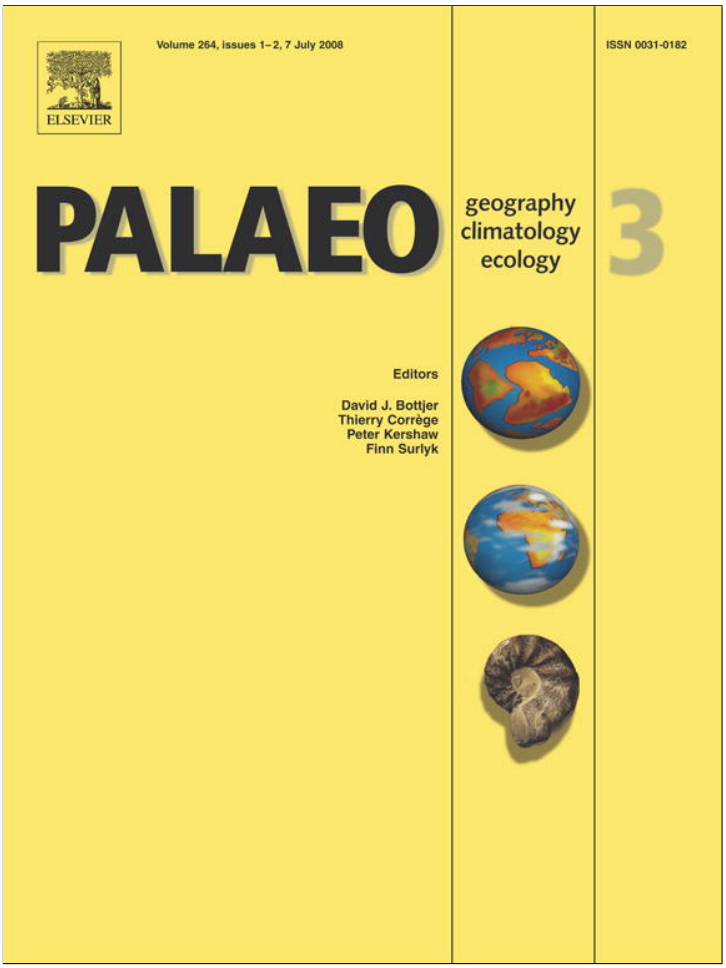
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Palaeogeography, Palaeoclimatology, Palaeoecology 264 (2008) 128–139

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Terrestrial crustacean breeding trace fossils from the Cretaceous of Patagonia (Argentina): Palaeobiological and evolutionary significance

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

[a] CONICET. Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100 Trelew, Chubut, Argentina
[b] CONICET. Universidad Nacional de La Pampa, Av. Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina

ARTICLE INFO

Article history:
Received 30 August 2007
Received in revised form 27 February 2008
Accepted 3 April 2008

Keywords:
Trace fossils
Terrestrial crustaceans breeding structures
Palaeobiology
Evolution
Cretaceous
Patagonia

ABSTRACT

The breeding trace fossils described herein along with the high density of *Loloichnus baqueroensis* in the Cretaceous formations of Patagonia suggest that crayfishes were soil engineers along the Cretaceous in southern South America, and that they had acquired many of the K-breeding behaviours recorded by insects in latest and post-Cretaceous soils, such as pelletal constructions and excavation of breeding cells. The K–T event was probably responsible for changes in environmental conditions in such a way that crayfishes finally became restricted to two small distributional areas in southern South America, and K-breeding insects replaced them as keystone organisms in Cainozoic and modern soils. *Dagnichnus titoi* igen. and isp. nov. and *Cellicalichnus meniscatus* isp. nov., are created to include the new trace fossils attributable to crayfishes from the Cretaceous of Patagonia, Argentina. The attribution to crayfishes is based on their association and morphological affinities with the crayfish fossil burrows *L. baqueroensis* from the same geologic units. *D. titoi* is represented by hemispherical chambers surrounded by thick and short, meniscate burrows, which can be arranged in two or three tight whorls in the more regular specimens. Meniscate burrows are curved downwards and have no neck. Walls are unlined. *C. meniscatus* are necked, horizontal, and straight cells, showing meniscate fillings, attached to sub-vertical shafts, which are relatively much wider than the neck of cells. Both, shafts and cells show a thin and smooth lining. The presence of cells or burrows smaller than the putative parental burrows and comparisons with breeding traces of marine Decapoda support the interpretation of breeding traces, Calichnia, of terrestrial crustaceans. *C. meniscatus* is interpreted as cells excavated from parental burrows, whereas *D. titoi* are probably breeding structures completely produced in a different palaeoenvironment where the female release juveniles.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

K-strategy, represented by adults showing parental care of offspring, is shown by ecological keystone groups of insects, such as ants, termites, bees, predatory wasps, and dung-beetles, among others. Many species of these groups nest in soils, and their trace fossils are the most common in post-Cretaceous palaeosols (Genise, 2004). Soils give the suitable support for making and provisioning cells in nests in which to lay eggs and to develop up to adults, a complex behaviour that finally allowed insects to colonize most terrestrial environments, even the most arid ones, and to achieve all their ecological importance. In parallel with insects, freshwater crayfishes are also considered keystone components of continental aquatic ecosystems (Horwitz, 1995). Brood care is rare among crustaceans, and usually eggs hatch in water where larvae and juvenile develop (Powers and Bliss, 1983). However, K-strategy cases occur particularly in terrestrial decapods, in which the female carry on her offspring until they reach the adult stage (Horwitz and Knott, 1983; Horwitz et al., 1985a; Turvey and Merrick, 1997; Rudolph 2002). Until now, reports of breeding trace fossils for crustaceans are scarce in the bibliography and in all cases involve marine examples (Verde and Martínez, 2004; Lewy and Goldring, 2006 and references therein).

Ichnological data presented herein shows that in southern South America, during the Cretaceous, terrestrial crayfishes shown some of the behaviours that K-breeding insects utilized later to become ecological keystone organisms in terrestrial ecosystems and particularly in soils. Crayfish trace fossils have been extensively described from North America (Hasiotis and Mitchell, 1993; Hasiotis and Honey, 2000 and references therein). Only recently, they have been recorded from South America (Bedatou et al., 2006, 2008), and no nesting structure has been described until now. Also recently, different breeding trace fossils, attributed to marine decapods, have been described (Curran, 1976; Verde and Martínez, 2004; Lewy and Goldring, 2006 and references therein). Abundant and diverse crayfish burrows, included in the proposed ichnotaxon *Loloichnus baqueroensis* (Bedatou et al., 2008), along with the new ichnotaxa, *Dagnichnus titoi* igen. and isp. nov. and *Cellicalichnus meniscatus* isp. nov., are outstanding individual

* Corresponding author. Tel.: +54 2965 432100.
E-mail address: jgenise@mef.org.ar (J.F. Genise).

0031-0182/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2008.04.004

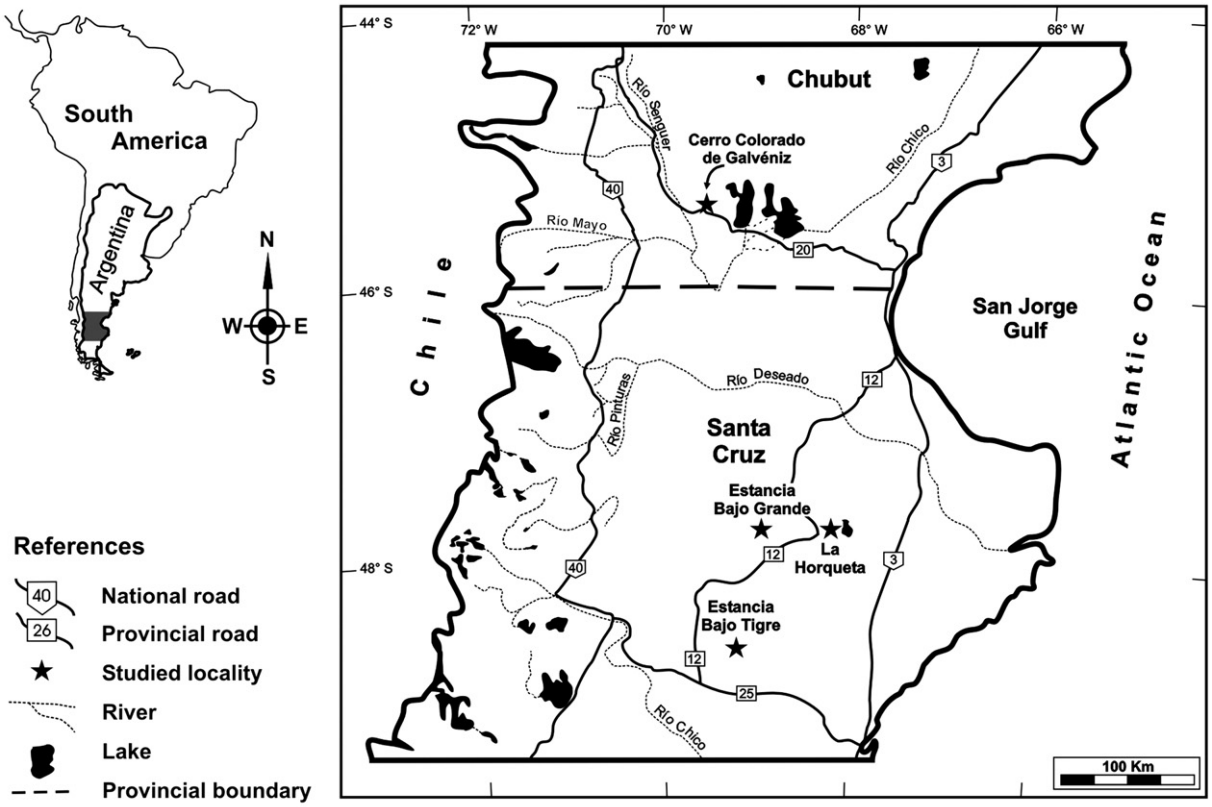
Author's personal copy

components of an ichnofabric that dominate Cretaceous palaeosols along hundreds of square kilometres in southern South America.

The objectives of this contribution are: (1) to describe for the first time breeding trace fossils from terrestrial crustaceans; (2) to provide an ichnotaxonomical treatment for them; (3) to analyze the evolutionary and palaeobiological significance of terrestrial crustacean breeding trace fossils.

2. Geological setting

The trace fossils described in this paper were recovered from three Cretaceous units of central Patagonia: the Bajo Tigre and Punta del Barco formations of the Baqueró Group and the Laguna Palacios Formation of the Chubut Group. The Baqueró Group represents Early Cretaceous (Barremian to Aptian–early Albian) (Cladera et al., 2002; Corbella, 2005) continental volcaniclastic sedimentation in the southern area of the Deseado Massif (Santa Cruz Province), whereas the Chubut Group corresponds to Late Cretaceous (Sciutto, 1981) sedimentation in lacustrine, fluvial, and pyroclastic settings in the San Jorge Basin (Chubut Province) (Fig. 1). The Bajo Tigre Formation is characterized by volcaniclastic gravity-flow deposits composed of tuffaceous breccias and massive, bioturbated tuffites, which are arranged in fining-upward cycles (Cladera et al., 2002; Bedatou et al., 2008). The Punta del Barco Formation contains lithic, massive conglomerates deposited by braided rivers, which are replaced upward by thick primary and reworked pyroclastic deposits with weakly developed palaeosols (Cladera et al.,



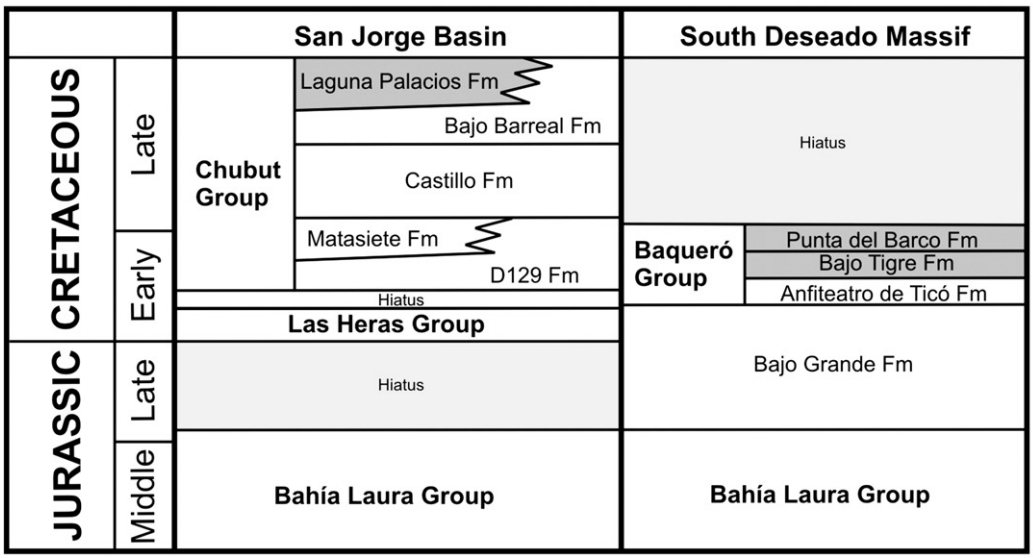


Fig. 1. Location map of studied localities (stars) and simplified stratigraphic chart of the Cretaceous continental units in the surveyed areas. Studied units in dark grey.

Author's personal copy

2002). The Laguna Palacios Formation is the younger unit of the Chubut Group and has been constrained to the Santonian–early Maastrichtian interval (Sciutto, 1981; Fitzgerald et al., 1990; Bridge et al., 2000). The Laguna Palacios Formation is an orange to reddish-grey, tuffaceous loess–palaeosol succession, which records the final terrestrial sedimentation in marginal areas of the San Jorge Basin (Sciutto, 1981; Bellosi and Sciutto, 2002). The mentioned formations display a diversity of complex ichnofabrics and discrete trace fossils, including *Loloichnus baqueroensis* (Bedatou et al., 2008) and insect trace fossils, which are restricted to the Laguna Palacios and Bajo Barreal formations, including *Cellicalichnus chubutensis*, *Rebuffoichnus casamiquelai,* and *R. sciuttoi* (Genise et al., 2002, 2007).

The four studied localities were: Cerro La Horqueta (47°42′58″S; 68°07′48″W) at Monumento Nacional Bosques Petrificados in northwestern Santa Cruz Province; Estancia Bajo Grande (47°47′32″S; 68°44′55″W) a few kilometres to the west of the later; Estancia Bajo Tigre (48°29′26″S; 69°07′10″W) in the centre of the Santa Cruz Province and; Cerro Colorado de Galveniz (45°25′42″S; 69°46′59″W) in the south of the Chubut Province. In the first three localities the Bajo Tigre Formation is exposed, in the third locality the Punta del Barco Formation is also exposed, and the fourth locality contains outcrops of the Laguna Palacios Formation (Figs. 1–3).

2.1. Lithofacies and palaeoenvironments

2.1.1. Bajo Tigre Formation

The Bajo Tigre Formation is characterized by extensive outcrops of tabular and laterally continuous beds of primary ash fall deposits and fluvial and aeolian reworked tuffaceous deposits (Fig. 2A). The typical cycles of this unit are poorly-developed at Cerro La Horqueta locality, which corresponds to the upper section of the formation. The studied interval (Fig. 3F) exhibits a dominance of white or light-gray massive tuffs of silt to fine-grained sands with occasional incipient reddening and abundant rhizoliths. Rare decimetre-thick intercalations of fine-grained breccia beds with scarce specimens of *Loloichnus baqueroensis*, are present. The most common trace fossils at this locality are 1–15 mm thick rhizoliths, which can be locally very abundant, and the new ichnotaxon *Dagnichnus titoi*. Estancia Bajo Grande is a classical palaeontological locality for the Baqueró Group (Archangelsky, 1967; Cladera et al., 2002; Petrulevicius and Nel, 2002) (Fig. 3D–E). At this locality, the sedimentary succession is very similar to that from Cerro La Horqueta. *D. titoi* occurs in an immature palaeosol, along with rhizoliths and meniscate burrows, isolated and in tangled groups (Fig. 6D). The Bajo Tigre Formation has been interpreted as a sediment of unconfined gravity flows followed by diluted flows in a low-lying relief, represented by the mentioned cycles, with strong pyroclastic input and subsequent palaeosol development, evidenced by massive tuffaceous beds and by soil structures (Cladera et al., 2002; Bedatou et al., 2008). This late scenario would be the best represented at La Horqueta. The palaeonvironmental scenario for the Bajo Tigre Formation at Cerro La Horqueta and Bajo Grande localities is envisaged as a lowland area located distally in relation with coeval pyroclastic eruptions. Fine grained and massive tuffs and tuffites have been mostly transported or reworked by aeolian processes. Localized reworking by aqueous currents is suggested by laminated intervals showing breccia clasts. These substrates supported incipient soil-forming processes, as suggested by reddening and presence of rhizoliths.

2.1.2. Punta del Barco Formation

This unit was studied at Estancia Bajo Tigre, where the dominant facies is fine-grained tuffites with sparse intraclasts, erosive bases, and normal grading. Beds are 0.5–1.5 m thick and display sparse to abundant *Loloichnus baqueroensis*, meniscate burrows and common root traces (up to 30 mm wide) in the upper part, along with occasional mottling, reddening and prismatic peds (Bedatou et al., 2008) (Fig. 2C). The upper part of the section is composed of laminated tuffites with erosive bases (relief about 0.5 m) that are replaced upward by structureless tuffites with Fe–Mn nodules. The latter bed contains abundant rhizoliths with a strong axial development, one stump cast, sparse *L. baqueroensis* and the new ichnotaxa *Dagnichnus titoi* and *Cellicalichnus meniscatus* (Fig. 3A–B). The Punta del Barco Formation facies suggest prevailing of dilute fluvial flows and a greater degree of development of palaeosols. The upper part of the section contains finer-grained sediments with Fe–Mn nodules that suggest a transient water logging during the soil development.

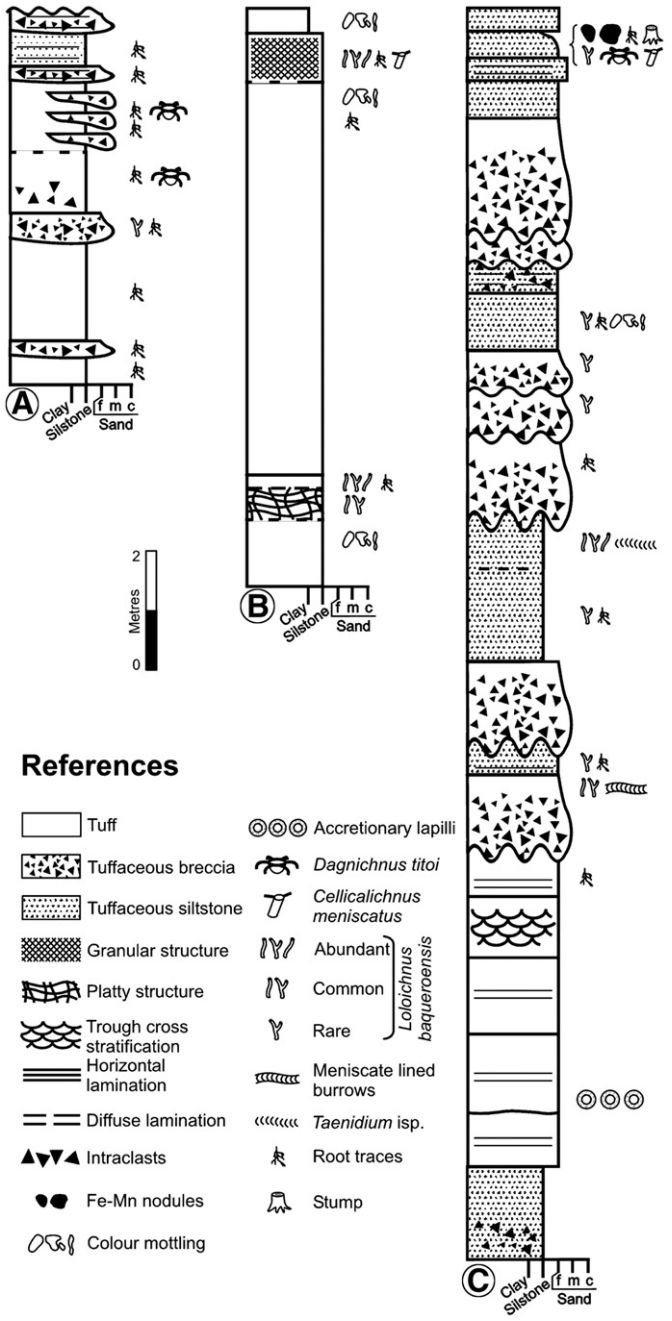


Fig. 2. Sedimentary logs of: A) Bajo Tigre Formation at Cerro La Horqueta; B) Laguna Palacios Formation at Cerro Colorado de Galvéniz; and C) Punta del Barco Formation at Estancia Bajo Tigre.

2.1.3. Laguna Palacios Formation

The Laguna Palacios Formation was studied at Cerro Colorado de Galveniz locality, where the middle member of the unit is exposed (Fig. 3C). The section is characterized by an extensive development of

Author's personal copy

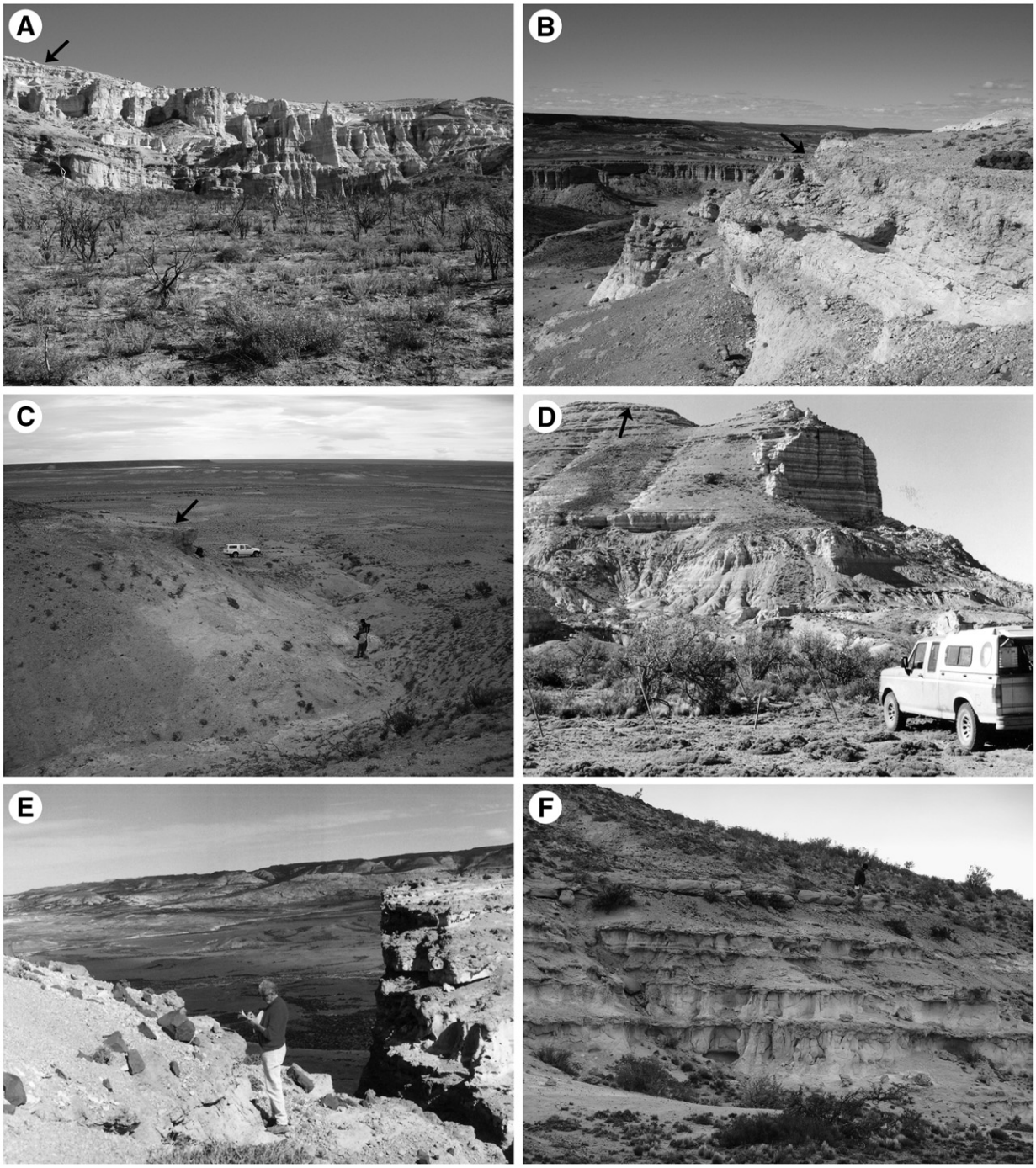


Fig. 3. Studied localities. (A) Punta del Barco Formation at Ea. Bajo Tigre. (B) Detail of the stratigraphic level bearing *D. titoi* and *C. meniscatus* at Ea. Bajo Tigre. (C) Laguna Palacios Formation at Cerro Colorado de Galvéniz. (D) Bajo Tigre Formation at Ea. Bajo Grande. (E) Detail of the stratigraphic level bearing *D. titoi* at Ea. Bajo Grande (the man in the picture is Prof. Tito Andreis). (F) Bajo Tigre Formation at Cerro La Horqueta. Arrows show stratigraphic levels with trace fossils.

mature tuffaceous palaeosols, which are more indurated than the rest of the rock, forming cornices (Fig. 2B). Macroscopic soil structure includes granular peds, root traces, colour mottling and incipient reddening of the upper horizon. Microscopically, mosaic speckled b-fabric and clay coatings in pores and clasts are the most common soil features; all terms after Bullock et al. (1985). The palaeosols contain abundant *Loloichnus baqueroensis* and rare *Cellicalichnus meniscatus*. The Laguna Palacios Formation is usually interpreted as deposited in broad fluvial plains, where frequent ash fall deposits were reworked by rivers and by wind action (Sciutto, 1981; Genise et al., 2002). Soil formation processes were very common in this unit, specially in the middle section.

3. Systematic ichnology

The material examined herein is housed at the ichnological collection of the Museo Regional Provincial "Padre Manuel Jesús Molina" Río Gallegos, Santa Cruz, Argentina (MPM-PIc) and at the ichnological collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN-Icn).

Author's personal copy

3.1. Cellicalichnus Genise 2000

Diagnosis: Rows or whorls of tear-shaped or ellipsoidal cells attached by means of short necks to main tunnels (Genise, 2000).

Type ichnospecies: *Cellicalichnus dakotensis* Elliott and Nations (1998).

Remarks: The ichnogenus *Ardelia* Chamberlain and Baer (1973) was briefly described as composed of short, small radiating burrows associated to larger, principal ones, roughly resembling the bauplan of *Cellicalichnus*. However, the illustrations of *Ardelia* show a very different morphology from that of *Cellicalichnus*. Curran and White (1999) described unnamed stellate burrows from the Holocene carbonate eolianites from Bahamas, resembling the bauplan of *Cellicalichnus*. Upward ramification of shafts and upward orientation of radiating burrows, in contrast to the described ichnospecies of *Cellicalichnus*, suggest a crustacean breeding structure more likely than bee trace fossils as suggested therein. Recently, Martin (2006) proposed that those were composite trace fossils composed of bee cells attached to abandoned land crab burrows. Alternatively Martin (2006), based on the morphology and interpretation of the ichnogenus *Maiakarichnus*, also proposed a crustacean breeding structure for those trace fossils.

3.2. Cellicalichnus meniscatus isp. nov.

Etymology: After the meniscate fillings of cells (Fig. 4A–D).

Diagnosis: Necked, horizontal and straight cells, showing meniscate fillings, attached to sub-vertical shafts, which are relatively much wider than the neck of cells. Both, shafts and cells show a thin and smooth lining.

Remarks: None of the described ichnospecies of *Cellicalichnus* has meniscated cells, although one of the specimens illustrated by Elliott and Nations (1998; Fig. 5E) shows a rough patterned structure inside, which is not commented by authors. In any other ichnospecies the difference in diameter between cell neck and main shaft is so large as in *C. meniscatus*.

Holotype: The only collected specimen of this ichnospecies is represented by a cell attached to the shaft in a piece of palaeosol bearing other burrows from Estancia Bajo Tigre (Lower Cretaceous Punta del Barco Formation) (Departamento Gregores, Santa Cruz, Argentina) (MPM-PIc 3789) (Fig. 4A–B).

Examined material: Apart from the holotype other two specimens were examined, measured, and photographed in the field (Fig. 4C–D). One of them occurs in the same deposit of the holotype, and the other is from Cerro de Galveniz (Late Cretaceous Laguna Palacios Formation) (Departamento Sarmiento, Chubut, Argentina).

Description: In the field, the holotype occurred in a naturally exposed horizontal bedding plane as a cross-section of a thinly lined shaft, connected with a single, radiating, meniscate cell, 22 mm long, and 16 in maximum thickness. The cell shows a neck, 14 mm wide, and a 1 mm thin lining, which is similar and continuous with that of the shaft. The concavity of cell menisci, which are 1 mm wide, faces the shaft (Fig. 4A–B). There are no differences between the rock matrix and the fillings of the burrow and cell. In the same bed, and included in a cone truncated structure, which can be interpreted as a cast of a tree stump, occurs a second example, which was also naturally

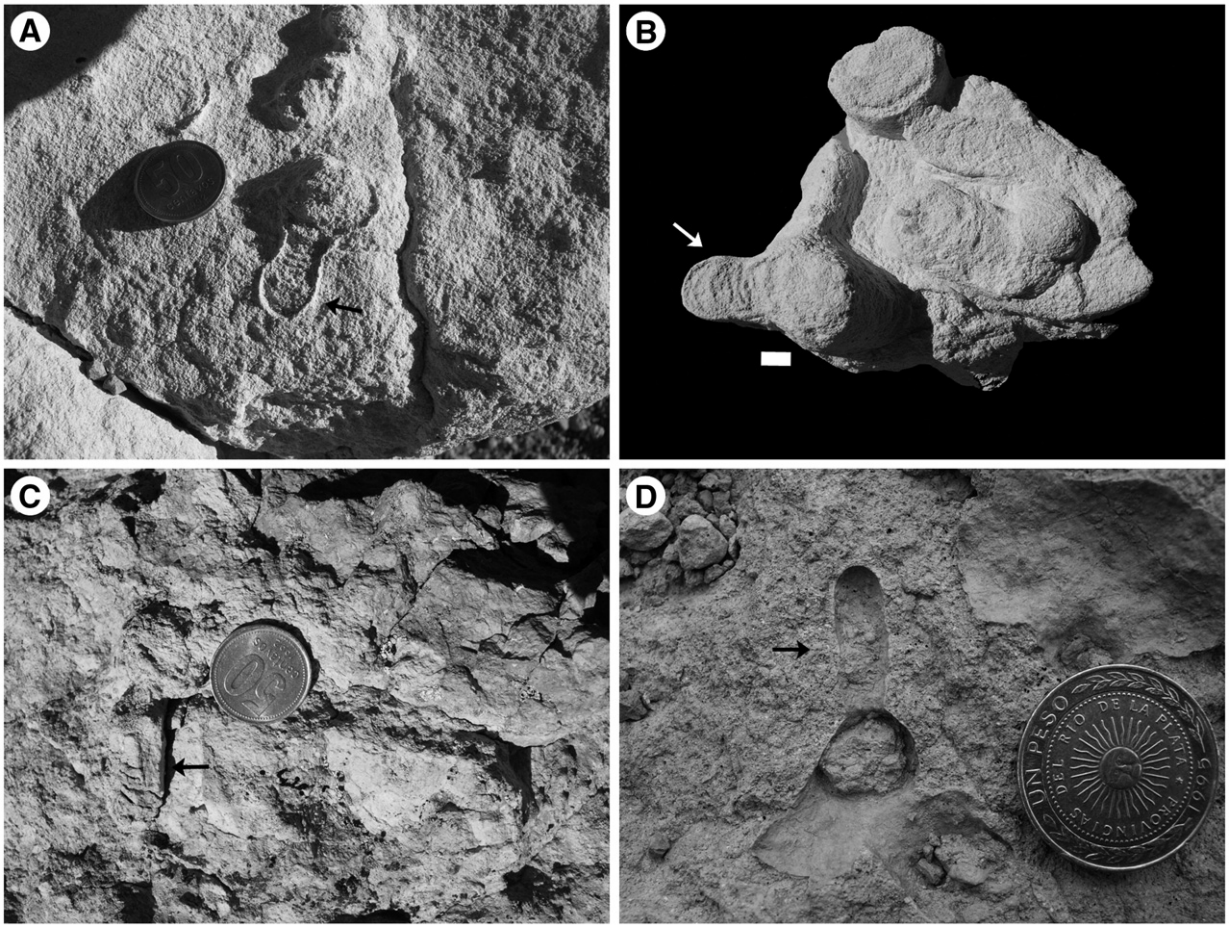


Fig. 4. *Cellicalichnus meniscatus* isp. nov. (A) Holotype (MPM-Pic 3789) as found in the field from the Punta del Barco Formation at Estancia Bajo Tigre. Coin: 25 mm. (B) Holotype after preparation in laboratory, note other burrows that were not evident in the field. Bar: 10 mm. (C) Another specimen from the same stratigraphic level, note the meniscate filling of the cell. Coin: 2.5 mm. (D) Specimen from the Laguna Palacios Formation at Cerro Colorado de Galvéniz. Coin: 23 mm. Arrows indicate cells.

Author's personal copy

exposed in cross-section (Fig. 4C). This specimen was composed of a vertical shaft, 25 mm in diameter, showing a 3 mm thin lining, and an attached necked cell showing also a 3 mm thin lining. The cell, which is 34 mm long and 15 mm in maximum diameter, has 1 mm thick menisci whose concavities face the shaft. The neck is 11 mm wide. Fillings of the shaft and the cell are similar to the rock matrix (Fig. 4C).

The other specimen, from the Laguna Palacios Formation, exposed in cross-section on a horizontal bedding plane, is different from the previous ones in lacking fillings in the cells. The vertical shaft is 10 mm in diameter, whereas the cell is 16 mm long and 6 mm wide, with a neck of 4 mm. The presence of a very thin lining can be recognized by a smoother and darker film than the rock matrix. The filling of the shaft is similar to the rock matrix, whereas the cell lacked the fillings probably by weathering (Fig. 4D).

3.3. *Dagnichnus igen. nov.*

Etymology: Derivated from the Mapuche language of Patagonia, *Dañe* meaning nest, and from the Greek Ikhnos, meaning trace.

Diagnosis: Hemispherical chamber surrounded by thick and short, meniscate burrows, which can be arranged in two or three tight whorls in the more regular specimens. Meniscate burrows are curved downwards and have no neck. Walls are unlined.

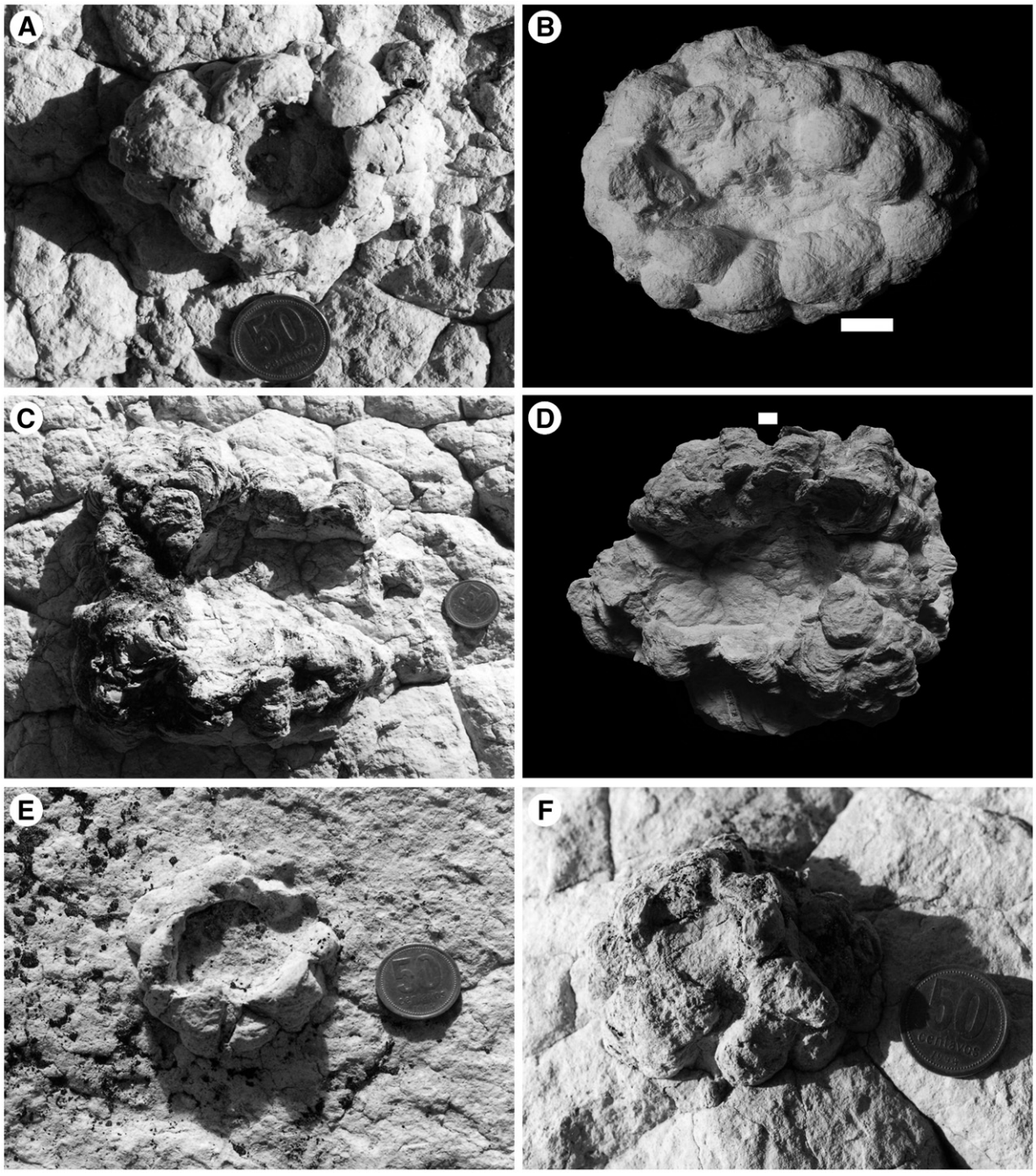


Fig. 5. *Dagnichnus titoi* igen. and isp. nov. from Bajo Tigre Formation at Estancia Bajo Grande. (A) Holotype (MPM-Pic 3790) as found in the field. (B) Back aspect of the holotype after preparation. (C) The largest specimen (MPM-Ic 3791) as found in the field. (D) Specimen (MPM-Ic 3791) after preparation in laboratory. (E) Specimen (MPM-Pic 3792) as found in the field. (F) Non-collected specimen. Coin: 2.5 cm. Scale bar: 10 mm.

Author's personal copy

Remarks: It can be distinguished from *Maiakarichnus* (Verde and Martínez, 2004) because it lacks a complete spherical chamber, and the radiating burrows are thick, short, meniscate, and connected to the bottom and equator of the chamber. *Phoebichnus* (Bromley and Asgaard, 1972) is also comparable with *Dagnichnus*, however the former show long radiating burrows with annulated mantle.

Type ichnospecies: *Dagnichnus titoi*, only known ichnospecies.

3.4. *Dagnichnus titoi isp. nov.*

2001 Meniscate trace Genise, p. 43 (Figs. 5A–E and 6A–C).

Etymology: Dedicated to Professor Renato "Tito" Andreis, friend, sedimentologist, and one of the pioneers on palaeosol research in South America, who participated in several field trips with one of us (JFG), and particularly in that in which the first specimens were found.

Holotype: A specimen in which meniscate burrows surround the chamber entirely with a very regular arrangement. The Lower Cretaceous Bajo Tigre Formation of Cerro Bayo (47°47′32″S; 68°44′55″), Departamento Gregores, Santa Cruz, Argentina. (MPM-PIc 3790) (Fig. 5A–B).

Paratype: One specimen similar to the holotype, in which some of the lateral burrows are covered by rock matrix; from the Lower Cretaceous Bajo Tigre Formation of Cerro Madre e Hija at Cerro La Horqueta, Monumento Nacional Bosques Petrificados, Santa Cruz, Argentina (MACN-Icn 2322) (Fig. 6A).

Examined material: Three specimens from the type locality (MPM-PIc 3791–3793). Other three specimens examined and photographed in the field from the Lower Cretaceous Punta del Barco Formation, Estancia Bajo Tigre (Departamento Gregores, Santa Cruz, Argentina) and two specimens from the Lower Cretaceous Bajo Tigre Formation, Cerro Madre e Hija (Monumento Nacional Bosques Petrificados, Santa Cruz, Argentina).

Diagnosis: Only known ichnospecies, same as for the ichnogenus.

Description: The holotype (MPM-PIc 3790) is composed of a subcircular half chamber, 30–35 mm in diameter and 20 mm deep, surrounded by about 25 short (24–29 mm) and thick (11–15 mm) meniscate burrows radiating in all directions, around the perimeter, and also at the bottom of the chamber. The menisci are scarcely marked. Burrows arise beneath the chamber margin, and curve upwards. They have a regular arrangement in two whorls, in lateral view, and up to three in one side. There are no differences between the rock matrix and the fillings of the burrows or the chamber. No lining or surface texture can be observed in this specimen, which is one of the smallest but regularly arranged specimen (Fig. 5A–B). The paratype (MACN-Icn 2322) is an elliptical chamber, 30 mm in long axis, 20 mm in short axis, and 15 mm deep, surrounded by about 18 short (24–26 mm) and thick (12–14 mm) meniscate burrows radiating in all directions, around the perimeter, and also at the bottom of the chamber. In some parts the boundaries between burrows are poorly preserved. The menisci are also scarcely marked. Burrows arise beneath the chamber margin and curve upwards. There are no differences between the rock matrix and the fillings of the burrows or the chamber. No lining or surface texture can be observed (Fig. 6A). The largest specimen (MPM-PIc 3791) is in plain view a semisphere, elliptical, 80 mm in long axis, and 60 mm in short axis, about 30 mm deep, surrounded by about 19 short (32–60 mm) and thick (16–

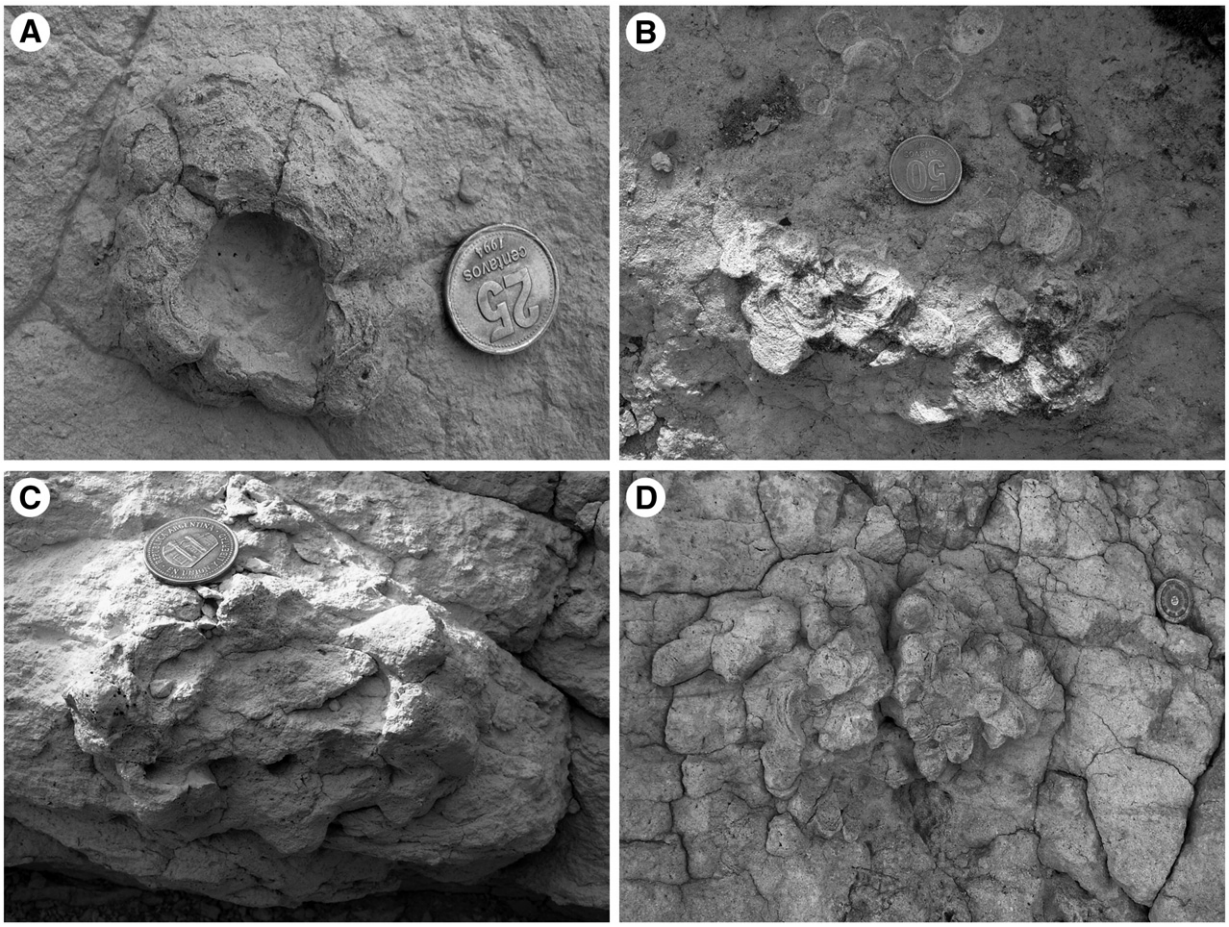


Fig. 6. (A) to (C) *Dagnichnus titoi* igen. and isp. nov. from Bajo Tigre Formation at Cerro la Horqueta. (A) Paratype (MACN-Icn 2322) as found in the field. Coin: 24 mm. (B) and (C) Non-collected specimens. Coin: 25 mm. (D) Tangled group of meniscated burrows commonly associated with *Dagnichnus titoi*. Coin: 23 mm.

Author's personal copy

22 mm) meniscate burrows radiating all around the chamber, except for a short, probably broken section of 20 mm. The menisci are about 2 mm thick and their concavities face the chamber. Some of the burrows arise at the same depth of the chamber bottom, being curved and directed upwards to connect with the chamber. The bottom of this specimen, partly covered with matrix, shows no burrows. There are no differences between the rock matrix and the fillings of the burrows or the chamber. No lining or surface texture can be observed (Fig. 5C–D). The specimen (MPM-PIc 3792) is mostly similar to the holotype, but more elliptical and not so well preserved. The elliptical semichamber is 44 mm in long axis, 34 mm in short axis, and 12 mm deep. Eleven short (25–30 mm) and thick (10–12 mm) burrows showing poorly preserved menisci surround the chamber perimeter. They arise at some depth and curve upwards to connect with the chamber. Burrows are undistinguishable at the bottom of this chamber. There are no differences between the rock matrix and the fillings of the burrows or the chamber. No lining or surface texture can be observed in this specimen (Fig. 5D). The remaining collected specimen (MPM-PIc 3793) is a broken one, preserving part of the chamber perimeter with 12 meniscate burrows, 20 to 48 mm long, and 11 to 14 mm thick. Menisci, facing to the chamber, 1 to 2 mm thick, are well preserved and similar in composition to the rock matrix. Burrows are arranged in three oblique rows, as seen laterally. Specimens examined in the field show similar morphologies and sizes that those described herein (Fig. 6B–C).

4. Discussion

Three basic questions are to be answered for both *Cellicalichnus meniscatus* and *Dagnichnus titoi* for understanding the evolutionary and paleobiological significance of these trace fossils: (1) what are the probable trace makers, (2) what is the function of these structures, and (3) how were palaeoenvironmental conditions during their production.

4.1. Trace makers

The attribution of *Dagnichnus titoi* and *Cellicalichnus meniscatus* to crustaceans is based on their relationships with *Loloichnus baqueroensis*, which has been attributed to crayfishes based on burrow morphology, wall surface texture, association with root traces, and sedimentological evidence contrasted with possible environments habited by different groups of land and freshwater crustaceans (Bedatou et al., 2008). *L. baqueroensis* was proposed for vertical to sub-vertical thickly lined burrows, in some cases Y-branched; passively filled, less commonly showing pelletal filling; and with a grooved inner surface texture. All these features are consistent with those of extant crayfishes and also with previously described fossil crayfish burrows (Bedatou et al., 2008).

Cellicalichnus meniscatus, *Dagnichnus titoi* and *Loloichnus baqueroensis* occur in the same formations, although with different densities. In those stratigraphic levels in which *L. baqueroensis* is abundant, *D. titoi* is lacking, whereas in those in which *D. titoi* occurs, *L. baqueroensis* is scarce, probably reflecting different palaeoenvironmental conditions for the occurrence of both that are analyzed below. *C. meniscatus* occurs in low numbers with *D. titoi* in the Punta del Barco Formation at Estancia Bajo Tigre and with abundant *L. baqueroensis* in the Laguna Palacios Formation at Cerro de Galveniz. The occurrence of breeding structures and undisputed crustacean trace fossils in the same beds, in some cases in connection, have been already used by former authors, such as Curran (1976), Verde and Martínez (2004), and Lewy and Goldring (2006) to attribute breeding structures to decapods in absence of modern analogues or homologues of such trace fossils. The similarity between *Dagnichnus* and *Maiakarichnus* bauplans, and other decapod trace fossils discussed below also support this assertion. The holotype and the paratype show a central chamber whose diameter is only a bit larger than the shaft of *L. baqueroensis*, suggesting that the radiating tunnels arose originally from a slightly enlarged bottom of *L. baqueroensis*. Finally, specimens of *C. meniscatus* represent cells associated with shafts that according to their morphology, lined wall, and diameter correspond to those of *L. baqueroensis*.

4.2. Function

Different functions were reported and postulated in the literature for chambers and small burrows associated with crustacean extant traces and trace fossils: (1) food storage and/or gardening (Frey and Howard, 1975; Grow, 1981; Richardson, 1983; D'Alessandro and Bromley, 1995; Dworschak, 2002; Dworschak et al., 2006; Lewy and Goldring, 2006; Nesbitt and Campbell, 2006), (2) gardening for offspring feeding (Bromley in Frey and Howard, 1975; Bottjer, 1985), (3) associated organisms (Hogue and Bright, 1971; Suter and Richardson, 1977; Powers and Bliss, 1983; de Gibert et al., 2006), (4) breeding of juveniles (Forbes, 1973; Frey and Howard, 1975; Curran, 1976; de Gibert et al., 1999; Verde and Martínez, 2004; de Gibert et al., 2006; Lewy and Goldring, 2006), (5) turnovers and terminal chambers (Grow, 1981; Hobbs, 1981; Horwitz et al., 1985a; Horwitz and Richardson, 1986; Bromley, 1990), (6) storage of garbage (coarse material) related with feeding and pumping (Tudhoppe and Scoffin, 1984; Dworschak and Ott, 1993; Dworschak et al., 2006; Lewy and Goldring, 2006), and (7) storage of pellets (Kilian, 1959; Rudolph, 1997).

Some of these functions are very unlikely for *Dagnichnus titoi* and *Cellicalichnus meniscatus*. Turnovers and terminal chambers (5) are enlargements located along or at the bottom of tunnels, which is not the case presented herein. Similarly, chambers for pellets (7) are also reported to be enlargements of tunnels, and more important, pellets were not found in the trace fossils studied herein. Food storage chambers or bacterial gardens have been postulated for some trace fossils based mostly on negative evidence (1). Only Nesbitt and Campbell (2006) have recently identified remains of organic matter inside chambers. In all cases these structures are also enlargements of tunnels. D'Alessandro and Bromley (1995) interpreted the chambers associated to *Spongeliomorpha sicula* as microbial gardens, and Dworschak (2002) and Dworschak et al. (2006) interpreted those associated with burrows of two species of callianassid as storage chambers. Tudhoppe and Scoffin (1984) described *Callianassa* burrows with chambers from which short tunnels radiate, in whose enlarged bottoms, bivalve shells were accumulated (6). The structures described by Tudhoppe and Scoffin (1984) match the bauplan of *D. titoi*. However, these authors considered the terminal chambers at the bottom of the radiating burrows as a kind of garbage room where coarse sediments accumulate during callianasid burrowing activity. Lewy and Goldring (2006) interpreted these accumulations as passive. Whereas, Dworschak and Ott (1993) and Dworschak et al. (2006) also found shell particles accumulated in chambers in callianassid burrows as a by-product of feeding on fine material. There are neither remains of organic matter nor coarse material in *D. titoi* or *C. meniscatus* to postulate their function as storage or garbage chambers or bacterial gardens. The latter is not an enlargement of a tunnel, and even when the central chamber of the first may be interpreted as a storage chamber, the radiating meniscate burrows suggest that this function would not be the single one for this structure. The possibility of a composite trace fossil (3) can be analyzed only for *C. meniscatus* since in the case of *D. titoi*, the meniscate burrows are not associated with a shaft that could be attributed to other organism. Martin (2006) analyzed the possibility for the stellate burrows of Bahamas described by Curran and White (1999) of being composite trace fossils produced by crabs and bees. However, as stated in that contribution the upward orientation and other characters of those cells, and also its construction in abandoned tunnels, are unlikely for bees. In addition, the regular co-occurrence, the large number, and the regular arrangement of cells in burrows suggest that more probably they are an important

Author's personal copy

part of a structure constructed by a single producer and not an additional trace added by another.

Apart from this negative evidence, there is a positive one that suggests that *Cellicalichnus meniscatus* and *Dagnichnus titoi* may be breeding structures, or at least structures constructed partly by juveniles. The diameter of meniscate burrows in *D. titoi* (mean=16 mm, *N*=89) and that of cell necks of *C. meniscatus* (mean=9 mm, *N*=4) is smaller than that of *Loloichnus baqueroensis*, (mean=20 mm, *N*=167) (Bedatou et al., 2008) suggesting juvenile instead of adult activity. *C. meniscatus* is probably a more simple structure than *D. titoi* composed only of one or more radiating cells, from a central, non-enlarged shaft, which correspond to those of *L. baqueroensis*. The size of the cell and particularly the neck diameter, which is much smaller than the shaft, suggests that juveniles excavate cells instead of adults, as is the case of other small burrows associated to parental ones discussed below. The recorded cases of marine nests support this hypothesis, not to mention the potential impossibility of the adult to excavate a cell smaller than its own body size. An important difference between *C. meniscatus* and *D. titoi*, is that radiating burrows are not comparable with the cells of the former. Radiating burrows of *D. titoi* are not necked, not lined, and they are curved downward. *C. meniscatus* would represent cells radiating from the parental one, indicating that juveniles were released in the same habitat where the adults live. Forbes (1973) found that burrows of juveniles of *Callianassa kraussi* (Thalassinidea) taper off slightly before they join the parent burrow, as in the cases shown here. The necessity of juveniles for constructing their own small burrows may be based on cannibalism by parents as reported for several crustaceans (Powers and Bliss, 1983; Alcorlo et al., 2004).

Crustacean breeding traces are few and briefly described, probably because brood care is rare in this group of organisms, and usually eggs hatch in water where larvae and juvenile develop. Exceptions occur particularly in some terrestrial decapods, in which the female carry on her offspring until they reach the adult stage (e.g. Horwitz and Knott, 1983; Powers and Bliss, 1983; Horwitz et al., 1985a; Rudolph 2002). However, different extant and fossil traces attributed to crustacean breeding behavior have been reported until now from marine environments (e.g. Forbes, 1973; Frey and Howard, 1975; Curran, 1976; Bottjer, 1985; Curran and White, 1999; de Gibert et al., 1999; Shimoda and Tamaki, 2004; Verde and Martínez, 2004; Lewy and Goldring, 2006). They follow two basic types: small tunnels radiating from a host burrow as in *Cellicalichnus meniscatus*, or radiating from a chamber as in *Dagnichnus titoi*.

The first type was formerly described by Forbes (1973), who reported small tunnels at the non-enlarged bottom of the parent burrow in *Callianassa kraussi*. Particularly interesting is that the small burrows show a neck nearby the parent burrow, which can be compared with those shown by chambers in *Cellicalichnus meniscatus*. Frey and Howard (1975) described small burrows in the parent burrows of *Upogebia affinis*, which might be associated with terminal enlarged chambers, or directly with the non-enlarged burrows, showing that both types may be present in the tunnel system of the same species. They also reported apertural necks in the juvenile burrows, and discussed the possibility that the chamber represented a provision chamber, in which plant material stored served as medium of culture of bacteria that would be used as food for juveniles (Bromley, in Frey and Howard, 1975). The latter possibility was not considered by Nesbitt and Campbell (2006) in their comment on *Maiakarichnus* preserving organic matter in the central chamber. Similar small burrows radiating from a central chamber were described by Curran (1976) and later included in the ichnogenus *Maiakarichnus* by Verde and Martínez (2004). In addition, Frey and Howard (1975) described two trace fossils from the Cretaceous of Utah that follow the same patterns described herein. One of them shows clusters of small burrows occurring at many places along a host burrow resembling the pattern of *C. meniscatus*, and in the other, the tiny burrows are clustered in small depressions (Frey and Howard, 1975, Fig. 7), resembling the bauplan of *Dagnichnus titoi*. Bottjer (1985) described chambers in *Thalassinoides* accepting the proposal by Bromley (in Frey and Howard, 1975) that they might represent bacterial cultures for feeding adults and brooded offspring. Curran and White (1999) and Martin (2006) described trace fossils from the Holocene carbonate aeolianites from Bahamas showing Y-branched shafts and upward orientated radiating burrows, suggesting another crustacean breeding structure similar to *C. meniscatus*. Lewy and Goldring (2006) went further, proposing that one type of the chambers they described associated with an *Spongeliomorpha* tunnel system was performed by the adult female for laying eggs, and for protecting them during the development of the hatching, even when no crustacean is known to show this type of breeding strategy similar to insects. The other type of chamber was interpreted as a storage chamber in which also juveniles might be housed.

Genise (2001) described briefly *Dagnichnus titoi*, without naming it, concluding that it might be considered as a kind of nest of an unknown group of organisms that could have dominated soils previous to nest producing insects during the Lower Cretaceous. Such prediction is confirmed with the data presented herein, where in addition, other type of breeding trace fossil, *Cellicalichnus meniscatus*, is also described. As *Maiakarichnus*, the new ichnogenus *Dagnichnus* can be included in the ethological category for nests, calichnia, proposed by Genise and Bown (1994).

4.3. Palaeobiological inferences

Terrestrial crustaceans show larval recruitment and parental care, however, no trace fossils have been described until now for them and the records of modern ones are few and brief described. Juveniles of terrestrial crabs were found inside parental burrows (Litulo, 2005; Hartnoll and Clark, 2006), and at least in one case they are reported to excavate small burrows (=diverticula) inside them (Vannini et al., 2003). For crayfishes, different behaviors were reported. In some cases, juveniles are released in the parental burrow, or at least adults of different sizes are found in the burrows, although these construct no particular diverticula or small burrows (Williams et al., 1974; Lake and Newcombe, 1975; Suter and Richardson, 1977; Hobbs, 1981; Horwitz et al., 1985a,b; Rudolph, 1997). In others, juveniles inhabiting the parental burrows are reported to construct small burrows or enlarge mating chambers (Horwitz et al., 1985b; Horwitz and Richardson, 1986). However, even in these latter cases there are no records of the more complex structures described for marine decapoda. Horwitz et al. (1985a) proposed that crayfishes that are more independent from water bodies or water table release juveniles in the parental burrow, whereas, other species that burrow in or close to water bodies, release juveniles into or nearby these water bodies. For Cambaridae, the common North American crayfishes, Hobbs (1981) found that in hundreds of burrows studied of primary burrowers (i.e. those that spent most of their lives in burrows) none contained juveniles or small tunnels connected. Only in secondary and tertiary burrowers that live increasingly in superficial waters, juveniles were found in parental burrows, although without excavating apparently their own tunnels (Hobbs, 1981). In contrast to the Southern Hemisphere Parastacidae, in Cambaridae, the occurrence of members of more than two generations in the same burrow is occasional (Hobbs, 1988). Some species of Parastacidae, which live in water bodies, are known to burrow in soils when the female is gravid (e.g. Horwitz and Richardson, 1986) or seek for a more appropriate aquatic environment to release juveniles (e.g. Rudolph, 2002). In contrast, other species inhabit burrows close to a water body, where females move to release juveniles, which are never found in parental burrows (e.g. Borsboom, 1998) as in most Cambaridae. Juvenile release is seasonal (Bocic et al., 1988; Rudolph, 2002) and occurs mostly in summer (Honan and Mitchell, 1995). In some species, release of juveniles is gradual (e.g.

Author's personal copy

Lake and Newcombe, 1975; Suter, 1977; Bocic et al., 1988), whereas in other it is synchronized (i.e. Borsboom, 1998).

Evidence presented herein suggests that *Cellicalichnus meniscatus* and *Dagnichnus titoi* might represent different breeding strategies. *C. meniscatus* occurs always in few numbers in the study cases, in beds where *Loloichnus baqueroensis* are present (Laguna Palacios Formation), and also where *D. titoi* occurs (Punta del Barco Formation). Whereas, *D. titoi* occurs in deposits, where *L. baqueroensis* and *C. meniscatus* are scarce, suggesting that it reflects a different breeding strategy probably controlled by environmental conditions or seasonality. In addition, in those deposits where *D. titoi* is abundant also occur tangled groups of meniscate burrows (Fig. 6D) of similar diameter to those of *D. titoi*, suggesting another behaviour of the same juveniles. Frey and Howard (1975) found for the same thalassinidean shrimp, tunnels of juveniles directly radiating from the host burrow or from chambers. Turvey and Merrick (1997) proposed that even different reproductive strategies, such as K and R, could be present in the same population of one species of *Euastacus* (Parastacidae) to deal with different environmental conditions.

If high densities of *Loloichnus baqueroensis* reflect the best palaeoenvironmental conditions for its potential producers (adult decapods), then *Dagnichnus titoi* will reflect the best palaeoenvironmental conditions for nesting and young larvae development. The gravid females of an Australian crayfish, which inhabits open water, burrow in a drier location not connected with the water body (Horwitz and Richardson, 1986). Juveniles of *Cambarus fodiens* congregate in pools in the drying stream-bed, but none showed any signs of burrowing (Williams et al., 1974). Others release juveniles seasonally in a more appropriate environment, for instance in water bodies with greater rotten organic matter content (Rudolph, 2002). Honan and Mitchell (1995) distinguished for crayfishes between winter brooders (Astacidae), having long breeding periods and releasing juveniles in spring or summer, and summer brooders (Cambaridae), having short breeding periods during summer. Although many species release larvae, juveniles or miniature adults in groups, there are still others that release juveniles individually and gradually (Lake and Newcombe, 1975; Suter, 1977; Bocic et al., 1988). Non-social gregariousness is known in terrestrial crustaceans, mostly produced by environmental constraints (Powers and Bliss, 1983; Horwitz and Richardson, 1986).

Sedimentological data presented herein show that the most suitable environmental conditions for juvenile crayfish (as suggested by the join occurrence of *Dagnichnus titoi* and *Cellicalichnus meniscatus*) can be found at the Punta del Barco Formation, reflecting lowland areas filled with fluvial deposits showing weak soil development and hydromorphic features. This was also a tolerable setting for adults, according to the few *Loloichnus baqueroensis* also present there, although the high density of *Loloichnus* burrows found in the Bajo Tigre Formation suggests that the most appropriate for adults were lowland areas with well-drained soil profiles, incipient soil development, probably under a seasonal climate (Bedatou et al., 2008). In addition, *D. titoi* was also recorded in low-relief areas with well-drained, poorly-developed soil profiles, where the wind action was important for transport of pyroclastic detritus (Cerro La Horqueta and Estancia Bajo Grande localities).

The interpretation of the breeding strategy represented by *Dagnichnus titoi* is complex. The size of the chamber is directly related to the size and number of meniscate burrows, suggesting that the fillings from the meniscate burrows come at least in part from the excavation or enlargement of the central chamber. The dispersion in diameters of meniscate burrows from different specimens shows that organisms of different size excavate them. If only one species of producer is involved, this evidence shows that juveniles in different developmental stages may produce the original structure. In all cases the size of meniscate burrows is slightly smaller than the shaft of *Loloichnus baqueroensis*, suggesting that juveniles are more likely involved than adults. On the other hand, the holotype and paratype of *D. titoi* achieve a so regular arrangement and optimal use of space that they seems to have been produced by a single breeding female instead of a group of non-cooperative group of juveniles. As mentioned previously, the chamber of *D. titoi* may be involved in juvenile development. For instance, the chamber would act as a pool in waterlogged soils, collecting water where offspring can live for some time before beginning adult life and constructing their own burrows. Suter and Richardson (1977) found that chambers of *Engaeus cisternarius* were very efficient for collecting soil water even when the water table was not available. Similarly, the central chamber may be involved in food provisioning. For developing, the immature stages should feed. Larvae of crayfishes feed on egg yolk for a long period time up to reaching the juvenile stage (Rudolph, 2002). Different marine and terrestrial crustaceans are known to feed inside burrows and are supposed to store plant material that would allow the culture of bacteria on which juveniles may feed on (i.e. Frey and Howard, 1975; Green, 2004; Lewy and Goldring, 2006 and references therein). Crayfishes usually feed on decaying organic matter and/or root mats that develop inside burrows favoured by the availability of oxygen (e.g. Richardson, 1983; Growns and Richardson, 1988; Richardson and Wong, 1995). The presence of a central chamber in *D. titoi* may indicate the storage of decaying organic matter or a suitable locus for the developing of root mats.

4.4. Evolutionary significance

The recent record of dense crayfish burrows (Bedatou et al., 2006, 2008) and the new breeding structures presented herein from different Cretaceous palaeosols of southern South America indicate that crayfishes were probably the ecosystem engineers of those Cretaceous soils. In addition, that by the Early Cretaceous, crustaceans probably acquired complex behaviors that at the same time or probably later appeared in ecological keystone groups of insects, as shown by the ichnofossil record (Genise, 2004). Extant burrows of crayfishes show thick lined walls constructed with soil pellets (Kilian, 1959; Hobbs, 1981; Rudolph, 1997; Bedatou et al., 2008). Such behaviour can be traced back up to the Triassic (Hasiotis and Mitchell, 1993) and perhaps up to the Permian for marine decapods (Chamberlain and Baer, 1973). In contrast, the use of soil pellets in insect constructions can be traced back with certainty up to the Late Cretaceous (Genise, 2004; Genise et al., 2007). The advantages of burrowing in soils for crayfishes, such as protection for predators, access to underground food and water, and creation of microhabitats with optimal moisture, temperature and oxygen (Horwitz and Knott, 1983), may be similar to those found by insects. For achieving all these objectives, the possibility of constructing thick linings for walls is essential. In addition, trace fossils presented herein indicate that crayfishes also burrowed in soils during the Cretaceous for making breeding structures in which juveniles found an optimal microenvironment for developing. The same K-breeding strategy recorded for ecological keystone groups of insects along the Cainozoic as shown by the ichnofossil record (Genise, 2004; Genise and Bown, 1994).

Crustaceans probably made their best attempt to dominate the driest land environments and particularly soils during the Cretaceous in Southern South America. However, their keystone role in Southern South American Cretaceous soils was interrupted during the K–T boundary, as shown by their trace fossils, which almost disappear from palaeosols, to remain present in few Cainozoic localities (Genise, unpubl. data). Finally, extant soil crayfishes became restricted to two small distributional areas in Chile (west) and South Brasil and Uruguay (east) (Morrone and Lopretto, 1994). Probably, their condition of water-breathers, in contrast with air-breather insects, environmental changes during the K–T boundary, and the subsequent diversification of mammals and birds, their main predators (Gherardi et al., 2000; Rudolph, 2002) finally aborted the crustacean realm, and settled insects as dominant invertebrates in post-Cretaceous soils.

Hasiotis (2000, 2004) postulated that trace fossils of crayfishes, but also of mud-loving and carrion beetles, bees, wasps, ants, and termites

Author's personal copy

among other insects could be recognized in North American Mesozoic soils. Those proposals were criticized based on the poor documentation presented for supporting the attributions of trace fossils (Bromley et al., 2007 and references therein). The new evidence presented herein, along with other scattered in the literature (e.g. Martin, 2006), shows that crustaceans were capable of constructing nests and cells, suggesting the possibility that some of the North American trace fossils recognized as produced by insects, were actually produced by crustaceans. At least, in southern South America, Cretaceous paleosols are dominated by ichnofabrics of crayfish trace fossils, whereas insect trace fossils are mostly absent during the Cretaceous (and the rest of the Mesozoic) only appearing in the latest Cretaceous (Genise, 2004; Genise et al., 2007).

5. Concluding remarks

- Two new ichnotaxa from the Cretaceous of Patagonia, *Dagnichnus titoi* igen. and isp. nov. and *Cellicalichnus meniscatus* isp. nov., are created to include trace fossils attributable to crayfishes based on their association and morphological affinities with *Loloichnus baqueroensis*.
- *Dagnichnus titoi* and *Cellicalichnus meniscatus* are interpreted as breeding traces, calichnia, based on the presence of cells or burrows of small diameter and by comparison with breeding traces of marine Decapoda. Both trace fossils are the first breeding traces recorded from terrestrial crustaceans.
- Both ichnotaxa would represent two different breeding strategies: while *Cellicalichnus meniscatus* is interpreted as cells excavated from parental burrows, *Dagnichnus titoi* would be breeding structures completely produced in a different palaeoenvironment where the female probably released juveniles.
- The high density of *Loloichnus baqueroensis* parental burrows and the association to breeding trace fossils described herein indicate that crayfishes were soil engineers along the Cretaceous in southern South America, and that they had acquired many of the K-breeding behaviours recorded by insects in latest and post-Cretaceous soils, such as pelletal constructions and excavation of breeding cells.
- The K–T event probably changed environmental conditions in such a way that crayfishes finally became restricted to two small distributional areas in southern South America, and K-breeding insects replaced them as keystone organisms in Cainozoic and modern soils.

Acknowledgements

Authors thank to Gerardo Cladera for field guidance in the Baqueró locality, and to Claudio Iglesias and Minera Piedra Grande authorities and staff for assistance and hosting during our field research at Baqueró locality. Thanks to Eduardo Bellosi, Mariano Verde, María Victoria Sánchez, Laura Sarzetti, Marcelo Krause, Juan Farina and Daniel Speranza for assistance during the field research at the Baqueró locality. Thanks to Ricardo Britapaja, Major of Sarmiento City, for his permanent help during our research along years in Late Cretaceous localities of Sarmiento Department in Chubut Province. Thanks to two anonymous reviewers for improvement of the original manuscript. This research was supported by grant PICT 13286, from the Agencia Nacional de Promocion Cientifica y Tecnologica (Argentina) to Jorge F. Genise.

References

Alcorlo, P., Geiger, W., Otero, M., 2004. Feeding preferences and food selection of the red swamp crayfish, *Procambarus clarkii*, in habitats differing in food item diversity. Crustaceana 77, 435–453.

Archangelsky, S., 1967. Estudio de la Formación Baqueró, Cretácico Inferior de Santa Cruz, Argentina. Revista Museo La Palta (n. s.) Paleontología, vol. 5, pp. 63–171.

Bedatou, E., Melchor, R.N., Bellosi, E.S., Genise, J.F., 2006. Trazas fósiles de decápodos continentales en el Jurásico y Cretácico de Santa Cruz, Argentina. 4° Congreso Latinoamericano de Sedimentología y 11° Reunión Argentina de Sedimentología. San Carlos de Bariloche, p. 54. Abstract Volume.

Bedatou, E., Melchor, R.N., Bellosi, E.S., Genise, J.F., 2008. Crayfish burrows from Late Jurassic–Late Cretaceous continental deposits of Patagonia, Argentina. Their palaeoecological, palaeoclimatic and palaeobiogeographical significance. Palaeogeography, Palaeoclimatology, Palaeoecology 257, 169–184.

Bellosi, E.S., Sciutto, J.C., 2002. Laguna Palacios Formation (San Jorge Basin, Argentina): an Upper Cretaceous loess–paleosol sequence from Central Patagonia. 9th Reunión Argentina de Sedimentología, p. 15. Abstracts.

Bocic, V., Rudolph, E., López, D., 1988. Biología reproductive y dinámica poblacional del camarón de río, *Samastacus spiniformis* (Philippi, 1882) (Decapoda: Parastacidae). Boletin de la Sociedad de Biología de Concepción, Chile 59, 9–21.

Borsboom, A., 1998. Aspects of the biology and ecology of the Australian freshwater crayfish, *Euastacus urospinosus* (Decapoda: Parastacidae). Proceedings of the Linnean Society of New South Wales 119, 87–100.

Bottjer, D.J., 1985. Trace fossils and paleoenvironments of two Arkansas Upper Cretaceous discontinuity surfaces. Journal of Paleontology 59, 282–298.

Bridge, J., Jalfin, G., Georgieff, S., 2000. Geometry, lithofacies, and spatial distribution of Cretaceous fluvial sandstone bodies, San Jorge Basin, Argentina: outcrop analog for the hydrocarbon-bearing Chubut Group. Journal of Sedimentary Research 70, 341–359.

Bromley, R.G., 1990. Trace Fossils. Unwin Hyman, London. 280 pp.

Bromley, R.G., Asgaard, U., 1972. A large radiating burrow-system in Jurassic micaceous sandstones of Jameson Land, East Greenland. Grønlands Geologiske Undersøgelse. Rapport, vol. 49, pp. 23–30.

Bromley, R., Buatois, L., Genise, J.F., Labandeira, C., Mángano, G., Melchor, R., Schlirf, M., Uchman, A., 2007. Comments on the paper "Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses" by Stephen T. Hasiotis. Sedimentary Geology 200, 141–150.

Bullock, P., Federoff, N., Jongerius, A., Stoops, G., Tursina, T., 1985. Handbook for Soil Thin Section Description. Waine Research Publications, Albrighton. 152 pp.

Chamberlain, C.K., Baer, J.L., 1973. *Ophiomorpha* and a new thalassinid burrow from the Permian of Utah. Brigham Young University, Geology Studies 20, 79–94.

Cladera, G., Andreis, R., Archangelsky, S., Cúneo, R., 2002. Estratigrafía del Grupo Baqueró, Patagonia (provincia de Santa Cruz, Argentina). Ameghiniana 39, 3–20.

Corbella, H., 2005. Nuevas determinaciones de edad absoluta para el Grupo Baqueró, Macizo del Deseado, Patagonia extrandina. 16° Congreso Geologico Argentino, Actas, vol. 1, pp. 69–74.

Curran, H.A., 1976. A trace fossil brood structure of probable callianassid origin. Journal of Paleontology 50, 249–259.

Curran, H.A., White, A., 1999. Ichnology of Holocene carbonate eolianites on San Salvador Island, Bahamas: diversity and significance. In: Curran, A.H., Mylroie, J.E. (Eds.), Proceedings of the 9th Symposium on the Geology of the Bahamas and Other Carbonate Regions. Bahamian Field Station, San Salvador, pp. 22–35.

D'Alessandro, A., Bromley, R., 1995. A new ichnospecies of *Spongeliomorpha* from the Pleistocene of Sicily. Journal of Paleontology 69, 393–398.

de Gibert, J.M., Jeong, K., Martinell, J., 1999. Ethologic and ontogenic significance of the trace fossil *Sinusichnus sinuosus*, Pliocene, northwestern Mediterranean. Lethaia 32, 31–40.

de Gibert, J.M., Netto, R.G., Tognoli, F.M.W., Grangeiro, M.E., 2006. Commensal worm traces and possible juvenile thalassinidean burrows associated with *Ophiomorpha nodosa*, Pleistocene, southern Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 230, 70–84.

Dworschak, P.C., 2002. The burrows of *Callianassa candida* (Olivi 1792) and *C. whitei* Sakai 1999 (Crustacea: Decapoda: Thalassinidea). In: Bright, M., Dworschak, P.C., Stachowitsch, M. (Eds.), The Vienna School of Marine Biology: a Tribute to Jörg Ott. Facultas Universitätsverlag, Wien, pp. 63–71.

Dworschak, P.C., Ott, J.A., 1993. Decapod burrows in mangrove-channel and back-reef environments at the Atlantic Barrier Reef, Belize. Ichnos 2, 277–290.

Dworschak, P.C., Koller, H., Abed-Navandi, D., 2006. Burrow structure, burrowing and feeding behaviour of *Corallianassa longiventris* and *Pestarella tyrrhena* (Crustacea, Thalassinidea, Callianassidae). Marine Biology 148, 1369–1382.

Elliott, D.K., Nations, J.D., 1998. Bee burrows in the Late Cretaceous (Late Cenomanian) Dakota Formation, Northeastern Arizona. Ichnos 5, 243–253.

Fitzgerald, M.G., Mitchum Jr., R.M., Uliana, M.A., Biddle, K.T., 1990. Evolution of the San Jorge Basin, Argentina. Bulletin American Association of Petroleum Geologists 74, 879–920.

Forbes, A.T., 1973. An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea). Marine Biology 22, 361–365.

Frey, R.W., Howard, J.D., 1975. Endobenthic adaptations of juvenile thalassinidean shrimp. Bulletin of the Geological Society of Danmark 24, 283–297.

Genise, J.F., 2000. The ichnofamily Celliformidae for *Celliforma* and allied ichnogenera. Ichnos 7, 267–284.

Genise, J.F., 2001. Una nueva traza meniscada en paleosuelos de la Formación Bajo Tigre (Cretácico Inferior) de Santa Cruz (Argentina). Resúmenes de la IV Reunión Argentina de Icnología y Segunda Reunión de Icnología del Mercosur, Tucumán, p. 43.

Genise, J.F., 2004. Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, termites and ants. In: McIlroy, D. (Ed.), The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Special Publications of the Geological Society of London, vol. 228, pp. 419–453.

Genise, J.F., Bown, T.M., 1994. New Miocene scarabeid and hymenopterous nests and Early Miocene (santacrucian) paleoenvironments, Patagonian Argentina. Ichnos 3, 107–117.

Genise, J.F., Sciutto, J.C., Laza, J.H., González, M.G., Bellosi, E.S., 2002. Fossil bee nests, coleopteran pupal chambers and tuffaceous paleosols from the Late Cretaceous Laguna Palacios Formation, Central Patagonia (Argentina). Palaeogeography, Palaeoclimatology, Palaeoecology 177, 215–235.

Author's personal copy

Genise, J.F., Melchor, R.N., Bellosi, E.S., Krause, M., 2007. New insect pupation chambers (Pupichnia) from the Late Cretaceous of Patagonia (Argentina). Cretaceous Research 28, 545–559.
Gherardi, F., Barbaresi, S., Salvi, G., 2000. Spatial and temporal patterns in the movement of *Procambarus clarkii*, an invasive crayfish. Aquatic Sciences 62, 179–193.
Green, P.T., 2004. Burrow dynamics of the red land crab *Gecarcoidea natalis* (Brachyura, Gecarcinidae) in rain forests on Christmas Islands (Indian Ocean). Journal of Crustacean Biology 24, 340–349.
Grow, L., 1981. Burrowing behaviour in the crayfish, *Cambarus diogenes diogenes* Girard. Animal Behaviour 29, 351–356.
Growns, I.O., Richardson, A.M., 1988. Diet and burrowing habits of the freshwater crayfish, *Parastacoides tasmanicus tasmanicus* Clark (Decapoda: Parastacidae). Australian Journal of Marine and Freshwater Research 39, 525–534.
Hartnoll, R.G., Clark, P.F., 2006. A mass recruitment event in the land crab *Gecarcinus ruricola* (Linnaeus, 1758) (Brachyura: Grapsoidea: Gecarcinidae), and a description of the megalop. Zoological Journal of the Linnean Society 146, 149–164.
Hasiotis, S.T., 2000. The invertebrate invasion and evolution of Mesozoic soil ecosystems: the ichnofossil record of ecological innovations. In: Gastaldo, R.A., DiMichele, W.A. (Eds.), Phanerozoic Terrestrial Ecosystems. The Paleontological Society Papers, vol. 6, pp. 141–169.
Hasiotis, S.T., 2004. Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. Sedimentary Geology 167, 177–268.
Hasiotis, S.T., Mitchell, C.E., 1993. A comparison of crayfish burrow morphologies: Triassic and Holocene paleo- and neoichnological evidence, and the identification of their burrowing signatures. Ichnos 2, 291–314.
Hasiotis, S.T., Honey, J.G., 2000. Paleohydrologic and stratigraphic significance of crayfish burrows in continental deposits: examples from several Paleocene Laramide basins in the Rocky Mountains. Journal of Sedimentary Research 70, 127–139.
Hobbs, H.H., 1981. The Crayfishes of Georgia. Smithsonian Contributions to Zoology 318, 1–536.
Hobbs, H.H., 1988. Crayfish distribution, adaptive radiation and evolution. In: Holdich, D.M., Lowery, R.S. (Eds.), Freshwater Crayfish: Biology, Management and Exploitation. Croom Helm, London, pp. 167–212.
Hogue, C.L., Bright, D.B., 1971. Observations on the biology of land crabs and their burrow associates on the Kenya coast. Contributions in Science 210, 1–10.
Honan, J.A., Mitchell, B.D., 1995. Reproduction of *Euastacus bispinosus* Clark (Decapoda: Parastacidae), and trends in the reproductive characteristics of freshwater crayfish. Marine and Freshwater Research 46, 485–499.
Horwitz, P., 1995. The conservation status of Australian freshwater crayfish: review and update. Freshwater Crayfish 10, 70–80.
Horwitz, P., Knott, B., 1983. The burrowing habit of the koonac *Cherax plebeius* (Decapoda: Parastacidae). West Australian Naturalist 15, 113–117.
Horwitz, P.H., Richardson, A.M., 1986. An ecological classification of the burrows of Australian freshwater crayfish. Australian Journal of Marine and Freshwater Research 37, 237–242.
Horwitz, P.H., Richardson, A.M., Cramp, P.M., 1985a. Aspects of the life history of the burrowing freshwater crayfish *Engaeus leptorhyncus* at Rattrays Marsh, North East Tasmania. The Tasmanian Naturalist 82, 1–5.
Horwitz, P.H., Richardson, A.M., Boulton, A., 1985b. The burrow habitat of two sympatric species of land crayfish, *Engaeus urostrictus* and *E. tuberculatus* (Decapoda: Parastacidae). Victorian Naturalist 102, 188–197.
Kilian, E.F., 1959. La construcción de los tubos habitacionales del *Parastacus nicoleti* (Philippi). Facultad de Estudios Generales, Universidad Austral de Chile, vol. 1, pp. 1–7.
Lake, P.S., Newcombe, K.J., 1975. Observations on the ecology of the crayfish *Parastacoides tasmanicus* (Decapoda: Parastacidae) from South-Western Tasmania. Australian Zoology 18, 197–214.
Lewy, Z., Goldring, R., 2006. Campanian crustacean burrow system from Israel with brood and nursery chambers representing communal organization. Palaeontology 49, 133–140.
Litulo, C., 2005. Population structure and breeding biology of the hairy crab *Pilumnus vespertilio* (Fabricius, 1973) (Crustacea: Brachyura: Pilumnidae) in southern Mozambique. Journal of Natural History 39, 1359–1366.
Martin, A.J., 2006. A composite trace fossil of decapod and hymenopteran origin in the Rice Bay Formation (Holocene), San Salvador, Bahamas. The 12th Symposium on the Geology of the Bahamas and other Carbonate Regions, pp. 99–112.
Morrone, J.J., Lopretto, E.C., 1994. Distributional patterns of freshwater Decapoda (Crustacea: Malacostraca) in southern South America: a panbiogeographic approach. Journal of Biogeography 21, 97–109.
Nesbitt, E.A., Campbell, K., 2006. Fossil pantries crustacean debris storage chambers in late Cenozoic estuarine sands. Abstracts of the Philadelphia Annual Meeting of the Geological Society of America, pp. 178–182.
Petrulevicius, J., Nel, A., 2002. Oldest Petalurid dragonfly (Insecta: Odonata): a Lower Cretaceous specimen from south Patagonia, Argentina. Cretaceous Research 24, 31–34.
Powers, L.W., Bliss, D.E., 1983. Terrestrial adaptations. The Biology of Crustacea, vol. 8. Academic Press, New York, pp. 271–333.
Richardson, A.M., 1983. The effect of the burrows of a crayfish on the respiration of the surrounding soil. Soil Biology and Biochemistry 15, 239–242.
Richardson, A.M., Wong, V., 1995. The effect of a burrowing crayfish, *Parastacoides* sp., on the vegetation of Tasmanian wet Heathlands. Freshwater Crayfish 10, 174–182.
Rudolph, E.H., 1997. Aspectos fisicoquímicos del habitat y morfología de las galerias del camaron excavador *Parastacus nicoletti* (Philippi, 1882) (Decapoda: Parastacidae) en el sur de Chile. Gayana Zoología 61, 97–108.
Rudolph, E.H., 2002. Sobre la biología del camarón de río *Samastacus spinifrons* (Philippi 1882) (Decapoda: Parastacidae). Gayana 66, 147–159.
Sciutto, J.C., 1981. Geología del codo del Río Senguerr, Chubut, Argentina. VIII Congreso Geológico Argentino, San Luis, Actas, vol. III, pp. 203–219.
Shimoda, K., Tamaki, A., 2004. Burrow morphology of the ghost shrimp *Nihonotrypaea petalura* (Decapoda: Thalassinidea: Callianassidae) from western Kyushu, Japan. Marine Biology 144, 723–734.
Suter, P.J., 1977. The biology of two species of *Engaeus* (Decapoda: Parastacidae) in Tasmania II. Life history and larval development, with particular reference to *Engaeus cisternarius*. Australian Journal of Marine and Freshwater Research 28, 85–93.
Suter, P.J., Richardson, A.M., 1977. The biology of two species of *Engaeus* (Decapoda: Parastacidae) in Tasmania III. Habitat, food, associated fauna and distribution. Australian Journal of Marine and Freshwater Research 28, 95–103.
Tudhoppe, A.W., Scoffin, T.P., 1984. The effect of *Callianassa* bioturbation on the preservation of carbonate grains in Davis Reef lagoon, Great Barrier Reef, Australia. Journal of Sedimentary Petrology 54, 1091–1096.
Turvey, P., Merrick, J.R., 1997. Reproductive biology of the freshwater crayfish, *Euastacus spinifer* (Decapoda: Parastacidae), from the Sydney region, Australia. Proceedings of the Linnean Society of New South Wales 118, 131–155.
Vannini, M., Cannicci, S., Berti, R., Innocenti, G., 2003. *Cardisoma carnifex* (Brachyura): where have all the babies gone? Journal of Crustacean Biology 23, 55–59.
Verde, M., Martínez, S., 2004. A new ichnogenus for crustacean trace fossils from the late Miocene Camacho Formation of Uruguay. Palaeontology 47, 39–49.
Williams, D.D., Williams, N.E., Hynes, H.B., 1974. Observations on the life history and burrow construction of the crayfish *Cambarus fodiens* (Cottle) in a temporary stream in southern Ontario. Canadian Journal of Zoology 52, 365–370.