

## The First Fossil Tody (Aves: Todidae) from Cuba

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Received August 25, 2019; revised September 2, 2019; accepted October 25, 2019

**Abstract**—Todies (Aves: Todidae)—endemic to the Greater Antilles and one of the most characteristic components of the modern fauna of Cuba—have not yet been represented in the island’s fossil record. This article describes the first fossil find of a representative of this family in Cuba. A coracoid from the Upper Pleistocene of the cave El Abrón (Pinar-del-Río province) in general morphology and size is similar to that of the modern Cuban Tody *Todus multicolor*, but differs in structural details and thus can represent a distinct species. The distinctiveness of the Late Pleistocene tody from Cuba may also indicate an increased morphological variability of todies, which in most cases is not typical for birds.

**Keywords:** Cuba, Pleistocene, endemic taxa, Todidae

**DOI:** 10.1134/S0031030120040164

Modern todies (family Todidae; order Coraciiformes) are very small tropical insectivorous birds with unusual external and internal morphology, relict distribution and a mysterious evolutionary history. The family includes one genus *Todus* with five species distributed exclusively on the Greater Antilles. Two species are found in Haiti and further two on the islands of Jamaica and Puerto Rico. The Cuban Tody inhabits Cuba, the nearby island of Juventud, and a number of smaller adjacent islands.

Todies’ evolutionary history is poorly understood. Traditionally, the family was included in the order Coraciiformes, and already earlier authors (Murie, 1872; Sclater, 1872) considered momots (family Momotidae) and kingfishers (Alcedinidae) as the closest relatives of todies in the modern fauna. Nevertheless, many prominent morphologists and systematists emphasized the morphological uniqueness of todies, as a result of which they placed these birds in a separate order (Todiformes or Todi; Forbes, 1882; Lowe, 1948; Stresemann, 1959). Forbes (Forbes, 1882) considered todies to represent a possible morphological prototype of Anomalognatae (a non-monophyletic group of modern birds identified by the absence of m. ambiens in the hind limb and including Strigiformes, Caprimulgiformes, Apodiformes, Coliiformes, Trogoniformes, Piciformes, Passeriformes, and Coraciiformes; Beddard, 1898). Since the end of the 20th century (Feduccia, 1977), todies, together with momots and kingfishers, are most often placed to a superfamiliar taxon (usually called Alcedinoidea or Alcediniformes) within the order Coraciiformes (see

Cracraft, 2013). According to modern molecular data, todies are the most basal representatives of this group (Prum et al., 2015).

The morphological distinctiveness of todies, noted by many authors, undoubtedly indicates a long-standing divergence of this group. Molecular data in combination with fossil calibrations date todies divergence relative to other Alcedinoidea to the Eocene (Early or Late; Prum et al., 2015; Claramunt and Cracraft, 2015). The Early Eocene *Quasisyndactylus* from Germany is characterized by a noticeable similarity with modern todies in the structure of the beak and is probably a stem representative of Alcedinoidea (Mayr, 2004). The genus *Palaeotodus* with three described species, known from the Early Oligocene of Wyoming (USA) and the Late Eocene—Early Oligocene of Germany and France, is referred to the family Todidae (Olson, 1976; Mourer-Chauviré, 1985; Mayr and Knopf, 2007; Mayr and Micklich, 2010). *Palaeotodus* differ from modern *Todus*, in particular, in the proportionally larger forelimbs, which suggests better flying abilities of these birds compared to modern Todidae (Olson, 1976). Representatives of *Palaeotodus* (except for one species) are also characterized by larger sizes.

The history of the settlement of the Caribbean islands by Todidae remains unclear, since starting from the Late Oligocene, representatives of this group almost completely disappear from the fossil record. The only exception is the find of two modern tody species (*Todus subulatus* Gray, 1847 and *T. angustirostris* Lafresnaye, 1851), which were identified from Quaternary (apparently Late Pleistocene) sediments of the

Cerro de San Francisco cave in the Dominican Republic (Bernstein, 1965). The divergence of these species is probably related to the episode of the existence of two islands at the place of the modern island of Haiti in the Plio-Pleistocene (Pregill and Olson, 1981). The fact that todies are represented in the modern fauna by morphologically very close species (sometimes even interpreted as one “superspecies”) indicates that radiation of representatives of the genus *Todus* should have taken place in the recent past: not older than the early Pleistocene in the modern interpretation (Bond, 1963; Kepler, 1977). Thus, this group of birds, being one of the characteristic and endemic to the Antilles, may have a relatively recent history in this region. In accordance with this concept, the ancestors of *Todus*, already isolated from the phylogenetic lineage leading to motmots, settled the Greater Antilles, like many other representatives of the Caribbean fauna, from Central America through the Yucatan Peninsula, which was separated from Cuba by a less wide water barrier at the time of the sea level drop in the Pleistocene (Bond, 1963; Olson, 1976; Kepler, 1977; Pregill and Olson, 1981). At the same time, the Cuban Tody seems to be closest to the ancestral form (Kepler, 1977) and gave rise to other species—primarily, the sister Haitian species *T. angustirostris* (Overton and Rhoads, 2004).

The Late Pleistocene—Early Holocene avifauna of Cuba, which preceded the large-scale Holocene vertebrate extinction in the Caribbean (Tyberg, 2009; Cooke et al., 2017; Upham, 2017), was significantly different from the modern one and included a significant number of extinct species or species that no longer occur on the island (Orihuela, 2019). A similar pattern was reported for other islands of the West Indies, in particular, the Bahamas (Steadman and Franklin, 2015). Especially noteworthy are findings of small poorly flying suboscine passerine birds *Scytalopus* in the Quaternary sediments of Cuba and Juventud Island—*Scytalopus* represent a South American group completely absent today on West Indies (Olson and Kurochkin, 1987). In this regard, it should be noted that the latest temporal episode of the last glacial maximum was characterized in Cuba by the coolest and the driest climate during the latest 82 kya (Warken et al., 2019). These climatic conditions question the survival of various components of the tropical fauna on Cuba during the latest Pleistocene, in particular the todies, which so far were not represented in the fossil record of the island. This paper describes the first find of a fossil tody from Cuba—a coracoid from the Late Pleistocene (the latest phase of the last glacial maximum; see below) of El Abrón cave (Pinar-del-Río province) is similar to that of the modern Cuban Tody *Todus multicolor* in size and general morphology, but differs in a number of structural details, thus most likely representing a different species.

The find described in this work is the first evidence of the existence of the genus *Todus* in the Pleistocene

faunas of Cuba, but in order to establish the exact systematic position of the fossil form, a comparison with a greater variety of modern representatives of the genus is necessary (comparisons were only made with the skeleton of *T. multicolor*). The differences between the Late Pleistocene Cuban Tody and the modern one can be interpreted in two ways: either the Late Pleistocene Cuban fauna of todies differed from the present one (for example, included a greater variety of species), or todies (all or only the Cuban Tody) are characterized by a noticeable morphological variability or evolution during the interval from the late Pleistocene to the Present. The second interpretation, although possible, is still very unusual for birds, because modern species (or complexes of closely related species) display stable morphology since the Early–Middle Pleistocene (Zelenkov, 2013, 2014, 2016).

The noticeable morphological evolution of todies, incapable of long-distance flights, at the turn of the Pleistocene and Holocene could be explained by significant rearrangement of landscape and climatic conditions (climatic factors account for a significant part of vertebrate extinctions on the Bahamas in the same time period; Steadman et al., 2015). At the same time, the very fact of the presence of todies in the Late Pleistocene faunas cannot serve as an indicator of any specific environmental conditions, since modern todies are extremely eurybiontic. In particular, the Cuban Tody inhabits various stations: from coastal beach *Coccoloba unifera* sea grape thickets and xerophytic shrubs to high mountain rain forests (up to 2840 m above sea level) (Kepler, 1977). It is possible that such environmental tolerance may be associated with a greater morphological plasticity, in turn expressed in an increased individual skeleton variability—similar to that which is found in the European dabbling ducks (Zelenkov, 2019).

#### LOCALITY DATA

El Abrón Cave (22°40 N, 83°28 W) is located in the western part of Cuba in the Pinar-del-Río province (Fig. 1). Excavations in the cave were carried out by the Department of Paleogeography and Paleobiology of the National Museum of Natural History of Cuba in Havana (hereinafter MNHN), where the described material is stored. During the excavations, Pleistocene deposits were discovered up to 2.85 m deep, among which 9 layers were identified, some containing rich osteological material (for details of the geology of the locality see: Suárez and Díaz-Franco, 2003, 2011). The accumulation of vertebral bones in El Abrón Cave is believed to be associated with the activity of barn owls (Suárez and Díaz-Franco, 2003, 2011; Suárez, 2004). For layer VII, from which the described in this article fragment originates, radiocarbon date of  $17406 \pm 161$  BP was obtained from the bone of the extinct barn owl *Tyto noeli* Arredondo, 1972 (Suárez and Díaz-Franco, 2003, 2011).

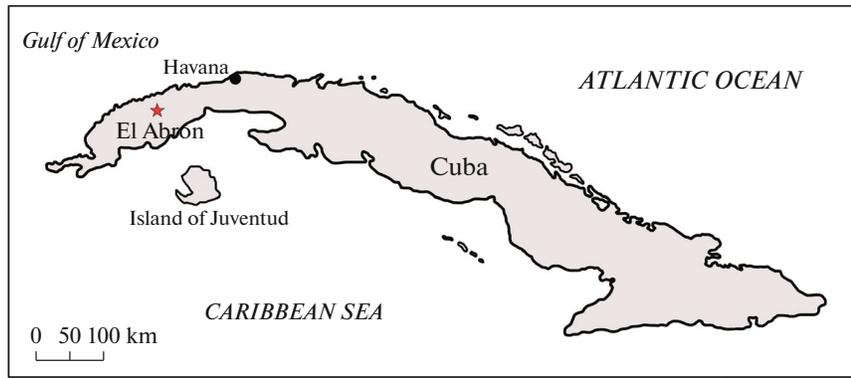


Fig. 1. Map showing the location of El Abrón Cave in Cuba.

The fauna of the locality includes several bird species, including the extinct *Falco kurochkini* Suarez et Olson, 2001, *Capella* sp. *Tyto noeli*, and *Siphonornis daiquiri* Olson, 1985, several modern ones (Suarez, 2004; Suarez and Díaz-Franco, 2011), as well as a number of mammals (Suarez and Díaz-Franco, 2003; Díaz-Franco, 2001; González, 2015). Of the diverse herpetofauna, only amphisbaenians have been described so far (Syromyatnikova et al., 2020).

#### DESCRIPTION OF MATERIAL

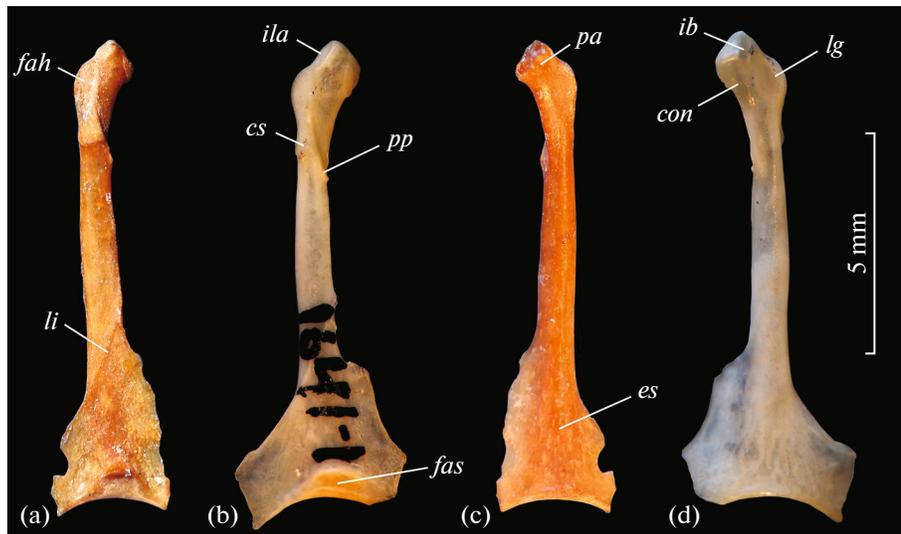
The complete left coracoid (specimen MNHN, no. 73.5395; Fig. 2) from layer VII of El Abrón Cave is fairly well preserved—only the outer parts of the lateral and medial processes of the extremitas sternalis are broken off, the shape of which in most birds are subject to individual variation; the medial apex of the processus acrocoracoideus is slightly damaged. The general outline of the coracoid, like that of other representatives of Alcedinoidea and unlike the rest of Coraciiformes, is gracile, the shaft is thin and elongated, the processus acrocoracoideus is moderately developed, has a pineal shape in ventral view and slightly protrudes medially relative to the shaft. As in Momotidae and Alcedinidae, the processus acrocoracoideus is craniomedially oriented and slightly inclines ventrally. In Momotidae, the processus acrocoracoideus is much more robust and has a craniocaudally wide base. In Alcedinidae, the general form of the processus acrocoracoideus is similar to that of the fossil specimen and modern *Todus*, but this process is fused with the processus procoracoideus.

In ventral view, the processus acrocoracoideus is noticeably less massive compared to that of *T. multicolor*. In its central part, closer to the caudal margin, there is an unclear ridge coming from the impressio bicipitis in the caudolateral direction and implicitly passing caudally into the ventral ridge of the shaft. Laterally to this rib on the process there is a concavity, bordering the slightly protruding labrum glenoidale.

In modern *T. multicolor*, the labrum glenoidale is noticeably more protruding, and the ridges on the processus acrocoracoideus and the cranial half of the shaft are expressed more clearly than in the fossil specimen; on the ventral surface of the processus acrocoracoideus, this crest is noticeably offset relative to the caudal edge of the process in *T. multicolor*. This position of the crest is due to the fact that the caudal part of the base of the processus acrocoracoideus in *T. multicolor* is expanded (this ensures the massiveness of the process) and distally it passes into the ridge medially protruding relative to the sulcus supracoracoidei and ending caudally at the level of the apex of the processus procoracoideus. In MNHN, no. 73.5395, the latter ridge is absent. In addition, in *T. multicolor*, more medially than the aforementioned ridge, on the ventral surface of the processus acrocoracoideus there is a shallow, but pronounced depression, absent in the fossil specimen. Impressio bicipitis in MNHN, no. 73.5395 is not very well preserved, but, apparently, had the shape of an elongated rectangle, as in modern *T. multicolor*.

In medial view, the processus acrocoracoideus protrudes ventrally and forms a rather sharp peak (blunter in *T. multicolor*). The facies articularis clavicularis occupies the apex of the processus acrocoracoideus and is partially medially oriented. The sulcus supracoracoideus is a narrow obliquely oriented groove near the processus procoracoideus, but it becomes more convex cranially, actually passing to the edge of the ridge. The impressio lig. acrocoracohumeralis is slightly elongated, oval and practically not curved.

The facies articularis humeralis is craniocaudally elongated and narrow, as in Todidae and Alcedinidae, it is not clearly narrowed caudally (in Momotidae the facies is short and wide, especially in its caudal part). The lateral surface of the facies articularis humeralis near the contact with the cotyla scapularis is slightly concave; cranially the facies is only slightly expanding (widened), which differs from the markedly expanded



**Fig. 2.** Fossil tody (Aves: Todidae) from the Upper Pleistocene of Cuba in comparison with the modern Cuban Tody (*Todus multicolor*): (a, c) specimen MNHN, no. 73.5395, complete left coracoid; locality El Abrón Cave (Pinar-del-Río Province), Upper Pleistocene; (b, d) *Todus multicolor* Gould, specimen PIN, no. 1641-1, modern (Cuba). Designations: *con*—depression in the caudal part of the processus acroracoideus; *cs*—cotyla scapularis; *es*—extremitas sternalis; *fah*—facies articularis humeralis; *fas*—facies articularis sternalis; *ib*—impressio bicipitalis; *ila*—impressio lig. acroracoideus; *lg*—labrum glenoidale; *li*—linea intermuscularis; *pa*—processus acroracoideus; *pp*—processus procoracoideus. (a, b) dorsal view; (c, d) ventral view.

facies articularis humeralis of modern *T. multicolor*. The cotyla scapularis, subtriangular in shape, is a continuation of the facies articularis humeralis (as in Todidae and Alcedinidae) and is unclearly raised relative to the latter in its cranial part. The caudal part of the cotyla is markedly elevated relative to the adjacent dorsal surface of the shaft and is separated from it by a low ridge. The dorsal surface of the cotyla scapularis is faintly convex in its lateral part and faintly concave in the medial part; medial margin of the cotyla caudally transforms into a rudimentary (unlike Momotidae) processus procoracoideus, whose apex is noticeably shifted caudally relative to the caudal margin of the cotyla. The cranial sloped edge of the processus procoracoideus carries on its medial surface an articular surface for the acromion of the scapula. Distally, the processus procoracoideus continues into a long and medially oriented ridge, extending along the shaft and marking the protruding edge of the shaft caudally up to the extremitas sternalis, as in Todidae. In modern *T. multicolor*, this crest protrudes somewhat more medially, especially in its caudal part. The foramen n. supracoracoidei is absent.

In the extremitas sternalis, the medial and lateral ridges, which are wing-like extensions, are well developed. The medial ridge begins from the described above medial ridge of the shaft somewhat distal to the origin of the impressio m. sternocoracoidei. It is not possible to establish the exact shape of the medial ridge, since its outer part is not well preserved. The lat-

eral ridge begins somewhat caudal to the medial one and its outer edge is a continuation of the above-mentioned muscular line. The outer part of this ridge is also broken off. The dorsal surface of the extremitas sternalis is flat or slightly convex in its middle part and distinctly concave in the region of the lateral crest. The dorsal surface of the medial ridge is concave only in its most caudal third, closer to the angulus medialis. In the cranial part of the impressio m. sternocoracoidei there is another unclear muscular line positioned close to the cranial edge of the impressio. The facies articularis sternalis, when viewed from the dorsal side, has a domed shape with a somewhat narrowed cranial apex framed by a distinct crest (crista dorsalis; Elzanowski et al., 2012) and elongated “tongues” of the base extending laterally and medially to almost the entire caudal edge of the bone. In modern *T. multicolor*, these caudal “tongues” are practically not expressed and the facies on the dorsal side have more extended outlines.

In ventral view, the extremitas sternalis is pronouncedly convex in its cranial part (continuation of the convexity of the shaft) and flattened distally, medially and laterally. The caudal margin is uniformly concave; the facies articularis sternalis does not extend to the ventral surface of the bone.

Measurements of the specimen MNHN, no. 73.5395 (mm): total length across the medial margin of the bone—10.6; minimal mediolateral width of the shaft—0.9; minimal dorsoventral height of the shaft—0.6.

## ACKNOWLEDGMENTS

The authors thank E. Pérez Lorenzo, J.M. Pajon, and R. Rojas Consuegra (Havana) for discussion and access to collections (for the senior author), E.V. Syromyatnikova (PIN RAS) for assistance with laboratory work and map preparation, as well as reviewers A.V. Panteleyev and A.B. Savinetsky.

## FUNDING

The present study was funded by RFBR (Russian Foundation for Basic Research) and CITMA (Ministerio de Ciencia, Tecnología y Medio Ambiente) under the research project no. 18-54-34004 (“Late Quaternary Cuban vertebrates: relictual faunas on the eve of the Holocene extinction”).

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