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New specimens of the early Eocene frigatebird *Limnofregata* (Pelecaniformes: Fregatidae), with the description of a new species

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Abstract

Four additional specimens from the Green River Formation of Wyoming are referred to the Eocene frigatebird *Limnofregata azygosternon* Olson, originally described from a nearly complete skeleton and two partial paratypes. Two skulls with mandibles and a partial postcranial skeleton are described as a new species, *Limnofregata hasegawai*, characterized by much larger size and a proportionately longer bill. One of the referred specimens of *L. azygosternon* is from Eocene Lake Gosiute, whereas all of the other specimens of *Limnofregata* are from Fossil Lake. The species of *Limnofregata* would have taken advantage of frequent periodic dieoffs of fish in the Green River lakes. Geological and climatic factors that may have influenced the paleoecology, distribution, and size variation in frigatebirds in the Cenozoic are reviewed.

Key words: Eocene, fossil birds, *Fregata*, Fregatidae, frigatebirds, *Limnofregata*, paleoecology, Pelecaniformes, sexual dimorphism, Wyoming

Introduction

Modern frigatebirds are oceanic, aerial, predatory and kleptoparasitic Pelecaniformes with extremely long, narrow wings, long forked tails, and very reduced legs and feet used only for perching during the breeding season. Until now, the only Tertiary fossil record of the family consisted of three specimens of a primitive genus and species, *Limnofregata azygosternon*, from the early Eocene Green River Formation of Wyoming (Olson, 1977). The only other fossils of the family known are Quaternary remains of living species from oceanic islands (Olson, 1985).

Although fairly numerous fossil birds have been recovered from lacustrine deposits of the Green River Formation in Wyoming, Utah, and Colorado, most of them are small,

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arboreal land birds (Grande, 1984). Although a few specimens show similarities to the modern order Gruiformes (Grande, 1984; Hesse, 1992), it is not known to what extent these may have been forest dwellers rather than aquatic. Waterfowl and flamingos are represented in the Green River Formation by *Presbyornis* and *Juncitarsus*, respectively (Ericson, 1997, 1999, 2000; Peters, 1987), which were long-legged inhabitants of shorelines and shallow flats. Neither genus is known from the classic deep-water shales that have produced the well-known slab birds of the Green River Formation.

Thus, *Limnofregata* is the only truly aquatic bird yet reported from these shales. Seven new specimens described herein now indicate that the genus was more diverse and contained at least two species.

Order Pelecaniformes
Family Fregatidae
Subfamily Limnofregatinae Olson, 1977
Genus *Limnofregata* Olson, 1977

Type-species: *Limnofregata azygosternon* Olson, 1977.
Included species: *L. azygosternon* Olson, 1977: *L. hasegawai*, new species.

***Limnofregata azygosternon* Olson, 1977**
Figs. 1–4

This species was described from a nearly complete skeleton with feather impressions (holotype USNM 22753) and two paratypes consisting of most of a right wing and shoulder girdle (UWY 6919) and the proximal end of an ulna (USNM 243766). Here we identify four additional specimens that can also be referred to the species *Limnofregata azygosternon*.

Referred specimen 1: GMNH PV 167, postcranial skeleton with impressions of remiges and contour feathers (Fig. 1). Bone color brown, feathers black. Collected by Tom Lindgren. The specimen consists of all elements of the appendicular skeleton except the proximal portion of the right humerus, plus the complete pectoral girdle and pelvis. It is lacking the skull and mandible, a number of ribs, and the entire pre- and postsacral vertebral column except for three thoracic and a caudal vertebra. Very distinct carbonized impressions of feathers can be identified as primaries, secondaries, and wing coverts.

Locality: Smith Hollow Quarry, Lewis Ranch (Locality B of Grande and Buchheim, 1994), Lincoln County, Wyoming.

Horizon: Beds about 4 m above the “18 inch layer,” Fossil Butte Member of the Green River Formation, late early Eocene.

Measurements (mm): See Table 1.

FIGURE 1. *Limnofregata azygosternon*, referred postcranial skeleton with feather impressions GMNH PV 167.

FIGURE 2. *Limnofregata azygosternon*, referred posterior portion of skeleton FMNH PA 723.

Referred specimen 2: FMNH PA 723, posterior portion of an associated skeleton consisting of the last 3 thoracic vertebrae, pelvis, caudal vertebrae and pygostyle, both hindlimbs complete with all toe bones, and assorted ribs (Fig. 2).

Locality: Thomson Ranch (Locality H of Grande and Buchheim, 1994), ca. 14 km W of Kemmerer, Lincoln County, Wyoming.

Horizon: F-2 facies, Fossil Butte Member of the Green River Formation, late early Eocene.

Measurements (mm): See Table 1.

TABLE 1. Length measurements (mm) of bones in four specimens of *Limnofregata*.

Measurement	*L. azygosternon*					*L. hasegawai*
	USNM 22753 Holotype	GMNH PV 167 Referred	UWY 6919 Paratype	FMNH PA 723 Referred	FMNH PA 720 Referred	BMS E25336 Paratype
Scapula	67.6	73.7	67.7			
Coracoid (maximum)	ca. 72	71.2	68+			
Humerus	ca 140	147.7	138.3			
Ulna	178	176.5	166		173+	
Carpometacarpus	80	80.3	79.6		79.3	
Major digit phalanx 1, 2	39.8, 33.3	41.9, 35.0			40.0, 35.3	
Synsacrum	61.5	61.2		66		73
Femur	~55	56.0		56.8		66
Tibiotarsus	67	67.9		67		72.6
Tarsometatarsus	26.7	27.3		26.8		
Digit I total length	22.7	22.6		22.5		
Digit II total length	45.8	44.4		43.1		
Digit III total length	62.4-	63.5		63.3		
Digit IV total length	51.3	52.3		52.6		

Referred specimen 3: FMNH PA 720, complete left wing distal to the humerus (Fig. 3).

Locality: Warfield Springs (NW1/4, Sec. 5, T19N, R117W; locality K of Grande and Buchheim, 1994), ca. 14 km SW of Kemmerer, Lincoln County, Wyoming, on the SE shore of Eocene Fossil Lake.

Horizon: F-2 facies equivalent, Fossil Butte Member of the Green River Formation, late early Eocene.

Measurements (mm): See Table 1.

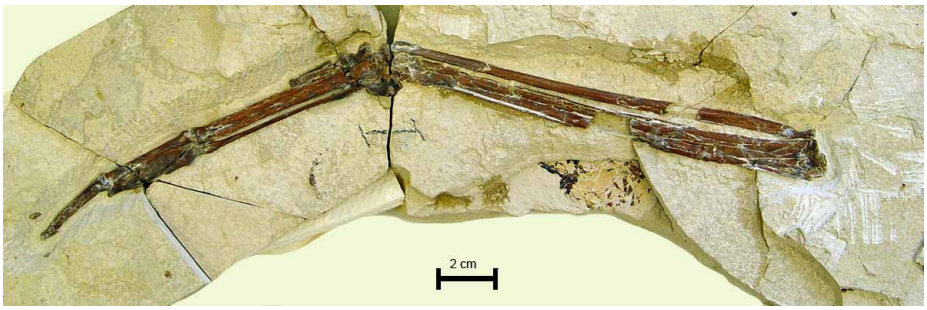

FIGURE 3. *Limnofregata azygosternon*, referred left wing FMNH PA 720.

Referred specimen 4: USNM 447002, left side of cranium with quadrate and associated posterior portion of mandible (Fig 4). The base of the bill and the occiput were preserved as a mold that has now been replaced with embedding compound.

Locality: Ca. 12 km NE of Fontanelle Reservoir Dam on N shore at autumn water level, Sweetwater County, Wyoming. This locality is in beds of the Eocene Lake Gosiute, whereas all the other specimens of *Limnofregata* to date have come from deposits in Fossil Lake.

Horizon: Laney Shale Member of the Green River Formation, lower middle Eocene.

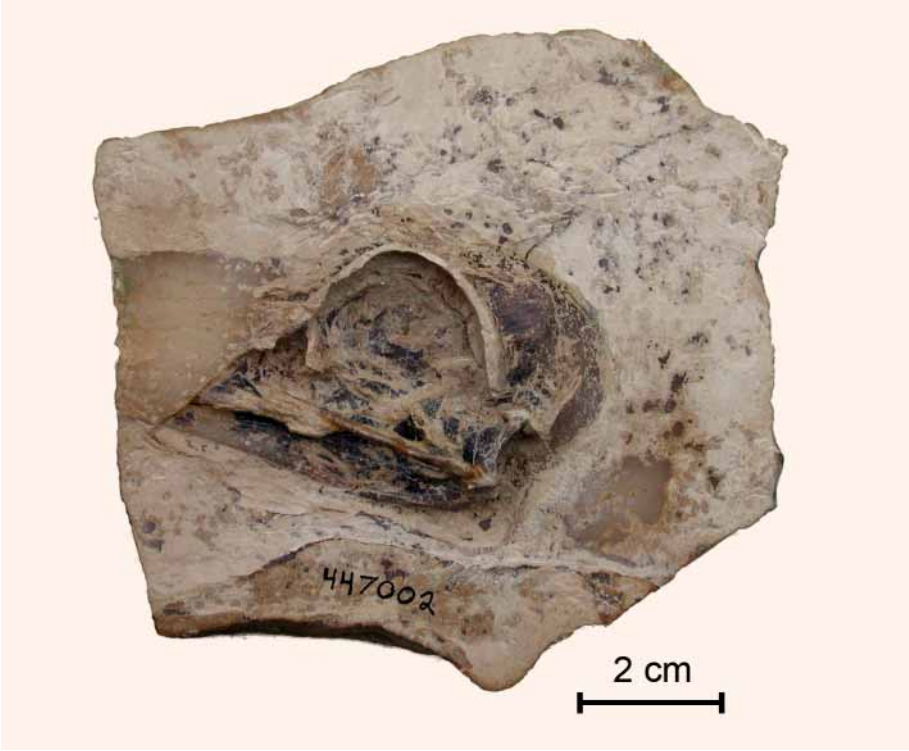

FIGURE 4. *Limnofregata azygosternon*, referred cranium and posterior portion of mandible USNM 447002. The orbit is perhaps overemphasized by matrix remaining along the margin.

Measurements (mm): Quadrate: distance from posterior margin of mandibular articulation to tip of otic process, ca. 13.4.

Description: Although USNM 447002 is very fragmentary, it is in places less crushed than other skulls of the genus. It shows a well-developed ectethmoid plate extending laterally from the mesethmoid, whereas the ectethmoid is much more reduced in *Fregata*. It emphasizes the large size of the orbit in *Limnofregata*, suggesting that the birds may have been partially nocturnal or crepuscular.

In GMNH PV 167, the toes of the right foot appear to be in their naturally maximal spread position, and shows the much better development of the foot in *Limnofregata* compared with *Fregata*. Assuming that the foot was totipalmate, as in all modern Pelecaniformes, the area of the webbing was on the order of 20 cm^2. In the largest and best preserved of the primary feathers in GMNH PV 167, the tip is much less attenuated and sharply pointed than in *Fregata*.

For FMNH PA 723, new information not preserved with the holotype concerns the tail. The number of free caudal vertebrae anterior to the pygostyle appears to be seven, as in *Fregata*. The pygostyle of *Limnofregata* was previously unknown, this element being entirely missing in the holotype of *L. azygosternon*. It is a broad plate as in *Phaethon* and *Fregata*, and completely unlike the pygostyle in the Sulidae, which is very thick and somewhat cylindrical proximally, tapering to a long, thin spine. In *Limnofregata*, the ventral margin of the pygostyle (Fig. 2) is rectilinear, the dorsal margin is curved, and the tip is broadly rounded.

***Limnofregata hasegawai*, new species**
(Figs. 5–7)

Holotype: GMNH PV 170, skull and mandible with quadrates, lacrimals, palatines, atlas, axis, and cervical vertebrae 3–7 (Fig. 5). Color brownish black. The skull is preserved in right dorso-lateral view with the mandible and right quadrate still in articulation. The left quadrate has been displaced and lies upside-down, with the mandibular articulation visible along the edge of the left orbit. The lacrimals are still nearly in articulation with the frontals, the right palatine is exposed but neither pterygoid is visible.

Locality: Smith Hollow Quarry, Lewis Ranch (Locality B of Grande and Buchheim, 1994), Lincoln County, Wyoming.

Horizon: Said to have been collected "2–3 m" from Referred Specimen 1 of *L. azygosterno*n (GMNH PV 167). Presumably this distance is intended as vertical as the matrix and the coloration of the bone (blackish vs. brown) are different. Fossil Butte Member of the Green River Formation, late early Eocene.

Etymology: To our esteemed colleague and friend Yoshikazu Hasegawa of the Gunma Museum of Natural History in recognition of his many contributions to vertebrate paleontology.

Diagnosis: Much larger than *L. azygosternon*. Rostrum proportionately much longer, 1.6 times as long as the cranium, vs. 1.4 in *L. azygosternon.*

FIGURE 5. *Limnofregata hasegawai*, new species, holotype GMNH PV 170 (above), compared with skull and mandible of the holotype of *L. azygosternon* USNM 22753 (below).

Measurements (mm) of holotype: Measurements that are comparable to those published for *Limnofregata azygosternon* appear in Table 2. Additional measurements are: Cranium: width at nasofrontal hinge, 16.8. Lacrimal: length, 17.1. Quadrate: length of articulation with mandible (left), 15.8. Atlas: width 11.9. Axis: width 13.1. Cervical vertebra 3: length, 16.1. Cervical vertebra 5: length, 22.8.

Paratype 1: FMNH PA 719, complete skull and mandible with left quadrate, both lacrimals and pterygoids, assorted sclerotic plates, atlas, axis, and cervical vertebra 3 (Fig. 6). The skull is preserved in dorsal and partial left lateral view with the entire left quadratojugal bar visible. The ventral surface of the mandible can be seen in its entirety.

Locality: Thomson Ranch (Locality H of Grande and Buchheim, 1994), ca. 14 km W of Kemmerer, Lincoln County, Wyoming.

Horizon: F-2 facies, Fossil Butte Member of the Green River Formation, late early Eocene.

Measurements (mm): The following are in addition to those in Table 2. Cranium: width at nasofrontal hinge, ca. 22. Pterygoid: length, 23.1. Quadrate: depth, 20.6; width of mandibular articulation, 15.7; length of otic process along dorsal edge, 12.2. Lacrimal: length, 18.1; depth including descending process, 19.0; depth of descending process, 12.5; greatest depth of corpus at posterior end 7.9. Mandible: posterior width (distance between external margins of articulations), 50.7; width of articulation, 17.3. Atlas: width and depth, 12.6 X 10.9.

FIGURE 6. *Limnofregata hasegawai*, new species, paratype, FMNH PA 719, skull and mandible. Scale = 2 cm. Inset: right and left lacrimal bones showing pneumatic foramina in the corpus.

TABLE 2. Cranial measurements of two species of *Limnofregata* compared

Measurement	*L. azygosternon* USNM 22753 Holotype	*L. hasegawai* GMNH PV 170 Holotype	*L. hasegawai* FMNH PA 719 Paratype 1
Total length of skull and rostrum	132.1	158.4	156.1+
Length of cranium to nasofrontal hinge	55.3	60.1	ca. 63
Length of rostrum from nasofrontal hinge	76.8	98.3	100.6
Length from posterior margin of postorbital process to tip of premaxillary	118.8	141.2	136+
Total length of mandible	120.6	149.4	149.4
Length of quadratojugal bar	50.0	66.2	65.8
Greeatest depth of mandible	9.5	12.2	—

Paratype 2: BMS E25336, pelvis with associated right and left femora and tibiotarsi, the first 5 free caudal vertebrae, and 10 presacral vertebrae (Fig. 7). Collected by Verl and Rick Hebdon and acquired by the Buffalo Museum of Science in 1982.

FIGURE 7. *Limnofregata hasegawai*, paratype, BMS E 25336 associated pelvis and hindlimbs without feet.

Locality: Warfield Fossil Quarries at Warfield Springs (NW1/4, Sec. 5, T19N, R117W; locality K of Grande and Buchheim, 1994), ca. 14 km SW of Kemmerer, Lincoln County, Wyoming.

Horizon: F-2 facies equivalent, Fossil Butte Member of the Green River Formation, late early Eocene. The specimen is from a 1.5 m thick layer of precipitated limestone overlying a 30–45 cm thick layer of bluish shale.

Measurements: See Table 1.

Description: As in *L. azygosternon* the nostril is long and open, the posteriormost corner being about 1 cm anterior to the naso-frontal hinge. The anterior margin can now be clearly discerned as extending nearly to the premaxillary symphysis.

The configuration of the quadrate in ventral view in *Limnofregata* shows some distinctive features. In *Phaethon* the medial and lateral condyles are in the same transverse plane with practically no development of a posterior condyle. In *Fregata*, the medial condyle extends posterolaterally as a more constricted crest, which then bends at nearly a right angle to the lateral condyle, the bend forming a rather weak posterior condyle with a deep depression anterior to it. The configuration in the Sulidae is more complex, with the posterior condyle completely separate from the medial condyle. *Limnofregata* is most similar to *Fregata*, with the medial condyle forming a long rolling crest with only an incipient posterior condyle and the lateral condyle is only slightly angled off of the long axis of the articular surface. The depression seen in *Fregata* is shallower in *Limnofregata*.

The pterygoids are relatively much longer in *Limnofregata* than in *Fregata*, with slightly curved rather than straight shafts that appear to be terete, without the flattened surfaces seen in *Fregata* or the Sulidae. They are quite unlike the very long, straight, and slender pterygoids in *Phaethon*.

The mandibular articulations are much heavier in *Limnofregata* than in *Fregata*, the rami much thicker and deeper, and the mandibular symphysis shorter. In the ventral view afforded by the paratypical skull of *L. hasegawai*, the internal processes of the articulations are shorter, thicker, and much less distinctly set off from the heavy proximal portion of the rami than in *Fregata*.

The one visible lacrimal in the holotype of *L. azygosternon* is partially obscured and was misinterpreted in the original description. The entire structure is beautifully revealed in paratype FMNH PA 719 of *L. hasegawai* in which both lacrimals are preserved with the entire external surface exposed (Fig 6). The corpus of the bone that articulates with the cranium is much larger than in *Fregata*, with the posterior portion broad and truncated. There are two small pneumatic foramina in the corpus, just anterior to the descending process. The descending process is very long and slender, with a very small expansion on the posterior margin about 2/3 the distance to the ventral extremity. The lacrimal in *Fregata* is very different, with a small, nonpneumatic corpus and a greatly expanded, inflated descending process that bears a single pneumatic foramen.

The postcranial specimen of *L. hasegawai* is not in particularly good condition, but has the pelvis preserved in dorsal view and the thoracic vertebrae are better preserved than in the holotype of *Limnofregata azygosternon*. These do not differ greatly from those in *Fregata*. The specimen confirms that the distinctive notch in the posterior margin of the innominate bone in the area of fusion of the ischim and ilium (Olson, 1977:15) is the normal condition. As in the holotype of *L. azygosternon*, the pygostyle is missing, suggesting that it may have floated away with the presumably enlarged rectrices.

Size in *Limnofregata*. The seven available specimens now assigned to *L. azygosternon* are remarkably homogeneous in size and those for which comparable length measurements are available are practically identical (Table 1), especially given the variation induced by crushing and other vicissitudes of preservation. In the two skulls of *L. hase-*

gawai such factors of preservation have doubtless contributed to inaccuracies in the measurements of the cranium and rostrum. For example, in the paratype FMNH PA 719, the skull is broken across the nasofrontal hinge and the anterior margin of the cranium has been shoved under the posterior margin of the rostrum perhaps as much as 6 mm. On the other hand, the length measurements of the two known mandibles of *L. hasegawai* and in the holotype of *L. azygosternon* are unequivocal. The two mandibles of *L hasegawai* are identical in length and are 20% larger than in the holotype of *L. azygosternon.* The postcranial paratype of *L hasegawai* basically agrees in size, as the femur is 17% larger and the pelvis 20% larger than in *L. azygosternon.* The tibiotarsus seems disproportionately small, however, as it is only 7% larger. The same appears to apply within modern frigatebirds, however, as the tibiotarsus of the largest species, *F. minor*, is proportionately smaller than in *F. ariel*, the smallest species (Table 3).

TABLE 3. Range and mean and ratio of skeletal measurements (n = 6 for both species) of the smaller sex of the smallest modern species and the larger sex of the largest modern species of frigatebirds (*Fregata*).

Measurement	*F. ariel* males	*F. minor* females	Ratio of *F. minor*/*F. ariel*
Total skull length	130–135.1 (132.3)	149.5–166.8 (159.2)	1.20
Width across antitrochanters	40.0–43.0 (41.4)	51.0–55.3 (52.4)	1.26
Humerus length	149.5–152.8 (150.9)	172.1–185.8 (179.7)	1.19
Femur length	41.2–43.3 (42.5)	47.7–52.0 (50.1)	1.18
Tibiotarsus length	59.0–60.8 (60.1)	63.5–69.3 (66.8)	1.11

The differences in size between *L. azygosternon* and *L. hasegawi* are as great as between the smallest and largest individuals of modern *Fregata*, which comprises 5 sexually dimorphic species (females larger). Thus, on size alone, *Limnofregata* would have to be divided into two species-level taxa, as the differences could not be due to differences between sexes, especially as the species of *Limnofregata* are unlikely to have been sexually dimorphic (see discussion below). The differences in bill proportions, with *L. azygosternon* having proportionately a much shorter bill, would also not be expected within a single species.

Evolution and morphology

Differences in the quadrate articulation and mandibular morphology of *Limnofregata* indicate that food processing and swallowing were probably different from that of *Fregata*. Whether any of these differences may be correlated with the inflation of the throat pouch into a large balloon in displaying males of *Fregata* would require detailed functional anatomical studies of the modern species.

In modern frigatebirds, the foot is greatly reduced in size and the extent of webbing is also reduced. These birds rarely if ever alight on water and use the feet only for perching. Although the tarsometatarsus is already considerably shortened in *Limnofregata*, it is not reduced to the great extent it is in *Fregata*. Furthermore, the toes are long and well-developed. Such a foot obviously would still form a very effective paddle, so that *Limnofregata* could have moved effectively about on the surface of the water.

It has been suggested that the lacustrine *Limnofregata* may have occupied a niche somewhat similar to modern gulls (Laridae), which are opportunistic predators and scavengers. A late Eocene or early Oligocene supposed gull from the Phosphorites de Quercy has been re-evaluated and gulls are not otherwise known prior to the late Oligocene (Mourer-Chauviré, 1982, 1995, 2004). If gulls of the genus *Larus* provide a valid analogy, then we can envision a sympatric assemblage of several species of *Limnofregata* that differ very little from one another osteologically except in size and perhaps bill shape.

Modern gulls are not greatly sexually dimorphic in size, whereas modern frigatebirds (*Fregata*) are, with females being larger than males. That *Limnofregata* was sexually dimorphic in size is unlikely. The 7 specimens of *L. azygosternon* are all the same size and it is highly improbable that all are of the same sex. The specimens of *L. hasegawai* are so much larger that the differences from *L. azygosternon* are approximately as great as between males (the smaller sex) of the smallest living frigatebird *Fregata ariel* (G. R. Gray) and females of the largest species *F. minor* (Linnaeus) (Table 3).

The various hypotheses proposed to explain size dimorphism, particularly reverse sexual size dimorphism (females larger than males), were examined at length by Schreiber and Schreiber (1988) in connection with modern frigatebirds and none were found to be applicable. Females of *Fregata* have a higher wing-loading than males and the sexes may be differentially distributed because of subtle differences in wind conditions from one locality to another (Harrington et al., 1972). The extremely long, pointed wings, and very long, deeply forked tail of *Fregata* are probably specializations for soaring flight associated with a dependence upon wind that would only exist in oceanic conditions. Sexual size dimorphism probably arose in connection with these specializations to a pelagic environment. Therefore it is a reasonable assumption that *Limnofregata* was not sexually dimorphic and that the size differences observed in the fossils reflect differences between species rather than sexes.

Paleoecology

The Green River Formation, one of the world's largest systems of lacustrine sediments, consists of independent units accumulated in three adjacent intermontane basins in which formed Lake Uinta, Lake Gosiute, and Fossil Lake (Grande, 1984). Sediments were laid down in Lake Uinta from the late Paleocene through the late Eocene, and for shorter periods of the early and middle Eocene in the other two lakes.

Apart from the one cranium from Lake Gosiute, all fossils of *Limnofregata* discovered so far have come from Fossil Lake. This is most likely an artifact of intensive commercial quarrying for fossil fish in the Fossil Lake sediments, during which fossil birds, including *Limnofregata*, are incidentally encountered. Fish are abundant throughout the Green River sediments and were undoubtedly the principal, if not sole prey of all species of *Limnofregata*. Most abundant of all were fishes of the genus *Knightia*, a true herring (Clupeidae; Grande, 1982) that occurred in all three lake systems. With a maximum total length of 25 cm and an average of about 15 cm, *Knightia* would have been of ideal size as prey for *Limnofregata*.

Various fish in the Green River lakes, but especially *Knightia*, were subject to frequent periodic dieoffs, possibly due to algal blooms or to turnover in thermally stratified layers of lake water that would have produced toxic amounts of gases such as hydrogen sulfide (McGrew, 1975). From differential degrees of decomposition of fish fossils and variations in amount of deposition of calcium carbonate that would have enhanced preservation, McGrew (1975) hypothesized that fish dieoffs in Fossil Lake took place in early and late summer and early fall. This appears to be borne out at least in part by isotopic analyses of carbonate in the Green River Formation showing precipitation of primary carbonate to be promoted by processes of photosynthesis-respiration (Pitman, 1996). Similarly, Grande (1984: 84) cited examples of dieoff of modern clupeids during summer months.

Frigatebirds, like gulls, will scavange voraciously on dead floating fish. Thus, the breeding season of the Green River frigatebirds may well have been timed to take advantage of summer fish dieoffs for a superabundance of food to be obtained with very little expenditure of energy.

During periods of carbonate precipitation, which is when both fish and frigatebirds were best preserved, Green River lake waters were brackish to slightly saline (Pitman, 1996). All modern Pelecaniformes have salt glands for excretion of excess sodium chloride and *Limnofregata* may be assumed to have been similarly equipped. In the Pelecaniformes, however, the salt glands are inside the orbit rather than in grooves on the dorsal surface of the skull as in most other marine birds; because of distortion and crushing in the known skulls of *Limnofregata* the impressions of the salt glands cannot be discerned.

The flora and sediments of the Green River lakes indicate a warm, equable, subtropical climate, with the vegetation having most similarities to floras now found at about the latitude of Monterrey or Mazatlan, Mexico (MacGinitie, 1969). These latitudes today are near the northern limits of breeding distribution of frigatebirds in the New World. There is no fossil record as yet to indicate whether Paleogene frigatebirds were also coastal or could take advantage of smaller bodies of fresh water in the manner of modern gulls. Regardless, the infilling and dessication of the Green River lakes during mid and late Eocene time (McGrew and Casilliano, 1976) obliterated this resource for frigatebirds. Furthermore, the first of major Cenozoic cooling events took place in the early middle Eocene (McGowran, 1990), initiating the retreat of tropical climates to lower latitudes

later in the Cenozoic. Such events, perhaps in concert with the ascendency of potential competitors such as gulls, probably caused frigatebirds to withdraw to the strictly tropical, pelagic niche that they occupy today.

Museum abbreviations

BMS—Buffalo Museum of Science, Buffalo, New York.; FMNH—Field Museum of Natural History, Chicago, Illinois; GMNH—Gunma Museum of Natural History, Tomioka, Gunma Pref., Japan; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UWY—University of Wyoming, Laramie, Wyoming.

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