Revalidation of *Promops davisoni* Thomas (Molossidae)

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Abstract
This paper focuses on the study of inter- and intraspecific variation within the genus *Promops* in order to evaluate the taxonomic status of some taxa, particularly *P. davisoni* Thomas, 1921. We analyzed 183 specimens representing all nominal taxa described for the genus, and studied pelage and morphometric characters seeking understanding of the taxonomy of *Promops*. Based mainly on size allied to pelage characters, we have recognized P. davisoni as a valid species. Relationships of *P. davisoni* are uncertain, though light brown dorsal pelage in most specimens seems more related to the *P. nasutus* than *P. centralis*. *Promops davisoni* presented cis-Andean allopatric distribution in accordance with range patterns of other bat species.
Key words: Davison´s mastiff bat, taxonomy, Andes

Introduction

The genus *Promops* Gervais, 1856 currently encompasses two species, *Promops nasutus* (Spix, 1823) and *P. centralis* Thomas, 1915 (Eger, 2007). The first species is exclusively South American, occurring from Venezuela to southern Brazil and northern Argentina, but there is no known record in the Amazon basin and portions of central Brazil (Eger, 2007). *Promops centralis* occurs from Mexico (Yucatán and Jalisco) throughout South America, on the northern coast (Brazil, Guianas, Venezuela, and Colombia), along the western Andes (Colombia, Ecuador, and Peru), the Amazon basin in Brazil, western Bolivia, Paraguay, and northeastern Argentina (Simmons, 2005; Eger, 2007; Pacheco et al., 2009). Koopman (1994) and Simmons (2005) recognized three subspecies of *P. nasutus* together with the nominal one [(*P. n. ancilla* Thomas, 1915, *P. n. downsi* Goodwin & Greenhall, 1962, and *P. n. pamana* (Miller, 1913)], and two subspecies of *P. centralis* (*P. c. davisoni* Thomas, 1921, and *P. c. occultus* Thomas, 1915). An updated South American molossid species account (Eger, 2007) considered all of these subspecies as junior synonyms of nominal ones. Indeed, subspecies of *P. nasutus* do not show substantial differences in the characters defining them to support their validity. On the other hand, subspecies of *P. centralis*, particularly *P. c. davisoni*, show some morphological and morphometrical distinctiveness. *Promops c. davisoni* presents an exclusive set of characters of pelage, skull and body dimensions that permits its recognition regarding *P. c. centralis* and *P. c. occultus* (e.g., Ojasti & Linares, 1971; Genoways & Williams, 1979; Simmons & Voss, 1998; Gregorin & Taddei, 2000).

Description of *P. davisoni* was based on two specimens from Chosica, Department of Lima, Peru (Thomas, 1921). Data of the holotype obtained from the original description (Thomas, 1921) describe an adult male (BM 21.5.21.1), with forearm 51.5 mm, greatest skull length 19.2 mm, and dorsal pelage cocoa-brown with whitish basal band of dorsal hairs. A reanalysis of the holotype shows forearm 50.7 mm and skull length 19.9 mm; the dorsal pelage was very dark brown with the whitish basal band occupying about half the total length of the hair. For a long time, *P. davisoni* was considered valid (e.g., Cabrera, 1958; Brosset, 1965; Albuja, 1982), but Handley (1966), Tuttle (1970), and Ojasti & Linares (1971) suggested the subspecific status for the taxon. Koopman (1978) firstly mentioned the trinomial use and thus formalized the new name combination, *P. centralis davisoni* (see synonym in Eger, 2007). It is striking that neither of these authors explained the reasons for pooling the taxon with *P. centralis* instead of *P. nasutus*, and this latter alternative hypothesis was first proposed by Genoways & Williams (1979). More recently, the taxon was synonymized with *P. centralis* (e.g., Ascorra et al., 1993; Pacheco et al., 1995; Eger, 2007) or eventually maintained as a subspecies of *P. centralis* (Simmons, 2005). Koopman (1994) stated that, although he recognized *P. c. davisoni*, the taxon may be more related to *P. nasutus* in accordance with Genoways & Williams (1979), and recently followed by Pacheco et al. (2009). This uncertain position of the *P. davisoni* bears upon the exclusive combination of characters found in *P. davisoni*, being closer to *P. centralis* due to the chocolate brown pelage present in a few specimens (e. g., the holotype); and similar to *P. nasutus* in body dimensions and lighter brown

pelage. Gregorin & Taddei (2000) applied the t-test and showed that the samples from the Pacific slopes of Peru and Ecuador (at that time referred to as *P. c. davisoni*) were smaller than the other samples of *P. centralis* from South America and Central America (referred to as *P. c. centralis* and *P. c. occultus*).

Recently, the number of molossid species has increased due to new descriptions and revalidations based on applied current species concepts (phylogenetic and genetic), such as *Eumops floridanus*, *E. patagonicus*, *E. delticus*, *E. nanus*, *E. ferox*, *E. wilsoni*, and *Molossus coibensis* (e.g., Eger, 2007; McDonough et al., 2008; Baker et al. 2009). There is consensus that South American molossid genera need taxonomic review in order to determine with accuracy the specific and subspecific composition within each genus, such as *Promops*, *Nyctinomops*, and *Molossus*. This study aims to analyze the morphological and morphometric variation within the genus *Promops* to revalidate *P. davisoni* Thomas, and to provide an updated definition of the species within the genus, formalizing a new taxonomic arrangement.

Material and Methods

One hundred and eighty-three specimens of *Promops* were studied (Appendix 1) in the following institutions: the American Museum of Natural History (AMNH), New York; the British Museum (BMNH), London; Coleção de Mamíferos da Universidade Federal de Lavras (CMUFLA), Lavras; Coleção de Mamíferos da Universidade Federal de Viçosa (CMUFV); Laboratório de Chiroptera da Universidade Estadual Paulista (DZSJRP), São José do Rio Preto; Museo Argentino de Ciências Naturales "Bernardino Rivadavia" (MACN), Buenos Aires; Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul (MCN); Porto Alegre; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; the Museum of Vertebrate Zoology (MVZ), Berkeley; the Royal Ontario Museum (ROM), Toronto; the Field Museum (FMNH), Chicago; and the United States National Museum (USNM), Smithsonian Institution, Washington DC.

Definition of the morphometrical variables taken from skull and teeth follow Vizzoto & Taddei (1973) and Kalko & Handley (1994): greatest length of skull (GLS), condyle-incisive length (CIL), maxillary toothrow length (C-M), lower toothrow length (c-m), greatest length of mandible (GLM), postorbital breadth (POB), upper molar breadth (M-M), upper canine breadth (C-C), mastoid breadth (MAB), zygomatic breadth (ZB), and braincase breadth (BCB). External variables taken from dried and alcohol-preserved specimens were: total length of forearm (FOA), total length of third metacarpal (III met), total length of fourth metacarpal (IV-met), and total length of fifth metacarpal (V-met). All measurements are in millimeters, and measurements were taken only adult specimens; age estimate was based on epiphyses cartilage fusion.

The statistical analyses performed comprise descriptive analysis; Student t test and Analysis of Variance (ANOVA), both univariate; Principal Component Analysis (PCA) and Discriminant Analysis (DA), both multivariate. Firstly, t-test was applied to evaluate the sexual dimorphism, comparing sexes within selected samples in each species and that presented higher number of specimens. The descriptive analysis and ANOVA were applied to comparing samples geographically pooled in order to assess geographical variation (many of these samples represent nominal taxa of species-group taxa within *Promops*, in which has recently been invalidated), and the level of divergence among the presently valid species (following taxonomic arrangement of Eger, 2007). Exception was to the samples from the Pacific Andean slopes of Peru and Ecuador, named *P. davisoni*, that were initially considered distinct from *P. nasutus* and *P. centralis*, and its validity is a hypothesis to be tested. Samples were compared along transects on a north-south axis.

The map in Figure 1 shows the geographical range of pooled samples for statistical comparisons, hence the map does not indicate the geographic distribution of the taxa. *Promops centralis* was pooled in three samples: 1) northern and middle Central America (MEX – specimens from Mexico, Honduras and Guatemala), 2) northern South

America, including Colombia, Venezuela, the Guianas, and northern Brazil (state of Pará) (SAM) (both samples are usually referred to as *P. c. centralis*), and 3) meridional portions of South America, the eastern Andes, in Bolivia, Paraguay, and the Peruvian Amazon (PAR) (sample usually

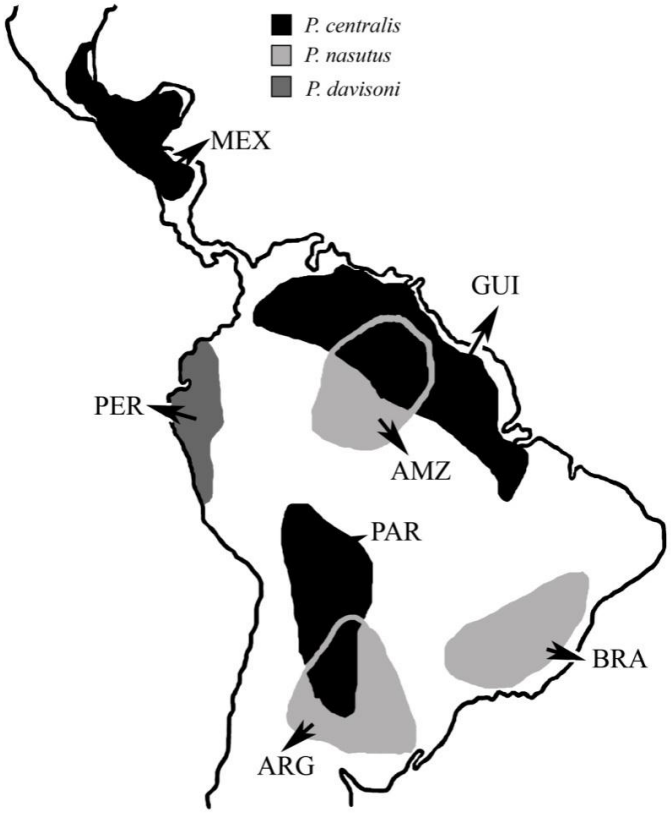

Figure 1 – Map of Neotropical region showing the grouping used for the statistical analysis and study of geographical comparisons. Definition of the acronyms is in text.

referred to as *P. c. occultus*). Samples of *P. centralis* from Panama were used only in descriptive statistics due to the low number of specimens available to apply the t-test. Samples from the Pacific slopes of the Andes, in Ecuador and Peru (PER) were studied separately. *Promops nasutus* was grouped in three samples: 1) northern South America including Venezuela, the Guianas, and Brazil (GUI), 2) eastern and southeastern Brazil (BRA – states of São Paulo, Bahia and Minas Gerais), and 3) southern sample, including southern Brazil (state of Rio Grande do Sul State), Bolivia, Argentina, and Paraguay (ARG). The latter was previously separated into Argentina (referred to as *P. s. ancilla*) and Paraguay (referred to as *P. n. fosteri*), but statistical tests resulted in non-significant differences, and the specimens were grouped in only one sample. Also, the t-tests resulted in non-significant differences for sexes in all samples analyzed, and they were grouped together.

External qualitative characters of skull and dentition were examined but they did not show variation among the specimens.

Results and discussion

Morphometric variation in *P. centralis* and comparison with *P. davisoni* – Table 1 shows the results of descriptive statistics for three samples of *P. centralis* and one sample of *P. davisoni*. It is noteworthy that there is a gradual decrease in the mean (Table 1) in samples from Central America (MEX – typically *P. c. centralis*) to the southernmost one (PAR – typically P. c. occultus); individuals from intermediate geographic sites in north-southern axis (northern South America - referred to in the literature as *P. c. centralis*) more similar with Paraguayan specimens. The results of ANOVA comparing all the samples are presented in Table 2. Data indicate that the sample of *P. centralis* from Mexico, Honduras, and Guatemala (MEX) presents only three distinct variables as compared with samples of *P. centralis* from northern South America (SAM), and the latter has only one statistically significant difference from sample PAR (Table 2). This level of variation among samples previously defined as pertaining to *P. centralis* is reduced to consider them as distinct taxa. But the level of differences increases with 10 of 15 analyzed variables comparing extreme samples (MEX vs. PAR).

Table 1. Descriptive statistics of the three samples of *P. centralis* (MEX, SAM, PAR), and one of *P. davisoni* (PER). Note the decreasing dimensions of samples from northern Central America (MEX) to southern South America (PAR) in *P. centralis.* Upper data in each variable denote mean, standard deviation, and sampling; bottom line in each variable denotes range.

Variables/Samples	MEX	SAM	PAR	PER
GLS	20.9 ± 0.4 (11) 18.8-21.9	20.5 ± 0.5 (9) 19.8-21.1	20.3 ± 0.4 (17) 19.8-21.2	19.5 ± 0.4 (17) 18.7-20.2
CIL	19.8 ± 0.5 (10) 19.0-20.4	19.2 ± 0.5 (9) 18.5-19.8	19.0 ± 0.5 (17) 17.5-19.8	18.1 ± 0.5 (17) 17.3-19.0
POB	4.2 ± 0.1 (11) 4.0-4.4	3.9 ± 0.2 (9) 3.6-4.2	4.0 ± 0.1 (17) 3.7-4.3	3.9 ± 0.1 (17) 3.7-4.2
C-M	7.9 ± 0.3 (11) 7.4-8.3	7.7 ± 0.2 (9) 7.3-7.9	7.4 ± 0.3 (17) 7.0-8.2	7.1 ± 0.2 (17) 6.9-7.4
M-M	9.4 ± 0.2 (11) 9.0-9.7	9.0 ± 0.3 (9) 8.6-9.3	8.9 ± 0.3 (17) 8.2-9.5	8.6 ± 0.2 (17) 8.3-9.0
C-C	5.2 ± 0.1 (11) 5.0-5.4	5.0 ± 0.2 (9) 4.7-5.3	4.8 ± 0.3 (17) 4.0-5.1	4.8 ± 0.2 (17) 4.5-5.1
ZB	12.5 ± 0.2 (11) 12.0-12.8	12.2 ± 0.2 (8) 11.9-12.4	12.4 ± 0.4 (17) 11.2-13.0	11.4 ± 0.3 (17) 11.0-12.0
MAB	11.9 ± 0.3 (10) 11.5-12.3	11.4 ± 0.3 (8) 11.0-11.7	11.7 ± 0.4 (16) 10.7-12.2	11.0 ± 0.2 (17) 10.7-11.3
BCB	10.3 ± 0.3 (11) 9.6-10.6	10.0 ± 0.1 (8) 9.9-10.2	10.0 ± 0.3 (17) 9.5-10.5	9.6 ± 0.1 (17) 9.4-9.9
GLM	14.3 ± 0.6 (10) 13.3-15.1	14.4 ± 0.7 (9) 13.2-15.3	13.9 ± 0.7 (16) 12.1-14.8	12.9 ± 0.3 (17) 12.2-13.7
c-m	8.5 ± 0.3 (10) 8.2-8.9	8.5 ± 0.3 (9) 8.1-9.0	8.2 ± 0.3 (17) 7.5-8.6	8.0 ± 0.5 (17) 7.5-9.9
FOA	53.4 ± 1.9 (12) 50.0-56.7	53.1 ± 1.6 (13) 50.0-56.4	50.7 ± 1.2 (21) 47.0-52.6	49.5 ± 1.1 (23) 47.6-52.0
III MET	56.6 ± 1.6 (12) 53.3-59.8	56.2 ± 1.9 (14) 53.0-59.0	53.9 ± 1.4 (21) 49.6-56.1	52.5 ± 1.4 (24) 48.8-54.7
IV MET	54.7 ± 1.7 (11) 51.9-57.8	54.1 ± 1.7 (14) 51.1-56.7	52.2 ± 1.7 (21) 48.3-54.5	50.5 ± 1.6 (24) 46.3-53.0
V MET	34.3 ± 0.8 (11) 33.4-353.6	34.6 ± 1.5 (14) 31.5-37.1	34.4 ± 1.7 (16) 30.7-36.9	32.6 ± 1.2 (24) 30.4-34.5

These data suggest that samples of *P. centralis* from the Amazon in western Brazil, Bolivia and part of Peru are biometrically closer to samples from southern South America (referred to as *P. c. occultus*) than those from Central America. These results can be explained by means clinal variation in *P. centralis*, with northward population along the distribution (Central American ones) larger than those southernmost ones (Paraguayan and Bolivian ones). Indeed, an adult female from the western Brazilian Amazon (state of Acre – Nogueira & Peracchi, 1999) has a 51.25 forearm and GLS 19.1 mm. It is more similar to the mean recorded for the Paraguayan and Bolivian samples (usually named *P. c. occultus*) than that of the samples of typical *P. c. centralis* (from Mexico and adjacent countries). On the other hand, we have considered the morphometric variation very complex and somewhat mosaic in *P. centralis*, with specimens with forearms as long as 55.2 and 53.7m, such as the Venezuelan and Suriname ones (Ojasti & Linares, 1971; Genoways & Williams, 1979). Also, specimens from the southern limit of the distribution of *P. centralis* (Argentina – Masoia, 1976) have long forearms varying from 53.0 to 55.0 mm, as long as typical *P. centralis* from Central America.

Table 2 – Results of ANOVA comparing all pooled samples of *P. centralis* (MEX, SAM, and PAR), *P. davisoni* (PER), and P. nasutus (GUI, BRA, and ARG). Note that the specimens from the Pacific slopes of Peru and Ecuador (PER) are highly divergent from the rest of the other samples. Bolded numbers indicate significantly distinct variables ($p \leq 5\%$).

Variables	F	MEX vs. SAM	MEX vs. PAR	MEX vs. GUI	MEX vs. BRA	MEX vs. ARG	SAM vs. PAR	SAM vs. GUI	SAM vs. BRA	SAM vs. ARG	PAR vs. GUI	PAR vs. BRA	PAR vs. ARG	GUI vs. BRA	GUI vs. ARG	BRA vs. ARG	PER vs. MEX	PER vs. SAM	PER vs. PAR	PER vs. GUI	PER vs. BRA	PER vs. ARG
GLS	52.49	0.214	**0.019**	**0.000**	**0.000**	**0.000**	1.000	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.968	0.987	0.324	**0.000**	**0.001**	**0.000**	**0.004**	**0.000**	**0.001**
CIL	9.18	**0.002**	**0.012**	**0.000**	0.631	0.106	0.812	0.892	0.065	0.178	**0.046**	0.421	0.812	**0.000**	**0.000**	0.966	**0.000**	1.000	0.622	0.693	**0.007**	**0.020**
POB	58.02	0.063	**0.001**	**0.000**	**0.000**	**0.000**	0.999	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.770	1.000	0.320	**0.000**	**0.000**	**0.000**	**0.010**	**0.000**	**0.000**
C-M	45.71	0.180	**0.000**	**0.000**	**0.000**	**0.000**	0.731	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.994	0.959	0.398	**0.000**	**0.002**	**0.028**	**0.002**	**0.000**	**0.001**
M-M	53.47	**0.002**	**0.000**	**0.000**	**0.000**	**0.000**	1.000	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.674	0.516	1.000	**0.000**	0.120	**0.011**	**0.000**	**0.000**	**0.000**
C-C	21.35	0.268	**0.000**	**0.000**	**0.000**	**0.000**	0.730	**0000**	**0.033**	**0.000**	**0.000**	0.336	**0.000**	**0.034**	0.741	0.184	**0.000**	0.323	0.980	**0.001**	0.843	**0.002**
ZB	55.20	0.249	0.952	**0.000**	**0.000**	**0.000**	0.668	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.840	0.108	0.829	**0.000**	**0.000**	**0.000**	**0.003**	0.083	0.444
MAB	34.39	**0.018**	0.822	**0.000**	**0.000**	**0.000**	0.190	**0.000**	**0.004**	**0.000**	**0.000**	**0.000**	**0.000**	0.866	0.987	0.988	**0.000**	0.070	**0.000**	0.194	0.858	0.245
BCB	22.12	0.397	**0.035**	**0.000**	**0.000**	**0.000**	0.999	**0.019**	**0.000**	**0.001**	**0.009**	**0.000**	**0.000**	0.155	0.999	0.077	**0.000**	**0.006**	**0.001**	1.000	0.063	0.999
GLM	37.66	0.998	0.557	**0.000**	**0.000**	**0.000**	0.324	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.468	0.804	0.974	**0.000**	**0.000**	**0.000**	0.946	**0.016**	**0.045**
c-m	26.06	1.000	0.238	**0.000**	**0.000**	**0.000**	0.628	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	1.000	1.000	1.000	**0.005**	0.061	0.660	**0.003**	**0.000**	**0.000**
FOA	39.90	0.988	**0.000**	**0.000**	**0.000**	**0.000**	**0.007**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.997	0.134	0.293	**0.000**	**0.000**	**0.033**	**0.001**	**0.001**	0.197
III MET	25.09	0.984	**0.001**	**0.000**	**0.000**	**0.000**	0.081	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	0.926	0.410	0.997	**0.000**	**0.000**	**0.038**	**0.013**	0.444	0.509

IV MET	23.55	0.965	**0.008**	**0.000**	**0.000**	**0.000**	0.293	**0.000**	**0.000**	**0.000**	**0.000**	**0.002**	**0.000**	0.401	0.066	1.000	**0.000**	**0.000**	**0.007**	**0.004**	0.869	0.877
V MET	17.01	0.994	0.985	**0.000**	**0.006**	**0.012**	1.000	**0.000**	**0.002**	**0.003**	**0.000**	**0.000**	**0.000**	0.098	**0.000**	0.914	**0.008**	**0.002**	**0.000**	**0.000**	0.956	1.000

Promops davisoni (sample PER) was shown to be statistically very distinct regards all three samples of *P. centralis* (MEX, PAR, and SAM) with highly significant results (Table 2): 12 variables are statistically different comparing PER with PAR, 10 with SAM and all 15 variables with MEX.

The results obtained in univariate statistics may also be graphically noted in Figure 2, which expresses the results of the PCA. Figure 2 shows that PC1 was responsible for 76.11% of the variation of variables, PC 2 for 7.11%, and both PCs explain 83.21% of the total variation. The variables that most significantly contributed to the variation of PCs 1 and 2 can be viewed in Table 3.

Table 3 - Results of two first Principal Components (PC). Variables are presented in log10.

Variables	PC1	PC2
GLS	0.01960	-0.00039
CIL	0.00348	0.01733
POB	0.02149	-0.00118
C-M	0.02598	-0.00087
M-M	0.02232	0.00228
C-C	0.02571	0.00945
ZB	0.02032	0.00141
MAB	0.01681	0.00213
BCB	0.01081	0.00104
GLM	0.02816	-0.00542
c-m	0.02649	-0.00634
FOA	0.01489	-0.00364
% of variance	76.11	7.11

The data in Figure 2 show that the specimens previously identified as *P. centralis* have a cohesive distribution, except for one outlier: USNM 121430 from Villa Rica, Paraguay - very small in skull and forearm dimensions. Analysis of the data (Fig. 2) also reveals that the specimens of *P. centralis* closest to *P. davisoni* come from Paraguay, Bolivia, Colombia and Panama, and they are smaller in size within *P. centralis* as previously discussed. Specimens of *P. centralis* that are more distinct from *P. davisoni* in PCA analysis are from Mexico, Honduras, Guatemala, Trinidad, and several localities from the Guiana shield. Only two specimens of *P. davisoni* have overlap with *P. centralis* on the graph, both (AMNH 81176 and 81178) being from Lambayeque, Peru. Specimens of *P. davisoni* (Fig. 2) also showed a cohesive distribution of the dots, except for one outlier (FMNH 179331, from Piura). The specimens representing *P. davisoni* in Figure 2 clearly present an intermediate morphological distribution between specimens of *P. centralis* and *P. nasutus*, although *P. davisoni* is closer to *P. nasutus*. Indeed, six specimens of *P. davisoni* overlap with *P. nasutus* (FMNH 81170, 81172, and 81175 from Lambayeque, Peru; AMNH 34300, 34382, and 53543 from Manavi, Ecuador).

The graphic resulted of Discriminant Analysis scores also shows three distinctive groups (Fig. 3). Along first Discriminant function (DF1), responsible for 91.4 % of variation, the *P. nasutus* scores assumed negative values, *P. centralis* positive values and, *P. davisoni* scores assumed values around zero, getting between two others species as a distinctive group. The influence of each variable on the analysis is plotted in Table 4.

Morphometric variation in *P. nasutus* and comparison with *P. davisoni* – Table 5 shows the results of descriptive analysis for the samples of *P. nasutus*. ANOVA comparing the three samples of *P. nasutus* resulted in non-significant differences in all variables. In order to test the validity of the two taxa described by Thomas, ANOVA includes also specimens of *P. nasutus* from Argentina and Paraguay. Indeed, there is some discussion regarding the validity of the two taxa described by Thomas: *P. fosteri* from Villa Rica, Paraguay (Thomas, 1901), and *P. ancilla* from Cachi, Argentina (Thomas, 1921) (e. g., Genoways & Williams, 1979; Myers & Wetzel, 1983). Both taxa were described based on the hue of the pelage, size and morphology of the basicranium. However, Thomas (1912) himself has suspected the validity of these species, suggesting a conspecific status with *P. nasutus*. All 15 variables tested were statistically similar ($p > 5\%$) regard samples from Argentina and Paraguay. The PCA results (Figure 2) also do not permit a clear morphological distinction among individuals from Argentina and Paraguay, and we are considering both taxa junior synonyms of *P. nasutus* in accordance with Eger (2007).

ANOVA with samples of *P. davisoni* (sample PER) and all three samples of *P. nasutus* from southern South America resulted in significant statistical differences (Table 2). Sample PER (P. davisoni) is very distinct from the sample from northern South America (GUI) and southeastern Brazil (BRA), with 11 and eight statistically distinct variables, respectively. *P. davisoni* is distinct from *P. nasutus* from ARG in eight variables too.

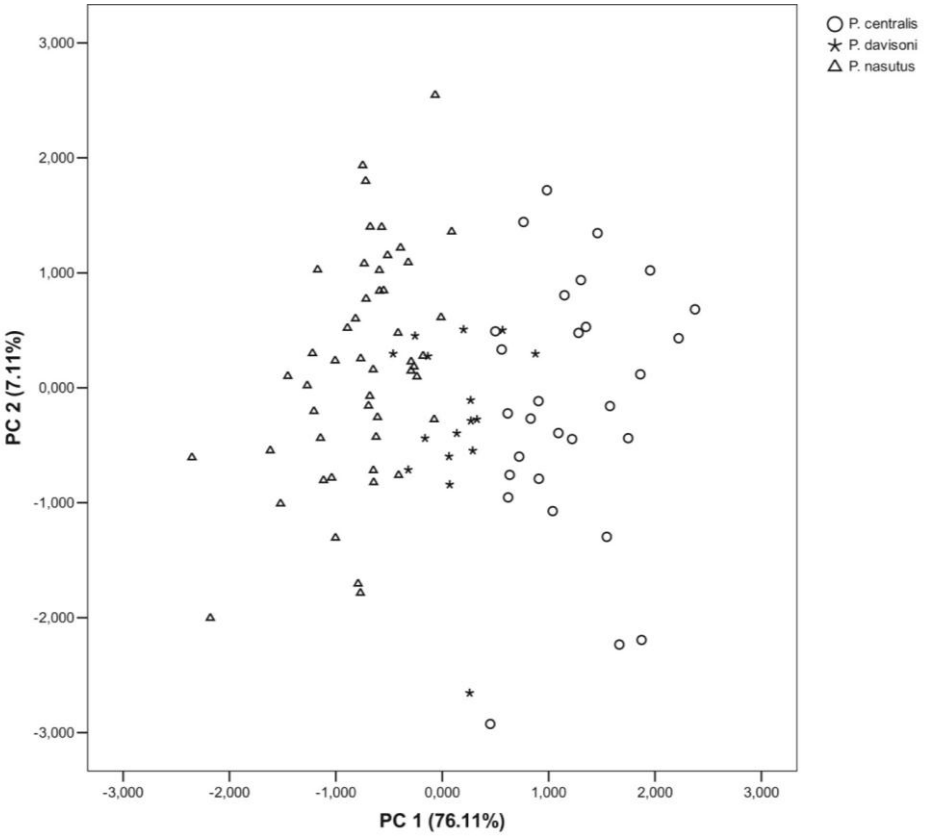

Figure 2 - Graph of PCA analysis (first two PCs) of *Promops*. Note the spatially intermediate, cohesive distribution of *P. davisoni* specimens.

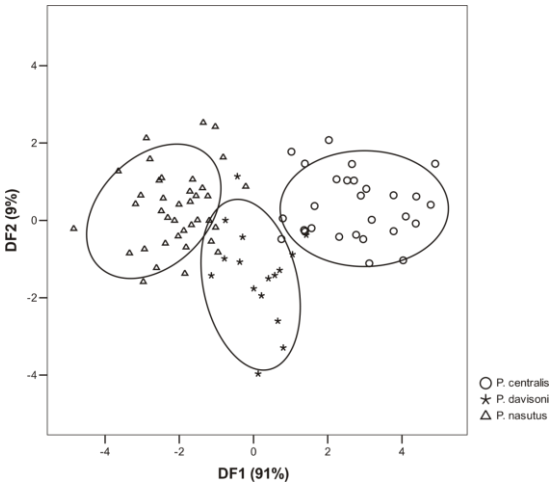

Figure 3 - Graph of Discriminant analysis (first two DFs) of *Promops*. Note the spatially intermediate, cohesive distribution of *P. davisoni* specimens.

The PCA results (Fig. 2) show that specimens of *P. nasutus* from southern Brazil (Taquari, state of Rio Grande do Sul - MCN 245, 249, 250, 252, 253, 254) are morphologically closest to P. davisoni.

Pelage variation in *Promops* –dorsal pelage in *P. davisoni* varies from blackish cocoa-brown, like in the holotype and one specimen from Piura (MACN 16696), to very light brown or cinnamon-brown or light chocolate-brown, as observed in most specimens. The whitish basal band in the dorsal hairs usually corresponds to half (like the holotype) or 3/4 of the total length of the hair (e.g. specimens from Lambayeque).

Table 4 – Scores of Discriminant Analysis of two first Discriminant Factors (DF). Variables are presented in log10.

Variables	DF1	DF2
GLS	0.416	0.236
CIL	-0.260	0.351
POB	-0.139	-0.266
C-M	0.422	-0.064
M-M	0.190	-0.711
C-C	-0.298	-0.419
ZB	0.255	0.542
MAB	0.249	0.388
BCB	-0.090	-0.102
GLM	0.028	0.795
c-m	0.130	-0.762
FOA	0.168	0.273
eigenvalue	4.708	0.468
% of variance	0.91	0.09

Peru), and it is abruptly replaced by a brown apical band, resulting in a clearly dichromic appearance in the dorsal hairs. Some *P. davisoni*

specimens from Peru (e. g. FMNH 81170-79) presented apparently faded pelage, but the dorsal hairs are still dichromic. Ventral coloration of most specimens is light cinnamon brown, contrasting with the dorsal coloration.

Specimens of *P. centralis* (samples from MEX, PAR, and SAM) have dorsal pelage coloration varying from blackish, like a specimen from Guiana (ROM 6067), to dark cocoa brown, like most specimens from Central America and French Guiana, or reddish dark brown, like the specimens from Trinidad (AMNH 175652, 179987, 178634, 175652-53, 178692-93). *Promops centralis* have the darkest pelage among the species of the genus. *Promops centralis* have the whitish basal band occupying about one fifth of the total length of the hair, except in AMNH 269114 from French Guiana and AMNH 261851 from Santa Cruz, Bolivia, which presented a basal band for about two fifths of the total length. Ventral pelage is slightly paler than that of the dorsal portion.

Overall dorsal pelage in *P. nasutus* is less variable than that of the other two taxa of *Promops*, and usually it is homogenously light brown; some Argentinean and Paraguayan specimens have slightly grayish-brown dorsal coloration. Thus, dorsal pelage coloration in *P. nasutus* resembles that of specimens of *P. davisoni* from Piura and Lambayeque, western Peru, but not the banding pattern of dorsal hair. Indeed, the banding of the dorsal hairs in *P. nasutus* is less varied with the whitish or very light brown basal band, which occupies about one fifth to a quarter of the total length of the hair, like in *P. centralis*. The paler (not whitish) basal bands in many specimens of *P. nasutus* have resulted in a weakly dichromic banding pattern in the dorsal hairs.

Taxonomic account

Promops davisoni Thomas, 1924

Diagnosis – medium size *Promops* (Figure 4) with total skull length ranging from 18.7 to 20.2 mm and length of forearm from 47.6 to 52.0 mm (for other variables, see Table 1). Dorsal pelage is usually light brown or cinnamon brown, although the holotype is blackish cocoa-brown. Ventral pelage is lighter, contrasting sharply with the dorsal pelage. Dichromism in dorsal hairs is usually evident with a long whitish basal band occupying about half the total length of the hairs; total length of dorsal hairs (in shoulder region) varies from 7.5 to 8.5 mm.

A comparative description of *P. davisoni* compared with *P. nasutus* and *P. centralis* is provided below in the description of variation. Synonym list followed Eger (2007). Geographic distribution – *P. davisoni* occurs on Pacific Andean slopes in Peru and Ecuador (Figure 5). Specimens from Pacaritambo, Ecuador (Brosset, 1965), were previously identified as *P. davisoni*, but the author did not provide any diagnostic characters of the pelage; the forearm length of specimens (51.0 to 52.0 mm) overlaps with *P. centralis* from western Amazon and the Paraguayan ones, and only this morphometric variable does not permit accurate identification. The habitat where specimens of *P. davisoni* have been recorded is usually arid in most of their coastal portions (Tuttle, 1970), but there is news of specimens occurring in moister habitats (Brosset, 1965).

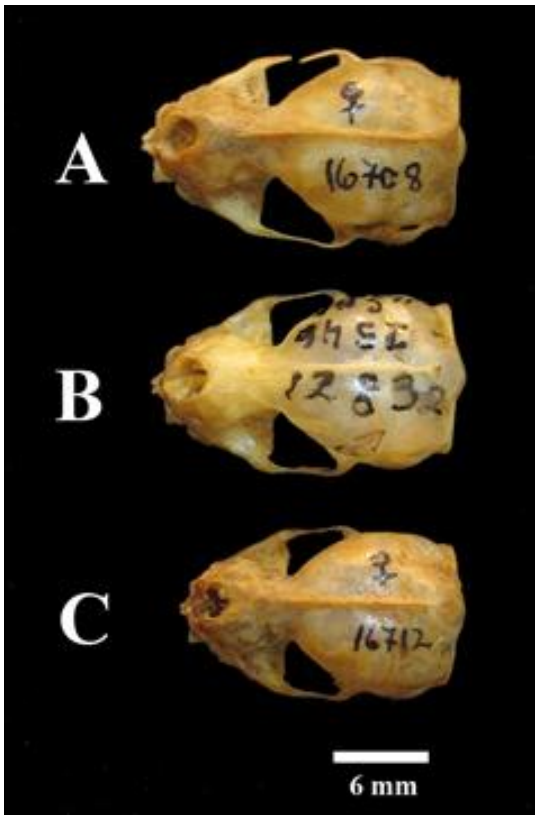

Figure 4 – Skulls of *Promops* in dorsal view. A – *P. centralis* from Formosa, Argentina (MACN 16708), B – *P. davisoni* from Piura, Peru (MACN 16696), and *P. nasutus* from Salta, Argentina (MACN 16712). Note the intermediate average overall size of *P. davisoni* as compared with *P. centralis* and *P. nasutus*.

Table 5. Descriptive statistics in three samples of *Promops nasutus*. Upper data in each variable denote mean, standard deviation, and sampling; bottom line in each variable denotes range.

Variables/Samples	GUI	BRA	ARG
GLS	18.7 ± 0.2 (14)	18.5 ± 0.4 (17)	18.7 ± 0.5 (60)
	18.5-1.0	18.1-19.4	17.6-19.7
CIL	17.4 ± 0.4 (14)	17.2 ± 0.4 (17)	17.6 ± 0.4 (61)
	17.0-18.8	16.7-18.1	16.3-18.3
POB	3.8 ± 0.1 (14)	4.1 ± 0.4 (16)	4.1 ± 0.2 (61)
	3.6-4.0	3.9-4.3	3.4-4.4
C-M	6.7 ± 0.2 (14)	6.7 ± 0.3 (16)	6.8 ± 0.3 (62)
	6.4-7.1	6.3-7.4	6.1-7.2
	8.0 ± 0.1 (14)	8.2 ± 0.19 (17)	8.1 ± 0.3 (62)
M-M	7.9-8.2	7.8-8.4	7.4-8.8
C-C	4.3 ± 0.1 (13)	4.7 ± 0.2 (16)	4.5 ± 0.3 (62)
	4.2-4.5	4.4-5.0	3.9-4.9
ZB	11.0 ± 0.2 (14)	11.1 ± 0.2 (14)	11.2 ± 0.3 (58)
	10.7-11.7	10.5-11.5	10.4-11.8
MAB	10.7 ± 0.1 (14)	10.8 ± 0.2 (15)	10.8 ± 0.3 (51)
	10.5-11.0	10.5-11.2	9.7-11.3
BCB	9.6 ± 0.1 (14)	9.4 ± 0.2 (17)	9.6 ± 0.2 (60)
	9.4-9.8	9.2-10.0	9.1-10.1
GLM	12.6 ± 0.1 (14)	12.3 ± 0.3	12.5 ± 0.5 (59)
	12.0-13.3	11.6-12.8	11.2-13.5
c-m	7.5 ± 0.2 (14)	7.5 ± 0.3 (16)	7.5 ± 0.3 (61)
	7.0-7.7	6.9-7.9	6.7-8.1
FOA	47.4 ± 1.2 (16)	47.7 ± 0.3 (16)	48.2 ± 1.5 (55)
	43.5-48.7	45.6-49.0	45.5-51.8
III MET	50.2 ± 1.8 (16)	51.2 ± 1.0 (9)	51.3 ± 1.7 (38)
	44.9-51.9	48.3-53.0	48.71-55.1
IV MET	47.8 ± 2.2 (16)	49.6 ± 1.1 (9)	49.6 ± 1.8 (38)
	42.3-49.7	47.6-51.5	46.8-54.0
V MET	30.4 ± 0.9 (16)	32.1 ± 1.2 (8)	32.7 ± 1.6 (24)
	28.3-31.5	30.2-33.5	29.9-36.3

Final considerations

Recent study focusing on the diversity and endemism in Peru (Pacheco et al., 2009) synonymized *P. davisoni* with *P. nasutus*, based on the small size and light brown dorsal pelage presented by two specimens from Lima and Piura, following Genoways and Williams (1979). In this sense, *P. nasutus* occurs on the Pacific coast of Peru (areas 3, 4, and 5 of Pacheco et al., 2009). Specimens from Pampa del Heath previously reported as *P. nasutus* were reidentified as *P. centralis* by Pacheco et al. (2009) and then this species occurs in the southeast in a small area of savannah with palms (area 10).

In addition with diagnostic characters as long and dichromatic dorsal hairs and intermediate size as compared with other two species, *P. nasutus* and *P. centralis*, the validity of *P. davisoni* is reinforced by its allopatric trans-Andean distribution, as currently recorded for other bat species, such as *Mormopterus kalinowski*, *Platyrrhinus chocoensis*, *Artibeus fraterculus*, *Eptesicus innoxius*, and *Eumops wilsoni*. Tuttle (1970) and Koopman (1978) discussed on the zoogeographical patterns of bats in the Peruvian Andes, and concluded that the bat fauna of the Pacific slopes of Peru may share elements with that of Ecuador (like *P. davisoni*) as well as with that of the Peruvian Amazon, but, usually, it is recognized that the Andes play an important role as an effective barrier to dispersion and genetic flow for many vertebrate taxa along a

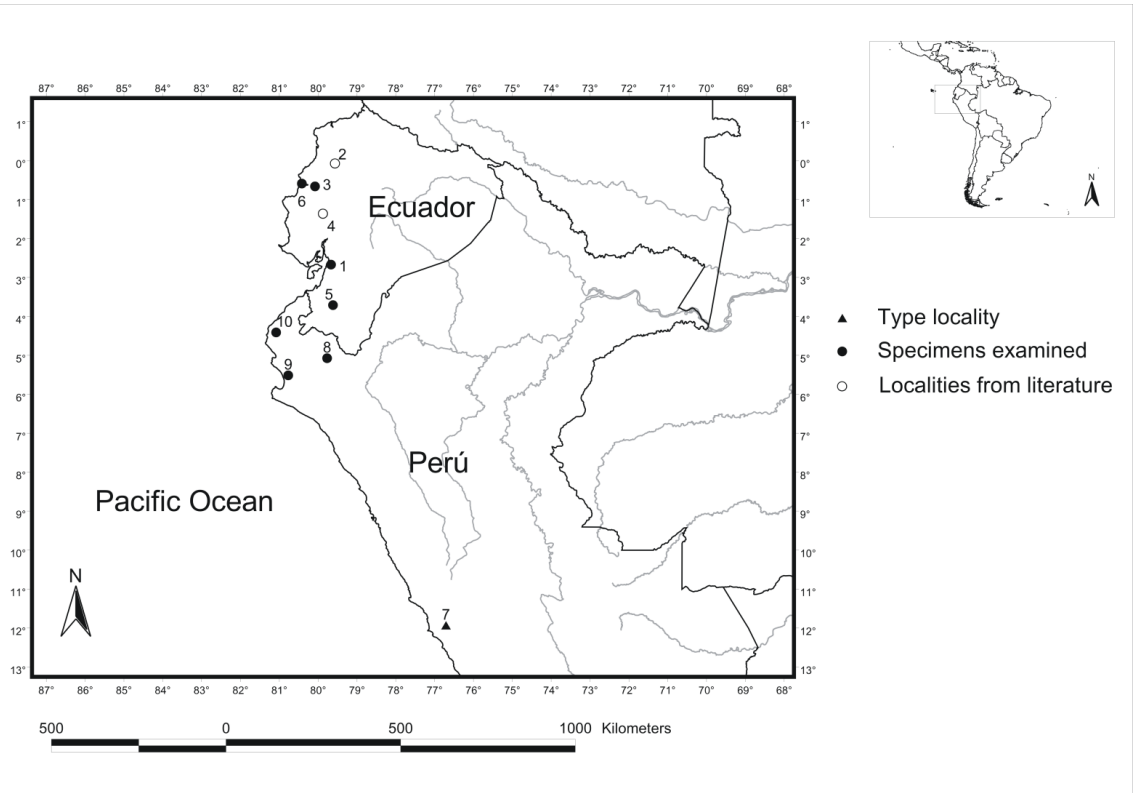

Figure 5 – Map of distribution of *P. davisoni* in Peru and Ecuador. 1 – Bucay, 2 – Hacienta Pacaritambo (Brosset, 1965), 3 – Manabí, 4 – La Papaya (Manabí) (Albuja, 1982), 5 – Portovelo, 6 – Rio de Oro, 7 – Chosica, 8 – Olmos, Lambayeque, 9 – Piura, and 10 – Talara.

west-east corridor. Indeed, the west-east connection is in northern Peru, and there is no record suggesting the connection evolving populations considered as *P. davisoni* and *P. nasutus* (or *P. centralis*), reinforcing the allopatry of both taxa.

Regards the substantial intraspecific geographical variation and the interspecific overlapping of the characters as usually employed in the taxonomy of *Promops* (e. g. pelage coloration and morphometrics), we concluded that there are at least three valid species for the genus: *P. centralis*, *P. nasutus*, and *P. davisoni*. We also concluded that to precisely define the taxa, analysis must be based on a set of characters studied together, including morphometrics, dorsal pelage coloration, and the banding pattern of the dorsal hairs. In this regard, *P. davisoni* is defined as presenting light or cinnamon brown dorsal pelage, a long whitish basal band in the dorsal hairs, and an intermediate size between the small *P. nasutus* and the large *P. centralis* (Figs. 2 and 4). We addressed that further analysis using more sensitive markers, like molecular ones, shall contribute to the better understanding of *Promops* taxonomy such as to evaluate the status of populations of *P. centralis* in Paraguay and Bolivia (namely *P. occultus*).

Acknowledgments

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Examined material

Promops centralis (total 63) – ARGENTINA: Formosa, Pirané MACN 16704, 16707-08. **BOLIVIA**: Roboré, Santa Cruz AMNH 260273-74. **BRAZIL**: Bragança, Pará USNM 392990. **COLOMBIA**: Pasto, Putamayo ROM 40361; Popayai, Cauca AMNH 181521; Rio Negro, Antioquia AMNH 149260. **GUATEMALA**: Coban, Verapaz AMNH 265131; Onimas (?) BM 75.2.27.59; Salama Baja, Verapaz FMNH 42087-88. **GUIANA**: Nappi Creek, Lethem ROM 6067. **FRENCH GUIANA**: Paracou, Sinnamary AMNH 269114. **HONDURAS**: El Pedrero, La Paz AMNH 126854-55; Los Encuentros, La Paz AMNH 126828. **PANAMA**: Ancon, Canal Zone AMNH 183871; Corozal, Canal Zone USNM 313048; Fort Amador, Canal Zone USNM 312119; Fort Clayton, Canal Zone AMNH 183866, 183899, USNM 317632; Fort Gulick, Canal Zone AMNH 183162. **PARAGUAY**: Altos (Departamento Cordillera) MVZ 145054-55; Concepción MVZ 145052; Filadelfia FMNH 157157-60; Mission Chaco BM 21.12.18.3; Recoleta, Asunción MVZ 145053, 145122; Sapucay BM 2.11.7.24 (holotype of *P. occultus*),

2.4.7.54, 2.4.7.58, FMNH 44099, USNM 116783, 121429, 121431; Villarica USNM 121430; 275 km from Villa Hayes MVZ 145056; **PERU**: Cuzco USNM 582879; La Concension USNM 577960-61. **MEXICO**: Tacarigan, Trinidad MVZ 167688; Tehuantepec, Oaxaca AMNH 178741-42, 232468, USNM 22036; Yucatán BM 94.2.5.3, 94.2.5.4 (holotype of *P. centralis*) USNM 37653; Yaxcach, Yucatán USNM 172076. **TRINIDAD**: George Village, Tableland AMNH 175652; San Fernando AMNH 179987; Tableland AMNH 178634, 175652-53, 178692-93. **VENEZUELA**: Rancho Grande AMNH 144838.

Promops nasutus (total 98) – **ARGENTINA**: Candelaria, Salta MACN 16712-16715; Cashi, Salta BM 6.5.8.4 (holotype of *P. ancilla*); Pellegrini, Santiago Del Estero MACN 16675-78, 16680-81, 16683, 16685, 16697-98, 16700, 16702; Tucumán BM 3.6.6.6; Yuto-Jujuy AMNH 184647-48. **BOLIVIA**: Cerro Amboro, Río Pitasamna, Santa Cruz AMNH 261851; Comapara, Santa Cruz AMNH 230603. **BRAZIL**: Bauru, São Paulo USNM 123826, MZUSP 502, 1305; Camarão, Bahia BM 3.9.5.24; Hyutanahan (=Huitanaã), Lavras, Minas Gerais CMUFLA 64-66, 162, 328; Rio Purus, Amazonas USNM 105528 (holotype of *P. pamana*); Itapé, Pará USNM 105595-97; Lageado, Rio Grande do Sul MCN 232-34, 238, 240; Rio Preto, Bahia FMNH 20884-86, 20888; Taquari, Rio Grande do Sul MCN 240-43, 245, 248-57, 1024; Viçosa, Minas Gerais CMUFV 1379, 1500, 1567, 1805. **GUIANA**: Dadanawa ROM 48864, 48870, 48872, 48874, 48878, 48881, 48884, 48887, 48890; Nappi Creek, Lethem ROM 31741, 31746, 31799. **PARAGUAY**: Parque Nacional Teniente Enciso, Nueva Asunción USNM 555683; Sapucay BM 3.4.7.8, 1.8.1.16, 1.8.1.18, USNM 102944, 102949, 114950, 121108, 121427-28, 121432-34; Villa Rica BM 1.8.1.17 (holotype of *P. fosteri*), 1.8.1.20, 1.8.1.21, USNM 105677, 114948. **TRINIDAD**: Port of Spain AMNH 186947 (holotype of *P. nasutus downsi*); **VENEZUELA**: Bolívar (near Caicara) USNM 405879; El Dorado, Bolívar USNM 387798; Río Manapiari, San Juan, Amazonas USNM 409633.

Promops davisoni (total 22) – **ECUADOR**: Bucay, Guayas AMNH 61481; Portovelo, El Oro AMNH 60532; Río de Oro, Manaví AMNH 34300, 34382; Manabe (=Manabí) FMNH 53543; La Papaya, Manabí FMNH 53510. **PERU**: Chosica, Lima BM 21.5.21.1 (holotype of *P. davisoni*), 21.5.21.2; Olmos, Lambayeque FMNH 81170-79; 81469-70; Suyo, Piura MACN 16696; Vale Poarinas, Talara, Piura FMNH 54949-50; Piura USNM 179330-31.