New evidence of *Ara autochthones* from an archeological site in Puerto Rico: a valid species of West Indian macaw of unknown geographical origin (Aves: Psittacidae)

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ABSTRACT.—The exinct macaw *Ara autochthones*, previously known only from a single bone from an archeological site on St. Croix, Virgin Islands, is here identified from several associated bones from an archaeological site in south-central Puerto Rico. The species belongs to a distinctive intermediate size-class and was larger than the Cuban Macaw *Ara tricolor*. It is assumed to have been endemic to the West Indies, but prehistoric interisland transport of parrots by humans makes interpreting the natural distribution of the species impossible in the absence of fossils. Historical reports of macaws elsewhere in the West Indies are rendered dubious for the same reason.

KEYWORDS.—*Amazona*, biogeography, extinction, human transport, parrots.

INTRODUCTION

The history and natural distribution of macaws (*Ara*) in the West Indies are clouded with uncertainties. The only specimen evidence apart from archeological remains is of the Cuban Macaw *Ara tricolor*, known from about nineteen skins and extinct since about 1864 (Greenway 1958, Olson and Suárez, in press). Contrary to previous belief, there is no historical evidence for a macaw from Hispaniola (Olson 2005), the second largest of the Antillean islands. From Jamaica, Guadeloupe, Martinique, Dominica, and an unknown West Indian island, there are 18th and 19th century visitors' accounts of various macaws to which no fewer than seven scientific names have been applied (Clark 1905a,b; 1908; Rothschild 1905, 1907a,b), although these are all rightly to be considered entirely hypothetical (Prestwich 1970). In addition, Fisher and Warr (2003) discovered and reproduced a previously unknown painting of a macaw supposedly from Jamaica dating from about 1765.

From an archeological deposit on St. Croix in the Virgin Islands, Wetmore (1937) described and named a new species of macaw as *Ara autochthones*, based on a single tibiotarsus of an immature bird. Nothing further regarding this species has turned up in the 60 years since it was described and there has been no further evaluation of the species, which has been mentioned occasionally in various checklists and compilations; e.g. the curious statement by Prestwich (1970: 199) that: "Nothing appears to have been recorded concerning this rather primitive macaw."

Here we report on several associated skeletal elements from another archeological site in central Puerto Rico that we refer to *Ara autochthones.* These confirm the validity of the species and provide proof of the existence of a second species of macaw endemic to the West Indies. Information that we supplied concerning this material formed the basis for Wiley et al. (2004:96) reporting "*Ara* unknown sp." from Puerto Rico. Unfortunately, as the with archeological specimens of parrots from elsewhere in the West Indies reported by Williams and Steadman (2001), and in the absence of a fossil record, it is not possible to determine on which island this species of macaw

originally evolved because of the potential for extensive trade in parrots among Amerindians of the Antilles.

MATERIALS AND METHODS

Comparative material examined.—Skeletons: *Anodorhynchus hyacinthinus* MHNT 1045, 1057, 1064, 1496, 1693, 1695, USNM 291249, 319969, 345230, 345854; *A. leari* FMNH 337716, 337860, 379161, MHNT 1540, 1547; *Ara ambiguus* LSUMZ 90381; USNM 224811; *A. ararauna* MHNT 242, 983, 1165, 1604, USNM 19355, 49891, 223952, 223993, 318791, 322286, 322337, 345207, 345848, 345849, 428243, 489411, 498698, 502499, 502500; *A. auricollis* USNM 345846, 345847, 345851, 345852; *A. chloropterus* MHNT 825, 1653, USNM 225132, 226876, 345850, 490125; *A. couloni* FMNH 291744; *A. glaucogularis* FMNH 337727, LSUMZ 168622; *A. macao* MHNT 753, USNM 18508, 18988, 226164, 288772, 290508, 321173, 321981, 322058, 322212, 430513, 430516, 431614, 502497, 502498; *A. manilatus* USNM 344700, 345853, 621711, 621949, 622388; *A. maracana* FMNH 337756, 390830, 398918, USNM 320003, 344670; *A. militaris* USNM 288554, 288605, 344772, 344848; *A. nobilis* USNM 344080, 344081, 502284, 502503, 622355; *A. rubrogenys* FMNH 291402, 291404, 337744, MHNT 1812; *A. severus* FMNH 104484, 290489, 337748, MHNT 388, USNM 19115, 502504; *Cyanopsitta spixii* MHNT 820, USNM 346722. Measurements were also taken from X-radiographs of two mounted specimens of *Ara tricolor* USNM 135137, 171767. Qualitative comparisons were made with skeletons of *Ara glaucogularis* ("*Ara caninde*" auct. FMNH 337727), *Anodorhynchus leari* (FMNH 337716), and *Amazona imperialis* (USNM 318792, USNM 321883).

RESULTS

Genus *Ara* Lacépède, 1799

The new archaeological material is referable to *Ara*, rather than *Amazona*, the only other genus of large parrots in the West Indies, by the following characters: coracoid more elongate with relatively narrower shaft, ventral lip of glenoid facet more protrudent; humerus with ectepicondylar process and attachment of pronator brevis situated decidedly more proximad; carpometacarpus proportionately much longer, process of alular metacarpal not curved proximad; femur with head proportionately larger; tibiotarsus very distinctive in having the inner cnemial crest more pointed and extending farther proximad, internal condyle much narrower. Although we have followed David and Gosselin (2002) in treating the generic name *Ara* as masculine, we do not endorse splitting the genus into three by resurrecting the names *Primolius* and *Orthopsittaca* (Tavares et al. 2006). Recognition of monophyly of the true macaws would be better served by including *Cyanopsitta* in *Ara* as it has long been delimited.

Ara autochthones Wetmore, 1937

Holotype.—USNM 483530, left tibiotarsus; vertebrate paleontological collections (formerly USNM 343033 in the bird collections). Collected in kitchen midden deposits from Concordia, southwestern St. Croix, Virgin Islands, in 1934 by L. J. Korn (Wetmore 1937).

Referred material.—USNM 448344 vertebrate paleontological collections: left coracoid lacking a portion of the head, proximal and distal ends of left humerus, proximal end of right radius, left carpometacarpus lacking minor metacarpal, left femur lacking distal end, right tibiotarsus lacking external part of proximal articular surface, proximal fragment and worn distal portion of left tibiotarsus, fragment of shaft (humerus?), unidentified fragment (perhaps not avian). These bones are evidently all from a single individual.

Locality and age.—Collected by Maíz during an excavation conducted in March and April 1987 at the Hernández Colón (PO-13) archaeological site. The site, UTM E 755665/N1998980, represents an inland Saladoid/Ostionoid pre-Columbian Indian village of approximately 15,000 m^2. It is located on the eastern bank of the Cerrillos-Bucaná River, south central Puerto Rico, NE of the city of Ponce, Barrio Cerrillos (18°

04′ 05″ N; 66° 35′ 09 W). It lies at 76m amsl, 13.5 river km from the Caribbean Sea. Physiographically, the Hernández Colón site is situated in an alluvial terrace within the Semiarid Southern Foothills of Puerto Rico.

Ten 2 × 1 m stratigraphic pits were excavated after mapping the site. The pottery seriation and two radiocarbon dates revealed a multi-component site, with a local sequence of three archaeological phases: Pomarrosa Phase, Cerrillos Phase, and Maragüez Phase. The Pomarrosa phase is stylistically related to the Hacienda Grande ceramic style (ca. 200 B.C.-400 A.D.) as defined for Puerto Rico by Alegría (1965) and Rouse & Alegría (1990). The Cerrillos and Maragüez phases are in turn related to the Cuevas (400-600 A.D.) and Early Ostiones (600-900 A.D.) styles as defined by Rouse (1952, 1992). The Hacienda Grande style is included within the Cedrosan Saladoid subseries of the Saladoid series and corresponds with the first horticultural and ceramics groups that migrated to Puerto Rico from northeastern South America (Rouse, 1992). All cultural and faunal remains were collected using three gauges of screens: 6 mm (1/4 inch), 3 mm (1/8 inch) and 1.5 mm (1/16 inch). This archaeological recovery technique provided abundant zooarchaeological remains. The macaw bones came from pit 8, level 30-40 cm below surface (cmbs), from a midden deposit that is located at the base and beginning of the Pomarrosa phase (Maíz López 2002) within the local sequence. The beginning of the Pomarrosa phase at the Hernández Colón site is dated at ca. A.D. 300, based on a charcoal sample measurement (2 sigma–cal. 420-870 A.D.-Beta 23902).

Measurements (mm) of referred material.—Coracoid: estimated length from head to internal corner of sternal facet 43.5 (42.5 as preserved), length from base of procoracoid process to internal corner of sternal facet 26.5, length and width of glenoid facet 10.5 × 6.1, width and depth of shaft at midpoint 5.2 × 4.4, width of sternal facet 10.5. Humerus: proximal width 19.9, depth through external tuberosity 12.8, depth of head 6.2, estimated distal width 15.5, height and width of radial condyle 7.4 ×

5.0. Carpometacarpus: length 55.8, proximal depth 14.3, width of trochlea 5.7, width and depth of shaft at midpoint 4.5 × 5.0. Radius: greatest proximal diameter 6.0. Femur: estimated length 51.5, proximal width 12.5, depth through trochanter 8.2, depth of head 6.2, width and depth of shaft at midpoint 4.9 × 5.4. Tibiotarsus: length from proximal articulating surface 74.5, length from distal end of fibular crest to external condyle 47.2, depth through inner cnemial crest 11.4, width and depth of shaft at midpoint 5.2 × 4.0, distal width 10.1.

Comparisons.—The referred tibiotarsus is essentially identical in size with the holotype of *Ara autochthones* and the referred material from Puerto Rico is therefore identified as that species. As Wetmore (1937) noted, the holotype is from a juvenile individual, so the new material is all the more important for establishing the nature of the species. In size, most living species of macaws fall into two separate clusters representing large species and smaller species (Table 1). *Ara autochthones* is distinct in being intermediate between these two clusters. Only *Ara glaucogularis* and *Anodorhynchus leari* (and presumably the very closely related *A. glaucus*, which may be only sub-

TABLE 1. Length measurements (range and mean in mm) of macaw bones (*Anodorhynchus, Ara, Cyanopsitta*). Species are arranged by decreasing mean of the length of the tibiotarsus.

Species	n	Carpometacarpus	Tibiotarsus
An. hyacinthinus	10	61.3-73.2 (67.9)	87.2-99.1 (93.6)
A. ambiguus	2	66.2-69.8 (68.0)	88.6-91.9 (90.2)
A. chloropterus	6	63.5-67.9 (65.9)	85.3-89.5 (87.6)
A. macao	15	59.3-68.1 (63.5)	79.7-89.2 (85.0)
A. militaris	4	61.0-65.6 (63.9)	80.4-85.2 (82.8)
A. ararauna	19	58.0-71.3 (63.9)	77.6-87.9 (82.7)
An. leari	5	56.3-60.3 (58.0)	77.0-82.6 (79.6)
A. autochthones	1	55.8	74.5
A. glaucogularis	2	53.4-57.6 (55.5)	67.8-70.7 (69.3)
A. rubrogenys	4	46.9-49.9 (48.3)	66.3-68.1 (67.0)
A. tricolor	2	42.6-45.2 (43.9)	63.5-64.7 (64.1)
A. severus	6	39.3-45.6 (41.3}	56.2-61.6 (58.5)
C. spixii	2	43.0-43.3 (43.1)	54.4-56.2 (55.3)
A. couloni	1	39.2	54.2
A. manilatus	5	40.4-44.5 (41.1)	50.3-55.4 (53.0)
A. auricollis	4	35.5-36.4 (35.7)	48.6-51.6 (50.5)
A. maracana	5	33.8-37.8 (35.7)	47.6-52.5 (50.4)
A. nobilis	5	27.1-28.5 (27.9)	40.3-43.4 (41.9)

specifically distinct [Alvarenga 2007]) are similar in size. Although these species are very far removed geographically from the West Indies, it is still useful to make qualitative comparisons of them with *Ara autochthones* to reduce the influence of possible size-related differences.

Compared with *Ara glaucogularis* and *Anodorhynchus leari*, in the humerus of *Ara autochthones* the pectoral attachment is less excavated and the capital groove is wider; the femur has a more massive head and in posterior view is more excavated under the head, neck, and trochanter—the more robust shaft agrees with that in *Ara* and differs from that of *Anodorhynchus*; the tibiotarsus is more robust with the distal extremity more flared. In length the coracoid, carpometacarpus, and femur are smaller than in either species although the tibiotarsus is longer than in *Ara glaucogularis* but shorter than in *Anodorhynchus leari*.

Additional archeological specimens attributed to Ara.—Two other specimens reported as macaws are known from West Indian archeological sites. A nearly complete coracoid from Montserrat was stated to be "smaller than in *Ara ararauna* but larger than in *A. severa* or *A. manilata*, although closer in size to the last two" (Williams and Steadman 2001: 180). Examination of this specimen (UF 4416) shows it to have the more pointed head of *Ara* versus that of *Amazona*. The head is broken in the specimen of *Ara autochthones* but the bone from Montserrat is slightly smaller (head to internal distal angle 41.6 vs. ca. 43.6 mm). This might be within the range of variation in *A. autochthones*, or possibly even that of *A. tricolor*. Its identity will have to remain uncertain in the absence of more material but at this point it cannot be used to establish the existence of a third species of macaw in the West Indies.

An ulna from an archeological site on Marie Galante was thought by Williams and Steadman (2001) likely to be referable to the hypothetical species *Ara guadeloupensis* Clark (1905a). We examined this specimen (UF archeological collections Folle Anse 68, Box 68-10), which is lacking the proximal articulation. The distal end is somewhat worn and abraded so that such features as may possibly be diagnostic in this area have been altered to varying degrees. There does seem to be a notch between the internal condyle and carpal tubercle, however, which is like *Amazona* and unlike *Ara*. In size and robustness, the specimen is perfectly intermediate between the two individuals of *Amazona imperialis* that we examined, and we consider that it is probably best referred to that species. *Amazona imperialis* is probably the same as *A. violacea*, which is known only from descriptions of birds from Guadeloupe. From the same site on Marie Galante as the ulna, Williams and Steadman referred a tibiotarsus to *A violacea* on the basis of its similarity to *A. imperialis*.

DISCUSSION

Ara autochthones was a decidedly larger bird than the Cuban *A. tricolor* (Table 1). It cannot be referred to any other known species of macaw and must be considered a valid, extinct species. Although Amerindians could have transported macaws from the mainland to the West Indies, it is far less likely that a mainland species would have been driven to extinction than a species restricted to one or more islands in the Antilles. Therefore, we assume that *Ara autochthones* was a West Indian endemic.

The specific name *autochthones* was probably one of the worst possible choices for this bird, as it is unlikely that it ever occurred naturally on St. Croix. We may question even whether it occurred naturally on Puerto Rico. Although fossil remains of both *Amazona* and *Aratinga* have been recovered from a number of pre-human sites in Puerto Rico (Olson, unpublished data), no fossils of *Ara* have yet been recovered. This is, however, not at all conclusive, as macaws are unlikely to occur in cave deposits on an island where the only known cave-inhabiting predator was a relatively small barn owl (*Tyto*). The only fossils of macaws found to date in a paleontological context in the West Indies are three bones of *Ara tricolor*, two of which were found in aquatic depositional environments (Wetmore 1928, Olson and Suárez in press).

The indigenous natives of the West Indies were excellent boatsmen and engaged in extensive interisland trade involving various commodities including parrots and feathers (Sauer 1966; Rouse 1986, 1992; Keegan 1992). That parrots were important in their culture was apparent from the outset of interaction with Europeans. When Christopher Columbus first landed in the New World in 1492, somewhere in the Bahamas, the inhabitants "brought to us: parrots, balls of cotton thread, (wooden) spears, and many other things" (Tyler 1998: 38). "In the early years [of Spanish colonization] parrots were frequently mentioned in the islands as well as on Tierra Firme, by the Old World names of *papagayo* and *perico*, and the long-tailed brilliantly colored ones [macaws] by the Arawak name *guacamayo*. Along with doves and pigeons, they were appreciated as food by Spaniards as well as by natives, and were very abundant" (Sauer 1966: 184).

Various other animals, both indigenous and otherwise, were moved about by Amerindians, doubtless as living individuals, and were reared in captivity in places where some species did not occur naturally (Wing 2001). Agoutis (*Dasyprocta*) were transported from South America through the Lesser Antilles at least as far north as St. Kitts and St. Eustatius (Wing 1989). The large rodent *Capromys pilorides*, native to Cuba, was transported from that island to Hispaniola, where remains were found in an archeological context (Rímoli 1974). Another large rodent, *Isolobodon portoricensis*, which occurs in pre-human contexts only in Hispaniola, was transported from there to Mona Island, Puerto Rico, and the Virgin Islands, including St. Croix, in all of which places it is found only in midden deposits (Olson and Pregill 1982, Woods 1989, Frank and Benson 1998). The extinct flightless rail *Nesotrochis debooyi* occurs both in paleontological and archeological contexts in Puerto Rico and has been found in middens in the Virgin Islands, including St. Croix (Olson and Pregill 1982) and isolated Mona Island (Olson unpublished). St. Croix is separated from the Puerto Rican Bank by a deep oceanic trench and hence was never connected to other islands (Heatwole and Mackenzie

FIG. 1. Comparison of appendicular bones of macaws: in each group of three, *Ara glaucogularis* FMNH 337727 is on the left, *Anodorhynchus leari* FMNH 337716 is on the right, and *Ara autochthones* USNM 448344 (archeological specimen from Puerto Rico) is in the middle; h = *Ara autochthones* USNM 483530 holotypical left tibiotarsus (juvenile). A, left humeri in anconal view; B, left carpometacarpi in internal view; C, left femora in anterior view; D, right tibiotarsi in anterior view. Scale = 2 cm.

1967, Pregill 1981). If it had had a native species of flightless rail, one would not expect it to be identical to *N. debooyi*, so that human transport and captive rearing of that species is a logical conclusion.

In northern Mexico and the American southwest, in areas where they do not occur naturally, macaws (mostly *Ara macao*) were an important item of commerce and ritual among Amerindians and large captive breeding facilities were maintained to sustain ritual sacrifices (Hargrave 1970, Minnis et al. 1993, Creel and McKusick 1994). Being the largest and most colorful of the highly esteemed parrots of the West Indies, it is altogether probable that macaws were likewise items of great prestige and value in the Antilles and would doubtless have been traded far and wide. Europeans likewise valued macaws and would have carried them between islands and the mainland from the beginning of commerce with the New World. Therefore, 18th and 19th century accounts of macaws in Jamaica

FIG. 2. Comparison of appendicular bones of macaws: in each group of three, *Ara glaucogularis* FMNH 337727 is on the left, *Anodorhynchus leari* FMNH 337716 is on the right, and *Ara autochthones* USNM 448344 (archeological specimen from Puerto Rico) is in the middle; h = *Ara autochthones* USNM 483530, holotypical left tibiotarsus (juvenile). A, left humeri in palmar view; B, left carpometacarpi in external view; C, left femora in posterior view; D, right tibiotarsi in posterior view. Scale = 2 cm.

FIG. 3. Comparison of coracoids of macaws (upper row, dorsal view; lower row, ventral view): A, *Ara glaucogularis* FMNH 337727; B, *Ara autochthones* USNM 448344 (archeological specimen from Puerto Rico); C, *Ara* sp. UF 4416 archeological specimen from Montserrat (image has been reversed to facilitate comparison); D, *Anodorhynchus leari* FMNH 337716. Scale = 2 cm.

and the Lesser Antilles could be based on species originating almost anywhere in the Caribbean region, including the mainland.

The macaw illustrated by Fisher and Warr (2003: 156) from several volumes of paintings by a Lt. L. J. Robins entitled *The Natural History of Jamaica* and dated to 1765, is stylized to a greater or lesser degree, but the overall plumage pattern is very similar to that of the Cuban Macaw *Ara tricolor* and it may well represent an example of that species that had been taken to Jamaica from Cuba.

Although human-caused extinctions on islands has in many cases been rampant (e.g. Olson and James 1982, Steadman 2006), we very much doubt that "each Greater Antillean and Lesser Antillean island once sustained one or two indigenous if not endemic species of *Ara*" (Williams and Steadman 2001: 176). There is no credible evidence in support of such a belief and the only relatively concrete evidence now available—the archeological record—

suggests just the opposite—that there may have been only one other macaw in the Antilles apart from the Cuban Macaw *Ara tricolor*. If so, the Antillean island most likely to have harbored a macaw larger than *Ara tricolor* would be Hispaniola, based on land area alone. It may be significant that if macaws were once present on Hispaniola then they seem to have disappeared before the first Spanish chroniclers began documenting the fauna of the island in the 16th century (Olson 2005).

To paint a completely hypothetical picture, a Hispaniolan macaw may have been so precious a commodity that every possible nest was sought to procure the young

for trade. By such a means a large and comparatively uncommon species might conceivably be reduced to extinction in the wild over the nearly two millennia that Amerindians occupied Hispaniola. The birds could have been maintained in captivity in native villages through many other parts of the Antilles, but with the collapse of Taino culture shortly following the arrival of Europeans (Rouse 1992), the macaw would then have become extinct.

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