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A Lower Eocene Frigatebird from the Green River Formation of Wyoming (Pelecaniformes: Fregatidae)

Storrs L. Olson

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ABSTRACT

Olson, Storrs L. A Lower Eocene Frigatebird from the Green River Formation of Wyoming (Pelecaniformes: Fregatidae). *Smithsonian Contributions to Paleobiology,* number 35, 33 pages, 31 figures, 1977.—A new subfamily, Limnofregatinae, is erected for the first known Tertiary specimens of the pelecaniform family Fregatidae. These are described as a new genus and species, *Limnofregata azygosternon*. The holotype is a nearly complete skeleton with feather impressions. Two additional specimens, consisting of a partial skeleton and a fragment of ulna, are referred to the same species. All are from freshwater lake deposits in the Lower Eocene Green River Formation of Wyoming, which are roughly 50 million years old. The principal differences between *Limnofregata* and modern frigatebirds *(Fregata)* are seen in its shorter and less hooked rostrum, proportionately shorter wings and longer hindlimb, in the lack of fusion in the pectoral girdle, and in the lack of extensive pneumatization of the skeleton. The fossil form is, nevertheless, well advanced along the lines of modern frigatebirds and nothing in its morphology seems to preclude its being ancestral to *Fregata*. The fossil provides additional support for placing the suborder Fregatae between the more primitive tropicbirds (suborder Phaethontes) and the members of the suborder Pelecani. Frigatebirds in the early Tertiary evidently occupied different habitats or a wider range of habitats than the modern forms and have only subsequently been restricted to a purely oceanic environment.

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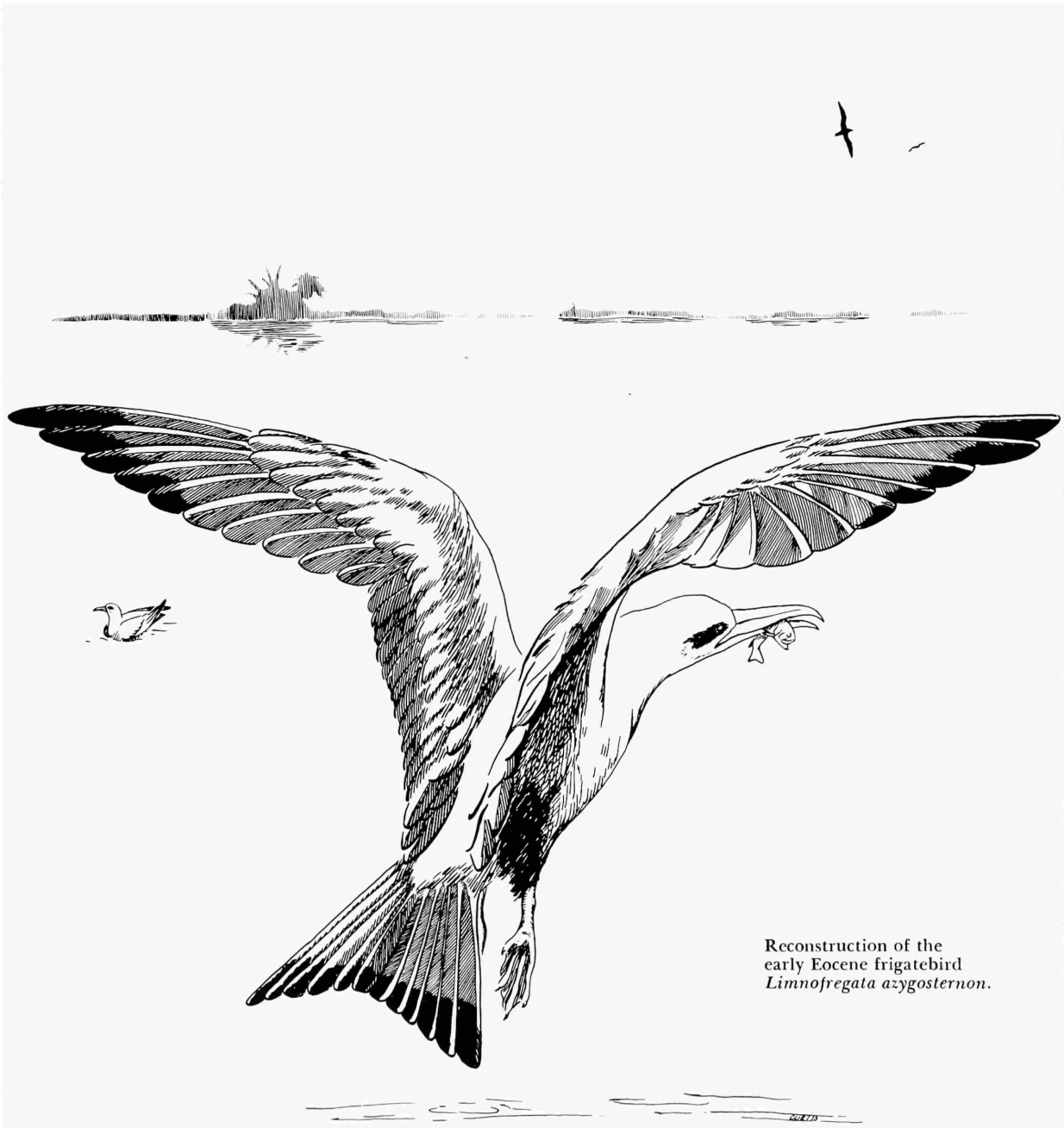

Reconstruction of the
early Eocene frigatebird
Limnofregata azygosternon.

A Lower Eocene Frigatebird from the Green River Formation of Wyoming (Pelecaniformes: Fregatidae)

Storrs L. Olson

Introduction

Among paleontologists it is often said that the best collecting is to be done in museums. The truth of this became quite evident to me in 1973, when in the collections of the National Museum of Natural History I encountered a nearly complete skeleton of an unidentified bird from the Green River Formation of Wyoming. This had been accessioned in 1960 but had never been studied subsequently. After a bit of chipping away at the matrix covering critical portions of the skeleton, I was soon convinced of the importance of this specimen, and further preparation revealed it to be of considerable significance in interpreting aspects of the evolution of the Pelecaniformes.

The modern members of the order Pelecaniformes are placed in three suborders and six essentially monogeneric families: Phaethontes (Phaethontidae, tropicbirds), Fregatae (Fregatidae, frigatebirds), and Pelecani (Pelecanidae, pelicans; Sulidae, gannets and boobies; Phalacrocoracidae, cormorants; Anhingidae, anhingas). The first two suborders are considered to be the most aberrant of the order and it has at times been suggested that each might be more closely related to some avian order other than the Pelecaniformes (see Sibley and Ahlquist, 1972, for a summary of the history of classification of Pelecaniformes).

Until now, there has been no fossil record of the Fregatidae other than Pleistocene to Recent specimens of extant species of *Fregata* found on St. Helena (Olson, 1975) and Fernando de Noronha (Olson, in prep.) in the South Atlantic. Thus, the Eocene fossil that is the subject of this paper is of great interest, for it is unquestionably a frigatebird. Although it is a primitive frigatebird, within the order it is sufficiently specialized to be regarded as belonging to the same family as the modern genus *Fregata*. It is certainly as much a frigatebird as its contemporary *Hyracotherium* (="*Eohippus*") is a horse. *Hyracotherium* is placed in the family Equidae, along with modern horses, but is maintained in a separate subfamily. I propose a similar treatment for the Eocene frigatebird.

It is often not generally appreciated that the addition of a new genus to a monogeneric family necessitates a redefinition of that family, and likewise that the erection of a new subfamily within such a family requires a diagnosis for the newly formed nominate subfamily as well. Therefore, I have briefly attempted such diagnoses in the following pages, these being based entirely on osteological characters, inasmuch as these are all that are available for the fossil form.

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ACKNOWLEDGMENTS.—The careful preparation of the holotype of the new species was undertaken by Leroy Glenn, who spent many hours at this task. I am grateful to the Division of Vertebrate Paleontology, National Museum of Natural History, Smithsonian Institution, and particularly to Nicholas Hotton III, for allowing this work to be done. I thank Harrison Sheng and Daniel J. Stanley for X-ray photographs of the specimen that facilitated its preparation. I am indebted to Paul O. McGrew for providing information and for photographs of the University of Wyoming specimen, to Pierce Brodkorb for calling it to my attention, and to Alan Feduccia for lending a cast. Lloyd F. Gunther is acknowledged for his kind donation of the paratypic ulnar fragment. The drawings (except Figures 3, 6, and 8) are the work of Deborah R. Horner; the life reconstruction was done by Anne Curtis; and the photographs (except Figure 4) were taken by Victor E. Krantz. I thank these people for helping to make the subject of this paper one of the best illustrated of Tertiary birds. For comments and criticisms that have much improved the manuscript I am indebted to John Farrand, Jr., M. Ralph Browning, Robert J. Emry, Frances C. James, Larry D. Martin, and David W. Steadman.

Order PELECANIFORMES Sharpe, 1891

Suborder FREGATAE (Sharpe, 1891)

INCLUDED FAMILY.—Fregatidae.

DIAGNOSIS.—As for the family.

Family FREGATIDAE Garrod, 1874

INCLUDED SUBFAMILIES.—Fregatinae, new rank; Limnofregatinae, new subfamily.

DIAGNOSIS.—Hindlimb more reduced than in other Pelecaniformes. Tarsometatarsus proportionately the shortest of the order, less than 20% of total hindlimb length (23% to 26% in other families). Sternum short, width as great as or greater than length (length greater than width in remainder of order). Cervical vertebrae longer and narrower than in *Phaethon* and lacking the hemal arches and the abrupt change in structure within the series that characterize the Pelecani. Deltoid crest of humerus large and triangular (unlike the Pelecani in which this crest is greatly reduced) and not situated as far distally as in the Phaethontes.

Subfamily FREGATINAE, new rank

INCLUDED GENUS.—*Fregata* Lacépède, 1799.

DIAGNOSIS.—Rostrum dorsoventrally flattened, strongly hooked at tip. In adults, bony nostril open only posteriorly. Rostrum twice as long as cranium. Furcula fused both to sternum and to coracoids. Scapular facet of coracoid convex; coracoidal articulation of scapula indistinct. Posterior border of sternum between posterolateral processes entire. Posterior portion of pubis expanded. Humerus with deltoid crest sharply triangular; bicipital surface oval, inflated, and extending distally well down the shaft. Wing long in proportion to body; hindlimb short, tarsometatarsus greatly reduced, only about 15% of total length of hindlimb. Skeleton highly pneumatized nearly throughout.

Subfamily LIMNOFREGATINAE, new subfamily

INCLUDED GENUS.—*Limnofregata,* new genus.

DIAGNOSIS.—Rostrum not markedly flattened dorsoventrally and only moderately hooked at tip. Bony nostril open in a long slit. Rostrum only 1.5 times as long as cranium. Furcula entirely free from sternum and coracoids. Scapular facet of coracoid concave; coracoidal articulation of scapula prominent. Posterior border of sternum four-notched. Pubis of nearly uniform width. Deltoid crest of humerus not acutely pointed; bicipital surface and crest reduced, not extending distally down the shaft and not inflated. Wing about 12% shorter in proportion to body size than in Fregatinae; hindlimb relatively longer, tarsometatarsus forming 19% of total length of hindlimb. Skeleton not highly pneumatic, apparently only the humerus and perhaps the femur with small pneumatic openings.

Limnofregata, new genus

TYPE-SPECIES.—*Limnofregata azygosternon,* new species.

DIAGNOSIS.—As for the subfamily.

ETYMOLOGY.—From the Greek *limne* (a marshy lake) and the generic name *Fregata* (from Italian

fregata, a swift warship, a frigate; used as the generic name of modern frigatebirds after that applied in the vernacular by pre-Linnean authors who were alluding to the superior flying ability and piratical habits of these well-known seabirds). The generic name of the fossil form is intended to refer to the lacustrine habitat in which its remains were interred.

Limnofregata azygosternon, new species

HOLOTYPE.—Nearly complete, partially flattened skeleton with feather impressions, vertebrate paleontological collections of the National Museum of Natural History, USNM 22753 (Figures 1, 2, and others); collected in 1960 or previously by M. L. Larsen.

TYPE-LOCALITY.—"On the north side of Highway 30 North. At an elevation of 7250 ft [2250 m] near the old diggings of Dave Haddenhams at Fossil, [Lincoln County], Wyoming" (M. L. Larsen *in litt.* to G. A. Cooper, 24 January 1961). This locality is now within Fossil Butte National Monument.

HORIZON.—Fossil Butte Member, Green River Formation, late early Eocene.

ETYMOLOGY.—From the Greek *azygos* (unyoked) and *sternon* (breast or chest), in allusion to the lack

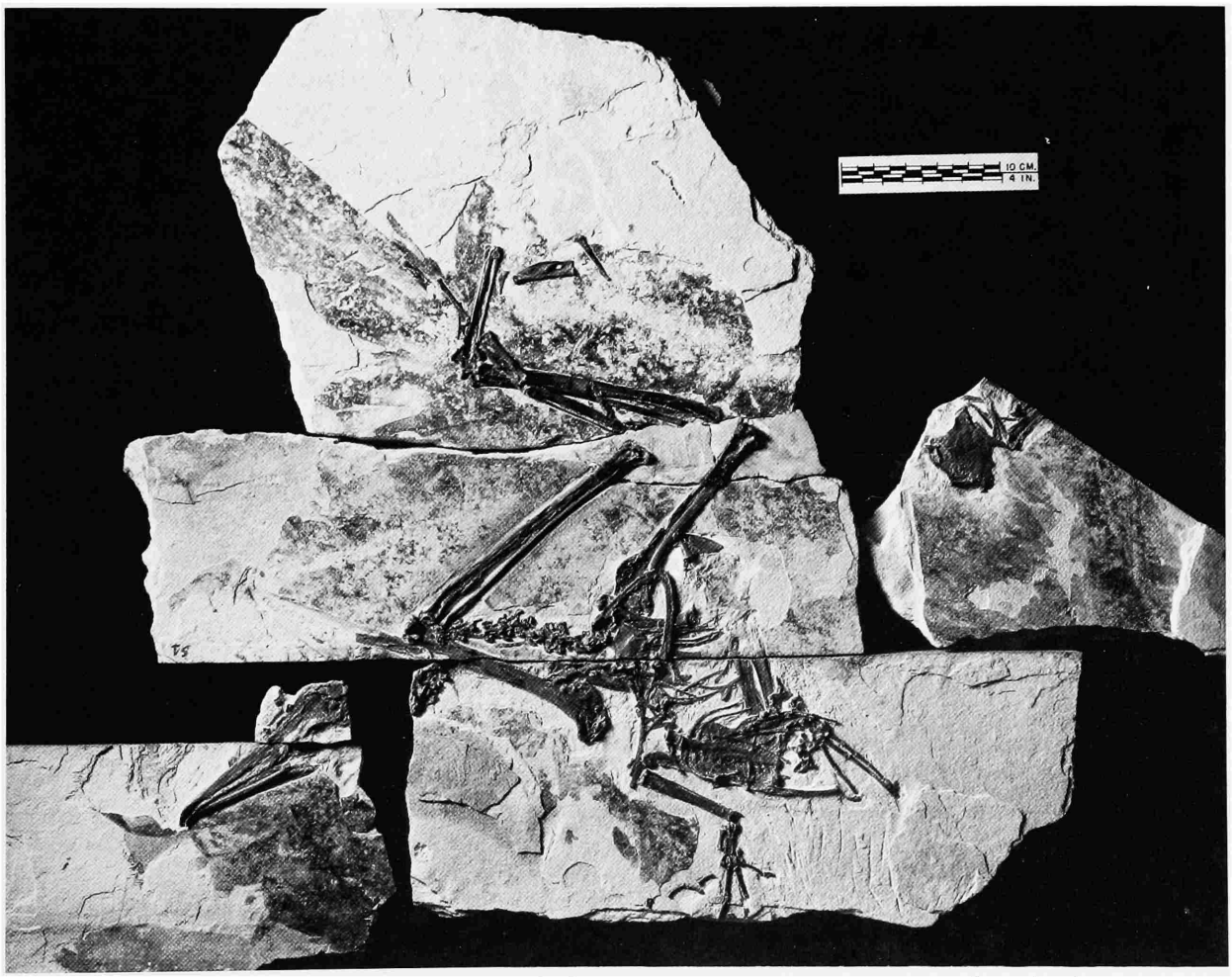

FIGURE 1.—Holotype (USNM 22753) of *Limnofregata azygosternon,* new genus and species, in three pieces of slab and two of counterslab before any of the individual bones were removed from the matrix.

of fusion in the elements of the pectoral girdle. The specific name is a neuter noun in apposition.

PARATYPES.—University of Wyoming 6919 (Figure 4); partial skeleton; from SE 1/4, Sec 16, T21N, R117W, Lincoln County, Wyoming; Fossil Butte Member, Green River Formation, probably Lost Cabinian, late early Eocene; collected by Carl Ulrich.

USNM 243766 (Figure 22); proximal fourth of right ulna; collected from the Green Riven Formation near Kemmerer, Lincoln County, Wyoming, by Lloyd F. Gunther.

MEASUREMENTS.—Unless otherwise indicated, the following measurements are taken from the holotype of *Limnofregata azygosternon*. All are in millimeters.

SKULL AND MANDIBLE.—Length of mandible 122.7; length of rostrum from posterior margin of nostril to tip 67.6; greatest depth of mandible (at surangular) 9.6; least depth of mandible 4.5; height of quadrate from posterior portion of mandibular articulation to tip of otic process 15.3; width of interorbital bridge ca. 17; length of lacrimal attachment 12.2.

VERTEBRAE (measurements in parentheses are from a small male of *Fregata ariel,* USNM 497972, of the same body size as *L. azygosternon*).—Height of atlas from ventral margin of centrum to dorsal margin of lateral process 9.0 (9.0); length of axis from anterior surface of centrum to posterior margin of hypapophysis 9.4 (8.1); length of 3rd cervical from anterior margin of prezygapophysis to posterior margin of anapophysis 13.6 (13.0); length of 4th cervical taken in the same manner 15.0 (14.0); length of centrum of 5th cervical 10.8 (12.0); length of centrum of 8th cervical 11.8 (12.7); length of centrum of 10th cervical 11.4 (13.0); length of centrum of 15th cervical 7.6 (10.0); length of centrum of 16th vertebra 7.2 (9.9); length of centrum of 19th vertebra 8.9 (9.2); height of 5th caudal 8.9 (9.9); width across transverse processes of 6th caudal 14.8 (18); height of 6th caudal 10.8 (11.7).

PELVIS.—Length of synsacrum 61.5; width across anterior expansion of ilia 33.2; length of ilium ca. 82; width across antitrochanters ca. 40.

CORACOID.—Length from head to internal distal angle 61.8; length of glenoid facet 12.0; length from head to lowest point of glenoid facet 17.9; width of sternal end ca. 25.

SCAPULA (measurements in parentheses from cast of University of Wyoming specimen).—Length 67.6 (67.7); width of proximal end 11.4 (11.6); width of shaft at midpoint, [obscured in holotype] (5.0).

FURCULA.—Length from anterior initiation of coracoidal expansion to tip of hypocleidium 57.8.

STERNUM.—Length from internal anastamosis of sulci to xiphium ca. 45; width at level of 1st costal facet 52 (estimated); distance from carinal apex to xiphium 56.6; length from first to last costal facet 16.7.

HUMERUS.—Overall length ca. 140; proximal width (above deltoid crest) 25.7; length of deltoid crest 29.5; length of external condyle 10.6; approximate distal width 18.5.

ULNA.—Length 166 (from cast of University of Wyoming specimen). Depth of distal end ca. 12.5 (estimated from holotype). The following measurements are from the paratype USNM 243766: proximal width 10.1; proximal depth 14.2; length of prominence for anterior articular ligament 14.0.

RADIUS.—Depth of distal end ca. 9.5; shaft width at midpoint 4.0.

RADIALE.—Greatest diameter 10.5.

ULNARE.—Greatest diameter 11.7.

CARPOMETACARPUS.—Length 80; length of intermetacarpal space 51.4; proximal depth ca. 17.5; length of metacarpal I 10.2; depth of distal end 10.8.

PHALANGES OF MANUS.—Digit I, length 25.2, proximal depth 5.5; digit II phalanx 1, length 39.8, distal depth 10.1; digit II phalanx 2, length 33.3, proximal depth 6.7; digit III, length 15.8, proximal depth 4.4.

FEMUR.—Length ca. 55; distal depth ca. 10; transverse diameter of head 5.3.

TIBIOTARSUS.—Overall length 67; width through condyles 8.4.

FIBULA.—Proximal depth of head 3.6.

TARSOMETATARSUS.—Overall length 26.7; proximal width 9.6; least width of shaft 5.6; width across trochleae 11.3; width of middle trochlea 3.5.

METATARSAL I.—Length 10.4.

PHALANGES OF PES (lengths). Digit I: phalanx 1, 15.1; phalanx 2, 8.1. Digit II: phalanx 1, 19.3; phalanx 2, 18.1; phalanx 3, 9.2. Digit III: phalanx 1, 19.3; phalanx 2, 19.8; phalanx 3, 18.0; phalanx 4, lacking. Digit IV: phalanx 1, 12.2; phalanx 2, 11.0; phalanx 3, 10.4; phalanx 4, 13.3; phalanx 5, 7.5.

PRESERVATION AND PREPARATION OF THE SPECIMENS.—The greater part of the holotype skeleton is preserved on a large slab of soft, cream-colored, varved oil shale, now broken into three pieces, one of the breaks being due to a natural cleavage in the rock. Most of the skull and the sternum were in smaller pieces of the counterslab (Figure 1). Numerous fragments of both slab and counterslab bear feather impressions. All of the bones are a rich, dark brown in color; the feather impressions are black and are mostly indistinct except for the primaries of the right wing, the tips of which are lacking.

As now viewed (Figures 1, 2), the specimen appears to be lying more or less on its back, with the right side uppermost. The pelvis faces ventral side upward, and both wings extend out in front of the body with their internal aspect upward. The skull and mandible had been broken into four pieces, but when these were united very little was found to be missing, although the resulting specimen is greatly flattened and difficult to interpret. The neck extends forward over the right wing and there appears to have been a postmortem separation of the cervical vertebrae where they cross over the right humerus. On the right wing, impressions of the alula and some of the primaries are clearly preserved. A section of the shafts of the radius and ulna (restored with wax for the photographs) and the proximal end of the carpometacarpus and the carpals are missing from the right wing. Part of the proximal end of the left humerus is covered by the left coracoid, and most of its distal end (restored), as well as the proximal ends of the left radius and ulna, are missing; the distal elements of this wing, however, are all present and well preserved. Bones of the thoracic region are jumbled and overlap each other considerably. The external surface of the right coracoid is exposed, but the bone has been cleft by a fault in the shale and is poorly preserved. Most of the left coracoid is exposed in internal view, being partly overlain by the furcula, ribs, and right coracoid. Most of the furcula is exposed in anterior view. Most of the right scapula is exposed, while all but the posteriormost part of the left scapula is obscured. The pelvis, with the last thoracic vertebra, is clearly exposed in ventral view and overlaps all but the head and the internal distal aspect of the right femur and much of the trochanter of the left femur. The tibiotarsi and tarsometatarsi on both sides are seen in posterior view, whereas the toes on both sides are seen in anterior view. It is difficult to conceive of just how the tibiotarsi and tarsometatarsi of this specimen could have turned over completely on their longitudinal axes without being displaced laterally or affecting the orientation of the femora and toes. Three whole phalanges and two halves are missing from the right foot and the ungual phalanx of the left third toe is also lacking. Caudal vertebrae, perhaps as many as seven, are scattered over and under the left foot and posterior portions of the pelvis. Unfortunately, the pygostyle appears to be absent and there are no remaining impressions of tail feathers. Most of the sternum, the distal portion of the left femur, and the proximal portion of the left tibiotarsus came away with a small piece of counterslab. The sternal carina remained on the main slab.

In preparing the holotype, all the portions of the skull and mandible were united and entirely removed from the matrix. The right humerus and right tibiotarsus, tarsometatarsus, and toes were likewise freed in order to be able to study both sides of the specimens. Also, the carina was removed from the main slab and joined with the rest of the sternum.

Of the paratype at the University of Wyoming (Figure 4), I have studied an accurate cast and photographs. The specimen consists of most of the right wing, lacking only phalanx 2 and the distal half of phalanx 1 of digit II. The humerus is in palmar view, whereas the rest of the wing is seen from the opposite side. Also present are most of the vertebral column, ribs, and the right scapula, right coracoid and the furcula in right lateral view. The specimen is identical in size and all other respects to the holotype and there is no question that the two specimens are referable to the same species.

The paratypic proximal end of an ulna (Figure 22) would probably have been unidentifiable by itself. When compared with the ulna of the holotype, however, it was found to be morphologically identical. The specimen is black in color and is very little distorted by compression.

Description

In the illustrations and descriptions, *Limnofregata* has been compared chiefly with *Sula* and

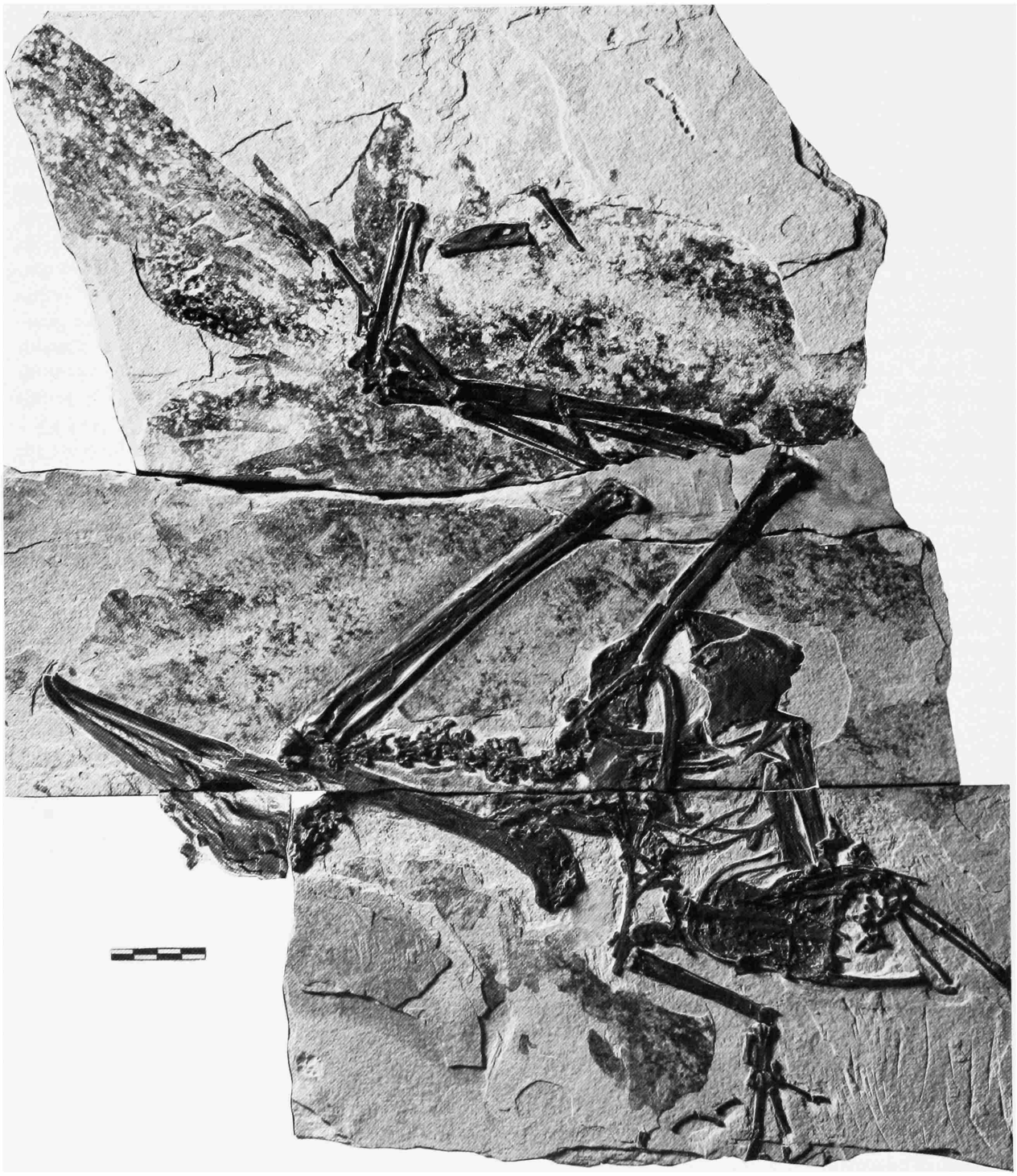

FIGURE 2.—Retouched photograph of the holotype of *Limnofregata azygosternon* (USNM 22753). The skull, body of the sternum, distal end of the left femur, and proximal end of the right tibiotarsus are shown in reverse in order to present the entire specimen associated as it was originally preserved. (Scale = 40 mm)

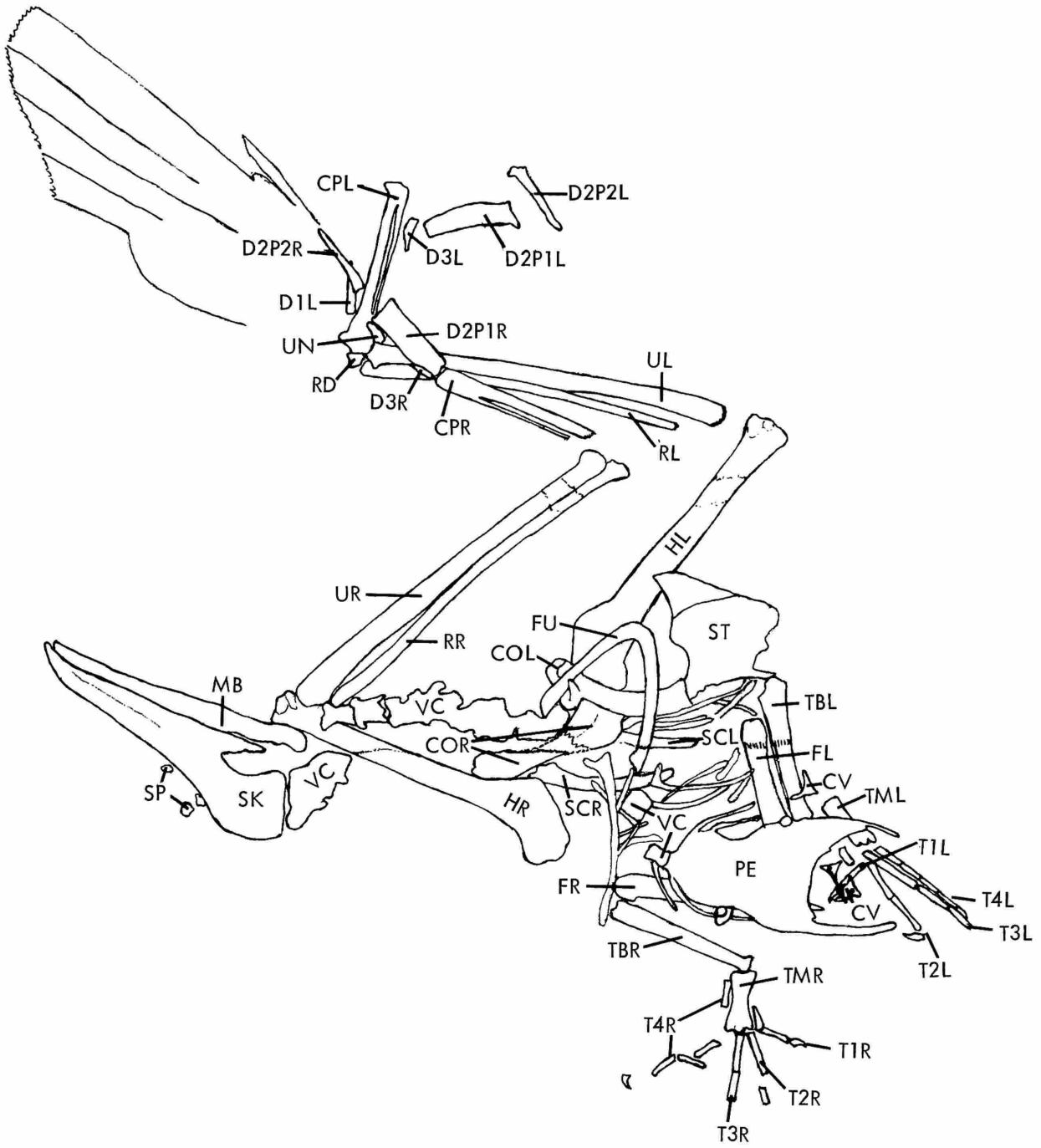

FIGURE 3.—Diagram identifying various parts of the specimen shown in Figure 2. (Abbreviations ending with L indicate the element is from the left side, while R indicates the right side; CO = coracoid, CP = carpometacarpus, CV = caudal vertebra, D1 = first digit, D2P1 = second digit first phalanx, D2P2 = second digit second phalanx, D3 = third digit, F = femur, FU = furcula, H = humerus, MB = mandible, PE = pelvis, R = radius, RD = radiale, SC = scapula, SK = skull, SP = sclerotic plates, ST = sternum, TB = tibiotarsus, TM = tarsometatarsus, T1 = first toe, T2 = second toe, T3 = third toe, T4 = fourth toe, U = ulna, UN = ulnare, VC = vertebral column.)

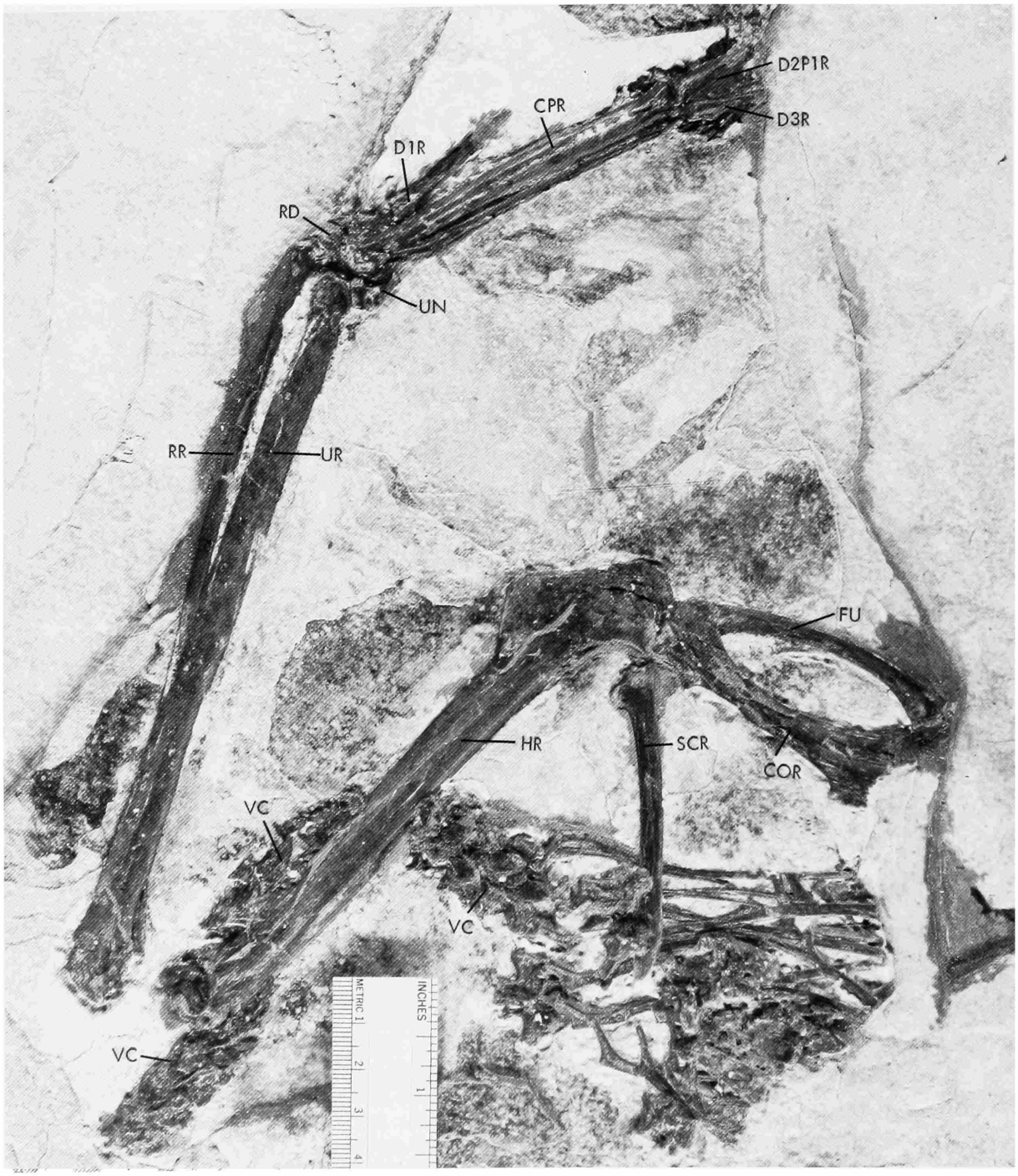

FIGURE 4.—Partial skeleton of *Limnofregata azygosternon*, paratype, University of Wyoming 6919. (Abbrevations as in Figure 3.)

Fregata, the intention being to show how the two genera of frigatebirds differ from each other and how both differ from the Pelecani. *Sula* was selected to represent the Pelecani, the Sulidae being the most primitive family of that suborder and, therefore, the most likely to share any characters with frigatebirds. More extensive comparisons of *Limnofregata* with the Phaethontes are planned for a later paper dealing with the fossil forms of that group. For the time being it can be said that *Limnofregata* is very distinct from the Lower Eocene genus *Prophaethon* Andrews, for which Harrison and Walker (1976) have recently created a new order, Prophaethontiformes. Their interpretation seems extreme and I believe that *Prophaethon* is best retained in the Pelecaniformes, within which it is on a line quite separate from *Limnofregata.*

Compared to modern frigatebirds, *Limnofregata* is decidedly small. The pelvis and sternum are very close in size to those of males (the smaller sex) of the modern species *Fregata ariel,* the smallest living member of the family. Therefore, *F. ariel* provides a convenient standard for comparing the limb proportions of the fossil and modern forms (Figure 31), since all the species of *Fregata* have very similar proportions. The following descriptions are based on the holotype of *L. azygosternon* unless otherwise stated. The degree of ossification of the limb bones of the holotype indicates that it was an adult, there being no sign of the porosity characteristic of juveniles. The three known individuals of *Limnofregata azygosternon* are virtually the same in size; either all three are of the same sex or there was no sexual dimorphism in size in the fossil form.

Skull and Mandible

The skull and mandible have been considerably flattened and are now essentially two-dimensional, the dorsal and left lateral aspects being seen on one side (Figures 5, and 6) and the ventral and right lateral aspects on the other (Figures 7, 8). The general shape of the bill is intermediate between that of *Sula* and *Fregata* (Figure 9). The tip of the rostrum is wider and not as deeply hooked as in *Fregata,* and probably did not curve downward past the tip of the mandible as in that genus. The tip of the rostrum is only slightly hooked in *Sula,* being most distinctly curved in *Sula sula.* The rostrum of *Limnofregata* bears no evidence of having been dorsoventrally compressed in life, as in *Fregata,* and in this respect is more similar to *Sula.* Compared to *Fregata,* the cranium in *Limnofregata* is proportionately larger and the bill shorter and again is more similar to that of *Sula* (the length of the rostrum is 1.5 times the length of the cranium in *Sula* and *Limnofregata,* and 2 times as long in *Fregata*).

Due to crushing it is difficult to determine the full extent of the nostril in *Limnofregata.* The posterior margin is distinct and lies a little less than 10 mm in front of the nasofrontal hinge. The nostril continues anteriorly as a well-defined open slit for at least 30 mm, beyond which the two sides have been pressed together, but it appears as though the nostril actually continued out nearly to the beginning of the hooked portion of the rostrum. In adults of *Fregata* the nostril is open only posteriorly (<5 mm in *F ariel,* for example) and in adults of the Sulidae it is closed altogether. In the juvenile stages of these and other Pelecaniformes, however, the nostrils are present as narrow openings running nearly the entire length of the rostrum (Figure 9). These become occluded by bone in later stages of development. Obviously, a long, open nostril is the primitive condition and this appears to have been retained in adults of the Eocene frigatebird.

There are other indications that the skull of *Limnofregata* was less ossified than in adults of *Fregata* and more similar to juveniles of that genus. In ventral aspect there is less ossification between the anterior portions of the palatine and quadratojugal bar. In lateral aspect there is less ossification in the space between the quadratojugal bar and the nasal. The quadratojugal bar is straight and narrow, slightly more expanded posteriorly. It is quite similar to that of *Fregata,* but proportionately heavier, and it lacks the great expansion in the anterior portion seen in the Sulidae. It is broader posteriorly than in *Phaethon.*

There are no grooves for salt glands on the dorsal surface of the skull. If salt glands were present in *Limnofregata,* they would have to have been inside the orbit, as in all other Pelecaniformes. The orbits are proportionately much larger than in *Sula* or *Fregata,* their size being more like that of *Phaethon,* although the greater curvature of the dorsal

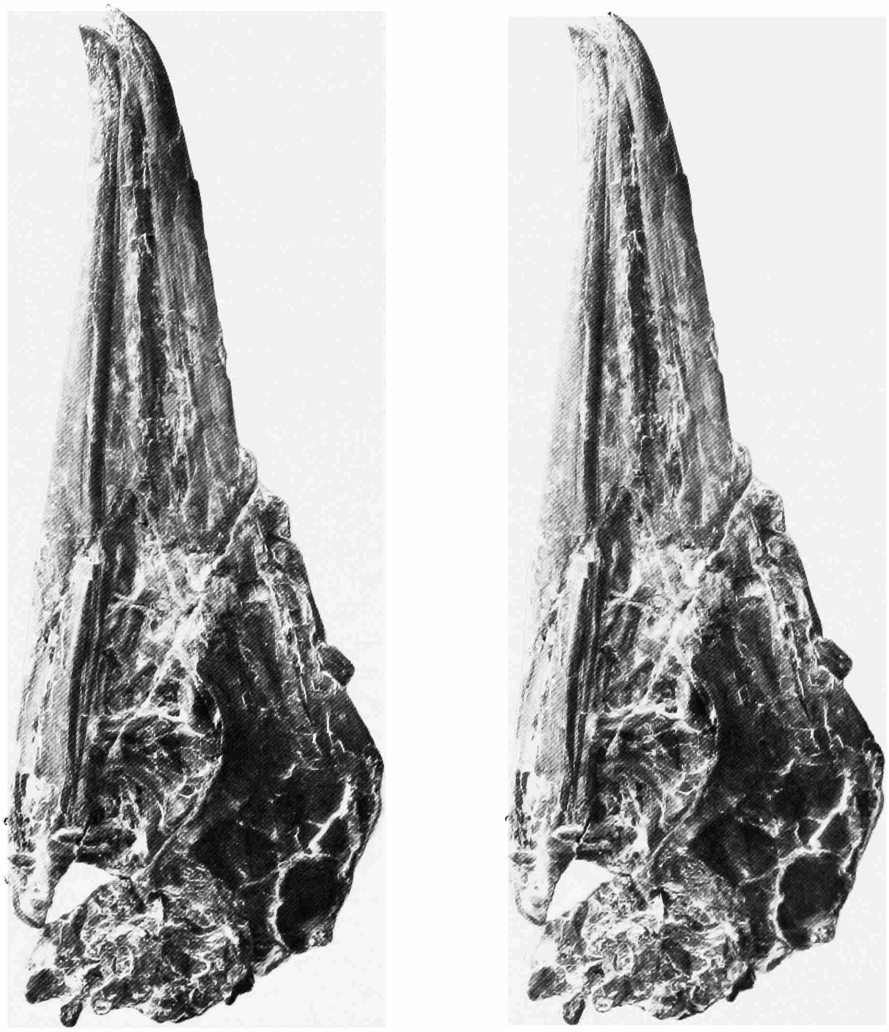

FIGURE 5.—Dorsolateral view of the skull and mandible of the holotype of *Limnofregata azygosternon*. (Stereopair, natural size)

rim is more similar to *Fregata*. The orbital rims are thin and turn upwards more than in *Fregata*. The postorbital process is shorter and more blunt than in *Fregata* or *Phaethon,* but is unlike the short expanded process of *Sula*. The otic area, with the quadrate articulation, is very similar to that of *Fregata* and differs markedly from *Phaethon* and also from *Sula,* in which the opisthotic is directed posteriorly rather than ventrally as in *Fregata* and *Limnofregata*. The occipital condyle is larger and more bulbous than in *Fregata,* in which the occipital condyle is slightly notched and somewhat triangular. The occipital condyle is proportionately much larger in *Phaethon* and smaller in *Sula* than in *Limnofregata*.

Except for part of the right palatine, most of the palate is obscured. The palatine is long and narrow, not inflated, and more closely resembles the juvenile than the adult condition of *Fregata*. Enough of the left pterygoid is visible to show that it is similar to that of *Fregata,* though slightly stouter, and unlike the long slender rod of *Phaethon* or the flat, expanded pterygoid of *Sula*. The lacrimal is free and differs considerably from that of *Fregata* and other known Pelecaniformes. The body of the bone is long, oriented nearly horizontally,

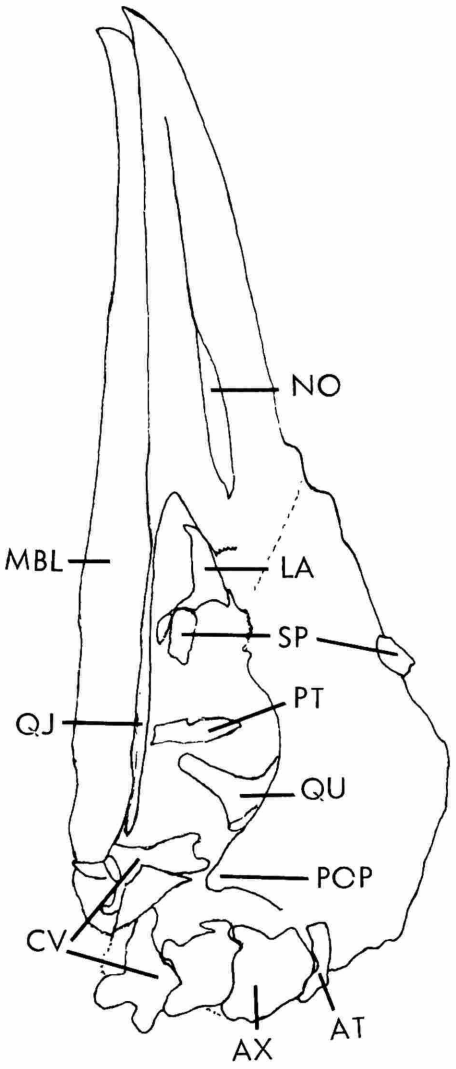

FIGURE 6.—Diagram of the specimen shown in Figure 5 (AT = atlas, AX = axis, CV = cervical vertebrae, LA = lacrimal, MBL = left mandibular ramus, NO = nostril, POP = postorbital process, PT = pterygoid, QJ = quadratojugal, QU = left quadrate, SP = sclerotic plates).

and is distinctly pointed both anteriorly and posteriorly. In *Fregata* the body of the lacrimal is short, oriented more vertically and is broad and rounded posteriorly. In *Limnofregata* the descending process of the lacrimal comes more from the posterior than the anterior portion of the bone and appears to be rather short and pointed. However, there is another small piece of bone extending ventroposteriorly from this process and abutting the quadratojugal (Figure 5); this may represent part of the lacrimal or possibly the os uncinatum. There is a thin elongate scar on the frontal for the attachment of the lacrimal. The left quadrate is preserved upside-down in the left orbit, with much of its internal aspect visible on the left side of the specimen and the articular socket for the quadratojugal protruding on the other side near the right mandibular articulation. It is distinctive in that the otic process is very elongate. As in *Fregata,* the quadrate appears almost single-headed, lacking the deep notch between the heads that is typical of *Sula.*

The mandible is more similar to that of *Fregata* than it is to any of the other members of the order. It differs from *Fregata* as follows: dentary proportionately shorter and postdentary portion of mandible longer; rami much deeper, not markedly narrowed as in *Fregata*; mandibular symphysis shorter and less deeply hooked; notch for articulation of quadrate in lateral view noticeably deeper. The different proportions of the mandible are in accordance with the proportionately shorter rostrum and longer cranium of *Limnofregata.*

PRESACRAL VERTEBRAE

Although the vertebral column is imperfectly preserved, a number of important features can be discerned. In general, the presacral vertebral series of *Limnofregata* is much more similar to that of *Fregata* than to other Pelecaniformes. A positive count cannot be made, but it is almost certain that *Limnofregata* had the same number of vertebrae as *Fregata* (15 cervicals and 4 thoracics). It did not have the larger number of cervicals (17 to 20) found in the higher pelecaniform families. The cervicals are fairly elongate, as in *Fregata,* and are quite distinct from the short, wide cervicals of *Phaethon.*

The atlas of *Limnofregata* is seen in left ventrolateral view and is very similar to that of *Fregata,* though slightly thicker anteroposteriorly, lacking the expanded neural arch of *Sula* and being lower and broader than in *Phaethon.* The axis can be seen in left lateral and partial right lateral view and is still articulated with the atlas. It differs most notably from *Sula* in that the hypapophysis is not an elongated, posteriorly directed spine. From *Phaethon* it differs in its less developed neural spine. It resembles the axis of *Fregata* but is proportionately larger and heavier, with the distance from

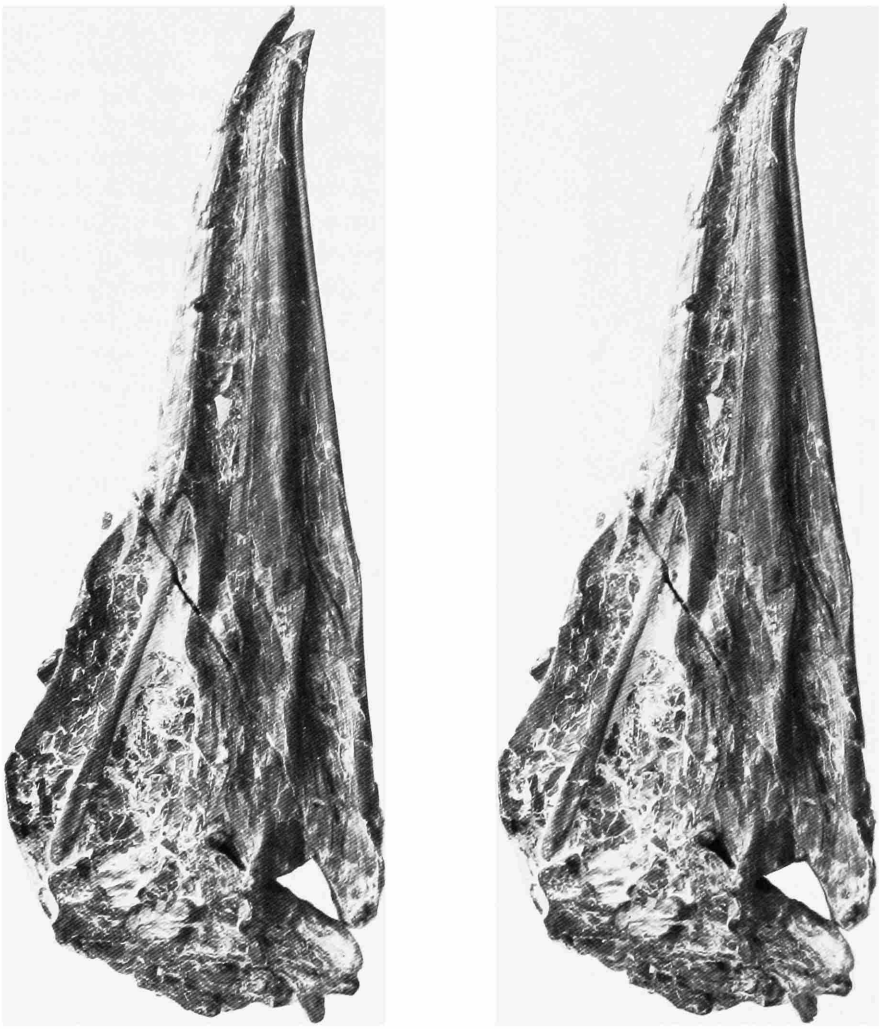

FIGURE 7.—Ventrolateral view of the skull and mandible of the holotype of *Limnofregata azygosternon*. (Stereopair, natural size)

the anterior surface of the centrum to the beginning of the hypapophysis being greater, and the neural spine being lower, directed more posteriorly, and not being inflated.

The third cervical is partially disarticulated and is displaced ventrally and laterally from the axis, though it still presents its left lateral aspect. Like the axis, this vertebra differs from *Sula* in the much lesser development of the hypapophysis. It resembles that of *Fregata* and *Phaethon* but differs from the former in having the styliform process much smaller (although larger than in *Phaethon*) and from the latter in the larger, more inflated anapophysis.

The fourth cervical is turned so that it is seen principally in dorsal, and partly in ventral, view. It is markedly different from that of *Sula*. In dorsal view the notch between the postzygapophyses is deeper and U-shaped, and it is quite different from the very deep and V-shaped notch of *Phaethon*. In ventral view, the articular surfaces of the postzygapophyses are seen to be markedly longer and narrower (4.0 × 1.8 mm) than in *Fregata*, in which these surfaces are more rounded (3.4 × 2.3 mm in

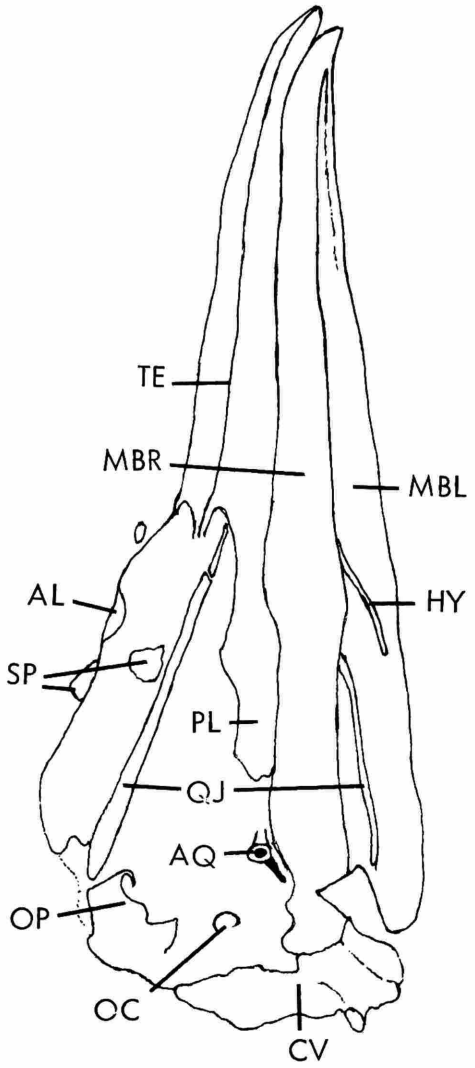

FIGURE 8.—Diagram of the specimen shown in Figure 7 (AL = articular surface for lacrimal, AQ = quadratojugal articulation of left quadrate, CV = cervical vertebrae, HY = hyoid, MBL = left mandibular ramus, MBR = right mandibular ramus, OC = occipital condyle, OP = opisthotic, PL = palatine, QJ = quadratojugal, SP = sclerotic plates, TE = right tomial edge of rostrum).

♂ *F. ariel*). In *Phaethon* the postzygapophyses of the fourth cervical are extremely attenuated, unlike either genus of frigatebird.

The fifth cervical is completely detached from the fourth and lies with its ventral side up in the posterior corner of the orbit, the posterior end overlapping the left mandibular articulation. A small triangular piece of bone and matrix is missing from this region in the holotype but it does not appear extensive enough to have held another vertebra. The fifth cervical of *Limnofregata* is longer and narrower than the corresponding vertebra in *Phaethon* or *Sula* and lacks the high neural crest of the latter. It is very similar to that of *Fregata* but is proportionately shorter, with longer styloid processes and a deeper posterior surface of the centrum.

The remainder of the cervical series of the holotype lies in a more or less articulated row, ventral side uppermost. As mentioned, there appears to have been a natural postmortem separation of the neck where it crossed the right humerus. If so, the next vertebra in the series is indeed the sixth. This is further supported by counting anteriorly from the reference point provided by the noticeable transition between the 12th and the 13th cervicals, which is present in both the modern and fossil forms.

Vertebrae 6 through 9 are similar to each other and, as far as can be seen, are very similar to those of *Fregata,* the only difference noted being that the articular surfaces of the postzygapophyses are proportionately larger in *Limnofregata,* while the overall size of the vertebrae is smaller. In both genera these vertebrae possess two well-developed catapophyses. The anterior portion of the 9th cervical is obscured in the holotype of *Limnofregata,* but beginning with the 10th and continuing through the 12th vertebra there is a fairly well-developed semilunar hypapophyseal crest on the anterior half of the centra. No such crests are present in *Fregata;* the 10th vertebra still has two prominent catapophyses, the 11th has these much reduced and placed closer together, and the 12th has only a single small protuberance on the anteroventral surface of the centrum. Vertebrae 10–12 of *Limnofregata* are otherwise quite similar to those of *Fregata. Sula* is very different in that vertebrae 9 through 13 have large hemal arches, a feature totally lacking in either genus of frigatebird.

Only the centrum of the 13th cervical is clearly discernable in *Limnofregata* and, as in *Fregata,* this is noticeably shorter than that of the 12th cervical. A low, thickened hypapophysis with a ridge running the length of the centrum in *Limnofregata* is nearly absent in *Fregata.*

Posterior to the 13th cervical is an area of crushed bone that must represent the 14th cervical, but it is too distorted to be interpreted. This is succeeded

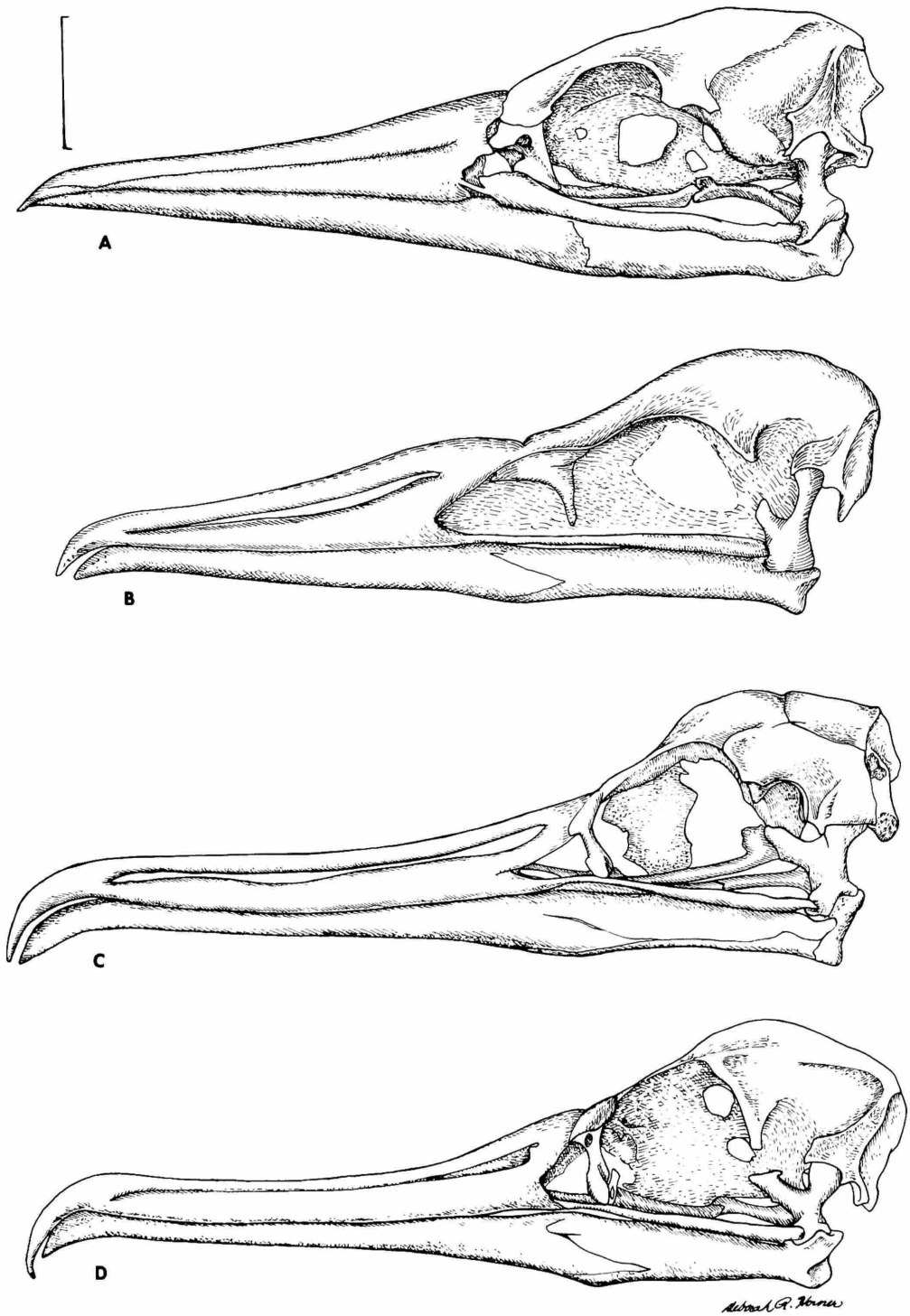

FIGURE 9.—Skulls and mandibles in left lateral view: A, *Sula sula;* B, *Limnofregata azygosternon* (the drawing is very generalized due to the difficulties in interpreting the crushed skull of the holotype and is not to be relied on for details); C, juvenile *Fregata minor* showing the very long, open nostril and the reduced ossification; D, adult *Fregata ariel.* (Scale = 20 mm)

by a centrum in ventral view, no doubt that of the 15th cervical. The ventral surface of this centrum is flat and ridged, as in the 15th and 16th vertebrae of *Fregata* and unlike the centra of vertebrae 17 through 19, which are more rounded.

The next visible vertebra is likewise represented by a centrum in ventral view. This is completely disassociated from the anterior series and lies between the right coracoid and scapula on the opposite side of the natural cleavage running through the holotype slab. The ventral surface of this centrum is also flat, suggesting, by analogy to *Fregata,* that this is the 16th vertebra.

Only two other presacral vertebrae are visible. If the vertebral count is the same in *Limnofregata* as in *Fregata* these would be by their positions certainly the 19th and probably the 18th, suggesting that it is the 17th vertebra that is missing or obscured. This is highly likely, since it is this area of the specimen that has suffered the most destruction by cleavage and that has the most overlap of bone.

What I am regarding as the 18th vertebra lies in left lateral view amid a tangle of ribs and its orientation is reversed so that the anterior end points more or less posteriorly. It is quite similar to the corresponding vertebra of *Fregata,* with a well-developed neural crest. The 19th vertebra is still in articulation with the synsacrum and is seen in ventral view. The barrel-like centrum is similar to that of *Fregata* except that the margins of the articulations form more distinct rims, giving the centrum slightly more of an hour-glass shape.

Pelvis

The pelvis (Figure 10) of *Limnofregata* is short, wide, and shallow, unlike any of the Pelecaniformes except *Fregata* and *Phaethon.* In the other families of the order, the pelvis is long, laterally compressed (particularly in the diving forms, such as cormorants) and deep (Figure 11). *Limnofregata* agrees with *Fregata* and differs from *Phaethon* in the greater expansion of the preacetabular ilia into broad, rounded shields. In *Fregata* the pubis is greatly attenuated in its anterior half, expanding to nearly thrice its former width in the area of contact with the ischium. In *Limnofregata* the width of the pubis is about the same throughout its length. In the synsacrum of *Limnofregata* the transverse processes of the preantepenultimate vertebra are conspicuously larger than those of the other vertebrae and extend laterally to abut against the internal side of the antitrochanter, whereas in *Fregata* the transverse processes are nearly uniform from one vertebra to the next, and none extends as far as the antitrochanter.

An interesting feature in *Limnofregata* is that in the posterior margin of the innominate there is a distinct notch and a resulting projection approximately in the area of fusion of the ilium and ischium. This is altogether absent in *Fregata,* but a somewhat similar condition, though much less distinct, is found in some individuals of *Phaethon,* and a possibly homologous structure is prominent in a more posterior position in *Sula.*

Caudal Vertebrae

In the holotype of *Limnofregata* I can account for 6 and possibly 7 free caudal vertebrae, although only four of these are not obscured by the pelvis (Figure 10). In *Fregata* there may be either 6 or 7 free caudals, the first of these often fusing to the synsacrum (Figure 11c). Of the exposed caudals in *Limnofregata,* three can definitely be determined as representing numbers 5, 6, and 7. The other is probably the first or second free caudal. The caudals of *Limnofregata* and *Fregata* are distinct from those of *Phaethon,* in which the transverse processes are much longer and narrower, or *Sula,* in which these processes are expanded at their tips. In both *Fregata* and *Limnofregata* the sixth and seventh caudals differ from the remainder of the series in having well-developed hemapophyses which are larger in the seventh than in the sixth. The transverse processes of the seventh caudal are better developed in *Limnofregata* than in *Fregata.* The hemapophyses of the sixth caudal in *Limnofregata* are slightly shorter and are well separated, rather than being fused as in *Fregata.* All of the caudal vertebrae of *Limnofregata* differ from those of *Fregata* in not being inflated and, except for the 7th, in having shorter and wider transverse processes. From this, one can infer that the structure and shape of the tail of *Limnofregata* was probably different from that of *Fregata.* It was almost certainly not as long or as deeply forked, and it may have appeared as hypothesized in the frontispiece, though unfortu-

FIGURE 10.—Pelvis, most of the left hindlimb, right femur, and caudal vertebrae of the holotype of *Limnofregata azygosternon*. (Scale = 20 mm)

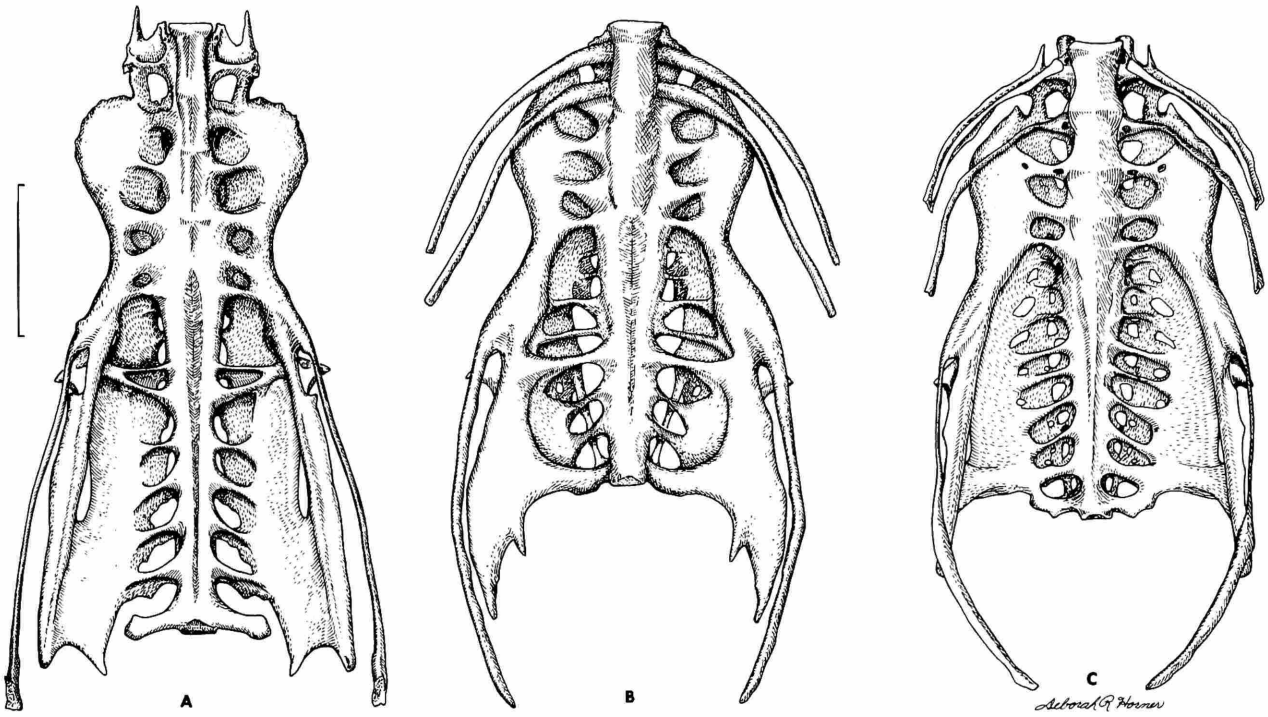

FIGURE 11.—Pelves in ventral view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

nately no impressions of the rectrices are preserved in the holotype.

RIBS

The ribs of *Limnofregata* are generally similar to those of *Fregata* but have decidedly longer uncinate processes. These processes agree with *Fregata* and differ from the Sulidae in being oriented more nearly perpendicular to the shaft of the rib, rather than being angled sharply dorsally.

CORACOID

Both coracoids of the holotype of *Limnofregata* are damaged or partly obscured (Figure 12). Fortunately, the right coracoid, which is split by a fault in the slab, is preserved with the ventral side up, while the left is preserved with the dorsal side up.

In overall proportions, the coracoid of *Limnofregata* is fairly similar to that of *Phaethon.* It is longer and more slender than in *Sula* or *Fregata* (Figure 13), but not so much as in *Anhinga* or *Phalacrocorax.* The most striking feature is that the coracoids of *Limnofregata* are not fused with the furcula as is the case in *Fregata.* The area of the furcular facet is considerably produced, however, to an extent greater than in other Pelecaniformes, although somewhat like *Phaethon.* The glenoid facet is large with a well-developed rim, unlike *Phaethon,* and is narrower and less rounded than in *Fregata,* being more similar to *Sula.* In ventral view the medial side of the sternal end bears a wide, shallow depression that is lacking in *Sula,* but present to a varying extent in *Fregata* and also present in *Phaethon, Anhinga,* and *Phalacrocorax.*

The scapular facet in *Limnofregata* is distinctly concave and cuplike, though not as deep or rounded as in *Pelecanus.* In *Phaethon* there is only a slight concavity and in the other modern genera of the order, including *Fregata,* the scapular facet is essentially convex and indistinct. The procoracoid process is short, rounded, and imperforate, unlike the thin, broad, perforate, bladelike procoracoid of *Phaethon* or the elongate, pointed process of *Sula* and *Fregata.*

The ventral sternal facet in *Limnofregata* is a

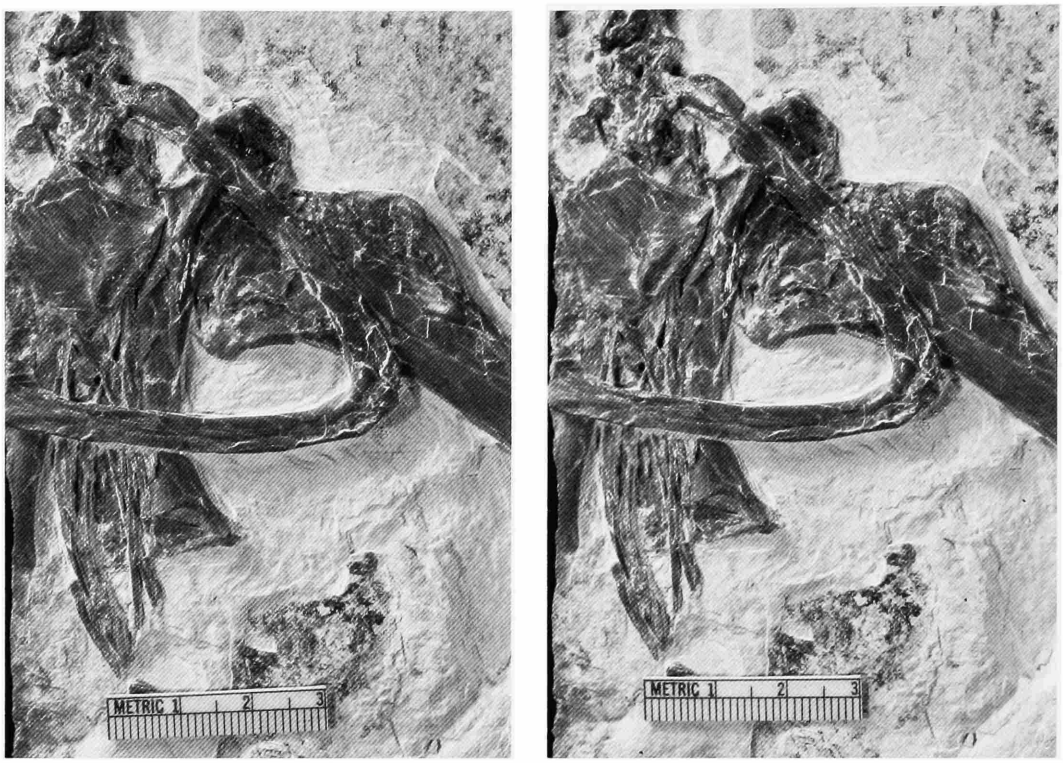

FIGURE 12.—Furcula, left coracoid (dorsal aspect), sternal end of right coracoid (ventral aspect), and proximal end of left humerus of the holotype of *Limnofregata azygosternon*. (Stereopair, natural size)

low ridge on the medial fourth of the sternal end of the coracoid, much better developed than in *Phaethon* but not as deep as in *Fregata* and wider than in *Sula*. The dorsal sternal facet in *Limnofregata* is quite distinct from that of *Fregata*, presenting a deep face situated high on the shaft, as in *Sula*, but not situated as close to the medial margin of the shaft. This facet in *Phaethon* is similar in position to that of *Limnofregata*, but is not as deep.

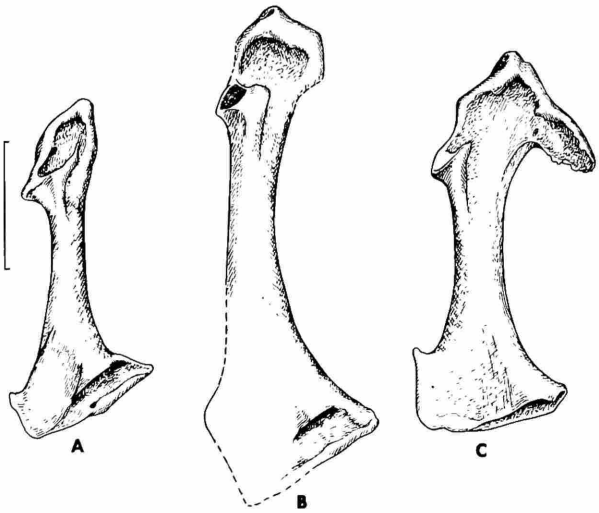

FIGURE 13.—Left coracoids in dorsal aspect: A, *Sula sula*; B, *Limnofregata azygosternon*; C, *Fregata ariel*. (Scale = 20 mm)

SCAPULA

The scapula of *Limnofregata* (Figure 14) is proportionately longer than in *Fregata*. The acromion is more weakly developed than in any modern pelecaniform but is more similar to that of *Phaethon* or *Fregata* than to the greatly elongated and pointed acromion in other members of the order (Figure 15). The coracoidal articulation is more prominent in *Limnofregata* than in any modern pelecaniform genus except *Pelecanus*, in which the coracoidal articulation is a large, distinct ball. This corresponds with the deeper scapular facet of the coracoid in both of these genera. The blade of the

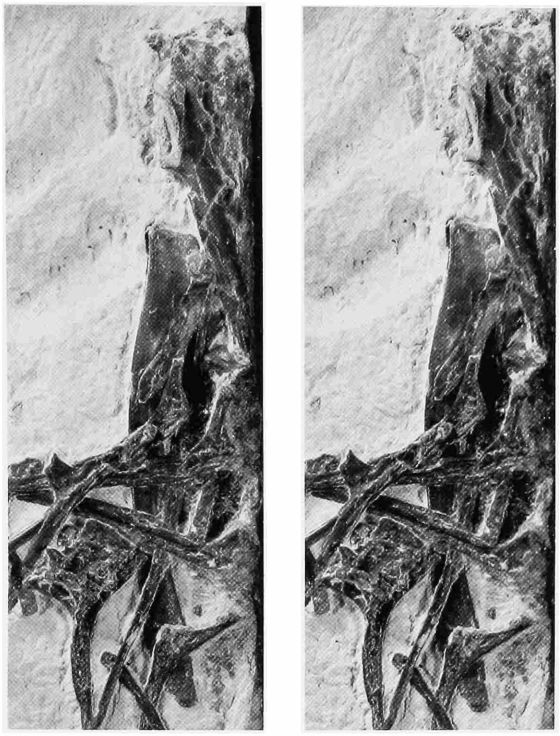

FIGURE 14.—Right scapula (dorsal aspect) and the scapular end of the right coracoid (ventral aspect) of the holotype of *Limnofregata azygosternon*. (Stereopair, natural size)

scapula is thin and flat and appears to be of a more uniform width than that of *Fregata, Sula,* or *Phaethon,* the tip being less acutely pointed than in those genera.

FURCULA

The ventral face of the furcula is exposed in the holotype of *Limnofregata* (Figure 12), with all of the anterior articulation obliterated on the right side and the scapular tuberosity obscured on the left. In the University of Wyoming specimen, most of the right ramus is visible in lateral view. Comparison of the furcula of *Limnofregata* with that of *Fregata* is rendered difficult because in the latter this bone is broadly fused posteriorly with the sternum and anteriorly with the coracoids, whereas there is no such fusion in *Limnofregata.* The furcula in *Limnofregata* is in the shape of a broad V, with the arms not as divergent and U-shaped as is the case in the Sulidae, Anhingidae, Phalacrocoracidae, and Pelecanidae. There is no indication of the strong rounded coracoidal facets seen in those families, although there is a distinct expansion below the scapular tuberosity. The scapular tuberosity appears to have been rather elongate and pointed as is also evident in *Fregata,* in spite of the fusion. The rami are broad and deep and there is a small, pointed hypocleidium but no evidence of a large sternal articulation or of the small pointed epicleidium seen in *Fregata* and *Sula.* The furcula of *Phaethon* is simple and U-shaped with almost no modification of the anterior ends. Despite the fact that it is not fused to the rest of the pectoral girdle, the furcula of *Limnofregata* appears to be more similar to that of *Fregata* than to other members of the order.

STERNUM

The sternum in the holotype of *Limnofregata* is well preserved and is seen in the ventrolateral aspect of the left side (Figure 16). The body of the

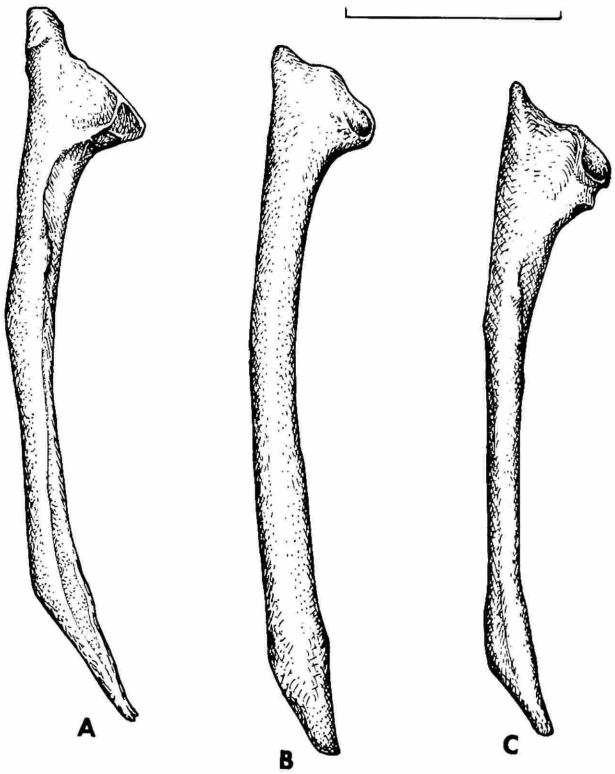

FIGURE 15.—Right scapulae in dorsal view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

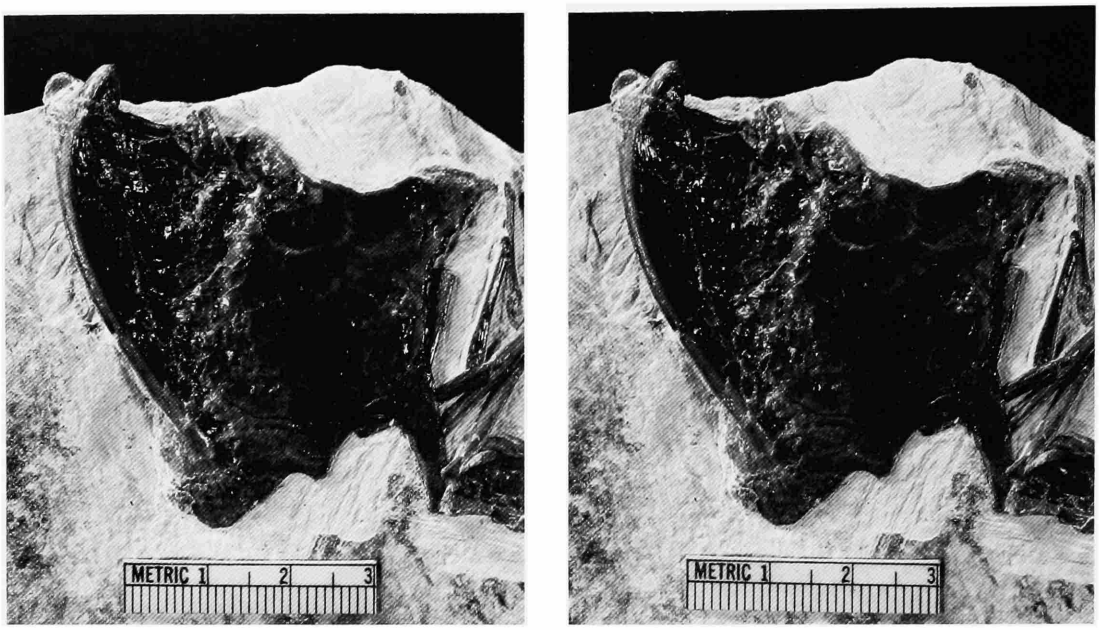

FIGURE 16.—Ventrolateral view of the sternum of the holotype of *Limnofregata azygosternon.* (Stereopair, about natural size)

sternum is very short, so that the width is equal to or exceeds the length, a condition found in modern Pelecaniformes only in *Fregata* (Figure 17). The carina extends posteriorly the full length of the bone, which is also characteristic only of *Fregata,* although *Phaethon* is close. The carina in lateral view is not as rounded as in *Fregata.* The carinal apex is distinctly bifurcate and the only modern pelecaniform showing a tendency towards such a condition is *Phaethon,* in which, however, the bifurcation is indistinct and lies anterior to a large round furcular facet, a feature not found in *Limnofregata.* The carinal apex of the Lower Eocene pelecaniform *Prophaethon shrubsolei* is also distinctly bifurcated (Harrison and Walker, 1976:12, fig. 6c), but this, too, has a large furcular facet as in *Phaethon.* In *Fregata* this area is entirely obliterated through fusion with the furcula.

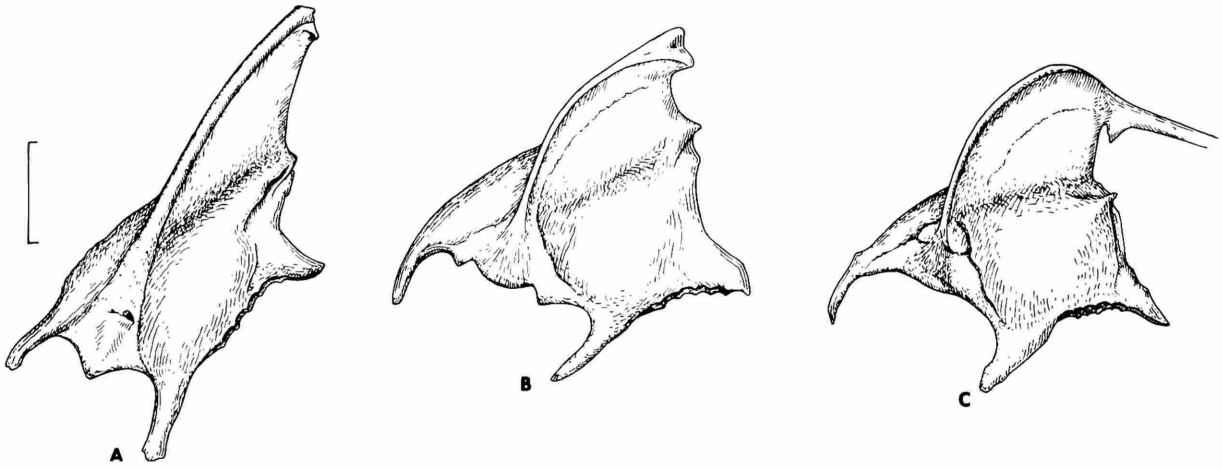

FIGURE 17.—Sterna in ventrolateral view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

The sterno-coracoidal processes are slender and pointed in *Limnofregata,* but not as much as in *Fregata,* and differ from *Sula* and *Phaethon,* in which the sterno-coracoidal processes are short and triangular. *Phaethon, Fregata,* and *Limnofregata* have six costal facets on the sternum, whereas there are five in all the Pelecani except *Anhinga,* which has only four. The posterior margin of the sternum in *Limnofregata* is definitely 4-notched, the lateral notch on each side being rather deep and the posterior lateral processes being slender and elongate. *Phaethon* also has a 4-notched sternum but in this genus the medial notches are the larger and the lateral ones are very reduced, sometimes to different degrees on either side of the same individual. In all other pelecaniform genera the sternum is broadly 2-notched and in *Fregata* the xiphial area does not form a projection, so that the posterior border between the posterior lateral processes is entire.

The sternum in *Limnofregata* is decidedly closer to that of *Fregata* than to any other modern genus of the order. The 4-notched posterior border and the lack of fusion with the furcula are primitive characters, while the very short, broad shape appears to be a derived condition.

Humerus

The humerus of *Limnofregata* (Figure 18) resembles that of *Phaethon* and *Fregata* and differs from that of any of the Pelecani in having a large triangular deltoid crest. The shaft appears to have been relatively stouter than in *Fregata* or *Phaethon* but this may in part be due to distortion of the fossil specimens.

The humerus of *Limnofregata* is in many respects more similar to that of *Phaethon* than *Fregata,* the principal differences from *Phaethon* being that the deltoid crest is of a very different shape (Figure 19), the bicipital crest is much less prominent, and the tricipital fossa appears to have been smaller. Although much crushed, in the right humerus of the holotype of *L. azygosternon* it can be seen that the tricipital fossa was pneumatic, and what appear to be small trabeculae can still be discerned in what is left of the foramen.

The humerus in *Fregata* presents a number of striking specializations as compared to *Limnofregata* (Figures 19, 20). To begin with, it is very highly pneumatic, with foramina evident in several places in the tricipital fossa, bicipital furrow, brachial depression, and olecranal fossa. The bicipital crest is inflated and bulbous and extends distally for a considerable length, whereas in *Limnofregata* the bicipital crest is all but lacking. The deltoid crest in *Fregata* has a distinctly projecting apex whereas in *Limnofregata* the apex is broadly rounded. The attachment for M. pectoralis major on the palmar surface of the deltoid crest of *Limnofregata* has several protuberances and rugosities that are more complex than in *Fregata,* although the most distal and best developed of these appears to be homologous to one in a similar position in *Fregata.* No other modern pelecaniform has such a distinct attachment for M. pectoralis major. Both *Limnofregata* and *Fregata* have a well-defined oval scar for M. latissimus dorsi posterioris on the midline of the anconal surface of the shaft at the level of the apex of the deltoid crest. This scar is less distinct in *Phaethon* and is situated off the midline, more towards the deltoid crest, as is the condition in the other modern members of the Pelecaniformes in which this scar is at all apparent.

The distal end of the humerus in *Limnofregata* differs considerably from that of *Fregata* and is more similar to that of *Phaethon* or even *Sula. Fregata* differs in possessing a greatly inflated, elongate ridge extending proximally from the entepicondylar prominence, in the much greater development of the ectepicondylar area, and in the more bulbous and inflated external condyle, which lacks the slight hook at the proximal end seen in *Limnofregata. Limnofregata* differs from *Phaethon* and *Sula* and is closer to *Fregata* in its much greater attachment of the anterior articular ligament and the greater development of the ectepicondylar area. The brachial depression is larger and deeper than in *Phaethon* but not nearly as extensive as in *Sula.*

Ulna and Radius

As does the humerus, the ulna of *Limnofregata* in most details bears more resemblance to that of *Phaethon* than *Fregata.* The papillae for the secondaries are not nearly as well developed as in *Fregata* (Figure 21), although it appears that the internal surface of the shaft was probably more rounded, as in *Fregata,* rather than being somewhat flattened

FIGURE 18.—Stereoviews of the right humerus of the holotype of *Limnofregata azygosternon:* A, anconal aspect (× 7/10); B, palmar aspect (× 7/10); C, distal end in palmar aspect (about × 1.3).

as in *Phaethon.* The most distinctive feature of the ulna of *Limnofregata* is the very large, roughly triangular prominence for the anterior articular ligament (Figure 22), which has a tapering extension along the lower margin of the impression of M. brachialis anticus. This is most similar to the condition seen in *Phaethon* and very different from the reduced and more rounded prominence of *Fregata* or that of any of the other modern Pelecaniformes. The impression of M. brachialis anticus is deeper than in either *Fregata* or *Phaethon,* but like the latter has no pneumatic foramina, in contrast to

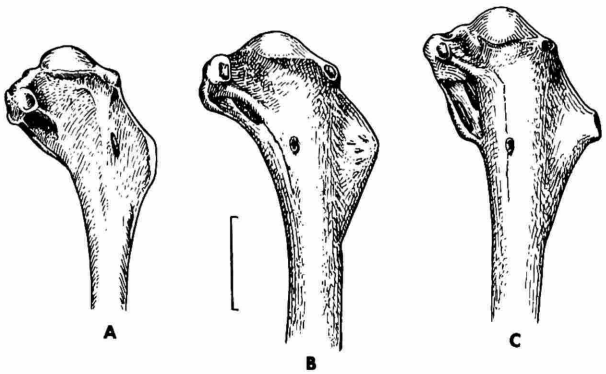

FIGURE 19.—Proximal ends of humeri in anconal view: A, *Phaethon aethereus;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

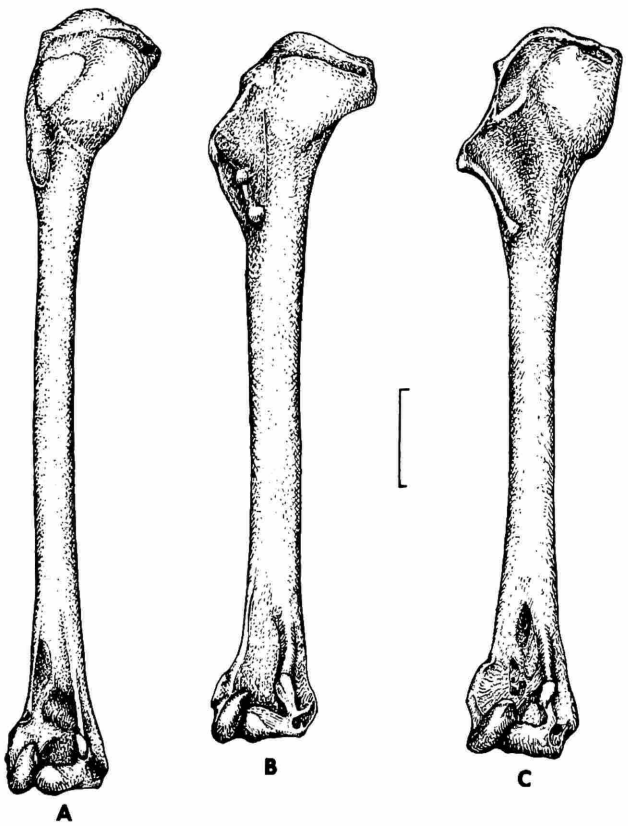

FIGURE 20.—Humeri in palmar view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

Fregata. The olecranon is narrower and projects farther proximally than in *Fregata* or *Phaethon* and is more sharply set off from the internal cotyla. The proximal radial depression is not as deep as in *Fregata* but the tendinal attachment along its

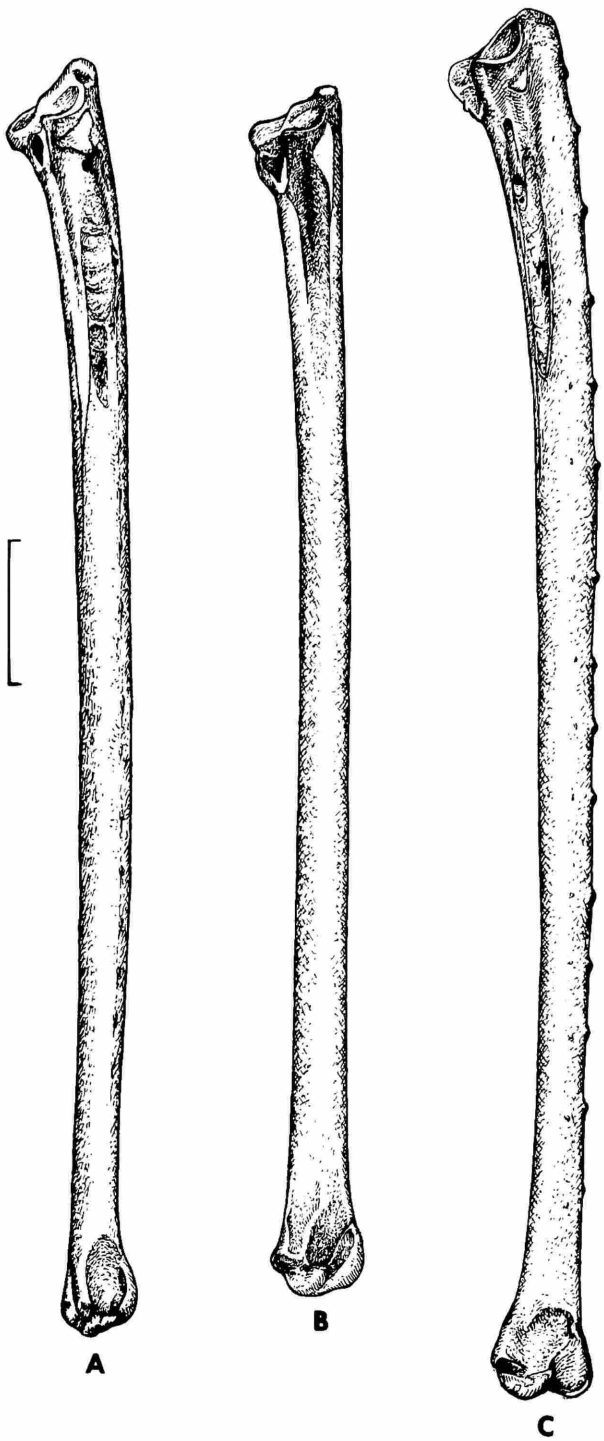

FIGURE 21.—Ulnae in internal view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

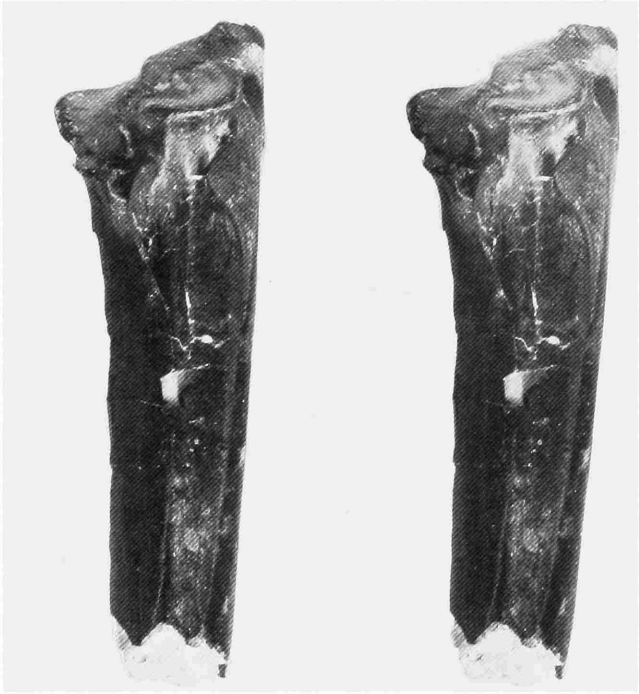

FIGURE 22.—Proximal end of right ulna of *Limnofregata azygosternon*, paratype, USNM 243766. (Stereopair, about × 1.8)

anterior margin is oriented nearly parallel to the long axis of the shaft, as in *Fregata,* rather than nearly perpendicular, as in *Phaethon.* The distal end of the ulna in *Limnofregata* is fairly similar to that of *Fregata* and differs markedly from *Phaethon,* in which the carpal tuberosity is large and hooked and bears a deep groove between it and the internal condyle.

The radius of *Limnofregata* is more sharply triangular in cross section than in *Fregata* and is thus more like *Phaethon.* The distal end is not greatly inflated as in *Fregata,* although the ligamental prominence is decidedly larger than in *Phaethon,* as it is also in *Fregata.*

Free Carpals

The left radiale of the holotype of *L. azygosternon* is seen in its proximo-internal aspect. It is more similar to that of *Sula* and *Fregata* than to *Phaethon,* in which last the medial surface between the articulating facets is narrower. In *Limnofregata* this surface lacks the pneumatic foramina that are present in *Fregata.*

The left ulnare of the holotype is seen mainly in its internal aspect and this bears a tendinal groove that is much deeper than in either *Fregata* or *Sula* but which is similar to that seen in *Phaethon.*

Carpometacarpus

The carpometacarpus of *Limnofregata* (Figure 23) resembles that of *Fregata* in having metacarpals II and III parallel throughout their lengths rather than diverging distally as in *Phaethon* and *Sula.* Metacarpal I is lower than in *Fregata* and the pisiform process is less bulbous and does not project as far outward; in these respects *Limnofregata* is closer to *Phaethon.* The distal metacarpal symphysis is longer in *Limnofregata* than in *Sula* or *Phaethon* and the tuberosity of metacarpal II is not crescentic nor as high as in *Phaethon.* In these respects, *Limnofregata* is fairly similar to *Fregata* (Figure 24). There are no pneumatic foramina (at least not on the internal face) in the carpometacarpus of *Limnofregata,* unlike *Fregata,* in which such foramina occur in several places.

Phalanges of Manus

Digit I of *Limnofregata* is not greatly expanded proximally as it is in *Fregata* and is fairly similar to that of *Phaethon,* but it is not as attenuated distally and is proportionately shorter (33% of length of carpometacarpus in both genera of frigatebirds, vs. 40% in *Phaethon).*

In phalanx 1 of digit II of *Limnofregata* the distal margin is truncate, whereas in *Phaethon* there is a distally projecting ventral lobe and in *Fregata* there is a large dorsal projection as well. In both the right and left elements of the holotype of *L. azygosternon* there is an irregular fenestra in the distal third of the blade, as in *Fregata.*

Phalanx 2 of digit II is more similar to that of *Fregata* than to the other genera compared. Both possess a small foramen on the dorso-internal corner of the proximal end. This is pneumatic in *Fregata* but appears to have been a nutrient foramen in *Limnofregata.* The proximal end is not as expanded and projects more distinctly from the shaft in *Limnofregata* than in *Fregata.* The distal end bears a hooked ventral process, as in *Fregata* and *Phaethon,* but the remaining distal portion is much

FIGURE 23.—Distal portions of right and left wings of the holotype of *Limnofregata azygosternon*.

shorter than in either genus and is not greatly attenuated as in *Phaethon*.

Digit III differs markedly from that of *Phaethon*, which is very elongate and slender, extending over half the length of digit II. This element is rather similar to that of *Fregata* but it is proportionately much shorter and more closely resembles that of *Sula*.

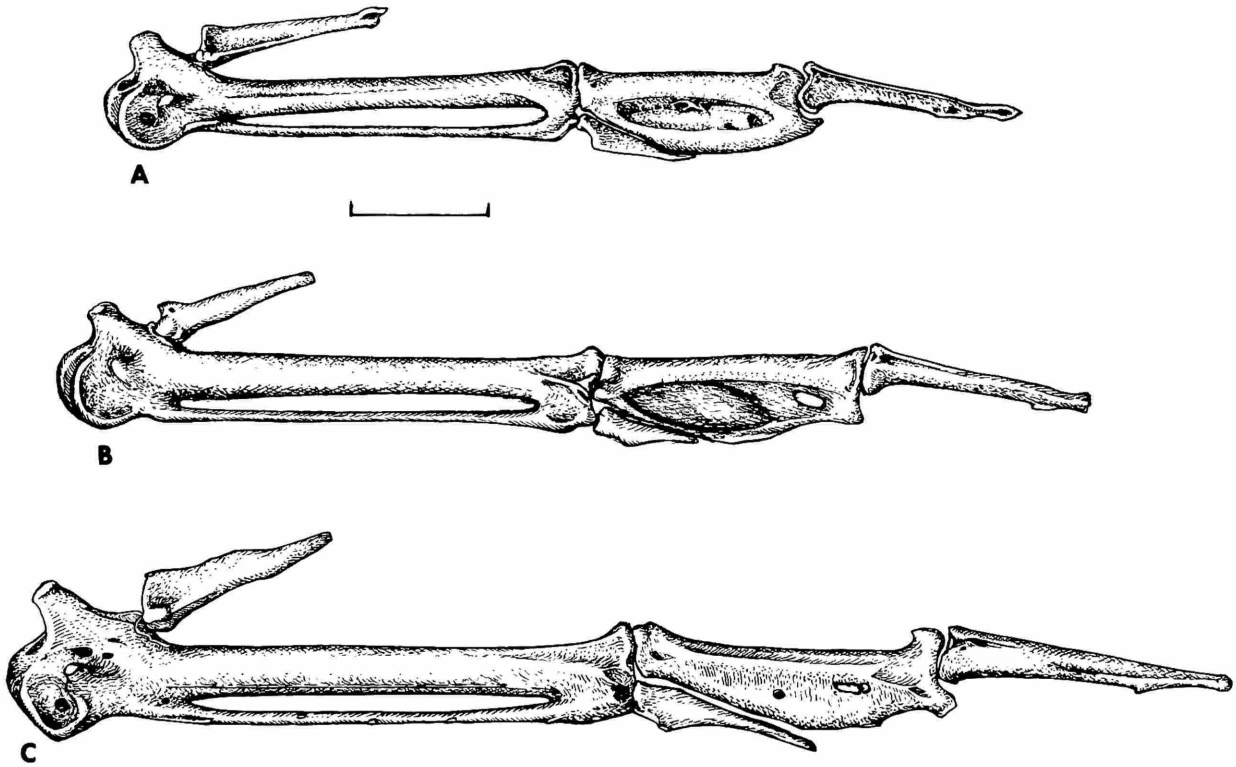

FIGURE 24.—Carpometacarpi in internal view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

FEMUR

The femora of the holotype of *Limnofregata azygosternon* are somewhat difficult to interpret since both are partially obscured. Nevertheless, a number of important features can be discerned. The femur of *Limnofregata* differs markedly from that of *Phaethon* as follows: shaft much stouter; head flattened proximally, not spherical; trochanter higher than head; fibular groove much deeper. In having the head flattened and lying below the level of the trochanter, *Limnofregata* differs from *Phaethon* and all of the Pelecani and agrees only with *Fregata* (Figure 25). The femur of *Limnofregata* differs from that of *Fregata* in being proportionately longer, in having the attachment for the ligamentum teres deeper and more distinct, and in the somewhat greater development of the fibular condyle. In the left femur of the holotype there is barely visible the outline of what may have been a small pneumatic foramen in the trochanter, now mostly obscured by crushing and by the overlapping of the pelvis. The femur is pneumatic in both *Fregata* and *Sula* but not in other modern Pelecaniformes.

TIBIOTARSUS AND FIBULA

The tibiotarsus of *Limnofregata* (Figure 26) is somewhat longer proportionately than in *Fregata* and has a decidedly heavier shaft than either *Fregata* or *Phaethon.* The fibula is likewise heavier than in either of these genera and extends farther distally and apparently was fused at its distal extremity, as in *Sula.* In its overall build the tibiotarsus of *Limnofregata* is more similar to *Sula* than to other Pelecaniformes (Figure 27), but it differs in a number of details, many of which are more similar to *Fregata.*

The inner cnemial crest in *Limnofregata* is larger and projects farther anteriorly than in *Phaethon* or *Fregata,* in both of which this crest is greatly reduced. Although folded over in the best preserved of the two tibiotarsi of *L. azygosternon,* the inner cnemial crest appears to have extended farther ante-

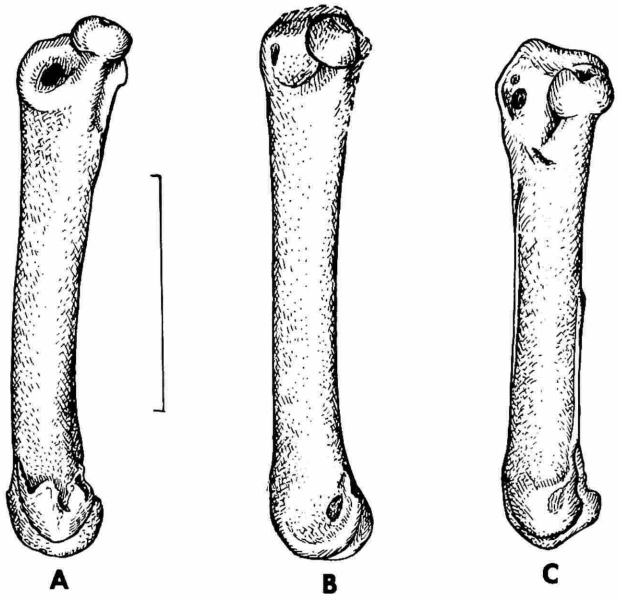

FIGURE 25.—Femora in medial view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

riorly even than in *Sula* and was thinner and more bladelike. Its proximal extent, however, is not as great as in *Sula* and in this respect it more closely resembles *Fregata.* The outer cnemial crest, too, is well developed and unciform, being less reduced than in any of the modern Pelecaniformes except *Phalacrocorax* and *Anhinga,* which are otherwise quite different. The head of the fibula is relatively and absolutely smaller than in *Fregata* or *Sula.*

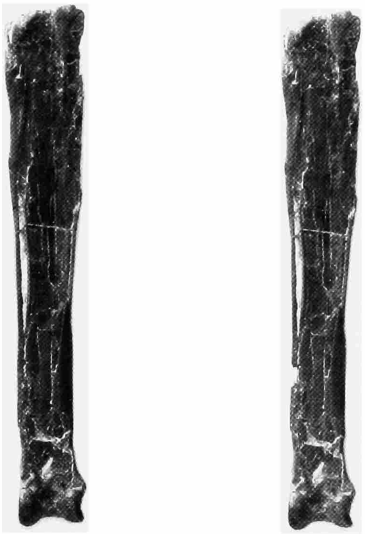

FIGURE 26.—Right tibiotarsus of the holotype of *Limnofregata azygosternon,* anterior view. (Stereopair, natural size)

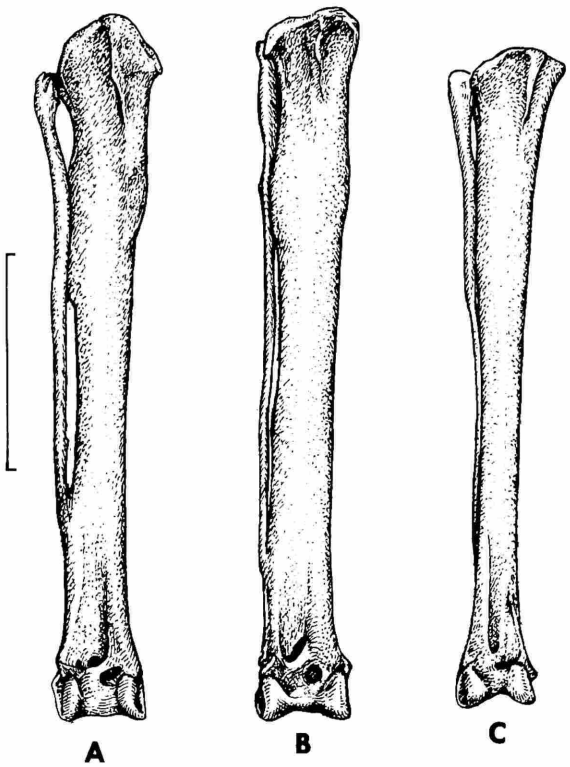

FIGURE 27.—Tibiotarsi in anterior view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

The distal end of the tibiotarsus of *Limnofregata* is similar to that of *Fregata* and differs from the other genera compared in having a distinct internal ligamental process. In anterior view both the internal and external condyles in *Limnofregata* are roughly triangular in shape, the apex of the triangles pointing towards the midline. This shape is still evident in *Fregata,* although somewhat modified, but in the other genera compared the condyles in anterior view are oblong and of nearly uniform width. The distal opening of the tendinal groove is rounded as in *Fregata* and *Phaethon,* and is not a transverse oval as in *Sula.* In posterior view the crest of the internal condyle is better developed than in *Sula* or *Phaethon* and more closely resembles the condition in *Fregata.* The anterior intercondylar fossa is narrower in *Limnofregata* than in *Sula,* but is wider than in *Fregata* and is not too different from that of *Phaethon.*

TARSOMETATARSUS

The tarsometatarsus of *Limnofregata* (Figure 28) is quite distinctive. It bears little resemblance to

FIGURE 28.—Right tarsometatarsus of the holotype of *Limnofregata azygosternon:* A, anterior view; B, posterior view. (Stereopairs, × 2)

the peculiar tarsometatarsus of *Phaethon,* which is slender and has a very deep anterior groove. In its overall proportions the tarsometatarsus of *Limnofregata* is intermediate between the greatly reduced and "degenerate" tarsometatarsus of *Fregata* and the more elongate element of *Sula* (Figure 29). It differs from *Sula* and agrees with *Fregata* in having the external cotyla projecting laterally beyond the line of the external margin of the shaft and in having a lower and less pointed intercotylar prominence. The cotylae are deeper in *Limnofregata* than in *Fregata* and the internal cotyla is proportionately smaller and does not extend as far anteriorly. The anterior metatarsal groove is fairly deep, and the various tendinal tubercles and foramina are developed about as in *Sula,* whereas in *Fregata* the anterior face of the bone is much modified, the most conspicuous feature being the ridges and grooves, which indicate the positions of the individual metatarsal elements, and the medial displacement of the tubercle for the tibialis anticus.

The hypotarsus of *Limnofregata* is quite different from that of either *Sula* or *Fregata* and actually bears more resemblance to that of *Phaethon.* In *Sula* the hypotarsus has a very large, posteriorly directed inner calcaneal ridge and contains two completely enclosed canals. In *Fregata* the hypotarsus is an irregularly shaped block containing a single large enclosed canal. In *Limnofregata* there are no closed canals and the hypotarsus consists of three calcaneal ridges separated by two grooves, the inner calcaneal ridge being the largest and swollen, the

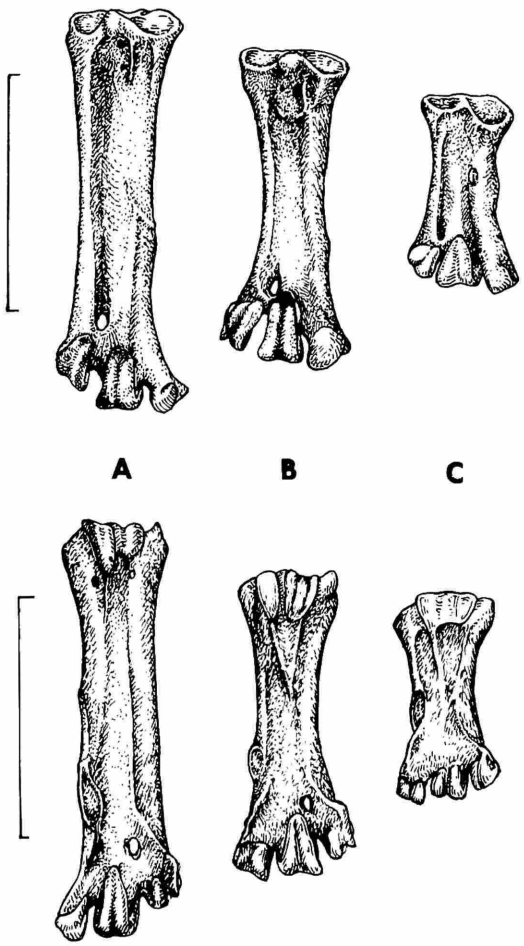

FIGURE 29.—Tarsometatarsi in anterior (*top*) and posterior (*bottom*) views: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

two outer ridges being thinner and equally developed. A similar condition exists in *Phaethon* except that the outer ridge is the largest and most swollen and the middle ridge is noticeably smaller than the other two.

The distal foramen is well developed and circular in *Limnofregata* and exits on the posterior surface of the shaft, in all respects being similar to *Sula* though relatively smaller. In *Fregata* the distal foramen seen in anterior view is greatly reduced and it exits between trochleae III and IV so that it is not visible in posterior view.

The trochleae of *Limnofregata* in anterior view may be characterized as follows: external trochlea longer and more slender than in *Fregata,* more like *Sula* but with the posterior wing less distinct; middle trochlea much longer, more deeply grooved, and not projecting sharply anteriorly from the shaft as in *Fregata,* more similar to *Sula* but longer and angling laterally instead of medially; internal trochlea about as in *Fregata,* not as long and slender as in *Sula* and not projecting as far medially. In posterior view the most notable feature of the trochleae of *Limnofregata* is that the articulating surface of the middle trochlea extends proximally in an elongate triangular shape as in *Sula* and is not short and truncate as in *Fregata.* Both genera of frigatebirds and *Sula* differ from *Phaethon* in having the internal rather than the middle trochlea extending farthest distally.

Toes

The "toe formula" in *Limnofregata,* going from longest to shortest, is 3–4–2–1. *Fregata* and *Pelecanus* have the same formula, as does *Phaethon,* except that in the last-named genus digits 4 and 2 are about equal. In all other Pelecaniformes the fourth toe is longer and either equals (*Sula*) or greatly exceeds (*Phalacrocorax* and *Anhinga*) the middle toe in length, the formula being 4 = 3–2–1, or 4–3–2–1.

The toes of *Limnofregata* (Figure 30), while proportionately longer, are nevertheless much more similar to those of *Fregata* than to those of *Sula* or *Phaethon* in that they are considerably heavier and have the phalanges of digit IV much shorter. The phalanges of *Limnofregata* differ from *Fregata* in that they are longer, more slender, and the articulating ends are much less expanded relative to the width of the shafts; the ungual phalanges are less curved.

Discussion

Limnofregata affords some new information on the affinities of the Fregatidae, since it presents us with a frigatebird without many of the obfuscating specializations of *Fregata.* The following are some of the characters that are shared by the Phaethontidae and Fregatidae but not found in the families of the suborder Pelecani: 15 cervical vertebrae, all lacking hemal arches and changing only gradually in shape through the series (see Mivart, 1878); absence of coracoidal facets on furcula (not ascertainable for the Fregatidae until now); 6 costal facets on sternum (versus 5 or 4 in the Pelecani); humerus with a large, triangular deltoid crest; width of pelvis across antitrochanters greater than 80% of length of dorsal portion of ilium (25–65% in Pelecani). With the possible exception of the short, broad pelvis, which may have evolved independently in each of these two aerially adapted families, all of the above characters appears to be primitive and thus are not evidence for a close relationship between tropicbirds and frigatebirds. They do, however, definitely support the phylogeny advocated by Lanham (1947), who treated the Phaethontes and Fregatae as being primitive within the order, to be followed by the more specialized families of the Pelecani. This is in contrast to such classifications as those of Peters (1931) and Wetmore (1960) where the frigatebirds are placed in a terminal position, separated from the Phaethontes by the Pelecani—a sequence that cannot be justified by the facts available now.

Limnofregata and *Phaethon* share some characters that are not seen in *Fregata:* the proportions of the coracoid, certain aspects of the humerus, the conformation of much of the proximal end of the ulna, the nature of the hypotarsus, and the 4-notched sternum. The last-named is without doubt a primitive character and most or all of the others could be also. Collectively, however, they might be taken as a possible indication that frigatebird morphology could have been derived from that of some primitive phaethontid-like ancestor.

In only a few characters can *Limnofregata* be

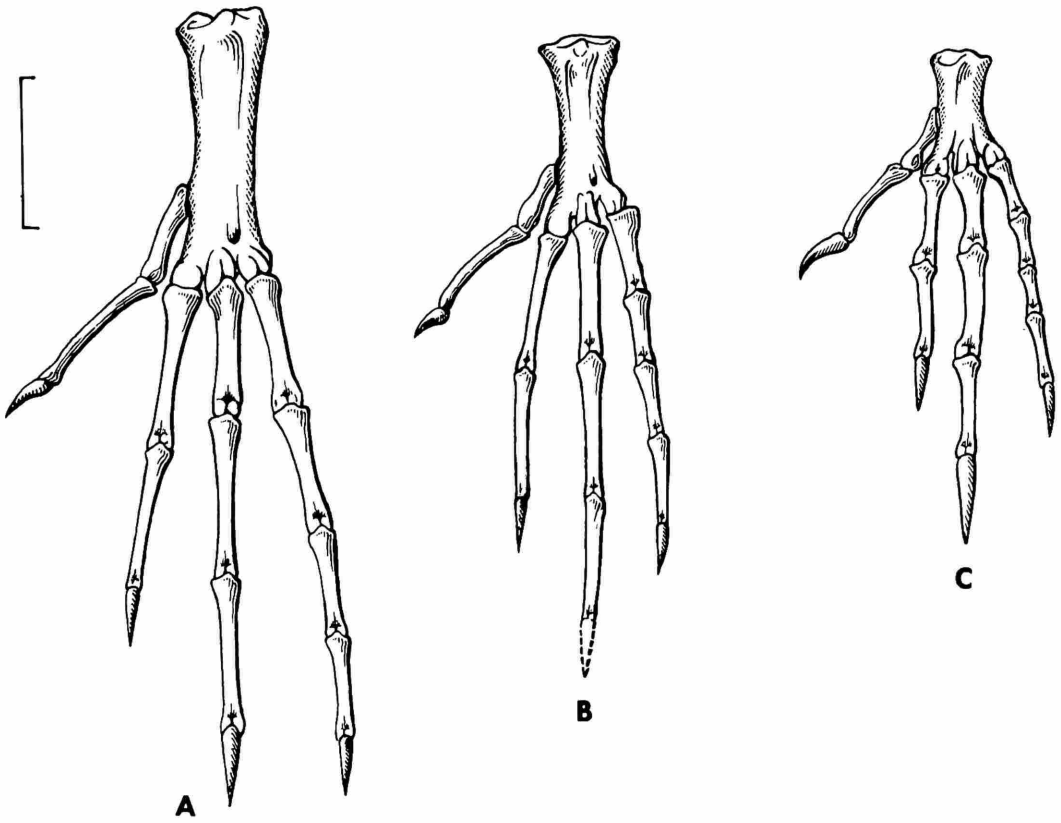

FIGURE 30.—Tarsometatarsi and toes in anterior view: A, *Sula sula;* B, *Limnofregata azygosternon;* C, *Fregata ariel.* (Scale = 20 mm)

said to resemble the Pelecani (particularly *Sula*) more than either *Phaethon* or *Fregata*. The ratio of cranium to bill length appears to be like that of *Sula* but this hardly appears to be of significance, since the condition in *Limnofregata* is intermediate between that of *Phaethon* and *Prophaethon* and that of *Fregata*. The tibiotarsus and tarsometatarsus of *Limnofregata* resemble *Sula* rather closely in several respects. This, however, could be attributable to the fact that these bones in both *Phaethon* and *Fregata* are highly modified, whereas the Sulidae, which appear to stem from near the base of the Pelecani, could be expected to retain a rather primitive morphology in the hindlimb. Thus, while the conformation of the tarsometatarsus and tibiotarsus cannot be cited as showing a close relationship between *Limnofregata* and the Sulidae, it does support their allocation to the same order.

Despite its primitiveness, the skeleton of *Limnofregata* has many more similarities to *Fregata* than to any other pelecaniform genus. The conformation of the otic area, pterygoid, mandible, cervical vertebrae, carpometacarpus, femur, and toes; the great reduction of the hindlimb; the proportions of the sternum and the general structure of the furcula; the size and position of the scar for M. latissimus dorsi posterioris and some other details of the humerus all resemble *Fregata* more closely than *Phaethon* or any of the Pelecani.

Although at first *Limnofregata* seems very different from modern frigatebirds, on closer examination the differences are actually rather less significant than might be expected (Figure 31) in view of the relatively great age of the fossil (ca. 50 million years BP). The proportionately longer, more dorsally compressed and strongly hooked bill of modern frigatebirds probably reflects increased specialization for feeding from the surface of the water and perhaps for taking marine animals, such as squid, rather than freshwater fish. Possibly corre-

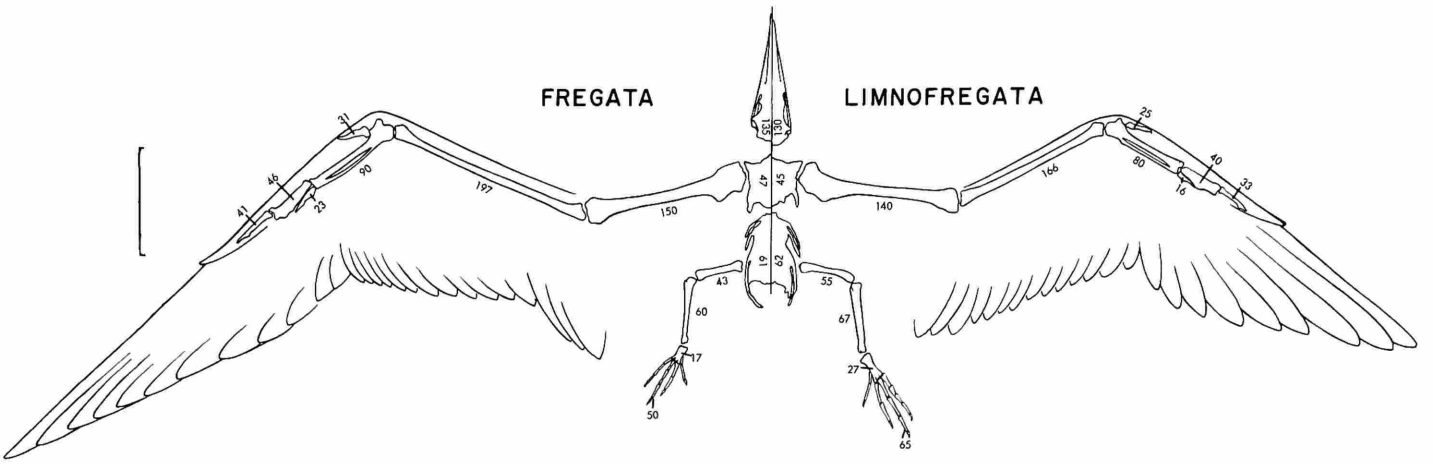

FIGURE 31.—Outline comparing the overall skeletal proportions of modern and fossil frigatebirds. *Fregata* is depicted on the left half of this composite individual and *Limnofregata* is pictured on the right. The numbers refer to the actual length measurements (mm) of individual bones in the holotype of *Limnofregata azygosternon* and in a small male of *Fregata ariel* (USNM 497972). Note that the body size of the two species is virtually the same, as evidenced by the lengths of the sterna and pelves. (Scale = 100 mm)

lated with this is the increased ossification of the skull in *Fregata*. This may represent a general evolutionary trend in various seabirds; three skulls of a Miocene albatross from Oregon, as in *Limnofregata,* are more similar to juveniles of modern species than to adults (Olson, notes).

Although the hindlimb of *Fregata* is more reduced than in *Limnofregata,* that of the latter shows that by the early Eocene the hindlimb of frigatebirds had already become more shortened than in other Pelecaniformes. Other specializations of *Fregata* appear to be correlated with an increasingly aerial existence. These include lengthening of the wing, fusion in the pectoral girdle, and extensive pneumatization of the skeleton. This pneumatization has in some instances resulted in fairly dramatic changes in morphology compared to *Limnofregata,* the most extreme example being the humerus. The resultant morphological changes, however, represent specializations peculiar to *Fregata* and are departures from all other Pelecaniformes. The fact that they also differ from *Limnofregata* is not of particular concern in assessing the relationships of the fossil. There is nothing that I can detect in the skeleton of *Limnofregata* that precludes its being directly ancestral to *Fregata*. The fact that by the early Eocene it was already markedly specialized along much the same lines as the modern genus renders this possibility plausible.

The completeness of the material of *Limnofregata* prompts me to make some observations and speculations about the taxonomic conclusions that might have been drawn had only parts of its skeleton been discovered and studied. The pelvis and probably the sternum are the only elements of *Limnofregata* that by themselves would most likely be recognized as being similar to those elements in the Fregatidae. The skull and possibly the tarsometatarsus, taken in their entirety but alone, might also have been properly assigned by an alert paleontologist. The humerus, radius, ulna, carpometacarpus, coracoid, furcula, scapula, tibiotarsus and probably the femur, if found in isolation, either whole or in part, would have stood very little chance of being correctly identified as once having formed a part of a frigatebird, and almost any one of them might have been said to constitute a new family, although it is far from certain that in every instance each specimen would have been assigned to the proper order. The distal end of the tarsometatarsus or that of the tibiotarsus might well have been referred to the Sulidae, whereas the proximal end of the tarsometatarsus would have proved impossible to assign to a modern family. The inadvisability of basing higher taxonomic categories of Paleogene birds on fragmentary limb elements, particularly when these bear no close resemblance to modern taxa, thus becomes evident.

Modern frigatebirds are confined to tropical oceans and breed exclusively on islands. The known environment of *Limnofregata,* on the other hand, was one of expansive inland freshwater lakes containing a variety of fish that were subject to periodic catastrophic die-offs (McGrew and Casilliano, [1976]). From its structure one may conjecture that *Limnofregata* probably occupied a niche somewhat similar to that of modern gulls of the genus *Larus.* It was better suited for flapping flight than is *Fregata* and was probably able to alight on and take off from the surface of the water or even the shore, unlike *Fregata,* for which the proportions of its limbs present nearly insurmountable obstacles to such activity. *Limnofregata* was no doubt a predator and scavenger on the multitudes of clupeiform fish found in the Green River lakes. It is possible that it preyed upon chicks of the flamingo-like wader *Presbyornis pervetus,* which nested in huge colonies around the early Eocene lakes of Wyoming, Colorado, and Utah (McGrew and Feduccia, 1973; Feduccia and McGrew, 1974).

It appears that frigatebirds were not entirely, if at all, marine in the early Tertiary, and this may perhaps have been true of other groups that are now entirely pelagic. Quite possibly the frigatebirds, sulids, tropicbirds, Procellariiformes, and certain primitive terns, such as *Anous,* may originally have been more diverse ecologically but were subsequently replaced in continental habitats by more advanced groups, with the result that they have been restricted to a purely oceanic environment where they now exist in a sense as relicts.

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