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Termite Traces on Bones from the Late Pleistocene of Argentina

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Insect activity during the late Cenozoic of the Pampean Region (Argentina) has been recorded mainly as fossil nests of ants, termites, flies and beetles. We present new evidence of insect activity based on the presence of traces on bones from a late Pleistocene site in the Quequén Grande Basin. Potential tracemakers were evaluated by comparing these scratches with both modern and ancient bone modifications produced by insects and other organisms. The marks reported here show radiate morphology, linear arrangement, opposite disposition of simple grooves, small size and association of irregular and star-like marks, and some are located on cracks. These characteristics link the traces to insects, specifically termites. Based on an associated radiocarbon date, the marks were shaped under climatic conditions of the last part of OIS 3, where some abrupt warm episodes were documented.

Keywords Taphonomy, Grooves, Coleoptera, Isoptera, Climate

INTRODUCTION

The activity of insects during the late Cenozoic in the Pampean Region is mainly recorded as fossil nests of ants, termites, flies and beetles (Bravard, 1857; Laza, 1995, 2006; Tonni et al., 1996; Genise, 1997; Voglino and Pardiñas, 2005). These records are important not only from an entomological perspective (since insect specimens are very scarce in the fossil record) but also as climatic indicators. Laza et al. (2003) described ichnological successions from the late Cenozoic of the Pampean region and reported ant hills and Scarabaeinae nests for the late Pleistocene. Another information system about insect occurrence in the fossil record may be recovered from marks preserved on bones. Ever since the Triassic, several orders of insects altering bones with their mandibles as part of their feeding and reproductive strategies (Derry, 1911; Behrensmeyer, 1978; Watson and Abbey, 1986; Wylie et al., 1987; Kreutzer, 1996; Hasiotis et al., 1990; Tappen, 1994; Kaiser, 2000; Paik, 2000; Kaiser and Katterwe, 2001; Genise et al., 2004; Fejfar and Kaiser, 2005; Roberts et al., 2007; West and Hasiotis, 2007; Britt et al., 2008; Bader et al., 2009; Dominato et al., 2009).

In this note we report particular marks found on bones from a late Pleistocene site of the Quequén Grande Basin (Buenos Aires Province, Argentina). We discuss the potential trace makers by comparing these bone modifications with those produced by modern animals (insects) and previous reports of insect borings in the fossil record. Finally, this record is discussed in a paleoclimatic framework taking into account the sensitivity of insects to local conditions (e.g., humidity, temperature, light) and available radiocarbon date for the assemblage.

ASSEMBLAGE DATA

Site Paso Otero P1 (POP1) is located alongside the middle course of Quequén Grande River, in southern Buenos Aires Province, Argentina (Fig. 1). This river runs across the Buenos Aires Inter-Hills Area, from the Tandil Hill System to the Atlantic Ocean. The present-day climate in the area is typically temperate, with local mean annual temperatures between 13 and 14.1°C. The monthly mean minimum temperature is higher than 6°C in the winter, and the monthly mean maximum does not exceed 22°C in the summer. Mean annual precipitation is 830 mm and North/North-West winds are predominant in these highly productive ecosystems (Campo de Ferreras and Píccolo, 1997).

The fossil bed is 20–45 cm thick and presents a normal gradation from fine gravels to sandy silts. The sandy silts are massive and contain almost all the specimens of the fossil assemblage. This level has a high concentration of shells affected by corrosion. Both levels, along with a gray fine sand facies without fossils, fill a depression excavated on top of the La Chumbiada Member of the Luján Formation (late Pleistocene) and are covered by the floodplain facies of the Guerrero Member also belonging to the Luján Formation. Prado et al. (1987) attributed the fossil level to a channel of an uncertain lithostratigraphic position. Radiocarbon analysis

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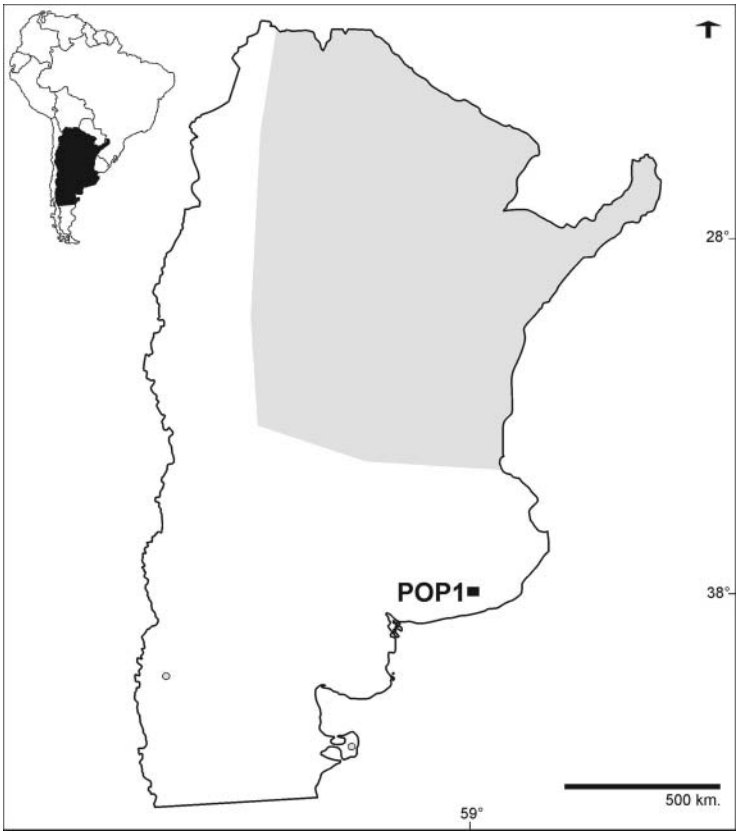

FIG. 1. Location of Paso Otero P1 Site (quadrate). Shaded area and circles: current distribution of Isoptera in Argentina (modified from Torales et al., 1997).

of the abundant freshwater gastropod shells (mostly *Chillina fluminea*) accumulated with the modified bones, indicates an age of 37,800 ± 2,300 radiocarbon years BP (LP-1928).

The POP1 fossil assemblage comprises approximately 1,500 specimens that include several orders of fishes, anurans, birds and mammals. These are part of Paleovertebrate Collection of La Plata Museum (MLP). Although numerous marks on bones were observed, the present analysis is focused on the specimens MLP 09-X-1-2: left femur of an indeterminate Caviidae; MLP 09-X-1-2: complete mobile osteoderm of *Eutatus* sp.; and MLP 09-X-1-3: distal right humerus of indeterminate *Polyborus* sp.

DESCRIPTION

The femur MLP 09-X-1-2 presents a single groove mark on a condyle. The osteoderm MLP 09-X-1-1 bears three irregular and radiate marks on its internal side. Some of the radiate grooves are curved and two appear on the scute margin. The most interesting specimen is the bird bone MLP 09-X-1-3. This specimen presents cracks on both sides that have been filled by matrix, exposition of trabecular bone at its distal condyles, and an oblique-steeped fracture with rounded fracture edges on its diaphysis. The bone surface shows eight small marks. Under light microscope, these marks are differentiated into three types according to the presence or absence of a central depression and the development of radiate grooves (Fig. 2A), groups of superposed parallel marks forming a circular figure (Fig. 2B) or isolated scratches. Two of the marks are arranged opposite to each other, with an unmarked surface between them (Fig. 2C). Three of the marks on the posterior surface of the bone are star-shaped and arranged in a straight line. Two marks lie over a crack in the bone. Some of these marks are filled with fine matrix. Diameters of the marks on the three specimens vary between 1.25 and 2.05 millimeters.

DISCUSSION

Tracemaker

Members of the highly diverse order Coleoptera are part of the typical fauna found on corpses in the latter stages of decomposition (Kulshresta and Satpathy, 2001). Beetles are primarily predaceous on fly eggs and larvae; however, some silphids, dermestids, nitulids and clerids feed on carrion (Haskell et al., 1997) or directly on bones (Schroeder et al., 2002). For instance, these taxa represent 2.32% of the arthropods present in the species succession on carcasses from central Argentina, 50% of which are dermestids (Horenstein et al., 2005). Britt et al. (2008) referred the marks preserved on bones of *Camptosaurus* to dermestid beetles based on the presence

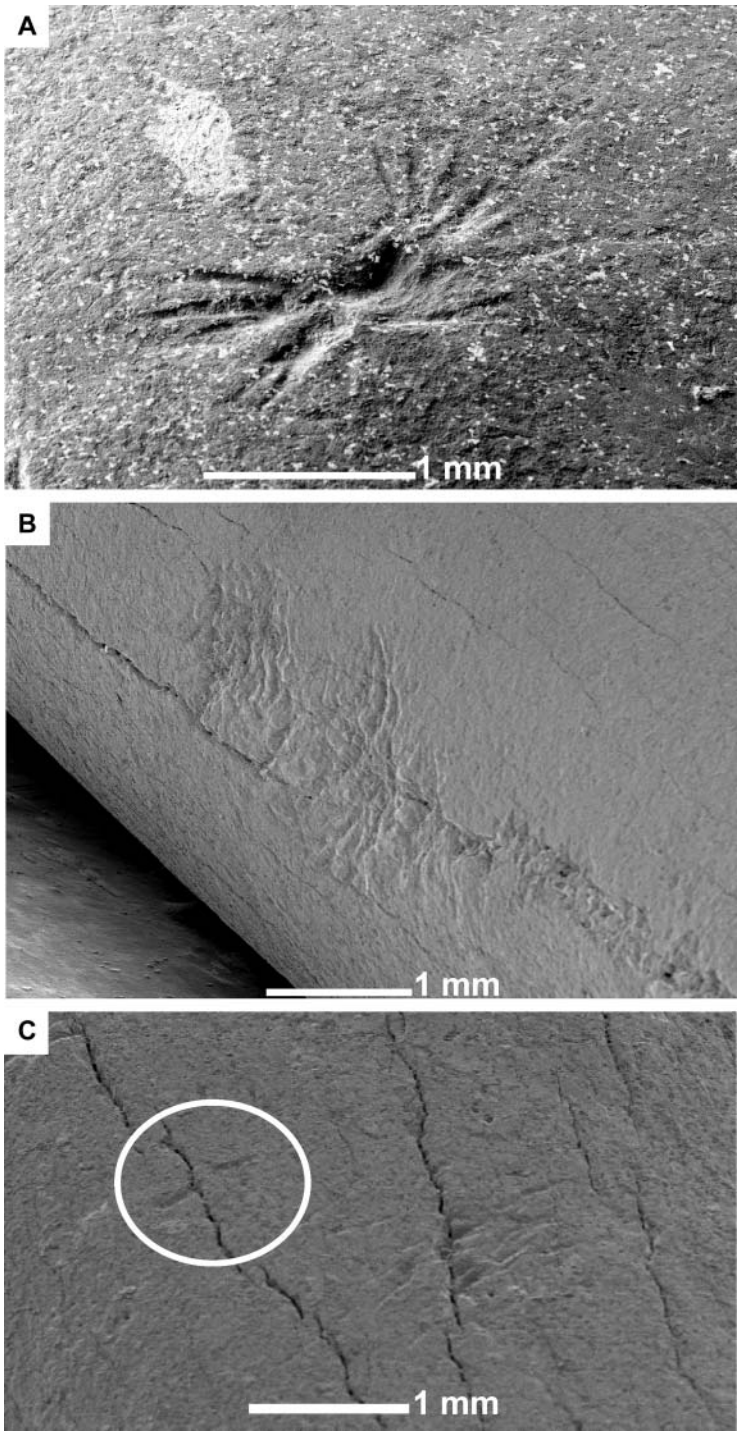

FIG. 2. SEM images of preserved marks in MLP 09-X-1-3. **A.** Star-like mark. **B.** Irregular marks over cracks. **C.** Opposite marks.

of opposing sets of parallel grooves that indicate they were produce by two apical teeth of symmetrical mandibles. In the cases of irregular and star-shaped marks recognized in MLP 09-X-1-3, the traces can be explained by multiple chewing acts that produced overlapping grooves. In this sense, these differ from the circular pits figured by Britt et al. (2008, fig. 1D) by the presence of single grooves at the bottom of the pits.

Another beetle family, the Tenebrionidae, includes necrophagous larvae which inhabit Buenos Aires province and the desert environments of Patagonia (Flores, 1998; Sackmann

and Flores, 2009). This family was dismissed as the possible tracemakers due to their U-shaped morphology and relative large groove size.

Termites (Isoptera) are the other probable tracemakers. Kaiser (2000) and Fejfar and Kaiser (2005) distinguished three classes of bone modification in fossil samples from the Pliocene of Africa (star-shaped pit marks, broad surface erosion and subcortical cavities) and referred these to termite action. Watson and Abbey (1986) performed the first experiments to test their bone-modification behavior by offering fresh, weathered and fossil bones to various termite species. They concluded that, although termites could modify the three types of bones under laboratory conditions, fossil specimens are not particularly attractive for them, since these insects prefer bones with higher concentration of nitrogen and phosphorus. Kaiser and Katterwe (2001) published experiments involving *Mastotermes darwiniensis* and documented paired and stepped grooves with crest-shaped structure that show the action of two opposite mandibles. Specimen MLP 09-X-1-3 shows a similar pair of opposite scratches, separated by an unmarked surface and associated to a crack due to weathering (Fig. 2C). The scratches on MLP 09-X-1-3 reflect the use of two opposite mandibles and a single tooth.

Timing of Modification

Bone modification by dermestids is basically linked to the skeletonization phase of decomposition. Their activity does not occur on submerged material and is prevented by rapid burial (Martin and West, 1995; in contrast to Britt et al., 2008, and Paik, 2000). McBrearty (1990) stressed the importance of termites as postdepositional disturbers of vertebrate assemblages. Derry (1911), for example, analyzed mummies from Egyptian graves affected by termites that reached the embedded bone by tunneling across mud or protective substances (see also Dangerfield et al., 2005). On the other hand, Thorne and Kimsey (1983) reported active carrion eating of exposed fresh carcasses by South American termites.

The facts related to the problem are (1) the location of some of the marks above cracks, (2) absence of tunnels in a profile of POP1, (3) fluvial accumulation of the bone assemblage, and (4) presence of marks in few bone specimens. The first issue is important because it indicates that the marks were developed after the opening of cracks. These cracks represent stage 1 of bone weathering (Behrensmeyer, 1978; Behrensmeyer et al., 2003) and point out that the traces were made after skeletonization of the bird carcass (months to years), in the absence of soft tissue remains and perhaps when the bone was already disarticulated.

Climate Context

Insect traces can be an exceptional source of data on temperature and moisture of past environments (Martin and West, 1995). Tonni et al. (1999) analyzed the mammalian record from Buenos Aires province and proposed a dramatic faunal change associated with the development of cold arid environments, which involved the deposition of the Guerrero Member of the Luján Formation (see Tonni et al., 2003). On the other hand, the faunal assemblage of the La Chumbiada Member indicated more humid and warm conditions (Prado et al., 1987).

According to the radiocarbon date, the fossil level was deposited during the Oxygen Isotope Stage 3 (OIS 3). The presence of *Lundomys* sp. (Sigmodontinae, Mammalia) in the POP1 assemblage has been used by Teta and Pardiñas (2006) to refer this level to a warm period. Abrupt warm episodes were recorded during the last part of OIS 3 (Huber et al., 2006; Hodgson et al., 2009). However, the association of this sigmodontine (confirmed by new discoveries in recent excavations of POP1) with xeric mammals such as *Lama gracilis* (cited as *Lama cf. vicugna* by Prado et al., 1987) and *Lestodelphys sp*., suggests a nonanalogous assemblage. Alternatively, the association of species with different ecological requirements can respond to an average time represented in the deposits, during which occurred rapid climate changes.

Termites are a predominantly tropical order of insects (Emerson, 1955), now cosmopolitan, and present in South America since at least the upper Cretaceous (Genise, 1995). In Buenos Aires province, termites have been recorded from the Upper Pliocene to the middle Pleistocene (Laza, 1995; Genise, 1997; Laza, 2006). According to previous climatic assumptions and because of the absence of fossil nests, Laza (2006) proposed that the colder trend occurring towards the late Pleistocene forced the retraction of termites north in Buenos Aires province. Today, the northeastern sector of this province is inhabited by *Rugitermes rugosus* and *Anoplotermes meridianus* (Torales et al., 1997). Genise (1997) mentions a personal communication about the presence of *Cortaritermes* sp. from Tandilia Hills System. The only two species distributed south from POP1 (Fig. 1) were deemed to be rare taxa by Torales (1998) and in one case as a recent case of transport by humans (Gomez and Torales, 2004). Watson and Abbey (1986) proposed that the osteophagic behaviour of termites probably functions to alleviate nitrogen deficiencies. Such behavior has also been recorded for *Nasutitermes* sp. during drought periods in a Panamanian rainforest (Thorne and Kimsey, 1983).

CONCLUSIONS

The scratches reported here are referred to insect activity, particularly to the Order Isoptera, by the following characteristics: (1) a pair of single grooves opposite to each other, (2) marks located on weathering cracks, (3) linear arrangement, (4) small size, and (5) association of irregular and star-shaped marks in the same specimen. The moment in which these marks were produced is not clear, but it probably was a perthotaxic process prior to the final burial of specimens.

These new discoveries extended the continuous record of the Isoptera from the Upper Pliocene to the late Pleistocene in the

Pampean Region. The ichnites described here were found in a basin that is not currently occupied by termites and far from the modern ecosystems with their high diversity and abundance of termites.

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