NOTES ON THE PHYLOGENY OF THE PELECANIFORMES

BY URLESS N. LANHAM

CERTAIN aspects of the phylogeny of the order Pelecaniformes are obscured by the arrangement of its three living suborders in the standard classifications. The sequence as given by Wetmore (1940) and Peters (1931) is: PHAËTHONTES (Tropic-birds), PELECANI (Pelicans, Boobies, Cormorants, Snake-birds), and FREGATAE (Frigate-birds). The tropic-birds and frigate-birds, although widely divergent, show basic structural similarities which indicate both to be primitive members of the order, and which link the order with the Procellariiformes.

The fundamental similarity of *Phaëthon* and *Fregata* has been recognized in the older work on the comparative osteology of the group. Mivart (1878), from a study of the axial skeleton, came to the conclusion that *Phaëthon* and *Fregata* possessed common characters which sharply distinguished them from the other steganopodes, and, in fact, could find no characters to unite them with the rest of the steganopodous genera to form a natural group. The generalized condition of the cervical vertebrae of these two genera, in contrast to the specialization in the rest of the order, and certain primitive skull characters are largely self-evident and may have escaped emphasis for this reason. Shufeldt (1894) states that " . . . Steganopodes are more closely connected with the Tubinares than they are with the Longipennes." Murphy (1936) recognizes the generalized character of the skull of *Phaëthon,* and the affinity of the Pelecaniformes with the Procellariiformes; these two facts, at least, are implicit in modern classifications.

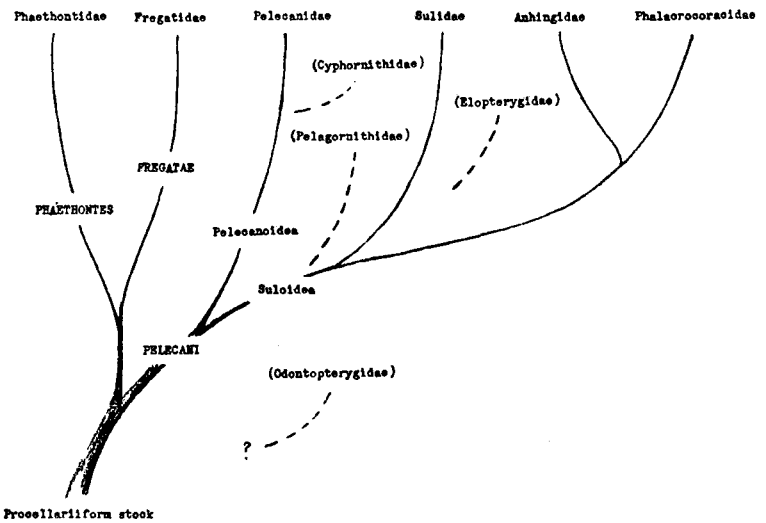
The more obvious skeletal characters common to *Phaëthon* and *Fregata,* and common also to the procellariiforms, may be summarized as follows:

Vomer present; maxillopalatines forming two conspicuous separate lobes on the palatal surface of skull near anterior end of palatines; occipital condyle well underneath skull, so that condyle is anterior to coronal crest. Fifteen cervical vertebrae present; normal, with serial change in shape gradual.

Corresponding characters of the suborder Pelecani are:

Vomer absent; maxillopalatines not visible on palatal surface, or (in *Pelecanus*) visible on surface and lobed, but fused in midline and reduced. Occipital condyle in line with or posterior to the coronal crest. Seventeen to twenty cervical vertebrae; articulation of cervical vertebrae peculiar, eighth or ninth pressed back at pre-axial end; posterior forking of neural arches appearing suddenly on seventh or eighth vertebrae.

The relationship of *Phaëthon* and *Fregata* to each other and to



TEXT-FIGURE 1.—Phylogeny of the Pelecaniformes.

the Procellariiformes is further suggested by the fact that all generally lay a single egg (usually two or more in the Pelecani).

Axial skeleton characters listed by Mivart (1878) as indicating the affinity of *Phaëthon* and *Fregata* include the very large acetabular fossae of these two genera (as compared with the moderate or small fossae in other pelecaniforms), the complete lack of haemal arches on any of the vertebrae (present on some vertebrae in the rest, although incomplete in *Phalacrocorax*), and the shape of the post-acetabular part of the ileum, described as being broad and dorsally convex, arching backwards and downward in a way not found in the rest of the order.

The striking difference in beak structure of the two genera—simple and tern-like in *Phaëthon,* compound and albatross-like in *Fregata*—could be compared to a similar (although less marked) difference in beak structure between the anhingas and cormorants, which are without doubt closely allied. In this view, the beak structure of *Phaëthon* and *Anhinga* would represent independent specializations. Of greater significance are anatomical differences which indicate a long period of separation of *Phaëthon* and *Fregata* stocks. Data on musculature given by Beddard (1898) include: leg musculature *AXY— in Phaëthon* (although Beddard was unable to find the ambiens in this genus, he states that Fürbringer and Gadow mark it as present), *A*+ in *Fregata,* biceps slip present in *Phaëthon,* absent in *Fregata.* The sternum of *Phaëthon* has two notches and processes

posteriorly, while that of *Fregata* is truncate. There are also differences in the articulation of the pectoral girdle.

The basic similarities of the Phaëthontes and Fregatae raise the question as to whether or not the two should be merged into a single suborder. Coues (1903) gives the essential facts which justify the separation of the two into separate suborders in stating that the families "Phaëthontidae and Fregatidae differ as much from each other as both do from the other four—Phalacrocoracidae, Anhingidae, Sulidae, and Pelecanidae being more closely related to one another. Such inter-relationships might serve for formal division of the order into three suborders . . ." If the formal classification were to express perfectly the supposed phylogency of the order, as illustrated in the accompanying diagram, then a pair of names of the same grade of category would have to be applied to each branch. *Phaëthon* and *Fregata* taken together would then constitute a taxonomic category equivalent to the rest of the order taken together. An inspection of the diagram will show further that two other grades of categories between suborder and family rank would have to be supplied to express the details of phylogeny. Such a formal classification would not, however, give any direct indication of the relative degrees of difference existing between the families. It would seem better to strike an average between the demands of phylogeny and relative difference by retaining the three suborders (meeting the latter requirement), and by altering the sequence, so that Fregatae follows Phaëthontes (meeting the requirements of phylogeny).

When expressing the phylogeny of a group in the manner of the diagram given here, with the primitive members to the left and the dominant, more evolutionally active members to the right, the degree of morphologic difference between the same grade of category will in a general way decrease from left to right. This is probably the result of longer operation of factors producing divergence, or apparent divergence (extinction of annectant forms), in the more ancient groups.

Although *Phaëthon* and *Fregata* differ widely from the Pelecani, there seems to be little doubt that the three constitute a natural order. Anatomical characters such as the absence of basipterygoid processes (Beddard, 1898: 409, thinks certain processes on the skull of *Pelecanus rufescens* may be rudiments of the basipterygoid processes) and the totipalmate foot are strengthened by other similarities. All (except *Phaëthon*) have similar eggs, and all (except possibly some anhingas) are fish-eaters. Murphy (1936) has pointed out the similarity of the young in all families, and notes that the young *Fregata*

is long-legged. In addition, the fossil *Prophaëthon* seems to be intermediate in some respects between *Phaëthon* and the rest of the steganopodes (Lambrecht, 1933), serving to unify the group.

Pelicans can be regarded as a specialized branch in which the ambiens has been lost, but in which the primitive maxillo-palata structure has been to some extent retained. In the superfamily Sulides, the ambiens muscle is retained (except possibly in some species of cormorants), and the maxillopalatines are not evident parts of the palatal surface. The Sulidae may be differentiated from the cormorants and anhingas by the fusion of the lachrymals to the skull, and (Beddard, 1898: 405) by the presence of 18 cervical vertebrae (20 in the cormorants and anhingas). The Phalacrocoracidae and Anhingidae are the most closely related families of the order. Cormorants are the least specialized of the two. Anhingas have a spear-like beak with serrated margins, and have lost the right carotid artery.

The geographical distribution of the order is that of an ancient group, and perhaps was accomplished, at least as far as continental distribution was concerned, by early Tertiary times. The continental families Pelecanidae and Anhingidae are found on all the major land masses. All families are represented in Australasia. Anhingidae are the most land-bound of the order, and the remaining families, arranged in order of increasingly greater oceanic distribution are (Murphy, 1936) Pelecanidae, Phalacrocoracidae, Fregatidae, Sulidae, and Phaëthontidae. The last are truly pelagic.

Fossil representatives of the Pelecaniformes are fairly numerous, and indicate the group to be an ancient one, being well diversified at the beginning of the Tertiary. The suborder Odontopteryges, from the Eocene, had tooth-like serrations on the margins of the beak; it is generally agreed that they did not posses true teeth. *Odontopteryx,* the type genus, is steganopodous in character, but cannot be referred to any of the living subdivisions of the order. *Pseudodontornis,* of unknown age, also had tooth-like pegs in the beak, and was evidently a large fish-eating bird. It is referred provisionally to the order by Lambrecht (1933). *Prophaëthon,* of Eocene age, is intermediate in many respects between the suborder Phaethontes and the rest of the Pelecaniformes. *Cyphornis* and *Paleochenöides,* from the Miocene of North America, are referred by Wetmore (1928) to a single family, Cyphornithidae, which is most nearly related to the pelicans. *Cyphornis* was a gigantic bird, about twice as large as a modern pelican. Both genera show suloid characters, and are somewhat intermediate between the superfamilies Pelecanoidea and Suloi-

dea. The genera *Pelagornis* (Miocene) and *Argillornis* (Eocene) are placed by Lambrecht in the superfamily Suloidea; they show some relationship to *Sula*. For convenience, both may be put arbitrarily into a single family, Pelagornithidae. The family Elopterygidae contains three genera: *Elopteryx* (Cretaceous), *Eostega* (Eocene), and *Actiornis* (Eocene). They show relationship to both the Sulidae and Phalacrocoracidae. The family may provisionally be considered as an intermediate group. *Miosula,* placed in the Sulidae, is annectant between the gannets and cormorants, as Miller (1925), has pointed out. Fossil cormorants, hardly different from living genera, are found in the Oligocene. *Protoplotus,* from the early Tertiary (probably Eocene), is referred by Lambrecht to the Anhingidae. This early differention of the anhingid stock implies the existence of cormorants in early Tertiary times, since the anhingids were undoubtedly derived from them.

The relationship between the Pelecaniformes and Procellariiformes is of such a nature as to suggest the former to have been derived from a primitive procellariiform stock. It seems likely that the broad lines of phylogenesis were accomplished in Crataceous times.

A hypothetical phylogeny is presented in the accompanying chart. The classification here used may be expressed in tabular form as follows:

ORDER PELECANIFORMES
- SUBORDER PHAËTHONTES
  - FAMILY PHAËTHONTIDAE
- SUBORDER FREGATAE
  - FAMILY FREGATIDAE
- SUBORDER PELECANI
  - SUPERFAMILY PELECANIDES
    - FAMILY PELECANIDAE
    - CYPHORNITHIDAE (extinct)
  - SUPERFAMILY SULIDES
    - FAMILY PELAGORNITHIDAE (extinct)
    - SULIDAE
    - ELOPTERYGIDAE (extinct)
    - ANHINGIDAE
    - PHALACROCORACIDAE
- SUBORDER ODONTOPTERYGES (extinct) (of uncertain position)
  - FAMILY ODONTOPTERYGIDAE
  - PSEUDODONTORNITHIDAE (of uncertain position)

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VARIATIONS IN COLOR OF THE SHOULDERS OF THE MALE GOLDFINCH

BY HORACE GROSKIN

DURING the six-year period, 1940 to 1946, I banded 1,249 Eastern Goldfinches, *Spinus tristis tristis,* in Ardmore, Montgomery County, Pennsylvania. Forty-two birds (3.36%) returned to Ardmore in the following years. Some returned one year after banding and again a second and third year, while others were not recaptured until two or three years after banding.

When the birds were banded, their wings were measured. The closed-wing measurement, or the chord, was taken of a series of 1,027