

A NEW SPECIES OF PALM SWIFT (*TACHORNIS*: APODIDAE) FROM THE PLEISTOCENE OF PUERTO RICO

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ABSTRACT.—A new species of palm swift, *Tachornis uranocetes*, is described from a late Pleistocene cave deposit in central Puerto Rico, the only Greater Antillean island on which swifts of the genus *Tachornis* are not now resident. The fossil species differs most conspicuously from the living species *T. phoenicobia* in being larger. The extinction of *T. uranocetes* probably resulted from the disappearance of open, dry savanna with scattered palm groves. This corroborates other evidence that shows decreasing aridity in the West Indies to have been a major cause of habitat alteration and extinction at the end of the Pleistocene. Received 24 August 1981, accepted 4 November 1981.

THE discovery of fossils of extinct mammals and birds in Puerto Rico in the early part of this century (Anthony 1918; Wetmore 1920, 1922) marked the beginning of concerted paleontological studies of Antillean vertebrates. In 1976 and 1977, expeditions conducted under the auspices of the Smithsonian Institution located many additional fossil deposits in Puerto Rico, some of which appear to be older than any of those previously reported. The use of more refined collecting techniques permitted the recovery of bones of very small vertebrates. As a consequence, the number of taxa known as fossils was greatly expanded. The fossil amphibians and reptiles of Puerto Rico have been analyzed in detail by Pregill (1981), whose publication should be consulted for information on the geology, physiography, and taphonomy of the fossil sites. Although the thousands of new specimens of birds have been only partially identified, it is already evident that the collections contain a number of taxa not previously known from Puerto Rico. Many of these are living species that are found elsewhere in the West Indies, but at least three represent undescribed, endemic taxa: a new genus and species of emberizine finch (Olson and McKittrick 1982), a very small, delicate form of burrowing owl (*Athene*) (see Pregill and Olson 1981), and a new species of palm swift of the genus *Tachornis*, described herein.

Although fossils have been collected in many different caves in Puerto Rico, bones of *Tachornis* were found only in one of these—Blackbone Cave. This may be an artifact of collect-

ing, as Blackbone Cave was the site that was most intensively screened for very small vertebrates. Nevertheless, had fossils of *Tachornis* been present in reasonable numbers in any of the other sites, some of the larger skeletal elements, such as carpometacarpi and ulnae, would almost certainly have been recovered. The deposits from Blackbone Cave are believed to be among the oldest yet encountered in Puerto Rico, and they have yielded other species that are lacking in the majority of Puerto Rican fossil sites (Pregill 1981, Olson and McKittrick 1982), implying that these species became extinct before the other deposits formed.

Fossils at Blackbone Cave were originally deposited in owl pellets (Pregill 1981), a few of which were found still intact. These were doubtless cast by the extinct barn owl *Tyto cavatica* (Wetmore 1920, 1922). This owl was a very proficient and opportunistic predator, as may be inferred from the hummingbirds and swifts, as well as many other species of birds, bats, insectivores, reptiles, and amphibians, in the deposits.

MATERIALS AND METHODS

Some of the fossils, particularly ulnae and carpometacarpi, were recovered at the fossil site with the use of 1/8-inch (0.3-cm) mesh screen, but the smaller specimens were obtained by transporting 135 kg of screened matrix to the laboratory and passing it through finer mesh (1.5 mm or less). The resulting concentrate was picked with the aid of a magnifying lamp and dissecting microscope. In addition to

bones of *Tachornis*, this procedure also yielded abundant remains of hummingbirds (Trochilidae) and many minute specimens of reptiles and amphibians (Pregill 1981). The importance of using very fine-mesh screens at productive West Indian fossil sites cannot be overemphasized. The fossil specimens of *Tachornis* were compared with 13 skeletons of *T. phoenicobia* in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), American Museum of Natural History (AMNH), and Pierce Brodkorb (PB). Skeletons of other genera of swifts in the Smithsonian collections were also used in the comparisons. Measurements were made through a dissecting microscope with dial calipers read to the nearest 0.05 mm. Specimens to be photographed were first coated with ammonium chloride to enhance detail.

SYSTEMATICS

Family Apodidae

Genus *Tachornis* Gosse 1849

The following characters refer the Puerto Rican fossils to the genus *Tachornis* (*sensu stricto*) and distinguish them from other genera of swifts: (1) ulna with distinct pointed olecranon, unlike Cypseloidinae (see Collins 1976); (2) distal condyles of tibiotarsus not projecting far posteriorly as in *Apus* and, to a lesser extent, in *Aeronautes*; (3) tarsometatarsus short and stout, unlike that in *Collocalia*, *Cypsiurus*, or *Chaetura*; (4) proximal end of tibiotarsus deflected strongly medially; (5) inner trochlea of tarsometatarsus extending distally well past the middle trochlea, and the outer trochlea situated well proximad to middle trochlea; (6) procoracoid process expanded (characters 4–6 separate *Tachornis*, *Panyptila*, and *Reinarda* from other genera of swifts); (7) shaft of tarsometatarsus not as laterally compressed, and inner and outer trochleae not rotated as far posteriorly as in *Reinarda*, but similar to *Tachornis* and *Panyptila*; (8) slitlike medial proximal foramen present, as in *Tachornis* and *Reinarda* (absent in *Panyptila*); the fossils agree with *Tachornis* and differ further from *Panyptila* in having (9) fenestra in proximal end of tarsometatarsus large, (10) distal foramen oval rather than more elongate, and (11) postero-proximal flange of outer trochlea not expanded.

The highly distinctive tarsal morphology of *Panyptila*, *Tachornis*, and *Reinarda* separates these genera from all other swifts. (Skeletons of the presumably related genus *Micropanyptila* are not available.) Within this group, a

number of authors (e.g. Lack 1956, Brooke 1970) have merged *Reinarda* and *Micropanyptila* with *Tachornis*, while keeping *Panyptila* separate. The tarsal morphology of *Reinarda*, however, is more specialized than that of either *Tachornis* or *Panyptila*, which are more similar to each other than either is to *Reinarda*. Thus, it would appear that, if *Reinarda* and *Tachornis* are merged, *Panyptila* would have to be included also. In the present consideration, the point is moot, as *Tachornis* has priority over the other two names, and the nomenclature of the Puerto Rican bird would not be affected.

Tachornis uranocetes, new species

(Figs. 1, 2)

Holotype.—Right tarsometatarsus, collections of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, USNM 311979 (Fig. 1d, e). Collected 28 April 1977 by Storrs L. Olson and J. Phillip Angle.

Locality.—North-central Puerto Rico; "Black-bone Cave I" (Cueva del Infierno), 1.2 km south of Iglesia Ascension, village of Barahona, 2 km northeast of Ciales (18°20'55"N; 66°26'57"W).

Chronology.—Late Pleistocene. Radiometric dates indicate a possible age of between 17,000 and 21,000 yr B.P. for this deposit; other evidence also supports a Wisconsinan age (Pregill 1981, Olson and McKittrick 1982).

Horizon.—Unconsolidated, unstratified cave sediments that probably formed beneath a former roost of the extinct barn owl, *Tyto cavatica*.

Measurements of holotype.—Length, 7.50 mm; proximal width, 2.15 mm; least width of shaft, 1.15 mm; distal width measured diagonally across the trochleae, 2.25 mm.

Paratypes.—All are topotypes; USNM 311980–312005. Anterior portion of sternum; 2 left and 1 broken right coracoids; 3 left and 2 right humeri; 4 left and 2 right ulnae; 4 left and 4 right carpometacarpi; 1 broken right femur; 2 right tibiotarsi.

Measurements of paratypes.—See Table 1.

Etymology.—Greek *ouranos*, sky, and *keles*, a racer. The name is proposed as a noun in apposition.

Diagnosis.—Differs from *Tachornis phoenicobia* Gosse 1849 as follows: (1) size larger (see Table 1); (2) posterior surface of proximal half



Fig. 1. Hindlimb elements of *Tachornis*: A, B, C, the living species *T. phoenicobia*; D, anterior view of tarsometatarsus of *T. uranocetes*, new species (holotype, USNM 311979); E, same, posterior view; F, anterior view of tibiotarsus of *T. uranocetes* (USNM 311999). Scale = 5 mm.

of shaft of tarsometatarsus more deeply excavated; (3) distal portion of inner trochlea heavier, more bulbous; (4) anterior surface of shaft of tarsometatarsus more deeply excavated; (5) anterior distal pit of middle trochlea much deeper; (6) procoracoid process of coracoid larger and projecting farther medially; (7) sterno-coracoidal process of coracoid wider, not as pointed or distally protrudent. No consistent differences, other than size, were found in the wing elements, except that in certain specimens of *T. uranocetes* the processes (e.g. internal tuberosity of humerus) were heavier than in any of the specimens of *T. phoenicobia*.

Remarks.—The greater size of *Tachornis uranocetes* is evident from the figures and from

Table 1. There is no overlap in the measurements of the coracoid, humerus, tibiotarsus, or tarsometatarsus, and only two of the six fossil ulnae fall within the range of variation of *T. phoenicobia*. All but two of the eight fossil carpometacarpi, however, fall within the upper limits of the living species. This might suggest that the carpometacarpus is proportionately shorter in *T. uranocetes*, but the intramembral ratios of the mean lengths of the wing elements are identical for both species.

DISCUSSION

The Antillean Palm Swift, *Tachornis phoenicobia*, is resident on Cuba, Hispaniola, and Ja-

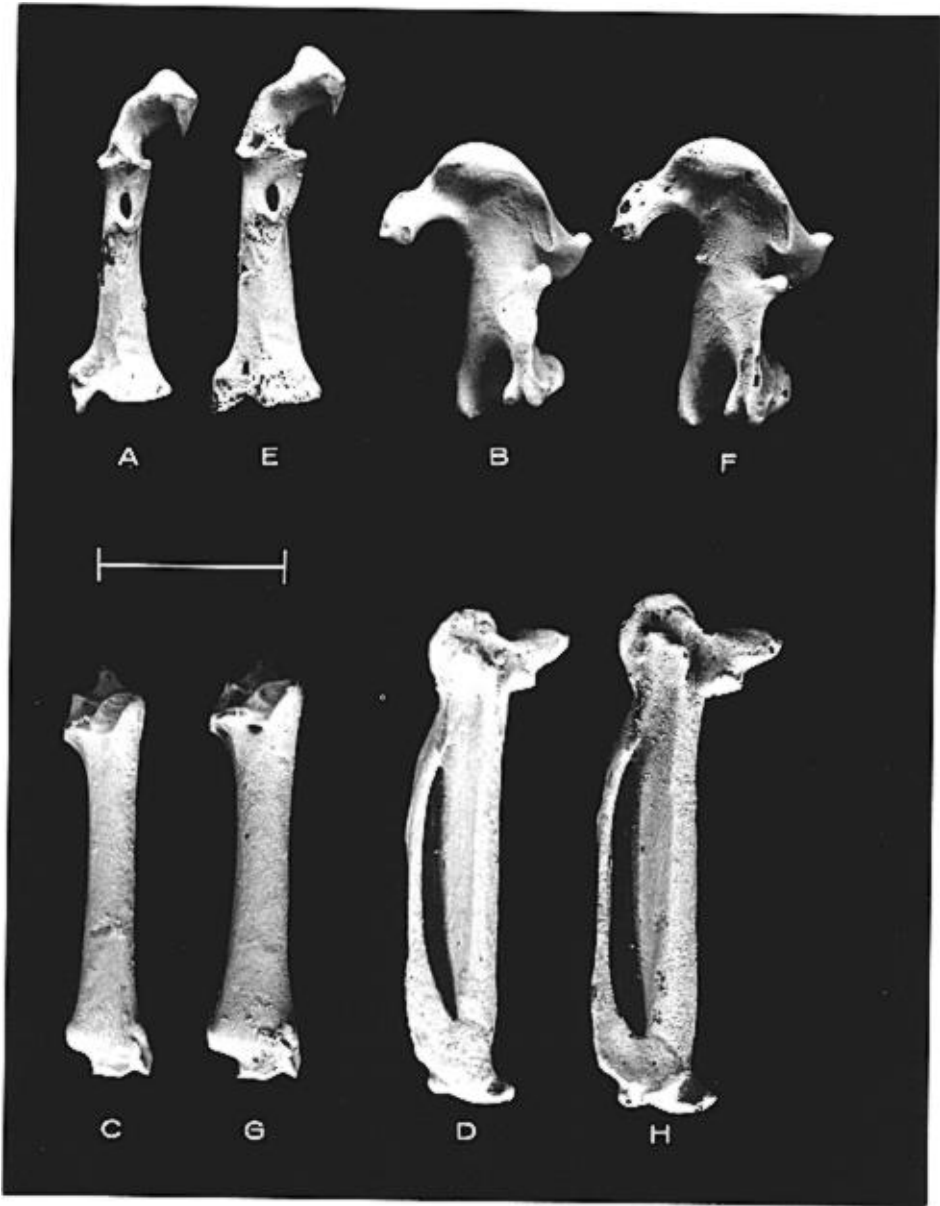


Fig. 2. Wing elements of *Tachornis*: A, B, C, D, the living species *T. phoenicobia*; E, dorsal view of coracoid of *T. uranocetes*, new species (USNM 312001); F, anconal view of humerus of *T. uranocetes* (USNM 311995); G, dorsal view of ulna of *T. uranocetes* (USNM 311988); H, ventral view of carpometacarpus of *T. uranocetes* (USNM 311980). Scale = 5 mm.

maica but is known only as a casual vagrant to Puerto Rico (Kepler 1971). Kepler's observation demonstrates that the species is still capable of dispersing to the island, and the discovery of *Tachornis uranocetes* shows that palm swifts indeed occurred on Puerto Rico in the Pleistocene. The absence of *Tachornis* in Puerto Rico

today prompted Kepler (1971) to speculate that the island must lack suitable ecological conditions for these birds. As we shall see, this is quite probably the case.

One of the better impressions of the habitat of *Tachornis phoenicobia* is given by Barbour (1943: 90), who observed that in Cuba "the lit-

TABLE 1. Length measurements (mm) of skeletal elements of living and fossil species of *Tachornis*.

Element	<i>T. phoenicobia</i>			<i>T. uranocetes</i>		
	<i>n</i>	Range	Mean	<i>n</i>	Range	Mean
Coracoid	13	7.55–8.10	7.85	2	8.45–8.75	8.60
Humerus	13	6.35–7.10	6.85	5	7.15–7.40	7.30
Ulna	13	8.70–9.70	9.35	6	9.35–10.25	9.85
Carpometacarpus	12	11.75–13.25	12.40	8	12.60–13.45	13.05
Tibiotarsus	12	11.05–11.70	11.35	2	12.10–12.50	12.30
Tarsometatarsus	13	6.60–7.30	6.90	1	7.50	—

tle palm swift is gregarious, and the colonies are scattered widely over vast areas of sterile, semi-arid grasslands in which grow scattered clumps of various palmetto-like palms. Among the dry, pendent dead fans of these trees the swifts stick their watchpocket nests . . . colonies do not occur in all of the localities which strike one as being most suitable." In Jamaica, Gosse (1849: 62) described these swifts as occurring "over the grass-pieces and savannas of the lowlands, the marshy flats at the seaward mouths of the valleys, as well as the pens of the mountain slopes." He described nests as being found in coconut palms (*Cocos*) and "palmetto (*Chaemerops*)" [probably = *Sabal*]. It is now somewhat difficult to determine the original habitat of *T. phoenicobia* in Hispaniola and Jamaica because the most readily observed colonies are found in exotic palms in botanical gardens and parks or even in the thatched roofs of dwellings. Wetmore and Swales (1931: 265) mention observing the birds "alighting among the dead hanging fronds of the royal palms" (probably not *Roystonea*, however; see below), and Lack (1976: 276) states that in Jamaica they are found especially in "the thatch palm *Sabal jamaicensis*." Orlando A. Garrido (pers. comm.) informs me that in Cuba *Tachornis* nests in *jata* palms, a name applied to a number of species of *Copernicia*, many of which grow in isolated groves in open country.

I suspect that the original habitat of *Tachornis phoenicobia* is much as portrayed by Barbour (1943)—open, rather arid grassland or savanna with isolated clumps of palms of a type that retain their dead fronds hanging alongside the trunk. In Brazil, the closely related swift *Reinarda squamata* nests in exactly similar situations in palms of the genus *Mauritia*, as de-

scribed and illustrated by Sick (1948). The only nest yet reported for *Micropanyptila* was stated to be similar to that of *Tachornis* (Bond 1956).

Puerto Rico now has a rather depauperate palm flora. Most of the species either grow in wet forest or probably do not present the right growth form to be attractive to *Tachornis*. Kepler (1971: 310) mentions that the endemic royal palm *Roystonea borinquena* appears "to offer similar ecological conditions" to those of species of *Roystonea* elsewhere. The Puerto Rican species, however, occurs in "hillsides and forest . . . in moist or wet districts" (Britton and Wilson 1923: 112), which does not conform with the preference of *Tachornis* for drier, open areas. Furthermore, the species of *Roystonea* do not retain pendent dead fronds alongside the trunk.

It is possible that one or more species of palm in which *T. uranocetes* nested became entirely extinct in Puerto Rico or became so reduced that there were no longer sufficient numbers to support viable populations of *Tachornis*. It is worth noting that two species of palms, *Gaussia attenuata* and *Sabal causiarum*, are either nearly restricted to, or are most abundant in, the arid southwestern part of Puerto Rico (Britton and Wilson 1923), where relict dry forest has been able to persist. The dead fronds are not retained in *Gaussia*, however, so it is unlikely that palms of this genus were ever important in the economy of *Tachornis*. In Puerto Rico today, the lower fronds of *Sabal* are so consistently stripped for use in mats and baskets (Robert W. Read, Dept. Botany, Smithsonian Institution, pers. comm.) that almost no suitable nesting sites remain for any individuals of *Tachornis phoenicobia* that might potentially colonize the island.

There is considerable evidence to show that

xeric habitats were more prevalent in Puerto Rico, and in the West Indies generally, during the last glacial advance (Pregill 1981, Pregill and Olson 1981, Olson 1982). At the end of the Pleistocene the West Indies evidently became more mesic, with the result that open, arid habitats contracted or disappeared. This caused the extinction or reduction in range of diverse species of vertebrates (Pregill and Olson 1981). I interpret the presence of *Tachornis uranocetes* in the Pleistocene of Puerto Rico as indicating that open prairie or savanna, with isolated groves of large palms, occurred in the area of the caves where the fossils were deposited. This habitat was replaced by the Subtropical Moist Forest that characterizes the region today (Pregill 1981, Fig. 3), with the result that the palms and their attendant populations of *Tachornis* could no longer survive. The reduction or loss of areas of open savanna suitable as foraging sites for *T. uranocetes* probably played as significant a role in the extinction of that species as the loss of nesting sites.

ACKNOWLEDGMENTS

I am indebted to the many people who participated in the Smithsonian fossil collecting expeditions (see Pregill 1981) and must particularly single out Noel Snyder, who provided the impetus for the entire project as well as boundless enthusiasm for finding new fossil deposits. Frederick V. Grady, in addition to taking part in the field work, spent countless hours picking fine concentrate, and the fossils described here are a testimony to the keenness of his eye. J. Phillip Angle assisted me on a return trip to Puerto Rico to collect matrix for fine screening and to obtain skeletal material of recent birds for comparative purposes. This trip was made possible through a grant from the National Geographic Society. Comparative material of *Tachornis* was kindly lent by Pierce Brodkorb and Charles T. Collins. The photographs of the minute bones are the exacting work of Victor E. Krantz. I am also grateful to K. Jeffrey Bickart, Charles T. Collins, Gregory K. Pregill, Robert W. Read, and David W. Steadman for their comments on the manuscript.

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