

PERUVIAN TENEBRIONIDAE: A REVIEW OF PRESENT KNOWLEDGE AND BIODIVERSITY

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Abstract.— A review of several aspects dealing with Tenebrionidae in Peru is presented. The study includes a taxonomic history, depositories of type specimens, taxonomic diversity, endemism, ecological studies, and other research involving Peruvian tenebrionids in medicine, agriculture, food protection and production. Analyses of the geographic distribution, habitats and estimation of the species richness are performed. A final recommendation suggesting the development of four main lines of research on Peruvian tenebrionids is presented, including: 1) systematics and biogeography, 2) spatial and temporal patterns of epigaeic assemblages, 3) morphological adaptations to aridity, and 4) preserving material of some representatives of Peruvian taxa for molecular studies.



Key words.— darkling beetles, species description process, taxonomic diversity, endemism, geographic distribution, Peru

INTRODUCTION

The family Tenebrionidae includes about 20,000 species and 2,300 genera worldwide, mainly distributed in tropical and temperate latitude areas (Matthews *et al.* 2010). It is one of the richest families in species of Coleoptera, ranking sixth in Australia (Matthews and Bouchard 2008), seventh in the Neotropics (Martín-Piera *et al.* 2000) and seventh at global scale (Finlay *et al.* 2006).

The fossil record of the family includes 112 species, the oldest specimens dating from the Jurassic period (Kirejtshuk *et al.* 2008, 2010). Most of them are known from Baltic and Dominican amber and predominantly species inhabiting forests. Samples of insect remains recovered from Late Pleistocene tar-seeps of Talara (Peru) mostly belong to the beetle families Hydrophilidae and Tenebrionidae (Churcher 1966). This material

includes many elytra, prothoraces and other parts of different sizes and forms attributed to tenebrionid beetles, but no attempts at generic classification were made because no reference collection was available at that time.

Adult tenebrionids are highly variable in terms of color (from black or brown to a wide variety of bright or metallic colors), size (from approximately 1.0–80.0 mm), and morphology (from flat flightless species to elongate cylindrical taxa capable to flight). In fact, some Neotropical genera resemble superficially beetles belonging to other families as was pointed by Champion (1884–1888). For example: *Adelina* Dejean to Cucujidae, *Blapida* Perty to Buprestidae and Elateridae, *Cuphotes* Champion to Erotylidae, *Nilio* Latreille to Coccinellidae and Endomychidae, *Paratenetus* Spinola to some Cryptophagidae, *Phrenapates* Gray to Passalidae, *Statira* Serville to Carabidae, and

Uroplatopsis Champion to some Chrysomelidae and Lycidae. However, with few exceptions tenebrionids can be identified based on their 5-5-4 tarsal formula (rarely 4-4-4 or 3-3-3); antennal insertions concealed under frons; five visible abdominal sternites, with the basal two sternites connate and the apical three hinged; and 10 to 11-segmented antennae (rarely 9-segmented). Detailed descriptions, including for immature stages, are provided in Aalbu *et al.* (2002) and Matthews *et al.* (2010).

The objectives of this study are to present several aspects dealing with Tenebrionidae in Peru: taxonomic history, depositories of type specimens, taxonomic diversity, endemism, geographic distribution and habitats, ecological studies, estimation of species richness, and other subjects such as medicine, agriculture, food protection and production.

Taxonomic diversity of Peruvian Tenebrionidae

The most recent classification of the family recognizes nine subfamilies (Matthews *et al.* 2010). Taking in account this classification, in Peru inhabit 8 subfamilies, 37 tribes, 105 genera, and 357 darkling beetle species or subspecies (Smith *et al.* 2015). In this study, we update this checklist to 108 genera and 359 species or subspecies. Four genera are added to the list: *Narsodes* Campbell, *Schizaraeus* Kulzer, *Entomochilus* Solier, and *Uleda* Laporte. Eight species are added: *Adelina frontalis* (Champion), *Cymatodes hieroglyphicus* (Perty), *Cymatodes nebulosa* (Fabricius),

Entomochilus nitens Kulzer, *Psammotichus lavalleyi* Murphy, *Uleda grossa* Champion, an undescribed species of *Narsodes* and an undescribed species of *Schizaraeus*. The genus *Lagriola* Kirsch was recently synonymized with *Paratenetus* (Matthews and Lawrence 2015) and six taxa are excluded of the list based on a carefully revision of the literature and type specimens: *Cosmonota picta erythropus* Gebien, *Nilio latipennis* Pic, *Nilio margaritaceus* Brèthes, *Statira anthicoides staudingeri* Pic, *Statira pallidipes* Pic and *Strongylium rubrithorax* Brèthes. The tenebrionid fauna of Peru, as many other arthropod groups in the country, is still poorly known. The total number of Peruvian species will almost certainly increase greatly as further sampling is undertaken. The number of species reported here is almost four times the 91 tenebrionid species reported in an overview of Peruvian insects based on a published catalogue (Aguilar *et al.* 1994). In comparison with the values reported for some other countries, the position of Peru is intermediate as it befits its territorial area (Table 1). However, Chile and Spain have higher tenebrionid species richness despite their smaller land area. This could be an indication of a greater collecting effort in these countries, although there are many other factors promoting species richness. In the case of Canada and Poland, species richness is lower than expected for countries with their spatial surface, because the high latitude significantly reduces tenebrionid diversity (Matthews *et al.* 2010).

Based on the endemic tribal areas identified for the world by Matthews *et al.* (2010) and on their

Table 1. Species richness of Tenebrionidae of sixteen countries reported in recent studies. Data in ascending order of territorial area of the countries.

Country	Species-group richness	Area (Km ²)	References
1 Malta	61	316	Lillig <i>et al.</i> (2012)
2 Portugal	173	88 940	Martín-Piera <i>et al.</i> (2000)
3 French Guiana	164	89 150	Touroult <i>et al.</i> (2014)
4 New Zealand	159	268 800	Watt (1992)
5 Italy	320	301 245	Lillig <i>et al.</i> (2012)
6 Poland	73	312 679	Iwan <i>et al.</i> (2012)
7 Spain	451	504 782	Martín-Piera <i>et al.</i> (2000)
8 Chile	487	756 630	Vidal and Guerrero (2007)
9 Colombia	250	1 141 748	Martín-Piera <i>et al.</i> (2000)
10 Peru	359	1 285 216	reported here
11 Mexico	1 248	1 972 545	Cifuentes-Ruiz and Zaragoza-Caballero (2014)
12 Argentina	488	2 780 090	Flores (1998)
13 Australia	1 595	7 618 000	Matthews and Bouchard (2008)
14 Brazil	1 317	8 547 379	Spiessberger <i>et al.</i> (2016)
15 USA	1 184	9 809 378	Aalbu <i>et al.</i> (2002)
16 Canada	141	9 970 610	Bousquet <i>et al.</i> (2013)

panropical distributions without evident high-level endemism, we concluded that the Peruvian tenebrionid fauna is composed of four biogeographic lineages: Panropical, Arid South America, Neotropical, and Gondwanan Relict. The tribes, number of genera and number of species included in each biogeographic component are summarized in Table 2. One Paleotropical genus, *Alphitobius* Stephens, is not considered in this analysis because the only species (*A. diaperinus* Panzer) was introduced in the country.

Historical knowledge of Peruvian Tenebrionidae

Peruvian species of Tenebrionidae have been described over the last two hundred and forty five years. This description process has been uneven, with very productive decades and decades with little input. The most productive decades were the 1830s, 1840s, 1870s, 1910s, 1920s and 1950s with over twenty species described in each of these decades (Fig. 1). This pattern is explained by the unequal contribution of taxonomists. The most productive author was Kulzer with 20% of the total species described, followed by Erichson (9%), Borchmann (7%), Champion (6%), Pic (6%), Gebien (6%) and a long list of authors providing minor contributions (Fig. 2). Basically, there were four generations of entomologists describing most of the Peruvian tenebrionids: The first generation (1830–1849) composed of the French F. Guérin-Méneville, F. Laporte, A. Solier and the German W. Erichson; the second generation (1870–1879) including the English H. Bates, the Finnish F. Mäklin, the German T. Kirsch, and the French L. Fairmaire and L. Chevrolat; the third generation (1910–1929) with the English G. Champion, the Germans F. Borchmann and H. Gebien, and the French J. Brèthes and M. Pic; the fourth generation (1950–1969) comprising the Hungarian Z. Kaszab, the Italian G. Marcuzzi, and the Germans H. Freude and H. Kulzer.

The taxonomic and systematic studies on Peruvian tenebrionid taxa since the second half of twentieth century are summarized in Table 3. Most studies are focused on the Pimeliinae, and were conducted during 1950–1969 by the fourth generation of entomologists, plus the more recent Chilean entomologist Luis E. Peña. The remaining subfamilies have received much less attention, but there have been noteworthy contributions to the Diaperinae (Diaperini, Hypopphaeini, Phaleriini) by Ardoin (1977) and Triplehorn (1991, 1994, 1998, 2006), to the Lagriinae (Goniaderini) by Ferrer and Moragues (2000), Ferrer and Delatour (2007) and Ferrer (2009b), and also to the Stenochiinae (*Othryoneus* Champion and *Cyrtosoma* Perty) by Ferrer (2009a) and Marcuzzi (1976, 1991, 2002). Particularly striking is the scarcity of recent studies on the tribes Alleculini, Lagriini, Stenochiini and Ulomini, which are taxa with a high species richness and endemism in the Amazonian rainforest (Smith *et al.* 2015).

Type specimens and collections

Most Peruvian tenebrionid type specimens are housed in foreign collections. The main are: British Museum Natural History (London, UK), Natural History Museum Basel (Switzerland) housing the former collection at George Frey München Museum (Germany), Hungarian Natural History Museum (Budapest, Hungary), Museum für Naturkunde der Humboldt Universität (Berlin, Germany), Muséum d'Histoire Naturelle (Paris, France), Zoologischen Museums der Universität Hamburg (Germany), California Academy of Sciences (San Francisco, USA), Field Museum of Natural History (Chicago, USA), The Ohio State University Insect Collection (Columbus, USA), United States National Museum of Natural History-Smithsonian Institution (Washington DC, USA), Fundación e Instituto

Table 2. Biogeographic components of Peruvian tenebrionid fauna.

Biogeographic components	Tribes and subtribes	n° genera	n° species
Pantropical	Alleculini, Amarygmmini, Belopini, Bolitophagini, Cnemeplatiini, Cnodalonini, Crypticini, Diaperini, Goniaderini, Hypopphaeini, Lagriini, Opatrini, Penetini, Phaleriini, Stenochiini, Stenosini, Tenebrionini, Toxicini-Eudysantina, Triboliini, Ulomini	64	188
Arid South America	Cossyphodini-Esemephina, Edrotini, Epitragini, Nycteliini, Physogasterini, Praociini, Scotobiini, Thinobatini, Trilobocarini	25	127
Neotropical	Acropterini, Alleculini-Xystropodina, Nilionini, Phrenapatini, Talanini	8	17
Gondwanic Relict	Caenocrypticini, Elenophorini, Evaniosomini	8	24

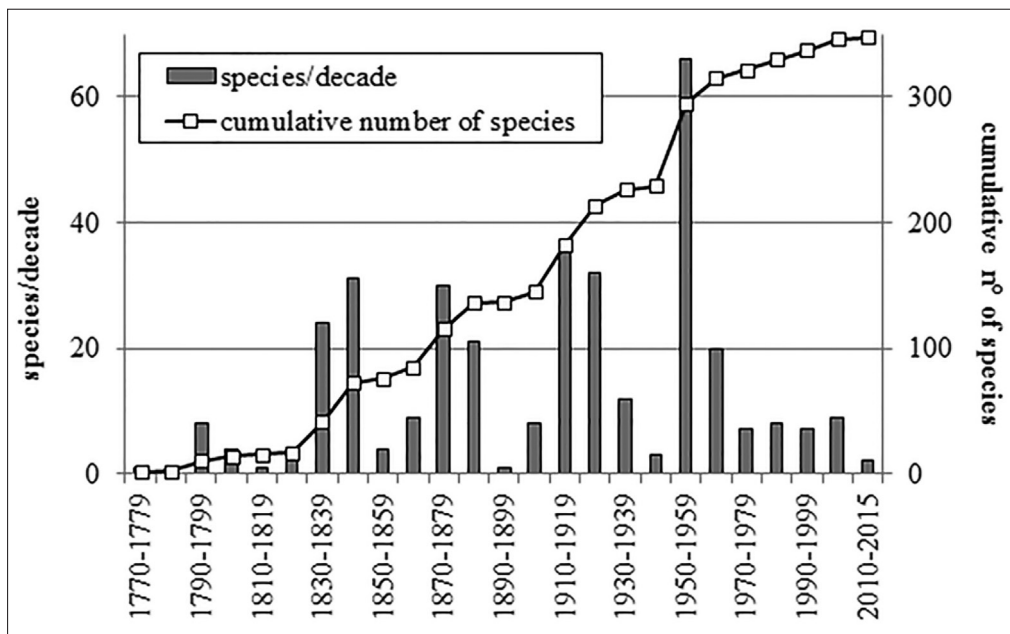


Figure 1. Description of Peruvian tenebrionid species by decades, from 1770 to 2015.

Miguel Lillo (Tucumán, Argentina), Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” Buenos Aires, Argentina), and Museo de La Plata (Argentina). Two Peruvian collections housed a reduced number of types: Museo de Entomología “Klaus Raven Büller” – Universidad Nacional Agraria La Molina (Lima, Peru)

and Museo de Historia Natural “Javier Prado” – Universidad Nacional Mayor de San Marcos (Lima, Peru) but according to the current layout the primary types of future species described for the country should be deposited in Peruvian collections as it happened recently (Silvestro *et al.* 2015).

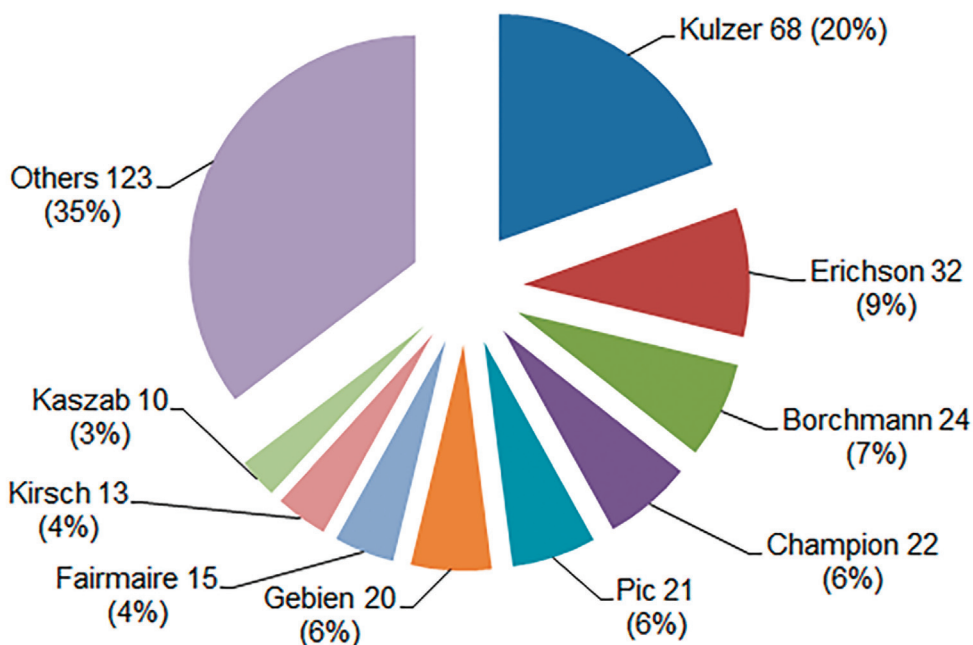


Figure 2. Numbers and percentages of Peruvian tenebrionid species described according to the author.

Table 3. Taxons of Tenebrionidae from Peru with taxonomic treatment since the second half of twentieth century. Subfamilies and tribes are listed in alphabetical order countries.

Subfamilies	Tribes	Genera	References
Diaperinae	Diaperini	<i>Adelina, Cosmonota, Liodema, Neomida, Platydema</i>	Kulzer (1961), Ardoin (1977), Triplehorn (1994, 1998, 2006) Bremer and Triplehorn (1999) Triplehorn (1991)
	Hypophaleini	<i>Corticeus</i>	
	Phaleriini	<i>Phaleria</i>	
Lagriinae	Goniaderini	<i>Goniadera, Phymatestes</i>	Ferrer and Moragues (2000), Ferrer and Delatour (2007), Ferrer (2009b)
Pimeliinae	Caenocrypticini	<i>Caenocrypticoides</i>	Endrödy-Younga (1996), Flores and Pizarro-Araya (2004) Steiner (1980) Kaszab (1964, 1981, 1985) Kulzer (1955), Peña (1973a) Freude (1967, 1968) Kulzer (1950, 1956), Flores and Aballay (2015) Kulzer (1954), Peña (1985) Kulzer (1956), Peña (1980), Kaszab (1981) Kulzer (1952, 1958), Flores (2001), Flores and Pizarro-Araya (2012, 2014) Kulzer (1956), Kaszab (1969), Aalbu and Andrews (1996) Peña (1974)
	Cossyphodini	<i>Esemephe</i>	
	Edrotini	<i>Hylithus, Kocakia, Prohylithus</i>	
	Elenophorini	<i>Psammetichus</i>	
	Epitragini	<i>Epitragopsis, Epitragus, Hemasodes, Omopheres, Parepitragus, Phytophilus</i>	
	Evaniosomini	<i>Achanius, Melaphorus, Vaniosus</i>	
	Nycteliini	<i>Pilobalia, Psectrascelis</i>	
	Physogasterini	<i>Philorea, Physogasterinus</i>	
	Praociini	<i>Parapraocis, Pilobaloderes, Praocidia, Platyholmus, Praocis</i>	
	Stenosini	<i>Discopleurus, Grammicus</i>	
Thinobatini	<i>Cordibates</i>		
Stenochiinae	Cnodalonini	<i>Cyrtosoma, Mylaris, Othryoneus, Taphrosoma</i>	Marcuzzi (1976, 1991, 2002), Ferrer and Siliansky (2008), Ferrer (2009a)
Tenebrioninae	Scotobiini	<i>Ammophorus, Pumiliofossorum, Scotobius</i>	Van Dyke (1953), Kulzer (1955), Silvestro et al. (2015) Ferrer (2011) Steiner (2005)
	Tenebrionini	<i>Zophobas</i>	
	Triboliini	<i>Hypogena</i>	

Endemicity

Of the 108 genera reported for the country only 16 (15%) are restricted to Peru. By the contrary, of 359 species and subspecies inhabiting Peru, 216 (60%) are endemic to it (Table 4).

At subfamily level, the Pimeliinae and Lagriinae have the greatest values of species richness and a high percentage of endemism, while the Alleculinae and Stenochiinae combine lower values of species richness with a high percentage of endemism (Fig. 3). At tribal and generic level, the taxa highlighted for their contribution to diversity can be divided into two groups:

Endemic genera (all known species are Peruvian), with low to moderate species richness. This group includes sixteen genera in the following tribes, Cossyphodini (*Esemephe* Steiner), Edrotini (*Kocakia* Kaszab, *Prohylithus* Kaszab), Epitragini (*Phytophilus* Guérin-Méneville), Evaniosomini (*Chorasmius* Bates, *Evaniosomus* Guérin-Méneville), Goniaderini (*Gamaerus* Bates), Lagriini (*Gebienia* Borchmann, *Thoracostira* Borchmann), Physogasterini (*Physogasterinus* Kaszab), Praociini (*Parapraocis* Kulzer, *Pilobaloderes* Kulzer, *Praocidia* Fairmaire), Scotobiini (*Pumiliofossorum* Silvestro & Giraldo), Stenochiini (*Strongylacanthus* Brèthes) and Ulomini (*Apteruleda* Gebien).

Table 4. Taxonomic diversity of subfamilies of Tenebrionidae from Peru.

Subfamily	Number of tribes	Number of genera	Number of species	Endemic genera	Endemic species
Alleculinae	1	7	17	0	11
Diaperinae	4	10	27	0	6
Lagriinae	3	12	64	3	44
Nilioninae	1	1	7	0	1
Phrenapatinae	2	3	3	0	1
Pimeliinae	13	34	137	10	99
Stenochiinae	3	19	45	1	33
Tenebrioninae	10	22	59	2	21
Total	37	108	359	16	216

Genera with high proportion of endemic species regarding the number of species inhabiting in Peru (proportion of endemic species = 0.6–1.0), with moderate to high species richness. This group includes 13 genera in the following tribes, Alleculini (*Lobopoda* Solier), Cnodalonini (*Cyrtosoma*), Evaniosomini (*Achanius* Erichson), Lagriini (*Colparthrum* Kirsch, *Statira*), Nycteliini (*Pilobalia* Burmeister, *Psectrascelis* Solier), Physogasterini (*Philorea* Erichson), Praociini (*Platyholmus* Solier, *Praocis* Eschscholtz), Stenochiini (*Poecilosthus* Blanchard, *Strongylium* Kirby) and Thinobatini (*Cordibates* Kulzer).

Among the major factors promoting increasing species richness and endemism of tenebrionid taxa are the orographic barriers resulting from the uplift of the Andes mountain range. Vicariant effects of the Andean uplift have acted on different taxonomic levels (genera and species), generating four patterns of distribution: taxa endemic to the east of the Andes, taxa endemic to the west of the Andes, taxa widely distributed on both sides of the Andes, and taxa inhabiting high altitudes in the Andes (Flores and Pizarro-Araya 2006). In the coastal desert, speciation is probably promoted by landscape configuration. Coastal desert tenebrionids inhabit patchy ecosystems surrounded by vast areas of extreme aridity, so that populations are eventually disconnected from each other. In Amazonia, altitudinal gradients in the Eastern Andes range and temporary flooding in the Amazonian Plain have potential as factors promoting speciation. However, their relevance to tenebrionid richness and endemism has not been studied and is still largely unknown.

Estimating species richness

Estimating the number of species of any taxon is not an easy task due to the complexity of ecological and historical factors involved. The data presented here

can be useful, using species-area and species accumulation- time relationships. The data shown in Table 1 were log-transformed (Ln) and used to establish a linear regression between number of species (Y) and land area (X) (Fig. 4). The equation used yielded an estimated value of about 433 species. The data in the historical knowledge section was used to establish Michaelis-Menten and Logistic relationships between cumulative number of species (Y) and decades from 1770 to 2015 (Fig. 5). The equations yielded estimated values of about 498 and 385 species respectively. Combining both approaches, the true value of species richness should be within the range of 385 to 498 species.

Another way to estimate species richness is to calculate the percentage of undescribed species observed in collecting trips and collections. Specimens that appear to be new species are common in some genera with high endemism such as *Philorea* or *Pilobalia* (AEG pers. obs.). However, more detailed studies on the systematics and morphology of these genera are required to provide accurate inferences. An estimation of the diversity of the whole genus *Praocis* (Praociini), which comprises 77 species and 8 subspecies arranged in nine subgenera, has been recently proposed (Flores and Pizarro-Araya 2014). Taking into account 34 currently undescribed species identified by the authors on collecting trips or from collections, the genus would have 119 species/subspecies, with a 47 percent increase in the number of species in the entire genus (Flores and Pizarro-Araya 2014).

Geographic distribution and habitat preferences

The geography of Peru is complex and rich in ecosystems, vegetation types and habitats because the interaction of the Humboldt Current and the Andes

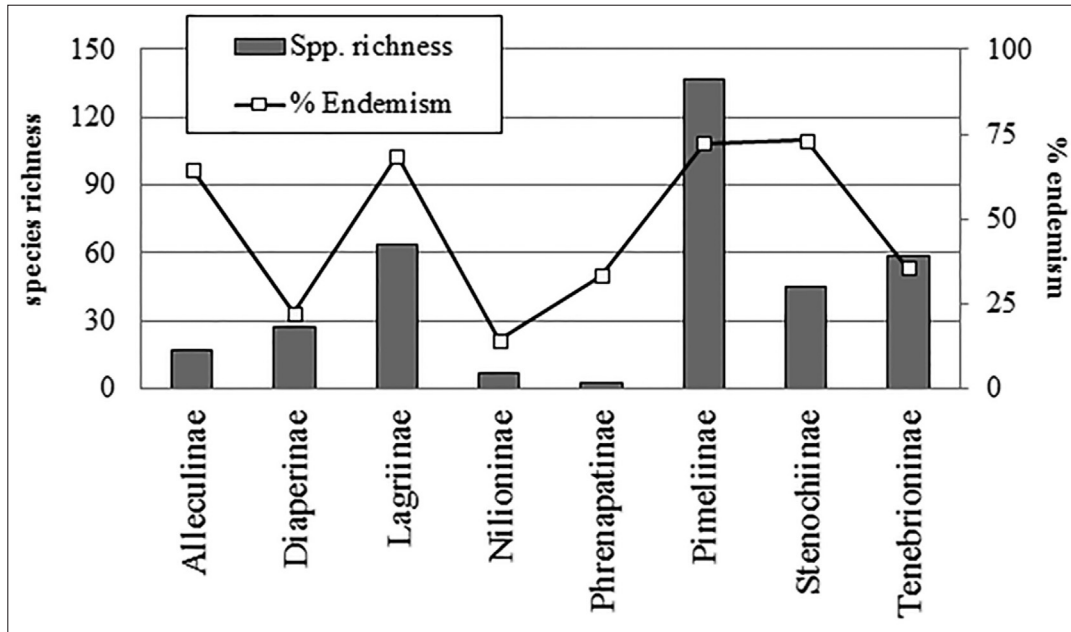


Figure 3. Species richness and endemism (%) of tenebrionid subfamilies in Peru.

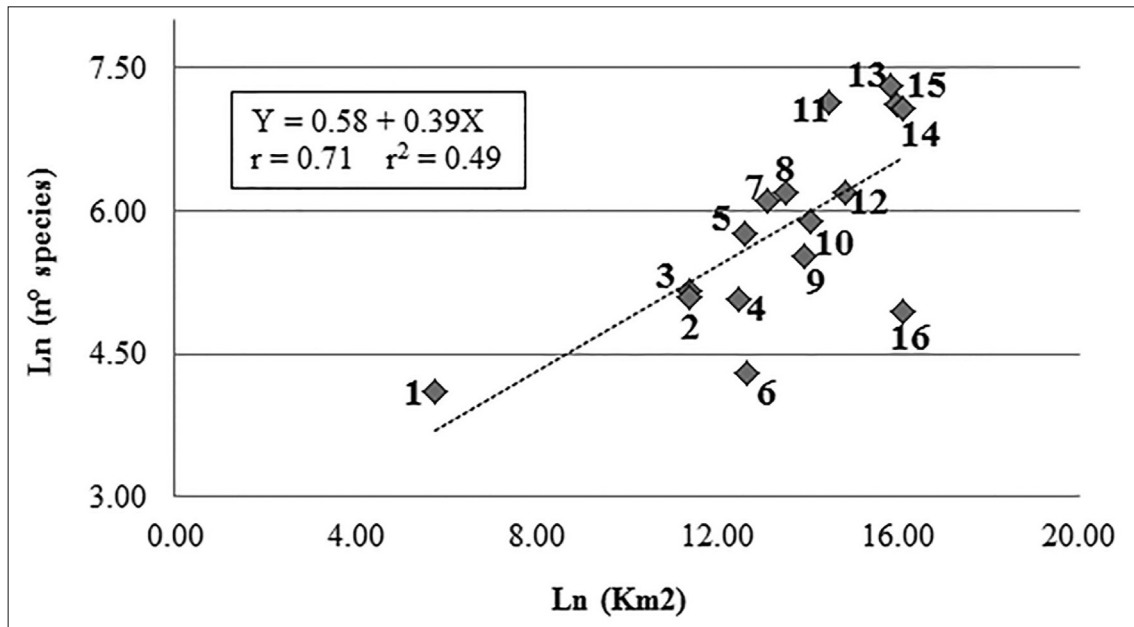


Figure 4. Linear relationship between the species richness (Y) and area (X) of sixteen countries. The countries are designated by the numbers 1–16 as in Table 1. Peru is number 10 on the graph.

Mountain range. Roughly, to the west of the Andes there are arid conditions, on the slopes and plateaus of this mountain range the weather is cold, while to the east of the Andes the climate is tropical, typical of low latitudes (0–18°S). Tenebrionid species are found in the full range of environmental extremes and, according to their geographical distribution, they can be classified into five groups:

Desert taxa distributed in the coastal deserts (0–1000 m) and the equatorial dry forest (0–2800 m) located west of the Andes. The tribes and genera registered in this area include Caenocrypticini (*Caenocrypticoides* Kaszab), Edrotini (*Kocakia*), Elenophorini (*Psammotichus* Latreille), Epitragini (*Parepitragus* Casey, *Hemasodes* Casey, *Omopheres* Casey), Evaniosomini (*Aryenis* Bates, *Chorasmius*,

Evaniosomus, *Melaphorus* Guérin-Méneville), Physogasterini (*Physogasterinus*), Praociini (*Parapraocis*), Thinobatini (*Cordibates*), Opatrini (*Blapstinus* Sturm), Scotobiini (*Ammophorus* Guérin-Méneville, *Pumiliofossorum*), Stenosini (*Grammicus* Waterhouse), and Tenebrionini (*Hipalmus* Bates). These genera are mostly epigeaic detritivores whose larvae live in sandy soils of alluvial origin. Overall, they are nocturnal insects that seek shelter under rocks (eg:

Caenocrypticoides, *Psammetchus*), get half-buried in small dunes (*Cordibates*) or are burrowers in sandy stream banks (*Blapstinus*) (Champion 1884–1888, Aguilar 1954, Peña 1973a, 1974, Flores & Pizarro-Araya 2004). Some Edrotini and Epitragini climb bushes or shrubs, maybe seeking refuge from high soil surface temperatures or drinking the water condensed in foliage (AEG pers. obs.). The vegetation types in the area they live in include coastal dunes, herbaceous

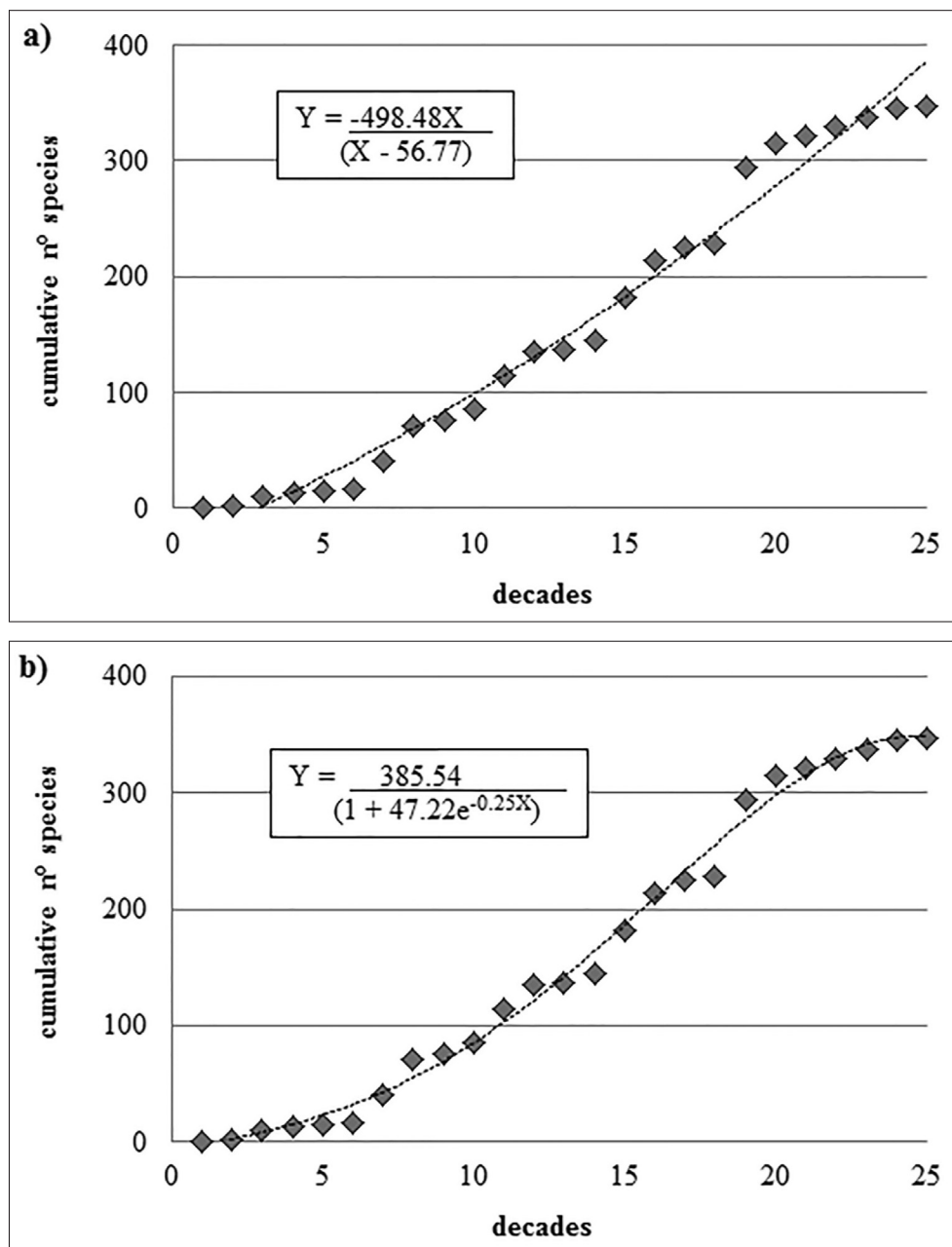


Figure 5. Relationships between the accumulated species richness (Y) and decades (X); a) Michaelis-Menten, b) Logistic. Data are the same as in Figure 1.

and shrubby plants associated to fog catchment (named “lomas”), dry scrubs, and more sparingly in riparian thickets and wetlands. The Evaniosomini and Physogasterini (also *Philorea* see below) included in this group belong to the low to medium-altitude eremic elements of Pierre (1980).

Andean taxa distributed along the Western Andes range (1000 m – 3800 m), in inter-Andean valleys (1500 m – 3300 m), and in the high plateaus or “Puna” (3800 m – 5000 m). The tribes and genera registered in this area include Alleculini (*Narsodes*), Edrotini (*Hylithus* Guérin-Méneville), Evaniosomini (*Vaniosus* Kulzer), Nycteliini (*Pilobalia*, *Psectrascelis*), Physogasterini (*Entomochilus*), Praociini (*Praocis*, *Praocidia*, *Pilobaloderes*, *Platyholmus*), and Stenosini (*Schizaraeus*). These genera are mostly epigaeic detritivores whose larvae live in several types of soil, including alluvial, calcareous, organic or volcanic, as reported by Pierre (1980) for sites south of 14° S. The Nycteliini are diurnal (*Pilobalia*) or nocturnal (*Psectrascelis*) walking insects, during their downtime they seek shelter under tussocks, rocks, logs and dry cattle dung (Peña 1973b, 1985). The vegetation types in their area of occurrence include cacti aggregations, grasslands, lawns and scrubs. The Edrotini, Praociini and Nycteliini included in this group belong to the medium- to high-altitude xerophilic elements of Pierre (1980).

Amazonic taxa distributed along the Eastern Andes range (800 m–3500 m), in the Amazonian plain (0–800 m) and in the Pacific tropical forest (0–500 m). The tenebrionids inhabiting montane and lowland forests can be found on three main habitats (Champion 1884–1888): upon foliage, leaves and branches, including those still attached to fallen trees; beneath loose bark of decaying or fallen trees; and in or around fungi growing on decaying or fallen trees. The first group is represented by the tribes Acropterini, Alleculini, Amarygmini, Cnodalonini (*Blapida*, *Camaria* Serville, *Cyrtosoma*, *Epicalla* Champion, *Isicercus* Champion, *Sycophantes* Kirsch, *Tenebriocamaria* Pic), Goniaderini, Lagriini, Stenochiini and Talanini. The second group includes Cnodalonini (*Choastes* Champion, *Mylaris* Pallas, *Nuptis* Motschulsky, *Paroeatus* Gebien, *Taphrosoma* Kirsch), Diaperini (*Adelina*, *Corticeus* Piller & Mitterpacher), Penetini, Tenebrionini (*Rhinandrus* LeConte, *Zophobas* Dejean), Toxicini, Triboliini (*Hypogena* Dejean) and Ulomini. The third group includes Bolitophagini, Diaperini (*Cosmonota* Blanchard, *Liodema* Horn, *Neomida* Latreille, *Platydema* Laporte & Brullé) and Nilionini (*Nilio*). Occasionally, some taxa of the first group can be found beneath loose bark, associated with fungi or on the ground beneath fallen timber or stones. The sub-social wood-boring genus *Phrenapates* is more specialized, since it lives in colonial assemblages of adults, larvae, and pupae in tunnels constructed in wood

partially decomposed by fungal activity (Nguyen *et al.* 2006). In general, the larvae of all these taxa grow in decaying wood or in fungoid growths.

Taxa widely distributed in the coastal deserts and along the Andes. The genera *Achanius* (Evaniosomini), *Prohylithus* (Edrotini) and *Epitragopsis* Casey (Epitragini) are found in coastal desert and interandean valleys. *Philorea* (Physogasterini) and *Scotobius* Germar (Scotobiini) are found from coastal deserts to high plateaus.

Taxa found in specialized habitats. The genus *Phaleria* Latreille inhabits sandy beaches and is frequently founded beneath decaying seaweed. The genera *Esemephe* (Cossyphodini) and *Discopleurus* Lacordaire (Stenosini) are myrmecophilous (Steiner 1980, Aalbu and Andrews 1996). The genera *Lepidocnemeplatia* Löbl & Merkl (Cnemeplatini), *Alphitobius* (Alphitobiini), *Tribolium* MacLeay (Triboliini), *Gnatocerus* Thunberg and *Ulomoides* Blackburn (Diaperini) are invasive cosmopolitan species associated with stored grains, poultry farms, and other anthropogenic environments (Spilman 1991). The genera *Blapstinus* and *Psammetchus* have been recorded from islands with sea-birds colonies (Murphy, 1925). The genus *Zophobas* has been recorded from caves (Ferrer 2011).

Collecting methods

Due to the different habitats that tenebrionids occupy, there are different methods for collecting whose applicability depends on the ecosystem explored.

Passive methods suitable for collecting tenebrionids include pitfall, flight-intercept and light traps. Pitfall traps are particularly useful in the coastal deserts and the Andes, where most ecosystems have low structural complexity and sometimes significant portions of bare soil. These traps have been successfully employed to describe spatial and temporal patterns of epigaeic arthropod assemblages (including Tenebrionidae) in arid zones of Peru (Aguilar 1977, Giraldo and Arellano 2003). According to available tests, the most effective pitfall traps for collecting tenebrionids were those uncovered (without funnels or roofs) and filled with preservative solutions, which also serve as attractants (Cepeda-Pizarro 1987). In short periods, live pitfall trapping is also feasible, without risk of escape of wingless species or sex-biased samples induced by pheromonal attraction (McIntyre 1998, Henschel *et al.* 2010). Flight-intercept traps such as Malaise and window traps are effective devices for collecting the understory coleopteran fauna in tropical forests of the Neotropics, although the second kind of trap seems to be more effective since beetles tend to fall on impact with a vertical surface (Steiner 2006). Concerning light traps,

tenebrionid specimens that are attracted to black and UV light sources belong to the genera *Cordibates* (Peña 1974), *Lepidocnemeplatia* (Triplehorn 1987), *Phaleria* (Triplehorn 1991), *Zophobas* (Champion 1884–1888), *Achanius* (*Ambigatus*) Fairmaire (Flores and Aballay 2015), and *Cyrtosoma*, *Goniadera* Perty and *Statira* (Jean-Hervé Yvinec pers. comm.). Yellow bowl traps buried at ground level are used less frequently and have proved to be useful at collecting some species of Alleculiini, Branchini and Opatrini in tropical forest of Central America (Steiner 2006).

Active methods suitable for collecting tenebrionids include direct searching and beating. Direct searching should be focused on habitats or “shelters” where darkling beetles live. Their preferred habitats are the following: 1) beneath decaying seaweed, carcasses or guano deposits in the intertidal zone (Triplehorn 1991), 2) below decaying leaves, dry cow dung, logs, shrubs and stones; also inside rock crevices and ground bird nests in coastal deserts (Aguilar 1954), 3) under stones, logs, dry cow dung and plants, especially those with padded or tussock structures in high Andean plains (Elgueta 1988), and 4) below loose bark, under fallen timber or stones and on surface of fungoid growths in tropical forests (Champion 1884–1888). In Peruvian Amazonia, specimens of the genera *Cuphotes*, *Cymatodes* Dejean and *Poecilosthus* were collected using these direct searching methods (Jean-Hervé Yvinec pers. comm.). Direct searching is an especially valuable collecting method in Andean highlands, where tenebrionid density and activity are low due to the strong daily variation in temperature (0°C at night). In tropical forests, direct searching may be improved by using a headlamp at night and fumigating dead trees with pyrethrum compounds (Bouchard and Yeates 2001). Using beating on leaves and branches is useful for collecting specimens of the tribes Acropteronini, Alleculiini, Amarygmini, Cnodalonini, Epitragini, Goniaderini, Lagriini, Strongyliini and Talanini. Collecting methods in the canopy of tropical forests include building cranes for direct searching and beating canopy tops or dislodging insects on foliage by fogging. These special techniques have been useful for finding new tenebrionid species in Central America (Ferrer and Ødegaard 2005).

Sensitivity to anthropogenic disturbance

Tenebrionidae and other faunal components are mainly affected by landscape transformation caused by human activities such as agriculture, deforestation, oil and gas extraction, mining and urbanization. The intensity of these activities is not uniform across the country, agriculture and urbanization are more important in the coastal deserts, mining in Andean slopes

and plateaus, and deforestation and oil and gas extraction in the Amazonian forests. The common pattern of these disturbances is the accelerated replacement of large continuous natural areas by fragments, which are progressively degraded until they are unsuitable for viable populations.

Responses of tenebrionids to anthropogenic disturbance have been identified and proposals for their conservation have been made in different parts of the world. In the Mediterranean region, data on species richness and species geographical distribution have been used to establish conservation priority of islands affected by human activities, mainly tourism (Cartagena 2002, Cartagena and Galante 2002, Fattorini and Dapporto 2014). Other topics studied are long-term extinction caused by urbanization in Rome (Fattorini 2011) and recovery of epigaeic assemblages in response to habitat restoration in Guadiamar River Basin (Cárdenas *et al.* 2011). In Southern South America, conservation priorities have been suggested, based on phylogenetic information obtained from cladistic analysis of some Nycteliini and Praociini genera, such as *Callyntra* Solier (Flores and Vidal 2000), *Epi-*pedonota** Solier (Flores and Roig-Juñent 2001), and *Platysthes* Waterhouse (Flores 2004). Tenebrionidae have been suggested as bioindicators for measuring the effects on invertebrate biota of many kinds of anthropogenic disturbances such as fragmentation, fire regimes, habitat restoration and pollution (Michaels 2007).

In this regard, the information for Peru is scarce and often limited to environmental assessment documents for private use related to mining, gas and oil extraction activities. Peruvian legislation on animal species at risk of extinction includes only seven Coleopteran species and none of them belongs to the Tenebrionidae (MINAGRI 2014). This situation could be changed by conducting studies about the geographic patterns of tenebrionid richness and endemism and improving communication with environmental authorities.

Studies about Peruvian tenebrionids

The studies about Peruvian tenebrionids are mostly devoted to applied subjects, including agriculture, food protection and production, forestry and medicine. Several genera have been reported as potential pests of crops including *Parepitragus* in potato (Vergara and Amaya de Guerra 1978), *Pilobalia* in quinoa (Rasmussen *et al.* 2003), *Epitragopsis* and *Parepitragus* in yacón (Narrea 2004), and *Blapstinus* and *Epitragopsis* in sweet potato (Rondón and Vergara 2004). Among the cosmopolitan species associated with stored grains, the biological cycle, morphology and

behaviour of *Alphitobius diaperinus* have been studied (Vergara and Gazani 1996). The larvae of *Tenebrio molitor* Linnaeus have been employed in assays for production of edible oil (Valdez and Untiveros 2010). In a list of insects of concern for forestry, Dourojeanni (1963) mentioned the occurrence of *Mylaris* larvae (as *Nyctobates* Guérin-Méneville) in rotten wood, but pointing out its scant impact compared to other beetle taxa, such as Cerambycidae, Passalidae or Curculionidae: Scolytinae. *Zophobas* species have been proposed as a food item of high nutritive value for insectivorous vertebrates in captivity (Schulte 1996, Morote 2004). Regarding medicine research, some species have been recognized as potential vectors of parasitic helminths, including *Ammophorus peruvianus* Guérin, *A. rubripes* Solier, *Epitragus* sp. (probably *Parepitragus* sp.), *Gnatocerus cornutus* (Fabricius) and *Tribolium castaneum* (Herbst) (Cáceres and Guillén de Tantaléan 1972, Arrojo *et al.* 2004, Gómez-Puerta *et al.* 2014).

Other studies included tenebrionid species as members of biotic assemblages. In the guano islands at the Peruvian coast, Murphy (1925) recorded 27 invertebrate species, including three tenebrionids: *Blapstinus* sp., *Psammetichus costatus* Guérin-Méneville and *Psammetichus lavellei*. In the northern coast, Carbajal *et al.* (1995) studied the macroinfauna communities of sandy beaches, finding great number of crustaceans, molluscs and polychaetes, but also an unidentified species of the genus *Phaleria*. In the central coast, the patches of coastal vegetation named “lomas” were explored by the entomologist Pedro Aguilar during three decades. His contributions contain information about diversity, habitat selection, spatial distribution, and seasonal cycles of tenebrionids (Aguilar 1954, 1963, 1964, 1976, 1977, 1981, 1985, Aguilar and Turkowsky 1977). Later, the overall family and some abundant species of Tenebrionidae were recognized as relevant components to explain the changes in diversity and structure of the epigaeic beetle assemblages sampled in Lachay lomas during years influenced by the El Niño event 1997–98 (Giraldo 2002, Giraldo and Arellano 2003). In Paracas Bay, Catenazzi and Donnelly (2007) studied the trophic interactions in animal communities of intertidal zone and adjacent sand dunes. Three tenebrionid species were found, *Phaleria subparaella* Chevrolat (as *Atahualpina peruviana* Español) linked to algae deposits on the seashore, *Cordibates fuscus* Kulzer feeding on vegetal detritus of marine or terrestrial origin, and *Psammetichus costatus* feeding mainly on detritus of animal origin (dead invertebrates, guano, vertebrate carcasses). In the Amazonian forest, Dourojeanni and Tovar (1972) described the food web of “Las Lechuzas” cave in Tingo María (Huánuco). They found a remarkable abundance and biomass of cockroaches and

darkling beetles, the latter were preliminarily identified as near *Nyctobates* and later as *Zophobas atratus* (Fabricius) (Ferrer 2011).

Although the studies reviewed cover many features of Peruvian tenebrionids, there is still much we need to know about them. More collecting efforts are required to cover the type and unexplored localities, obtain topotypes, determine the distribution patterns of known species and look for new taxa. For this purpose, the basic information presented in the section “Collecting methods” is the starting point for designing protocols or combinations of methods that are efficient and suitable for each ecosystem. Specimens collected in this way, properly preserved in public collections and labeled with as much information as possible will be the basis for future research.

We suggest the development of four main lines of research on Peruvian tenebrionids: 1) systematics and biogeography, using biodiversity and cladistic tools to elucidate the influence of altitude, latitude, orographic barriers and major vegetation types on richness and endemism; 2) Spatial and temporal patterns of epigaeic assemblages, such as daily and seasonal cycles, microhabitat preferences and soil type selection; 3) Morphological adaptations to aridity, i.e. finding connections between environmental preferences and body models; and 4) preserving material of some representatives of Peruvian taxa (especially the endemic ones) for molecular studies with colleagues who will take charge of this study.

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