OSTEOLOGICAL CHARACTERS FOR THE IDENTIFICATION OF CARIBBEAN COLUMBIDS

Caracteres osteológicos para la identificación de los colúmbidos del Caribe

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ABSTRACT

Columbid remains are commonly recovered from Caribbean archaeological and paleontological sites. Identifying specimens to species level is therefore likely to yield a wealth of information concerning species diversity and changes in their distribution over time. Here we examine the metrical data and 42 osteological characters of eight skeletal elements of 80 specimens belonging to 12 species from five genera that represent most of the indigenous taxa of the West Indies. Our new data provide a reliable means for identifying these birds in the Caribbean fossil and subfossil record.

Keywords: Columbidae, pigeons, doves, osteology, Antilles.

RESUMEN

La recuperación de restos de colúmbidos en yacimientos arqueológicos y paleontológicos del Caribe es habitual. En consecuencia, su identificación a nivel de especie puede generar una gran cantidad de información relativa a la diversidad de las especies y a los cambios en su distribución a lo largo del tiempo. Aquí, examinamos los datos métricos y 42 caracteres osteológicos de ocho elementos esqueléticos, de 80 especímenes, pertenecientes a 12 especies de cinco géneros distintos, la mayoría taxones nativos de las Antillas. Nuestros nuevos datos proporcionan un medio fiable para identificar estas aves en el registro fósil y subfósil en el Caribe.

Palabras clave: Columbidae, palomas, tórtolas, osteología, Antillas.

INTRODUCTION

Among the birds that provide the most information for changes in bird community through time, pigeons and doves occupy a special place in Caribbean avifauna. First, the Caribbean currently hosts some twenty Columbidae species (Raffaele *et al*., 2003), making this family well represented in the region. Second, members of this family are good ecological markers, as several species occur on most islands with each species occupying a specific or, at least, partially distinct habitat (e.g. Baptista *et al*., 1997; Gibbs *et al*., 2001; Wells & Wells, 2001). Several studies have described the past diversity and abundance of Columbidae in the Greater Antilles and Bahamian Archipelago. The initial work of Wetmore (1920, 1922a, 1922b, 1925, 1937) and more recent research in Cuba (Arredondo, 1984; Jiménez-Vázquez, 2001; Jiménez-Vázquez & Arrazcaeta, 2008, 2015; Olson & Wiley, 2016; Orihuela *et al*., 2020) and the Bahamas (e.g. Brodkorb, 1959; Olson & Hilgartner, 1982; Steadman & Franklin, 2020) has documented about 15 columbid taxa from late Pleistocene to historical period. However, in other areas of the Caribbean, namely the Lesser Antilles, the fossil and subfossil records remain poorly documented, comprising not

more than 8 columbid taxa, most of which have been identified on the islands of Montserrat, Antigua and Sint Eustatius (Steadman *et al*., 1984a, 1984b; Van der Klift, 1992; Pregill *et al*., 1994). In other Lesser Antilles islands, columbid birds are usually not attributed beyond genus (Grouard, 2001, 2013; Newsom & Wing, 2004). In fact, identifying columbid bones from archaeological and paleontological sites to species remains difficult, especially for medium-sized species (Olson & Hilgartner, 1982; Steadman *et al*., 1984b; Goldberg, 1999; Olson, 2011). One reason for this is the substantial inter- and infraspecific variability that complicates reliably determining fossil remains, meaning that, while quantitatively well represented in fossil assemblages, a large number of columbid bones cannot be assigned to species. Moreover, only limited and partial data is available to identify the bones of several columbid species in the Caribbean and Bermuda (Wetmore, 1922a; Olson & Hilgartner, 1982; Steadman *et al*., 1984b; Worthy, 2001; Tellkamp, 2005; Olson, 2011).

OBJECTIVES

- Provide new osteological descriptions and quantitative data from the morphometric analysis of modern pigeons and doves for the reliable identification of Caribbean columbid bones from both archaeological and paleontological contexts.

MATERIALS AND METHODS

Specimens. The reference material for this study comes from the skeletal collection of the PACEA laboratory, University of Bordeaux, as well as the American Museum of Natural History of New York (AMNH), Musée Edgar Clerc (MEC), Muséum National d'Histoire Naturelle (MNHN), Natural History Museum (NHMUK), University of Florida-Florida Museum of Natural History (UF), and the Smithsonian Institution-National Museum of Natural History (USNM).

The sample included all pigeon species, resident or seasonal, currently present in the Antilles. The 3 species recently introduced to the Caribbean (*Columba livia, Streptopelia decaocto* and *Streptopelia chinensis*) and species with a limited distribution in the Western Caribbean (e.g., *Columba caribaea, Geotrygon caniceps*, *Geotrygon versicolor*) were excluded. The overall sample includes 80 more or less complete modern specimens of Columbidae (Appendix A), encompassing 5 genera, 12 species: the Scaly-naped Pigeon *Patagioenas squamosa* (n = 10), White-crowned Pigeon *P. leucocephala* (n = 11), Plain Pigeon *P. inornata* (n = 8), Common Ground Dove *Columbina passerina* (n = 2), Ruddy Quail-Dove *Geotrygon montana* (n = 5), Key West Quail-Dove *G. chrysia* (n = 7), Bridled Quail-Dove *G. mystacea* (n = 6), White-winged Dove *Zenaida asiatica* (n = 8), Zenaida Dove *Z. aurita* (n = 15), Eared Dove *Z. auriculata* (n = 5), and Mourning Dove *Z. macroura* (n = 2). A virtual specimen of the rare species Grenada Dove *Leptotila wellsi* was also included in the sample. Sex, age, and locality of origin were recorded for each specimen. Skeletal maturity is almost complete in some specimens, and several characters are evident even when the bird displayed juvenile plumage (subadult osteological specimens).

Methodology. We analysed 8 skeletal elements commonly found in the archaeological and paleontological record: coracoideum, scapula, humerus, ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus.

Bone orientation and descriptions of anatomical features follow the terminology of Baumel and Witmer (1993), with some exceptions. Osteological features on some elements of different European and Neotropical columbids identified by Wetmore (1922a), Fick (1974),

Olson and Hilgartner (1982), Steadman *et al.* (1984b), Worthy (2001), Tellkamp (2005), and Tomek and Bochenski (2009) have been integrated into this study. The anatomical features used in the description of characters are illustrated for each bone, and characters are described respecting their anatomical position (from proximal to distal bone portions). The description and a photo are provided for the different states (from 2 to 4, A-D) of each morphological character. Specimens were assigned to intermediate states when they displayed less expressed characters or those falling between two states. The referred specimen, the percentage of states, and sample size (n) are provided for each taxon.

Measurements follow those described by von den Driesch (1976) but with two additions for the coracoideum: the proximal end (Bp) and smallest breadth (SC), (Appendix B). All bones were measured with a digital caliper to the nearest 0.1 mm and primarily concerned right-side bones. Mean, maximum, and minimal values of repeated measurements are provided in Appendix C. Some samples could not be fully measured due to damage (e.g. broken bone), anatomical connections, pathologies, or time contraints. For the 3–D models, the measurements were derived with the Avizo and Meshlab software packages. Measurements were compared with those provided by Goldberg (1999) for American Southwestern Columbidae (*Z. asiatica*, *Z. macroura* and *C. passerina*), with size classes based on those proposed by Steadman *et al.* (1984b) for pigeons and doves from the Lesser Antilles (*P. squamosa, P. leucocephala, G. mystacea, G. montana, Z. aurita, C. passerina*).

A single observer (MG) scored all criteria and measured all specimens. Only characters that occurred in at least 60 % of specimens are presented. *Columbina passerina,* the smallest species in the sample, cannot be confused with other species and is therefore included in the metric data excluded for describing specific characters. Detailed information (measurements and characters of each modern specimen) and illustrations of the 8 bones of the 4 genera are provided in the appendices (D-V).

RESULTS

A total of 42 morphological characters (7 for the coracoideum, 3 for the scapula, 6 for the humerus, 5 for the ulna, 11 for the carpometacarpus, 3 for the femur, 4 for the tibiotarsus, 3 for the tarsometatarsus) were selected. Due to the lack of sex data for numerous specimens, we excluded sexual dimorphism when discussing our results. However, male and female pigeons and doves are roughly similar in size, with appreciable dimorphism between sexes recorded only for *Zenaida* species (i.e. males larger than females; Wiley, 1991; Baptista *et al.,* 1997).

Coracoideum

Coracoidea from 73 specimens were analyzed (Appendix D). When complete, this bone is easily distinguishable between genera. The coracoideum of *Patagioenas* has a much longer, broader, and robust shaft (corpus coracoidei) than the other 3 genera, whereas in *Geotrygon,* the shaft is long and narrow, and in *Zenaida,* it is short and wide (Fig. 1; Appendix E). Seven osteological characters and their states allow for a more detailed diagnosis (Fig 2). Five of these diagnostic characters concern the omal portion of the coracoideum, while the two others are typical of the distal portion and allow different *Zenaida* species to be distinguished (see also Appendix F). The percentage and distribution of states for each taxon are reported in Table I.

Margin of the facies articularis humeralis and cotyla scapularis (COR_FAH)

Referred material. *Geotrygon mystacea* PACEA–O–858 for state A and *Zenaida aurita* PACEA–O–865 for state B (Table I).

The margin of facies articularis humeralis and cotyla scapularis in dorsal view is broader in state A than in state B (Fig. 2).

All *Zenaida* specimens present a narrow margin, which sets them apart from the single *L. wellsi* specimen in the sample (Table I). Conversely, most *Patagioenas* and *Geotrygon* specimens exhibit a broad margin whose form differs according to species.

Shape of the area between the facies articularis clavicularis and the processus procoracoideus (COR_FAC)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A, *Zenaida asiatica* PACEA–O–1063 for state B, *P. leucocephala* PACEA–O–493 for state C, and *Z. aurita* PACEA–O–708 for state D (Table I).

In dorsal view, this element is oval in *Geotrygon* (Fig. 2; Table I). It is large in *G. mystacea* and most individuals of *G. montana* (state A) and narrow in *G. chrysia* (state D). Except for a single specimen of *P. leucocephala*, all *Patagioenas* specimens present a generally large, oval-shaped area between the articularis clavicularis and the processus procoracoideus.

In the single *L. wellsi* specimen and most *Zenaida* specimens, this area is rounded and narrow (state B), except in *Z. asiatica,* in which only two of the seven individuals present this character. In the other specimens assigned to this species it is narrow and oval, while in *Z. auriculata* it appears large and rounded (state C).

Pneumatic foramen (COR_PN)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A, *Geotrygon montana* PACEA–O–492 for state B, *Zenaida auriculata* PACEA–O–498 for state C, and *Z. asiatica* PACEA–O–707 for state D (Table I).

A pneumatic foramen is visible in medial view and can be found in the dorsal, central, or ventral portion of the bone. It is positioned dorsally (state A) in the upper part of the sulcus musculi supracoracoidei in *Patagioenas* (Fig. 2).

In *Geotrygon*, the presence of a pneumatic foramen is exclusive to *G. montana*, occurring centrally (state B) or in an intermediate position between the dorsal and midpoint of the bone (state A/B). This character is absent (state D) in the other two species (*G. chrysia* and *G. mystacea)* of this genus and in *L. wellsi*.

The absence of a marked pneumatic foramen is systematic in *Zenaida*, although a deep depression is occasionally present in the sulcus musculi supracoracoidei or below the facies articularis clavicularis (ventral position, state C): *Z. aurita* and *Z. auriculata*.

Tuberculum caudale (COR_TC)

Referred material. *Zenaida asiatica* PACEA–O–707 for state A, *Patagioenas leucocephala* PACEA–O–970 for state B, and *Geotrygon montana* PACEA–O–847 for state C (Table I).

In medial view, the tuberculum caudale (Fick, 1974) appears very prominent (projects dorsally) in several cases, as in *Zenaida asiatica* (state A) and half of the coracoidea of *Z. auriculata,* whereas the two congeneric species have a prominent (state B) or non-prominent tuberculum (state C), (Fig. 2).

In *Geotrygon*, the tuberculum caudale is slightly or not prominent and absent in state A. While attributions to *P. squamosa* or *P. leucocephala* based on this character are less certain, the *P. inornata* primarily lacks a prominent tuberculum caudale. A single specimen of *L. wellsi* has a prominent tuberculum.

Processus acrocoracoideus (COR_PA)

Referred material. *Geotrygon montana* PACEA–O–847 for state A and *Zenaida asiatica* PACEA–O–707 for state B (Table I).

In ventral view, the processus acrocoracoideus in *Geotrygon* is more often distinctly raised (state A) and upwardly projected compared to state B (Fig. 2). This character is also observed in *P. squamosa* and some individuals of *Z. aurita* (Table I).

This element is less distinctly raised (state B) in *P. inornata, Z. asiatica*, *Z. auriculata*, and in the single *Z. macroura* and *L. wellsi* individuals. The processus acrocoracoideus is either distinctly raised or raised in *P. leucocephala* and *Z. aurita*.

Additionaly, 3 omal characters are described in the appendix (Appendix F).

Facies articularis sternalis near the angulus medialis (COR_FAS)

Referred material. *Zenaida asiatica* PACEA–O–707 for state A and *Z. aurita* PACEA–O–865 for state B (Table I).

This character and all of the following ones describe the area of the angulus medialis and allow different *Zenaida* species to be identified (Fig. 3).

In ventral view, the facies articularis sternalis near the angulus medialis is distinctively large for all individuals of *Z. asiatica* (state A, Fig. 3A), while this portion of the articular surface is quite narrow in *Z. aurita* (Fig. 3B), Z. *auriculata* (Fig. 3C), and Z. *macroura* (Fig. 3D).

Angulus medialis (COR_AM)

Referred material. *Zenaida asiatica* PACEA–O–707 for state A and *Z. aurita* PACEA–O–865 for state B (Table I).

In sternal view, the angulus medialis is straight in *Z. asiatica* (state A, Fig. 3E). All coracoidea of *Z. aurita* except one present a concavity on the labrum internum coracoidei (Livezey & Zusi, 2006), (state B, Fig. 3F). As all coracoidea present an intermediate state A/B (Fig. 3G-H), it is impossible to attribute specimens to either *Z. auriculata* or *Z. macroura* based on this character.

Coracoideum measurement

As expected, while genera are well differentiated, different species within each genus are less so (Fig. 4; Appendix C). Our results are in perfect agreement with those of Goldberg (1999), although the limited representation of certain taxa in our sample suggests a poor estimation of interspecific variability (Fig. 4). With that said, our data paints a more complex situation than previously assumed (Steadman *et al*., 1984b). Metrical data for the coracoideum does not separate *Geotrygon mystacea* and *montana*, and *Geotrygon mystacea* and *Patagioenas leucocephala* are only partially differentiable. In the latter case, despite a non-negligible overlap between the coracoideum measurements of these two taxa, the difference in mean coracoideum length is very close to being significant (t-student, $p = 0.097$). This is because smaller of the *G. mystacea* fall outside the size range of *P. leucocephala* while the larger of the latter taxon is outside the variability of the quail-doves. Overall, 5 distinct size classes are observable: *P. squamosa* = *P. inornata* > *P. leucocephala* ~= *G. mystacea* ~= *G. montana* > *G. chrysia* = *Z. asiatica* = *Z. aurita* > *Z. auriculata* = *Z. macroura* >> *C. passerina*.

Apart from being comparable in size to the different species of *Zenaida*, the small sample size for *L. wellsi* does not allow us to place this taxon within a particular size class.

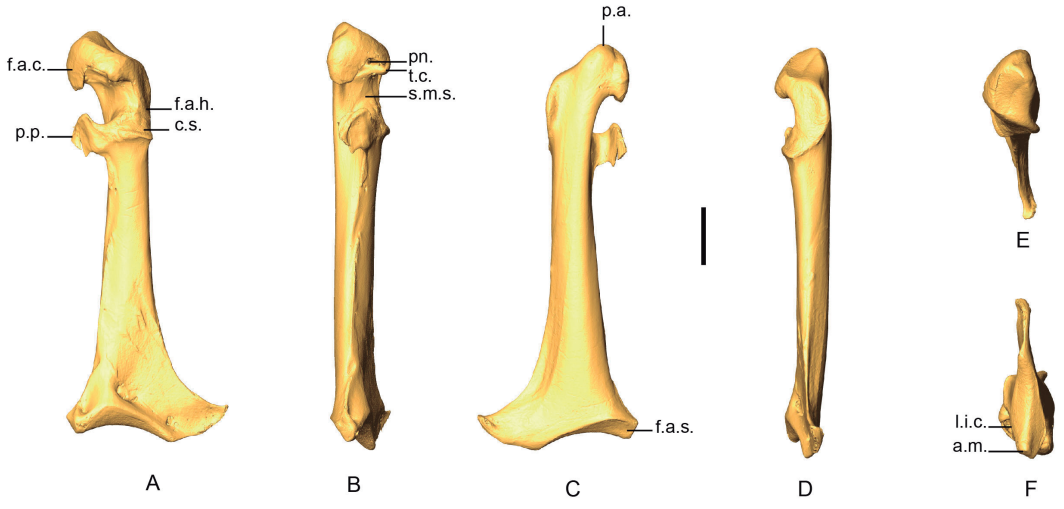


Figure 1. 3D – model of a right coracoideum of *Patagioenas inornata* USNM 226458 in dorsal (A), medial (B), ventral (C), lateral (D), proximal (E), and distal (F), views. Abbreviations: a.m., angulus medialis; c.s., cotyla scapularis; f.a.c., facies articularis clavicularis; f.a.h., facies articularis humeralis; f.a.s., facies articularis sternalis; l.i.c., labrum internum coracoidei; p.a., processus acrocoracoideus; pn., pneumatic foramen; p.p., processus procrocoracoideus; s.m.s., sulcus musculi supracoracoidei; t.c., tuberculum caudale. Scale bar equals 5 mm.

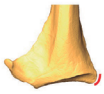
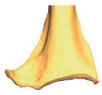
Code	States			
	A	**B**	**C**	**D**
COR_FAH **Margin of the facies articularis humeralis and cotyla scapularis in dorsal view**	Broad  *Geotrygon montana* MNHN-ZO-AC-1993-116	Narrow  *Zenaida asiatica* PACEA-O-707		
COR_FAC **Shape of the area between the facies articularis clavicularis and the processus procoracoideus in dorsal view**	Large and oval  *Geotrygon montana* MNHN-ZO-AC-1993-116	Narrow and rounded  *Zenaida asiatica* PACEA-O-707	Large and rounded  *Patagioenas leucocephala* PACEA-O-493	Narrow and oval  *Geotrygon chrysia* USNM 292518
COR_PN **Pneumatic foramen in medial view**	Dorsally  *Patagioenas inornata* USNM 226458	Centrally  *Geotrygon montana* PACEA-O-492	Ventrally  *Zenaida auriculata* PACEA-O-498	Absent  *Zenaida asiatica* PACEA-O-707
COR_TC **Tuberculum caudale in medial view**	Very prominent  *Zenaida asiatica* PACEA-O-707	Prominent  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1	Not prominent  *Patagioenas inornata* USNM 226458	
COR_PA **Processus acrocoracoideus in ventral view**	Distinctly raised  *Geotrygon montana* PACEA-O-847	Raised  *Zenaida asiatica* PACEA-O-707		
COR_FAS **Facies articularis sternalis near the angulus medialis in ventral view**	Large  *Zenaida asiatica* PACEA-O-707	Narrow  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1		
COR_AM **Angulus medialis in sternal view**	Straight  *Zenaida asiatica* PACEA-O-707	Concave  *Zenaida aurita* PACEA-O-865		

Figure 2. States of the osteological characters described for the coracoideum.

Table I. Coracoideum characters. Sample size (n) and percentage of states (A-D) and intermediate state (A/B, B/C, B/D) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
COR_FAH	**n**	8	9	3	5	3	5	1	7	15	4	1
	A	87	100	33	100	33	60	100				
	B	13		67		67	40		100	100	100	100
COR_FAC	**n**	8	9	4	5	3	6	1	7	15	4	1
	A	100	89	75	80		100					
	B							100	29	60	75	100
	C		11								25	
	D			25	20	100			71	27		
	B/D									13		
COR_PN	**n**	8	9	5	5	3	5	1	7	15	4	1
	A	100	89	60								
	A/B				60							
	B				40							
	B/C			20								
	C		11							7	25	
	D			20		100	100	100	100	93	75	100
COR_TC	**n**	8	9	4	5	3	5	1	8	15	4	1
	A		22						63		50	
	A/B	37	11									
	B	37	44	25		67	60	100	37	60	50	100
	B/C				40					7		
	C	25	22	75	60	33	40			33		
COR_PA	**n**	8	8	5	5	3	6	1	7	15	4	1
	A	75	13		80	33	100			40	25	
	A/B	25	50			67				20		
	B		37	100	20			100	100	40	75	100
COR_FAS	**n**	7	9	3	5	3	5	1	7	15	4	1
	A	43	22	33	80	67	20		100			
	A/B			67								
	B	57	78		20	33	80	100		100	100	100
COR_AM	**n**	5	8	2	5	3	5	1	7	14	4	1
	A	80	63	100	40	67	60		100			
	A/B	20	37		60		20	100		21	100	100
	B					33	20			79		

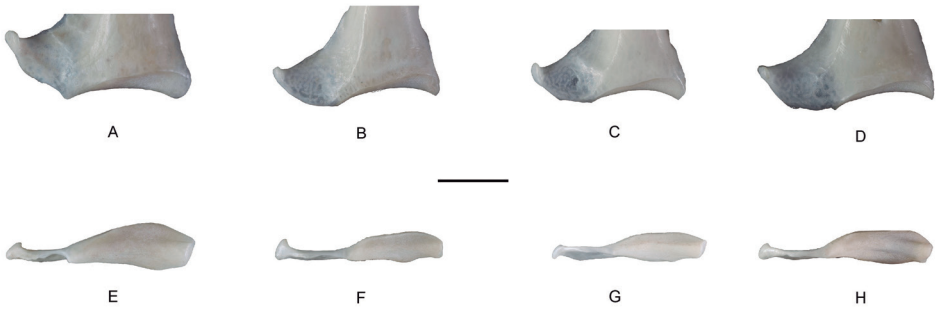


Figure 3. Distinctive characters of facies articularis sternalis and angulus–medialis in ventral (A–D) and sternal (E–H) views of coracoideum of *Zenaid*a; A, E, *Z. asiatica* PACEA–O–707; B, F, *Z. aurita* PACEA–O–865; C, G, *Z. auriculata* PACEA–O–498; D, H, *Z. macroura* PACEA–O–493. Right side. Scale bar equals 1 cm.

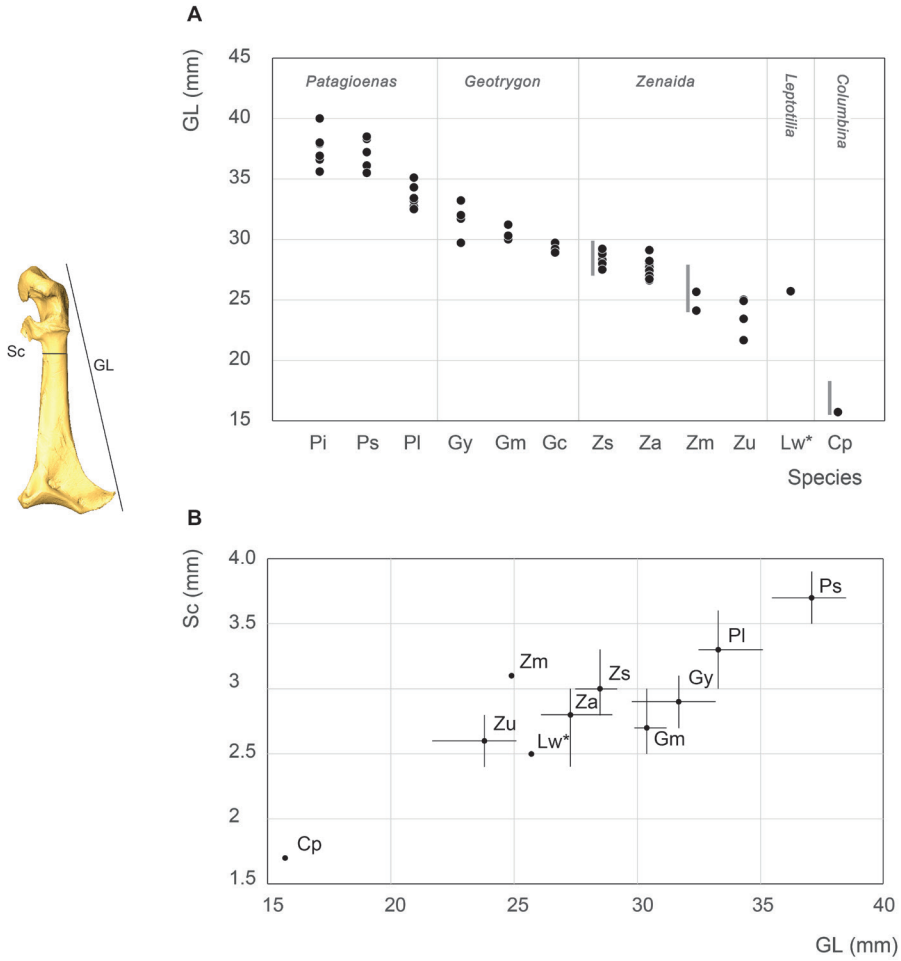


Figure 4. Coracoideum measurement in mm: GL, Greatest length (A), Sc, smallest breadth of the corpus and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

Scapula

Scapulae from 66 specimens have been considered (Appendix G). The observations of complete bones demonstrate scapulae of *Patagioenas* (Fig. 5) and *Zenaida* to primarily exhibit a more curved ventral margin of the shaft (corpus scapulae) in medial or lateral view compared to those of the 2 other genera *Geotrygon* and *Leptotila* (Appendix H).

However, the substantial degree of inter-specific variability of this bone in the 4 genera complicates the recognition of diagnostic characters. Three osteological criteria and associated states of the articular portion of the scapula, two in articular view and one in medial view medial, are illustrated in Figure 6. The percentage and the distribution of states for each taxon are reported in Table II.

Shape of acromion (SCA_A)

Referred material. *Zenaida aurita* PACEA–O–708 for state A, *Geotrygon montana* PACEA–O–1055 for state B, and *Patagioenas squamosa* PACEA–O–442 for state C (Table II).

In medial view, the acromion is flat and rounded (state A) in *Zenaida* (Fig. 6). The medial apex is flattened, and the lateral apex is rounded while in state B the medial apex is flattened and the lateral apex is angular. This latter character is observed in *Geotrygon* and in *L. wellsi* (Appendix H).

In *Patagioenas inornata* and two congeneric species, the medial apex is larger than in other species and the lateral apex is rounded (state C, Fig. 6).

Pneumatic foramen (SCA_PN)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A and *Z. aurita* PACEA–O–708 for state B (Table II).

In articular view, a large pneumatic foramen is visible on the acromion (state A) in *Patagioenas* specimens, while in *Geotrygon*, *Zenaida*, and *Leptotilia* this foramen is absent (state B), (Fig. 6).

Medial margin between facies articularis humeralis and medial apex (SCA_MM)

Referred material. *Geotrygon montana* PACEA–O–847 for state A, *Zenaida aurita* PACEA–O–710 for state B, *Patagioenas squamosa* PACEA–O–442 for state C, and *G. mystacea* PACEA–O–766 for state D (Table II).

In articular view, the shape of the medial margin differs from one species to another (Fig. 6; Table II). This margin is convex and projects medially (state A) in 2 species: *G. montana* (except one scapula in Appendix I) and *Z. asiatica.*

In *Z. aurita*, *Z. macroura*, and most of the *Z. auriculata* individuals, the medial margin is concave (i.e. U-shaped) in state B. State C is slightly different but clearly distinguisable from state B; the two portions of the margin are more oblique and the margin is an open V-shape: *P. squamosa, P. leucocephala, G. mystacea* and *L. wellsi*.

One specimen of *P. inornata* exhibits characters of both B and C states. In rare cases, a relatively straight margin (state D) is present, as observed in the two *G. chrysia* specimens and the single specimens of *P. leucocephala* and *G. mystacea.*

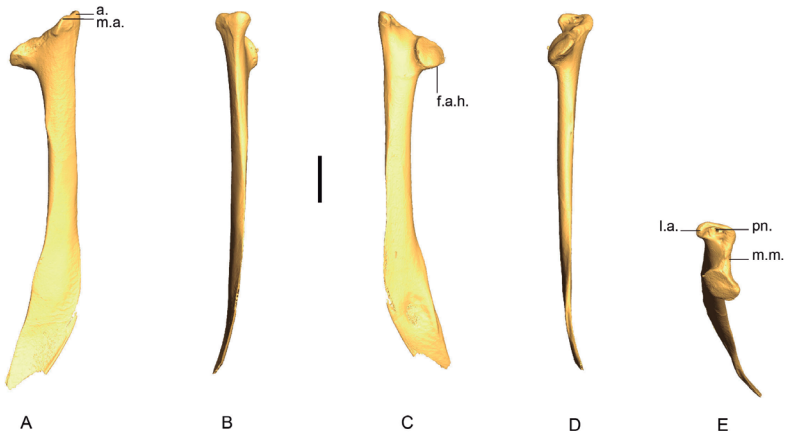


Figure 5. 3D – model of a right scapula of *Patagioenas inornata* USNM 290977 in medial (A), dorsal (B), lateral (C), ventral (D) and articular (E) views. Abbreviations: a., acromion; f.a.h., facies articularis humeralis; l.a., lateral apex; m.a., medial apex; m.m., medial margin; pn., pneumatic foramen. Scale bar equals 5 mm.

Code	States			
	A	**B**	**C**	**D**
SCA_A **Shape of acromion in medial view**	Flat and rounded  *Zenaida aurita* PACEA-O-865	Flat and angular  *Geotrygon montana* MNHN-ZO-AC-1993-116	Large and rounded  *Patagioenas inornata* USNM 290977	
SCA_PN **Pneumatic foramen in articular view**	Present  *Patagioenas inornata* USNM 290977	Absent  *Geotrygon montana* MNHN-ZO-AC-1993-116		
SCA_MM **Medial margin between facies articularis humeralis and medial apex in articular view**	Convex  *Geotrygon montana* PACEA-O-847	Concave  *Geotrygon montana* MNHN-ZO-AC-1993-116	V-shaped  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1	Relatively straight  *Geotrygon chrysia* MNHN-ZO-AC-1931-525

Figure 6. States of the osteological characters described for the scapula.

Table II. Scapula characters. Sample size (n) and percentage of states (A-D) and intermediate state (B/C) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
SCA_A	**n**	6	8	1	4	2	5	1	7	14	5	1
	A								100	100	100	100
	B				100	100	100	100				
	C	100	100	100								
SCA_PN	**n**	6	8	1	4	2	5	1	7	14	5	1
	A	100	100	100								
	B				100	100	100	100	100	100	100	100
SCA_MM	**n**	6	8	1	4	2	5	1	7	14	5	1
	A				75				71		20	
	B				25				29	100	80	100
	B/C			100								
	C	100	87				80	100				
	D		13			100	20					

Scapula measurements

Given the fragility of its extremity, only a limited number of scapulae could be measured in their entirety (Appendix C). Despite this limitation, the proximal width of the scapula is greater in *Patagioena* compared to the other three genera (Fig. 7).

Scapula measurements were similar to those reported by Goldberg (1999) but differ from those of Steadman *et al*. (1984b); the larger *P. leucocephala* has a longer scapula than *G. mystacea*, while scapula length in *G. mystacea* and *G. montana* appear indistinguishable and *Z. aurita* has a shorter scapula compared to *G. montana*.

The same five size classes identified for the coracoideum are equally evident in *the greatest length* of scapula, including the same degree of uncertainty for the position of *L. wellsi* which, reflects the single scapula measurement for this species.

Humerus

Humeri from 66 specimens have been considered (Appendix I). Extremely difficult to distinguish between different genera, even when complete, the humerus of *Patagioenas* is generally long and robust (Fig. 8). Distinguishing the genera *Geotrygon* and *Zenaida* based on metrical data is difficult, even if the humerus of *Geotrygon mystacea* is generally longer. The humerus is more curved in *Zenaida* compared to the other genera (Appendices J-K).

Six osteological criteria are defined and illustrated (Fig. 9). The distribution of the different states by species is reported in Table III. Four of these diagnostic characters were found in the proximal portion of the bone, while the two others describe the distal portion.

Caput humeri (HUM_CH)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A and *Geotrygon montana* MNHN–ZO–AC–1993–116 for state B (Table III).

In cranial view, the caput humeri projects ventrally beyond the shaft axis (state A) in *Patagioenas* as well as in *G. chrysia* (Fig. 9). The caput is more centrally positioned (state B) in *G. montana*, *G. mystacea,* and *L. wellsi.* This character is present in the two states in *Zenaida* specimens.

Ventral margin of the shaft and crista bicipitalis (HUM_VM)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A, *P. inornata* USNM 290977 for state B, and *Zenaida asiatica* PACEA–O–707 for state C (Table III).

In cranial view, the crista bicipitalis and the corpus humeri form a large, rounded arch (state A) in *Patagioenas* and *Geotrygon* (Fig. 9). In state B, the ventral margin is more tightly rounded than in state A (*L. wellsi*). In *Zenaida*, the ventral margin is angular (state C, see appendix K for an additional character of this genus).

Tuberculum dorsale (HUM_TD)

Referred material. *Patagioenas squamosa* PACEA–O–486 for state A, *Zenaida aurita* PACEA–O–710 for state B, *P. leucocephala* PACEA–O–822 for state C, and *G. mystacea* PACEA–O–494 for state D (Table III).

This character was recognized by Steadman *et al.* (1984b) as distinguishing *P. leucocephala* from *G. mystacea*. Our results are consistent with this distinction and also allow *Zenaida* to be individualized from *Patagioenas*.

The tuberculum dorsale can be wide and well developed (state A) or narrow (state B) and in many cases is associated with a depression in the cranial margin of the crista deltopectoralis (states C-D), (Fig. 9). Several obvious differences are evident on the two reference specimens of *Patagioenas* and *Zenaida*, although numerous variations between the two genera make it difficult to refer some specimens to a state. Moreover, in *Geotrygon*, a well-developed depression is evident in *G. mystacea* but is less marked in *G. montana*, where a slight depression is present. Therefore, some specimens of this genus present intermediate states (state B/D).

However, the tuberculum dorsale is generally well developed in *Patagioenas* (state A) and in some cases projects cranially and dorsally. In *Zenaida*, this element is narrow (states B or D) and in *L. wellsi* it is narrow with a depression (state D).

Ventral margin of the sulcus ligamentus transversus of the caput humeri (HUM_SLT)

Referred material. *Geotrygon mystacea* PACEA–O–494 for state A, *G. montana* MNHN–ZO–AC–1993–116 for state B and *Zenaida aurita* PACEA–O–710 for state C (Table III).

This character is visible in both proximal and ventral view and allows *G. mystacea* to be distinguished from *G. montana.* In the first species, the ventral margin of the sulcus ligamentus transversus of the caput humeri has a rounded profile (state A) while in *G. montana* this margin is oblique (state B, Fig. 9). A straighter margin (state C) is evident in some specimens of *Zenaida*.

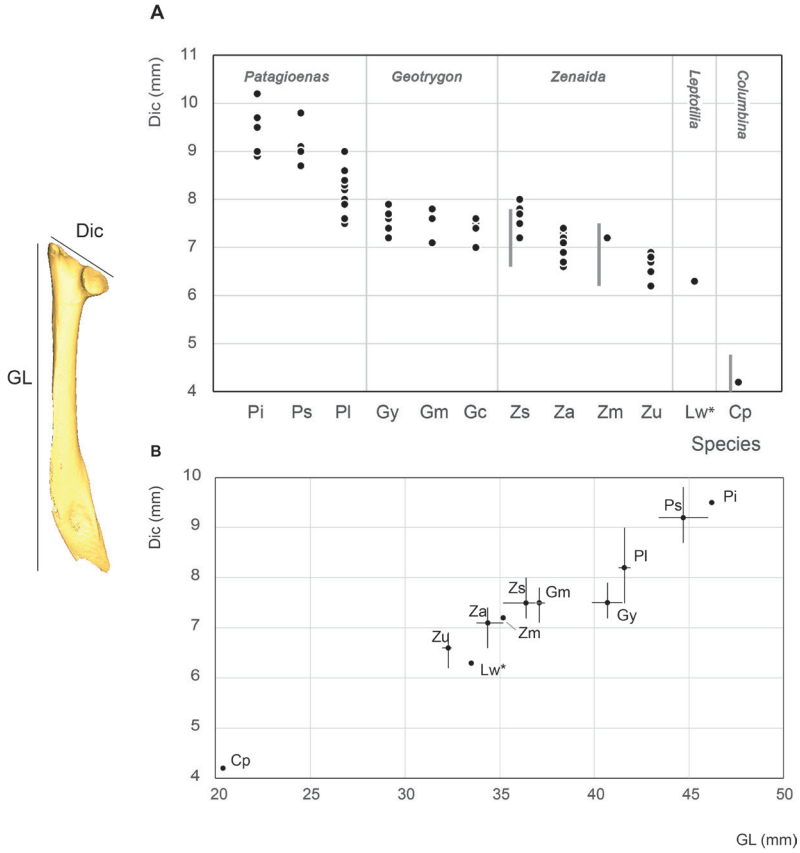


Figure 7. Scapula measurement in mm: Dic, (Greatest) cranial diagonal (A), Dic, (Greatest) cranial diagonal and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

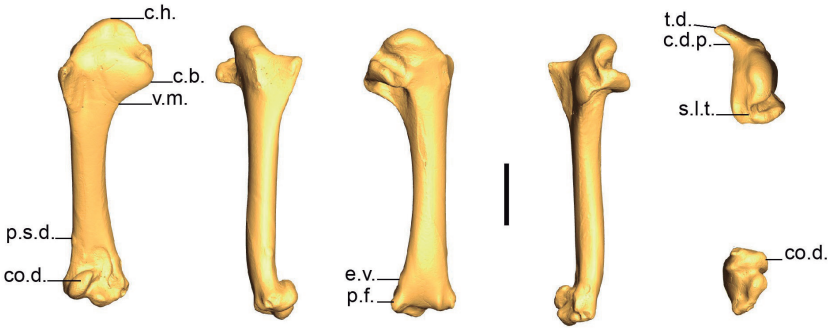


Figure 8. 3D – model of a right humerus of *Patagioenas inornata* USNM 226458 in cranial (A), dorsal (B), caudal (C), ventral (D), proximal (E), and distal (F), views. Abbreviations: c.b. crista bicipitalis; c.d.p., crista deltopectoralis; c.h., caput humeri; co.d., condylus dorsalis; e.v., epicondylus ventralis; p.f., processus flexorius; p.s.d., processus supracondylaris dorsalis; s.l.t., sulcus ligamentus transversus of caput humeri; t.d., tuberculum dorsale; v.m., ventral margin. Scale bar equals 1 cm.

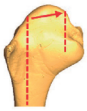
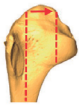
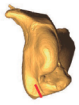
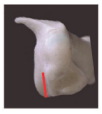
Code	States			
	A	B	C	D
HUM_CH Caput humeri in cranial view	Projected ventrally  *Patagioenas inornata* USNM 226458	Centrally located  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1		
HUM_VM Ventral margin of the shaft in cranial view	Rounded and large  *Patagioenas inornata* USNM 226458	Rounded and tight  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1	Angular  *Zenaida asiatica* PACEA-O-707	
HUM_TD Tuberculum dorsale in proximal view	Wide  *Patagioenas inornata* USNM 226458	Narrow  *Zenaida aurita* PACEA-O-710	Wide with depression  *Patagioenas leucocephala* PACEA-O-822	Narrow with depression  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1
HUM_SLT Ventral margin of sulcus ligamentus transversus of caput humeri in proximal view	Rounded  *Geotrygon chrysia* USNM 292518	Oblique  *Geotrygon montana* MNHN-ZO-AC-1993-116	Straight  *Zenaida aurita* PACEA-O-710	
HUM_PSD Processus supracondylaris dorsalis in cranial view	Near to the condylus dorsalis  *Geotrygon montana* MNHN-ZO-AC-1993-116	Far to the condylus dorsalis  *Patagioenas inornata* USNM 290977		
HUM_PF Processus flexorius in caudal view	Projected far from the shaft in ventral side  *Patagioenas inornata* USNM 226458	Projected far from the shaft in ventral side and aligned with epicondylus ventralis  *Zenaida aurita* PACEA-O-865	Projected little from the shaft and aligned with epicondylus ventralis  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1	Projected little from the shaft  *Geotrygon chrysia* USNM 292518

Figure 9. States of the osteological characters described for the humerus.

Table III. Humerus characters. Sample size (n) and percentage of states (A-D) and intermediate states (A/B, B/C, C/D, B/D) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
HUM_CH	**n**	6	8	2	4	2	4	1	7	14	5	1
	A	100	100	50		100			100	100		
	B			50	100		100	100			100	100
HUM_VM	**n**	6	8	2	4	3	5	1	7	14	4	1
	A	100	100	50	100	67	100					
	B			50		33		100				
	B/C											100
	C								100	100	100	
HUM_TD	**n**	5	8	2	3	2	5	1	7	14	5	1
	A	80	87	100		50						
	B				33					14	100	
	C	20	13									
	C/D				33	50						
	D						100	100		43		100
	B/D				33				100	43		
HUM_SLT	**n**	6	8	2	4	2	5	1	7	14	5	1
	A		13			50	100		71	21	20	100
	A/B		37						14			
	B	100	37	50	100	50		100		64		
	B/C		13	50					14	7	60	
	C									7	20	
HUM_PSD	**n**	6	8	2	4	2	5	1	7	14	5	1
	A	33	37		75	100	100					
	A/B	33	63	50	25				29			100
	B	33		50				100	71	100	100	
HUM_PF	**n**	6	8	2	3	2	5	1	6	14	5	1
	A	50	50	100					17	57		
	A/B	17	13									
	B	33	37							7		
	C				67	50	60	100	83	29		100
	C/D						20					
	D				33	50	20			7	100	

Processus supracondylaris dorsalis (HUM_PSD)

Referred material. *Geotrygon montana* MNHN–ZO–AC–1993–116 for state A and *Zenaida asiatica* PACEA–O–707 for state B (Table III).

The processus supracondylaris dorsalis (ectepicondylar prominence) has been previously used by Olson & Hilgartner (1982) to distinguish *G. chrysia* from *Z. aurita*. We equally observed this character in other species, indicating it to reliably distinguish the two genera *Geotrygon* and *Zenaida*. As in *G. chrysia*, the processus supracondylaris dorsalis is closer to the condylus dorsalis than in the two other *Geotrygon* species (state A, Fig. 9). In *Zenaida*, the processus supracondylaris dorsalis is positioned away from the condylus dorsalis (state B).

Processus flexorius (HUM_PF)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A, *Zenaida aurita* PACEA–O–865 for state B, *Geotrygon mystacea* PACEA–O–494 for state C, and *G. montana* PACEA–O–847 for state D (Table III).

The processus flexorius projects significantly from the shaft on the ventral side in *Patagioenas* (state A). In some cases, it is aligned with the epicondylus ventralis (state B) (Fig. 9). Conversely, in *Geotrygon* and *L. wellsi*, the processus flexorius projects only slightly from the shaft and is either aligned (state C) or unaligned (state D) with the epicondylus ventralis. This character is present in the four states in *Zenaida* specimens. Additionaly, one distal character is described in the appendix (Appendix K).

Humerus measurement

Our humerus measurements for *Z. asiatica* do not differ from those of Goldberg (1999) (Fig. 10). On the other hand, our *Z. macroura* and *C. passerina* specimens fall outside the variability documented for these two species in the southwestern United States in that they are, respectively, slightly larger and smaller than the specimens reported by Goldberg (1999).

Humerus length measurements are more evenly distributed compared to the two bones of the upper girdle (coracoideum and scapula). The different size classes are clearly evident in all three bones, although some differences in the distributions of taxa within each category are evident; humerus size in *P. squamosa* and *P. inornata* fall within the variability of large pigeons while *P. leucocephala* is within the small pigeon category. All *Geotrygon* specimens, the large *Zenaida* (*Z. asiatica* and *Z. aurita*) and *Leptotila* are classed as large doves. The small doves, *Z. macroua*, *Z. auriculata* and *C. passerina,* are easily distinguished by the very small size of their humerus. Unlike Steadman *et al.* (1984b) data, our measurements do not distinguish *G. mystacea*, *G. montana* and *Z. aurita.*

Ulna

Ulnae from 63 specimens have been considered (Appendix L). The complete ulnae of *Patagioenas* are longer and their shafts are more robust than the other 3 genera (Fig. 11; Appendix M). Distinguishing *Geotrygon* from *Zenaida* based on size is, however, difficult, even if the *Geotrygon* specimens are generally longer. Several morphological differences do exist between these two genera. We described 5 osteological criteria (4 on the proximal and 1 on the distal parts) for the 4 genera (Fig. 12) that distinguish different *Geotrygon* species, but which do not always separate them from certain forms of *Zenaida*. It is equally difficult to consistently distinguish different *Zenaida* species due to the variable expression of these characters (Table IV).

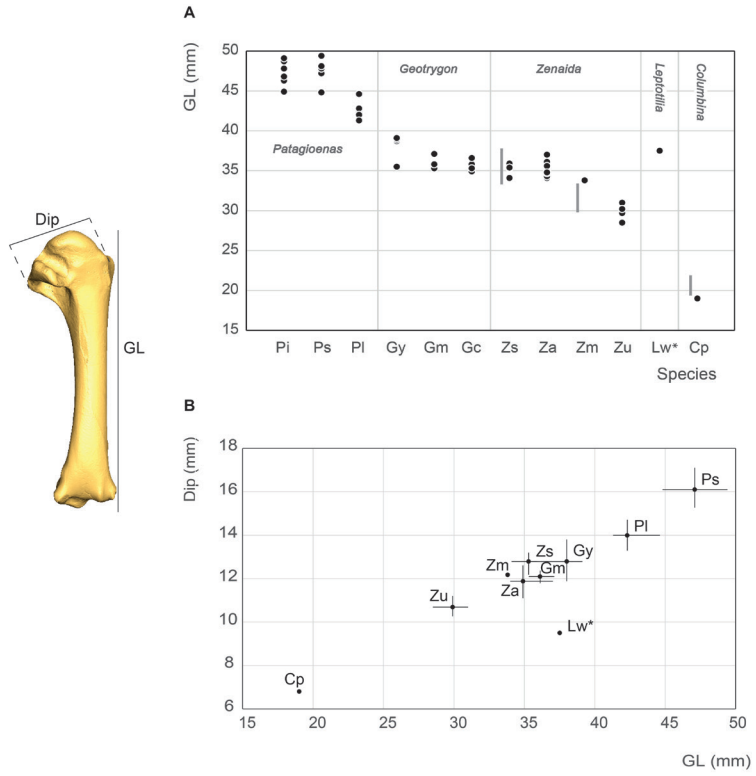


Figure 10. Humerus measurement in mm: GL, Greatest length (A), Dip, (Greatest) diagonal of the proximal end and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

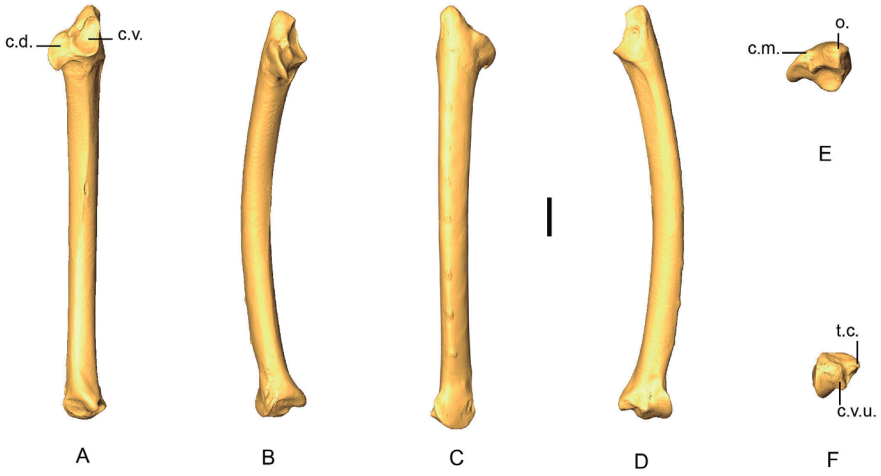


Figure 11. 3D – model of a right ulna of *Patagioenas inornata* USNM 226458 in cranial (A), dorsal (B), caudal (C), ventral (D), proximal (E), and distal (F), views. Abbreviations: c.m., caudal margin; c.d., cotyla dorsalis; c.v., cotyla ventralis; c.v.u., condylus ventralis ulnae; o., olecranon; t.c., tuberculum carpale. Scale bar equals 5 mm.

Code	States		
	A	**B**	**C**
ULN_CD1 Cotyla dorsalis in cranial view	Pointed  *Patagioenas inornata* USNM 226458	Rounded  *Geotrygon chrysia* USNM 292518	
ULN_CD2 Cotyla dorsalis in cranial view	Displaced distally compared to the cotyla ventralis  *Patagioenas inornata* USNM 226458	Not displaced distally compared to the cotyla ventralis  *Geotrygon montana* PACEA-O-847	
ULN_CV Cotyla ventralis in cranial view	Straight  *Patagioenas inornata* USNM 226458	Angular  *Geotrygon chrysia* USNM 292518	With depression  *Patagioenas squamosa* PACEA-O-442
ULN_CM Caudal margin in proximal view	Straight  *Patagioenas inornata* USNM 226458	Cotyla dorsalis projected caudally  *Geotrygon montana* MNHN-ZO-AC-1993-116	
ULN_TC Tuberculum carpale in distal view	Slightly projected cranially  *Patagioenas inornata* USNM 226458	Strongly projected cranially  *Geotrygon chrysia* USNM 292518	

Figure 12. States of the osteological characters described for the ulna.

Table IV. Ulna characters. Sample size (n) and percentage of states (A-D) and intermediate states (A/B, B/C) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
ULN_CD1	**n**	6	8	2	4	1	5	1	7	14	5	1
	A	50	75	50			100		100	93	100	
	A/B		25									
	B	50		50	100	100		100		7		100
ULN_CD2	**n**	6	8	2	4	1	5	1	7	14	5	1
	A	100	100	100		100	100	100	100	86	100	100
	B				100					14		
ULN_CV	**n**	6	8	2	4	1	5	1	7	14	5	1
	A	17	25	50				100		7		
	A/B			50								100
	B		37		100	100	100		100	71	60	
	B/C									7		
	C	83	37							14	40	
ULN_CE	**n**	6	8	2	4	1	5	1	7	14	5	1
	A	17	50	100	25	100		100		7	80	
	B	83	50		75		100		100	93	20	100
ULN_TC	**n**	6	7	2	4	1	5	1	7	14	5	1
	A	100	100	50				100	100	50	40	100
	A/B									36	20	
	B			50	100	100	100			14	40	

Cotyla dorsalis (ULN_CD1)

Referred material. Patagioenas leucocephala PACEA–O–493 for state A and *Geotrygon montana* PACEA–O–847 for state B (Table IV).

The distal part of the cotyla dorsalis, in cranial view, has a pointed margin on most columbid specimens in our sample (state A), (Fig. 12). Some specimens exhibit a rounded cotyla dorsalis (state B): all specimens of *G. montana*, some of the *P. squamosa* and *P. inornata* specimens, as well as *G. chrysia*, *L. wellsi* and *Z. macroura.*

Cotyla dorsalis (ULN_CD2)

Referred material. *Geotrygon mystacea* PACEA–O–494 for state A and *G. montana* PACEA–O–847 for state B (Table IV).

In cranial view, the cotyla dorsalis is displaced distally compared to the cotyla ventralis (state A) or positioned at the same level (state B); (Fig. 12). In *Geotrygon*, this character is distinctive of *G. montana.*

Cotyla ventralis (ULN_CV)

Referred material. *Patagioenas leucocephala* PACEA–O–821 for state A, *Zenaida aurita* PACEA–O–865 for state B, and *P. squamosa* PACEA–O–442 for state C (Table IV).

In cranial view, the ventral margin of the cotyla ventralis is relatively straight and vertical (state A) in the *L. wellsi* specimen as well as several other species (Fig. 12). This state is absent from *Geotrygon* and rare in the other genera. In *Geotrygon*, the ventral margin is angular, the distal part of the ventral margin is relatively straight, and the proximal portion near the olecranon is oblique (state B). In addition, the cotyla ventralis of *G. montana* is more curved than in *G. mystacea*.

The cotyla ventralis of most *P. squamosa* specimens projects ventrally and has a depression in the distal part (state C). Three *P. leucocephala* specimens and four *Zenaida* specimens also exhibit this character.

Caudal margin of proximal end (ULN_CM)

Referred material. Patagioenas squamosa PACEA–O–442 for state A and Zenaida aurita PACEA–O–865 for state B (Table IV).

In the proximal view, the caudal margin of the proximal portion of the ulna is relatively straight and the cotyla dorsalis is aligned with the olecranon (state A) or projects caudally (state B), (Fig. 12). This latter state is observed in most *Geotrygon* specimens except for *G. chrysia,* in *Zenaida* apart from *Z. auriculata* and in *P. squamosa.*

Problematic species: no characteristic states in *P. leucocephala.*

Tuberculum carpale (ULN_TC)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A and *Geotrygon montana* PACEA–O–492 for state B (Table IV).

In distal view, the tuberculum carpale is slightly projected cranially and the cranial margin between the condylus ventralis ulnae and the tuberculum carpale is relatively straight (state A), (Fig. 12). This state is observed in most of the *Patagioenas* and *Zenaida* specimens, and in *L. wellsi*. The tuberculum projects heavily cranially and the cranial margin is angular in *Geotrygon* (state B).

Ulna measurement

Our ulna and humerus measurements differ in the same way as those reported by Goldberg (1999), namely a smaller-winged *C. passerina* specimen and a larger-winged *Z. macroura* specimen (Fig. 13).

The same five groupings of taxa for the humerus sample are equally evident amongst the ulna although slightly less clearly expressed; the largest small pigeons (*P. leucocephala*) are indistinct from the smallest individuals of the large pigeons (*P. squamosa* and *P. inornata*). Moreover, *L. wellsi* is closer to the small rather than the large doves; however, it should be noted that is this based on a single specimen of *L. wellsi* in our sample

Like the humerus, *G. mystacea*, *G. Montana*, and *Z. aurita* cannot be distinguished based on ulna length, an observation inconsistent with the data reported by Steadman *et al.* (1984b).

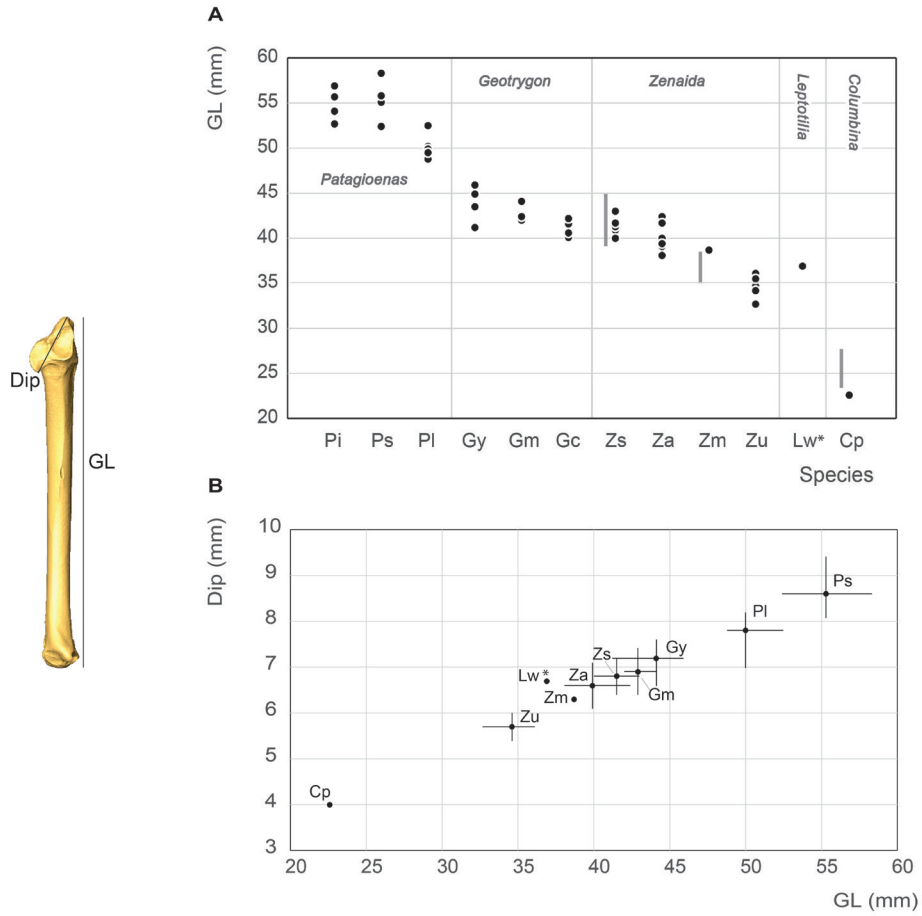


Figure 13. Ulna measurement in mm: GL, Greatest length (A), Dip, diagonal of the proximal end and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

Carpometacarpus

Our sample comprises 68 specimens (Appendix N). The complete carpometacarpi of *Patagioenas* are longer and more robust than those of other genera (Fig. 14; Appendix O). Morphological differences between the 4 genera are based on 11 osteological criteria, which also are used to identify species (Fig. 15; Table V). Seven characters describe the proximal part of the bone, 1 the shaft and 3 the distal portion.

Dorsal margin of the os metacarpale minus near trochlea carpalis (CMC_OMM)

Referred material. Geotrygon mystacea PACEA–O–494 for state A and *Patagioenas squamosa* PACEA–O–442 for state B (Table V).

In dorsal view, the margin of the os metacarpale minus in its proximal part, near the trochlea carpalis, is wide (state A) in *L. wellsi, G. chrysia, G. mystacea* and some *G. montana* (Fig. 15, State 1). It is narrower (state B or intermediate state A/B) in the other specimens or species studied.

Trochlea carpalis (CMC_TC1)

Referred material. *Patagioenas leucocephala* PACEA–O–970 for state A, *Geotrygon mystacea* PACEA–O–494 for state B, *G. montana* PACEA–O–492 for state C, and *Zenaida auriculata* PACEA–O–498 for state D (Table V).

On the proximal portion of carpometacarpus, the trochlea carpalis in dorsal view is well-developed upwards (projecting well beyond the processus extensorius) and rounded (state A) in *P. inornata* (Fig. 15, State 1). It is developed upwards (projecting slightly from the processus extensorius) and flattened (state B) in *G. mystacea* and part of the *P. leucocephala* specimens. Some specimens of Eastern Caribbean columbids have a weakly developed trochlea (reaching approximately the same level as the processus extensorius) that is either rounded, as in some *Patagioenas*, *Geotrygon* and *Zenaida* species (state C), or flattened, as in *Leptotila wellsi* (state D).

Problematic species: no characteristic states in *Z. aurita.*

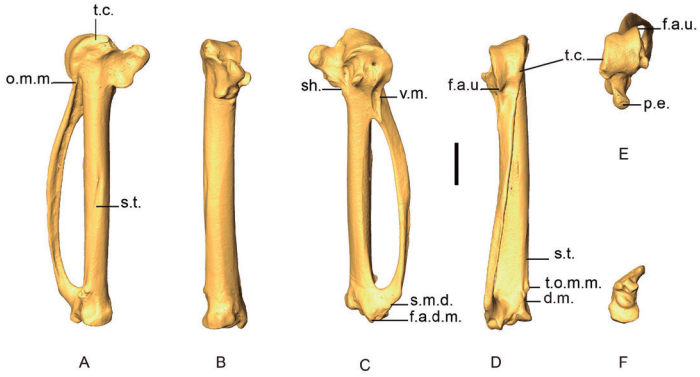


Figure 14. 3D – model of a right carpometacarpus of *Patagioenas inornata* USNM 226458 in dorsal (A), caudal (B), ventral (C), cranial (D), proximal (E), and distal (F), views. Abbreviations: d.m., dorsal margin; f.a.d.m., facies articularis digitalis major; f.a.u, facies articularis ulnocarpalis; o.m.m., os metacarpale minus; p.e., processus extensorius; sh., shaft; s.m.d., symphysis metacarpalis distalis; s.t., sulcus tendinous; t.c, trochlea carpalis; t.o.m.m., tuberosity of os metacarpale majus; v.m., ventral margin. Scale bar equals 5 mm.

Distal dorsal margin of trochlea carpalis (CMC_TC2)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A, *Zenaida a. asiatica* PACEA–O–707 for state B and *Geotrygon montana* PACEA–O–492 (Table V).

In caudal view, there is a distinct eminence on the distal dorsal margin of the trochlea carpalis (state A) in all or most of the observed specimens of *P. inornata*, *G. chrysia* and *G. mystacea* (Fig. 15, State 1). This eminence is less prominent (state B) in *Z. asiatica*, *Z. aurita* and *Z. macroura.* The dorsal margin does not present an eminence (state C) in *G. montana* and *L. wellsi.*

Problematic species: depending on the individual, the 3 states are observed in *P. leucocephala*, and this eminence is relatively indistinct or absent in *Z. auriculata*. *P. squamosa* presents a distinct eminence or no eminence at all.

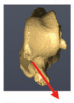
Code	States			
	A	B	C	D
CMC_OMM Dorsal margin of os metacarpale minus near trochlea carpalis in dorsal view	Wide  *Geotrygon montana* MNHN-ZO-AC-1993-116	Narrow  *Zenaida asiatica* PACEA-O-707		
CMC_TC1 Trochlea carpalis in dorsal view	Well-developed upwards and rounded  *Patagioenas inornata* USNM 226458	Developed upwards and flattened  *Geotrygon mystacea* PACEA-O-494	Poorly developed and rounded  *Geotrygon montana* MNHN-ZO-AC-1993-116	Poorly developed and flattened  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1
CMC_TC2 Distal dorsal margin of trochlea carpalis in caudal view	Distinct eminence  *Patagioenas inornata* USNM 226458	Eminence  *Zenaida asiatica* PACEA-O-707	Eminence absent  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1	
CMC_FAU1 Ventral margin of facies articularis ulnocarpalis in caudal view	Aligned with ventral margin of os metacarpale minus  *Zenaida asiatica* PACEA-O-707	Oblique  *Geotrygon montana* MNHN-ZO-AC-1993-116		
CMC_FAU2 Ventral margin of facies articularis ulnocarpalis in proximal view	Curved dorsally  *Patagioenas inornata* USNM 226458	Curved dorsally with depression  *Patagioenas squamosa* PACEA-O-487	Straight  *Geotrygon chrysia* USNM 292518	
CMC_PE Processus extensorius in proximal view	Large and projected ventrally  *Zenaida asiatica* PACEA-O-707	Large and projected centrally  *Patagioenas squamosa* PACEA-O-487	Small and projected ventrally  *Zenaida aurita* PACEA-O-449	Small and projected centrally  *Geotrygon montana* MNHN-ZO-AC-1993-116

Figure 15, State 1. States of the osteological characters described for the carpometacarpus.

Code	States			
	A	B	C	D
CMC_VM Ventral margin of os metacarpale minus in ventral view	Broad and straight  *Patagioenas inornata* USNM 226458	Broad and curved  *Zenaida asiatica* PACEA-O-707	Narrow and curved  *Zenaida aurita* PACEA-O-987	Narrow and straight  *Geotrygon montana* MNHN-ZO-AC-1993-116
CMC_SH Shaft of the major metacarpal towards the processus alularis in ventral view	Straighter and slopes up proximally  *Geotrygon chrysia* USNM 292518	Very slightly bowed and does not slope up as markedly  *Zenaida asiatica* PACEA-O-707		
CMC_SMD Symphysis metacarpalis distalis in ventral view	Straight  *Patagioenas inornata* USNM 226458	Straight with eminence  *Patagioenas squamosa* PACEA-O-442	Curved with eminence  *Zenaida asiatica* PACEA-O-707	
CMC_FADM Facies articularis digitalis minor in ventral view	More projected distally than the facies articularis digitalis major  *Patagioenas inornata* USNM 226458	Less projected distally than the facies articularis digitalis major  *Zenaida asiatica* PACEA-O-707	Aligned with the facies articularis digitalis major  *Geotrygon montana* MNHN-ZO-AC-1993-116	
CMC_DM Dorsal margin between distal part of sulcus tendineus and tuberosity of os metacarpale majus in caudal view	Large and concave  *Patagioenas inornata* USNM 226458	Narrow and concave  *Zenaida asiatica* PACEA-O-707	Straight  *Geotrygon montana* MNHN-ZO-AC-1993-116	

Figure 15, State 2. States of the osteological characters described for the carpometacarpus.

Ventral margin of the facies articularis ulnocarpalis (CMC_FAU1)

Referred material. *Zenaida aurita* PACEA–O–865 for state A and *Geotrygon montana* PACEA–O–492 for state B (Table V).

In caudal view, the ventral margin of the facies articularis ulnocarpalis and the ventral margin of the proximal part of the os metacarpale minus are aligned in *Zenaida* (state A) and *P. inornata* (Fig. 15, State 1). The ventral margin of the facies articularis ulnocarpalis is oblique compared to the ventral margin of the os metacarpale minus (state B) in *Geotrygon, L. wellsi* and *P. squamosa*.

Ventral margin of the facies articularis ulnocarpalis (CMC_FAU2)

Referred material. Patagioenas leucocephala PACEA–O–493 for state A, *P. squamosa* PACEA–O–487 for state B, *Geotrygon montana* PACEA–O–492 for state C (Table V).

In proximal view, the ventral margin of the facies articularis ulnocarpalis curves dorsally (state A) in most *Patagioenas* specimens (Fig. 15, State 1), *L. wellsi*, *Z. auriculata* and *Z. macroura.* In rare cases, a depression is present in state B, as observed in the two *P. squamosa* specimens.

A straight ventral margin of the facies articularis ulnocarpalis (state C) is characteristic of *G. montana* and the carpometacarpi of *G. mystacea.*

Problematic species: no characteristic states are evident in *G. chrysia, Z. asiatica* and *Z. aurita.*

Processus extensorius (CMC_PE)

Referred material. Patagioenas squamosa PACEA–O–442 for state A, *P. leucocephala* PACEA–O–970 for state B, *Zenaida aurita* PACEA–O–449 for state C, and *Z. asiatica* PACEA–O–1013 for state D (Table V).

In proximal view, the processus extensorius is large and its caudal extremity projects ventrally (state A) in most of the *P. squamosa* specimens (Fig. 15, State 1). It is large and oriented centrally (state B) in *P. leucocephala* and *Z. macroura*.

A small processus extensorius oriented ventrally (state C) or centrally (state D) is typical of *Geotrygon*, except for one of the two *G. chrysia* individuals.

Problematic species: *Z. aurita* and, to a lesser extent, Z. *asiatica* and *Z. auriculata*, present intermediate states or uncharacteristic features.

Ventral margin of the os metacarpale minus (CMC_VM)

Referred material. *Patagioenas squamosa* PACEA–O–443 for state A, *Zenaida asiatica* PACEA–O–707 for state B, *Geotrygon montana* PACEA–O–492 for state C, and *Z. aurita* PACEA–O–987 for state D (Table V).

In ventral view, the proximal end of the os metacarpale minus has a shallow groove that connects it to the facies articularis ulnocarpalis; the ventral margin of this portion is broad and straight (state A) in *P. leucocephala* and *P. inornata* (Fig. 15, State 2).

The ventral margin is curved in *Zenaida,* broad (state B) in *Z. asiatica* and *Z. macroura*, and narrow (state C) in *Z. aurita, Z. auriculata. L. wellsi* also has a narrow and curve ventral margin.

The carpometacarpi of *G. montana* and *G. mystacea* have a narrow, straight ventral margin (state D).

Problematic species: broad ventral margin in *P. squamosa* and straight ventral margin in *G. chrysia.*

Shaft of the major metacarpal towards the processus alularis (CMC_SH)

Referred material. Geotrygon chrysia USNM 292518 for state A and *Zenaida aurita* PACEA–O–865 for state B (Table V).

In ventral view, the character described by Olson and Hilgartner (1982) as distinguishing the two species *G. chrysia* and *Z. aurita* can also be used to identify other species. The shaft is straighter and slopes upward proximally in *G. chrysia* (state A, Fig. 15, State 2), *G. mystacea*, and *P. inornata*. The shaft is very slightly bowed and does not slope up as markedly in *Z. aurita* (state B) and in all other studied species, including *G. montana*.

Symphysis metacarpalis distalis (CMC_SMD)

Referred material. *Geotrygon montana* PACEA–O–492 for state A, *Patagioenas squamosa* PACEA–O–442 for state B and *Zenaida asiatica* PACEA–O–707 for state C (Table V).

In ventral view, the symphysis metacarpalis distalis is straight (states A-B) in almost all specimens (Fig. 15, State 2; Table V). One feature distinguishing the two states is the presence (state B) or absence of an eminence (state A) on the caudal margin of the os metacarpale minus.

Only a few specimens of *P. squamosa*, *Z. asiatica* and *Z. aurita* have a curved symphysis metacarpalis distalis with an eminence (state C).

Problematic species: no characteristic states in *P. leucocephala*.

Facies articularis digitalis minor (CMC_FADM)

Referred material. *Patagioenas inornata* USNM 226458 for state A, *P. squamosa* PACEA–O–442 for state B, and *Geotrygon mystacea* PACEA–O–858 for state C (Table V).

In ventral view, the facies articularis digiti minor is more projected distally than the facies articularis digitalis major (state A) in *P. inornata* (Fig. 15, State 2). These two surfaces are closer (state B) in *P. squamosa, P. leucocephala, L. wellsi* and almost all specimens of *Zenaida*. The two surfaces are aligned (state C) in a few *Geotrygon* and *Zenaida* specimens.

Problematic species: this character is present in the same proportions as the two states in *G. montana* and *G. chrysia.*

Dorsal margin between the distal part of the sulcus tendineus and tuberosity of the os metacarpale majus (CMC_DM)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A, *Zenaida asiatica* PACEA–O–707 for state B, and *G. montana* PACEA–O–492 for state C (Table V).

In caudal view, the dorsal margin between the distal part of the sulcus tendineus and the tuberosity of the os metacarpale majus is large and concave (state A) in *Patagioenas* genus (Fig. 15, State 2) and *Z. aurita* (Table V).

It is narrow and concave (state B) in *G. chrysia, L. wellsi*, *Z. asiatica*, *Z. auriculata* and *Z. macroura.* It is straight (state C) in most of the *G. montana* specimens.

Problematic species: *G. mystacea* present two states.

Carpometacarpus measurement

Carpometacarpus measurements were similar to those provided by Goldberg (1999). In our study, *G. mystacea* appears smaller rather than similar in size to *P. leucocephala*, as reported by Steadman *et al.* (1984b), (Fig. 16). The 5 size ranges of pectoral and wing bones described above are equally evident in the carpometacarpus sample. Several *P. leucocephala* individuals are similar in size to the other two large pigeons, and *Lepotilia* falls within the

range of small doves. The range of carpometacarpus measurements differs from that of the humerus but is in good agreement with those for the ulna. The length distribution of this element overlaps significantly with *G. mystacea* and *Z. asiatica, G. chrysia*, *G. montana* and, particularly, *Z. aurita*. However, the length of this bone compared to other elements of the wing appears more discriminating within the group of large doves, in that it distinguishes large specimens of *G. mystacea* and *Z. aurita* from *G. montana*.

Table V. Carpometacarpus characters. Sample size (n) and percentage of states (A-D) and intermediate states (A/B, A/C, B/C, C/D, B/D) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
CMC_OMM	**n**	6	8	2	4	2	5	1	7	14	5	1
	A				25	100	100	100	14			
	A/B			50						14		100
	B	100	100	50	75				86	86	100	
CMC_TC1	**n**	6	8	2	4	2	5	1	7	14	5	1
	A		12	100								
	A/B									29		
	B	33	63				100		29	29		
	B/C									29		
	C	67	25		100	100			71		80	100
	C/D									7		
	D							100		7	20	
CMC_TC2	**n**	5	8	2	4	2	5	1	7	14	5	1
	A	60	50	100		100	80		43	21		
	B		37		25				57	79	40	100
	B/C										40	
	C	40	13		75		20	100			20	
CMC_FAU1	**n**	6	8	2	4	2	5	1	7	14	5	1
	A		25	100					100	100	100	100
	A/B						20					
	B	100	75		100	100	80	100				
CMC_FAU2	**n**	6	8	2	4	2	5	1	7	14	5	1
	A	67	100	100		50		100	29	14	100	100
	A/B									29		
	B	33							43	29		
	C				100	50	80		29	21		
	A/C						20			7		

Table V. Continuation

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
CMC_PE	**n**	6	8	2	4	2	5	1	7	14	4	1
	A	67		50					29	21	25	
	A/B									21		
	B	33	100						29	7		100
	B/C									7		
	C						40			14		
	C/D				75				29	21	25	
	D			50	15	50	60	100	14	7	50	
	B/D					50						
CMC_VM	**n**	6	8	2	4	2	5	1	7	14	5	1
	A	50	75	100		50						
	B	50	12						72		20	100
	C						40	100	29	71	80	
	C/D									29		
	D		12		100	50	60					
CMC_SH	**n**	6	8	2	4	2	4	1	7	13	5	1
	A			100		100	100			23		
	B	100	100		100			100	100	77	100	100
CMC_SMD	**n**	6	8	2	4	2	5	1	7	14	5	1
	A			50	100	50	60					
	B	83	37	50		50	40	100	86	93	100	100
	B/C		63									
	C	17							14	7		
CMC_FADM	**n**	6	8	2	4	2	5	1	7	13	5	1
	A			100		50						
	B	100	100		50		40	100	100	93	60	100
	B/C					50						
	C				50		60			7	40	
CMC_DM	**n**	6	8	2	4	2	5	1	7	14	5	1
	A	100	88	100						100	20	
	B		12			100	40	100	86		80	100
	B/C				25				14			
	C				75		60					

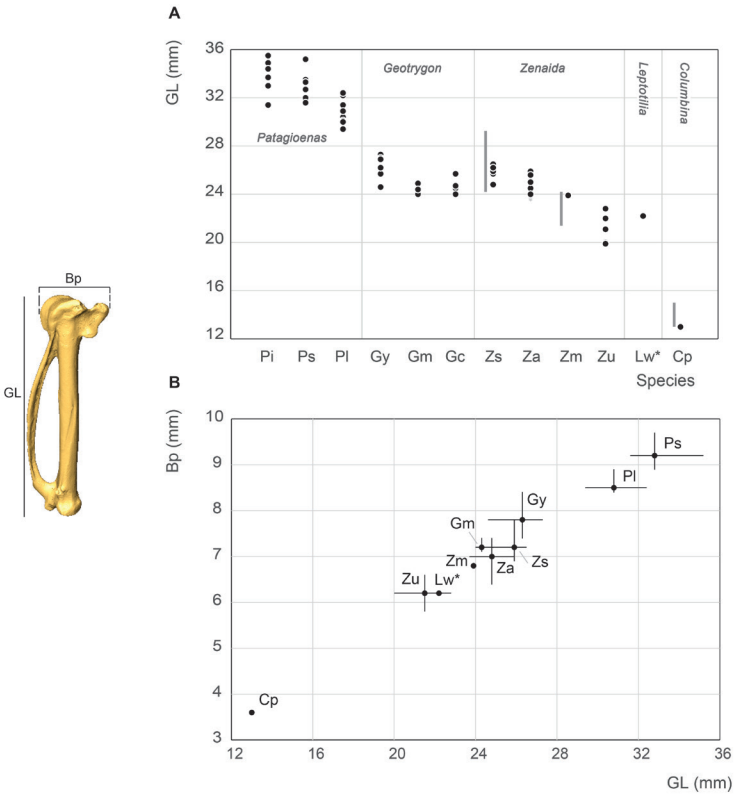


Figure 16. Carpometacarpus measurement in mm: GL, Greatest length (A), Bp, breadth of the proximal end and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

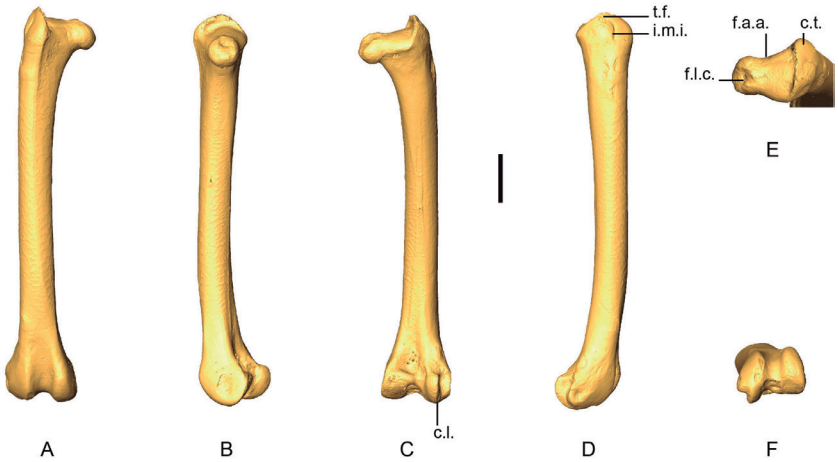


Figure 17. 3D – model of a right femur of *Patagioenas inornata* USNM 226458 in cranial (A), medial (B), caudal (C), lateral (D), proximal (E), and distal (F), views. Abbreviations: c.l., condylus lateralis; c.t., crista trochanteris; f.a.a., fascies articularis antitrochanterica; f.l.c., fovea ligamentum capitis; i.m.i., impressio musculi iliotrochantericus; t.f., trochanter femoris. Scale bar equals 5 mm.

Femur

Femora from 73 specimens were examined (Appendix P). The overall morphology of this bone reflects the terrestrial mode of life of *Geotrygon*. *Zeinada aurita* among *Zeinada* species has a relatively longer femur. Three osteological criteria of the femur and the features involved in character descriptions are illustrated in figure 17. Two criteria describe the proximal part of the bone and one the distal part (Fig. 18; Table VI).

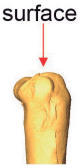
Code	States		
	A	B	C
FEM_FAA Facies articularis antitrochanterica in proximal view	Straight  *Geotrygon montana* MNHN-ZO-AC-1993-116	Rounded near fovea ligamentum capitis  *Patagioenas inornata* USNM 226458	Concave  *Zenaida aurita* PACEA-O-865
FEM_IMI Position of impressio musculi iliotrochantericus in lateral view	In the middle of the lateral surface of trochanter femoris  *Geotrygon montana* MNHN-ZO-AC-1993-116	Cranially located  *Zenaida aurita* PACEA-O-865	
FEM_CL Condylus lateralis in caudal view	Pointed  *Geotrygon montana* MNHN-ZO-AC-1993-116	Rounded  *Zenaida asiatica* PACEA-O-707	

Figure 18. States of the osteological characters described for the femur.

Table VI. Femur characters. Sample size (n) and percentage of states (A-D) and intermediate states (A/B, B/C) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
FEM_FAA	**n**	6	8	2	4	2	5	–	7	13	5	1
	A	17	87		100		80			54	50	
	A/B								14			
	B	50	13	100		100	20		71		25	100
	B/C	33										
	C								14	38	25	
FEM_IMI	**n**	6	8	2	4	2	5	1	7	13	5	1
	A	100	100		100	100	80	100	100	8		
	A/B			50			20					
	B			50						92	100	100
FEM_CL	**n**	5	6	2	4	2	5	1	7	14	5	1
	A	60	33	50	75	100	100		14	57	60	
	A/B		50		25				14	29	20	
	B	40	17	50				100	71	7	20	100

Facies articularis antitrochanterica (FEM_FAA)

Referred material. *Patagioenas leucocephala* PACEA–O–493 for state A, *P. squamosa* PACEA–O–442 for state B, and *Zenaida aurita* PACEA–O–865 for state C (Table VI).

In proximal view, the cranial margin of the facies articularis antitrochanterica is straight (state A) or nearly straight (state B), (Fig. 18). The portion of the facies closest to the fovea ligamentum capitis distinguishes the two states: it is angular in state A as observed in *G. montana* and *G. mystacea* and more rounded in state B in *G. chrysia*. The concave facies articularis antitrochanterica between the crista trochanteris and fovea ligamentum capitis (state C) is a character found only in a very small sample of *Zenaida* femurs.

Problematic species: several states are observed in *P. squamosa, Z. aurita* and *Z. auriculata*. This character is also not observable in the pathologically–altered femur of *L. wellsi*.

Position of the impressio musculi iliotrochantericus (FEM_IMI)

Referred material. *Patagioenas squamosa* PACEA–O–442 for state A and *Zenaida aurita* PACEA–O–865 for state B.

The impressio musculi iliotrochantericus is most frequently located at the middle of the lateral surface of the trochanter femoris (state A) in *Geotrygon*, *Leptotila* and *Patagioenas*, except for *P. inornata* (Fig. 18; Table VI). Apart from *Z. asiatica*, in *Zenaida* this impressio is more cranially oriented (state B) compared with state A.

Condylus lateralis (FEM_CL)

Referred material. *Geotrygon montana* PACEA–O–847 for state A and *Zenaida asiatica* PACEA–O–707 for state B (Table VI).

In caudal view, two states are observable with the condylus lateralis (Fig. 18): pointed (state A) for *Geotrygon* or rounded (state B) for *Leptotila*.

The distribution of character states does not distinguish *Patagioenas* nor *Zenaida* species.

Femur measurement

Our femur measurements for *Z. asiatica* and *C. passerina* do not differ from those reported by Goldberg (1999), (Fig. 19), although the *Z. macroura* specimen in our sample is larger. The *G. montana* femur is much longer than those attributed to *Z. aurita*, a result inconsistent with Steadman *et al.* (1984b) data for the same species.

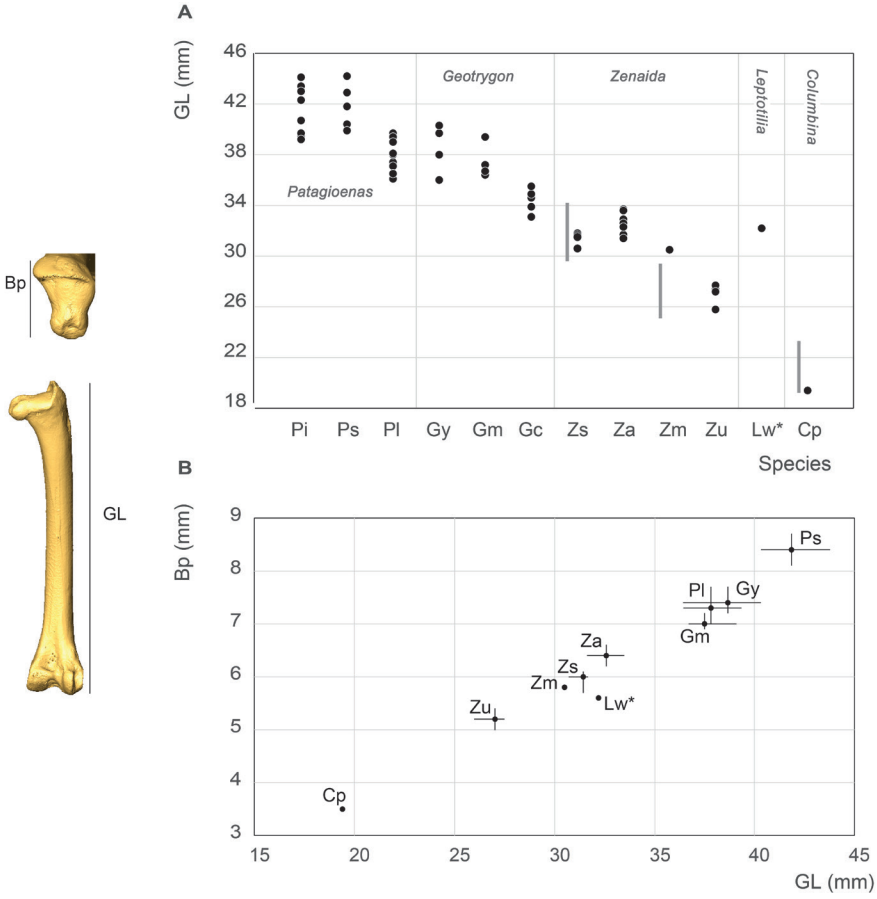


Figure 19. Femur measurement in mm: GL, Greatest length (A), Bp, breadth of the proximal end and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

P. squamosa and *P. inornata* fall within the variability of large pigeons. The substantial overlap in femur size between *P. leucocephala, G. mystacea,* and *G. montana* makes distinguishing these three taxa based solely on metrtical data difficult, especially given their anatomical similarity. *Leptotilia* overlaps with the large *Zenaida* species (*Z. asiatica,* Appendix Q, and *Z. aurita*) and *G. chrysia* with large doves, as observed for the humerus. With that said, the proximal end of *Leptotila* femur is slenderer than in *Zenaida*. Our femur measurements group *Z. macroua* and *Z. auriculata* in the category of small doves.

Tibiotarsus

Sixty-four tibiotarsi were examined (Appendix R). Complete *Patagioenas* and *Geotrygon* tibiotarsi, although difficult to separate based only on maximal length, can be distinguished based on shaft robusticity (Fig. 20; Appendix S). The terrestrial behavior of *Geotrygon* is reflected in a relatively long tibiotarsus (Baptista *et al.,* 1997) that potentially overlaps with some *Patageonias* species.

Morphological differences between genera and species are explored based on four osteological criteria, one found in the proximal portion and three in the distal portion of the tibiotarsus (Fig. 21; Table VII).

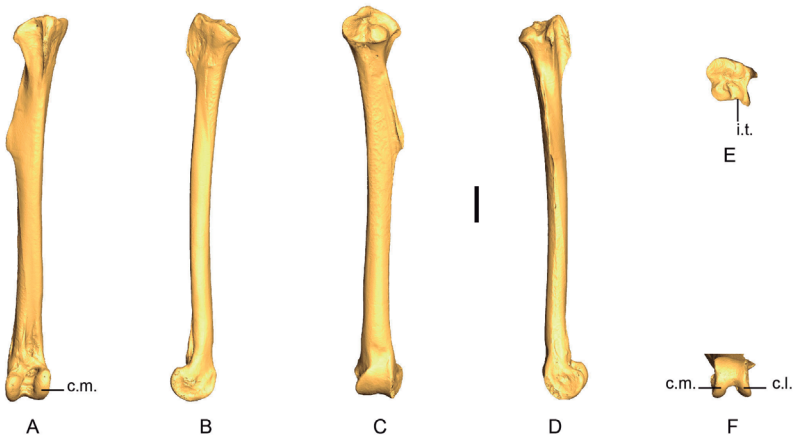


Figure 20. 3D – model of a right tibiotarsus of *Patagioenas inornata* USNM 290977 in cranial (A), medial (B), caudal (C), lateral (D), proximal (E) and distal (F) views. Abbreviations: c.l., condylus lateralis; c.m., condylus medialis; i.t., incisura tibialis. Scale bar equals 5 mm.

Incisura tibialis (TIB_IT)

Referred material. *Zenaida aurita* PACEA–O–865 for state A, *Patagioenas squamosa* PACEA–O–442 for state B (Table VII).

In proximal view, the lateral margin of the incisura tibialis is curved (state A), (Fig. 21) in all species except for *P. squamosal,* which has a straight incisura tibialis in most specimens (state B).

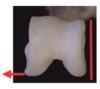
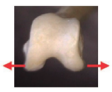
Code	States			
	A	B	C	D
TIB_IT Incisura tibialis in proximal view	Curved  *Geotrygon montana* MNHN-ZO-AC-1993-116	Straight  *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1		
TIB_C1 Condyles in distal view	Nearly parallel condyles  *Patagioenas inornata* USNM 226458	Condylus lateralis projected laterally  *Geotrygon montana* MNHN-ZO-AC-1993-116	Condylus medialis projected medially  *Patagioenas squamosa* PACEA-O-705	Condylus lateralis projected laterally and condylus medialis projected medially  *Zenaida aurita* PACEA-O-865
TIB_C2 Condyles in distal view	Condyles equally developed cranially  *Patagioenas inornata* USNM 226458	Condylus lateralis elongated cranially  *Zenaida asiatica* PACEA-O-707	Condylus medialis elongated cranially  *Geotrygon montana* MNHN-ZO-AC-1993-116	Narrow with saddle
TIB_CM Condylus medialis in cranial view	Medial margin oriented in accordance with the bone axis  *Zenaida asiatica* PACEA-O-707	Obliquely oriented compared to the bone axis  *Zenaida aurita* PACEA-O-710		

Figure 21. States of the osteological characters described for the tibiotarsus.

Condyles (TIB_C1)

Referred material. *Patagioenas inornata* USNM 226458 for state A, *Geotrygon mystacea* PACEA–O–1085 for state B, *P. squamosa* PACEA–O–705 for state C, and *Zenaida aurita* PACEA–O–865 for state D (Table VII).

The relative orientation of the condylus lateralis and condylus medialis in distal view distinguish four states; the condyles are nearly parallel (state A), a character observed uniquely in a few *Patagioenas* specimens, or are non-parallel (states B, C, D), (Fig. 21). In these latter cases, the cranial extremity of the condylus lateralis projects laterally (state B), the cranial extremity of the condylus medialis is oriented medially (state C) or, in most cases (primarily in *Z. asiatica*), both condyles project in the opposite direction (state D).

Condyles (TIB_C2)

Referred material. Zenaida aurita PACEA–O–865 for state A, Z. *asiatica* PACEA–O–1004 for state B, and *Geotrygon mystacea* PACEA–O–494 for state C (Table VII).

In distal view, the cranial extremities of the condyles are equally developed cranially (state A, Fig. 21), especially in *P. leucocephala.* In specimens when the condyles are not equally developed, the condylus lateralis extends more cranially than the condylus medialis (state B), as is the case with the tibiotarsus of *Z. asiatica* and *Z. auriculata*, or conversely (state C), as frequently observed in *Geotrygon* and the single specimen of *L. wellsi.*

Table VII. Tibiotarsus characters. Sample size (n) and percentage of states (A-D) and intermediate states (A/B, B/D) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
TIB_IT	**n**	5	7	2	4	1	4	1	7	14	4	1
	A	20	100	100	100	100	100	100	100	100	100	100
	B	80										
TIB_C1	**n**	6	8	1	4	2	5	1	6	14	5	1
	A	50	12	100								
	B				25	100	20	100		36	80	100
	C	17										
	D	33	88		75		60		100	43	20	
	B/D						20			21		
TIB_C2	**n**	6	8	2	4	2	5	1	6	14	5	1
	A	50	62	50	25		20		33	50	40	100
	B								67		60	
	C	50	38	50	75	100	80	100		50		
TIB_CM	**n**	6	8	1	4	2	5	1	6	13	5	1
	A	17	13		25	100			86	23		
	A/B		13	100	25			100				
	B	83	75		50		100		14	77	100	100

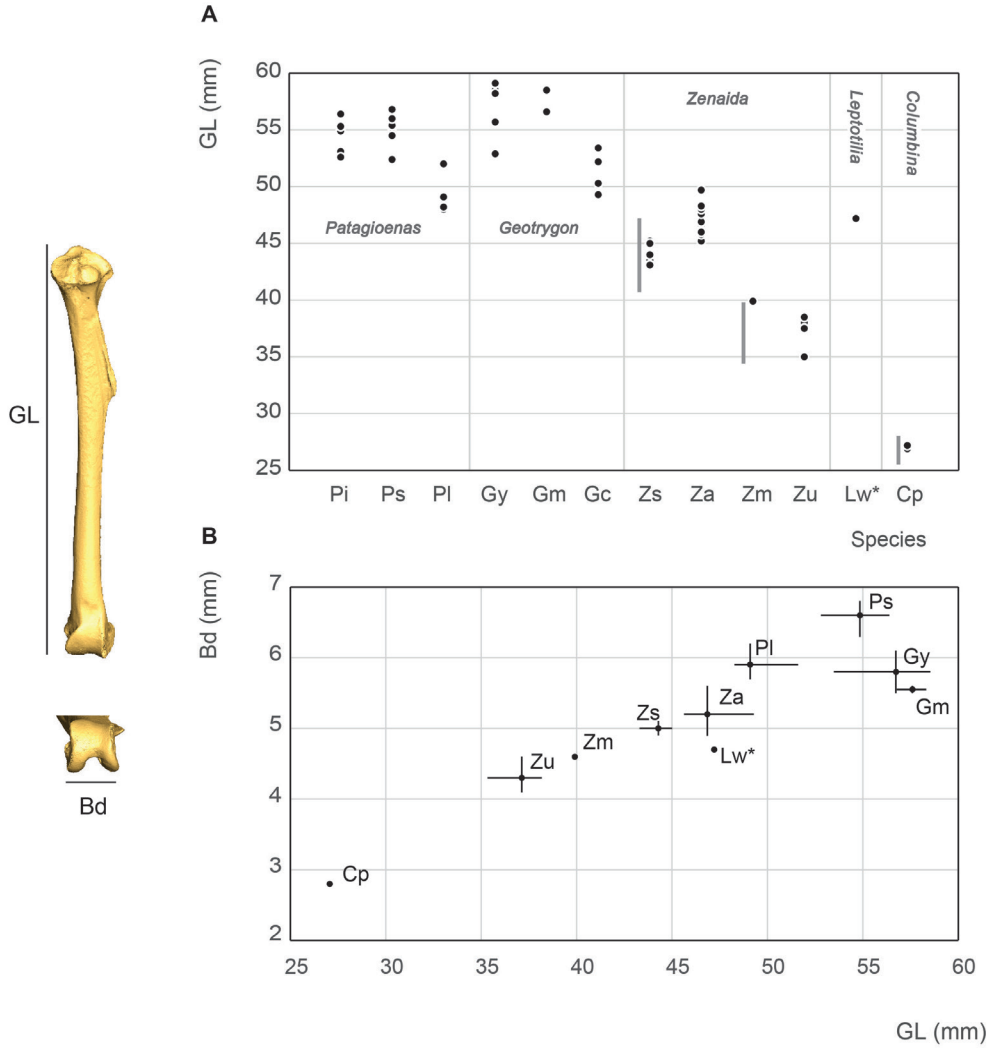


Figure 22. Tibiotarsus measurement in mm: GL, Greatest length (A), Bd, breadth of the distal end and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

Condylus medialis (TIB_CM)

Referred material. *Zenaida asiatica* PACEA–O–707 for state A and *Z. aurita* PACEA–O–865 for state B (Table VII).

In cranial view, the medial margin of the condylus medialis is oriented along the axis of the bone (state A) in almost all *Z. asiatica* specimens. This character distinguishes this species from the other 3 congeners, which have a tibiotarsus with an oblique condyle (state B), (Fig. 21). This character distinguishes *G. mystacea* and *G. chrysia.*

Problematic species: no characteristic states in *G. montana.*

Tibiotarsus measurement

The *Zenaida macroura* tibiotarsus measurements are comparable with the largest values reported by Goldberg (1999) while *Z. asiatica* and *C. passerina* fall within the variability of North American columbid species (Fig. 22). *G. mystacea* has a longer tibiotarsus than *P. leucocephala* (Steadman *et al*., 1984b), which in turn, is longer than *G. montana*. Our measurements depict a slighty different pattern; *G. montana* tibiotarsus length falls within the variability of *G. mystacea* and both species have a longer tibiotarsus than *P. leucocephala.* It is also worth noting that the order of the size classes of taxa based on pectoral and wing bones is not the same, primarily due to the greater relative length of *Geotrygon* tibiotarsus. This leads to the two Lesser Antilles quail-doves (*G. mystacea* and *G. montana*) appearing comparable in size to large pigeons, and *G. chrysia* being the same size as the small pigeon *P. leucocephala*. However, this pattern reflects *Geotrygon's* distinctive slender form, with the GL/Bp ratio setting it apart from other West Indian columbids.

Tarsometatarsus

Tarsometatarsi from 67 specimens have been considered (Appendix T). The comparably longer leg bones of *Geotrygon* linked to their more terrestrial behavior is even more pronounced with the tarsometatarsus, which had led some to consider the relative gracility of this bone (long and slender) as particular to *Geotrygon* in comparison to *Patagioenas* and *Zenaida* (Steadman *et al.,* 1984b; Olson & Hilgartner, 1982), (Appendix U). Three osteological criteria (2 proximal and 1 distal) and the anatomical features used in the description are illustrated in Figure 23. Among these, the distal character distinguishes *Zenaida* species (Fig. 24; Table VIII).

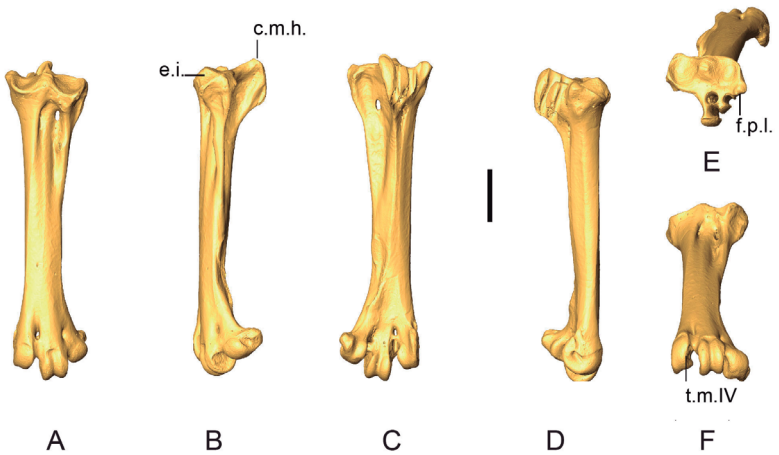


Figure 23. 3D – model of a right tarsometatarsus of *Patagioenas inornata* USNM 226458 in dorsal (A), medial (B), plantar (C), lateral (D), proximal (E) and distal (F) views. Abbreviations: c.m.h., crista medialis hypotarsi; e.i., eminentia intercotylaris. f.p.l., fossa parahypotarsalis lateralis; t.m.IV., trochlea metatarsi IV. Scale bar equals 5 mm.

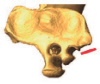
Code	States		
	A	**B**	**C**
TMT_CMH Crista medialis hypotarsi in medial view	More projected proximally than eminentia intercotylaris  *Patagioenas inornata* USNM 226458	At the same level than eminentia intercotylaris  *Geotrygon montana* MNHN-ZO-AC-1993-116	Less projected than eminentia intercotylaris  *Zenaida aurita* PACEA-O-448
TMT_FPL Fossa parahypotarsalis lateralis in proximal view	Present  *Geotrygon montana* MNHN-ZO-AC-1993-116	Absent  *Patagioenas inornata* USNM 226458	
TMT_TMIV Trochlea metatarsi IV in distal view	With notch  *Zenaida asiatica* PACEA-O-707	Straight  *Zenaida aurita* PACEA-O-865	

Figure 24. States of the osteological characters described for the tarsometatarsus.

Table VIII. Tarsometatarsus characters. Sample size (n) and percentage of states (A-D) and intermediate states (A/B, B/C) for each taxon

		P. squamosa	*P. leucocephala*	*P. inornata*	*G. montana*	*G. chrysia*	*G. mystacea*	*L. wellsi*	*Z. asiatica*	*Z. aurita*	*Z. auriculata*	*Z. macroura*
TMT_CMH	**n**	6	8	2	4	1	5	1	7	14	5	1
	A	83	75	100		100	20			14	40	
	A/B						20					
	B	17	25		75		40	100	72	36	60	100
	B/C								14	7		
	C				25		20		14	43		
TMT_FPL	**n**	7	9	1	4	1	5	1	7	14	4	1
	A	43	78		100	100	100	100	57	86	50	100
	B	57	22	100					43	14	50	
TMT_TMIV	**n**	6	8	2	4	1	5	1	7	14	5	1
	A								100		20	
	A/B	17										
	B	83	100	100	100	100	100	100		100	80	100

Crista medialis hypotarsi (TMT_CMH)

Referred material. Patagioenas squamosa PACEA–O–442 for state A, *Geotrygon montana* PACEA–O–492 for state B, and *Zenaida aurita* PACEA–O–448 for state C (Table VIII).

In medial view, the summit of the crista medialis hypotarsi projects more proximally than the eminentia intercotylaris (state A) in *Patagioenas* (Fig. 24). Among representatives of *Geotrygon*, the single *G. chrysia* specimen exhibits state A while in *G. montana* the summit of the crista medialis hypotarsi and the eminentia intercotylaris are at the same level (state B). This latter state is also observed in *L. wellsi, Z. asiatica* and *Z. macroura.* In some specimens, the crista medialis hypotarsi projects less proximally than the eminentia intercotylaris (state C).

All three states as well as intermediate states are found in *G. mystacea* and *Z. aurita.*

Fossa parahypotarsalis lateralis (TMT_FPL)

Referred material. *Geotrygon montana* PACEA–O–492 for state A and *Patagioenas squamosa* PACEA–O–443 for state B (Table VIII).

In proximal view, the depth of the fossa parahypotarsalis lateralis varies (state A) in all *Geotrygon* specimens, most *P. leucocephala* and *Z. aurita,* and the single specimens of *L. wellsi* and *Z. macroura* (Fig. 24).

The plantar margin of the cotyla lateralis is straight or oblique and the fossa parahypotarsalis lateralis is absent in *P. inornata* (state B, Fig. 24).

Problematic species: no characteristic states in *P. squamosa*, *Z. asiatica* and *Z. auriculata.*

Trochlea metatarsi IV (TMT_TMIV)

Referred material. Zenaida asiatica PACEA–O–707 for state A and *Zenaida aurita* PACEA–O–865 for state B (Table VIII).

In distal view, the morphology of the trochlea metatarsi of the fourth digit is characteristic of two states in *Zenaida* (Fig. 24; Table VIII). In the *Z. asiatica,* there is a clear notch on the plantar margin of trochlea (state A), while in the other species this margin is straight (state B).

Tarsometatarsus measurement

In our study, length measurements for *Zenaida asiatica* are comparable with the lowest values reported by Goldberg (1999), (Fig. 25). Our *Z. macroura* specimen is substantially longer than those in Goldberg's (1999) study. *G. montana* is much longer than *G. mystacea* compared to the observations of Steadman *et al*. (1984b). The comparably longer leg bones of the tarsometatarsus in columbid genera with more terrestrial behavior is more important than seen in the other leg bones, with *Geotrygon* specimens having the longest values. Lower length values for *G. chrysia* overlap with the higher value of the large pigeons *P. inornata* and *P. squamosa*. The two large *Zenaida* and *Leptotilia* fall within the range of *Patagioenas*. Similir to the tibiotarsus, this overlap reflects the more slender form of *Geotrygon* and *Leptotilia*. Unlike the tibiotarsus, this more gracile aspect, although slight, is neverless more evident in *Zenaida* than *Patagioeonas*.

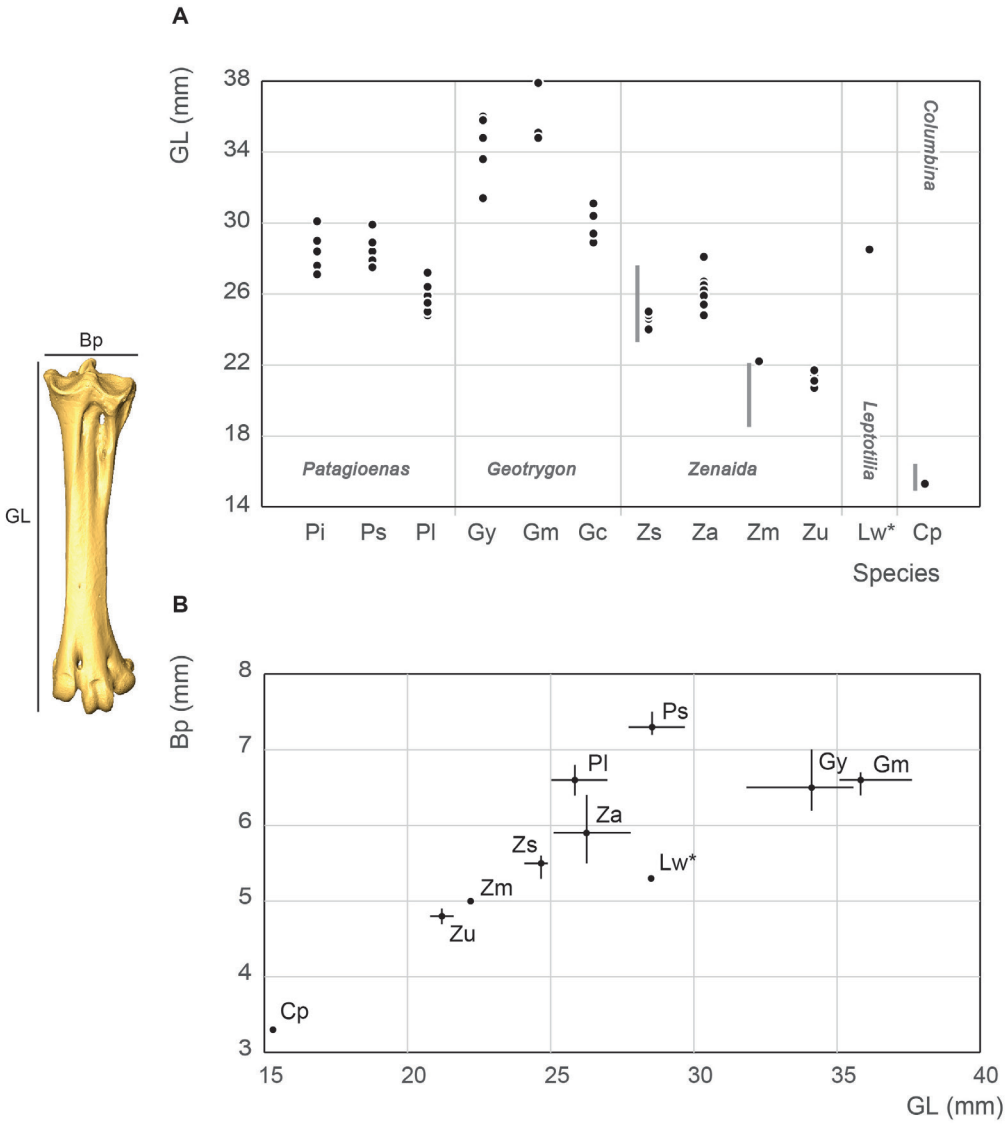


Figure 25. Tarsometatarsus measurement in mm: GL, Greatest length (A), Bp, breadth of the proximal end and GL, Greatest length (B). See Appendix C. Abbreviations: Cp, *Columbina passerina*; Gc, *Geotrygon chrysia*; Gm, *Geotrygon montana*; Gy, *Geotrygon mystacea*; Lw, *Leptotila wellsi*; Pi, *Patagioenas inornata*; Pl, *Patagioenas leucocephala*; Ps, *Patagioenas squamosa*; Za, *Zenaida aurita*; Zm, *Zenaida macroura*; Zs, *Zenaida asiatica*; Zu, *Zenaida auriculata*. (*) 3D measurement; the grey vertical line in panel A indicates Goldberg's measurements (1999).

Table IX. The most discriminating character for the 8 analyzed bones: coracoideum (COR), scapula (SCA), humerus (HUM), ulna (ULN), carpometacarpus (CMC), femur (FEM), tibiotarsus (TIB) and tarsometatarsus (TMT) for each taxon: Ps, *Patagioenas squamosa;* Pl, *Patagioenas leucocephala;* Pi, *Patagioenas inornata;* Cp, *Columbina passerina nigrirostris;* Gm, *Geotrygon montana;* Gc, *Geotrygon chrysia;* Gy, *Geotrygon mystacea;* Lw, *Leptotila wellsi;* Zs, *Zenaida asiatica asiatica;* Za, *Zenaida aurita aurita;* Zu, *Zenaida auriculata stenura;* Zm, *Zenaida macroura*. Range of sample size (n). Distribution of states: bold 100 %, bold–italics 80–100 %, normal 75–100 % and italics 60–100 %. See tables I-VIII for character codes

Code	*Ps*	*Pl*	*Pi*	*Gm*	*Gc*	*Gy*	*Lw*	*Zs*	*Za*	*Zu*	*Zm*
n	5-8	6-9	1-5	3-5	1-3	4-5	1	6-8	13-15	4-5	1
COR_FAH							Broad	Narrow			
COR_FAC	*Large and oval*			Oval			Narrow and rounded	*Narrow*			
COR_PN	*Dorsally*			*Dorsally-centrally*	Absent			Absent			
COR_TC								*Very prominent*			
COR_PA				*Distinctly raised*							
COR_FAS								Large	Narrow		
COR_AM	*Straight*							Straight	Concave		
SCA_A	Large and rounded			Flat and angular				Flat and rounded			
SCA_PN	Present			Absent							
SCA_MM	*V-shaped*			Convex	Straight	*V-shaped*	V-shaped	Convex	*Concave*		
HUM_CH	Projected ventrally			Centrally located	Projected ventrally	Centrally located		Projected ventrally		Centrally located	
HUM_VM	Rounded and large			*Rounded and large*			Rounded and tightly	Angular			
HUM_TD	*Wide*					Narrow with depression		Narrow			

Table IX Continuation

Code	*Ps*	*Pl*	*Pi*	*Gm*	*Gc*	*Gy*	*Lw*	*Zs*	*Za*	*Zu*	*Zm*
n	5-8	6-9	1-5	3-5	1-3	4-5	1	6-8	13-15	4-5	1
HUM_SLT				Oblique		Rounded					
HUM_PSD				Near to the condylus dorsalis				*Far to the condylus dorsalis*			
HUM_PF	Projected far from the shaft and/not aligned with epicondylus ventralis			Projected little from the shaft and/not aligned with epicondylus ventralis							
ULN_CD1				Rounded		Pointed	Rounded	*Pointed*			Rounded
ULN_CD2	Displaced distally compared to the cotyla ventralis			Not displaced	Displaced distally compared to the cotyla ventralis			*Displaced distally compared to the cotyla ventralis*			
ULN_CV	*With depression*			Angular			Straight	*Angular*			
ULN_CM	*Cotyla dorsalis projected caudally*		Straight	Cotyla dorsalis projected caudally	Straight	Cotyla dorsalis projected caudally	Straight	*Cotyla dorsalis projected caudally*		*Straight*	Cotyla dorsalis projected caudally
ULN_TC	Slightly projected cranially			Strongly projected cranially			Slightly projected cranially				Slightly projected cranially
CMC_OMM	Narrow			Narrow	Wide		Wide	*Narrow*			
CMC_TC1	*Poorly developed and rounded*	*Developed upwards and flattened*	Well-developed upwards and rounded	Poorly developed and rounded		Developed upwards and flattened	Poorly developed and rounded	Poorly developed and rounded		*Poorly developed and rounded*	
CMC_TC2				Eminence absent	*Distinct eminence*						
CMC_FAU1	Oblique		Aligned with ventral margin of os metacarpale minus	*Oblique*			Oblique	Aligned with ventral margin of os metacarpale minus			

Code	*Ps*	*Pl*	*Pi*	*Gm*	*Gc*	*Gy*	*Lw*	*Zs*	*Za*	*Zu*	*Zm*
n	5-8	6-9	1-5	3-5	1-3	4-5	1	6-8	13-15	4-5	1
CMC_FAU2	*Curved dorsally*			Straight		***Straight***	**Curved dorsally**			**Curved dorsally**	
CMC_PE	*Large and projected ventrally*	**Large and centrally located**		**Small**							
CMC_VM	***Broad***			**Narrow and straight**		*Narrow and straight*	**Narrow and curved**	*Curved*			
CMC_SH	**Very slightly bowed and does not slope up as markedly**		**Straighter and slopes up proximally**	**Very slightly bowed and does not slope up as markedly**	**Straighter and slopes up proximally**		**Very slightly bowed and does not slope up as markedly**	Very slightly bowed and does not slope up as markedly			
CMC_SMD				**Straight with/without eminence**			**Straight with eminence**	***Straight with eminence***			
CMC_FADM	**Less projected distally than the facies articularis digitalis major**		**More projected distally than the facies articularis digitalis major**			*Aligned with the facies articularis digitalis major*	**Close but lower than the facies articularis digitalis major**	*Close but lower than the facies articularis digitalis major*			
CMC_DM	***Large and concave***			Straight	**Narrow and concave**	*Straight*	**Narrow and concave**	***Concave***			
FEM_FAA				**Straight**	**Rounded near fovea ligamentum capitis**	***Straight***					

Table IX. Continuation

Code	*Ps*	*Pl*	*Pi*	*Gm*	*Gc*	*Gy*	*Lw*	*Zs*	*Za*	*Zu*	*Zm*
n	5-8	6-9	1-5	3-5	1-3	4-5	1	6-8	13-15	4-5	1
FEM_IMI	**In the middle of the lateral surface of trochanter femoris**			***In the middle of the lateral surface of trochanter femoris***			**In the middle of the lateral surface of trochanter femoris**		***Cranially located***		
FEM_CL				Pointed			**Rounded**	*Rounded*	*Pointed*		**Rounded**
TIB_IT	*Straight*	**Curved**									
TIB_C1				Condylus lateralis projected laterally and condylus medialis projected medially	**Condylus lateralis projected laterally**	*Condylus lateralis projected laterally and condylus medialis projected medially*		**Condylus lateralis projected laterally and condylus medialis projected medially**			
TIB_C2				Condylus medialis elongated cranially							
TIB_CM					**Medial margin oriented in accordance with the bone axis**	**Obliquely oriented compared to the bone axis**		***Medial margin oriented in accordance with the bone axis***	Obliquely oriented compared to the bone axis		
TMT_CMH	More projected proximally than eminentia intercotylaris			At the same level than eminentia intercotylaris							
TMT_FPL		Present	**Absent**	**Present**							
TMT_TMIV	***Straight***			**Straight**			**Straight**	**With notch**	***Straight***		

DISCUSSION

A comparison of osteological and biometrical data for the 8 bones of the upper and lower limbs and pectoral girdle of pigeons and doves demonstrate the 12 taxa in our analysis to differ in several morphological traits and/or in size. The most frequently recorded states of the 42 osteological characters described for the eight analyzed postcranial skeleton elements are available as Table IX.

Two characters evident on elements of the pectoral girdle (COR_FAC and SCA_A) distinguish specimens of the four genera in our sample (*Patagioenas*, *Geotrygon*, *Zenaida* and *Leptotila*). Several wing bone characters equally separate *Patagioenas* and *Geotrygon* (HUM_VM) and *Geotrygon* and *Zenaida* (ULN_CV). One character state of the coracoideum (COR_PN), in addition to being present in *Patagioenas,* is also exhibited in one *Geotrygon* species. Six characters of the coracoideum, humerus, and carpometacarpus are distinguishing characteristics separating *Patagioenas* from *Geotrygon* (HUM_PF), *Patagioenas* from *Zenaida* (HUM_TD), *Geotrygon* from *Zenaida* (HUM_VM, HUM_PSD and CMC_FAU1), and *Zenaida* from *Leptotila* (COR_FAH).

Apart from the humerus, seven bones separate the different genera*: Patagioenas* (COR_AM, SCA_PN and TMT_CMH), *Geotrygon* (COR_PA, ULN_TC, FEM_CL, TIB_C2 and TMT_FPL) and *Zenaida* (CMC_SH and CMC_SMD). Four bones lend themselves for identification to species level: *P. squamosa* (TIB_IT), *P. leucocephala* (CMC_PE), *G. mystacea* (CMC_FADM), *G. montana* (COR_PN and ULN_CD2) and *Z. asiatica* (COR_TC, TIB_C1 and TMT_TMIV).

In addition, the absence of some character states can help in identifying columbid bones and distinguish between different genera: *Patagioenas* (SCA_MM, HUM_PF, CMC_FAU2, CMC_FADM, CMC_DM and TMT_CMH), *Geotrygon* (COR_TC, HUM_SLT, HUM_PF, CMC_PE, CMC_SMD, CMC_DM, FEM_FAA) and *Zenaida* (SCA_MM, CMC_VM and CMC_FADM). *Patagioenas* and *Geotrygon* both share two characters (CMC_TC1 and TIB_C2).

Interspecific differences can be observed in three genera. One character of the carpometacarpus and two of the humerus distinguish three *Patagioenas* species (HUM_CH, HUM_VM and CMC_TC1). On the other hand, multiple characters reliably separate *Geotrygon* species: *G. chrysia* differs from the congeneric species in five characters (HUM_CH, ULN_CM, CMC_DM, FEM_FAA and TIB_C1); *G. montana* differs in two characters on the carpometacarpus (CMC_TC2 and CMC_OMM) and *G. mystacea* in two characters (ULN_CD1 and CMC_TC1). One character on the humerus distinguishes *G. mystacea* from *G. montana* (HUM_SLT). Three characters found on the coracoideum, femur and tibiotarsus distinguish *Z. asiatica* from congeneric species (COR_FAS, FEM_IMI and TIB_CM) or from *Z. aurita* (COR_AM). Two characters on the humerus (HUM_CH) and carpometacarpus (CMC_FAU2) distinguish *Z. asiatica* and *Z aurita* from *Z. auriculata* and *Z. macroura.*

Overall, our measurements evince five size categories: large (*P. inornata* and *P. squamosa*) and small pigeons (*P. leucocephala*), large (*Geotrygon* spp., *Z. asiatica* and *Z. aurita*), medium (*Z. macroura* and *Z. auriculata*), and small doves (*C. passerina*). Independent of the skeletal element considered, *Columbina passerina* is always the smallest species and no overlap in size can be observed with the other Caribean columbids. The position of the single *L. wellsi* specimen amongst medium or large doves varies between skeletal elements, indicating the need for additional data for this species. More specifically, this size ordering changes depending on body size, which varies as a function of the terrestrial habits of birds (Baptista *et al.,* 1997). Hence, the size and shape of complete pectoral (coracoideum and scapula) and wing bones (humerus, ulna and carpometacarpus) reliably separate large

and small pigeons from large and medium doves. For wing bones, *P. leucocephala* occupies an intermediate position between the large pigeons and the quail-doves, the latter being grouped with the large *Zenaida* (*Z. asiatica* and *Z. aurita*). The relative position of the *Geotrygon* changes according to the leg bones considered; the two large pigeons generally have longer femurs than *G. mystacea* and *G. montana*, with *P. leucocephala* grouped with the latter. The opposite is true for the tarsometatarsus, with the tibiotarsus occupying an intermediate position. Clear differences are also evident between these limb elements in terms of robusticty. The allometry evident between wing and leg bones of New World quail-doves (*Geotrygon*) compared to the other genera potentially reflects an adaptation to terrestrial behavior (Wetmore, 1922; Baptista *et al*., 1997).

When compared with data provided by Goldberg (1999), several minor metrical differences emerge. The place of *Geotrygon* within Antillean columbids in our study also differs from that reported by Steadman *et al.* (1984b), except for the femur and tarsometatarsus. This discrepancy potentially reflects different populations in the two samples, as our *Geotrygon mystacea* and *G. montana* specimens come uniquely from the Guadeloupe Islands while the Smithsonian Institute *G. montana* sample used by Steadman *et al*. (op. cit.) includes numerous continental specimens. These difference could also reflect a limited sample that underestimates intra-specific variability.

The precise origin of each specimen in this study (Appendix A) and associated metric data (Appendices C, D, G, I, L, N, P, R, T) can be integrated in future studies to better identify potential regional variability in Columbidae.

CONCLUSIONS

The morphometric analysis of the postcranial skeleton of the main Caribbean pigeons and doves demonstrates identifying avian remains to species can be difficult even with a large modern osteological sample. The five size classes identified and 42 diagnostic characters described in our study reliably distinguish skeletal elements of different columbid species. Combining several characters and measurements on complete bones will undoubtedly help in the determination of columbid remains recovered from archaeological and paleontological deposits, especially those from sites excavated in the French West Indies over the past 60 years.

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APPENDIX A

Modern comparative specimens. (F) female and (M) male. Unavailable data is indicated by a dash, 3D–models with an asterisk

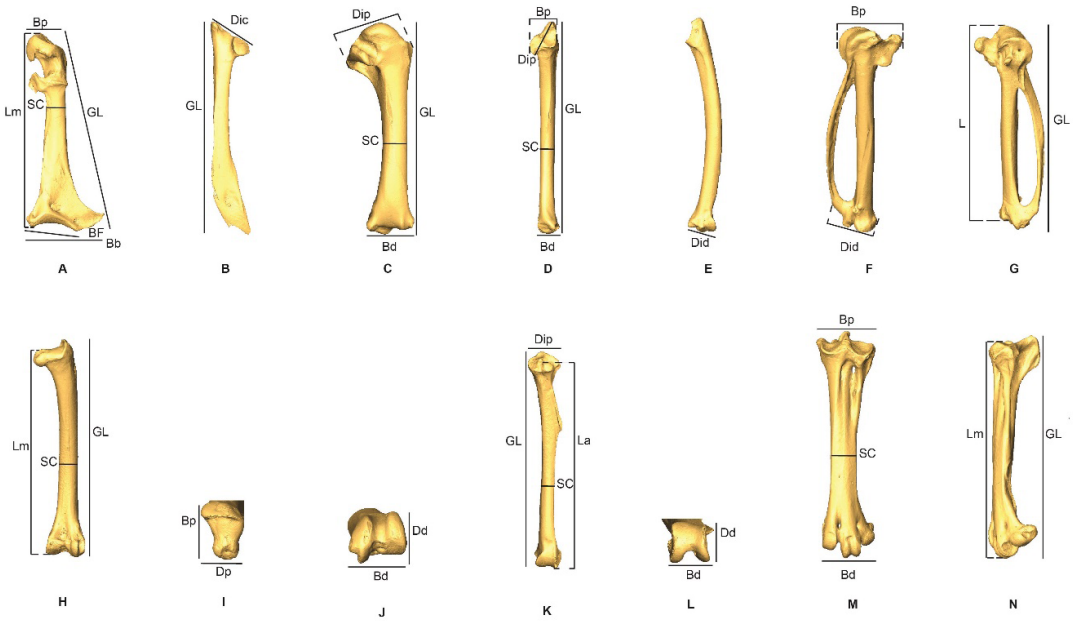
Taxon	Catalog Number	Sex	Age	Locality
Patagioenas squamosa	PACEA-O-442	F	Adult	Saint Martin
Patagioenas squamosa	PACEA-O-443	-	Adult	Saint Martin
Patagioenas squamosa	PACEA-O-486	M	Adult	Basse-Terre
Patagioenas squamosa	PACEA-O-487	F	Adult	Basse-Terre
Patagioenas squamosa	PACEA-O-704	M	Subadult	Basse-Terre
Patagioenas squamosa	PACEA-O-705	-	Adult	Basse-Terre
Patagioenas squamosa	MEC 041112-E	-	-	Guadeloupe
Patagioenas squamosa	MEC 100513-A	-	-	Marie-Galante
Patagioenas squamosa	USNM 225865	F	-	Haiti
Patagioenas squamosa	USNM 501768	M	-	Puerto Rico
Patagioenas leucocephala	PACEA-O-493	M	Adult	Grande-Terre
Patagioenas leucocephala	PACEA-O-706	-	Adult	Marie-Galante
Patagioenas leucocephala	PACEA-O-821	M	Adult	Basse-Terre
Patagioenas leucocephala	PACEA-O-822	M	Adult	Basse-Terre
Patagioenas leucocephala	PACEA-O-970	M	Adult	Grande-Terre
Patagioenas leucocephala	PACEA-O-1065	F	Adult	Grande-Terre
Patagioenas leucocephala	PACEA-O-1066	F	Adult	Grande-Terre
Patagioenas leucocephala	PACEA-O-1117	-	Adult	Saint Barthélemy
Patagioenas leucocephala	MEC 171112-C	-	-	Marie-Galante
Patagioenas leucocephala	USNM 554982	M	-	Antigua
Patagioenas leucocephala	USNM 556833	M	-	Bahamas
Patagioenas inornata	USNM 7021	-	-	Jamaica
*Patagioenas inornata**	USNM 226458	M	-	Dominican Republic
Patagioenas inornata	USNM 289629	M	-	Haiti
Patagioenas inornata	USNM 289630	M	-	Haiti
*Patagioenas inornata**	USNM 290977	F	-	Haiti
Patagioenas inornata	USNM 292505	F	-	Haiti
Patagioenas inornata	USNM 292506	F	-	Haiti
Patagioenas inornata	USNM 582879	F	-	Puerto Rico
Columbina passerina nigrirostris	MEC 041112-A	-	Adult	Guadeloupe
Columbina passerina nigrirostris	PACEA-O-904	-	Adult	Guadeloupe
Geotrygon montana	PACEA-O-492	M	Adult	Basse-Terre
Geotrygon montana	PACEA-O-847	F	Adult	Basse-Terre
Geotrygon montana	PACEA-O-1055	M	Adult	Grande-Terre
*Geotrygon montana**	MNHN-ZO-AC-1993-116	F	Adult	Locality Unknown
Geotrygon montana	MEC 150414-A	-	-	Guadeloupe
Geotrygon chrysia	USNM 290993	F	-	Haiti

Taxon	Catalog Number	Sex	Age	Locality
*Geotrygon chrysia**	USNM 292518	F	-	Haiti
Geotrygon chrysia	USNM 292519	F	-	Haiti
Geotrygon chrysia	USNM 318870	M	-	Haiti
Geotrygon chrysia	USNM 554602	F	-	Dominican Republic
*Geotrygon chrysia**	MNHN-ZO-AC-1931-525	M	Adult	Locality Unknown
Geotrygon chrysia	UF 49970	F	Adult	Bahamas
Geotrygon mystacea	PACEA-O-494	-	Adult	Basse-Terre
Geotrygon mystacea	PACEA-O-713	-	Adult	Marie-Galante
Geotrygon mystacea	PACEA-O-766	-	Adult	Marie-Galante
Geotrygon mystacea	PACEA-O-858	M	Adult	Guadeloupe
Geotrygon mystacea	PACEA-O-1085	M	Adult	Guadeloupe
Geotrygon mystacea	MEC 041112-I	-	-	Guadeloupe
*Leptotila wellsi**	NHMUK-ZOO-1898.9.20.1	M	Adult	Tobago
*Zenaida asiatica asiatica**	PACEA-O-707	F	Adult	Guadeloupe
Zenaida asiatica asiatica	PACEA-O-1004	F	Adult	Grande-Terre
Zenaida asiatica asiatica	PACEA-O-1013	-	Adult	Grande-Terre
Zenaida asiatica asiatica	PACEA-O-1061	M	Adult	Grande-Terre
Zenaida asiatica asiatica	PACEA-O-1062	F	Adult	Grande-Terre
Zenaida asiatica asiatica	PACEA-O-1063	F	Adult	Grande-Terre
Zenaida asiatica asiatica	PACEA-O-1064	F	Adult	Grande-Terre
Zenaida asiatica asiatica	USNM 553875	-	Adult	Florida
Zenaida aurita aurita	PACEA-O-430	-	Adult	Basse-Terre
Zenaida aurita aurita	PACEA-O-440	F	Adult	Saint Martin
Zenaida aurita aurita	PACEA-O-441	M	Subadult	Saint Martin
Zenaida aurita aurita	PACEA-O-448	M	Adult	Martinique
Zenaida aurita aurita	PACEA-O-449	M	Adult	Martinique
Zenaida aurita aurita	PACEA-O-708	-	Adult	Basse-Terre
Zenaida aurita aurita	PACEA-O-709	M	Adult	Basse-Terre
Zenaida aurita aurita	PACEA-O-710	-	Subadult	Guadeloupe
Zenaida aurita aurita	PACEA-O-795	M	Adult	Grande-Terre
Zenaida aurita aurita	PACEA-O-865	-	Adult	Guadeloupe
Zenaida aurita aurita	PACEA-O-987	-	Adult	Guadeloupe
Zenaida aurita aurita	PACEA-O-995	-	Adult	Guadeloupe
Zenaida aurita aurita	PACEA-O-996	-	Adult	Guadeloupe
Zenaida aurita aurita	PACEA-O-1001	-	Adult	Guadeloupe
Zenaida aurita aurita	MEC 130513-G	-	-	Guadeloupe

Appendix A. Continuation

Taxon	Catalog Number	Sex	Age	Locality
Zenaida auriculata stenura	PACEA-O-495	-	Adult	Martinique
Zenaida auriculata stenura	PACEA-O-496	-	Adult	Martinique
Zenaida auriculata stenura	PACEA-O-497	-	Subadult	Martinique
Zenaida auriculata stenura	PACEA-O-498	M	Adult	Martinique
Zenaida auriculata stenura	PACEA-O-499	-	Adult	Martinique
Zenaida macroura	PACEA-O-963	M	-	United States
Zenaida macroura	USNM 622529	F	-	Florida

APPENDIX B



Measurements of the Columbidae modified from von den Driesch (1976). A, coracoideum in dorsal view; B, scapula in lateral view; C, humerus in caudal view; D–E, ulna in cranial and ventral views; F–G, carpometacarpus in dorsal and ventral views; H–J, femur in caudal, proximal and distal views; K-L, tibiotarsus in caudal and distal views; M–N, tarsometatarsus in dorsal and medial views. Abbreviations: Bb, (greatest) basal breadth; Bd, breadth of the distal end; BF, breadth of facies articularis basalis; Bp, breadth of the proximal end; Dd, depth of the distal end; Dic, (greatest) cranial diagonal; Did diagonal of the distal end; Dp, (greatest) depth of the proximal end; Dip, (greatest) diagonal of the proximal end; GL, greatest length; L length of the metacarpus II; La, axial length; Lm, medial length; Sc, smallest breadth of the corpus.

APPENDIX C

Measurements (in mm) for Columbidae. Unavailable data is indicated by a dash, 3D–models with an asterisk. See Appendix B for significance of the measurements

		Patagioenas squamosa				*P. leucocephala*				*P. inornata*				*Columbina passerina*				*Geotrygon montana*				*G. chrysia*				*G. mystacea*			
		n	min	max	mean	n	min	max	mean	n	min	max	mean	n	min	max	mean	n	min	max	mean	n	min	max	mean	n	min	max	mean
COR	GL	5	35.5	38.5	37.1	8	32.5	35.1	33.3	8	35.6	40.0	37.5	1	-	-	15.7	3	29.9	31.2	30.4	3	28.9	29.7	29.3	4	29.8	33.2	31.7
	Lm	4	34.9	37.0	36.0	8	31.4	33.7	32.0	-	-	-	-	1	-	-	15.4	3	29.0	30.2	29.6	-	-	-	-	4	29.1	32.8	31.1
	Bp	6	7.2	7.7	7.5	8	6.1	6.9	6.5	3	7.9	8.5	8.1	1	-	-	3.3	3	5.4	5.8	5.6	-	-	-	-	5	5.5	5.9	5.7
	SC	4	3.5	3.9	3.7	8	3.0	3.6	3.3	-	-	-	-	1	-	-	1.7	2	2.5	3.0	2.7	-	-	-	-	5	2.7	3.1	2.9
	Bb	5	13.5	14.7	13.9	8	11.9	13.8	12.9	-	-	-	-	1	-	-	6.4	4	10.3	11.9	11.0	-	-	-	-	6	11.6	13.0	12.3
	BF	5	7.9	10.7	9.3	8	8.3	9.5	8.9	-	-	-	-	1	-	-	4.5	4	6.5	7.8	7.3	-	-	-	-	6	7.6	9.2	8.5
SCA	GL	2	43.4	46.0	44.7	2	41.3	41.9	41.6	1	-	-	46.2	1	-	-	20.4	2	36.9	37.2	37.1	-	-	-	-	2	39.9	41.5	40.7
	Dic	6	8.7	9.8	9.2	10	7.5	9.0	8.2	6	8.9	10.2	9.5	1	-	-	4.2	4	7.1	7.8	7.5	4	7.0	7.6	7.4	5	7.2	7.9	7.5
HUM	GL	7	44.8	49.4	47.1	10	41.3	44.6	42.3	6	44.9	49.1	47.3	1	-	-	19.0	3	35.3	37.1	36.1	4	34.9	36.6	35.6	5	35.5	39.1	38.0
	Dip	6	15.3	17.1	16.1	8	13.3	14.7	14.0	-	-	-	-	1	-	-	3.8	3	11.8	12.4	12.1	-	-	-	-	5	11.9	13.8	12.8
	SC	6	4.6	5.3	5.1	8	4.3	4.9	4.6	-	-	-	-	1	-	-	2.3	3	3.9	4.4	4.1	-	-	-	-	5	4.0	4.2	4.1
	Bd	6	11.2	11.8	11.4	8	9.8	10.4	10.0	-	-	-	-	1	-	-	4.8	3	8.9	9.3	9.1	-	-	-	-	5	8.6	10.2	9.4
ULN	GL	5	52.4	58.3	55.3	6	48.8	52.5	50.0	5	52.7	56.9	54.7	1	-	-	22.6	3	42.0	44.1	42.9	4	40.1	42.2	41.1	5	41.2	45.9	44.1
	Dip	5	8.1	9.4	8.6	6	7.0	8.2	7.8	-	-	-	-	1			4.0	4	6.4	7.4	6.9	-	-	-	-	5	6.6	7.6	7.2
	Bp	5	7.0	7.9	7.4	6	6.4	6.8	6.6	-	-	-	-	1	-	-	3.2	4	5.6	6.1	5.8	-	-	-	-	5	5.6	6.7	6.1
	SC	5	3.3	3.5	3.5	6	3.1	3.3	3.1	-	-	-	-	1	-	-	1.5	4	2.6	2.8	2.7	-	-	-	-	5	2.8	2.9	2.8
	Bd	4	5.7	6.4	6.1	6	5.3	6.0	5.6	-	-	-	-	1			2.8	3	4.9	5.1	5.0	-	-	-	-	5	4.9	5.5	5.1
	Did	4	6.6	7.1	6.9	6	5.8	6.4	6.0	-	-	-	-	1	-	-	3.0	3	5.1	5.3	5.2	-	-	-	-	5	5.0	6.0	5.5
CMC	GL	7	31.6	35.2	32.8	9	29.4	32.4	30.8	6	31.4	35.5	33.8	1	-	-	13.0	4	24.0	24.9	24.3	4	24.0	25.7	24.7	6	24.6	27.3	26.3
	L	6	30.8	34.3	32.3	8	28.4	31.5	29.7	-	-	-	-	1	-	-	12.3	3	23.3	24.6	23.8	-	-	-	-	5	23.8	26.0	25.4
	Bp	6	8.9	9.7	9.2	8	8.4	8.9	8.5	-	-	-	-	1	-	-	3.6	4	7.1	7.4	7.2	-	-	-	-	6	7.4	8.4	7.8
	Did	6	5.6	5.9	5.7	8	5.1	5.8	5.4	-	-	-	-	1	-	-	2.6	4	4.1	5.0	4.6	-	-	-	-	5	4.1	5.0	4.6
FEM	GL	5	39.9	44.2	41.8	10	36.1	39.7	37.8	8	39.2	44.1	41.5	1	-	-	19.4	4	36.4	39.4	37.4	5	33.1	35.5	34.4	5	36.0	40.3	38.8
	Lm	6	37.9	42.6	40.3	9	34.4	38.2	36.2	-	-	-	-	1	-	-	18.5	4	34.6	37.6	35.5	-	-	-	-	5	33.9	38.2	36.6
	Bp	6	8.1	8.7	8.4	9	7.0	7.7	7.3	-	-	-	-	1	-	-	3.5	4	6.9	7.2	7.0	-	-	-	-	5	7.2	7.7	7.4
	Dp	6	5.2	5.5	5.3	9	4.5	5.1	4.8	-	-	-	-	1	-	-	2.3	4	4.1	4.5	4.2	-	-	-	-	5	4.3	4.7	4.5
	SC	6	3.4	3.7	3.5	8	2.9	3.4	3.1	-	-	-	-	1	-	-	1.7	4	2.8	3.0	2.9	-	-	-	-	5	2.9	3.3	3.1
	Bd	7	7.1	7.9	7.4	8	6.2	7.1	6.6	-	-	-	-	1	-	-	3.3	4	6.4	6.8	6.6	-	-	-	-	6	6.6	7.3	7.1
	Dd	6	6.0	6.4	6.2	7	5.4	5.9	5.5	-	-	-	-	1	-	-	2.7	3	5.2	5.8	5.4	-	-	-	-	5	5.6	6.0	5.7
TIB	GL	6	52.4	56.8	54.9	8	47.9	52.0	48.9	6	52.6	56.4	54.8	2	26.9	27.2	27.1	2	56.6	58.5	57.6	4	49.3	53.4	51.3	5	52.9	59.1	56.9
	La	6	51.5	55.9	54.3	8	47.4	51.2	48.3	-	-	-	-	2	26.7	26.8	26.7	2	56.0	57.8	56.9	-	-	-	-	5	52.2	58.5	56.2
	Dip	6	7.6	8.0	7.8	8	6.7	7.5	6.9	-	-	-	-	2	3.6	3.9	3.8	2	7.3	7.4	7.3	-	-	-	-	4	7.5	8.8	8.1
	SC	6	3.1	3.5	3.2	8	2.7	3.0	2.9	-	-	-	-	2	1.3	1.4	1.3	2	2.5	2.5	2.5	-	-	-	-	5	2.4	3.0	2.7
	Bd	6	6.3	6.8	6.6	8	5.7	6.2	5.9	-	-	-	-	2	2.8	2.8	2.8	2	5.5	5.6	5.6	-	-	-	-	5	5.5	6.1	5.8
	Dd	6	6.3	6.7	6.5	8	5.7	6.0	5.8	-	-	-	-	2	2.8	3.0	2.9	2	5.9	6.5	6.2	-	-	-	-	5	5.6	6.3	6.0
TMT	GL	7	27.5	29.9	28.5	9	24.8	27.2	25.8	6	27.1	30.2	28.7	1	-	-	15.3	4	34.8	37.9	35.7	4	28.9	31.1	30.0	6	31.4	36.0	34.2
	Bp	7	7.2	7.5	7.3	9	6.4	6.8	6.6	-	-	-	-	1	-	-	3.3	4	6.4	6.7	6.6	-	-	-	-	6	6.2	7.0	6.5
	SC	6	3.5	3.7	3.6	9	3.0	3.2	3.1	-	-	-	-	1	-	-	1.7	4	2.2	2.5	2.4	-	-	-	-	6	2.5	2.7	2.6
	Bd	7	7.0	8.0	7.3	9	6.0	6.7	6.4	-	-	-	-	1	-	-	3.8	4	6.7	7.0	6.8	-	-	-	-	6	6.7	7.7	7.0

Appendix C. Continuation.

		*Leptotila wellsi**		*Zenaida asiatica*			*Z. aurita*				*Z. auriculata*				*Z. macroura*			
		n	mean	n	min	max	mean	n	min	max	mean	n	min	max	mean	n	min	max	mean
COR	GL	1	25.7	9	27.5	29.2	28.5	13	26.1	29.0	27.3	4	21.7	25.1	23.8	2	24.1	25.6	24.9
	Lm	1	24.4	7	26.8	28.4	27.8	15	24.7	28.0	26.0	4	21.0	24.2	23.0	1	-	-	24.5
	Bp	1	4.7	7	3.0	7.0	5.6	14	4.9	5.9	5.5	5	4.6	5.4	5.1	1	-	-	5.7
	SC	1	2.5	7	2.8	3.3	3.0	14	2.4	3.0	2.8	4	2.4	2.8	2.6	1	-	-	3.1
	Bb	1	10.0	7	10.8	11.9	11.4	12	10.8	11.5	11.1	5	9.6	10.3	10.0	1	-	-	11.0
	BF	1	6.6	7	7.3	8.3	7.8	13	6.5	8.9	7.7	5	6.3	6.9	6.6	1	-	-	9.0
SCA	GL	1	33.5	6	35.2	37.4	36.4	5	33.8	35.2	34.4	4	32.0	32.5	32.3	1	-	-	35.2
	Dic	1	6.3	7	7.2	8.0	7.5	9	6.6	7.4	7.1	5	6.2	6.9	6.6	1	-	-	7.2
HUM	GL	1	37.5	7	34.1	35.9	35.3	14	34.0	37.0	34.9	5	28.5	31.0	29.9	1	-	-	33.8
	Dip	1	9.5	7	12.2	13.2	12.8	14	11.1	12.6	11.9	5	10.3	11.2	10.7	1		-	12.2
	SC	1	3.4	7	3.8	4.2	3.9	14	3.4	4.1	3.9	5	3.3	3.6	3.4	1	-	-	4.3
	Bd	1	7.6	7	8.2	8.8	8.6	14	7.9	8.7	8.3	5	7.0	7.4	7.2	1	-	-	8.4
ULN	GL	1	36.9	7	40.0	43.0	41.5	8	38.1	42.4	39.9	5	32.7	36.1	34.6	1	-	-	38.7
	Dip	1	6.7	7	6.4	7.2	6.8	8	6.1	7.1	6.6	5	5.4	6.0	5.7	1	-	-	6.3
	Bp	1	4.6	7	5.4	6.0	5.8	8	5.1	6.0	5.5	5	4.8	5.2	5.1	1	-	-	5.4
	SC	1	2.2	7	2.5	3.1	2.7	8	2.3	2.8	2.6	5	2.2	2.4	2.3	1	-	-	2.7
	Bd	1	4.8	7	4.7	5.0	4.8	8	4.3	5.0	4.7	5	4.0	4.2	4.1	1	-	-	5.0
	Did	1	5.0	7	5.1	5.7	5.3	8	4.7	5.3	4.9	5	4.2	4.5	4.3	1	-	-	5.0
CMC	GL	1	22.2	7	24.8	26.5	25.9	15	23.7	25.9	24.8	4	20.0	22.8	21.5	1	-	-	23.9
	L	1	21.7	7	24.3	26.2	25.3	14	23.3	25.4	24.3	4	19.6	22.4	21.0	1	-	-	23.3
	Bp	1	6.2	7	6.9	7.8	7.2	15	6.4	7.4	7.0	4	5.8	6.6	6.2	1	-	-	6.8
	Did	1	4.1	7	4.0	4.9	4.5	15	3.9	5.5	4.4	4	3.5	4.1	3.8	1	-	-	4.0
FEM	GL	1	32.2	7	30.6	31.8	31.5	11	31.4	33.7	32.6	5	25.8	27.7	27.1	1	-	-	30.5
	Lm	1	29.8	7	28.9	30.4	30.0	10	29.9	33.0	31.1	5	24.5	26.1	25.7	1	-	-	28.9
	Bp	1	5.6	7	5.7	6.1	6.0	10	6.2	6.6	6.4	5	5.0	5.4	5.2	1	-	-	5.8
	Dp	1	4.1	7	3.7	4.0	3.8	10	3.7	4.8	4.1	5	3.3	3.5	3.4	1	-	-	4.0
	SC	1	2.4	7	2.4	2.7	2.6	10	2.5	3.1	2.8	5	2.1	2.4	2.3	1	-	-	2.7
	Bd	1	5.2	6	5.4	5.8	5.6	10	5.7	6.4	6.0	5	4.7	5.1	4.9	1	-	-	5.4
	Dd	1	4.3	6	4.4	4.7	4.5	9	4.3	5.1	4.7	5	3.8	4.2	4.0	1	-	-	4.2
TIB	GL	1	47.2	6	43.1	45.2	44.3	14	45.2	49.7	46.7	4	35.0	38.5	37.2	1	-	-	39.9
	La	1	46.7	6	42.8	44.6	43.7	14	44.5	48.3	45.9	4	34.6	38.2	36.9	1	-	-	39.4
	Dip	1	6.5	7	6.2	6.8	6.5	13	6.2	7.2	6.8	5	2.1	5.8	4.9	1	-	-	6.2
	SC	1	2.4	6	2.4	2.5	2.5	14	2.1	2.8	2.5	5	2.0	4.3	2.6	1	-	-	2.3
	Bd	1	4.7	6	4.9	5.1	5.0	14	4.9	5.6	5.2	5	4.1	4.6	4.3	1	-	-	4.6
	Dd	1	4.2	6	4.8	5.1	4.9	14	4.8	5.4	5.2	5	4.0	4.7	4.4	1	-	-	4.9
TMT	GL	1	28.5	7	24.0	25.0	24.7	10	24.8	28.1	26.2	5	20.7	21.7	21.2	1	-	-	22.2
	Bp	1	5.3	7	5.3	5.6	5.5	10	5.5	6.4	5.9	5	4.7	4.9	4.8	1	-	-	5.0
	SC	1	2.1	7	2.5	2.9	2.7	10	2.4	2.8	2.7	5	2.2	2.5	2.4	1	-	-	2.5
	Bd	1	5.1	7	5.3	5.9	5.5	10	5.4	6.2	5.9	5	5.0	5.5	5.3	1	-	-	5.1

APPENDIX D

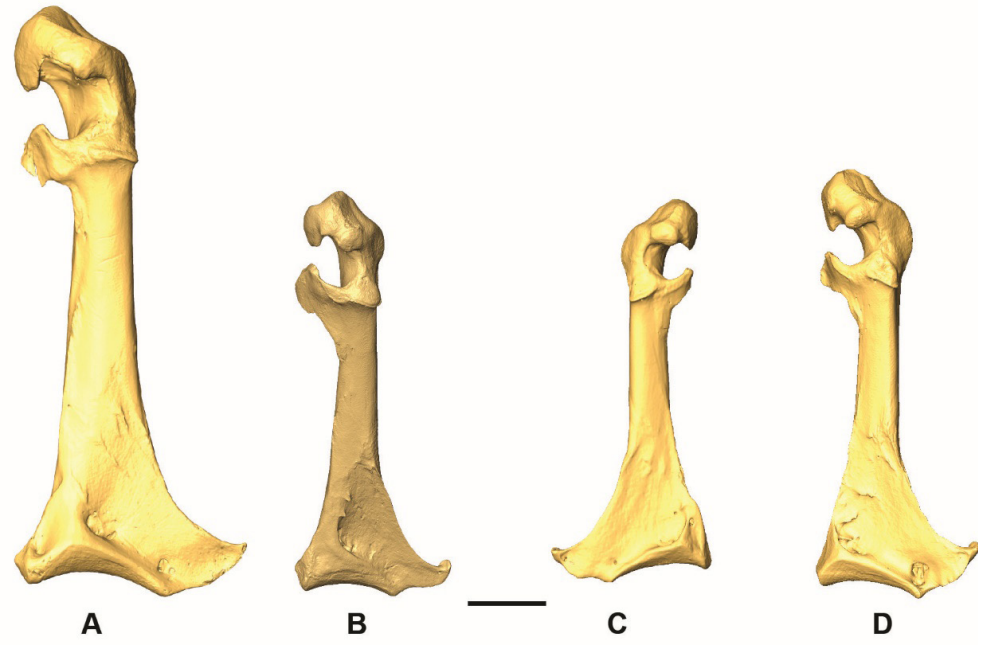
Measurements (in mm) and characters of coracoideum from modern specimens (character states see Fig. 2). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	Lm	Bp	Sc	Bb	BF	COR_FAH	COR_FAC	COR_PN	COR_TC	COR_PA	COR_FAS	COR_AM
Patagioenas_squamosa	PACEA_O_442	36.1	34.9	7.2	3.9	-	8.3	A	A	A	A/B	A/B	B	A
Patagioenas_squamosa	PACEA_O_443	35.5	-	7.5	3.8	-	-	A	A	A	A/B	A	-	-
Patagioenas_squamosa	PACEA_O_486	38.3	37.0	7.5	3.6	13.8	9.5	A	A	A	C	A	B	A/B
Patagioenas_squamosa	PACEA_O_487	-	-	7.6	-	13.8	10.7	B	A	A	C	A	A	A
Patagioenas_squamosa	PACEA_O_704	-	-	7.3	-	13.5	10.3	A	A	A	A/B	A	A	A
Patagioenas_squamosa	PACEA_O_705	37.2	35.4	7.7	3.5	13.6	7.9	A	A	A	B	A/B	A	A
Patagioenas_squamosa	MEC_041112_E	-	-	-	-	-	-	A	A	A	B	A	B	-
Patagioenas_squamosa	MEC_100513_A	38.5	36.7	-	-	14.7	10.8	A	A	A	B	A	B	-
Patagioenas_leucocephala	PACEA_O_493	32.8	31.4	6.1	3.2	12.5	9.1	A	C	A	A	B	B	A
Patagioenas_leucocephala	PACEA_O_706	32.7	31.6	6.6	3.3	11.9	8.6	A	A	A	C	A/B	B	A/B
Patagioenas_leucocephala	PACEA_O_821	32.7	31.4	6.6	3.0	12.3	8.3	A	A	C	A/B	A/B	B	A
Patagioenas_leucocephala	PACEA_O_822	-	-	6.3	3.4	13.0	8.6	A	A	A	B	-	B	A
Patagioenas_leucocephala	PACEA_O_970	33.2	32.0	6.9	3.6	13.1	8.7	A	A	A	B	A/B	B	A/B
Patagioenas_leucocephala	PACEA_O_1065	32.5	31.4	6.6	3.2	12.5	9.1	A	A	A	B	A/B	A	A/B
Patagioenas_leucocephala	PACEA_O_1066	33.4	31.7	6.8	3.2	-	-	A	A	A	C	B	B	A
Patagioenas_leucocephala	PACEA_O_1117	35.1	33.7	6.6	3.6	13.7	9.5	A	A	A	A	A	A	A
Patagioenas_leucocephala	MEC_171112_C	34.3	33.0	-	-	13.8	10.2	A	A	A	B	B	B	-
Patagioenas_inornata	USNM_7021	40.0	-	-	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_226458	38.0	-	-	-	-	-	B	A	A	C	B	A/B	A
Patagioenas_inornata	USNM_289629	37.9	-	8.0	-	-	-	-	D	B/C	B	B	-	-
Patagioenas_inornata	USNM_289630	38.0	-	8.5	-	-	-	-	-	D	-	B	-	-
Patagioenas_inornata	USNM_290977	36.6	-	-	-	-	-	B	A	A	C	B	A/B	A
Patagioenas_inornata	USNM_292505	36.9	-	-	-	-	-	A	A	A	C	B	A	-
Patagioenas_inornata	USNM_292506	35.6	-	-	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_582879	36.9	-	7.9	-	-	-	-	-	-	-	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	15.7	15.4	3.3	1.7	6.4	4.5	-	-	-	-	-	-	-
Geotrygon_montana	PACEA_O_492	-	-	5.4	-	-	7.7	A	A	B	B/C	A	A	A/B
Geotrygon_montana	PACEA_O_847	30.0	29.0	5.5	2.5	10.3	6.5	A	A	A/B	C	A	B	A/B
Geotrygon_montana	PACEA_O_1055	31.2	30.2	5.8	3.0	11.9	7.8	A	A	A/B	B/C	A	A	A/B
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	-	-	-	-	A	A	A/B	C	A	A	A
Geotrygon_montana	MEC_150414_A	30.3	29.6	-	-	11.1	6.6	A	D	B	C	B	A	A
Geotrygon_chrysia	USNM_290993	29.7	-	-	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_292518	29.2	-	-	-	-	-	B	D	D	B	A	B	B
Geotrygon_chrysia	USNM_292519	28.9	-	-	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	MNHN_ZO_AC_1931_525	-	-	-	-	-	-	B	D	D	B	A/B	A	A
Geotrygon_chrysia	UF_49970	-	-	-	-	-	-	A	D	D	C	A/B	A	A
Geotrygon_mystacea	PACEA_O_494	29.7	29.1	5.5	2.8	11.6	7.6	B	A	D	B	A	B	A
Geotrygon_mystacea	PACEA_O_713	31.7	31.0	5.5	2.8	11.8	8.5	A	A	D	C	A	A	A/B
Geotrygon_mystacea	PACEA_O_766	32.0	31.4	5.9	2.8	12.4	9.2	B	A	D	B	A	B	A
Geotrygon_mystacea	PACEA_O_858	-	-	5.7	2.7	11.9	8.5	A	A	D	C	A	B	A
Geotrygon_mystacea	PACEA_O_1085	33.2	32.8	5.9	3.1	12.9	9.0	A	A	D	B	A	B	B
Geotrygon_mystacea	MEC_041112_I	-	-	-	-	13.0	8.5	-	A	-	-	A	-	-

Appendix D. Continuation

Taxon	Catalog_Number	GL	Lm	Bp	Sc	Bb	BF	COR_FAH	COR_FAC	COR_PN	COR_TC	COR_PA	COR_FAS	COR_AM
*Leptotila_wellsi**	NHMUK_ZOO_1898_9_20_1	25.7	24.4	4.7	2.5	10.0	6.6	A	B	D	B	B	B	A/B
Zenaida_asiatica_asiatica	PACEA_O_707	28.3	27.4	6.0	2.9	11.4	7.9	B	B	D	A	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1004	29.0	28.2	5.6	3.1	11.8	8.3	B	D	D	A	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1013	27.9	26.8	6.2	2.8	10.8	7.3	B	D	D	A	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1061	29.2	28.4	7.0	3.3	11.9	8.2	B	D	D	A	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1062	28.0	27.6	5.4	2.8	11.2	7.6	B	D	D	B	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1063	28.8	27.6	5.9	3.1	11.2	7.6	B	B	D	B	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1064	29.2	28.4	5.6	3.0	11.2	7.7	B	D	D	A	B	A	A
Zenaida_asiatica	USNM_553875	27.5	-	-	-	-	-	-	-	-	B	-	-	-
Zenaida_aurita_aurita	PACEA_O_430	29.1	28.0	5.7	2.7	11.5	7.9	B	B	D	C	A	B	B
Zenaida_aurita_aurita	PACEA_O_440	27.2	25.9	5.6	2.8	11.0	7.8	B	B	D	B	B	B	B
Zenaida_aurita_aurita	PACEA_O_441	-	25.2	5.0	2.4	-	6.6	B	B	D	C	A	B	B
Zenaida_aurita_aurita	PACEA_O_448	27.0	25.2	5.5	2.7	11.1	8.9	B	B/D	D	B	A	B	B
Zenaida_aurita_aurita	PACEA_O_449	28.0	27.2	5.5	2.8	11.2	8.9	B	B	D	B	A/B	B	A/B
Zenaida_aurita_aurita	PACEA_O_708	26.6	25.1	5.5	3.0	11.1	7.3	B	D	D	C	A	B	B
Zenaida_aurita_aurita	PACEA_O_709	27.7	26.8	5.6	2.7	11.1	7.5	B	D	D	B	A/B	B	A/B
Zenaida_aurita_aurita	PACEA_O_710	28.2	26.9	5.6	2.8	11.2	7.9	B	D	D	B	B	B	B
Zenaida_aurita_aurita	PACEA_O_795	27.4	26.3	5.9	3.0	11.1	7.2	B	B	D	B	B	B	B
Zenaida_aurita_aurita	PACEA_O_865	27.0	25.9	5.3	2.7	10.8	6.5	B	B/D	D	B	A/B	B	B
Zenaida_aurita_aurita	PACEA_O_987	-	25.0	4.9	2.6	-	7.1	B	B	D	C	A	B	B
Zenaida_aurita_aurita	PACEA_O_995	26.9	25.6	5.6	2.8	11.4	-	B	B	C	C	B	B	A/B
Zenaida_aurita_aurita	PACEA_O_996	-	25.8	5.5	3.0	-	-	B	B	D	B	B	B	B
Zenaida_aurita_aurita	PACEA_O_1001	27.0	25.9	5.7	3.0	10.8	8.2	B	B	D	B	A	B	B
Zenaida_aurita_aurita	MEC_130513_G	26.7	24.7	-	-	11.1	8.3	B	D	D	B/C	B	B	-
Zenaida_auriculata_stenura	PACEA_O_495	-	-	5.4	-	-	6.9	B	B	D	B	A	B	A/B
Zenaida_auriculata_stenura	PACEA_O_496	21.7	21.0	4.6	2.8	9.6	6.7	-	-	-	-	-	-	-
Zenaida_auriculata_stenura	PACEA_O_497	23.4	22.5	4.7	2.7	10.1	6.4	B	B	D	B	B	B	A/B
Zenaida_auriculata_stenura	PACEA_O_498	25.0	24.2	5.4	2.7	10.4	6.1	B	C	C	A	B	B	A/B
Zenaida_auriculata_stenura	PACEA_O_499	24.9	24.1	5.2	2.4	10.0	6.3	B	B	D	A	B	B	A/B
Zenaida_macroura	PACEA-O-963	25.7	24.6	5.7	3.1	11.0	9.0	B	B	D	B	B	B	A/B
Zenaida_macroura	USNM_622529	24.1	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX E



3D – models of coracoidea in dorsal view. A, *Patagioenas inornata* USNM 226458; B, *Geotrygon montana* MNHN-ZO-AC–1993–116; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA–O–707. A-B, D, right side; C, left side. Scale bar equals 5 mm.

APPENDIX F

Additional characters of the coracoideum.

The following omal characters allow distinguish *Geotrygon* from *Zenaida*.

In agreement with Olson and Hilgartner, in *G. chrysia,* the glenoid facet (facies articularis humeralis) in lateral view is smaller than in *Z. aurita* and the "scapular facet is not situated as far sternally on the shaft as *Z. aurita*" (Olson & Hilgartner,1982 p. 35).

Two characters (shape of cotyla scapularis) are unreliable for identifying specimens to species due to the substantial variability of *Geotrygon* and *Zenaida*.

In dorsal view, the shape of cotyla scapularis is triangular in *Geotrygon* and uncharacteristic in *Zenaida* (irregular form, rounded or triangular).

In medial view, the cotyla scapularis is most often rounded in *G. montana* and straight in *Z. asiatica* and some individuals of *Z. aurita*.

In addition, the 2 distal characters are situated in the area of the facies articularis sternalis and the angulus medialis. The facies articularis sternalis of *G. montana* in sternal view is triangular in 60 % of specimens.

In medial view, the angulus medialis of *Z. asiatica* is often large with a symmetric rhomboid shape.

LITERATURE CITED

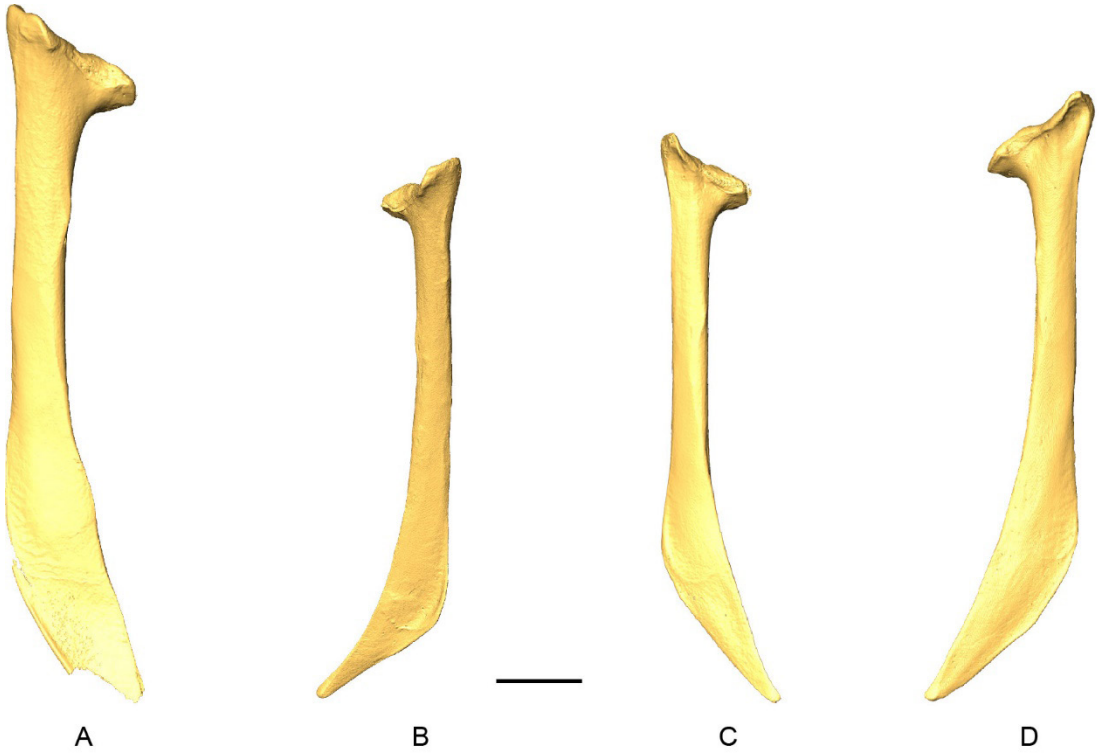
Olson, S. L., & W. B. Hilgartner. 1982. Fossil and subfossil birds from the Bahamas (25–55). *In*: Olson, S. L. (Ed.). *Fossil vertebrates from the Bahamas*. Smithsonian Institution Press, Washington D.C., *Smithsonian Contributions to Paleobiology*, 48.

APPENDIX G

Measurements (in mm) and characters of scapula from modern specimens (character states see Fig. 6). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	Dic	SCA_A	SCA_PN	SCA_MM
Patagioenas_squamosa	PACEA_O_442	-	9.0	C	A	C
Patagioenas_squamosa	PACEA_O_443	-	9.8	C	A	C
Patagioenas_squamosa	PACEA_O_486	-	9.1	C	A	C
Patagioenas_squamosa	PACEA_O_487	43.4	8.7	C	A	C
Patagioenas_squamosa	PACEA_O_704	-	9.0	C	A	C
Patagioenas_squamosa	PACEA_O_705	46.0	9.8	C	A	C
Patagioenas_leucocephala	PACEA_O_493	41.9	8.2	C	A	C
Patagioenas_leucocephala	PACEA_O_706	-	7.5	C	A	C
Patagioenas_leucocephala	PACEA_O_821	41.3	8.2	C	A	C
Patagioenas_leucocephala	PACEA_O_822	-	7.6	C	A	C
Patagioenas_leucocephala	PACEA_O_970	-	8.0	C	A	C
Patagioenas_leucocephala	PACEA_O_1065	-	7.9	C	A	C
Patagioenas_leucocephala	PACEA_O_1066	-	8.3	C	A	D
Patagioenas_leucocephala	PACEA_O_1117	-	8.6	C	A	C
Patagioenas_leucocephala	USNM_554982	-	9.0	-	-	-
Patagioenas_leucocephala	USNM_556833	-	8.4	-	-	-
Patagioenas_inornata	USNM_7021	-	10.2	-	-	-
Patagioenas_inornata	USNM_290977	46.2	8.9	C	A	B/C
Patagioenas_inornata	USNM_292505	-	9.5	-	-	-
Patagioenas_inornata	USNM_292506	-	9.0	-	-	-
Patagioenas_inornata	USNM_582879	-	9.7	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	20.4	4.2	-	-	-
Geotrygon_montana	PACEA_O_492	-	7.6	B	B	A?
Geotrygon_montana	PACEA_O_847	36.9	7.1	B	B	A
Geotrygon_montana	PACEA_O_1055	-	7.8	B	B	A
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	B	B	B
Geotrygon_montana	MEC_150414_A	37.2	7.6	-	-	-
Geotrygon_chrysia	USNM_290993	-	7.5	-	-	-
Geotrygon_chrysia	USNM_292518	-	-	B	B	D
Geotrygon_chrysia	USNM_292519	-	7.6	-	-	-
Geotrygon_chrysia	USNM_318870	-	7.4	-	-	-
Geotrygon_chrysia	USNM_554602	-	7.0	-	-	-
Geotrygon_chrysia	MNHN_ZO_AC_1931_525	-	-	-	B	D
Geotrygon_mystacea	PACEA_O_494	-	7.2	B	B	C
Geotrygon_mystacea	PACEA_O_713	-	7.6	B	B	C
Geotrygon_mystacea	PACEA_O_766	-	7.4	B	B	D
Geotrygon_mystacea	PACEA_O_858	39.9	7.7	B	B	C
Geotrygon_mystacea	PACEA_O_1085	41.5	7.9	B	B	C
*Leptotila_wellsi**	NHMUK_ZOO_1898_9_20_1	33.5	6.3	B	B	C
Zenaida_asiatica_asiatica	PACEA_O_707	36.7	7.8	A	B	A
Zenaida_asiatica_asiatica	PACEA_O_1004	36.4	7.7	A	B	A
Zenaida_asiatica_asiatica	PACEA_O_1013	35.2	7.2	A	B	B
Zenaida_asiatica_asiatica	PACEA_O_1061	-	8.0	A	B	A
Zenaida_asiatica_asiatica	PACEA_O_1062	35.9	7.2	A	B	A
Zenaida_asiatica_asiatica	PACEA_O_1063	36.8	7.5	A	B	A
Zenaida_asiatica_asiatica	PACEA_O_1064	37.4	7.2	A	B	B
Zenaida_aurita_aurita	PACEA_O_430	-	7.3	A	B	B
Zenaida_aurita_aurita	PACEA_O_440	-	7.2	A	B	B
Zenaida_aurita_aurita	PACEA_O_441	-	6.6	A	B	B
Zenaida_aurita_aurita	PACEA_O_448	33.8	6.9	A	B	B
Zenaida_aurita_aurita	PACEA_O_449	-	-	A	B	B
Zenaida_aurita_aurita	PACEA_O_708	-	-	A	B	B
Zenaida_aurita_aurita	PACEA_O_709	34.6	7.4	A	B	B
Zenaida_aurita_aurita	PACEA_O_710	35.2	6.7	A	B	B
Zenaida_aurita_aurita	PACEA_O_795	34.4	7.2	A	B	B
Zenaida_aurita_aurita	PACEA_O_865	34.1	7.1	A	B	B
Zenaida_aurita_aurita	PACEA_O_987	-	-	A	B	B
Zenaida_aurita_aurita	PACEA_O_995	-	-	A	B	B
Zenaida_aurita_aurita	PACEA_O_996	-	-	A	B	B
Zenaida_aurita_aurita	PACEA_O_1001	-	7.4	A	B	B
Zenaida_auriculata	PACEA_O_495	32.0	6.7	A	B	B
Zenaida_auriculata	PACEA_O_496	-	6.2	A	B	A
Zenaida_auriculata	PACEA_O_497	32.5	6.5	A	B	B
Zenaida_auriculata_stenura	PACEA_O_498	32.4	6.9	A	B	B
Zenaida_auriculata	PACEA_O_499	32.3	6.8	A	B	B
Zenaida_macroura	PACEA_O_963	35.2	7.2	A	B	B

APPENDIX H



3D-models of scapulae in medial view. A, *Patagioenas inornata* USNM 290977; B, *Geotrygon montana* MNHN-ZO-AC-1993-116; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA-O-707. B, D, right side; A, C, left side. Scale bar equals 5 mm.

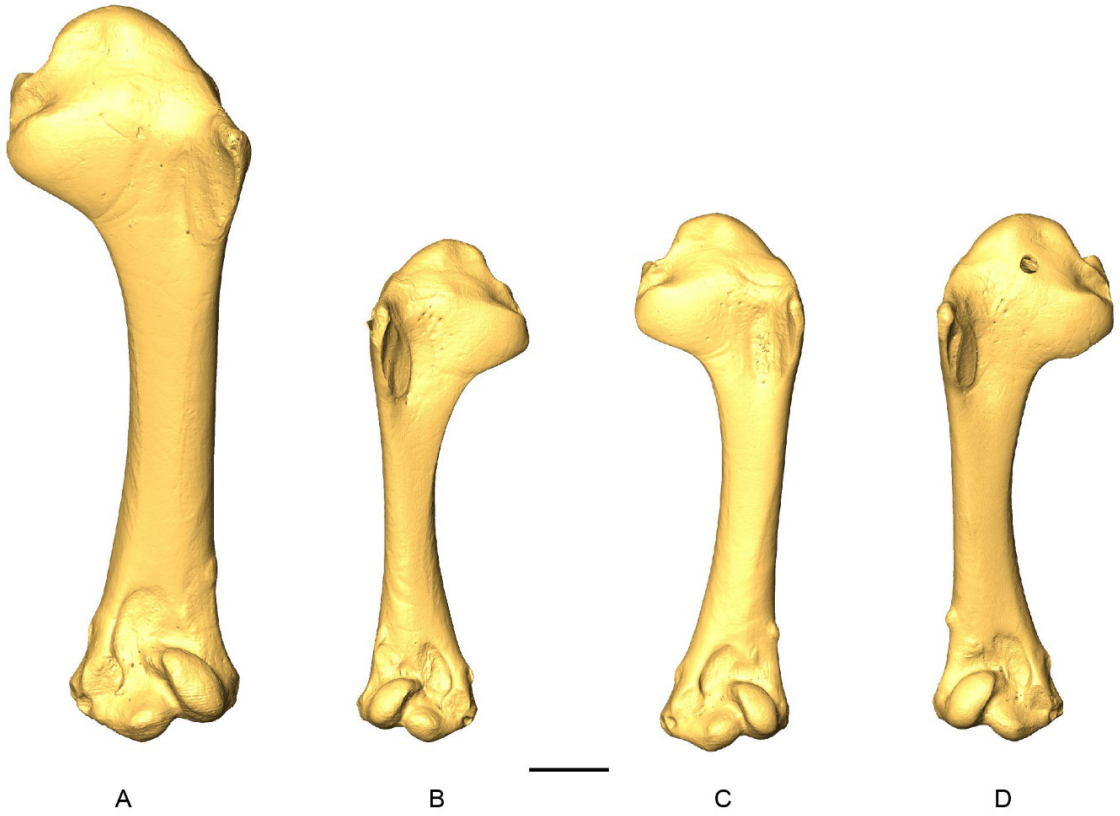
APPENDIX I

Measurements (in mm) and characters of humerus from modern specimens (character states see Fig. 9). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	Dip	Sc	Bd	HUM_CH	HUM_VM	HUM_TD	HUM_SLT	HUM_PSD	HUM_PF
Patagioenas_squamosa	PACEA_O_442	47.4	15.8	5.1	11.2	A	A	C	B	A	A
Patagioenas_squamosa	PACEA_O_443	47.2	16.3	5.2	11.2	A	A	-	B	B	A
Patagioenas_squamosa	PACEA_O_486	49.4	17.1	5.3	11.8	A	A	A	B	A	A
Patagioenas_squamosa	PACEA_O_487	44.9	15.3	5.2	11.7	A	A	A	B	A/B	B
Patagioenas_squamosa	PACEA_O_704	47.8	15.9	4.6	11.3	A	A	A	B	A/B	B
Patagioenas_squamosa	PACEA_O_705	48.1	16.1	5.2	11.3	A	A	A	B	B	A/B
Patagioenas_squamosa	USNM_225865	44.8	-	-	-	-	-	-	-	-	-
Patagioenas_leucocephala	PACEA_O_493	42.8	14.2	4.7	9.9	A	A	A	A/B	A	A
Patagioenas_leucocephala	PACEA_O_706	41.9	13.3	4.3	10.0	A	A	A	B/C	A/B	A
Patagioenas_leucocephala	PACEA_O_821	41.7	13.9	4.7	10.2	A	A	A	A/B	A	A
Patagioenas_leucocephala	PACEA_O_822	42.3	13.7	4.6	10.2	A	A	C	B	A	A
Patagioenas_leucocephala	PACEA_O_970	42.8	13.7	4.7	9.8	A	A	A	A	A/B	B
Patagioenas_leucocephala	PACEA_O_1065	42.0	14.7	4.9	9.8	A	A	A	A/B	A/B	B
Patagioenas_leucocephala	PACEA_O_1066	41.8	14.1	4.6	10.4	A	A	A	B	A/B	B
Patagioenas_leucocephala	PACEA_O_1117	42.0	14.4	4.6	9.9	A	A	A	B	A/B	A/B
Patagioenas_leucocephala	USNM_554982	44.6	-	-	-	-	-	-	-	-	-
Patagioenas_leucocephala	USNM_556833	41.3	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_226458	48.7	-	-	-	A	A	A	B/C	A/B	A
Patagioenas_inornata	USNM_289629	47.8	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_289630	49.1	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_290977	46.3	-	-	-	B?	B	A	B	B	A
Patagioenas_inornata	USNM_292505	46.8	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_292506	44.9	-	-	-	-	-	-	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	19.0	6.8	2.3	4.8	-	-	-	-	-	-
Geotrygon_montana	PACEA_O_492	35.3	11.8	4.0	9.1	B	A	-	B	A	-
Geotrygon_montana	PACEA_O_847	35.8	12.4	3.9	8.9	B	A	B/D	B	A/B	D
Geotrygon_montana	PACEA_O_1055	37.1	12.2	4.4	9.3	B	A	B	B	A	C
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	-	-	B	A	C/D	B	A	C
Geotrygon_chrysia	USNM_292518	34.9	-	-	-	A	A	A	A	A	D
Geotrygon_chrysia	USNM_292519	35.8	-	-	-	-	B	-	-	-	-
Geotrygon_chrysia	USNM_318870	36.6	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_554602	35.3	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	MNHN_ZO_AC_1931_525	-	-	-	-	A	A	C/D	B	A	C
Geotrygon_mystacea	PACEA_O_494	35.5	11.9	4.2	8.6	B	A	D	A	A	C
Geotrygon_mystacea	PACEA_O_713	38.7	12.8	4.2	9.4	B	A	D	A	A	C/D
Geotrygon_mystacea	PACEA_O_766	38.9	12.9	4.0	9.3	B	A	D	A	A	C
Geotrygon_mystacea	PACEA_O_858	39.1	12.9	4.2	9.5	B	A	D	A	A	D
Geotrygon_mystacea	PACEA_O_1085	-	13.8	-	10.2	-	A	D	A	A	C

Taxon	Catalog_Number	GL	Dip	Sc	Bd	HUM_CH	HUM_VM	HUM_TD	HUM_SLT	HUM_PSD	HUM_PF
*Leptotila_wellsi**	NHMUK_ZOO_1898_9_20_1	37.5	9.5	3.4	7.6	B	B	D	B	B	C
Zenaida_asiatica_asiatica	PACEA_O_707	35.3	13.0	4.0	8.6	A	C	B/D	A	B	C
Zenaida_asiatica_asiatica	PACEA_O_1004	35.4	12.2	3.8	8.2	A	C	B/D	A	B	C
Zenaida_asiatica_asiatica	PACEA_O_1013	34.1	12.7	3.9	8.4	A	C	B/D	A/B	B	C
Zenaida_asiatica_asiatica	PACEA_O_1061	35.9	13.2	4.2	8.8	A	C	B/D	B/C	A/B	C
Zenaida_asiatica_asiatica	PACEA_O_1062	35.4	12.8	3.9	8.6	A	C	B/D	A	A/B	C
Zenaida_asiatica_asiatica	PACEA_O_1063	35.4	12.7	3.9	8.8	A	C	B/D	A	B	A
Zenaida_asiatica_asiatica	PACEA_O_1064	35.4	12.8	3.9	8.6	A	C	B/D	A	B	-
Zenaida_aurita_aurita	PACEA_O_430	37.0	12.6	4.1	8.7	A	C	D	B	B	C
Zenaida_aurita_aurita	PACEA_O_440	34.8	12.0	4.0	8.6	A	C	B/D	B	B	A
Zenaida_aurita_aurita	PACEA_O_441	34.2	11.4	3.4	8.2	A	C	B/D	B/C	B	D
Zenaida_aurita_aurita	PACEA_O_448	34.8	12.4	3.9	8.1	A	C?	B/D	B	B	A
Zenaida_aurita_aurita	PACEA_O_449	-	12.0	4.1	8.5	A	C	D	A	B	C
Zenaida_aurita_aurita	PACEA_O_708	34.0	11.9	3.8	8.3	A	C?	D	B	B	A
Zenaida_aurita_aurita	PACEA_O_709	36.1	12.0	3.8	8.6	A	C	D	B	B	A
Zenaida_aurita_aurita	PACEA_O_710	34.9	11.3	4.0	8.0	A	C	B	C	B	C
Zenaida_aurita_aurita	PACEA_O_795	35.6	12.1	4.1	8.4	A	C?	D	A	B	A
Zenaida_aurita_aurita	PACEA_O_865	34.1	11.8	3.9	8.2	A	C	B/D	B	B	B
Zenaida_aurita_aurita	PACEA_O_987	34.4	11.1	3.5	7.9	A	C	B/D	B	B	C
Zenaida_aurita_aurita	PACEA_O_995	34.3	11.6	4.0	8.5	A	C?	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_996	34.7	11.9	4.0	8.2	A	C	D	A	B	A
Zenaida_aurita_aurita	PACEA_O_1001	34.8	12.2	4.0	8.2	A	C	B/D	B	B	A
Zenaida_auriculata_stenura	PACEA_O_495	30.3	11.2	3.5	7.4	B	C	B	B/C	B	D
Zenaida_auriculata_stenura	PACEA_O_496	28.5	10.3	3.5	7.3	B	C	B	B/C	B	D
Zenaida_auriculata_stenura	PACEA_O_497	29.7	10.7	3.3	7.0	B	C	B	A	B	D
Zenaida_auriculata_stenura	PACEA_O_498	31.0	10.7	3.6	7.3	B	C	B	B/C	B	D
Zenaida_auriculata_stenura	PACEA_O_499	30.2	10.5	3.4	7.1	B	-	B	C	B	D
Zenaida_macroura	PACEA_O_963	33.8	12.2	4.3	8.4	B	B/C	D	A	A/B	C

APPENDIX J



3D-models of humeri in cranial view. A, *Patagioenas inornata* USNM 290977; B, *Geotrygon montana* MNHN-ZO-AC-1993-116; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA-O-707. B, D, right side; A, C, left side. Scale bar equals 5 mm.

APPENDIX K

Additional characters of humerus. The presence of an eminence on the ventral margin of crista bicipitalis is an additional proximal character of the humerus linked to HUM_VM observed in *Zenaida asiatica* that distinguishes it from *Zenaida aurita* and other 2 congeneric.

Right humeri in cranial view. A, *Zenaida aurita* PACEA-O-865; B, *Zenaida asiatica* PACEA-O-707. Scale bar equals 5 mm.

An additional distal character was recognized by Wetmore (1922). Based on the form of the fossa olecrani, this author suggested a shared behavior (flight) linking the three species of *Patagioenas*. The fossa olecrani in *P. inornata* bears an "inner wall merging with adjacent entepicondylar process in a gentle slope (forming a basin-like depression)" while in *P. leucocephala* and *P. squamosa* it has a "deeper, inner wall abrupt, forming a distinct pit at base of entepicondylar process" (Wetmore op. cit.: 318). These latter species are migratory unlike the *P. inornata*, which is more sedentary.

LITERATURE CITED

Wetmore, A. 1922. Bird remains from the caves of Porto Rico. *Bulletin of the American Museum of Natural History*, 46: 297–333.

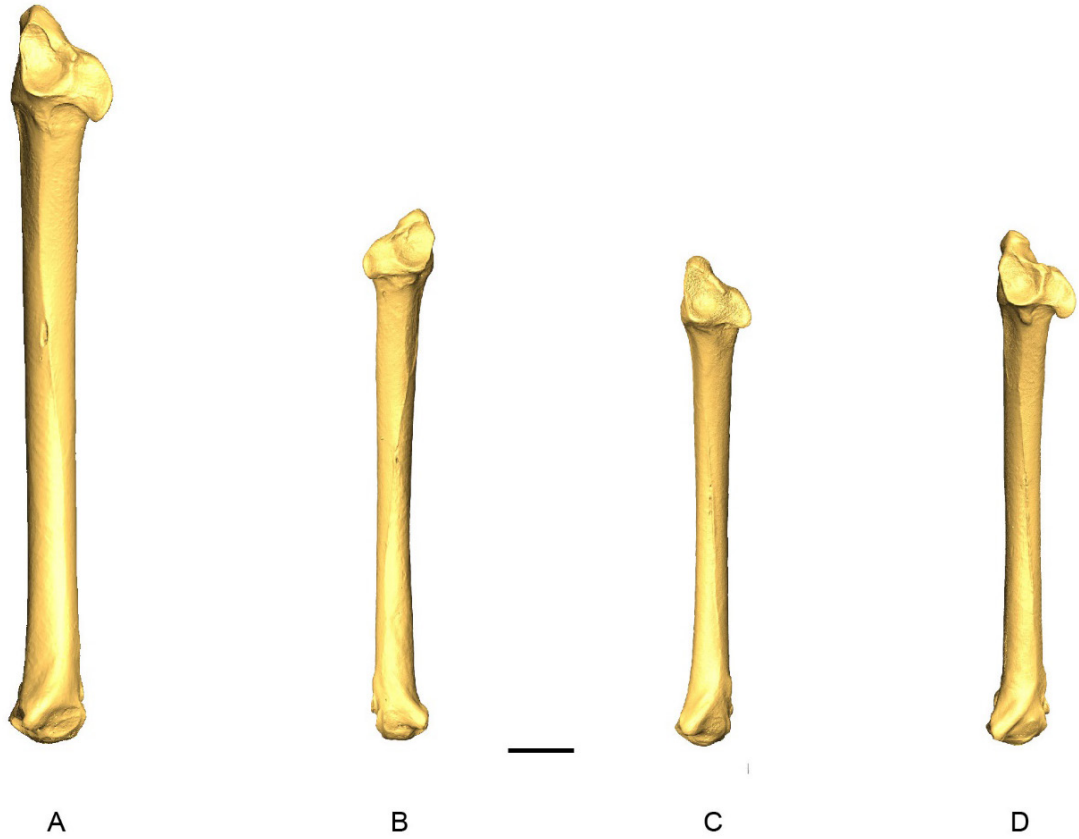
APPENDIX L

Measurements (in mm) and characters of ulna from modern specimens (character states see Fig. 12). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	Dip	Bp	Sc	Did	Bd	ULN_CD1	ULN_CD2	ULN_CV	ULN_CM	ULN_TC
Patagioenas_squamosa	PACEA_O_442	55.1	9.4	7.3	3.5	6.6	6.1	A	A	C	A	A
Patagioenas_squamosa	PACEA_O_443	55.1	8.1	7.0	3.3	7.1	6.2	A	A	A	B	A
Patagioenas_squamosa	PACEA_O_486	58.3	8.5	7.2	3.5	7.0	6.4	B	A	C	B	A
Patagioenas_squamosa	PACEA_O_487	52.4	8.4	7.5	3.5	6.8	5.7	B	A	C	B	A
Patagioenas_squamosa	PACEA_O_704	-	-	-	-	-	-	A	A	C	B	A
Patagioenas_squamosa	PACEA_O_705	55.8	8.6	7.9	3.5	-	-	B	A	C	B	A
Patagioenas_leucocephala	PACEA_O_493	50.2	8.2	6.6	3.2	6.0	5.7	A	A	C	A	A
Patagioenas_leucocephala	PACEA_O_706	49.2	7.0	6.4	3.1	5.9	5.4	A/B	A	B	A	A
Patagioenas_leucocephala	PACEA_O_821	-	-	-	-	-	-	A/B	A	A	A	A
Patagioenas_leucocephala	PACEA_O_822	49.9	7.8	6.7	3.1	6.0	5.7	A	A	B	B	A
Patagioenas_leucocephala	PACEA_O_970	-	-	-	-	-	-	A	A	B	B	A
Patagioenas_leucocephala	PACEA_O_1065	48.8	7.7	6.5	3.1	5.8	5.3	A	A	A	A	A
Patagioenas_leucocephala	PACEA_O_1066	49.5	7.9	6.7	3.2	5.9	5.6	A	A	C	B	A
Patagioenas_leucocephala	PACEA_O_1117	52.5	8.2	6.8	3.3	6.4	6.0	A	A	C	B	-
Patagioenas_inornata	USNM_226458	-	-	-	-	-	-	A	A	A	A	A
Patagioenas_inornata	USNM_289629	55.7	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_289630	56.9	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_290977	54.0	-	-	-	-	-	B	A	A/B	A	B
Patagioenas_inornata	USNM_292505	54.1	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_292506	52.7	-	-	-	-	-	-	-	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	22.6	4.0	3.2	1.5	3.0	2.8	-	-	-	-	-
Geotrygon_montana	PACEA_O_492	42.0	6.4	5.6	2.8	5.1	5.0	B	B	B	A	B
Geotrygon_montana	PACEA_O_847	42.4	6.8	5.6	2.6	5.2	4.9	B	B	B	B	B
Geotrygon_montana	PACEA_O_1055	44.1	7.0	5.9	2.7	5.3	5.1	B	B	B	B	B
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	-	-	-	-	B	B?	B	B	B
Geotrygon_montana	MEC_150414_A	-	7.4	6.1	2.6	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_292518	40.1	-	-	-	-	-	B	A?	B	A	B
Geotrygon_chrysia	USNM_292519	41.6	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_318870	42.2	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_554602	40.6	-	-	-	-	-	-	-	-	-	-
Geotrygon_mystacea	PACEA_O_494	41.2	7.6	5.6	2.8	5.0	4.9	A	A	B	B	B
Geotrygon_mystacea	PACEA_O_713	43.5	6.6	6.1	2.8	5.6	4.9	A	A	B	B	B
Geotrygon_mystacea	PACEA_O_766	45.0	6.8	5.9	2.9	5.4	5.1	A	A	B	B	B
Geotrygon_mystacea	PACEA_O_858	44.9	7.2	6.7	2.8	5.5	5.2	A	A	B	B	B
Geotrygon_mystacea	PACEA_O_1085	45.9	7.6	6.2	2.9	6.0	5.5	A	A	B	B	B

Leptotila_wellsi	NHMUK_ZOO_1898_9_20_1	36.9	6.7	4.6	2.2	4.8	5.0	B	A	A	A	A
Zenaida_asiatica_asiatica	PACEA_O_707	40.9	6.5	6.0	2.6	5.1	4.8	A	A	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1004	41.4	7.0	5.7	2.5	5.4	4.7	A	A	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1013	40.0	6.8	5.4	2.6	5.2	4.7	A	A	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1061	43.0	7.2	5.9	3.1	5.7	4.9	A	A	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1062	41.8	6.9	5.8	2.7	5.5	4.9	A	A	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1063	41.3	6.4	6.0	2.7	5.3	5.0	A	A	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1064	41.7	6.9	6.0	2.8	5.3	4.8	A	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_430	42.4	6.8	6.0	2.8	5.3	4.9	A	A	C	B	A
Zenaida_aurita_aurita	PACEA_O_440	39.1	6.7	5.4	2.7	4.9	4.7	A	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_441	39.1	6.1	5.3	2.3	4.7	4.3	B	B	A	A	A/B
Zenaida_aurita_aurita	PACEA_O_448	40.0	6.8	5.3	2.5	4.9	4.7	A	B?	B	B	B
Zenaida_aurita_aurita	PACEA_O_449	-	-	-	-	-	-	A	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_708	38.1	6.2	5.4	2.5	4.9	4.8	A	A	B	B	B
Zenaida_aurita_aurita	PACEA_O_709	-	-	-	-	-	-	A	A	B	B	A/B
Zenaida_aurita_aurita	PACEA_O_710	39.1	6.2	5.6	2.6	4.7	4.7	A	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_795	41.7	7.1	5.7	2.7	5.0	5.0	A	A	B	B	A/B
Zenaida_aurita_aurita	PACEA_O_865	-	-	-	-	-	-	A	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_987	-	-	-	-	-	-	A	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_995	-	-	-	-	-	-	A	A	C	B	A
Zenaida_aurita_aurita	PACEA_O_996	-	-	-	-	-	-	A	A	B	B	A/B
Zenaida_aurita_aurita	PACEA_O_1001	39.4	6.8	5.1	2.7	4.9	4.7	A	A	B/C	B	A/B
Zenaida_auriculata_stenura	PACEA_O_495	34.7	6.0	5.2	2.4	4.4	4.2	A	A	C	A	B
Zenaida_auriculata_stenura	PACEA_O_496	32.7	5.4	5.1	2.3	4.2	4.1	A	A	B	A	A
Zenaida_auriculata_stenura	PACEA_O_497	34.2	5.7	4.8	2.2	4.2	4.0	A	A	C	B	A
Zenaida_auriculata_stenura	PACEA_O_498	36.1	5.5	5.2	2.4	4.5	4.2	A	A	B	A	B
Zenaida_auriculata_stenura	PACEA_O_499	35.5	5.8	5.0	2.3	4.4	4.2	A	A	B	A	A/B
Zenaida_macroura	PACEA_O_963	38.7	6.3	5.4	2.7	5.0	5.0	B	A	A/B	B	A

APPENDIX M



3D-models of ulnae in cranial view. A, *Patagioenas inornata* USNM 290977; B, *Geotrygon chrysia* USNM 292518; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA-O-707. B, right side; A, C-D, left side. Scale bar equals 5 mm.

APPENDIX N

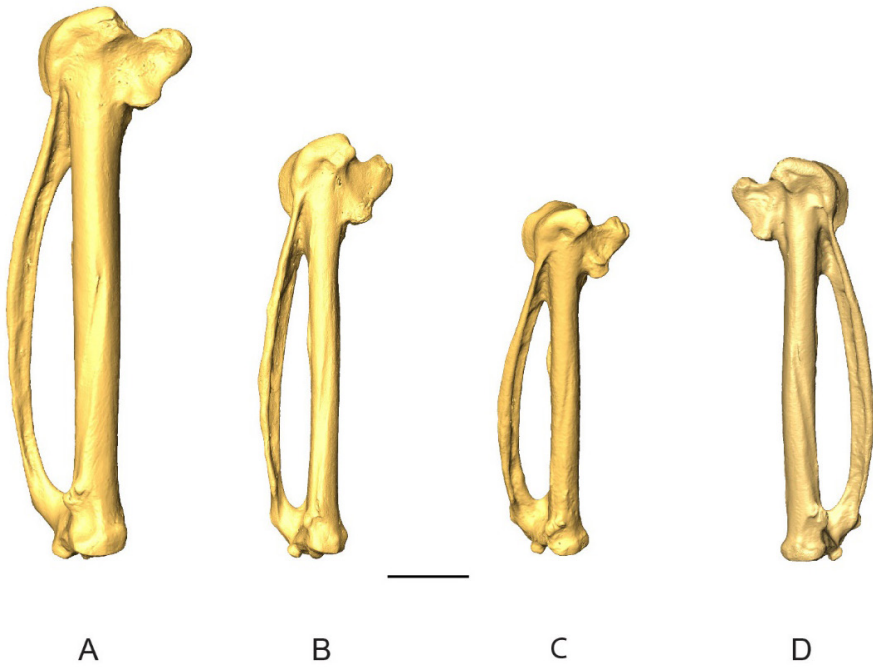
Measurements (in mm) and characters of carpometacarpus from modern specimens (character states see Fig. 15). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	L	Bp	Did	CMC_TC1	CMC_TC2	CMC_OMM	CMC_PE	CMC_FAU1	CMC_FAU2	CMC_A	CMC_VM	CMC_SH	CMC_SMD	CMC_FADM	CMC_DM
Patagioenas_squamosa	PACEA_O_442	33.5	33.1	9.3	5.7	B	A	B	A	B	A	B	B	B	B	B	A
Patagioenas_squamosa	PACEA_O_443	32.7	31.7	8.9	5.8	C	C	B	A	B	A	C	A	B	B	B	A
Patagioenas_squamosa	PACEA_O_486	35.2	34.3	9.4	5.9	C	A	B	A	B	A	B	B	B	B	B	A
Patagioenas_squamosa	PACEA_O_487	31.6	30.8	9.2	5.6	B	A	B	B	B	B	B	B	B	B	B	A
Patagioenas_squamosa	PACEA_O_704	32.0	31.2	9.1	5.7	C	-	B	A	B	A	C	A	B	B	B	A
Patagioenas_squamosa	PACEA_O_705	33.3	32.9	9.7	5.6	C	C	B	B	B	B	B	A	B	C	B	A
Patagioenas_squamosa	USNM_501768	31.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patagioenas_leucocephala	PACEA_O_493	30.4	29.6	8.5	5.4	B	A	B	B	B	A	A/B	B	B	B	B	A
Patagioenas_leucocephala	PACEA_O_706	30.1	29.4	8.6	5.2	B	C	B	B	A	A	C	A	B	B/C	B	B
Patagioenas_leucocephala	PACEA_O_821	30.1	29.4	8.5	5.5	B	A	B	B	B	A	A/B	A	B	B/C	B	A
Patagioenas_leucocephala	PACEA_O_822	31.4	30.8	8.4	5.5	C	B	B	B	B	A	A/B	A	B	B	B	A
Patagioenas_leucocephala	PACEA_O_970	30.9	29.9	8.6	5.1	A	B	B	B	B	A	C	A	B	B/C	B	A
Patagioenas_leucocephala	PACEA_O_1065	29.4	28.4	8.5	5.6	C	B	B	B	B	A	A/B	D	B	B	B	A
Patagioenas_leucocephala	PACEA_O_1066	30.0	28.9	8.5	5.2	B	A	B	B	B	A	A/B	A	B	B/C	B	A
Patagioenas_leucocephala	PACEA_O_1117	32.2	31.5	8.9	5.8	B	A	B	B	A	A	A/B	A	B	B/C	B	A
Patagioenas_leucocephala	USNM_554982	32.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_226458	34.9	-	-	-	A	A	B	D	A	A	B	A	A?	A	A	A
Patagioenas_inornata	USNM_289629	34.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_289630	35.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_290977	33.7	-	-	-	A	A	A/B	A	A	A	B/C	A	A?	B	A	A
Patagioenas_inornata	USNM_292505	33.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_292506	31.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	13.0	12.3	3.6	2.6	-	-	-	-	-	-	-	-	-	-	-	-
Geotrygon_montana	PACEA_O_492	24.0	23.3	7.2	4.6	C	C	B	C/D	B	C	A	D	B	A	B	C
Geotrygon_montana	PACEA_O_847	24.0	23.5	7.1	4.1	C	C	B	C/D	B	C	A	D	B	A	C	B/C
Geotrygon_montana	PACEA_O_1055	24.9	24.6	7.4	4.6	C	C	B	C/D	B	C	A	D	B	A	B	C
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	-	-	C	B	A	D	B	C	A	D	B	A	C	C
Geotrygon_montana	MEC_150414_A	24.4	-	7.2	5.0	-	-	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_292518	24.5	-	-	-	C	A	A	B/D	B	C	B	D	A	A	A	B
Geotrygon_chrysia	USNM_292519	24.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_318870	25.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_554602	24.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	MNHN_ZO_AC_1931_525	-	-	-	-	C	A	A	D	B	A	C	A	A	B	B/C	B
Geotrygon_mystacea	PACEA_O_494	24.6	23.8	7.6	4.1	B	A	A	D	A/B	C	A	C	-	A	B	C
Geotrygon_mystacea	PACEA_O_713	25.7	25.4	7.7	5.0	B	A	A	D	B	C	A/B	D	A	B	C	C
Geotrygon_mystacea	PACEA_O_766	27.3	26.0	7.7	4.6	B	C	A	D	B	C	A	D	A	A	B	B
Geotrygon_mystacea	PACEA_O_858	26.2	25.8	7.4	4.6	B	A	A	C	B	A/C	A	D	A	B	C	C
Geotrygon_mystacea	PACEA_O_1085	27.0	26.0	8.4	5.0	B	A	A	C	B	C	A/B	C	A	A?	C	B
Geotrygon_mystacea	MEC_041112_I	26.9	-	8.1	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix N. Continuation

Taxon	Catalog_Number	GL	L	Bp	Did	CMC_TC1	CMC_TC2	CMC_OMM	CMC_PE	CMC_FAU1	CMC_FAU2	CMC_A	CMC_VM	CMC_SH	CMC_SMD	CMC_FADM	CMC_DM
*Leptotila_wellsi**	NHMUK_ZOO_1898_9_20_1	22.2	21.7	6.2	4.1	D	C	A	D	B	A	A/B	C	B	B	B	B
Zenaida_asiatica_asiatica	PACEA_O_707	26.0	25.3	7.2	4.3	C	B	B	A	A	A	A/B	B	B	C	B	B
Zenaida_asiatica_asiatica	PACEA_O_1004	25.7	25.1	6.9	4.9	C	A	B	C/D	A	C	A/B	C	B	B	B	B
Zenaida_asiatica_asiatica	PACEA_O_1013	24.8	24.3	7.0	4.6	B	B	B	D	A	C	A/B	B	B	B	B	B/C
Zenaida_asiatica_asiatica	PACEA_O_1061	26.5	26.2	7.8	4.7	C	B	B	B	A	B	A/B	B	B	B	B	B
Zenaida_asiatica_asiatica	PACEA_O_1062	26.2	25.8	7.2	4.2	C	A	B	A	A	B	A/B	B	B	B	B	B
Zenaida_asiatica_asiatica	PACEA_O_1063	25.9	25.2	7.3	4.0	B	B	A	C/D	A	A	A/B	B	B	B	B	B
Zenaida_asiatica_asiatica	PACEA_O_1064	26.2	25.5	7.4	4.8	C	A	B	B	A	B	A/B	C	B	B	B	B
Zenaida_aurita_aurita	PACEA_O_430	25.9	25.4	7.3	4.7	B	A	B	A	A	A/B	B/C	C/D	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_440	24.9	24.3	7.1	4.0	B/C	A	B	B/C	A	B	B	C	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_441	23.7	23.4	6.7	3.9	D	B	B	A	A	B	B	C	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_448	25.0	24.6	7.1	4.1	B/C	B	B	C	A	C	B/C	C	A	C	B	A
Zenaida_aurita_aurita	PACEA_O_449	25.5	25.2	6.9	4.7	A/B	B	B	C	A	C	A/B	C	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_708	23.8	23.3	7.1	4.2	A/B	B	B	C/D	A	B	A	C/D	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_709	25.9	25.2	7.2	4.5	B	B	A/B	C/D	A	B	B	C	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_710	24.8	24.3	6.9	4.0	C/D	B	B	C/D	A	A	A	C/D	B	B	C	A
Zenaida_aurita_aurita	PACEA_O_795	25.6	25.1	7.4	4.4	A/B	B	A/B	A	A	A/C	B	C	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_865	24.6	23.8	7.3	4.7	B/C	B	B	D	A	A/B	B	C/D	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_987	23.9	23.3	6.4	4.7	B/C	B	B	B	A	A	B	C	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_995	24.5	24.0	6.7	4.2	B	A	B	A/B	A	C	B/C	C	B	B	B	A
Zenaida_aurita_aurita	PACEA_O_996	24.5	23.7	6.8	4.2	B	B	B	A/B	A	A/B	A/B	C	A	B	B	A
Zenaida_aurita_aurita	PACEA_O_1001	25.0	24.0	7.0	4.4	A/B	B	B	A/B	A	A/B	B	C	B	B	B	A
Zenaida_aurita_aurita	MEC_130513_G	24.0	-	6.6	5.5	-	-	-	-	-	-	-	-	-	-	-	-
Zenaida_auriculata_stenura	PACEA_O_495	20.0	19.6	5.8	3.5	C	B/C	B		A	A	B	C	B	B	B	B
Zenaida_auriculata_stenura	PACEA_O_496	19.9	19.3	5.9	3.5	C	B/C	B	A	A	A	B	C	B	B	C	B
Zenaida_auriculata_stenura	PACEA_O_497	21.1	20.7	6.0	3.7	C	C	B	D	A	A	C	C	B	B	B	B
Zenaida_auriculata_stenura	PACEA_O_498	22.8	22.4	6.4	4.1	D	B	B	D	A	A	A	C	B	B	B	A
Zenaida_auriculata_stenura	PACEA_O_499	22.0	21.5	6.6	4.0	C	B	B	C/D	A	A	B	B	B	B	C	B
Zenaida_macroura	PACEA_O_963	23.9	23.3	6.8	4.0	C	B	A/B	B	A	A	B	B	B	B	B	B

APPENDIX O



3D-models of carpometacarpi in dorsal view. A, *Patagioenas inornata* USNM 226458; B, *Geotrygon montana* MNHN-ZO-AC-1993-116; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA-O-707. A-C, right side; D, left side. Scale bar equals 5 mm.

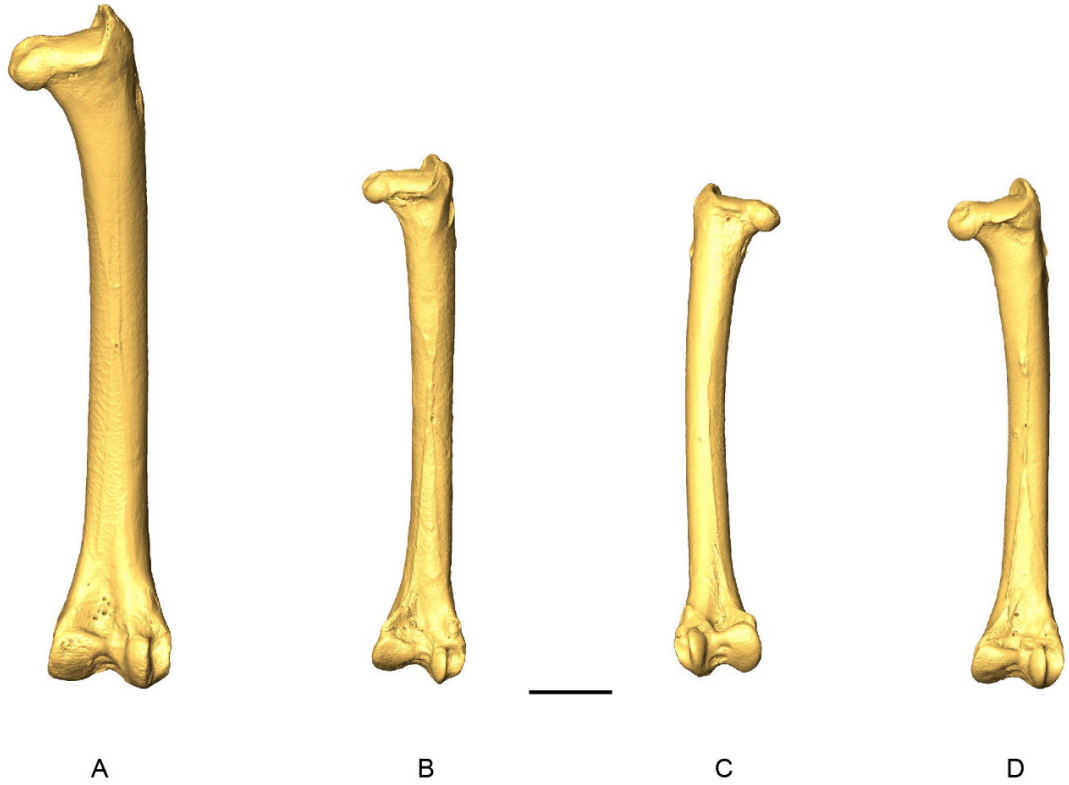
APPENDIX P

Measurements (in mm) and characters of femur from modern specimens (character states see Fig. 18). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	Lm	Bp	Dp	Sc	Bd	Dd	FEM_FAA	FEM_IMI	FEM_CL
Patagioenas_squamosa	PACEA_O_442	40.4	39.3	8.1	5.2	3.4	7.1	6.2	B	A	A
Patagioenas_squamosa	PACEA_O_443	41.8	40.1	8.4	5.2	3.6	7.2	6.4	B	A	B
Patagioenas_squamosa	PACEA_O_486	44.2	42.6	8.7	5.4	3.7	7.9	6.3	B	A	B
Patagioenas_squamosa	PACEA_O_487	39.9	37.9	8.6	5.4	3.4	7.6	6.0	A	A	A
Patagioenas_squamosa	PACEA_O_704	-	40.9	8.2	5.5	3.5	7.4	6.2	B/C	A	-
Patagioenas_squamosa	PACEA_O_705	42.9	41.2	8.3	5.2	3.7	7.6	6.3	B/C	A	A
Patagioenas_squamosa	MEC_100513_A	-	-	-	-	-	7.3	-	-	-	-
Patagioenas_leucocephala	PACEA_O_493	37.1	36.2	7.6	5.1	3.2	6.5	5.4	A	A	A/B
Patagioenas_leucocephala	PACEA_O_706	-	-	7.3	4.9	-	-	-	A	A	-
Patagioenas_leucocephala	PACEA_O_821	37.4	35.9	7.1	4.5	3.0	6.6	5.4	A	A	B
Patagioenas_leucocephala	PACEA_O_822	37.1	35.6	7.2	4.6	3.1	6.5	5.4	A	A	A
Patagioenas_leucocephala	PACEA_O_970	38.0	36.5	7.4	4.7	3.3	6.4	5.6	A	A	A/B
Patagioenas_leucocephala	PACEA_O_1065	36.1	34.4	7.0	4.8	3.0	6.6	5.4	A	A	A/B
Patagioenas_leucocephala	PACEA_O_1066	36.5	35.0	7.2	4.7	2.9	6.2	5.4	A	A	A
Patagioenas_leucocephala	PACEA_O_1117	39.7	38.2	7.7	5.1	3.2	-	5.9	B	A	-
Patagioenas_leucocephala	MEC_171112_C	39.4	37.6	7.4	5.1	3.4	7.1	-	-	-	-
Patagioenas_leucocephala	USNM_554982	39.0	-	-	-	-	-	-	-	-	-
Patagioenas_leucocephala	USNM_556833	38.1	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_7021	44.1	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_226458	43.4	-	-	-	-	-	-	B	A/B	A
Patagioenas_inornata	USNM_289629	42.3	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_289630	43.0	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_290977	39.5	-	-	-	-	-	-	B	B	B
Patagioenas_inornata	USNM_292505	39.7	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_292506	39.2	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_582879	40.7	-	-	-	-	-	-	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	19.4	18.5	3.5	2.3	1.7	3.3	2.7	-	-	-
Geotrygon_montana	PACEA_O_492	37.2	34.9	7.2	4.2	2.8	6.4	5.2	A	A	A
Geotrygon_montana	PACEA_O_847	36.4	34.7	6.9	4.1	2.9	6.7	5.4	A	A	A
Geotrygon_montana	PACEA_O_1055	39.4	37.6	7.1	4.5	3.0	6.8	5.8	A	A	A/B
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	-	-	-	-	-	A	A	A
Geotrygon_montana	MEC_150414_A	36.7	34.6	7.0	4.2	2.9	6.6	-	-	-	-
Geotrygon_chrysia	USNM_290993	34.6	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_292518	33.1	-	-	-	-	-	-	B	A	A
Geotrygon_chrysia	USNM_292519	34.9	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_318870	35.5	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_554602	33.9	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	MNHN_ZO_AC_1931_525	-	-	-	-	-	-	-	B?	A	A
Geotrygon_mystacea	PACEA_O_494	36.0	33.9	7.2	4.3	2.9	6.6	5.6	B	A/B	A
Geotrygon_mystacea	PACEA_O_713	38.0	35.8	7.3	4.3	3.1	7.1	5.7	A	A	A
Geotrygon_mystacea	PACEA_O_766	39.7	37.4	7.2	4.6	2.9	7.3	5.7	A	A	A
Geotrygon_mystacea	PACEA_O_858	39.7	37.6	7.5	4.6	3.0	7.3	5.7	A	A	A
Geotrygon_mystacea	PACEA_O_1085	40.3	38.2	7.7	4.7	3.3	7.3	6.0	A	A	A
Geotrygon_mystacea	MEC_041112_I	-	-	-	-	-	7.1	-	-	-	-

Taxon	Catalog_Number	GL	Lm	Bp	Dp	Sc	Bd	Dd	FEM_FAA	FEM_IMI	FEM_CL
*Leptotila_wellsi**	NHMUK_ZOO_1898_9_20_1	32.2	29.8	5.6	4.1	2.4	5.2	4.3	-	A	B
Zenaida_asiatica_asiatica	PACEA_O_707	31.8	30.4	6.0	4.0	2.5	5.7	4.6	A/B	A	B
Zenaida_asiatica_asiatica	PACEA_O_1004	31.7	30.4	6.1	3.8	2.6	5.8	4.6	B	A	B
Zenaida_asiatica_asiatica	PACEA_O_1013	30.6	28.9	5.7	3.7	2.5	5.5	4.5	B	A	B
Zenaida_asiatica_asiatica	PACEA_O_1061	31.5	30.0	6.0	3.9	2.7	5.5	4.7	B	A	B
Zenaida_asiatica_asiatica	PACEA_O_1062	31.5	30.0	6.1	3.7	2.6	5.4	4.4	B	A	B
Zenaida_asiatica_asiatica	PACEA_O_1063	31.6	30.2	6.0	4.0	2.5	5.6	4.5	B	A	A/B
Zenaida_asiatica_asiatica	PACEA_O_1064	31.5	29.9	5.9	3.7	2.4	-	-	C	A	A
Zenaida_aurita_aurita	PACEA_O_430		33.0	6.6	4.5	2.9	6.3	4.8	A	-	B
Zenaida_aurita_aurita	PACEA_O_440	32.9	30.8	6.3	4.1	2.8	6.0	5.1	C	B	A
Zenaida_aurita_aurita	PACEA_O_441	32.3	30.7	6.2	3.7	2.5	5.7	4.3	A	-	A
Zenaida_aurita_aurita	PACEA_O_448	33.7	32.2	6.4	4.8	3.1	5.9	4.9	C	B	A
Zenaida_aurita_aurita	PACEA_O_449	-	-	-	-	-	-	-	C	A	A/B
Zenaida_aurita_aurita	PACEA_O_708	31.7	30.0	6.3	3.8	2.6	5.9	4.7	A	B	A
Zenaida_aurita_aurita	PACEA_O_709	32.6	-	-	-	-	-	-	A	B	A
Zenaida_aurita_aurita	PACEA_O_710	32.3	31.0	6.6	4.0	2.9	6.2	4.8	C	B	A
Zenaida_aurita_aurita	PACEA_O_795	33.6	31.8	6.5	4.1	2.8	6.4	4.9	A	B	A/B
Zenaida_aurita_aurita	PACEA_O_865	31.4	29.9	6.5	3.9	2.9	6.1	4.6	C	B	A/B
Zenaida_aurita_aurita	PACEA_O_987	-	-	-	-	-	-	-	A	B	A
Zenaida_aurita_aurita	PACEA_O_995	-	-	-	-	-	-	-	-	B	A/B
Zenaida_aurita_aurita	PACEA_O_996	-	-	-	-	-	-	-	A	B	A
Zenaida_aurita_aurita	PACEA_O_1001	32.5	31.1	6.5	4.0	3.0	5.9	4.7	A	B	A
Zenaida_aurita_aurita	MEC_130513_G	32.6	31.0	6.4	3.9	2.5	5.8	-	-	A	-
Zenaida_auriculata_stenura	PACEA_O_495	27.5	25.9	5.3	3.5	2.3	5.1	4.0	A	B	A
Zenaida_auriculata_stenura	PACEA_O_496	25.8	24.5	5.0	3.4	2.3	4.9	4.2	-	B	A/B
Zenaida_auriculata_stenura	PACEA_O_497	27.4	26.1	5.0	3.3	2.2	4.7	3.8	A	B	B
Zenaida_auriculata_stenura	PACEA_O_498	27.7	26.1	5.4	3.4	2.4	4.9	4.0	C	B	A
Zenaida_auriculata_stenura	PACEA_O_499	27.2	25.9	5.4	3.5	2.1	4.9	4.0	B	B	A
Zenaida_macroura	PACEA_O_963	30.5	28.9	5.8	4.0	2.7	5.4	4.2	B	B	B

APPENDIX Q



3D-models of femora in caudal view. A, *Patagioenas inornata* USNM 226458; B, *Geotrygon montana* MNHN-ZO-AC-1993-116; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA-O-707. A–B, D, right side; C, left side. Scale bar equals 5 mm.

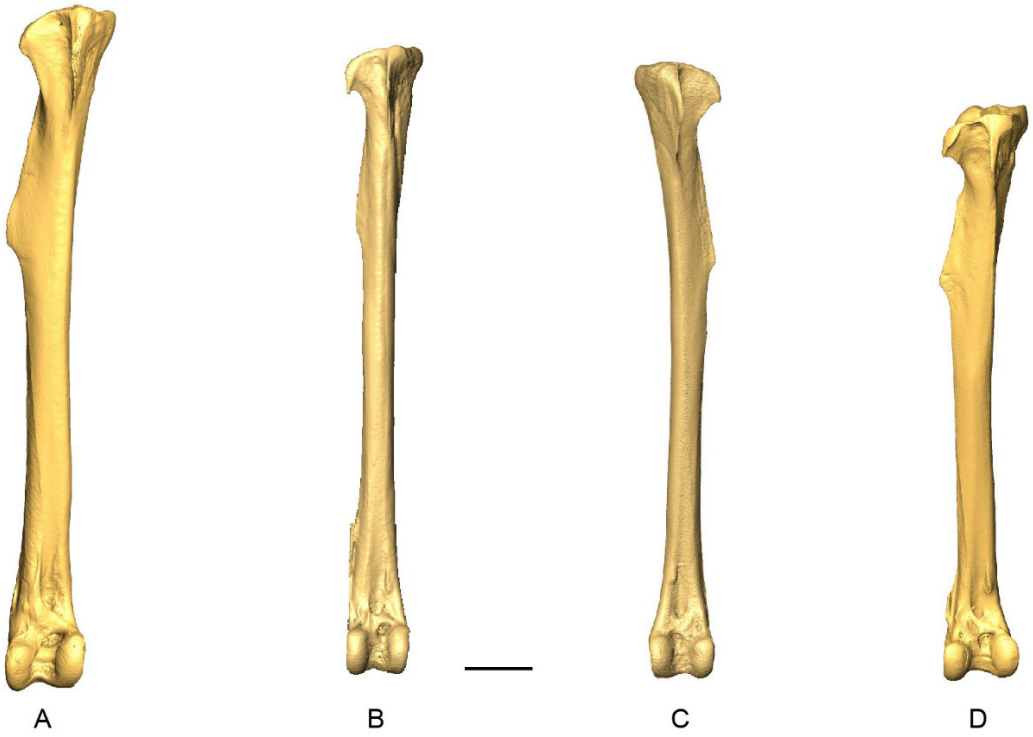
APPENDIX R

Measurements (in mm) and characters of tibiotarsus from modern specimens (character states see Fig. 21). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	La	Dip	Sc	Bd	Dd	TIB_IT	TIB_C1	TIB_C2	TIB_CM
Patagioenas_squamosa	PACEA_O_442	55.4	54.8	7.7	3.5	6.5	6.7	B	A	C	B
Patagioenas_squamosa	PACEA_O_443	55.3	54.3	7.7	3.1	6.3	6.4	B	A	A	B
Patagioenas_squamosa	PACEA_O_486	56.8	55.9	7.6	3.1	6.8	6.3	A	D	C	B
Patagioenas_squamosa	PACEA_O_487	52.4	51.5	7.9	3.4	6.7	6.6	B	D	A	B
Patagioenas_squamosa	PACEA_O_704	56.0	55.4	7.8	3.1	6.7	6.4	-	A	A	B
Patagioenas_squamosa	PACEA_O_705	54.5	53.7	8.0	3.3	6.7	6.4	B	C	C	A
Patagioenas_leucocephala	PACEA_O_493	48.7	47.9	7.0	2.8	5.8	5.9	A	D	C	B
Patagioenas_leucocephala	PACEA_O_706	48.5	48.1	6.8	2.9	5.7	5.9	A	A	C	A/B
Patagioenas_leucocephala	PACEA_O_821	47.9	47.4	6.8	2.9	5.7	5.7	A	D	A	A
Patagioenas_leucocephala	PACEA_O_822	48.9	48.5	6.7	3.0	6.0	5.9	-	D	A	B
Patagioenas_leucocephala	PACEA_O_970	49.1	48.4	6.8	2.9	6.1	5.9	A	D	C	B
Patagioenas_leucocephala	PACEA_O_1065	48.0	47.4	7.0	2.7	5.8	5.7	A	D	A	B
Patagioenas_leucocephala	PACEA_O_1066	48.2	47.4	6.8	2.8	6.0	5.8	A	D	A	B
Patagioenas_leucocephala	PACEA_O_1117	52.0	51.2	7.5	2.9	6.2	6.0	A	D	A	B
Patagioenas_inornata	USNM_226458	56.3	-	-	-	-	-	A	A	A	A/B
Patagioenas_inornata	USNM_289629	54.9	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_289630	56.4	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_290977	55.3	-	-	-	-	-	A	-	C	-
Patagioenas_inornata	USNM_292505	53.1	-	-	-	-	-	-	-	-	-
Patagioenas_inornata	USNM_292506	52.6	-	-	-	-	-	-	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	26.9	26.7	3.9	1.4	2.8	3.0	-	-	-	-
Columbina_passerina_nigrirostris	PACEA_O_904	27.2	26.8	3.6	1.3	2.8	2.8	-	-	-	-
Geotrygon_montana	PACEA_O_492	-	-	5.5	-	5.6	5.8	A	D	A	B
Geotrygon_montana	PACEA_O_847	56.6	56.0	7.3	2.5	5.5	5.9	A	D	C	A/B
Geotrygon_montana	PACEA_O_1055	58.5	57.8	7.4	2.5	5.6	6.5	A	D	C	B
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	-	-	-	-	A	B	C	A
Geotrygon_chrysia	USNM_292518	49.3	-	-	-	-	-	A	B	C	A
Geotrygon_chrysia	USNM_292519	52.2	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_318870	53.4	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	USNM_554602	50.3	-	-	-	-	-	-	-	-	-
Geotrygon_chrysia	MNHN_ZO_AC_1931_525	-	-	-	-	-	-	A	B	C	A
Geotrygon_mystacea	PACEA_O_494	52.9	52.2	7.5	2.4	5.5	5.6	A	B/D	C	B
Geotrygon_mystacea	PACEA_O_713	55.7	55.0	-	2.7	5.6	6.0	-	D	C	B
Geotrygon_mystacea	PACEA_O_766	58.5	57.7	8.2	2.7	5.9	6.0	A	D	C	B
Geotrygon_mystacea	PACEA_O_858	58.2	57.5	8.1	2.7	5.7	6.0	A	D	A	B
Geotrygon_mystacea	PACEA_O_1085	59.1	58.5	8.8	3.0	6.1	6.3	A	B	C	B

Taxon	Catalog_Number	GL	La	Dip	Sc	Bd	Dd	TIB_IT	TIB_C1	TIB_C2	TIB_CM
*Leptotila_wellsi**	NHMUK_ZOO_1898_9_20_1	47.2	46.7	6.5	2.4	4.7	4.2	A	B	C	A/B
Zenaida_asiatica_asiatica	PACEA_O_707	43.5	42.8	6.8	2.5	5.1	4.9	A	D	A	A
Zenaida_asiatica_asiatica	PACEA_O_1004	44.0	43.7	6.2	2.5	4.9	4.8	A	D	B	A
Zenaida_asiatica_asiatica	PACEA_O_1013	43.1	42.8	6.4	2.5	4.9	4.8	A	D	B	A
Zenaida_asiatica_asiatica	PACEA_O_1061	45.2	44.2	6.4	2.5	4.9	5.1	A	D	B	A
Zenaida_asiatica_asiatica	PACEA_O_1062	45.0	44.6	6.4	2.4	5.1	5.0	A	D	A	B
Zenaida_asiatica_asiatica	PACEA_O_1063	45.0	44.5	6.7	2.5	5.0	5.0	A	D	B	A
Zenaida_asiatica_asiatica	PACEA_O_1064	-	-	6.3	-	-	-	A	D	-	A
Zenaida_aurita_aurita	PACEA_O_430	49.7	48.3	7.2	2.6	5.4	5.3	A	B	A	B
Zenaida_aurita_aurita	PACEA_O_440	46.6	45.8	7.0	2.6	5.2	5.4	A	B	A	B
Zenaida_aurita_aurita	PACEA_O_441	46.1	45.1	6.2	2.1	4.9	4.9	A	D	A	-
Zenaida_aurita_aurita	PACEA_O_448	46.9	46.3	6.9	2.4	5.1	4.8	A	D	A	B
Zenaida_aurita_aurita	PACEA_O_449	47.6	47.1	6.7	2.5	5.0	5.2	A	D	C	B
Zenaida_aurita_aurita	PACEA_O_708	45.2	44.5	6.7	2.5	5.3	5.4	A	D	C	B
Zenaida_aurita_aurita	PACEA_O_709	48.0	47.3	7.0	2.5	5.2	5.4	A	D	A	B
Zenaida_aurita_aurita	PACEA_O_710	46.1	45.2	6.7	2.5	4.9	5.0	A	B	C	B
Zenaida_aurita_aurita	PACEA_O_795	48.3	47.7	7.0	2.2	5.1	5.4	A	B	C	B
Zenaida_aurita_aurita	PACEA_O_865	46.1	45.3	6.9	2.6	5.6	5.0	A	D	A	B
Zenaida_aurita_aurita	PACEA_O_987	45.8	45.0	-	2.3	5.1	5.1	A	B/D	A	A
Zenaida_aurita_aurita	PACEA_O_995	46.0	45.2	6.9	2.6	5.2	5.3	A	B	C	A
Zenaida_aurita_aurita	PACEA_O_996	46.1	45.2	7.0	2.8	5.1	5.3	A	B/D	C	B
Zenaida_aurita_aurita	PACEA_O_1001	46.0	45.2	6.8	2.5	5.0	5.2	A	B/D	C	A
Zenaida_auriculata_stenura	PACEA_O_495	38.0	37.8	4.3	2.1	4.3	4.5	A	D	B	B
Zenaida_auriculata_stenura	PACEA_O_496	35.0	34.6	5.6	2.0	4.1	4.0	A	B	B	B
Zenaida_auriculata_stenura	PACEA_O_497	-	-	5.5	2.2	4.1	4.2	A	B	B	B
Zenaida_auriculata_stenura	PACEA_O_498	38.5	38.2	5.7	2.2	4.6	4.6	A	B	A	B
Zenaida_auriculata_stenura	PACEA_O_499	37.5	37.0	5.8	2.3	4.3	4.7	A	B	A	B
Zenaida_macroura	PACEA_O_963	39.9	39.4	6.2	2.3	4.6	4.9	A	B	A	B

APPENDIX S



3D-models of tibiotarsi in cranial view. A, *Patagioenas inornata* USNM 226458; B, *Geotrygon montana* MNHN-ZO-AC-1993-116; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA-O-707. A-B, D, right side; C, left side. Scale bar equals 5 mm.

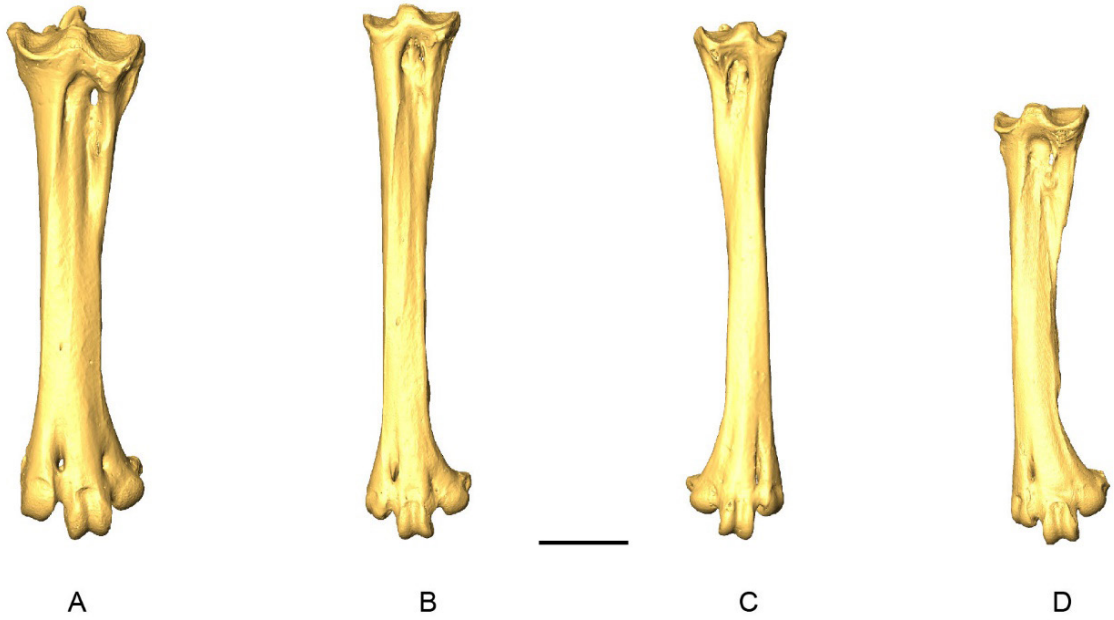
APPENDIX T

Measurements (in mm) and characters of tarsometatarsus from modern specimens (character states see Fig. 24). Unavailable data is indicated by a dash, 3D–models with an asterisk

Taxon	Catalog_Number	GL	Bp	Sc	Bd	TMT_CMH	TMT_FPL	TMT_TMIV
Patagioenas_squamosa	PACEA_O_442	28.9	7.4	3.7	7.3	A	A	B
Patagioenas_squamosa	PACEA_O_443	28.4	7.3	3.5	7.2	A	B	B
Patagioenas_squamosa	PACEA_O_486	29.9	7.5	3.5	8.0	A	B	B
Patagioenas_squamosa	PACEA_O_487	27.6	7.3	3.6	7.2	A	B	B
Patagioenas_squamosa	PACEA_O_704	27.9	7.2	3.5	7.0	B	B	B
Patagioenas_squamosa	PACEA_O_705	28.9	7.3	3.7	7.0	A	A	A/B
Patagioenas_squamosa	MEC_100513_A	27.5	7.2	-	7.4	-	A	-
Patagioenas_leucocephala	PACEA_O_493	24.8	6.4	3.0	6.1	B	A	B
Patagioenas_leucocephala	PACEA_O_706	25.8	6.7	3.2	6.2	A	A	B
Patagioenas_leucocephala	PACEA_O_821	25.5	6.5	3.2	6.5	B	B	B
Patagioenas_leucocephala	PACEA_O_822	25.9	6.7	3.1	6.0	A	A	B
Patagioenas_leucocephala	PACEA_O_970	26.4	6.8	3.1	6.5	A	B	B
Patagioenas_leucocephala	PACEA_O_1065	25.0	6.6	3.0	6.3	A	A	B
Patagioenas_leucocephala	PACEA_O_1066	25.5	6.6	3.1	6.5	A	A	B
Patagioenas_leucocephala	PACEA_O_1117	27.2	6.6	3.2	6.6	A	A	B
Patagioenas_leucocephala	MEC_171112_C	26.4	6.4	3.2	6.7	-	A	-
Patagioenas_inornata	USNM_226458	30.2	-	-	-	A	B	B
Patagioenas_inornata	USNM_289629	28.4	-	-	-	-	-	-
Patagioenas_inornata	USNM_289630	30.1	-	-	-	-	-	-
Patagioenas_inornata	USNM_290977	29.0	-	-	-	A	-	B
Patagioenas_inornata	USNM_292505	27.6	-	-	-	-	-	-
Patagioenas_inornata	USNM_292506	27.1	-	-	-	-	-	-
Columbina_passerina_nigrirostris	MEC_041112_A	15.3	3.3	1.7	3.8	-	-	-
Geotrygon_montana	PACEA_O_492	35.1	6.5	2.2	6.8	B	A	B
Geotrygon_montana	PACEA_O_847	35.1	6.4	2.5	6.7	C	A	B
Geotrygon_montana	PACEA_O_1055	37.9	6.7	2.5	7.0	B	A	B
Geotrygon_montana	MNHN_ZO_AC_1993_116	-	-	-	-	B	A	B
Geotrygon_montana	MEC_150414_A	34.8	6.7	2.4	6.8	-	-	-
Geotrygon_chrysia	USNM_292518	28.9	-	-	-	A	A	B
Geotrygon_chrysia	USNM_292519	30.4	-	-	-	-	-	-
Geotrygon_chrysia	USNM_318870	31.1	-	-	-	-	-	-
Geotrygon_chrysia	USNM_554602	29.4	-	-	-	-	-	-
Geotrygon_mystacea	PACEA_O_494	31.4	6.2	2.5	6.8	B	A	B
Geotrygon_mystacea	PACEA_O_713	33.6	6.3	2.6	6.7	B	A	B
Geotrygon_mystacea	PACEA_O_766	34.8	6.6	2.6	6.7	A/B	A	B
Geotrygon_mystacea	PACEA_O_858	33.6	6.4	2.5	7.2	A	A	B
Geotrygon_mystacea	PACEA_O_1085	36.0	7.0	2.7	7.7	C	A	B
Geotrygon_mystacea	MEC_041112_I	35.8	6.7	2.5	6.7	-	-	-

Taxon	Catalog_Number	GL	Bp	Sc	Bd	TMT_CMH	TMT_FPL	TMT_TMIV
*Leptotila_wellsi**	NHMUK_ZOO_1898_9_20_1	28.5	5.3	2.1	5.1	B	A	B
Zenaida_asiatica_asiatica	PACEA_O_707	24.6	5.5	2.5	5.4	B/C	B	A
Zenaida_asiatica_asiatica	PACEA_O_1004	24.8	5.4	2.6	5.9	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1013	24.0	5.3	2.7	5.3	B	B	A
Zenaida_asiatica_asiatica	PACEA_O_1061	25.0	5.5	2.9	5.4	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1062	25.0	5.6	2.7	5.5	C	A	A
Zenaida_asiatica_asiatica	PACEA_O_1063	25.0	5.5	2.8	5.8	B	A	A
Zenaida_asiatica_asiatica	PACEA_O_1064	-	5.6	-	5.4	B	A	A
Zenaida_aurita_aurita	PACEA_O_430	28.1	6.4	2.8	6.0	B	A	B
Zenaida_aurita_aurita	PACEA_O_440	26.7	6.0	2.8	5.9	C	A	B
Zenaida_aurita_aurita	PACEA_O_441	25.6	5.6	2.4	5.4	B	B	B
Zenaida_aurita_aurita	PACEA_O_448	26.7	5.8	2.6	6.4	C	A	B
Zenaida_aurita_aurita	PACEA_O_449	26.1	5.7	2.4	5.9	C	B	B
Zenaida_aurita_aurita	PACEA_O_708	25.6	5.8	2.7	5.8	B	A	B
Zenaida_aurita_aurita	PACEA_O_709	26.5	6.0	2.7	6.0	C	A	B
Zenaida_aurita_aurita	PACEA_O_710	26.1	5.7	2.7	5.8	C	A	B
Zenaida_aurita_aurita	PACEA_O_795	26.5	5.8	2.5	5.8	B	A	B
Zenaida_aurita_aurita	PACEA_O_865	26.2	6.2	2.7	6.2	A	A	B
Zenaida_aurita_aurita	PACEA_O_987	24.9	5.3	2.3	5.5	B	A	B
Zenaida_aurita_aurita	PACEA_O_995	25.5	5.5	2.5	5.8	B/C	A	B
Zenaida_aurita_aurita	PACEA_O_996	25.9	5.9	2.7	6.3	A	A	B
Zenaida_aurita_aurita	PACEA_O_1001	25.4	5.5	2.7	6.0	C	A	B
Zenaida_aurita_aurita	MEC_130513_G	24.8	6.0	2.7	5.7	-	-	-
Zenaida_auriculata_stenura	PACEA_O_495	21.4	4.8	2.2	5.4	B	B	B
Zenaida_auriculata_stenura	PACEA_O_496	-	4.9	2.5	5.5	A	A	B
Zenaida_auriculata_stenura	PACEA_O_497	20.7	4.8	2.4	5.0	A	B	B
Zenaida_auriculata_stenura	PACEA_O_498	21.7	4.9	2.4	5.5	B	A	B
Zenaida_auriculata_stenura	PACEA_O_499	21.1	4.7	2.3	5.3	B	-	A?
Zenaida_macroura	PACEA_O_963	22.2	5.0	2.5	5.1	B	A	B

APPENDIX U



3D-models of tarsometatarsi in dorsal view. A, *Patagioenas inornata* USNM 226458; B, *Geotrygon montana* MNHN-ZO-AC-1993-116; C, *Leptotila wellsi* NHMUK-ZOO-1898.9.20.1; D, *Zenaida asiatica* PACEA-O-707. A-B, D, right side; C, left side. Scale bar equals 5 mm.