

FIRST FOSSIL ASSEMBLAGE OF DARKLING BEETLES (COLEOPTERA: TENEBRIONIDAE) FROM BUENOS AIRES, ARGENTINA: EVIDENCE OF DRY CLIMATE DURING THE LATE PLEISTOCENE IN THE HUMID PAMPAS

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Abstract.— Late Pleistocene outcrops exposed in Buenos Aires province, Argentina, represent one of the most informative sources for paleoecological studies on South American fauna and flora. Several proxies have been used for studying Pleistocene environmental conditions in the Pampas, but only a few were based on paleoentomological data. The aims of this study are to present the first record of three species of darkling beetles from the late Pleistocene of Buenos Aires province and to provide new paleoenvironmental information. The sediments containing fossil insects correspond to the Guerrero Member of the Luján Formation and were dated between $12,100 \pm 100$ 14C BP and $13,400 \pm 200$ 14C BP. Specimens of *Nyctelia picipes* (Billberg), *Epipedonota cristallisata* Waterhouse and *Scotobius pilularius* Germar were identified. To provide information about past climate, the particular climate requirements of these species were analyzed by using the Mutual Climatic Range method. This association could indicate the first pulse of post-glacial climate recovery and the replacement by the insect fauna currently inhabiting the area. This study is one of the first approaches to the Quaternary paleoentomology of Argentina, and highlights the potential of paleoentomological information, when evaluated in combination with previous knowledge on global climate conditions after the last glacial maximum.



Key words.— Fossil Tenebrionidae, Late Pleistocene, Luján Formation, *Nyctelia picipes*, *Epipedonota cristallisata*, *Scotobius pilularius*, Argentina.

INTRODUCTION

The Tenebrionidae, also known as darkling beetles, are one of the most diverse families in the animal

kingdom, with about 20,000 species and 2,300 genera worldwide (Matthews *et al.* 2010). In Argentina, the family is represented by seven subfamilies with 488 species, most of them endemic to the country (Flores

1998, Matthews *et al.* 2010). Although the Tenebrionidae are quite a large beetle group, relatively little has been published on their representation in the fossil record. Approximately 115 fossil taxa of darkling beetles are currently known, most of them from Baltic and Dominican amber, and most known fossils belong to forest inhabiting groups (Kirejtshuk *et al.* 2008, Nabozhenko *et al.* 2015 and references therein). The historical development and fossil record of the family are considered in Kirejtshuk *et al.* (2008) and in the catalogue by Ponomarenko and Kirejtshuk (2010).

Despite the number of deposits studied in Argentina, the only recorded fossil tenebrionid for country (and for South America) is *Tenebrionites inclinans* which was described by Cockerell (1928) from Maiz Gordo Formation, Jujuy Province, northern Argentina, Paleocene (?Eocene). This specimen was allocated to the collective group *Tenebrionites*. In this work an assemblage of three tenebrionid species found in sediments referred to the Guerrero Member of the Luján Formation (late Pleistocene) in northeast Buenos Aires Province, Argentina is presented.

From a biogeographic point of view, the deposit where this assemblage was found is located in the humid Pampas ecoregion (Fig. 1), based on the ecoregions used in Olson *et al.* (2001). Currently, there is controversy over the climatic conditions found during the late Pleistocene in this ecoregion. Several authors who have studied the Pleistocene paleoclimate support the existence of cold and arid environmental conditions during the deposition of the Guerrero Member of the Luján Formation (ca. 21,000–13,000 yr BP) (e.g., Clapperton 1993; Tonello and Prieto 2010). On the other hand, Scanferla *et al.* (2013 and references therein) suggested hot and humid climate conditions. The assemblage of tenebrionids found in this deposit can help to elucidate climate conditions in this region during the late Pleistocene, as they are sensitive to several environmental variables and have previously been considered indicators of different climate conditions (Cepeda-Pizarro *et al.* 2005).

The fossil tenebrionids found in the Pampas are particularly useful as paleoclimatic proxies as they are all still extant species (Carrara *et al.* 2011). As such, information on current species distribution patterns is available, which can be compared with data obtained for the deposit during the late Pleistocene. The tenebrionid species assemblage found in the deposit area no longer exist in the region at the present time. This could have been caused by at least two factors: first, climate conditions in the late Pleistocene changed through time, making it currently impossible for these three species to subsist; or second, climate conditions did not change and species were driven to local

extinction by factors other than climate. Taking into account that these three species are at present locally abundant in their current distribution area (Carrara and Flores, personal observations) and widely distributed in southern South America (Kulzer 1963, Flores and Vidal 2001, Carrara *et al.* 2016 this volume), it is unlikely that factors other than climate caused the present expatriations observed in the deposit area. Thus, it is feasible to reconstruct paleoclimate scenarios by overlapping present-day climatic tolerance ranges of these living species (Sinka and Atkinson 1999) as an indicator of climate conditions that promoted the species assemblage found during the late Pleistocene.

The objectives of this work are: to present the first record of a darkling beetle assemblage from the late Pleistocene of Buenos Aires Province; to assess whether climate has modified species distribution by comparing late Pleistocene with present-day conditions and, if so, to provide new paleoclimate evidence to clarify the debate regarding climate in the humid Pampas in the late Pleistocene.

MATERIALS AND METHODS

Study area and geological settings

The Salado river basin covers an area of approximately 186,000 km² and is located between 35°00' and 37°37'S, and 56°52' and 60°38'W. Geomorphologically, the basin lies in the area that Frenguelli (1950) and Fidalgo (1992) called “depressed Pampa” (Fig. 1), and is the area with the lowest slope in Buenos Aires province, which makes it easily floodable (Fidalgo 1992). Because of the low slope, large volumes of water can accumulated rapidly, and leading to persistent flooding (Brandizi and Labraga 2012). Another factor contributing to flooding in the area is the predominance of soils with low capacity to infiltrate water when saturated (INTA 1977, Provincia de Buenos Aires – Consejo Federal de Inversiones 1981, Miaczynski 1995).

The current climate in this ecoregion is temperate and humid, without a dry season (Quiros 2005, Magrin *et al.* 2007). Average annual rainfall is 855 mm and there is a general upward trend in average rainfall from south to north. Average annual temperature varies from north to south between 13.8 and 15.9°C (Halcerow and Partners 1999, Diaz and Mormeneo 2002). Temperature in the northwest varies between 24°C in summer and 10°C in winter, while in the southwest it varies between 20°C and 7°C respectively. The flora associated with the Salado River is part of the sub-humid temperate grasslands found in South America, specifically in the Pampas ecoregion (Soriano

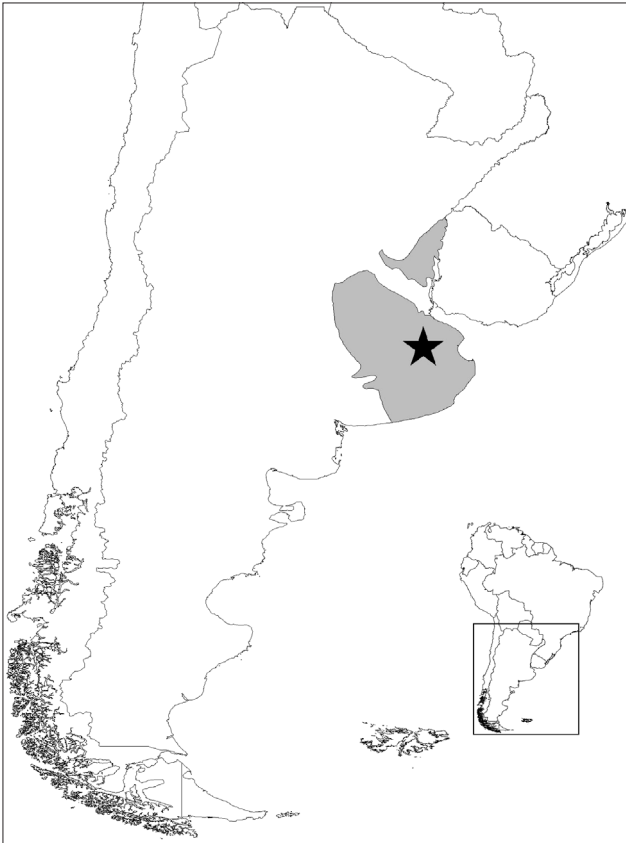


Figure 1. Geographic location of General Belgrano deposit (black star) in the ecoregion of Humid Pampas (grey area).

1991). This vegetation is influenced by temporary periods of drought, excess water during periods of flooding, and by high salinity both the in water and soil (Apóstolo 1999). Because of this, Canevari *et al.* (1999) considered the Salado river basin one of the major wetlands in the Pampas.

The outcrop was exposed on the left margin during the work of dredging and channeling the Salado River. The fossiliferous strata consist of greenish brown sandy clays deposited in a small paleopond environment that was filled by fluvial sediments, exhibiting abundant organic matter, gypsum, and carbonate concretions (Scanferla *et al.* 2013). The age of the sediments containing fossil insects ranges between $12,100 \pm 100$ 14C BP and $13,400 \pm 200$ 14C BP and was obtained by radiocarbon analysis of bone collagen (Scanferla *et al.* 2013) and molluscan shells (Fucks *et al.* 2012). These deposits correspond to the time span represented by the Guerrero Member of the Luján Formation (Fidalgo *et al.* 1973). The deposition of the Guerrero Member began around the Last Glacial Maximum (ca. 21,000 yr BP) and continued at least until ca. 10,000 yr BP (Tonni *et al.* 2003).

Data collection

The techniques used for extraction and concentration of fossil insect material were summarized by Elias (1994). However, an alternative method to kerosene flotation, the most common method, was used in this study. Before treating the sediments with a defloculant (calgon), the clay blocks were checked for conspicuous pieces of insects. Once disaggregated, the material was analyzed under the microscope. This method allows recovery of fragments from heavy, non-floating, insects (such as tenebrionids) and prevents damage to the material during sieving and detergent washing. Moreover, the material remains suitable for radiocarbon dating. The remains were stored in small vials of 70% ethanol. The remains were identified by comparison with modern specimens of material deposited in the Entomological collection of IADIZA (Instituto Argentino de Investigaciones de las Zonas Áridas) and using identification keys and revisions from Kulzer (1955, 1963) and Flores and Vidal (2001).

Species distribution

Data on species distributions were obtained by studying material from several collecting trips and the following museum collections: Argentina: Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, Sergio Roig-Juñent), Mendoza; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires (Arturo Roig Alsina); Museo de La Plata, La Plata (Nora Cabrera); Fundación e Instituto Miguel Lillo, San Miguel de Tucumán (Emilia Pérez); Museo Municipal Lorenzo Scaglia, Mar del Plata (Juan Farina); Instituto Patagónico de Ciencias Naturales, San Martín de los Andes, Neuquén (now deposited at IADIZA), Instituto Patagónico para el Estudio de los Ecosistemas Continentales (CENPAT, Germán Cheli), Universidad Nacional de San Luis, Cátedra de Zoología, San Luis (Ana Medina); Chile: Museo Nacional de Historia Natural, Santiago (Mario Elgueta D.); Brazil: Museu de Ciências Naturais, Porto Alegre, RS (Luciano Moura); Germany: Museum für Naturkunde der Humboldt Universität, Berlin (Manfred Uhlig and Bernd Jaeger).

The specimens were georeferenced according to their collection information and their geographical location of the collection site (latitude and longitude). It should be noted that any specimen that was found more than once with the same collection information and georeference was considered a duplicate data point. These combined data points were entered into the database as a single record.

Paleoclimate analyses

Mutual Climatic Range (MCR) approach was used. This method avoids the use of indicator species and accounts for the ephemeral presence of some species during intervals of rapid climate change by concentrating on the analysis of entire assemblages, employing presence of species rather than relative abundance (which may change depending on the depositional environment). From the climate information about sites where the species were recorded, T_{\max} (mean temperature and precipitation of the warmest month) were plotted versus T_{range} (temperature range between the warmest and coldest months), and P_{\max} (mean precipitation of the wettest month) versus P_{range} (precipitation range between the wettest and driest months). To this end, climate information from the WorldClim database (www.worldclim.com) at a resolution of approximately 5×5 km and the DIVA-GIS software (www.divagis.org) was used to extract climate information from each species' presence record. Then, all species' climate ranges were plotted together to obtain the area of maximum overlap, which is recognized as the climate conditions where the species can subsist as an assemblage.



Figure 2. *Scotobius pilularius* Germar, 1823, fossil of the elytra and ventrites articulated. Scale bars: 5 mm.

RESULTS

Systematic Paleontology

Family **Tenebrionidae** Latreille, 1802

Subfamily **Tenebrioninae** Latreille, 1802

Tribe **Scotobiini** Solier, 1838

Genus **Scotobius** Germar, 1823

Scotobius pilularius Germar, 1823

(Fig. 2)

Description. The fossil consists of the elytra and ventrites articulated.

Label: “*Scotobius pilularius* MHM-PI 33/Col. Ramírez, L.C. 2013”

Diagnosis. See Aballay *et al.* 2016 (this volume).

Modern collection localities. Argentina: provinces of Buenos Aires, Chubut, Córdoba, Corrientes, Entre Ríos, Formosa, La Pampa, La Rioja, Mendoza, Neuquén, Río Negro, San Luis, Tucumán; Uruguay: departments of Canelones, Lavalleja, Montevideo; Brazil: state of Rio Grande do Sul; Chile: Cautín province (Silvestro and Flores 2016, this volume).

Subfamily **Pimeliinae** Latreille, 1802

Tribe **Nycteliini** Solier, 1834

Genus **Epipedonota** Solier, 1836

Epipedonota cristallisata Waterhouse, 1844

(Fig. 3)

Description. The fossil consists of a fragment of the left elytron.

Label: “*Epipedonota cristallisata* MHM-PI 32/Col. Ramírez, L.C. 2013”

Diagnosis. See Flores and Vidal 2001: 36.

Modern collection localities. Argentina: provinces Buenos Aires (south), Chubut, La Pampa, Mendoza, Neuquén, Río Negro, and Santa Cruz (Flores and Vidal 2001).

Genus **Nyctelia** Berthold, 1827

Nyctelia picipes (Billberg, 1815)

(Figs. 4: A–B)

Description. The fossil consists of a specimen partially articulated.

Label: “*Nyctelia picipes* MHM-PI 31/Col. Ramírez, L.C. 2013”

Diagnosis. See Kulzer 1963: 61 as *Nyctelia brun-nipes* Latreille.



Figure 3. *Epipedonota cristallisata* Waterhouse, 1844, fossil consists of a fragment of the left elytron. Scale bars: 5 mm.

Modern collection localities. Argentina: provinces Buenos Aires, Catamarca, Chubut, Córdoba, Entre Ríos, La Pampa, La Rioja, Mendoza, Río Negro, San Juan, San Luis, Santa Fe, and Santiago del Estero; Uruguay: departments Rocha, Maldonado, and Montevideo (Kulzer 1963, Silvestro and Flores 2016, this volume).

Species biogeographic distributions

A review of modern specimen records shows no recent occurrences for two of the fossil species (*E. cristallisata* and *N. picipes*) in the deposition area. Considering the first two species, it was recognized that they exhibited different spatial distribution patterns in relation to the General Belgrano deposit. On the one hand, the nearest modern spatial record of *E. cristallisata* is located 400 km from the deposit, and all records are from areas that are drier than the current conditions in the deposit area (Fig. 5); the nearest spatial record of *N. picipes* is located 200 km from the deposit but in similar climate areas (Fig. 6). Instead, *S. pilularius* was recently found in the same area of the present deposit, which proves that this species still survives under the climate conditions in the deposit area (Fig. 7).

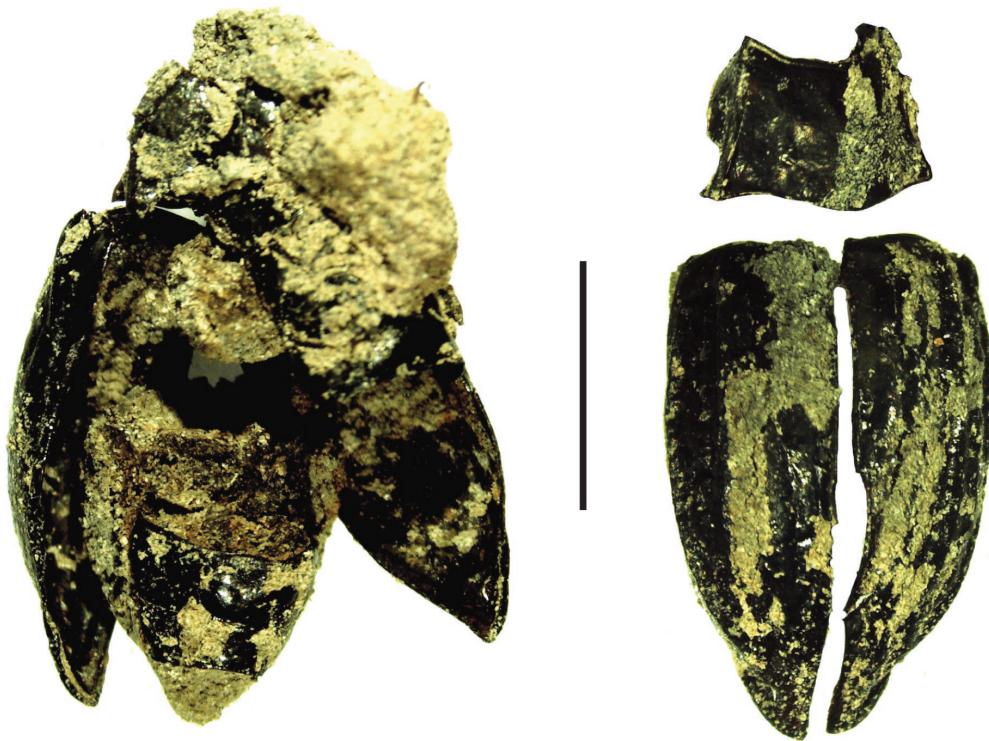


Figure 4. *Nyctelia picipes* (Billberg, 1815), fossil consists of a specimen partially articulated: (A) ventral view before cleaning; (B) dorsal view of pronotum and elytra. Scale bars: 5 mm.

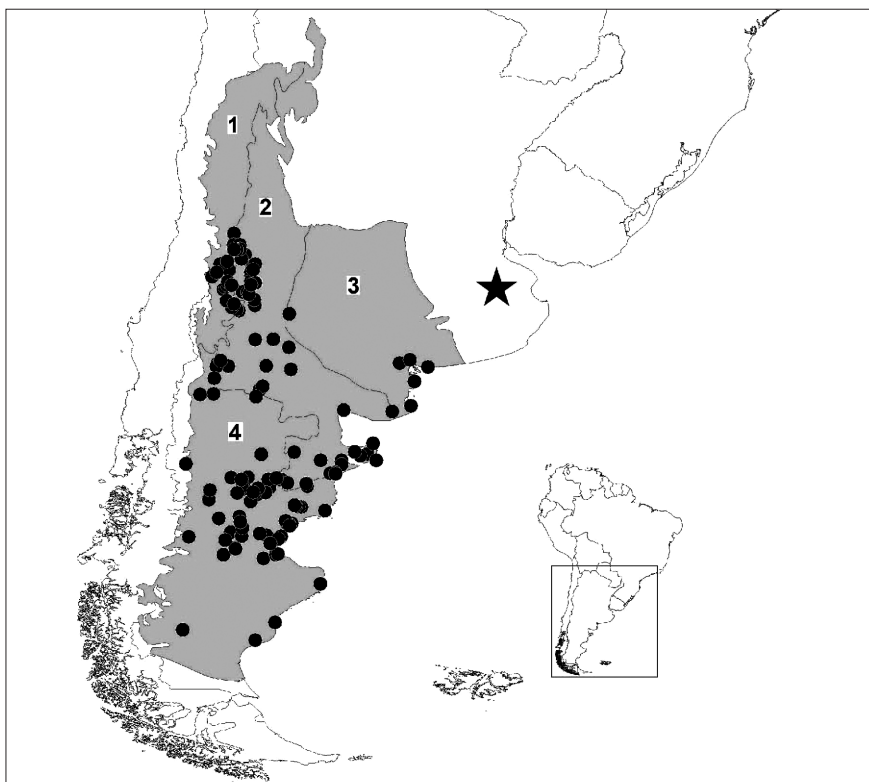


Figure 5. Geographic distribution of *Epipedonota cristillisata* (black circles) through different terrestrial ecoregions (grey area): 1 – Southern Andean steppe; 2 – Argentine Monte; 3 – Semi-arid Pampas; 4 – Patagonian steppe. Black star represents the spatial location of the deposit.

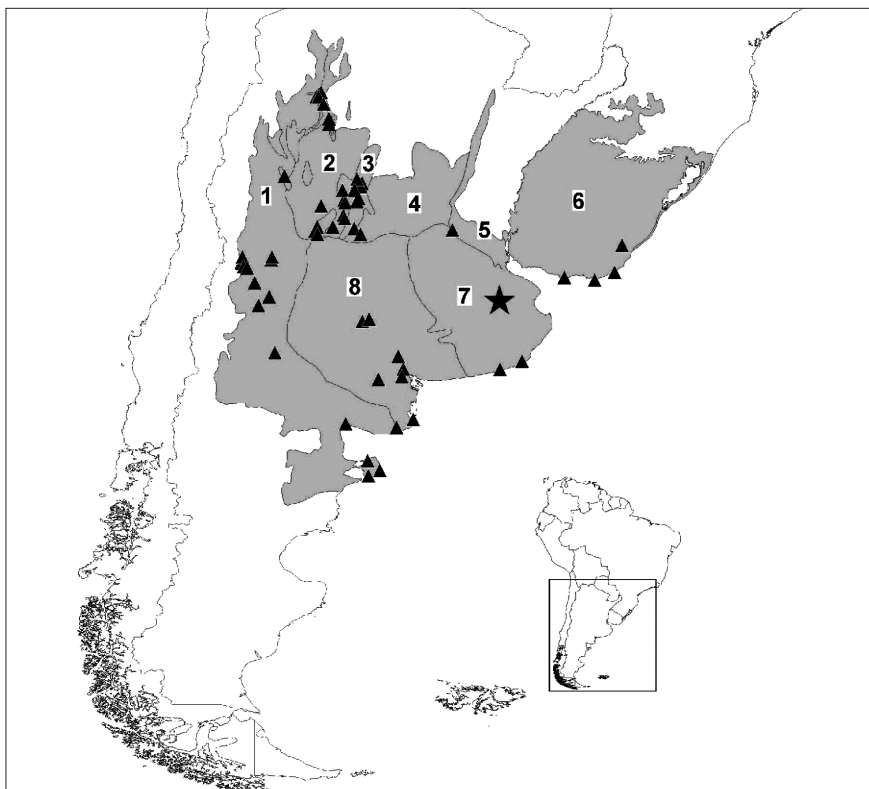


Figure 6. Geographic distribution of *Nyctelia picipes* (black triangles) through different terrestrial ecoregions (grey area): 1 – Argentine Monte; 2 – Arid Chaco; 3 – Córdoba montane savanna; 4 – Argentine espinal; 5 – Paraná flooded savanna; 6 – Uruguayan savanna; 7 – Humid Pampas; 8 – Semi-arid Pampas. Black star represents the spatial location of the deposit.

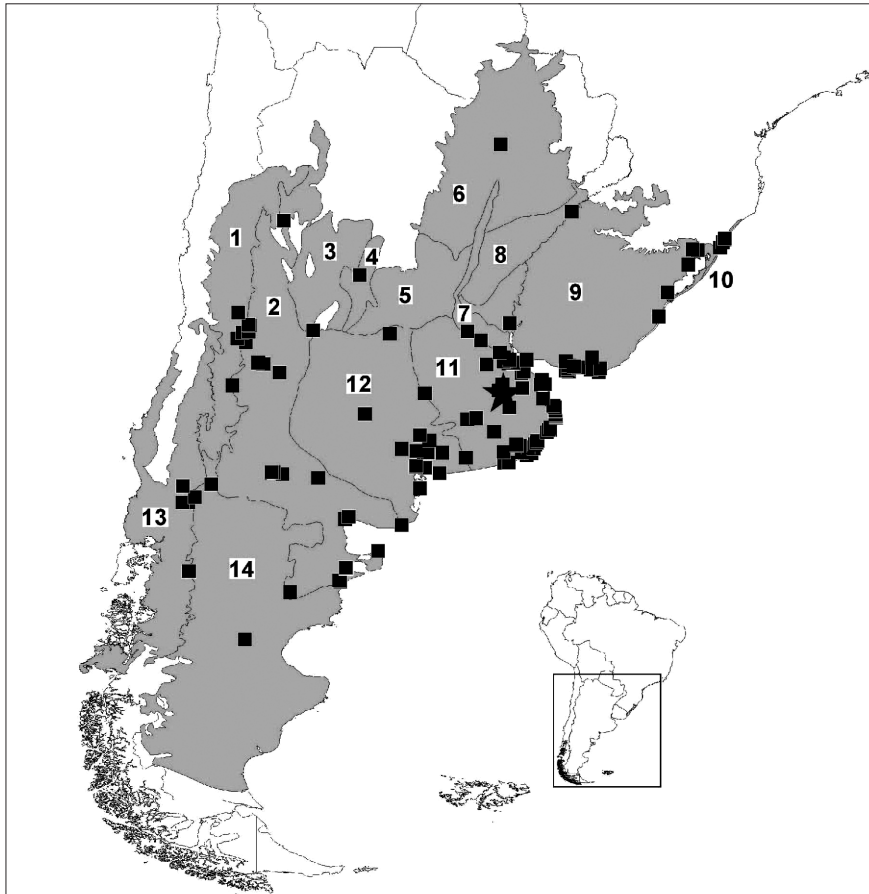


Figure 7. Geographic distribution of *Scotobius pilularius* (black squares) through different terrestrial ecoregions (grey area): 1 – Southern Andean steppe; 2 – Argentine Monte; 3 – Arid Chaco; 4 – Córdoba montane savanna; 5 – Argentine espinal; 6 – Humid Chaco; 7 – Paraná flooded savanna; 8 – Southern Cone Mesopotamian savanna; 9 – Uruguayan savanna; 10 – Atlantic Coast restingas; 11 – Humid Pampas; 12 – Semi-arid Pampas; 13 – Valdivian temperate forest; 14 – Patagonian steppe. Black star represents the spatial location of the deposit.

Paleoclimate analyses

The MCR results showed that the values for temperature variables in the area of maximum overlap of the superimposed climate ranges of all three species were T_{\max} 21–31°C and T_{range} 21.8–31.5°C (Fig. 8). The values for precipitation variables were P_{\max} 12–70 mm and P_{range} 20–85 mm (Fig. 9). These climate ranges did not differ from the current climate conditions in the deposit area in temperature (T_{\max} 30.5°C and T_{range} 26.2°C) but were lower for precipitation (P_{\max} 103 mm and P_{range} 52 mm).

DISCUSSION

This study is one of the first approaches to the Quaternary paleoentomology of Argentina, and highlights the potential of paleoentomological information, when

evaluated in combination with previous knowledge on global climate conditions after the last glacial maximum. The species found here belong to the tribes Nyciteliini and Scotobiini, which were assigned by Matthews *et al.* (2010) as endemic tribes of Arid South America. This area is formed in America mainly south of the 25th parallel S, not including southern Chile which was assigned to the Austral region (Morrone 2015), or eastern Argentina which has mainly Neotropical elements (Flores 1998), but including arid areas further north (Matthews *et al.* 2010) such as the Peruvian coastal desert and ranges, Bolivian altiplano, and Galapagos Islands, as well as north-eastern Brazil which has xerophilic elements (Flores and Triplehorn 2002).

Current occurrences for two species appear to exclude areas of high precipitation, such as the humid Pampas. In the fossiliferous locality there are no current records for *E. cristallisata* or *N. picipes*. This finding suggests that weather conditions in General

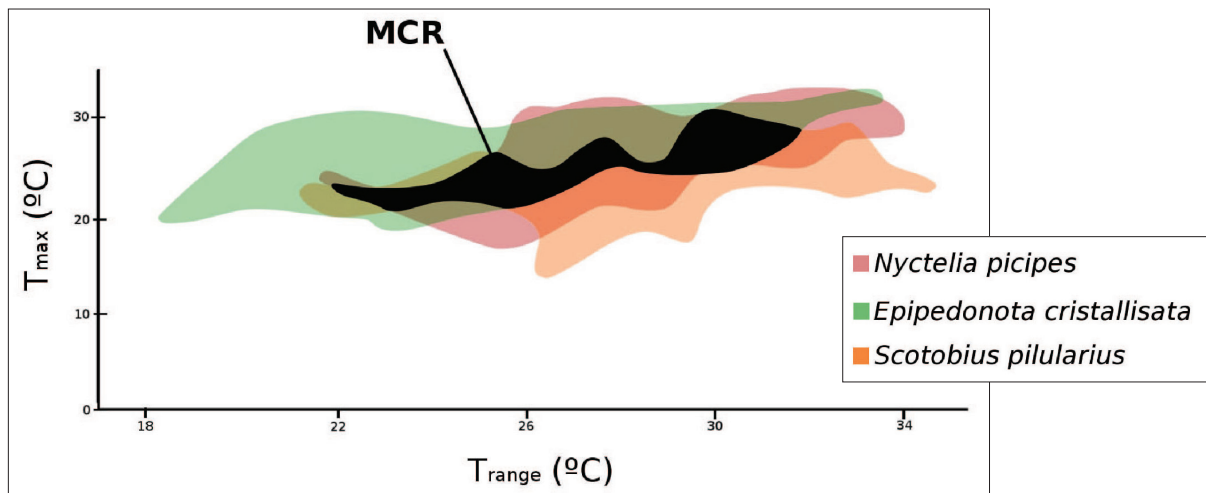


Figure 8. Mutual climatic range of *Nyctelia picipes*, *Epipedonota cristallisata* and *Scotobius pilularius*: colored areas represent the amplitude for maximum temperature (T_{max}) and temperature ranges (T_{range}) that each species can tolerate and black area, pointed as MCR, represents the amplitude of conditions that the three species share.

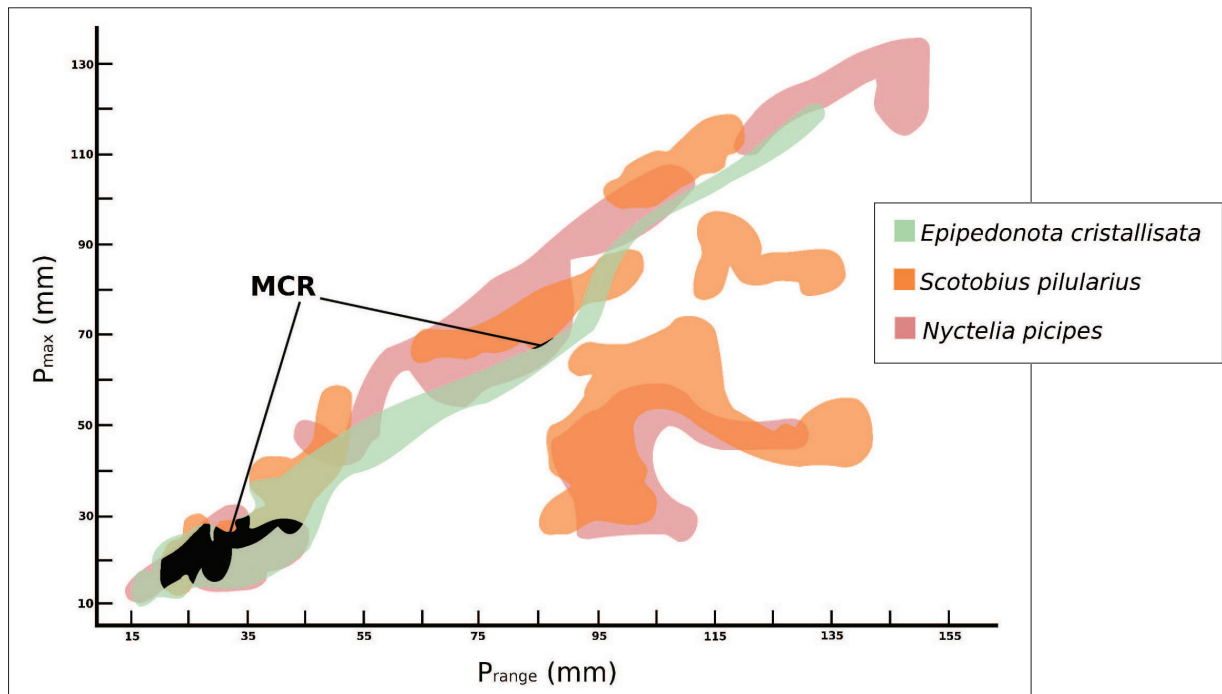


Figure 9. Mutual climatic range of *Nyctelia picipes*, *Epipedonota cristallisata* and *Scotobius pilularius*: colored areas represent the amplitude for maximum precipitations (P_{max}) and precipitations ranges (P_{range}) that each species can tolerate and black area, pointed as MCR, represents the amplitude of conditions that the three species share.

Belgrano were different from the current ones at the time of deposition.

Temperature, both maximum and range, and precipitation range values obtained by the MCR method about 13000 years BP in General Belgrano, are similar to those prevailing in the present day and do not represent a barrier to the coexistence of the three species.

However, the inferred maximum precipitation value suggests that climate conditions could have been drier than in the late Pleistocene. Specifically, precipitation appears to be one of the most restrictive variables in regard to the present distribution of *E. cristallisata*, which currently inhabits only arid or semi-arid environments (Flores and Vidal 2001). Thus, the presence

of this species at the site supports the idea of prevailing arid or semi-arid climate at deposition time. Considering that the taphonomic conditions are the same (depositional environment energy and chemical conditions), the complete absence of *E. cristallisata* and abundance of other insect remains observed upward in the profile lead us to think that this could have been one of the last time intervals where arid conditions reached the center-east of the province of Buenos Aires. These findings are concordant with the impact of “Draw-down” of water-tables on atmospheric humidity and on forest and grass cover (Clapperton 1993), and with the pollen sequences studied by Tonello and Prieto (2010) that indicate sub-humid to semi-arid conditions during the late Pleistocene with precipitation values lower than current ones. However, our findings are in contrast to those of Scanferla *et al.* (2003) who suggested that humid conditions prevailed in the Salado river basin because of the presence of a large amount of rhizoconcretions and the predominance of fluvial and fluvio-lacustrine deposits found in the deposits, and to those of Tonni *et al.* (1999), Vizcaíno (2000), Prevosti and Vizcaíno (2006), Bargo and Vizcaíno (2008), who found megafauna in the deposit associated with warm and humid conditions. It is hypothesized that probably the use of tenebrionid beetles as bioproxies could provide more precise information about paleoclimate, as the distributions of these insects are strongly constrained by climate conditions (Cloudsley-Thompson 2001, Matthews *et al.* 2010); particularly members of the tribes Nycteliini and Scotobiini are successful in arid environments with adaptations to life in xerophilic habitats (Flores 1997, Silvestro *et al.* 2012).

Finally, it is hypothesized that the characterization of Quaternary climate based on insects as bioindicators is novel and promising. An important advantage is that insects differ from other bioproxies in the level of detail of the environmental information they provide. Most bioproxies can only be identified to generic or family level, while insects can often be identified to species. This feature makes them excellent bioproxies. Future work, including sampling from a greater number of species and other localities will allow us to adjust the inferences made herein.

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