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The diversity and biogeography of late Pleistocene birds from the lowland Neotropics

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ABSTRACT

The Neotropical lowlands sustain the world's richest bird communities, yet little that we know about their history is based on paleontology. Fossils afford a way to investigate distributional shifts in individual species, and thus improve our understanding of long-term change in Neotropical bird communities. We report a species-rich avian fossil sample from a late Pleistocene tar seep (Mene de Inciarte) in northwestern Venezuela. A mere 175 identified fossils from Mene de Inciarte represent 73 species of birds, among which six are extinct, and eight others no longer occur within 100 km. These 14 species consist mainly of ducks (Anatidae), snipe (Scolopacidae), vultures/condors (Vulturidae), hawks/eagles (Accipitridae), and blackbirds (Icteridae). Neotropical bird communities were richer in the late Pleistocene than today; their considerable extinction may be related to collapse of the large mammal fauna at that time. The species assemblage at Mene de Inciarte suggests that biogeographic patterns, even at continental scales, have been remarkably labile over short geological time frames. Mene de Inciarte is but one of 300+ tar seeps in Venezuela, only two of which have been explored for fossils. We may be on the cusp of an exciting new era of avian paleontology in the Neotropics.

Introduction

The rich, diverse bird communities of the lowland Neotropics undoubtedly have been shaped by many historic processes, including the major climate fluctuations (glacial–interglacial cycles) over the past ~2.5 million yr (Rull, 2011; Turchetto-Zolet et al., 2012). Most of what we know about the evolution and historic biogeography of Neotropical birds is based on phylogenies inferred from the molecular data of modern species (Brumfield, 2012). Paleontology provides a complementary perspective through morphologically based identifications of species that, whether living or extinct, occurred at known times in the geological past. Furthermore, fossil-based evidence can help us to refine concepts of extinction, trophic cascades, and the long-term stability of species-specific habitat preferences (Semken et al., 2010; Terborgh and Estes, 2010; Oswald and Steadman, 2011). In this spirit, we studied a remarkably rich set of avian fossils from lowland Venezuela.

Mene de Inciarte (10°47′42.6″N, 72°14′20.8″W, elevation 115 m) is a surface asphalt deposit (tar seep) in Municipio Mara, Zulia State, northwestern Venezuela (Fig. 1). The site lies 90 km WNW of Maracaibo, in the lower foothills of the Sierra de Perijá. The semi-arid climate of the region supports patchy tropical dry forest dominated by trees and shrubs in the genera *Byrsonima* (Malpighiaceae), *Hura* (Euphorbiaceae), *Caesalpinia*, *Prosopis*, and *Enterolobium* (Fabaceae), *Bulnesia* and *Guaiacum* (Zygophyllaceae), and *Tabebuia* (Bignoniaceae), with grasses, sedges, and cacti also common (Fajardo et al., 2005; Rincón et al., 2008). Discovered in 1997, Mene de Inciarte is ~1200 m long and up to ~500 m wide. The fossiliferous asphaltic sediment, which varies from liquid to consolidated, overlies unmapped, presumably Pleistocene alluvial terraces that it penetrated from below through fissures. The late Pleistocene fauna of Mene de Inciarte features many small vertebrates (amphibians, reptiles, and small mammals) that are only beginning to be studied (Czaplewski et al., 2005) and extinct species of large mammals such as the ground sloth *Eremotherium* sp., glyptodont *Glyptodon clavipes*, pampatheres *Holmesina occidentalis* and *Pampatherium humboldtii*, armadillos *Dasypus sabanicola* and *Propraopus sulcatus*, toxodont *Mixotoxodon larensis*, litoptern *Macrauchenia patachonica*, proboscidean *Stegomastodon waringi*, horse *Equus* (*Amerihippus*) *santaeelenae*, camel *Paleolama* sp., sabercat *Smilodon populator*, and wolves *Canis dirus* and *Protocyon troglodytes* (Rincón, 2011a,b; Rincón et al., 2006; Prevosti and Rincón, 2007). The region supports a much less diverse large mammal community today, with only five species exceeding 50 kg body mass (tapir *Tapirus terrestris*, white-tailed deer *Odocoileus virginianus*, puma *Felis concolor*, jaguar *Panthera onca*, and capybara *Hydrochaeris hydrochaeris* (Eisenberg, 1989)).

Two geochemically defensible accelerator-mass spectrometer (AMS) radiocarbon (^{14}C) dates exist for the vertebrate fauna from

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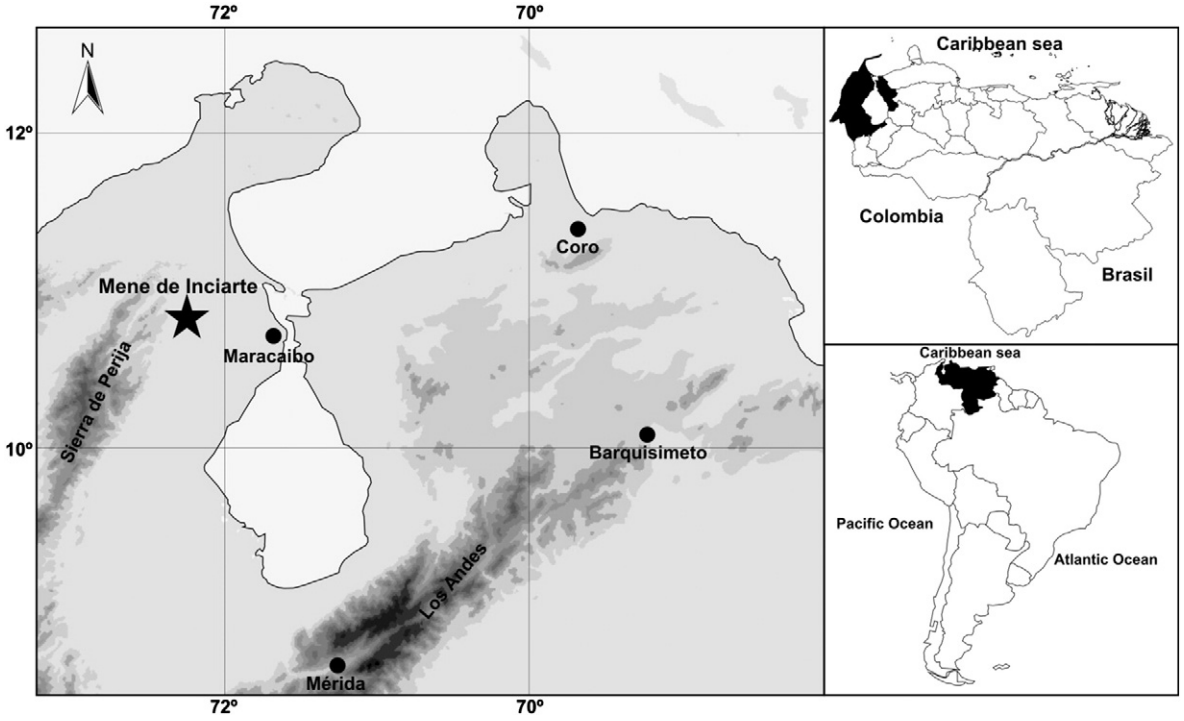

Figure 1. Location of Mene de Inciarte, northwestern Venezuela.
From Rincón et al. (2008: Fig. 1).

Mene de Inciarte, namely 25,500 ± 600 ^{14}C yr BP (28,456–30,878 cal yr BP) and 27,980 ± 370 ^{14}C yr BP (31,165–32,843 cal yr BP) for different collagenous fractions of a single specimen of *G. clavipes* (Jull et al., 2004). Three older and less precise AMS ^{14}C dates (from 41,000 ± 1300 to 46,900 ± 2600 ^{14}C yr BP, or 42,440–46,776 to 45,655–[50,000] cal yr BP) were based on non-collagenous fractions of a single specimen of *H. occidentalis*, and thus are likely to be contaminated with old ("dead") carbon from the asphalt (Jull et al., 2004). In order to see if we could improve on this chronology, we attempted to isolate collagen in two unidentified avian fossils, but without success. None of the fauna recovered thus far from Mene de Inciarte would argue for a Holocene rather than late Pleistocene age, whether based on taxonomy or preservation.

Materials and methods

The methods of excavating and preparing the fossils are described in Rincón et al. (2008) and Czaplewski et al. (2005). The avian fossils that we studied are from a systematically collected 50 cm × 50 cm × 50 cm block of highly fossiliferous asphaltic sediment with a depth from the surface that ranged from 25 to 75 cm. The upper 45 cm of this 50-cm interval (25 to 70 cm below the surface) consists of slightly sandy asphalt, underlain by sandier asphalt at depths greater than 57 cm (Czaplewski et al., 2005: Fig. 1). The sample of avian fossils that we studied is but a miniscule fraction of the fossils that will eventually be available with more field work and sediment-processing at Mene de Inciarte. The total depth of the fossil deposit is unknown, nor have test excavations been done across the tar seep, which measures ca. 1200 m NE–SW and up to 400 m wide (Rincón et al., 2008).

All avian fossils from Mene de Inciarte are disarticulated, as is generally the case in asphaltic deposits (Friscia et al., 2008). For the most commonly recorded families of birds, the percentage of complete specimens was 44% for Vulturidae (condors and vultures; 7 of 16), 48% for Tytonidae + Strigidae (owls; 13 of 27), 68% for Anatidae (ducks; 15 of 22), and 98% for Scolopacidae (sandpipers; 41 of 42). These data suggest less post-mortem movement for fossils of aquatic birds than for landbirds, the reason(s) for which are not clear.

We identified the avian fossils through direct comparisons with skeletons of living species from the Florida Museum of Natural History, University of Florida (UF), supplemented with specimens from the Louisiana State University Museum of Natural Science (LSUMNS). Comparisons were also made with extinct, late Pleistocene fossil species from UF, the Natural History Museum of Los Angeles County (LACM), the Royal Ontario Museum (ROM), and from the literature (Alvarenga and Olson, 2004; Olson, 2007). The fossil specimens from Mene de Inciarte are deposited in the Museo de Biología, La Universidad del Zulia (MBLUZ), Maracaibo, Venezuela. The specimens reported in this paper are listed in Appendix 1. Habitat preferences and modern geographic distributions of extant species were derived from Stotz et al. (1996), Hilty (2003), and our own field observations. Calibrated ages for radiocarbon dates (cal yr BP, at 2σ) were done using the program Calib 7.0 (Calib.qub.ac.uk/calib/calib.html).

The only other extensive sources of late Pleistocene avian fossils from tropical South America are from the arid Tumbesian region of southwestern Ecuador (La Carolina; Campbell, 1976) and northwestern Peru (Talara; Campbell, 1979). To compare the relative species richness of non-passerine birds identified from these three sites, we performed a rarefaction analyses in the R package vegan (Oksanen et al., 2013) using the RAREFY function based on the formulation of Hurlbert (1971) and standard errors (SE) as computed by Heck et al. (1975). These analyses provide the expected species richness at La Carolina and Talara if the same number of fossils were recovered from each site as in Mene de Inciarte.

Results

We identified 175 avian fossils from Mene de Inciarte that represent at least 73 species (57 resident, 16 migratory) in 58 genera and 25

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Table 1
Birds identified from late Pleistocene fossils at Mene de Inciarte, Zulia Province, Venezuela. Status categories — ER, extralocal resident; M, migrant; LR, local resident; †, extinct species. NISP, the number of identified fossil specimens.

	Status	NISP
Waterbirds (total 25 species, 73 specimens)		
CICONIIDAE — STORKS		
Ciconiidae sp. (large) — unknown stork	LR	3
ARDEIDAE — HERONS, EGRETS		
Tigrisoma sp. — tiger-heron	LR	1
Ardeidae sp. (medium; size of *Egretta thula*) — unknown egret	LR	2
ANATIDAE — DUCKS, GEESE		
Dendrocygna autumnalis — black-bellied whistling-duck	LR	1
Dendrocygna bicolor — fulvous whistling-duck	LR	1
Cairina moschata — muscovy duck	LR	2
Sarkidiornis melanotos — comb duck	ER	1
Anas bahamensis — white-cheeked pintail	LR	3
Anas clypeata — northern shoveler	M	4
Anas discors — blue-winged teal	M	7
Netta erythrophthalma — southern pochard	ER	2
Nomonyx dominica — masked duck	LR	1
ARAMIDAE — LIMPKINS		
Aramus guarauna — limpkin	LR	2
CHARADRIIDAE — PLOVERS		
Charadrius vociferus — killdeer	M	1
SCOLOPACIDAE — SANDPIPERS		
Tringa melanoleuca — greater yellowlegs	M	5
Tringa flavipes — lesser yellowlegs	M	1
Tringa solitaria — solitary sandpiper	M	8
Calidris canutus — red knot	M	2
Calidris fuscicollis — white-rumped sandpiper	M	3
Calidris sp. (small) — "peep" sandpiper	M	6
Phalaropus tricolor — Wilson's phalarope	M	4
Phalaropus lobatus — red-necked phalarope	M	1
Gallinago paraguaiae — Paraguayan snipe	ER	5
Gallinago sp. 2 (small) — unknown snipe	?	4
Gallinago sp. 3 (large) — unknown snipe	ER	3
Scavengers & raptors (total 21 species, 62 specimens)		
VULTURIDAE — VULTURES, CONDORS		
Sarcoramphus new sp. — "King-like" vulture	†	1
Coragyps cf. *C. atratus* — "Black" vulture	LR	2
Cathartes sp. — turkey/yellow-headed vulture	LR	1
Wingegyps new sp. (small) — micro-condor	†	6
Unknown genus (large; not *Vultur* or *Gymnogyps*) — extinct condor	†	6
ACCIPITRIDAE — HAWKS, EAGLES		
Buteogallus aequinoctialis — rufous crab-hawk	LR	1
Buteogallus meridionalis — savanna hawk	LR	1
Buteogallus new sp. — long-legged hawk/eagle	†	4
Geranoaetus melanoleucus — black-chested buzzard-eagle	ER	1
Buteo sp. — unknown buteo	?	2
Gypaetinae sp. — Old World vulture	†	1
Accipitridae sp. 7 — unknown hawk	?	1
Accipitridae sp. 8 — unknown eagle	?	1
FALCONIDAE — FALCONS, CARACARAS		
Falco sparverius — American kestrel	LR	3
Falco peregrinus — peregrine falcon	M	2
Caracara cheriway — crested caracara	LR	2
TYTONIDAE — BARN-OWLS		
Tyto alba — common barn-owl	LR	12
STRIGIDAE — TYPICAL OWLS		
Athene cunicularia — burrowing owl	LR	7
Bubo sp. — "Great Horned" owl	LR	6
Strix virgata — mottled owl	LR	1
Asio stygius — stygian owl	ER	1
Other landbirds (total 27 species, 40 specimens)		
ODONTOPHORIDAE — NEW WORLD QUAILS		
Colinus cristatus — crested bobwhite	LR	2
RALLIDAE — RAILS		
Aramides cajanea — gray-necked wood-rail	LR	1
BURHINIDAE — THICK-KNEES		
Burhinus sp. — unknown thick-knee	LR	1
COLUMBIDAE — PIGEONS, DOVES		
Patagioenas sp. (size of *P. cayennensis*) — unknown pigeon	LR	2
Zenaida cf. *Z. auriculata* — eared dove	LR	3
Columbina sp. (*talpacoti* or *passerina*) — unknown ground-dove	LR	1
CUCULIDAE — CUCKOOS		
Coccyzus americanus — yellow-billed cuckoo	M	1
CAPRIMULGIDAE — NIGHTJARS		
Caprimulgus sp. — unknown nightjar	LR	3
TROCHILIDAE — HUMMINGBIRDS		
Trochilidae sp. — unknown hummingbird(s)	LR	3
BUCCONIDAE — PUFFBIRDS		
Malacoptila sp. — whiskered-type puffbird	LR	1
FURNARIIDAE — OVENBIRDS		
Furnariidae sp. — medium-sized ovenbird	LR	1
TYRANNIDAE — FLYCATCHERS		
Arundinicola leucocephala — white-headed marsh-tyrant	LR	2
Pitangus sulphuratus — great kiskadee	LR	1
Pitangus lictor — lesser kiskadee	LR	1
Myiozetetes similis — social flycatcher	LR	1
Tyrannus melancholicus — tropical kingbird	LR	1
Tyrannus dominicensis — gray kingbird	M	1
VIREONIDAE — VIREOS		
Hylophilus flavipes — scrub greenlet	LR	1
HIRUNIDINIDAE — SWALLOWS		
Petrochelidon pyrrhonota — cliff swallow	M	1
EMBERIZIDAE — EMBERIZID FINCHES		
Volatinia jacarina — blue-black grassquit	LR	1
Sicalis flaveola — saffron finch	LR	2
ICTERIDAE — BLACKBIRDS, ORIOLES, MEADOWLARKS, ETC.		
Chrysomus icterocephalus — yellow-hooded blackbird	LR	1
Sturnella magna — eastern meadowlark	LR	1
Euphagus cf. *E. magnirostris* — large-billed blackbird	†	1
Quiscalus lugubris — Carib grackle	ER	2
Icterus spurius — orchard oriole	M	2
Gymnomystax mexicanus — oriole blackbird	ER	2
Total species/total NISP	73/175	

Species total — † = 6; ER = 8; M = 16; LR = 43; ? = 1.

families (Table 1). Of the 56 non-passerine species, 33 (59%) are from just four families, namely sandpipers and snipes (Scolopacidae, 11 spp.), ducks (Anatidae, 9 spp.), hawks and eagles (Accipitridae, 8 spp.), and vultures and condors (Vulturidae, 5 spp.). The heavy representation of scolopacids and anatids may be due to these mostly migratory birds landing on shallow water covering the tar seeps after rains and then becoming mired. Waterbirds also make up a large percentage of the avian fossils at two South American late Pleistocene sites (La Carolina, Ecuador and Talara, Peru) that are in places even more arid than Mene de Inciarte (Campbell, 1976, 1979; Tables 2, 3 herein). In arid habitats, any surface water "is a magnet for birds" (Taylor, 2010: 7). Seasonal rainfall, not an overall wetter climate, is all that is required to account for the large representation of waterbirds at natural traps such as tar seeps, where the struggling or deceased birds would then attract predators and scavengers (hawks, eagles, vultures, condors; see Discussion).

Five of the six extinct species are scavengers or raptors (Table 1), none of which are previously described. The femur and tarsometatarsus of *Buteogallus* new sp. (Fig. 2) are indistinguishable qualitatively, and intermediate in size, from those of the living *Buteogallus meridionalis* (smallest) and the extinct, late Pleistocene *B.* (*Wetmoregyps*) *daggetti* (largest). Measurements of these three species are as follows: distal width of femur — 14.5, 18.9, and 23.8 mm; and distal width of tarsometatarsus — 13.4, 17.4, and 23.0 mm. The qualitative similarity between *B. meridionalis* and *Buteogallus daggetti* was first noted by Olson (2007). The new species of *Buteogallus* from Mene de Inciarte represents another extinct, highly terrestrial raptor in this lineage. The gypaetine vulture is the first record for this subfamily for South America; while known from Pleistocene and earlier fossils in North America (Emslie, 1998), gypaetine vultures occur today only in Africa and Eurasia.

The other extinct species is the blackbird *Euphagus magnirostris* (Fig. 3), known previously only from late Pleistocene fossils in the southern United States. The maximum depth of the mandible in the Mene de Inciarte specimen is 3.13 mm. In the two extant species of

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Table 2
Family-level summary (% of total identified fossils) of non-passerine birds from late Pleistocene Neotropical sites. Data sources: Mene de, Inciarte, Venezuela (herein); La Carolina, Ecuador (Campbell, 1976) and Talara, Peru (Campbell, 1979). Only non-passerines are considered because the passerine fossils have not yet been identified comprehensively at La Carolina or Talara.

Family	Inciarte, Venezuela	La Carolina, Ecuador	Talara, Peru
Waterbirds	48	44	69
Podicipedidae — grebes	–	–	<1
Phalacrocoracidae — cormorants	–	–	<1
Ciconiidae — storks	2	–	1
Threskiornithidae — ibises	<1	–	<1
Ardeidae — herons	2	<1	1
Anatidae — ducks	14	22	55
Aramidae — limpkins	<1	–	–
Jacanidae — jacanas	–	–	<1
Recurvirostridae — stilts	–	<1	–
Charadriidae — plovers	<1	3	1
Scolopacidae — sandpipers, phalaropes	27	17	7
Laridae — gulls, terns	–	<1	2
Scavengers & raptors	41	6	18
Vulturidae — vultures, condors	10	<1	3
Accipitridae — hawks, eagles	8	1	3
Falconidae — falcons, caracaras	5	5	9
Tytonidae — barn-owls	8	<1	1
Strigidae — typical owls	10	<1	2
Other landbirds	11	50	13
Tinamidae — tinamous	–	–	<1
Cracidae — guans	–	–	<1
Odontophoridae — New World quail	1	–	–
Rallidae — rails	<1	–	<1
Thinocoridae — seedsnipes	–	<1	<1
Burhinidae — thick-knees	<1	1	<1
Columbidae — pigeons, doves	4	4	11
Psittacidae — parrots	–	45	<1
Cuculidae — cuckoos	<1	–	–
Caprimulgidae — nightjars	2	–	<1
Trochilidae — hummingbirds	2	–	–
Bucconidae — puffbirds	<1	–	–
Number of identified fossils	153	1611	6258

Table 3
Number of species of non-passerine birds at Mene de Inciarte, Venezuela compared to those from La Carolina, Ecuador (Campbell, 1976), and Talara, Peru (Campbell, 1979).

Family	Inciarte, Venezuela	La Carolina, Ecuador	Talara, Peru
Waterbirds	26	32	51
Podicipedidae — grebes	–	–	2
Phalacrocoracidae — cormorants	–	–	2
Ciconiidae — storks	1	–	2
Ardeidae — herons	2	1	6
Threskiornithidae — ibises	1	–	4
Anatidae — ducks	9	5	9
Aramidae — limpkins	1	–	–
Jacanidae — jacanas	–	–	–
Recurvirostridae — stilts	–	1	–
Charadriidae — plovers	1	5	7
Scolopacidae — sandpipers, phalaropes	11	18	17
Laridae — gulls, terns	–	2	2
Scavengers & raptors	21	14	23
Vulturidae — vultures, condors	5	3	6
Accipitridae — hawks, eagles	8	5	7
Falconidae — falcons, caracaras	3	4	6
Tytonidae — barn-owls	1	1	1
Strigidae — typical owls	4	1	3
Other landbirds	10	7	14
Tinamidae — tinamous	–	–	1
Thinocoridae — seedsnipes	–	1	3
Psittacidae — parrots	–	2	1
Cracidae — guans	–	–	1
Odontophoridae — New World quail	1	–	–
Rallidae — rails	1	–	1
Burhinidae — thick-knees	1	1	1
Columbidae — pigeons, doves	3	3	4
Cuculidae — cuckoos	1	–	–
Caprimulgidae — nightjars	1	–	2
Trochilidae — hummingbirds	1	–	–
Bucconidae — puffbirds	1	–	–
Total families	20	15	23
Total genera	42	42	67
Total species	56	53	89
Total identified fossils	153	1611	6258

Euphagus, this measurement is 2.47–2.55 mm in *Euphagus carolinus* males (N = 3), 2.22–2.52 mm in *E. carolinus* females (N = 4), 2.84–3.11 mm in *Euphagus cyanocephalus* males (N = 2), and 2.66–2.78 mm in *E. cyanocephalus* females. With further studies that include more sites, it could be that *E. magnirostris* will be found to be a large temporal form of *E. cyanocephalus*.

The eight extant but extralocal species feature six species that live in or near freshwater wetlands, typically in areas of greater rainfall (two ducks, two snipes, a grackle, and blackbird) and two upland species (a buzzard-eagle and owl) that today prefer non-forested or sparsely forested habitats. Detailed estimates of long-term changes in species richness await thorough censuses of the modern local bird community, as well as availability of a larger sample of fossils.

Also found at Mene de Inciarte are avian groups with little or no fossil record in the Neotropics, such as hummingbirds, puffbirds, and various suboscine and oscine passerines. Of the 17 passerine taxa identified, 12 (71%) are represented by only two families, the flycatchers (Tyrannidae) and blackbirds (Icteridae). The passerines include the first fossil evidence in South America of migratory songbirds that breed in North America or the West Indies (the kingbird *Tyrannus dominicensis*, swallow *Petrochelidon pyrrhonota*, and oriole *Icterus spurius*). The 14 resident passerine species inhabit wetlands, grasslands, or forest-edge habitats today; species characteristic of forest interiors are absent.

Based on published fossil identifications (Campbell, 1976, 1979) and our rarefaction analyses based on samples of 153 non-passerine fossils, the expected species richness was 22.2 (SE = 2.6) for La Carolina, Ecuador. For Talara, the expected species richness was 30.4 (SE = 2.9). Thus these two sites had estimated late Pleistocene species richness values of non-passerine birds that were only 40–54% (respectively) of that found (56 species) at Mene de Inciarte.

Discussion

As mentioned previously, the only rich collections of late Pleistocene avian fossils from tropical South America are from the arid Tumbesian region of southwestern Ecuador (La Carolina; Campbell, 1976) and northwestern Peru (Talara; Campbell, 1979). In spite of lying in different climatic zones (La Carolina and Talara near the Pacific Ocean vs. Mene de Inciarte on the Caribbean slope), the non-passerine family-level compositions of these three Pleistocene avifaunas are fairly similar; the largest differences are the greater abundance of scavengers and raptors at Mene de Inciarte and of parrots at La Carolina (Table 2). In terms of non-passerine species richness, Mene de Inciarte is richer (56 spp.) than La Carolina (53 spp.) in spite of only 153 identified specimens from the former site vs. 1611 from the latter (Table 3). The larger total of non-passerine species from Talara (89) reflects the much larger number of identified specimens (6258) from that site.

Moving to passerine birds, Mene de Inciarte resembles late Pleistocene sites from Mexico and southern United States in having a passerine assemblage dominated by species of the New World-restricted Icteridae (blackbirds, meadowlarks, oriole, grackles, cowbirds (Lundelius et al., 1983; Oswald and Steadman, 2011)). Today, many extant species of icterids live in close association with large introduced mammals such as cattle and horses. For example, meadowlarks (*Sturnella* spp.) often forage for seeds in mammal dung (Lanyon, 1995) and brown-headed

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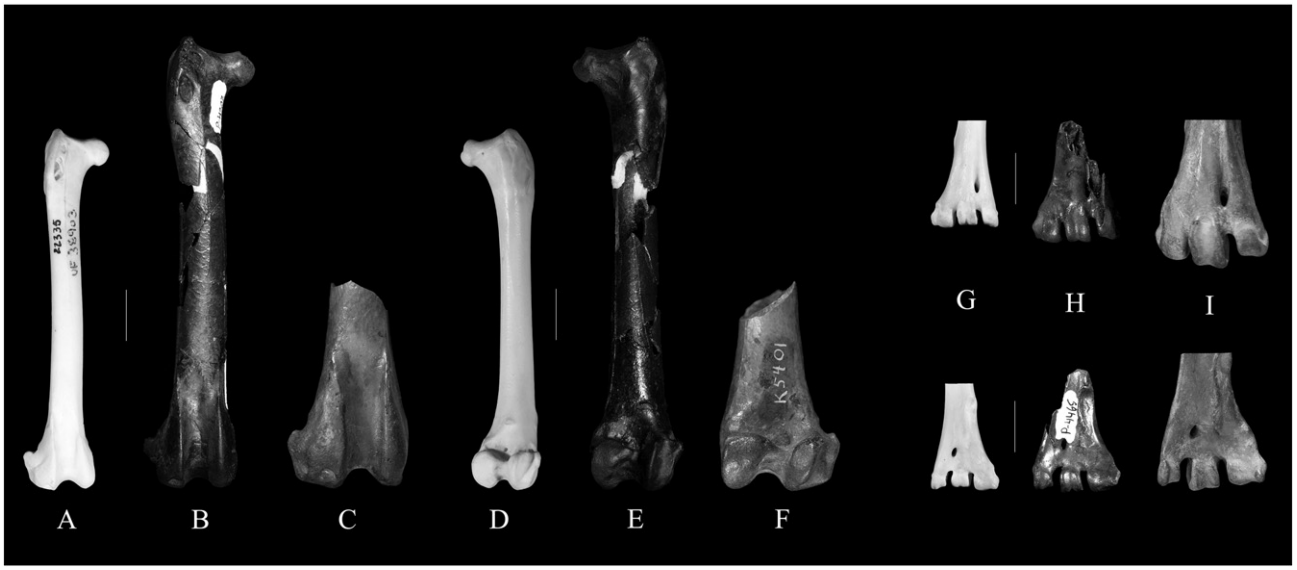

Figure 2. The right femur (A–F) in dorsal (A–C) and ventral (D–F) aspects, and the left tarsometatarsus (G–I) in acrotarsial (upper) and plantar (lower) aspects of selected living and extinct species of *Buteogallus*. A, D, and G. *Buteogallus meridionalis*, UF 38903. B, E, and H. *Buteogallus* new sp., MBLUZ P-4202, P-4465, Mene de Inciarte, Venezuela. C, F, and I. *Buteogallus daggetti*, LACM K5401, L493, Rancho La Brea tar pits, California. Scale bars = 10 mm.

cowbirds (*Molothrus ater*) and Brewer's blackbirds (*E. cyanocephalus*) forage for insects and seeds alongside grazing mammals (Friedmann, 1929; Martin, 2002). Many Pleistocene icterids, such as *E. magnirostris*, probably depended on megamammals to maintain open habitats and facilitate foraging opportunities in a similar way that elephants (and other large mammals) affect habitat structure in African savannas (Laws, 1970). The modern range of the extant congeneric blackbird *E. cyanocephalus*, which does not occur south of Mexico, has increased by hundreds of kilometers over just the past century (Martin, 2002), with deforestation, cattle, and horses acting as non-native analogs for the late Pleistocene grasslands and large mammals.

The combination of human impact and major climatic change that took place during the late Pleistocene (glacial) to Holocene (interglacial) transition is believed to have fueled high levels of extinction among large mammals in the Americas (Lorenzen et al., 2011). For birds, the species that may have depended on large mammals for foraging (including scavenging) were especially susceptible to extinction at this time (Steadman and Martin, 1984). One such species from Mene de Inciarte was described originally from the Rancho La Brea Tar Seeps in Los Angeles, California, a site famous for its spectacularly large mammalian herbivores and carnivores (Coltrain et al., 2004). This extinct bird is the large-billed blackbird *E. magnirostris* (Miller, 1929), which had been known previously only from late Pleistocene sites in the southwestern U.S. and northern Mexico (Lundelius et al., 1983; Steadman and Mead, 2010). Widespread species are generally believed to be more resilient to extinction than more specialized, small-ranged species (Mayr, 1942; Warren et al., 2013). The loss of *E. magnirostris* demonstrates that a widespread distribution is not always a safeguard against extinction.

During the last glacial interval, the climate of northern South America was somewhat drier and cooler than today (Bradbury et al., 1981; Curtis et al., 1999; Kanner et al., 2012). Whether lying on the Pacific slope (La Carolina, Talara) or Caribbean/Atlantic slope (Mene de Inciarte), cooler temperatures in the late Pleistocene were associated with a southward displacement of the Intertropical Convergence Zone (ITCZ; Peterson et al., 2000; Chiang et al., 2003; Kienast et al., 2006). The ITCZ is linked to the modern climate along the Venezuelan coast (and at Mene de Inciarte) resulting in the modern wet–dry season and a semi-arid climate; its southern shift during glacial periods would have resulted in a decrease in precipitation in the region (Peterson et al., 2000). This decrease would seem to contradict the discovery of large numbers of ducks and other waterbirds at the site, although waterbirds in fact are common fossils in arid environments (see Results). Furthermore, most of the non-aquatic species of birds that we recorded as fossils at Mene de Inciarte are compatible with an arid or semi-arid climate in the past. While the loss of microhabitats may have resulted in the extirpation of species such as the blackbird *Gymnomystax mexicanus* (which prefers forested river margins), a habitat-based cause for the extirpation or extinction of the other species is less likely than some direct or indirect association with the extinct large mammals. The rodent fossils from Mene de Inciarte, which have not yet been studied, may eventually yield more evidence for paleohabitat.

Scolopacid shorebirds are represented at all three late Pleistocene South American fossil sites by more species than any other family of birds (Table 3). At least eight of the eleven species of scolopacids identified at Mene de Inciarte are long-distance migrants that breed today (and presumably in the Pleistocene as well) in North America. Perhaps less familiar with the local landscape than resident species, these migrants may be especially vulnerable to entrapment in tar, where shallow pools of water accumulate after rains. The overrepresentation of vultures, condors, hawks, eagles, falcons, and caracaras may be because these predatory and scavenging birds were attracted to struggling or dead animals in the tar seeps but then became stuck themselves, much as has been suggested for Rancho La Brea (Stock, 1956).

Fossils enable direct observations of range changes and extinction that may not be evident from phylogenetic trees of extant species. Estimations of extinction rates from molecular phylogenies are often incredibly low (Quental and Marshall, 2010), yet 8% of the avian taxa sampled from the late Pleistocene of Mene de Inciarte are extinct. In addition, by identifying the blackbird *Euphagus magnirostris* ca. 5300 km from where it was first discovered in California, it is evident that we are in the early stages of estimating the extent that distributions of species have contracted (or expanded) since the late Pleistocene.

We expect that considerable additional avian diversity awaits discovery at Mene de Inciarte, especially among the "Other Landbirds" with 17 of 27 species identified thus far (63%) being known from a single fossil (Table 1), compared to nine of 26 species (35%) in

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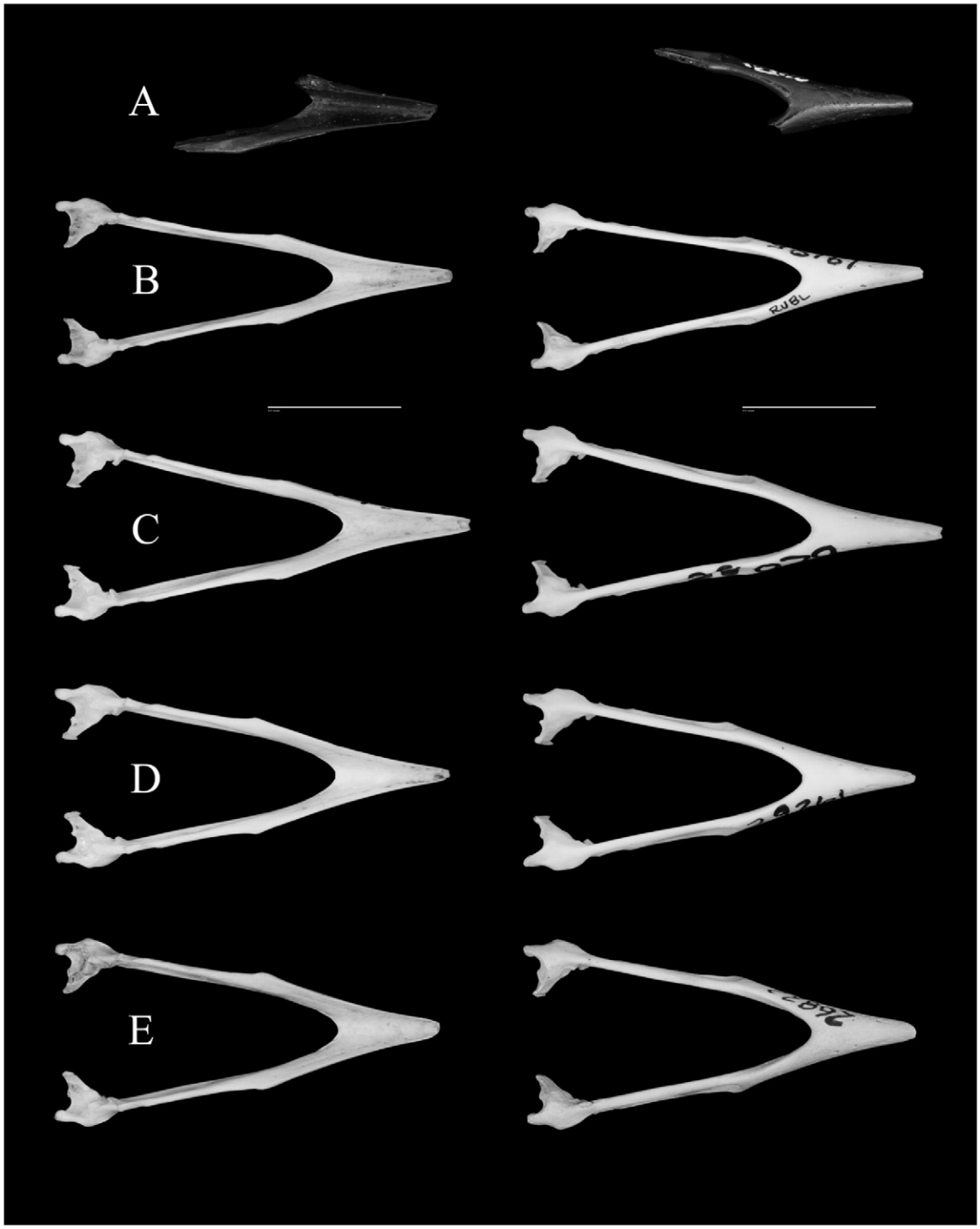

Figure 3. Fossil mandible of the extinct large-billed blackbird *Euphagus magnirostris* from Mene de Inciarte, Venezuela (A, MBLUZ P-2880) compared to mandibles of living congeners (B–E). B, Rusty blackbird *E. carolinensis* ♀, UF 33134; C, *E. carolinensis* ♂, UF 31110; D, Brewer's blackbird *E. cyanocephalus* ♀, UF 31115; E, *E. cyanocephalus* ♂, UF 31114. Scale bars = 10 mm.

"Waterbirds" and ten of 21 species (48%) in "Scavengers & Raptors." In other words, our currently available sample of bird fossils is nowhere near reaching diminishing returns. We note that Mene de Inciarte is one of perhaps 300+ tar seeps in northern Venezuela (ranging in age from late Pliocene through Pleistocene; Rincón, 2011a,b), only two of which have been explored for fossils. We hope that our research will stimulate new efforts to discover, excavate, and study vertebrate fossils in Venezuela and elsewhere in the Neotropics, and thus improve our understanding of the dynamic processes that have affected this region's extraordinary faunal diversity.

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Appendix 1. Catalog of fossil bird specimens from Mene de Inciarte, Venezuela, reported in this paper. C, complete; I, incomplete; *, not included in text or tables because of imprecise identification

Catalog Number	Taxon	I/C	Skeletal element	Remarks
P-2078	*Tyto alba*	C	Coracoid	
P-2151	*Buteogallus meridionalis*	I	Tarsometatarsus	Distal end
P-2195	*Sarcoramphus* sp.	I	Coracoid	Sternal end
P-2200	*Coragyps* cf. *atratus*	I	Rostrum	Two pieces
P-2204	Accipitridae sp. 8	I	Ungual phalanx	Lacking tip
P-2210	*Wingegyps* new sp.	C	Coracoid	
P-2337	*Wingegyps* new sp.	I	Humerus	Distal third
P-2410	*Cairina moschata*	C	Manual phalanx	Pit wear
P-2424	Vulturidae sp. (large)	I	Femur	Distal end
P-2454	*Gallinago* sp. 2 (small)	C	Coracoid	
P-2473	*Buteogallus aequinoctialis*	I	Carpometacarpus	Lacking proximal end
P-2494	*Gallinago* sp. 3 (large)	C	Carpometacarpus	
P-2562	*Tringa solitaria*	C	Carpometacarpus	
P-2570	*Calidris fuscicollis*	C	Ulna	
P-2573	*Netta erythrophthalma*	C	Coracoid	
P-2618	*Quiscalus lugubris*	C	Humerus	
P-2622*	Non-bird (marsupial)	C	Femur	
P-2627	*Geranoetus melanoleucus*	I	Carpometacarpus	Proximal half
P-2644	*Tringa solitaria*	C	Humerus	
P-2647	*Tringa melanoleuca*	I	Tarsometatarsus	Distal half
P-2845	*Petrochelidon pyrrhonota*	C	Humerus	
P-2847	*Strix virgata*	I	Carpometacarpus	Lacking proximal end
P-2855	*Anas clypeata*	C	Carpometacarpus	
P-2880	*Euphagus* cf. *magnirostris*	I	Mandible	Symphysis
P-2881	*Tringa solitaria*	C	Ulna	
P-2891	*Anas clypeata*	C	Coracoid	
P-2912	*Sarkidiornis melanotus*	C	Coracoid	Pit wear
P-2979	*Tyto alba*	I	Tarsometatarsus	Distal half
P-3014	Trochilidae sp.	C	Carpometacarpus	
P-3015	*Gallinago* sp. 3 (large)	C	Carpometacarpus	
P-3028	Vulturidae sp. (large)	C	Cervical vertebra	
P-3058	*Anas discors*	C	Ulna	
P-3062	*Dendrocygna bicolor*	C	Carpometacarpus	
P-3144	*Buteogallus new sp.*	C	Ungual phalanx	
P-3153	*Cairina moschata*	I	Tarsometatarsus	Distal end; pit wear
P-3156	*Calidris* sp. (small)	C	Ulna	Two fitted pieces
P-3158*	Passeriformes sp.	C	Carpometacarpus	
P-3163	*Gallinago paraguaiae*	C	Tarsometatarsus	
P-3164	*Anas clypeata*	C	Tarsometatarsus	
P-3167	*Chrysomus icterocephalus*	C	Tarsometatarsus	
P-3176	*Calidris* sp. (small)	C	Coracoid	
P-3181	*Tyrannus dominicensis*	C	Coracoid	
P-3183	*Tringa flavipes*	C	Humerus	
P-3186	*Arundinicola leucocephala*	C	Humerus	
P-3187	*Athene cunicularia*	C	Coracoid	
P-3193	*Charadrius vociferus*	C	Humerus	
P-3197	*Hylophilus flavipes*	C	Coracoid	
P-3200	*Calidris* sp. (small)	C	Humerus	
P-3208*	Passeriformes sp.	C	Carpometacarpus	
P-3209	*Icterus spurius*	C	Carpometacarpus	
P-3220	*Tringa solitaria*	C	Tarsometatarsus	
P-3239	*Calidris canutus*	C	Humerus	
P-3248	Trochilidae sp.	C	Carpometacarpus	
P-3258	*Tringa melanoleuca*	C	Carpometacarpus	
P-3261	*Anas discors*	C	Humerus	
P-3270*	Passeriformes sp.	C	Coracoid	
P-3273	*Phalaropus lobatus*	C	Carpometacarpus	
P-3313	*Phalaropus tricolor*	C	Coracoid	
P-3355	Vulturidae sp. (large)	C	Quadrate	
P-3356	Ciconiidae sp.	C	Quadrate	
P-3360	Ardeidae sp. (medium)	C	Ungual phalanx	
P-3362	*Athene cunicularia*	C	Tarsometatarsus	
P-3380	*Gallinago paraguaiae*	C	Coracoid	
P-3598	*Phalaropus tricolor*	C	Coracoid	
P-3602	*Falco peregrinus*	I	Carpometacarpus	
P-3605	*Tringa melanoleuca*	C	Carpometacarpus	
P-3609	Vulturidae sp. (large)	I	Tarsometatarsus	Distal end
P-3613	*Sicalis flaveola*	I	Rostrum	Lacking lateral bars
P-3631	*Coccyzus americanus*	I	Coracoid	Lacking sternal end
P-3636	*Bubo* sp.	I	Mandible	Lacking articulations
P-3637	*Bubo* sp.	I	Rostrum	Lacking nasals

(continued on next page)

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Appendix 1 (*continued*)

Catalog Number	Taxon	I/C	Skeletal element	Remarks
P-3638	*Tringa solitaria*	C	Carpometacarpus	
P-3642*	Tyrannidae sp.	C	Coracoid	
P-3655	*Zenaida* cf. *auriculata*	C	Tarsometatarsus	
P-3658	*Zenaida* cf. *auriculata*	C	Coracoid	
P-3661	*Calidris fuscicollis*	C	Tarsometatarsus	
P-3663	*Athene cunicularia*	C	Tarsometatarsus	
P-3664	*Phalaropus tricolor*	C	Tarsometatarsus	
P-3665	*Gallinago paraguaiae*	C	Tarsometatarsus	
P-3667	*Colinus cristatus*	C	Coracoid	
P-3669*	Passeriformes sp.	C	Coracoid	
P-3671	*Gallinago paraguaiae*	C	Coracoid	
P-3672*	Passeriformes sp.	C	Femur	
P-3681	*Wingegyps* new sp.	I	Humerus	Distal end
P-3682	*Calidris canutus*	C	Humerus	
P-3692	*Athene cunicularia*	C	Optic ossicles	Two ossicles
P-3693	*Tyto alba*	C	Manual phalanx	
P-3696	*Bubo* sp.	C	Tarsometatarsus	
P-3703	*Wingegyps* new sp.	C	Humerus	Shaft in many pieces
P-3708	*Calidris* sp. (small)	C	Humerus	
P-3733	*Caracara cheriway*	C	Quadrate	
P-3739	*Gymnomystax mexicanus*	C	Carpometacarpus	
P-3767	*Sicalis flaveola*	I	Mandible	Articulation
P-3781	*Caprimulgus* sp.	C	Coracoid	
P-3783	Ardeidae sp. (medium)	C	Ungual phalanx	
P-3785	*Gallinago* sp. 2 (small)	C	Carpometacarpus	
P-3786	*Gallinago* sp. 2 (small)	C	Coracoid	
P-3795	Vulturidae sp. (large)	I	Tarsometatarsus	Proximal end
P-3819	*Patagioenas* sp.	C	Manul phalanx	
P-3840	*Zenaida* cf. *auriculata*	C	Carpometacarpus	
P-3841	*Athene cunicularia*	C	Ungual phalanx	
P-3858	*Calidris* sp. (small)	C	Carpometacarpus	
P-3869	*Caprimulgus* sp.	C	Coracoid	
P-3875	*Cathartes* sp.	I	Mandible	Articulation
P-3914	*Falco sparverius*	C	Coracoid	
P-3916	*Nomonyx dominica*	C	Carpometacarpus	
P-3920	*Tyrannus melancholicus*	C	Ulna	
P-3926	*Tringa solitaria*	C	Humerus	
P-3937	*Caracara cheriway*	I	Rostrum	Lacking nasals
P-3942	Furnariidae sp.	C	Coracoid	
P-4002	*Netta erythrophthalma*	C	Carpometacarpus	
P-4006	*Anas discors*	C	Ulna	
P-4068	*Volatinia jacarina*	C	Humerus	
P-4106	*Tyto alba*	I	Tarsometatarsus	Lacking proximal end
P-4134	*Quiscalus lugubris*	I	Coracoid	Lacking sternal end
P-4202	*Buteogallus new sp.*	C	Femur	
P-4219	*Dendrocygna autumnalis*	C	Femur	
P-4256	*Tringa solitaria*	C	Humerus	
P-4257	*Calidris fuscicollis*	C	Coracoid	
P-4267	*Wingegyps* new sp.	C	Coracoid	
P-4269	*Tringa melanoleuca*	C	Humerus	
P-4275	Gypaetinae sp.	I	Humerus	Distal end
P-4277	*Buteo* sp.	C	Coracoid	
P-4308*	Accipitridae sp.	C	Ungual phalanx	
P-4315	*Gallinago* sp. 2 (small)	C	Coracoid	
P-4316	*Coragyps* cf. *atratus*	C	Ungual phalanx	
P-4345	*Tyto alba*	C	Femur	Pit wear
P-4352	*Anas discors*	C	Coracoid	
P-4353	*Pitangus sulphuratus*	C	Tarsometatarsus	Glued
P-4361	*Athene cunicularia*	C	Coracoid	
P-4379*	Aves sp.	C	Ungual phalanx	
P-4388	*Malacoptila* sp.	C	Tarsometatarsus	Glued
P-4395	*Wingegyps* new sp.	C	Coracoid	
P-4425	*Calidris* sp. (small)	C	Coracoid	
P-4426	*Athene cunicularia*	I	Rostrum	Lacking nasals
P-4461*	Passeriformes sp.	C	Femur	
P-4464	Ciconiidae sp.	I	Tarsometatarsus	Proximal end
P-4465	*Buteogallus new sp.*	I	Tarsometatarsus	Distal end
P-4468	*Tringa melanoleuca*	C	Coracoid	
P-4471	Ciconiidae sp.	I	Coracoid	Sternal end
P-4529	*Phalaropus tricolor*	C	Coracoid	
P-4536	*Aramides cajanea*	C	Femur	
P-4557	*Myiozetetes similis*	C	Coracoid	
P-4579	*Gallinago paraguaiae*	C	Coracoid	
P-4666	*Falco peregrinus*	I	Coracoid	Lacking humeral end
P-4709	*Anas discors*	C	Coracoid	

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Appendix 1 (*continued*)

Catalog Number	Taxon	I/C	Skeletal element	Remarks
P-4728	*Icterus spurius*	C	Coracoid	
P-4732	*Bubo* sp.	I	Rostrum	Lacking premaxilla
P-4758*	Tyrannidae sp.	C	Coracoid	
P-4761	*Tringa solitaria*	C	Humerus	
P-4765	*Bubo* sp.	C	Optic ossicle	
P-4781	*Pitangus lector*	C	Carpometacarpus	
P-4804	*Arundinicola leucocephala*	C	Humerus	
P-4808	*Gymnomystax mexicanus*	C	Coracoid	
P-4811	Trochilidae sp.	C	Coracoid	
P-4854	*Gallinago* sp. 3 (large)	C	Coracoid	
P-4856*	Passeriformes sp.	C	Humerus	
P-4867	Vulturidae sp. (large)	C	Pedal phalanx	
P-4873	*Colinus cristatus*	C	Carpometacarpus	
P-4878	*Anas discors*	C	Carpometacarpus	
P-4913*	Non-bird (Chiroptera)	I	Radius	Distal end
P-4920	*Columbina* sp.	C	Carpometacarpus	
P-5908*	Passeriformes sp.	I	Scapula	Lacking blade
P-5910	*Anas clypeata*	I	Radius	Distal end
P-5912*	Passeriformes sp.	C	Scapula	
P-5916	*Buteo* sp.	I	Tarsometatarsus	Distal end
P-5921	*Tyto alba*	I	Fibula	Proximal half
P-5925	*Buteogallus new sp.*	I	Carpometacarpus	Distal end
P-5935	*Anas bahamensis*	I	Humerus	Distal end
P-5936	*Aramus guarauna*	I	Tibiotarsus	Distal end
P-5938	*Falco sparverius*	I	Tarsometatarsus	Distal half
P-5961*	Passeriformes sp.	I	Ulna	Distal half
P-5964	*Tyto alba*	I	Radius	Distal end
P-5967	*Anas bahamensis*	I	Humerus	Proximal end
P-5975	*Asio sygius*	I	Tarsometatarsus	Proximal third
P-5983*	Tyrannidae sp.	I	Coracoid	Lacking sternal end
P-5984*	Passeriformes sp.	I	Scapula	Lacking blade
P-5986*	Passeriformes sp.	I	Radius	Proximal end
P-5989*	Passeriformes sp.	I	Rostrum	Lacking nasals
P-5998*	Passeriformes sp.	C	Coracoid	
P-6013	*Sturnella magna*	I	Dentary	Ramus
P-6014	*Falco sparverius*	C	Coracoid	
P-6022*	Passeriformes sp.	C	Humerus	
P-6023	*Tyto alba*	I	Radius	Proximal end
P-6024	*Tyto alba*	I	Carpometacarpus	Proximal symphysis
P-6025	*Tyto alba*	I	Manual phalanx	Distal half
P-6027	*Burhinus* sp.	I	Tibiotarsus	Distal third
P-6032	*Bubo* sp.	C	Quadrate	
P-6039	*Caprimulgus* sp.	I	Tarsometatarsus	Distal end
P-6051	*Anas discors*	I	Furcula	Symphysis
P-6053	*Tyto alba*	I	Coracoid	Lacking sternal end
P-6054	*Tyto alba*	I	Coracoid	Lacking both ends
P-6062	*Anas bahamensis*	I	Scapula	Articulation
P-6070*	Passeriformes sp.	I	Ulna	Proximal half
P-6071*	Passeriformes sp.	I	Ulna	Distal half
P-6074*	Passeriformes sp.	C	Carpometacarpus	
P-6077	*Tigrisoma* sp.	I	Carpometacarpus	Distal end
P-6078	Accipitridae sp. 7	I	Femur	Proximal third; pit wear
P-6079	*Aramus guarauna*	I	Femur	Proximal end
P-6080*	Aves sp.	I	Tibiotarsus	Proximal half; pit wear
P-6084*	Aves sp.	I	Tarsometatarsus	Proximal half
P-6085	*Patagioenas* sp.	I	Tarsometatarsus	Lacking both ends

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