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ABSTRACT.—**Squamate remains from fossil-bearing deposits are difficult to identify on the basis of their morphology, because their modern relatives lack osteological description. In addition, intraspecific morphological variability of modern taxa is mostly understudied, making taxonomic identification of subfossil bones even more difficult. The aim of this study was to investigate osteological differences between two sympatric gecko species, *Thecadactylus rapicauda* and *Hemidactylus mabouia*, both currently occurring in the Lesser Antilles and in the subfossil assemblages of the region. Comparison of several modern museum specimens reveals the intraspecific osteological variability of these lizards and how difficult it is to distinguish between their bones, even though they are from two distant families. This study presents nine osteological characters, allowing for a fully reliable distinction of these two gecko species. These characters are applied to the specific identification of gecko species subfossil remains unearthed from the Pointe Gros Rempart 6 Hole (La Désirade Island, Guadeloupe). Our results confirm the past occurrence of *T. rapicauda* as well as the historical introduction of *H. mabouia* on La Désirade Island.**

RESUMEN.—**La identificación de depósitos fósiles de reptiles escamados usando morfología es difícil debido a la falta de datos osteológicos de especies actuales cercanas. Por eso, la variación morfológica intraespecífica de especies actuales está poco estudiada, lo cual hace que la identificación de huesos subfósiles sea aún más compleja. El objetivo de este estudio es investigar las diferencias osteológicas de dos especies de geckos simpátricos que viven en las Antillas Menores y que además están representadas en ensambles subfósiles de la región: *Thecadactylus rapicauda* y *Hemidactylus mabouia*. Al comparar varios especímenes de museos, se encontró variación morfológica intraespecífica en estos lagartos. También resultó difícil distinguir estas dos especies, incluso considerando que pertenecen a dos familias diferentes. Sin embargo, encontramos nueve diferencias osteológicas que permiten diferenciar estas dos especies con confidencia. Estos caracteres se presentan para identificar a nivel de especie el material de geckos descubierto en Pointe Gros Rempart 6 depósito (isla La Désirade Island, Guadalupe). Los resultados obtenidos confirman la presencia de *T. rapicauda* en la isla, como también la introducción moderna de *H. mabouia* a La Désirade Island.**

Precise identification of squamate osteological remains from subfossil and modern bone accumulations is critical for tackling a wide spectrum of questions related to paleobiogeography, evolution, and biodiversity changes across time. In addition, modern bone accumulations of raptor regurgitation pellets allow direct predator/prey relations to be established. Squamate bones found in both modern owl pellets and subfossil bone accumulations mostly correspond to modern species or closely related taxa, allowing a direct comparison with modern specimens for identification purposes. Taxonomic attribution of these remains is difficult, however, mostly because of the lack of detailed osteological descriptions of modern taxa and the limited comparative material available in museum collections (Bell and Mead, 2014; Villa et al., 2017). In addition, squamate species often present important intraspecific variability that is generally overlooked in morphological studies. Therefore, the comparative process requires the use of a large series of museum specimens to reveal morphological criteria relevant for taxonomic identification (e.g., Bochaton et al., 2016b).

Here we describe the morphological differences between one medium-sized (*Hemidactylus mabouia* [Moreau de Jonnès, 1818]) and one large-sized (*Thecadactylus rapicauda* [Houttuyn, 1782]) gecko species co-occurring both in Guadeloupe and in most other Lesser Antillean islands (Powell and Henderson, 2012). *Thecadactylus* Oken, 1817, includes only three species (Bergmann and Russell, 2007; Köhler and Vesely, 2011), two of which occur in the Lesser Antilles: *T. rapicauda*, with a widespread distribution in Central America, South America, and several Caribbean islands, and *Thecadactylus oskrobapreinorum* (Kôhler and Vesely, 2011), restricted to St. Martin Island. *Hemidactylus* Oken, 1817, is a widespread genus represented mainly by a single species in the Lesser Antilles, *H. mabouia*, probably introduced around the 17th century (Carranza and Arnold, 2006; Gamble et al., 2011). A second *Hemidactylus* species, the South American species *Hemidactylus palaichthus*, occurs in the Lesser Antilles on Saint Lucia Island and some of its offshore islets (Lewis, 2001; Powell and Henderson, 2012).

A third gecko genus, *Sphaerodactylus* Wagler, 1830, is known to occur in Guadeloupe and across the Lesser Antilles. This genus is represented in this region by small-sized lizards <29 mm SVL (Schwartz and Henderson, 1991). Their identification in bone assemblages can be based on size (Pregill et al., 1994); however, discrimination on the basis of size is not well defined among the other gecko species because body size overlaps between *T. rapicauda* (maximum SVL 121 mm) and *H. mabouia* (maximum SVL 70 mm) (Breuil, 2002).

Morphological osteological differences between *T. rapicauda* and *H. mabouia* are of interest in the Lesser Antilles for the study of raptor feeding habits based on their regurgitation pellets (Stoetzel et al., 2016). These two gekkotan species are especially relevant for the study of raptor behaviors, because they are

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generally not found in the same habitats. *Hemidactylus mabouia* is more adapted to urbanized environments, whereas *T. rapicauda* is commonly found in undisturbed areas (Vitt and Zani, 1997; Howard et al., 2001). Morphological differences between these two taxa and evaluation of their intraspecific variability are also of primary interest for the study of their recent history in the Lesser Antilles with the use of subfossil remains. Unfortunately, no osteological criteria allowing for the clear distinction of *H. mabouia* and *T. rapicauda* osteological remains have been described, and the distinction of their fossil remains in previous studies relies mostly on size data (Pregill et al., 1994; Bailon et al., 2015; Kemp and Hadly, 2016).

The osteology of these species was previously considered in a phylogenetic context by Abdala (1996), who pointed out differences in the degree of the interorbital constriction of the frontal bone; however, no detailed osteological analysis was available. In this article, we provide detailed morphological comparisons between *H. mabouia* and *T. rapicauda*, using isolated cranial and postcranial bones most frequently found in fossil-bearing deposits. This study also provides additional osteological information of these two wide-ranging but still poorly known taxa. Therefore, we will apply the osteological criteria presented in this article to the taxonomic identification of a Lesser Antillean subfossil assemblage of gekkotan remains collected in the Late Holocene subfossil deposit of the Pointe Gros Rempart 6 Cave (Boudadi-Maligne et al., 2016) on La Désirade Island (Guadeloupe archipelago, French West Indies).

To illustrate the potential of subfossil material to obtain precise data concerning the status and the introduction periods of *T. rapicauda* and *H. mabouia* on this island, we tested the hypothesis that all gekkotan remains from pre-European contact layers will be attributable to *Thecadactylus*, whereas those found in layers that are more recent will also include *Hemidactylus*.

Materials and Methods

Comparative Specimens.—Diagnostic osteological characters were defined with the use of a sample of 24 skeletonized specimens: 14 specimens of *H. mabouia*, 9 specimens of *T. rapicauda*, and 1 specimen of *T. oskrobapreinorum* (see Appendix). Skeletons were obtained from individuals of varying ages and sizes, representing the intraspecific variability of *T. rapicauda* and *H. mabouia*. We did not take sexual dimorphism into consideration, because the sex of the museum specimens was mostly not documented. Specimens from four collections located in three institutions were examined: Museum national d'Histoire naturelle, Paris, France (MNHN-ZA-AC and MNHN-UMR 7209); PACEA laboratory at the University of Bordeaux, France (PACEA); and Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ-RA) (see Appendix).

Method of Analysis.—Osteological characters were first observed on six specimens (three from *H. mabouia* and three from *T. rapicauda*), followed by additional observations in the remaining specimens to corroborate our initial observations. Cranial and postcranial bones considered in this study include parietal, frontal, maxilla, pterygoid, quadrate, articular, coronoid, dentary, scapulocoracoid, ilium, humerus, femur, and tibia. For each character described, we specified the number of specimens on which it was recordable (number of observations referred to as NO) and the correct identification rate (CIR). The CIR corresponds to the percentage of the specimens presenting the expected character state and not the character state expected from the other taxa. Characters were considered reliable and reported in this study only if their global CIR was >80%. Such reliable characters were absent on investigated pterygoid, quadrate, and articular bones. Morphological comparisons were mainly between *H. mabouia* and *T. rapicauda*; one specimen of *T. oskrobapreinorum* was used to check if the morphological characters of *T. rapicauda* extend to other species of the same genus.

Osteological nomenclature used mostly follows Smith (2011) and Klembara et al. (2010). These terms are completed by some others used by Daza et al. (2008), Evans (2008), and Bailon (1991) for cranial bones, and Lécuru (1969) for humeri. Measurements used are those described by Bochaton (2016).

Subfossil Material.—Subfossil material originated from the Pointe Gros Rempart 6 site (16°19′41.56″N, 61°0′49.18″W WGS 84), which is a collapsed opening on the coastal plain on La Désirade, one of the Guadeloupe islands. This site was first excavated by M. Boudadi-Maligne in 2011 (Boudadi-Maligne et al., 2016). It is a stratified fossil-bearing deposit with three periods represented: the pre-Columbian Ceramic period (layers 4 and 3); the Colonial period (layer 2), which on la Désirade starts with the permanent French settlement in 1728 AD; and modern times (layer 1). The pre-Columbian Ceramic period ranges in Guadeloupe from around 80 AD to around 1700 AD (Hofman et al., 1999; Keegan et al., 2013; Fitzpatrick, 2015), and the ceramic shreds recovered in pre-Columbian layers are not diagnostic enough to derive a precise estimate of the age of the basal part of the deposit. Nonetheless, a radiocarbon dating of 1143–1650 calibrated BP obtained from the layer 3 demonstrated the final part of pre-Columbian period to be represented in the site. These chronological characteristics make the site especially suitable for the study of the history of the squamate diversity of La Désirade, including *T. rapicauda* and *H. mabouia*, which are currently occurring on the island (Powell and Henderson, 2012). From the 2011 excavation, six remains of Gekkonidae were collected and attributed to cf. *Thecadactylus rapicauda* because of their sizes and geographical arguments. These remains were all from the pre-Columbian layer 3 of the site or from the contact between this first layer and underlying colonial period layer 2 (Boudadi-Maligne et al., 2016). A subsequent paleontological investigation on the site was conducted by A. Lenoble in 2016 to constitute a more substantial paleontological collection documenting the timing of extinction, extirpation, and introduction of the vertebrate fauna. This new excavation led to the discovery of 106 new gecko remains that are studied using the results of our osteological investigation.

Results

General Gekkota Morphological Characters.—Both taxa share the following general features (Evans, 2008): frontal fused in adults with cristae cranii that meet and fuse below olfactory tract, paired parietals with short posteromedian extension (this character is not present in eublepharids and some gekkonids), reduced postparietal processes, pineal foramen and posteroventral pit for the processus ascendens tecti synotici absent (Daza et al., 2013), maxilla with a short anteromedial premaxillary process (extensive in some geckos, e.g., *Pristurus* [Kluge, 1995]), quadrate with narrow medial crest and inflated posterolateral conch, dentary with tubular Meckelian canal, coronoid extending laterally onto the lateral side of the dentary (Daza et al., 2015), surangular and articular fused and presenting an elongated articular condyle with anteroposterior ridge and a "spoon-shaped" retroarticular process laterally notched (absent in pygopods).

Osteological Differences between T. rapicauda *and* H. mabouia.—We found 18 osteological characters that we considered as relevant for the distinction between *T. rapicauda* and *H. mabouia* bones. These characters are described below and their respective NO and CIR reported in Table 1.

Maxilla (Fig. 1A): A1: The ratio between the number of dental positions and the length of the dental row of the maxilla (LDR) in millimeters (number of dental position per millimeter) is <4 in *T. rapicauda* and >4 in *H. mabouia*. Although this could not be used as a distinctive character, we observed that the number of dental positions of the maxilla shows intraspecific variation in both species, between 23 and 37 in *H. mabouia* and between 31 and 47 in *T. rapicauda*. A2: In lateral view, the anterodorsal corner of the facial process projects anteriorly into a well-defined narrow process in *T. rapicauda*; the same part in *H. mabouia* is reduced. This process constitutes the dorsal border of the osseous nares and as a consequence, the border of the osseous naris is nearly as high as it is deep in *T. rapicauda* and very shallow in *H. mabouia*. A3: In ventral view, the anteromedial premaxillary process or maxillary lappet (Evans, 2008) extends more anteriorly than the anterolateral premaxillary process in *T. rapicauda*. It is the reversed condition in *H. mabouia*, in which the anterolateral premaxillary process extends more anteriorly than the anteromedial premaxillary process.

Tooth morphology (maxilla and dentary) (Fig. 1B): B: Teeth present blunt crowns in *T. rapicauda* and are more pointed in *H. mabouia*.

Frontal bone (Fig. 1C): C: The anterior margin of the frontal is concave in *T. rapicauda*; in *H. mabouia* it has an anterior process. Also in *T. rapicauda*, the prefrontal bone is more recessed than in *H. mabouia*, leaving a more uneven lateral outline. No difference in orbital constriction was observed between these two taxa.

Parietal bone (Fig. 1D): D1: The posteromedial margin of the bone presents a median extension of the parietal (sensu Evans, 2008) that is pointed in *T. rapicauda* and truncated in *H. mabouia*. D2: In ventral view, the postorbitofrontal facet is well-defined in the anterolateral corner of the parietal in *T. rapicauda*. This facet is not visible in *H. mabouia*, where the postorbitofrontal has a laminar suture.

Coronoid bone (Fig. 1E): E: In medial view, the anteromedial process of the coronoid is short and has subequal height and length in *T. rapicauda*. In *H. mabouia*, the same process is slender and several times longer than high.

Dentary (Fig. 1F): F1: In lateral view, the coronoid facet extends beyond the level of the last dental position in *T. rapicauda*, whereas in *H. mabouia*, the facet ends posterior to the last mandibular tooth. F2: The ratio between the number of dental positions and the LDR in millimeters (number of dental position per millimeter) of the dentary is <4 in *T. rapicauda* and >4 in *H. mabouia*. The number of dental positions of the dentary shows intraspecific variation, as in the maxilla for both species, between 25 and 40 in *H. mabouia* and between 30 and 50 in *T. rapicauda*. This, however, does not constitute a clearly distinctive character.

Scapulocoracoid bone (Fig. 2A): G1: In lateral view, the posterior extremity of the scapular ray is pointed in *T. rapicauda* and square in *H. mabouia*. G2: In lateral view, the first coracoid ray is taller than the base of the scapular ray in *T. rapicauda*. This condition is reversed in *H. mabouia*. G3: There is an anteroventral lamina connecting the body of the coracoid with the second coracoid ray in *H. mabouia*. This lamina is absent in *T. rapicauda*.

Ilium bone (Fig. 2B): H: In lateral view, the base of the iliac blade bears a small tubercle that is poorly developed in *T. rapicauda* and more prominent in *H. mabouia*.

Humerus (Fig. 2C): I1: In ventral view, the deltopectoral crest of the humerus of *H. mabouia* presents two longitudinal cristae; the same surface is smooth in *T. rapicauda*. I2: In ventral view, the

TABLE 1. List of the distinctive characters between *T. rapicauda* and *H. mabouia*. NO, number of observations; CIR, correct identification rate.

	T. rapicauda	*H. mabouia*	Total
Maxilla			
A1			
NO	9	14	23
CIR	100	100	100
A2			
NO	9	14	23
CIR	100	93	96
A3			
NO	4	14	18
CIR	100	86	89
Teeth			
B			
NO	9	14	23
CIR	100	100	100
Frontal			
C			
NO	3	13	16
CIR	67	100	94
Parietal			
D1			
NO	9	12	21
CIR	78	100	90
D2			
NO	6	12	18
CIR	100	100	100
Coronoid			
E			
NO	3	14	17
CIR	100	100	100
Dentary			
F1			
NO	9	13	22
CIR	100	877	86
F2			
NO	9	14	23
CIR	100	100	100
Scapulocoracoid			
G1			
NO	7	14	21
CIR	57	100	86
G2			
NO	6	13	19
CIR	100	100	100
G3			
NO	7	12	19
CIR	57	100	84
Ilium			
H			
NO	7	14	21
CIR	100	93	96
Humerus			
I1			
NO	7	14	21
CIR	100	100	100
I2			
NO	7	14	21
CIR	86	93	90
Femur			
J			
NO	8	13	21
CIR	100	100	100
Tibia			
K			
NO	6	13	19
CIR	100	100	100

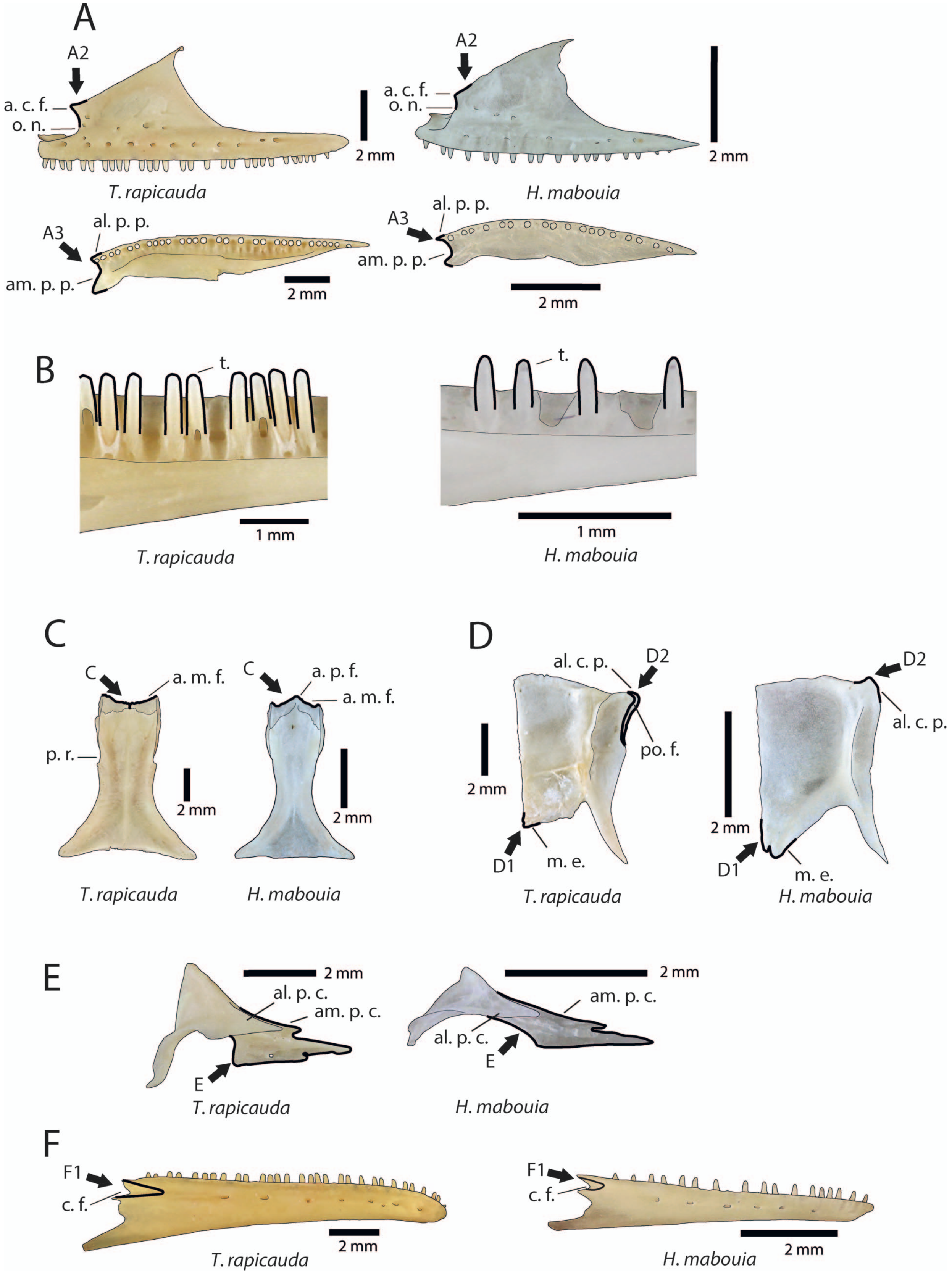

FIG. 1. Osteological differences between *Thecadactylus rapicauda* and *Hemidactylus mabouia* observed on (A) maxilla (left; lateral view [A2] and ventral view [A3]); (B) teeth (medial view); (C) frontal bone (dorsal view); (D) parietal bone (left; ventral view); (E) coronoid bone (right; lateral view); (F) dentary (right; lateral view). Abbreviations: a. c. f.: anterodorsal corner of the facial process, a. m. f.: anterior margin of the frontal, a. p. f.: anterior process of the frontal, al. c. p.: anterolateral corner of the parietal, al. p. c.: anterolateral process of the coronoid, al. p. p.: anterolateral premaxillary process, am. p. c.: anteromedial process of the coronoid, am. p. p.: anteromedial premaxillary process, c. f.: coronoid facet, m. e.: median extension of parietal, o. n.: osseous nares, p. r.: prefrontal recess, po. f.: post-frontal facet, t.: teeth.

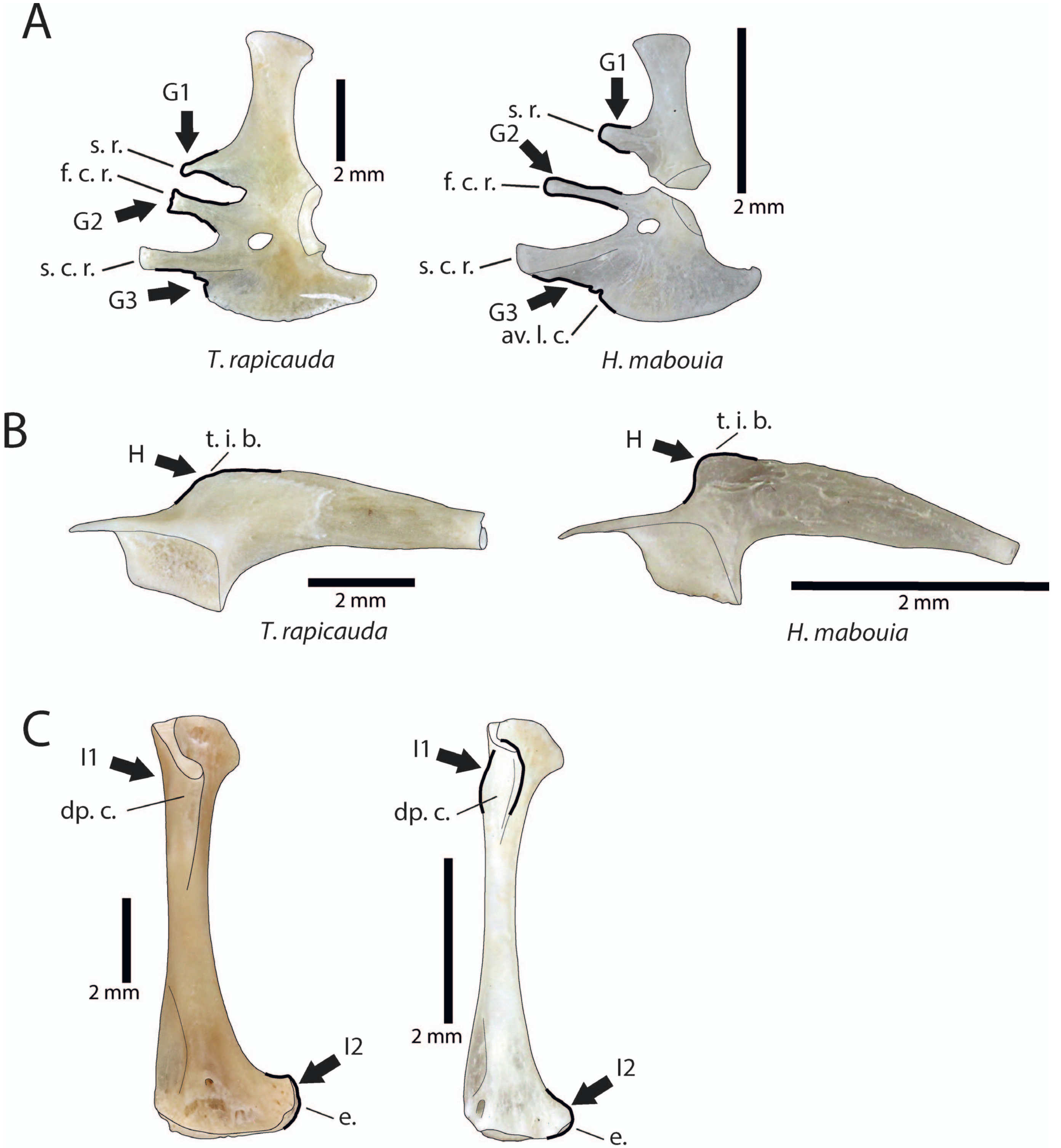

FIG. 2. Osteological differences between *Thecadactylus rapicauda* and *Hemidactylus mabouia* observed on (A) scapulocoracoid bone (left; lateral view), (B) ilium bone (left; lateral view), (C) humerus bone (left; ventral view). Abbreviations: av. l. c.: anteroventral lamina of the coracoid; dp. c.: deltopectoral crest, e.: entepicondyle, f. c. r.: first coracoid ray, s. c.: scapular ray, s. c. r.: second coracoid ray, t. i. b.: tubercle of the iliac blade.

entepicondyle is more prominent and square-like in *T. rapicauda* than in *H. mabouia*.

Femur: J: The femur is slenderer in *H. mabouia* than in *T. rapicauda*. The ratio between the greatest length of the bone (GL) and its dorsoventral width at middiaphysis (dvWD) is <13 (mean = 11.8) in *T. rapicauda* and >14 (mean = 16.9) in *H. mabouia*.

Tibia: K: The tibia is slenderer in *H. mabouia* than in *T. rapicauda*. The ratio between its GL and its dvWD is >13 (mean = 10.3) in *T. rapicauda* and >18 (mean = 20.7) in *H. mabouia*.

TABLE 2. Number of Gekkonidae remains identified from the different layers of Pointe Gros Rempart 6 paleontological deposit.

Identification	Layer 1	Layer 2	Layer 2/3	Layer 3	Layer 3/4	Layer 4
Gekkonidae	12	6	4	21	1	13
H. mabouia	4		1			
T. rapicauda	2	8	1	24	2	7
Total	18	14	6	45	3	20

We did not record any morphological differences between *T. rapicauda* and our single specimen of *T. oskrobapreinorum*, which bears all the characters we found to occur on *T. rapicauda*.

Paleontological Application.—From the 106 investigated Gekkonidae remains, 44 were attributed to *T. rapicauda*, 5 to *H. mabouia* (Fig. 3), and 57 were left specifically unidentified because they correspond to anatomical parts on which we did not observe any osteological character allowing for a specific attribution or to broken elements impossible to characterize. *Thecadactylus rapicauda* remains were found in all of the four layers of the site, whereas *H. mabouia* remains were identified only from Layer 1 (four remains), with the exception of one remain (a dentary illustrated in Fig. 3) from Layer 2/3 (Table 2). The remains attributed to *T. rapicauda* include dentaries (13), humerus (9), maxilla (7), parietals (7), femurs (6), and ilium (2). The remains attributed to *H. mabouia* include dentaries (3), parietal (1), and femur (1). This anatomical distribution of identified elements (see Table 3) is related to differential conservation and differential recovery. Indeed, specifically identified bones tend to be the largest and most robust ones, making them more likely to be recovered in a conservation state allowing for identification. At the opposite, none of the 14 frontal bones recovered was identifiable at the species level, because the very fragile anterior part useful for identification was not preserved in the material.

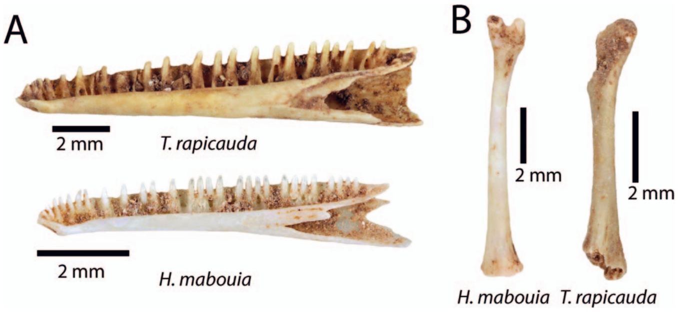

FIG. 3. Fossil dentaries (A) and femora (B) of *Thecadactylus rapicauda* and *Hemidactylus mabouia* recovered in the Pointe Gros Rempart 6 assemblage.

DISCUSSION

We describe 18 osteological characters allowing the distinction between *H. mabouia* and *T. rapicauda*/*T. oskrobapreinorum*. Nine of these characters are fully reliable on the basis of the collection of modern skeletons used in this study (Table 1): the ratio between length of the dental row and number of teeth and shape of these teeth on maxilla and dentary, the development of the postorbitofrontal facet of the parietal, the length of the anteromedial process of the coronoid bone, the morphology of the scapulocoracoid bone, the morphology of the deltopectoral crest of the humerus, and the ratio between width of the diaphysis and length of the femur and tibia (Table 1). Two other characters were 95% to 99% accurate: the morphology of the anterodorsal corner of the facial process of the maxilla, and the shape of the iliac blade of the ilium (Table 1). These results show that even among phylogenetically distant species, observation of reliable identification characters on a single bone can still be challenging. Even though the two studied taxa are from different families, the intraspecific variability affects our results and shows morphological overlap between the two taxa for some characters (Table 1). These results support the idea of the necessity to consider intraspecific variation to assess the reliability of used characters (Bell and Mead, 2014). Despite this consideration, our results clearly indicate that isolated bones of *T. rapicauda* and *H. mabouia* can be distinguished with rigorously tested morphological arguments.

From a wider perspective, our study sheds light on new osteological characters possibly relevant for systematic studies of Gekkota. Our results constitute a major improvement for the documentation of the skeletal morphology of the studied taxa, which have been exposed only briefly in previous studies (see Wellborn, 1933; Fabián-Beurmann et al., 1980; Abdala, 1996). A difference in the width of the midsection of the frontal bone between *H. mabouia* and *T. rapicauda* was previously hypothesized (Abdala, 1996); however, this character is directly related to orbital constriction that changes along the ontogenetic

TABLE 3. Table showing the details of the anatomical parts attributed to each taxon in Pointe Gros Rempart 6 fossil material. NR, number of remains.

	NR		NR		NR	NR total
Gekkonidae	57	*Hemidactylus mabouia*	5	*Thecadactylus rapicauda*	44	106
Articular	4	Dentary	3	Coxal	2	
Quadrate	2	Femur	1	Dentary	13	
Coxal	1	Parietal	1	Femur	6	
Dentary	2			Humerus	9	
Femur	1			Maxilla	7	
Frontal	13			Parietal	7	
Maxilla	3					
Prefrontal	2					
Premaxilla	1					
Pterygoid	5					
Basi-sphenoid	1					
Surangular	1					
Caudal vertebra	4					
Sacral vertebra	1					
Trunk vertebra	16					

trajectory. This variation was recorded in our sample, and has been reported in other squamate taxa (see, e.g., *Anolis*: Etheridge, 1959; *Pholidoscelis*: Bochaton et al., 2017). Characters described here help us understand the morphological differences between two gekkotans living in sympatry. Additionally, the differences identified between *H. mabouia* and *T. rapicauda* also served to distinguish the single specimens of *T. oskrobapreinorum* from *H. mabouia*. Observed characters on the maxilla in our *Thecadactylus* specimens also occurs on *Thecadactylus solimoensis*, considering the bone described and figured by Daza et al. (2017). The variability of the characters derived from this study, however, needs to be tested on a larger set of taxa to assess their potential phylogenetic meaning.

The results we obtained on paleontological material with these new characters demonstrate the importance of carefully investigated osteological criteria by adding robust data concerning the past occurrence of *H. mabouia* and *T. rapicauda* on La Désirade Island. Although previously hypothesized, the past occurrence of *T. rapicauda* on La Désirade during pre-Columbian time was lacking clear osteological evidence, and the identification of its osteological remains was uncertain (Boudadi-Maligne et al., 2016). Thanks to the investigated osteological characters, we confirmed this hypothesis on the basis of morphological data. Fossil data also confirm the hypothesis of the introduction of *H. mabouia* during historical times (Kluge, 1969); however, the precise period remains difficult to address. The occurrence of a *H. mabouia* remain, identified with fully reliable criteria in layer 2/3 of Pointe Gros Rempart 6 site, could indicate the occurrence of this lizard on la Désirade Island since the beginning of European colonization during the 18th century. This result would match with the results obtained on other taxa showing a strong anthropogenic impact on this island since the beginning of historical times (Boudadi-Maligne et al., 2016). The dating of this *H. mabouia* remain is still uncertain, however, because an isolated bone could indicate contamination from another layer. This problem could be resolved with radiocarbon dating directly from this microremain (Cersoy et al., 2017), but this would require the destruction of the material.

The identification of subfossil material relies on comparison with modern taxa to obtain precise taxonomic allocation; however, because of intraspecific variation of modern taxa, this process is very complex, especially in squamates, as we demonstrate in this study. Bone identification should follow criteria of established systematic and taxonomic value (see, e.g., Evans, 2008). These criteria still have to be established on a large number of taxa and specimens, and be rigorously tested to avoid identification error, a time-consuming task requiring an adequate collection of comparative specimens. Often, such collections are very difficult to obtain, especially concerning protected or endangered species, which is the case for many squamates. Regardless, these comparative studies are the only way to obtain trustworthy data, as well as to test previously obtained identifications (e.g., archaeological iguanas: Bochaton et al., 2016a).

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LITERATURE CITED

ABDALA, V. 1996. Osteología craneal y relaciones de los geconinos sudamericanos (Reptilia: Gekkonidae). Revista Española de Herpetología 10:41–54.

BAILON, S. 1991. Amphibiens et Reptiles du Pliocéne et du Quaternaire de France et d'Espagne: Mise en place et évolution des faunes. Unpubl. Ph.D. diss., University Paris VII, France.

BAILON, S., C. BOCHATON, AND A. LENOBLE. 2015. New data on Pleistocene and Holocene herpetofauna of Marie-Galante (Blanchard Cave, Guadeloupe Islands, French West Indies): insular faunal turnover and human impact. Quaternary Science Reviews 128:127–137.

BELL, C. J., AND J. I. MEAD. 2014. Not enough skeletons in the closet: collections-based anatomical research in an age of conservation conscience. The Anatomical Record 297:344–348.

BERGMANN, P. J., AND A. P. RUSSELL. 2007. Systematics and biogeography of the widespread Neotropical gekkonid genus *Thecadactylus* (Squamata), with the description of a new cryptic species. Zoological Journal of the Linnean Society 149:339–370.

BOCHATON, C. 2016. Describing archaeological *Iguana* Laurenti, 1768 (Squamata: Iguanidae) populations: size and skeletal maturity. International Journal of Osteoarchaeology 26:716–724.

BOCHATON, C., S. BAILON, I. INEICH, M. BREUIL, A. TRESSET, AND S. GROUARD. 2016a. From a thriving past to an uncertain future: zooarchaeological evidence of two millennia of human impact on a large emblematic lizard (*Iguana delicatissima*) on the Guadeloupe Islands (French West Indies). Quaternary Science Reviews 150:172–183.

BOCHATON, C., S. GROUARD, M. BREUIL, I. INEICH, A. TRESSET, AND S. BAILON. 2016b. 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. Journal of Herpetology 50:295–305.

BOCHATON, C., R. BOISTEL, S. GROUARD, I. INEICH, A. TRESSET, AND S. BAILON. 2017. Evolution, diversity and interactions with past human populations of recently extinct *Pholidoscelis* lizards (Squamata: Teiidae) from the Guadeloupe Islands (French West-Indies). Historical Biology, doi:10.1080/08912963.2017.1343824

BOUDADI-MALIGNE, M., S. BAILON, C. BOCHATON, F. CASSAGRANDE, S. GROUARD, N. SERRAND, AND A. LENOBLE. 2016. Evidence for historical human-induced extinctions of vertebrate species on La Désirade (French West Indies). Quaternary Research 85:54–65.

BREUIL, M. 2002. Histoire naturelle des Amphibiens et Reptiles terrestres de l'archipel Guadeloupéen. Publications Scientifiques du Muséum National d'Histoire Naturelle, France.

CARRANZA, S., AND E. N. ARNOLD. 2006. Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 38:531–545.

CERSOY, S., A. ZAZZO, J. ROFES, A. TRESSET, S. ZIRAH, C. GAUTHIER, E. KALTNECKER, F. THIL, AND N. TISNERAT-LABORDE. 2017. Radiocarbon dating minute amounts of bone (3–60 mg) with ECHoMICADAS. Scientific Reports 7:7141.

DAZA, J. D., V. ABDALA, T. RICHARD, AND A. M. BAUER. 2008. Skull anatomy of the miniaturized gecko *Sphaerodactylus roosevelti* (Squamata: Gekkota). Journal of Morphology 269:1340–1364.

Daza, J. D., A. M. Bauer, and E. Snively. 2013. *Gobekko cretacicus* (Reptilia: Squamata) and its bearing on the interpretation of gekkotan affinities. Zoological Journal of the Linnean Society 167:430–448.

Daza, J. D., A. M. Bauer, C. Sand, I. Lilley, T. A. Wake, and F. Valentin. 2015. Reptile remains from Tiga (Tokanod), Loyalty Islands, New Caledonia. Pacific Science 69:531–557.

Daza, J. D., L. B. Price, C. Schalk, A. Bauer, A. R. Borman, and J. K. Peterhans. 2017. Predation on Southern Turnip-tailed geckos (*Thecadactylus solimoensis*) by a Spectacled Owl (*Pulsatrix perspicillata*). Cuadernos de Herpetología 31:37–39.

Etheridge, R. 1959. The Relationships of the Anoles (Reptilia: Sauria: Iguanidae): An Interpretation Based on Skeletal Morphology. Unpublished Ph.D. diss., University of Michigan, USA.

Evans, S. E. 2008. The skull of lizards and Tuatara. Pp. 1–347 in C. Gans, A. S. Gaunt, and K. Adler (eds.), The Skull of Lepidosauria. Society for the Study of Amphibians and Reptiles, USA.

Fabián-Beurmann, M., M. Ibarra-Vieira, and M. Alves. 1980. Estudo osteológico comparativo do cranio de *Hemidactylus mabouia* (Morreau de Jonnes, 1818) e Homonota uruguayensis (Vaz Ferreira & Sierra de Soriano, 1961) (Lacertilia, Gekkonidae). Revista Brasileira de Biologia 40:187–202.

Fitzpatrick, S. M. 2015. The pre-columbian Caribbean: colonization, population dispersal, and island adaptations. PaleoAmerica 1:305–331.

Gamble, T., A. M. Bauer, G. R. Colli, E. Greenbaum, T. R. Jackman, L. J. Vitt, and A. M. Simons. 2011. Coming to America: multiple origins of New World geckos. Journal of Evolutionary Biology 24:231–244.

Hofman, C. L., M. L. P. Hoogland, and A. Delpuech. 1999. New perspectives on a Huecan Saladoid assemblage on Guadeloupe: the case of Morel I. Pp. 303–310 in C. L. Hofman and M. L. Hoogland (eds.), Archaeological Investigations on St. Martin (Lesser Antilles): The Sites of Norman Estate, Anse des Pères and Hope Estate with a Contribution to the 'La Hueca Problem.' Leiden University, Netherland.

Howard, K. G., J. S. Parmerlee, and R. Powell. 2001. Natural history of the edificarian geckos *Hemidactylus mabouia*, *Thecadactylus rapicauda*, and *Sphaerodactylus sputator* on Anguilla. Caribbean Journal of Science 37:285–288.

Keegan, W. F., C. L. Hofman, and R. R. Ramos. 2013. The Oxford Handbook of Caribbean Archaeology. Oxford University Press, United Kingdom.

Kemp, M. E., and E. A. Hadly. 2016. Early Holocene turnover, followed by stability, in a Caribbean lizard assemblage. Quaternary Research 85: 255–261.

Klembara, J., M. Böhme, and M. Rummel. 2010. Revision of the anguine lizard *Pseudopus laurillardi* (Squamata, Anguidae) from the Miocene of Europe, with comments on paleoecology. Journal of Paleontology 84:159–196.

Kluge, A. G. 1969. The evolution and geographical origin of the new world *Hemidactylus mabouia-brookii* complex (Gekkonidae, Sauria). Miscellaneous Publications of the Museum of Zoology, University of Michigan 138:1–78.

Kluge, A. G. 1995. Cladistic relationships of sphaerodactyl lizards. American Museum Novitates 3139:1–23.

Köhler, G., and M. Vesely. 2011. A new species of *Thecadactylus* from Sint Maarten, Lesser Antilles (Reptilia, Squamata, Gekkonidae). ZooKeys 118:97–107.

Lécuru, S. 1969. Étude morphologique de l'humérus des lacertiliens. Annales Des Sciences Naturelles, Zoologie 12:1–47.

Lewis, T. R. 2001. Reptile observations on the Maria Islands: two satellite islands of St. Lucia (West Indies). Herpetological Bulletin 77:25–28.

Powell, R., and R. W. Henderson. 2012. Island list of West Indian amphibians and reptiles. Bulletin of Florida Museum of Natural History 51:85–166.

Pregill, G. K., D. W. Steadman, and D. R. Watters. 1994. Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. Bulletin of Carnegie Museum of Natural History 30:1–51.

Schwartz, A., and R. W. Henderson. 1991. Amphibians and Reptiles of the West-Indies: Descriptions, Distributions and Natural History. University of Florida Press, USA.

Smith, K. T. 2011. The evolution of mid-latitude faunas during the Eocene: late Eocene lizards of the Medicine Pole Hills reconsidered. Bulletin of the Peabody Museum of Natural History 52:3–104.

Stoetzel, E., A. Fraysse, S. Grouard, C. Bochaton, M. Gala, A. Lenoble, and C. Denys. 2016. Diet of the Lesser Antillean barn owl *Tyto insularis* (Aves: Strigiformes) in Dominica, Lesser Antilles. Caribbean Journal of Science 49:91–100.

Villa, A., E. Tschopp, G. L. Georgalis, and M. Delfino. 2017. Osteology, fossil record and palaeodiversity of the European lizards. Amphibia-Reptilia 38:79–88.

Vitt, L. J., and P. A. Zani. 1997. Ecology of the nocturnal lizard *Thecadactylus rapicauda* (Sauria: Gekkonidae) in the Amazon region. Herpetologica 53:165–179.

Wellborn, V. 1933. Vergleichende osteologische Untersuchungen an Geckoniden, Eublephariden und Uroplatiden. Otto Dornbluth nachf, Germany.

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Appendix 1

The following museum specimens were used to describe morphological differences between investigated taxa. For museum acronyms, see Materials and Methods section.

Hemidactylus mabouia.—MNHN-UMR 7209-14, MNHN-UMR 7209-166, MNHN-UMR 7209-170, MNHN-UMR 7209-404d(1), MNHN-UMR 7209-404d(2), MNHN-UMR 7209-409, MNHN-UMR 7209-697, MNHN-ZA-AC 2016-4, MNHN-ZA-AC 2016-5, PACEA 051112A, PACEA 111111B, PACEA 141112B, PACEA 181112A, PACEA 251112Q.

Thecadactylus rapicauda.—MCZ-RA 15714, MCZ-RA 32234, MCZ-RA 119677, MCZ-RA 131549, MCZ-RA 131550, MCZ-RA 145322, MNHN-ZA-AC 2016-7, PACEA 160312A, PACEA A1.

Thecadactylus oskrobapreinorum.—MNHN-ZA AC-2016-6.