Ancient trouble in paradise: seed beetle predation on coconuts from middle–late Paleocene rainforests of Colombia

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Abstract

Modern Neotropical rainforests are characterized by the high intensity and host specificity with which insects feed on plants. Previous studies have shown that, during the middle–late Paleocene, the leaves of the early evolving Neotropical rainforests of tropical South America were heavily herbivorized by insects. Yet, less attention has been given to insect damage found on fossil fruits and seeds, despite the host specialization of many disseminule predators in modern forests. Here, we present and describe borings found on a fruit compression fossil of cf. *Cocos* (coconut) from the middle–late Paleocene Cerrejón Formation (58–60 Ma) of Colombia. We interpret the borings as constructed by palm seed beetles (Chrysomelidae: Bruchinae: Pachymerina) based on size, number, position, plant reaction tissue, and plant host selection. This occurrence provides the earliest record of an ecological interaction between seed beetles and palms, suggesting that this host-specific interaction has been consistently maintained for several tens of millions of years.

Keywords: *Cocos*, Seed predation, Host-specialized interactions, Fossil fruits, Paleobotany, Paleoecology

1. Introduction

A defining feature of modern Neotropical rainforests is the high intensity and host specificity with which insects feed on plants (Dyer et al., 2007). Host-specific herbivory is a major factor in plant population dynamics, as it creates density-dependent restrictions on population growth and contributes to local and regional patterns of species diversity (Comita et al., 2014; Forrister et al., 2019; Terborgh, 2012). Abundant insect-mediated leaf damage found in middle–late Paleocene deposits of tropical South America indicates that herbivory of leaves was intense during the early evolution of modern-like Neotropical rainforests (Carvalho et al., 2021; Giraldo et al., 2021; Wing et al., 2009). Yet, much less attention has been given to insect damage found on fossil fruits and seeds, even though many insect seed predators are specialized to varying extent (Lewis and Gripenberg, 2008) and the host-specific nature of seed-predating insects is of major importance to the evolution and maintenance of tropical forest diversity (Connell, 1971; Janzen, 1970). Seed predation is a form of insect (or arthropod) attack that involves the penetration of the outer seed coat and targeting of the seed's internal tissues, typically resulting in the inviability of the new plant. Evidence of this form of feeding extends back to the Early Pennsylvanian (Jennings, 1974; Labandeira, 2006; Scott and Taylor, 1983) and is recorded as various types of scars and damaged tissues resulting from the attack. These include numerous kinds of individual or grouped punctures and cratered pits into the seed main body, indicating the removal and hollowing out of embryonic tissues, and circular to elliptical exit holes (e.g., Barbosa dos Santos et al., 2020; Labandeira et al., 2007)

Currently, numerous species representing six major orders of insects are known to feed on seeds, including true bugs (Hemiptera), thrips (Thysanoptera), flies (Diptera), moths (Lepidoptera), wasps (Hymenoptera) (Lewis and Gripenberg, 2008; Louda, 1982; Roques et al., 2016; Sweet, 1960), and, especially beetles (Coleoptera) (Janzen, 1980; Lewis and Gripenberg, 2008). Seed beetles (Chrysomelidae: Bruchinae), for instance, spend their larval period feeding on –and living in– seeds (Johnson et al., 1995; Nilsson and Johnson, 1993), often being specific to seeds of particular plant genera or species (Johnson and Slobodchikoff, 1979). Approximately 85% of bruchine larvae live inside legume seeds (Fabaceae), 4% within palms (Arecaceae), another 4% in the morning glory family (Convolvulaceae), and 2% in the mallow family (Malvaceae), whereas the remaining 4% are distributed among 29 other angiosperm plant families (Borowiec, 1987; Nilsson and Johnson, 1993). Female bruchids oviposit on a fruit or seed, where the first instar larva bores through the fruit and/or seed coat and enters the seed cavity (Johnson et al., 1995). While inside, the larva molts into a legless grub and feeds on the endosperm and embryonic tissues throughout another three molts before the larva pupates within the seed (Johnson et al., 1995). Prior to pupation, the larva excavates a round exit hole –either within the seed or from the seed and the fruit– which the emerging adult finishes (Johnson et al., 1995). Adult bruchines feed on nectar and pollen and are not known to feed on seeds or fruits (Johnson et al., 1995; Nilsson and Johnson, 1993).

Phylogenetically nested within the Bruchinae are the palm bruchines (subtribe Pachymerina), which feed almost exclusively on palm seeds (Delobel et al., 1995; Johnson et al., 1995; Nilsson and Johnson, 1993). Palm bruchines are restricted to the New World, and although most species are tropical, some occur as far north as Texas and as far south as Argentina (Johnson et al., 1995; Nilsson and Johnson, 1993). Currently, four palm bruchine genera are recognized: *Caryoborus*, *Caryobruchus*, *Pachymerus* and *Speciomerus* (Nilsson and Johnson, 1993), with varying degrees of palm host specificity. Species of *Caryobruchus* show a clear preference for palms in the tribes Corypheae (gebang, talipot, and buri palms), Phoeniceae (date palms) and Chamaedoreeae (bamboo and parlor palms), whereas the seeds of the Phytelepheae (ivory and tagua palms) and Cocoseae (coconut, oil, and jelly palms) are consumed by species of *Caryoborus*, *Speciomerus* and most extensively by species of *Pachymerus* (Johnson et al., 1995).

Here, we present and describe an example of host-specific seed predation found on a fruit compression of cf. *Cocos* sp. (Arecaceae) (Gomez- Navarro et al., 2009), a coconut from a middle–late Paleocene rainforest from northern South America. Borings and exit holes observed are consistent with those made by palm bruchines (Pachymerina), based on size, number, position, plant reaction tissue, and plant host selection. This occurrence provides the earliest record of an ecological interaction between seed beetles and palms. It also indicates that the specific behavior of palm-feeding bruchines dates back to at least 60 Ma and suggests the antiquity of this type of host-specific interaction through geologic time.

2. Methods

2.1 Geological and environmental setting

The Cerrejón Formation is a ~700 m thick sequence of sandstones, mudstones, claystones and coals (Jaramillo et al., 2007) that are exposed along the Cerrejón open-pit coal mine, located in the Ranchería Basin of northeastern Colombia (Figure 1). These deposits accumulated in coastal plains that transitioned from estuarine to fluvial and lacustrine-influenced depositional systems in an environment of warm temperatures and high precipitation (Head et al., 2012; Jaramillo et al., 2011, 2007). Pollen zonation, correlations with stable carbon isotopic data and marine microfossils from the Cerrejón Formation indicate a middle–late Paleocene age for the entire sequence (ca. 58–60 Ma) (Jaramillo et al., 2011, 2007).

Along with the middle–late Paleocene Bogotá flora (Giraldo et al., 2021), the Cerrejón flora localities are the earliest known examples of Neotropical rainforests (Carvalho et al., 2021; Jaramillo et al., 2007; Wing et al., 2009). Extinction and turnover related to the end-Cretaceous ecological crisis led to the assembly of modern-like Neotropical rainforests (Carvalho et al., 2021), characterized by flowering plant dominance (Carvalho et al., 2021; Jaramillo et al., 2007; Wing et al., 2009), closed, multistratal canopy structure (Graham et al., 2019), abundance of legumes (Herrera et al., 2019), and hot, humid climate (Carvalho et al., 2021; Wing et al., 2009). The coastal, peat-accumulating rainforests of Cerrejón included tropical tree lineages such as mallows and kapok trees (Malvaceae: Malvoideae and Bombacoideae; Carvalho et al., 2011);

epiphytic and semiaquatic aroids (Araceae; Herrera et al., 2008); abundant vines such as moonseeds (Menispermaceae; Doria et al., 2008; Herrera et al., 2011) and species of Icacinaceae (Stull et al., 2012); and diverse palms (Arecaceae; Gomez- Navarro et al., 2009). Non-monocot flowering plants were heavily herbivorized, as nearly half of their leaves show signs of leaf chewing, galling, mining and piercing marks (Wing et al., 2009). The overall richness of insect damage on leaves is nonetheless low for the Cerrejón flora, when compared to coeval floras around the world (Giraldo et al., 2021).

2.2 Studied material

This study is based on palm fruit compressions collected from the STRI localities 0317 (11°14'N; 72°57'W), 0319 (11°66'N; 73°31'W), 0324 (11°62'N; 73°32'W), and La Puente-pit (11°90'N; 72°30'W) (Gomez- Navarro et al., 2009; Wing et al., 2009), Cerrejón coal mines of northern Colombia (Figure 1). Although the fossil fruits do not preserve internal structure, multiple morphological characters (e.g., shape, longitudinally oriented fibers, inconspicuous longitudinal ridges, and very large size) and the regular co-occurrence with palm leaves are indicative of an Arecaceae affinity (Gomez- Navarro et al., 2009). All specimens are deposited at the Paleontological Museum Royo y Gómez, Servicio Geológico Colombiano, Bogotá, Colombia.

Examples of extant borings on palm fruits and seeds were surveyed from the available entomological and forestry literature. We focused on examples that described the feeding behaviour of insect larvae and/or adults on palm fruits and reported plant host and insect species, plant tissue consumed, features of the borings such as size, shape and circularity of the exit holes, and reaction rims (see electronic supplementary material). Additionally, the herbarium collections of the Jardín Botánico Joaquín Antonio Uribe (JAUM), in Medellín, Colombia, were surveyed for modern examples of borings in palm fruits. Although borings in fossil palm fruits have been previously described (El Hedeny et al., 2021; Moreno-Dominguez et al., 2016), these are bivalve-mediated and morphologically very distinct from the damage here described, and were not considered in further comparisons.

Specimens were examined with a Nikon SMZ 1500 stereoscope. Fossils and botanical samples were photographed using Canon EOS 5DS R and Canon EOS 5D Mark III cameras, respectively. Reversible image adjustments such as white balance, temperature and contrast were made using Adobe Photoshop 2021. The diameter of the borings and associated reaction tissues were measured using ImageJ v1.53e (Schneider et al., 2012). The displacement of each boring, or change in position in the three-dimensional space, was tracked based on the relative change in position of the centroid of each boring from the outer to the innermost layers of the mesocarp.

2.3 Bruchine systematics

We treat Bruchinae (seed beetles) as a subfamily of Chrysomelidae (leaf beetles) (Farrell and Sequeira, 2004; Gómez-Zurita et al., 2008; Morse, 2014) and have adjusted previously published ranks (*sensu* Nilsson and Johnson, 1993) accordingly. Thus, palm bruchines (considered as tribe Pachymerini by Nilsson and Johnson, 1993) are here adjusted to subtribe Pachymerina (see Archibald et al., 2014 for a similar approach). Pachymerines have a fossil record that extends to the Late Cretaceous (Poinar, 2005), ca. 20 million years earlier than the fossil described here.

3. Results

3.1 Borings description

Of 17 palm fruits recovered from the Cerrejón locality, one specimen displayed evidence of borings. Six borings were recorded in the fibrous mesocarp of specimen STRI-9938 (Plate I; numbered arrows), described as cf. *Cocos* (Gomez- Navarro et al., 2009). The borings are circular (3.8–7.5 mm in maximum diameter) to broadly elliptical (7.5–8.3 mm long by 3.6–3.8 mm wide) in shape, discernable by an outer ring of indurated reaction tissue 0.3–0.9 mm in width. This fruit is preserved as an outer impression (Plate I, 1, 3) and a modular, inner compression (Plate I, 2, 4) that we interpret as the innermost mesocarp layers. The preservation of the mesocarp in distinct layers allows tracking of the borings in a three-dimensional manner.

Four borings (Plate I; arrows 1, 2, 4, 6) are easily tracked from the outer surface and into the inner layers of the mesocarp. The borings show an overall expansion in diameter from the outer (Plate I, 1, 3) to the innermost layers (Plate I, 2, 4), as well as some displacement in the three-dimensional space. Boring 1 is 3.8 mm in diameter at the outer layer and has a 0.4 mm thick reaction tissue; in the inner section, the centroid of the boring shifts 8.6 mm exmedially and 5 mm basally, and its diameter and reaction tissue expand to 6.3 mm and 0.7 mm, respectively. Boring 2 is 5.3 mm in diameter and bears a reaction rim 0.4 mm thick at the outer section; its diameter expands to 7.5 mm and reaction tissue increases to a thickness of 0.5 mm in the inner section. The centroid of boring 2 shifts 2.9 mm admedially and 4 mm basally in the inner section of the fruit. Boring 4 does not change in diameter (7.5 mm long by 3.6 mm wide) or reaction rim thickness (0.3 mm thick) across the outer and inner mesocarp layers but it shifts 8.3 mm exmedially and 14.9 mm basally in the inner mesocarp layer. Boring 6 is 4.6 mm across and has a 0.3 mm thick reaction rim; this boring expands to 6.8 mm in diameter on the inner mesocarp layer and shifts 1.5 mm admedially and 12.5 mm basally. The reaction rim of boring 6 is 0.9 mm, on the inner layer.

Borings 3 and 5 are only visible in the outer but not the inner sections. Boring 3 is 4.8 mm in diameter, associated with a 0.4 mm thick reaction rim. Boring 5 is 8.3 mm long by 3.8 mm wide, with a reaction rim 0.3 mm in width. Since these two borings are not discernible in the inner sections, the displacement in the three-dimensional space (if any) cannot be ascertained.

Palm bruchine borings on modern palm fruits (Plate II) are similar in size, position, and reaction tissue thickness. Although smaller borings are seen in modern specimens, their position at the medial portion of the fruits is consistent with those seen in the fossil coconut. Furthermore, the thickness of the reaction tissue is similar in both the fossil specimen (0.3–0.9 mm) and modern palm fruits (0.1–0.6 mm). Even though not all borings on palm fruits induce such a thick reaction rim (Plate II, 1–4), most of them do (Plate II, 5–10). Importantly, in all instances where there is a thick reaction tissue (Plate II, 5–6, 8–9), these are outwardly directed, as seen in the fossil coconut borings (Plate I).

3.2 Modern palm-boring insects

We compiled 244 cases describing the feeding by beetles on the fruits and seeds of extant palms (electronic supplementary material). Each entry is a unique beetle-to-palm association, with curated taxonomy for both groups, geographic location, and –when available– size of the insect exit hole (or entrance hole for Curculionidae; see Discussion section 4.1 below). These cases included 21 species of Chrysomelids (leaf beetles), 15 species of Curculionidae (weevils) and one species of Cerambycidae (longhorned beetles).

4. Discussion

4.1 The culprit

The borings preserved in the compression fossil of a coconut from Cerrejón are consistent with those made by living palm bruchines of the subtribe Pachymerina. This interpretation is based on the unique combination of size, number, location, presence of a thick and outwardly positioned reaction rim, and plant host selection. The thickened, outwardly flared reaction tissue along the periphery of the borings define an exit hole, typical for bruchines, rather than an entrance hole, as is the case with the feeding behavior of bark beetles of the tribe Scolytini (see below). The size of Pachymerina exit holes depends on the size of the insects fabricating the borings (Nilsson and Johnson, 1993). Exit holes as small as 3 mm and as large as 8 mm in diameter have been reported across species of Pachymerina (see electronic supplementary material for a complete list of palm bruchine species, their palm hosts and –when available– exit hole size), whereas other potential culprits, such as weevils, produce exit holes of much smaller diameter. The location of these borings in the central portion of the fruit also allows the elimination of other potential culprits such as the longhorn beetle *Pterolophia apiceplagiata* Breuning (see below). Furthermore, it is common for multiple palm bruchines to develop within the same seed and produce multiple exit holes, as in the fossil coconut, especially among larger seeds (Dracxler et al., 2011; Lau et al., 2014; Pedersen, 1995) such as those of *Cocos*. The occurrence of multiple exit holes in close proximity to each other suggests that the developing larvae were not cannibalistic, a behavior observed among some species of bruchids, such as *Megaceros discoidus* (Say), when resources are limited (Wang and Kok, 1986).

Alternative insect culprits could be affiliated to other coleopteran lineages such as Curculionidae or Cerambycidae, or even piercing-and-sucking hemipterans such as leaf-footed bugs (Coreidae) or seed bugs (Lygaeidae). However, the damage made by these insects is inconsistent with the overall morphology, size, number of borings, reaction tissue or position –or a combination of these– seen in the fossil coconut. Bark beetles in the subtribe Scolytini such as *Dactylotrypes*, *Hypothenemus* and especially *Coccotrypes* are particularly prolific consumers of palm seeds (Atkinson and Peck, 1994; Beaver, 1987; Dracxler et al., 2011; Jansen et al., 2010; LaBonte and Takahashi, 2012; Siviero and Montesdeoca, 1990; Spennemann, 2019; Villalobos and Blanco-Metzler, 2006; Wood, 1986). These female beetles bore into and oviposit within the seed (Jansen et al., 2010; Wood, 1986), wherein multiple generations and up to 100 individuals can coexist, depending on the size of the seed (Spennemann, 2019). When seed resources are exhausted, adults emerge through the same entrance hole that the first female beetle created (Spennemann, 2019). These entrance holes are usually less than 1 mm in diameter (Dracxler et al., 2011; Jansen et al., 2010) and rarely approach 1.5 mm (Siviero and Montesdeoca, 1990) (see electronic supplementary material for a complete list of palm seed predating curculionids, their palm hosts and, when available, entrance hole size). Although it is common for multiple females to attack the same seed (Jansen et al., 2010) and abandon multiple holes as in the fossil coconut, the hole diameters are 2.5–5 times smaller than the borings described herein. Importantly, as the boring is excavated by the mouthparts of the female while entering the seed (Anderson, 1995), the reaction tissue is not outwardly flared but rather inwardly directed. We consider that it is consistent with what is known about the life habits of weevils, and this group is discarded as the culprit for the damage seen in the Paleocene coconut from Cerrejón.

Although less common, longhorned beetles also feed on palm seeds. A report of one such cerambycid, *Pterolophia apiceplagiata* Breuning, feeding on coconut fruits in Sumatra, Indonesia (de Chenon et al., 1991), shows that females are likely to oviposit at the remnant tissue surfaces of the calyx, given that the entrance hole made by the larva is always at the attachment of the fruit to the rachillae (de Chenon et al., 1991). The larva bores through the fibrous mesocarp until it reaches the germination pores, where it preferentially feeds. After obtaining sufficient nutrition, the larva bores a 6 cm long gallery from the germination pores to the periphery, creating a pupal chamber 18–28 mm long by 14.4–21 mm wide, followed by pupation, and ending in the adult exiting the fruit through an elliptical hole 5 mm long by 3.9 mm wide (de Chenon et al., 1991). The size of this cerambycid exit hole is slightly less in maximum dimension than the elliptical borings seen in the fossil coconut (7.5–8.3 mm long by 3.6–3.8 mm wide); however, only a single larva develops per fruit (de Chenon et al., 1991). It is likely that the number of cerambycid larvae that develop on each fruit is restricted due to nutritional constraints imposed by the coconut mesocarp tissues available, as the larvae cannot penetrate the endocarp (de Chenon et al., 1991). Notably, in the fossil coconut, there is no evidence of a boring near the point of attachment to the rachillae, and species of *Pterolophia* are not found in the New World. Taking these observations into account, we consider that the damage found in the fossil is not attributable to a cerambycid culprit.

Sufficiently similar lesions are caused by the coreid bug *Pseudotheraptus wayi* Brown on coconuts of East Africa (Brown, 1955; Way, 1953). Females oviposit on the surfaces of flowers or young fruits, and both nymphal and adult stages feed on young stems, leaves, inflorescences and, especially, fruits (Egonyu et al., 2013). The damage on the fruits consists of piercing-and-sucking punctures which, due to the toxic saliva of the coreid, induce sunken lesions and surrounding necrotic tissue in an unorganized manner (Way, 1953). The lesions widen as the fruit expands, and occasionally develop into deep slits into the exocarp (Way, 1953). Although no measurements are reported for these lesions, given the necrotic nature of the damage, the lack of a reaction rim along the lesion periphery, and its generalized slit-like shape, we consider that the damage found on the fossil coconut is not that of a coreid.

Most seed bugs (Lygaeidae) are lacerate-flush feeders (Burdfield-Steel and Shuker, 2014), feeding mainly on mature seeds and occasionally on developing fruits (Sweet, 1960; Sweet et al., 2000). Their feeding behavior creates lesions in parenchymatous tissues, emptying cells of their content as insects pierce-and-suck through the surface (Panizzi et al., 2021), and often these insects aggregate in large groups that can cause wilting and deformation of developing fruits (Burdfield-Steel and Shuker, 2014; Sweet et al., 2000). There is no evidence of wilting or deformation on the fossil coconut that could be attributed to group feeding of seed bugs; moreover, the size, morphology, and reaction rim of the exit holes does not match that of piercing-and-sucking marks.

4.2 Plant host specificity

Overall, bruchines are typically monophagous or oligophagous (Borowiec, 1987; Kergoat et al., 2004), and exhibit strong conservatism in host-plant use (Kergoat et al., 2007). Studies on host preference have shown that oviposition substrate affects the evolution of host-plant affiliation and dietary specialization (Morse and Farrell, 2005), and presently, palm bruchines feed almost exclusively on palm seeds (Nilsson and Johnson, 1993). The only possible exception is a dubious record (Johnson et al., 1995) of *Pachymerus abruptestriatu*s (Gyllenhal) in the seeds of *Diospyros* sp. (Ebenaceae) (Bondar, 1941). The borings on the cf. *Cocos* fruit from the Paleocene of Colombia are the first known case of palm bruchine feeding behaviour in the fossil record.

Inferences on the origin and history of coevolutionary relationships between herbivorous insects and their hosts are typically based on phylogenetics and divergence-age estimations of living plant hosts and their pests (e.g., Kergoat et al., 2015), but rarely have there been fossil occurrences for support. The specific feeding behaviour of palm bruchines observed in the borings of the cf. *Cocos* fruit shows that palm bruchines have used (and likely lived in) palm fruits and seeds since minimally 60 Ma and documents a coevolutionary relationship in deep time. The association between palm bruchines and palms could have arisen as early as the Late Cretaceous, as the fossil record of both palms (Matsunaga and Smith, 2021) and palm bruchines (Poinar, 2005; see 4.3 below) extend back to this time. Early records of crown-group Cocoseae include permineralized fruits of subtribe Attaleinae recovered from Danian deposits in Patagonia, Argentina (Futey et al., 2012), indicating that the Cocoseae most likely diverged during the Late Cretaceous, as is also suggested by divergence-age estimations (Meerow et al., 2015).

While it would be impossible to pinpoint a particular genus within Pachymerina as the culprit of the damage found in the cf. *Cocos* fruit, most of the seeds of the tribe Cocoseae (coconuts, oil and jelly palms) are predated by *Pachymerus* (Johnson et al., 1995; and see electronic supplementary material). *Pachymerus bactris* L. and *P. nucleorum* Fabricius are the only palm bruchines reported in *Cocos nucifera* L. seeds (see electronic supplementary material). Our finding highlights the evolutionary connection between Pachymerina and palms in deep-time, which extends to the early evolution of modern-like Neotropical rainforests (Carvalho et al., 2021). The borings found on the cf. *Cocos* fruit also add yet another form of ecological interaction between primary producers (vascular plants) and consumers (herbivorous insects) in the Paleocene rainforests of northern South America (Carvalho et al., 2021). Moreover, the pachymerine seed beetle–coconut palm association emphasizes that host-specific interactions are a defining feature of lowland tropical rainforests (Dyer et al., 2007).

4.3 Biogeography and fossil record of palm bruchines

The occurrence of palm bruchines in the Cerrejón flora is consistent with their current Neotropical distribution and previous findings in the Americas. Fossils of Pachymerina are known from the Late Cretaceous of southern Canada (Poinar, 2005), and are a common element in the early Eocene Okanagan Highland fossil sites of the Pacific Northwest of North America (Archibald et al., 2014; Archibald and Mathewes, 2000). Pachymerina are also found in the late Eocene Florissant Formation, Colorado (Archibald et al., 2014; Kingsolver, 1965) and the early Neogene of the Dominican Republic (Poinar, 1999). A single species preserved in Late Eocene Baltic amber remains the only known record of palm bruchines outside the Americas (Legalov, 2016). The presence of an extralimital occurrence of a bruchine outside of the Americas is a common biogeographic pattern in Cenozoic insect lineages, whereby a formerly cosmopolitan taxon is currently restricted to a region of the Southern Hemisphere, a prominent example of which is the tsetse fly *Glossina* (Lambrecht, 1980). The Cerrejón borings on the arecaceous fruit indicate that palm bruchines lived in northern South America by the middle–late Paleocene, where palms were already one of the most abundant and diverse elements of the flora (Gomez-Navarro et al., 2009; Wing et al., 2009). The ages and localities of known fossil occurrences of Pachymerina suggest that their current Neotropical distribution is a relict from a much wider distribution observed during warmer Cretaceous and Paleogene ages. The fossil record may also suggest a north-to-south migration pattern, perhaps through the Late Cretaceous/Paleocene Proto-Greater Antilles Island bridge (Poinar, 2005). Nonetheless, the fossil record of palm bruchines is scant, and therefore a detailed interpretation of their biogeographic history remains tentative.

5. Conclusion

Borings on an early cf. *Cocos* fruit from the middle–late Paleocene Cerrejón Formation provide the earliest record of the ecological interaction between palm bruchine seed beetles (Pachymerina) and coconut palms. This suggests that palm bruchines have consistently been seed predators of palm fruits for minimally 60 Ma, and highlights host-specific interactions –that likely act as plant diversity-promoting agents– as a defining feature of modern Neotropical rainforests.

Data availability. The compilation of modern instances of beetles feeding on palm fruits and seeds is provided in the electronic supplementary material. Further details on samples and localities can be accessed through the Geologic sample Database of the Smithsonian Tropical Research Institute at https://biogeodb.stri.si.edu/jaramillosdb/web/fossils/

Declaration of competing interests. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Text to figures

Figure 1. Collection site of cf. *Cocos* fruits of the Cerrejón Formation, Colombia, indicated by a star.

Plate I. Palm bruchine borings (numbered arrows) on cf. *Cocos* fruit (STRI-9938) of the Cerrejón Formation. Given that the fossil specimen is roughly fractured transversely, outer (**1** and **3**) and inner (**2** and **4**) mesocarp sections are discernible. Note that all the borings are circular or broadly elliptical, with a thick reaction tissue flanking the periphery of the damage. Borings 1, 2, 4 and 6 are observable at the outer and inner mesocarp sections, allowing for a tracking of the damage in a three-dimensional manner. By contrast, borings 3 and 5 are visible along the outer but not the inner section. Borings are numbered clockwise.

Plate II. Palm bruchine borings on modern palm fruits. **1.** Tunnel on the mesocarp of *Astrocaryum malybo* H. Karst. (JAUM 073119), enlarged at **2** (see arrow). **3.** Hole on the exocarp and mesocarp of *Bactris brongniartii* Mart. (JAUM 066644), enlarged at **4. 5.** Circular hole on the exocarp and mesocarp of *Bactris chocoensis* R. Bernal, Galeano, Copete & Cámara-Leret (JAUM 079698), enlarged at **6** (note the thick and outward flaring reaction tissue). **7.** Circular hole on the calyx remnants, exocarp and mesocarp of *Bactris macana* (Mart.) Pittier (JAUM 050273). **8.** Two circular holes of different sizes on the exocarp and mesocarp of *Chamaedorea pinnatifrons* (Jacq.) Oerst. (JAUM 007592); we interpret the small hole (marked with an arrow) as the entrance boring made by a larval stage bruchine, while the large one represents the exit hole made by the adult. **9.** Circular holes on the exocarp and mesocarp of two fruits of *Prestoea ensiformis* (Ruiz & Pav.) H.E. Moore (JAUM 058644) (note the thick reaction tissue surrounding the hole of the fruit on the right). **10.** Circular and broadly elliptical holes on the exocarp, mesocarp and endocarp of four fruits of the palmetto *Sabal mauritiiformis* (H. Karst.) Griseb. & H. Wendl. (JAUM 072846), together with the palm bruchines that made the damage (possibly *Caryobruchus gleditsiae* L.; see electronic supplementary material and Nilsson and Johnson, 1993). Note that there is one palm bruchine still inside a fruit (marked arrow).

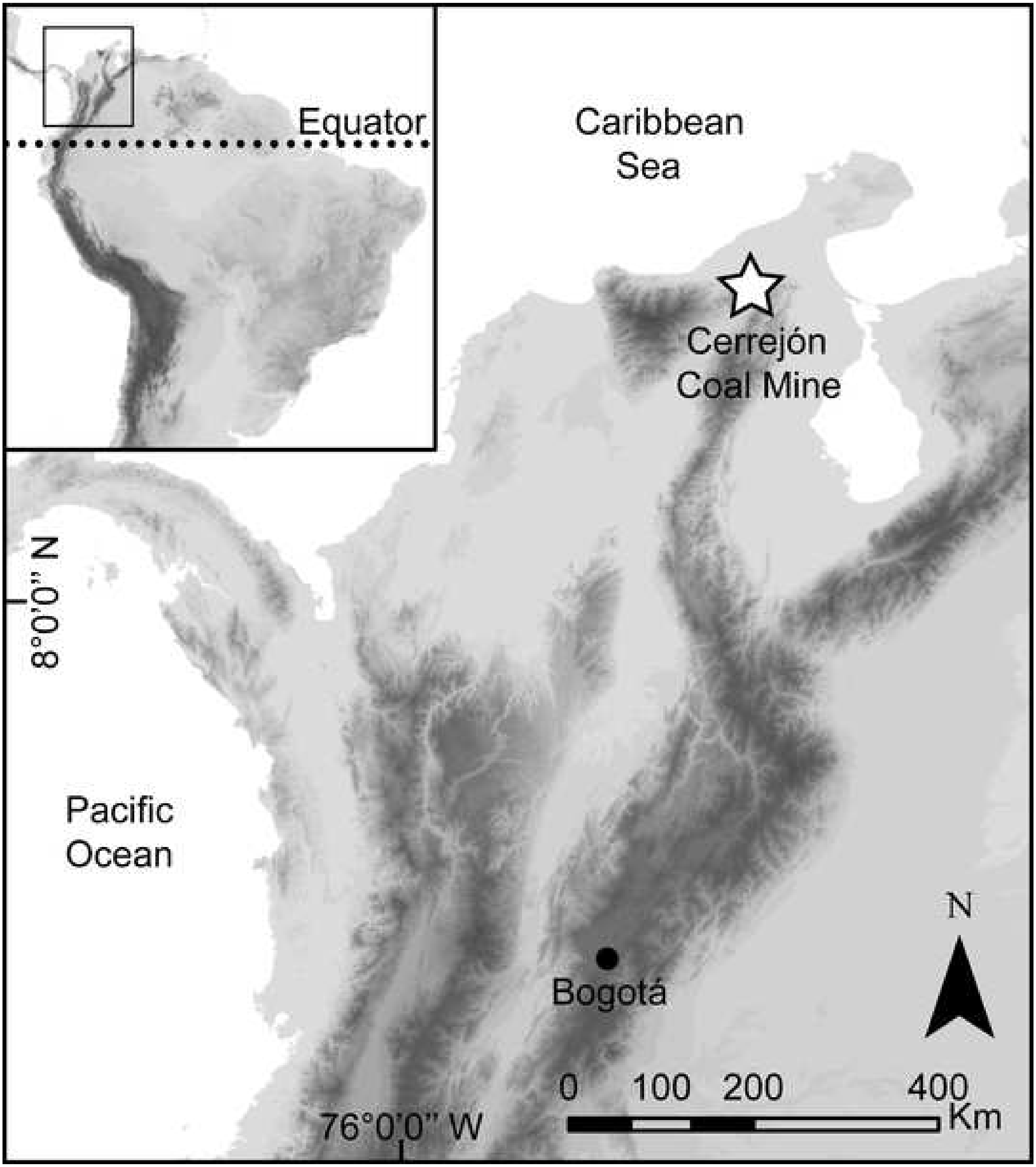
Equator
Caribbean Sea
Cerrejón Coal Mine
8°0'0" N
Pacific Ocean
Bogotá
N
0
100
200
400
Km
76°0'0" W

Plate I

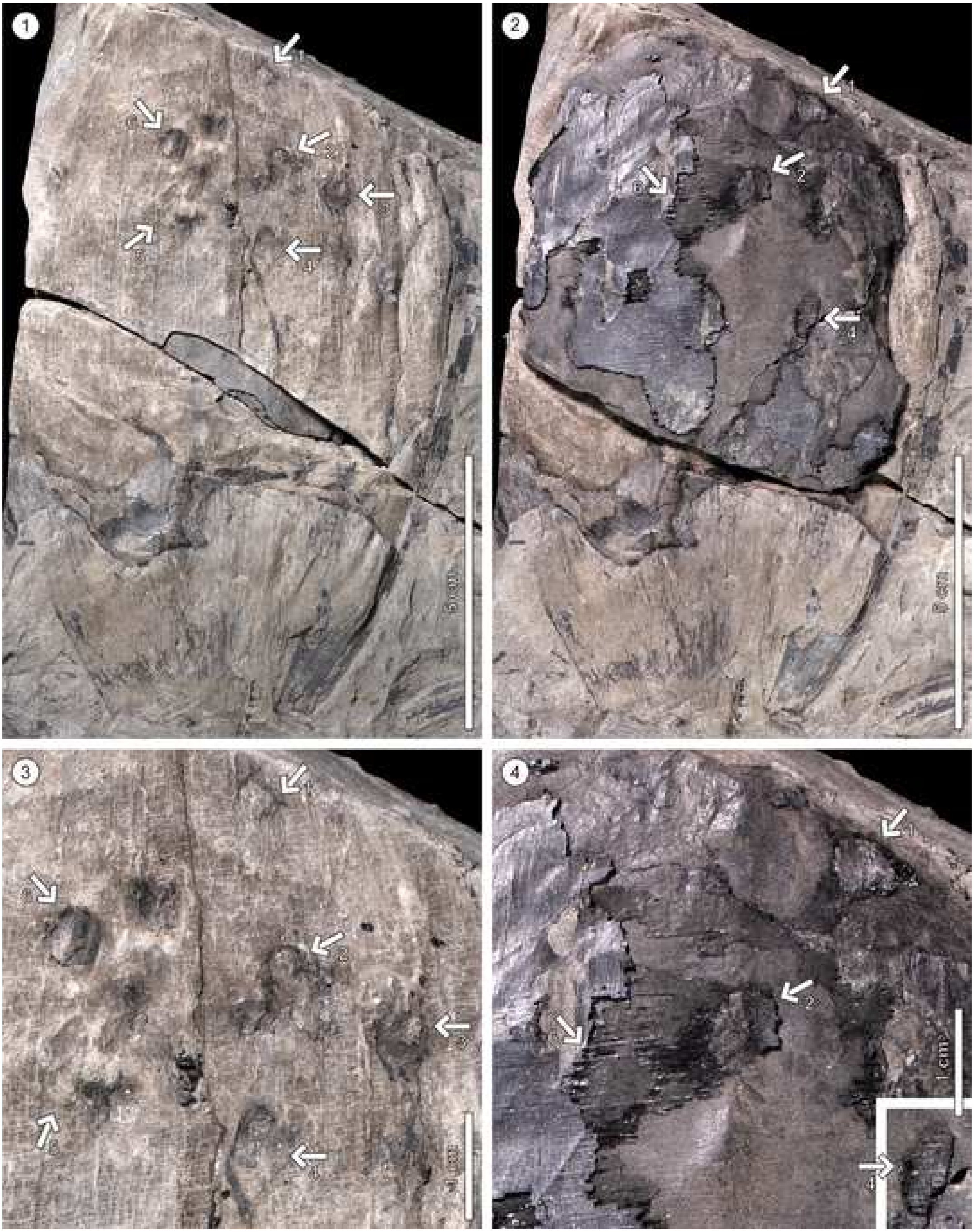

Plate II

Supplementary Material. Database of seed predating beetles and their palm hosts