a flamingo. That it properly belongs to the same genus as *A. laurillardii* may be questioned, particularly as it is geologically much younger and also nearly contemporaneous with *Palaelodus* and the earliest known form of *Phoenicopterus*, with both of which it needs comparison.

Lydekker (1891) described a coracoid from the upper Eocene of England, referring it with a query to Milne-Edwards' genus *Agnopterus* as *A. hantoniensis*. Harrison and Walker (1976b) referred a humerus to this species, and made it the type of a new genus, *Headonornis*, of Telmabatidae, either overlooking or ignoring the fact that Feduccia and McGrew (1974) had synonymized this family with the Presbyornithidae. Harrison and Walker's diagnosis of *Headonornis* does not diagnose the genus, nor do they explain why the taxon was referred to the Telmabatidae or how it differs from *Telmabates* (= *Presbyornis*). Their illustration of the humerus shows it to be quite different from that of flamingos, but the same may not be true of the type coracoid. Until a proper comparative study is made, the significance of these specimens to the evolution of either flamingos or the Presbyornithidae cannot be determined.

The nomenclatural and taxonomic status of *Elornis littoralis* and *E. grandis*, from the lower

Oligocene of France, was reviewed by Olson (1978). The specimens on which these names were based have been lost and the taxa are now known only from Milne-Edwards' (1867–1871) illustrations and descriptions. These do not preclude phoenicopterid affinities for these taxa, but beyond this little else can be said. *Elornis anglicus* Lydekker, from the upper Eocene of England, was synonymized by Harrison and Walker (1976b) with *Actiornis anglicus* Lydekker, formerly of the Phalacrocoracidae, which they then transferred to the Threskiornithidae. Any supposed phoenicopterid affinities of this taxon are thus doubtful.

Tiliornis senex Ameghino (1899), based on an unillustrated coracoid from the Lower Oligocene of Argentina and assigned to the Phoenicopteridae, is a meaningless name until the type is located and restudied.

Hitherto, the earliest unequivocal flamingos based on sufficient material to have some evolutionary significance have come mainly from late Oligocene or early Miocene (Aquitanian) deposits in France. These consist of an extinct species in a modern genus, *Phoenicopterus croizeti*, and several species in the extinct genus *Palaelodus*. Six species of the latter have been named, mostly distinguished on size. Although known from abundant material, no modern comparative study has ever been made of *Palaelodus* and a revision would no doubt result in the recognition of fewer species. One species, *Palaelodus steinheimensis* Fraas (1840), from the late Miocene of Germany, is misidentified to family, being based on what appears to be the distal end of a tibiotarsus of a large anseriform (Olson, pers. obs.). Species larger than any of those of *Palaelodus* have been named in the genus *Megapalaelodus*, from the early Miocene and early Pliocene of North America (A. H. Miller, 1944; Brodkorb, 1961; Howard, 1971). We have examined additional specimens of *Megapalaelodus* from the middle Miocene (Clarendonian) of Texas (AMNH 9109) and the Aquitanian of France (USNM 18497). This genus is very similar to, and may not be separable from, *Palaelodus*.

Palaelodus and *Megapalaelodus* are usually sepa-

rated from the Phoenicopteridae as a distinct family, Palaelodidae. Most skeletal elements of *Palaelodus* agree well with the Phoenicopteridae. The cervical vertebrae are greatly elongated as in modern flamingos, and the humerus is decidedly flamingo-like as well. The specimen of bill previously assigned to *Palaelodus* by Milne-Edwards (1867–71, vol. 2), was referred by Cracraft (1973: 87–88) to the gruiform species *Probalaerica problematica*, the type of which is also a bill. In our opinion, the true identity of these Aquitanian rostra, as well as the skull that forms the type of the supposed ibis *Ibidopodia palustris* Milne-Edwards, remains problematical. The latter needs comparison with the cranium illustrated by Rothausen (1966) that was found in association with postcranial elements of *Palaelodus*. In any case, the morphology of the bill of *Palaelodus* is not certainly known.

The most obvious difference between *Palaelodus* and modern flamingos is the shorter tibiotarsus and the shorter and more laterally compressed tarsometatarsus of the former. These modifications suggest that the species of *Palaelodus* may have occupied more of a duck-like swimming niche than do typical flamingos. The differences in the proportions of the hindlimb between typical flamingos and *Palaelodus* are hardly greater than seen between the genera of recent Recurvirostridae (Figure 19). Although the osteology and systematics of *Palaelodus* and *Megapalaelodus* require further study, we believe that they are clearly flamingos and should be included in the Phoenicopteridae.

Contemporaneous with *Palaelodus* in the Aquitanian of France is a typical flamingo, *Phoenicopterus croizeti* Gervais, known from a number of specimens, including cranial material. Harrison and Walker (1976a) have recently proposed a new genus, *Gervaisia*, with *P. croizeti* (which they consistently misspell "croiseti") as the type. They based their diagnosis solely on fragments of bill that they happened to have on hand, evidently without consulting any of the more diagnostic material that is available in various other museums. As happens too frequently with Harrison

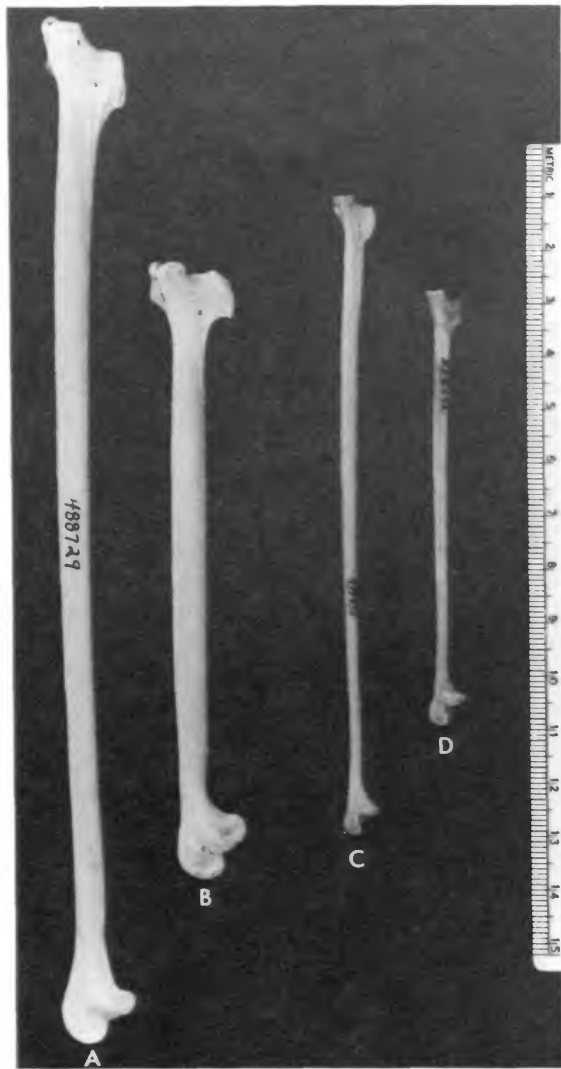


FIGURE 19.—Right tarsometatarsi in medial view: *a*, *Phoeniconaias minor*, Phoenicopteridae; *b*, *Palaelodus* sp., Phoenicopteridae; *c*, *Himantopus mexicanus*, Recurvirostridae; *d*, *Cladorhynchus leucocephalus*, Recurvirostridae. Note that the difference in proportions between the two genera of flamingos is about the same as that between the two recurvirostrids. (Scale in cm.)

and Walker, their name was preoccupied, in this case thrice over. Kashin (1978) noted that *Gervaisia* Bonaparte, 1854 (Aves), *Gervaisia* Waga, 1858 (Myriapoda), and *Gervaisia* Robineau-Des-

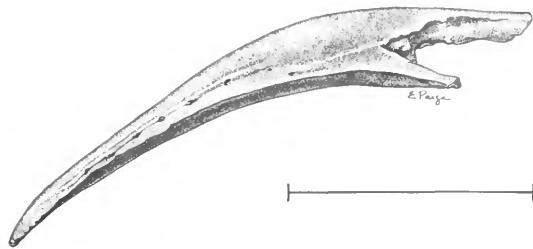
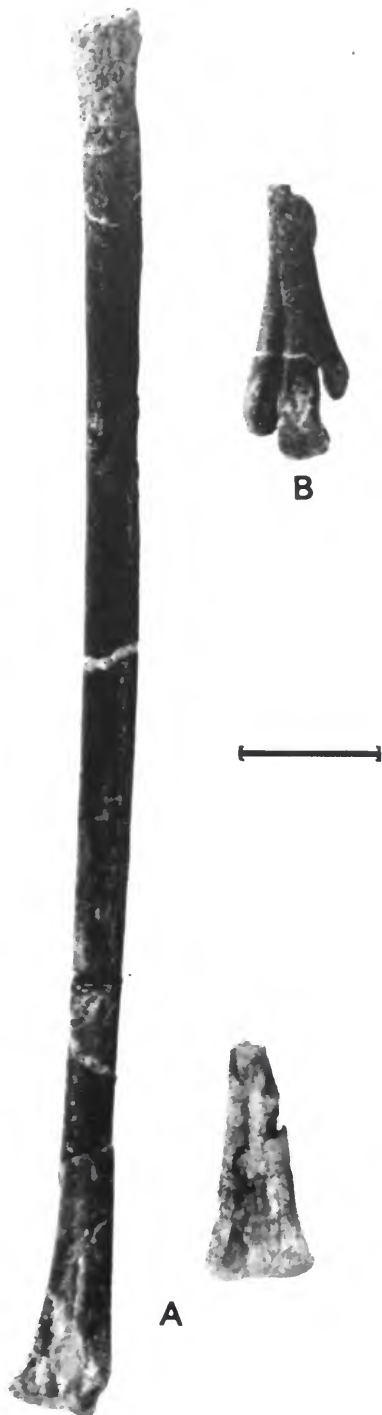


FIGURE 20.—Rostrum of the Miocene flamingo *Phoenicopterus croizeti*, drawn from a cast of a specimen in the Naturhistorisches Museum, Basel. The curvature is less than in adults of modern species of *Phoenicopterus* but is similar to that seen in their earlier developmental stages (see Figure 38c). (Scale = 3.5 cm.)

voidy, 1863 (Insecta), all antedate *Gervaisia* Harrison and Walker, 1976a, and he therefore proposed the name *Harrisonavis* as a substitute. The distinguishing feature of the supposed new genus was said by Harrison and Walker to be the less bent bill with a broader tip. Figure 20 illustrates a nearly complete rostrum of *P. croizeti* and shows the less bent nature of the bill, the shallower keel, and the broader tip, all of which occur in the developmental stages of modern *Phoenicopterus* (see Figure 38c). Thus *P. croizeti* does not possess characters of generic significance as compared to extant taxa, the morphology of the bill being precisely what would be expected in an earlier, somewhat more primitive form of *Phoenicopterus*. We regard *Gervaisia* Harrison and Walker, 1976a, and *Harrisonavis* Kashin, 1978, as junior synonyms of *Phoenicopterus* Linnaeus, 1758.

From Australia, A. H. Miller (1963) described two flamingos of roughly the same age as *Palaelodus* and *Phoenicopterus croizeti*. One of these was referred to a modern genus as *Phoenicopterus novae-hollandiae*, and the other was described in a new genus as *Phoeniconotius eyrensis*. The latter was based on the distal end of a tarsometatarsus and two phalanges and was characterized as being more massive and less specialized for swimming than modern flamingos. All fossil flamingos subsequent to the early Miocene (except a few specimens of *Megapalaelodus*) have been referred to modern genera.



The fossil record of flamingos hitherto known can be summarized as follows. None of the Mesozoic and early Tertiary fossils said to represent flamingos have been identified with certainty and for the present they may be discounted. In the late Oligocene or early Miocene of Europe occurs a species in the modern genus *Phoenicopterus* having a somewhat more primitive bill structure than recent forms. Contemporaneously, there was a radiation of shorter-legged flamingos (*Palaelodus* and *Megapalaelodus*), apparently more specialized for swimming. At least one species of these persisted until the early Pliocene. None of these fossils gives any better clue to the ancestry of flamingos than do the modern forms themselves.

To the foregoing may now be added a new genus and species of middle Eocene flamingo. This is the earliest certain member of the Phoenicopteridae and is based on a meaningful representation of the skeleton. It is particularly significant in showing an even closer approach to the Charadriiformes than do recent flamingos.

A New Stilt-like Flamingo from the Middle Eocene of Wyoming

Among the many fossil birds that had been submitted to the late Alexander Wetmore for study and which had remained unidentified, was a small series of bones from a single locality in the middle Eocene Bridger Formation of Wyoming. These were collected in 1946 and 1947 by C. Lewis Gazin, Franklin L. Pearce, and G. F. Sternberg. According to Pearce's recollection, the fossil birds at this locality all came from the same level and from a relatively small area, although no specimens were found in association.

Other than a single, undiagnostic distal end of a femur of a yet unidentified larger bird (USNM 244323), apparently found somewhat apart from the other specimens, all of the avian fossils from

FIGURE 21.—Bones of very young individuals referred to *Juncitarsus gracillimus*: a, two portions of tibia tarsi; b, distal end of tarsometatarsus. These probably indicate the presence of a breeding colony. (Scale = 1 cm.)

this site appear to be from a single species. At least three adults or sub-adults are represented, along with several bones, possibly from a single juvenile individual (Figure 21) that was almost certainly too young to fly at the time of death, thus suggesting the possibility of a breeding aggregation. The individuals vary in size (Figure 22), perhaps indicating that the species was sexually dimorphic.

This species was intermediate in size between the larger extant Charadrii and the smallest extant flamingos. Its osteology shows a mosaic of characters of both groups, but its presumably derived features are those of flamingos, thereby providing the earliest definite record of the Phoenicopteridae. In the following descriptions we have included some comparisons with *Presbyornis* (Presbyornithidae) in order to facilitate identification of specimens in the event that additional material comes to light.

Order CHARADRIIFORMES Huxley, 1867

Suborder CHARADRII Huxley, 1867

Family PHOENICOPTERIDAE Bonaparte, 1831

Juncitarsus, new genus

TYPE-SPECIES.—*Juncitarsus gracillimus*, new species.

DIAGNOSIS.—Referable to the Phoenicopteridae by having the humerus with a single pneumatic foramen, a distinct oval scar for *M. scapulo-humeralis cranialis*, and the ectepicondylar spur lacking; cervical vertebrae modified similarly to modern Phoenicopteridae; intercotylar knob of tarsometatarsus high and broad. Tarsometatarsus extremely long and slender, most similar to *Himantopus* (Recurvirostridae); proximal end of hypotarsus level with cotylae; hypotarsus complex, with closed canals; scar for hallux present; distal foramen large and elongate; inner trochlea markedly retracted posteriorly, with distinct wing; posteroproximal border of middle trochlea truncate. Attachment for anterior articular ligament of



FIGURE 22.—Anterior view of proximal ends of three tarsometatarsi of *Juncitarsus gracillimus* showing variation in size. (Natural size.)

humerus sloping steeply. Thoracic vertebrae not fused into a notorium.

ETYMOLOGY.—Latin *juncus* (a reed or rush) plus *tarsus*, latinized from Greek *tarsos* (ankle), in reference to the extremely slender tarsometatarsus; the generic name is masculine.

Juncitarsus gracillimus, new species

FIGURES 23, 24b, 25–27a, 28–31

HOLOTYPE.—Left tarsometatarsus lacking only a portion of the anterior part of the proximal end; hypotarsus slightly abraded. Vertebrate paleontological collections of the National Museum of Natural History, USNM 244318 (Figures 23, 25, 26b,c); collected in 1947 by C. Lewis Gazin (original number 140-47).

TYPE-LOCALITY.—Wyoming, Sweetwater County, “low buttes to extreme NE of Twin Buttes and within Bridger” (C. L. Gazin, 1946 field catalog), in “yellow layer near base of buttes, beneath a hard grayish green sandstone” (C. L.



FIGURE 23.—Holotype, left tarsometatarsus of *Juncitarsus gracillimus* (USNM 244318): a, anterior view; b, posterior view; c, lateral view; d, medial view. (Natural size.)

Gazin, 1947 field catalog). Although Gazin (pers. comm.) indicated that these buttes were those indicated in the SE corner of section 33, T15N, R109W (Buckboard Quadrangle, U.S. Geological Survey 15 minute series topographic map, 1966), successive searches of this locality in 1976, 1977, and 1978 by Arnold D. Lewis, R. J. Emry, and Olson, disclosed no vertebrate fossils other than a few turtles. We later found that Gazin's 1946 field catalog refers to the locality as "near 1/4 section 22/27 corner," which would place it slightly farther to the north (McKinnon Junction Quadrangle); outcrops fitting the above descriptions were located here in 1979 by Olson and Lewis, but no additional bird remains were found.

HORIZON.—Middle Eocene, Bridger Formation. The site is very low in the Bridger, hence the specimens are earliest middle Eocene in age.

ETYMOLOGY.—Latin *gracillimus* (very slender).

PARATYPES.—Proximal two-fifths of right tarsometatarsus lacking hypotarsus and not completely ossified, USNM 244319 (Figure 26a); proximal two-thirds of right tarsometatarsus with associated fragments of inner and outer trochleae, USNM 244322; distal end of right tarsometatarsus of a very young individual, USNM 244327; left tibiotarsus of very young individual lacking tarsals and with proximal end unossified, USNM 244334; distal end of right tibiotarsus of juvenile lacking tarsals, USNM 244337; abraded distal end of right femur, USNM 244320; pedal phalanx 1 of right digit II, USNM 244329; distal two-thirds of pedal phalanx, USNM 244335; worn proximal half of left humerus, USNM 244325 (Figure 27a); distal end of left humerus, USNM 244330 (Figure 28b); proximal fourth of left ulna, USNM 244326 (Figure 28d); portion of a shaft of an ulna, USNM 244324; left radiale, USNM 244333 (Figure 28c); anterior two-thirds of left scapula of a juvenile, USNM 244328 (Figure 28a); unfused frontal bone of a juvenile, USNM 244336 (Figure 31); anterior half of cervical vertebra similar to the 6th cervical of *Phoenicopterus*, USNM 244338 (Figure 30a,b); cervical vertebra similar to the 16th of *Phoenicopterus*, USNM 244321 (Figure 29); thoracic vertebrae

possibly equivalent to the 17th and 18th vertebrae of *Recurvirostra*, USNM 244332 and 244331 (Figure 30c). All from the same locality and horizon as the holotype; C. L. Gazin field numbers 40–46, 139–47, 141–47, and 142–47.

MEASUREMENTS (in mm).—*Holotype*: Total length 182, depth through hypotarsus about 12, greatest proximal width about 10.5, least width of shaft 3.8, least depth of shaft 4.0, width of shaft at midpoint 3.9, depth of shaft at midpoint 5.1, greatest width through trochleae 10.6, greatest depth through trochleae 11.9, width of middle trochlea 3.9, depth of middle trochlea 6.0, depth through inner trochlea 6.3, depth through outer trochlea 6.7.

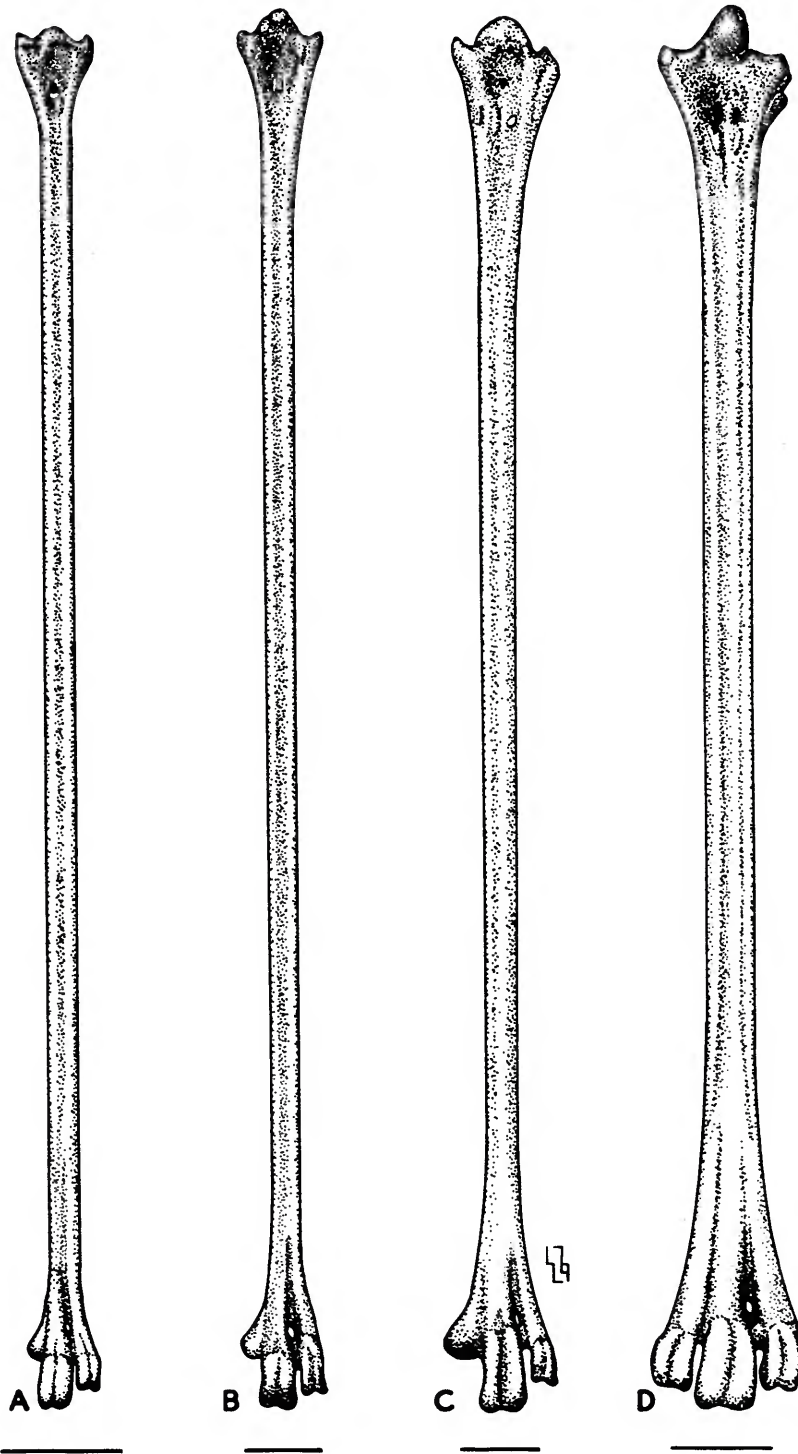
Paratypes: Tarsometatarsus USNM 244322, proximal width 9.6; ulna USNM 244326, proximal depth 9.7, proximal width 6.7, distance from tip of olecranon to distal extent of attachment of anterior articular ligament 8.3; humerus USNM 244325, distance from head to distal end of pectoralis attachment 24.5, length of scar for M. scapulohumeralis cranialis 4.0; humerus USNM 244330, distal width 13.2, depth through external condyle 7.4, diagonal length of external condyle 6.1 (humerus length estimated at 100); radiale USNM 244333, greatest diameter 7.6; pedal phalanx 1 digit II USNM 244329, length 19.1; thoracic vertebra USNM 244331, length of centrum 10.3; cervical vertebra USNM 244321, length through centrum 14.4.

DIAGNOSIS.—As for the genus. Smaller than any other known species of Phoenicopteridae; larger than any member of the Recurvirostridae.

DESCRIPTION.—*Tarsometatarsus*: The extraordinary tarsometatarsus of this species is somewhat smaller than that of the smallest living flamingo, *Phoeniconaias minor*, but is much more slender (Figure 24), its proportions being approached among recent birds only by the stilts (*Himantopus*; Recurvirostridae). This element, in fact, is so nearly identical in morphological details to that of *Himantopus*, that without the associated material it would probably have been referred to the Recurvirostridae, and within that family would have been regarded as a close relative of *Himantopus*. Only in the following details can the tarsometatarsus of *Juncitarsus* be distinguished from that of *Himantopus*: larger size; distal foramen larger and more elongate (Figure 25d,e); middle trochlea without the slight lateral deflection of *Himantopus* but identical to *Recurvirostra*; distinct, small scar for hallux (Figure 25e) (hallux lacking in *Himantopus*); wing of outer trochlea narrower and slightly more produced posteriorly (Figure 25f); attachment for M. tibialis cranialis more distinct and elongate (Figure 25a); intercotylar knob markedly higher and broader (Figure 26a). The last feature is the only salient character separating the tarsometatarsus of *Juncitarsus* from that of the Recurvirostridae and the only one that shows a closer approach to a condition in modern flamingos.

The tarsometatarsus of *Juncitarsus* can be distinguished from that of modern flamingos by the following features: outer trochlea narrower, with wing in lateral view more perpendicular to the shaft, not angling distally (Figure 25f); distal foramen larger and more elongate; proximal border of posterior face of middle trochlea truncate (Figure 25e), not tapering proximally to form a distinct V as in modern flamingos, but exactly duplicating the condition in *Recurvirostra*; inner trochlea rotated farther medially, giving the distal end of the bone a narrower aspect than in modern flamingos (Figure 24), and in medial view with a wing distinctly set off from the body of the trochlea (Figure 25c), as in recurvirostrids; hypotarsus more complex (Figures 25b, 26b), with closed canals matching *Himantopus*, not consisting of two high calcaneal ridges with no canals as in modern flamingos; hypotarsal block in proximal view (Figure 26b) more pedicilate and in lateral view (Figure 23c) at nearly the same level as the cotylae (also true of *Palaelodus*), not set well below the cotylae as in modern flamingos; base of hypotarsus extending distally as a ridge on shaft (Figure

FIGURE 24.—Anterior view of left tarsometatarsus: (a) stilt, *Himantopus mexicanus* (Recurvirostridae); (b) *Juncitarsus gracilimus* (Phoenicopteridae; reconstructed from two specimens); (c) flamingo, *Phoeniconaias minor* (Phoenicopteridae); (d) stork, *Ciconia abdimii* (Ciconiidae). (Scales = 1 cm.)



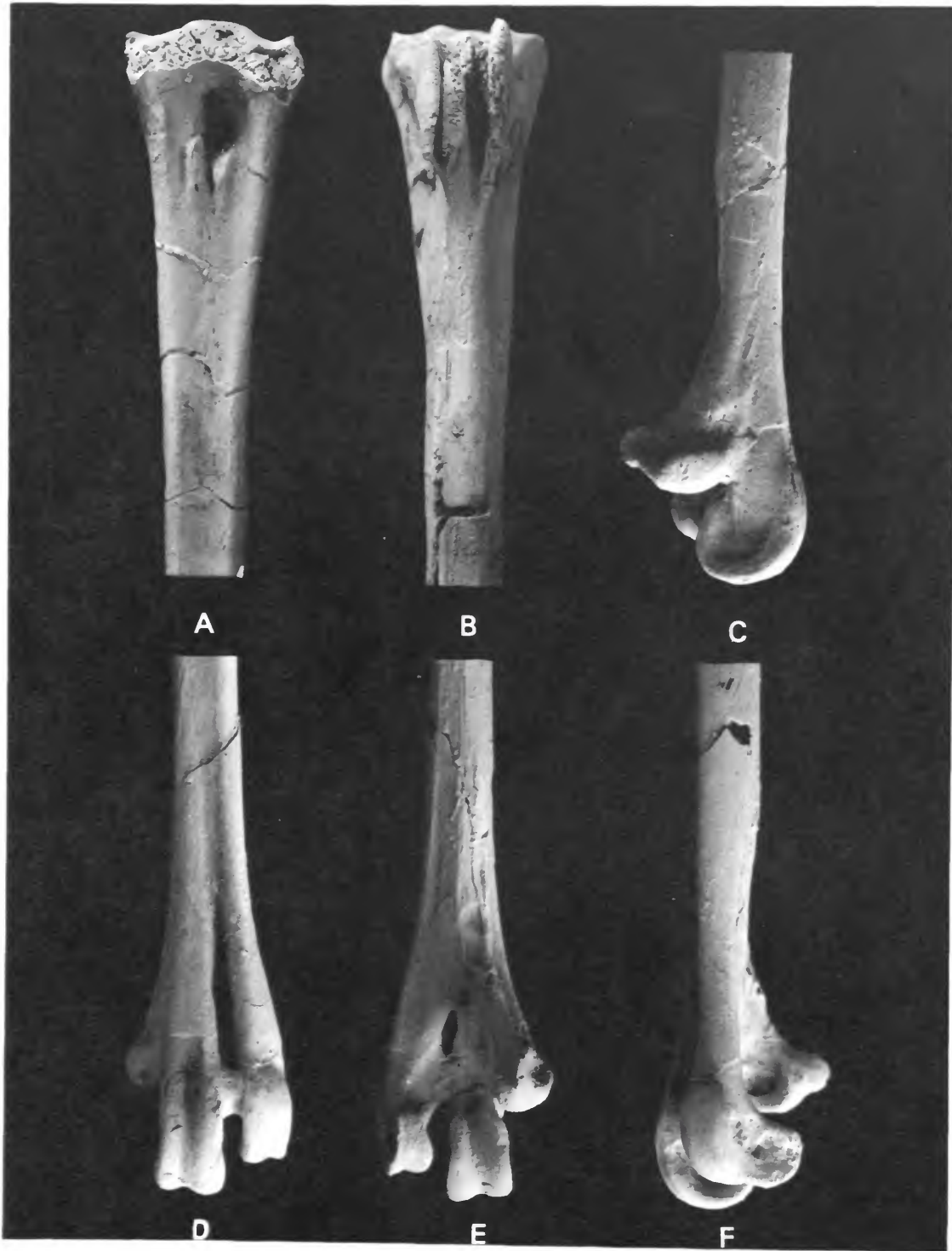


FIGURE 25.—Details of holotype tarsometatarsus of *Juncitarsus gracillimus* (USNM 244318): *a*, proximal end, anterior view; *b*, proximal end, posterior view; *c*, distal end, medial view; *d*, distal end, anterior view; *e*, distal end, posterior view; *f*, distal end, lateral view. (Specimen coated with ammonium chloride; $\times 3$.)

25*b*), much more pronounced than in modern flamingos but similar to *Himantopus*.

The tarsometatarsus of *Juncitarsus* is more slender and elongate than in either *Presbyornis* or *Palaelodus*. In *Palaelodus* (Figure 19*b*) the shaft is much deeper and more laterally compressed, the hypotarsus more complex, the proximal end proportionately wider, the intercotylar knob heavier,



FIGURE 26.—Tarsometatarsi of *Juncitarsus gracillimus*: *a*, proximal end in anterior view, paratype of subadult (USNM 244319) to show development of intercotylar knob; *b*, holotype (USNM 244318), proximal view; *c*, same, distal view. ($\times 3$.)

the inner trochlea much deeper and more rounded, and in posterior view more elongate. In *Presbyornis*, the hypotarsus is much wider basally, has no closed canals, the inner calcaneal ridge is reduced and the outer one produced distally as a hook; the distal end of the tarsometatarsus differs from that of *Juncitarsus* in that the inner trochlea is less retracted posteriorly and lacks a distinct wing; the middle trochlea is more elongate and not truncate on the posterior face, and the outer trochlea is deeper. The tarsometatarsus of *Juncitarsus* bears no resemblance to that of any member of the Ciconiiformes (e.g., Figure 24).

Humerus: The two portions of humerus of *Juncitarsus*, unlike the tarsometatarsus, bear no resemblance to the humerus in recurvirostrids. The proximal end (Figure 27*a*) appears to have been pneumatic (a small portion of the border of the pneumatic foramen remains in the one specimen) and does not have the deeply excavated, nonpneumatic tricypital fossae that are characteristic of the Recurvirostridae, most other Charadriiformes, and *Presbyornis*. In the distal end, the distinct ectepicondylar spur characteristic of recurvirostrids and most other shorebirds is absent, as in flamingos.

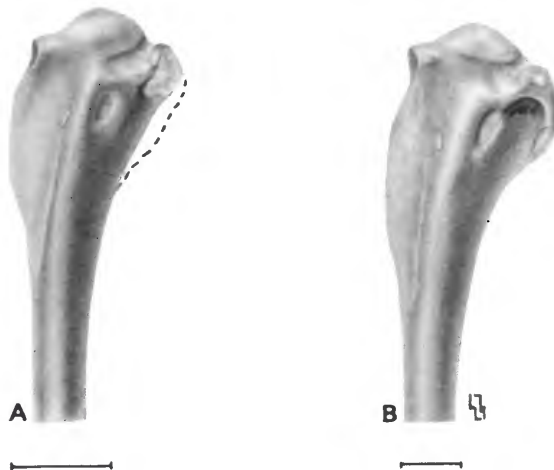


FIGURE 27.—Proximal ends of left humeri of fossil flamingos: *a*, *Juncitarsus gracillimus* (USNM 244325); *b*, *Palaelodus* sp. (Scales = 1 cm).

The most characteristic feature of the proximal end of the humerus in *Juncitarsus* is a distinct elliptical scar for *M. scapulohumeralis cranialis* (the "supraspinatus" scar of Howard, 1929), distal to the pneumatic foramen and lying between that opening and the midline of the shaft. A similar deep scar is characteristic also of *Palaelodus* (Figure 27*b*) and may be faintly seen in those individuals of modern flamingos in which the pneumatic foramen is less extensive and does not obliterate this area. We regard the resemblance of this scar in *Juncitarsus*, *Palaelodus*, and modern flamingos as significant, as we have not seen a similar condition in any modern group of birds, including the Ciconiiformes, Anseriformes, or Charadriiformes. The overall configuration and details of the proximal end and shaft of the

humerus in *Juncitarsus* very closely resemble that in *Palaelodus* and modern flamingos. In all of these forms, the margin of the deltoid crest describes a long, gentle curve extending well down the shaft, in contrast to that seen in Ciconiiformes, in which the deltoid crest is variable but always shorter and more angular, as, for example, in storks and herons. Likewise, in *Juncitarsus*, *Palaelodus*, and modern flamingos, the scar of *M. latissimus dorsi pars cranialis* is quite similar, being situated midway between the midline and the external margin of the shaft, whereas in Ciconiiformes this scar is either on the midline or lies between it and the internal margin of the shaft.

The single distal end of humerus available for *Juncitarsus* (Figure 28*b*) has the anconal surface and the area of the brachial depression crushed

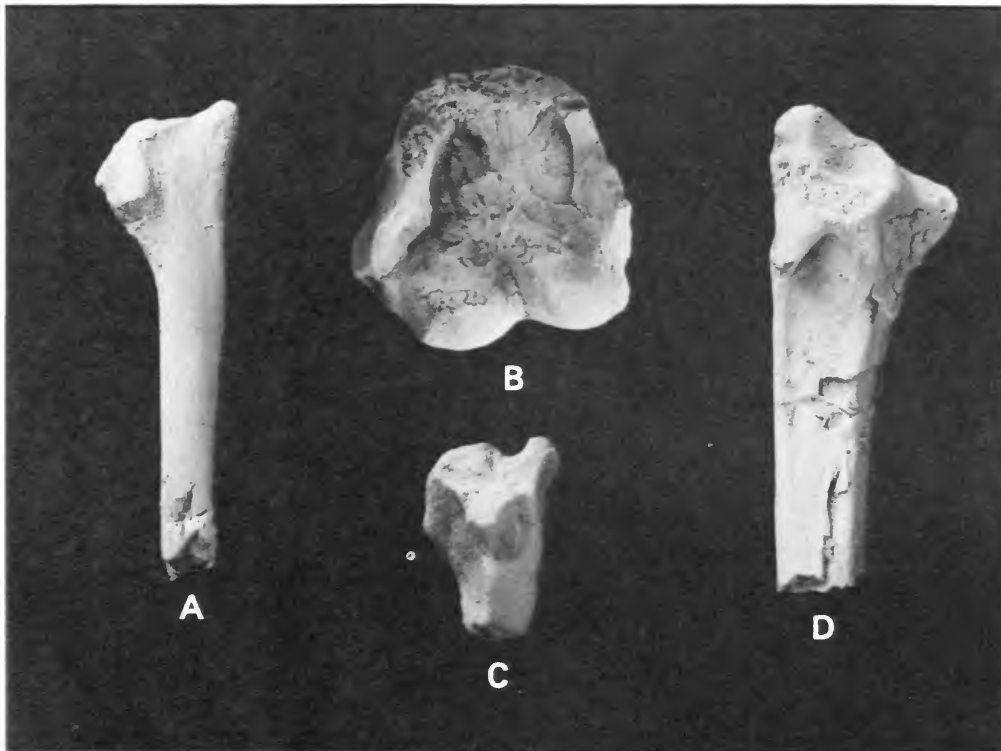


FIGURE 28.—Paratypes of *Juncitarsus gracillimus*: *a*, left scapula, dorsal view (USNM 244328); *b*, distal end of left humerus, palmar view (USNM 244330); *c*, left radiale, proximal view (USNM 244333); *d*, left ulna, internal view (USNM 244326). (× 3.)

and is therefore not particularly useful. One distinctive feature is the raised internal margin and steeply angled surface of the attachment of the anterior articular ligament. From *Presbyornis* it differs further in having the internal condyle in distal and palmar views more rounded and the external condyle relatively narrower. *Palaelodus* and modern flamingos differ from *Juncitarsus* in having the external condyle curved internally at the proximal tip.

Ulna: The proximal end of an ulna of *Juncitarsus* (Figure 28d) is generally similar to that in modern flamingos, but the attachment of the anterior articular ligament is broadly triangular and does not extend distally along the impression of *M. brachialis*. In this respect *Juncitarsus* more nearly resembles the *Recurvirostridae* and differs greatly from *Palaelodus*—in which the attachment of the anterior articular ligament is very narrow and elongate. The proximal radial depression in *Juncitarsus* is deeper than in the forms just mentioned.

Radiale: A well-preserved left radiale (Figure 28c) is generally similar to that of modern flamingos, although we have not made extensive comparisons of this element. It agrees with flamingos, as opposed to *recurvirostrids*, in being more elongate and in having a distinct notch in the dorsal surface. It is proportionately narrower than in modern flamingos, but otherwise is more similar to the *Phoenicopteridae* than to the *Ciconiiformes* or *Charadriiformes*.

Scapula: The only available scapula of *Juncitarsus* (Figure 28a) is the anterior portion from a juvenile. The coracoidal articulation is perhaps slightly better developed than in *Phoenicopterus* but not as distinctly produced as in *Palaelodus* or *Presbyornis*, nor a distinct ball as in storks and herons. The acromion is not as elongate and pointed as in *Presbyornis*, *Palaelodus*, or modern flamingos, and is not unlike that of *Himantopus*. The shaft is narrow, rather rounded in cross-section, and deflected ventrally, as in *Palaelodus*, *Presbyornis*, and modern flamingos, and quite unlike the broad flattened condition in *Ciconiiformes*.

Vertebrae: We undertook comparisons of the four vertebrae included among the material of *Juncitarsus* with little anticipation of discovering much of interest. We found, however, these specimens were of great value in assessing the affinities and adaptations of the bird.

The most complete specimen corresponds very closely with the 16th cervical of *Phoenicopterus* (15th of *Phoeniconaias*), differing mainly in the narrower and longer prezygapophyses and the narrower and deeper articular surfaces of the centrum. In modern flamingos, this vertebra occurs at the point of transition from the greatly elongated anterior cervicals to the shortened prethoracic cervicals. It is characterized by having the ventral surface of the centrum elongate and flat, with two distinct anterior hemapophyses, and by having a large, sloping, expanded neural crest. The agreement of the fossil with modern flamingos is striking (Figure 29), particularly since we found no vertebra comparable in proportions and details in any of the other orders of birds possibly related to flamingos, including the *Charadriiformes*. In the *Recurvirostridae* the equivalent vertebra is much shorter, has no neural crest, and has only a single hemapophysis. In the *Anatidae*, the vertebrae in this area are somewhat similar but are not as elongate and do not possess a combination of a high neural crest and double hemapophyses. The transitional cervical vertebrae in the families of *Ciconiiformes* are not as well demarcated, except in herons. There is considerable difference between the families, but none approaches the condition in flamingos. In herons, for example, the ventral surface of the most nearly comparable vertebra bears a large, thin crest, totally unlike the double hemapophyses and flattened and elongated centrum of modern flamingos and *Juncitarsus*.

A fragmentary anterior portion of an anterior cervical of *Juncitarsus* (Figure 30a,b) indicates a very elongate and slender vertebra with a distinctly oval cross-section (Figure 30a) such as seen in modern flamingos. It is most similar to the 6th cervical in *Phoenicopterus*, differing in having the hemal spines reduced and more widely divergent



A



A'



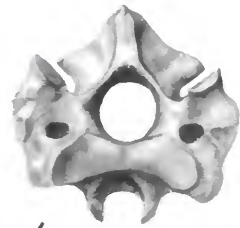
D



B



B'



D'



C



C'



E



E'

FIGURE 29—Cervical vertebra of *Juncitarsus gracillimus* (paratype USNM 244321) compared with the 15th cervical vertebra of the modern flamingo *Phoeniconaias minor* (primed letters): a, lateral view; b, dorsal view; c, ventral view; d, anterior view; e, posterior view of centrum. (*Juncitarsus* \times 2.6; *Phoeniconaias* \times 2).

and the ventral surface of the centrum forming a slight crest rather than being flattened; in the last feature it is like *Himantopus*. Only the Ardeidae have comparably elongated vertebrae. The fossil agrees with flamingos and differs from herons in the deeper anterior articular surface and the shallower depression on the ventral surface posterior to the articulation.

Another vertebra of *Juncitarsus* (Figure 30c) bears a costal facet and therefore formed part of

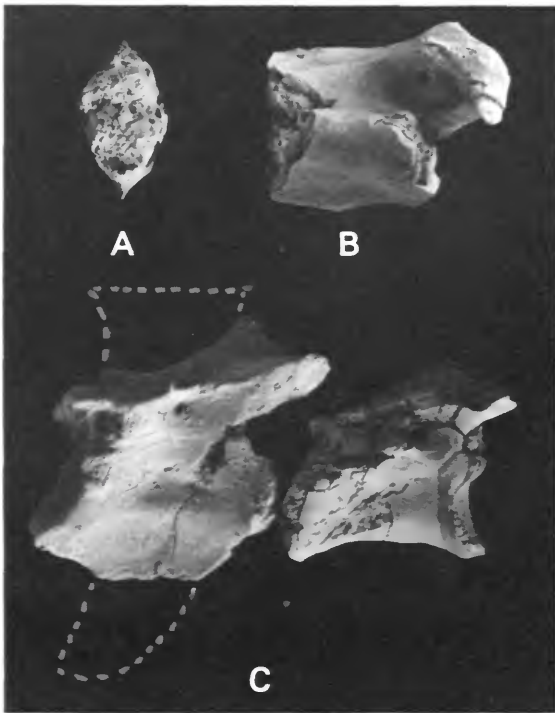


FIGURE 30.—Paratypical vertebrae of *Juncitarsus gracillimus*: a, anterior cervical equivalent to 6th cervical vertebra of *Phoenicopterus*, cross section (USNM 244338); b, same, lateral view of right side; c, thoracic vertebrae equivalent to the 17th and 18th vertebrae of *Recurvirostra*, lateral view of left side (USNM 244332, 244331). (\times 3.)

the thoracic series. It bears the remains of a single large hemal spine and thus came from the anterior portion of the series. In modern flamingos these vertebrae are fused into a notorium and the neural spines are less prominent. The present vertebra had a large neural spine and was unfused. It bears no resemblance to any of the thoracic vertebrae of modern flamingos but agrees very closely with the 17th vertebra (2nd thoracic) of *Recurvirostra*.

A second specimen of thoracic vertebra (Figure 30c) was also unfused and bears a costal facet. The centrum is laterally compressed unlike modern flamingos. This vertebra also agrees well with *Recurvirostra* and appears to be the one succeeding the previously mentioned thoracic.

The resemblance of the thoracic vertebrae of *Juncitarsus* is closest to the Charadriiformes. As with the cervicals, there is great variation in the thoracic vertebrae between the families of Ciconiiformes, none of which have the centra as compressed as in *Juncitarsus*. In storks and herons none of the thoracics bear well-developed hemal spines. In ibises some of the thoracics are fused into a notorium, but this involves a different series of vertebrae than that of modern flamingos.

Frontal Bone: Associated with the other material of *Juncitarsus* is a small unfused frontal bone, the sutures of which obviously had not closed. It is important in showing in the supraorbital area a distinct impression for a salt gland (Figure 31), in the same position as seen in modern flamingos.

Pedal Phalanx: A toe bone appears to be phalanx 1 of right digit II. The element differs from modern flamingos in being less laterally compressed, and from storks and herons in being less elongate. Its resemblances are closer to the *Recurvirostridae*.

Femur: An abraded distal end of a femur referred to *Juncitarsus* preserves no useful characters.

DISCUSSION.—*Juncitarsus* is the earliest known fossil that is definitely referable to the Phoenicopteridae. It is known as yet only from the earliest Middle Eocene. *Presbyornis*, a colonial charadriiform near the ancestry of Anseriformes, is abundant in early Eocene deposits and thus

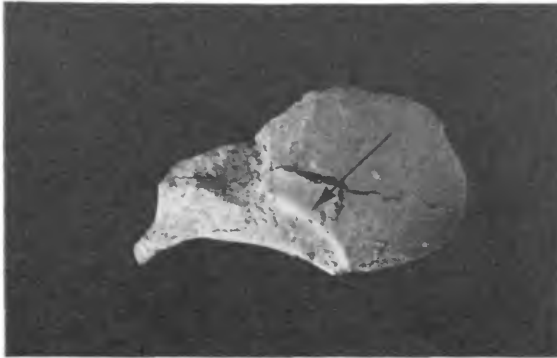


FIGURE 31.—Unfused frontal bone of juvenile specimen of *Juncitarsus gracillimus* (USNM 244336) showing depression for salt gland (arrow). ($\times 3$.)

must have been contemporaneous with the ancestors of *Juncitarsus*.

The available evidence indicates that *Juncitarsus* may have nested colonially. It had salt excreting glands and therefore inhabited saline environments at least intermittently, if not entirely. Both of these conditions are typical of modern flamingos.

Juncitarsus possessed apparently derived characters of the cervical vertebrae and humerus which ally it with the Phoenicopteridae, although it retains the morphology of the Charadriiformes in the thoracic vertebrae and most features of the tarsometatarsus. The last element is particularly similar to that of the Recurvirostridae, corroborating our proposed relationship between the Phoenicopteridae and the Recurvirostridae. That the cervical vertebrae of *Juncitarsus* are specialized like those of modern flamingos suggests that some of the aspects of the highly modified feeding apparatus of flamingos had evolved by the Middle Eocene. The thoracic vertebrae of *Juncitarsus* are unfused, indicating that the notorium of modern flamingos evolved subsequent to the specializations of the neck.

Juncitarsus provides a mosaic of phoenicopterid and charadriiform characters and in size bridges the gap between the modern members of the Recurvirostridae and the Phoenicopteridae. It shows no approach to the morphology of either Ciconiiformes or Anseriformes.

Aspects of Evolution of Filter Feeding

The most characteristic feature of flamingos is their filter-feeding apparatus, which has been likened to that of the Anseriformes and therefore has been cited as evidence for a relationship between the two groups. Greatly detailed descriptions of the structure and function of the feeding apparatus are available for flamingos (Jenkin, 1957) and for ducks (Goodman and Fisher, 1962; Zweers, 1974; Zweers et al., 1977). These lack, however, a more general overview of evolutionary events that may have led to development of such adaptations.

Filter feeding is commonly employed in diverse groups of invertebrates and in some fishes and tadpoles. Among higher vertebrates, however, well-developed straining devices have evolved only in baleen whales and in three groups of birds: flamingos, ducks, and one genus of petrels (*Pachyptila*, Procellariidae). Certain penguins (Spheniscidae) and auks (Alcidae) show some of the structures needed for feeding on small organisms but have not evolved lamellate strainers. It is instructive to examine their adaptations first. Zusi (1974a) has provided a valuable account of feeding adaptations in penguins, and Bédard (1969) has discussed those of alcids. The plankton-eating forms of these groups are characterized by an enlarged tongue, a broadened rostrum, and cornified papillae on the roof of the mouth and, in the case of penguins, on the tongue, inner surface of lower jaw, and larynx also. The enlarged tongue may be accommodated in two ways; either by a distensible gular pouch as in alcids, or by a deepening of the bones of the lower jaw, best exemplified in penguins by species of the genus *Eudyptes*. The penguins and alcids thus adapted, feed largely on small crustaceans which are thought to be taken individually rather than with a netlike scooping (Zusi, 1974a:76). Prey is taken very rapidly, however, and is held and manipulated toward the throat by action of the tongue.

The next steps in the evolution of filter feeding are well illustrated by the petrels of the genus *Pachyptila*, sometimes known as whalebirds, on account of the baleen-like feeding apparatus in

some species. In *Pachyptila* there is a continuum of variation in bill shape, from proportions nearly typical of other members of the family (*P. belcheri*) to the grotesquely broadened bill of *P. vittata* (see illustrations in Murphy, 1936; Fleming, 1941). All have an enlarged tongue, which, as with the plankton-feeding alcid, is accommodated by a distensible gular pouch rather than by a deep lower jaw. Each possesses at least the rudiments of lamellae, always on the inner surface of the edge of the upper jaw, with more pronounced development posteriorly than anteriorly. In the narrow-billed species these "lamellae" are very small transverse projections extending medially less than a millimeter from the cutting edge of the bill. They reach their extreme in *P. vittata*, which possesses a bona fide straining device consisting of a series of plate-like lamellae extending ventrally some 3.5 mm from a ridge inside the edge of the bill.

Although Murphy (1936:614) held that in the narrow-billed forms of *Pachyptila* "it would be hard to believe that the faint striations [in the upper jaw] could have any function whatsoever," it is more difficult to believe that such structures would evolve without having some function. Quite probably the rudimentary lamellae in the less specialized filter-feeding petrels provide gaps for the expulsion of water while the prey is held in place with the tongue. With increasing specialization, the lamellae enlarge and begin to assume the role of food retention while the tongue forces out water and moves the prey toward the throat. As with penguins (Zusi, 1974a) and flamingos (Jenkin, 1957), increasing specialization of the feeding apparatus in *Pachyptila* is correlated with a decrease in size of prey (Watson, 1975).

The filter-feeding petrels thus illustrate several important points. First, the initial adaptation for filter-feeding is enlargement of the tongue. This is accompanied or followed by widening and deepening of the bill and the development of lamellae. Secondly, the initial function of lamellae may be to permit the expulsion of water rather than to retain prey. Third, the species of *Pachyptila* show progression from a primitive, nearly unmodified species, to a highly evolved lamellate filter

feeder within a single extant genus, suggesting that the great broadening of the bill and the development of a fine strainer may occur rapidly in birds. Fleming (1941) considered speciation in *Pachyptila* to be the result of climatic changes associated with Pleistocene glacial events, which, if true, would make the more specialized filter-feeding adaptations in the genus of very recent origin.

Flamingos are the most specialized of avian filter feeders. The peculiarly bent bill, used in an "upside down" attitude when feeding, separates the living flamingos from all known birds. Two strikingly different modifications of the bill occur in flamingos, the least specialized being that of *Phoenicopterus*, the most derived condition being that found in *Phoenicoparrus* and *Phoeniconaias*. In all flamingos the lower jaw is deep and swollen and the upper jaw is narrow. In *Phoenicopterus* (Figure 32), the lower jaw is essentially a large cylinder housing an immense tongue equipped with a series of spiny protuberances. Fine ridges lying transverse to the long axis of the bill occur on the narrow dorsal surface of the two sides of the lower jaw. The upper jaw is rather flat, with a slightly developed median keel. Coarse hooklike lamellae are present on the outer edge of the upper jaw, inside of which is a series of diagonally-oriented, fine plate-like lamellae lying in a narrow band between the outer edge of the jaw and the bare median keel.

In *Phoenicoparrus* and *Phoeniconaias* the upper jaw is much narrower and bears a deep median keel (Figure 39a), with long rows of exceedingly fine microscopic, feather-like lamellae. The coarse lamellae along the edge of the jaw are much finer and less hooklike than in *Phoenicopterus*. In the lower jaw, the space for the tongue is greatly reduced because the dorsal lamellate ridges seen in *Phoenicopterus* have expanded and are turned inward and downward to provide a greater surface area for rows of fine lamellae opposing those of the keel on the upper jaw. *Phoeniconaias* feeds on much smaller food particles than does *Phoenicopterus* (Jenkin, 1957).

The filtering apparatus in the Anatidae is quite different from that of flamingos but the essential

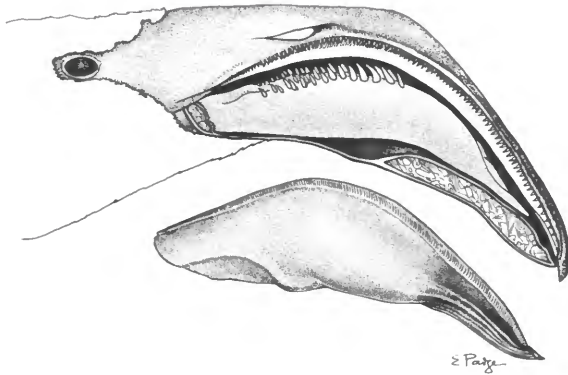


FIGURE 32.—Head of the flamingo *Phoenicopterus ruber*. Lower jaw removed and displaced below, viewed from the external surface. Note that the tongue is housed in the lower jaw and that neither the lower jaw nor the keel on the upper jaw are as deep as in *Phoeniconaias* (see Figure 39).

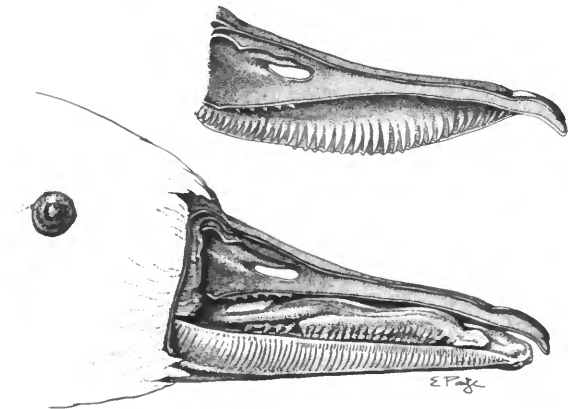


FIGURE 33.—Head of a Mallard Duck, *Anas platyrhynchos*. Upper jaw removed and displaced above, viewed from the internal surface and reversed to preserve the same orientation. Note that the tongue is accommodated by the upper jaw and that there are two bulges in the tongue that form a double piston suction pump, unlike the mechanism in the flamingo.

structures are all present: enlarged tongue, broad bill, and lamellae. The bill shape of ducks is too familiar to need description but perhaps it has not been realized that it presents an adaptation not found in other filter-feeding vertebrates: the enlarged tongue is accommodated by the upper

rather than the lower jaw (Figure 33). This is a fundamental difference between ducks and flamingos and one that has not been emphasized by those attempting to ally the two groups. Furthermore, the underlying bony structure of the tongue is very different in the two groups. In ducks, the paraglossale, the terminal bone of the hyoid apparatus supporting the tongue, is a distinctive expanded, spatulate bone, whereas in flamingos it is slender and more rodlike, as is typical of most birds.

In typical anatids, rows of lamellae lie along the inner surfaces of both the upper and lower jaws, the latter series being divided into upper and lower rows. The morphology of these lamellae may vary considerably, even within a genus. In *Anas*, the lamellae may be coarse, hard plates, as in the Mallard *Anas platyrhynchos*, or they may be prolonged into fine hairlike fringes as in the congeneric Shoveler *Anas clypeata*. Again, as in *Pachyptila*, the evolution of fine lamellate structures seems to be accomplished with relative ease. In no case, however, are the lamellae in ducks like the rows of platelets or feather-like strainers of flamingos.

The process of filtration in flamingos is quite different from that of ducks. In flamingos, the mouth is opened and water enters along the entire gape, which then closes, the tongue forcing water back through the filtering devices. In the normal feeding process of *Phoeniconaias* and when *Phoenicopterus* feeds on mud, this process is modified so that the outer lamellae function as excluders, keeping out larger inorganic particles (Jenkin, 1957). In ducks, the bill and tongue act as a suction pressure pump consisting of two pistons in a cylinder (Figure 33), with the water entering at the tip of the bill and being expelled posteriorly (Zweers et al., 1977).

The advocates of ciconiiform relationships of flamingos have not hypothesized how the complicated filter-feeding apparatus might have evolved from the hard, pointed bill of a stork; indeed it is difficult to envision such a transformation taking place. Several authors (Reichenow, 1877; Jenkin, 1957; Sibley et al., 1969) have



FIGURE 34.—Bills of two specimens of the African Open-bill Stork, *Anastomus lamelligerus*, to show the variation in development of the bristly pads on the rhamphotheca. It is obvious by their placement that these structures could have no filtering function.

mentioned the so-called “lamellae” of the open-bill storks, *Anastomus*, in connection with the evolution of straining devices in flamingos, but the analogy is invalid. The structures on the rhamphothecae of *Anastomus* (Figure 34) are in no way comparable to lamellae. Kahl (1971:27) much more appropriately refers to them as “leathery columnar ‘pads.’” He has shown that the open-bill structure in *Anastomus* provides a forceps-like action of the bill tips that functions in preying on mollusks, particularly large snails, which are the chief item of diet in these storks.

The bristly pads on the rhamphothecae of *Anastomus* probably do not function in feeding. They occur along the edges of the gap in the bill and their relative prominence appears to be correlated with the age of the individual, as there is considerable variation in development (Figure 34). In most birds, the edges of the upper and

lower jaws come in contact, serving to keep the horny rhamphothecae worn down and probably sharpened as well (Tunnicliffe, 1973). Such contact is not possible in *Anastomus*, however, and the rhamphothecae appear to be unable to check each other against continued outgrowth. Thus the bristly pads in this genus may well be purely adventitious structures. Regardless, *Anastomus* does not represent any stage in the evolution of filter feeding.

Because we propose a shorebird ancestry both for flamingos and for ducks (Olson and Feduccia, in press), there should be taxa among the Charadriiformes having morphological precursors of phoenicopterid and anatid feeding adaptations. Within the Recurvirostridae, *Recurvirostra* and *Cladorhynchus* are adapted for feeding rapidly on large numbers of small prey items. Accordingly, the tongue is enlarged and is short, broad, and

fleshy (Figure 35), to facilitate movement of small prey into the throat. The development of a large, fleshy tongue, as we have noted, is the first major step involved in the evolution of filter feeding. In storks, however, the tongue is rudimentary (Gardner, 1925).

An unrecognized example of a shorebird showing the beginning stages in the development of filter feeding is the Red Phalarope, *Phalaropus fulicarius* (Phalaropodidae). In the other two members of the Phalaropodidae (*Lobipes lobatus* and *Steganopus tricolor*) the bill is extremely slender, pointed, and needlelike (Figure 36b), but in *Phalaropus* the bill is broad, deep, and subspatulate in shape (Figures 36a, 37b, 38a), with wide, flexible margins. The tongue is correspondingly enlarged and from the postero-lingual rims of the lower jaw project a few well-developed, narrow papillae that may function as strainers (Figure 36a). In other phalaropes the tongue is narrow and papillae in the lower jaw are absent or very rudimentary (Figure 36b). *Phalaropus fulicarius* feeds mainly on small insects and crustaceans and is reported to take food at a much faster rate than other phalaropes (Bent, 1927). Harold Mayfield (in litt. to Olson, 17 January 1978) writes that on the breeding grounds, *Phalaropus* may be seen to feed by extracting chironomid midge larvae from floating vegetation and often is observed with strands of vegetation hanging from the mouth.

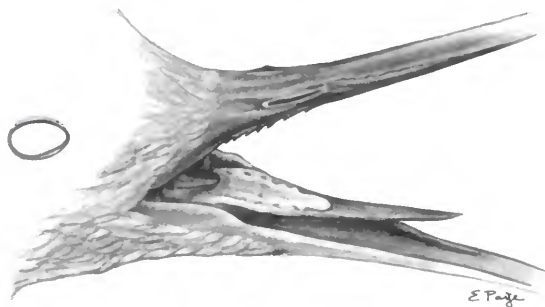


FIGURE 35.—Mouth of the American Avocet, *Recurvirostra americana*, to show the broad, fleshy tongue. The acquisition of such a tongue is the first step in the development of filter-feeding.

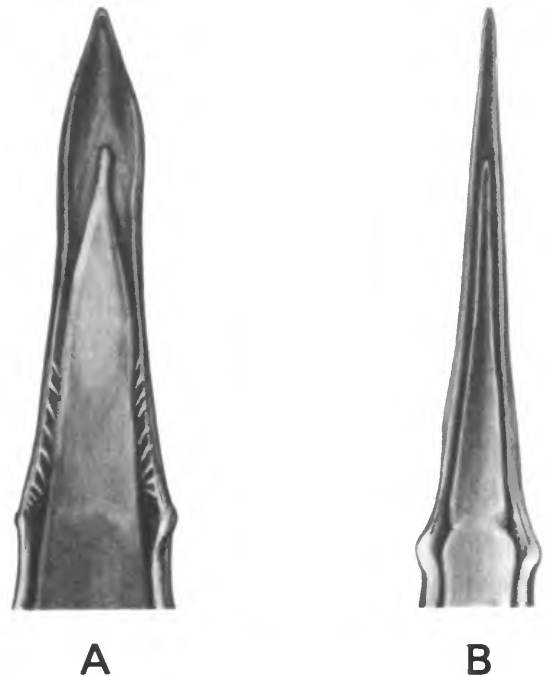


FIGURE 36.—Dorsal view of the lower jaw and tongue of a Red Phalarope, *Phalaropus fulicarius* (a), and a Northern Phalarope, *Lobipes lobatus* (b). The broad bill, enlarged tongue, and papillae of *Phalaropus* probably indicate a capacity for primitive filter-feeding.

He reports that stomachs almost always contain bits of vegetation apparently taken in accidentally while feeding. Thus it appears that *Phalaropus* actually engages in a primitive straining type of filter-feeding as would be predicted from its morphology.

The bill in most Charadriiformes is typically rather weak and flexible, due in large measure to the long schizorhinal nostrils and the short premaxillary and mandibular symphyses. This has proved to be a very plastic structure, and consequently the Charadriiformes exhibit the greatest diversity in feeding adaptations of any order of birds (see examples illustrated in Zusi, 1974b). Contrast, for example, the bill of a Spoonbill Sandpiper (*Eurynorhynchus*) with that of a skimmer (*Rynchops*).

It is well known that the bill in young flamingos is straight and only later in ontogeny develops the characteristic crook. This has received only passing comment in the literature, with most authors stating that the flamingo bill is "goose-like" in its early stages. The bill in flamingos is never really gooselike but in its earliest stages can better be likened to that of a shorebird such as *Phalaropus*, being rather long and narrow with somewhat flexible margins (Figure 37). In lateral view, the bill is deeper than usual for most Charadrii (Figure 38*b*) and ontogenetic changes involve increasing the depth of the mandible and

the curvature of both jaws (Figure 38*c,d*). At one point in the development of *Phoenicopterus ruber*, the bill is shaped almost exactly as in the early Miocene species *P. croizeti* (Figures 20, 38*c*), and the ontogeny of the bill in modern flamingos appears to reflect rather closely their phylogeny. To evolve such a structure from the condition typical of the Charadrii would mainly require fusion by increased ossification of various separate elements, whereas to evolve the flamingo feeding apparatus from the already greatly fused cranial structure of a stork would involve a series of highly improbable intermediate stages.

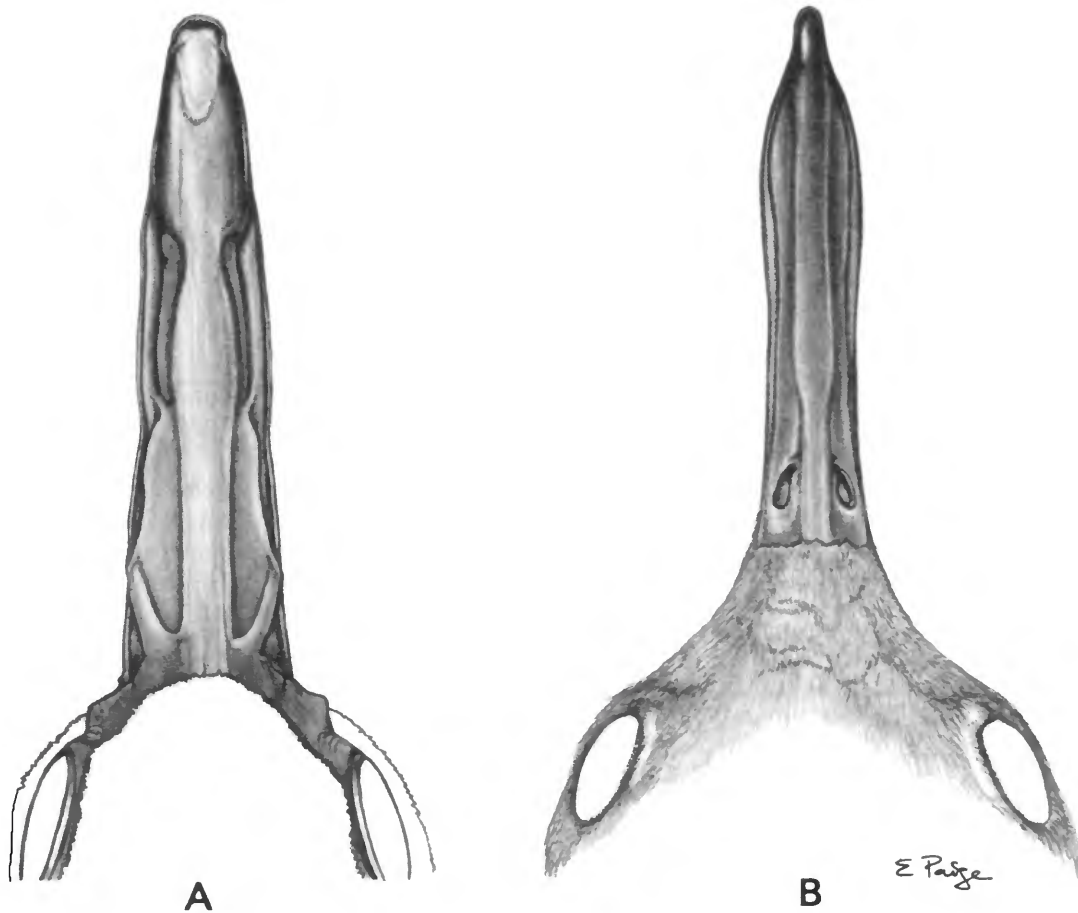


FIGURE 37.—Dorsal view of bill of downy chick of a flamingo, *Phoenicopterus ruber* (a) compared to an adult Red Phalarope, *Phalaropus fulicarius* (b).

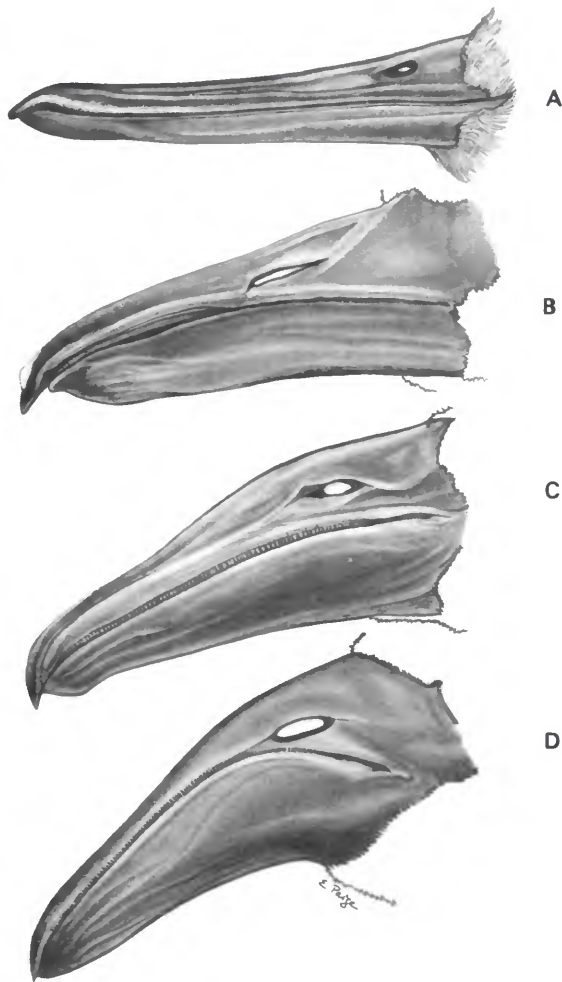


FIGURE 38.—Lateral view of bill: *a*, Red Phalarope, *Phalaropus fulicarius*; *b-d*, progressive developmental stages of flamingos: *b*, downy chick of *Phoenicopterus ruber* less than a week old; *c*, chick of *P. ruber* about 30 days old; *d*, chick of *Phoeniconaias minor* 7 weeks old (adapted from Kear and Duplaix-Hall, 1975, plate 48). Note the progressive deepening of the mandible and bending of the bill with increasing age.

Although the filtering techniques of flamingos and ducks are entirely different from one another, both methods require repeated and rapid opening of the bill, which can be accomplished by moving either the upper or the lower jaw, or both. Because M. depressor mandibulae causes protract-

tion of the upper jaw as well as depression of the mandible (Zusi, 1967), it has a very important role in the feeding process in flamingos and in ducks. The enlarged bladeliike retroarticular processes of the mandible in both groups provide increased area for the insertion of the depressor mandibulae. The retroarticular processes and depressor mandibulae are well-developed in several groups of shorebirds, notably so in *Recurvirostra* (Burton, 1974), and although not as exaggerated as in flamingos and ducks, are quite suitable as precursors. Such retroarticular processes are lacking in storks and herons, however. Because of the importance of the depressor mandibulae in filter-feeding, regardless of how such filtering is accomplished, it is not improbable that the enlarged retroarticular processes of flamingos arose independently of those in ducks.

The astute naturalist Stejneger (1885:153) noted in passing the resemblance between the feeding apparatus of flamingos and that of baleen whales, but devoted only a sentence to it. The similarity between the head of a flamingo and that of the right and bowhead whales (*Eubalaena* and *Balaena*) is quite striking. In these whales the upper jaw is quite narrow, with a ventral keel bearing long plates of baleen. The lower jaw is very deep and swollen, accommodating a huge tongue and rising up so as to cover the baleen plates of the upper jaw when the mouth is closed. Unlike flamingos, there are no straining devices on the lower jaw, but otherwise the general appearance of the head is so like that of flamingos (Figure 39) as to be one of the more outstanding examples of convergence in the animal kingdom.

The resemblances extend to the skeleton as well. The rostrum in *Eubalaena* and *Balaena*, particularly as compared to that in other baleen whales such as *Balaenoptera*, is markedly crooked and bent downward so that it is superficially like that of a flamingo (Figure 40). The bony structure of the lower jaw is not like that of flamingos because the great depth of the lower jaw in *Balaena* is achieved by a mass of connective tissue built up on a mandible not substantially different from that of other baleen whales.

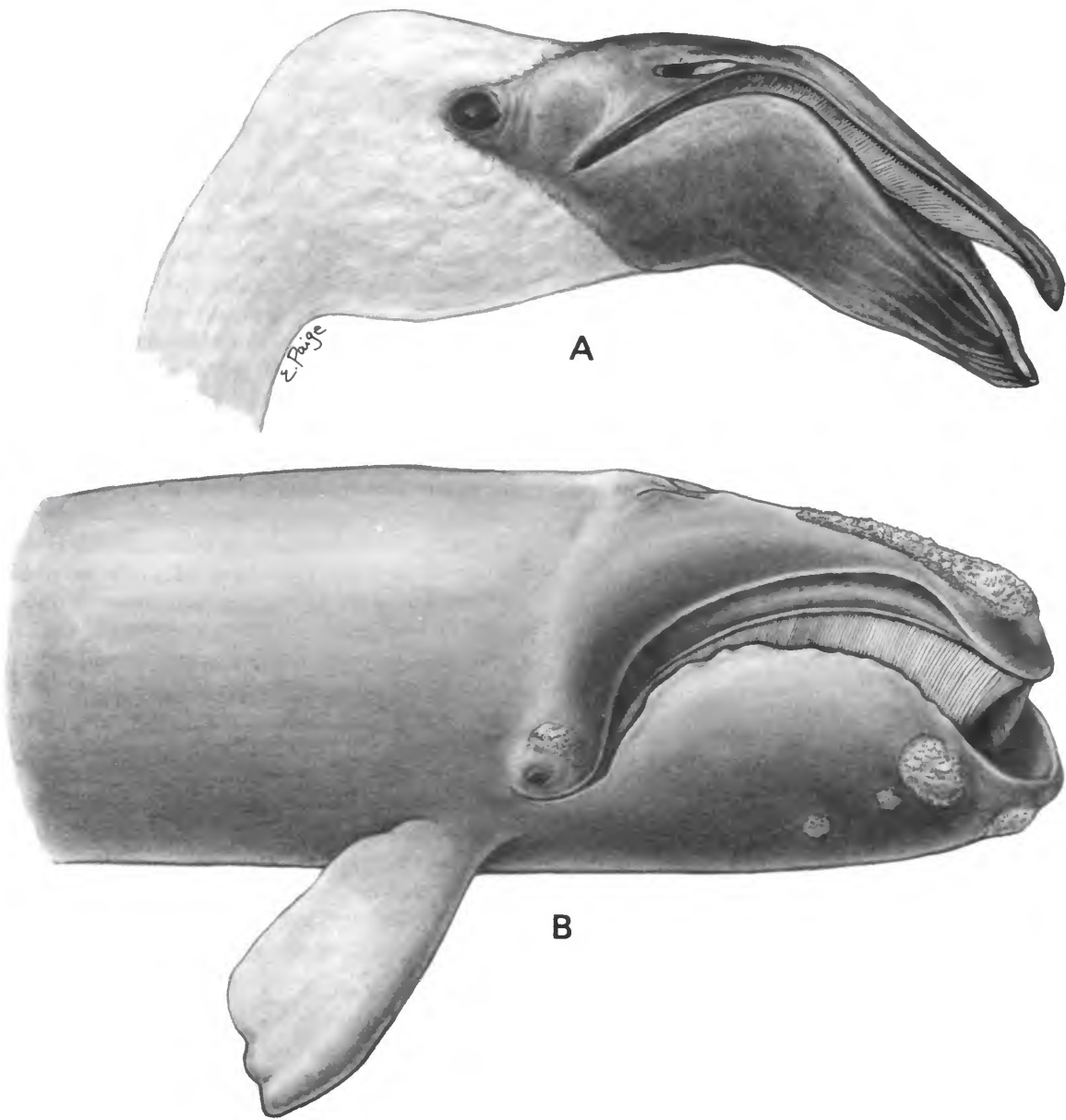


FIGURE 39.—Head of a Lesser Flamingo, *Phoeniconaias minor* (a), compared with that of a Black Right Whale, *Eubalaena glacialis* (b), to show the convergent similarities in the filter-feeding apparatus.

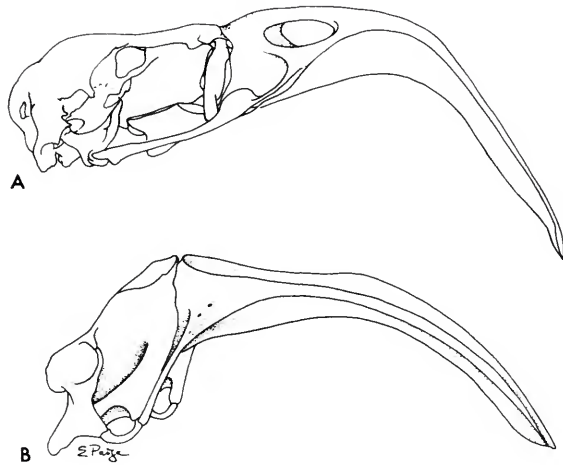


FIGURE 40.—Skull of a Lesser Flamingo, *Phoeniconaias minor* (a), compared with that of a Black Right Whale, *Eubalaena glacialis* (b), to show the similarity in the shape of the long, decurved bony structure of the rostrum.

The bend in the rostrum of *Balaena* and in the deep-keeled flamingos confers one obvious advantage: it allows the filtering devices in the middle portions of the rostrum to become much longer and more extensive. *Balaena* has the longest and finest baleen of any of the filter-feeding whales and as a consequence feeds on smaller organisms.

The bent rostrum must confer other advantages, however, for *Phoenicopterus* has no deep keel. First of all, it provides space for an enlarged tongue while still allowing the tips of the jaws to come together, thereby permitting flamingos to pick up individual food items (Rooth, 1965) and to manipulate nesting material. More importantly, the bend in the bill also allows the entire length of the gape to be opened with a minimum of movement of the jaws (Jenkin, 1957). At least in flamingos, the bend must first have arisen for these purposes, being followed by its use for expansion of the filtering apparatus in the more advanced species.

The similarity of the heads of flamingos and whales is probably a good indication that the bent structure of the flamingo bill arose in accordance with the constraints of filter feeding alone, the "upside-down" feeding posture having evolved secondarily. The more primitive baleen

whales, with their straighter and wider upper jaws, might provide useful analogs to the morphological stages through which flamingos may have passed during their evolution, although this is demonstrated just as well in the ontogeny of living species (Figure 38).

Modern flamingos feed in highly saline waters and the available evidence indicates that the earliest fossil flamingo, *Juncitarsus*, may have occurred in a similar habitat. The same is true of *Presbyornis*, a filter-feeding charadriiform near the ancestry of ducks. Highly saline lakes provide abundant food in the form of swarms of brine-adapted arthropods and growths of algae. The small size of these organisms, however, would necessitate a filtering device for effective feeding. Furthermore, in such habitats there would be strong selection for feeding methods that prevent the ingestion of water, in order to avoid the higher energetic cost of metabolic excretion of salt. Thus, highly saline lakes may have been the original habitat for both flamingos and Anseriformes. There, selection would have favored the development of specialized filtering mechanisms that might never have evolved under less strenuous conditions.

To summarize, the filter-feeding adaptations of flamingos are seen to be entirely different from those of the Anseriformes and are not indicative of a relationship between these two groups. Morphological precursors for such adaptations exist among the Charadriiformes but not in storks.

Conclusions

The association of the Phoenicopteridae with the Ciconiiformes has resulted solely from historical traditions and misconceptions. We have shown that there is no substantial or convincing evidence of relationship between flamingos and either the Ciconiiformes or Anseriformes, whereas all of the attributes of flamingos are compatible with a charadriiform origin, including those that once seemed inexplicable when flamingos were considered as bewildering mosaics of ciconiiform and anseriform characters.

If flamingos were derived from Ciconiiformes

and converged towards Charadriiformes, one would expect fossil flamingos to have more stork-like characters than modern flamingos (which have no stork-like characters anyway). This is definitely not the case, for the earliest known flamingo, *Juncitarsus*, has no similarities to the Ciconiiformes and in many respects is more similar to the Recurvirostridae than are modern flamingos. We cannot see that convergent evolution is really responsible for the confusion surrounding the classification of flamingos; their similarities to storks go no farther than the similarities between all birds with long legs and long necks.

The Anseriformes likewise prove unsatisfactory as ancestors of flamingos. Although members of both groups have webbed feet, swim and tip up while feeding, and have honking vocalizations, so, too, do members of the charadriiform family Recurvirostridae. The fact that both flamingos and ducks are filter feeders is of no systematic consequence because their basic structural adaptations for filtering are completely dissimilar and evolved independently of one another. Flamingos and Anseriformes share similar mallophagan parasites, but new knowledge of the evolutionary history of these two groups provides a logical explanation for this that does not involve a close relationship of the hosts: the ancestors of both flamingos and ducks originally evolved in the same harsh saline environments and probably had similar breeding habits that would have promoted transfer of parasites between the downy young. No anatomical evidence exists that supports an ancestral-descendant relationship for Anseriformes and flamingos.

On the other hand, in virtually all of their features that are not unique, flamingos resemble the Charadriiformes. This is supported by osteology, myology, behavior, internal parasites, and by the existence of a fossil form intermediate between the Recurvirostridae and modern flamingos.

In their predilection for highly saline environments, their coloniality, simplified breeding displays, habit of feeding on very small prey, en-

larged fleshy tongue, and large retroarticular processes of the mandible, the Recurvirostridae possess the necessary ecological, behavioral, and morphological precursors of the more specialized features of flamingos. Furthermore, modern flamingos and the recurvirostrid *Cladorhynchus* share certain characters that are either derived for all birds (*M. iliotibialis* medialis; breeding habits) or are derived within the Charadriiformes (two coats of white, unpatterned nestling down; elongated tertiaries). *Cladorhynchus* is nevertheless clearly a member of the Recurvirostridae. Thus the evidence suggests that flamingos evolved directly from the Recurvirostridae rather than from a proto-recurvirostrid. Otherwise, it would have to be assumed either that all the derived characters shared by *Cladorhynchus* and flamingos evolved twice, which is implausible, or that all recurvirostrids once possessed these characters and that *Recurvirostra* and *Himantopus* have lost them and "re-evolved" all their primitive, more typically charadriiform characters, which is even less likely. If flamingos evolved directly from the Recurvirostridae, then it must be assumed that the Recurvirostridae were in existence before the middle Eocene, when the first flamingos appear. As yet, the only fossils possibly belonging to the Recurvirostridae are a few fragmentary bones of Miocene age.

The principal differences between modern flamingos and the Recurvirostridae are in the highly modified feeding apparatus, the increased number and specialization of the cervical vertebrae, and the pneumaticity of the proximal end of the humerus, with the associated changes in osteology and myology of the shoulder. These characters can then be said to define the family Phoenicopteridae. Although the nature of the feeding apparatus is not known for the fossil genera *Juncitarsus* and *Palaelodus*, both taxa possess modified humeri and cervical vertebrae and therefore are clearly referable to the Phoenicopteridae.

Within the Phoenicopteridae there are three basic generic groups: *Juncitarsus*, from the middle Eocene; *Palaelodus*, from the late Oligocene or early Miocene to early Pliocene; and "Recent"

flamingos, from the late Oligocene or early Miocene to the present. None of the known features of the long-legged *Juncitarsus* would preclude it from being very close to or on a direct line with Recent flamingos, whereas the *Palaelodus* group represents a separate, shorter-legged swimming lineage. There is, as yet, no evidence to indicate whether *Palaelodus* diverged from the more typical flamingos before or after the evolution of *Juncitarsus*.

The Phoenicopteridae are shorebirds with a highly evolved feeding apparatus. They are derived not only from members of the suborder Charadrii, but from a particular family of that suborder, the Recurvirostridae. Their distinctive

peculiarities entitle them to rank as a separate family, but it is not possible to accord them any higher position, such as a suborder or order, without raising each genus or family of Charadriiformes with a specialized feeding adaptation to an equivalent rank—an obviously undesirable procedure. To add proper perspective, it should be observed that flamingos differ no more from the Recurvirostridae than, for example, the Anhingidae differ from the Sulidae, yet these last two families are almost always included in the same suborder of Pelecaniformes.

Therefore, we place the Phoenicopteridae in the order Charadriiformes, suborder Charadrii, immediately following the Recurvirostridae.

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