

Synopsis of the Colombian Stag Beetles: A baseline for conservation assessments

Sinopsis de los escarabajos ciervo de Colombia: Una línea de base para evaluaciones de conservación

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ABSTRACT

Stag beetles, or Lucanidae (Insecta: Coleoptera: Scarabaeoidea), are among the most charismatic groups of scarab beetles. However, their ecology and natural history are largely unknown, partly due to their rarity in the field and in biological collections. This contribution summarizes the status of knowledge of the Colombian Lucanidae, based for the most part in bibliographic research and personal observations from fieldwork and biological collections in Colombia and Brazil. Bibliographic records are supplemented by data from the Global Biodiversity Information Facility (GBIF), including field observations recorded through the online platform iNaturalist. In the literature, we found 19 species of stag beetles recorded for Colombia, belonging to five genera, three tribes, and two subfamilies. Bibliographic records are concentrated in the Andean region of Colombia, with some records in the Caribbean and Pacific regions. The lowlands of the Amazon and Orinoco regions lack any records for lucanid beetles. The diversity and ecology of stag beetles in Colombia are discussed in the light of current environmental threats. By presenting diagnoses and an identification key to the lucanid genera present in the country, along with known distributional data, and a discussion about their ecology, this contribution constitutes the first step towards proposing Colombian lucanids as species in need of conservation efforts.

Keywords. Biodiversity, conservation, scarab beetles, species list.

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RESUMEN

Los escarabajos ciervo de la familia Lucanidae (Insecta: Coleoptera: Scarabaeoidea) están entre los grupos más carismáticos de escarabajos. Sin embargo, su ecología e historia natural en la región Neotropical permanecen ampliamente desconocidas, parcialmente debido a su rareza tanto en campo como en colecciones biológicas. Este trabajo resume el estado del conocimiento de los Lucanidae colombianos, basado principalmente en búsquedas bibliográficas junto con observaciones de campo y colecciones biológicas en Colombia y Brasil. Los registros bibliográficos se complementaron con datos de la Global Biodiversity Information Facility (GBIF), y observaciones en campo registradas a través de la plataforma en línea Naturalista. Encontramos 19 especies de escarabajos ciervo registradas para Colombia en la literatura, pertenecientes a cinco géneros, tres tribus y dos subfamilias. Los registros bibliográficos se concentran en la región andina de Colombia, con algunos registros en las regiones Caribe y Pacífico. Las tierras bajas de la Amazonia y Orinoquia carecen de registros de escarabajos lucánidos. Adicionalmente, se discute la diversidad y ecología de los escarabajos ciervo en Colombia, a la luz de las amenazas ambientales actuales. Mediante la presentación de diagnóstico y una clave de identificación de los géneros de Lucanidae presentes en el país, además de datos conocidos de distribución y una discusión sobre su ecología, esta contribución constituye el primer paso hacia proponer a los lucánidos de Colombia como especies que necesitan esfuerzos de conservación.

Palabras clave: Biodiversidad, conservación, escarabajos, lista de especies.

INTRODUCTION

Stag beetles (Coleoptera: Lucanidae) are a small family in the superfamily Scarabaeoidea represented by approximately 1500 species in 115 genera, distributed worldwide (Bouchard *et al.* 2017). According to Holloway (1960, 1968, 1969, 2007), Lucanidae is composed of four extant subfamilies: Aesalinae MacLeay, 1819; Lampriminae MacLeay, 1819; Syndesinae MacLeay, 1819; and Lucaninae Latreille, 1804, which is the most diverse, representing around 90 % of the described species. Traditionally, Lucanidae has attracted the attention of the scientific community and non-scientific public, and even in the absence of identification keys, it is possible to identify them at least to supraspecific levels.

Lucanid beetles can be recognized by the following combination of characters: size 3–120 mm, body flattened to weakly convex; antennae usually with ten antennomeres, with tomentose and unopposable lamellae; labrum usually continuous with clypeus, which is fused with frons; legs serrate; protibiae with one apical spur; meso- and metatibiae with two spurs (Ratcliffe 2002). There is evident sexual dimorphism in most species of the family (somewhat reduced in Aesalinae), where males present greatly enlarged

and symmetric mandibles, whereas females show reduced and frequently asymmetric mandibles (compare fig. 3B, male, with 4f, female; Kim and Farrel 2015). There are also other differences such as stronger body punctation and reduced antennal club in females. The development of male mandibles is allometric, with a significant reduction in minor males, producing a close resemblance to females, characterized by not only the reduction in size but also a reduction in body vestiture, sometimes making it difficult to distinguish both sexes (Kawano 2000).

Most taxa are extremely under-represented in collections, being more commonly found in private collections where access is restricted, making it difficult for taxonomists to study them. This may be one of the reasons why lucanid classification is highly inconsistent, especially at the suprageneric level (Smith 2006, Holloway 2007). Due to a lack of taxonomic revisions and available identification keys, the most common way to identify them is through images provided in books such as Fujita (2010) and Bartolozzi *et al.* (2017), or updated catalogs like Paulsen (2019).

Besides taxonomic limitations, lucanid beetles are extremely rare in nature, which has made it difficult to conduct studies on ecology and life history of this family. Despite

this, it is well-known that stag beetles are saproxylic, with larvae feeding on dead wood; the females oviposit either directly in decaying wood, at the soil-wood interface beneath logs, or in the soil (Huang 2018). Their role as decomposers and ecosystem engineers are key for maintaining forest ecological dynamics (Fierro and Vergara 2019, Crespin and Barahona-S 2022).

According to Paulsen (2019), stag beetles from the Americas represent around 15 % of the total described species, with representatives of all four subfamilies: Aesalinae (four genera, 18 species), Lampriminae (one genus, one species), Lucaninae (32 genera, 215 species), and Syn-desinae (three genera, twelve species). In the Neotropical region, lucanids can be found in most countries, with no records from Belize, Suriname, and the Caribbean Islands (Fig. 1), except for an amber fossil from the Dominican Republic described by Woodruff (2009).

In South America most species have been described from Brazil, Ecuador, and Peru. Most taxa are associated with high elevation ecosystems of high conservation value, as the majority of the known localities are distributed across some of the most important biodiversity hotspots, such as the Tropical Andes and the Brazilian Atlantic Forest (Myers 2000). However, only *Chiasognathus grantii* Stephens, 1831 from Chile (Vergara and Jerez 2009), and species of the Brazilian endemic genus *Altitaiayus* Weirich, 1960 (Ministério do Meio Ambiente 2022) have been included in national conservation strategies.

For the specific case of Colombia, current knowledge is scarce. Only 19 species in five genera are known for the country: *Sphaenognathus* Buquet, 1838, *Aegognathus* Leuthner 1883, *Cantharolethrus* Thomson, 1862, *Onorelucanus* Bartolozzi and Bomans, 1989, and *Psilodon* Perty, 1830. Some lucanid species are only known from their original descriptions, with no known recent material available for study. Lucanids are underrepresented in Colombian scientific collections; in some cases, private collections have more and rare material for study, but are essentially inaccessible for research. With no catalogs, identification keys, accurate distributional data, or scientific researchers focused on the taxon, the need for taxonomic, evolutionary, and conservation studies regarding Colombian stag beetles is evident. This work is the first summarized contribution to the knowledge of Colombian Lucanidae, providing basic but fundamental information that serves as the baseline for

ecological studies, and the first step towards evaluating extinction risks for Colombian lucanid beetles.

MATERIALS AND METHODS

The list of species of Lucanidae was initially extracted from Paulsen's online annotated checklist of the Lucanidae of the Americas (Paulsen 2019). Additional references for each taxon were revised to extract locality information in Colombia, including the original description for each species, available catalogs, and taxonomic or faunistic revisions for the world and the region. The list was formatted as a Darwin Core Checklist available through the Global Biodiversity Information Facility - GBIF (Cáceres *et al.* 2022).

The core checklist dataset includes the extensions Reference, Types and Specimen, and Species Profile, to accommodate the following information: (1) valid/accepted scientific name; (2) author and year of description; (3) relevant bibliographic resources, including original description, checklists, and catalogs; (4) Colombian localities where the species has been documented; (5) information on type material when it was readily available from publications; (6) origin (native vs. introduced); (7) endemism: taxa are considered Colombian endemics if no records from other countries were found in the published literature; (8) general ecological habit of each species.

In addition, we downloaded all the records for observation data for Lucanidae from Colombia from iNaturalist (up to November 4, 2022; Supplementary Material 1). We also downloaded data from GBIF by searching occurrence data by 'Country or area' Colombia and 'Scientific name' Lucanidae (GBIF.org 2022), which includes observation data along with information on preserved specimens from collections. We assumed that identifications for preserved specimens from GBIF are correct.

Using these data, we constructed a distribution map including the Colombian species of stag beetles (Fig. 2). To build the map, we used QGIS v.3.10, using as a base layer a shapefile for South America (provided by the Environmental Systems Research Institute-ESRI), available at <http://tapiquen-sig.jimdo.com>. We included an additional layer containing a Digital Elevation Model for South America, published by the Center for Earth Resources Observations and Science, available at <http://databasin.org/datasets/d8b7e23f724d46c99db1421623fd1b4f.c>.

Morphological diagnoses for all subfamilies and genera present in Colombia (Supplementary Material 2) and an identification key to the Colombian genera were generated by studying specimens deposited in the “Coleção Entomológica da Universidade Federal Rural de Pernambuco – CERPE” (Brazil) and the “Sección Entomología, colecciones biológicas, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt – IAvH-E” (Colombia), along with the revision of original descriptions. The terminology used for the descriptions follows Holloway (1960, 1968, 1969, 2007), Paulsen (2005), Lawrence *et al.* (2011), and Cristóvão and Vaz-de-Mello (2021).

RESULTS

Colombian lucanid records from the literature

According to the literature, there are 19 species of Lucanidae recorded from Colombia, grouped in five genera, three tribes, and two subfamilies (Table 1). Eight of those species are considered Colombian endemics. Most species (17) belong to the subfamily Lucaninae. With twelve species, the genus *Sphaenognathus* is the most diverse lucanid genus in the country; the remainder genera are represented by one or two species.

Descriptions of lucanid species recorded from Colombia are scattered through time and by author: Parry (1872, 1874, 1875) described four species; Boileau (1904, 1911) and Buquet (1838, 1840, 1843), each described three species. Most of the type material is deposited at the Muséum national d’Histoire naturelle (MNHN) in Paris, France, followed by The Natural History Museum (NHMUK) in London, United Kingdom. Most species were described between 1911 and 1938. Only one recent taxonomic revision (Cáceres and Grossi 2023) has included Colombian material. During the last decade two new species of Lucanidae have been described from the Colombian Andes (*Psilodon paschoali* Pardo-Locarno and Ríos-Málaver, 2011 and *Aegognathus dulima* Cáceres, Ríos-Málaver and Grossi, 2019).

As for distributions, according to the literature, Colombian lucanids are more diverse in the Andean region (Antioquia, Boyacá, Caldas, Risaralda, Norte de Santander, Santander, Tolima), with some representatives in the Caribbean (Cesar, Magdalena) and Pacific (Cauca, Chocó, Valle del Cauca), and one species from the Orinoco region of the country (Meta) (Fig. 2). No specific localities are known for one species (*Aegognathus leuthneri* van de Poll, 1886).

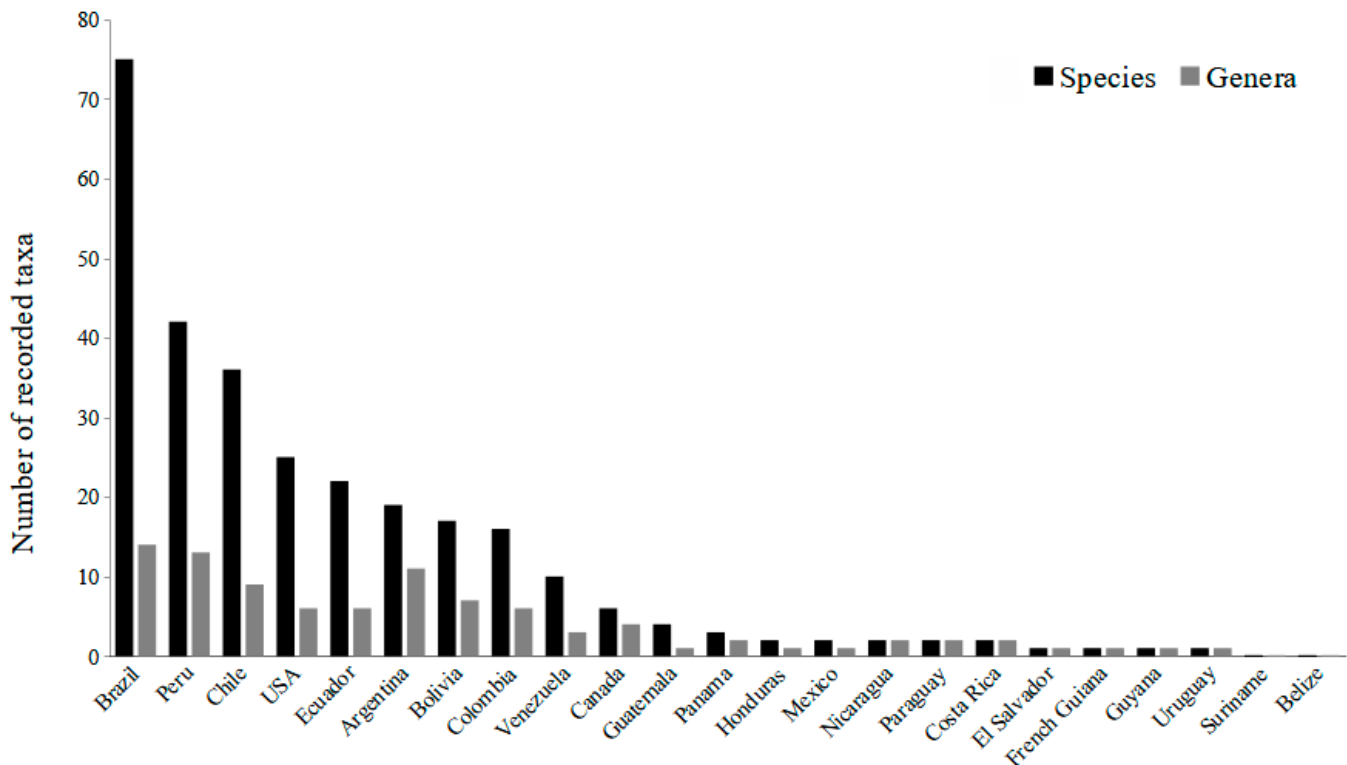


Figure 1. Number of lucanid taxa per country across the Americas.

Colombian lucanid records from online platforms

We recovered 140 records from iNaturalist (Supplementary Material 1; Fig. 2), from which 120 were identified to species (Cáceres and Ríos-Málaver verified the identifications). The records correspond to fourteen species, from which 122 specimens belong to the genus *Sphaenognathus*, with *Sphaenognathus feisthamelii* (Guérin-Méneville, 1838) representing the highest number of records (46) and the broadest distributional range (Antioquia, Boyacá, Cundinamarca, Norte de Santander, Risaralda, Santander, and Valle del Cauca), followed by *Sphaenognathus bellicosus* Boileau, 1904 (26 records; Cesar, Magdalena).

Records from GBIF were very heterogeneous in the information provided. Out of the 348 downloaded records

(GBIF.org), 232 corresponded to preserved specimens identified at various taxonomic categories. Three species (one record each: *Lucanus capreolus* (Linnaeus, 1763), *Odontolabis bellicosa* (Castelnau, 1840), and *Platycerus scarabeoides* -which is not an existing name) were excluded from the list due to evident errors or inaccuracies in the data: *Lucanus* species have Nearctic and Palearctic distributions; the specimen identified as *L. capreolus* is recorded from Soacha (Cundinamarca), but it is likely a misidentification. The species *O. bellicosa* is not currently recognized as a valid species, the valid name is *Odontolabis dalmani* (Hope, 1845) and its distribution is restricted to Indonesia and Malaysia; the specimen in question is housed at the Museo Entomológico Francisco Luis Gallego in Medellín, but has no locality data; it is likely a misidentification.

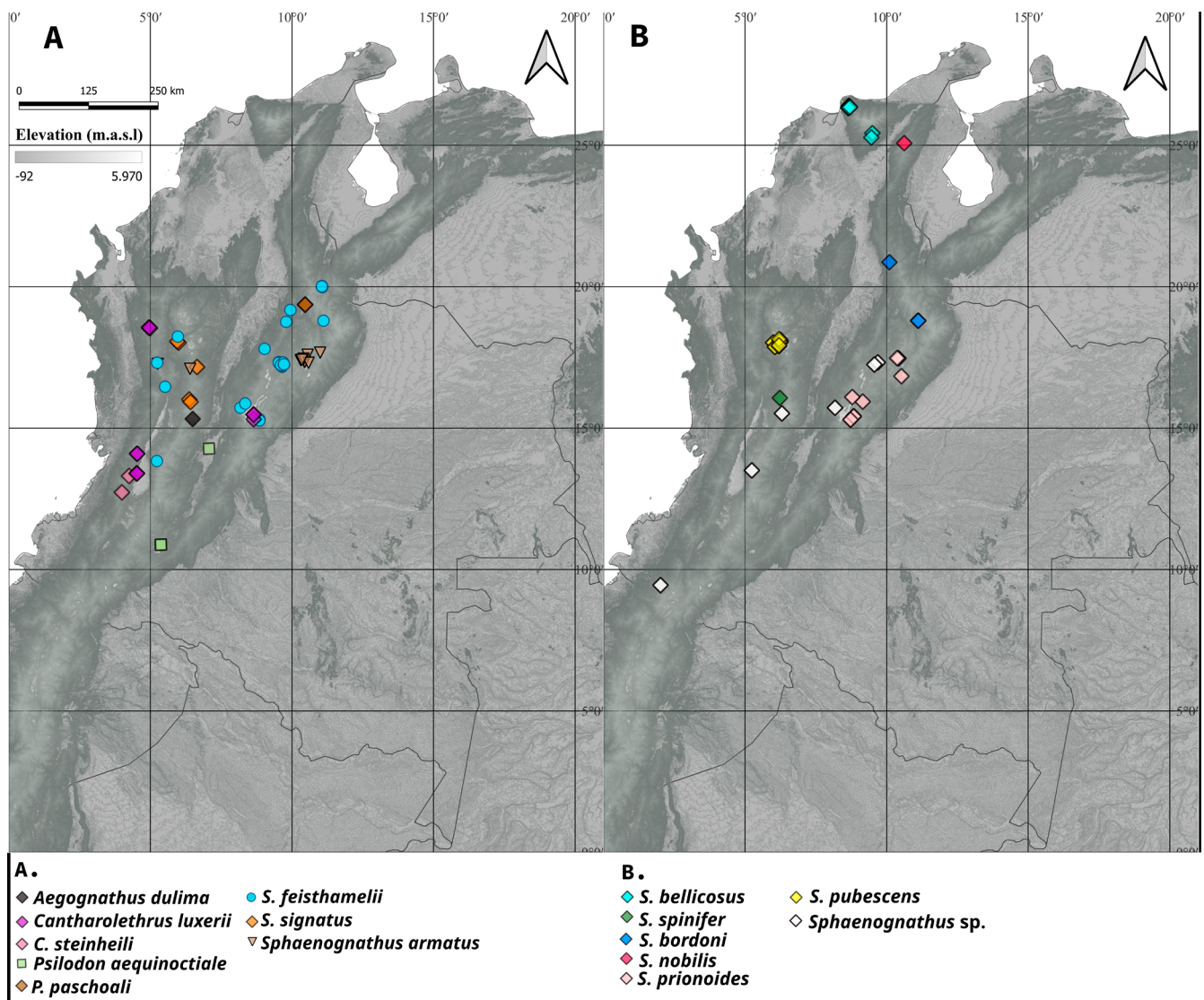


Figure 2. Distribution map of the Colombian species of stag beetles. Note that *O. pulverosus* and *A. leuthneri* do not have accurate distribution data available.

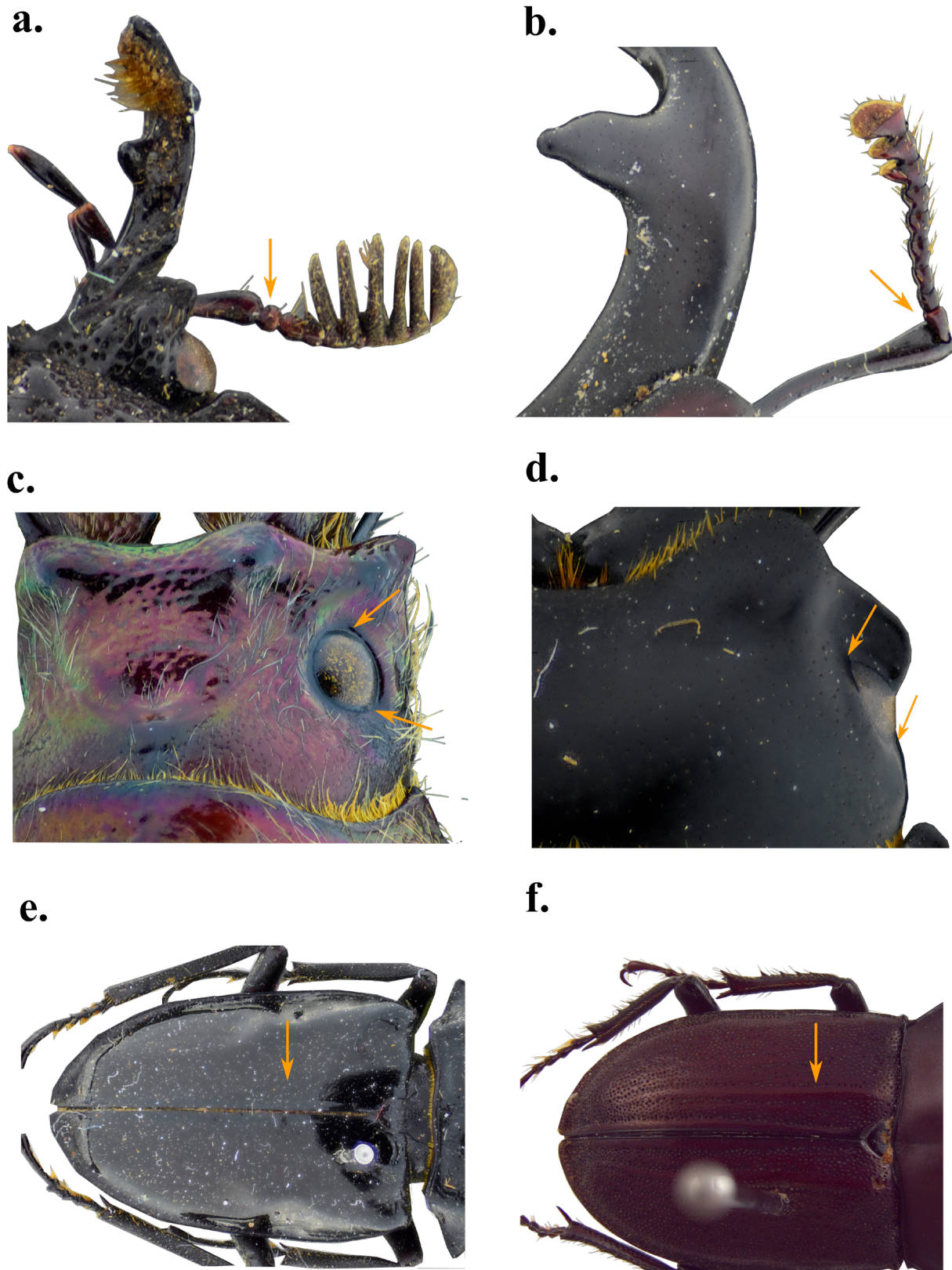


Figure 3. Morphological features of male Lucanidae. **a.** Antennae of *Psilodon aequinoctiale*, arrow showing pedicel insertion, non-geniculate (scale bar 1 mm); **b.** Antennae of *Aegognathus leuthneri*, arrow showing pedicel insertion, geniculate (scale bar 1 mm); **c.** Ocular canthus complete of *Sphaenognathus nobilis* (scale bar 1mm); **d.** Ocular canthus incomplete of *Aegognathus. dulima* (scale bar 1 mm); **e.** Elytra of *Cantharolethrus luxerii luxerii*, surface without longitudinal costae (scale bar 10 mm); **f.** Elytra of *Onorelucanus pulverosus*, surface with few longitudinal costae (scale bar 20 mm) Photo courtesy P. Grossi.

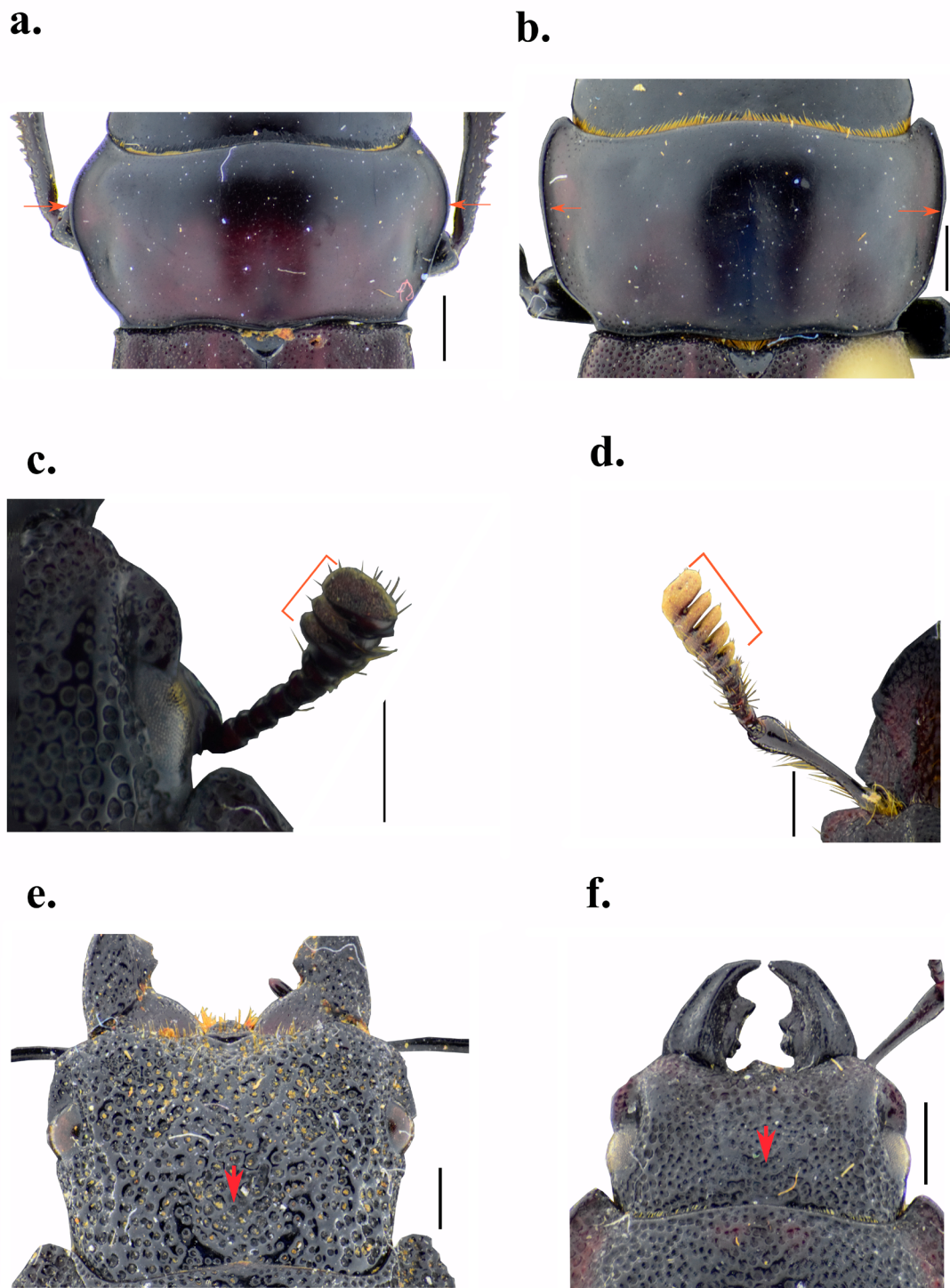


Figure 4. Morphological features of Lucanidae. **a.** Male pronotum of *Onorelucanus pulverosus*, arrows showing strongly convex lateral margins; **b.** Male pronotum of *Aegognathus dulima*, arrows showing nearly straight to slightly convex lateral margins; **c.** Female antennal club of *Aegognathus leuthneri*, with three lamellae; **d.** Female antennal club of *Sphaenognathus nobilis*, with five lamellae; **e.** Female head of *Cantharolethrus luxerii luxerii*, arrow showing the strongly excavated vertex; **f.** Female head of *A. leuthneri*, arrow showing the non-excavated vertex. Scale bars 1 mm.

Table 1. Species of Lucanidae recorded from Colombia. Species marked with an asterisk (*) are considered Colombian endemic. For additional details on localities see Cáceres *et al.* (2022). All the original descriptions are cited in Supplementary Material 2.

Subfamily	Species	Distribution by department
	<i>Aegognathus dulima</i> Cáceres, Ríos-Málaver & Grossi, 2019*	Tolima
	<i>Aegognathus leuthneri</i> Van der Poll, 1886	No known localities
	<i>Cantharolethrus luxerii luxerii</i> (Buquet, 1843) (Fig. 6a, c)	Antioquia, Chocó, Valle del Cauca
	<i>Cantharolethrus steinheili steinheili</i> Parry, 1875	Antioquia, Caldas, Cauca, Risaralda, Valle del Cauca
	<i>Onorelucanus pulverosus</i> (Westwood, 1875)	Boyacá
	<i>Sphaenognathus armatus</i> Parry, 1872* (Fig. 6o)	Boyacá, Cauca, Quindío, Risaralda, Valle del Cauca
	<i>Sphaenognathus bellicosus</i> Boileau, 1904* (Fig. 6j, k)	Cesar, Magdalena
	<i>Sphaenognathus bordoni</i> Brochier & Chalumeau, 2000*	Norte de Santander, Meta
Lucaninae	<i>Sphaenognathus feisthamelii</i> (Guérin-Méneville, 1838) (Fig. 6l, m, n)	Boyacá, Cundinamarca, Santander, Tolima, Valle del Cauca
	<i>Sphaenognathus mandibularis</i> Boileau, 1911*	Antioquia
	<i>Sphaenognathus metallescens</i> DeLisle, 1967*	Cauca
	<i>Sphaenognathus nobilis</i> Parry, 1874	Cundinamarca, Magdalena
	<i>Sphaenognathus prionoides</i> Buquet, 1838 (Fig. 6h)	Cundinamarca, Boyacá, Risaralda, Valle del Cauca, Tolima
	<i>Sphaenognathus pubescens</i> (Waterhouse, 1873)	Antioquia, Tolima
	<i>Sphaenognathus rotundatus</i> Lacroix, 1987	Santander
	<i>Sphaenognathus signatus</i> Parry, 1874 (Fig. 6d, e)	Boyacá, Huila, Quindío, Tolima, Valle del Cauca
	<i>Sphaenognathus spinifer</i> Boileau, 1904* (Fig. 6f)	Caquetá, Huila, Putumayo, Quindío, Tolima
Syndesinae	<i>Psilodon aequinoctiale</i> (Buquet, 1840)*	Tolima, Huila
	<i>Psilodon paschoali</i> Pardo-Locarno & Ríos-Málaver, 2011 (Fig. 6a)	Santander

We recovered twelve species of three genera, recorded from Amazonas, Antioquia, Atlántico, Boyacá, Caquetá, Cauca, Cundinamarca, Huila, Magdalena, Norte de Santander, Risaralda, and Valle del Cauca. *Cantharolethrus luxerii* (Buquet, 1843) was the most widespread species and with the highest number of records (Amazonas, Boyacá, Cundinamarca, Huila, and Valle del Cauca; 71 records). For four of the identified species (*Psilodon aequinoctiale* (Buquet, 1840) - one record, *Sphaenognathus albofuscus* Blanchard, 1842 - a junior synonym of *S. prionoides* Buquet, 1838 - three records, *S. rotundatus* Lacroix, 1987 - one record, and *S. taschenbergi* Parry, 1874 - one record), no spe-

cific localities were provided. Specimens of *S. albofuscus* and *S. taschenbergi* belong to the NHMUK and are likely old specimens, as evidenced by the scarceness of the available information. It is likely that such localities have been recorded as Colombia for old specimens labeled as “New Granada”, which nonetheless, encompassed parts of what is nowadays Brazil, Ecuador, Guyana, Peru, and Venezuela.

Colombia has representation of 6.4 % of the genera and 5.5 % of the lucanid species recorded for the Americas (Fig. 1). Considering only South America, Colombia has 8.1 % of the genera and 6.6 % of the described species.

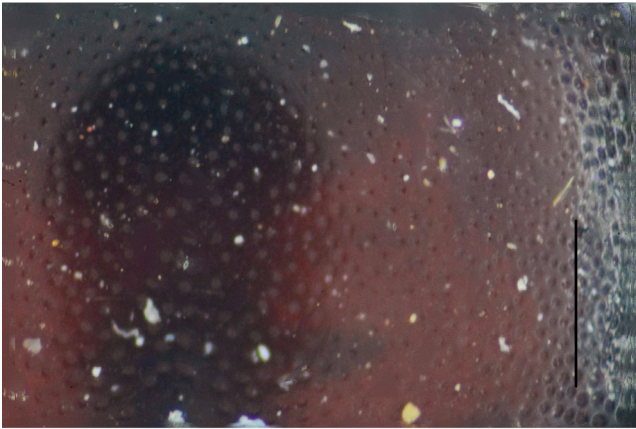
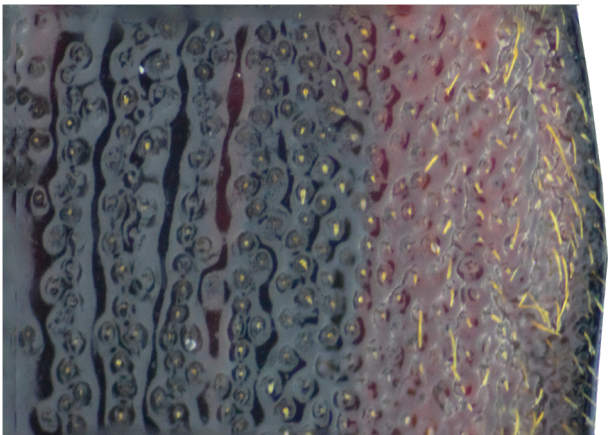
a.**b.**

Figure 5. Elytral surface of lucanid females. **a.** *Onorelucanus pulverosus*, with moderate to large and dense punctation; **b.** *Aegognathus leuthneri*, with coarse and contiguous punctation. (Scale bars 1 mm).

Identification key to the males of lucanid genera present in Colombia

1. Antennae non-geniculate (pedicel inserted on the apex of the antennal scape, at 180°; Fig. 3a)... Syndesinae, Syndesini, ***Psilodon***
- 1'. Antennae geniculate (pedicel inserted on the anterodorsal face of the apical region of the antennal scape at an oblique angle, forming a 90° angle with scape; Fig. 3b)... 2
2. Ocular canthus entire, dividing eyes into dorsal and ventral faces (Fig. 3c)... Chiasognathini, ***Sphaenognathus***
- 2' Ocular canthus not entirely dividing eyes, covering anterior third or half of eyes (Fig. 3d)... Sclerostomini... 3
3. Elytral costae absent; body entirely black (Fig. 3e)... ***Cantharolethrus***

3'. Elytra with few to several longitudinal costae; body color, variable, often with reddish and bluish reflections, somewhat black on head (Fig. 3f)... 4

4. Lateral margins of pronotum strongly convex (Fig. 4a)... ***Onorelucanus***

4'. Lateral margins of pronotum nearly straight, abruptly narrowed at anterior and posterior angles (Fig. 4b)... ***Aegognathus***

Identification key to the females of lucanid genera present in Colombia

1. Antennal club with three lamellae (Fig. 4c)... Sclerostomini... 2
- 1'. Antennal club with five or more lamellae (Fig. 4d)... Chiasognathini, ***Sphaenognathus***
2. Head vertex with a strongly excavated spot (Fig. 4e)... ***Cantharolethrus***
- 2'. Head vertex without excavations, flattened to slightly convex (Fig. 4f)... 3
3. Dorsal surface of body with dense and moderate to large punctation, somewhat contiguous along lateral portion of elytra (Fig. 5a)... ***Onorelucanus***
- 3'. Dorsal surface of body with coarse, contiguous punctation (Fig. 5b)... ***Aegognathus***

DISCUSSION

Colombian stag beetles in the Neotropical context

The known diversity of stag beetles in Colombia can be considered low, especially when compared with Peru, which has more than double the number of species in a slightly larger area (1 139 vs. 1 285 million km², respectively) or Ecuador (283 560 km²), which with about one-fourth of the territory has a slightly larger number of species. Considering the known Andean affinities of some lucanid taxa, these differences can be attributed to revisionary studies involving new species from Ecuador (e.g., Bartolozzi et al. 1992) and Peru (e.g., Arnaud and Bomans 2007), but lacking in Colombia.

On the other hand, Brazil is the country with the highest number of described lucanid taxa across the Americas,



Figure 6. Some representative species of the Lucanidae fauna of Colombia, observed in their natural habitats. **a.** *Psilodon paschoali* ♂, Cerro de la Uchata, Serranía de los Yariguíes, Santander, 2200 m.a.s.l.; **b.** *Cantharolethrus luxerii* ♂, Calima, Darien, Valle del Cauca, 1300 m.a.s.l.; **c.** *C. luxerii* ♀, PNN Las Orquídeas, Antioquia, 1300 m.a.s.l.; **d.** *S. signatus* ♂, La Gruta, Villa María, Caldas, 3300 m.a.s.l.; **e.** *S. signatus* (♂ mayor) Reserva Forestal Protectora, Bosques de la CHEC, Manizales, 2500 m.a.s.l.; **f.** *S. spinifer* ♂, Farallones de Cali, Valle del Cauca 1700 m.a.s.l.; **g.** *S. bordoni* ♀, Carcasí, Santander 3200 m.a.s.l.; **h.** *S. nobilis* ♂, Serranía del Perijá, Colombia, 3000 m.a.s.l.; **i.** *S. prionoides* ♀, Carcasí, Santander 3200 m.a.s.l.; **j.** *S. bellicosus* ♂, Filo de San Lorenzo, Sierra Nevada de Santa Marta, Magdalena 2500 m.a.s.l.; **k.** *S. bellicosus* ♀, Filo de San Lorenzo, Sierra Nevada de Santa Marta, Magdalena 2500 m; **l.** *S. feisthamelii* (♂ mayor), Pamplona, Norte de Santander, 2600 m.a.s.l.; **m.** *S. feisthamelii* ♀, Galán, Santander Serranía de los Yariguíes, 2700 m.a.s.l.; **n.** *S. feisthamelii* ♀ Arcabuco, Boyacá 2300 m.a.s.l.; **o.** *S. armatus* ♀ Duitama, Boyacá, 3000 m.a.s.l.. Photos by Indiana Cristo.

with 76 species classified in fourteen genera, of which eleven are endemic. Most Brazilian lucanids are restricted to the eastern highlands of the Atlantic Forest and to a lesser extent, distributed across the Amazonian biome (Vulcano and Pereira 1961, Grossi and Aguiar 2014). There are several factors contributing to the large number of species known from Brazil: (1) a large territory in a tropical region; (2) the existence of a monograph treating the Brazilian fauna of stag beetles (Luederwaldt 1935), that served as the baseline for recent studies; (3) the presence of a highly trained specialist, Paschoal C. Grossi, who has been contributing to Lucanid knowledge since 2003, and has not only been focused on Brazilian diversity, but also has made significant contributions to the taxonomy of Andean Stag Beetles (Grossi and Paulsen 2009, Grossi 2011, Grossi and Bartolozzi 2011). These key factors have resulted in the existence of an updated catalog for Brazil (Grossi 2023). With this kind of information, Brazilian researchers brought attention to the conservation needs of these beetles, considering vulnerable all seven species of the endemic genus *Altitaiayus* Weinreich, 1960, now included in the list of species threatened by extinction (Ministério do Meio Ambiente 2022). These and *Chiasognathus granti* Stephens, 1831, a rare and vulnerable species from Chile (Vergara and Jerez 2009), are the only protected lucanid species in South America.

The local context of Colombian lucanids

There is evidence that our knowledge about biodiversity in Colombia is biased towards increased data and studies in the Andean region (Arbeláez-C 2013). In the case of lucanids, this bias is actually a reflection of the ecological habits of these beetles. Colombian lucanids are mostly restricted to high elevation ecosystems along the Andes, in an altitudinal range between 1300 and 3900 meters above sea level (m.a.s.l.). Most of the species are associated with montane forests and paramos, which are ecosystems characterized by their high biodiversity, high levels of endemism (Young and Leon 2000, Etter and van Wyngaarden 2000, Larsen *et al.* 2011, Madriñán *et al.* 2013, Cuesta *et al.* 2017, Hazzi *et al.* 2018), and high conservation value (Bush *et al.* 2007, Russi *et al.* 2013).

Besides distributional data for Colombian lucanids we found information about their seasonality (Ríos and Salazar 2005, Salazar *et al.* 2010), which along with field observations (by ICRM and JSDC), suggest that stag beetle populations are more frequently observed during higher

rainfall peaks in the Andean region (April–May and October–November), which is consistent with the close relationship between different beetle taxa and humid seasons (Ortega-E *et al.* 2019, García *et al.* 2021).

Observations from iNaturalist represent the most recent records for *Psilodon*, *Cantharolethrus*, and *Sphaenognathus* species, as well as additional phenological information. In addition, there are records of rare and little-known species that allow for a better understanding of their ecological habits. This shows that community science is a powerful tool to assist formal research teams in the absence of enough available material in national collections and scarce fieldwork.

On the other hand, the armed conflict in Colombia has generated isolation in regions of high interest for their biodiversity (Arbeláez-C 2013). The lack of guaranteed safety for researchers in the field has restricted opportunities to explore and study Colombian Lucanidae in high mountain landscapes of high interest, in areas of the departments of Antioquia, Cauca, Cesar, Córdoba, Chocó, Huila, Magdalena, Valle del Cauca, and Norte de Santander.

Taxonomic studies involving Colombian stag beetles are lacking, which makes it difficult to conduct ecological, populational, and evolutionary studies, as well as to assess conservation status. This situation is compounded by the absence of funding for basic research, the lack of experienced taxonomists, and the limited access to type material, which is for the most part, deposited in European collections (Girón *et al.* 2021). Even when this scenario is not promising, this work represents the first effort to summarize information about this charismatic and yet neglected group of beetles in Colombia.

Towards conservation assessments for Colombian stag beetles

The constant transformation of highland landscapes, where the greatest richness and endemism of these rare beetles is concentrated in Colombia, increases their extinction risk (Ríos and Salazar 2005). Human activities including deforestation, agriculture, illegal mining, and hydropower production (Huang 2018, Bax and Francesconi 2018, Bax *et al.* 2019) are key causes of habitat loss that can have detrimental effects on stag beetle populations across the Andes. There is at least one Colombian endemic lucanid species (*Sphaenognathus mandibularis* Boileau, 1911) that is only known from its original description and has

apparently never been collected again. The natural Andean forest areas in the vicinity of the type locality (Medellín, Antioquia), have undergone intense transformation by human activities in the last century, especially urbanization and forest monocultures, which has possibly negatively impacted the populations of this extremely rare species.

Neotropical lucanids are among the most desired groups of insects by collectors worldwide (Goka *et al.* 2004; Crespin and Barahona-S 2022). Illegal trade of species constitutes a latent threat (New 2010) to Colombian stag beetles, especially considering the rarity of their populations. This is especially evident in the relatively large series of specimens that are present in foreign (including private) collections.

For Lucanidae, the combination of widespread rarity of the species, the lack of data about population dynamics, the significant gaps in ecological knowledge, and the low number of regional specialists, hinder the development of conservation strategies for this beetle family. Given the tight ecological association between lucanids and fragile montane habitats (see Fig. 2), the conservation status of Colombian lucanids must be evaluated urgently. This contribution constitutes a baseline for the analysis of geographic distributions, habitat specificity, and threats that are needed (*e.g.*, Fallon *et al.* 2021) to propose Colombian lucanids as species in need of conservation efforts. We envision the stag beetles of Colombia as objects of conservation efforts that can promote evaluations for other beetles, other insects, and invertebrates in general.

AUTHORS' CONTRIBUTIONS

JSDC: investigation, data curation, writing - original draft, visualization; ICRM: investigation, writing - review and editing, visualization. JCG: conceptualization, data curation, writing - review and editing.

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The Grupo Coleoptera de Colombia (<https://sites.google.com/view/coleopcol/inicio>), with its effort to generate beetle species lists for the country, brought us together to produce this manuscript.

Supplementary Material 1. Comma Separated values file downloaded from iNaturalist on November 10 2022, for data for Lucanidae from Colombia.

Supplementary Material 2. Morphological diagnoses and additional information for lucanid taxa present in Colombia.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

LITERATURE CITED

- Arbeláez-CE. 2013. Knowledge of Colombian biodiversity: published and indexed. *Biodivers. Conserv.* 22(12):2875–2906. doi: <https://doi.org/10.1007/s10531-013-0560-y>
- Arnaud P, Bomans H. 2007. Descriptions de trois nouvelles espèces de Coléoptères Lucanidae du Pérou. *Besoiro.* 16:2–5. https://www.researchgate.net/publication/318888953_Descriptions_de_trois_nouvelles_especes_de_Coleopteres_Lucanidae_du_Perou
- Bartolozzi L, Bomans HE. 1989. *Onorelucanus aequatorianus* n. gen., n. sp. di Lucanidae dell'Ecuador (Coleoptera). *Boll. Soc. ent. Ital.* 121(1):53–58.
- Bartolozzi L, Bomans HE, Onore G. 1992. Contributo alla conoscenza dei Lucanidae dell'Ecuador (Insecta, Coleoptera). *Frustula Entomol.* 14:143–246.
- Bartolozzi L, Zilioli M, De Keyzer R. 2017. The Stag Beetles of Australia, New Zealand, New Caledonia and Fiji. Hradec Králové: Taita Publishers, s.r.o. 176p.

- Bax V, Francesconi W. 2018. Environmental predictors of forest change: An analysis of natural predisposition to deforestation in the tropical Andes region, Peru. *Appl. Geogr.* 91:99–110. doi: <https://doi.org/10.1016/j.apgeog.2018.01.002>
- Bax V, Francesconi W, Delgado A. 2019. Land-use conflicts between biodiversity conservation and extractive industries in the Peruvian Andes. *Environ. Manag.* 232:1028–1036. doi: <https://doi.org/10.1016/j.jenvman.2018.12.016>
- Boileau H. 1904. Description de Coléoptères nouveaux. *Le Naturaliste.* 26:284–285.
- Boileau H. 1911. Description de quelques espèces nouvelles de Lucanides appartenant aux collections du British Museum. *Trans. Entomol. Soc. Lond.* 59(2):426–451. <https://www.biodiversitylibrary.org/page/14765450>
- Bouchard P, Smith ABT, Douglas H, Gimmel ML, Brunke AJ, Kanda K. 2017. Chapter 11. Biodiversity of Coleoptera. In: Foottit RG, Adler PH, editors. *Insect Biodiversity: Science and Society*. Vol. 1. Second Edition. Hoboken: Wiley-Blackwell. p. 337–417. doi: <https://doi.org/10.1002/9781118945568.ch11>
- Buquet L. 1838. Genre Sphenognathe, *Sphoenognathus*. *Revue. Zool.* 1838:104. <https://www.biodiversitylibrary.org/page/2328183>
- Buquet ML. 1840. D'une nouvelle espèce de Lucanidae. *Ann. Soc. Ent. Fr.* 1840: 375–377. <https://www.biodiversitylibrary.org/page/14220284>
- Buquet ML. 1843. Communication. *Ann. Soc. Entomol. Fr.* 1843: LI-LII. <https://www.biodiversitylibrary.org/page/8258647>
- Bush MB, Hanselman JA, Hooghiemstra H. 2007. Andean montane forests and climate change. In: Bush MB, Flenley J, Gosling W. *Tropical rainforest responses to climatic change*. Berlin: Springer. doi: <https://doi.org/10.1007/978-3-642-05383-2>
- Cáceres JSD, Ríos-M C, Grossi PC. 2019. Taxonomic contribution on the Andean species of *Aegognathus* (Coleoptera: Lucanidae) with two new species from Colombia and Peru. *J. Nat. His.* 53(35–36):2145–2164. doi: <https://doi.org/10.1080/00222933.2019.1692089>
- Cáceres JSD, Clavijo J, Ríos-M C. 2022. Listado de las especies de Lucanidae (Coleoptera: Scarabaeoidea) de Colombia. Checklist dataset <https://doi.org/10.15472/p9fc2m> accessed via GBIF.org on 2023-04-24.
- Cáceres JSD, Grossi PC. 2023. Taxonomic revision of *Aegognathus* Leuthner, 1883 (Coleoptera: Lucanidae). *J. Nat. Hist. In press*. doi: <https://doi.org/10.1080/00222933.2023.2198736>
- Crespin SJ, Barahona-S RM. 2022. The risk of rediscovery: fast population decline of the localized endemic Chilean stag beetle *Sclerostomulus nitidus* (Coleoptera: Lucanidae) suggests trade as a threat. *Insect. Conserv. Diver.* 14(1):107–116. doi: <https://doi.org/10.1111/icad.12445>
- Cristóvão JP, Vaz-de-Mello FZ. 2021. The terminalia of the superfamily Scarabaeoidea (Coleoptera): specific glossary, dissecting methodology, techniques and previously unrecorded sexual dimorphism in some difficult groups. *Zool. J. Linn. Soc.* 191(4):1001–1043. doi: <https://doi.org/10.1093/zoolinnean/zlaa079>
- Cuesta F, Muriel P, Llambí LD, Halloy S, Aguirre N, Beck S, Carilla J, Meneses RI, Cuello S, Grau A, Gámez LE, Irazábal J, Jácome J, Jaramillo R, Ramírez L, Samaniego N, Suárez-D D, Thompson N, Tupayachi A, Viñas P, Yager K. Becerra MT, Pauli H, Gosling WD. 2017. Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes. *Ecography.* 40:1–14. doi: <https://doi.org/10.1111/ecog.02567>
- Etter A, van Wyngaarden W. 2000. Patterns of landscape transformation in Colombia, with Emphasis in the Andean Region. *AMBIO.* 29:432–439. doi: <https://doi.org/10.1579/0044-7447-29.7.432>
- Fallon CE, Walker AC, Lewis S, Cicero J, Faust L, Heckscher CM, Pérez-H CX, Pfeiffer B, Jepsen S. 2021. Evaluating firefly extinction risk: Initial red list assessments for North America. *PLOS ONE.* 16(11):e0259379. doi: <https://doi.org/10.1371/journal.pone.0259379>
- Fierro A, Vergara PM. 2019. A native long horned beetle promotes the saproxylic diversity in exotic plantations of Monterrey pine. *Ecol. Indic.* 96:532–539. doi: <https://doi.org/10.1016/j.ecolind.2018.09.018>
- Fujita, H. 2010. *The Lucanid Beetles of the World. Vol II.* Japan: Mushi-sha.
- García K, Martínez NJ, Botero JP. 2021. Diversity of longhorned beetles (Coleoptera: Cerambycidae) in the Caribbean region of Colombia: temporal variation between two fragments of tropical dry forest. *Biota. Neotrop.* 21(3):1–10. doi: <https://doi.org/10.1590/1676-0611-BN-2020-1136>
- GBIF.org (04 November 2022) GBIF Occurrence Download. <https://doi.org/10.15468/dl.xpzh7g>
- Girón JC, García GA, Botero JP, Cardona-D J, Clavijo-B J, Díaz-D C, García JH, García K, López W, Lugo-d A, Neita JC, Ramírez-S JM, Taboada-V C, Uchima-T D, Viasus-B A. 2021. Consideraciones sobre el estado del conocimiento de la diversidad de Coleoptera (Arthropoda: Insecta) en Colombia. *Rev. Colomb. Entomol.* 47(2):e10717. doi: <https://doi.org/10.25100/socolen.v47i2.10717>
- Goka K, Kojima H, Okabe K. 2004. Biological invasion caused by commercialization of stag beetles in Japan. *Global Environ. Res.* 8(1):67–74.
- Grossi PC, Paulsen MJ. 2009. Generic limits in South American stag beetles: taxa currently misplaced in *Sclerostomus* Burmeister (Coleoptera: Lucanidae: Lucaninae: Sclerostomini). *Zootaxa.* 2139:23–42. doi: <https://doi.org/10.11646/zootaxa.2139.1.2>
- Grossi PC. 2011. Review of *Incadorcus* Arnaud & Bomans with the description of three new species from the Yungas of Peru and Bolivia (Coleoptera: Lucanidae: Lucaninae). *Zootaxa.* 2750(1): 1–14. doi: <https://doi.org/10.11646/zootaxa.2750.1.1>

- Grossi PC, Bartolozzi L. 2011. Description of a new genus and species of stag beetle (Coleoptera: Lucanidae: Lucaninae) from the Peruvian Andes. *Coleop. Bull.* 65(4):387–392. doi: <https://doi.org/10.1649/072.065.0414>
- Grossi PC, Aguiar NO. 2014. Discovery of a third stag beetle genus in the Amazonian Region, with description of a new species of *Psilodon* Perty (Coleoptera: Lucanidae: Syndesinae: Syndesini). *Coleop. Bull.* 68(1): 83–90. doi: <https://doi.org/10.1649/0010-065X-68.1.83>
- Grossi PC. 2023. Lucanidae in Catálogo Taxonômico da Fauna do Brasil. PNUD. [Revised in: 9 Nov 2022] <http://fauna.jbrj.gov.br/fauna/faunadobrasil/124549>
- Guérin MFE. 1838. Sur un insecte coléoptère nouveau du genre *Chiasognathus* de Stephens. *Rev. Zool.* 1838: 287–288. <https://www.biodiversitylibrary.org/page/2328468>
- Hazzi NA, Moreno JS, Ortiz-M C, Palacio RD. 2018. Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *P. Natl. Acad. Sci-Biol.* 115(31):7985–7990. doi: <https://doi.org/10.1073/pnas.1803908115>
- Holloway BA. 1960. Taxonomy and phylogeny in the Lucanidae (Insecta: Coleoptera). *Rec. Dom. Mus.* 3:321–365.
- Holloway BA. 1968. The relationship of *Syndesus* MacLeay and *Sinodendron* Schneider (Coleoptera: Lucanidae). *New. Zeal. J. Sci.* 11:264–269.
- Holloway BA. 1969. Further studies on generic relationships in Lucanidae (Insecta: Coleoptera) with special reference to the ocular canthus. *New. Zeal. J. Sci.* 12:958–977.
- Holloway BA. 2007. Lucanidae (Insecta: Coleoptera). *Fauna of New Zealand Vol 6*. First edition. Wellington: PrintLink Ltd.
- Huang TI. 2018. Diversity and ecology of stag beetles (Lucanidae). In: Ulyshen MD. *Saproxyllic Beetles, Diversity, Ecology and Conservation*. Cham: Springer International Publishing. doi: https://doi.org/10.1007/978-3-319-75937-1_4
- Kawano K. 2000. Genera and allometry in the stag beetle family Lucanidae, Coleoptera. *Ann. Entomol. Soc. Am.* 93(2):198–207. doi: [https://doi.org/10.1603/0013-8746\(2000\)093\[0198:GAAITS\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[0198:GAAITS]2.0.CO;2)
- Kim SI, Farrell BD. 2015. Phylogeny of world stag beetles (Coleoptera: Lucanidae) reveals a Gondwanan origin of Darwin's stag beetle. *Mol. Phylogenet. Evol.* 86:35–48. doi: <https://doi.org/10.1016/j.ympev.2015.02.015>
- Lacroix JP. 1987. Description de *Sphaenognathus* (Col: Lucanidae) nouveaux de la faune Sud américaine. *Bull. Soc. Sci. nat.* 56: 11–13.
- Larsen TH, Escobar F, Armbrrecht I. 2011. Insects of Tropical Andes: Diversity patterns, processes and global change. In Herzog SK, Martinez R, Jorgensen PM, Tiessen H, editors. *Climate Change and Biodiversity in the Tropical Andes*. Inter-American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE).
- Latreille PA. 1804. *Histoire naturelle, générale et particulière des crustacés et des insectes*. Tome Dixième. Paris: L'Imprimerie de F. Dufart. <https://www.biodiversitylibrary.org/page/15587272>
- Lawrence JF, Slipiński A, Seago AE, Thayer MK, Newton AF, Marvaldi AE. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Ann. Zool.* 61(1):1–217. doi: <https://doi.org/10.3161/000345411X576725>
- Leuthner F. 1883. *Aegognathus waterhousei*, a new genus and species of Dorcinae from Peru. *Trans. Entomol. Soc. Lond.* 445–446. <http://www.archive.org/stream/transactionsofen1883roya#page/445/mode/1up>
- Luederwaldt H. 1935. *Monographia dos Lucanideos Brasileiros*. *Rev. Mus. Pau.* 19: 448–574.
- MacLeay WS. 1819. Appendix. Genera entomologica ad animadversiones praecedentes illustrandas, necnon queadam nova ad natralem Petalocerorm ordinem detegendum nune primum constructa. *Horae entomol.* 1:95–160. <https://www.biodiversitylibrary.org/page/33071033>
- Madriñán S, Cortés AJ, Richardson JE. 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Front. Genet.* 4:1–7. doi: <https://doi.org/10.3389/fgene.2013.00192>
- Ministério do Meio Ambiente. 2022. Portaria MMA Nº148, de 7 de junho de 2022 [Revised in: 9 Nov 2022] <https://in.gov.br/en/web/dou/-/portaria-mma-n-148-de-7-de-junho-de-2022-406272733>
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature.* 403:853–858. doi: <https://doi.org/10.1038/35002501>
- New T. 2010. *Beetles in conservation*. Chichester: Wiley-Blackwell.
- Ortega-E C, Navas-S GR, Noriega JA. 2019. Seasonality of the assemblage of dung beetles (Coleoptera: Scarabaeinae) of the botanical garden of Cartagena “Guillermo Piñeres” Bolívar-Colombia. *Caldasia.* 41(1):124–138. doi: <https://doi.org/10.15446/caldasia.v41n1.72107>
- Pardo-L LC, Ríos-M C. 2011. *Psilodon paschoali* n. sp. y descripción de la hembra de *Psilodon aequinoctiale* Buquet (Coleoptera: Lucanidae) en la región Norandina de Colombia. *Bol. cient. mus. hist. nat.* 15(1):246–250. <https://revistasoj.s.ucaldas.edu.co/index.php/boletincentifico/article/view/4442/4075>
- Parry FJS. 1872. Descriptions of new species of Lucanoid Coleoptera; with remarks on the genus *Cantharolethrus*, and supplementary list. *Trans. Entomol. Soc. Lond.* 20(1): 73–84. <https://www.biodiversitylibrary.org/page/14778313>
- Parry FJS. 1874. Further descriptions of Lucanoid Coleoptera. *Trans. Entomol. Soc. Lond.* 22(3): 365–372. <https://www.biodiversitylibrary.org/page/14921679>
- Parry FJS. 1875. Description of a new species of the Lucanoid genus *Cantharolethrus*, Thomson. *Cistula Entomol.* 2: 51–52. <https://www.biodiversitylibrary.org/page/10890677>

- Paulsen MJ. 2005. A revision of the southern South American stag beetles of the genus *Sclerostomus* Burmeister (Coleoptera: Scarabaeoidea: Lucanidae). *Zootaxa* 1060(1):1–26. doi: <https://doi.org/10.11646/zootaxa.1060.1.1>
- Paulsen MJ. 2019. Annotated Checklist of the New World Lucanidae (Coleoptera: Scarabaeoidea) [Reviewed on: 07 nov 2022] <https://unsm-ento.unl.edu/Guide/Scarabaeoidea/Lucanidae/Lucanidae-Catalog/LucanidaeC.htm>
- Perty JAM. 1830. De Insectorum in America Meridionali habitantium vitae genere, moribus ac distributione geographica, observationes nonnullae. In: Spix J, Martius C, editors. *Delectus animalium*. 1830–1834: 53–54. <https://www.biodiversitylibrary.org/page/57932815>
- Ratcliffe BC. 2002. Lucanidae. In Arnett RH, Thomas MC, Skelley PE, Frank JH, editors. *American Beetles*. Vol. 2. First edition. Boca Raton: CRC Press LLC. p. 6–9.
- Ríos IC, Salazar JA. 2005. Coleóptera (IV) Sobre algunas localidades colombianas para conocer y estudiar a *Cantharolethrus luxerii* (Buquet); *Sphaenognathus hemiphanestus* (Delisle) & *Sph. feisthamelii* (Guérin-Ménéville) (Col. Lucanidae). *Bol. Cient. Mus. Hist. Nat. U. Caldas*. 9:167–177. <https://revistasoj.s.ucaldas.edu.co/index.php/boletincentifico/article/view/6010>
- Russi D, Ten-B P, Farmer A, Badura T, Coates D, Förster J, Kumar R, Davidson N. 2013. *The economics of ecosystems and biodiversity for water and wetlands*. London and Brussels: IEEP, Ramsar Secretariat, Gland.
- Salazar JA, Ríos-M C, Martínez-A JF. 2010. Coleoptera (VII) Noticias sobre los lucánidos colombianos *Sphaenognathus pubescens* (Wartherhouse), *S. bordoni* (Brochier & Chalumeau); *S. bellicosus* (Boileau) y *S. nobilis colombiensis* (Moxey) (Coleoptera: Lucanidae). *Bol. Cient. Mus. Hist. Nat. U. Caldas*, 14(2):141–154. <https://revistasoj.s.ucaldas.edu.co/index.php/boletincentifico/article/view/5265>
- Smith BT. 2006. A review of the family-group names for the superfamily Scarabaeoidea (Coleoptera) with corrections to nomenclature and a current classification. *Coleopt. Bull.* 60(mo5):144–204. [https://doi.org/10.1649/0010-065X\(2006\)60\[144:AROTFN\]2.0.CO;2](https://doi.org/10.1649/0010-065X(2006)60[144:AROTFN]2.0.CO;2)
- Stephens JF. 1831. Description of *Chiasognathus grantii*, a new lucanideous insect forming the type of an undescribed genus, together with some brief remarks upon its structure and affinities. *Trans. Cambridge Philos. Soc.* 4(2):209–219. <https://www.biodiversitylibrary.org/page/13266035>
- Thomson J. 1862. Catalogue des Lucanides. *Ann. Soc. Entomol. Fr.* 4(2):392–436. <https://www.biodiversitylibrary.org/page/8239334>
- Van de Poll JRH. 1886. Description of a second species of the lucanoid genus *Aegognathus* Leuthner. *Tijdschr. Entomol.* 29:153–154. <https://www.biodiversitylibrary.org/page/10851883>
- Vergara OE, Jerez V. 2009. Estado de conservación de *Chiasognathus grantii* Stephens, 1831 (Coleoptera: Lucanidae) en Chile. *Rev. Chil. Hist. Nat.* 82:565–576. doi: <http://dx.doi.org/10.4067/S0716-078X2009000400010>
- Vulcano MA, Pereira FS. 1961. A Subfamília Penichrolucaninae representada em América. *Stud. Entomol.* 4(1–4): 471–480.
- Weinreich E. (1960). Revision südamerikanischer Lucanidae II. Die Gattungen *Charagmophorus*, *Metadorcus*, *Scortizus*, *Apterodorcus*, *Beneshius*, *Sclerostomus* und *Pycnosiphorus*. *Senck. Biol.* 41(1–2):41–95.
- Woodruff RE. 2009. A new fossil species of stag beetle from Dominican Republic amber, with Australasian connections (Coleoptera: Lucanidae). *Insecta Mundi* 0098:1–10. <https://digitalcommons.unl.edu/insectamundi/621/>
- Young KR, León B. 2000. Biodiversity conservation in Peru's Eastern montane forests. *Mt. Res. Dev.* 20(3):208–211. doi: [https://doi.org/10.1659/0276-4741\(2000\)020\[0208:BCIPSE\]2.0.CO;2](https://doi.org/10.1659/0276-4741(2000)020[0208:BCIPSE]2.0.CO;2).