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L'EVOLUTION DES OISEAUX D'APRES LE TEMOIGNAGE DES FOSSILES

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AN EARLY EOCENE OILBIRD
FROM THE GREEN RIVER FORMATION OF WYOMING
(CAPRIMULGIFORMES : STEATORNITHIDAE)

Storrs L. OLSON

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UN GUACHARO DANS L'EOCENE INFERIEUR
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Storrs L. OLSON *

Abstract

The first diagnostic fossils of an oilbird (*Steatornithidae* : *Caprimulgiformes*), two nearly complete skeletons, are described as a new genus and species from the early Eocene Green River Formation of Wyoming. The fossil form is smaller than the living Oilbird (*Steatornis caripensis*) but had the characteristically shortened tarsometatarsus and distinctive mandibular morphology. The sternum and pelvis are more primitive than in *Steatornis* and the less specialized structure of the humerus, toes, and tail suggests that the fossil form was not adapted for hovering flight or for life in caves. Although the family *Steatornithidae* is now confined to South America and has been regarded as one of the endemic elements in the avifauna of that continent, the distribution of the family is now seen to be relictual. *Steatornis* is the only herbivorous member of the *Caprimulgiformes*. The same families and even genera of plants that predominate in the diet of *Steatornis* also occur as fossils in the Green River Formation, suggesting that herbivory could have arisen in the *Steatornithidae* during or prior to the early Eocene. Because these birds would have been effective disseminators of large angiosperm seeds, rapid coevolution of both seed plants and their avian dispersal agents at the beginning of the Tertiary is likely.

KEY-WORDS : *Aves*, Eocene, Green River Formation, *Steatornithidae*, *Caprimulgiformes*, *Coraciidae*, *Coraciiformes*, Biogeography, Angiosperm Co-evolution.

Résumé

Les premiers restes de Guacharos (*Steatornithidae*, *Caprimulgiformes*), représentés par deux squelettes presque complets provenant de l'Eocène inférieur de la Green River Formation, dans le Wyoming, sont décrits sous le nom de *Prefica nivea*, n. gen. n. sp. La forme fossile est de taille inférieure à celle du Guacharo actuel (*Steatornis caripensis*) mais elle possède un tarsométatarse raccourci de façon caractéristique et une morphologie distinctive de la mandibule. Le sternum et le pelvis sont plus primitifs que dans le genre *Steatornis* et la structure moins spécialisée de l'humérus, des doigts postérieurs et de la queue suggère que la forme fossile n'était pas adaptée au vol sur place ou à la vie dans les cavernes. Bien que la famille des *Steatornithidae* soit actuellement limitée à l'Amérique du Sud et ait été considérée comme l'un des éléments endémiques de l'avifaune de ce continent, la distribution de cette famille doit maintenant être considérée comme relictuelle. Les *Steatornithidae* sont les seuls engoulevants végétariens. Les mêmes familles de plantes, ou parfois même les mêmes genres, qui prédominent dans le régime alimentaire de *Steatornis* sont connus à l'état fossile dans la Green River Formation, suggérant que les *Steatornithidae* pouvaient déjà être végétariens à l'Eocène inférieur ou même à une époque antérieure. Ces oiseaux ont pu être des agents efficaces pour la dissémination des grosses graines d'Angiospermes.

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et donc une coévolution rapide à la fois des plantes à graines et des oiseaux qui les dispersent semble avoir eu lieu dès le commencement du Tertiaire.

MOTS-CLES : Oiseaux, Eocène, Formation de Green River, *Steatornithidae*, *Caprimulgiformes*, *Coraciidae*, *Coraciiformes*, Biogéographie, Coévolution des Angiospermes.

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I. INTRODUCTION

The Oilbird, or Guácharo (*Steatornis caripensis* HUMBOLDT, 1817) is one of the most peculiar of all living birds. It constitutes a monotypic family in the order Caprimulgiformes, which is composed of nonraptorial nocturnal birds such as nightjars, frogmouths, and potoos. *Steatornis* is remarkable for nesting and roosting in caves, echolocating, having an extremely long nestling period and fatty young, and for being the only vegetarian member of the order, feeding mainly on the fruits of palms and laurels. The Oilbird is confined almost entirely to South America (only two records from Panama) and is regarded as one of the characteristic endemic elements of the South American avifauna. Until very recently, there has been no fossil record whatever for the family (Brodtkorb, 1971).

This changed with the discovery of a nearly complete skeleton (USNM 336278) of a new genus and species of *Steatornithidae* in the early Eocene (ca. 50 MYA) Fossil Butte Member of the Green River Formation in Wyoming. After the analysis and description of this specimen was nearly completed, I came to the realization that another specimen from the Green River Formation that I had previously suggested was close to the roller genus *Eurystomus*, in the family *Coraciidae* (Olson, 1985 : fig. 4), must belong to the same species. Together, these specimens provide not only an unexpected insight into the early history of the *Steatornithidae*, but also important new information concerning the origins of the order Caprimulgiformes.

II. SYSTEMATICS

Order *Caprimulgiformes* RIDGWAY, 1881
Family *Steatornithidae* GRAY, 1846

Included subfamilies

Steatornithinae, new status ; *Preficinae*, new subfamily.

Diagnosis

Anisodactyl land birds with wide mouths and reduced, non-raptorially adapted feet ; mandibular rami strong, not wide and flattened dorsoventrally but widely divergent posteriorly, symphysis short ; tarsometatarsi reduced, less than 17 % of total hindlimb length, but not grotesquely reduced with widely splayed trochleae as in the *Nyctibiidae*.

Subfamily *Steatornithinae*, new status

Included genus

Steatormis HUMBOLDT, 1814

Diagnosis

Head small in relation to body, rostrum relatively narrow with the bones strongly co-ossified and the nostrils reduced ; posterior margin of sternum shallowly two-notched ; innominates strongly fused to sacrum ; transverse processes of caudal vertebrae very wide, pygostyle elongated ; humerus relatively stout with greatly enlarged pectoral crest, ventral epicondyle protrudent, with distinctive postero-distal facet ; certain phalanges of pes differentially reduced.

Subfamily *Preficinae*, new subfamily

Included genus

Prefica, new genus.

Diagnosis

Differs from *Steatornithinae* as follows : head large in proportion to body, rostrum wide and not heavily ossified, nostrils large ; sternum 4-notched ; innominates not fused to sacrum ; transverse processes of caudal vertebrae and pygostyle less developed ; humerus relatively longer, without greatly expanded pectoral crest and ventral epicondyle ; phalanges of pes not differentially reduced.

***Prefica*, new genus**

Type species

Prefica nivea, new species.

Diagnosis

As for the subfamily.

Etymology

Latin, f. *praefica*, a woman hired to lament at the head of a funeral procession, in reference to the wailing cries of *Steatormis* that give rise to its Spanish name.

***Prefica nivea*, new species
(pl. 1-3)**

Holotype

Nearly complete, flattened skeleton preserved in a slab of unvarved, cream-colored shale ; vertebrate paleontological collections of the National Museum of Natural History, Smithsonian Institution, USNM 336278 (pl. 1-3). The specimen was probably in quite good condition originally, but before it was acquired by the Smithsonian it had been prepared by an inexperienced person using a pneumatic abrasive device ; consequently the exposed surfaces are in some cases worn and indistinct. Although the mandible is nearly intact, lacking only the very tip, all that remains of the skull are barely interpretable portions of the cranium, a quadrate, and possibly the quadratojugals. Both wings and both hindlimbs are present, although the proximal end of the left humerus is missing, little remains of the right tibio-tarsus, and the left femur, left scapula, and furcula are obscured. There is no trace of the left innominate, which was either lost prior to preservation or is located undiscovered elsewhere in the slab.

Type locality

Northeast of Kemmerer, Lincoln County, Wyoming. From Fossil Lake, locality F-2, as mapped and discussed by Grande (1984). Collected in 1981.

Horizon

Fossil Butte Member of the Green River Formation, Lost Cabinian substage of the Wasatchian land mammal age, late early Eocene.

Etymology

Latin, *nivea*, of snow, dedicated to David W. Snow for his excellent investigations into the life history of *Steatornis caripensis* (Snow, 1961 ; 1962). Without such general biological knowledge it is impossible to understand the evolutionary context of an organism and even more difficult to appreciate the significance of fossils such as those of *Prefica*. Unfortunately, because such studies are inherently descriptive, they are now usually disdained in favor of vacuous «hypothesis-testing» and contrived experimentation that serve mainly to provide statisticians with sufficient «scientifically» quantified material with which to revile one another, while around them most of the natural world disappears before it can begin to be understood. In light of this, we can be all the more grateful to have Snow's contribution to the behavior and ecology of *Steatornis*.

Diagnosis

As for the subfamily ; smaller than *Steatornis caripensis* HUMBOLDT, 1817.

Referred material

An excellent complete skeleton exposed in dorsal aspect in the Landessammlungen für Naturkunde Karlsruhe (see Olson, 1985 : fig. 4). This is also from locality F-2 in the Green River Formation of Wyoming. As yet I have been able to study only a photograph of this specimen but this is sufficient to establish its probable identity with the holotype of *Prefica nivea*.

Comparative material examined

Five skeletons of the living species *Steatornis caripensis* : AMNH 3426 (male), AMNH 3167, UMMZ 157205 (male), USNM 19878, YPM 1936. Except for the two specimens indicated, the remainder were of undetermined sex. Representative skeletons of all the families of Caprimulgiformes and Coraciiformes were also examined.

Measurements of holotype

Measurements are in mm and are of the length of the element unless otherwise specified. The number in parentheses is the average of five modern specimens of *Steatornis caripensis*, although not all measurements were available for each specimen and those for the ungual phalanges were taken from USNM 19878 only.

Mandible, 48.5 (53.2) ; coracoid, ca. 26 (37.4) ; length and depth of sternal carina, ca. 35 x 11.5 (48.6 x 17.3) ; humerus, ca. 63 (72.7) ; ulna 77.7 (111.6) ; radius, 72.2 (114.5) ; carpometacarpus, 35.6 (45.4) ; phalanx 1 of major alar digit, 18.0 (23.4) ; phalanx 2 of major alar digit, 16.0 (17.7) ; minor alar digit, 7.7 (12.3) ; femur, ca. 30 (36.4) ; tibiotarsus, ca. 37 (47.6) ; tarsometatarsus, 11.8 (18.1) ; pedal phalanges—dII p1, 6.3 (9.5) ; dII p2, 5.6 (9.8) ; dII p3, 5.0 (8.7) ; dIII p1, 6.8 (8.7) ; dIII p2, 7.0 (6.6) ; dIII p3, 8.1 (9.5) ; dIII p4, 6.5 (9.2) ; dIV p1, 5.1 (7.1) ; dIV p2, 4.6 (3.5) ; dIV p3, 3.5 (3.2) ; dIV p4, 4.1 (7.0) ; dIV p5, 5.3 (8.6).

A. DESCRIPTION AND COMPARISONS

The two specimens in question are clearly anisodactyl land birds with a very wide gape. The weak feet and claws remove owls (Strigiformes) from consideration and therefore the only modern groups that require detailed comparison are the Coraciiformes and Caprimulgiformes.

Because of the very roller-like aspect of *Prefica*, especially as seen in the Karlsruhe specimen, it is first necessary to discuss the differences between the fossils and the *Coraciidae*. Probably most important in this regard is the mandible (pl. 2), which is visible only in the holotype. The form of the mandible in *Prefica* is strikingly similar to that in *Steatornis* and differs from *Eurystomus*, which has the widest bill of any of the *Coraciidae*, in having the rami more strongly bowed, contributing to a wider angle between them. The rami are thicker posteriorly than in *Eurystomus* and do not become flattened and expanded as they approach the symphysis. Although the tip of the symphysis is missing in the holotype of *Prefica nivea*, the part that remains is like the very short symphysis in *Steatornis* rather than the longer and more expanded symphysis of *Eurystomus*. Also, the tarsometatarsus in *Prefica* is shorter and stouter than in *Eurystomus*, constituting only about 17 % of the total hindlimb length, as opposed to about 21 % in *Eurystomus*. A similarly shortened tarsometatarsus is characteristic of *Steatornis*. Among the Caprimulgiformes, only the *Nyctibiidae* have a shorter tarsometatarsus, but in that family the bone is grotesquely abbreviated, with distinctively splayed trochleae.

Clearly visible in both specimens of *Prefica* are the two equal notches on the left side of the posterior border of the sternum (pl. 3). In the *Coraciidae* these notches are deeper, the lateral ones being

much larger than the medial notches, whereas in *Steatornis* there is only a single, wide, shallow notch on either side of the sternum. The reduction in the lateral notch of *Prefica* may foreshadow the condition in *Steatornis*. The transition from a 4-notched to a 2-notched sternum is a pattern that is repeated in many unrelated groups of birds, with the primitive four-notched condition being present in Eocene forms and lost in their modern derivatives (e.g. *Limnofregata*, *Presbyornis* Olson, 1977 ; Olson and Feduccia, 1980).

A very wide mouth, and consequently the presence of widely divergent mandibular rami, is characteristic of the Caprimulgiformes in general. In the *Aegothelidae*, *Nyctibiidae*, and *Caprimulgidae*, however, the rami are very weak and thin anteriorly, unlike the fossil and recent *Steatornithidae*. In the *Podargidae* the mandibular rami are stout but extremely broad and flattened, and thus quite different from either of the steatornithids.

The configuration of the mandible and tarsometatarsus of *Prefica* indicate that its closest living relative is *Steatornis*. Although *Prefica* is extremely primitive, its relationship to *Steatornis* is best reflected at the familial level, whereas the differences are certainly sufficient to require their separation at the subfamilial level, as in the case of the early Eocene frigatebird *Limnofregata* (Olson, 1977).

As seen in the Karlsruhe specimen, the skull of *Prefica* differs greatly from that of *Steatornis* in having long, open nostrils with a distinct median bar, appearing somewhat similar to the skull in *Eurystomus*, in which, however, the nostrils are considerably ossified. In *Steatornis*, the rostrum is heavily ossified and reinforced, with small, anteriorly situated narial openings. The width of the skull at the nasofrontal hinge is much less in *Prefica* than in *Eurystomus* and there is no evidence of the presence of lacrimals. Both of these characters, if the lacrimals are indeed absent, are also found in *Steatornis*.

The very poorly preserved skull of the holotype shows well developed temporal fossae, as in *Eurystomus* and *Steatornis*. There is also a large, elongate postorbital process quite unlike the short, wide, triangular process of *Steatornis*. Although the exact configuration of this process cannot be made out in the fossil (further preparation of the Karlsruhe specimen could be revealing in this regard), a strong, elongate postorbital process that descends almost to the jugal bar is a distinctive character of the entire roller group (Olson, 1983), but occurs in modern Caprimulgiformes only in the *Podargidae*. On either side of the skull of the holotype are obscure elongated structures that may possibly be the quadratojugal bars (pl. 3). If this interpretation is correct, the quadratojugal bar in *Prefica* is much more expanded anteriorly than in *Steatornis* and would therefore be more similar to that in *Eurystomus*.

Apart from the notches in the posterior margin, discussed above, the overall configuration of the sternum in *Prefica* is similar to that of *Steatornis*, with the anterior apex of the carina being rounded rather than pointed as in the *Coraciidae*.

In *Prefica*, the innominates are not fused to the sacrum, whereas in *Steatornis* these bones are heavily co-ossified, with obscure sutures. The innominates are also fused in the *Coraciidae* and some of the Caprimulgiformes. The unfused condition is clearly primitive, whereas fusion has apparently taken place independently in many different lines, similar to the transformation of the 4-notched to the 2-notched sternum. The anterior iliac shields are larger in *Prefica* than in either *Eurystomus* or *Steatornis*, being somewhat more similar to the condition in the *Podargidae* or *Leptosomidae*. The posterior iliac shields are short and wide, perhaps foreshadowing the very wide condition seen in *Steatornis*.

There appear to be six free caudals between the pygostyle and the sacrum, as in *Steatornis*, but the transverse processes in *Prefica* are blunt and not nearly as well developed as in *Steatornis*. The pygostyle is likewise not as large and elongated, so the tail was almost certainly smaller than in the modern bird.

The humerus in *Steatornis* is unique and differs greatly from that in any of the Coraciiformes or other Caprimulgiformes in being relatively shorter and stouter, with a much more expanded pectoral crest and a distinctive faceted projection of the ventral epicondyle that probably serves as an expanded area of attachment for the carpal flexors. Increased action at the wrist joint is doubtless needed in hovering flight, as shown in photographs of *Steatornis* hovering in caves (Snow, 1961 : pl. II, fig. 5 ; Ross, 1965). *Prefica* shows none of these specializations and the humerus is not substantially different from that of rollers or primitive Caprimulgiformes such as the *Podargidae*.

Steatornis has a relatively shorter humerus and a longer ulna than in *Prefica*, whereas in both genera the carpometacarpus makes up 20 % of the length of the three elements combined. The intramembral proportions of the hindlimb are roughly the same in these two genera. The head of *Prefica* is considerably larger relative to body size than in *Steatornis*. Whereas the mandible is nearly the same

absolute size in both genera, *Steatornis* is nearly 40 % larger in body size than *Prefica*. A large head relative to body size is one of the most noticeable characteristics of the Caprimulgiformes and is likely to be the primitive condition.

The proportions of the phalanges of the toes in *Prefica* are similar to those in rollers. Taking the lengths of the individual phalanges as a percent of coracoid length, which provides some measure of overall body size, it is seen that in *Steatornis* phalanges 2 and 3 of digit IV, and phalanx 2 of digit III, are greatly reduced, and phalanx 3 of digit III is somewhat reduced, as compared to *Prefica*. The proportions of the other pedal phalanges are otherwise very nearly the same in these two genera. All of the phalanges are more laterally compressed in *Steatornis* than in *Prefica*.

B. PHYLOGENY

Prefica allows us to examine a steatornithid without the more extreme specializations that obscure the affinities of *Steatornis*. The great similarity of most of its skeleton to that in the *Coraciidae* lends support to the suggested derivation of the Caprimulgiformes from the Coraciiformes (Olson, 1985). The early Eocene was a time of great diversification of the coraciiform lineage, at least in North America and Europe, where there is now an excellent fossil record, and it is clear that the appearance of nocturnal birds that resulted in the Caprimulgiformes and Strigiformes is a manifestation of this great coraciiform radiation. *Prefica* is scarcely more than a short-legged roller with a large, somewhat modified head. It shows no characters to ally it with any of the Caprimulgiformes, other than *Steatornis*, that are not also shared with the Coraciiformes. Therefore the *Steatornithidae* may have arisen near the base of the caprimulgiform radiation.

As in the case of *Limnofregata* and *Fregata* (Olson, 1977), there are no characters of *Prefica* that would preclude it from being on a line directly ancestral to *Steatornis*. Although *Prefica* may have had a «sister-group» relationship to *Steatornis*, it has not a single morphological feature that would favor this hypothesis over one of direct ancestry.

III. CONCLUSIONS

A. EVOLUTION AND PALEOECOLOGY

The basic facts concerning the life history of the living oilbird, *Steatornis caripensis*, may be summarized from Snow (1961, 1962). Oilbirds are nocturnal and nest and roost in caves. At night they range considerable distances from their nesting caves to feed gregariously on the fruits of various kinds of trees, principally palms and species of *Lauraceae*. The birds feed mainly by hovering, although they may at times land on clusters of fruit. Hovering flight is also necessary in the restricted confines of the nesting caves, the well developed tail being extensively used in this connection, but only rarely as a prop when clinging to cave walls, as the birds usually perch horizontally on narrow ledges. In the absence of sufficient light, flight through caves is aided by audible clicks that function in echolocation. The nesting period is very long, during which time the young become extremely fat, eventually exceeding adult weight by as much as 50 %.

Snow (1961 : 44-45) presents a most plausible discussion of the factors that were probably important in the evolutionary history of *Steatornis*. He proposed that *Steatornis* originally evolved from a nocturnal or crepuscular ancestor and that this was more closely related to Caprimulgiformes than to owls because the transition to fruit-eating is easier to envision in birds that seize food with the mouth and swallow it whole, rather than in birds that seize food with the feet and tear it up with the beak. Because many diurnal birds in the tropics eat fruit, it is logical that some nocturnal bird would also exploit this resource. The temporary and discontinuous nature of fruiting trees would make social feeding advantageous and the increase in size of *Steatornis* relative to other Caprimulgiformes would enable it to feed on larger fruit. Because the young of fruit-eating birds develop slowly, safer nesting sites would be required, which, in combination with the social behavior, would have favored cliff ledges or caves. Increasing specialization for cave nesting resulted in the evolution of echolocating mechanisms and, in combination with the feeding methods, in greater specialization for hovering flight.

With the fossils of *Prefica*, we may postulate what the initial stages may have been in the evolution of *Steatornis*. *Prefica* presents us with what must be one of the most primitive stages in steatornithid evolution in which very little has changed from the original roller-like ancestor. The most significant differences from rollers are in the skull and probably relate to feeding adaptations. The mandible is very

similar to that of *Steatornis* and, whereas the skull retains some primitive features, it had already become narrower in the naso-frontal region and the lacrimals may already have been lost. Because the mandible differs from that of related families, it may be reasonable to assume that the transition to fruit eating had already taken place or was in the process of evolving by the early Eocene, a possibility strengthened by the existence then of all the proper food sources (see below). The more arboreal and aerial behavior that resulted from eating fruit may concurrently have permitted the reduction of the hindlimb. The significance of further reduction of some of the pedal phalanges in *Steatornis* is difficult to surmise, although such reduction also took place in other Caprimulgiformes, especially the *Caprimulgidae*, in which one of the phalanges of digit IV is lost.

The smaller size of *Prefica* agrees with the ancestral condition as inferred by Snow. The fact that its head was virtually identical in size with the much larger *Steatornis* indicates that increased size in the latter was not an adaptation for swallowing larger fruit but probably for increasing the quantity of food that could be carried over a greater distance. Such an increase in flight range would be of advantage to a cavernicolous bird, given the spotty distribution of caves. *Prefica* had none of the specializations of the wing and tail that in *Steatornis* are probably correlated with hovering flight; therefore it almost certainly had not assumed a cavernicolous reproductive mode. The increase in ossification of the rostrum in *Steatornis* may represent a strengthening adaptation for increasingly specialized fruit feeding, but it would be difficult to imagine that the unique, peculiar configuration of the palatines (see Beddard, 1898 : fig. 120), which is not ascertainable in the fossils, is involved in feeding and I wonder if this might somehow be related to sound production in echolocation.

The Green River Formation was deposited in several very large lakes covering parts of what is now Wyoming, Colorado, and Utah (Grande, 1984). The climate in the early Eocene of northwestern North America was subtropical (Wolfe and Hopkins, 1967), with mild, equable winters, dry, hot summer and fall, and moderate rainfall in late spring and early summer (MacGinitie, 1969). No strictly comparable floras exist today, but «the closest resemblances in environment and composition are found in the savanna-woodland floras along the equatorward border of the dry tropics, east of Mazatlan, Mexico, and in the area of Santiago, Argentina, and the region around Monterrey, Mexico» (MacGinitie, 1969 : 2).

Despite the fact that there are many northern elements in the flora and that the vegetation would certainly not be characterized as that of a humid tropical forest, such as inhabited by *Steatornis* today, it is extremely interesting that practically all the major taxa of food plants preferred by *Steatornis* occur as fossils in the Green River Formation. Snow (1962) identified 112,717 individual fruits eaten by *Steatornis*. Of these, 74 % were of palms and *Lauraceae*. Several species of palms are known from the Green River Formation (Read and Hickey, 1972), although all are «form genera» based on leaves, so their precise relationships to living genera of palms is not known. Four genera of *Lauraceae* have been recorded from the Green River Formation (MacGinitie, 1969), including two, *Ocotea* and *Beilschmiedia* that are eaten by *Steatornis*. Fruits of *Ocotea* made up nearly 11 % of the diet of *Steatornis* sampled by Snow (1962) in Trinidad. The only other fruits that were taken in significant numbers by *Steatornis* were of *Burseraceae* (25 %), a family also represented in the Green River Formation. Of the seven additional plant families recorded as food of *Steatornis*, three (*Araliaceae*, *Oleaceae*, and *Anacardiaceae*) occur in the Green River Formation. Only 14 specimens of seeds, out of the 112,717 identified by Snow, came from families as yet unrecorded in the Green River Formation (*Myristicaceae*, *Sapotaceae*, *Boraginaceae*, *Malpighiaceae*).

Because all the appropriate food sources were present for *Prefica* to have become partly or completely frugivorous by the early Eocene, it is possible that the lineage leading to *Steatornis* has been feeding on essentially the same specialized diet for over 50 million years. This could be an interesting possibility to bear in mind for anyone who might wish to study the intestinal flora and parasites of *Steatornis*, as it is conceivable that the alimentary tract of *Steatornis* may represent an environment that has been absolutely stable for most of the Cenozoic era.

The appearance of birds capable of eating and dispersing large fruit by the early Eocene has interesting botanical implications as well. Tiffney (1985) and Wing and Tiffney (1987) have called attention to co-evolutionary patterns between angiosperms and their potential dispersers over the Cretaceous-Tertiary boundary. Angiosperms were not a dominant component in Cretaceous ecosystems, consisting mainly of and shrubs and insubstantial trees with small fruits and seeds. This changes dramatically in the early Tertiary, with «angiosperms becoming physiognomically-dominant plants of stable forest communities» (Tiffney, 1985 : 569). This is postulated to be the result of the simultaneous evolution of large seed size and suitable dispersal agents, mainly birds and mammals. The fossil record indicates an explosive radiation of birds in the early Tertiary (Olson, 1985), similar to that observed for mammals. The fossils of *Prefica* show that birds capable of consuming and dispersing quite large seeds were probably in existence for some time prior to the early Eocene. Thus there can be no question that adequate dispersal mechanisms were available for early Tertiary angiosperms.

B. BIOGEOGRAPHY

With *Steatornis* being entirely restricted in distribution to South America (fig. 1), it was logical to assume that the *Steatornithidae* were but one more bizarre element in the fauna of that «island continent» that evolved in «splendid isolation» (Simpson, 1980) during the Tertiary. The discovery of *Pre-fica* in the early Eocene of North America shows, however, at least that the family *Steatornithidae* probably differentiated outside of South America. Supporting this is Mourer-Chauviré's (1982) tentative identification of the anterior portion of a sternum from the late Oligocene of Quercy, France, as that of a steatornithid. Whether the extreme specializations of *Steatornis* evolved in South America or elsewhere remains unknown, but at the family level the *Steatornithidae* must be regarded as a relict in South America, rather than an autochthonous endemic.



Fig. 1 – Modern (black) and fossil (X) distribution of the *Steatornithidae* in the New World (modified from Ross, 1965).

Fig. 1 – Distribution actuelle (en noir) et fossile (X) des *Steatornithidae* du Nouveau Monde (d'après Ross, 1965, modifié).

It now appears that such relictual status must be conferred upon practically all the nonpasserine families of birds that have historically been considered to be endemic to the southern continents. Mourer-Chauviré (1982) has reviewed the numerous taxa from Quercy alone that belong to families now restricted to South America, the Antilles, Africa, or Australia. Among the Caprimulgiformes, the families *Podargidae* and *Aegothelidae* and the Neotropical family *Nyctibiidae* have all been recorded from Quercy (Mourer-Chauviré, 1982 ; in press). Thus, the occurrence of a steatornithid in North America no longer really seems anomalous.

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PLANCHE 1

Holotype of *Prefica nivea*, new species, USNM 336278 from the early Eocene Green River Formation of Wyoming.

Holotype de *Prefica nivea*, n. sp., USNM 336278 de l'Eocène inférieur de la Formation de Green River, Wyoming.

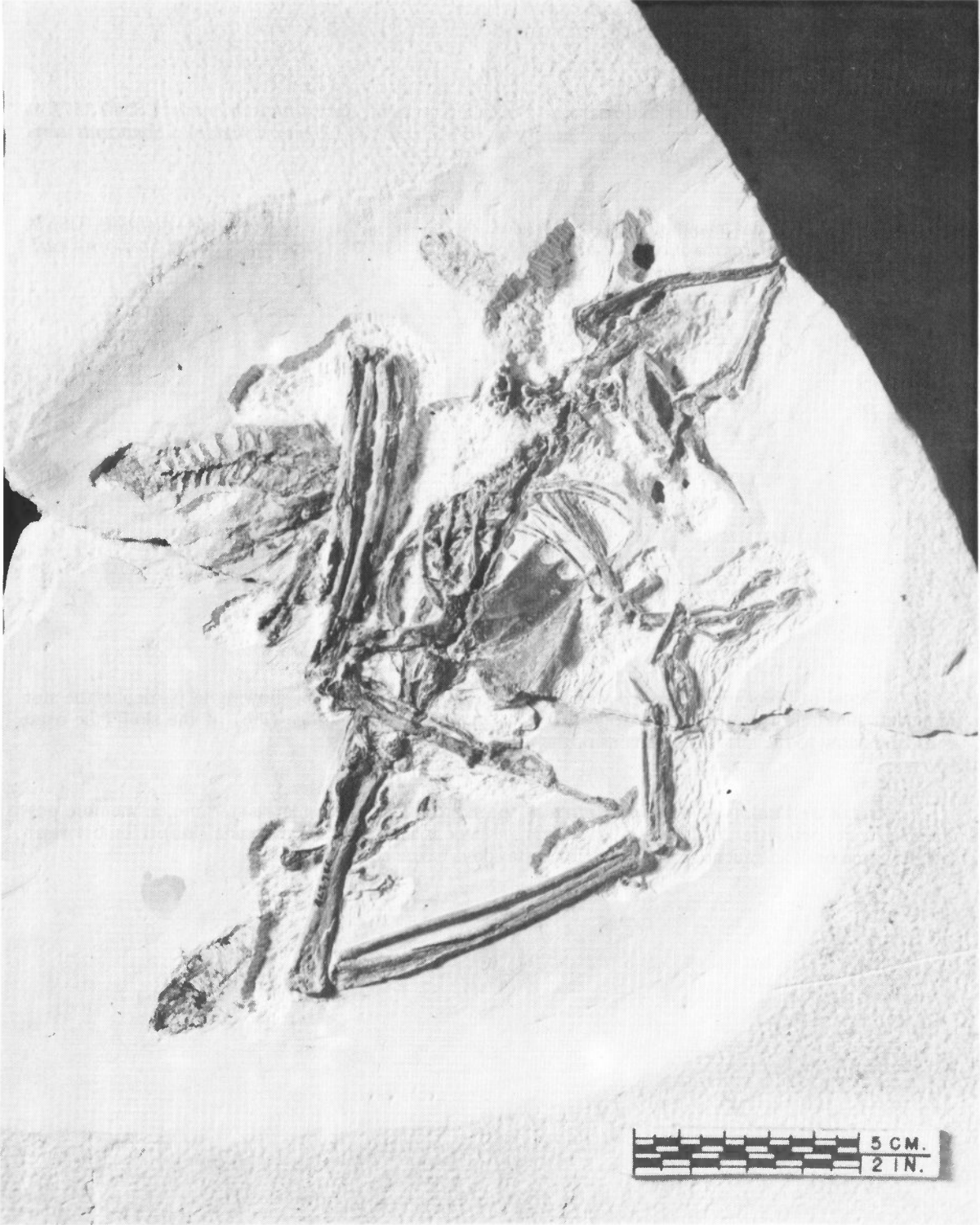


PLANCHE 2

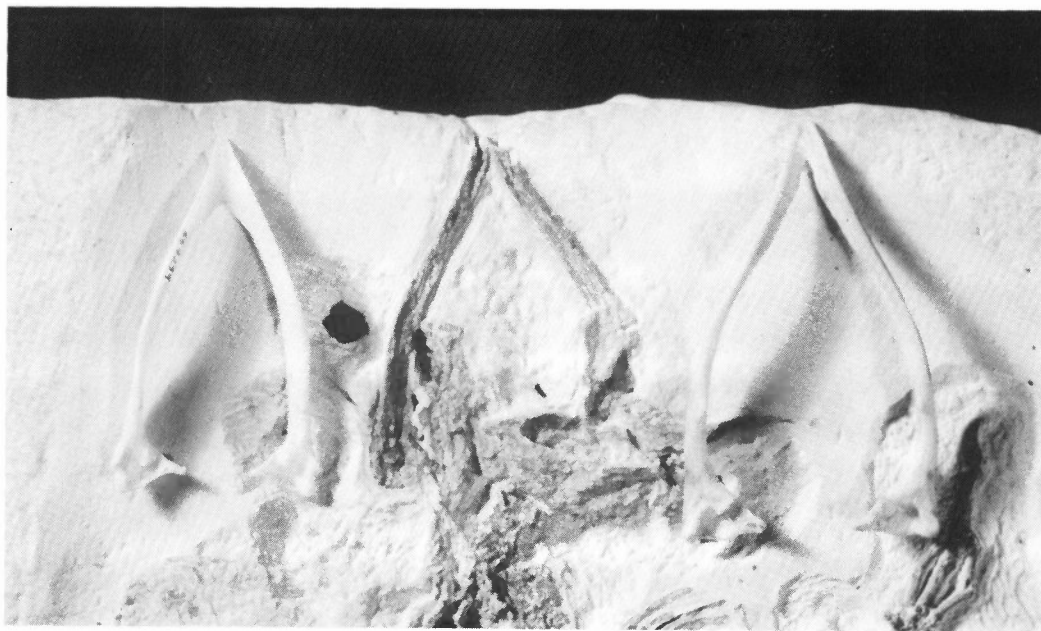
Comparison of mandibles in dorsal view : from left to right, *Eurystomus orientalis* USNM 557239 (*Coraciidae*) ; *Prefica nivea*, new species, holotype USNM 336278 (*Steatornithidae*) ; *Steatornis caripensis* USNM 19878 (*Steatornithidae*).

Comparaison des mandibules, face dorsale : de gauche à droite, *Eurystomus orientalis*, USNM 557239 (*Coraciidae*) ; *Prefica nivea* n. sp., holotype, USNM 336278 (*Steatornithidae*) ; *Steatornis caripensis* USNM 19878 (*Steatornithidae*).

PLANCHE 3

Detail of holotype of *Prefica nivea*, new species, USNM 336278, showing in particular the sternum, left hindlimb, possible quadratojugal (**qj** ?), and interorbital bridge (**iob**) of the skull (the ovate vertical shadow to the left is the remains of the brain pan).

Détail de l'holotype de *Prefica nivea* n. sp. montrant en particulier le sternum, le membre postérieur gauche, peut-être le quadratojugal (**qj** ?), et le pont interorbitaire du crâne (**iob**). L'ombre verticale de forme ovale, à gauche, correspond aux restes de la cavité cérébrale.



Pl. 3
Storrs L. Olson

