Crayfish burrows from Late Jurassic–Late Cretaceous continental deposits of Patagonia: Argentina. Their palaeoecological, palaeoclimatic and palaeobiogeographical significance

Emilio Bedatou [a,*], Ricardo N. Melchor [a], Eduardo Bellosi [b], Jorge F. Genise [c]

[a] *CONICET-Universidad Nacional de La Pampa, Av. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina*
[b] *CONICET-Museo Argentino de Ciencias Naturales, División Icnología, Av. Angel Gallardo 470, 1405 Buenos Aires, Argentina*
[c] *CONICET-Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut, Argentina*

Abstract

The trace fossil, *Loloichnus baqueroensis* igen. and isp. nov., from Late Jurassic–Late Cretaceous continental deposits of Patagonia, Argentina, includes thickly lined, mostly passively-filled, and Y-branched burrows. Other important features of this ichnofossil are the inner surface texture of lining showing transversal, elongated, and adjacent grooves, and less commonly, the pelletal filling of burrows. *L. baqueroensis* is recorded from the Bajo Grande, Bajo Tigre, Punta del Barco, and Laguna Palacios Formations, which were deposited in different volcaniclastic environments of the Deseado Massif and San Jorge Basin geological provinces, respectively. The described burrows are found in many levels of palaeosols developed in reworked piroclastic deposits, where they are the main component of the ichnofabrics, in association with meniscate and thinly lined burrows and a diffuse and complex boxwork of small diameter burrows. Root traces are also present, and in many cases, occur inside *L. baqueroensis*. Considering general morphology, surface texture, filling types, palaeoenvironments in which they occur, and comparisons with extant and fossil decapod burrows, the likely trace makers of *L. baqueroensis* were crayfishes (Decapoda: Astacidea), probably Parastacidae. The producers of *L. baqueroensis* inhabited soils, where their burrows probably reached the water table, and contained roots that were used for feeding. Considering climatic preferences of extant parastacids, it is proposed a temperate climate for central Patagonia during the deposition of the studied units. The widespread presence of crayfishes during Late Jurassic–Late Cretaceous times in central Patagonia, supports the monophyletic origin of this group during the Triassic, and suggests that the present restricted geographic distribution in southern South America is a relict of a broader one.
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1. Introduction

Decapod burrows are common in the geological record and display a wide range of morphologies. They usually show one ore more openings that sometimes can be connected downward forming complex networks (i.e. Frey et al., 1978; Ekdale et al., 1984; Uchman, 1995;

* Corresponding author. Tel.: +54 2954436787x13; fax: +54 2954 432535.
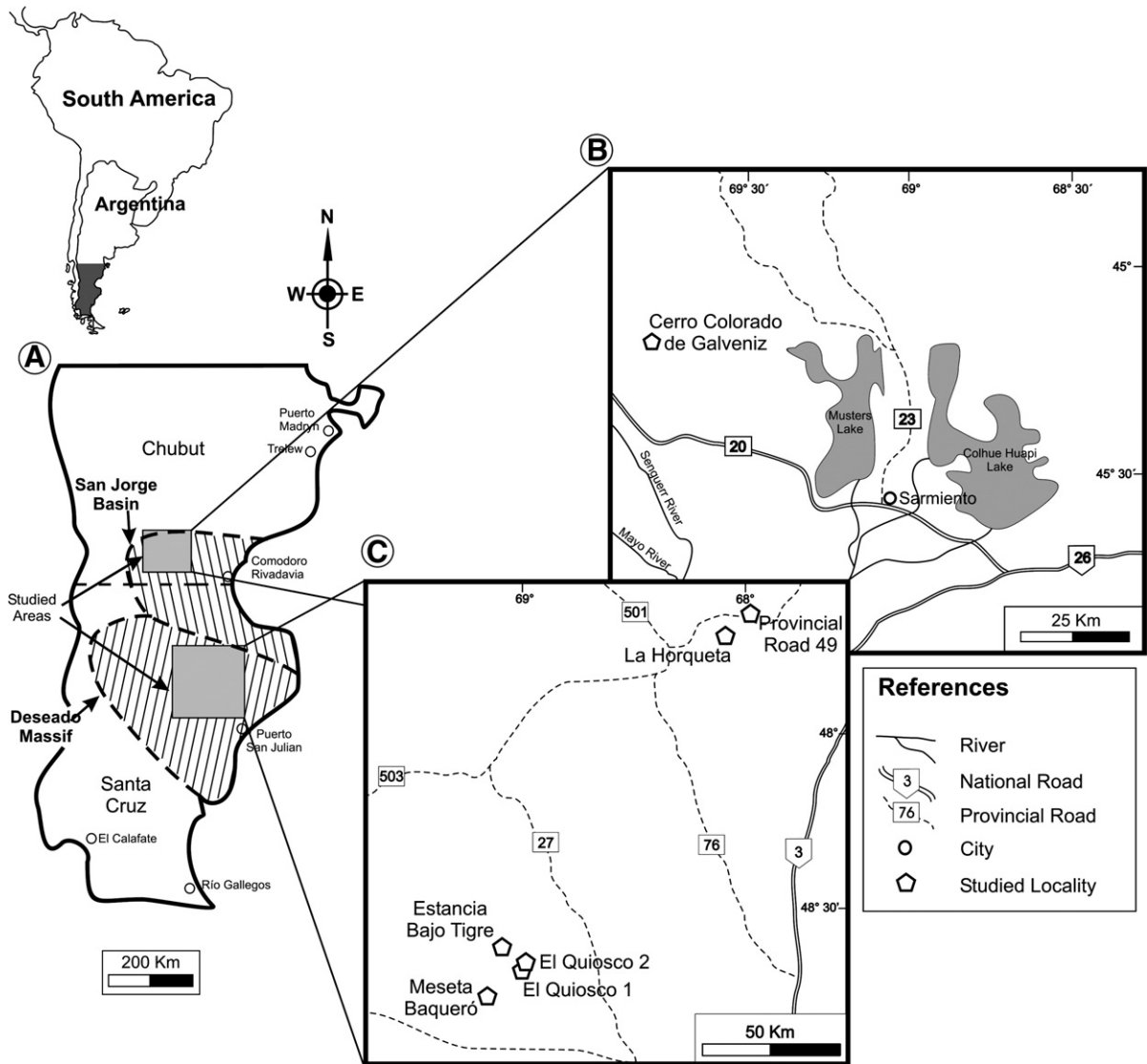 *E-mail address:* ebedatou@yahoo.com (E. Bedatou).

Fig. 1. Location map with studied localities.

Miller, 2003). In other cases, they can be very simple showing I, J, or U shape with a predominantly vertical orientation (i.e. Fürsich, 1981; Frey et al., 1984). Most common producers are marine decapods (including crabs, lobsters and shrimps) which construct burrows assigned to *Psilonichnus*, *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha* (Fürsich, 1973, 1981; Ekdale et al., 1984; Frey et al., 1984; Frey and Pemberton, 1987; Bromley and Ekdale, 1998; Nesbitt and Campbell, 2006).

Freshwater decapod trace fossils are less common in the geological record, although they have been described for several continental environments (i.e. Fürsich,

1981; Frey et al., 1984; Frey and Pemberton, 1987; Hasiotis and Mitchell, 1993; Bromley, 1996; Zonneveld et al., 2006). These include burrows assigned to crabs, shrimps and crayfishes. The described ichnogenera, which are attributed to crayfish burrows are *Camborygma* (Hasiotis and Mitchell, 1993) and *Lunulichnus* (Zonneveld et al., 2006). *Camborygma* is reported for continental deposits of North America (Hasiotis and Mitchell, 1993; Hasiotis and Honey, 2000; and references therein). *Lunulichnus* was recorded from the early Eocene of Wyoming, USA and its assignation to crayfishes is tentative. Crayfish trace fossils can be of simple bauplan (i.e. the simple, subvertical burrows of
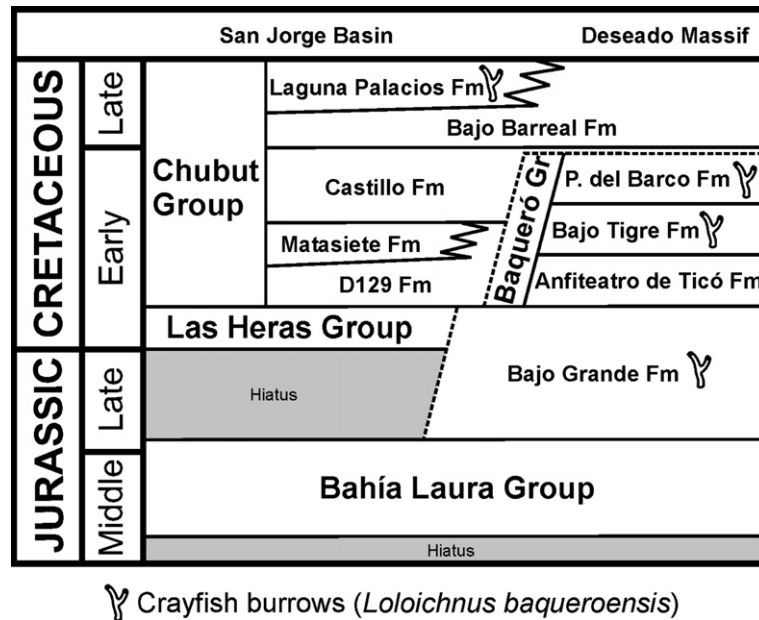
Fig. 2. Simplified stratigraphic chart of studied units. Units separated by zigzag lines display lateral transition and those separated by dashed lines are temporally equivalent, although not in contact. Not to scale.

Lunulichnus) or they can exhibit some complexity, as in the case of *Camborygma eumekenomos*; an ichnospecies showing bifurcations, corridors and chambers.

Herein they are reported, for the first time, crayfish burrows from the Southern Hemisphere, which occur in several continental units from central Patagonia ranging in age from Late Jurassic to Late Cretaceous. These units show, as the dominant trace fossil, thick-walled, Y-shaped burrows, first reported as "thick-walled tubes" by Melchor et al. (2004), Bedatou et al. (2005) and Bellosi et al. (2005). These burrows resemble some of the known crustacean trace fossils, particularly *Camborygma*. However, some characters such as its distinctive thick lining, its surface texture and absence of chambers or enlargements distinguished it from the known ichnogenera, supporting the proposal of the new ichnotaxon, *Loloichnus baqueroensis* n. igen n. isp. Frequently, these burrows, in association with other discrete trace fossils, originate a particular and complex ichnofabric, which will be described elsewhere (Bedatou et al., unpublished).

The objectives of this paper are 1) to describe for the first time these thick-walled burrows, 2) to provide an ichnotaxonomical treatment for them, 3) to discern the potential producers by comparison with modern and fossil structures and 4) to interpret their palaeoecological, palaeoclimatic and palaeobiogeographical significance, and their evolutionary implications.

2. Stratigraphy

L. baqueroensis is best represented in the Bajo Grande Formation (Upper Jurassic–Lower Cretaceous; de Barrio et al., 1999) and in the overlying Bajo Tigre and Punta del Barco Formations from the Baqueró Group (Barremian–Aptian) (Corbella, 2001, 2005; Cladera et al., 2002). This ichnotaxon also occurs in other Cretaceous units such as the Upper Cretaceous Laguna Palacios Formation, which is a part of the Chubut Group (Sciutto, 1981). In the Cenozoic of Patagonia, *L. baqueroensis* is restricted to a few beds from different stratigraphic units and its degree of preservation and density are lower than those in the Jurassic–Cretaceous outcrops described herein (Bedatou et al., 2005, 2006).

The Bajo Grande Formation and the Baqueró Group represents the Late Jurassic–Early Cretaceous continental sedimentation in the southern part of the Deseado Massif. The Laguna Palacios Formation records the terrestrial and fluvial accumulation in the NW sector of the San Jorge Basin, which is located northward of the Deseado Massif (Fig. 1A).

The Bajo Grande Formation displays angular unconformities at the base with the Bahía Laura Group and at the top with the Baqueró Group (Fig. 2). It is a 20 m to 300 m thick, volcaniclastic succession, typically composed of well-bedded, structureless or cross-bedded primary and

Table 1
Facies description and interpretation

Facies #	Description	Interpretation
1	Tuffaceous breccias, matrix supported, normally graded, subangular clasts, erosive base, relicts of horizontal or cross stratification. Scarce to moderate *L. baqueroensis*, scarce root traces.	Unconfined hyperconcentrated flows.
2	Massive tuffaceous sandstone, relicts of horizontal or cross stratification. Abundant *L. baqueroensis* burrows and root traces. Scarce mottling, Fe–Mn nodules and veins, carbonaceous remains.	Diluted unconfined flow, genetically related to facies 1. Posterior soil development.
3	Massive tuffaceous sandstone, highly bioturbated by diffuse boxwork of small diameter burrows and scarce *L. baqueroensis*. Root traces common. Reddening in some bed tops.	Soil formation process and biogenic imprint on a deposit similar to facies 2.
4	Tuffaceous siltstones and mudstones, rhizoliths and root traces moderately common, large extraclasts rare. Occasional occurrence of *L. baqueroensis*.	Settling from suspension and posterior.
5	Tuffs, horizontal lamination, mantle bedding, diffuse cross stratification, localized accretionary lapilli, scarce *L. baqueroensis* and root traces.	Ash fall events, weak soil development.
6	Massive tuffs, root traces can be locally abundant, scarce *L. baqueroensiss* and common meniscate burrows.	Ash fall deposits with scarce soil development.
7	Sandstone, horizontal lamination, common intraclasts.	Sheetflood events.

reworked tuffs and tuffaceous breccias, similar to the Bajo Tigre Formation, although the occurrence of breccias is more important in the latter. Both units also weather as step cliffs forming an organ-tube relief. The Bajo Grande Formation is separated from the overlying Baqueró Group by an angular unconformity. The Baqueró Group is composed of the Anfiteatro de Ticó, Bajo Tigre, and Punta del Barco Formations (Cladera et al., 2002; Fig. 2). *L. baqueroensis* was not recorded in the older formation; for this reason no further details of this unit are provided. The Bajo Tigre Formation (26–70 m thick) is characterized by tuffaceous breccias and massive, bioturbated tuffites, which are arranged in fining-upward cycles (Cladera et al., 2002). This unit is widely distributed and recognized for its laterally continuous horizontal beds that form cornices and for their light brown to light orange and gray colour. The Punta del Barco Formation (up to 110 m thick) displays a more restricted distribution and is also composed of volcaniclastic rocks. The lower half of the unit contains lithic, massive conglomerates deposited in deeply incised, linear erosive troughs cut in the underlying Bajo Tigre Formation. The upper half of the unit displays both primary and reworked tuffs containing accretionary lapilli and root traces (Cladera et al., 2002). This unit is separated from the underlying Bajo Tigre Formation and from the overlying marine Monte León Formation (Lower Miocene) by erosive unconformities. *L. baqueroensis* also occurs in the Laguna Palacios Formation, which is the uppermost unit of the Chubut Group and its outcrops
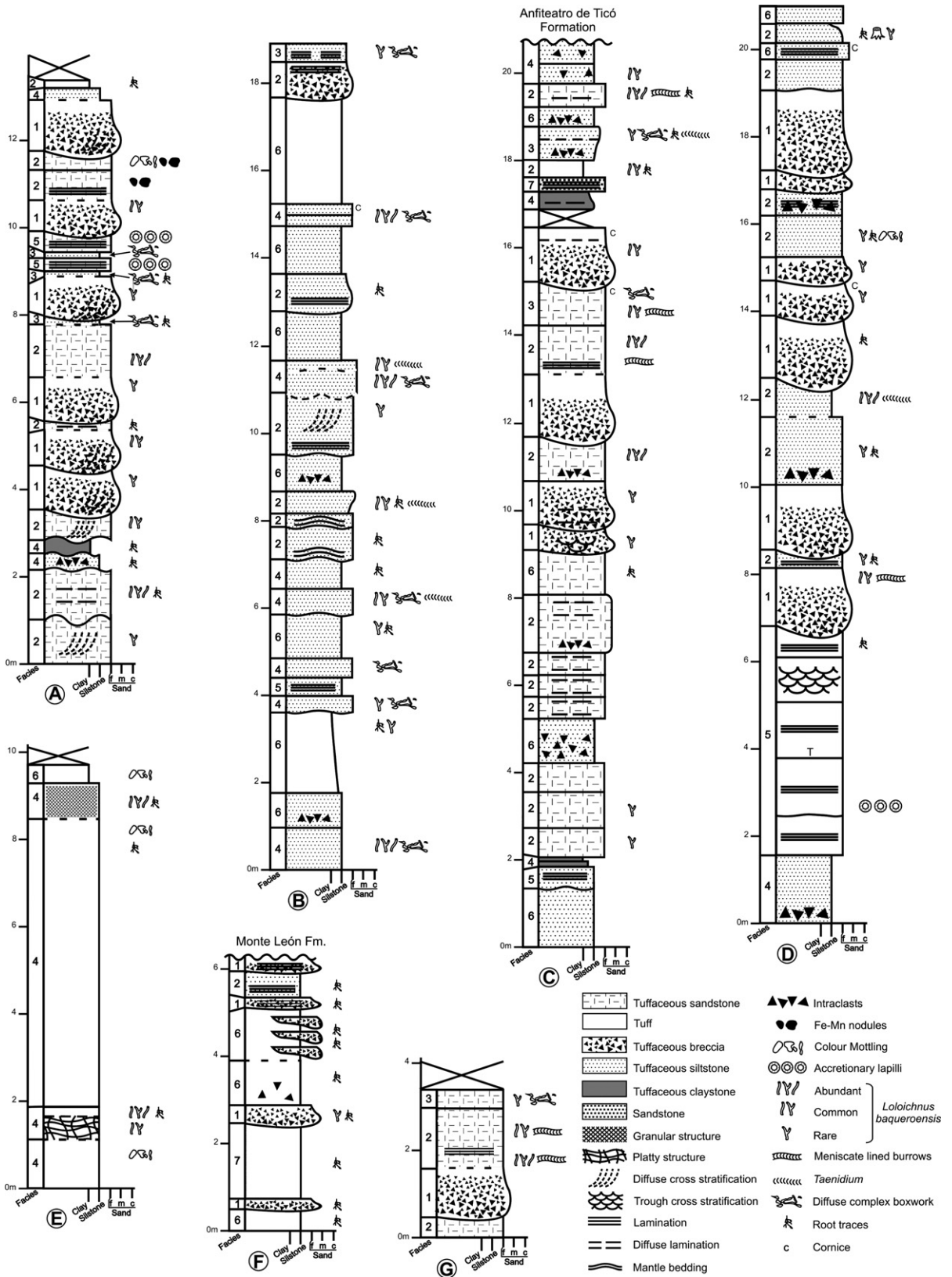
are found northward of the previously described units in marginal areas of the San Jorge Basin (Fig. 1B). Its stratigraphic relationships suggest a Santonian–Early Maastrichtian age (Sciutto, 1981; Fitzgerald et al., 1990; Bridge et al., 2000). The Laguna Palacios Formation is an orange to reddish-gray; tuffaceous succession, including primary deposits and reworked volcaniclastic deposits. Extensive development of palaeosols, usually stacked, is common especially in the middle member of the unit where *L. baqueroensis* occurs (Sciutto, 1981; Bellosi and Sciutto, 2002).

For this study, six localities were surveyed: El Quiosco-1 (48°32′29″S; 69°03′20″W), El Quiosco-2 (48°32′06″S; 69°03′32″W), Estancia Bajo Tigre (48°29′26″S; 69°07′10″W), Cerro La Horqueta (47°42′58″S; 68°07′48″W), and Provincial Road 49 (47°40′50″S; 68°06′32″W), all of them in the Santa Cruz Province (Fig. 1C). The two later localities belong to the Monumento Natural Bosque Petrificado, which is a national reserve area. The remaining surveyed locality was Cerro Colorado de Galvéniz (45°25′42″S; 69°46′59″W) in the south of the Chubut Province (Fig. 1B).

3. Lithofacies and palaeoenvironments

The studied lithostratigraphic units are dominantly composed of reworked and primary pyroclastic rocks. For this reason, a common scheme is adopted for the description and interpretation of lithofacies (Table 1).

Fig. 3. Measured sedimentologic logs of studied units. (A) Bajo Tigre Formation log at Estancia Bajo Tigre. (B) Bajo Tigre Formation section at Provincial Road 49. (C) Bajo Grande Formation log section at El Quiosco-1. (D) Punta del Barco Formation section at Estancia Bajo Tigre. (E) Laguna Palacios Formation section at Cerro Colorado de Galvéniz. (F) Bajo Tigre Formation section at La Horqueta. (G) Bajo Grande Formation log section at El Quiosco-2.

Anfiteatro de Ticó Formation

Monte León Fm.

Tuffaceous sandstone	▲▼▼▲	Intraclasts
Tuff	●◖	Fe-Mn nodules
Tuffaceous breccia	◯ᗷᵨ	Colour Mottling
Tuffaceous siltstone	◎◎◎	Accretionary lapilli
Tuffaceous claystone	ⲓᎩ⫽	Abundant
Sandstone	ⲓᎩ	Common
Granular structure	Ꭹ	Rare
Platty structure	⫸⫸⫸⫸⫸	Meniscate lined burrows
Diffuse cross stratification	⫷⫷⫷⫷⫷	*Taenidium*
Trough cross stratification	꒲	Diffuse complex boxwork
Lamination	ⱪ	Root traces
Diffuse lamination	c	Cornice
Mantle bedding		

Loloichnus baqueroensis

Facies are distinguished by their lithology, sedimentary and palaeosol structures, and also by its dominant trace fossils and ichnofabrics. Detailed sedimentologic logs of selected intervals bearing *L. baqueroensis* were measured at the mentioned localities (Fig. 3).

The most common facies of the studied sections are usually grouped in a distinctive cycle that is repeated several times in the Bajo Grande, Bajo Tigre, and Punta del Barco Formations. The cycle (Fig. 3G) is composed of: a) matrix-supported (tuffaceous sandstone) intraclast breccias with erosive base and normal grading (facies 1) showing a gradual transition to b) massive tuffaceous sandstone with abundant *L. baqueroensis* burrows and subordinate *Beaconites* burrows and root traces (facies 2). This is overlain by massive tuffaceous sandstone showing a dense ichnofabric composed of a diffuse complex boxwork of small diameter burrows, with few discrete trace fossils and scarce *L. baqueroensis*, that typically weather out as a cornice (facies 3). Genise and Bellosi (2004) referred the latter lithofacies was as "highly bioturbated tuffs" in deposits of the Laguna Palacios Formation. The transitional contact between facies 1 (below) and facies 2 (above) corresponds to the base of the bed with *L. baqueroensis* and is occasionally associated to poorly developed lamination. In some cases, facies 3 beds comprise thin mudstone/siltstone interbeds.

3.1. Bajo Grande Formation

This unit was logged in detail at the El Quiosco-1 and 2 localities (Fig. 3C and F), where it lies unconformably under the laminated tuffaceous sandstones and mudstones of the Anfiteatro de Ticó Formation (Fig. 3). The section exhibits a dominance of massive or poorly laminated tuffaceous sandstones with common angular intraclasts and occasional erosive bases (facies 2), as well as, breccia and bioturbated tuffaceous sandstone cycles (facies 1, 2, and 3). These breccia and bioturbated tuffaceous sandstone cycles range in thickness from 2.7 to 3.4 m and contain root traces in the upper part of the cycle (Fig. 3C). The identified microscopic pedofeatures are clay coatings (from thin to thick and laminated) and minor Fe–Mn oxides and Fe oxides coatings that, in some cases, can fill completely some pores.

The main depositional process in the analyzed section was the reworking of pyroclastic material by unconfined hyperconcentrated (facies 1) and dilute flows (sheet flows) (facies 2 and 3), as suggested by breccia and bioturbated tuffaceous sandstone cycles (Smith and Lowe, 1991). These deposits were followed by secondary modification by soil forming processes and bioturbation by different organisms.

3.2. Bajo Tigre Formation

The Bajo Tigre Formation was studied at Estancia Bajo Tigre, Cerro La Horqueta, and Provincial Road 49. These localities correspond to the upper section of the unit. At Estancia Bajo Tigre (Fig. 3A), about half of the measured thickness is composed by the described cycles of facies 1, 2 and 3. The remaining recognized facies at Estancia Bajo Tigre locality can be assigned to facies 4 and 5 (Table 1). At the other localities of the Bajo Tigre Formation most beds are finer-grained tuffaceous rocks showing greater participation of whitish, structureless or cross-bedded tuffs, with sparse *L. baqueroensis* and abundant rhizoliths; and a greater degree of bioturbation observed in facies 3. At Cerro La Horqueta, and Provincial Road 49 the breccia and bioturbated tuffaceous sandstone cycles are poorly developed or absent (Fig. 3B and F). Pedogenic features in thin sections are clay and Fe–Mn coatings (usually laminated), which locally fill completely the pores. The Bajo Tigre Formation, at the homonymus localty, has been interpreted as reflecting unconfined gravity flows followed by diluted flows in a low-lying relief with strong pyroclastic influence and later palaeosol development (Cladera et al., 2002). These processes are represented by the cycle composed of facies 1, 2, and 3. Scarcity of pedogenic structures probably reflects a higher recurrence of ash fall events. Laminated clay coatings suggest probable climate seasonality (dry and wet seasons) (Retallack et al., 2000).

3.3. Punta del Barco Formation

This formation was studied at Estancia Bajo Tigre locality, where one section was logged (Fig. 3D). The dominant facies are fine-grained tuffaceous sandstones with sparse intraclasts (facies 2) and matrix-supported tuffaceous breccias with erosive bases, and normal grading (facies 1). Beds display sparse to abundant *L. baqueroensis*, meniscate burrows and common root traces in the upper part, along with occasional mottling, reddening and prismatic peds. Clay coatings and scarce development of b-fabric are the most common pedofeatures in thin section.

The lithofacies assemblage of the Punta del Barco Formation suggests dominance of dilute fluvial flows and greater development of palaeosols. Possible channel-fill successions are less than 5 m thick. The upper part of the section (Fig. 3) contains finer-grained sediments and Fe–Mn nodules that would suggest transient water logging.
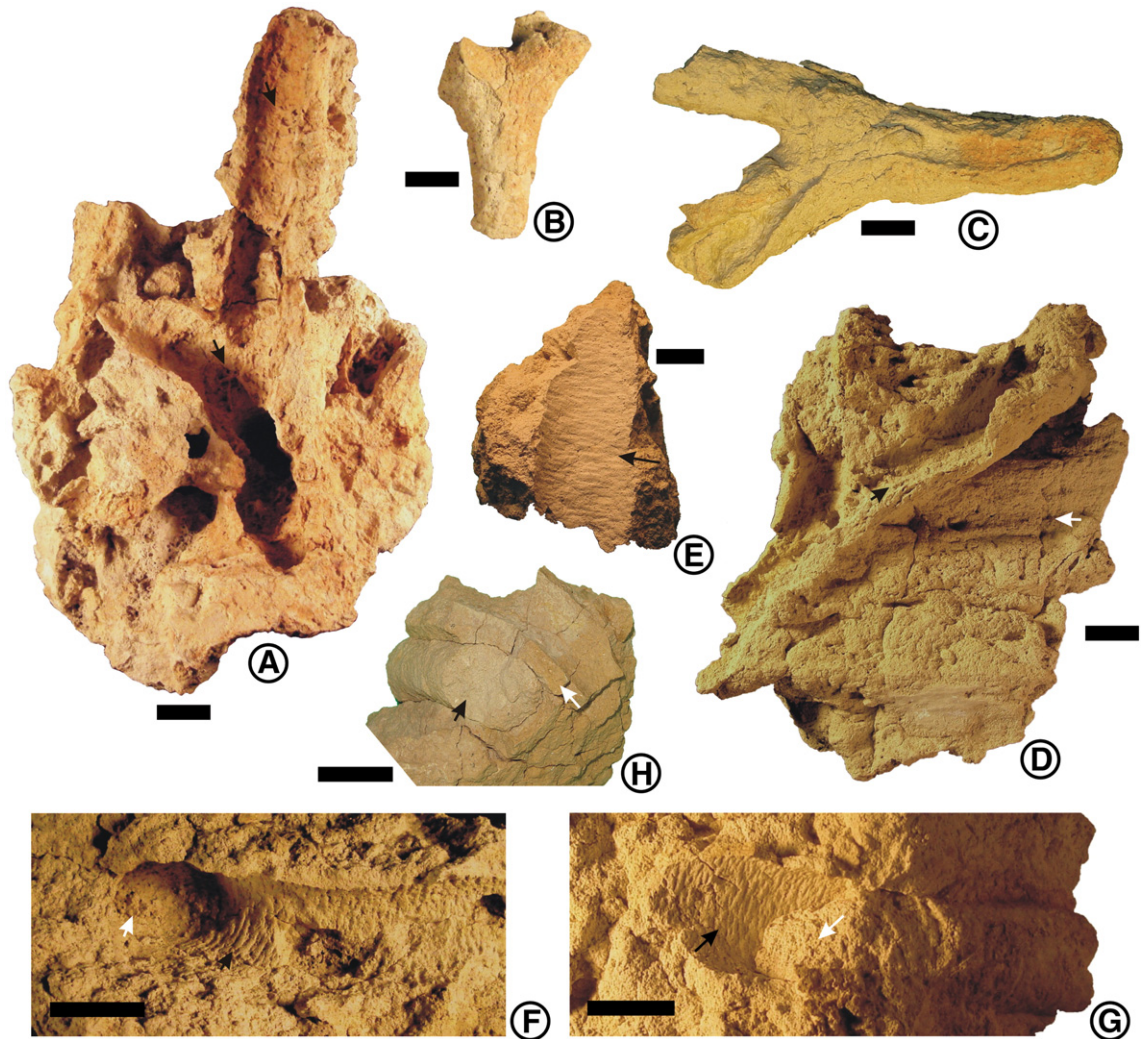
Fig. 4. Type material of *L. baqueroensis*. (A) Holotype, MPMP-Pic 3794 showing 80° Y-branching, and weathered filling with small rhizoliths (arrows). (B) Paratype MPMP-Pic 3795 showing 90° Y-branching. (C) Paratype MPMP-Pic 3796 showing 60° Y-branching. (D) Paratype MPMP-Pic 3797 branching is at 65°, note thick lining (black arrow) and position respect to bedding (white arrow). (E) Paratype MPMP-Pic 3798, incomplete specimen showing grooved wall texture (arrow). (F) Paratype MPMP-Pic 3799 with grooved wall texture (black arrow) and passive filling (white arrow). (G) Paratype MACN-Icn 2331 showing grooved wall texture (black arrow) and thick lining (white arrow). (H) Paratype MPEF-IC 1366 with passive filling (black arrow) and thick lining (white arrow). Figures A, B, C, and D, positioned as in the field. Scale bars are 20 mm.

3.4. Laguna Palacios Formation

The Laguna Palacios Formation was studied at Cerro Colorado de Galvéniz locality, where the middle member of the unit is exposed. The logged section is composed of thick massive red to orange tuffs; showing, at the top of beds, common *L. baqueroensis*, and macroscopic soil features as root traces, mottling and platy and granular peds. Pedofeatures identified under the microscope include illuvial clay coatings, surrounding grains or filling partial or totally the pores and scarce small Fe–Mn nodules. Tuffs were deposited by ash fall processes and later pedogenized and colonized by the producer of *L. baqueroensis* and by plants. Extensive development of palaeosols is characteristic of this member (Sciutto, 1981).

4. Systematic ichnology

Collected specimens are housed at Museo Regional Provincial "Padre Manuel Jesús Molina" (MPM-Pic) at Río Gallegos, Santa Cruz Province, Argentina; at the

Museo Paleontológico "Egidio Feruglio" (MPEF-IC), Trelew, Chubut Province, Argentina; and at the División Icnología of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Icn), Buenos Aires Province, Argentina.

4.1. *Loloichnus igen. nov.*

4.1.1. Etymology

Lolo, meaning animal burrow, derives from the Mapuche language of the aboriginal inhabitants of
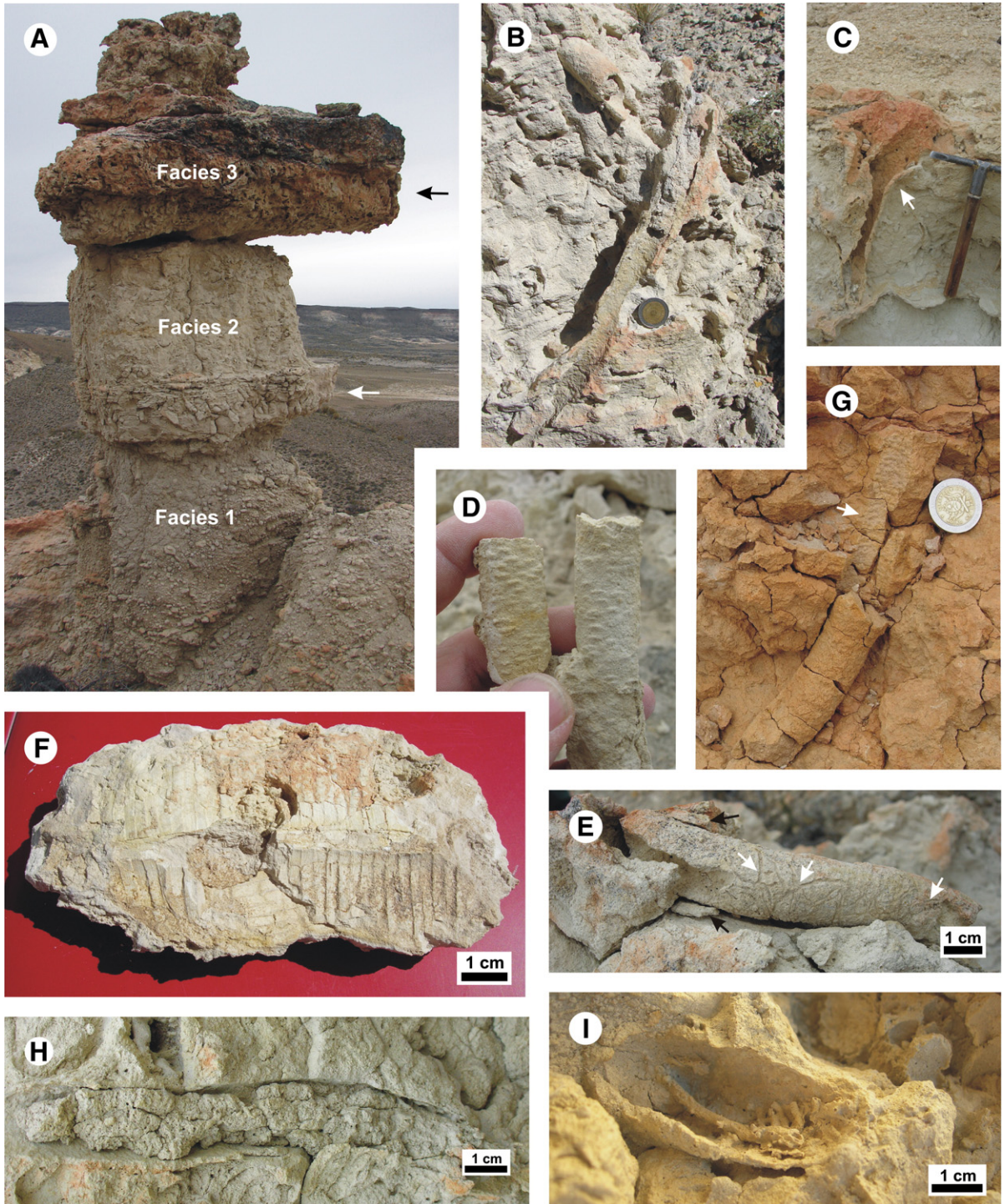
Patagonia, and *Ikhnos*, meaning trace, derives from the Greek.

4.1.2. Diagnosis

Mainly straight to gently curved, vertical to oblique, thickly lined burrows of constant diameter. They are mostly passively-filled and sub-circular in cross section, Upward Y-branching and pelletal fillings may be present. Inner surface of lining showing transversal, parallel, and adjacent elongated grooves, which are semicircular in cross section. The burrow filling, when detached from the lining may show a knobby surface texture. Burrow endings are blunt and chambers are absent.

4.1.3. Type ichnospecies L. baqueroensis (only known ichnospecies)

4.1.4. Remarks

The presence of Y-branching as well as lined walls preserving surface marks is typical of Decapoda burrows, which are features of ichnospecies of *Ophiomorpha*, *Thalassinoides*, *Spongeliomorpha*, *Psilonichnus*, *Lunulichnus* or *Camborygma* (Calzada, 1981; Fürsich, 1981; Frey et al., 1984; Hasiotis and Mitchell, 1993; Zonneveld et al., 2006). Several of these ichnogenera show an important development of horizontal burrow systems (*Ophiomorpha*, *Thalassinoides*, *Spongeliomorpha*), which is lacking in *Loloichnus*.

Camborygma has an overall shape and a surface texture similar to *Loloichnus* but differs from it by the presence of chambers, common corridors and multiple shafts, which are lacking in *Loloichnus*. *Psilonichnus* differs from *Loloichnus* because of its unlined walls and its morphology that usually includes "J" and "U" shapes, which are not present in the latter. Probably, the trace fossils described as *P. lutimuratus* by Nesbitt and Campbell (2002) should not be included in *Psilonichnus* since it is an ichnogenus created originally for unlined burrows (Fürsich, 1981; Frey et al., 1984). The ichnotaxonomical relationship between *P. lutimuratus* and *Loloichnus* would require further studies. *Lunulichnus* (Zonneveld et al., 2006) is quite similar to *Loloichnus*, particularly its surface texture; however, it is an unlined burrow.

Several of the mentioned ichnogenera (*Loloichnus*, *Camborygma*, *Lunulichnus* and *Psilonichnus*), which are produced by decapods, show a close morphological resemblance, particularly in architecture of the burrow systems and surface textures of lined walls, forming a consistent ichnotaxonomical group that would qualify for the ichnofamily rank (e. g. Psilonichnidae).

4.1.5. L. baqueroensis isp. nov.

2004. "Thick-walled tubes". Melchor, de Valais & Genise. p. 57
2005. "Tubos de pared gruesa". Bedatou, Melchor, Bellosi & Genise. p. 14R
2005. "Thick-walled tubes". Bellosi, Genise, Laza, & Sánchez. abst. 824
2006. "Excavaciones con pared". Bedatou, Melchor, Bellosi & Genise. p. 54

4.1.5.1. Diagnosis.
Only known ichnospecies, same as for ichnogenus.

4.1.5.2. Etymology.
After the Meseta Baqueró locality in Patagonia, where *L. baqueroensis* is one of the most common trace fossils.

4.1.5.3. Holotype.
MPM-Pic 3794, specimen showing 80° Y-branching, and weathered filling with small rhizoliths that are visible in the inner part of the wall. Bajo Tigre Formation at Estancia Bajo Tigre (Fig. 4A).

4.1.5.4. Paratypes.
Specimens MPM-Pic 3795 and MPM-Pic 3796 (Fig. 4B and C, respectively), Y-branched and passively-filled. Specimen MPM-Pic 3797 (Fig. 4D), Y-branched and preserving neither filling nor surface texture. Specimens MPM-Pic 3798, MPM-Pic 3799 MACN-Icn 2331 and MPEF-IC 1366 (Fig. 4E, F, G, and H, respectively), which are incomplete burrows where grooved wall texture is represented. All mentioned specimens are from the Bajo Tigre Formation at Estancia Bajo Tigre except MACN-Icn 2331, which is from Cerro La Horqueta, Monumento Natural Bosque Petrificado

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Fig. 5. Field examples of *L. baqueroensis* and associated facies. (A) Breccia-tuffaceous sandstone cycle composed by facies 1, 2, and 3. Note the cornice that coincides with the end of a large number of *L. baqueroensis* specimens (white arrow); and also note reddening and cornice in the palaeosol of facies 3 (black arrow). Facies 2 is 1,1 m thick. (B) Large segment of a gently curved *L. baqueroensis* specimen with partly weathered filling. (C) Specimen with an anterior portion of unusual large diameter (arrow) handle of hammer is 20 mm in diameter. (D) Knobby texture on the surface of loose burrow fillings. (E) Root traces on the surface of *L. baqueroensis* filling. Some of them are indicated by white arrows. Note preserved portions of wall lining (black arrows). (F) Two *L. baqueroensis* specimens cutting a *Ptilophyllum* (Bennettitales) leaf. Scale is in centimetres. (G) Passive filling of *L. baqueroensis*. Surface texture shown in the visible portion of lining (arrow). (H) *L. baqueroensis* with elongated pellets in the filling. (I) Free-standing rhizoliths in a specimen of *L. baqueroensis* with its filling missing. Ruler is in millimetres. Coin in B and G is 23 mm in diameter.
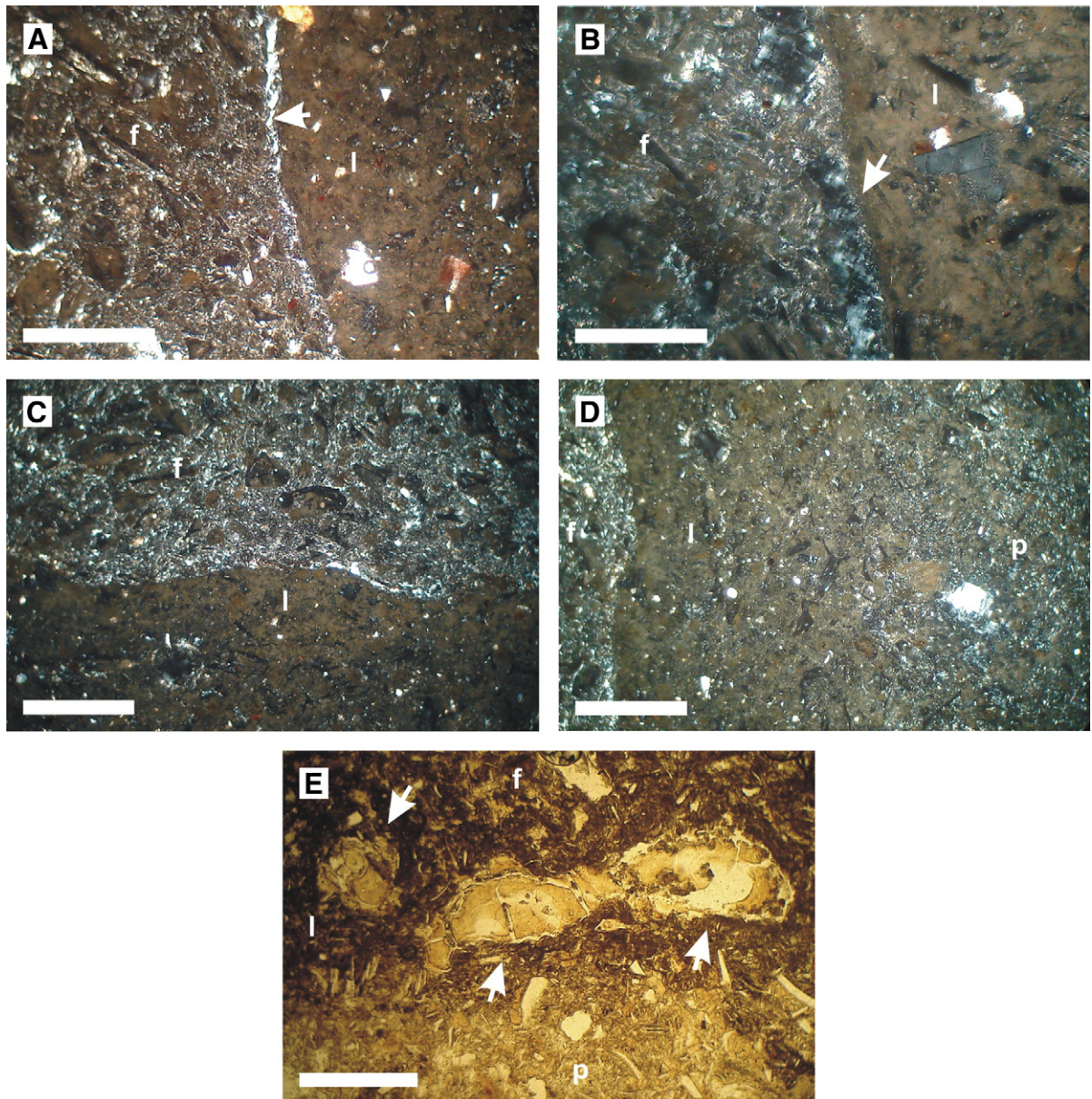
Fig. 6. Thin sections of *L. baqueroensis*. (A) Contact between burrow fill (f) and inner part of lining (l). Note the colour contrast between them and also note the thin illuvial clay layer in the contact (arrow). (B) Dark line adjacent to inner surface of lining (l) is a zone of clay and oxides concentration attributed to fluidization during construction of burrow; f is burrow filling. (C) Sinuous contact between burrow fill (f) and lining (l), probably reflecting the grooved surface texture. (D) Part of the burrow filling (f) and gradual transition from lining (l) to hosting palaeosol rock (p). (E) Large voids filled with clay in the lining (arrows), are the root traces. Figure A, B, C, and D, crossed nicols; Figure E, plane polarized light. Scale bars are 1 mm (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

and MPEF-IC 1366, which is from the Laguna Palacios Formation at Cerro Colorado de Galvéniz.

4.1.5.5. Examined material. 10 specimens from Bajo Grande Formation at Estancia Bajo Tigre (MPM-Pic 3813 to 3822); 17 specimens from Bajo Tigre Formation at Estancia Bajo Tigre (MPM-Pic 3794 to 3808, 3833 and 3834); 8 specimens from Bajo Tigre Formation at Monumento Natural Bosque Petrificado (MACN-Icn 2332 to 2339); 11 specimens from Punta del Barco Formation at Estancia Bajo Tigre (MPM-Pic 3823 to 3832); one specimen from Laguna Palacios Formation

at Cerro Colorado de Galvéniz (MEF-IC 1366); and two specimens, MPM-Pic 3833 and 3834, which consist each one of a *Ptilophyllum* (Bennettitales) leaf bored by several *L. baqueroensis* burrows. More than 200 specimens were studied, measured, and photographed in the field.

4.1.5.6. Description. Most specimens, which show a thick lined wall, are vertical to oblique burrows and only rarely they show horizontal portions (Fig. 4C). They are burrows of sub-circular section, passively-filled, blunt-ended, and sometimes with an upward branching. The angle of upward branching, in Y-shaped burrows ranges from 50° to 130° ($N=9$; mean$=81°$). Neither chambers nor other kind of enlargement of burrow were observed in all studied specimens, with exception of the specimen in Fig. 5C, which have an upper portion with a diameter of around 80 mm, which is reduced downward to a most common diameter. Internal diameter ranges from 11 mm to 26 mm ($N=371$; mean$=18$ mm) and wall thickness ranges from 1 mm to 7 mm ($N=167$; mean$=2$ mm). The longest observed burrow (not collected) is 0.5 m, but still this specimen was incomplete. The inner surface of lining, show in some cases, elongated, parallel and adjacent grooves, transverse to the long axis, which cover the entire surface. Individual grooves are up to 5 mm long and 1.5 mm wide and they are semicircular or V-shaped in cross section. A less common surface texture shown by the fillings are sparse protuberances 1–2 mm wide and less than 1 mm high, which result in a knobby surface. The protuberances may appear isolated or in small groups in different sections of the burrow. In many specimens both the inner surface of lining and the filling preserve root traces of different diameters. Internal rhizoliths (1–3 mm in diameter), detached from the wall were also observed when the filling is weathered. The most common type of filling is composed of material of similar composition to the enclosing rock, although more porous. Rarely, in the Bajo Grande Formation, burrow filling is formed by a massive, dark brown mudstone that contrast with the rest of the grayish white tuffaceous deposit. In the same unit, the filling of some burrows was active, showing ellipsoidal pellets, about 5 mm long and 3 mm wide. Pellets can fill the whole burrow or they can appear isolated or in small clusters. In the Bajo Tigre Formation the filling of some specimens is composed of tuffaceous mudstone with mud chips up to 0.7 mm in diameter. In the same unit, leaves of *Ptilophyllum* (Bennettitales) probably composing originally the soil litter, show perforations comparable in diameter with *L. baqueroensis* (Fig. 5F). *L. baqueroensis* typically occurs in

facies 2 which compose the breccia-bioturbated tuffaceous sandstone cycles. A few burrows continue below that facies, penetrating into the underlying bed, up to the level where the first gravel clasts occur (Fig. 5A). The endings of burrows usually compose a cornice that projects from the face of the outcrop.

In thin sections, burrows show an inner zone of structureless filling usually surrounded by a thick lining (>1 mm), although locally part of this lining can be thinner (<0.5 mm). The filling of the burrow is mainly composed of clear glass shards and pumice fragments surrounded by a matrix of clay and very fine glass shards; with rare subangular to subrounded quartz and plagioclase grains. This composition is similar to the surrounding palaeosol but the proportion of clay is greater in the filling of the burrow than in the rock (at least 10% larger). Pores are common both in host rock and in the filling. Pore spaces may be totally or partially filled with clay and Fe–Mn coatings (*sensu* Bullock et al., 1985). Contact between burrow fill and inner part of lining is sharp and is marked by the contrast between the light colour of the former and the dark colour of latter and by a thin layer of illuvial clay in the boundary (Fig. 6A). In some cases, it is also possible to observe a still thinner layer of clays probably produced by fluidization (Genise and Poiré, 2000), in the inner surface of the lining (Fig. 6B). Some specimens show a sinuous boundary between filling and lining probably reflecting the previously described grooved surface texture (Fig. 6C). The outer surface of the lining, in some specimens, shows a gradual transition to the palaeosol (Fig. 6D). This would be the reason why most burrow fillings are naturally removed from the matrix in weathered preserving no lining, which remains attached to the matrix. In other specimens, the contact between the outer surface of the lining and the palaeosol is sharp, and it is marked by a clear contrast of the dark colour of the former and the light colour of the later.

The dark colour of the lining is produced by the presence of iron oxides. The elongated grains, mainly glass shards, are oriented parallel to the burrow lumen in the lining, which is a typical character of arthropod constructions (Genise and Hazeldine, 1998). In some specimens, it is also possible to observe in the lining sub-circular voids that correspond to the root traces associated with burrows, as described previously (Fig. 6E). In the filling of some specimens it was possible to distinguish individual pellets (4.3 mm long axis; 2.8 mm short axis) formed by a dense core of clay and small fragments of volcanic glass followed by a ring of elongated volcanic glass fragments oriented parallel to the pellet boundary and surrounded by an oxidized

thin dark line. The same material of the rock matrix usually constitute the pellets, although the size of coarse minerals, fine to medium sand fraction, is less than those in the rock, which is of medium sand grain size. Voids in pellets are greatly reduced and packing of coarse material is very tight, reflecting mechanical compaction. In contrast, in the wall it was impossible to distinguish individual pellets in the thin sections prepared, probably because the producers welded strongly the pellets among them and with the soil matrix.

5. Discussion

5.1. Trace makers

L. baqueroensis is interpreted as produced by crayfishes according to its architectural bauplan, wall structure and surface texture, and the palaeoenvironment where it occurs.

Decapod burrows share some common features as vertical and sub-vertical development, common Y-branching, lined walls and surface textures (Fürsich, 1981; Frey et al., 1984; Bottjer, 1985; Hasiotis and Mitchell, 1993; Asgaard et al., 1997; Dworschak, 2002; Lewy and Goldring, 2006; Zonneveld et al., 2006). These common features are present in *L. baqueroensis* suggesting a decapod origin for this trace fossil.

Burrowing crayfishes and crabs show different terrestrial adaptations including the construction of structures similar to *L. baqueroensis* for colonizing soils (Power and Bliss, 1983). However, the palaeoenvironments described herein are more compatible with those inhabited by crayfishes than by crabs. *Gecarcinidae* and *Coenobitidae* (Brachyura), the typical land crabs, inhabit areas up to 5 km from the sea, where they need to release their marine larvae (Vannini et al., 2003). The deposits where *L. baqueroensis* occur lack any evidence of marine influence, or lateral facies relationships with marine rocks. The freshwater crabs, which inhabit inland environments, excavate its burrows along the sides of drainage ditches or river banks (Maitland and Maitland, 1985; Melchor et al., personal observations). Representatives of southern South American freshwater crabs, such as *Aegla* spp. are fully aquatic organisms that move to land only for mating and build no burrows (Bond-Buckup and Buckup, 1994; Morrone and Lopretto, 1994; Jara et al., 2006), whereas Trichodactylidae excavate burrows along river feed wetlands (Melchor et al., unpublished). In contrast, different extant southern South American crayfishes are associated with soils, where they excavate their burrows, showing no connection with water courses (i.e. Rudolph,

1997; Rudolph and Crandall, 2005). Even when fluvial channel are present in studied sections, they are rare, and mostly *L. baqueroensis* is not related to them or any other courses of water. Additionally, *L. baqueroensis* is mostly present in palaeosols as inferred from macroscopic features such as root traces and mottling, and micromorphological features, such as abundant illuvial clay and Fe–Mn oxides coatings and some scarce and small Mn nodules. Also, in the Bajo Tigre Formation, some burrows cut *Ptilophyllum* (Bennettitales) leafs, which are interpreted as being part of the soil litter. Thus, the palaeoenvironmental evidence in relation to the ecological preferences of potential producers indicates that *L. baqueroensis* was constructed more likely by crayfishes than by crabs.

The simple architectural design that shows *L. baqueroensis*, consisting of a near vertical tube, in some cases Y-branched and lacking of chambers, matches with those that extant crayfish are capable to build (Hobbs, 1981). Horwitz and Richardson (1986) also described some Australian crayfish burrows showing such simple architecture. Horwitz and Knott (1983) for *Cherax plebejus* (Parastacidae) and Grow (1981) for *Cambarus diogenes diogenes* (Cambaridae) described simple burrow systems consisting of a semi-vertical burrow with one or two entrances usually ending in a small terminal chamber. Chambers in extant crayfish burrows are common but they are not invariably present (Horwitz and Richardson, 1986; Horwitz and Knott, 1983). For fossil burrows, it has been reported that in a population of burrows apparently produced by the same organisms only some of them show chambers (Hasiotis and Mitchell, 1993).

Specimens of *L. baqueroensis* mostly end at a level bearing the coarser gravel clasts of the deposits. Lake and Newcombe (1975) observed this large-size clast avoidance in *Parastacoides tasmanicus* burrows. Similar observations were made by Barbaresi et al. (2004) for *Procambarus clarkii*.

Characters of wall also suggest crayfishes as producers of *L. baqueroensis*. Kilian (1959) described in detail how *Parastacus nicoleti* (Parastacidae) constructs a lining producing soil pellets with its appendages and pushing and knocking them against the burrow wall. Rudolph (1997) notes the presence of pellets inside abandoned burrows. Hobbs (1981) also reports the production of soil pellets for construction of chimney and as active fillings of burrows. Individual pellets were recorded in the burrow fillings of *L. baqueroensis*. The lined burrows of *L. baqueroensis* are compatible with these of extant South American crayfishes, and also with fossil examples described from North America (Hasiotis and Mitchell, 1993).

Texture of the inner surface of the wall in *L. baqueroensis* is another component shared with other decapod burrows. Hasiotis and Mitchell (1993) analyzed the surface texture of extant crayfishes and found a close similarity between those of some Cambaridae and the surface texture preserved in *Camborygma*. The surface texture of representatives of this ichnogenus, formed by transversal short grooves covering the surface of burrow, is similar to that of *L. baqueroensis*. Other ichnogenera with similar surface texture is *Lunulichnus* (Zonneveld et al., 2006) also interpreted as produced by crayfishes.

The present distribution shows that Parastacidae is the only family of crayfishes represented in southern South America (Hobbs, 1981, 1988; Rode and Babcock, 2003) indicating that parastacids are the most probable trace makers of *L. baqueroensis*.

5.2. Palaeoecological implications

Hobbs (1942, 1981) and Horwitz and Richardson (1986) proposed classifications for modern North American and Australian crayfish burrows, respectively. These schemes are based on burrow morphology and on its relationship with the water table. In Hobbs's classification, the architecture of *L. baqueroensis* matches with those of the tertiary burrowers, which are simple burrow systems formed by a single subvertical shaft connected to the water table. In the Australian classification (Horwitz and Richardson, 1986), *L. baqueroensis* can be compared with the Type 2 burrows. This type of burrow is an equivalent to those of the secondary and tertiary burrowers of Hobbs (1981). Crayfish burrows are commonly, but not invariably, related to the water-table position. Hasiotis and Mitchell (1993) and Hasiotis and Honey (2000) used the position of burrow termination as indicators of palaeo water-table levels. However, even when many species of extant crayfishes construct their burrows up to a few centimetres below the water-table level (Grow, 1981; Hobbs, 1981; Horwitz and Knott 1983; Horwitz and Richardson, 1986, Welch and Eversole, 2006), other species construct burrows that have no relation with the groundwater and depend on rainwater (Suter and Richardson, 1977; Horwitz et al., 1985; Horwitz and Richardson, 1986; Welch and Eversole, 2006). In the best exposed sections, showing the most complete specimens of *L. baqueroensis* (Fig. 5A) most burrows end abruptly at the same level, which show a greater consolidation forming a cornice. It is possible that this level represents the palaeowater table. However, the level with the larger clasts mentioned previously is immediately below this cornice, suggesting also this lithological factor as a potential reason for burrow ending.

The close association between root traces and *L. baqueroensis* (Fig. 5E) is compatible with the feeding habitats of some extant crayfishes. Land crayfish preferentially locate their burrows under the base of plants on whose roots they feed (Lake and Newcombe 1975; Suter and Richardson 1977; Grow 1981; Horwitz and Knott 1983; Horwitz et al., 1985; Horwitz and Richardson 1986). Growns and Richardson (1988) recorded a dense mat of roots and rootlets inside the burrows of *Parastacoides tasmanicus tasmanicus*, which were used for feeding. In addition, Rudolph (1997) mentioned portions of blind burrows of *Parastacus nicoleti* penetrated from above by roots and rootlets. Plant material (fresh and rotten) is one of the main components in parastacid diet together with organic debris (Suter and Richardson, 1977; Growns and Richardson, 1988). Accumulation of plants remains inside crayfish burrows is also common (Sherman, 2003; Alcorlo et al., 2004; Nordhaus et al., 2006).

5.3. Palaeoclimate

Crayfish burrows can be useful palaeoclimatic indicators considering that most extant crayfishes are mainly located in medium to high latitude regions with seasonal and temperate to cold climates (Hobbs, 1988). Particularly the Parastacidae, which are the proposed producers of *L. baqueroensis*, inhabit temperate and seasonal regions of the Southern Hemisphere. Most of the few species that inhabit tropical areas colonized mountain settings (>700 m a.s.l. in Madagascar and >1500 m a.s.l. in New Guinea) where the temperature is lower (Hobbs, 1988). Climatic preferences of extant Parastacidae are in accordance with previous palaeoclimatic interpretations for the Baqueró Group. Archangelsky (1967), using palaeobotanical evidence of the Anfiteatro de Ticó and Punta del Barco Formations, suggested a temperate climate. Isotopic analysis on kaolinites from the Anfiteatro de Ticó Formation (Cravero et al., 1991) suggests a humid and temperate climate. According to the same authors this climate was quite uniform and stable during the lapse Late Jurassic–Early Cretaceous. Petrulevicius and Nel (2003) suggested cold and humid forests in the Anfiteatro de Ticó Formation based on the finding of a petalurid dragonfly (Insecta: Odonata).

5.4. Palaeobiogeography

Previous records of fossil crayfish burrows and fossil body remains are not very common and they were reported mainly from North America (Feldman et al., 1981; Hasiotis and Mitchell, 1993; Hasiotis and Honey,

2000; and references therein). In Patagonia, the only previous record of crayfish is several specimens of Parastacidae from the Oligocene levels of the Ñirihuau Formation (Aguirre-Urreta, 1992). *L. baqueroensis* extends the record of crayfish activity in southern South America back to the Late Jurassic. The wide area with outcrops bearing *L. baqueroensis* and its large number and density indicates that crayfishes were well-established in this part of Gondwana by those times. The new data presented are useful evidence to contribute with the reconstruction of the evolutionary and biogeographic history of crayfishes (Crandall et al., 2000; Rode and Babcock, 2003). A monophyletic origin for crayfishes during the Triassic is generally accepted today (Ortmann, 1902; Scholtz, 1993, 2002; Crandall et al., 2000; Rode and Babcock, 2003). The presence of *L. baqueroensis* in Late Jurassic-Late Cretaceous successions from Patagonia supports this hypothesis.

Extant crayfishes belong to Astacidae, Cambaridae and Parastacidae families of the Astacidea infraorder (Hobbs, 1981; Taylor et al., 1999). Astacidae and Cambaridae are now distributed in North America, in northern part of South America, in Europe and in the south east of Asia; while the Parastacidae are widespread in the southern hemisphere, mainly in Oceania, in southern south America and in Madagascar but they are not present in continental Africa and in Antarctica (Hobbs, 1981, 1988; Babcock et al., 1998; Taylor et al., 1999; Rode and Babcock, 2003). In South America, there are only two genera of Parastacidae, whose species were studied by Kilian (1959); Buckup and Rossi (1980); Morrone and Lopretto (1994), and Rudolph (1997, 2002), among others. They are located in two separated areas, one in central and south of Chile; and the other in Uruguay, south of Brazil and north-east of Argentina (Morrone and Lopretto, 1994). The extended distribution of *L. baqueroensis* in Patagonia during Late Jurassic and Cretaceous times suggests the possibility that the present distribution would be a relict of a broader one in southern South America that included a large area in central Patagonia. This reduction of crayfish distribution would have been induced, probably, by climatic changes.

6. Conclusions

1) A new ichnotaxon, *L. baqueroensis* igen. and isp. nov., is recorded from palaeosols of the Late Jurassic–Late Cretaceous Bajo Grande, Bajo Tigre, Punta del Barco, and Laguna Palacios Formations of Patagonia, Argentina.
2) *L. baqueroensis* includes trace fossils whose principal features are: vertical to subvertical and in some cases Y-branched burrows, thick linings, passive, or less common, pelletal fillings, and grooved inner surface texture.
3) Considering morphological characters, palaeoenvironments in which it occurs, and extant distribution of families, *L. baqueroensis* is attributed to crayfishes, and particularly to Parastacidae.
4) Trace makers of *L. baqueroensis* inhabited soils, where their burrows probably reached the water table, and contained roots that were likely used for feeding, as in extant crayfishes.
5) In accordance with previous palaeoclimatic evidence, it is proposed a temperate climate for Central Patagonia during the deposition of the studied units, considering climatic preferences of extant parastacids.
6) The widespread presence of crayfishes during Late Jurassic–Late Cretaceous times in Central Patagonia, supports the monophyletic origin of this group during the Triassic, and suggests that the present restricted geographic distribution in southern South America is a relict of a broader one.

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