

Osteological Differentiation of the *Iguana Laurenti*, 1768 (Squamata: Iguanidae) Species: *Iguana iguana* (Linnaeus, 1758) and *Iguana delicatissima* Laurenti, 1768, with some Comments on their Hybrids

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ABSTRACT.—The origins of the two iguana species (*Iguana delicatissima* [Lesser Antillean Iguana] and *Iguana iguana* [Green Iguana]) occurring today in the Lesser Antilles are frequently questioned using mostly historical and genetic data. Osteological remains of iguanas are common in archaeological and paleontological deposits in the Lesser Antilles, however, and they could be important for understanding the past colonization processes of these two iguana species and subsequent sympatry. Unfortunately, although numerous questions exist about the past occurrence of those two species and their respective arrival dates, no osteological study has led to proper identification of subfossil iguana skeletal elements. Here we present a series of characters that allow for distinguishing the two species using isolated bones and emphasize the reliability of each recognized specific character. We also provide some comments about skeletal morphology of hybrids between both species and their identification based on osteology.

RÉSUMÉ.—L'origine des deux espèces d'iguanes peuplant actuellement les Petites Antilles (*Iguana delicatissima* et *Iguana iguana*) est souvent sujette à question notamment via l'utilisation des sources historiques et génétiques. Cependant, les restes ostéologiques d'iguanes sont fréquemment retrouvés dans les sites archéologiques et paléontologiques des Petites Antilles et pourraient être de première importance pour comprendre les processus de colonisation de la zone par ces deux espèces. Malheureusement, bien que de nombreuses questions persistent quant à la présence passée et aux périodes d'arrivées de ces deux taxons, aucune étude ostéologique ne permet d'aboutir à une identification satisfaisante de leurs restes sub-fossiles. Nous présentons ici une série de caractères permettant d'identifier ces deux espèces via des fragments osseux isolés tout en discutant la fiabilité de chacun des caractères. Nous émettons également quelques commentaires relatifs à la morphologie squelettique des hybrides de ces deux espèces et à leur identification via des restes osseux.

The genus *Iguana* (Laurenti, 1768) includes two species, both of which currently occur in the Lesser Antilles. The Lesser Antillean Iguana, *Iguana delicatissima* (Laurenti, 1768), is distributed only in the Lesser Antilles; two subspecies of the Green Iguana, *Iguana iguana* (Linnaeus, 1758), are also distributed in Central [*Iguana iguana iguana* (Linnaeus, 1758)] and South America [*Iguana iguana rhinolopha* (Wiegmann, 1834)].

Iguana iguana was recently introduced in the Greater Antilles, in Florida and Hawaii, United States, and in Israel (Malone and Davis, 2004; Henderson and Powell, 2009; Breuil, 2013); its history in the Lesser Antilles is more paradoxical. It probably was introduced to the Lesser Antilles during modern times from both South and Central America, but this is obscured by possible endemic forms that exist on Saba, Montserrat, and Saint Lucia islands (Malone and Davis, 2004; Breuil, 2013; Stephen et al., 2013). *Iguana iguana* and *I. delicatissima* are morphologically and molecularly distinct yet can hybridize (Day and Thorpe, 1996; Malone and Davis, 2004; Breuil, 2013; Stephen et al., 2013). The common assumption is that hybridization has endangered the survival of *I. delicatissima* following island introduction of the continental *I. iguana* (Breuil, 2002; Day et al., 2000; Breuil, 2009; Lorvelec et al., 2011; Knapp et al., 2014). The discovery of a possibly ancient, introduced *I.*

iguana population in the Lesser Antilles at Montserrat, St. Lucia, and Saba, however, and the weak genetic diversity of the *I. delicatissima* populations among islands, make the island colonization and evolution scenario of these two iguanas difficult to understand. Approaching such questions can be done using genetic data (Malone and Davis, 2004; Stephen et al., 2013; Valette et al., 2013), but subfossil remains preserved in archaeological and paleontological deposits also can provide direct evidence of past iguana populations to suggest new hypotheses or test genetic assumptions. Such material is available in the Lesser Antilles, where there exist dozens of archaeological sites of pre-Columbian age that contain iguana remains (Grouard, 2001, 2007, 2010, 2013).

Despite an abundance of data, studies on osteological differences between *I. iguana* and *I. delicatissima* remain rare. A previous work of Conrad and Norell (2010) led to the identification of complete skulls of the two species, but this is not helpful for making proper species identification of osteological remains collected in subfossil deposits, which are mainly isolated and fragmented skeletal elements. In addition, inter-specific hybrids have received no attention in the literature.

Martin (2009) also conducted a study on osteological differences between *I. iguana* and *I. delicatissima*, but distinctive osteological characters of the two species were built on a very small comparative sample (5 *I. delicatissima* and 10 *I. iguana* specimens from Muséum national d'Histoire naturelle [MNHN, Paris,

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France)), all of which have been re-examined in our study. In addition, Martin (2009) considered five *I. iguana* museum specimens, included in its comparative collection, to be hybrids without any supporting argument. For all those reasons, the whole characters described by Martin (2009) were tested in our study.

The main purpose of our work is to provide a set of useful characters on isolated and fragmented *Iguana* skeletal elements that will allow for a clear distinction between *I. iguana*, *I. delicatissima*, and their hybrids in Holocene subfossil remains. We also evaluate the reliability of those characters to avoid identification mistakes because of intraspecific variability of both taxa.

MATERIAL AND METHODS

Comparative Material.—We examined 69 specimens of *Iguana* spp. collected during the two past centuries: 44 *I. iguana*, 18 *I. delicatissima*, and 7 interspecific hybrids. These specimens come from Muséum national d'Histoire naturelle (MNHN - Paris, France) collections (Comparative Anatomy - MNHN-ZA-AC-, Reptile and Amphibians - MNHN-RA-, and UMR 7209 "Archéozoologie et Archéobotanique" "Caraïbes" - MNHN-UMR7209- collections); UMR 5199 CNRS "De la Préhistoire à l'Actuel, Culture, Environnement, Anthropologie" (PACEA - Bordeaux, France), and Museum of Comparative Zoology (MCZ - Harvard, Cambridge, Massachusetts, United States). Newly collected specimens were imported to the MNHN in conformity with the French and international regulation under the permits no. 11629 and no. 11631 in Saint Barthelemy and in accordance with the Direction de l'Environnement, de l'Aménagement et du Logement (DEAL) and Direction Régionale de l'Environnement (DIREN) organizations in la Martinique and Guadeloupe (permit delivered 18 October 2010, 28 November 2011, and 29 May 2013). Sex, origin, collector, and collection year for each specimen are listed in Appendix 1. Adults of both sexes and juveniles were included in this sample.

Species identification was verified using external morphology for all specimens collected after 2000 following the criteria established by Breuil (2013). The main characters used rely on the presence (*I. iguana*) or absence (*I. delicatissima*) of a large, subtympenic scale, the sublabial region morphology that contained a mosaic of flat scales in *I. iguana* and a single row of domed scale in *I. delicatissima*, and the gular spines that are restricted to the dewlap straight edge (they are less numerous [<6] in *I. delicatissima* whereas in *I. iguana* they are more numerous [6–10] and more-extended ventrally on the dewlap). More criteria can be found in Breuil (2013). Hybrids also were identified following the same morphological criteria; as in other squamate hybrids (see Ernst et al., 2014), they usually present intermediate states for all the characters of the two parental species (F1 hybrids) or a patchwork of *I. delicatissima* and *I. iguana* character states (post F1 hybrids) (Breuil, 2013). Following those characters, two of our hybrids (MNHN-UMR 7209-529 and MNHN-UMR 7209-715) could be F1 hybrids and the others post F1 hybrids (Fig. 1).

The Osteological Criteria.—We observed each skeletal element separately and did not consider characters concerning contact or relative position of different bones (connections between unfused bones are rarely preserved in fossil assemblages). We observed each element of the skeleton and paid particular attention to those that usually are well represented in fossil remains.

Only the genus *Iguana* (including hybrids) is included in this study. We consequently did not have any assumption about the phylogenetic significance of the diagnostic characters. Our goal

was limited to establishing clear osteological differences between *I. iguana*, *I. delicatissima*, and their hybrids. Some of the characters on the frontal and coronoid bones can be influenced by ontogenetic variation; therefore, we discuss the ontogenetic variability of these skeletal elements to help the reader establish the juvenile or adult condition of the bone prior to identification. All the others characters can be used regardless of the specimen maturity. Each feature is identified by a letter and a number; all characters situated on the same skeletal element bear the same letter and are numbered.

Methodology.—All characters were first established using a subset of samples before being tested on the whole set of reference specimens. To describe the reliability of each character, we used a correct identification rate (CIR), which corresponds to the percentage of correct identifications using the character. The characters presenting a CIR lower than 80% were automatically discarded; all other characters were kept. Because of the intraspecific morphological variability of the two species, however, characters with a CIR of 100% were rare. For this reason, the numbers of observations of each character along with their CIR for each species are presented in this study (Table 1). We also report the occurrence of nonrecordable intermediate and juvenile bone condition. When combined with good comparative material, this approach could avoid false identification based on non-fully reliable characters by providing a degree of confidence for each criterion. We also report observed skeletal elements and characters that were considered as nonreliable for distinguishing between the two *Iguana*.

We observed hybrids separately to see if some significant characters could be recognized. In addition, all previously identified diagnostic characters were examined in our hybrid sample.

We also tried to recognize sexually dimorphic characters in both species but failed to observe any characters linked to sex rather than to age or size of a specimen. Through this process, we also ensured that sex had no effect on the state of the distinctive characters.

The terminology used to describe the anatomical structures is that used by Fejérvary-Langh (1923), Lécure (1969, 1968), Evans (2008), Klembara et al. (2010), and Smith (2011).

RESULTS

Distinctive Characters Between *I. delicatissima* and *I. iguana* (Table 1).—Maxilla (two characters: CIR = 84–90%): Two maxilla characters allow a reliable discrimination of the two species. In dorsal and medial views, the infraorbital foramen (i. f.) (superior alveolar foramen sensu Smith, 2011) is anteriorly located on the suprudental shelf (s. s.) (sensu Rage and Augé, 2010) and can reach the transversal crest (t. c.) (crista transversalis sensu Smith, 2011) in *I. delicatissima*. This foramen is more-posteriorly located in *I. iguana* (character A1 in Fig. 2). The second character is the exonarial margin (e. m.) of the facial process (f. p.) in lateral view, which forms an obtuse angle with premaxillary process (p. p.) in *I. delicatissima* and a right angle in *I. iguana* (character A2 in Fig. 2). These two features already have been reported by Martin (2009). Nasal (one character: CIR = 100%): The nasals of the two species are very different, as was previously highlighted by Conrad and Norel (2010), who relied mainly on the nasal region to distinguish the skulls of the two iguanas. The *I. delicatissima* nasal bone is as long as it is wide whereas that of *I. iguana* is clearly longer than wide. In addition, the naris (n.) (fenestra exonarina sensu [Gauthier et al., 1988]) of *I. delicatissima* is more-posteriorly

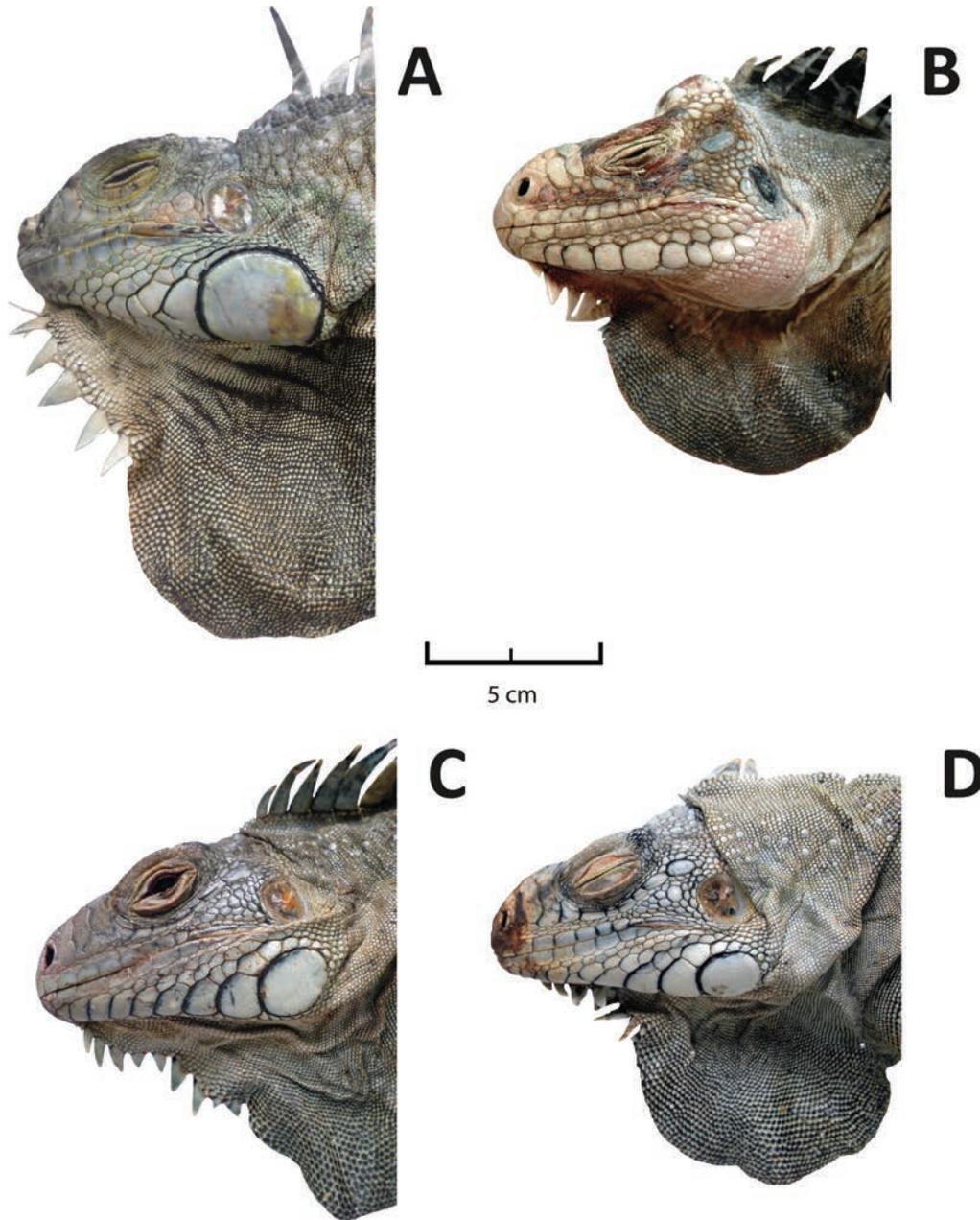


FIG. 1. Head lateral view of (A) *I. iguana* (MNHN-ZA-AC 2014-35), (B) *I. delicatissima* (MNHN-ZA-AC 2014-24), (C), F1 hybrid (MNHN-ZA-AC 2014-18), and (D) post F1 hybrid (MNHN-ZA-AC 2014-14). Pictures: E. Pellé.

extended in dorsal view than in *I. iguana*, and the anteromedial process (a. p.) is more-anteriorly extended in *I. delicatissima* than in *I. iguana* (character B in Fig. 3). Among our hybrids, a specimen shows an intermediate morphology combining general morphology and nasal margin depth of each parental species.

Frontal (three characters: CIR = 88–100%): The frontals also are easily identifiable. As reported by Conrad and Norell (2010), in dorsal view on adult specimens, the *I. delicatissima* frontal is wider and the interorbital constriction weaker than in *I. iguana* (character C1 in Fig. 4). The smallest width of the interorbital constriction (1) is below 50% of the maximal lateral length (2) of the bone in *I. iguana* and above 50% in *I. delicatissima*. This character cannot be used on juvenile specimens because the interorbital constriction is strong in juveniles of both species (see Fig. 4), but other characters can be used independently of the

specimen's age. The posterolateral processes (p. p.) are differentially oriented in both species. In *I. delicatissima*, these processes are oriented posterolaterally, and articular facets with the parietal (a. f. p.) are oriented dorsally and well visible in dorsal view (character C2 in Fig. 4). In *I. iguana* the frontal posterolateral processes are oriented laterally and the articular facets with the parietal are oriented posteriorly, almost not visible in dorsal view. A particular condition can be observed in some hybrids where the posterolateral processes can be very short and blunt. Another difference is that *I. delicatissima* frontal bones bear a posterior braincase depression (p. b. d.) in ventral view which tends to be absent in *I. iguana* (character C3 in Fig. 4). Conrad and Norell (2010) also observed differences of overlapping between nasal and frontal bones of both species, but we do not assess the reliability of this character because the anterior part of the frontal

TABLE 1. Numbers of observations of each character state on *I. delicatissima*, *I. iguana*, and hybrid specimens of the comparative sample (*n*), correct identification rate (CIR) between *I. iguana* and *I. delicatissima* for each character, and occurrence of nonrecorded intermediate condition (NC).

Bone	Character	State	Comparative specimens						
			<i>I. delicatissima</i>		<i>I. iguana</i>		CIR (%)	Hybrids	
			<i>n</i>	NC	<i>n</i>	NC		<i>n</i>	NC
Maxilla	A1	<i>I. iguana</i>	0	0	20	1	84	4	2
		<i>I. delicatissima</i>	12		6			1	
	A2	<i>I. iguana</i>	0	0	33	0	90	4	1
		<i>I. delicatissima</i>	14		5			2	
Nasal	B	<i>I. iguana</i>	0	0	38	0	100	3	1
		<i>I. delicatissima</i>	15		0			3	
Frontal	C1	<i>I. iguana</i>	2	0	31	0	88	4	0
		<i>I. delicatissima</i>	13		4			3	
	C2	<i>I. iguana</i>	0	0	36	1	100	0	1
		<i>I. delicatissima</i>	15		0			0	
		hybrid	0		0			6	
	C3	<i>I. iguana</i>	0	0	27	1	91	5	0
		<i>I. delicatissima</i>	13		3			2	
Parietal	D1	<i>I. iguana</i>	0	1	35	1	90	5	1
		<i>I. delicatissima</i>	14		3			1	
	D2	<i>I. iguana</i>	0	0	19	3	85	0	1
		<i>I. delicatissima</i>	10		5			6	
Postorbital	E	<i>I. iguana</i>	0	0	34	4	98	5	0
		<i>I. delicatissima</i>	14		1			2	
Jugal	F	<i>I. iguana</i>	0	0	31	1	88	4	1
		<i>I. delicatissima</i>	15		6			2	
Pterygoid	G1	<i>I. iguana</i>	0	1	29	11	100	5	2
		<i>I. delicatissima</i>	15		0			0	
	G2	<i>I. iguana</i>	0	1	40	0	100	6	0
		<i>I. delicatissima</i>	15		0			1	
	G3	<i>I. iguana</i>	0	0	25	12	94	3	3
		<i>I. delicatissima</i>	15		3			1	
Sphenoid	H	<i>I. iguana</i>	0	3	34	2	98	4	2
		<i>I. delicatissima</i>	12		1			1	
Dentary	I	<i>I. iguana</i>	0	0	23	0	100	6	0
		<i>I. delicatissima</i>	13		0			1	
Coronoid	J1	<i>I. iguana</i>	1	0	29	1	88	5	0
		<i>I. delicatissima</i>	15		5			1	
	J2	hybrid	0		0			1	
		<i>I. iguana</i>	0	16	4	31	100	3	3
		<i>I. delicatissima</i>	0		0			0	
Articular	K1	<i>I. iguana</i>	5	0	30	0	82	5	1
		<i>I. delicatissima</i>	10		4			1	
	K2	<i>I. iguana</i>	0	0	21	0	73	4	1
		<i>I. delicatissima</i>	15		13			2	
	K1 + K2	<i>I. iguana</i>	0	4	17	17	100	1	5
		<i>I. delicatissima</i>	11		0			1	
Surangular	L	<i>I. iguana</i>	2	1	17	3	86	5	0
		<i>I. delicatissima</i>	10		2			2	
Axis	M	<i>I. iguana</i>	0	0	27	2	90	1	1
		<i>I. delicatissima</i>	13		4			5	
Caudal vertebrae	N	<i>I. iguana</i>	0	0	32	2	100	3	1
		<i>I. delicatissima</i>	14		0			3	
Scapula	O1	<i>I. iguana</i>	0	13	24	12	100	2	4
		<i>I. delicatissima</i>	0		0			0	
	O2	<i>I. iguana</i>	2	0	28	3	83	1	5
		<i>I. delicatissima</i>	13		6			1	
	O3	<i>I. iguana</i>	1	1	34	2	95	3	4
		<i>I. delicatissima</i>	12		1			0	
Coxal	P1	<i>I. iguana</i>	0	4	14	21	100	0	4
		<i>I. delicatissima</i>	11		0			2	
	P2	<i>I. iguana</i>	0	0	31	0	92	3	0
		<i>I. delicatissima</i>	15		4			4	
	P3	<i>I. iguana</i>	1	1	27	1	100	3	0
		<i>I. delicatissima</i>	13		0			4	
	P4	<i>I. iguana</i>	0	0	24	1	94	5	0
		<i>I. delicatissima</i>	13		3			2	
	P5	<i>I. iguana</i>	1	1	28	3	89	4	0
		<i>I. delicatissima</i>	13		4			3	
Humerus	Q	<i>I. iguana</i>	0	0	27	0	93	4	0
		<i>I. delicatissima</i>	15		2			3	

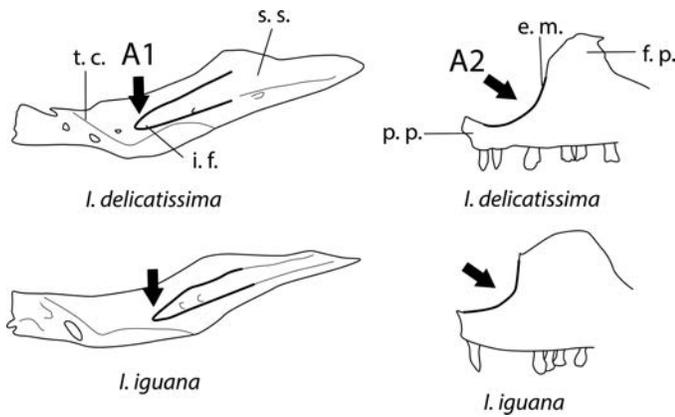


FIG. 2. Left maxilla, dorsal (A1) and labial (A2) views.

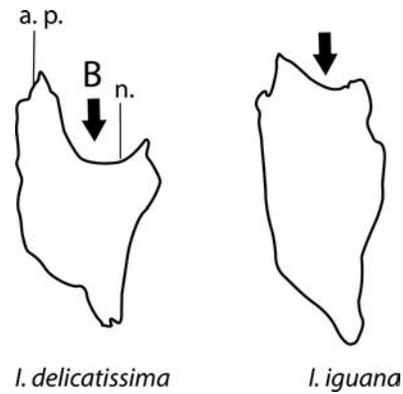


FIG. 3. Right nasal, dorsal view.

is very thin and often broken, even on our modern specimens. The few times we observed entire elements, the nasal impression (n. i.) on the frontal did not seem to be a valuable distinctive character.

Parietal (two characters: CIR = 85–90%): The parietal presents an important variability across our comparative sample, especially between juvenile and adult individuals. The shape of the entire bone is modified across ontogeny, from the juvenile to the adult form (Fig. 5). The posterior processes become longer, the median constriction stronger, and the parietal crests (well individualized on the young specimens) are fused together and extended posteriorly on the adult specimens (Fig. 5). We did not see any clear differences in the ontogenetic variability of *I. iguana* and *I. delicatissima*, but we identified two characters that can be used on juveniles and adult of both species. The first is the pineal foramen (p. f.), highly visible on the *I. iguana* parietal/frontal margin and usually less conspicuous on the *I. delicatissima* parietal (character D1 in Fig. 5). The second criterion concerns articular facets with the frontal bone (a. f.) that are oriented ventrally and highly visible in ventral view in *I. delicatissima* and oriented anteriorly and less visible in *I. iguana* (character D2 in Fig. 5).

Postorbital (one character: CIR = 98%): The articulation between the jugal and the postorbital is different in the two species. The contact between the jugal and the postorbital is mainly ventral in *I. iguana* and mainly medial in *I. delicatissima*. Consequently, the postorbital articular facet with the jugal (a. f. j.) is ventrally directed and nearly nonvisible in medial view in *I. iguana*, while this facet is oriented medially and well visible in medial view in *I. delicatissima* (character E in Fig. 6). In addition, the articular facets with the jugal and squamosal form a continuous slender articular facet in *I. iguana* but two individualized facets in *I. delicatissima* (character E in Fig. 6).

Jugal (one character: CIR = 88%): In *I. delicatissima*, the dorsal view of the jugal suborbital ramus bears an anteromedial expansion (a. e.) between the palatine and ectopterygoid insertion regions. The same expansion tends to be less developed in *I. iguana* (character F in Fig. 7).

Pterygoid (three characters: CIR=94–100%): Three characters can be used to separate both species according to their pterygoids, but two of them are subject to ontogenetic variations. Consequently, establishing the adult or juvenile state of the bone prior to identification is a necessity. Unfortunately, we lack morphological characters to do this on isolated pterygoid bones, so we will only consider the maximal width of the bone in ventral view (at the level of the ectopterygoid process [e. p.]), which is <7 mm on our juvenile

specimens. The first distinctive character is the number of pterygoidian dental rows: *I. delicatissima* and juvenile *I. iguana* bear only one dental row (d. r.), but adult *I. iguana* show two or more rows (character G1 in Fig. 8). Second, the dental row is less-posteriorly expanded in *I. delicatissima* than in *I. iguana*, where it can be prolonged near the ectopterygoid process (e. p.) posterior margin (character G2 in Fig. 8). Third, pterygoid lateral area (l. a.) tends to be concave near the dental row in *I. iguana* and flat in *I. delicatissima* and juvenile *I. iguana* (character G3 in Fig. 8).

Sphenoid (one character: CIR = 98%): In ventral view, the sphenoid ventral crests (v. c.) joining basal tubercle (b. t.) to basiptyergoid process (b. p.) tend to be straight in *I. iguana* and sigmoid in *I. delicatissima* (character H in Fig. 9).

Dentary (one character: CIR = 100%): Only one character seems to be reliable to sort the two iguana dentaries: the intra-mandibular lamella (sensu Smith, 2011) corresponding to the anteromedial coronoid branch insertion. This lamella is anteriorly extended in *I. iguana* under the third to sixth last dental positions and shorter in *I. delicatissima* under the first to second dental position (character I). Martin (2009) proposed some characters regarding teeth shape. According to our observations, teeth morphology is highly variable depending on the species and the size of each specimen but also depending on the wear and the relative position of each tooth on the dentary.

Coronoid (two characters: CIR = 88–100%): The morphology of the coronoid, and especially of the coronoid process (c. p.), is highly variable in *I. iguana* but consistent in *I. delicatissima*. In lateral view, the *I. delicatissima* coronoid process tends to be slightly higher and more-dorsally rounded (character J1 in Fig. 10) than in *I. iguana*. In some cases it bears a small posterior protuberance (p. p.) (character J2 in Fig. 10). In *I. iguana*, the coronoid process is slightly lower (character J1 in Fig. 10) and can present a well-developed posterior protuberance (character J2 in Fig. 10). In addition, *I. iguana* presents a wide range of wide coronoid process morphologies (Fig. 10), easily distinguishable from the typical *I. delicatissima* morphology illustrated. The juvenile *I. delicatissima* coronoids bear a more-dorsally pointed coronoid process oriented dorsally without a posterior process (Fig. 10); it differed from the coronoid process in juvenile *I. iguana* by being more-posteriorly directed (Fig. 10). In addition, one of seven examined hybrids presented an original morphology with a square-shaped coronoid process because of an especially wide posterior protuberance.

Articular (one character: CIR = 100%): The articular bone also is highly variable, but a combination of two characters effectively distinguishes between both iguanas. The retroarticular process (r.

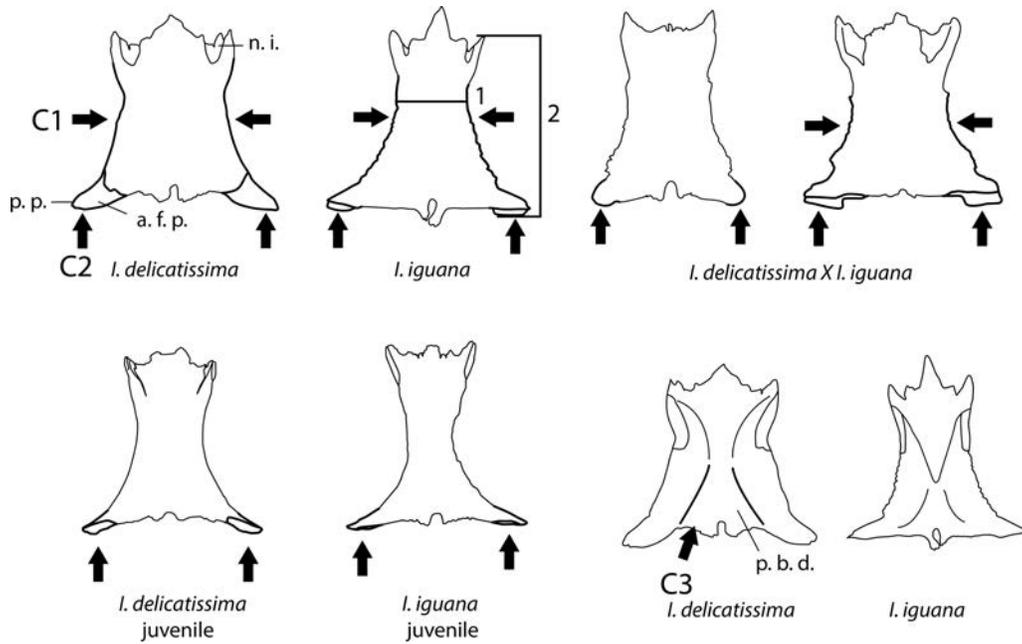


FIG. 4. Frontal, dorsal (C1 and C2) and ventral (C3) views.

p.) tends to be shorter in *I. delicatissima*, where its length (1) is <150% of the length of the articular fossa (2), than in *I. iguana* where its length is >150% of the length of the articular fossa (a. f.) (character K1 in Fig. 11). In addition, the tympanic crest (t. c.) (3) tends to be wider than the angular crest (a. c.) (4) in *I. delicatissima*, a condition that is reversed in *I. iguana* (character K2 in Fig. 11). Those characters cannot be used separately because they are highly variable depending on specimen size. They can be considered only if they are combined (see Table 1).

Surangular (one character: CIR = 86%): The surangular coronoid process (c. p.) is pointed in *I. delicatissima* and rounded in *I. iguana* (character L in Fig. 12).

Axis (one character: CIR = 90%): The proportion between minimal neural arch (n. a.) length (1) and the posterior neural arch breadth comprising the postzygapophysis (2) is smaller in *I. delicatissima* (<0.65) than in *I. iguana* (>0.68) (character M in Fig. 13).

Caudal vertebrae (one character: CIR = 100%): As previously reported by De Queiroz (1987) and later by Breuil (2013), *I.*

I. iguana parietal ontogenetic variability

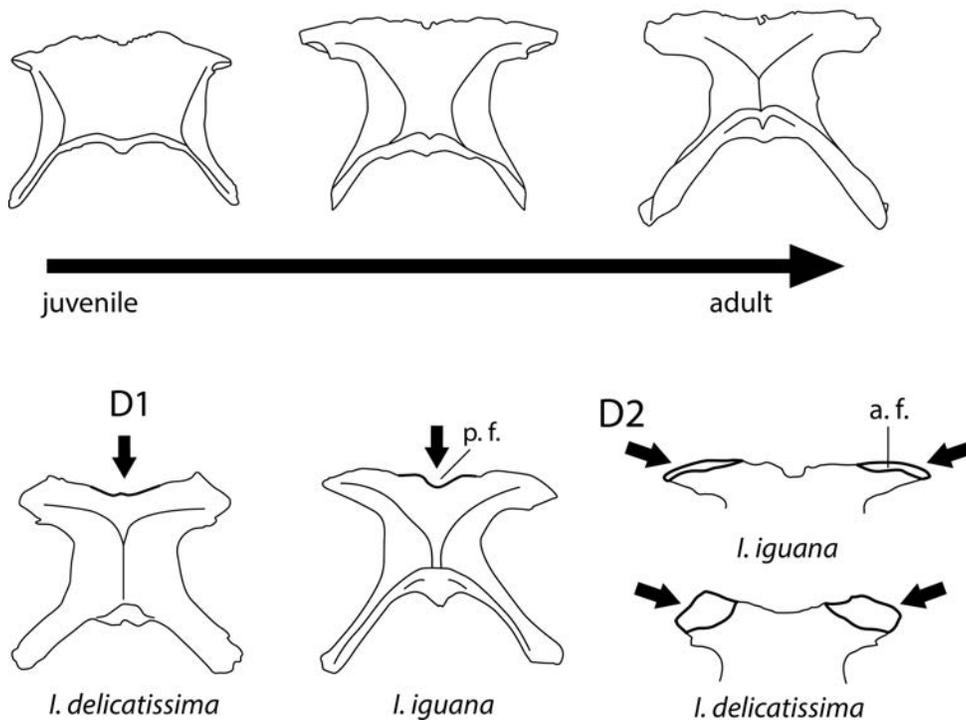


FIG. 5. Parietal, dorsal (ontogenetic variability and D1) and ventral (D2) views.

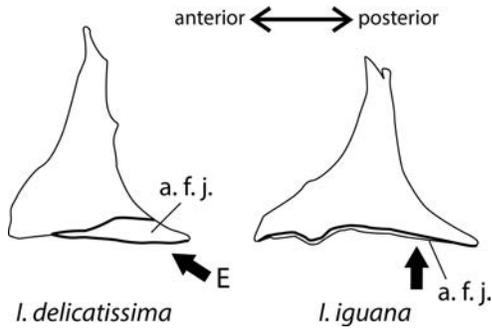


FIG. 6. Left postorbital, medial view.

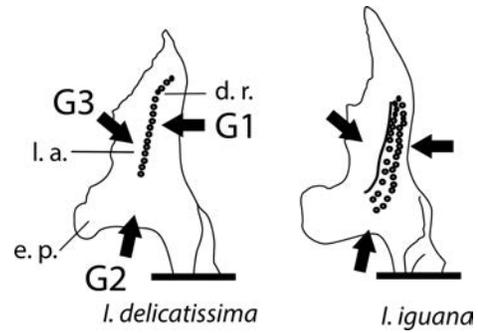


FIG. 8. Right pterygoid, ventral view.

delicatissima lacks caudal autotomy planes (a. p.) (character N in Fig. 14), unlike *I. iguana*. These autotomy planes can be fused in adult *I. iguana* but still remain clearly visible, unlike in *I. delicatissima* where they do not occur. These planes occur in the first anterior quarter of the posterior caudal vertebrae bearing no or two lateral process(es), just as described by Etheridge (1967), but tend to be absent or not visible on most caudal vertebrae.

Scapulocoracoid (three characters: CIR = 83–100%): Three characters can be used on the scapulocoracoid to distinguish between both *Iguana* species. A small posterolateral protuberance (pl. p.), marking the attachment of scapulohumeral ligament (Russel and Bauer, 2008), occurs in two thirds of our *I. iguana* specimens but is systematically absent in *I. delicatissima* (character O1 in Fig. 15). In *I. delicatissima*, the coracoid process (c. p.) is more robust than in *I. iguana*, where it is slender (character O2 in Fig. 15). The width of the *I. delicatissima* coracoid process (1) is >40% of its length (2), and in *I. iguana* its width is <40% of its length. In lateral view, the posterior coracoid fenestra (p. c. f.) opening (3) is wider than the mesocoracoid (mc.) (4) in *I. iguana* and narrower in *I. delicatissima* (character O3 in Fig. 15).

Pelvic bone (five characters: CIR = 89–100%): The pelvis bears five characters, allowing a reliable distinction between the two iguanas. The ilium dorsal crest (d. c.) tends to be convex in *I. delicatissima* and concave in *I. iguana* (character P1 in Fig. 16), a character also mentioned by Martin (2009). It also bears a ventral edge (v. e.), short and curved in *I. delicatissima* but long and straight in *I. iguana* (character P2 in Fig. 16). The posterior section of ilium (Il.) is subtriangular in *I. delicatissima* and oval in *I. iguana* (character P3 in Fig. 16). The anterior section of the pubis (P.) forms a triangle with an acute angle apex in *I. delicatissima* and a straight angle apex in *I. iguana* (character P4 in Fig. 16). The posterior margin of ischium (Is.) is more concave in *I. delicatissima* than in *I. iguana* (character P5 in Fig. 16).

Humerus (one character: CIR = 93%): The foramen of the supracondylar fossa was first observed by Hoffstetter (1946) but not clearly mentioned as a distinctive character of *I. delicatissima*.

Martin (2009) also mentioned this character but judged it as unreliable for distinguishing both iguanas; however, we found the character to be reliable. The foramen of the supracondylar fossa (sc. f.) is largely open in *I. delicatissima* and narrow in *I. iguana* (character Q in Fig. 17).

Unreliable Skeletal Elements and Characters.—Regarding the previously discussed skeletal elements, we described anatomical structures that were considered reliable characters for distinguishing only between *Iguana* species. We tried to observe the whole morphology of each bone so that undescribed structures can be considered unreliable for identification. We also observed skeletal elements on which we failed to distinguish reliable characters: the occipital, palatine, quadrate, ectopterygoid, splenial, radius, ulna, femur, tibia, fibula, calcaneus, talus, metapodial, and phalanx.

Hybrid Osteology.—The hybrid osteology was highly variable and did not show many typical osteological characters. Indeed, only two characters observed on the hybrids were absent in both *I. iguana* and *I. delicatissima*. First, a frontal morphology with very short and blunt posterolateral processes or an intermediate morphology, with a wide frontal and articular facets with the parietal forming a right angle, which makes them partially visible in dorsal view (character C2 in Fig. 4). Second, a coronoid bone that has a wide and short coronoid process with a prominent secondary process (characters J1 & J2 in Fig. 10). The two frontal hybrid morphologies occur on six of our seven hybrids and the hybrid coronoid morphology on only one specimen. All other characters are similar to those described for *I. iguana* and *I. delicatissima*. The hybrids possess primarily an assemblage of characters of both parental species and cannot be distinguished based on loose skeletal elements. Therefore, only a combination of several characters from both *I. iguana* and *I. delicatissima* found on a whole skeleton can allow proper identification of a hybrid. In our sample, all examined complete

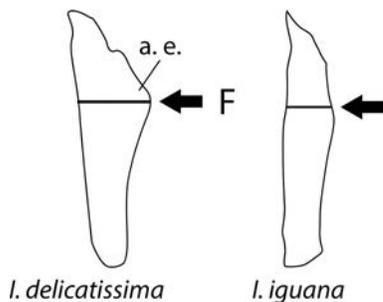


FIG. 7. Left jugal, dorsal view.

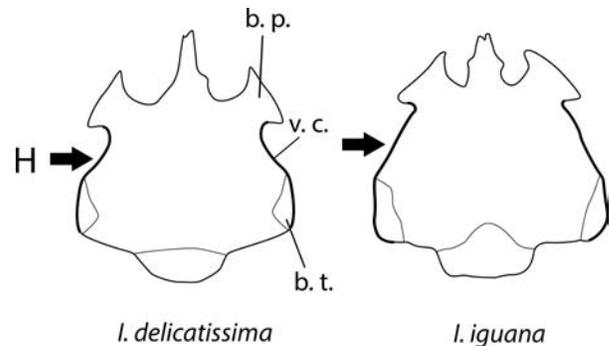


FIG. 9. Sphenoid, ventral view.

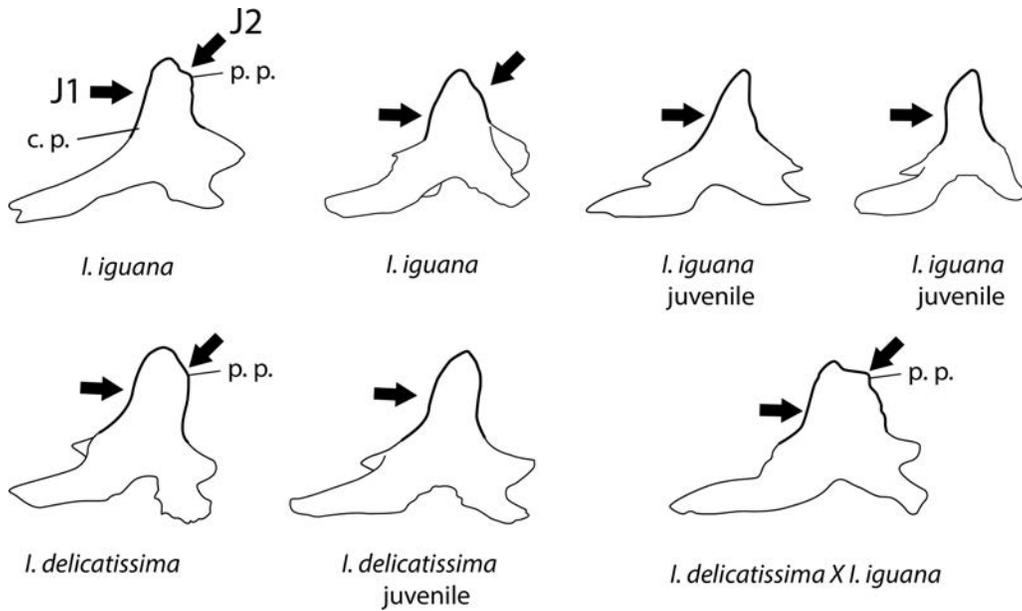


FIG. 10. Right coronoid, lingual view.

hybrid skeletons bear <80% of the characters of one of the parental species. This combination of characters probably reflects the genotype and the importance of each parental species in its skeletal shape, but this observed variability makes the identification of hybrid isolated skeletal elements impossible except in the case of the occurrence of the two previously mentioned specific characters.

DISCUSSION

We give evidence of 32 diagnostic characters distributed on 17 iguana skeletal elements. Most, but not all, of these characters are present on the skull elements and partly reflect the difference of head shape between the two *Iguana* species, especially those dealing with the nasal and frontal morphology that tend to be shortened in *I. delicatissima* as compared to *I. iguana*.

Among all the characters, 11 are 100% reliable, 3 are 99–95% reliable, 9 are 95–90% reliable, 6 are 90–85% reliable, and 4 are 80–85% reliable for separating both species (see Table 1). This clearly shows that *Iguana* isolated bones coming from archae-

ological and paleontological contexts can now be identified at the species level.

Interestingly, only 34% of the characters (see Table 1) seem to be 100% reliable. This clearly shows there to be important intraspecific variability in both species as well as strong morphological overlap between *I. iguana* and *I. delicatissima* for most skeletal elements. Interpreting this overlap is far beyond the scope of this work and would require genetic studies to know if it reflects a recent speciation or a complex history of repeated hybridizations. The morphological variability of *I. iguana* also could reflect the large distribution of this taxon and the existence of unrecognized subspecific diversity (Breuil, 2013), but the small number of specimens, and the lack of precise geographical origins for most of them, did not allow us to approach this question (see Appendix 1).

Our study also shows the importance of establishing a strong, broad, comparative collection to include the intraspecific variability. This high variability and morphological overlap, along with the large amount of skeletal elements that had been unconsidered because of the lack of reliable characters, demonstrates that building dichotomous keys for closely related species can be difficult. Our study shows that a dichotomous

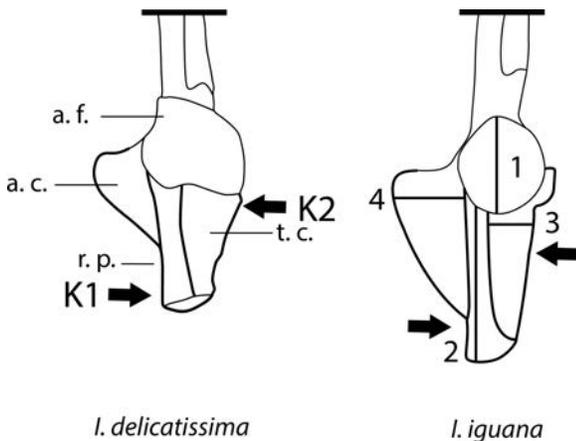


FIG. 11. Right articular, dorsal view.

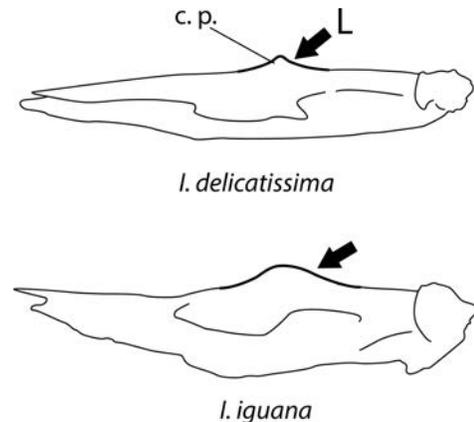


FIG. 12. Right surangular, medial view.

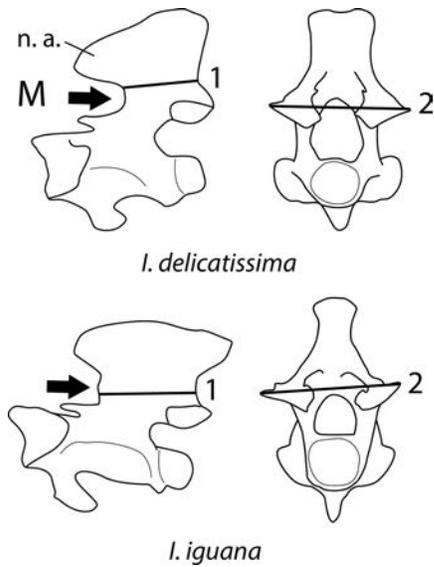


FIG. 13. Axis, lateral and posterior views.

key based on <10 specimens of each species is not reliable and can lead to misidentifications. We show the importance of assessing the reliability of each character to interpret the results obtained by using comparative material in zooarchaeological and paleontological studies. Indeed, such studies are limited by the number of remains available because of the scarcity of subfossil material, and a single wrong attribution can easily lead to important misinterpretations. Therefore, disclosing a confidence level for each character can be a critical element to understand the obtained results.

Unsurprisingly, our study shows a huge morphological variability among the hybrids, probably reflecting the effect of different cross statuses of these hybrids. Moreover, we failed to establish a link between the external morphology attribution (F1 or post F1 hybrids) and the observed skeletal morphology. Based on external morphology, our two putative F1 hybrids show very different osteological characters, and the external morphology criteria of intermediate characters (F1 hybrids) or the patchwork of characters of both parental species (post F1 hybrids) does not seem correlated with skeletal morphology. The main reason for this could be that our characters are not suitable for describing intermediate states. Indeed, because of the important *I. iguana* variability, our characters focused on undoubtedly *I. delicatissima* character states, and any variation led to an undetermined or an *I. iguana* state identification. This is highly visible in our hybrids for which we coded mainly *I. iguana* states ($n = 110$) rather than *I. delicatissima* states ($n = 60$) and with many undetermined states ($n = 46$) (Table 1). Further investigations are required to establish a link between hybrid genotypes and skeletal phenotypes. However, our characters still reliably identify a hybrid whole skeleton which, following

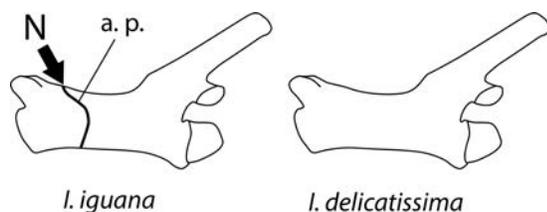


FIG. 14. Posterior caudal vertebra, lateral view.

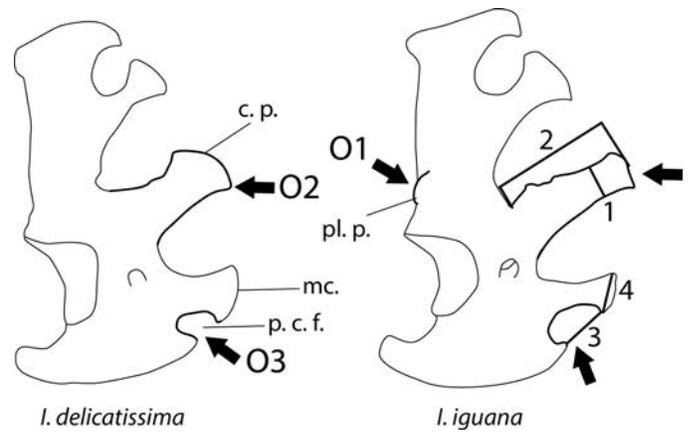


FIG. 15. Right scapulocoracoid lateral view.

our observations, would possess at least one of the following attributes: it bears <80% of each parental species characters and has one or both of the peculiar hybrid character state on frontal and coronoid bones.

Comparisons to previous studies show our results to match those of Conrad and Norell (2010) but strongly diverge with those of Martin (2009). Indeed, among the 36 characters observed by the later author on whole iguana skeletons, only three (two on maxilla and one on ilium bones) match our results. An observed character on the humerus was signaled as a nondiscriminant character by the same author. All other characters indicated by Martin (2009) seem only to reflect intraspecific variability and prove that trying to distinguish close taxa without taking this variability into account by using a large number of reference specimens is worthless.

We demonstrate that several osteological characters will allow reliable species identifications for *Iguana* subfossil remains in the Lesser Antilles. Among others, we identified eleven osteological characters that reliably distinguish the two *Iguana* species 100% of the time (see Table 1): (B) the nasal bone morphology; (C2) the orientation of the frontal bone posterior processes; (G1) the number of tooth rows and (G2) their position on the pterygoid; (I) the length of the intramandibular lamella of the dentary; (J2) the presence-absence of a well-developed coronoid posterior process; (K1+K2) the morphology of the retroarticular process and tympanic crest of the articular bone; (N) the presence-absence of fracture planes on the caudal vertebrae; (O1) the presence-absence of a posterolateral protuberance on the scapulocoracoid; and (P1) morphology of the dorsal crest and (P3) posterior section of the ilium. We also show that hybridization can be tracked under certain modalities using frontal and coronoid bones. This new tool will allow for the study of past iguana colonization by enabling species identification of *Iguana* remains from the numerous archaeological sites in the Lesser Antilles. With such confident identification, we can solve different questions regarding past occurrence and interactions of *I. iguana* and *I. delicatissima* on those islands.

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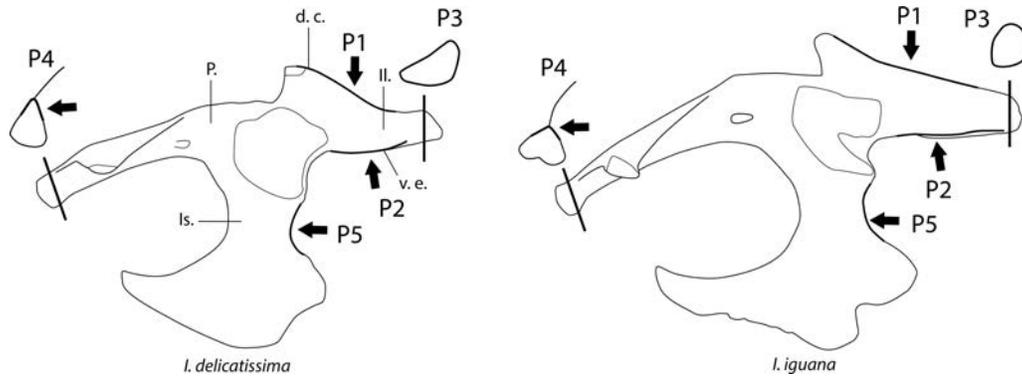


FIG. 16. Left pelvic girdle, lateral view.

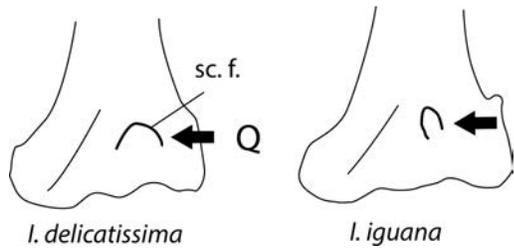


FIG. 17. Left humerus, ventral view.

and the two anonymous reviewers who helped us improve the quality of this manuscript. We also thank the Museum of Comparative Zoology (J. Rosado), which lent us their *I. delicatissima* specimens; the UMR 5199 CNRS "PACEA" that kindly send us their iguanas; and the MNHN collection curators and technicians who helped us find collection specimens and their corresponding collection information. And of course, we thank E. Pellé and the MNHN osteological preparation service which prepared the recently collected iguanas.

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APPENDIX 1

The following specimens were used to describe osteological differences between *Iguana iguana*, *Iguana delicatissima*, and their hybrids. We list sex, maturity, collection location, collector, and year of collection for each specimen (specimen No./sex/maturity/origin/collector/date). Nonavailable information is signaled by NA. For museum acronyms, see Material and Methods.

Iguana iguana.—MNHN-RA 1985.0431/NA/adult/found in Paris airport/NA/1885; MNHN-RA 1987.0940/NA/adult/NA/NA/prepared in 1910; MNHN-RA 1988.6632/NA/adult/NA/NA/prepared in 1929; MNHN-RA 1992.0017/NA/adult/NA/NA/NA; MNHN-RA 1991.4264/NA/adult/NA/NA/NA; UMR 5199 010311A/NA/adult/Guadeloupe: Basse-Terre /Lenoble/2011; UMR 5199 150312A/female/adult/Guadeloupe: Grande-Terre/Lenoble/2012; MNHN-UMR 7209-15/NA/adult/Les Saintes: Terre-de-Bas/Grouard/1995; MNHN-UMR 7209-319/NA/adult/Guyane/Grouard/1996; MNHN-UMR 7209-352/NA/adult/Les Saintes: Terre-de-Bas/Vigne/1999; MNHN-UMR 7209-538/NA/adult/Nicaragua/Grouard/2008; MNHN-UMR 7209-540/NA/adult/Guadeloupe: Morel/Grouard/1995; MNHN-ZA-AC A5382/NA/adult/America/NA/NA; MNHN-ZA-AC V221/NA/adult/NA/NA/NA; MNHN-ZA-AC 1874-365(1)/NA/adult/NA/NA/1874; MNHN-ZA-AC 1874-365(2)/NA/juvenile/NA/NA/1874; MNHN-ZA-AC 1889-96/NA/juvenile/kept alive at the Ménagerie du Jardin des Plantes/NA/1889; MNHN-ZA-AC 1892-

74/Female/adult/kept alive at the Ménagerie du Jardin des Plantes/NA/1892; MNHN-ZA-AC 1896-188/NA/adult/NA/NA/1896; MNHN-ZA-AC 1910-29/NA/adult/kept alive at the Ménagerie du Jardin des Plantes/NA/1910; MNHN-ZA-AC 1912-135/NA/adult/kept alive at the Ménagerie du Jardin des Plantes/NA/1912; MNHN-ZA-AC 1912-136/NA/juvenile/NA/NA/1874; MNHN-ZA-AC 1939-53/NA/adult/NA/NA /1939; MNHN-ZA-AC 1953-50/NA/adult/kept alive at the Ménagerie du Jardin des Plantes/NA/1953; MNHN-ZA-AC 1973-137/male/adult/kept alive at the Ménagerie du Jardin des Plantes/NA/1973; MNHN-ZA-AC 1974-129/NA/adult/NA/NA/1874; MNHN-ZA-AC 2002-47/NA/juvenile/NA/NA/1874; MNHN-ZA-AC 2014-27/male/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-28/female/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-29/male/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-30/female/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-31/male/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-32/male/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-33/female/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-34/male/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-35/female/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-36/female/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-37/male/juvenile/Martinique/Breuil/2011; MNHN-ZA-AC 2014-38/female/juvenile/Martinique/Breuil/2011; MNHN-ZA-AC 2014-39/female/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-40/male/adult/Martinique/Breuil/2011; MNHN-ZA-AC 2014-41/NA/juvenile/Martinique/Breuil/2011; MNHN-ZA-AC 2014-42/male/adult/Martinique /Breuil/2011; MNHN-ZA-AC 2014-43/male/juvenile/Salvador/NA/2013.

Iguana delicatissima.—MCZ R-6097/NA/adult/Nevis/Lagois/NA; MCZ R-10975/NA/adult/Les Saintes/Noble/1914; MCZ R-16157/NA/adult/Anguilla/Peters/1922; MCZ R-60823/NA/adult/Dominica/Lazell/1959; MCZ R-75388/NA/adult/St Eustatius/Allen/1963; MCZ R-83228/NA/adult/St Eustatius/Ray/1963; UMR 5199 231111B/NA/juvenile/La Désirade/Lenoble/2011; MNHN-UMR 7209-411(1)/NA/adult/Saint-Barthélemy/Breuil/2000; MNHN-UMR 7209-411(2)/NA/adult/Saint-Barthélemy/Breuil/2000; MNHN-UMR 7209-530/NA/adult/Guadeloupe: Basse-Terre/Moinecourt/2010; MNHN-ZA-AC 1941-215/NA/adult/NA/NA/1941; MNHN-ZA-AC 2014-20/male/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-21/NA/juvenile/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-22/female/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-23/female/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-24/male/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-25/NA/adult/La Désirade /Lenoble/2008; MNHN-ZA-AC 2014-26/female/adult/Saint-Barthélemy/Breuil/2011.

Iguana iguana × *Iguana delicatissima*.—MNHN-ZA-AC 2014-13/female/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-14/female/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-15/female/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-16/female/adult/Guadeloupe: Basse-Terre/Breuil/2011; MNHN-ZA-AC 2014-17/female/adult/Guadeloupe: Basse-Terre/Breuil/2011; MNHN-ZA-AC 2014-18/female/adult/Saint-Barthélemy/Breuil/2011; MNHN-ZA-AC 2014-19/NA/juvenile/Guadeloupe: Basse-Terre/Breuil/2011.