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A new subspecies of hutia (*Plagiodontia*, Capromyidae, Rodentia) from southern Hispaniola

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Abstract

Continued uncertainty persists over the taxonomic status of many threatened Caribbean mammal populations. Recent molecular analysis has identified three genetically isolated allopatric hutia populations on Hispaniola that diverged during the Middle Pleistocene, with observed levels of sequence divergence interpreted as representing subspecies-level differentiation through comparison with genetic data for other capromyids. Subsequent analysis of existing museum specimens has demonstrated biogeographically congruent morphometric differentiation for two of these three populations, *Plagiodontia aedium aedium* (southwestern population) and *P. aedium hylaeum* (northern population). We report the first craniodental material for the southeastern Hispaniolan hutia population, and demonstrate that this population can also be differentiated using quantitative morphometric analysis from other Hispaniolan hutia subspecies. The holotype skull of *P. aedium aedium*, of unknown geographic provenance within Hispaniola, clusters morphometrically with the southwestern population. The southeastern Hispaniolan subspecies is described as *Plagiodontia aedium bondi* **subsp. nov.**, and is assessed as Endangered under Criterion B1a,biii,v on the IUCN Red List.

Key words: Bond's Line, craniodental morphometrics, Dominican Republic, endangered, Haiti, phylogeography

Introduction

The caviomorph family Capromyidae is a clade of large-bodied rodents known as hutias, which constitutes one of only two native non-volant land mammal families that still survive in the insular Caribbean. The family formerly comprised c.30 species distributed across the Greater Antilles and neighboring islands (Woods & Sergile 2001). However, the Caribbean land mammal fauna experienced a severe series of extinctions during the Late Quaternary, and most of the capromyid evolutionary radiation disappeared during the prehistoric Holocene and post-AD 1500 historical era due to human activities (MacPhee & Flemming 1999; MacPhee 2009; Turvey 2009), with only eight currently recognized species probably still extant (Borroto-Páez & Mancina 2011; IUCN 2013).

Reconstructing the magnitude, dynamics and drivers of Caribbean Late Quaternary extinctions is complicated by continued uncertainty over the taxonomic status of many of the region's extinct and extant mammals. Most strikingly, whereas 27 Late Quaternary–Recent capromyid species were recognized from Cuba during the late twentieth century, 16 are now considered dubious or invalid (Díaz-Franco 2001; Silva Taboada *et al.* 2007; Borroto-Páez & Mancina 2011). Similarly, recent analysis of Hispaniola's plagiodontine hutias has reduced the number of Late Quaternary species from eight to four (Hansford *et al.* 2012). Conversely, the status of numerous extinct and extant Caribbean mammal populations has not been assessed using modern quantitative morphometric

or molecular analyses (Turvey & Cooper 2009), and some of these understudied populations may represent distinct taxa.

Hispaniola, divided politically into the Dominican Republic and Haiti, is one of the few Caribbean islands to retain native capromyids, referred to the endemic genus *Plagiodontia* Cuvier, 1836. The taxonomic history of Hispaniolan hutias is complex. Two distinct taxa, *P. aedium* Cuvier, 1836 (described from an animal collected at an unknown locality on Hispaniola) and *P. hylaeum* Miller, 1928 (established to describe hutias from the northern Dominican Republic), have been proposed and variously interpreted as sympatric species (Miller 1929, 1930; Mohr 1939; Tate 1948; Rímoli 1976), allopatric species (Johnson 1948; Woods 1989), allopatric subspecies (Anderson 1965; Woods *et al.* 2001; Wilson & Reeder 2005) or morphologically indistinguishable synonyms (Woods & Howland 1979; Woods 1981). Although the collection locality of the holotype of *P. aedium* is unknown, this name has generally been attached to animals from southern Haiti following apparent soft-tissue similarities with an individual from Miragoâne (Johnson 1948).

Two recent studies have greatly clarified this taxonomic confusion. Firstly, Brace *et al.* (2012) used mitochondrial DNA (cytochrome *b*) analysis of 27 *Plagiodontia* samples to confirm that distinct hutia sister taxa occur allopatrically across Hispaniola, with a primary phylogenetic division into northern and southern lineages that diverged c.594,000 years ago (95% credibility interval=765,000–433,000 years ago), and further subdivision of the southern population into eastern and western lineages that diverged c.436,000 years ago (95% credibility interval=572,000–312,000 years ago). Exceptionally low levels of migration were detected between all three populations (modal rate $\leq 4.57 \times 10^{-5}$ individual migrants per generation), indicating that they are almost certainly all genetically isolated.

These molecular data are biogeographically congruent with Hispaniola's geotectonic history (Figure 1). Hispaniola consists of independent northern and southern palaeo-islands that docked through plate-tectonic movement in the late Miocene (Mann *et al.* 1991; Iturralde-Vinent & MacPhee 1999), but remained separated by the Neiba Valley, a prominent depression periodically or permanently inundated by a narrow seaway until the late Pleistocene (Maurrasse *et al.* 1982; Graham 2003). The southern palaeo-island or Presqu'île du Sud is further subdivided into two major physiographic provinces (the western Massif de la Hotte and the eastern Massif de la Selle–Sierra de Bahoruco) separated by the Jacmel–Fauché depression, which bisects the peninsula and was also inundated by a seaway during some or all of the Plio-Pleistocene (Maurrasse *et al.* 1982). All three regions are biogeographically distinct and characterized by substantial endemism in many terrestrial vertebrates, invertebrates and plants (e.g. Williams 1961; Schwartz 1980; Hedges 1999), with the Jacmel–Fauché depression referred to as 'Bond's Line' after the ornithologist James Bond (Latta *et al.* 2006). The three allopatric hutia populations recognized by Brace *et al.* (2012) correspond closely to these three major biogeographic provinces. However, the two southern hutia subclades are not completely congruent with the south palaeo-island's east-west division, as samples from localities closely adjacent to the Jacmel–Fauché depression (Miragoâne and western Massif de la Selle) are nested within clades otherwise comprising samples from the other side of Bond's Line, suggestive of secondary migration across a transient biogeographic barrier. The small level of secondary contact between *Plagiodontia* populations across this biogeographic barrier is comparable to the geographically restricted "hybrid zone" documented in the Massif de la Selle for *Phaenicophilus* palm-tanagers (McDonald & Smith 1994), which otherwise also display clear allopatric divergence across Bond's Line (Sly *et al.* 2010).

Estimates of sequence divergence between allopatric *Plagiodontia* populations based on the entire cytochrome *b* region (northern–southern populations=2.86%, southeastern–southwestern populations=1.03%) are lower than interspecific divergence values for Cuban capromyid species based on the first 415 base pairs of this gene (3.0–20.4%), but are higher than most values similarly calculated between subspecies of the Cuban hutia *Capromys pilorides* (0.4–1.9%) (Borroto-Páez *et al.* 2005); these latter values may represent an underestimate of comparative levels of sequence divergence in other hutias, as the first half of cytochrome *b* evolves at a slower rate than the second half (Irwin *et al.* 1991; Spotorno *et al.* 2004). Brace *et al.* (2012) therefore conservatively recognized only one *Plagiodontia* species. They assigned the available names *aedium* and *hylaeum* at the subspecies level to describe the primary phylogenetic division within *Plagiodontia* between Hispaniola's two palaeo-islands: *P. aedium aedium* (combined southern populations, following usage of previous authors) and *P. aedium hylaeum* (northern population). Subsequent genetic analysis of the almost 200-year-old holotype specimen of *P. aedium* failed to yield amplifiable DNA, making it impossible to associate the name *aedium* with a specific population using molecular techniques (Hansford *et al.* 2012). However, although they only formally assigned names to two populations, Brace *et al.* (2012) recognized all three *Plagiodontia* populations as distinct at the subspecific level, and recommended that they should all be treated as distinct evolutionary units for conservation management.

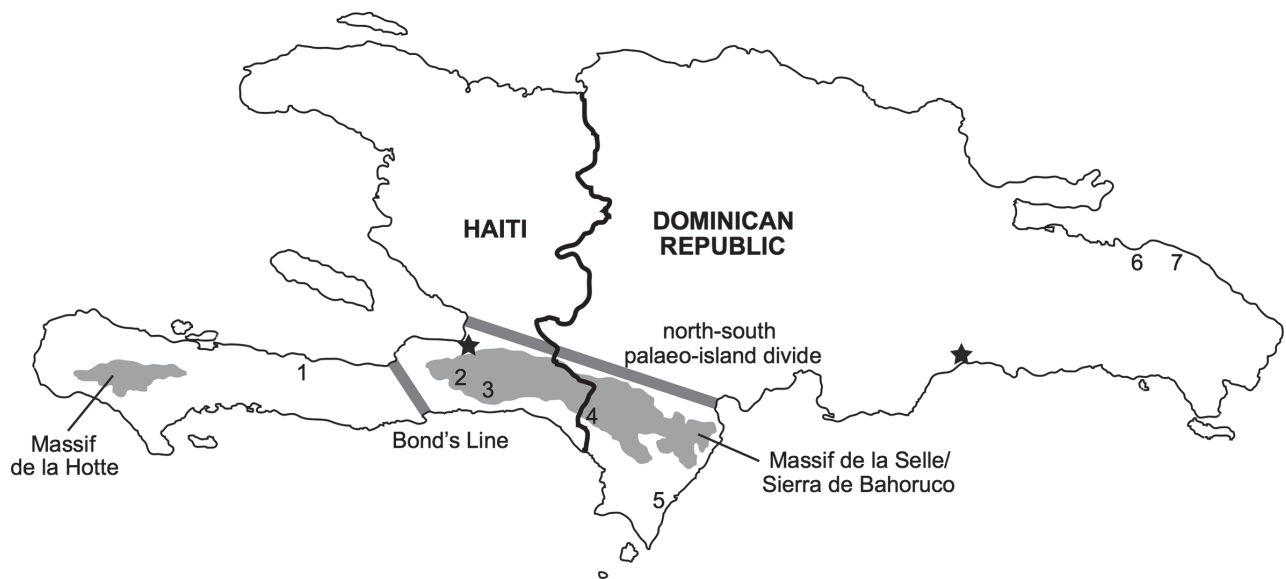


FIGURE 1. Map of Hispaniola, showing geotectonic boundaries and localities indicated in the text. Capital cities indicated with filled stars. Key: 1, Miragoâne; 2, Morne Cabiao; 3, Morne La Visite/Riviere Blanche; 4, Mencia; 5, Laguna Oviedo/Parque Nacional Jaragua; 6, El Jovero; 7, Guarabo.

These phylogenetic conclusions are further supported by quantitative morphometric analyses (Hansford *et al.* 2012). These authors used a dataset of 67 craniodental measurements representing two of the three genetically identifiable populations, and demonstrated significant separation between populations in 14 measurements. Further comparison between extant *Plagiodontia* populations and the extinct species *P. spelaenum* demonstrated that morphological variation between living hutias is lower than between well-defined Late Quaternary species, supporting interpretation of living allopatric populations as subspecies rather than species. The holotype skull of *P. aedium* was morphometrically closest to the southwestern population in 12 out of 14 measurements that differed between living populations and clustered with southwestern specimens, supporting use of this name for representatives of the southern palaeo-island clade.

However, whereas Brace *et al.* (2012) identified three lineages within *Plagiodontia*, only two scientific names are available for these subspecies. No craniodental material from the southeastern population has previously been available for comparative analysis. The only skull available from southeastern Hispaniola, collected from Morne Cabiao, Massif de la Selle (UF 15246), a locality close to the Jacmel–Fauché depression, clusters with the southwestern population in genetic analysis (Brace *et al.* 2012). Other existing hutia material from southeastern Hispaniola consists of postcranial bone fragments from Morne la Visite, Massif de la Selle (UF 23288) recovered from dog feces in the 1980s (Woods & Ottenwalder 1992) that cluster with the southeastern population in genetic analysis (Brace *et al.* 2012); and a recently collected hutia skeleton lacking a skull from Terre Chaude (c.10.5 km southeast of Morne La Visite), Massif de la Selle (LDUCZ Z2717), of unknown genetic status. A specimen from Miragoâne, southern Haiti (USNM 282552), which also clusters with the southeastern population in genetic analysis (Brace *et al.* 2012), is preserved in fluid and is not available for craniodental morphometric analysis.

During fieldwork in 2011 on a long-term research programme into the ecology and status of Hispaniola's endemic land mammals, the bodies of two hutias were recovered from the Sierra de Bahoruco region of southeastern Hispaniola. Although phylogenetic affinities of these specimens have not been assessed using genetic analysis, they were collected from the vicinity of the same village as three previously sampled wild-caught and re-released individuals which all showed identical cytochrome *b* haplotypes that fell securely within the southeastern genetic lineage (unique identifier=Q_{1,3} in Brace *et al.* 2012); we can therefore confidently interpret the new specimens as also being referable to the southeastern population. Complete skeletons of both individuals were preserved, permitting new investigation into whether the previously undescribed southeastern hutia population displays any morphometric variation that can differentiate it from other genetically distinct hutia populations on Hispaniola.

Material and methods

Specimens and measurements. Repositories of described or cited specimens are: LDUCZ, Grant Museum of Zoology, London; MNHN, Muséum National d'Histoire Naturelle; UF, Florida Museum of Natural History, Gainesville; USNM, United States National Museum.

The two new specimens were compared with the holotype skull of *Plagiodontia aedium* (MNHN 2M-MO-1982-894), and with 31 complete/almost complete recent hutia specimens assignable to the northern or southwestern Hispaniolan populations on the basis of genetic analysis of samples from the same collection locality by Brace *et al.* (2012) (Appendix 1). It was not possible to use the full series of 67 craniodental measurements originally used by Hansford *et al.* (2012) due to minor damage to some specimens. The following reduced series of 62 measurements for comparison with northern specimens, and 65 measurements for comparison with southwestern specimens, were used for comparative analysis:

Skull: (1) greatest occipitonasal length; (2) height of skull above palate; (3) height of braincase; (4) width across braincase; (5) width of occipital region; (6) internal width across occipital condyle; (7) width across paroccipital processes (measurement only available for comparison with southwestern population); (8) height of occipital region excluding paroccipital processes; (9) width across auditory bullae; (10) width across zygomatic arches; (11) minimum breadth of zygomatic plate; (12) maximum interorbital width; (13) minimum anterior interorbital width; (14) minimum posterior interorbital width; (15) maximum width of frontals; (16) width of nasals; (17) width of single incisor (only versus southwest); (18) length of diastema (from posterior incisor margin); (19) length of incisive foramina; (20) width of incisive foramina; (21) internal width across bony palate at PM4; (22) external width across bony palate at PM4; (23) internal width across bony palate at M3; (24) external width across bony palate at M3; (25) length from interior alveolus of PM4 to back of palate; (26) width of mesopterygoid fossa; (27) postpalatal length (to occipital foramen); (28) crown length of cheek tooth row; (29) alveolar length of cheek tooth row; (30) maximum alveolar width of cheek tooth row; (31) crown length of PM4; (32) crown width of PM4; (33) crown length of M1; (34) crown width of M1; (35) crown length of M2; (36) crown width of M2; (37) crown length of M3; (38) crown width of M3.

Mandible: (39) mandible length (incisor base to condyle); (40) mandible length (incisor base to angular process); (41) width of incisor (only versus southwest); (42) length of symphysis; (43) length of diastema; (44) length from incisor base to posterior bulb of incisor root; (45) crown length of cheek tooth row; (46) alveolar length of cheek tooth row; (47) maximum alveolar width of cheek tooth row; (48) crown length of pm4; (49) crown width of pm4; (50) crown length of m1; (51) crown width of m1; (52) crown length of m2; (53) crown width of m2; (54) crown length of m3; (55) crown width of m3; (56) maximum width of entire mandibular body; (57) maximum width of angular process; (58) internal height of mandible (base to alveolar lip); (59) internal height of mandible (base to tooth crown); (60) height of toothrow at pm4 (internal aspect); (61) height of toothrow at m3 (internal aspect); (62) breadth across distal end of condyle; (63) coronoid–condyle length; (64) coronoid–angular length; (65) condyle–angular length.

Statistical analyses. Morphometric data were analyzed in R 2.10.1 (R Development Core Team 2011). The new specimens were compared with northern and southwestern samples to identify whether any quantitative morphometric differences could differentiate them from either of these formally recognized subspecies. Methods closely followed Hansford *et al.* (2012): individual Analyses of Variance (ANOVAs) were first used to identify and eliminate craniodental characters that were not significantly different between the new samples and either the northern or the southwestern population, and then a Multivariate Analysis of Variance (MANOVA) using this new reduced dataset was conducted to assess whether these significant differences provided a consistent separation of the new samples between geographically distinct hutia populations. It was not statistically possible to conduct MANOVAs using the entire measurement dataset, as the number of dependent variables is considerably greater than the overall sample size, thus violating statistical assumptions. Principal Component Analysis (PCA) was also conducted on both the non-reduced and reduced datasets to further determine whether the new samples fell within or outside the primary morphometric variation shown by either formally recognized subspecies, and to assess whether the holotype specimen of unknown geographic provenance was morphometrically closer to the new samples or the southwestern population.

Results

Individual ANOVAs showed statistically significant differences at $\alpha=0.05$ for 13 characters in the two available specimens from the southeastern Hispaniolan hutia population compared with available material from the southwestern population (and for two characters under Bonferroni correction at $\alpha=0.0008$), and for two characters compared with the smaller available sample of the northern population (with a further three characters of borderline statistical significance for comparison with the northern population). In all cases, the southeastern samples show greater measurement values compared to other populations (Tables 1–2). MANOVAs using the reduced dataset consisting of only these significant characters found a significant separation of all three populations ($F=6.008$, $p<0.001$). There is complete separation of all three populations in PCA using the reduced dataset, and complete separation (for southwestern population) or almost complete separation (for northern population) between the new samples and the two formally recognized subspecies in PCA using the non-reduced dataset (Figures 2–3). The holotype of *Plagiodontia aedium aedium* clusters within the southwestern population sample and is morphometrically far from the new samples on PCA axis 2 (Figures 2–3).

The statistically significant morphometric differences demonstrated between the two specimens from the Sierra de Bahoruco and craniodental samples from both the southwestern and northern populations are congruent with the substantial genetic differences and genetic isolation previously identified between all three allopatrically segregated populations, demonstrating that the southeastern population can be differentiated from other populations on both morphometric and genetic grounds. As the other two populations are formally recognized as distinct subspecies, and the holotype specimen of *Plagiodontia aedium aedium* clearly clusters with the southwestern population in PCA, a new subspecies name therefore needs to be established for the currently unnamed distinct southeastern population.

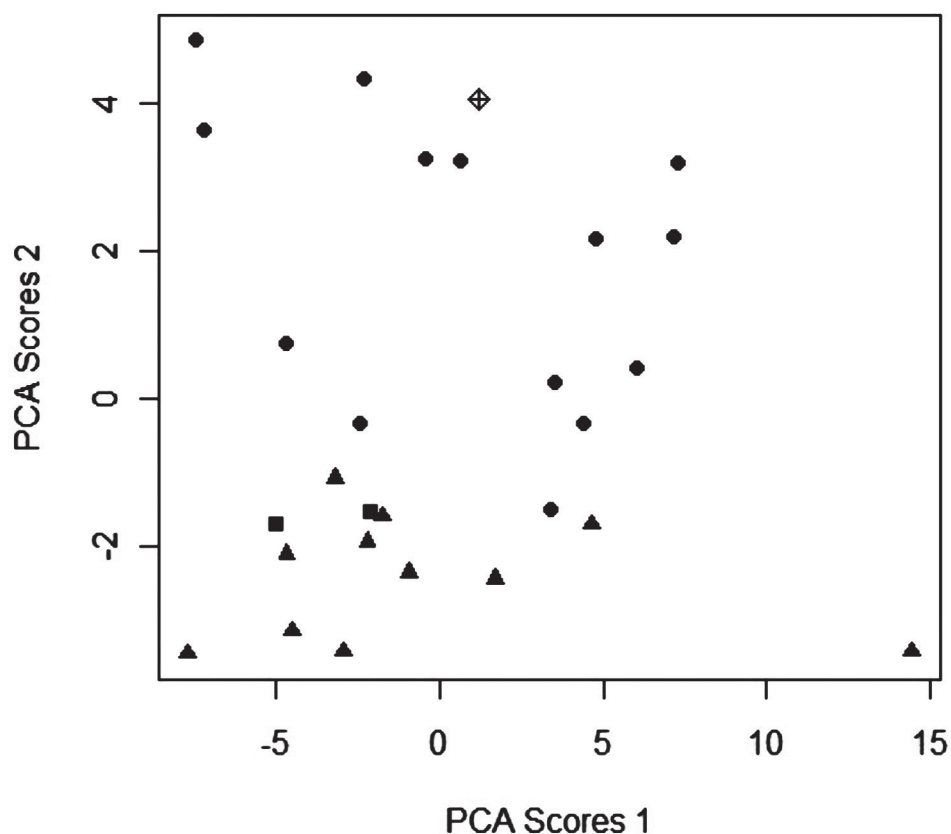


FIGURE 2. Principal Component Analysis for non-reduced dataset of craniodental measurements of southeastern palaeo-island hutias (squares), *Plagiodontia aedium hylaeum* (triangles), *Plagiodontia aedium aedium* (circles), and holotype of *Plagiodontia aedium aedium* (diamond). Percentage variation explained by PCA: axis 1, 43.41%; axis 2, 11.36%; cumulative variation, 54.78%.

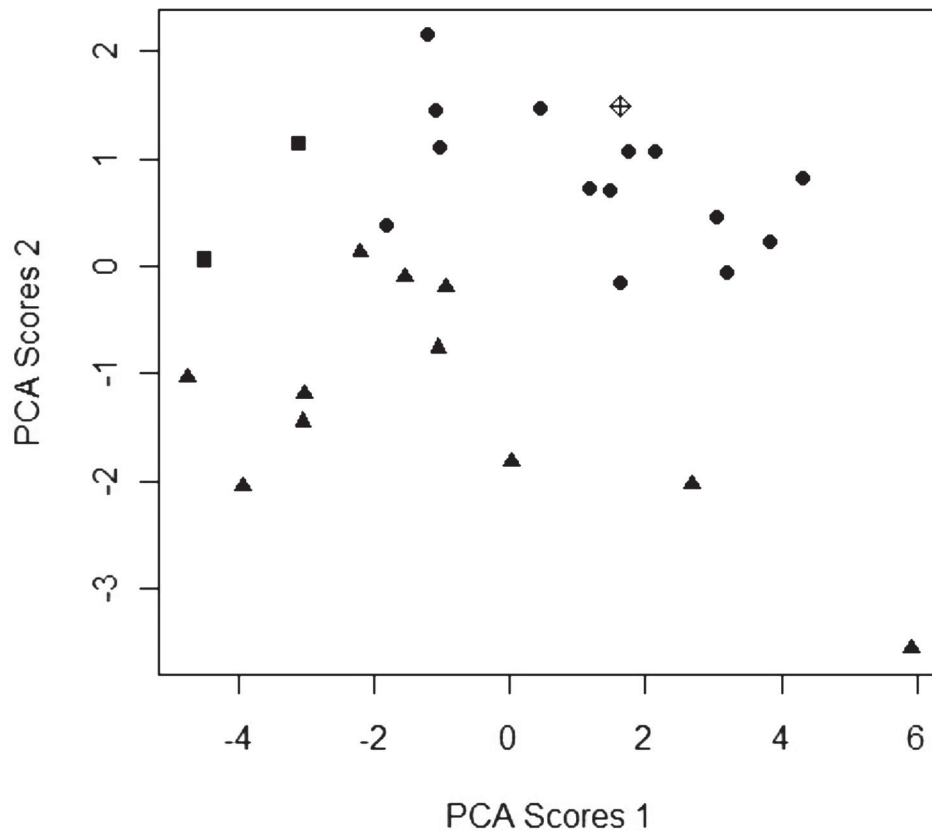


FIGURE 3. Principal Component Analysis for reduced dataset of craniodental measurements of southeastern palaeo-island hutias (squares), *Plagiodontia aedium hylaeum* (triangles), *Plagiodontia aedium aedium* (circles), and holotype of *Plagiodontia aedium aedium* (diamond). Percentage variation explained by PCA: axis 1, 56.63%; axis 2, 12.06%; cumulative variation, 69.23%.

TABLE 1. Craniodental measurements displaying statistically significant ($\alpha=0.05$) differences between populations of *Plagiodontia aedium* from the southwestern and southeastern palaeo-islands of Hispaniola, showing mean and measurement range for each character, and *p* values for ANOVA analysis of population-level differences. Asterisks indicate *p* values that remain statistically significant after Bonferroni correction ($\alpha=0.0008$).

Measurement	Southwestern specimens (n=20): mean, range (mm)	Southeastern specimens (n=2): mean, range (mm)	<i>p</i> value
Coronoid–condyle length	16.19 (13.18–18.76)	17.05 (15.74–18.36)	>0.0001*
Coronoid–angular length	25.79 (23.30–31.68)	30.63 (30.12–31.14)	>0.0001*
Length of incisive foramina	6.13 (4.94–7.08)	7.67 (7.00–8.34)	0.0015
Minimum anterior interorbital width	18.23 (16.66–20.06)	20.07 (19.64–20.50)	0.0043
External width across bony palate at PM4	13.04 (11.86–15.37)	14.74 (both specimens)	0.0077
Maximum interorbital width	21.26 (19.16–25.62)	24.59 (24.18–25.00)	0.0080
Crown width of pm4	4.35 (3.90–4.80)	4.91 (4.76–5.06)	0.0083
Crown length of M3	4.23 (3.38–4.97)	4.93 (4.84–5.02)	0.0084
Crown width of m1	5.12 (4.60–6.06)	5.82 (5.76–5.88)	0.0118
Width of incisive foramina	2.52 (2.12–2.97)	3.05 (2.80–3.30)	0.0124
Crown width of M1	5.21 (4.74–5.86)	5.86 (5.75–5.96)	0.0139
Crown width of M2	4.95 (4.44–5.49)	5.46 (5.30–5.62)	0.0341
Crown width of PM4	4.94 (4.06–5.58)	5.61 (5.36–5.85)	0.0383

TABLE 2. Craniodental measurements displaying statistically significant ($\alpha=0.05$, indicated with asterisks) or nearly significant differences between populations of *Plagiodontia aedium* from the northern and southeastern palaeo-islands of Hispaniola, showing mean and measurement range for each character, and *p* values for ANOVA analysis of population-level differences.

Measurement	Northern specimens (n=11): mean, range (mm)	Southeastern specimens (n=2): mean, range (mm)	<i>p</i> value
Crown length of M2	4.35 (3.87–4.63)	4.85 (4.70–4.99)	0.0167*
Width of incisive foramina	2.50 (2.04–3.15)	3.05 (2.80–3.30)	0.0346*
Crown length of M3	4.06 (2.50–4.62)	4.93 (4.84–5.02)	0.0653
Coronoid–condyle length	15.53 (14.10–16.90)	17.05 (15.74–18.36)	0.0767
Height of tooththrow at pm4 (internal aspect)	3.15 (2.24–3.72)	3.82 (3.44–4.20)	0.0792

Systematic taxonomy

Rodentia Bowditch, 1821

Hystricognathi Tullberg, 1899

Caviomorpha Wood, 1955

Capromyidae Smith, 1842

Plagiodontia F. Cuvier, 1836

Plagiodontia aedium F. Cuvier, 1836

Plagiodontia aedium bondi subsp. nov. (James Bond's hutia)

Holotype. LDUCZ-Z2807, complete skeleton of adult individual (Figure 4). Found dead in ravine, apparently after fatal fall from tree branch; collected by Ramon “Moncho” Espinal on 25 October 2011.

Paratype. LDUCZ-Z2808, complete skeleton of young adult with full tooth eruption and substantial but not complete closure of ectocranial sutures; possibly offspring of holotype individual. Collected at same location and date as holotype.

Etymology. Named after the ornithologist James Bond (1900–1989), to acknowledge his recognition of the biogeographic line in southern Hispaniola that represents the allopatric barrier between the new subspecies and *P. aedium aedium*.

Local names. This subspecies is referred to by local informants in southeastern Haiti and the southwestern Dominican Republic by several names, including *jutía* (commonest name used in Dominican Republic), *kochondenn* (commonest name used in Haiti), *solenodon*, *kombee*, and *rata*, reflecting confusion with other native and introduced co-occurring land mammals (Turvey *et al.* 2014).

Type locality. Vicinity of Mencia village, Pedernales Province, Dominican Republic (18°10'10N, 71°44'25W), in area of primary broadleaf forest at elevation of 460 m.

Distribution. The southern palaeo-island of Hispaniola south of the Neiba Valley and east of the Jacmel–Fauché depression; found in both southeastern Haiti (departments Ouest and Sud-Est) and southwestern Dominican Republic (Barahona, Independencia and Pedernales provinces). Hutias are known to occur in the Massif de la Selle (Haiti), and the Sierra de Bahoruco mountain range and Barahona Peninsula (Dominican Republic) (Sullivan 1983; Woods *et al.* 1985; Woods 1986; Woods & Ottenwalder 1992; Turvey *et al.* 2014).

Diagnosis. Subspecies of Hispaniolan hutia which is significantly larger than the closely related *Plagiodontia aedium aedium* in the following craniodental characters: maximum interorbital width, minimum anterior interorbital width, length and width of incisive foramina, external width across bony palate at PM4, crown width of PM4, M1 and M2, crown length of M3, crown width of pm4 and m1, coronoid–condyle length, and coronoid–

angular length. Significantly larger than *P. aedium hylaeum* in width of incisive foramina and crown length of M2, and somewhat larger than this subspecies in crown length of M3, height of toothrow at pm4, and coronoid–condyle length. Postcranial and soft-tissue differences between all three subspecies are unknown.

Description. Craniodental anatomy of *Plagiodontia aedium*, including material from Pedernales Province referable to the new subspecies, described in detail by Woods & Howland (1979) and Woods (2001). Nasals slightly anteriorly inflated. No supraorbital ridge; slight postorbital process. Zygomatic arch broad, with greatest width opposite M3; well-defined lateral jugal fossa present, restricted to level of molar toothrow. Superior zygomatic root of maxillary broad, inferior zygomatic root narrow, with well-developed masseteric tuberosity on ventral surface; posterior zygomatic root formed by squamosal. Incisive foramen distinct, relatively short and broad; septum formed mainly by premaxillary. Alisphenoid canal forms crescent-shaped fissure in rear wall of orbit, with optic foramen small and deep within this fissure; no sphenopalatine foramen on medial canal wall. Posterior margin of palate with V-shaped mesopterygoid fossa extending opposite M3, and with long, delicate lateral pterygoid processes. Large pterygoid plate extends medially posterior to M3, contacting base of pterygoid process; masticatory foramen in middle of pterygoid plate; lateral pterygoid ridge absent. Pterygoid fossa restricted by pterygoid plate; medial to M3. Paroccipital process long and broad; closely associated with short, spike-like lateral process that is independent from bullae. Incisors not procumbent; upper incisors strongly curved; alveolar capsule of lower incisors terminates below m1. Molariform cheek teeth hypsodont and rootless; upper and lower toothrows both parallel. Cheek teeth with enamel ridges forming deeply overlapping cement-filled oblique re-entrant folds oriented at 45° angle to body axis; upper cheek teeth with one labial re-entrant fold and one lingual re-entrant fold; lower cheek teeth with one labial re-entrant fold and two lingual re-entrant folds. Anterior margin of upper cheek teeth sigmoid; lower cheek teeth not sigmoid. Mandible with well-developed coronoid process, and angular process with masseteric crest and broad, flat-bottomed pterygoid shelf; mental foramen absent; retromolar fossa present as large pit with mandibular foramen in its centre.

New subspecies distinguished phenotypically from other subspecies of *P. aedium* in this study on the basis of morphometric analysis using quantitative character measurements; no qualitative differences in craniodental character states are recognized. Craniodental measurements are as follows, taken from both individuals in type series unless indicated:

Skull: greatest occipitonasal length, 74.16–77.6 mm; height of skull above palate, 19.58–21.24 mm; height of braincase, 17.20–18.12 mm; width across braincase, 21.86–23.16 mm; width of occipital region, 27.76–28.22 mm; internal width across occipital condyle, 10.30–11.50 mm; width across paroccipital processes, 27.32–27.38 mm; height of occipital region excluding paroccipital processes, 17.56–17.60 mm; height of occipital region including paroccipital processes, 25.85–27.40 mm; width across auditory bullae, 28.74–29.05 mm; width across zygomatic arches, 41.00–41.64 mm; minimum breadth of zygomatic plate, 4.38–4.88 mm; maximum interorbital width, 24.18–25.00 mm; minimum anterior interorbital width, 19.64–20.50 mm; minimum posterior interorbital width, 18.72–19.78 mm; maximum width of frontals, 23.58–25.50 mm; length of nasals, 25.10 mm (LDUCZ-Z2807 only); width of nasals, 9.20–9.60 mm; width of single incisor, 2.88–2.95 mm; length of diastema (from posterior incisor margin), 17.10–19.36 mm; length of incisive foramina, 7.00–8.34 mm; width of incisive foramina, 2.80–3.30 mm; internal width across bony palate at PM4, 2.54–2.60 mm; external width across bony palate at PM4, 14.74 mm (both specimens); internal width across bony palate at M3, 6.48–7.04 mm; external width across bony palate at M3, 15.55–15.96 mm; length from interior alveolus of PM4 to back of palate, 20.02–21.40 mm; width of mesopterygoid fossa, 4.24–4.56 mm; postpalatal length (to occipital foramen), 23.14–24.66 mm; crown length of cheek tooth row, 20.16–20.77 mm; alveolar length of cheek tooth row, 22.42–22.45 mm; maximum alveolar width of cheek tooth row, 5.94–6.58 mm; crown length of PM4, 6.18–6.26 mm; crown width of PM4, 5.36–5.85 mm; crown length of M1, 4.93–5.14 mm; crown width of M1, 5.75–5.96 mm; crown length of M2, 4.70–4.99 mm; crown width of M2, 5.30–5.62 mm; crown length of M3, 4.84–5.02 mm; crown width of M3, 4.58–4.64 mm.

Mandible: mandible length (incisor base to condyle), 50.64–50.98 mm; mandible length (incisor base to angular process), 51.58–55.34 mm; width of incisor, 2.70–2.78 mm; length of symphysis, 23.93–24.16 mm; length of diastema, 12.92–14.26 mm; length from incisor base to posterior bulb of incisor root, 21.52–22.34 mm; crown length of cheek tooth row, 19.09–20.16 mm; alveolar length of cheek tooth row, 21.92–21.96 mm; maximum alveolar width of cheek tooth row, 5.90–6.08 mm; crown length of pm4, 5.54–6.60 mm; crown width of pm4, 4.76–5.06 mm; crown length of m1, 4.76–5.00 mm; crown width of m1, 5.76–5.88 mm; crown length of m2, 4.32–4.68 mm; crown width of m2, 5.46–5.62 mm; crown length of m3, 4.00–4.36 mm; crown width of m3, 4.70–4.94

mm; maximum width of entire mandibular body, 21.00–22.09 mm; maximum width of angular process, 6.02–6.95 mm; internal height of mandible (base to alveolar lip), 13.50–14.24 mm; internal height of mandible (base to tooth crown), 16.06–16.27 mm; height of toothrow at pm4 (internal aspect), 3.44–4.20 mm; height of toothrow at m3 (internal aspect), 1.12–1.20 mm; breadth across distal end of condyle, 10.32–10.37 mm; coronoid–condyle length, 15.74–18.36 mm; coronoid–angular length, 30.12–31.14 mm; condyle–angular length, 25.92–26.70 mm.

Detailed description of soft-tissue characters for the two specimens reported here is unfortunately not possible, as they were almost completely decomposed by the time they became available for study. General external morphology of hutias from southern Haiti, representing individuals of both *P. aedium aedium* and the new subspecies, was described by Woods & Ottenwalder (1992), and live individuals encountered in the Sierra de Bahoruco during fieldwork by the authors in 2009–2013 match the broad description given by these authors (Figure 5a). However, previously published information on supposed differences in external body proportions and pelage characteristics between northern and southwestern Hispaniolan hutia populations (Miller 1928; Johnson 1948; Anderson 1965; Woods & Howland 1979) is conflicting and of uncertain taxonomic value, and identification of systematic soft-tissue differences between different subspecies requires further study. Seventeen adult hutias were captured and released around Mencia in 2011–2013 during field research into ranging behavior and habitat use; adult males have a mean body mass of 1322.9 g (n=12, range=1040–1795 g, SD=280.4), and adult females have a mean body mass of 1355.0 g (n=5, range=1180–1530 g, SD=157.9), with total mean body mass for all individuals of 1335.0 g. These values are higher than the mean body mass of 1018 g for eight wild-caught individuals of *P. aedium aedium* from the Massif de la Hotte reported by Woods & Ottenwalder (1992).

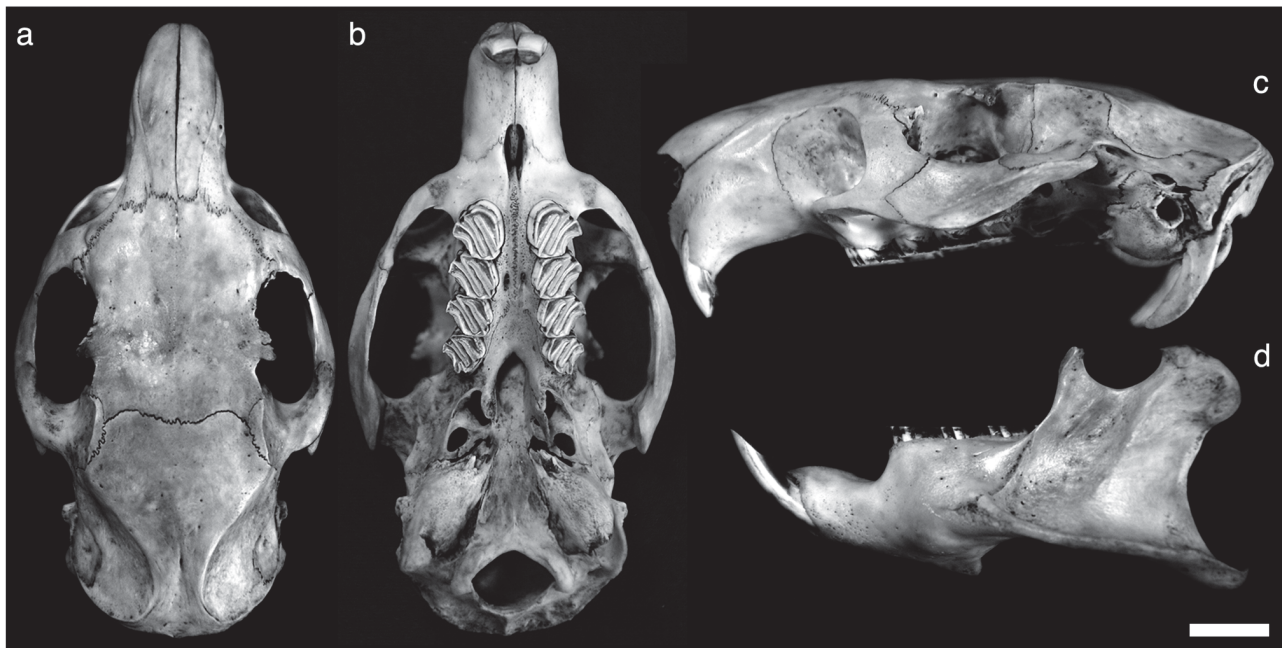


FIGURE 4. Holotype skull and mandible of *Plagiodontia aedium bondi* (LDUCZ-Z2807): a, dorsal view of skull; b, ventral view of skull; c, lateral view of skull; d, external view of mandible. Scale bar = 1 cm.

Biological and ecological data. Hispaniolan hutias are considered to be predominantly arboreal when in good-quality forest (Woods 1981; Sullivan 1983), but during the course of the 2011–2013 study some individuals were caught on the ground, and signs of feeding on saplings on the ground were often observed. Females caught on 6 January 2013 and 15 February 2013 were both pregnant, and a female caught on 14 September 2012 was lactating. Field observations and camera trap photos recorded young juveniles (200–350 g body mass) in separate family groups on 15 January 2012, 27 January 2012, 22 November 2012 and 11 January 2013, suggesting probable parturition during the autumn, with larger juveniles (420–500 g body mass) recorded on 12 May 2012 and 13 September 2012. Feeding signs detected during fieldwork and local reports suggest that hutias in the southeastern Dominican Republic feed upon a relatively wide variety of plants, including *Rauvolfia* (Apocynaceae), *Cleome* (Cleomaceae), *Clusia* (Clusiaceae), *Ipomoea* (Convolvulaceae), *Tragia* (Euphorbiaceae), *Acacia* and *Senna* (Fabaceae), *Ocotea* (Lauraceae), *Guarea* and *Trichilia* (Meliaceae), *Ficus* (Moraceae), *Trichostigma*

(Phytolaccaceae), *Gouania* and *Krugiodendron* (Rhamnaceae), *Chrysophyllum* and *Sideroxylon* (Sapotaceae), and *Guaiaacum* (Zygophyllaceae).

The relatively limited existing literature on previous field studies of Hispaniolan hutias provides some further information on habitat preferences and ecological requirements of the new subspecies. Sullivan (1983) reported the presence of hutias referable to this subspecies in low-elevation (0–234 masl) dry subtropical forest around Laguna Oviedo on the Barahona Peninsula, where they have also been observed by the current authors (Figure 5b), and also in humid subtropical forest in the Sierra de Bahoruco across an elevational gradient from mixed hardwood forest (500–900 masl) to deciduous vegetation in ravines within pine forest (1300–1500 masl), with all sites associated with rocky limestone substrate that provides suitable cavities and crevices for shelter. Hutias have also been recorded from the Massif de la Selle in southeastern Haiti in undisturbed broad-leaved forest (locally known as “rak bwa”) on the steep north slope of the main ridge (2160 masl) and along the ravine of the Riviere Blanche (1730 masl) (Woods *et al.* 1985; Woods 1986; Woods & Ottenwalder 1992), again near areas of exposed limestone.

Interestingly, albinism has been documented in a relatively large number of individuals in this subspecies. Two separate albino individuals were caught during fieldwork around Mencia in 2011 and 2012, and a further albino individual was observed in Parque Nacional Jaragua in 2009 (Figure 5b). A further “partially albinistic” individual “with pink eyes and unpigmented hands, feet and tail” from the “mountains of southern Haiti” (specific location unknown), which could refer either to the Massif de la Hotte in southwestern Haiti or the Massif de la Selle in southeastern Haiti, was described by Tate (1948).



FIGURE 5. Living individuals of *Plagiodontia aedium bondi*: a, typical individual, photographed on 5 November 2009 near Mencia (18°10'49"N, 71°44'40"W); b, albino individual, photographed on 29 November 2009 at Fondo Paradi, Parque Nacional Jaragua (17°47'36"N, 71°27'57"W).

Discussion

Following recognition of three phylogenetically distinct allopatric populations of *Plagiodontia* by Brace *et al.* (2012), and referral of the two available subspecies names to describe the morphologically diagnosed northern and southwestern populations by Brace *et al.* (2012) and Hansford *et al.* (2012), it is therefore necessary to also diagnose and name the third phylogenetically distinct Hispaniolan hutia population following collection of new craniodental material from this taxon. Our decision to recognize the southeastern population as a formally named taxon is strongly supported by the substantial morphometric differentiation shown from its phylogenetically closest relative, *P. aedium aedium*, from which it diverged during the Middle Pleistocene (Brace *et al.* 2012), and which is closely similar in magnitude (statistically significant differences demonstrated in 13 of 65 craniodental character measurements) to the level of morphometric differentiation observed between *P. aedium aedium* and *P. aedium hylaeum* by Hansford *et al.* (2012). Although the new subspecies shows fewer recognized morphometric differences from the more distantly related *P. aedium hylaeum* in our study, it can still be statistically differentiated from this subspecies, and we consider this apparently reduced variation most likely to reflect limited statistical

power associated with the markedly smaller craniodental sample size available for comparison with this subspecies. We encourage future study into soft-tissue differences between the three recognized Hispaniolan hutia subspecies, to identify further characteristics that can be used to distinguish these distinct taxa in the field.

Hispaniolan hutias are currently listed at the species level as Endangered by IUCN (2013), and the recommendation by Brace *et al.* (2012) that all three subspecies should also be treated as distinct evolutionary units for conservation management suggests that the status of the new subspecies should be separately evaluated. The new subspecies was estimated to have a mean effective female population size of 6,509 individuals (95% credibility interval=1,650–56,207 individuals) on the basis of genetic coalescent modeling (Brace *et al.* 2012), although this estimate will not reflect recent population declines resulting from human activities. It occurs in three nationally protected areas: La Visite National Park in Haiti, and Sierra de Bahoruco National Park and Jaragua National Park in the Dominican Republic, with the latter two protected areas forming part of the larger Jaragua-Bahoruco-Enriquillo Biosphere Reserve. However, severe deforestation driven largely by charcoal production and subsistence agriculture continues to reduce suitable hutia habitat across both sides of the international border in the Massif de la Selle and Sierra de Bahoruco, including within protected areas (Sergile & Woods 2001; Devenish *et al.* 2009). Hutia predation by dogs, especially free-roaming village dogs, is also likely to represent a major and possibly unsustainable threat (Sullivan 1983; Woods 1986; Turvey *et al.* 2014). The new subspecies is likely to now have an extent of occurrence of less than 5000 km² across southeastern Haiti and the southwestern Dominican Republic, is restricted to a small number of subpopulations, and is experiencing continuing declines in area, extent and quality of habitat and possibly also in number of mature individuals through dog predation. We therefore recommend that this subspecies is listed as Endangered under Criterion B1a,biii,v on the IUCN Red List (IUCN 2001).

Our morphometric analysis provides new support for the molecular-based hypothesis of allopatric differentiation of Hispaniola's hutia populations, and we recommend the use of a combined genetic-morphometric approach to clarify the evolutionary history and taxonomic status of other extant Caribbean mammal populations. In particular, similar research needs to be conducted to assess relationships between allopatric populations of the endangered Hispaniolan solenodon (*Solenodon paradoxus*), which has the same geographic distribution as *Plagiodontia aedium* and may therefore be expected to show congruent spatial patterns of population differentiation (Ottenwalder 2001); and also the taxonomic validity of the numerous currently recognized allopatric subspecies of *Capromys pilorides* and extant or recently extinct allopatric species of *Mesocapromys*, which have matching geographic distributions across mainland Cuba and its associated offshore island groups (Silva Taboada *et al.* 2007; Borroto-Páez & Mancina 2011). Some of these threatened populations are interpreted as representing top priorities for mammal conservation at a global level (Collen *et al.* 2011), so that establishing their status and relationships is an important goal for future Caribbean mammal research.

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APPENDIX 1. Other specimens examined.

Plagiodontia aedium aedium Cuvier, 1836, n=21: MNHN 2M-MO-1982-894 (holotype of *Plagiodontia aedium*), locality unknown; LDUCZ Z2708, LDUCZ Z2709, LDUCZ Z2712, LDUCZ Z2714, UF 6279, UF 12002, UF 14861, UF 14864, UF 14865, UF 14877, UF 14880, UF 15081, UF 15084, UF 18893, UF 18905, UF 18906, UF 25239, UF 25244, UF 30962, UF 30965, Duchity, Grande'Anse Department, Haiti. *Plagiodontia aedium hylaeum* Miller, 1928, n=11: USNM 239886, USNM 239887 (holotype of *Plagiodontia hylaeum*), USNM 239888, USNM 239889, USNM 239890, USNM 239891, USNM 239892, USNM 239893, USNM 239894, Guarabo, El Seibo Province, Dominican Republic; USNM 239895, USNM 239896, El Jovero, El Seibo Province, Dominican Republic.