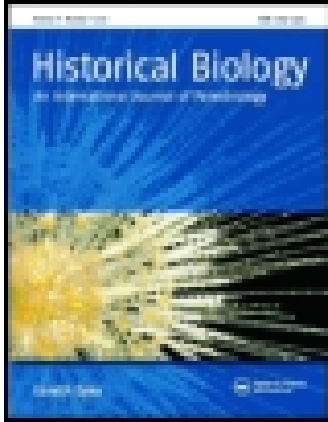


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Bioerosion trace fossils on bones of the Cretaceous South American theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005 (Deinonychosauria)

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Bioerosion trace fossils on bones of the Cretaceous South American theropod *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005 (Deinonychosauria)

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The ichnological record provides valuable information on the lifestyle, behaviour, and other palaeobiological and palaeoecological aspects of the biota. Here, we describe an interesting case of bioerosion trace fossils in bones of *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005, a deinonychosaurian theropod from the fossiliferous locality of La Buitrera, Río Negro, Patagonia, Argentina. The trace fossils are morphologically diverse and preserved in a great percentage of the skeleton, including the jaw, vertebrae and limbs. Four main groups of trace fossils have been informally named as Parallel-Edge Furrows, Overlapped Grooves, Punctures and Lined. Parallel-Edge Furrows are in turn subdivided into four subgroups: isolated furrows, parallel pairs, opposed pairs and a combination of parallel and opposed pairs. The bioerosion trace fossils were probably generated by scavenging activities, and the semi-articulated preservation of the skeleton and the small size of each individual trace indicate small-sized tracemakers. Mammals are the main candidates although some traces may have been generated by crocodyliforms and insects such as dermestids and termites. This evidence provides additional information about palaeoenvironmental conditions, taphonomic processes, taxonomic diversity and ecological relationships that characterised this part of northern Patagonia at Early Cretaceous times.

Keywords: ichnological evidence in bones; scavenging; *Buitreraptor gonzalezorum*; Patagonia; Cretaceous

1. Introduction

The evidence of fossil tetrapods is supported not only by the preservation of their hard anatomical parts such as bones, plates and teeth, but also by the ichnological data such as tracks, caves and egg nests. These latter data provide significant information about the lifestyle, behavioural biology, and palaeobiological and ecological aspects of the tracemakers, which are sometimes quite difficult to infer only from the evidence of osteological anatomy. Because the evidence of biotic interactions between tetrapods and other taxa are scarce in the fossil record (e.g. Jacobsen 1998; Roberts et al. 2007; Britt et al. 2008; Cione et al. 2010; de Valais et al. 2012; Pirrone et al. 2014), this ichnological record provides valuable information on palaeoecological aspects between animals such as predator-prey or scavenging relationship, and has great potential to elucidate functional ecosystems features.

Ichnological evidence is associated with important palaeoecological and palaeobiological implications, but also it is a valuable source of taphonomic information that helps in the reconstruction of the biostratinomic processes occurred from the death of an animal. Other taphonomic aspects, such as the degree of skeletal articulation or bone alteration and the patterns of spatial arrangement, are fundamental to infer taphonomic history (Behrensmeyer 1975, 1978, 1991; Behrensmeyer and Kidwell 1985;

Weigelt 1989; Martin 1999; Fernández López 2000). The environmental and sedimentological contexts are also basic aspects of taphonomic studies. Some processes that affect animal remains after death depend on the environmental conditions, and these processes result in general patterns of preservation that are characteristic of different physical settings (Behrensmeyer 1991). Thus, taphonomic characteristics combined with sedimentological information provide multiple lines of evidence, which may be useful to formulate and test hypotheses concerning taphonomic history (Behrensmeyer 1991).

In this contribution, we present the case of a dinosaur, *Buitreraptor gonzalezorum* Makovicky, Apesteguía and Agnolín, 2005, with abundant and diverse bioerosion activity on the surface of its skeleton. *Buitreraptor gonzalezorum* is a small non-avian coelurosaurian theropod, which was reported as the earliest dromaeosaurid from South America, yielded from the Candeleros Formation, at the fossiliferous locality known as La Buitrera, northern Río Negro Province, Argentina (Makovicky et al. 2005; Gianechini 2014). Its holotype (MPCA 245) is represented by an almost complete skeleton found in a semi-articulated condition. The preservation of many of their bones is very good with little alteration by non-biological erosion of the external surface. A complete study of the osteology of this theropod was developed

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(Gianechini 2014) revealing the presence of abundant trace fossils covering a large proportion of its skeleton, including the skull, vertebrae and limb bones. A previous publication reported two of these traces on the surface of the left dentary (i.e. MPCA 470-13a and 13b), interpreting them as feeding evidence (de Valais et al. 2012).

This paper presents and describes the abundant bioerosion trace fossil association preserved on the surface of the bones of MPCA 245, and analyses and interprets the identity and palaeobiology of the possible tracemakers. The evidence of the ecological relationships of the faunal components of the Cretaceous ecosystem from Gondwana is considered. Furthermore, taphonomic processes and the environmental conditions where the trace fossils were produced are analysed.

2. Geological setting

The specimen MPCA 245 has been recovered from the La Buitrera fossiliferous locality, from the upper levels of the Candeleros Formation (Cenomanian), the basal unit of the Río Limay Subgroup, Neuquén Group (Stipanovic et al. 1968; Cazau and Uliana 1973). In the studied area, the Candeleros Formation is unconformably underlain by the Lohan Cura Formation (late Aptian-Albian) and overlain by the Huincul Formation (Turonian; Corbella et al. 2004; Leanza et al. 2004).

The La Buitrera site is located 32 km NW of Cerro Policía, northern Río Negro Province, Argentina (Figure 1(a)). The Candeleros Formation here has a measured thickness reaching up to 95 m, and it is composed by quartzitic, coarse- to medium-grained sandstones, sabulitic and conglomerate lenses and frequent intercalation of siltstones and mudstones (Apesteguía 2008). The palaeoenvironment was interpreted as a meandering fluvial system, evidenced by the presence of channelised bodies with lateral accretion macroforms (Garrido 2010). Overbank deposits are abundant, mainly represented by levee, crevasse channels and crevasse splay deposits. The evidence of discontinuities in the sedimentation, represented by poorly developed palaeosols, is relevant for this study, and it was interpreted as a result of several events of periodical flooding followed by lapses of limited or no sedimentation and sub-aerial exposure (Apesteguía 2008).

Regarding the components of the palaeofauna of La Buitrera, they are mainly represented by small- to medium-sized continental tetrapod specimens, most of them found articulated or slightly disarticulated. Three-dimensional preservation with scarce or null deformation of skeletons is common. Taxonomically, the vertebrate palaeofauna is composed of diverse groups of reptiles, such as sphenodonts, crocodyliforms, snakes, theropod dinosaurs and pterosaurs (e.g. Apesteguía and Novas 2003; Pol and Apesteguía 2005; Apesteguía and Zaher 2006; Haluza and Canale 2009; Makovicky et al. 2012),

mammalian taxa (Rougier et al. 2011) and ceratodontiform dipnoans (Apesteguía, Agnolín, et al. 2007).

In the La Buitrera locality, two main taphonomic processes can be recognised. The first mode involves red fine-grained sandstones containing well-articulated specimens, representing immature palaeosols developed in water-saturated levee deposits. The second mode involves yellow medium-grained sandstones with disarticulated specimens, representing lateral accretion deposits and the sub-aerial top of point bars (Apesteguía, Garrido, et al. 2007; Apesteguía 2008). The preservation of the holotype of *Buitreraptor* is consistent with the first mode described.

3. Materials and methods

The trace fossils are preserved as negative epichnia (concave downward) on the surface of the bones of the holotype of *Buitreraptor gonzalezorum* (MPCA 245), which was found mostly articulated and later disarticulated during technical preparation. Two of these trace fossils (i.e. numbered MPCA 470-13a and 13b) have already been described by de Valais et al. (2012). All the specimens are housed, under the acronym MPCA, in the palaeontological collection of the Museo Provincial 'Carlos Ameghino', Cipolletti, Río Negro Province, Argentina. The trace-bearing bones are the left dentary, cervical and caudal vertebrae, and bones of the forelimbs and hindlimbs (Figure 1(c)). The trace fossils were characterised following the criteria of de Valais et al. (2012) and Pirrone et al. (2014). The list of the trace fossils, their collection number, the anatomical location on MPCA 245 and the classification adopted are compiled in Figure 2. The measurements on the trace fossils are summarised in Table 1.

Trace fossils were photographed with a digital camera SONY SX160 IS, both at normal view and using a binocular loupe Arcane Ztx-T. To evaluate the association between ichnofossils and the potential tracemakers, the whole fossil record from La Buitrera locality reported so far was considered. Palaeobiological aspects of the taxa involved have also been considered focusing on the anatomic structures that could produce traces on bones, such as teeth and jaws, and in the morphology and spatial distribution of them.

4. Description of the traces

The trace fossils preserved on the surface of MPCA 245 can be divided into four main groups, based on their morphology and spatial arrangement, informally named as Parallel-Edge Furrows ('Parallel Furrows' *sensu* de Valais et al. 2012), Overlapped Grooves, Punctures and Lined (Figure 2).

4.1 Parallel-Edge Furrows

These traces are composed by one or more straight furrows with parallel to sub-parallel edges, and are

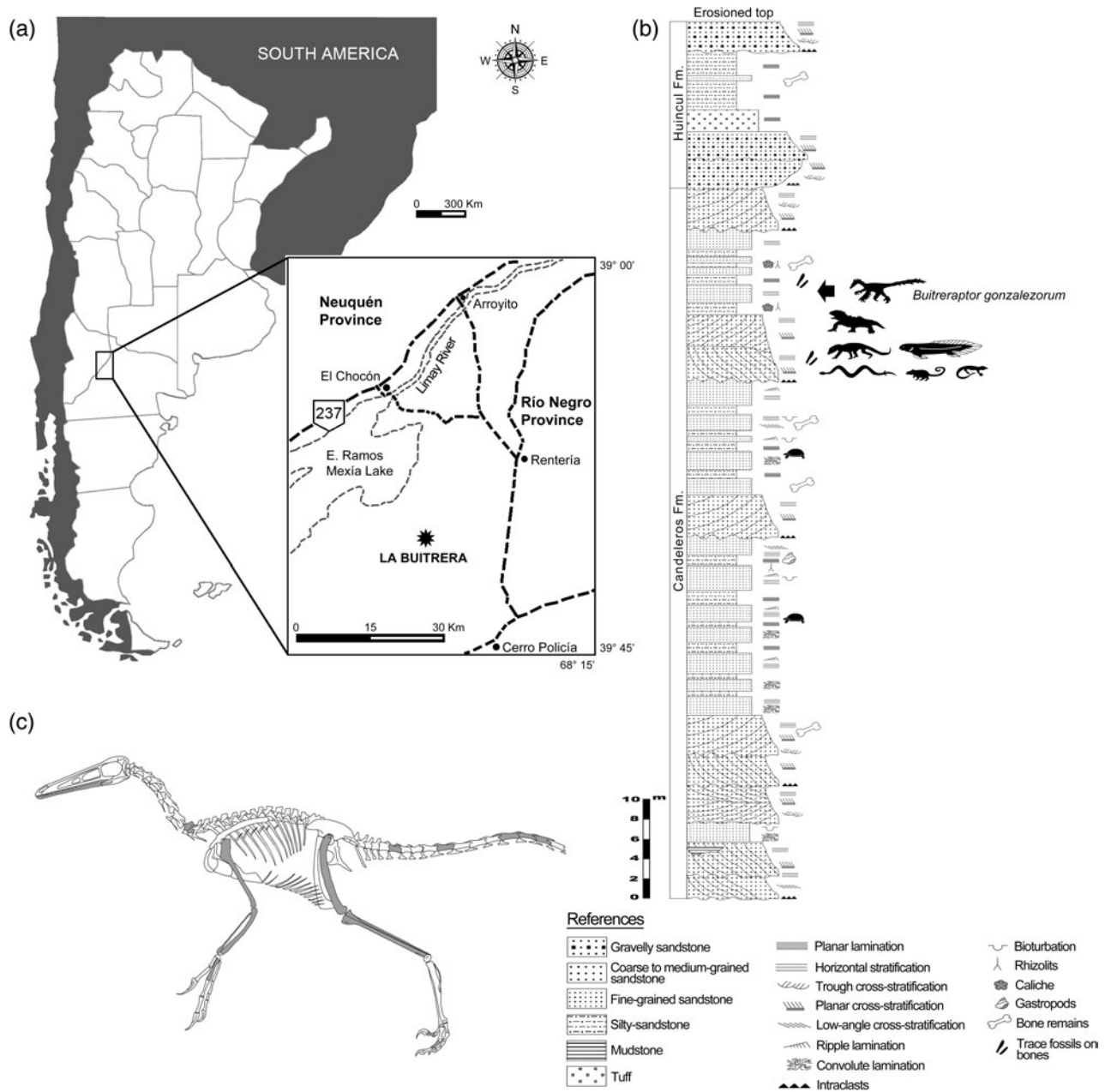


Figure 1. (a) Geographic location of La Buitrera, at NW Patagonia, Argentina. (b) Stratigraphic sequence of the Candeleros Formation showing the levels of provenance of the holotype of *Buitreraptor gonzalezorum* and the associated fauna (modified from de Valais et al. 2012). (c) Reconstruction of the skeleton of *Buitreraptor gonzalezorum* showing in grey the bones with trace fossils.

represented by MPCA 470-13a, 13b, 14–20, 22–31, 34–37, 40, 42, 43, 46, 48–53, 79, 80, 82 and 88 (Figures 3–6). The Parallel-Edge Furrows have a cross-sectional gradient, represented by two extreme morphologies (Figure 2): (1) with flat floor and walls roughly perpendicular to the external surface of the bone ('U-shaped'), and (2) with angular floor and oblique walls ('V-shaped'). Further subdivisions can be made on the basis of the spatial arrangement of the furrows: isolated (see Section 4.1.1), arranged in parallel rows (see Section 4.1.2.1), in opposed

pairs (see Section 4.1.2.2) or a combination of the last two (see Section 4.1.2.3).

4.1.1 Isolated furrows

This group includes those furrows morphologically unrelated to other grooves, although they may be preserved close to others. The specimens are numbered MPCA 470-13b, 19, 20, 25, 26, 27 and 29, and are observed on the surface of the right dentary, femur and fibula (Figures 2 and 3).












	Interpretation of the cross section	Plan view	Specimen	Location	
PUNCTURES			MPCA 470-72 MPCA 470-73 MPCA 470-75 MPCA 470-76	right fibula right fibula right ulna right fibula	
PARALLEL-EDGE FURROWS		Isolated furrows		MPCA 470-13b MPCA 470-19 MPCA 470-20 MPCA 470-25 MPCA 470-26 MPCA 470-27 MPCA 470-29	right dentary right femur right femur right femur right femur right femur right fibula
		Parallel pairs		MPCA 470-18 MPCA 470-31 MPCA 470-40 MPCA 470-88	left femur 9th cervical vertebra right femur right radius
		Opposed pairs		MPCA 470-16 MPCA 470-17 MPCA 470-82	right ulna right radius right humerus
		Opposed and parallel pairs		MPCA 470-13a MPCA 470-14 MPCA 470-15 MPCA 470-22 MPCA 470-23 MPCA 470-24 MPCA 470-28 MPCA 470-30 MPCA 470-34 MPCA 470-35 MPCA 470-36 MPCA 470-37 MPCA 470-42 MPCA 470-43 MPCA 470-46 MPCA 470-48 MPCA 470-49 MPCA 470-50 MPCA 470-51 MPCA 470-52 MPCA 470-53 MPCA 470-79 MPCA 470-80	right dentary right dentary right humerus right femur right tibia right tibia right tibia right dentary caudal vertebra right humerus right humerus right humerus right humerus left femur left femur right tibia right humerus right humerus right humerus left humerus right radius right femur right ulna caudal vertebra
OVERLAPPED GROOVES			MPCA 470-32 MPCA 470-33 MPCA 470-38 MPCA 470-39 MPCA 470-41 MPCA 470-44 MPCA 470-45 MPCA 470-54 MPCA 470-55 MPCA 470-56 MPCA 470-57 MPCA 470-58 MPCA 470-59 MPCA 470-60 MPCA 470-61 MPCA 470-62 MPCA 470-63 MPCA 470-64 MPCA 470-65 MPCA 470-66 MPCA 470-67 MPCA 470-68 MPCA 470-69 MPCA 470-70 MPCA 470-71 MPCA 470-74 MPCA 470-77 MPCA 470-78 MPCA 470-81	caudal vertebra caudal vertebra metacarpal II? caudal vertebra right femur left femur left femur caudal vertebra caudal vertebra caudal vertebra caudal vertebra caudal vertebra caudal vertebra caudal vertebra caudal vertebra right femur right femur right femur right femur right femur right femur right tibia right tibia right fibula pedal phalanx indet. right tibia right tibia right femur	
LINED			MPCA 470-47	right pedal phalanx II-2	

Figure 2. Trace fossils diversity observed on the bones of *Buitreraptor gonzalezorum* (MPCA 245), showing the different morphologies and the corresponding specimens with their locations in the skeleton.

Specimen MPCA 470-13b was previously described by de Valais et al. (2012), with a length of 0.70 mm and a maximum width of 0.30 mm (Figure 3(a),(e)). On the lateral surface of the right femur, several of those grooves were observed (i.e. MPCA 470-19, 20, 25, 26, 27 and 29). Among them, MPCA 470-20, located in the proximal region, is the shortest, 0.65 mm in length, but the widest, 0.37 mm in width (Figure 3(b),(e)). The specimens MPCA 470-19, 25, 26 and 27 are morphologically similar, consisting of narrow, elongated grooves with sharp ends (Figure 3(b),(c),(e)). The

specimen MPCA 470-29 is the only isolated furrow in the right fibula, in its proximal lateral surface (Figure 3(d),(e)).

4.1.2 Furrows in pairs

This subgroup includes traces composed of two or more grooves of straight edges, with variable spatial arrangement. These grooves may be parallel to each other, or opposed pairs facing each other or a combination of these two dispositions, namely opposed and parallel pairs.

Table 1. Measures of the trace fossils preserved on the bones of *Buitreraptor gonzalezorum* (MPCA 245).

Groups	Min.	Max.	Mean	n
<i>Parallel-Edge Furrows</i>				
Isolated				
W	0.08	0.37	0.19	7
L	0.65	3.1	1.59	7
Furrows in Parallel pairs				
W	0.1	0.58	0.23	8
L	1.09	1.84	2.3	8
Lateral Hiatus	0.56	1.7	1.06	4
Furrows in Opposed pairs				
W	0.1	0.77	0.35	6
L	1.12	4.2	2.21	6
Hiatus between internal ends	0.14	1.23	0.5	3
Opposed and parallel pairs				
W	0.1	0.2	0.15	12
L	0.3	1.5	0.83	12
Lateral Hiatus	0	0.9	0.42	10
Hiatus between internal ends	0	0.7	0.2	12
<i>Overlapped Grooves</i>				
Minor axis	0.53	3.65	1.36	29
Major axis	1.03	3.78	1.87	29
<i>Punctures</i>				
Minor axis	1.08	2.11	1.48	4
Major axis	1.2	2.43	1.66	4
<i>Lined</i>				
W	0.07	0.23	0.15	13
L	1.18	2.51	1.95	13

Notes: For the groups Parallel Edge-Furrows and Lined, the width (W) and length (L) of each furrow were measured. For the groups Overlapped Grooves and Punctures, the major and minor axes of the bioeroded surface were measured. Measures are in millimeters; Min, minimal measure; Max, maximum measure; n, amount corresponding to each type of trace.

4.1.2.1 Parallel pairs. These trace fossils are represented by specimens MPCA 470-18, 31, 40 and 88 (Figure 4).

MPCA 470-18 consists of two grooves (average length and width of 1.08 and 0.5 mm, respectively) disposed obliquely relative to the longitudinal axis on the posterior surface of the left femur, separated one from the other by 1.7 mm (Figure 4(a),(g)). The specimens MPCA 470-31 (on the ninth cervical vertebrae), 40 (on the right femur) and 88 (on the right radius) are morphologically similar, composed of two slender furrows with angular floor and oblique walls (Figure 4(b)–(d),(g)). The length of individual traces ranges from 1.30 to 2.30 mm, with an average of 1.84 mm, whereas the width, approximately 0.1 mm, does not present variability. The lateral distance between the two furrows is about 0.75 mm.

4.1.2.2 Opposed pairs. This type of traces consists of pairs of opposed grooves, arranged perpendicularly to sub-perpendicularly to the longitudinal axis of the bone, represented by specimens MPCA 470-16, 17 and 82 (Figures 2 and 4).

MPCA 470-16 is preserved on the lateral surface of the distal end of the right ulna (Figure 4(e),(g)). One of the

individual traces is deeply impressed and larger (1.30 mm long and 0.77 mm wide) than the other (0.7 mm long and 0.48 mm wide) and are separated by a hiatus of 1.23 mm. MPCA 470-17 is a small specimen, located in the distal end of the right radius (Figure 4(f),(g)), with a total length of 1.12 mm and a width of 0.17 mm; the hiatus between the opposed traces is of 0.14 mm. MPCA 470-82 is located on the medial surface of the right humerus, at the middle zone of the diaphysis, arranged obliquely in relation to the longitudinal axis of the bone (Figure 4(g),(h)). The total length and width is of 1.32 and 0.10 mm, respectively, with a hiatus of 0.14 mm.

4.1.2.3 Combination of opposed and parallel pairs.

Several trace fossils present a more complex morphology, which could be described as a combination of opposed and parallel pairs. The specimens are numbered as MPCA 470-13a, 14, 15, 22, 23, 24, 28, 30, 34–37, 42, 43, 46, 48–53, 79 and 80 (Figures 2, 3, 5 and 6). Most of the specimens are arranged perpendicularly or obliquely to the longitudinal axis of the bones, and the individual traces are similar to those of the subgroups opposed pairs and parallel pairs. In some cases, the furrows composing each combined trace are overlapped among themselves and with other isolated traces, thus making their interpretation difficult.

The simplest of such traces is MPCA 470-22 (Figure 5 (c),(l)), on the lateral surface of the right femur, which is formed by a pair of opposed furrows separated by 1.5 mm, and a smaller and less marked furrow parallel to the proximal trace of the opposed pair located at a distance of 1.61 mm.

There are several traces composed of two pairs of parallel furrows opposed to each other, represented by MPCA 470 13a, 14, 15, 23, 34, 48, 49, 51 and 80 (Figures 3, 5 and 6). MPCA 470-13a is the other trace fossil described by de Valais et al. (2012) (Figure 3(a),(e)), close to MPCA 470-13b and about 6 cm away from MPCA 470-14. The latter has an opposed pair with no internal hiatus (1.46 mm long and 0.15 mm wide), and the other is superficially preserved (each trace 0.3 mm long and 0.1 mm wide, hiatus 0.7 mm) (Figure 5(a),(l)). MPCA 470-23, on the right tibia, is similar to MPCA 470-14, but with the lateral hiatus between grooves of 0.29 mm (Figure 5 (d),(l)). MPCA 470-51 is located on the medial surface of the left humerus (Figure 6(e),(j)), also with a pair of opposed furrows in slight contact but the other with a separation of 0.1 mm, whereas the parallel pairs are separated by 1 mm. MPCA 470-15, 48, 49 and 80 exhibit a similar morphology and spatial distribution, formed by two pairs of opposed and parallel narrow furrows, arranged perpendicular to the long axis of the bearing bone (Figures 5(b),(l) and 6(c),(i),(j)). MPCA 470-34 is composed of individual traces with an average length and

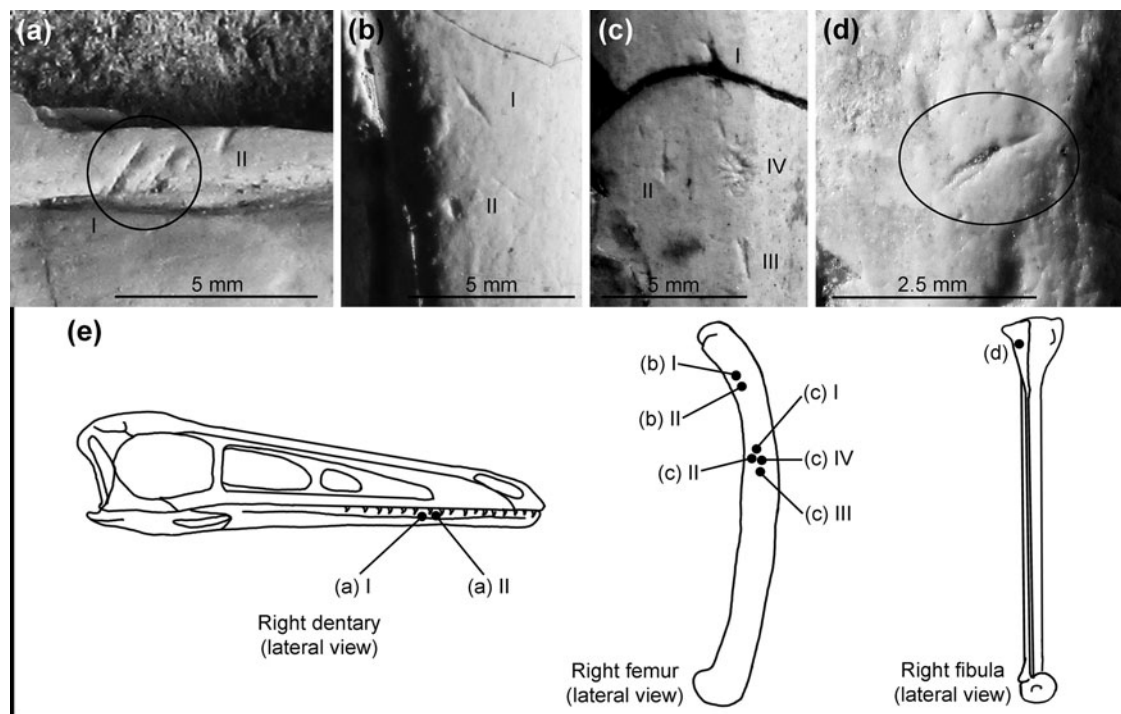


Figure 3. Isolated furrows, opposed and parallel pairs, and Overlapped Grooves on the bones of *Buitreraptor gonzalezorum* (MPCA 245). (a) MCPA 470-13a, an opposed and parallel pair identified as 'I', and MCPA 470-13b, an isolated groove identified as 'II'; (b) two isolated furrows, MCPA 470-19 (identified as 'I') and MCPA 470-20 (identified as 'II'); (c) three isolated furrows, MCPA 470-25 (identified as 'I'), MCPA 470-26 (identified as 'II') and MCPA 470-27 (identified as 'III'), and Overlapped Grooves, MCPA 470-68 (identified as 'IV'); (d) MCPA 470-29, an isolated furrow; (e) locations of the trace fossils showed in this figure.

width of 1.06 and 0.1 mm, respectively, with the opposed pairs disposed obliquely (Figure 5(g),(l)). MPCA 470-28 is a small trace, formed by two opposed pairs, and another parallel groove (Figure 5(f),(l)). MPCA 470-37, on the medial surface of the right humerus, is represented by two sets of two pairs of opposed and parallel furrows, side by side (Figure 5(j),(l)). The complete trace covers a total area of 4.02 mm × 1.29 mm.

MPCA 470-30 and MPCA 470-46 comprise three parallel and opposed pairs of short and relatively wide furrows (average 0.7 mm long and 0.2 mm wide). The first one is placed close to MPCA 470-14 and is a narrowly packed case with all the traces in slight contact (Figure 5(a),(l)), whereas the second one is located on the posteromedial area of the distal portion of the right tibia, perpendicularly to the longitudinal axis of the bone (Figure 6(b),(j)). The rest of the trace fossils of the group are more complex as they are composed of a greater amount of individual traces. The most representative specimen is MPCA 470-52, on the anterior surface of the medial-proximal zone of the diaphysis of the right radius (Figure 6(f),(j)). It is constituted by five opposed and parallel pairs, perpendicular to the major longitudinal axis of the bone. The individual traces composing the three central pairs have an average length

and width of 1.04 and 0.19 mm, respectively. The opposed pairs of the extremes are smaller and shallower, and have an average of 0.4 mm in length and 0.15 mm in width. MPCA 470-35, on the posterolateral surface of the right humerus, is composed of at least nine pairs of opposed and parallel grooves and isolated furrows (about 1.5 mm long and 0.19 mm wide), many of them overlapped, with a hiatus between opposed grooves of 0.9 mm in average (Figure 5(h),(l)). MPCA 470-53, perpendicular to the longitudinal axis of the right femur and similar to the former, is constituted of two sets of at least seven parallel and opposed pairs and isolated furrows, with poor preservation (Figure 6(g),(j)). MPCA 470-36, on the anteromedial surface of the right humerus, 42 and 43, both on the lateral surface of the left femur, are composed of several slender furrows, overlapped but distinguishable enough to note that there are several opposed and parallel pairs (Figures 5(i),(k), (l) and 6(a),(j)).

MPCA 470-50, a complex trace arranged in two sets at the proximal end of the right humerus, consists of many opposed and parallel pairs and isolated, shallow and poorly preserved furrows, distributed in an area of 5.43 mm in length (Figure 6(d),(j)). MPCA 470-24, on the proximal end of the right tibia, is a small trace fossil,

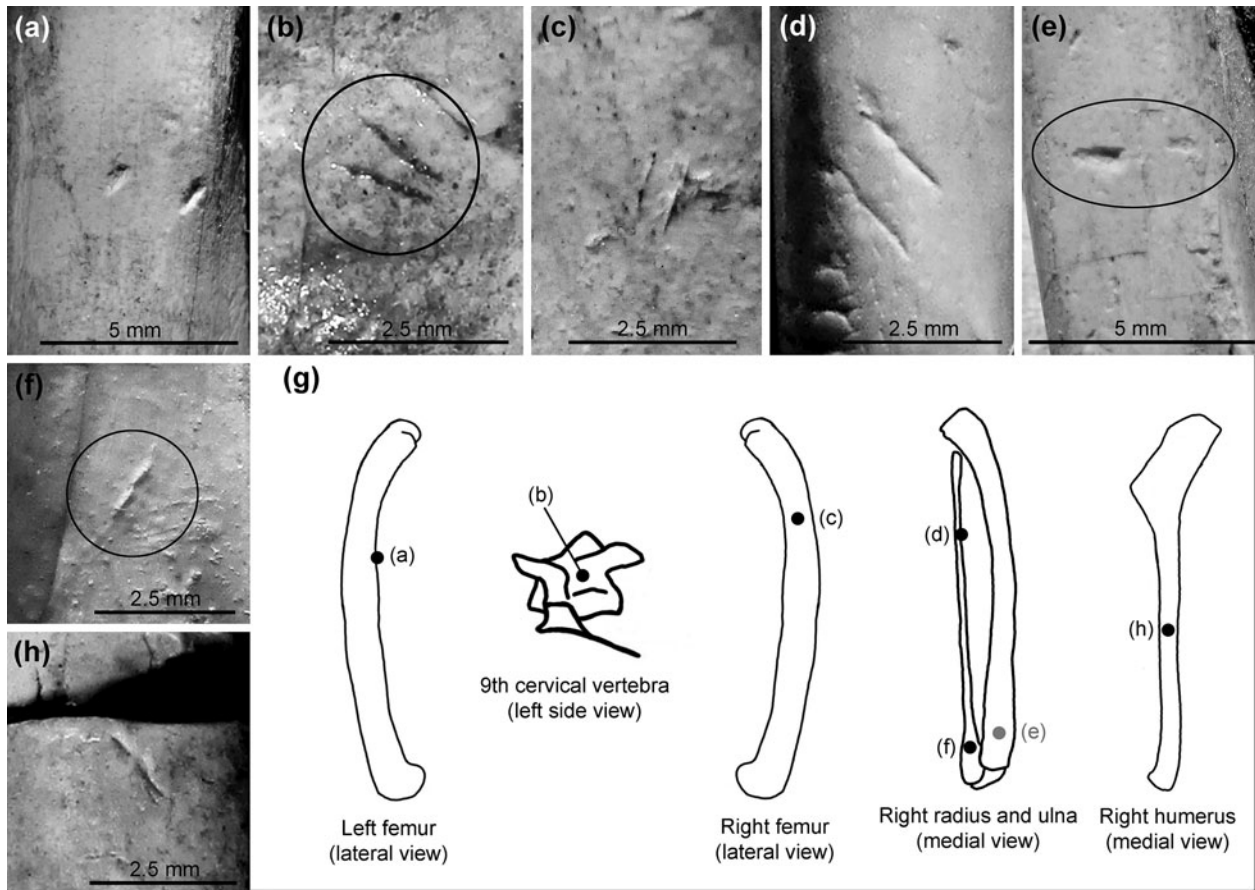


Figure 4. Parallel pairs and opposed pairs, on the bones of *Buitreraptor gonzalezorum* (MPCA 245). (a–d) Parallel pairs: (a) MPCA 470-18, (b) MPCA 470-31, (c) MPCA 470-40 and (d) MPCA 470-88; (e–g) opposed pairs: (e) MPCA 470-16, (f) MPCA 470-17 and (h) MPCA 470-82; (g) locations of the trace fossils showed in this figure, those in grey are located on the opposed surface of the bone.

composed of at least five individual traces (average length of 0.6 mm), showing a similar disposition of the opposed and parallel pairs, but the pairing arrangement is not clear (Figure 5(e),(l)).

4.2 Overlapped Grooves

This group is integrated by abundant specimens, numbered as MPCA 470-32, 33, 38, 39, 41, 44, 45, 54–71, 74, 77, 78 and 81 (Figures 2, 3, 7 and 8).

They are composed by overlapped narrow grooves, in some cases radiating from a central point. The number of grooves varies from just a few (e.g. MPCA 470-69, about seven grooves, Figure 8(b)) to several ones, where the high superposition makes the identification of each individual trace difficult (e.g. MPCA 470-70, Figure 8(c)). The bioeroded surfaces present variable sizes, with an average minor axis of 1.36 mm and an average major axis of 1.87 mm. In some cases, the radial arrangement produces shallow pits, with the greatest depth in the centre (Figures 7(e),(g),(h) and 8(a),(c)–(e),(g),(h)).

4.3 Punctures

Four specimens belong to this group, numbered as MPCA 470-72, 73, 75 and 76, consisting of circular and semi-circular holes, where the bone surface appears to have been compressed by a high punctual pressure, almost piercing the periosteum (Figures 2 and 9). MPCA 470-75 is a relative deeper pit, preserved on the medial surface of the proximal zone of the right ulna, with an irregular but well-demarcated border (Figure 9(b),(d)). Inside the drilling, at least three grooves are observed. MPCA 470-72, 73 and 76 are on the lateral surface of the proximal region of the right fibula (Figure 9(a),(d)). The first two do not show their periosteum completely perforated, being shallower than MPCA 470-76. The three specimens have roughly circular shape but no clear edges.

4.4 Lined

In the right pedal phalanx II-2, there is a series of grooves and furrows that constitute the specimen MPCA 470-47

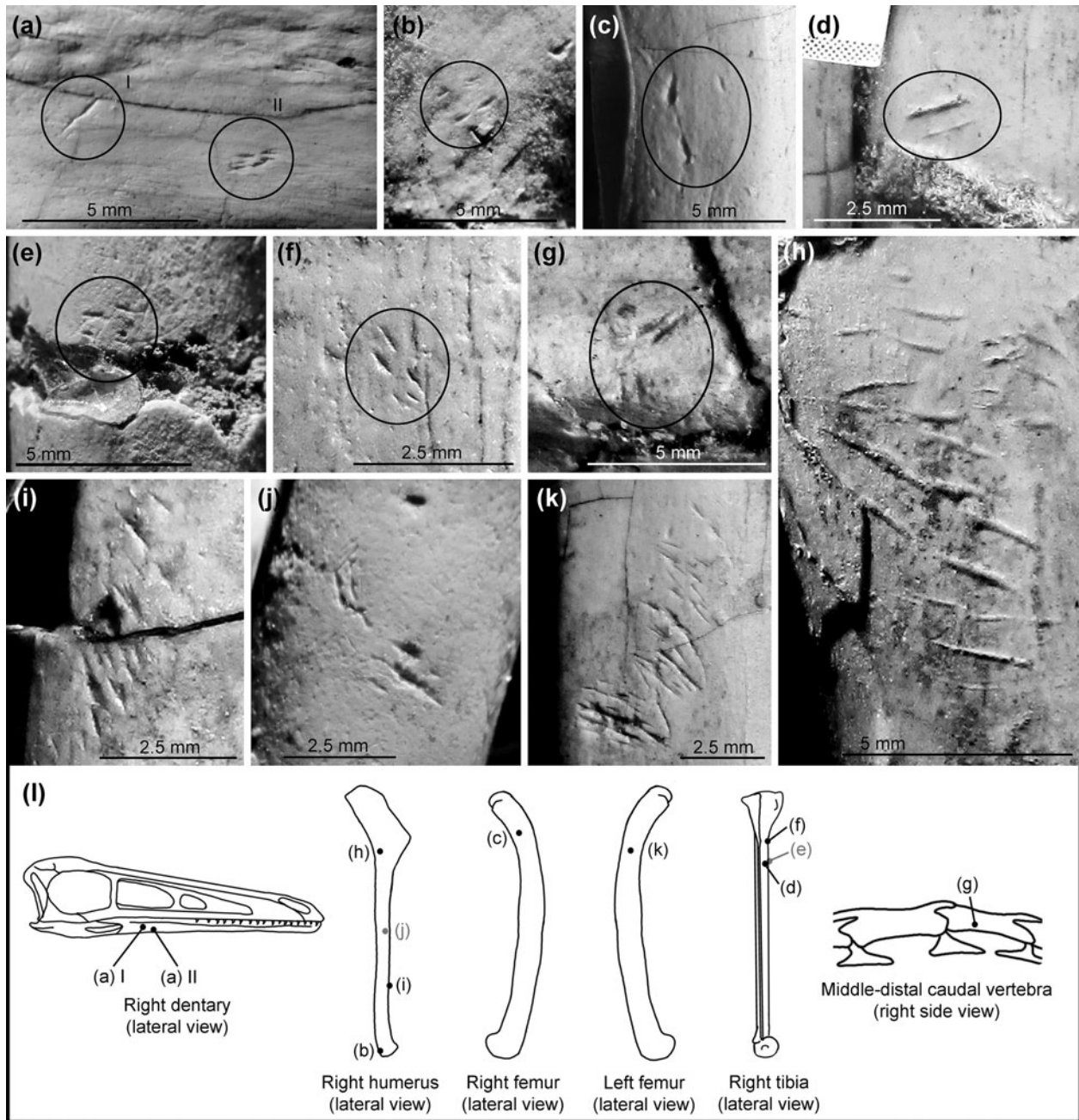


Figure 5. Combinations of parallel and opposed pairs on the bones of *Buitreraptor gonzalezorum* (MPCA 245). (a) MPCA 470-14 (identified as 'I') and MPCA 470-30 (identified as 'II'); (b) MPCA 470-15; (c) MPCA 470-22; (d) MPCA 470-23; (e) MPCA 470-24; (f) MPCA 470-28; (g) MPCA 470-34; (h) MPCA 470-35; (i) MPCA 470-36; (j) MPCA 470-37; (k) MPCA 470-42; (l) locations of the trace fossils showed in this figure, those in grey are located on the opposed surface of the bone.

(Figure 9(c),(d)). It is formed by several parallel grooves, where at least one opposed pair can be distinguished. The individual traces range 1.18–2.51 mm in length and 0.07–0.23 mm in width. The bioeroded area covers nearly all the medial surface of the phalanx, extending approximately 6.69 mm in the longitudinal axis and 4.75 mm in the dorsoventral axis of the bone.

5. Discussion

The trace fossils preserved on the surface of the bones of the holotype of *Buitreraptor gonzalezorum* represent a very interesting case, not only from the point of view of the traces themselves, but also considering the taphonomic, palaeobiological and palaeoecological aspects. There are several points to be taken into consideration in relation to

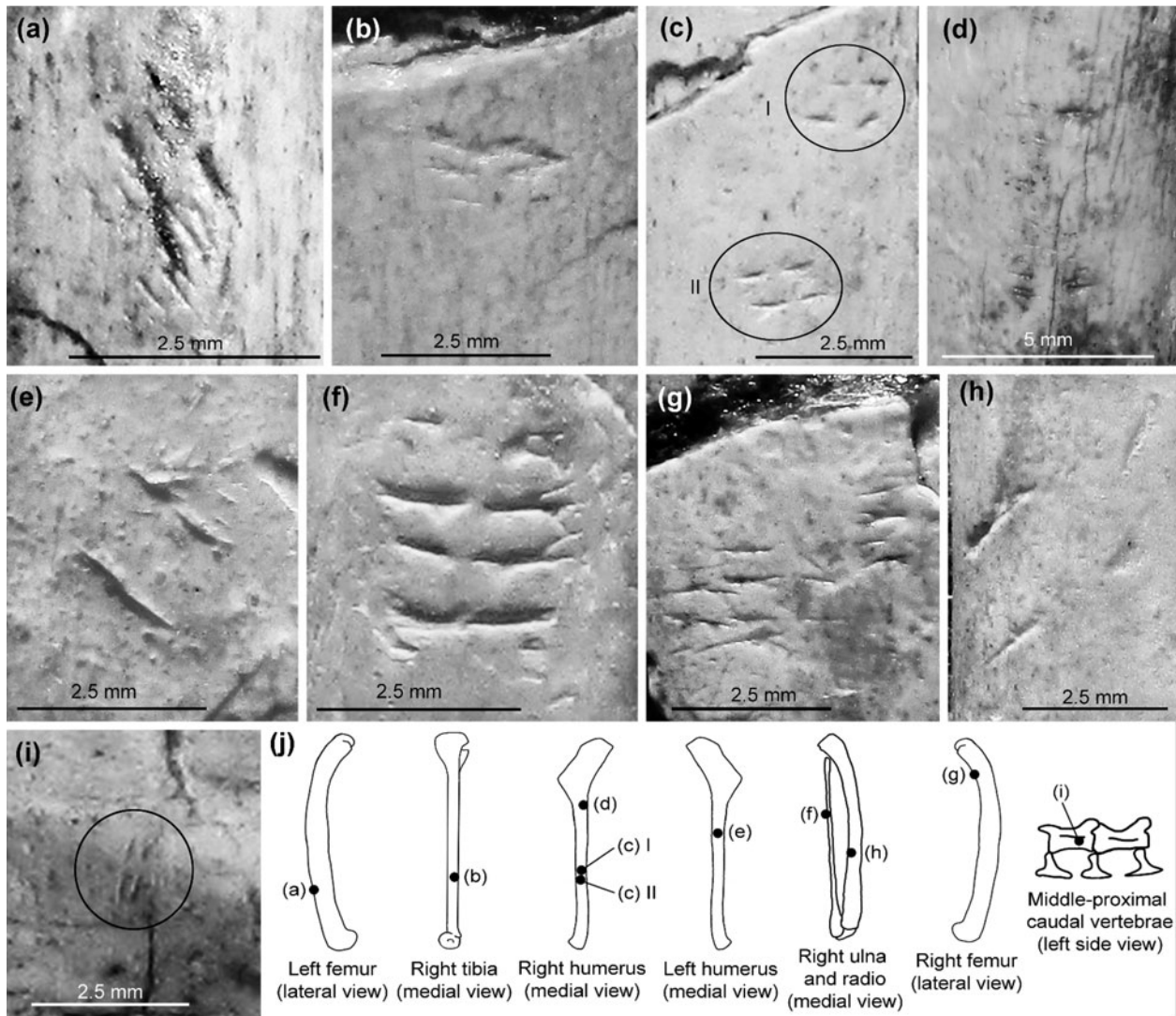


Figure 6. Combinations of parallel and opposed pairs on the bones of *Buitreraptor gonzalezorum* (MPCA 245). (a) MPCA 470-43; (b) MPCA 470-46; (c) MPCA 470-48 (identified as 'I') and MPCA 470-49 (identified as 'II'); (d) MPCA 470-50; (e) MPCA 470-51; (f) MPCA 470-52; (g) MPCA 470-53; (h) MPCA 470-79; (i) MPCA 470-80; (j) locations of the trace fossils showed in this figure.

this case: (1) the holotype specimen of *Buitreraptor gonzalezorum*, MPCA 245, was found almost complete and partially articulated; (2) the preservation of the bones of this specimen is very good, with the surface of the periosteum intact or almost unaltered in most cases – with the exception of the trace fossils studied; (3) the high number of trace fossils preserved on the bones; and (4) the diversity both in size and shape of the trace fossils. Each of these items can be analysed separately, although it can be considered that they are directly or indirectly related.

5.1 Taphonomic and palaeoenvironmental interpretations

The large amount of trace fossils indicates that they were produced after the death of the individual, or at least in a

position of weakness and inability of defence before death. In turn, the presence of these traces indicates that the body has spent a time of sub-aerial exposure. That means that it took a period of time long enough to expose the body at the mercy of the tracemakers. This time lapse is difficult to determine, but certain taphonomic issues can provide clues about its duration. For example, usually, one of the first parts to be separated from the rest of the skeleton is the jaw (Martin 1999; Fernández López 2000), because of the facility of detachment of the lower jaw and the symphysis and preferential attack by scavengers (Weigelt 1989). Although these observations were made on mammal corpses, we consider that they can be applied to dinosaurs, taking into account that the articular junction between the jaws and the cranium is not complex in theropods. Additional observations have revealed that most scattering

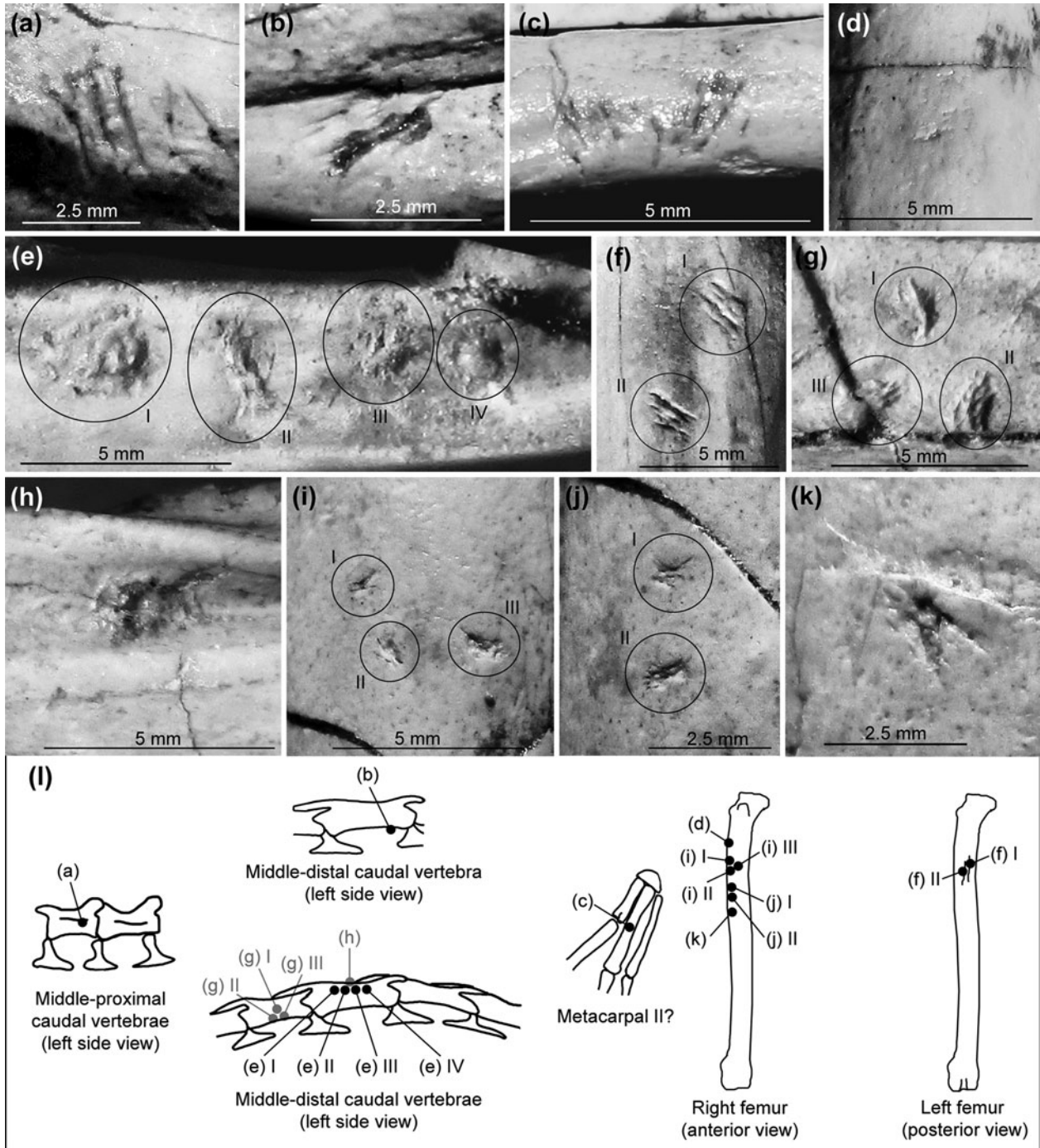


Figure 7. Overlapped Grooves on the bones of *Buitreraptor gonzalezorum* (MPCA 245). (a) MPCA 470-32; (b) MPCA 470-33; (c) MPCA 470-38; (d) MPCA 470-41; (e) MPCA 470-57 (identified as 'I'), MPCA 470-58 (identified as 'II'), MPCA 470-59 (identified as 'III') and MPCA 470-39 (identified as 'IV'); (f) MPCA 470-44 (identified as 'I') and MPCA 470-45 (identified as 'II'); (g) MPCA 470-54 (identified as 'I'), MPCA 470-55 (identified as 'II') and MPCA 470-56 (identified as 'III'); (h) MPCA 470-60; (i) MPCA 470-61 (identified as 'I'), MPCA 470-62 (identified as 'II') and MPCA 470-63 (identified as 'III'); (j) MPCA 470-64 (identified as 'I') and MPCA 470-65 (identified as 'II'); (k) MPCA 470-66; (l) locations of the trace fossils showed in this figure, those in grey are located on the opposed surface of the bone.

of disconnected bones occurs during the late stages of disarticulation after most digestible tissues have been lost (Toots 1965; Hill 1980), even though skeletons of current

medium-sized bovids were largely disarticulated after only a few weeks (Martin 1999). Highly disarticulated skeletons suggest prolonged exposure to air before final

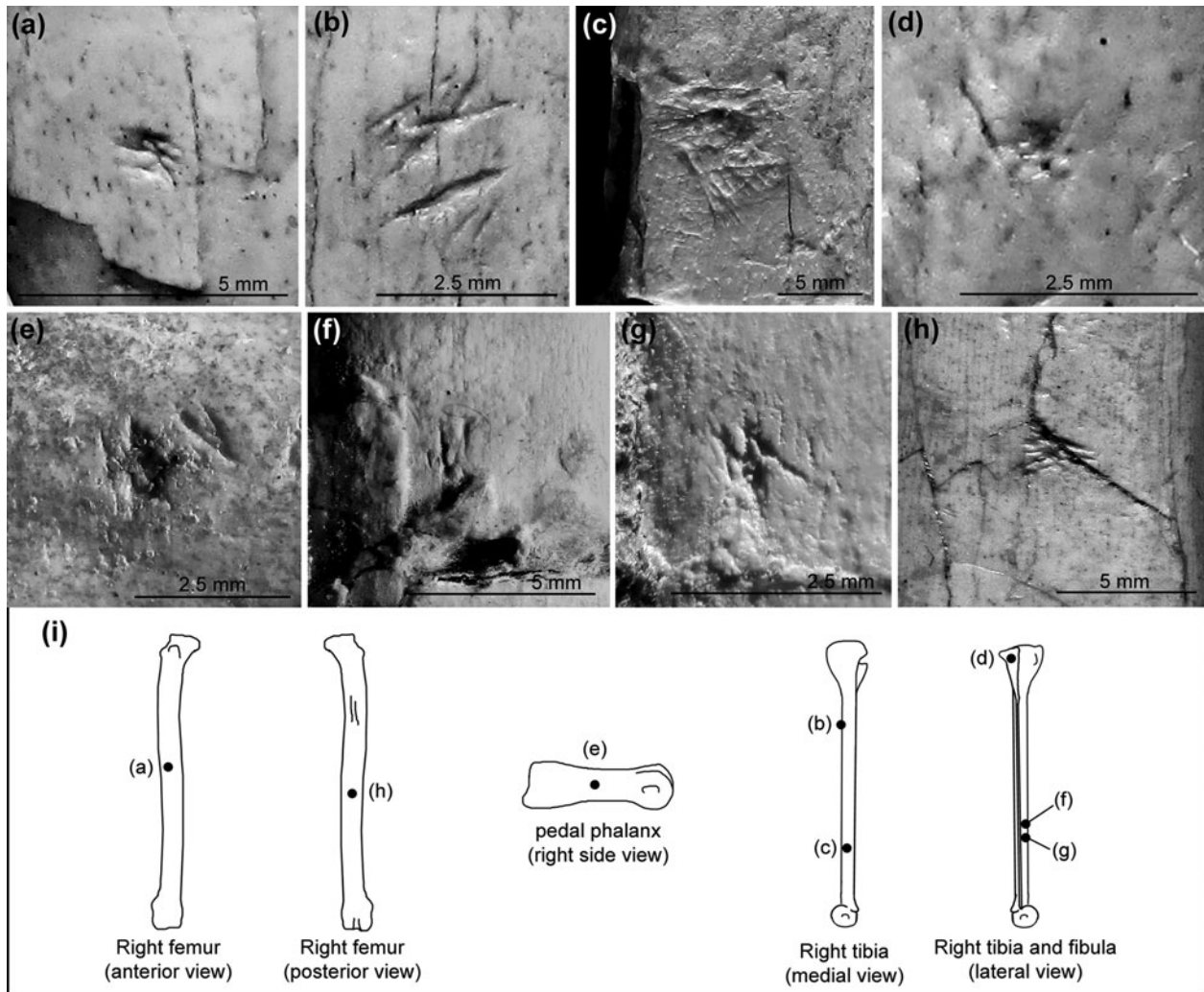


Figure 8. Overlapped Grooves on the bones of *Buitreraptor gonzalezorum* (MPCA 245). (a) MPCA 470-67; (b) MPCA 470-69; (c) MPCA 470-70; (d) MPCA 470-71; (e) MPCA 470-74; (f) MPCA 470-77; (g) MPCA 470-78; (h) MPCA 470-81; (i) locations of the trace fossils showed in this figure.

burial (Behrensmeier 1991; Martin 1999; Fernández López 2000). The holotype of *Buitreraptor* is semi-articulated with its jaw in occlusion, thus, based on the taphonomic issues outlined, the time span between the animal death and its final burial have been relative short, from days to a few weeks.

The type of environment where the individual inhabited is another topic to analyse, which, in turn, leads us to define the type and rate of sedimentation. The Candeleros Formation represents a predominantly fluvial system, which together with the development of palaeosols, indicate sub-aerial exposure conditions (Garrido 2011). However, edafized levels are poorly developed, with ferric specks, suggesting immature palaeosols affected by frequent floods (de Valais et al. 2012). Probably, the floods were not only relatively common but also occurred episodically, as isolated and sudden events

characterised by high rates of sedimentation. The tetrapod record from the La Buitrera locality in supposed 'escape' position due to a rapid burial suffered by animals during these events (de Valais et al. 2012) supports this hypothesis. However, in the case of MPCA 245, the abundant trace fossils on the bones indicate that the burial most likely occurred after the death of the animal and thus a sudden flood was not the cause of mortality. The semi-articulation of the specimen MPCA 245 suggests little or no post-mortem transport, indicating that the sedimentary process was represented by a sudden but low-energetic event. The sediment would have covered the individual relatively rapidly, but with little movement of the parts of the body.

Sites with mature soils often preserve less complete skeletons (Martin 1999). MPCA 245 may have died in an interval between floods. If the time of exposure would

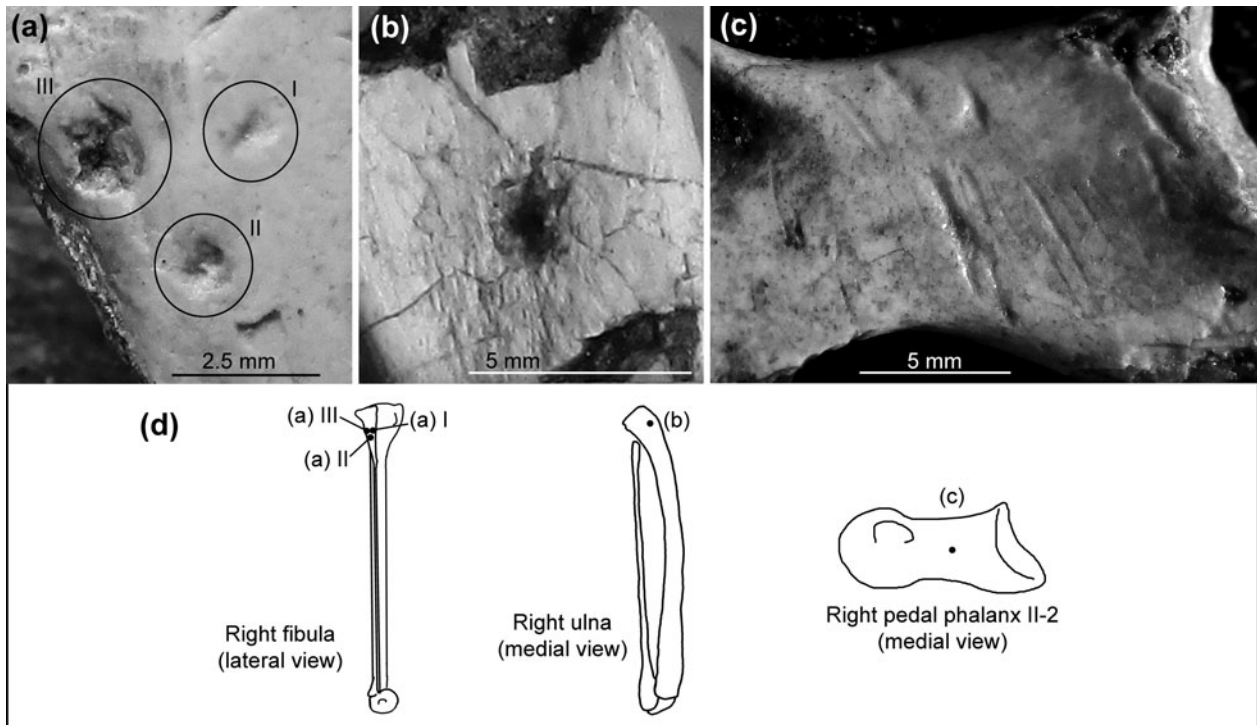


Figure 9. Punctures and Lined grooves on the bones of *Buitreraptor gonzalezorum* (MPCA 245). (a) Punctures, MPCA 470-72 (identified as 'I'), MPCA 470-73 (identified as 'II') and MPCA 470-76 (identified as 'III'); (b) a puncture, MPCA 470-75; (c) Lined grooves, MPCA 470-47; (d) locations of the trace fossils showed in this figure.

have been extensive, the corpse would have suffered a greater alteration, causing the incorporation of the bones into the soil, and thus generating their decay, dissolution or encrustation (Martin 1999). However, none of these alterations is observed in the slightly modified bones of *Buitreraptor*. In floodplain palaeosols, accumulation of remains over extended periods of time results in relatively unsorted disarticulated small bones with variable patterns of weathering (Behrensmeyer 1991).

5.2 Identity of the tracemakers and behavioural interpretations

The interpretation of how the traces were produced leads us to linking them with the behaviours of the tracemakers, i.e. make ethological inferences from the morphology of the traces (as was proposed by Seilacher 1953). Specifically in the case studied here, the extremely bioeroded skeleton of *Buitreraptor*, with some bones with a high density of traces, suggests that the producers had the freedom and the time necessary to attack the bones. As was mentioned above, this could only have occurred after the death of the individual, so these trace fossils are interpreted as scavenging activities. The bones of MPCA 245 have scarcely been moved from their original positions by the tracemakers; thus, the bioerosion trace

fossils on bones have been generated in the same place of death of the individual and without a relevant influence on the arrangement of the bones. This low alteration on the arrangement leads us to interpret that, along with the general small size of the traces, the producers would have been small animals, either adults of small taxa or youth of large-size animals. It has been observed that bones with several bite marks are typical of dining sites where juveniles mouth and play with the bones (Behrensmeyer 1991).

The trace fossils stand out not only for its abundance but also by their morphological assortment. The morphology and arrangement of the traces may be the main factor that allows an approach to the taxonomic identity of the producers, or at least they may allow the exclusion of certain potential taxa. However, ambiguities arise when trying to relate one ichnotaxon to a particular taxon, based on the ichnological principles that similar trace fossils can be generated by different producers or that the same taxon can generate different trace fossils (Ekdale et al. 1984; Bromley 1990, 1996). In reference to this latter principle, both wide and thin furrows form the Parallel-Edge Furrows on MPCA 245. This variability can be explained as: (1) the two types of grooves were generated by individuals of the same taxon but in different ontogenetic stages – however, it is observed that the

wide grooves mainly constitute smaller overall traces (e.g. MPCA 470-13a, 20, 18; Figures 3(a),(b) and 4(a)); (2) the same tracemaker generated different bite forces or applied forces in different angles or positions; and (3) tracemakers of different taxa but with comparable size had a similar behaviour, leaving similar trace fossils.

Based only on the morphology of the traces, the identity of the tracemakers is difficult to determine, although the diversity of the palaeofauna from La Buitrera locality offers a wide taxonomic range, including potential producers. Two of the trace fossils (i.e. MPCA 470-13a and 13b) have been previously analysed and included in the informal group 'Parallel Furrows', following the terminology of de Valais et al. (2012). These authors have mentioned several vertebrate taxa as potential tracemakers, such as crocodyliforms, snakes, mammals and dromaeosaurids, as they would have had predator and/or scavenger habits and would have been able to produce traces on the bones of their prey or dead animals.

According to the ichnological principles stated above, the morphology of a trace cannot be directly assigned to a particular taxon (i.e. a genus and/or species), although some types of traces may be restricted to certain animal groups. For example, pits or punctures, circular to oval in shape, can be generated both by mammals or crocodiles (Njau and Blumenschine 2006). In the fossil record, there are possible bite traces related to crocodyliforms represented by oval perforations or 'punctures' (e.g. Schwimmer 2010; Noto et al. 2012; Boyd et al. 2013). In addition, extant representatives of this group use the teeth to hold prey and not to cut or gnaw repeatedly in a particular area (Njau and Blumenschine 2006). Small-sized crocodyliforms, 1–2 m in length, with robust, conical teeth, with blunt apices, have been found in La Buitrera (e.g. Pol and Apesteguía 2005), so the morphology of the Punctures matches well with bites made by these animals. Crocodiles with these sizes may have led to a greater dissociation of the bones and a more significant damage, but it must be into account that Punctures are among the less frequent of the trace fossils found in the skeleton, so that the action of these animals may have been scarce. On the other hand, the Punctures also can be interpreted as results of individual bites of mammals. In reference to this, some of the traces observed in *Buitreraptor*, i.e. MPCA 470-72, 73 and 76 (Figure 9(a), (b)), resemble *Nihilichnus nihilicus* Mikuláš, Kadlecová, Fejfar and Dvořák, 2006, characterised by roughly triangular, circular or ovoid holes or external pits, with flat bottoms, occurring solitarily or in groups. When arranged in groups, they may show recurring patterns (often trapezoidal) that resemble the arrangement of dental nodes of mammalian carnivorous molars (Mikuláš et al. 2006). The specimens MPCA 470-72, 73 and 76 show signs of erosion, so the aspect of the bottom cannot be observed with confidence. The disposition of some of

these traces resembles the patterns observed in *Nihilichnus nihilicus*, supporting the possibility that these trace fossils have been generated by mammalian bites. At least two types of mammals have been found in La Buitrera: (1) dryolestoids, with two long canine-like teeth and well-developed acute molars (i.e. *Cronopio dentiacutus* Rougier, Apesteguía and Gaetano, 2011) and (2) homodonts, with cylindrical teeth, lacking enamel and with procumbent incisor-like teeth (Apesteguía 2008). Between them, *Cronopio* can be a probable tracemaker because although the distances between cusps of each molar are very small (1 mm or less), the distances between cusps of different molars may correspond to the punctures observed on the fibula. However, it is possible that the punctures represent isolated and successive bites and not necessarily that have been generated simultaneously by just one bite. Thus, two of the traces, possibly MPCA 470-76 and MPCA 470-72, can match the upper last premolar and the upper first molars of *Cronopio*, whereas MPCA 470-73 could correspond to a second bite.

Among the recorded taxa from La Buitrera, only the mammals possess the capacity and behaviour to generate the trace fossils included in the subgroups of Parallel-Edge Furrows and Lined. Mammals have the mandibular strength and the capacity of chewing movements to produce repeated traces on the bones, and small and long incisors able to crack and cause numerous opposed grooves of considerable depth. Many taxa of extant mammals have the capacity to generate this kind of traces, such as rodents, porcupines, canids, mustelids, hyenas and felids (Haynes 1980; Fisher 1995; Mikuláš et al. 2006; Quintana 2007; Reitz and Wing 2008). As was exposed above, among the mammals from La Buitrera, *Cronopio* could have been a tracemaker. Some authors claim that, according to their morphology, the canine-like teeth (as those present in *Cronopio*) would have produced punctures or broad scores (Haynes 1980; Mikuláš et al. 2006; Longrich and Ryan 2010), and that they would not be effective for gnawing the bones. Although *Cronopio* has sabertooth-type canines, probably not able to apply pressure on bones, it should be considered that *Cronopio* also has anteriorly located incisor teeth (Rougier et al. 2011), probably with the ability to gnaw hard surfaces. Furthermore, these mammals from La Buitrera are represented by very small individuals (estimated skull length of *Cronopio*: 27 mm) with millimetre-sized teeth, which match the size of the traces. Nevertheless, we do not claim a direct link between the traces and the mentioned taxon, but considering that mammals are recorded in this locality and the general taxonomic diversity, the existence of other mammalian taxa with the capacity to generate this kind of trace fossils is possible.

In the literature, there are some examples of bioerosion trace fossils in tetrapod bones, some of them quite similar to those preserved in *Buitreraptor gonzalezorum*, related to mammal activity (e.g. Cione et al. 2010; Longrich and

Ryan 2010). Cione et al. (2010) observed several grooves on penguin bones from the Miocene of Patagonia, which were attributed to mammalian scavengers. These grooves, some of them overlapping and almost perpendicular to the longitudinal axis of the bone, resemble some specimens in *Buitreraptor gonzalezorum* (e.g. MPCA 470-35, 42 or 47; Figures 5(h),(k) and 9(c)).

Trace fossils preserved on vertebrate bones from the Late Cretaceous Oldman and Dinosaur Park Formations from Canada have also been attributed to mammals (Longrich and Ryan 2010, Text-Figure 1). These traces are almost equal to opposed and parallel grooves present in *Buitreraptor gonzalezorum* (e.g. MPCA 470-46, 48–53, Figure 6(b)–(g)). Some of the Canadian examples are asymmetric pairs, with one of the grooves of the pair shorter than the other, interpreted as differences in the sizes between the upper and lower incisors (Longrich and Ryan 2010). Although this interpretation may be valid, another possibility is that the asymmetry is due only to topographic differences on the surfaces of the bones, in the forces applied by the teeth or in the bite angle. Another similarity between the traces studied by Longrich and Ryan (2010) and those observed in *Buitreraptor gonzalezorum* is that all of them are arranged at approximately 90° to the longitudinal axis of the bone. These authors attributed the trace fossils particularly to multituberculates, which present possible records in the Late Cretaceous of Argentina (Kielan-Jaworowska et al. 2007) and elsewhere in Gondwana (e.g. Parmar et al. 2013). Thus, it is possible that this lineage of mammals may have been part of the La Buitrera palaeofauna, but if they have not been present, it is likely that other lineages with similar dental morphologies and similar habits inhabited the area.

As already said, the abundance of trace fossils in some bones, especially in the limbs, is striking, which evidences the persistence and the successive attack directly on the bones or on the deep muscle masses in close contact with them. The depth of some of the traces indicates that the teeth of the producers have perforated hard on the periosteum, suggesting a clear intent to attack the bones or tissue in contact with them directly, and evidencing an active and persistent scavenging on the body.

Current non-carnivorous mammals, such as squirrels, porcupines and deer, among others, gnaw bones in order to obtain mineral from its surface (Guthrie 1990; Hansson 1990; Fisher 1995; Mikuláš et al. 2006; Klippel and Synstelién 2007; Longrich and Ryan 2010). However, removal of tissue that is attached to the bone, such as muscles, may also generate, as a secondary consequence, marks on the periosteum (Longrich and Ryan 2010). In this respect, the specimens MPCA 470-44 and 45 (Figure 7(f)), located on two flanges or ridges on the posterior surface of the femur, comprise deep and well-impressed grooves. In fact, these grooves are deep enough to interrupt the continuity of these ridges, altering its topography, being

more conspicuous in MPCA 470-45. We interpreted the bone elevations as muscle attachments; thus, the bioerosion may evidence that the tracemakers was trying to remove muscle tissue still attached to the bone.

Among theropods, the only small-sized taxa from La Buitrera so far are dromaeosaurids (i.e. *Buitreraptor gonzalezorum*) and alvarezsaurids (i.e. *Alnashetri cerropoliciensis* Makovicky, Apesteguía and Gianechini, 2012). *Alnashetri* has no preserved teeth, and only in a few alvarezsaurids, the teeth are known (e.g. *Shuvuuia deserti* Chiappe, Norell and Clark, 1998), which are small and lacking denticles. The teeth of *Buitreraptor gonzalezorum* are very small (average crown height: 2.19 mm) and with crowns separated by approximately 2 mm (Makovicky et al. 2005; Gianechini et al. 2011; Gianechini 2014). Given that most of the trace fossils are tiny, constituted by furrows separated by < 1 mm, even *Buitreraptor* teeth are too large to produce these traces. Nevertheless, considering that *Alnashetri* is smaller than *Buitreraptor* – measuring < 1 m in length – and the general minute teeth of alvarezsaurid, *Alnashetri* is not excluded as a possible tracemaker. It is important to note that it is necessary to find a specimen of this taxon with the teeth preserved to confirm this hypothesis.

In addition, snakes have been proposed as potential tracemakers (de Valais et al. 2012), which are abundant in La Buitrera (Apesteguía and Zaher 2006 and references therein). Snakes are active predators, with long needle-shaped teeth posteriorly curved with which they hold firmly to their prey (Edmund 1969; Kardong 2006). However, these animals do not generate chewing movements, but swallow the entire prey. The morphology of the trace fossils observed in *Buitreraptor*, such as opposed grooves, opposed and parallel grooves or the punctures, would not fit with the dental morphology of snakes.

Concerning the traces named as Overlapped Grooves, they are composed by small and thin grooves, and comprising semi-circular areas of < 4 mm in diameter. Some of them are represented by deeper and more concave marks, forming pits in different stages of development. MPCA 470-68 and 70 could represent pits in early stages (Figures 3(c) and 8(c)), whereas MPCA 470-54, 55, 56 and 60 (Figure 7(g),(h)) could correspond to more developed ones. MPCA 470-68 and 70 differ from the other specimens by having shallower and thinner grooves. Similar bioerosion trace fossils in bones have been associated with the activity of insects such as dermestids and termites (e.g. Watson and Abbey 1986; Fisher 1995; Kaiser 2000; Kaiser and Katterwe 2001; Roberts et al. 2003; Fejfar and Kaiser 2005; Roberts et al. 2007; Britt et al. 2008; Pomi and Tonni 2011; Backwell et al. 2012).

The dermestids are the most commonly cited insect linked to traces in fossil bones (Roberts et al. 2003). Britt et al. (2008) observed some overlapped thin grooves related to larvae of dermestid beetles, with a general

similar morphology to some specimens in *Buitreraptor* but mainly composed by clusters of grooves in pairs. Some traces attributed to these insects present the appearance of opposed grooves, which would match the mandibles of these animals (sensu Britt et al. 2008). However, in the opposed grooves observed in *Buitreraptor*, the distance between the grooves is greater. Furthermore, specimens consisting of the opposed and parallel grooves, such as MPCA 470-35, 48, 49 and 52 (Figures 5(h) and 6(c),(f)), usually have total dimensions and too large distances between grooves to have been produced by dermestids. On the other hand, the specimens classified as Overlapped Grooves, similar to those observed by Britt et al. (2008), may be assigned to dermestids.

The time to infest a dried vertebrate carcass may vary from days to months (Britt et al. 2008 and references herein). The larvae of dermestids feed mainly on soft tissue, such as muscles and ligaments but in a state of desiccation, when other soft tissues have been consumed by other taxa and when no other food supplies are present (Schroeder et al. 2002; Mairs et al. 2004; Britt et al. 2008). Under laboratory conditions, dermestids may attack bones when food sources or substrate (for pupation/shelter) are limited (Schroeder et al. 2002; Roberts et al. 2003; Mairs et al. 2004). However, this behaviour may be variable or dependent on the environmental conditions, given that for example some museum technicians who use dermestids to clean recent carcasses have never observed traces on bones made by these insects, even after several months of confinement in sealed containers with the skeletons (S. Bogan and M. Cárdenas, pers. comm., 2012). Further studies should be carried out in order to evaluate the capacity of dermestids to leave traces on bones.

In some cases, traces on vertebrate bones represented by clusters of striations, pits with radiating or opposed grooves have been attributed to mandibles of Isoptera insects, specifically termites (e.g. Watson and Abbey 1986; Kaiser 2000; Kaiser and Katterwe 2001; Fejfar and Kaiser 2005; Pomi and Tonni 2011; Backwell et al. 2012). In controlled experiments, bones exposed to these insects have presented this kind of traces (e.g. Watson and Abbey 1986; Backwell et al. 2012). The pits with radiating grooves (star-shaped marks) or clusters of striations reported by Backwell et al. (2012) are similar to some trace fossils observed in *Buitreraptor* (e.g. MPCA 470-68 and 70; Figures 3(c) and 8(c)). In other cases, traces attributed to termites are constituted by opposed grooves (Pomi and Tonni 2011), resembling some specimens observed in *Buitreraptor*. However, based on the arguments exposed above, the latter type of traces matches better with structures approximately equidistant from each other, such as teeth of tetrapods. It is considered that pits associated with radiating grooves or clusters of striations are more referable to insects (e.g. Watson and Abbey 1986; Backwell et al. 2012). Although

the Overlapped Grooves observed in *Buitreraptor* may be assigned to insects, it is difficult to implement a more accurate distinction between the morphology of the trace and the type of insect involved (i.e. dermestids or termites). For example, those traces formed by a central pit and radiating grooves (star-like pattern) that have been associated with termites have also been related to dermestids (Britt et al. 2008).

6. Conclusion

The abundance of bioerosion trace fossils in the holotype of *Buitreraptor gonzalezorum* suggests that they were generated by the attack of scavengers. A certain period of sub-aerial exposure of the body was necessary for scavengers to act before burying, whereas the taphonomic evidence (i.e. semi-articulation of the skeleton, with the jaws in occlusion, and little alteration of the bones) indicates that this time was short. The semi-articulated skeleton also indicates that it was covered by a low-energy event. The good preservation of the bones and their spatial arrangement, as well as the general small size of the traces, indicate that the scavengers were small animals, which fed without altering the original position of the bones or generating significant destruction or damage to the carcass. The sedimentological and additional taphonomic data (such as the 'scape' position of others skeletons from the locality) indicate that the environment of the area at that moment was characterised by a semi-arid climate, with periods of little or no sedimentation, evidenced by the presence of palaeosols, alternating with sudden floods. After death, the body was likely exposed for a few days, during which it was attacked by scavengers and then suddenly buried by one of these floods.

The morphology of the trace fossils is diverse and, although they cannot be directly related to a particular taxon (i.e. genus or species) some types of traces may be restricted to certain animal groups. As potential tracemakers, both tetrapods and insects have been considered. Among the different taxonomic groups present in La Buitrera area, it is likely that the Parallel-Edge Furrows and the Lined grooves may have been generated by mammalian bites, whereas the Punctures may be attributed to crocodyliforms or mammals. The Overlapped Grooves are related to the action of the mandibles of insects, such as dermestids and termites.

The trace fossils recorded in *Buitreraptor* document a very interesting part of the palaeoecology of La Buitrera. The abundance and variability of these traces complement the taxonomic diversity of this locality, which is also reflected by the abundant record of tetrapods of different taxa. Furthermore, it also reveals a highly active ecosystem, where the corpse of an animal was attacked in an intense way by different scavengers in a relatively short time. Thus, this ichnological case provides important data on the palaeobiology of the taxa involved and also on

the palaeoecology of this region of northern Patagonia during Cenomanian times.

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