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Photo: A. Lenoble

Birds Caribbean

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Monica Gala*[1,2], Véronique Laroulandie[1,3], Arnaud Lenoble[1,4]

Abstract This paper describes a partial pedal phalanx of an extinct species of barn owl from Guadeloupe. The morphology and size of the bone fragment allow it to be referred to as a giant *Tyto* without further specification. In addition to the *Tyto noeli* specimens described from a Quaternary deposit on Barbuda, this remain represents the second occurrence of a giant barn owl in the Lesser Antilles, and is the first record from Guadeloupe. The specimen was recovered from a pre-Columbian midden dated to between the 11th and 16th centuries, indicating that this tytonid had persisted in the Lesser Antilles up to the European colonization of the Caribbean. This is consistent with the hypothesis that the giant owl went extinct along with, and potentially because of, the disappearance of the endemic, medium-sized rodents on which they preyed.

Keywords extinction, giant barn owl, Late Quaternary, Lesser Antilles

Resumen Evidencia de una lechuza gigante del Holoceno tardío (Aves: Strigiformes: Tytonidae) en Guadalupe • En este artículo se describe una falange pedal parcial de una especie extinta de lechuza de Guadalupe (Antillas francesas). La morfología y el tamaño del fragmento óseo permiten atribuirlo a un *Tyto* gigante sin más especificaciones. Además de los ejemplares de *Tyto noeli* descritos en un yacimiento cuaternario de Barbuda, este resto representa la segunda aparición de una lechuza gigante en las Antillas Menores, y el primer registro en Guadalupe. El espécimen fue descubierto en un basurero precolombino fechado entre los siglos XI y XVI, lo que indica que esta lechuza persistió en las Antillas Menores hasta la colonización europea del Caribe. Esto concuerda con la hipótesis de que la lechuza gigante se extinguió al mismo tiempo que las especies endémicas de roedores de mediano tamaño sobre las que depredaba, y posiblemente como consecuencia de su desaparición.

Palabras clave Antillas Menores, Cuaternario tardío, extinción, lechuza gigante

Résumé Découverte d'une Effraie géante (Aves : Strigiformes : Tytonidae) à l'Holocène tardif en Guadeloupe • Cet article présente une phalange partielle de la patte d'une espèce éteinte de chouette découverte en Guadeloupe. La morphologie et les dimensions du fragment osseux permettent de l'attribuer à une *Tyto* géante sans plus de précision. En sus des spécimens de *Tyto noeli* décrits dans le dépôt quaternaire de Barbuda, ce vestige représente la deuxième occurrence d'une chouette effraie géante dans les Petites Antilles, et la première mention en Guadeloupe. Le spécimen a été recueilli dans un dépotoir précolombien daté entre le 11ème et le 16ème siècle, indiquant que ce Tytonidae a pu persister dans les Petites Antilles jusqu'à la colonisation européenne des Caraïbes. Cette hypothèse est cohérente avec celle selon laquelle les chouettes géantes se sont éteintes en même temps, et potentiellement en raison de la disparition des espèces endémiques de rongeurs de taille moyenne dont elles se nourrissaient.

Mots clés Chouette effraie géante, extinction, Petites Antilles, Quartenaire récent

The Caribbean was once home to a significant number of nocturnal raptors (e.g., Suárez 2020a, 2020b, Jiménez and Orihuela 2021); however, exactly how many of these bird species existed remains difficult to estimate accurately due to the scattered and fragmented nature of the region's paleontological record (e.g., Orihuela 2019). A recent revision of Caribbean specimens nevertheless identified at least four giant (Suárez and Olson 2015) and one small form (Suárez and Olson 2020) of tytonid owl (genus *Tyto*). The past presence of giant tytonid owls in the Caribbean is limited to the Greater Antilles and the Bahamas, with the only exception being fossil specimens originally described as *Tyto neddi* from a cave deposit on Barbuda (Steadman and Hilgartner 1999). These specimens have recently been reattributed to the Greater Antillean form *Tyto noeli*, the smallest of the giant barn owls (Suárez and Olson 2015). This owl is thought to have preyed on large forms of rice rat (Sigmodontinae) and was likely to have

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occurred wherever these rodents were found. Its distribution would therefore have spanned the entire Caribbean region, including most of the islands of the Lesser Antilles. The region's poorly documented paleontological record, however, makes it difficult to more precisely determine the past biogeography of this owl (Suárez and Olson 2015).

Here, we report a distal fragment of a large Tytonidae phalanx from a pre-Columbian midden in Guadeloupe. Although the fragmentary nature of the bone precludes its assignment to species level, its large size is consistent with it representing a now-extinct giant owl. We provide a detailed metrical and osteological description of this specimen and discuss its implications for the timing of and causes underlying the extinction of the giant owl in Guadeloupe.

Methods

The specimen was identified amongst terrestrial faunal remains from the Roseau vertebrate collection stored at the Regional Archaeology Service of Guadeloupe at Le Moule. This pre-Columbian village site is located on the southeastern shore of Basse Terre (16°5'42"N, 61°33'37"W), Guadeloupe. The site produced a multi-layered midden filling a gully on a beach. Initially discovered during surface surveys of archaeological material exposed following storms, the site was excavated in 2001 and 2002 (Richard 2003). The ceramic analysis and radiocarbon dating of various archaeological remains (charcoal, shells, and bones) indicate a succession of three main occupations corresponding, respectively, to the 11th and 12th centuries, 13th century, and 14th century, to which several more recent elements from the 16th century can be added (Bochaton *et al.* 2021).

A detailed zooarchaeological analysis of the faunal assemblage recovered during these excavations documented numerous fish remains complemented by those of squamates, turtles, birds, rodents, and manatees, all of which were interpreted as food waste associated with the pre-Columbian village (Bochaton *et al.* 2021). During this analysis, a bird bone was described simply as representing a giant owl of the genus *Tyto*. The specimen (Roseau archaeological site [ROS] catalogue number: ROS-O61) was found in a bag within a box numbered "B-9-1616" that contained all the vertebrate material from Roseau. More specifically, the specimen was identified in a bag labeled "unlabeled 2/2," which contained some of the bone material for which the stratigraphic provenance was lost since the excavation (Bochaton *et al.* 2021). This bag also contained bones of fish, rodents (agouti and rice rat), squamates, and sea turtles similar in every respect to the rest of the archaeological collection.

Osteological nomenclature herein follows Livezey and Zusi (2006: Fig. 35). We produced a high-resolution 3D model of the subfossil specimen using a GE v|tome|x s μCT scanner housed at the University of Bordeaux (UMS Placamat) to compare it with museum specimens preserved at the Smithsonian National Museum of Natural History (USNM). Strigiformes bone anatomy was assessed based on Kessler (2017) and the avian osteological collection of the PACEA laboratory at the University of Bordeaux (Lenoble *et al.* 2019).

Measurements of the subfossil distal width and distal depth were recorded using digital calipers to one-tenth of a millimeter. For Caribbean specimens, phalanx measurements of fossil

giant barn owls *T. noeli* and *T. ostologa*, as well as those from modern *Tyto alba furcata* and *T. a. pratincola*, are provided by Steadman and Hilgartner (1999). These measurements concern digit I, phalanx 1 (pha1I) and digit III, phalanx 2 (pha2III), which are not the same anatomical elements described here. To overcome the lack of metrical data for homologous phalanges, the width and depth of penultimate phalanges were estimated from available measurements of modern and fossil specimens. For this purpose, interspecific ratios were established for digit I, phalanx 1 of *Tyto a. alba* and digit I, phalanx 1 of the other species and subspecies (*T. a. pratincola*, *T. a. furcata*, *T. noeli*, T*. ostologa*). The same ratio was calculated for digit III, phalanx 2 of *Tyto a. alba* and digit III, phalanx 2 of the other species and subspecies. These ratios were subsequently used to extrapolate the width and depth measurements of digit II, phalanx 2 (pha2II), digit III, phalanx III (pha3III), and digit IV, phalanx 4 (pha4IV) for each of the past and current American barn owls (Appendix 1). This approach assumes that phalange proportions are the same between species. European specimens of *Tyto a. alba* from the PACEA laboratory collection were used for measurements and for generating the predicted values of homologous phalanges.

Finally, we incorporate additional comparative metric data for a fragmentary juvenile specimen of *Tyto noeli* from Barbuda (USNM 359244), which was reported but not described in detail by Steadman and Hilgartner (1999).

Results

While the exact stratigraphic provenance of the specimen has been lost, the pre-Columbian origin of the specimen is not in question, as the mixing of archaeological material in the Roseau midden can be ruled out. The degree of bone surface mineralization and its similar color to the other bones collected from the site suggest that it was not introduced into the deposit at a later date. Like the other bones from the site, the corrosion of the specimen's cortical surface makes direct dating impossible. For this reason, the precise age of the osteological material is based on dates obtained on dentin from rodent bones (Bochaton *et al.* 2021). As the subfossil specimen from Roseau could derive from any of the site's Amerindian occupations, it can safely be attributed to the period between the 11th and 16th centuries.

The specimen corresponds to a distal fragment of a pedal phalanx that presents a well-developed *fovea subtrochlearis* consistent with a penultimate phalanx of a Strigiformes (Fig. 1). The plantar depression which accommodates the *tuberculum flexorium* of the ungual phalange is not as pronounced as in a Strigidae, indicating it to belong to a Tytonidae. The relative lateral-medial enlargement of the subtrochlear zone, the circular morphology of the *fovea subtrochlearis*, and its distance from the condyle exclude its classification as the first phalanx of digit I (pha1I). The fragmentary nature of the bone precludes a more precise anatomical attribution: pha2II, pha3III, or pha4IV, and also makes it impossible to determine the lateral (left or right) orientation of the specimen.

With a maximal distal width of 5.5 mm and a distal depth of 6.7 mm, the specimen is slightly smaller than the fossil penultimate phalanx of a juvenile *T. noeli* from Barbuda (USNM PAL 359244), which has a distal width of 5.9 mm (Fig. 2).

A broader comparison of the Roseau specimen measurements with those of the small European Barn Owl *T. a. alba*, estimated
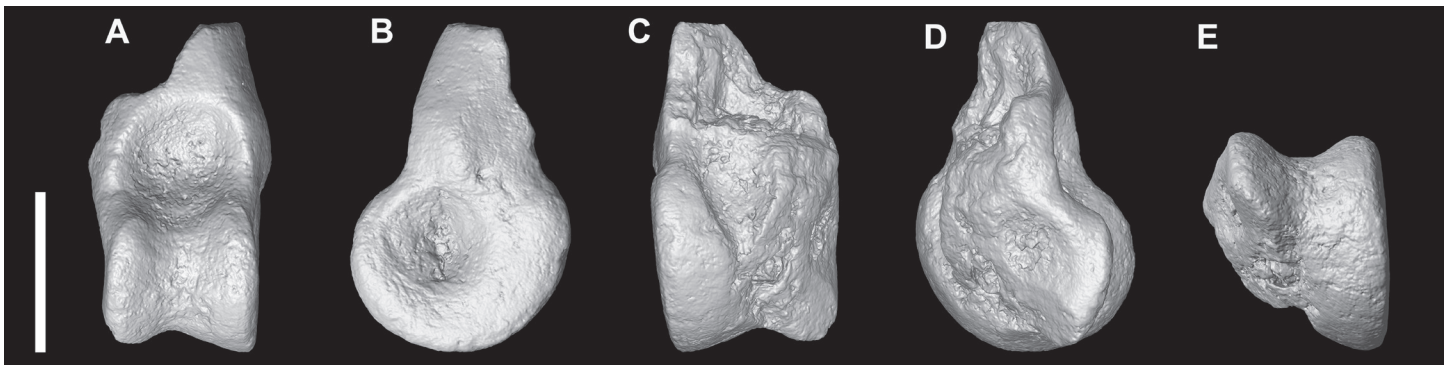
Fig. 1. Dorsal (A), plantar (C), side (B, D), and distal (E) views of the distal Tytonid phalanx from the pre-Columbian Roseau site, Guadeloupe. The scale bar represents 5 mm.
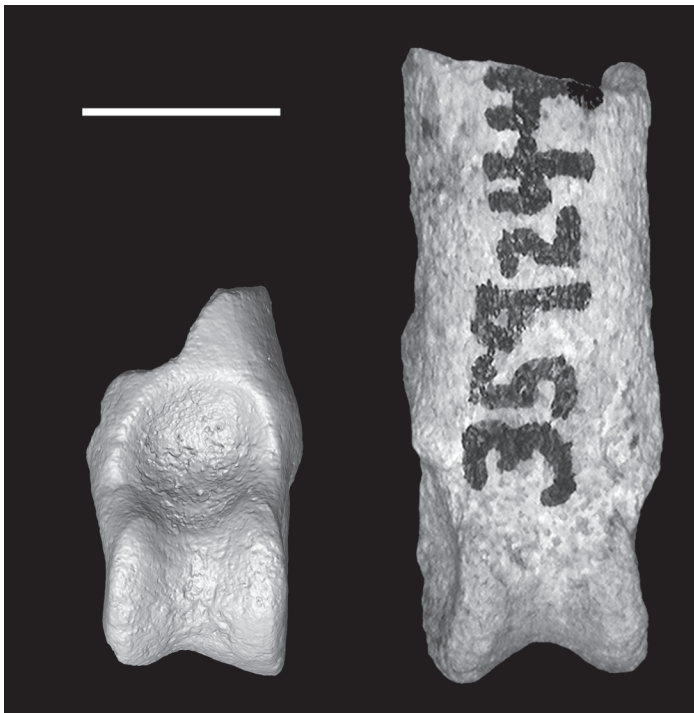

Fig. 2. Dorsal view of the Roseau fossil specimen (left) and a penultimate phalanx of a juvenile *Tyto noeli* individual, USNM 359244 (right). The scale bar represents 5 mm.

values for large present-day North American subspecies *T. a. pratincola* and *T. a. furcata*, and measurements for the Caribbean giant owls *T. noeli* and *T. ostologa*, revealed distinct patterns in phalanx size (Fig. 3). The larger North American barn owls had a 28–35% greater distal width and 36–42% greater distal depth than the smaller form, while *T. noeli* had 53% greater distal width and 22% greater distal depth than the extant larger form *T. a. furcata*. In comparison, the intra-population variability of the width and distal depth of the penultimate phalanges, as reflected in the mean values of the different phalanges of *T. a. alba*, is 16% for width and 12.5% for depth. This variation is significantly less compared to measurements between the different size groups, making it possible to reliably assign the Roseau fossil specimen to the giant owl fossil group.

Attributing the Roseau specimen to a particular species is,

however, less straightforward. Based on predicted values of homologous phalanges, the width of the Roseau fossil specimen is similar to the penultimate phalanges of *T. noeli,* while its depth is greater, distinguishing the specimen from the Barbuda fossils but making it comparable to specimens of *T. ostologa* (Fig. 3). This observation should be taken with some caution, as the phalanx size of *T. noeli* and *T. ostologa* are only known from a very limited number of elements. Consequently, the metric variability of the pedal phalanges of these species is currently difficult to reliably assess. Moreover, the available fossil material makes it impossible to rule out the Roseau bone belonging to another still undescribed giant owl species. We thus only consider the Roseau fossil specimen as evidence for the past occurrence of a giant owl of the genus *Tyto*.

Discussion

The discovery of a pedal phalanx fragment of a large Tytonid bird from the pre-Columbian site of Roseau suggests a giant barn owl occurred in Guadeloupe sometime between the 11th and 16th centuries. Nonetheless, it remains possible that this singular specimen was transported between islands by indigenous groups, for example in the form of a personal ornament (Laffoon 2018). However, considering that the bone was recovered from a midden (Bochaton *et al.* 2021) and the absence of evidence for the use of owl bones in Caribbean crafts, the most parsimonious interpretation of the Roseau specimen is the presence of a large owl in Guadeloupe during the pre-Columbian period. In addition to the Quaternary specimen previously reported from Barbuda (Steadman and Hilgartner 1999), the Roseau phalanx fragment is only the second instance of a giant owl documented in the Lesser Antilles. Based on biogeography, it is tempting to refer to the Roseau specimen as *Tyto noeli*, as it is the smallest and the most geographically proximal representative of the Caribbean giant barn owls; however, the bone is too fragmentary to be identified to species level.

The extinction of Caribbean giant owls has been explained by two non-mutually exclusive hypotheses, one focused on chronological factors in relation to human occupation and the other on ecological factors. The ecological hypothesis maintains that the absence of carnivorous mammals in the West Indies allowed large raptors to develop into super-predators heavily dependent on indigenous vertebrates (Arredondo 1976, Olson 1978). The
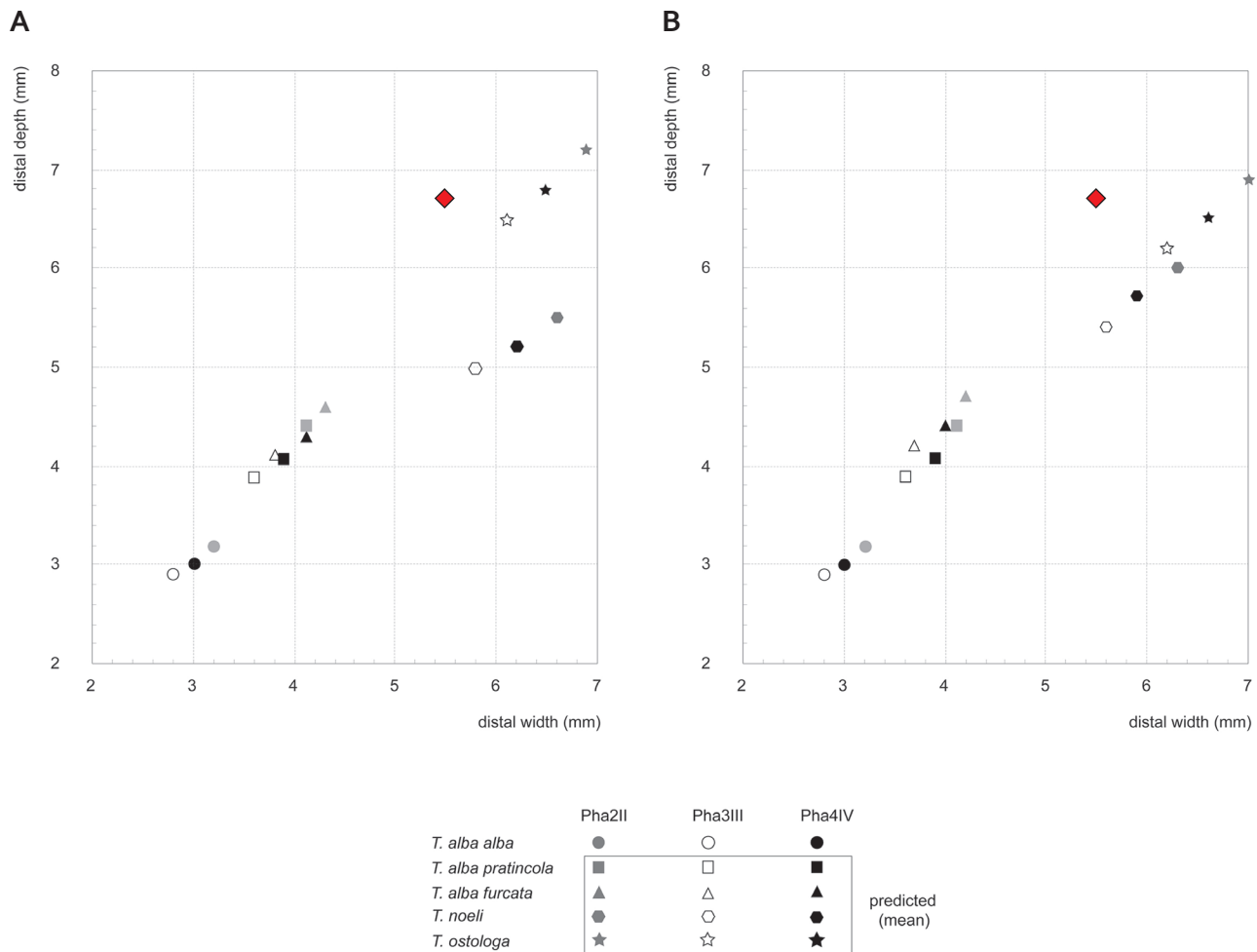
A

B

Fig. 3. Bivariate plot showing the distal width and depth measurements (mean) of the penultimate pedal phalanges (digit II, phalanx 2; digit III, phalanx 3; digit IV, phalanx 4) for extant European Barn owls (*Tyto a. alba*, *n* = 6) and predicted values of homologous phalanges of extant North American barn owls (*Tyto a. furcata* and *T. a. pratincola*) and extinct Caribbean giant barn owls (*T. noeli* and *T. ostologa*). Predicted values were calculated using available measurements for digit III, phalanx 2 (A) and digit I, phalanx 1 (B) of modern and fossil specimens (see Methods section for more details). The Roseau specimen is indicated by a red diamond.

loss of these prey species would have consequently led to the extinction of the giant owls in this region. This previously formulated hypothesis (Olson 1978, Steadman and Hilgartner 1999) is still valid today (Suárez and Olson 2015, 2020) and applies not only to owls, but to all large raptors (Steadman *et al.* 2019). In the specific case of owls, they would have primarily consumed mammals, which, unlike most birds or lizards, remain active at night (Suárez and Olson 2015).

A radiation of West Indian owls in relation to the availability of prey on each island has been proposed (Steadman and Hilgartner 1999), which may have led to variable body sizes throughout the subregion. This has led to the suggestion that large owls were more widely distributed in the Lesser Antilles, particularly on islands that supported sufficiently large rodents (Suárez and Olson 2015, 2020). As such, *Tyto noeli*, which is thought to have originated in Cuba, where fossils of the owl are abundant and widely distributed, would have spread to islands containing suitable prey species. In Barbuda, the extinct large rice rat, *Megalomys audreyae*, is assumed to have been the main prey of

this owl (Suárez and Olson 2015). While the past presence of *M. audreyae* in Barbuda has been questioned (Ray 1962), the presence of an even larger rodent, *Antillomys rayi*, has been reliably demonstrated (Brace *et al.* 2015). Weighing between 300–600 g (Goedert *et al.* 2020a), this rice rat could have been suitable prey for a large barn owl. In addition to the presence of *A. rayi* on Barbuda during the Pleistocene, this rodent also occurred in Guadeloupe, where bones recovered from paleontological deposits indicate its presence more than 2,000 years ago (Goedert *et al.* 2020a). These occurrences reflect the minimum amount of time during which favorable ecological conditions could have supported a giant owl in Guadeloupe.

The chronological hypothesis maintains that the disappearance of the giant barn owls was coincident with the extirpation of their prey (Steadman and Hilgartner 1999, Suárez and Olson 2015). However, as advanced by Suárez and Olson (2015), the disappearance of West Indian rodents coincided with the human occupation of the islands (Cooke *et al.* 2017) and therefore these large raptors, like many other now-extinct Caribbean endemics,

likely vanished after the arrival of humans in the Caribbean (Orihuela *et al.* 2020a, 2020b). The precise timing of their extinction, however, remains poorly documented.

Available data from Guadeloupe indicate that *Antillomys rayi* disappeared at the very beginning of the European occupation of the islands, possibly as a consequence of competition with the black rat (Goedert *et al.* 2020a). Black rats are smaller in size, with a body mass of between 125–200 g (Goedert *et al.* 2020b). They form the main part of the diet of the small endemic owl *Tyto insularis* on the neighboring island of Dominica (Stoetzel *et al.* 2016) as well as the barn owl in the Bahamas (Suárez and Olson 2020). These introduced mammals weigh only a third of the endemic rodent species *A. rayi* and therefore would not have been the main prey consumed by the giant owl. Among the several factors leading to the disappearance of the giant owls, the scarcity of suitable prey coincident with the onset of the colonial occupation likely played a major role.

The discovery of a pedal phalanx fragment of a giant barn owl from the pre-Columbian Roseau site indicates that a large owl was once present in Guadeloupe. It also suggests that this bird survived until sometime between the 11th and 16th centuries, a chronology that is consistent with both hypotheses explaining the disappearance of the Caribbean giant owls.

Acknowledgments

Title Page Illustration

The Roseau beach. Photograph taken on 26 July 2019 by A. Lenoble.

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Appendix 1. Measurements (mm) of the pedal phalanges (pha) of Tytonidae; *n* = sample size (see Methods for details).

Phalanx	Taxon	*n*	Distal width mean	Ratio pha2III	*n*	Distal depth mean	Ratio pha2III	Reference
Pha2III	*T. alba alba*	6	3.0		6	3.2		This work
	T. alba pratincola	11	3.8	0.78	11	4.4	0.73	Steadman and Hilgartner 1999
	T. alba furcata	4	4.0	0.74	4	4.6	0.70	Steadman and Hilgartner 1999
	T. noeli	1	6.1	0.49	1	5.6	0.58	Steadman and Hilgartner 1999
	T. ostologa	13	6.4	0.46	11	7.3	0.44	Steadman and Hilgartner 1999
Pha2II	*T. alba alba*	6	3.2		6	3.2		This work
	T. alba pratincola	-		4.1	-		4.4	Predicted
	T. alba furcata	-		4.3	-		4.6	Predicted
	T. noeli	-		6.6	-		5.5	Predicted
	T. ostologa	-		6.9	-		7.2	Predicted
Pha3III	*T. alba alba*	6	2.8		6	2.9		This work
	T. alba pratincola	-		3.6	-		3.9	Predicted
	T. alba furcata	-		3.8	-		4.1	Predicted
	T. noeli	-		5.8	-		5.0	Predicted
	T. ostologa	-		6.1	-		6.5	Predicted
Pha4IV	*T. alba alba*	5	3.0		5	3.0		This work
	T. alba pratincola	-		3.9	-		4.1	Predicted
	T. alba furcata	-		4.1	-		4.3	Predicted
	T. noeli	-		6.2	-		5.2	Predicted
	T. ostologa	-		6.5	-		6.8	Predicted
Pha1I	*T. alba alba*	6	2.8		6	3.2		This work
	T. alba pratincola	11	3.6	0.78	11	4.4	0.73	Steadman and Hilgartner 1999
	T. alba furcata	4	3.7	0.76	4	4.7	0.69	Steadman and Hilgartner 1999
	T. noeli	1	5.5	0.51	1	6.1	0.53	Steadman and Hilgartner 1999
	T. ostologa	5	6.1	0.46	5	7.0	0.46	Steadman and Hilgartner 1999
Pha2II	*T. alba alba*	6	3.2		6	3.2		This work
	T. alba pratincola	-		4.1	-		4.4	Predicted
	T. alba furcata	-		4.2	-		4.7	Predicted
	T. noeli	-		6.3	-	-	6.0	Predicted
	T. ostologa	-		7.0	-		6.9	Predicted
Pha3III	*T. alba alba*	6	2.8		6	2.9		This work
	T. alba pratincola	-		3.6	-		3.9	Predicted
	T. alba furcata	-		3.7	-		4.2	Predicted
	T. noeli	-		5.6	-	-	5.4	Predicted
	T. ostologa	-		6.2	-		6.2	Predicted
Pha4IV	*T. alba alba*	5	3.0		5	3.0		This work
	T. alba pratincola	-		3.9	-		4.1	Predicted
	T. alba furcata	-		4.0	-		4.4	Predicted
	T. noeli	-		5.9	-	-	5.7	Predicted
	T. ostologa	-		6.6	-		6.5	Predicted