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Beyond the carapace: skull shape variation and morphological systematics of long-nosed armadillos (genus *Dasypus*)

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Background. The systematics of long-nosed armadillos (genus *Dasypus*) has been mainly based on a handful of external morphological characters and classical measurements. Here, we studied the pattern of morphological variation in the skull of long-nosed armadillos species, with a focus on the systematics of the widely distributed nine-banded armadillo (*D. novemcinctus*). **Methods.** We present the first exhaustive 3D comparison of the skull morphology within the genus *Dasypus*, based on µCT-scans. We used geometric morphometric approaches to explore the patterns of the intra- and interspecific morphological variation of the skull with regard to several factors such as taxonomy, geography, allometry, and sexual dimorphism. **Results.** We show that the shape and size of the skull vary greatly between *Dasypus* species, with *D. pilosus* representing a clear outlier compared to other long-nosed armadillos. The study of the cranial intraspecific variation in *D. novemcinctus* evidences clear links to the geographic distribution and argue in favour of a revision of past taxonomic delimitations. Our detailed morphometric comparisons detected previously overlooked morphotypes of nine-banded armadillo, especially a very distinctive unit circumscribed to the Guiana Shield. **Discussion.** As our results are congruent with recent molecular data and analyses of the structure of paranasal sinuses, we propose that *D. novemcinctus* should be regarded either as a polytypic species (with three to four subspecies) or as a complex of several distinct species.

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Abstract

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Methods. We present the first exhaustive 3D comparison of the skull morphology within the genus *Dasypus*, based on μCT-scans. We used geometric morphometric approaches to explore the patterns of the intra- and interspecific morphological variation of the skull with regard to several factors such as taxonomy, geography, allometry, and sexual dimorphism.

Results. We show that the shape and size of the skull vary greatly between *Dasypus* species, with *D. pilosus* representing a clear outlier compared to other long-nosed armadillos. The study of the cranial intraspecific variation in *D. novemcinctus* evidences clear links to the geographic distribution and argues in favour of a revision of past taxonomic delimitations. Our detailed morphometric comparisons detected previously overlooked morphotypes of nine-banded armadillos, especially a very distinctive unit circumscribed to the Guiana Shield.

Discussion. As our results are congruent with recent molecular data and analyses of the structure of paranasal sinuses, we propose that *D. novemcinctus* should be regarded either as a polytypic species (with three to four subspecies) or as a complex of several distinct species.

Introduction

With their Pan-American distribution, long-nosed armadillos (genus *Dasypus*) constitute an understudied model for Neotropical biogeography. They are the most taxonomically diverse and widespread extant xenarthrans. The genus *Dasypus* traditionally comprises seven extant species (*D. novemcinctus*, *D. hybridus*, *D. septemcinctus*, *D. kappleri*, *D. pilosus*, *D. mazzai*, and *D. sabanicola*; Wetzel, 1985; Wilson & Reeder, 2005; Feijo & Cordeiro-Estrela, 2014) and two extinct ones (*D. bellus* and *D. punctatus*; Castro et al., 2013; Castro, 2015). In spite of being one of the earliest diverging cingulate lineages (Gaudin & Wible, 2006; Delsuc et al., 2012; Gibb et al., 2016), the dasypodid early evolutionary history remains poorly known (Castro, 2015). Only three extinct genera were recognized among the Dasypodini: *Anadasypus* from the middle Miocene of Colombia and late Miocene of Ecuador (Carlini, Vizcaíno & Scillato-Yané, 1997; Carlini et al., 2013), *Pliodasypus* from the late Pliocene of Venezuela (Castro et al., 2014), and *Propraopus* from the middle Pleistocene–early Holocene of South America (Castro et al., 2013a).

Aside the widespread nine-banded armadillo (*D. novemcinctus*), all extant long-nosed armadillos are restricted to South America. Some species are sympatric in certain areas resulting in competition and possibly supporting divergent behaviours and morphologies. The nine-banded armadillo is likely to be the most abundant armadillo in tropical forests (Wetzel & Mondolfi, 1979; Loughry & Mcdonough, 1998) and has the widest distribution of all extant xenarthran species. Its distribution is thought to cover much of South and Central America and parts of North America and ranges from the south-east United States to North western Argentina and Uruguay (McBee & Baker, 1982). The species ability to disperse quickly, as well as its opportunistic and generalist mode of life, could partly explain this large distribution (Smith &

Doughty, 1984; Loughry & Mcdonough, 1998) marked by its rapid historical expansion into the United States (Taulman & Robbins, 2014). Such a wide geographical distribution, combined with early-recognized morphological variations (Peters, 1864; Gray, 1873; Allen, 1911; Lönnberg, 1913; Russell, 1953), raise the possibility that major taxonomic subgroups have been overlooked, be it at the subspecific or even specific level.

As its vernacular name implies, the genus *Dasypus* is characterized by a long, slender rostrum, which represents at least more than 55% of the length of the head (Gardner, 2008). The different species are usually distinguished by body and cranial measurements, colour differences, and morphological features of the carapace such as the number of movable bands and scutes across the body and the number and shape of osteodermal foramina (Feijo & Cordeiro-Estrela, 2016). The carapace is a hallmark of armadillos, and constitutes such a unique feature for mammals that it has dominated the attention of early and modern anatomists and, as a result, partly jeopardized the classification of the group. Its morphology, chiefly the number of movable bands, has been intensively, if not abusively, used in systematic studies. However, even in the so-called nine-banded armadillo, the number of movable bands can vary from 7 to 10 (Wetzel & Mondolfi, 1979). Yet early on, in his Systema Naturae (ed. 10, p. 51), (Linnaeus, 1758) casted doubt on the use of the number of movable bands as a criterion to distinguish *Dasypus* species (*i.e.*, *D. septemcinctus* from *D. novemcinctus*). Since then, a number of authors have raised the question whether such external features could be confidently used for systematic purposes. Wetzel and Mondolfi (1979) argued that "although many scientific names of armadillos are based on the number of movable bands, it is proposed here that for vernacular names we discontinue using this variable characteristic and base names upon unique or more consistent features". In the early 20th century, Hamlett (1939) made similar observations when focusing on

the nine-banded armadillo; he considered as impossible to recognize external variations at a subspecific level and concluded that "cranial characters appear to offer the only promise for subspecific analysis of the species" (Hamlett 1939:335). We decided to take up and further discuss Hamlett's idea since no large review of the dasypodine cranial variation has been undertaken to date.

This study aims to further elucidate the pattern of morphological variation seen in the skull of long-nosed armadillos, with a focus on the nine-banded armadillo. Geometric morphometric data were collected for most *Dasypus* species using µCT-scans. The main questions asked in the present study were whether different patterns of variation in skull shape can be characterized among and within long-nosed armadillo species, and if those patterns could be linked to factors such as taxonomy, geographical distribution, skull size, or sexual dimorphism. Our ultimate goals are to reconstruct the details of the biogeographic distribution of the widespread nine-banded armadillo at the continental scale and to lay the path for a new integrative taxonomy of long-nosed armadillos. A greater understanding of the morphological diversity and patterns of evolution for long-nosed armadillos is timely to effectively conserve these species and will also serve to deepen our knowledge of their peculiar evolution and biology (Loughry & Mcdonough, 2013).

Materials & Methods

Biological samples

The material studied came from the collections of the *Muséum national d'Histoire naturelle* in Paris (MNHN, collections *Zoologie et Anatomie comparée, Mammifères et Oiseaux*), the Natural History Museum in London (BMNH), the Naturalis Biodiversity Center in Leiden (NBC), the

Royal Ontario Museum in Toronto (ROM), the Louisiana State University in Bâton-Rouge (LSU), the American Museum of Natural History in New York (AMNH), the National Museum of Natural History in Washington (USNM), the *Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá* in Macapá (IEPA), and the *Muséum d'Histoire naturelle* in Geneva, the KWATA association in Cayenne, and the Personal collection of Pierre Charles-Dominique. We analysed 128 skulls belonging to five *Dasypus* species (see Table S1 for a complete list of specimens): *D. novemcinctus*, *D. hybridus*, *D. septemcinctus*, *D. kappleri*, and *D. pilosus* (no data was available for *D. yepesi*, and *D. sabanicola*). With these data we performed a preliminary assessment of the average amounts of cranial variation at the specific level among different populations of *D. novemcinctus* from French Guiana, Guyana, Suriname, Ecuador, Brazil, Venezuela, Colombia, Costa Rica, Belize, Bolivia, Argentina, Paraguay, Uruguay, Panama, Nicaragua, Honduras, Guatemala, Mexico, Peru, and USA (Table S1). Juvenile, subadult, and adult specimens were considered in order to take into account the effect of age, size and differential growth on the dataset. Several studies (Hensel, 1872; Russell, 1953; Ciancio, Castro & Asher, 2012) showed that long-nosed armadillos possess tooth replacement, as typical for mammals, and that the eruption of permanent teeth occurs relatively late, as observed in afrotherians (Asher & Lehmann, 2008). Accordingly, we used eruption of the teeth, suture closure, and size as criteria to identify adult specimens in our dataset.

Geometric morphometric methods

Due to the limitations of the classical qualitative descriptive approach, geometric morphometrics represents a good complementary technique by which to examine intraspecific shape variation. Digital data of all specimens were acquired using X-ray micro-computed tomography (μCT) at

129 the University of Montpellier (France), at the Natural History Museum (London, UK), and at the
130 AST-RX platform MNHN (Paris, France). Three-dimensional reconstruction and visualization of
131 the skulls were performed using stacks of digital µCT images with AVIZO v. 6.1.1 software
132 (Visualization Sciences Group 2009). The mandibles and crania of armadillos were quantified
133 with 10 and 84 anatomical landmarks respectively (Fig. 1 and Tables 1 and 2) using ISE-
134 MeshTools (version 1.3.1; Lebrun, 2014). These landmarks were inspired by previous studies
135 performed on different mammalian taxa (Hautier, Lebrun & Cox, 2012; Hautier et al., 2014).
136 Considering the tendency to the reduction of the number of teeth in *Dasypus* specimens (Allen,
137 1911), which often lack the last dental locus and thus produce an artificial shortening of the
138 entire tooth row, we decided to place a landmark after the seventh teeth and not at the end of the
139 tooth row as it is usually the norm. Since skulls were often incomplete, the number of landmarks
140 was adjusted to account for the maximal morphological variation in a maximum number of
141 individuals; this number was then different whether we performed analyses considering all
142 *Dasypus* species (10 and 84 landmarks for the mandible and the cranium respectively) or only *D.*
143 *novemcinctus* (10 and 82 landmarks for the mandible and the cranium respectively).
144 All configurations (sets of landmarks) were superimposed using the Procrustes method of
145 generalized leastsquares superimposition (GLS scaled, translated, and rotated configurations so
146 that the intralandmark distances were minimized) following the methods of Rohlf (1999) and
147 Bookstein (1991). Subsequently, mandibular and cranial forms of each specimen were
148 represented by centroid size S, and by multidimensional shape vector v in linearized Procrustes
149 shape space. Shape variability of the skull and the mandible was analysed by Principal
150 Component Analysis (PCA) of shape (Dryden & Mardia, 1998). Analysis and visualization of
151 patterns of shape variation were performed with the interactive software package

MORPHOTOOLS (Specht, 2007; Specht, Lebrun & Zollikofer, 2007; Lebrun, 2008; Lebrun et al., 2010).

To account for the potentially confounding effects of size allometry on shape, size-corrected shapes were obtained as follows. In a first step, allometric patterns were obtained via regression of Procrustes coordinates against the logarithm of centroid size, yielding an allometric shape vector (ASV), which characterizes cranial allometric patterns. In a second step, regressions of Procrustes coordinates against the logarithm of centroid size were computed for all species, yielding species-specific allometric shape vectors (ASVs). The ASVs represent directions in shape space that characterize species-specific allometric patterns of shape variation. A common allometric shape vector (ASVc), obtained as the mean of all the ASVs, provided a direction in shape space that minimizes potential divergence in mandibular allometric patterns across species (see Lebrun et al., 2010 for further details concerning this methodology). PCres corresponds to principal components of a PCA performed on shape data corrected for allometry. The same analyses have been performed at the intraspecific level and regressions were then computed between the Procrustes coordinates and the logarithm of centroid size for all subgroups (defined at a country level).

Multivariate analyses of variance (MANOVA) were performed on the principal component scores of mandibular and cranial mean shapes (35 first PCs, i.e. 90% of the variance) in order to assess the effects of different factors on mandibular and cranial shape variation: clades (species), sex, and geographic distribution (countries). MANOVAs were performed with Past 2.06 (Hammer, Harper & Ryan, 2001). Linear discriminant analyses (LDA) of shape coordinates were performed on the same number of PCs to assess a potential discrimination of skull morphology in relation to phylogeny (*i.e.*, species) and geography (*i.e.*, countries). When a group included

only one individual, this specimen was integrated into the dataset as ungrouped cases. A skull from Panama (USNM 171052) was not complete enough to be considered in these analyses. We then decided to perform similar analyses with a reduced set of landmarks (71 landmarks on the cranium) to enable morphological comparisons with other specimens.

Linear measurements

Several linear measurements of the skull of *Dasypus* were calculated directly on 3D coordinates of landmarks (Fig. 2). These measurements were used to compare our results with traditional methods of species delineation.

Results

Interspecific variation of skull shape among long-nosed armadillos

A MANOVA performed on the first 35 PCs (i.e. 90% of the variance) indicates a significant morphological differentiation of the mandibles and crania relative to species delimitations (mandible Wilks' lambda=0.01164, $F=4.903$, $p<0.001$; cranium Wilks' lambda=0.0005897, $F=11$, $p<0.001$). A multivariate regression of the shape component on size, estimated by the logarithm of centroid size, was highly significant for the skull (mandible Wilks' lambda=0.2709, $F=6.637$, $p<0.001$; cranium Wilks' lambda=0.0632, $F=30.92$, $p<0.001$). When looking at the allometric shape vectors obtained with the centroid size, we found that size explains 18.99% and 25.58% of the variation in the whole mandibular and cranial data sets respectively (S2A and S3A).

Morphological differences occur among the mandibles of the five species of *Dasypus* (Fig. 3A). The first two principal components (24.73 % and 16.48% of total shape variation)

198 weakly discriminates *D. pilosus* (negative values) from *D. kappleri* (positive values) while all
199 specimens of *D. novemcinctus*, *D. hybridus*, and *D. septemcinctus* sit in the middle of the graph.
200 These axes separate mandibles having a slender horizontal ramus with an elongated anterior part
201 (located in front of the tooth row) and a short ascending ramus with a short coronoid process
202 anteriorly positioned and vertically oriented from mandibles showing a high horizontal ramus
203 with a short anterior part and a long ascending ramus with an elongated and distally oriented
204 coronoid process. Mandibles of different size are poorly discriminated along the first principal
205 component (Fig. 3B). Once the effect of allometry is removed (S4), no clear morphological
206 differentiation is visible along PCres1. All taxa but *D. pilosus* lay in the positive values of
207 PCres2 therefore the variation in this component is mostly restricted to this latter species.
208 The interspecific differences in the cranium of *Dasypus* are apparent in the morphospace
209 defined by the first two principal components. Except for *D. hybridus* and *D. septemcinctus*, all
210 species are well discriminated in the morphospace defined by the two first principal components
211 (Fig. 4A), which explain 28,4% and 14,6% of the variance respectively. The first principal
212 component unequivocally discriminates *D. hybridus* and *D. septemcinctus* from other species,
213 and negatively correlates with a shortened rostrum and enlarged basicranium and braincase (Fig.
214 4A). *D. pilosus* individuals are well discriminated on the second principal component. On PC2
215 (Fig. 4A), the crania of *D. pilosus* appear narrower with a long snout and smaller braincase
216 (positive values) whereas the crania of *D. novemcinctus*, *D. kappleri*, *D. hybridus*, and *D.*
217 *septemcinctus* are wider with a shorter snout and relatively small braincase (negative values). A
218 regression of the first principal component on the logarithm of the centroid size (Fig. 4B) clearly
219 shows that the five species show different size ranges. The biggest crania are long and display
220 longer and wider snout; whereas the smallest crania are short and wide posteriorly and

221 characterized by a short snout. *D. pilosus* clearly remains an outlier once the size effect is
222 removed (S5), while the other species appear less differentiated in the cranium morphospace.
223 The specific differentiation was checked by performing a discriminant analysis and using a
224 classification phase. The classification methods recovered 100% correct classification of
225 specimens.
226 We also performed the same analyses this time including juvenile specimens (S6) but
227 excluding *D. pilosus* since it represents a clear outlier in the morphospace. All juvenile
228 specimens of *D. novemcintus* tend to congregate in the negative values of the PC1 and then
229 appear more similar in shape to *D. septemcinctus* and *D. hybridus* than the adults. All juveniles
230 of *D. novemcinctus* and *D. septemcinctus* are located in more negative values of PC1 and more
231 positive values of PC2 relative to the adult individuals of their own species. Such a distribution
232 in the morphospace defined by PC1-2 suggests similar ontogenetic trajectories for the two
233 species.
234
235 ***Intraspecific variation of skull shape in nine-banded armadillos***
236 In specimens for which sex was available (22 females and 32 males for the mandible; 19 females
237 and 34 males for the cranium), a MANOVA shows that there is no sexual dimorphism present in
238 the cranial data (Wilks' lambda=0.2429, F=1.514, p=0.182), so sex is unlikely to be responsible
239 for the variation observed in the cranium of *D. novemcinctus*, while it might partly for the
240 mandible (Wilks' lambda=0.2292, F=2.579, p=0.0110). A multivariate regression of the shape
241 component on size was highly significant (mandible, Wilks' lambda=0.3468, F=3.454, $p < 0.001$;
242 cranium, Wilks' lambda=0.1447, F=8.446, $p < 0.001$). When looking at the allometric shape
243 vectors obtained with the centroid size (S2B and S3B), we found that size explains 14.14% and

244 14.32% of the variation in the whole mandibular and cranial data sets respectively. Shape data
245 corrected for allometry are presented in S7 and S8.
246 A weak intraspecific differentiation (per country) is noticeable on the mandibular
247 morphology (mandible, Wilks' lambda=0.0001404, F=1.523, p <0.001; Fig. 5A). The first
248 principal component (9.87% of total shape variation) weakly discriminates specimens from
249 Brazil, Bolivia, Paraguay, Uruguay (positive values) from other specimens (negative values).
250 This axis separates mandibles characterized by robust and short horizontal ramus and long
251 ascending ramus with a high coronoid, low condylar, and poorly individualized angular
252 processes from mandibles with slender and elongated horizontal ramus and short ascending
253 ramus with low coronoid, high condylar, and well individualized angular processes (Fig. 5A). In
254 terms of shape variation, PC2 (4.745% of total shape variation) separates mandibles that show
255 elongated anterior part of the horizontal ramus, short tooth row, high and distally oriented
256 coronoid process from mandibles having reduced anterior part of the horizontal ramus, an
257 elongated tooth row, and low coronoid process. We observed even less differentiation with shape
258 data corrected for allometry (S7), which indicates that some specimens differ significantly in
259 size. This is confirmed by a regression of the first principal component on the logarithm of the
260 centroid size (Fig. 5B) that shows that the specimens from Brazil, Uruguay, Paraguay, Bolivia,
261 Peru, Ecuador, Costa Rica, and Colombia are usually smaller.
262 A MANOVA was also used to explore if the cranial variation matches the geographical
263 distributions of *D. novemcinctus* (Wilks' lambda=2.97×10^{-6}, F=2.157, p <0.001). When looking
264 at the cranial morphological variation according to geographic origin (*i.e.*, countries) (Fig. 6),
265 several trends can be observed. PC1, accounting for 22.7% variation, demonstrates a change in
266 how domed the dorsal surface of the skull is and positively correlates with an increase in snout

length, a decrease in braincase size, jugals more extended dorsoventrally, and shorter pterygoid processes (Fig. 6A). Specific clusters are recognizable on the first principal component with specimens from Brazil, Paraguay, Venezuela (USNM 406700 from Clarines area, North), Ecuador (BMNH-14-4-25-86 from Gualaquiza, South East), Colombia (AMNH 136252 from Villavicencio area, Centre), Peru, Bolivia, Paraguay, and Uruguay that congregate in the negative values whereas all other specimens lay in the positive values. PC2 is responsible for 8.6% of the variance, and describes variation in the size of the posterior part of the rostrum; it also displays variation in length of the posterior part of the palate with an anterior border of the palatine that is well behind the posterior end of the tooth row in positive values. This axis mainly separates specimens from USA, Mexico, Belize, Honduras, Guatemala, and Nicaragua (negative values) from other specimens (positive values). We observed less specific differentiation with shape data corrected for allometry (S8), which shows that the different geographical subgroups differ significantly in size. This is confirmed by a regression of the first principal component to the logarithm of the centroid size (Fig. 7).

A Linear Discriminant Analysis (LDA) of shape coordinates was performed in order to take into account the entire morphological variation (*i.e.*, 35 first PCs that represent 90.6% of the variance) and to maximize discrimination among specimens belonging to different countries. Only countries for which we had several specimens could be considered here. Three main regional groups were clearly recovered by the analysis (Fig. 8A): a Northern morphotype, a Southern morphotype, and a group circumscribed to the Guiana Shield (GS). The first group from North and Central America includes specimens from the US, Mexico, Guatemala, and Belize. The South American group gathers specimens from Brazil, Uruguay, Bolivia, Peru, Colombia, and Venezuela. Finally, specimens from French Guiana, Suriname, and Guyana

290 congregate in a last distinctive group. Some specimens from Colombia, Venezuela, and Ecuador
291 do not gather with any of those groups and sit in the middle of the graph defined by the first two
292 discriminant axes; these specimens are however well discriminated on the third and fourth
293 discriminant axes (Fig. 8B) and might constitute a fourth individualized regional group among
294 *D. novemcinctus*, called hereafter the Central morphotype.
295 The discriminant model used to separate the regional groups was checked using a
296 classification phase and then used on under-sampled countries (*i.e.*, when n=1) to assess their
297 affiliation to one of the four abovementioned groups. This classification showed 95% correct
298 classification of specimens (S9). Most regional misclassifications were with specimens coming
299 from the limit of the distribution range of the groups. Two Brazilian specimens from Amapa are
300 put together with the Guianan specimens (S9) and confirmed previous results from the PCA
301 where these two specimens clearly depart from the rest of the Brazilian specimens (Fig. 6A).
302 Three specimens from Venezuela (USNM 406700 from Clarines area, North), Ecuador (BMNH-
303 14-4-25-86 from Gualaquiza, South East), and Colombia (AMNH 136252 from Villavicencio
304 area, Centre) were *a posteriori* classified as close to the Southern morphotype. All these
305 specimens were collected East of the Andes (Fig. 9) and grouped with Brazilian specimens in the
306 PCA analyses. Concerning the countries for which only one specimen was available, the
307 classification analyses gave congruent results with the grouping proposed by the principal
308 component analysis: specimens from Paraguay and Peru were classified as being part of the
309 Southern morphotype while specimens from Nicaragua, Honduras, and Costa Rica were
310 classified as grouping with the Northern morphotype (S9). Using a reduced set of landmarks, the
311 specimen from Panama was attributed to the Central morphotype. When performing these
312 classification methods using the four groups as factors (*i.e.*, Northern, Central, Southern, and

313 Guianan morphotypes; see S10), instead of countries, we retrieved 100% correct classification of
314 specimens.
315 We performed very similar analyses (PCA and LDA, see S11) using linear cranial
316 measurements traditionally used in systematic studies. In all cases, these analyses failed to
317 retrieve a clear-cut discrimination between the four groups defined above.
318

319 ## Discussion

320 ### *Morphological variation of skull among* Dasypus *species*

321 Skull ratios are commonly used to compare *Dasypus* species, especially the length of the palate
322 to length of skull (PL/CNL) and length of rostrum to length of skull (RL adj./CNL) (Wetzel,
323 1985). Three subgenera are commonly recognized on this basis: *Cryptophractus* (including *D.*
324 *pilosus*), *Hyperoambon* (including *D. kappleri*), and *Dasypus* (including all remaining species)
325 (Wetzel & Mondolfi, 1979). Our results are largely consistent with findings from previous
326 studies regarding existing differences between *Dasypus* species. Allometry substantially explains
327 cranial differences, with the exception of *D. pilosus* that does not follow the main dasypodine
328 allometric trend (Figs. 3 and 4). The hairy long-nosed armadillo clearly departs from the other
329 four *Dasypus* species in being mainly characterized by a lengthening of the snout and mandible
330 and a small development of the braincase and basicranium. All these characteristics were linked
331 to their unique diet, which might predominantly include ants and termites (Castro et al., 2015).
332 Considering these distinctive morphological features and a specific structure of its osteoderms,
333 Castro et al. (2015) recently proposed to include *D. pilosus* in a different genus, i.e.
334 *Cryptophractus*. However, recent molecular results (Gibb et al., 2016) did not support such a
335 taxonomic reassessment and argued for the conservation of the hairy long-nosed armadillo in the

genus *Dasypus*. *D. pilosus* thus likely represents a case of rapid acquisition (*i.e.*, 2.8 Ma as estimated by Gibb et al., 2016) of distinctive morphological traits in line with the shift to a divergent behaviour and ecology.

Both molecular and morphological data suggested that *D. kappleri* is broadly separated from the other *Dasypus* species (Wetzel & Mondolfi, 1979; Gibb et al., 2016). Mitogenomic data clearly identified *D. kappleri* as the sister group to all other *Dasypus* species from which it diverged more than 12 million years ago (Gibb et al., 2016) and suggested to place it in the distinct genus *Hyperoambon*, as originally proposed by Wetzel and Mondolfi (1979). We retrieved a significant morphological differentiation with all the specimens of *D. kappleri* congregating in the morphospace and being much larger than the other species. However, the cranial morphology of *D. kappleri* still remains very close to that of *D. novemcinctus* when compared to that of *D. septemcinctus*, *D. hybridus*, and *D. pilosus* (Fig. 4). Recently, Feijo and Cordeiro-Estrela (2016) proposed to recognize three species within *D. kappleri* based on morphological differences of the skull and carapace: *D. kappleri* distributed in the Guiana shield; *D. pastasae* occurring from the eastern Andes of Peru, Ecuador, Colombia, and Venezuela south of the Orinoco River into the western Brazilian Amazon; and finally *D. beniensis* that occurs in the lowlands of the Amazonian Brazil and Bolivia to the south of the Madre de Dios, Madeira, and lower Amazon rivers. We only had access to a limited number of specimens but did not retrieve such a clear geographical segregation in shape (S12A), while we observed a mild differentiation in size with the Guianan *D. kappleri* being usually bigger (S12B).

Wetzel and Mondolfi (1979:47) placed *D. septemcinctus*, *D. hybridus*, and *D. sabanicola* in the same subgenus together with *D. novemcinctus*. We observed that *D. hybridus* and *D. septemcinctus* group together in the morphospace, but are largely separated from *D.*

359 *novemcinctus*. These two species are usually distinguished by external features, *D. hybridus*
360 showing shorter ears and a longer tail than *D. septemcinctus* (Hamlett, 1939; Wetzel &
361 Mondolfi, 1979). Our morphometrical results showed that *D. hybridus* and *D. septemcinctus*
362 display very similar cranial and mandibular morphologies; they also display several cranial
363 characteristics in common with juvenile specimens of *D. novemcinctus*. Such morphological
364 similarities echo recent molecular findings (Gibb et al., 2016) that showed that mitogenomic
365 sequences of *D. hybridus* are almost identical to those of an Argentinian *D. septemcinctus*
366 (99.3% identity). The two species were considered as valid based on cranial and body
367 measurements (Hamlett, 1939; Wetzel, 1985) despite the fact that they display many external
368 resemblances and have very close geographical distribution. A recent study of their internal
369 cranial sinuses also failed to provide diagnostic characters for the distinction of these two genera
370 (Billet et al., unpublished data). Our samples were very limited for both *D. hybridus* (n=4) and
371 *D. septemcinctus* (n=3), but additional samplings will undoubtly help to define the systematic
372 status of the two species.
373 We did not have access to the two most recently recognized *Dasypus* species: the
374 Yunga's lesser long-nosed armadillo *D. mazzai* (Yepes, 1933), and the northern long-nosed
375 armadillo *D. sabanicola* (Mondolfi, 1967). The validity of the former was and is still hotly
376 debated (Wetzel & Mondolfi, 1979; Vizcaíno, 1995; Gardner, 2008; Feijo & Cordeiro-Estrela,
377 2014), while the specific status of the latter also remains controversial (Wetzel & Mondolfi,
378 1979; Wetzel, 1985). Cranial morphometric data might provide insightful arguments to discuss
379 the systematic status of the two species.
380
381 ***Morphological systematics and skull shape variation in* Dasypus**

Relative skull shape has previously been examined for systematics purposes in the genus *Dasypus* but never with a focus on patterns of intraspecific variation. Hamlett (1939) casted doubt on the possibility to identify different subgroups within *D. novemcinctus*, while early workers had already recognized several, either at a specific or at a subspecific level. Peters (1864) described *Dasypus fenestratus* from Costa Rica based on the position of the small and numerous major palatine foramina, some of which are connected to the incisive foramina through a groove, between (not in front of) the anterior teeth, its medially shorter palatine bones, the position of the palatine suture posterior to the end of the tooth row, the position of the lacrimal foramen closer to the orbital rim, as well as one character on the extent of the pelvic shield of the carapace. Gray (1873) tentatively recognized as many as seven species of nine-banded armadillos in South and Central Americas, among which five of them were new: *Tatusia* (=*Dasypus*) *granadiana*, *T. leptorhynchus*, *T. brevirostris*, *T. leptocephala*, and *T. boliviensis*. He also followed Peters (1864) and recognized *T. mexicana* (a variety of *D. novemcinctus* in Peters 1864), but decided to ignore *T. fenestratus*. Both Peters (1864) and Gray (1873) used a very small number of specimens and Gray (1873) distinguished all these species based mainly on the morphology of the lacrimal bones and minute morphological variation of the head scutes. Allen (1911) later considered *D. fenestratus* and *D. mexicanus* as synonym taxa of subspecific level (*D. novemcinctus fenestratus* Peters). He also described *D. novemcinctus hoplites* from Grenada, a subspecies that he considered to be distinctly characterized by a shorter tooth row due to the absence of the last tooth locus.

From the inspection of a series of specimens from Panama, Costa Rica, and Yucatan, Allen (1911) also distinguished a Central American morphotype. Compared to Brazilian specimens, Allen's Central American armadillo is characterized by short palatine bones that do

not reach the level of the most posterior teeth, an obvious inflation of the maxillary region located in front of the lacrimal bone, as well as a lateral margin of the skull that is largely convex at the level of the second or third tooth in ventral view. Based on size differences, Hagmann (1908) described the subspecies *D. n. mexianae*, which he thought was restricted to a small area close to the mouth of the Amazon River. Lönnberg (1913) defined *D. n. aequatorialis* from Ecuador, which McBee and Baker (1982) later proposed to consider as a probable synonym to *T. granadiana* Gray 1873. His comparisons were based on morphological characteristics of the carapace, *D. n. aequatorialis* showing differences of the occipital portion of the frontal shield as well as different proportions of the scales of the shoulder and pelvic shields. Later on, Russel (1953) proposed to recognize two subspecies in Mexico: *D. n. davisi* in north-western part of Mexico and *D. n. mexicanus* present in most of the country. Even if it is close morphologically to *D. n. mexicanus*, *D. n. davisi* is much smaller in size and displays a few distinctive features such as small maxillary teeth, a narrow mandible with an angular process posteriorly projected, and differences in suture closure patterns and shape with for instance the parietal-frontal sutures that lies well behind the posterior process of the zygomatic arch (Russell, 1953). Most of these early descriptions, be them at a specific and subspecific level, were based on subtle morphological differences and no proper quantification of the skull variation was undertaken up to now.

Our statistical analysis of the skull shape demonstrated that *D. novemcinctus* exhibits a significant level of intraspecific variation, with several clearly identified groups within the nine-banded armadillo. While male nine-banded armadillos tend to be slightly larger than females (McBee & Baker, 1982), our multivariate analyses first suggest the absence of sexual dimorphism in the cranium and a slight sexual dimorphism in the mandible. We also show that allometry is likely to explain a substantial part of the observed morphological variation,

428 including geographically. This echoes early findings by Wetzel and Mondolfi (1979) who
429 already pointed out size gradients between different populations of *D. novemcinctus*. Our
430 morphometric analysis successfully retrieved such a geographical differentiation, both in size
431 and shape. Interestingly, our geometric morphometric analyses permitted to define four discrete
432 phenotypic units. These units display very different cranial characters and occupy very distinct
433 geographical distributions, which are in essence allopatric.
434 Specimens from Brazil, Uruguay, Paraguay, Bolivia, Peru, and from regions of Ecuador,
435 Colombia, and Venezuela located east of the Andes make up most of one group and show a very
436 stable pattern of variation (Fig. 9); they are on average smaller than the three remaining groups.
437 Skulls of this Southern morphotype are clearly distinct by showing smaller and flatter skulls with
438 short frontal sinuses, a narrow snout with short premaxillar bones, a narrow interorbital width, a
439 long and slender jugal part of the zygomatic arch, longer pterygoid processes, and a basicranium
440 aligned with the palate in lateral view (Fig. 6). We found no sign of morphological
441 differentiation of specimens from the mouth of the Amazon River, as implied by the proposed
442 recognition of the subspecies *D. n. mexianae* (Hagmann, 1908). The area covered by the
443 specimens attributed to this morphological unit fully encompasses that of the Amazon basin and
444 seemed to be delimitated by the Andes on the western side. As a matter of fact, the single
445 Ecuadorian specimen coming from the eastern side of the Andes appeared to be distinct from
446 most other Ecuadorian specimens, but morphologically close to Brazilian and Bolivian
447 specimens. The same holds true for the Peruvian, Colombian, and Venezuelan specimens
448 collected east of the Andes. The distribution of this group is reminiscent of that of the subspecies
449 *D. novemcinctus novemcinctus* Linnaeus, except for the Guiana Shield area (Gardner, 2008). It
450 also recalls a similar lineage molecularly identified (Arteaga et al., unpublished data) and the

Southern morphotype evidenced by the analysis of paranasal spaces (Billet et al., unpublished data). Unfortunately the type specimen of *D. novemcinctus*; which is supposedly housed in the Swedish Museum of Natural History in Stockholm (Lönnberg, 1913), could not be included in our analyses. The type locality of *Dasypus novemcinctus* Linnaeus is "America meridionali" and is generally thought to be from the eastern coast of Brazil (Allen, 1911).

The next differentiated group is represented by individuals originating from the Guiana shield region including French Guiana, Guyana, Suriname, and Amapa in Brazil (Fig. 9). All the specimens belonging to this Guianan morphotype display large dome-shaped skulls that share distinctive morphological features including long frontal sinuses, a wide snout with long premaxillar bones, a large interorbital width, large lacrimal bones, a short and massive jugal part of the zygomatic arch, an anterior border of the palatine located well behind the posterior end of the tooth row, shorter pterygoid processes, and a basicranium situated above the palatal plane (Fig. 6). Studies of paranasal sinuses agree with the distinctness of this group and show that the dome-shaped frontal region of Guianan nine-banded armadillos is occupied by a characteristically inflated pair of frontal sinuses that extend posteriorly to the fronto-parietal suture (Billet al., unpublished data). No subspecies has ever been recognized or proposed in this part of South America, and such a clear-cut morphological divergence of Guianan specimens of *D. novemcinctus* is here proposed for the first time. These morphometric findings corroborate recent molecular studies, which showed that specimens from French Guiana are very distant from the US populations (Huchon et al., 1999) and represent a distinct branch in the dasypodine mitogenomic tree (Gibb et al., 2016; Arteaga et al., submitted).

The distribution of the third recognized morphological group is more limited. It is distributed from the western Andes of Ecuador, Colombia, Panama, and Venezuela to Costa Rica

(Fig. 9). This Central morphotype is characterized by high and short skulls having moderately developed frontal sinuses, long premaxillar bones, a narrow interorbital width (larger than Southern specimens but narrower than Guianan specimens), a massive anterior part of the zygomatic arch that is much larger than the posterior part, a short and high jugal part of the zygomatic arch that is largely convex ventrally, an anterior border of the palatine located well behind the posterior end of the tooth row, shorter pterygoid processes, and a basicranium well above the palatal plan (Fig. 6). This distribution roughly corresponds to the combined ranges of two previously described subspecies: *D. n. fenestratus* (Peters, 1864) and *D. n. aequatorialis* (Lönnberg, 1913). These close morphological resemblances suggest that these subspecies might be synonym taxa. However, we could not fully test this hypothesis since we had only access to one specimen from West of the Andes in Peru, Ecuador and southern Bolivia. Studies on the paranasal spaces (Billet et al., unpublished data) failed to recognize such a group, and instead gathered some specimens from these regions with specimens from North and Central America, while others (from the western parts of Colombia, Venezuela and from Panama) were judged impossible to be confidently referred to a given frontal sinus morphotype. In contrast, molecular studies recovered a lineage similar to the group recognized here distributing from the Northern Andes and Central America but expanding to western Mexico (Arteaga et al., unpublished data).

The last distinct morphotype occurs from Nicaragua to the Southern part of the US (Fig. 9). The range of this Northern morphotype spans the proposed distribution areas of the subspecies *D. n. mexicanus* and *D. n davisi*, as well as the northernmost part of the distribution range of *D. n. fenestratus*. All the skulls from this area display moderately developed frontal sinuses convergent toward the midline, long premaxillar bones, a narrow interorbital width (larger than Southern specimens but narrower than Guianan specimens), a long and slender jugal

497 part of the zygomatic arch that is largely convex ventrally, an anterior border of the palatine
498 located at the level of the posterior end of the tooth row, shorter pterygoid processes, and a
499 basicranium slightly above the palatal plan (Fig. 6). Contrary to Russel (1953), we did not find
500 major morphological cranial differences between north-western and eastern Mexican
501 populations. Our results thus cast doubts on the validity of the subspecies *D. n. davisi*. The
502 morphological homogeneity in this group is also at odds with the presence of two mitochondrial
503 lineages in Mexico (Arteaga et al., 2012, submitted) but is coherent with the presence of nuclear
504 gene flow between them (Arteaga et al., 2011). Within this Northern group, the invasive US
505 armadillo population derived from two geographical sources: one from Mexico and one from
506 south-central Florida where captive animals were presumably released (Loughry & Mcdonough,
507 2013). For a long time, the exact origin of the Floridian introduced population remained
508 uncertain. All the US specimens used in our analyses were proved to belong to the same
509 Northern morphotype. Echoing the results obtained on six microsatellite loci described by
510 Loughry et al. (2009), we interpret our findings as indicative of a close relationship between the
511 two US populations. The recognition of this Northern unit with individuals ranging from Central
512 to Northern America is also in agreement with their distinctive pattern of paranasal sinuses
513 (Billet et al., unpublished data).

514 The newly recognized subgroups within *D. novemcinctus* prompt questions about the role
515 of ecological factors likely to have influenced their morphological differentiation. Morphological
516 variation in skull morphology as a result of ecological factors has been studied in a number of
517 species over recent years (*e.g.*, Caumul and Polly, 2005; Wroe and Milne, 2007; Hautier et al.,
518 2012). Factors such as temperature, diet and competition may cause phenotypic variation and are
519 likely to explain some morphological differences between the identified groups. These ecological

520 factors vary in relation to geography, and differences in geographical distribution can drive
521 selection for different phenotypes, which may eventually lead to distinctive populations or even
522 new species. Since the four *D. novemcinctus* subgroups are not sympatric in most of their
523 respective natural range, we can hypothesize that environment and/or genetic drift, but not
524 competition, may be responsible for some of the observed intraspecific variation. The Northern
525 Andes constitute a clear geographical barrier, which limited contacts between Northern/Central
526 and Southern populations, and thus has likely played a major role in shaping the morphological
527 differentiation of the long-nosed armadillos. This biogeographical barrier seems to have played a
528 significant role in xenarthrans since it also marks the separation between the two living species
529 of tamanduas with *Tamandua mexicana* in the north and *T. tetradactyla* in the south (Superina,
530 Miranda & Abba, 2010), also within naked-tailed armadillos with *Cabassous centralis* in the
531 north and *C. unicinctus* in the south (Abba & Superina, 2010).
532 The geographical distribution of the divergent populations of *D. novemcinctus* recalls the
533 pattern of morphological differentiation recently proposed for the greater long-nosed armadillo
534 (*D. kappleri*), especially for the Guianan specimens (Feijo & Cordeiro-Estrela, 2016). However,
535 in the nine-banded armadillo, we did not find a clear morphological differentiation within the
536 Amazonian basin as defined on the opposite banks of the Madeira-Madre de Dios rivers (Feijo &
537 Cordeiro-Estrela, 2016), which separate *D. pastasae* from *D. beniensis*. Given the extent of
538 morphological variation reported within *D. kappleri*, Feijo and Cordeiro-Estrela (2016)
539 interpreted their findings as indicative of the fact that this species complex diverged earlier than
540 other *Dasypus* species, which would allow them to accumulate more differences. Such a
541 hypothesis seems difficult to conceive in view of the substantial morphological variation
542 observed among different populations of *D. novemcinctus*, which have diverged more recently

(3.7 Ma, Gibb et al., 2016). Feijo and Cordeiro-Estrela (2016) also proposed that such cumulative differences may result from strong environmental selective pressures. The newly discovered morphological diversity within *D. kappleri* and *D. novemcinctus* is likely to represent parallel cases of allopatric differentiation in response to diverging environmental pressures. In both cases, only the future collecting of large-scale genomic nuclear data will allow testing these taxonomic proposals based on morphological data.

Conclusions

Intraspecific variations can be the result of adaptation to varying local environmental conditions. We showed that morphometrical comparisons enable detection of previously overlooked morphotypes and yield new insights into factors likely to explain differences between populations inhabiting different areas. Our study of the intraspecific variation of the skull in *D. novemcinctus* evidences clear links to the geographic distribution and allows a revision of past taxonomic delimitations. Based on the cranial differences observed, we consider that *D. novemcinctus* should be regarded either as a polytypic species (with three to four subspecies) or as a complex of several species. In particular, a new unit of nine-banded armadillos from the Guiana Shield could be detected, which is in agreement with most recent investigations of molecular data and internal anatomy (Arteaga et al., unpublished data; Billet et al., unpublished data). The discovery of divergent populations within *D. novemcinctus* has implications for conservation of the species. In some areas, human activities have led to habitat degradation and fragmentation (Zimbres et al., 2013) or even to habitat loss. These divergent populations may be under threat and may require conservation measures, or at least a close re-examination of their conservation status. If we were to consider them as separate management unit and not as a single

566 species with a large distribution, the threat of endangerment to *D. novemcinctus* would need re-
567 evaluation since it is currently classified globally as 'Least Concern' by the IUCN (Loughry,
568 McDonough & Abba, 2014). In addition, our results demonstrate that specimens of *D.*
569 *novemcinctus* should be chosen with caution when making anatomical comparisons or
570 performing cladistic analyses (*e.g.*, Castro et al., 2015); their geographical distribution should be
571 at least specified in all cases. This morphological investigation needs to be extended to the other
572 parts of the body, the carapace in particular. The cranial differences detected among the defined
573 groups might be linked to previously detected differences in the number and shape of scutes on
574 the head shield (*e.g.*, Lönnberg, 1913). Geometric morphometric data holds out the possibility of
575 studying effectively covariation patterns between osteological parts and features of the carapace.
576 Given the quality of the cingulate fossil record, using geometric morphometric methods seems
577 equally conceivable on extinct forms and might also provide fruitful ways to interpret past
578 morphological diversity.
579

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The authors declare no competing interests.

Author Contributions

• Lionel Hautier conceived and designed the experiments, contributed materials, performed the experiments, analysed the data, wrote the paper.

• Guillaume Billet conceived and designed the experiments, contributed materials.

• Benoit de Thoisy contributed materials.

• Frédéric Delsuc conceived and designed the experiments, contributed materials.

• All authors read, discussed, corrected, and approved the final version of the paper.

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773
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775

776 Table legends

777 **Table 1.** Definitions of the landmarks used on the mandible.
778
779 **Table 2.** Definitions of the landmarks used on the cranium. Landmarks indicated with a star
780 were not used in the intraspecific comparisons.

Figure Legends

Figure 1. Landmarks digitized on the mandible and the skull. Dorsal (A), lateral (B), and ventral views of the cranium; medial (C) and lateral (D) views of the mandible.

Figure 2. Illustration of the skull linear measurements. In blue, traditional measurements used in Wetzel (1985). *Abbreviations*: LTC, length between the anterior tip of the nasal and the posteriormost point of the supraoccipital; LR, rostral length; IOB, interorbital breadth; ILFB, inter lacrimal foramina breadth; BB, distance between the left and right intersections between the frontal, parietal, and squamosal sutures; NB, nasal breadth; NL, nasal length; LCB, length between the anterior tip of the premaxillar and the condyles; TL, length of the tooth row; PB, palate breadth; BZP, distance between the infraorbital and the maxillary foramina; MB, inter-meatus breadth; OCB, breadth between the lateral border of the occipital condyle.

Figure 3. (**A**) Principal component analysis (PC1 *vs* PC2) and associate patterns of morphological transformation for the mandible of five *Dasypus* species. (**B**) Regression of the first principal component on the logarithm of the centroid size (R^2=0.23; p<0.001). *Symbols*: blue squares, *D. kappleri*; black crosses, *D. novemcinctus*; green triangles, *D. hybridus*; green diamonds, *D. septemcinctus*; red circles, *D. pilosus*.

Figure 4. (**A**) Principal component analysis (PC1 *vs* PC2) and associate patterns of morphological transformation for crania of five *Dasypus* species. (**B**) Regression of the first principal component on the logarithm of the centroid size (R^2=0.55; p<0.001). *Symbols*: blue

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805 diamonds, *D. septemcinctus*; red circles, *D. pilosus*.
806
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808 morphological transformation for mandibles of *Dasypus novemcinctus*. (**B**) Regression of the
809 first principal component on the logarithm of the centroid size (R^2=0,035; p=0.03). *Symbols*:
810 green diamonds, Bolivia; green triangle, Brazil (solid green triangles are for specimens from
811 Amapa); green circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars,
812 Venezuela; blue diamonds, Belize; blue "plus", Guatemala; blue bars, Honduras; Blue squares,
813 Mexico; blue crosses, Nicaragua; blue triangles, USA; blue circles, Costa Rica; black triangles,
814 Colombia; black crosses, Ecuador; black stars, Panama; orange squares, French Guiana; orange
815 crosses, Guyana; orange circles, Suriname.
816
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818 of morphological transformation for crania of *Dasypus novemcinctus*. *Symbols*: green diamonds,
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820 circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue
821 diamonds, Belize; blue "plus", Guatemala; blue bars, Honduras; Blue squares, Mexico; blue
822 crosses, Nicaragua; blue triangles, USA; blue circles, Costa Rica; black triangles, Colombia;
823 black crosses, Ecuador; orange squares, French Guiana; orange crosses, Guyana; orange circles,
824 Suriname.
825
826 **Figure 7.** Regression of the first cranial principal component (*Dasypus novemcinctus*) on the

827 logarithm of the centroid size (R^2=0.15; p<0.001). *Symbols*: green diamonds, Bolivia; green
828 triangle, Brazil (solid green triangles are for specimens from Amapa); green circles, Paraguay;
829 green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue
830 "plus", Guatemala; blue bars, Honduras; Blue squares, Mexico; blue crosses, Nicaragua; blue
831 triangles, USA; blue circles, Costa Rica; black triangles, Colombia; black crosses, Ecuador;
832 orange squares, French Guiana; orange crosses, Guyana; orange circles, Suriname.
833
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835 *Dasypus novemcinctus*. *Symbols*: green diamonds, Bolivia; green triangle, Brazil (solid green
836 triangles are for specimens from Amapa); green circles, Paraguay; green crosses, Peru; green
837 squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue "plus", Guatemala; blue
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839 triangles, Colombia; black circles, Costa Rica; black crosses, Ecuador; orange squares, French
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842 **Figure 9**. Summary map showing the geographical distribution of nine-banded armadillo
843 specimens investigated in this study and their attribution to one of the four main morphotypes
844 defined in this study: black, Central group; blue, Northern group; green, Southern group; orange,
845 Guianan group. Specimens lacking precise geographical information (other than country of
846 origin) are indicated with a square.

Supplemental Information

S1. List of measured specimens (used for linear measurements and/or geometric morphometric analyses). *Abbreviations:* MNHN, *Muséum national d'Histoire naturelle* in Paris (collections *Zoologie et Anatomie comparée, Mammifères et Oiseaux*); BMNH, Natural History Museum in London; NBC, Naturalis Biodiversity Center in Leiden; ROM, Royal Ontario Museum in Toronto; LSU, Louisiana State University in Bâton-Rouge; AMNH, American Museum of Natural History in New York; USNM, National Museum of Natural History in Washington; IEPA, *Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá* in Macapá; MHNG, *Muséum d'Histoire naturelle* in Geneva; KWATA, KWATA association; and PCDPC, Personal collection of Pierre Charles-Dominique.

S2. Regression of the common allometric shape vector (ASVc) on the logarithm of the centroid size for mandibles of five *Dasypus* species (A, R^2=0.50; $p<0.001$) and *D. novemcinctus* (B, R^2=0.34; $p<0.001$). Below, associate patterns of morphological transformation for mandibles with small (left) and large (right) centroid size. *Symbols*: same as in Figure 3 and 5.

S3. Regression of the common allometric shape vector (ASVc) on the logarithm of the centroid size for crania of five *Dasypus* species (A, R^2=0.72; $p<0.001$) and *D. novemcinctus* (B, R^2=0.48; $p<0.001$). Below, associate patterns of morphological transformation for crania with small (left) and large (right) centroid size. *Symbols*: same as in Figure 3 and 5.

S4. Principal component analyses with shape data corrected for allometry (PCres1 *vs* PCres 2)

and associate patterns of morphological transformation for mandible of five *Dasypus* species. *Symbols*: blue squares, *D. kappleri*; black crosses, *D. novemcinctus*; green triangles, *D. hybridus*; green diamonds, *D. septemcinctus*; red circles, *D. pilosus*.

S5. Principal component analyses with shape data corrected for allometry (PCres1 *vs* PCres 2) and associate patterns of morphological transformation for crania of five *Dasypus* species. *Symbols*: blue squares, *D. kappleri*; black crosses, *D. novemcinctus*; green triangles, *D. hybridus*; green diamonds, *D. septemcinctus*; red circles, *D. pilosus*.

S6. (**A**) Principal component analysis (PC1 *vs* PC2) and associate patterns of morphological transformation for crania of five *Dasypus* species, including juveniles (indicated with smaller symbols) and excluding *D. pilosus*. (**B**) Regression of the first principal component on the logarithm of the centroid size (R^2=0,63; p<0.001). *Symbols*: blue squares, *D. kappleri*; black crosses, *D. novemcinctus*; green triangles, *D. hybridus*; green diamonds, *D. septemcinctus*.

S7. Principal component analyses with shape data corrected for allometry (PCres1 *vs* PCres 2) and associate patterns of morphological transformation for mandibles of *Dasypus specimens*. *Symbols*: green diamonds, Bolivia; green triangle, Brazil (solid green triangles are for specimens from Amapa); green circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue “plus”, Guatemala; blue bars, Honduras; Blue squares, Mexico; blue crosses, Nicaragua; blue triangles, USA; blue circles, Costa Rica; black triangles, Colombia; black crosses, Ecuador; black stars, Panama; orange squares, French Guiana; orange crosses, Guyana; orange circles, Suriname.

S8. Principal component analyses with shape data corrected for allometry (PCres1 *vs* PCres 2) and associate patterns of morphological transformation for crania of *Dasypus specimens*. *Symbols*: green diamonds, Bolivia; green triangle, Brazil (solid green triangles are for specimens from Amapa); green circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue "plus", Guatemala; blue bars, Honduras; Blue squares, Mexico; blue crosses, Nicaragua; blue triangles, USA; blue circles, Costa Rica; black triangles, Colombia; black crosses, Ecuador; orange squares, French Guiana; orange crosses, Guyana; orange circles, Suriname.

S9. Results of *a posteriori* classifications for the discriminant analysis performed on the cranial shape coordinates of *Dasypus novemcinctus* using countries as factors. Specimens with a star (*) were integrated into the analyses as ungrouped cases.

S10. Results of *a posteriori* classifications for the discriminant analysis performed on the cranial shape coordinates of *Dasypus novemcinctus* using the four subgroups (*i.e*., Northern, Central, Southern, and Guianan morphotypes) as factors. Specimens with a star (*) were integrated into the analyses as ungrouped cases.

S11. (**A**) Principal component analysis (PC1 *vs* PC2) and associate patterns of morphological transformation for crania of *Dasypus kappleri*. (**B**) Regression of the first principal component on the logarithm of the centroid size (R^2=0.40; $p<0.001$). *Symbols*: green crosses, Peru; green bars, Venezuela; black triangles, Colombia; black crosses, Ecuador; orange squares, French

916 Guiana; orange crosses, Guyana; orange circles, Suriname.

Figure 1

Figure 1

Landmarks digitized on the mandible and the skull. Dorsal (A), lateral (B), and ventral views of the cranium; medial (C) and lateral (D) views of the mandible.

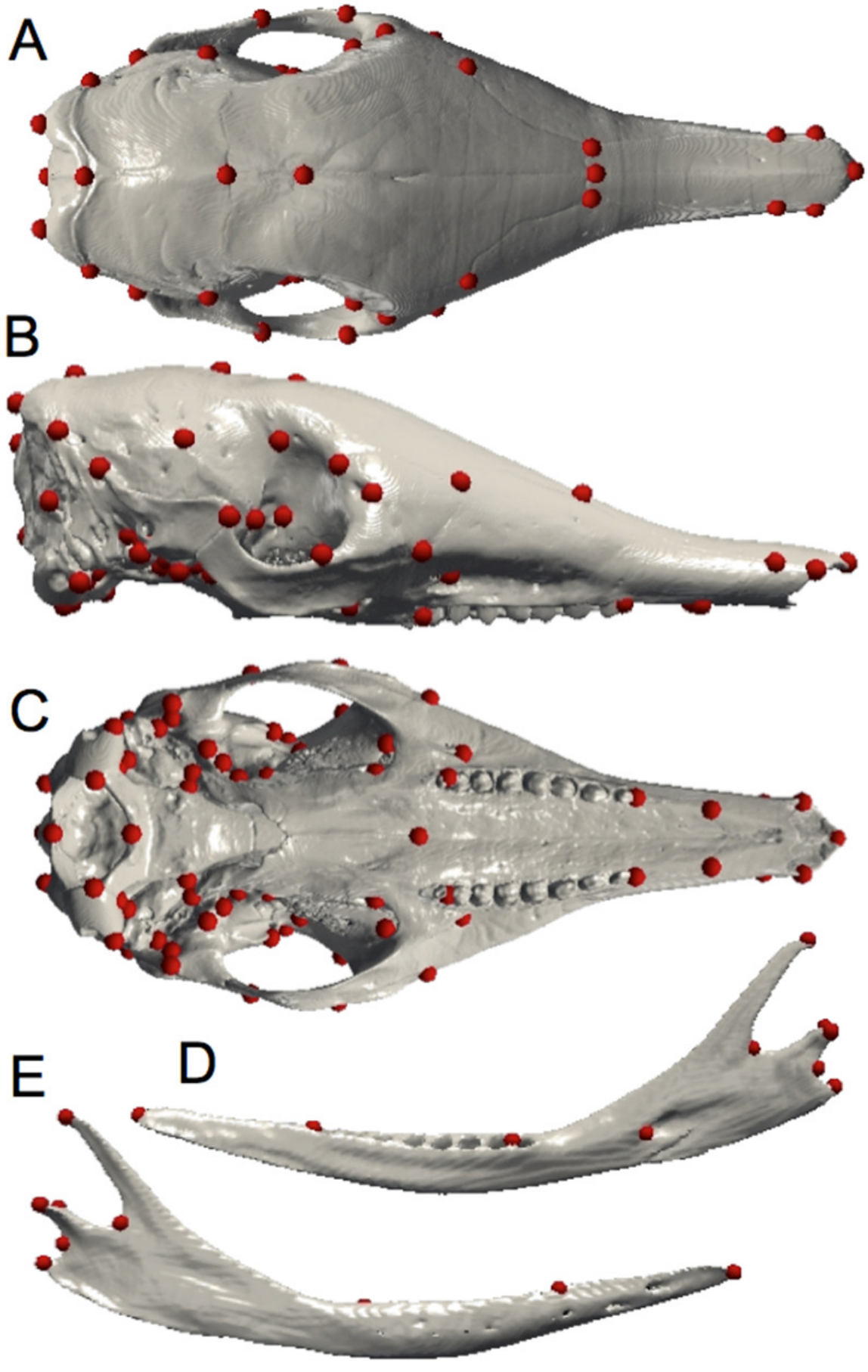
A
B
C
D
E

Figure 2

Figure 2

Illustration of the skull linear measurements. In blue, traditional measurements used in Wetzel (1985) . *Abbreviations*: LTC, length between the anterior tip of the nasal and the posteriormost point of the supraoccipital; LR, rostral length; IOB, interorbital breadth; ILFB, inter lacrimal foramina breadth; BB, distance between the left and right intersections between the frontal, parietal, and squamosal sutures; NB, nasal breadth; NL, nasal length; LCB, length between the anterior tip of the premaxillar and the condyles; TL, length of the tooth row; PB, palate breadth; BZP, distance between the infraorbital and the maxillary foramina; MB, inter-meatus breadth; OCB, breadth between the lateral border of the occipital condyle.

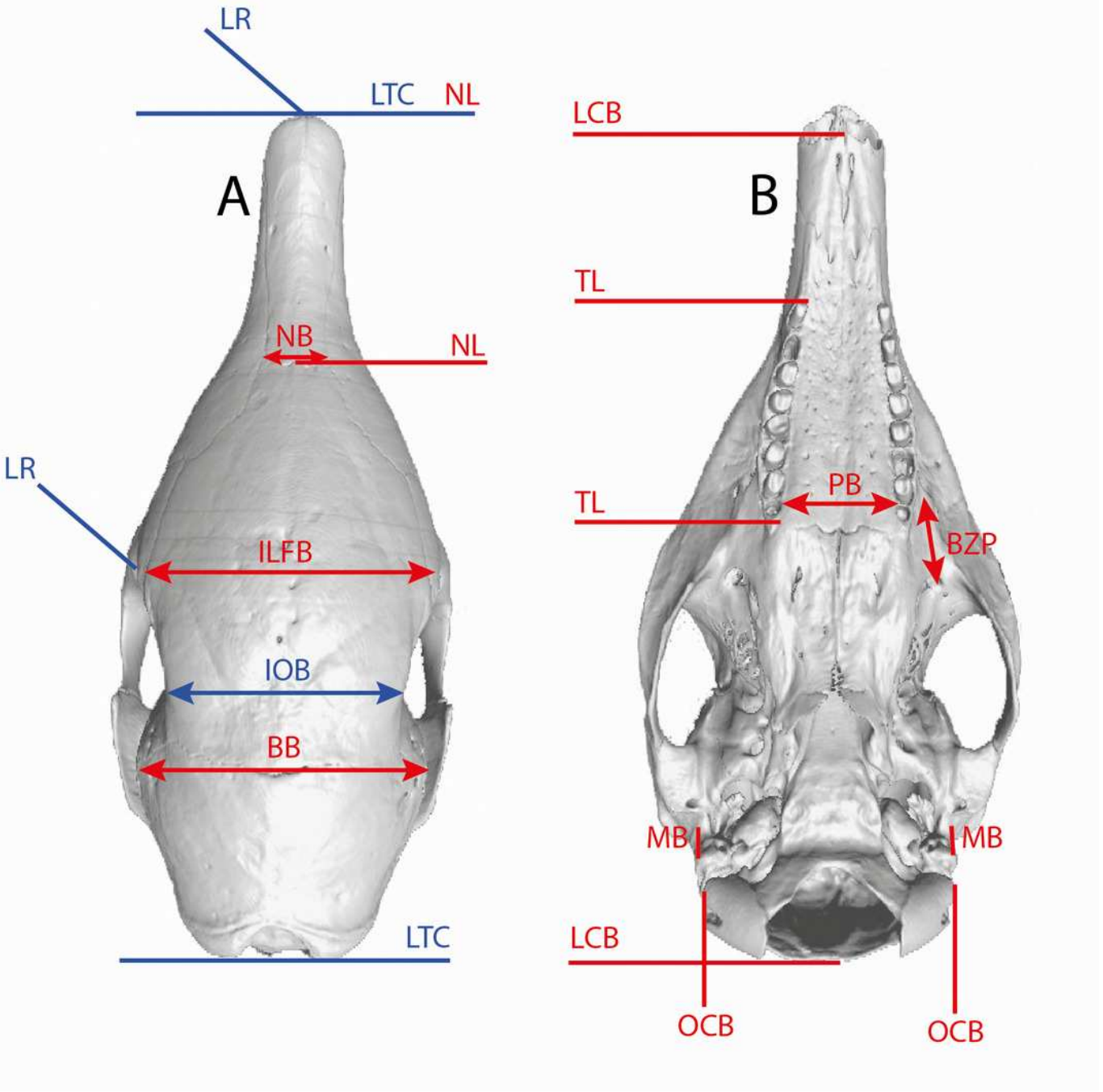
LR
LTC
NL
A
NB
NL
LR
ILFB
IOB
BB
LTC
LCB
B
TL
TL
PB
BZP
MB
MB
LCB
OCB
OCB

Figure 3

Figure 3

(**A**) Principal component analysis (PC1 *vs* PC2) and associate patterns of morphological transformation for the mandible of five *Dasypus* species. (**B**) Regression of the first principal component on the logarithm of the centroid size (R^2=0.23; p<0.001). *Symbols*: blue squares, *D. kappleri*; black crosses, *D. novemcinctus*; green triangles, *D. hybridus*; green diamonds, *D. septemcinctus*; red circles, *D. pilosus*.

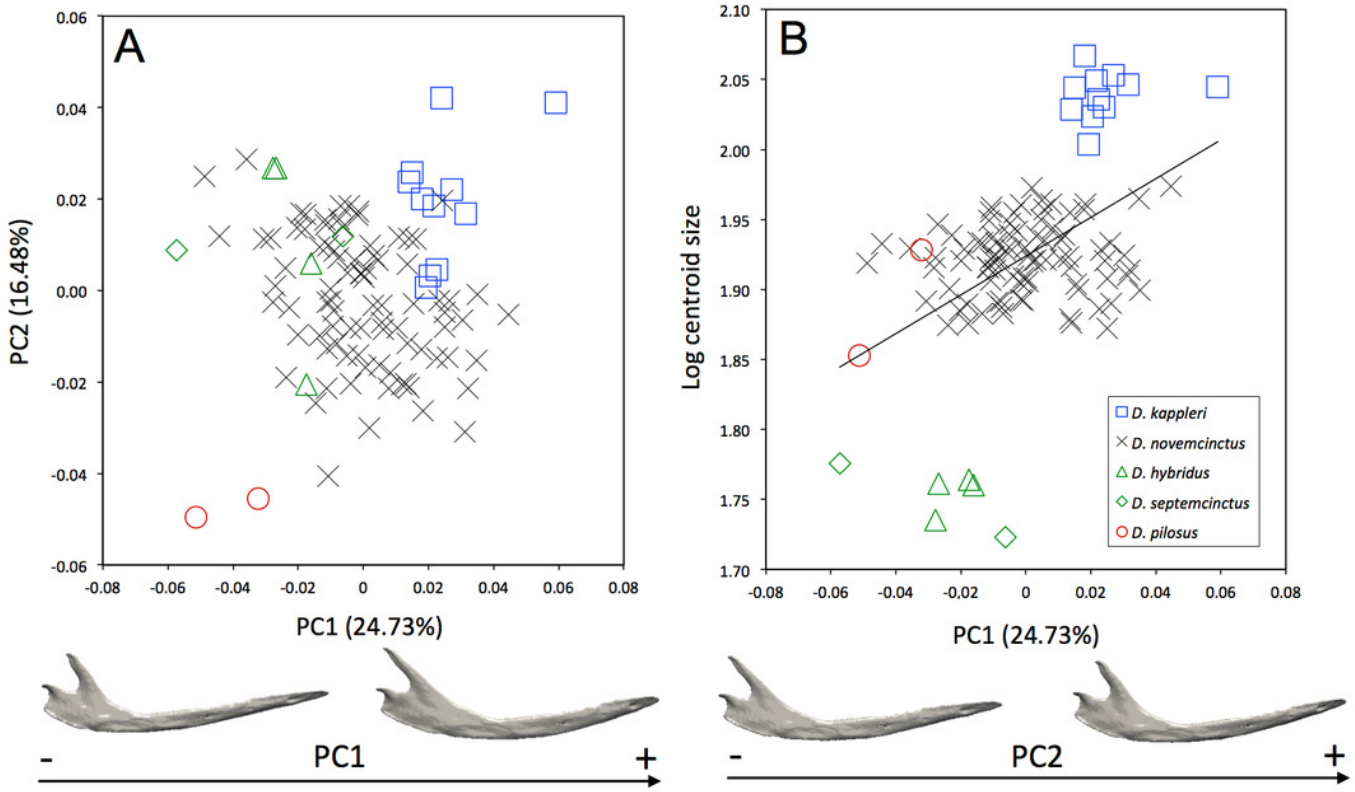

Figure 4

Figure 4

(**A**) Principal component analysis (PC1 *vs* PC2) and associate patterns of morphological transformation for crania of five *Dasypus* species. (**B**) Regression of the first principal component on the logarithm of the centroid size (R^2=0.55; p<0.001). *Symbols*: blue squares, *D. kappleri*; black crosses, *D. novemcinctus*; green triangles, *D. hybridus*; green diamonds, *D. septemcinctus*; red circles, *D. pilosus*.

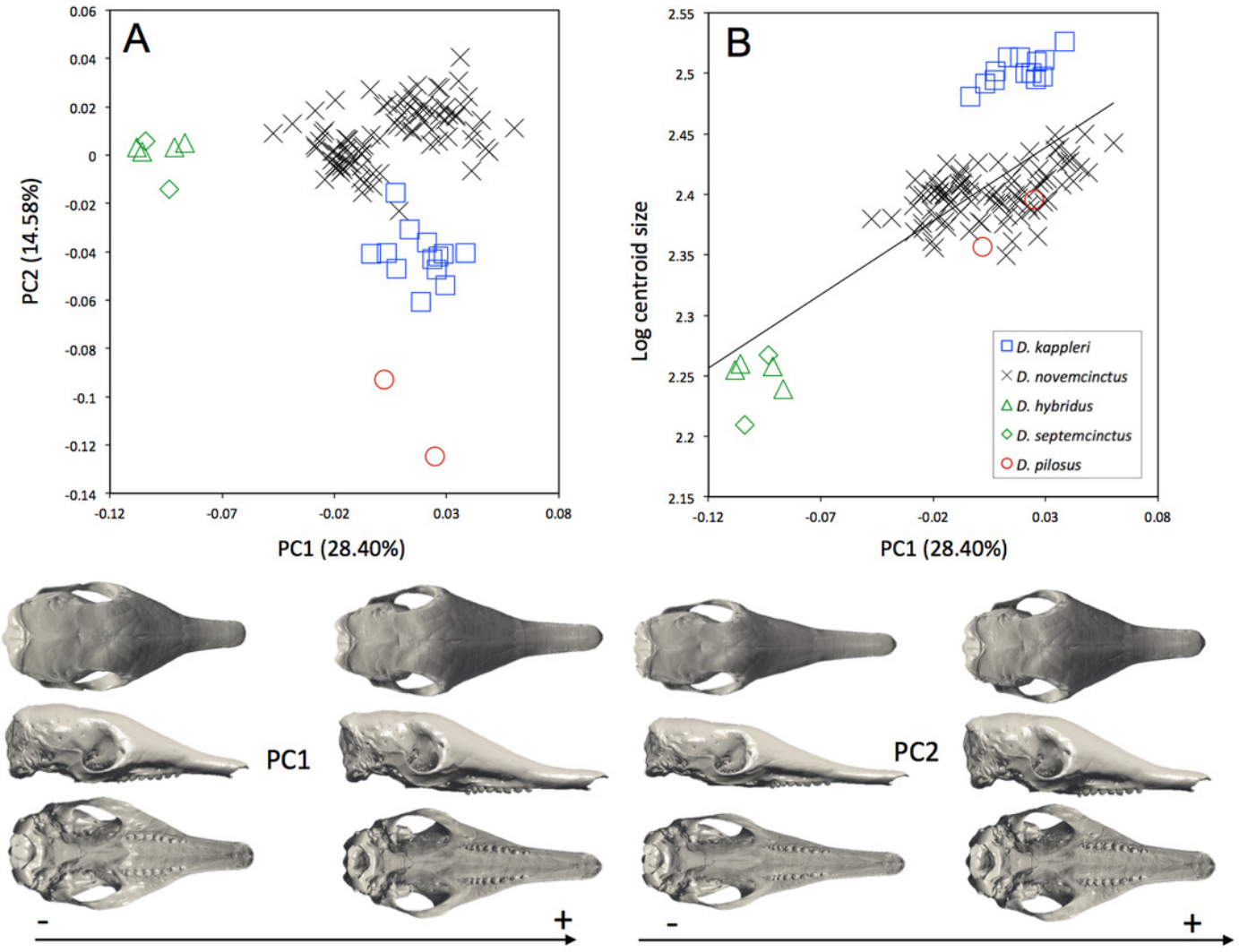

Figure 5

Figure 5

(**A**) Principal component analysis (PC1 *vs* PC2) and associate patterns of morphological transformation for mandibles of *Dasypus novemcinctus*. (**B**) Regression of the first principal component on the logarithm of the centroid size (R^2=0,035; p=0.03). *Symbols*: green diamonds, Bolivia; green triangle, Brazil (solid green triangles are for specimens from Amapa); green circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue “plus”, Guatemala; blue bars, Honduras; Blue squares, Mexico; blue crosses, Nicaragua; blue triangles, USA; blue circles, Costa Rica; black triangles, Colombia; black crosses, Ecuador; black stars, Panama; orange squares, French Guiana; orange crosses, Guyana; orange circles, Suriname.

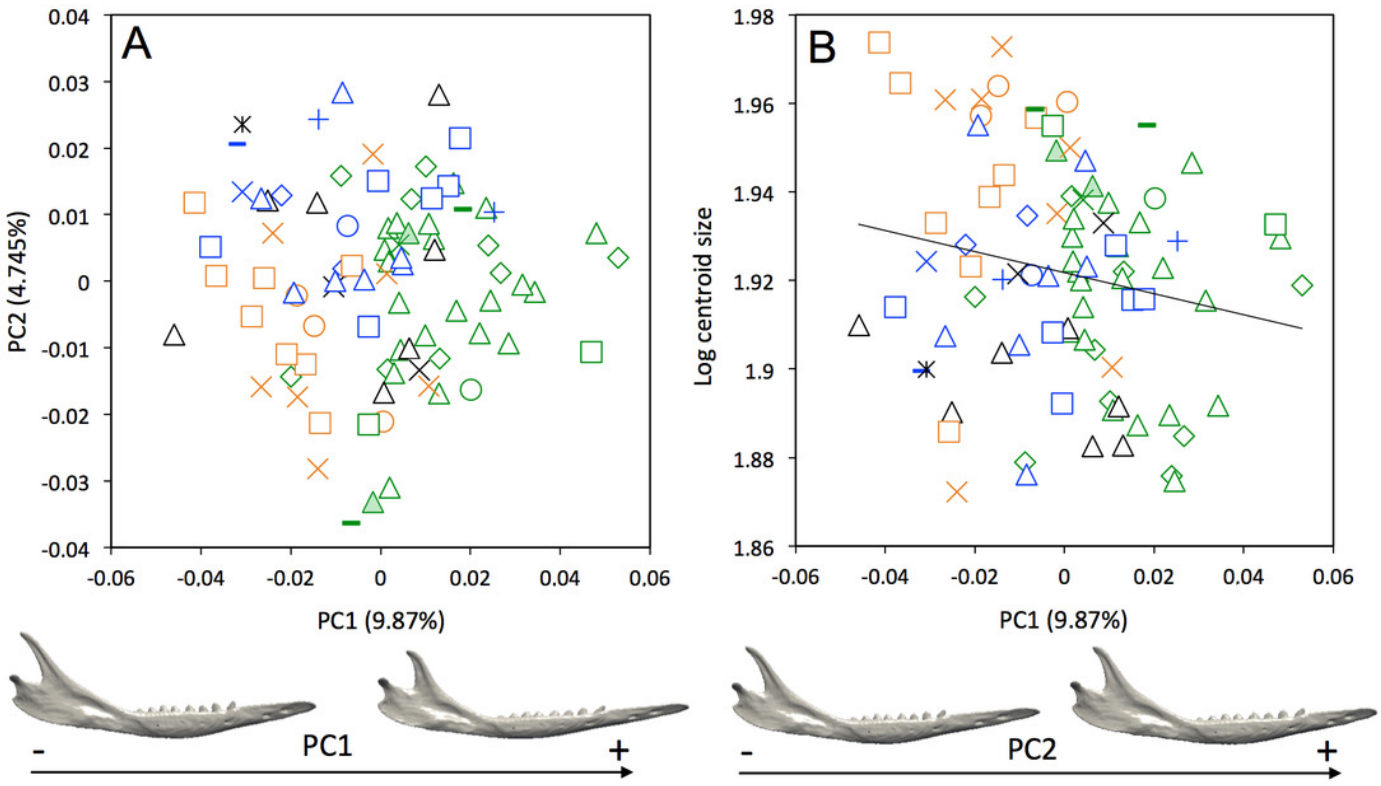

Figure 6

Figure 6

Principal component analysis (**A**, PC1 *vs* PC2; **B**, PC3 *vs* PC4) and associate patterns of morphological transformation for crania of *Dasypus novemcinctus*. *Symbols*: green diamonds, Bolivia; green triangle, Brazil (solid green triangles are for specimens from Amapa); green circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue “plus”, Guatemala; blue bars, Honduras; Blue squares, Mexico; blue crosses, Nicaragua; blue triangles, USA; blue circles, Costa Rica; black triangles, Colombia; black crosses, Ecuador; orange squares, French Guiana; orange crosses, Guyana; orange circles, Suriname.

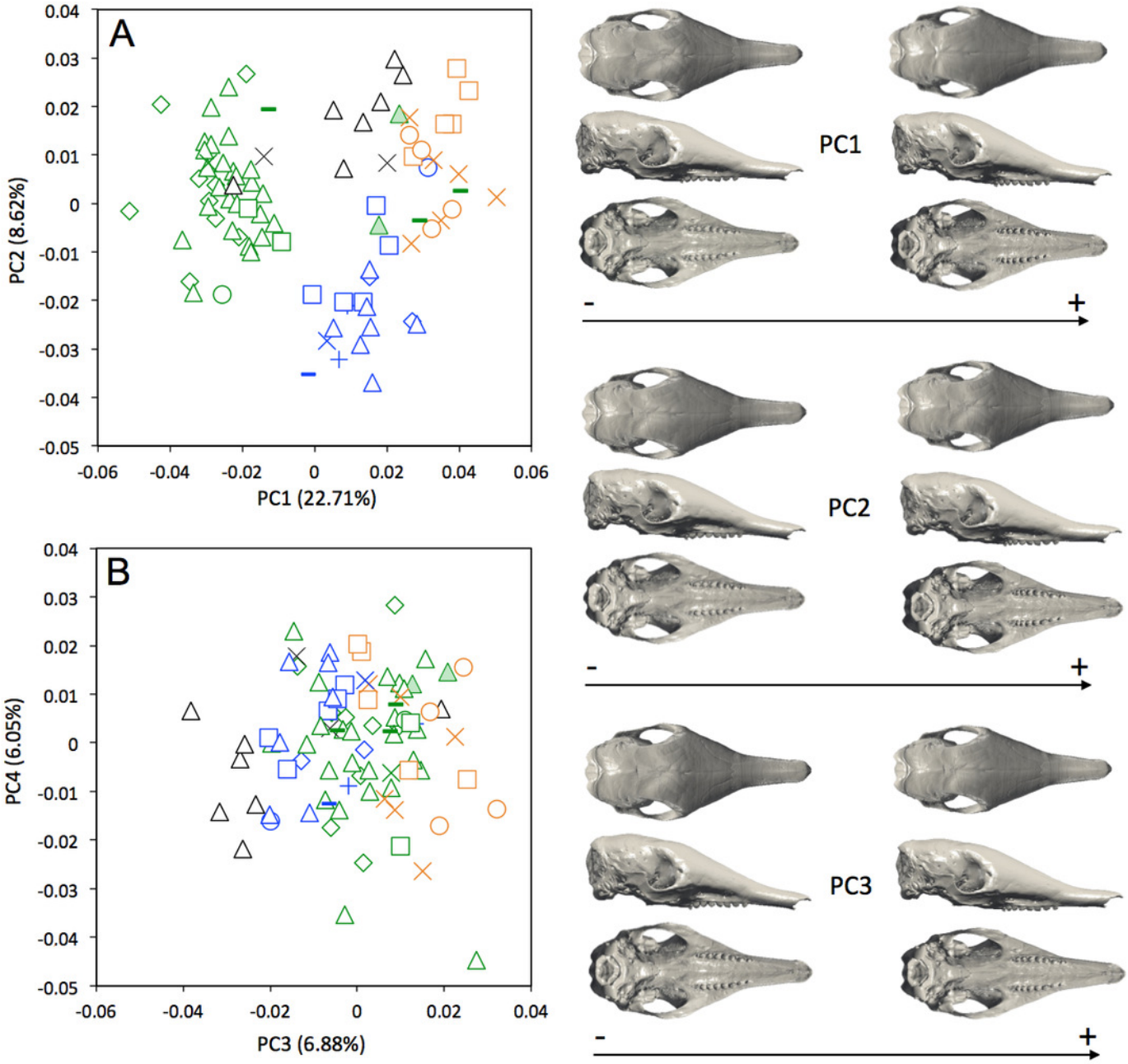
A
PC2 (8.62%)
PC1 (22.71%)
B
PC4 (6.05%)
PC3 (6.88%)
PC1
PC2
PC3
-
+

Figure 7

Figure 7

Regression of the first cranial principal component (*Dasypus novemcinctus*) on the logarithm of the centroid size (R^2=0.15; p<0.001). *Symbols*: green diamonds, Bolivia; green triangle, Brazil (solid green triangles are for specimens from Amapa); green circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue “plus”, Guatemala; blue bars, Honduras; Blue squares, Mexico; blue crosses, Nicaragua; blue triangles, USA; blue circles, Costa Rica; black triangles, Colombia; black crosses, Ecuador; orange squares, French Guiana; orange crosses, Guyana; orange circles, Suriname.

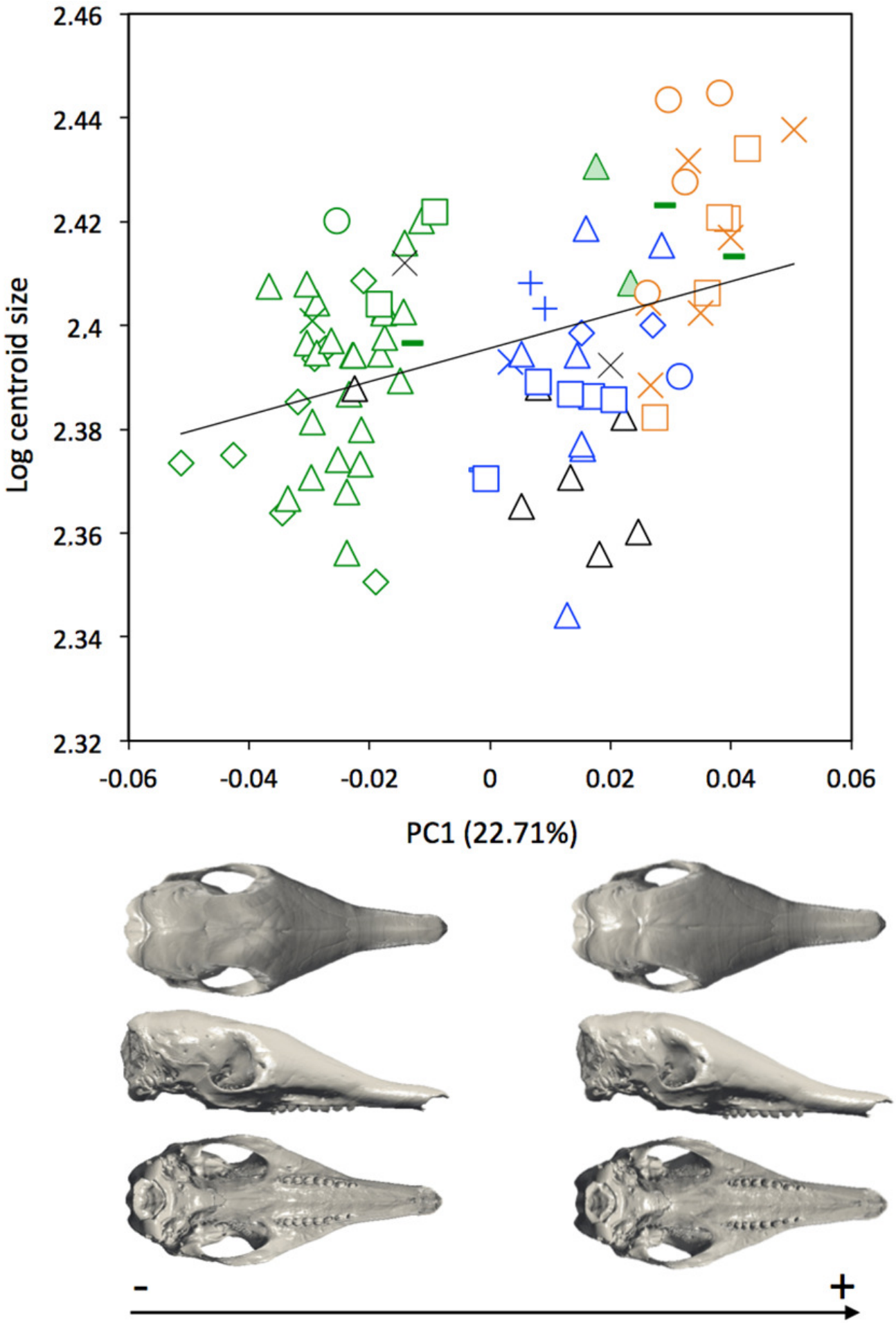
2.46
2.44
2.42
2.4
2.38
2.36
2.34
2.32
Log centroid size
-0.06
-0.04
-0.02
0
0.02
0.04
0.06
PC1 (22.71%)
-
+

Figure 8

Figure 8

Linear Discriminant Analysis (LDA) performed on cranial shape coordinates of *Dasypus novemcinctus*. *Symbols*: green diamonds, Bolivia; green triangle, Brazil (solid green triangles are for specimens from Amapa); green circles, Paraguay; green crosses, Peru; green squares, Uruguay; green bars, Venezuela; blue diamonds, Belize; blue “plus”, Guatemala; blue bars, Honduras; Blue squares, Mexico; blue crosses, Nicaragua; blue triangles, USA; black triangles, Colombia; black circles, Costa Rica; black crosses, Ecuador; orange squares, French Guiana; orange crosses, Guyana; orange circles, Suriname.

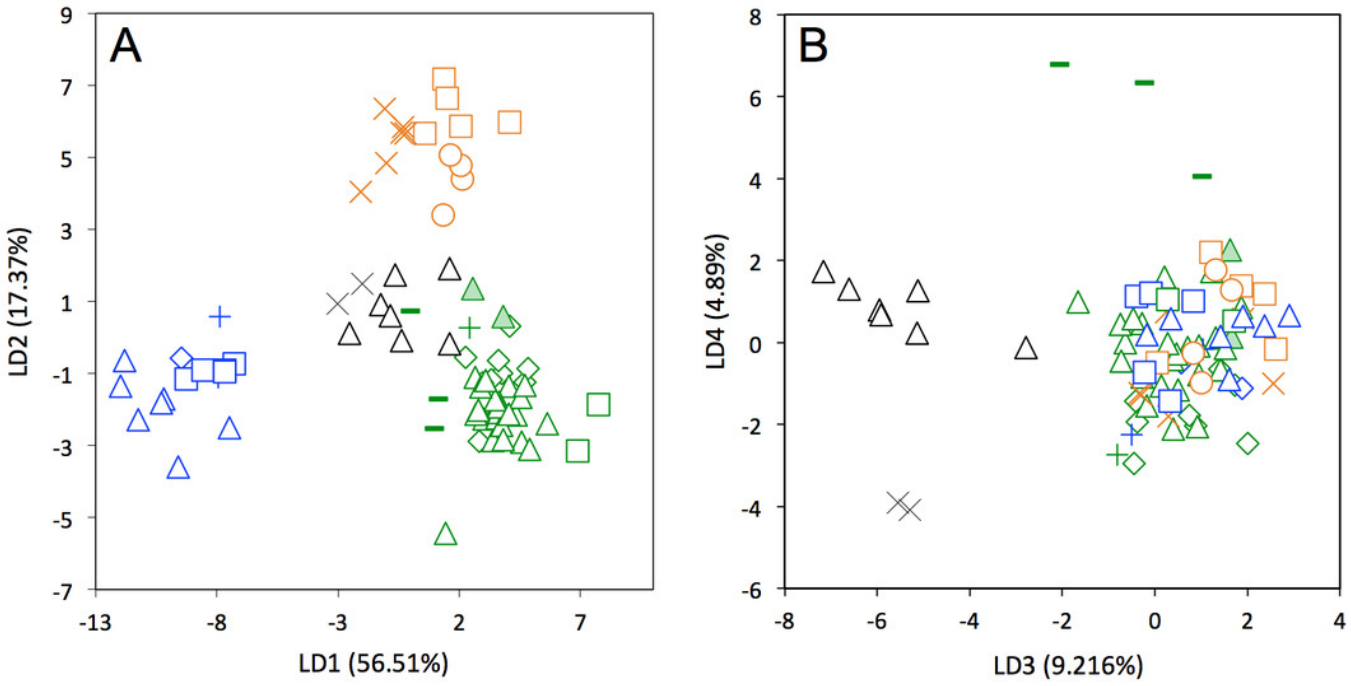

Figure 9

Figure 9

Summary map showing the geographical distribution of nine-banded armadillo specimens investigated in this study and their attribution to one of the four main morphotypes defined in this study: black, Central group; blue, Northern group; green, Southern group; orange, Guianan group. Specimens lacking precise geographical information (other than country of origin) are indicated with a square.

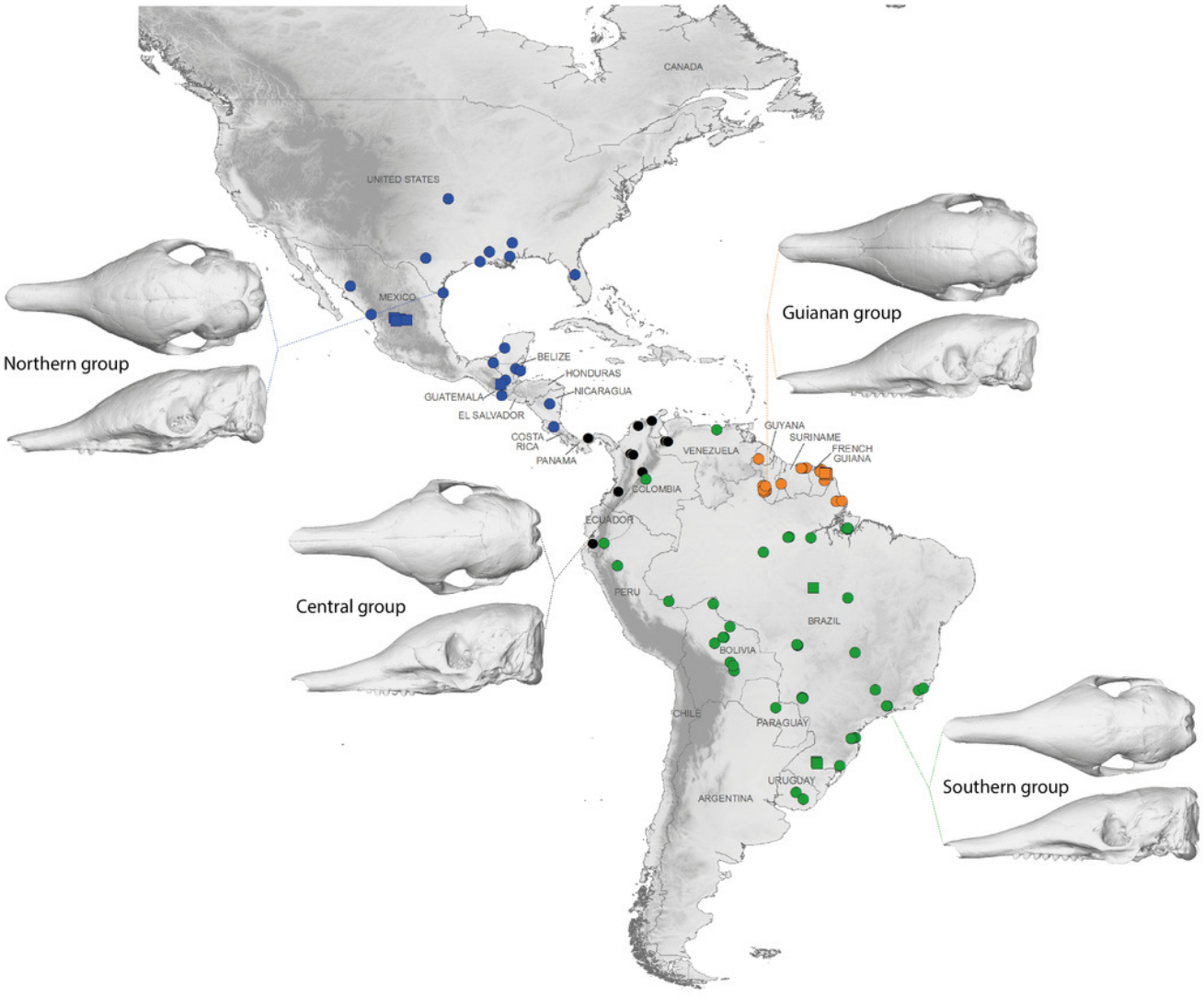

Table 1(on next page)

Table 1

Definitions of the landmarks used on the mandible

Numbers	Definition
1	Most anterior point of the mandible
2	Most anterior point of the alveolar margin of the tooth row
3	Most posterior point of the seventh tooth
4	Tip of the coronoid process
5	Point at the maximum of concavity between the coronoid and the condyloid processes
6	Most lateral point of the articular surface of the condyle
7	Most medial point of the articular surface of the condyle
8	Point at the maximum of concavity between the condyloid and the angular
9	Tip of the angular process
10	Mandibular foramen

1

Table 2 (on next page)

Table 2

Definitions of the landmarks used on the cranium. Landmarks indicated with a star were not used in the intraspecific comparisons.

Numbers	Definition
1	Most anterodorsal point of the nasal suture
2	Intersection between inter-nasal and inter-frontal sutures
3	Intersection between inter-parietal and inter-frontal sutures
4	Intersection between inter-parietal and supra-occipal
5	Most distal point of the supra-occipal
6 and 7	Intersection between frontal, maxillar, and nasal sutures
8 and 9	Most dorsomedial point of the orbit (i.e. minimal interobital length)
10 and 11	Most posterolateral point of the supra-occipital
12 and 28	Most anterolateral point of the premaxillar/nasal suture
13 and 29	Intersection between premaxillar, maxillar, and nasal sutures
14 and 30	Interection between the lacrimal, maxillar, and frontal sutures
15 and 31	Anteroventral margin of the lacrimal foramen
16 and 32	Anteroventral margin of the upper ethmoid foramen
17 and 33	Most anterior point of the squamosal, frontal, and alisphenoid sutures
18 and 34	Most dorsal point of the maxillary foramen
19 and 35	Most dorsal point of the infraorbital foramen
20 and 36	Most anteroventral point of the sphenopalatine fissure
21 and 37	Most dorsal point of the jugal/maxillar suture
22 and 38	Most dorsal point of the jugal/squamosal suture
23 and 39	Most posterior point of the postglenoid process
24 and 40	Most posterodorsal point of the zygomatic part of the squamosal
25 and 41	Intersection between the frontal, squamosal, and parietal sutures
26 and 42	Most dorsal point of sulcus for external acoustic meatus on squamosal
27 and 43	Intersection between the parietal, squamosal, and supraoccipital sutures
44 and 60	Most posterior point of the premaxillar/maxillar suture in ventral view
45 and 61	Most anterior point of the alveolar margin of the tooth row
46 and 62	Most posterior point of the alveolus of the seventh dental locus
47 and 63	Intersection between the lacrimal/maxillar suture and the zygomasseteric crest in ventral view
48	Intersection between maxillar and palatine sutures
49 and 64	Most posterolateral point of the pterygoid wings
50 and 65	Transverse canal foramen
51 and 66	Most anterodorsal point of the *foramen ovale*
52 and 67	Most ventral of the alisphenoid/squamosal suture
53 and 68	Most lateral point between the basioccipital/basisphenoid sutures
54 and 69	Most posterolateral point of the jugular foramen
55 and 70	Most posterolateral point of the hypoglossal foramen
56 and 71	Most anterolateral point of the occipital condyle
57 and 72	Intersection between the basioccipital, the occipital condyle, and the *foramen magnum*
58	Most antero-ventral point of the *foramen magnum*
59	Most postero-dorsal point of the *foramen magnum*
73 and 74	Intersection between the supraoccipital, exoccipital, and petrosal sutures
75 and 76	Most posterior point of the postglenoid foramen
77 and 78	Caudal palatine foramen
79* and 80*	Point of maximum concavity on the maxillar/frontal suture in dorsal view
81 and 82	Intersection between the lacrimal/frontal suture and the orbit
83	Most posterior point of the frontal sinuses in the midline
84	Ventral tip of the tentorial process

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