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Did Costa Rican Dung Beetles (Coleoptera: Scarabaeidae) Feed on Bison Dung Before the Arrival of Spanish Cattle?

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Abstract

An analysis based on fossilized animal tracks, oral tradition, archaeological findings, and the distribution and biology of dung beetles is presented to suggest that *Copris subpunctatus* Gillet (Coleoptera: Scarabaeidae) probably fed on bison dung and switched to cow dung after cattle were introduced by the Spanish colonizing effort. This transition probably took place before the bison apparently became extinguished in Costa Rica at the end of 19th or beginning of the 20th century.

Key Words: Scarabaeinae, *Copris*, Neotropics, Spanish colonization, megafauna, American buffalo

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The American plains bison (*Bison bison bison* Linnaeus), more commonly known as the American buffalo, was once widely distributed in recent times in the North American grasslands, ranging from south−central Canada to the Mexican states of Durango and Nuevo León (Gates and Aune 2008). Unfortunately, it faced near extinction through commercial and sport hunting at the end of the 19th century. The typical habitat of the plains bison is open or semi-open grasslands, sagebrush, semi-arid lands, scrublands, and lightly wooded areas in mountain valleys and plains up to 3,000 m elevation (Gates and Aune 2008). Plains bison migrate directionally, but also altitudinally (McHugh 1958), consuming shortgrass pasture during the warm season (Peden *et al.* 1974) and sedges and grasses on mixed prairies during the cool season (Popp 1981). They can roam great distances, moving continuously as they eat.

Pleistocene fossil remains of bison in Central America (Fig. 1) are reported in the literature from Hormiguero, El Salvador (Stirton and Gealey 1943, 1949; Webb and Perrigo 1984) and Jalapa, Río Viejo, and El Recreo, Nicaragua (Williams 1952; McDonald 1981; Lucas *et al.* 2007, 2008; Alvarado *et al.* 2008; Lockley *et al.* 2008). Williams (1952) assumed these fossils to be older than 2,000 years BP. The bison footprint locality of El Recreo is only 2.5 km from the human footprint locality of Acahualinca, Nicaragua. Although correlation of both localities is a valid process, it cannot be performed at present because the El Recreo locality has now been built upon (Alvarado *et al.* 2008).

However, Williams (1952) had already proposed the hypothesis that bison could have co-existed with humans in Central America during the Holocene, and Gómez (1986) suggested that they might have been present during recent times. This idea gained support when Bryan (1973) determined an age of 5,945 ± 145 ^{14}C years BP (recalibrating the old radiocarbon date using the high-precision radiocarbon calibration program Calib Rev7.1.0 (Stuiver and Reimer 1993). This would now be 4,857 ± 355 ^{14}C years BP for the Acahualinca human footprints. Later on, Schmincke *et al.* (2009) dated indirectly the Acahualinca human footprints at 2120 ± 145 ^{14}C years BP, using tephra correlation. Subsequently, Alvarado *et al.* (2008), correlating Schminke *et al.* (2009) data, rectified previous work that suggested an age of ~6,500 BP (Lockley *et al.* 2008), now assuming that the bison from El Recreo (Nicaragua)

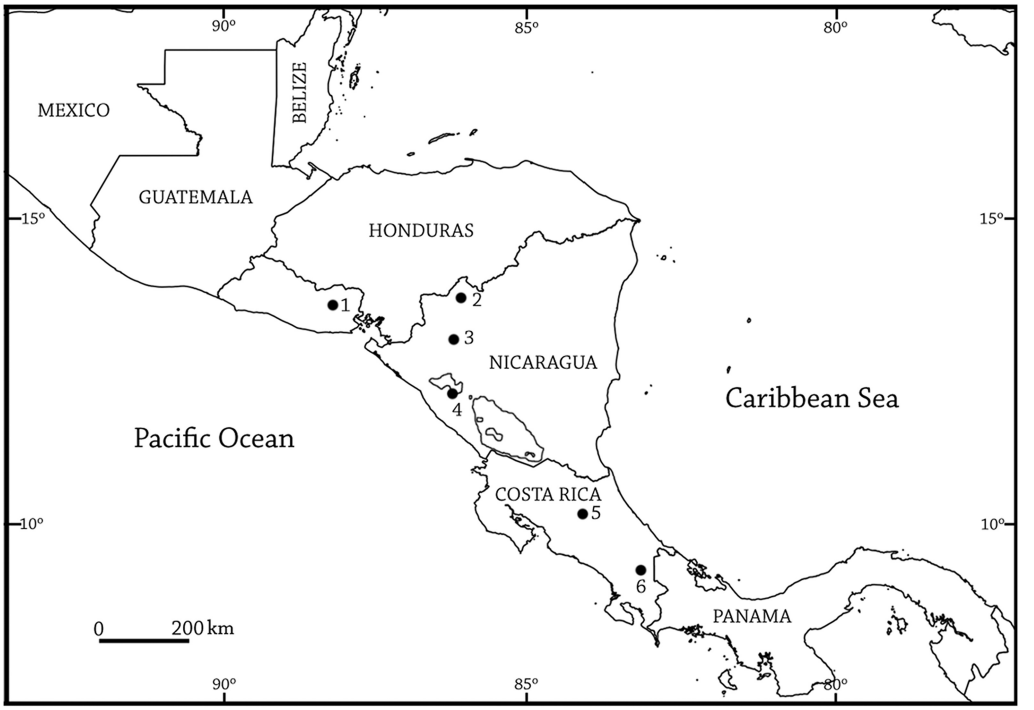

Fig. 1. Countries and localities mentioned in the text. 1. Hormiguero (El Salvador); 2. Jalapa (Nicaragua); 3. Río Viejo (Nicaragua); 4. El Recreo/Acahualinca (Nicaragua) 5. Toro Amarillo (Costa Rica); 6. Río Brujo (Costa Rica). Modified after Alvarado *et al.* (2008).

were still extant around 2,100 BP (*ca*. 100 BC) (Fig. 1). However, Lucas (2017) still is unconvinced about the precise age of the footprints. Further support of the possibility of bison reaching to Central America in historical times comes from a study by Alvarado *et al.* (2008), who present intriguing evidence.

Alvarado *et al.* (2008) report the finding of a pre-Columbian sculpture (Fig. 2). The sculpture is part of the collections of the National Museum of Costa Rica. This sculpture, found at the locality of Río Brujo in Costa Rica (Fig. 3), is made of yellowish stone pertaining to the Chiriquí period (700−1,500 BC) as established by Maureen Sánchez, archaeological expert of the southern region of Costa Rica. The sculpture is made of a sandy material of a medium-sized grain, rich in crystals of igneous origin, typical of the lithology of the Río Brujo area. The statuette strongly suggests a bison form, not only for its morphology, but also by the proportions of their measures, when comparing the archaeological piece with present-day bison proportions. This area is at present characterized by the existence of savanna-like vegetation (Kesel 1983; Gómez 1986), which is suitable habitat for bisons. Kesel (1983) indicates that this area represents probably the oldest recorded savanna for Latin America, according to radiocarbon dates (17,050 years BP), conditions becoming very similar to the present towards 8,800 years BP with grass savanna and scattered woodland.

Alvarado *et al.* (2008) also report the existence of an oral tradition that gave rise to the names of the towns of Toro Amarillo (Yellow Bull in Spanish) (1,400 m altitude) and Colonia Toro (Bull Colony) (740 m altitude), and of the Toro Amarillo River and Hill, all located in an intermontane valley in the Central Volcanic Cordillera of Costa Rica (Fig. 3). The oral tradition tells that when the first settlers arrived to this region in the 19th century, they found a type of "bull" living there that had a yellowish body color, horns turned backwards, pointed muzzle, and a deep bellow. This legend persists today and suggests the existence of probably very small and isolated bison populations during the Spanish colonization period of Costa Rica.

Recently, Solís and Kohlmann (2012) published a distribution atlas of the Costa Rican dung beetles. In this atlas, one species stands out because of its peculiar distribution: *Copris subpunctatus* Gillet (Coleoptera: Scarabaeidae) (Fig. 4). This species lives at middle altitudes (1,000−2,200 m) on mountain ranges and in open spaces, and its present-day diet is basically

Fig. 2. Bison-like sculpture made of yellow stone found at Río Brujo, Costa Rica.

composed of mostly cattle dung. Its distribution (Fig. 3) coincides with the inferred existence of Late Pleistocene savannas and meadowlands by Alvarado and Cárdenes (2015), as indicated by fossils of grazing animals, such as horses and mammoths.

In this paper, we hypothesize that *C. subpunctatus* was formerly associated with bison, feeding on their dung, which closely resembles cow dung, thus representing possible additional indirect evidence that bison were still present in Costa Rica during Spanish colonial times.

Evidence

Dung Beetles. Janzen (1983) writes the following comment:

"The present dung beetle fauna is probably only a remnant of what was supported by the Pleistocene megafauna. The patterns of horse and cow dung use by the contemporary dung beetle fauna may well be nothing more than an ecological response over the past 300 yrs. by species sufficiently flexible to have survived since the Pleistocene on the dung rain generated by a native tropical fauna poor in large mammals".

He explains the persistence of large, nocturnal dung beetles in Costa Rican deciduous forests and adjacent horse pastures on the grounds of the species´ ecological flexibility at surviving by using a depauperate dung resource. In the following section, we present the known autoecology of *C. subpunctatus* to emphasize its relative "flexibility" in relation to the model proposed by Janzen (1983).

In another study, Favila (2012) presents the thesis that the introduction of such an exotic resource, cattle dung, to the Americas posed no problems to the native dung beetle fauna. Favila (2012) indicates that the Native American dung beetle fauna was already preadapted to such type of dung, because they had been already eating dung from the existing megafauna, which included bisons. This fact permitted many of the open-space species to exploit this resource and thrive with the Spanish-induced anthropization of the landscape, such as man-made pastures. Favila (2012) cites two very close relatives of our study species, *Copris armatus* Harold and *Copris klugi* Harold, that also inhabit cattle dung in natural and man−made pastures in the highlands of central Mexico.

***Copris subpunctatus*.** This is a large species (Fig. 4), 17.0–24.5 mm in length. It is only known from the environs of Cartago and San José (1,000−2,200 m), although Matthews (1961) cites it also from Chiriquí, Panama, without further precise details, a record that should be confirmed. We have collected it only in open spaces and only in cow dung or attracted to light. The second author has collected it using pig manure- and human feces-baited traps. Not much more is known about its biology. There is no information about its dung-burial capacity, but another species, *Copris sierrensis* Matthews, which belongs to the same species-group and is slightly smaller, can bury 24.3 ± 8.5 g (dry weight) dung/pair (Anduaga and Huerta 2007). A smaller species, *Copris incertus* Say, can accumulate up to 50 g fresh dung/pair in a nest (C. Huerta, personal communication 2015).

New Evidence of Bison in Costa Rica. In a book published by Inksetter (1987) that tells about the history of the borough of Valverde Vega (Sarchí), it

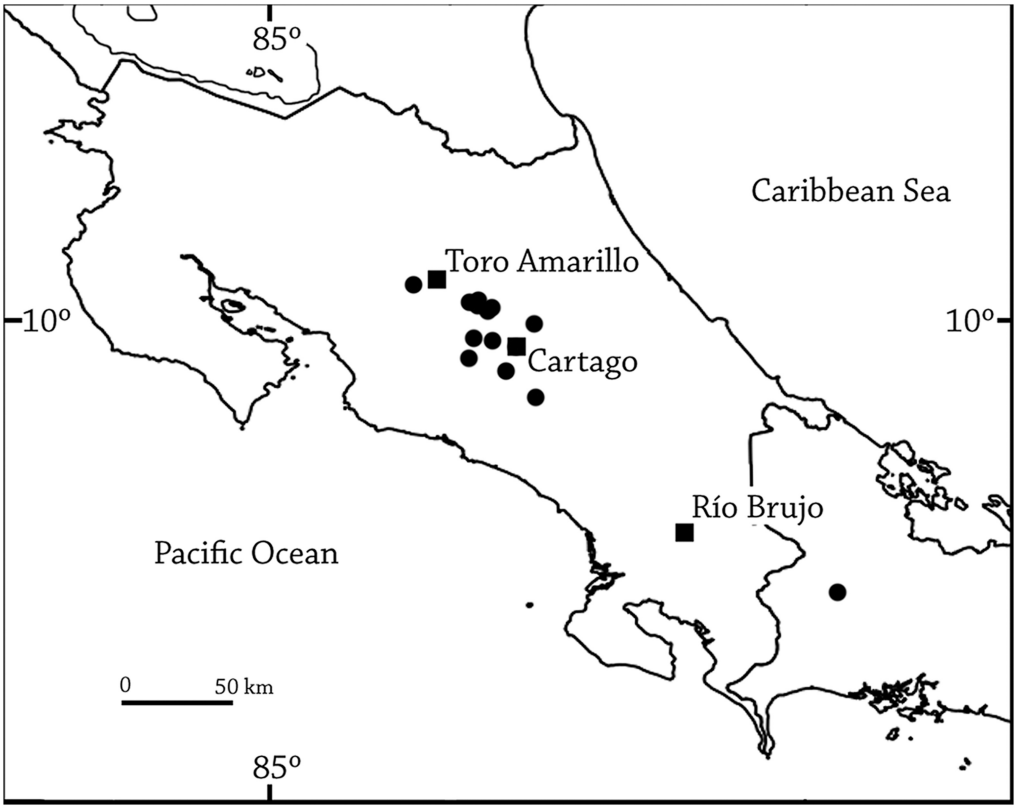

Fig. 3. Known distribution of *Copris subpunctatus* (filled circles) and the localities of Toro Amarillo, Río Brujo, and Cartago, Costa Rica (filled squares).

is written that two hunters arrived around 1870 to a valley, with a great clearing, inhabited by wild cattle. A big yellow bull attacked the hunters and forced them to flee to a tree.

Additionally, Mr. Alfredo Alfaro communicated in a letter to Mr. Hebly Inksetter that the cattle looked like a Cebu, but that it was totally yellow (A. Alfaro, *in litt.* 2015). Mr. Juvenal Alfaro (1891−1981) also communicated to his grandson, Mr. Alfredo Alfaro, that he had found in the area of the Barroso River, very close to Toro Amarillo, animals that looked very similar to a bison, with a hump on the back and a dark yellow color, but different from a Cebu or the Indobrasil cattle race, and that these same animals also lived in the Toro Amarillo Valley. These rare bulls lived still until around 1910 (A. Alfaro, *in litt*. 2015), although the first contact with these rare megamammals should have happened before 1870 (arrival time for the first Caucasian people in the Toro Amarillo Valley), because the name Toro Amarillo existed at least as early as 1861 (von Frantzius 1861).

When the Panamanian land bridge became connected in the middle Pliocene, horses, llamas, camels, *etc*. crossed from North America to South America (part of the so-called Great American Interchange of mammal evolution). Environments in the past did allow these large, open-habitat specialized mammals to enter Central America and eventually South America. Perhaps a bison population could have made some progress southward into Central America, too, but did not make it into South America and remained in Costa Rica as a relict population into modern times.

Discussion

Copris subpunctatus is presently living in open areas around Poás and Irazú volcanoes, where it eats cattle dung and needs great amounts of dung for nesting (about 24.3 ± 8.5 g of dung, dry weight/pair). What could this species have used as a food source before the introduction of Spanish cattle?

Tapir can range to higher elevation forests and produce the necessary quantities of dung to enable *C. subpunctatus* to nest. However, tapir dung is even more fibrous than that of horse dung, and we have not yet seen *C. subpunctatus* using horse dung, so

Fig. 4. Lateral and dorsal views of a male *Copris subpunctatus*.

we suspect it would not be attracted to tapir dung. Moreover, the tapir is a forest species that normally does not enter open spaces; it is well known that the tapir deposits its feces in brook pools inside the forest. The second author found that dung deposited inside the forest is usually riddled with many nesting holes made by *Ontherus pseudodidymus* Génier. It would therefore appear that tapir dung is not a likely source of food for *C. subpunctatus*.

Lucrecia Arellano (personal communication, 2015) observed that large coprophages, like *Dichotomius* Hope and *Phanaeus* MacLeay, that have a size similar to *C. subpunctatus*, are attracted to peccary dung. However, this mammal species, as the tapir, is reported as a forest inhabitant and does not usually penetrate into open spaces.

These realities leave us with the most probable explanation, that only a large, open-space living mammal could have sustained the *C. subpunctatus* populations. We suggest here that this species was the bison that, according to all the previously discussed indirect evidence. lived in the same area as *C. subpunctatus*, apparently until around 1910. Following Janzen´s (1983) proposal that the Costa Rican dung beetles survived the megafauna extinction because of an inherent ecological flexibility, *C. subpunctatus* would seem to follow Tiberg and Floate´s (2011) hypothesis that bison dung-associated insects are more responsive to changes in diet than to changes in host species and, therefore, this taxon now persists in the dung of cattle, because present day cattle have a similar diet as bisons did grazing local mountain grass.

The exact date of introduction of cattle into Costa Rica is not known. It is believed that cattle already existed in Guanacaste before 1561 due to commercial exchanges between Nicaragua and Panama along the Pacific coast. We know that by the year 1561 livestock arrived for the first time to the Gulf of Nicoya, brought by the Spanish conquistador Juan de Cavallón. By 1568, Álvaro de Acuña brought cattle to Sabana Grande in Cartago (Quirós 2006), a locality within the modern distribution range of *C. subpunctatus*. However, one could fairly expect that by the mid-19th century, Costa Rican cattle could have been making contact with *C. subpunctatus* populations at the Toro Amarillo locality and the bison-to-cow dung transition presumably started at this time, if not earlier. In conclusion, as a very intriguing hypothesis, we believe *C. subpunctatus* could have survived in very small, restricted areas together with the last bison in Costa Rica, and the dung beetle was saved from possible extinction by the timely arrival of the 'cowalry'.

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