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Ontogenetic and Sexual Variation in cranial characters of *Aegialomys xanthaeolus* (Thomas, 1894) (Cricetidae: Sigmodontinae) from Ecuador and Peru

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ABSTRACT

Aegialomys xanthaeolus *(Cricetidae: Sigmodontinae) inhabits the arid montane areas of western Ecuador and Peru, and higher elevations in the upper Marañón valley in northern Peru. Some researchers have included this species in broader systematic assessments over the years, but there are no comprehensive studies focusing on intraspecific variation. There are several sources of intraspecific phenotypic variation, including sexual dimorphism and age. These sources may confound the assessment of similarity/dissimilarity among populations, therefore it is essential that non-geographic variation is evaluated before studies on geographical variation and species delimitation are carried out. Here we summarize existing information regarding the geographical distribution of* A. xanthaeolus *and evaluate variation related to sex and age. We analyzed 19 traditional cranio-dental measurements taken from specimens housed in scientific collections, and organized the collecting localities of specimens examined in a gazetteer and plotted them on a distribution map. Uni and multivariate statistical analyses allow us to assert that age variation was significant, as age classes 3, 4 and 5 can be pooled for the subsequent analysis of geographic variation and that sexual dimorphism is not a consistent component of variation within this species in the continental samples, when considering samples from the same locality, or localities close to each other.*

Keywords: Geographic Distribution; Skull; Ontogeny; Sexual Dimorphism; Morphometrics.

INTRODUCTION

The cricetid rodents of the genus *Aegialomys* are a trans-Andean group, distributed throughout the open habitats of the western Peruvian and Ecuadorean Andes, including the Galapagos Island (Musser & Carleton, 2005). The most recent contribution (Weksler *et al.,* 2006) that studied the *xanthaeolus* species group of the former genus *"Oryzomys"* (sensu lato, see Musser *et al.,* 1998; Percequillo, 1998, 2003; Weksler, 2003; Musser & Carleton, 2005), proposed a new generic name, *Aegialomys,* and recognized two species: *Aegialomys galapagoensis* (Waterhouse, 1839) and *Aegialomys xanthaeolus* (Thomas, 1894).

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According to Weksler *et al.* (2006) *Aegialomys xanthaeolus* inhabit the dry montane areas at western regions of Ecuador and Peru, reaching the high elevations (about 2500 m) in the upper Marañon valley, northern Peru. These authors describe *A. xanthaeolus* as a medium size rodent, with very long and dense dorsal pelage, coarsely grizzled yellowish- or grayish-brown and ventral pelage paler, with ventral hairs always gray-based; with small pinnae and mystacial vibrissae not extending posteriorly beyond pinnae when laid back; with hind foot with conspicuous tufts of ungual hairs; with tail distinctly longer than head and body, weakly to distinctly bicolored. This species also exhibit small to moderately large skull, with strongly beaded supraorbital ridges, long incisive foramina, usually long palate, large sphenopalatine vacuities, the derived pattern of carotid circulation (type 3 of Voss, 1988), and large auditory bullae.

Over the years, few publications dealt with some biological aspects (karyology, morphological comparisons, phylogenetic position) of oryzomyine taxa, including *Aegialomys xanthaeolus* (Thomas, 1894; Heller, 1904; Cabrera, 1961; Gardner & Patton, 1976; Patton & Hafner, 1983; Weksler, 2003, 2006; Weksler *et al.,* 2006), but none of them studied the intra-specific variation structure, aiming to evaluate the validity of some species group taxa associated with this species (Weksler *et al.,* 2006).

According to Reis *et al.* (1990), description of patterns of variation in morphologic and genetic characters within and among populations is essential to detect independent evolutionary subunits, an important aspect to comprehend species variation and limits. Mayr (1969) stated that there are several sources of phenotypic variation among species, which he classified as non-genetic (ontogenetic, seasonal, social, ecologic and traumatic variation) and genetic (related to sex, continuous and discontinuous variation). These variations can obscure the evaluation and recognition of similarity and dissimilarity among populations (Abdel-Rahman *et al.,* 2008). It is therefore fundamental that non-geographic variation, such as sexual dimorphism and ontogenetic variation should be clarified before studies related to geographic variation and species delimitation are carried out (Thorpe, 1976; Patton & Rogers, 1983; Reis *et al.,* 1990, 2002). In studies focusing on rodents, sample sizes are frequently too small to enable the assessment of all these genetic and non-genetic variation. Therefore, the majority of non-geographic analyses only examine sexual dimorphism and ontogenetic variation (Abdel-Rahman *et al.,* 2008).

Although usually neglected in recent times, study of non-geographic variation attracts the interest of biologists since Darwin (Abdel-Rahman *et al.,* 2008). There are several examples that documented shape differences among individuals of one population or between co-specific populations, than among closely related species (Mayr, 1977). Among mammals, taxa that have noticeable difference in body size regarding sex belong to the orders Primates and Proboscidea, to the suborders Odontoceti, Pinnipedia, Ruminantia and to families Macropodidae and Mustelidae (Weckerly, 1998).

In the present contribution, we evaluate and describe non-geographic variation in *Aegialomys xanthaeolus,* especially related to sexual and age variation; and present information on the geographical distribution of this species.

MATERIAL AND METHODS

Samples

We examined specimens from the following museum collections: American Museum of Natural History, New York, United States (AMNH); Natural History Museum, London, England (BMNH); The Field Museum, Chicago, United States (FMNH); Louisiana State University, Museum of Zoology, Baton Rouge, United States (LSUMZ); Museum of Vertebrate Zoology, University of California, Berkeley, United States (MVZ); Smithsonian Institution National Museum of Natural History, Smithsonian Institution, Washington D.C., United States (NMNH).

Gazetteer

The collecting localities are organized in alphabetical order by country, state or province and locality. Descriptions of localities, geographical coordinates and elevation data were obtained as accurately as possible from specimen labels. The following sources were also used to obtain geographic coordinates: United States Board on Geographical Names (USBGN, NIMA; see http://gnswww.nga.mil/geonames/GNS/index.jsp), Stephens & Traylor (1983), and Paynter (1993).

Definition of Locality Clusters

In order to increase the sample size and to reduce the probability of geographic variation within samples, we pooled some closely geographic collection localities, and thus making more feasible analyses of non-geographic variance. We defined some criteria to pool these localities, in order to avoid the pooling of samples that could be subjected to geographic variation. We only clustered samples: from the same altitudinal gradient; that are not separated by large rivers or other geographic accident, such as cliffs, ravines, high mountains (*e.g.,* Andean Cordillera); and, that are surrounding a larger sample, within a radius of *ca.* 50 km.

On the other hand, in order to compare the non-geographic variation on the whole distribution of genus (except Galapagos Islands samples) with the non-geographic variation observed in the small clusters of localities, we also pooled all available samples in one large *Aegialomys* sample.

Cranio-Dental Measurements

We obtained measurements (in mm) from the skull and the teeth of all specimens examined. A 0.01 mm precision caliper was used to obtain the measurements of the following cranio-dental dimensions:

Total length of skull (TL): measured from the anterior margin of nasals to the posteriormost portion of the occipital;

Condylo-incisive length (CIL): measured from the greater curvature of the upper incisor to the articular surface of the occipital condyle, on the same side of the skull;

Length of diastema (LD): measured from the crown of the first upper molar to the inner side of the base of the upper incisor on the same side of the skull;

Length of molars (LM): measured from the anterior surface of the first upper molar to the posterior surface of the third upper molar, at the crown of the molars;

Breadth of M1 (BM1): greatest breadth of the first upper molar measure of the base crown, the height of the protocone;

Length of incisive foramen (LIF): the greatest length measured from the anterior edge to posterior edge of incisive foramen;

Breadth of incisive foramen (BIF): the greatest internal breadth, measured on the lateral margins of the incisive foramen;

Palatal breadth (PB): measured in the external lateral portion of the maxillary, between the second and third molar;

Breadth of interparietal (BIP): greatest breadth of interparietal bone;

Length of interparietal (LIP): greatest length (anteroposterior) of interparietal bone;

Breadth of rostrum 2 (BR2): measured across the rostrum, at the posterior extremity of the upper edge of the infraorbital foramen;

Length of nasal (LN): measured from the anteriormost end of the nasal to the naso-frontal suture;

Length of palatal bridge (LPB): measured from the posterior margin of incisive foramen to the anterior margin of mesopterygoid fossa;

Least interorbital breadth (LIB): shortest distance through the frontals in the orbital fossa;

Zygomatic breadth (ZB): greatest external distance of the zygomatic arches, close to the squamosal roots, measured across the skull;

Breadth of zygomatic plate (BZP): the shortest distance between the anterior and posterior margin of the inferior zygomatic root or zygomatic plate;

Condylo-zygomatic length (CZL): shortest distance between the posteriormost point of occipital condyle and the posteriormost point of the upper edge of the zygomatic notch;

Orbital fossa length (OFL): greatest dimension of the orbital fossa between the squamosal and maxillary roots of zygomatic arch;

Bullar breadth (BB): measured from the petrosal suture with the basioccipital to dorsal process of ectotympanic.

Sexual Dimorphism and Age Classes

Specimens were separated regarding sex, for the evaluation of sexual dimorphism. In addition, we classified specimens in age classes (1, 2, 3, 4 and 5), according to the eruption and wear of occlusal surfaces of molars, as well as aspects of the pelage, following Voss (1991) and Percequillo (1998):

Age class 1: First and second molars without apparent wear, with labial flexus open and conspicuous. Third molar is usually non-erupted or newly erupted, with the main cusps still closed, without dentine exposition. Dorsal pelage is predominantly gray and ventral pelage is grayish.

Age class 2: In this class, first and second molars with minor wear, with main cusps high and with small exposure of dentine; some flexi closed, forming fossets (especially anteroflexus and posteroflexus). Third molar already showing wear, but minimal to moderate. Dorsal pelage is predominantly gray and ventral pelage is grayish.

Age class 3: First and second molar in this class with medium wear, with the cusps conspicuously eroded and with large dentin exposure; nearly all labial flexi closed (especially para-, meso-, and metaflexus) and some fossetes (posterofessete). Third molar exhibit marked wear, with nearly flat to flat surface. Dorsal pelage is coarsely grizzled yellowish- or grayish-brown, with the aristiform hairs with the tip yellow and ventral pelage is pale yellow.

Age class 4: First and second molar with heavy wear, with flat and indistinct cusps and massive exposure of dentine; most fossetes eroded (para- and metafossete more persistent). Third molar appears quite flat, with major exposure of dentine. Dorsal pelage is coarsely grizzled yellowish- or grayish-brown, with the aristiform hairs with the tip yellow and ventral pelage is cream.

Age class 5: Three molars are completely worn, with large exposition of dentine. Dorsal pelage is coarsely grizzled yellowish- or grayish-brown, with the aristiform hairs with the tip yellow and ventral pelage is cream.

Statistical Analysis

The sample was first assessed for univariate normality, according to the Kolmogorov-Smirnov test (KS) and for multivariate normality, according the Mardia Kurtosis test (Sokal & Rohlf, 1997; Kankainen, *et al.* 2003).

We calculated descriptive statistics for samples and applied the *t* test to check for sexual dimorphism. We then employed analysis of variance (ANOVA and MANOVA) and Tukey's *post hoc* test to check for age variation. Firstly, in the *Aegialomys* sample we implemented the following analyses: age variation with males and females pooled, then age variation with sexes separated; sex variation, comparing males and females from age class 3 and class 4, separately. Secondly, we performed the same analyses in the selected largest available clusters of localities. This was conducted to evaluate different approaches to access non-geographic variation.

Principal Component Analysis and Discriminant Function Analysis were computed using a combination of cranio-dental measurements. Principal Components were extracted from the correlation matrix and canonical variables were extracted for the Discriminant Function Analysis (Johnson & Wichern, 1999; Manly, 2005). These multivariate analyses were performed with the *Aegialomys* sample, since as an *a priori* evaluation, PCA will summarize the entire variation of the sample, whether non-geographic or geographic.

RESULTS

Geographical Distribution

We examined 465 specimens (Appendix A), and based on the information provided by these we elaborated a gazetteer with 90 localities from Peru and Ecuador (Appendix B) and an updated distribution map for the species (Fig. 1 and 2).

The distribution of *Aegialomys xanthaeolus* is limited by Esmeraldas (Esmeraldas Province, Ecuador) to the north; by Chavina (Arequipa Department, Peru) to the south; by Hacienda Buena Vista, Chinchao (Huanuco Department, Peru) to the east; and the coastline of Ecuador and Peru to the west, except from its presence in a continental island, Isla Puna, in Ecuador. Altitudinal records of *A. xanthaeolus* range from sea level, in the localities Esmeraldas, Cuaque and Bahia de Caraquez (all located in Ecuador), to 2743 m in the locality 5 miles East of Yanyos (Peru).

This is a trans-Andean species, with most localities (*ca.* 66%) located on the coastal lowlands of Peru and Ecuador and part of collection samples (*ca.* 34%) located in the Andean Cordillera, on the upper part of mountain slopes and on the deep portions of river valleys.

Definition of Locality Clusters

Samples analyzed in this study were pooled into nine geographic clusters (Table 1 and Fig. 3); the numbers of localities in the Table 1 corresponds to the number shown in the gazetteer given in Appendix B.

Intraspecific variation: Age and Sex

The univariate normality test Kolmogorov-Smirnov was applied to each of the nine geographic groups, and all variables showed a normal distribution (results not shown). Accordingly to Manly (2005), if all the individual variables under study are normally distributed, then it is plausible to assume that the multivariate distribution is also normal. Nevertheless, we also performed Mardia Kurtosis test (p = 0,000) and its coefficient was 618.02, showing that all variables are also normally distributed in multivariate space.

Aiming to evaluate sex and age variation we perform a MANOVA with all specimens (*Aegialomys* sample) and in the Isla Puna, respectively. The results of first MANOVA for sex*ages effects are depicted in Table 2. Both age and sex, as well the interactions between factors were shown to be statistically different. The results of the MANOVA for Isla Puna sample for sex*ages effects revealed (Table 3) that age, sex and interaction between these factors was not statistically different.

These discrepant results lead us to investigate the variation of univariate level, and we first conducted a series of ANOVA's and Student's *t* analyses to test age and sex variation. Regarding age, we first compared the five age classes on the *Aegialomys* sample. The results (Table 4) showed that all variables, except LIP, showed differences among age classes. The *post hoc* Tukey test revealed significant difference between classes 1 and 2 for 12 variables, TL, CIL, LD, LM, LIP, BR2, LN, LPB, ZB, BZP, CZL and OFL; even when compared to other age classes, the class 1 is very different. Classes 2 and 3 differ in 12 variables TL, CIL, LD, LIF, BIF, BR2, BIP, LN, LPB, ZB, BZP,

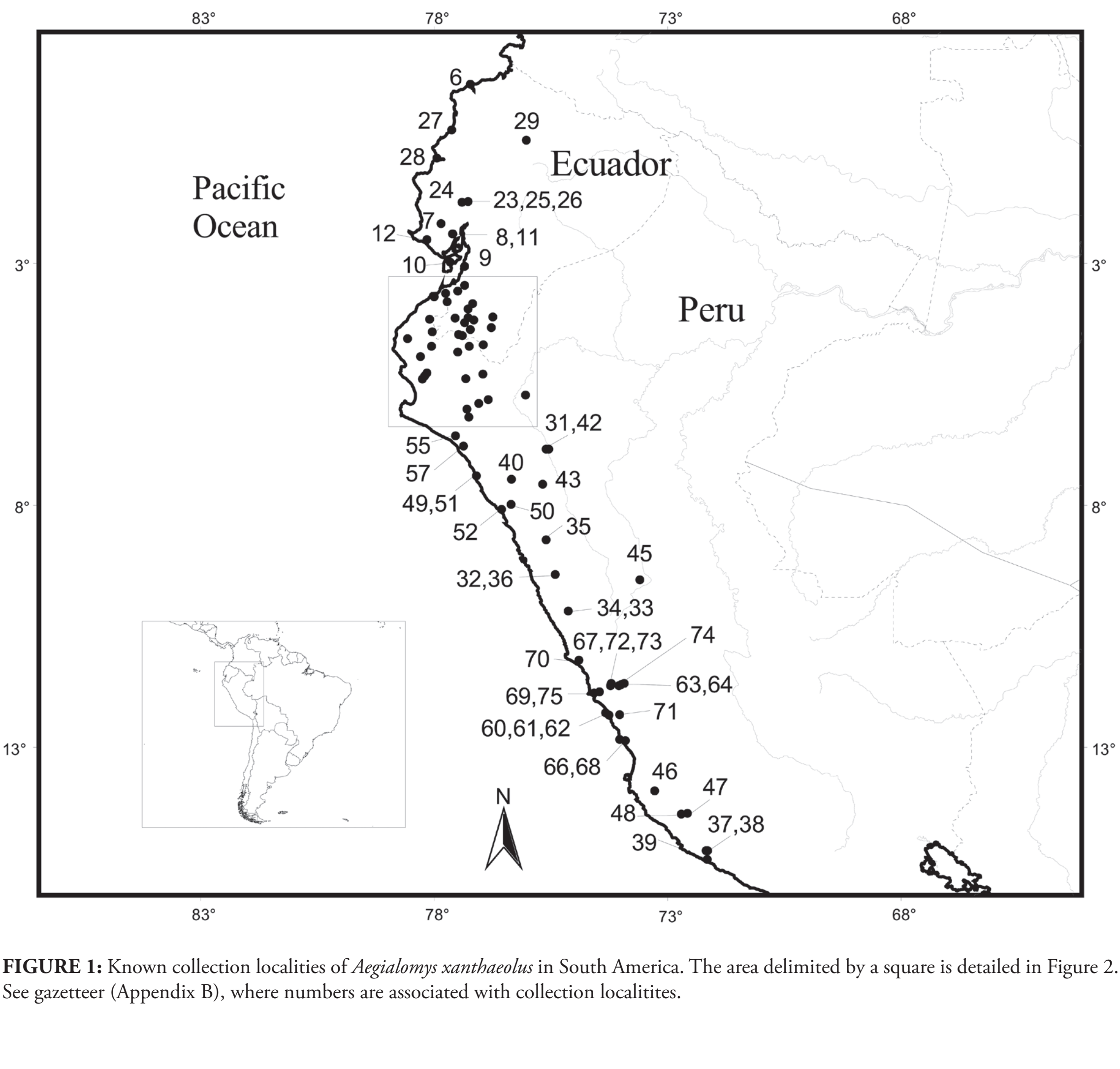

FIGURE 1: Known collection localities of *Aegialomys xanthaeolus* in South America. The area delimited by a square is detailed in Figure 2. See gazetteer (Appendix B), where numbers are associated with collection localitites.

TABLE 1: Composition of Clusters (The numbers preceding the names of localities correspond to the index localities and the number beside the name of the group correspond to the total number of the individuals of the cluster).

Cluster	Localities
I – Vinces (22)	26. Hacienda El Carmen, Vinces
	27. Hacienda Pijigual, Vinces
	28. Hacienda Santa Teresita (Abras de Mantequilla), *ca.* 12 km NE Vinces
	29. Vinces, near Puerto Nuevo and Vinces
II – Chongón (48)	11. Chongoncito, Guayaquil
	14. Rio Chongón. 1.5 km SE Chongón
III – Isla Puna (45)	13. Isla Puna, San Ramon, Guayaquil
IV – Pasaje-Zarumilla (39)	2. Pasage
	5. Santa Rosa
	91. Matapalo, Zarumilla
	92. Positos, Zarumilla
V – Portovelo (27)	1. 12 km E by road Portovelo
	3. Portovelo
	4. Rio Pindo, Portovelo
VI – Casanga (40)	18. Casanga River Valley
	20. Hacienda Casanga, Paltas
VII – Piura-La Arena (18)	78. Catacaos
	82. Hacienda San Luis, La Arena
	89. Piura
VIII – Trujillo (20)	52. Menocucho, Trujillo
	54. Trujillo
IX – Nazca (21)	49. Hacienda San Pablo, El Ingenio, 30 km Nasca
	50. San Javier, 13 km S Palpa

CZL and OFL. Classes 3 and 4 were different on 14 variables, TL, CIL, LD, BM1, LIF, PB, BR2, LN, LPB, ZB, BZP, CZL, OFL and BB. The classes 4 and 5 did not show significant differences.

In addition we performed an ANOVA for the age classes within each sex separately. First within males, the results (Table 5) showed that all variables, except BM1 and LIP, showed differences among age classes. The *post hoc* Tukey test revealed significant difference between classes 1 and 2 for 11 variables, TL, CIL, LD, LM, BR2, LN, LPB, ZB, BZP, CZL and OFL. Classes 2 and 3 are different for 12 variables TL, CIL, LD, LIF, BIF, BIP, BR2, LN, LPB, ZB, CZL and OFL. Classes 3 and 4 were different on 8 variables, TL, CIL, LD, BR2, LPB, ZB, BZP and CZL. The classes 4 and 5 did not show significant differences again. Second within females, the results (Table 6) showed that all variables showed differences among age classes, except LM and LIP. The *post hoc* Tukey test revealed significant difference between classes 1 and 2 for LPB and BZP. Classes 2 and 3 differ in 10 variables, TL, CIL, LD, LIF, BR2, LN, ZB, BZP, CZL and OFL. Classes 3 and 4 were different for 13 variables, TL, CIL, LD, BM1, LIF, PB, LIP, LN, ZB, BZP, CZL, OFL and BB. The classes 4 and 5 did not show significant differences.

Subsequently we evaluated the age variation within the best sample, Isla Puna, but this group did

TABLE 2: Results for the multivariate analysis of variance performed for the fixed effects of a priori ages, sex, and the interaction between them for total sample, on *Aegialomys xanthaeolus* specimens.

	Hotelling's Trace	*F*	Hypothesis df	Error df	Sig.
Age	1.347	3.744	84	934	0.000
Sex	0.150	1.679	21	235	0.035
Age*Sex	0.500	1.390	84	934	0.014

Values significant at the α = 0.05 level.

TABLE 3: Results for the multivariate analysis of variance performed for the fixed effects of a priori ages, sex, and the interaction between them for Isla Puna, on *Aegialomys xanthaeolus* specimens.

	Hotelling's Trace	*F*	Hypothesis df	Error df	Sig.
Age	16.346	0.000	36	0	0.890
Sex	34.277	1.904	18	1	0.971
Age*Sex	20.182	0.000	36	0	0.909

Values significant at the α = 0.05 level.

TABLE 4: ANOVA followed by Tukey test between age classes for the entire sample of 19 cranio-dental variables. Values in bold represent statistical difference at 5% in Tukey test and the * represent statistical difference at 5% in ANOVA.

Var	ANOVA	Tukey									
	F	1/2	1/3	1/4	1/5	2/3	2/4	2/5	3/4	3/5	4/5
TL	42.126*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.020**	0.393
CIL	48.206*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.378
LD	50.346*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.406
LM	4.763*	**0.009**	**0.001**	**0.000**	**0.021**	0.996	0.736	0.999	0.721	0.976	0.638
BM1	4.136*	0.875	0.996	0.685	0.946	0.811	**0.007**	0.172	**0.008**	0.413	0.961
LIF	26.749*	0.080	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	0.601
BIF	14.694*	0.265	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.335	0.316	0.991
PB	10.406*	0.701	**0.021**	**0.000**	**0.001**	0.103	**0.000**	**0.002**	**0.002**	0.158	0.993
BIP	8.168*	0.891	**0.009**	**0.001**	**0.002**	**0.002**	**0.000**	**0.001**	0.600	0.632	0.999
LIP	1.492	—	—	—	—	—	—	—	—	—	—
BR2	37.786*	**0.001**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.054
LN	36.085*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.002**	**0.000**	0.317
LPB	34.619*	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.008**	0.052	0.999
LIB	6.723*	0.298	**0.025**	**0.001**	**0.000**	0.741	**0.036**	**0.012**	0.101	**0.037**	0.887
ZB	7.077*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	0.228
BZP	37.215*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	0.053
CZL	59.810*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.583
OFL	46.110*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.003**	**0.000**	0.460
BB	35.266*	0.233	**0.008**	**0.000**	**0.000**	0.532	**0.005**	**0.022**	**0.033**	0.149	0.999

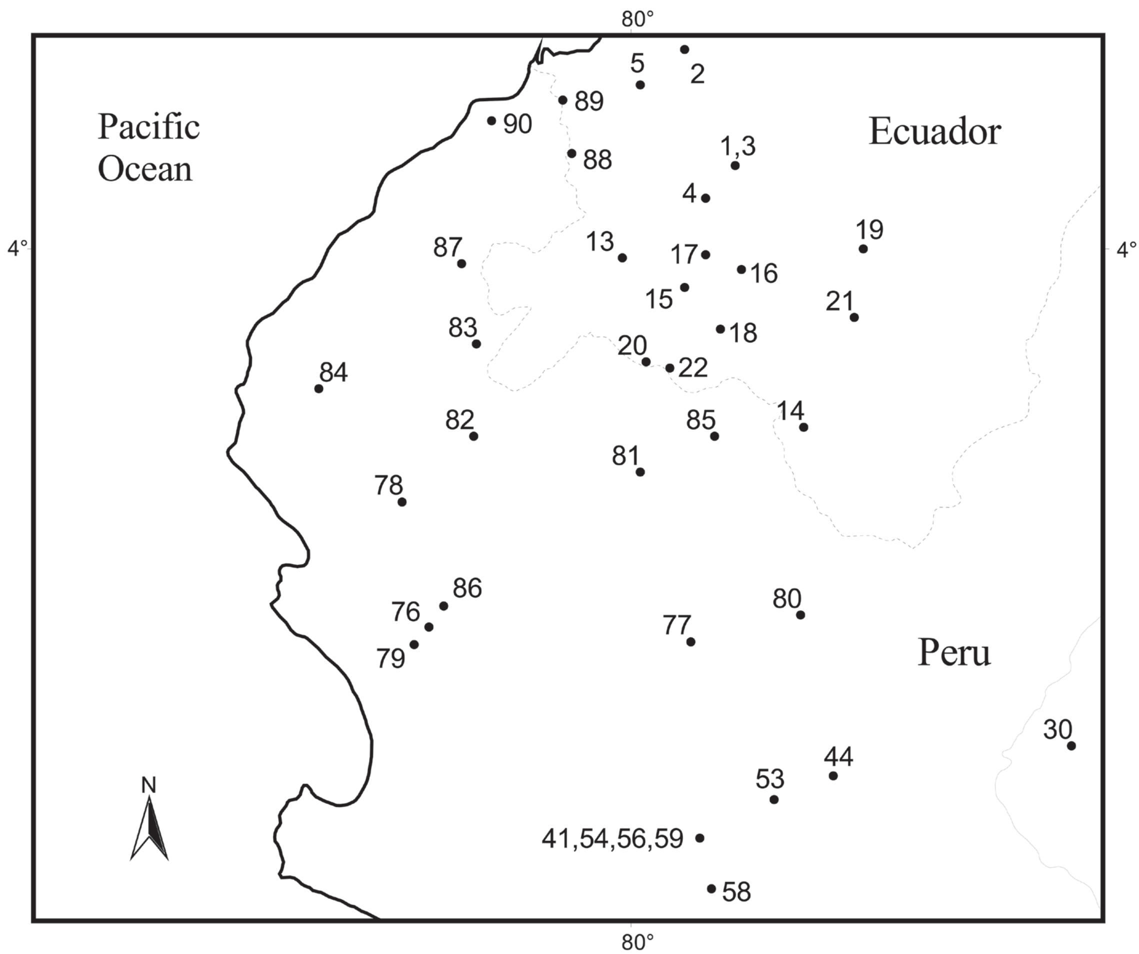

FIGURE 2: Detail of map showing known collection localities for *Aegialomys xanthaeolus*.

TABLE 5: ANOVA followed by Tukey test between age classes for the entire sample of 19 cranio-dental variables in males. Values in bold represent statistical difference at 5% in Tukey test and the * represent statistical difference at 5% in ANOVA.

Var	ANOVA	Tukey									
	F	1/2	1/3	1/4	1/5	2/3	2/4	2/5	3/4	3/5	4/5
TL	21.769*	**0.000**	**0.000**	**0.000**	**0.000**	**0.038**	**0.000**	**0.000**	**0.006**	0.173	0.997
CIL	27.638*	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.002**	0.054	0.999
LD	32.613*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.003**	0.058	0.999
LM	4.495*	**0.036**	**0.001**	**0.002**	0.204	0.856	0.835	0.949	0.999	0.421	0.433
BM1	1.672	—	—	—	—	—	—	—	—	—	—
LIF	15.199*	0.073	**0.000**	**0.000**	**0.000**	**0.002**	**0.000**	**0.000**	0.073	0.353	0.999
BIF	9.634*	0.600	**0.000**	**0.000**	**0.011**	**0.000**	**0.000**	0.114	0.993	0.943	0.878
PB	6.863*	0.662	**0.015**	**0.000**	**0.008**	0.109	**0.001**	0.068	0.119	0.788	0.988
BIP	3.848*	0.999	0.270	0.157	0.181	**0.034**	**0.022**	0.052	0.918	0.922	0.999
LIP	0.406	—	—	—	—	—	—	—	—	—	—
BR2	20.766*	**0.010**	**0.000**	**0.000**	**0.000**	**0.002**	**0.000**	**0.000**	**0.000**	**0.013**	0.998
LN	15.541*	**0.000**	**0.000**	**0.000**	**0.000**	**0.028**	**0.000**	**0.010**	0.112	0.574	0.999
LPB	26.138*	**0.000**	**0.000**	**0.000**	**0.000**	**0.032**	**0.000**	**0.000**	**0.005**	0.197	0.999
LIB	6.343*	0.370	**0.015**	**0.000**	**0.009**	0.456	**0.007**	0.235	0.058	0.806	0.949
ZB	21.085*	**0.000**	**0.000**	**0.000**	**0.000**	**0.004**	**0.000**	**0.000**	**0.022**	0.084	0.999
BZP	29.277*	**0.000**	**0.000**	**0.000**	**0.000**	0.053	**0.000**	**0.001**	**0.015**	0.109	0.999
CZL	25.836*	**0.000**	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.004**	0.167	0.995
OFL	18.714*	**0.000**	**0.000**	**0.000**	**0.000**	**0.007**	**0.000**	**0.001**	0.137	0.399	0.999
BB	4.759*	0.110	**0.002**	**0.000**	**0.012**	0.525	0.224	0.762	0.831	0.999	0.968

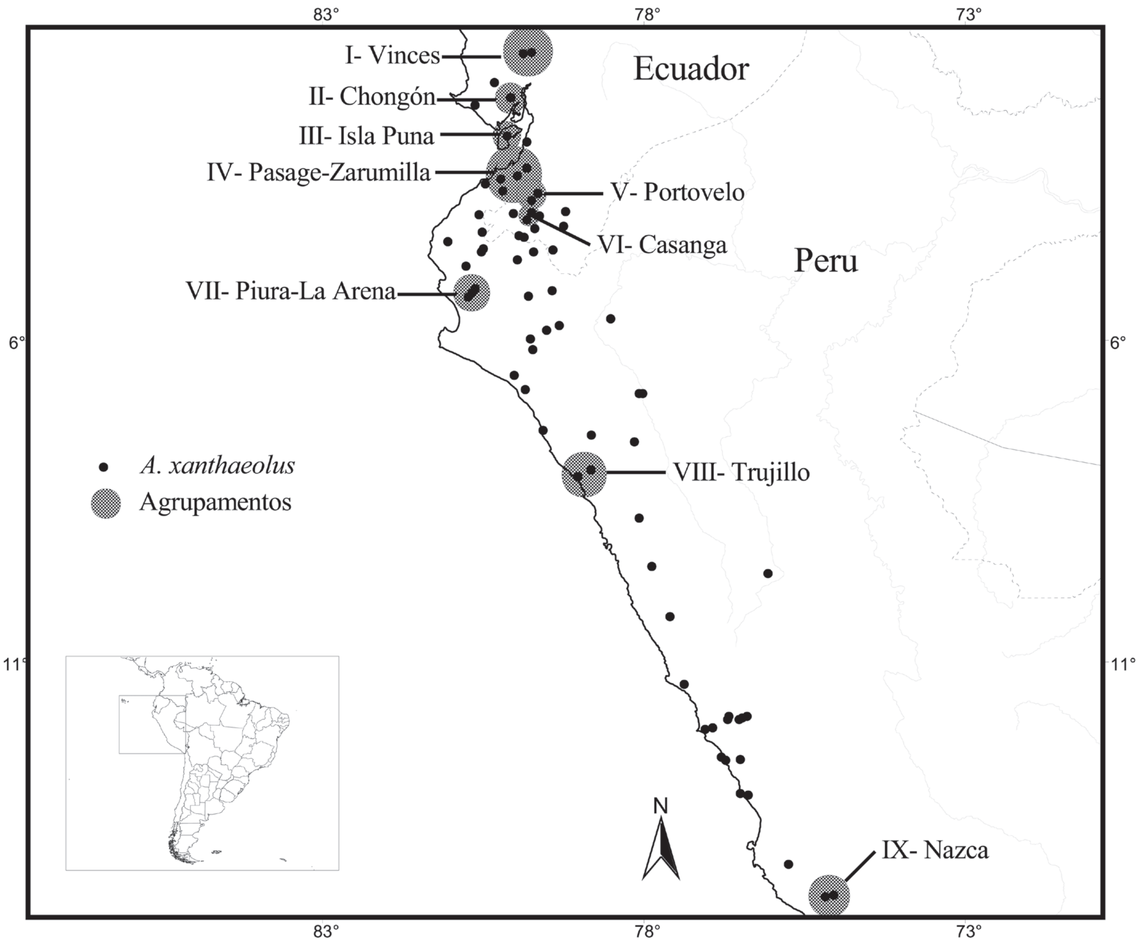

FIGURE 3: Clusters tested in this study.

TABLE 6: ANOVA followed by Tukey test between age classes for the entire sample of 19 cranio-dental variables in females. Values in bold represent statistical difference at 5% in Tukey test and the * represent statistical difference at 5% in ANOVA.

Var	ANOVA	Tukey									
	F	1/2	1/3	1/4	1/5	2/3	2/4	2/5	3/4	3/5	4/5
TL	24.278*	0.113	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.014**	**0.000**	0.085
CIL	24.760*	0.264	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.002**	**0.000**	0.123
LD	22.314*	0.245	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.027**	**0.000**	0.104
LM	1.789	—	—	—	—	—	—	—	—	—	—
BM1	2.965*	0.608	0.723	0.998	0.999	0.982	0.085	0.488	**0.032**	0.568	0.973
LIF	11.727*	0.995	0.128	**0.002**	**0.000**	**0.040**	**0.000**	**0.000**	**0.032**	**0.000**	0.397
BIF	6.521*	0.885	0.129	**0.005**	**0.003**	0.315	**0.006**	**0.004**	0.126	0.080	0.950
PB	4.327*	0.999	0.927	0.167	0.398	0.529	**0.005**	0.083	**0.034**	0.436	0.994
BIP	4.823*	0.929	0.096	**0.015**	**0.032**	0.128	**0.011**	**0.045**	0.565	0.777	0.999
LIP	1.560	—	—	—	—	—	—	—	—	—	—
BR2	19.150*	0.279	**0.000**	**0.000**	**0.000**	**0.007**	**0.000**	**0.000**	**0.050**	**0.000**	**0.036**
LN	23.660*	0.173	**0.000**	**0.000**	**0.000**	**0.001**	**0.000**	**0.000**	**0.007**	**0.000**	0.088
LPB	11.927*	**0.037**	**0.000**	**0.000**	**0.000**	0.074	**0.002**	**0.001**	0.340	0.154	0.907
LIB	3.721*	0.998	0.907	0.499	0.052	0.928	0.381	**0.016**	0.552	**0.015**	0.321
ZB	22.469*	0.361	**0.000**	**0.000**	**0.000**	**0.014**	**0.000**	**0.000**	**0.001**	**0.000**	0.081
BZP	33.039*	**0.000**	**0.000**	**0.000**	**0.000**	**0.004**	**0.000**	**0.000**	**0.030**	**0.000**	**0.002**
CZL	24.859*	0.229	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.004**	**0.000**	0.156
OFL	20.302*	0.441	**0.000**	**0.000**	**0.000**	**0.002**	**0.000**	**0.000**	**0.011**	**0.000**	0.206
BB	5.995*	0.999	0.942	0.125	**0.046**	0.905	**0.019**	**0.006**	**0.015**	**0.007**	0.902

not address all age classes, this way the analysis of age variation (ANOVA) were conducted only in the classes 3, 4 and 5 (Table 7) showing that for variables TL, CIL, LD, BR2, LN, LPB, ZB, BZP and CZL there are significant differences between these three age classes. The *post hoc* Tukey test showed that for 8 variables, TL, CIL, LD, BR2, LPB, ZB, BZP and CZL the age 3 is significantly different from the age 4; for CIL, ZB and BZP, age 3 is significantly different from age 5, and for any variable the class 4 is significantly different from class 5.

Regarding sexual dimorphism in *Aegialomys xanthaeolus,* we also compared males and females on *Aegialomys* sample with all age classes separately and then in the Isla Puna sample within classes 3 and 4 separately (we could not perform the analysis in class 5 due to small sample sizes), to avoid the influence of age variation in the samples. The results of the analysis in the *Aegialomys* sample are (see Table 8): in the class 1, only PB and BB showed significant difference between sexes; considering class 2, only TL and LN showed significant difference between sexes; regarding class 3, 13 variables showed significant difference: TL, CIL, LD, BIF, BR2, LN, LPB, LIB, ZB, BZP, CZL, OFL and BB; in class 4, only six variables showed significant difference, TL, CIL, LD, LIB, BR2 and CZL; and finally, specimens classified as class 5 exhibited no significant difference between sexes. On Isla Puna sample (Table 9), 13 variables showed significant difference between sexes, TL, CIL, LD, LM, BIF, PB, LPB, LIB, ZB, BZP, BR2, CZL and OFL, for age class 3. When considering class 4, only three variables (TL, CIL and LD), showed significant difference between sexes.

To verify how sexual dimorphism is structured along the geography, comparisons were performed

TABLE 7: ANOVA followed by Tukey test between age classes 3, 4 and 5 for the cluster Isla Puna of 19 cranio-dental variables. Values in bold represent statistical difference at 5% in Tukey test and the * represent statistical difference at 5% in ANOVA.

Variable	ANOVA	Tukey		
	F	3/4	3/5	4/5
TL	3.797*	**0.044**	0.185	0.919
CIL	6.841*	**0.007**	**0.029**	0.794
LD	4.927*	**0.016**	0.119	0.944
LM	0.166	—	—	—
BM1	0.896	—	—	—
LIF	0.203	—	—	—
BIF	1.510	—	—	—
PB	0.014	—	—	—
BIP	1.097	—	—	—
LIP	0.278	—	—	—
BR2	4.943*	**0.030**	0.055	0.699
LN	3.389*	0.069	0.158	0.877
LPB	4.404*	**0.034**	0.097	0.818
LIB	0.676	—	—	—
ZB	11.917*	**0.003**	**0.000**	0.145
BZP	5.956*	**0.040**	**0.013**	0.305
CZL	5.855*	**0.009**	**0.077**	0.938
OFL	1.262	—	—	—
BB	0.696	—	—	—

TABLE 8: Results of Student *t* tests between sexes for the total sample in each age class on 19 cranio-dental variables, containing the value of *t*. Values in bold represent statistical difference at 5%.

Variable	1	2	3	4	5
TL	-0.988	**2.691**	**2.745**	**2.194**	-0.711
CIL	-1.677	1.470	**2.923**	**2.146**	-0.431
LD	-1.936	1.887	**2.992**	**2.612**	0.133
LM	-0.850	-0.381	1.222	-0.557	-1.656
BM1	-1.286	-0.642	0.357	-0.586	-1.046
LIF	-1.883	0.306	1.760	1.017	-0.599
BIF	-0.855	-0.708	**2.726**	0.423	-1.156
PB	**-2.478**	-0.575	0.366	-0.023	-0.079
BIP	0.560	-0.057	1.343	0.432	0.860
LIP	-0.434	1.139	1.601	1.379	-0.585
BR2	-1.299	1.443	**3.015**	3.001	0.585
LN	-0.812	**2.993**	**2.797**	1.339	-1.323
LPB	-1.536	0.872	**2.210**	**2.926**	1.033
LIB	-1.109	1.096	**3.824**	**3.379**	0.428
ZB	-1.952	0.932	**2.689**	1.336	-0.830
BZP	-0.533	1.713	**2.155**	1.640	-1.658
CZL	-1.766	1.322	**2.900**	**2.090**	-0.578
OFL	-1.679	1.865	**3.167**	1.521	-0.589
BB	**-3.105**	0.343	**2.576**	-0.030	-0.867

TABLE 9: Results of Student *t* tests between sexes for the Isla Puna in age class 3 and 4 on 19 cranio-dental variables, containing the value of *t*. Values in bold represent statistical difference at 5%.

Variable	3	4
TL	**2.745**	**2.194**
CIL	**2.923**	**2.146**
LD	**2.992**	**2.612**
LM	1.222	-0.557
BM1	0.357	-0.586
LIF	1.760	1.017
BIF	**2.726**	0.423
PB	0.366	-0.023
BIP	1.343	0.432
LIP	1.601	1.379
BR2	**3.015**	3.001
LN	**2.797**	1.339
LPB	**2.210**	**2.926**
LIB	**3.824**	**3.379**
ZB	**2.689**	1.336
BZP	**2.155**	1.640
CZL	**2.900**	**2.090**
OFL	**3.167**	1.521
BB	**2.576**	-0.030

between male and female individuals with age classes separately for the clusters Pasaje-Zarumilla (IV), Casanga (VI) and Nazca (IX; see Table 10); the small sample size of the other clusters precluded us to conduct these comparative analyses. According to the availability of sample, differents age classes were tested in differents clusters. In the Pasage-Zarumilla (IV) sample, only class 3, 4 and 5 could be tested, the

TABLE 10: Results of Student *t* tests between sexes for the clusters IV, VI and IX, in age class 3, 4 and 5, on 19 cranio-dental variables, containing the value of *t*. Values in bold represent statistical difference at 5%.

Variable	IV			VI		IX	
	3	4	5	4	5	3	4
TL	1.101	1.308	-0.339	—	0.412	1.144	0.674
CIL	1.099	1.426	-0.301	—	0.534	1.216	0.759
LD	0.323	**3.295**	0.566	0.293	2.721	0.919	0.629
LM	-0.089	-0.607	-0.772	0.951	5.196	2.302	-2.050
BM1	-0.922	-0.300	0.077	0.266	-0.288	2.168	-2.301
LIF	0.503	0.350	-0.228	0.416	-0.336	1.529	1.034
BIF	0.366	1.463	-1.856	0.577	-0.522	1.761	0.519
PB	-0.428	-0.348	1.148	0.838	-5.196	1.280	-2.128
BIP	-0.822	-0.591	0.718	—	3.532	-0.984	-0.617
LIP	-0.590	-0.950	1.590	—	0.251	0.421	0.482
BR2	1.075	**3.224**	0.288	0.891	-0.782	0.668	0.870
LN	0.876	1.598	-0.132	0.264	10.199	1.009	0.321
LPB	1.164	**3.168**	0.530	0.104	3.676	1.485	0.940
LIB	1.579	**5.683**	0.632	0.705	7.949	**6.575**	1.833
ZB	1.973	0.191	-0.212	0.372	0.096	1.379	0.068
BZP	1.251	1.130	-0.300	0.288	-0.726	0.741	0.352
CZL	1.559	1.280	-0.189	—	0.927	1.093	1.010
OFL	1.093	1.017	-0.678	0.252	4.907	1.049	0.662
BB	2.218	0.405	-0.190	—	-0.125	**2.451**	**2.987**

TABLE 11: Result of Principal Component Analysis. Components that most influence the dispersion of scores are in bold.

Variable	Principal Components		
	First	Second	Third
TL	**0.975**	-0.156	-0.017
CIL	**0.967**	-0.167	-0.027
LD	0.935	-0.248	0.026
LM	0.670	**0.558**	-0.058
BM1	0.641	**0.613**	-0.107
LIF	0.897	0.121	-0.088
BIF	0.743	0.059	-0.058
PB	0.784	0.405	-0.069
BIP	0.557	0.190	0.443
LIP	0.266	0.098	**0.883**
BR2	0.892	-0.162	0.011
LN	0.947	-0.061	-0.025
LPB	0.559	**-0.636**	0.044
LIB	0.699	0.202	0.085
ZB	0.942	-0.137	-0.021
BZP	0.880	-0.204	-0.051
CZL	**0.963**	-0.197	-0.033
PFL	0.918	-0.145	-0.046
BB	0.725	0.312	**-0.149**
Eigenvalue	12.436	1.726	1.050
% Variance	65,45%	9,08%	5,52%

TABLE 12: Result of discriminant analysis based on the first nine principal components. Canonical Discriminant Function Coefficients, Wilk's Lambda, Eigenvalue and Variance (%) are presented.

		Canonical Discriminant Function			
		1º	2º	3º	4º
Principal Components	1º	-0.885	0.068	-0.185	0.308
	2º	0.659	-0.013	-0.368	0.328
	3º	-0.003	-0.033	0.526	-0.438
	4º	0.140	-0.009	0.596	0.714
	5º	0.159	-0.244	0.213	0.078
	6º	0.158	-0.259	-0.261	0.109
	7º	-0.021	0.465	0.048	0.124
	8º	0.209	0.814	-0.044	-0.056
	9º	-2.642	-0.143	-0.262	-0.053
Wilk's Lambda		0.526	0.875	0.949	0.983
Eigenvalue		0.662	0.084	0.035	0.016
% Variance		82.85	10.61	4.46	2.05

variables that showed significant difference between sexes were LD, BR2, LPB and LIB (all variables in class 4). In Nazca (IX), only class 3 and 4 were tested, and LIB and BB show difference in class 3 and BB show difference in class 4. In Casanga (VI) no variable showed significant difference.

Principal Component analysis was conducted on *Aegialomys* sample and our results showed that first principal component accounts for 65.45% of variation, the second for 9.08% and third for 5.52% of the variation (Table 11). The variables explaining the variation along the first component are TL, CIL, and CZL, all related to the overall size of the skull. The distribution of scores between the first and second components (Fig. 4) revealed a division between specimens assigned to classes 1 and 2 and to classes 4 and 5, without clear overlap between these classes. Nevertheless, specimens identified as class 3 are predominantly overlapped to specimens from classes 2 and 4. Plotting male and female individuals on this PCA analysis (Fig. 5), it is possible to observe no clear distinction between male and female through the multivariate space.

A discriminant analysis for the five age classes was performed on the *Aegialomys* sample, using the scores of the first nine principal components. Four Canonical Functions explain the total variance; the first is responsible for 82.85%, the second for 10.61%, the third for 4.46% and the fourth for 2.05% (Table 12). A scatterplot between the first and second canonical function (Fig. 6) evidences that specimens from classes 1 and 2 are nested in a cloud in the right corner of the graph. Specimens assigned to classes 4 and 5 are more restricted to the left portion of the scatter plot, whereas class 3 specimens occupy an intermediate position between these two major age groups. The first canonical function is influenced mainly by the first and fifth principal component, which are expressing variation on longitudinal skull size (TL, CIL, CZL) and interparietal size (BIP and LIP) of specimens examined, respectively. Thus, most of the differentiation of groups is distributed along the abcissa axis of the scatterplot graph; the absence of any discriminatory power for the second function is also evident; Wilk's Lambda shows that only the first and second canonical functions exhibit statistical significant differences between the age classes.

DISCUSSION

Quantitative comparisons of skulls and molars have traditionally been used in systematic studies of Muroidea and these measurements promote an important evidence of differences among populations (Voss, 1991), as documented in this study: we detected a significant variation related to age and also differences between males and females of *A. xanthaeolus*.

According to the univariate results described above, it seems that the age classes with minor tooth wear (1 and 2), are different among themselves and from all other age classes. In all analyses performed, individuals with moderate tooth wear, from class 3, are different from the adjacent age classes (2 and 4). The specimens classified as age classes 4 and 5, with intense to heavy wear, are similar in all analyses. It is noteworthy that despite the univariate analyses employed (all samples pooled, males and females separated, Isla Puna sample), all results were quite similar. The multivariate results showed no significant difference related to age in Isla Puna: this suggests that the evidence of significant differences provided by the individual variables on univariate approach is overcome by evidence of no difference provided by all variables together on the multivariate approach. Manly (2005) stated that the use of a multivariate test as distinct from a series of univariate tests is important to control the rates of type I error, *i.e.,* to find a significant result when there are no differences among samples.

We believe that the major variation found in class 3 within the *Aegialomys* sample (in multivariate and univariate analysis) could be due to several other factors than strictly age variation (like geographic, sex, environmental, and random factors) and could be misleading: thus, the comparisons we performed (with all pooled sample) suggest that such procedures should be avoided in age or sex analysis. We interpret the age variation observed in Isla Puna in the univariate analysis and the absence of such variation found in the multivariate results, as resultant from sexual dimorphism detected in this sample on age class. We believe that classes 3, 4 and 5 are similar (another evidence for that: age class 3 is less different from age

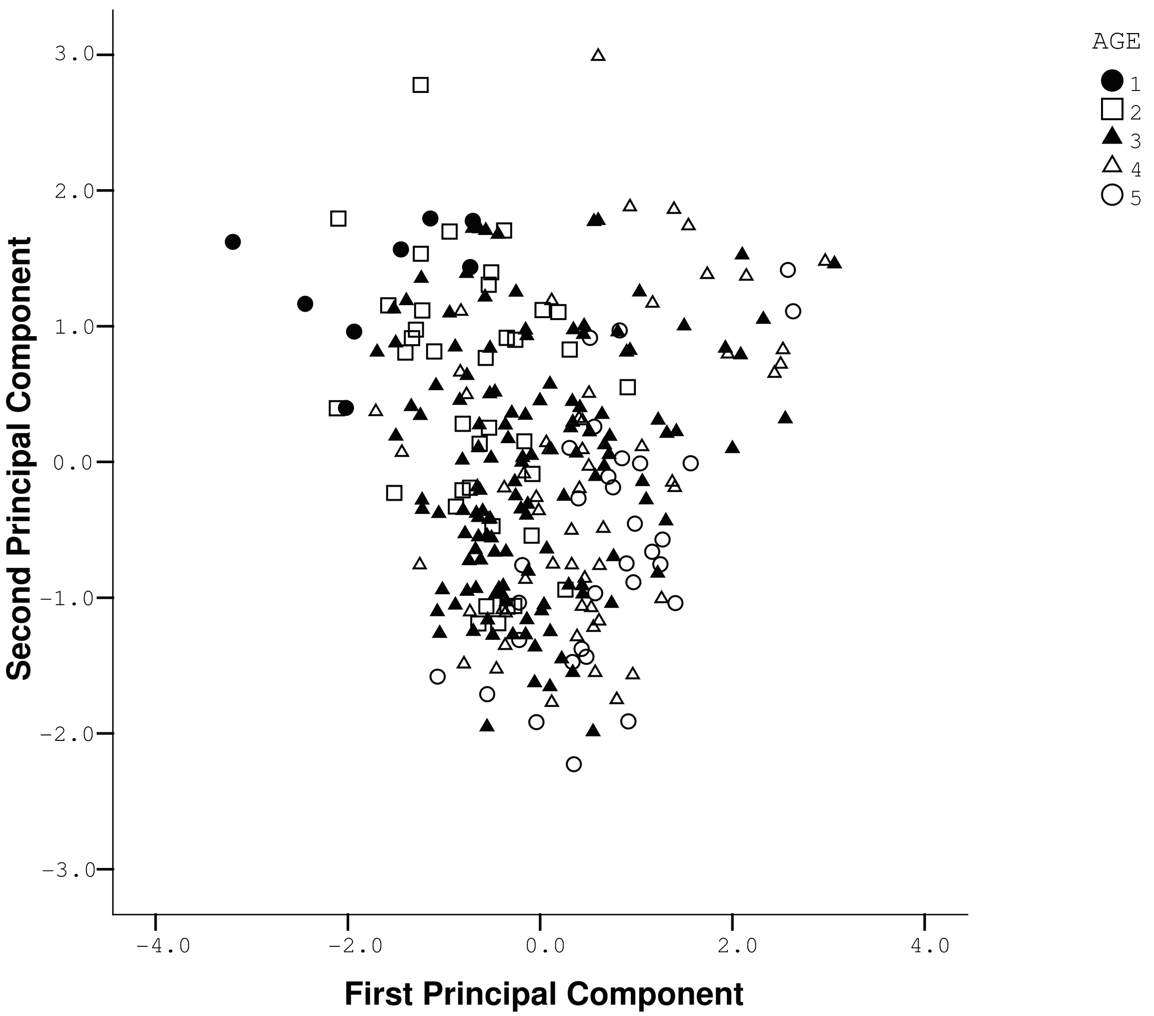

FIGURE 4: Scores of principal component analysis based on the values of 19 variables and designed in the first and second principal component, showing differentiation among age classes.

class 5, than to age class 4) and could be grouped to the posterior geographic analyses.

Our results also highlight age-related differences on cranial morphology, mainly including the rostrum (BR2, LN, LD), the zygomatic region (ZB, BZP, OFL) and the overall skull size (TL, CIL).

These trends indicate a pattern of postnatal growth that we can hypothesize to occur as follows: total length of skull condylo-incisive length indicate overall skull size, and which increases at the same rate as body size. As expected from other neurocranium components, the breadth of the bulla increases following the same pattern of HB and ZB. Temporal space expands by a combination of distance outside of zygomatic arches and breadth of zygomatic plate, the latter growing rapidly in classes 1, 2 and 3, stabilizing afterwards. This suggests an increase in the volume of masticatory muscles in adults, due to an increase of muscle insertion areas (ZB, BZP, OFL), especially for the temporal and masseteric muscles. Other facial skeleton dimensions (BR2, LN) show an elongation of the rostrum as the individual grows from classes 1 and 2 to classes 3, 4 and 5. On the other hand, both measurements on the molar series showed no significant variation in any age group, indicating that molars do not exhibit ontogenetic quantitative variation, despite noticeable qualitative variation described above on age classes (Carleton & Musser, 1989; Voss, 1991; Giannini *et al.* 2009). In general, this ontogenetic variation described for *A. xanthaeolus* followed the pattern described by Voss (1991) for *Zygodontomys,* and Carleton & Musser (1989) for *Microryzomys.* These authors stated that the variation is larger for most craniofacial and incisors measurements, because they have indeterminate growth, revealing a general expansion of the skull as the animal grows older. On

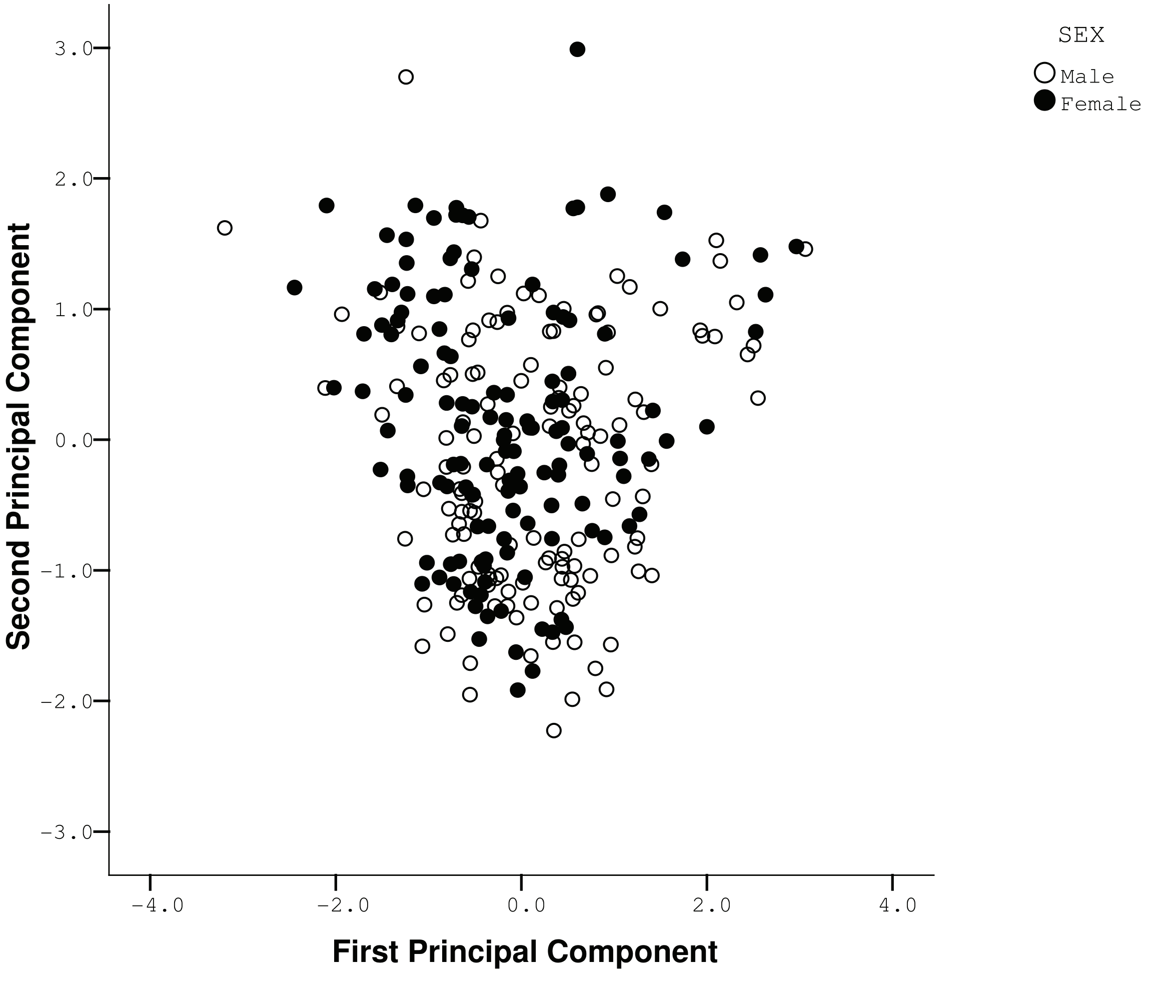

FIGURE 5: Scores of principal component analysis based on the values of 19 variables and designed in the first and second principal component, showing sexual differentiation.

contrary, the dimensions of molars and neurocranium are relatively less variable, which exhibit their growth early in postnatal life.

Proven sex-related differences (uni- and multivariate) only in the total sample, lead us to consider that this result may be due to geographic variation. Nevertheless, if this is true all age classes should exhibit a similar pattern, and this was not observed, only age class 3 exhibited sexual dimorphism. Furthermore, it is interesting the result of univariate analysis in Isla Puna that showed significant differences between sexes only in class 3 too (even though the multivariate analysis did not identify dimorphism in the sample).

The results of age and sex analysis show a great variation in the class 3 in *A. xanthaeolus.* Brandt & Pessôa (1994) also found that sexual dimorphism is a significant factor in age class 3 of a large sample of *Cerradomys langguthi* from Triunfo (Pernambuco, Brazil) for seven cranial characters, and considers that sexual dimorphism may be an important source of variation where specimens of age class 3 are considered. Camardella *et al.* (1998), evaluating a sample of *C. langguthi* from Viçosa and Palmeira dos Indios (Alagoas, Brazil), revealed that sexual dimorphism is not restricted to age class 3 (11 of 15 variables are dimorphic), being also observed in age classes 2, 4 and 5 (although less conspicuous; only 10 of 15, 6 of 15 and 3 of 15 variables for classes 2, 4 and 5, respectively).

It is probable that males and females indexed with tooth wear corresponding to class 3 exhibit different growth rates: males would begin to grow larger before females, resulting in sexual differences; supporting this assumption is the fact that in *Aegialomys* (and

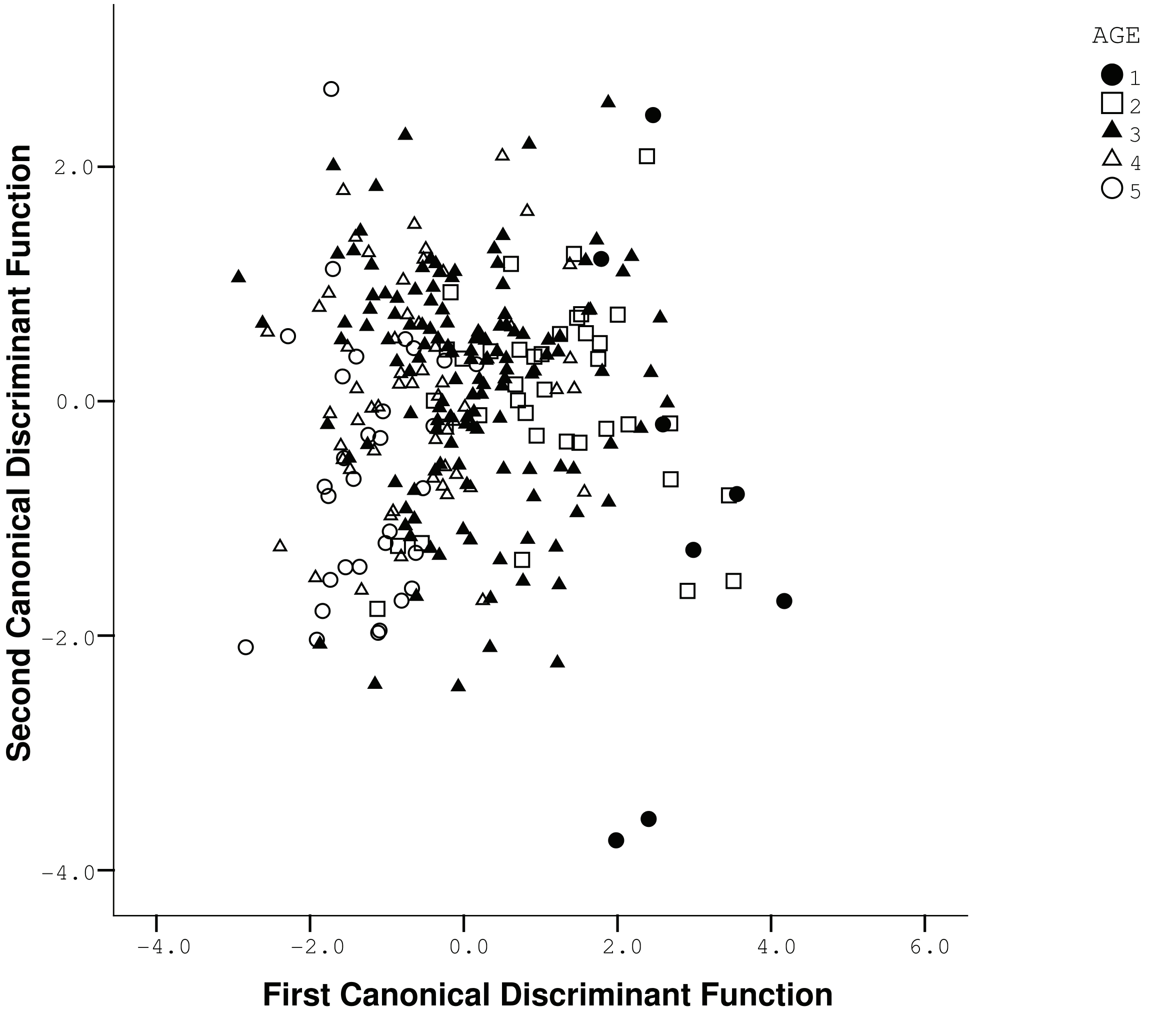

FIGURE 6: Scores based on the values of the first nine principal components and designed in the first and second canonical discriminant function.

also in *C. langguthi;* Brandt & Pêssoa, 1994) mature adults from age classes 4 and 5 are similar in all cranial measurements. It is also possible that age class 3 is inadequately defined ("First and second molar in this class with medium wear, with the cusps conspicuously eroded…"), thus encompassing specimens with wide range of cranial size. Another explanation could be related to dietary contents: some specimens (or specimens from a particular area, with more sand soils) could ingest more abrasive food (sometimes along with soil), resulting in relatively young individuals with advanced tooth wear (Patton & Rogers, 1983). This would increase the variation within this intermediate age class and, thus, cause confusion in the classification of age classes. Moreover, intersexual competition for food and predation may cause differences in body size between males and females (Shine, 1978).

Regarding body measurements, Clark (1980) found that males were heavier and exhibited longer head and body than females in *Aegialomys galapagoensis. A. galapagoenis* also displays sexual dimorphism for skull measurements (results not show), suggesting that there are some degree of sexual dimorphism within the genus. *Nesoryzomys swarthy,* another Galapagos Island endemic Oryzomyini, also exhibit sexual dimorphism, accordingly to Harris & MacDonald (2007). In Galapagos, reproduction is highly seasonal, with males of both genera defending larger home range that encompasses home ranges of several females, suggesting high competition for receptive females. Although these authors do not state it clearly, this life history will probably lead to sexual dimorphism. It is possible that the dimorphism observed on Isla Puna sample is similar as that observed in Galapagos, but as data on the life history of *A. xanthaeolus* is lacking, we are not able to provide any insight on this subject. It is also important to establish that Isla Puna is a continental island, and shares with the continent most of its fauna (see Chapman, 1926).

The absence of sexual dimorphism and pronounced age-related craniometric differentiation has been reported for some Muridae rodents, including *Dasymys incomtus* (Mullin *et al.,* 2001), *Aethomys chrysophilus, Micaelamys namaquensis* (Chimimba & Dippenaar, 1994), and *Taterillus gracilis* (Robbins, 1973); for some Cricetidae rodents, as *Transandinomys talamancae* (Musser & Williams, 1985), the genus *Microryzomys* (see Carleton & Musser, 1989), the genus *Zygodontomys* (see Voss, 1991), several Oryzomyini genera (Musser *et al.,* 1998), and the genus *Cerradomys* (see Percequillo *et al.,* 2008), and for *Proechimys brevicauda* from family Echimyidae (Patton & Rogers, 1983).

On the other hand, information available regarding the Akodontini tribe highlighted the existence of sexual dimorphism, even though it is not in all age groups (Macêdo & Mares, 1987; Oliveira, 1992). However, Ventura *et al.* (2000), evaluating several akodontine morphotypes, did not detect this type of variation. Within the Oryzomyini tribe, sexual dimorphism is a conspicuous feature in some skull characters of the genus *Oligoryzomys,* such as *O. nigripes, O. chacoensis* and *O. fornesi* (Myers & Carleton, 1981), and in some insular populations of *Aegialomys* (this study; Clark, 1980) and *Cerradomys* (Brandt & Pêssoa, 1994; Carmadella *et al.,* 1998). As the sexual variation observed in *A. xanthaeolus* is not consistent (sexual dimorphism was observed only in Isla Puna and in *Aegialomys* sample, which probably also includes geographic variation), we will pool both sexes to assess geographic variation throughout mainland samples and clusters; for insular populations we will keep males and females separated for all subsequent analysis.

CONCLUSION

Evaluating the non-geographic variation within *Aegialomys xantaheolus,* allowed us to assert that, regarding the samples available and cranial traits analyzed, sexual dimorphism is an important component of variation in class 3 for some samples of this species, differing from most taxa of the tribe Oryzomyini, in which morphometric studies found only a minor or negligible sexual variation in the measured variables. Nevertheless, considering the variation described here regarding age variation and sexual dimorphism, we recommend that non-geographic analysis should be performed as part of the protocol in morphometrical studies on sigmodontine rodents.

RESUMO

Aegialomys xanthaeolus *(Cricetidae: Sigmodontinae) habita principalmente as áreas montanas áridas do oeste do Equador e Peru, e ainda as altas elevações na parte superior do vale Marañón ao norte do Peru. No decorrer dos anos alguns trabalhos incluíram esta espécie, mas nenhum deles estudou profundamente a estrutura da variação dentro dela. Existem várias fontes de variação fenotípica intraespecífica, entre elas dimorfismo sexual e idade. Essas fontes podem confundir o acesso a similaridade/dissimilaridade entre populações, dessa maneira é fundamental que a variação não-geográfica seja esclarecida antes dos estudos relacionados à variação geográfica e* *delimitação de táxons. Este trabalho representa um estudo inicial com* A. xanthaeolus, *sumarizando a informação existente a respeito da sua distribuição geográfica e compreendendo sua variação relacionada ao sexo e à idade. Para tal nos baseamos nas análises de mensuração morfométrica tradicional de 19 medidas crânio-dentárias acessadas em coleções científicas, e organizamos as localidades de coleta dos espécimes examinados em um índice de localidades e um mapa de distribuição. A análise dos dados teve uma abordagem morfológica em nível quantitativo, através de análises estatísticas uni e multivariadas. Os resultados obtidos nos permitem afirmar que a variação ontogenética é significante, que as classes etárias 3, 4 e 5 podem ser agrupadas para as análises de variação geográfica e que o dimorfismo sexual não é um componente consistente de variação para esta espécie, quando consideramos amostras provenientes de uma mesma localidade, ou de localidades próximas umas as outras.*

PALAVRAS-CHAVES: Distribuição Geográfica; Crânio; Ontogenia; Dimorfismo sexual.

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APPENDIX A

Material Examined

ECUADOR: *El Oro:* 12 km E by road of Portovelo: M: NMNH 513559: F: NMNH 513560. Pasage: M: AMNH 61319, AMNH 61321, AMNH 61314, AMNH 61315, AMNH 61316, AMNH 61317, AMNH 61318, F: AMNH 61320, AMNH 61313. Portovelo: M: AMNH 47748, AMNH 47747, AMNH 47746, AMNH 47745, AMNH 47744, AMNH 47741, AMNH 47740; F: AMNH 47749, AMNH 47743, AMNH 47742, AMNH 47739. Rio Pindo, Portovelo: M: AMNH 47725, AMNH 47753, AMNH 47754, AMNH 47755, AMNH 47757; F: AMNH 47723, AMNH 47724, AMNH 47726, AMNH 47727, AMNH 47728, AMNH 47750, AMNH 47751, AMNH 47752, AMNH 47756. Santa Rosa: M: AMNH 61305, AMNH 61308, AMNH 61311, AMNH 61312; F: AMNH 61306, AMNH 61307, AMNH 61310. *Esmeraldas:* Esmeraldas: M: AMNH 33206, AMNH 33209, AMNH 33211; F: AMNH 33207, AMNH 33208, AMNH 33210. *Guayas:* Cerro Manglaralto, Santa Elena (part of Sierra de Colonche): M: AMNH 64707, AMNH 64708, AMNH 64713; F: AMNH 64709, AMNH 64710, AMNH 64711, AMNH 64712, AMNH 64714, AMNH 64715, AMNH 64716. Chongoncito, Guayaquil: M: AMNH 63252, AMNH 63254, AMNH 63255, AMNH 63256, AMNH 63259, AMNH 63260, AMNH 63261, AMNH 63264, AMNH 63268, AMNH 63269, AMNH 63038, AMNH 63271, AMNH 63274, AMNH 63275, AMNH 63276, AMNH 63278, AMNH 63280, AMNH 63281, AMNH 63283, AMNH 63289, AMNH 63291, AMNH 63292, AMNH 63295; F: AMNH 63253, AMNH 63257, AMNH 63258, AMNH 63262, AMNH 63263, AMNH 63265, AMNH 63266, AMNH 63267, AMNH 63270, AMNH 63272, AMNH 63273, AMNH 63277, AMNH 63279, AMNH 63282, AMNH 63284, AMNH 63285, AMNH 63286, AMNH 63287, AMNH 63288, AMNH 63290, AMNH 63293, AMNH 63294. Huerta Negra, 20 km ESE Balao, east of Tenguel: F: NMNH 534358, NMNH 534361. Isla Puna, San Ramon, Guayaquil: M: AMNH 66900, AMNH 66901, AMNH 66902, AMNH 66906, AMNH 66909, AMNH 66910, AMNH 66914, AMNH 66915, AMNH 66916, AMNH 66917, AMNH 66919, AMNH 66922, AMNH 66925, AMNH 66926, AMNH 66927, AMNH 66931, AMNH 66932, AMNH 66936, AMNH 66937, AMNH 66938, AMNH 66940; F: AMNH 66903, AMNH 66904, AMNH 66905, AMNH 66907, AMNH 66908, AMNH 66911, AMNH 66912, AMNH 66913, AMNH 66918, AMNH 66920, AMNH 66921, AMNH 66923, AMNH 66924, AMNH 66928, AMNH 66929, AMNH 66930, AMNH 66933, AMNH 66934, AMNH 66935, AMNH 66939, AMNH 66941, AMNH 66942, AMNH 66943; U: AMNH 66240. Rio Chongón. 1.5 km SE Chongón: M: NMNH 513543, NMNH 513545; F: NMNH 513544. San Rafael, 7 km S Balao: M: NMNH 498977. *Loja:* Alamor, San Agustin, Puyango: M: AMNH 213198. Amaluza: U: NMNH 461653. Casanga River Valley: U: AMNH 265355, AMNH 265356, AMNH 265357, AMNH 265358, AMNH 265359, AMNH 265360, AMNH 265361, AMNH 198695, AMNH 198696, AMNH 198697, AMNH 198698, AMNH 198699, AMNH 229727, AMNH 229728, AMNH 229729, AMNH 229730, AMNH 229731, AMNH 229732, AMNH 229733, AMNH 229734, AMNH 229735, AMNH 229736, AMNH 229737, AMNH 199545, AMNH 199546, AMNH 199547, AMNH 199548, AMNH 199549, AMNH 199550, AMNH 198700. Catacocho, Olmedo, Paltas: F: AMNH 213194. Hacienda Casanga, Paltas: M: AMNH 47736, AMNH 47735, AMNH 47732, AMNH 47731, AMNH 47730, AMNH 47729; F: AMNH 47737, AMNH 47734, AMNH 47733, AMNH 47738. Jatumpamba: M: NMNH 461647. Loja: U: NMNH 461652. Los Pozos, Macara: M: AMNH 67512, AMNH 67514, AMNH 67515, AMNH 67516, AMNH 67517; F: AMNH 67513. Malacatos: M: FMNH 53368, FMNH 53370; F: FMNH 53369, FMNH 53371, FMNH 53372, FMNH 53373. Sabiango, La Caprilla: F: NMNH 461645. *Los Rios:* Hacienda El Carmen, Vinces: F: AMNH 63298, AMNH 63299, AMNH 63300. Hacienda Pijigual, Vinces: M: AMNH 63302, AMNH 63303, AMNH 63304, AMNH 63305, AMNH 63306, AMNH 63308, AMNH 63312, AMNH 63099, AMNH 63296, AMNH 63297; F: AMNH 63301, AMNH 63307, AMNH 63309, AMNH 63310, AMNH 63311. Hacienda Santa Teresita (Abras de Mantequilla), *ca.* 12 km NE Vinces: M: NMNH 534364; F: NMNH 534365. Vinces, near Puerto Nuevo and Vinces: M: NMNH 534369; F: NMNH 534371. *Manabí:* Cuaque, Pedernales: M: AMNH 64718, AMNH 64719, AMNH 64721, AMNH 64722, AMNH 64723, AMNH 64724, AMNH 64725, AMNH 64726, AMNH 64727, AMNH 64729, AMNH 64730, AMNH 64731; F: AMNH 64720, AMNH 64728. Hacienda San Carlos, Bahia de Caraquez, Rio Briseño, Sucre: M: AMNH 64732, AMNH 64734, AMNH 64735, AMNH 64737, AMNH 64738, AMNH 64739, AMNH 64742, AMNH 64743, AMNH 64744,

AMNH 64746; F: AMNH 64740, AMNH 64741, AMNH 64745, AMNH 64747. *Pichincha:* Great Quito Railroad, Kilometer 8: M: AMNH 64756, AMNH 64755, AMNH 64752, AMNH 64751, AMNH 64749, AMNH 64748, AMNH 64753; F: AMNH 64758, AMNH 64757, AMNH 64754, AMNH 64750, AMNH 64759. **PERU:** *Amazonas:* 8 km WSW Bagua: F: MVZ 135667. Balsas, Chachapoyas: F: FMNH 19761. *Ancash:* 1 km N, 12 km E of Pariacoto: M: MVZ 135660; F: MVZ 135659. 4 km by road NE Chasquitambo, km 51: M: UMMZ 155915, UMMZ 155916. Macate, Santa: F: FMNH 20892. Pariacoto, Huaraz: M: FMNH 81381, FMNH 81382. *Arequipa:* $4^{1/2}$ mi. E Acari: M: MVZ 145532, MVZ 145533. $8^{1/2}$ mi. NNW Bella Union: M: MVZ 145537. Chavina, on the coast near Acari, Rio Lomos, Province Caravelli: M: NMNH 277572; F: NMNH 277571. *Cajamarca:* Cascas: M: NMNH 302994, NMNH 302995; F: NMNH 302996, NMNH 302997. El Arenal, Rio Huancabamba, 7 km, 50 km E, Olmos: M: MVZ 135668. Hacienda Limon, Celendin: M: FMNH 19448, FMNH 19760; F: FMNH 19447, FMNH 19759; U: FMNH 19647. Malca, Cajabamba: F: AMNH 11819/10111, AMNH 11820. Rio Chamaya, 35 km SE San Felipe: M: MVZ 135663; F: MVZ 135662, MVZ 135669. *Huanuco:* Hacienda Buena Vista, Chinchao: M: NMNH 304533. *Ica:* Hacienda San Jacinto, Ica: F: FMNH 53157, FMNH 53158. Hacienda San Pablo, El Ingenio, 30 km. Nazca: M: NMNH 277563, NMNH 277565, NMNH 277566, NMNH 277570; F: NMNH 277564, NMNH 277568, NMNH 277569. San Javier, 13 km S Palpa: M: FMNH 107365, FMNH 107380, FMNH 107383, FMNH 107386; F: FMNH 107363, FMNH 107364, FMNH 107370, FMNH 107371, FMNH 107376, FMNH 107377, FMNH 107378, FMNH 107379, FMNH 107381, FMNH 107382. *La Libertad:* 5 km NE Pacasmayo: F: MVZ 137944. Menocucho, Trujillo: M: FMNH 19433, FMNH 19438, FMNH 19440, FMNH 19450, FMNH 19451; F: FMNH 19431, FMNH 19432, FMNH 19434, FMNH 19435, FMNH 19436, FMNH 19437, FMNH 19439, FMNH 19441. Pacasmayo: FMNH 19445, NMNH 274572, NMNH 283172; F: FMNH 19442, FMNH 19443, FMNH 19444, FMNH 19461, FMNH 44433. Trujillo: M: FMNH 19452, FMNH 19453, FMNH 19459; F: FMNH 19455, FMNH 19456, FMNH 19458, FMNH 20891. *Lambayeque:* 2 km W Porculla Pass: M: MVZ 137943. 7.5 km N of Olmos: F: LSUMZ 21863. 8 km S Morrope: M: MVZ 135670. 12 mi. ENE Olmos: M: MVZ 137927. Chongoyape, Chiclayo: F: FMNH 81383. Hacienda El Carmen, Motupe: F: FMNH 81384. Olmos: M: FMNH 81387; F: FMNH 81385, FMNH 81386, FMNH 81388. *Lima:* 7 km SSE Chilca: M: MVZ 137588; F: MVZ 137589, MVZ 137590, MVZ 137593. 8 km SE Chilca: F: MVZ 137945. 10 km ENE Pucusana: F: MVZ 137594. 1 mi. W Matucana: M: MVZ 120214. 1 mi. W Surco: M: MVZ 120221, MVZ 120220. 5 mi. E Yanyos: M: MVZ 137597; F: MVZ 137595, MVZ 137598. Cerro Azul, Rio Cañete Valley: U: UMMZ 161219, UMMZ 161222. Chosica: F: FMNH 20893, FMNH 20894, FMNH 20895. Hacienda Casa Blanca, Cerro del Oro, Canete: U: FMNH 29434. Lima: F: NMNH 256515. Lomas de Lachay, 22 km N, 11 km W de Cancay: M: MVZ 135664, MVZ 135665; F: NMNH 507255. Loma Viscachera: F: FMNH 64342. Santa Eulalia: M: FMNH 23750; F: FMNH 23749. Santa Eulalia Cyn, 6 mi. NNE Chosica: M: FMNH 107348, FMNH 107349; F: FMNH 107356, FMNH 107358. Tornamesa: F: FMNH 53057. Vitarte: M: AMNH 42398. *Piura:* Catacaos: F: NMNH 304524, NMNH 304526, NMNH 304528; U: NMNH 304523. Chasquitambo, Julcan: F: NMNH 302987, NMNH 302988. Hacienda Bigotes, Morropon: M: FMNH 81389, FMNH 81391, FMNH 81393; F: FMNH 81390, FMNH 81392. Hacienda Mallares, Sullana: M: FMNH 81403, FMNH 81404, FMNH 81405, FMNH 81406; F: FMNH 81407. Hacienda San Luis, La Arena: M: FMNH 81397, FMNH 81400, FMNH 81402; F: FMNH 81395, FMNH 81396, FMNH 81398, FMNH 81399, FMNH 81401. Huancabamba: F: FMNH 81394. Laguna: F: NMNH 304522, NMNH 304527. Lancones, Sullana: M: NMNH 282282; F: FMNH 83442, NMNH 282284; U: NMNH 304558. Las Trancas, Cerro Cortezo, Sullana: M: NMNH 304557. Monte Grande, 14 km N, 25 km E de Talara: F: MVZ 135666. Paymas, Ayabaca: M: FMNH 81431. Piura: M: NMNH 177814, NMNH 177815, NMNH 177822; F: NMNH 177817, NMNH 177820; U: AMNH 18970. *Tumbez:* El Sauce: M: NMNH 304530; F: NMNH 304531. Matapalo, Zarumilla: M: FMNH 81408, FMNH 81410, FMNH 81411, FMNH 81413; F: FMNH 81409, FMNH 81412, FMNH 81414. Positos, Zarumilla: M: FMNH 81416, FMNH 81417, FMNH 81419, FMNH 81420, FMNH 81421, FMNH 81422, FMNH 81423, FMNH 81429; F: FMNH 81415, FMNH 81418, FMNH 81424, FMNH 81425, FMNH 81426, FMNH 81427, FMNH 81428, FMNH 81430. Tumbez: U: BMNH 854147.

APPENDIX B

Aegialomys xanthaeolus (Thomas, 1894)

Gazetteer

Ecuador

El Oro

1. 12 km E by road Portovelo [*ca.* 792 m]. Not located; here are employed the geographical coordinates of Portovelo. 03°20'S, 79°49'W.
2. Pasage [*ca.* 61 m]. 03°20'S, 79°49'W.
3. Portovelo [*ca.* 610 m]. 03°43'S, 79°39'W.
4. Rio Pindo, Portovelo [*ca.* 564 m]. 03°50'S, 79°45'W.
5. Santa Rosa [*ca.* 31 m]. 03°27'S, 79°58'W.

Esmeraldas

6. Esmeraldas [sea level]. 00°59'N, 79°42'W.

Guayas

7. Cerro Manglaralto, Santa Elena (part of Sierra de Colonche) [*ca.* 365 m]. Not located; here are employed the geographical coordinates of Colonche. 02°00'S, 80°20'W.
8. Chongoncito, Guayaquil [*ca.* 365 m]. 02°14'S, 80°05'W.
9. Huerta Negra, 20 km ESE Balao, east of Tenguel. 03°00'S, 79°46'W.
10. Isla Puna, San Ramon, Guayaquil [*ca.* 925 m]. 02°50'S, 80°08'W.
11. Rio Chongón. 1.5 km SE Chongón [*ca.* 70 m]. 02°14'S, 80°4'W.
12. San Rafael, 7 km S Balao. 03°59'S, 79°47'W.

Loja

13. Alamor, San Agustin, Puyango [*ca.* 1325 m]. 04°02'S, 80°02'W.
14. Amaluza. 04°36'S, 79°25'W.
15. Casanga River Valley [*ca.* 875 m]. Not located; here are employed the geographical coordinates of Rio Casanga. 04°08'S, 79°49'W.
16. Catacocho, Olmedo, Paltas [1872 m]. 04°04'S, 79°38'W.
17. Hacienda Casanga, Paltas [884 m]. 04°01'S, 79°45'W.
18. Jatumpamba (used the coordinates of Jatum Pamba). 04°16'S, 79°42'W.
19. Loja. 04°00'S, 79°13'W.
20. Los Pozos, Macara. 04°23'S, 79°57'W.
21. Malacatos. 04°14'S, 79°15'W.
22. Sabiango, La Caprilla. 04°24'S, 79°52'W.

Los Rios

23. Hacienda El Carmen, Vinces. Not located; here are employed the geographical coordinates of Vinces. 01°32'S, 79°45'W.

24. Hacienda Pijigual, Vinces. Not located; here are employed the geographical coordinates of Vinces. 01°32'S, 79°45'W.
25. Hacienda Santa Teresita (Abras de Mantequilla), *ca.* 12 km NE Vinces. Not located; here are employed the geographical coordinates of Vinces. *Aegialomys xanthaeolus,* 01°32'S, 79°45'W.
26. Vinces, near Puerto Nuevo and Vinces. 01°32'S, 79°45'W.

Manabí

27. Cuaque, Pedernales [sea level]. 00°00'S, 80°06'W.
28. Hacienda San Carlos, Bahia de Caraquez, Rio Briseño, Sucre [sea level]. 00°36'S, 80°25'W.

Pichincha

29. Great Quito Railroad, Kilometer 8. Not located; here are employed the geographical coordinates of Quito. 00°13'S, 78°30'W.

Peru

Amazonas

30. 8 km WSW Bagua [*ca.* 457 m]. 05°40'S, 78°31'W.
31. Balsas, Chachapoyas [*ca.* 854 m]. 06°50'S, 78°01'W.

Ancash

32. 1 km N, 12 km E of Pariacoto [*ca.* 2590 m]. 09°31'S, 77°53'W.
33. 4 km by road NE Chasquitambo, km 51. Not located; here are employed the geographical coordinates of Chasquitambo. 13°48'S, 73°23'W.
34. Chasquitambo, Julcan. 10°18'S, 77°36'W.
35. Macate, Santa [*ca.* 2712 m]. 08°46'S, 78°05'W.
36. Pariacoto, Huaraz [*ca.* 1239 m]. 09°32'S, 77°32'W.

Arequipa

37. $4^{1/2}$ mi. E Acari. Not located; here are employed the geographical coordinates of Acari. 15°26'S, 74°37'W.
38. $8^{1/2}$ mi. NNW Bella Union [*ca.* 731 m]. Not located; here are employed the geographical coordinates of Bella Union. 15°26'S, 74°39'W.
39. Chavina, on the coast near Acari, Rio Lomos, Province Caravelli. 15°37'S, 74°38'W.

Cajamarca

40. Cascas [*ca.* 1274 m]. 07°29'S, 78°49'W.
41. El Arenal, Rio Huancabamba, 7 km, 50 km E, Olmos [*ca.* 915 m]. 05°59'S, 79°46'W.
42. Hacienda Limon, Celendin [*ca.* 2048 m]. 06°50'S, 78°05'W.
43. Malca, Cajabamba [*ca.* 2440 m]. Type locality of *Oryzomys baroni.* 07°37'S, 78°03'W.
44. Rio Chamaya, 35 km SE San Felipe [*ca.* 762 m]. 05°46'S, 79°19'W.

Huanuco

45. Hacienda Buena Vista, Chinchao [*ca.* 1066 m]. Not located; here are employed the geographical coordinates of Chinchao. 09°38'S, 76°04'W.

Ica

46. Hacienda San Jacinto, Ica. 14°09'S, 75°45'W.
47. Hacienda San Pablo, El Ingenio, 30 km Nazca. Not located; here are employed the geographical coordinates of El Ingenio. 14°39'S, 75°05'W.
48. San Javier, 13 km S Palpa [*ca.* 275 m]. 14°32'S, 75°11'W.

La Libertad

49. 5 km NE Pacasmayo [*ca.* 61 m]. 07°24'S, 79°34'W.
50. Menocucho, Trujillo [*ca.* 500 m]. 08°01'S, 78°50'W.
51. Pacasmayo [*ca.* 8 m]. 07°24'S, 79°34'W.
52. Trujillo [*ca.* 34 m]. 08°07'S, 79°02'W.

Lambayeque

53. 2 km W Porculla Pass [*ca.* 1981 m]. Not located; here are employed the geographical coordinates of Porculla Pass. 05°51'S, 79°31'W.
54. 7.5 km N of Olmos [*ca.* 304 m]. Not located; here are employed the geographical coordinates of Olmos. 05°59'S, 79°46'W.
55. 8 km S Morrope [*ca.* 304 m]. Not located; here are employed the geographical coordinates of Morrope. 06°33'S, 80°01'W.
56. 12 mi. ENE Olmos [*ca.* 610 m]. Not located; here are employed the geographical coordinates of Olmos. 50°59'S, 79°46'W.
57. Chongoyape, Chiclayo [*ca.* 209 m]. 06°46'S, 79°51'W.
58. Hacienda El Carmen, Motupe [*ca.* 130 m]. 06°09'S, 79°44'W.
59. Olmos [*ca.* 175 m]. 05°59'S, 79°46'W.

Lima

60. 7 km SSE Chilca [*ca.* 2 m]. Not located; here are employed the geographical coordinates of Chilca. 12°32'S, 76°44'W.
61. 8 km SE Chilca [*ca.* 150 m]. Not located; here are employed the geographical coordinates of Chilca. 12°32'S, 76°44'W.
62. 10 km ENE Pucusana [*ca.* 250 m]. Not located; here are employed the geographical coordinates of Pucusana. 12°29'S, 76°48'W.
63. 1 mi. W Matucana [*ca.* 1981 m]. Not located; here are employed the geographical coordinates of Matucana. 11°51'S, 76°24'W.
64. 1 mi. W Surco [*ca.* 1828 m]. Not located; here are employed the geographical coordinates of Surco. 11°52'S, 76°28'W.
65. 5 mi. E Yanyos [*ca.* 2743 m]. Not located.
66. Cerro Azul, Rio Cañete Valley [*ca.* 100 m]. 13°03'S, 76°30'W.
67. Chosica [*ca.* 800 m]. 11°54'S, 76°42'W.

68. Hacienda Casa Blanca, Cerro del Oro, Canete. Not located; here are employed the geographical coordinates of Canete. 13°04'S, 76°23'W.
69. Lima [*ca.* 154 m]. 12°03'S, 77°03'W.
70. Lomas de Lachay, 22 km N, 11 km W of Cancay [*ca.* 396 m]. 11°21'S, 77°23'W.
71. Loma Viscachera. 12°31'S, 76°30'W.
72. Santa Eulalia [*ca.* 1036 m]. 11°51'S, 76°41'W.
73. Santa Eulalia Cyn, 6 mi. NNE Chosica. Not located; here are employed the geographical coordinates of Santa Eulalia. 11°51'S, 76°41'W.
74. Tornamesa. 11°54'S, 76°31'W.
75. Vitarte. 12°02'S, 76°56'W.

Piura

76. Catacaos. 05°16'S, 80°41'W.
77. Hacienda Bigotes, Morropon [*ca.* 200 m]. 05°19'S, 79°48'W.
78. Hacienda Mallares, Sullana. 04°53'S, 80°41'W.
79. Hacienda San Luis, La Arena. Not located; here are employed the geographical coordinates of La Arena. 05°20'S, 80°44'W.
80. Huancabamba [*ca.* 1929 m]. 05°14'S, 79°28'W.
81. Laguna [*ca.* 1150 m]. 04°41'S, 79°50'W.
82. Lancones, Sullana. 04°35'S, 80°30'W.
83. Las Trancas, Cerro Cortezo, Sullana. 04°53'S, 80°41'W.
84. Monte Grande, 14 km N, 25 km E of Talara. 04°28'S, 81°03'W.
85. Paymas, Ayabaca [*ca.* 700 m]. Coordenates of Ayabaca. 04°38'S, 79°43'W.
86. Piura [*ca.* 50 m]. 05°12'S, 80°38'W.

Tumbez

87. El Sauce. 07°06'S, 79°19'W.
88. Matapalo, Zarumilla [*ca.* 54 m]. 03°41'S, 80°12'W.
89. Positos, Zarumilla [*ca.* 25 m]. 04°16'S, 80°30'W.
90. Tumbez. Type locality of *Oryzomys xantheolus.* 03°34'S, 80°28'W.