

# TRACE FOSSILS OF CICADAS IN THE CENOZOIC OF CENTRAL PATAGONIA, ARGENTINA

by J. MARCELO KRAUSE\*, THOMAS M. BOWN†, EDUARDO S. BELLOSI‡ and JORGE F. GENISE§

\*FONCYT – Universidad Nacional de la Patagonia San Juan Bosco, Ruta Provincial N° 1 s/n, Comodoro Rivadavia 9000, Chubut, Argentina; e-mail: krausemarcelo@yahoo.com

†Erathem-Vanir Geological Inc., 10350 Dover Street No D32, Westminster, Colorado 80021, USA

‡CONICET – Museo Argentino de Ciencias Naturales, Avenida Angel Gallardo N° 470, Buenos Aires 1405, Argentina

§CONICET – Museo Paleontológico Egidio Feruglio, Av. Fontana N° 140, Trelew 9100, Chubut, Argentina

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**Abstract:** Hemispherical pan or dish-shaped trace fossils from the Cenozoic of the Central Patagonia are attributed to the burrowing action of cicadas. A new ichnotaxon, *Feoichnus challa* igen. et isp. nov. is characterized by its hemispherical shape, mostly subvertical orientation, smoothed internal lining showing knobbly surface texture, and rough and irregular external surface devoid of ornamentation. The wall is composed of a lining plus a layer of soil material consolidated passively by cicada excretions. In other specimens the wall shows a repetition of linings and soil layers reflecting changes in the position of the chambers. Grooves, which represent traces of roots originally related to the feeding activities of cicada nymphs, are located in the wall of many specimens of *F. challa*. These grooves are subvertical to subhorizontal and show smooth surfaces with longitudinal stria-

tions. The cicadan origin of these traces is supported by comparison of the fossils to modern cicada nymph chambers and by laboratory experiments. The most significant characters that emerged from the comparison are the differential preservation of the basal part of the chambers, the interior lining with similar surface texture, and the presence of root traces in the wall and in the interior of the chamber. Additional records of *F. challa* from the Cretaceous–Pliocene of the USA, the Oligocene of Ethiopia, and the Miocene of the United Arab Emirates and Kenya complete the current information yielded by the known body fossil record to help understand the evolutionary history of cicadas.

**Key words:** trace fossils, *Feoichnus*, cicada nymph chambers, palaeosol, Cenozoic, Central Patagonia, Argentina.

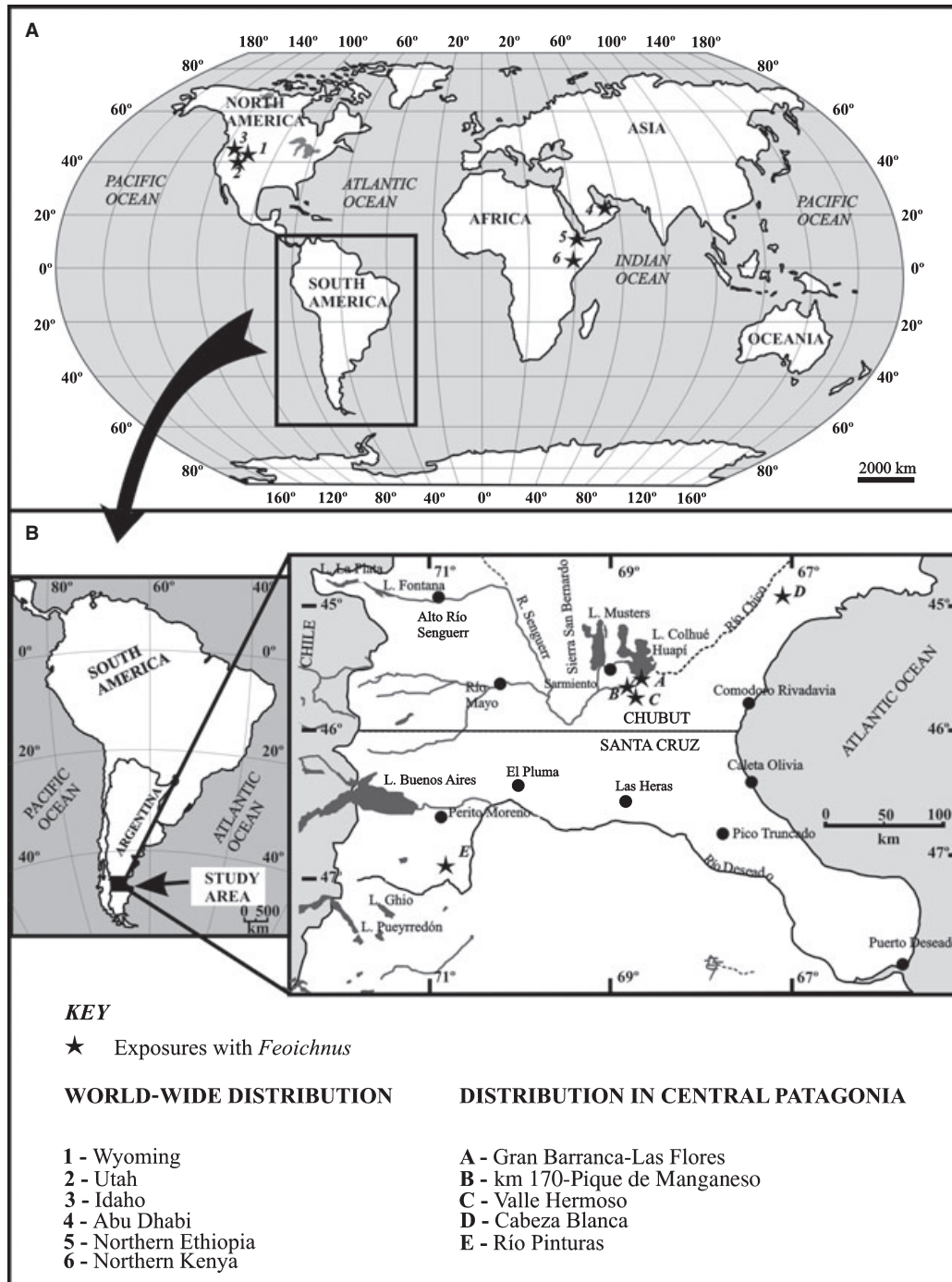
DURING recent years, sedimentological knowledge of Cenozoic continental units in central Patagonia (e.g. Simpson 1933; Feruglio 1949; Andreis *et al.* 1975; Spalletti and Mazzoni 1977, 1979; Bown and Larriestra 1990; Legarreta *et al.* 1990; Legarreta and Uliana 1994), has been complemented by new ichnological data (e.g. Bown and Ratcliffe 1988; Bown and Laza 1990; Genise and Bown 1990, 1994; Bellosi *et al.* 2001; Genise *et al.* 2001, 2002). Integration of this information has furthered our knowledge of the palaeoenvironmental conditions under which these Cenozoic units were deposited and of the evolutionary history of the organisms that produced the trace fossils (Genise, 2004). In this contribution, we focus on pan-shaped trace fossils first recognized in the Pinturas River area in Patagonia, and herein given the new name *Feoichnus challa*. This ichnofossil, recorded for the first time from palaeosols of the Lower–Middle Eocene Koluel Kaike Formation, had already been recorded from palaeosols of the Sarmiento (Middle Eocene–Lower Miocene) and the Pinturas (Lower–Middle Miocene) formations as a *nomen nudum* (e.g. Bellosi *et al.* 2001), ‘pan-shaped

traces’ (Bellosi 2004; Bellosi and Genise 2004; Genise *et al.* 2004) and ‘unattributed forms’ (Bown and Larriestra, 1990). However, until now the producer remained unknown. The principal goal of this contribution, resulting from the recognition and detailed analysis of several characters, is to identify cicadas as the producers of this trace fossil, and to provide a formal ichnotaxonomic treatment.

The importance of *Feoichnus challa* is based on its world-wide distribution. Additional records of one of us (TMB) include: the USA, where it occurs in the Upper Cretaceous Lance Formation (Wyoming), the Paleocene Fort Union Formation (Wyoming), the Paleocene–Eocene Claron Formation (Utah), the lower Eocene Colton Formation (Utah), the lower Eocene Willwood Formation (Wyoming), the Miocene Split Rock Formation (Wyoming), and the Miocene–Pliocene Glenns Ferry Formation (Idaho); the United Arab Emirates (continental Miocene of Abu Dhabi Emirate); northern Ethiopia (Chilga Formation, Upper Oligocene); and northern Kenya (Bulak Formation, Lower Miocene) (Text-fig. 1A).

These new records of *F. challa* complete the information yielded by the body fossil record to understand better the evolutionary history of cicadas, particularly those filling the gaps in the Cenozoic of South America and Africa. According to the body fossil record, true cicadas (Cicadoidea) extend back to the Early Jurassic in Europe,

and the digging habits of nymphs, documented by fossorial forelegs, can be traced to at least the Cretaceous of the USA. Cicadidae are known from the Eocene of the USA, whereas hairy cicadas included in different families come from the Jurassic and Cretaceous of South America, Europe and Asia (Grimaldi and Engel 2005).



TEXT-FIG. 1. Localities with *F. challa*. A, worldwide distribution. B, distribution in Central Patagonia.

## GEOLOGICAL SETTING

Specimens of *F. challa* examined for this contribution are from four localities of the Koluel Kaike and Sarmiento formations in south-central Chubut Province, Argentina: Gran Barranca, Las Flores, km 170, and Pique de Manganeso, all situated south of Colhué Huapi Lake (Text-fig. 1B). There, exposures consist of Lower Eocene–Lower Miocene rocks of the Río Chico Group and the Sarmiento Formation, both well known because of their important fauna of fossil mammals (Ameghino 1906; Simpson 1940; Cifelli 1985) and, more recently, for their ichnological record (Bellosi *et al.* 2001; Genise *et al.* 2001, 2004; Bellosi 2004; Bellosi and Genise 2004). In addition, other specimens examined come from localities of the Pinturas Formation, near the Pinturas River, in the north-west of Santa Cruz Province, Argentina.

The Koluel Kaike Formation forms the upper portion of the Río Chico Group (Legarreta and Uliana 1994) and is distinctive in being composed almost exclusively of pedogenically altered siliceous tuffs containing abundant ferric nodules. Despite the high degree of pedogenesis, rare trace fossils are entombed in the palaeosols.

The Sarmiento Formation is a dominantly pyroclastic succession rich in fossil mammals. It is largely composed of pyroclastic mudstones, with subordinate bentonites, sandstones and conglomerates (Spalletti and Mazzoni 1977, 1979). The origin of most of these deposits is attributed to aeolian processes (Mazzoni 1979; Spalletti and Mazzoni 1979). Another distinctive feature of the Sarmiento Formation is the high frequency of palaeosols, which bear an important ichnofauna comprising *Coprinisphaera*, *Teisseirei*, *Pallichnus*, *Celliforma*, and the pan-shaped trace fossil described herein (Bellosi *et al.* 2001; Bellosi 2004; Bellosi and Genise 2004; Genise *et al.* 2004). The formation consists of six members that are separated from each other by unconformities. These are the Gran Barranca, Rosado, Lower and Upper Puesto Almendra, Vera, and Colhué Huapi members (Spalletti and Mazzoni 1979; Bellosi and Genise 2004; Bellosi *et al.* 2005), all represented at the Gran Barranca locality. Although these members are similar lithologically, their separation by unconformities (Kay *et al.* 2001; Bellosi *et al.* 2002; Bellosi *et al.* 2005) illustrates their sequence-stratigraphic importance. The contact between the Sarmiento Formation and the underlying Koluel Kaike Formation is transitional, being defined by a 6–8-m layer of non-silicified tuffs containing ferric nodules (e.g. Las Flores, km 170).

The Pinturas Formation represents deposition of pyroclastic and epiclastic aeolian material (Bown and Larriestra 1990; Kramarz and Bellosi 2005). It crops out in north-west Santa Cruz Province, and represents infilling of an irregular topography. The relative development of

Pinturas palaeosols shows that deposition was characterized by a fluctuation in sedimentation rate, with the most mature palaeosols having been developed during periods of relatively low sedimentation rates (Bown and Larriestra 1990). Also rich in fossil mammals (Ameghino 1906; Frenguelli 1931; Pascual *et al.* 1965; Pascual and Odreman Rivas 1971; Bown and Larriestra 1990), the Pinturas Formation also contains an important ichnofauna in the form of trace fossils attributed to rodents, beetles, bees and termites (Bown and Larriestra 1990; Bown and Laza 1990; Genise and Bown 1994). It reflects a combination of humid and drier palaeoenvironments (Bown and Larriestra 1990; Kramarz and Bellosi 2005). Abundant rhizoliths, tree-hole steinkerns, platyrrhine primate remains, and termite nests indicate a humid climate (Bown and Larriestra 1990; Bown and Laza 1990; Genise and Bown 1994; Kramarz and Bellosi 2005). By contrast, dune deposits, astrapothere remains, bee and dung-beetle nests, and the absence of primates suggest a less humid to semi-arid, open herbaceous environment (Bown and Larriestra 1990; Genise and Bown 1994; Genise *et al.* 2000). In addition to the ichnofossils mentioned above, Bown and Larriestra (1990) recorded the presence of ‘unattributed forms’, which include those described herein.

## SYSTEMATIC ICHNOLOGY

All examined material is housed in the collections of the Museo Argentino de Ciencias Naturales, Buenos Aires (MACN-Icn); the Museo Desiderio Torres, Sarmiento, Chubut (MDT); the Museo Paleontológico Egidio Feruglio, Trelew, Chubut (MPEF-IC); and the Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Chubut (UNPSJB-IC).

### Ichnofamily PALLICHNIDAE Genise, 2004

#### Ichnogenus FEOICHNUS igen. nov.

- 1990 ‘unattributed forms’; Bown and Larriestra, p. 107.
- 2001 *Feoichnus* Bellosi *et al.*, p. 31 (*nomen nudum*).
- 2004 ‘pan-shaped traces’; Bellosi, p. 19.
- 2004 ‘pan-shaped traces’; Bellosi and Genise, pp. 20, 22, 25; figs 3–5.
- 2004 ‘pan-shaped traces’; Genise *et al.*, p. 369, fig. 6c; p. 371.

*Derivation of name.* One of us (TMB) informally named this trace fossil after Pinturas exposures along the watercourse known as Arroyo Feo, south of Perito Moreno, in north-west Santa Cruz Province, Argentina. It was from specimens found there that *Feoichnus* was originally recognized as a trace fossil. The name also derives from the Spanish word *feo*, meaning ugly, because of its quite irregular shape.

*Type and only ichnospecies. Feoichnus challa* isp. nov.

**Diagnosis.** Usually hemispherical, upwardly concave, pan- or dish-shaped structures, more rarely conical, and lacking any active filling. Internal surface is lined, smooth and regular, or in some cases with a surface texture constituted by irregular ridges with a knobby appearance. External surface is rough and irregular, without ornamentation. Some specimens may show a succession of several lined layers at the base or laterally. A common feature is the presence laterally of a small, subvertical to subhorizontal groove, which in some cases shows a smooth surface with longitudinal striations or arise from a hole in the wall.

**Remarks.** Isolated, thick-walled specimens can be confused with a half specimen of *Coprinisphaera*, a trace fossil attributed to dung beetle brood balls (Laza 2006). However, *Coprinisphaera* (Coprinisphaeridae) bears a constructed wall, whereas *Feoichnus* (Pallichnidae) has a lined one. When broken specimens of *Coprinisphaera* that resemble *Feoichnus* are found in the field, they are usually associated with complete specimens, and therefore allow unequivocal identification of these trace fossils. In contrast, however, many outcrops of various ages worldwide bear only *Feoichnus* specimens. Ichnogenera with roughly similar morphologies have been defined from marine deposits, among them *Conostichus*, *Bergaue-ria* and *Astropolichnus* (Branson 1959; Chamberlain 1971; Pfefferkorn 1971; Crimes *et al.* 1977). All of these are plug-shaped ichnofossils interpreted as cubichnia or domichnia, predominantly of actinarian sea anemones (Pemberton *et al.* 1988). These plug-shaped ichnogenera also have external ornamentation that probably relates to anatomical features of the tracemaker (Pemberton *et al.* 1988). Such a patterned surface texture is absent from *Feoichnus*.

*Feoichnus challa* isp. nov.

Plate 1, figures 1–6; Text-figs 2–4

**Derivation of name.** From the Mapuche (a Patagonian native language) word *challa*, meaning vessel for saucers.

**Holotype.** A pan-shaped specimen with well-developed internal surface texture (MPEF-IC 1469) (Text-figs 3A–C, 4C) from Gran

Barranca, Chubut, Argentina (Middle Eocene–Lower Miocene Sarmiento Formation).

**Paratypes.** A pan-shaped specimen with two coats and a groove (MACN-Icn 344) (Text-fig. 4D), from Gran Barranca; an elongate, subvertical specimen with two floors (MACN-Icn 365), from Gran Barranca; a conical specimen with a groove (MACN-Icn 366) (Text-fig. 4E), from Gran Barranca; an elongate, subhorizontal specimen with a groove (UNPSJB-IC 139) (Pl. 1, fig. 6), from Las Flores, Chubut (Lower–Middle Eocene Koluel Kaike Formation).

**Additional material.** 30 specimens from Las Flores, Chubut: UNPSJB-IC 135–144, MPEF-IC 1400–1414, MDT 486–490; 13 specimens from km 170, Chubut: UNPSJB-IC 145–151, MPEF-IC 1415–1420; 4 specimens from Pique de Manganeso, Chubut: MPEF-IC 1421–1424; all from the Lower–Middle Eocene Koluel Kaike Formation. 28 specimens from km 170, Chubut: UNPSJB-IC 152–159, MPEF-IC 1425–1444; 153 specimens from Gran Barranca, Chubut: MACN-Icn 242–251, 260–261, 336–369, 389–391, 1501–1517, 1557–1559, 1561–1565, 1575–1579, 1736; UNPSJB-IC 54, 56–61, 160–190, MPEF-IC 1445–1474, MDT 491–495; 10 specimens from Valle Hermoso, Chubut: MACN-Icn 1865–1866, 1873–1880; 9 specimens from Cabeza Blanca, Chubut: MACN-Icn 95; all from the Middle Eocene–Lower Miocene Sarmiento Formation. 67 specimens from Perito Moreno, Santa Cruz; Lower–Middle Miocene Pinturas Formation: MACN-Icn 84–90.

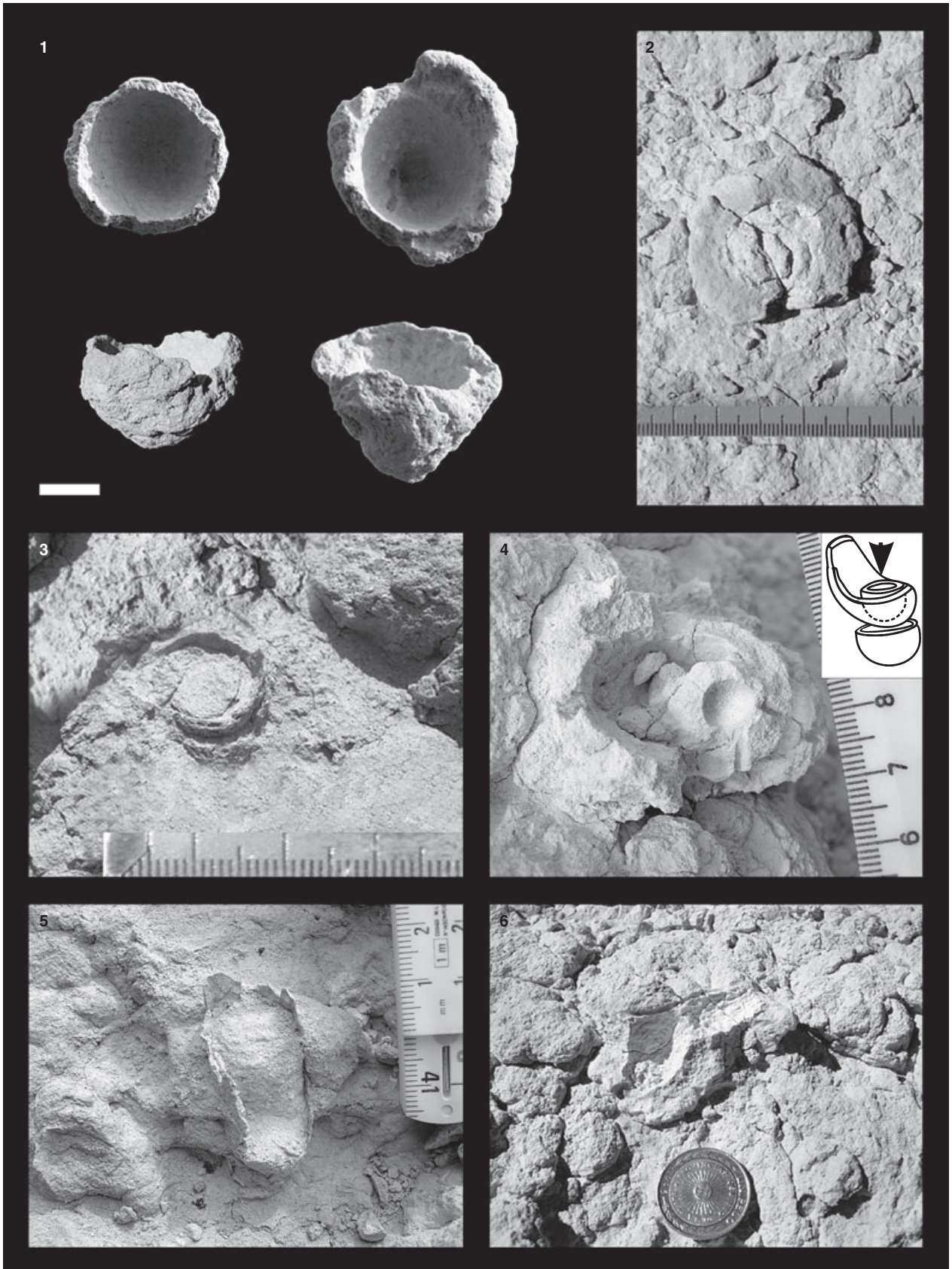
**Diagnosis.** As for the ichnogenus.

**Description.** The detailed examination of 204 specimens allowed the recognition of four main features, which are analyzed separately in this section.

1. Shape and orientation. The morphology of *Feoichnus challa* is relatively simple, albeit specimens range from showing clearly defined shapes to being very irregular. They are upwardly concave structures resembling little pans or dishes, or in some cases conical cups, and they show a predominant subvertical orientation (Pl. 1, figs 1–4). The upper boundary of *F. challa* is rarely flat and regular; instead an irregular upper edge is usual (Pl. 1, figs 1–6). Occasionally, the structures are grouped, either superimposed vertically or one within the other. Each of the individual specimens of a group preserves the typical shape and orientation (Pl. 1, fig. 4). Shape and orientation show certain degrees of variation, as exemplified by more elongated or ellipsoidal specimens, which occur in the Koluel Kaike and Sarmiento formations (Pl. 1, figs 5–6). However, these specimens share significant

#### EXPLANATION OF PLATE 1

Figs 1–6. *Feoichnus challa* igen. et isp. nov. 1, pan-shaped (MACN-Icn 260) and conical (MACN-Icn 363) specimens in plan and side views. 2, thick-walled specimen, UNPSJB-IC 145. 3, thin-walled specimen, UNPSJB-IC 187. 4, vertically superposed specimens (plan view), MPEF-IC 1413. 5, subvertical, elongate specimen, UNPSJB-IC 169. 6, subhorizontal, elongate specimen, paratype, UNPSJB-IC 139. Scale bar represents 1 cm; coin diameter is 2.2 cm.



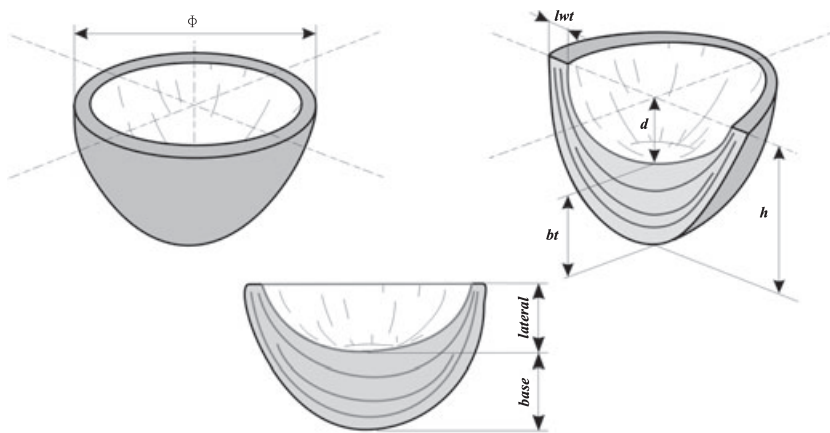
- features with the pan-shaped trace fossils: an internal lined surface with the same inner knobby texture, a rough and irregular external surface, and in some cases the presence of grooves. In addition, these structures show broken, irregular boundaries at one end and orientations that range from subvertical to subhorizontal (Pl. 1, figs 5–6).
2. Dimensions. Three measures were taken for the characterization of the hemi-chamber in all examined specimens (N = 204): external diameter, height and depth (Text-fig. 2). A fourth measure, wall thickness, is analyzed in the next section. Height is the distance from the upper boundary to the external surface of the wall at the base of the specimen; depth is the distance to the internal surface of this wall. The obtained ranges (Table 1) in diameter, height and depth were: 5.0–40.0 mm, 2.80–34.0 mm, and 0.60–16.0 mm, respectively (N = 204). The elongated specimens of *Feoichnus challa* range from 15.0 to 31.0 mm (N = 9) in equatorial diameter, 32.5 to 55.0 mm (N = 9) in height and 21.0 to 44.0 mm (N = 9) in depth.
  3. Wall. *Feoichnus challa* is usually removable from the rock matrix, showing a wall with a wide variation in thickness (Pl. 1, figs 2–3; Tables 1–2). The external aspect of this wall is irregular in shape and texture. The internal surface is more regular, and characterized by a more or less white, smooth, very thin (1.0–2.0 mm) layer. This layer has a knobby surface texture, consisting of irregular, very thin (1.0–2.0-mm wide) ridges (Text-fig. 4C).

In subvertical specimens, it is possible to divide the wall into a base and a lateral wall (Text-fig. 2). The base is upwardly concave, ranging from 1.3 to 23.5 mm in thickness (N = 204). Occasionally, when it is broken, a succession of stacked internal smooth surfaces, 1.0–2.0 mm thick, separated by unpatterned, fine material, is present. All of these layers are floors (Text-

fig. 4A). The lateral part of the wall can be defined as an upward extension of the base. Its height (the depth of the structure) ranges from 0.6 to 16.0 mm (N = 204) and its thickness from 0.5 to 12.0 mm (N = 204). Elongated specimens show an increase in wall thickness at both ends. Thickness ranges from 3.0 to 10.0 mm (N = 9) at the ends, and from 1.0 to 9.0 mm laterally (N = 9). In some specimens, the lateral wall also exhibits several smooth surfaces, similar in thickness to the floors, separated by unarranged material, which are called coats herein. These are usually concentrated only in one part of the lateral wall (Text-fig. 4B). The smooth surfaces, floors and coats, have a surface texture, thickness and colour similar to that of the inner surface of the wall, suggesting an identical origin.

The base is always thicker than the lateral wall (Table 1). It is noticeable that specimens of *F. challa* from Central Patagonia show a decrease in wall thickness from those of the Lower–Middle Eocene Koluel Kaike Formation to those of the Lower–Middle Miocene Pinturas Formation (Table 2).

Micromorphologically, volcanic glass fragments and subordinate quartz and plagioclase grains constitute the coarse fraction of the wall. This fraction is present in 5 per cent of the material. Voids amount to 30–40 per cent, particularly at the base. These, mainly without interconnection, are spherical to irregular and elongate, and in some cases almost parallel to the coats and floors. Clay minerals and iron and manganese sesquioxides are present. Both types of compound fill or coat fractures and voids within the wall, producing a differential impregnation within the wall, the filling and the rock matrix (Text-fig. 5A–C). The sesquioxides are useful for defining the external as well as the internal boundaries of the wall. Floors and coats are recognized by a dark, thin layer, which is a result of the strong staining with sesquioxides (Text-fig. 5A–D). Furthermore, the wall is more stained than the rock matrix or the filling (Text-



TEXT-FIG. 2. Measurements of *F. challa* specimens.

- Φ external diameter
- h height
- d depth
- lwt lateral wall thickness
- bt base thickness
- d/h depth-height ratio

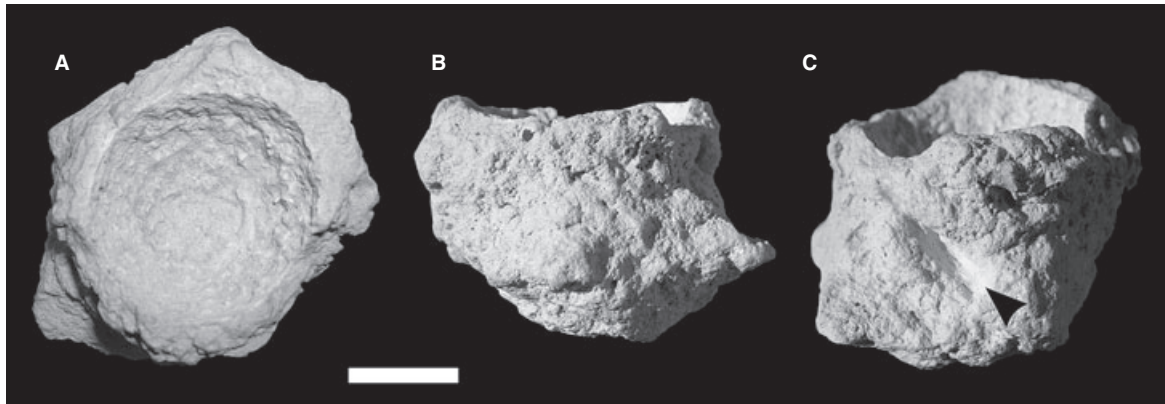
(pst) pan-shaped *F. challa* specimen  
 (ct) conical *F. challa* specimen

■ soil material  
 — lined surface

Where:  $h = d + bt$

and

(Φ = constant)  $d/h$  (pst) <  $d/h$  (ct)



**TEXT-FIG. 3.** *Feoichnus challa* igen. et isp. nov., holotype; MPEF-IC 1469. A, plan view. B, side view. C, front view showing a diagonal groove (black arrow). Scale bar represents 1 cm.

**TABLE 1.** Measurements of *F. challa*.

Shape		Dimensions (mm)		$\Phi$	$d$	$h$	$lwt$	$bt$
		Range	Mean					
Pan-shaped specimens (N = 204)	Range	5.0–40.0	0.6–16.0	2.8–34.0	0.5–12.0	1.3–23.5		
	Mean	21.5	7.2	15.3	3.1	8.8		
Elongated specimens (N = 9)	Range	15.0–31.0	21.0–44.0	32.5–55.0	1.0–9.0	3.0–10.0		
	Mean	24.2	33.1	42.3	3.4	4.5		

$\Phi$ , external diameter;  $d$ , depth;  $h$ , height;  $lwt$ , lateral wall thickness;  $bt$ , base thickness.

fig. 5A–C). In some cases, elongated grains which are close to floors and coats, are orientated parallel to these surfaces (Text-fig. 5D). The remaining part of the wall shows a random arrangement of grains.

4. Grooves. A thin, short groove is present in about 40 per cent of the specimens studied (Text-fig. 4D–E). This feature ranges from 1.0 to 7.0 mm in width and 1.1 to 25.0 mm in length (N = 32). These grooves are subvertical to subhorizontal with a smooth surface and some longitudinal striations. They arise in a notch of the upper edge or in a hole in the wall of some specimens, running along the outer surface (Text-figs 4D–E). Small holes lacking an associated groove, which are about 1.0 mm in diameter and have smooth internal surfaces, can be present in the wall.

## DISCUSSION

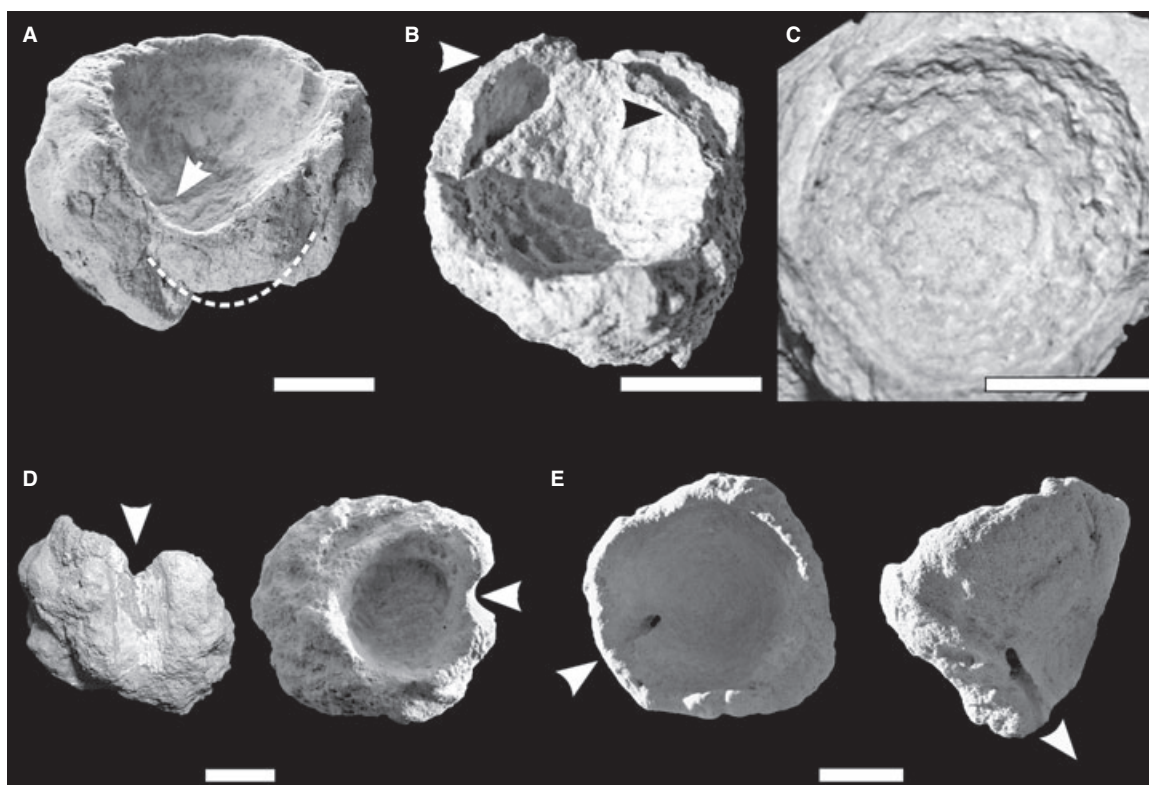
### Chamber

Most of the specimens observed in the Sarmiento Formation occur in alfisols and andisols in B horizons, which are subsurface horizons that can be recognized by clay illuviation (Bt horizon) or strong gleying (Bg hori-

zon). *Coprinisphaera* and *Celliforma*, which are completely underground chambers, also occur in these horizons. This shows that *F. challa* was not a structure intruded merely into the surface of the original soil, but buried to a certain depth. Being a completely underground chamber, it should have had a roof, no matter what its morphology and function. Hence, the trace fossil analyzed is only part of an original complete spherical or oval chamber, particularly its basal portion. The irregular upper boundary would be the result of disintegration of the roof by pedogenic processes (Text-fig. 6A–F). Given that differences in the original content of organic matter in traces control their potential for preservation (Genise and Bown 1994), it can be assumed that the basal portion had a higher content of organic matter than the upper part. Only in exceptional cases would this organic matter have reached the sides of the structure to some extent, resulting in the elongated specimens described above.

The organic matter involved should have been sufficiently fluidized to allow both the production of a lining in the interior of the chamber and the consolidation of a discrete wall, essentially composed of undisturbed soil material that lacks any evidence of moulding by the producer. Therefore, the pan-shaped specimens would result from differential moistening of the chamber. The dominant subvertical orientation would have favoured a major concentration of the organic liquid at the bottom of the chamber. Subhorizontal orientation would have allowed the preservation of other parts of the original chamber instead of only the base. Thus, ellipsoidal specimens record the more complete shape of the original chamber.

The pan-shaped traces can, therefore, be attributed to: (1) predominant subvertical orientation of chambers; (2) differential impregnation of the chamber bases with liquid organic matter; and consequently (3) differential preservation of the base (Text-fig. 6A–F).



**TEXT-FIG. 4.** Main features of *F. challa*. A, specimen showing the older (white dashed line) and the younger floor (white arrow); MACN-Icn 369. B, specimen showing two coats (white and black arrows); MACN-Icn 249. C, detail of the internal surface texture in the holotype; MPEF-IC 1469. D, side and plan views of a paratype, showing a subvertical groove in the wall (white arrows); MACN-Icn 344. E, plan and side views of a paratype, showing the hole and the groove produced by the feeding root (arrows show the inferred orientation of the root); MACN-Icn 366. Scale bars represent 1 cm.

A first approximation of the potential trace-maker can be made, considering the characters related to the shape described previously. Oval underground chambers, whose bottoms underwent impregnation with liquid organic matter, are compatible with those of cicadas (e.g. Marlatt 1907; Beamer 1928; Boulard 1965). The nymphs of these insects, such as most Sternorrhyncha (Boulard 1965), which excavate feeding chambers within the soil, commonly excrete abundant anal liquid. Furthermore, Torres (1953) recorded fifth instar cicada nymphs inhabiting mud cells with anal secretions filling up to half of the chamber. The size range of *Feoichnus* suggests different developmental stages of a single producer, or even individuals of the same stage and differences in food availability. White and Lloyd (1975) showed that differenced-sized cicada nymphs of the same age may be a result of differences in the availability of food.

Field research was carried out in a modern orchard in Lanús (Buenos Aires Province, Argentina) during December 2005, where cicada adults (*Dorisiana drewseni* Stål) were abundant in previous years. Soil under trees showing old exuviae of cicadas was excavated up to 30–50 cm from the surface, where nymphs inside oval, elongated,

cells were found (Text-fig. 7A). Complete cells resemble the elongate specimens of *Feoichnus* (Text-fig. 7C). In addition, while excavating the soil for extant cells, several pan-shaped structures, actually the bottoms of old cells, were recovered from the soil (Text-fig. 7B). These present-day specimens indicate that the impregnated bottoms of cells are capable of being preserved differentially in the soil, after pedogenic processes destroyed the upper part of the cells.

#### Wall

Most recorded insect trace fossils in palaeosols have two types of wall: lined or constructed (Genise 2004). Even when a thick wall suggests a constructed origin, its thickness is not sufficient to distinguish it from lined walls, as claimed by Genise (2004). A constructed wall is produced when the insect has processed all the soil material that constitutes the wall, e.g. by moulding pellets and then positioning them as bricks. This process results in both the internal and external surfaces of the wall being moulded and, as such, they have the potential to exhibit pat-



**TABLE 2.** Thickness of the lateral wall shown by specimens of *F. challa* in the formations studied in Central Patagonia.

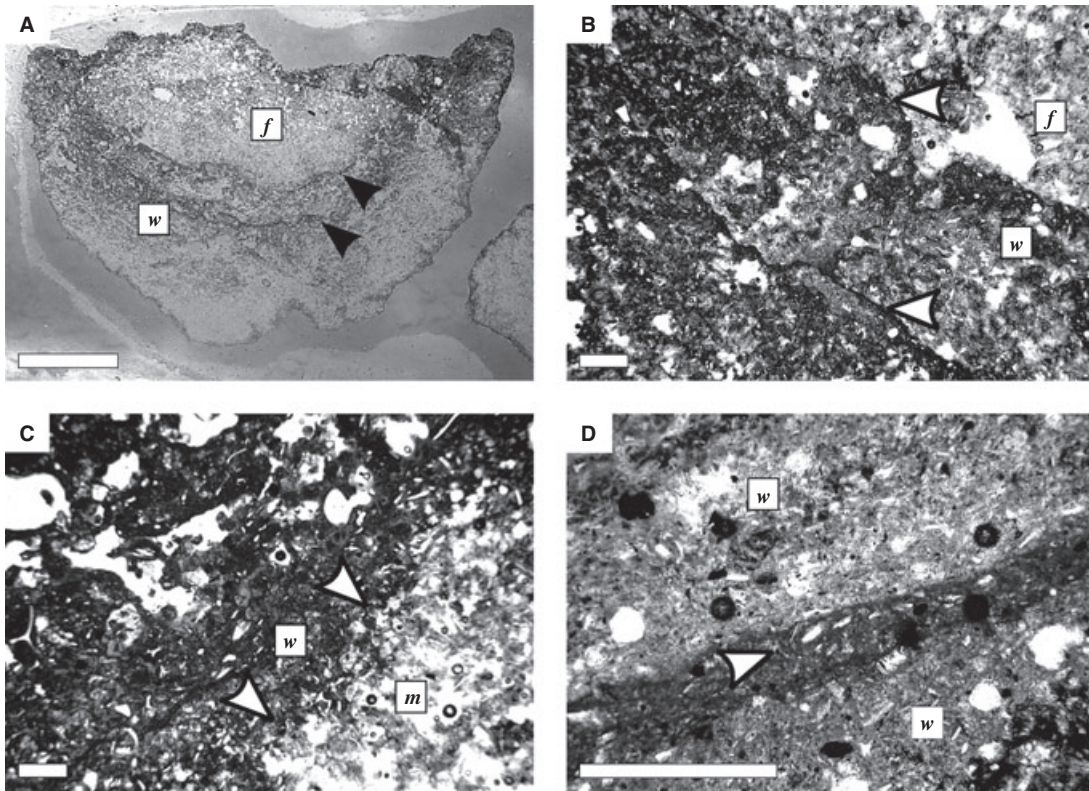
Stratigraphical Unit		Lateral wall thickness (mm)		
		Range	Mean	Wall thickness vs. age
Pinturas Formation (Lower–Middle Miocene) (N = 61)		0.4 – 5.7	1.9	
Sarmiento Formation (Middle Eocene–Lower Miocene)	Colhué Huapi Member (N = 27)	1.0 – 2.7	2.2	
	Puesto Almendra Member (N = 27)	1.8 – 4.5	2.6	
	Gran Barranca Member (N = 32)	1.3 – 7.6	3.4	
Koluel Kaike Formation (Lower–Middle Eocene) (N = 34)		1.0 – 11.0	5.8	

terned surface textures (bioglyphs). The external aspect of the wall of *Feoichnus challa* is irregular in shape and texture, indicating no interaction of the producer with this particular surface of the wall.

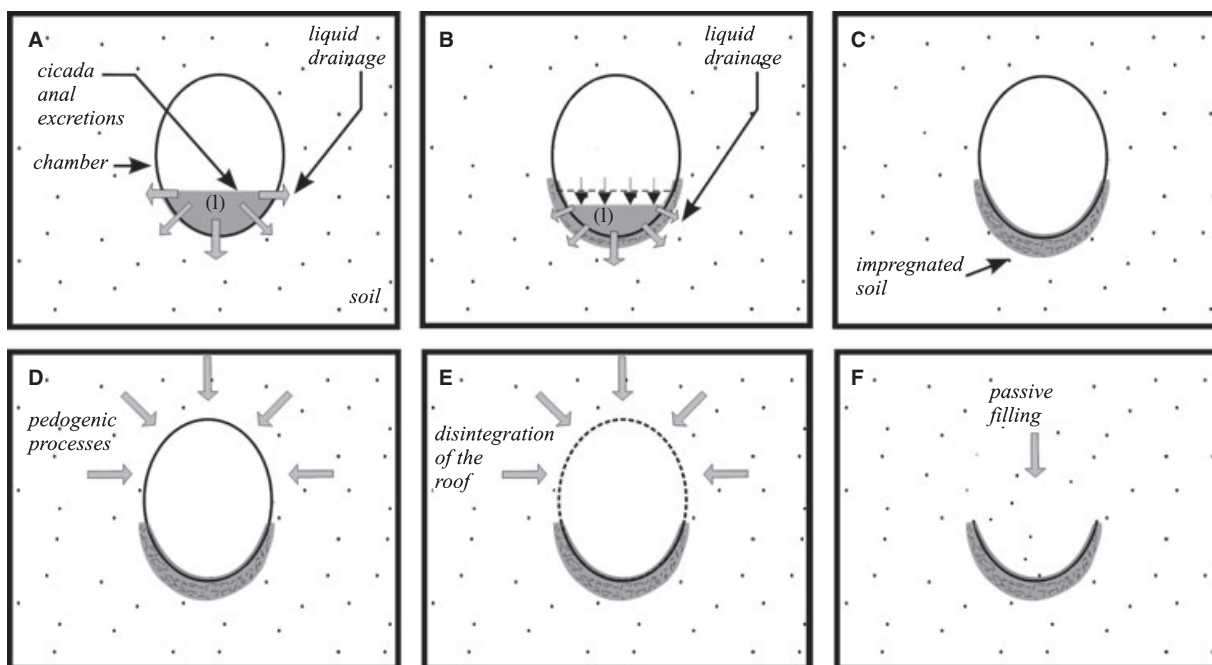
It is considered here that the *Feoichnus* wall corresponds to an inner, smooth lining that bears remains of the surrounding original soil which was passively impregnated with liquid organic matter. Micromorphologically, the smooth inner layers and the external wall lack any evidence of either pelletal structure or accumulation of fine material owing to fluidization. Both characters are typical of constructed walls (Genise and Hazeldine 1998; Genise and Poiré 2000).

In addition, in the laboratory, artificial pan-shaped structures were obtained by passive liquid diffusion, pouring dilute glue into hemispherical depressions in fine sand and ash dust. The liquid expands from the depression into the surrounding matrix, resulting in a pan-shaped structure that is easily removable (Text-fig. 8A–B). Wall thicknesses increased when more liquid was applied.

The wall of specimens of *Feoichnus challa* can be interpreted as an inner lining plus the part of the soil surrounding the excavated chamber that was originally impregnated with organic fluids. In those specimens showing tiered floors and coats they can be interpreted as a superposition of inner linings with intercalated soil



**TEXT-FIG. 5.** Micromorphology of *F. challa*. A, view of a thin section showing a lighter filling and a darker wall; floors and coats are recognized by the darkest thin lines; black arrows indicate the older and the younger floor. B, filling (lighter) and wall (darker); white arrows indicate two floors. C, contact (white arrows) between the rock matrix (lighter) and the wall (darker). D, detail of a floor, showing the orientation of elongated grains. Scale bars represent 0.5 mm. *f*, filling; *w*, wall; *m*, rock matrix.



**TEXT-FIG. 6.** Production and taphonomic processes involved in the preservation of *F. challa*. A–C, impregnation of the soil around the base of the chamber with the liquid organic matter (l) produced by the cicada nymph. D–E, progressive disintegration of the non-impregnated roof chamber by pedogenic processes. F, passive filling of the remaining basal hemi-chamber with soil material.

material among them. This origin is compatible with both thin and thick walls. The thickness of the wall could be the result of two different processes. In the first of these, the thickness may have been increased when more liquid organic matter, possibly favoured by more available water in the environment, was poured against the inner surface of the wall, as shown in specimens resulting from laboratory experiments. Accordingly, the decrease in the wall thickness higher up in the stratigraphic record would be a response to increasingly drier climates in Central Patagonia from the Eocene to the Miocene. The second process reflects the accumulation of layers composed of lined surfaces plus soil material. In this case, the thickness of the bottom or the side of the specimens increased when more stacked floors or coats were involved. This process may also have been enhanced by increasing incorporation of the organic fluids.

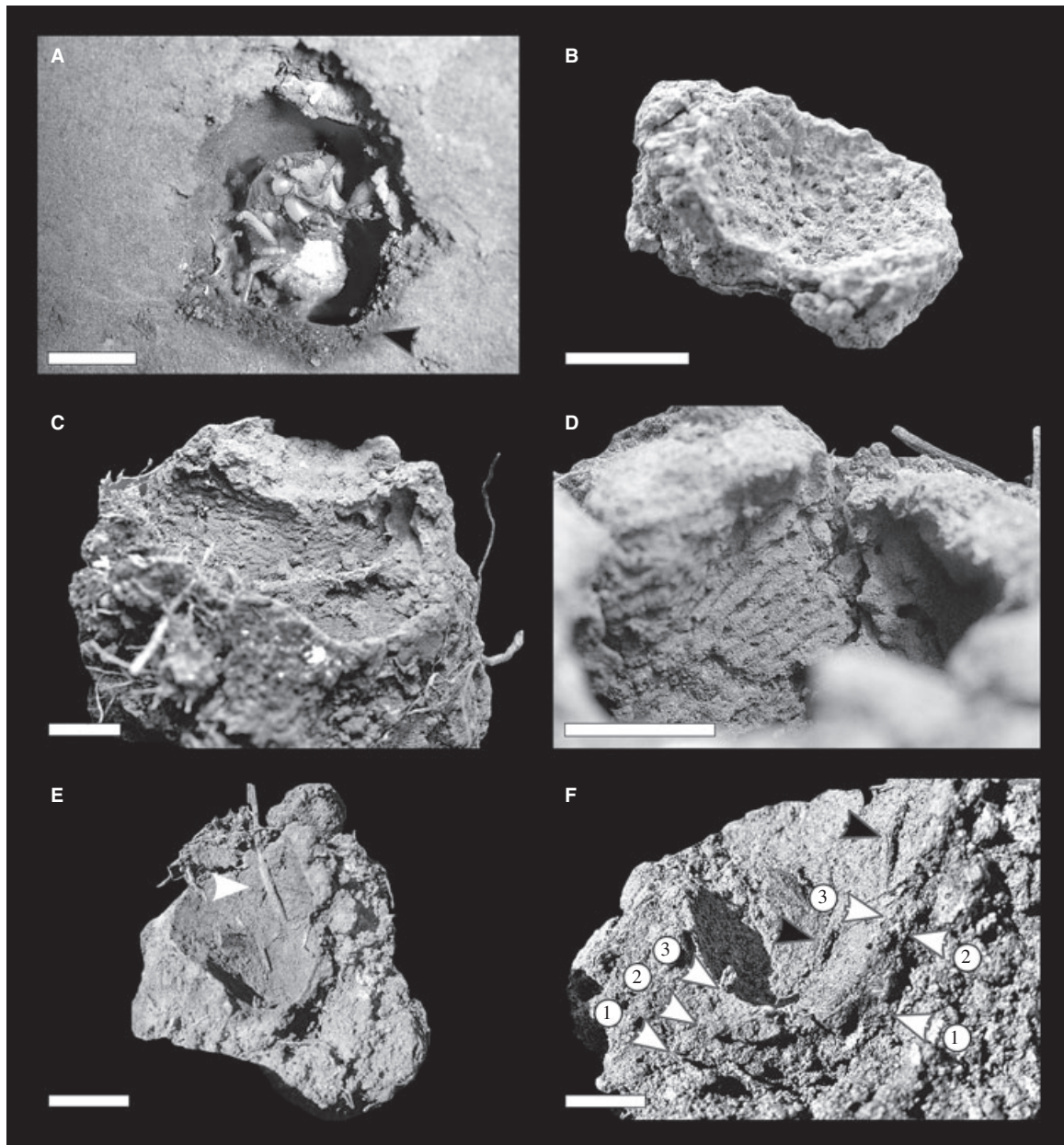
The repetition of floors and/or coats can be explained by the displacement of the chamber. As in other ichnofossils (e.g. *Conostichus*, *Bergaueria*), the vertical succession of several floors seems to have been related to the upward migration of the organism (Branson 1959; Chamberlain 1971; Pfefferkorn 1971). In the marine trace fossils above, the cause of the migration was an increment in the rate of sedimentation, whereas in *F. challa* the chamber displacement can be interpreted according to the behaviour of cicada nymphs. After hatching, the first instar nymph reaches the soil, digs downward and makes

a cell enclosing itself and a part of a root to feed on (e.g. Marlatt 1907; Beamer 1928; Dybas and Lloyd 1962). Chambers are then relocated or enlarged when the nymphs search for new roots or new parts of the same root on which to feed (Beamer 1928; Dybas and Lloyd 1962; Boulard 1965; White and Strehl 1978). An upward shift of the chamber is compatible with the presence of stacked floors. A new floor would be produced by smoothing the surface of removed material from the upper half of the chamber (Text-fig. 9A–C). In addition, a lateral displacement of the chamber would explain the presence of successive coats (Text-fig. 9A–C). In some chambers of *Dorisiana drewseni*, tiered floors and coats could be recognized (Text-fig. 7F).

#### Surface texture

The inner surface texture of *F. challa* is probably the result of anal secretions of cicada nymphs that moistened the wall. The secretions are used by some extant species to moisten the earth and remould their mud cells (Boulard 1965; White and Strehl 1978), thereby generating 'plastered' inner surfaces in the chambers (e.g. White *et al.* 1979).

Feeding chambers of *Dorisiana drewseni* show on the internal surface of their walls a texture composed of pits and scratches (Text-fig. 7B–D). The knobby texture is

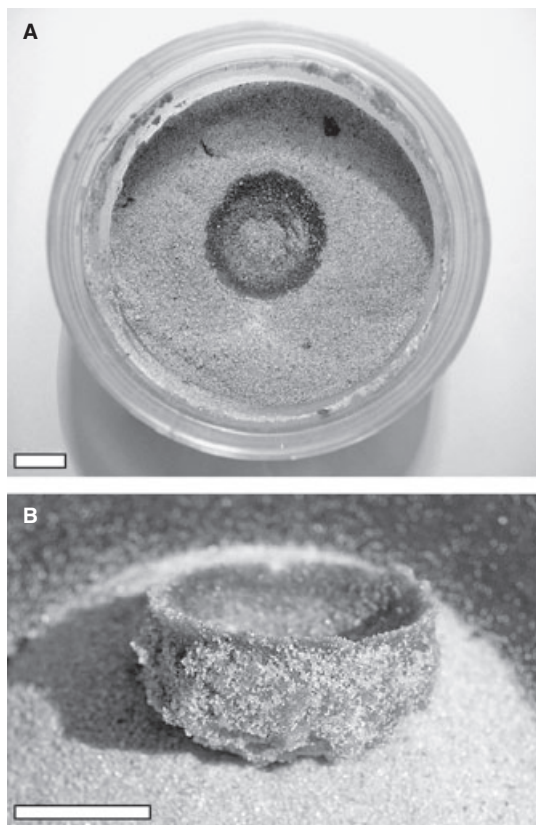


**TEXT-FIG. 7.** Extant cicada nymph feeding chambers. A, cicada nymph within its chamber; black arrow shows an impregnated soil part. B, bottom of one chamber, as found in the soil, resembling pan-shaped *F. challa* specimens, and showing a similar surface texture probably produced by trampling. C, longitudinal view of a chamber, resembling elongated *F. challa* specimens. D, internal surface texture composed of pits and scratches similar to that of elongated specimens illustrated in Plate 1, figure 6. E, chamber section showing the feeding root (white arrow). F, chamber section showing roots (black arrows) and distinctive surfaces in the wall (white arrows). 1, outer boundary of the wall; 2, older floor; 3, extant floor (inner surface of the wall). Scale bars represent 1 cm.

probably the indirect result of the insect trampling on the moistened inner surface of the chamber. In some chamber bottoms it is possible to recognize individual pits that probably correspond to tracks produced by legs (Text-fig. 7B). By contrast, the scratches are probably produced by digging movements in the drier lateral walls of chambers and are similar to those in elongated *F. challa* specimens (Pl. 1, fig. 6; Text-fig. 7C–D).

#### Grooves

Nearly 40 per cent of the specimens show lateral grooves, suggesting that such a character is significant for the interpretation of the origin of *Feoichnus*. The trace fossil *Monesichnus ameghinoi* frequently shows longitudinal grooves in the external wall (Genise and Laza 1998). However, in this case the groove is not in contact



**TEXT-FIG. 8.** A–B, plan and side views of artificial pan-shaped structures produced by pouring dilute glue into a depression made in sand. Scale bars represent 1 cm.

with the interior part of the trace fossil, as it is in *Feoichnus challa*. The surface of the grooves show parallel striations comparable with those seen in the roots of plants, particularly grasses. Thus, we interpret the chambers as occurring in association with roots, which not only were used as attachments but also traversed the interior structure, a feature that occurs in root-feeding

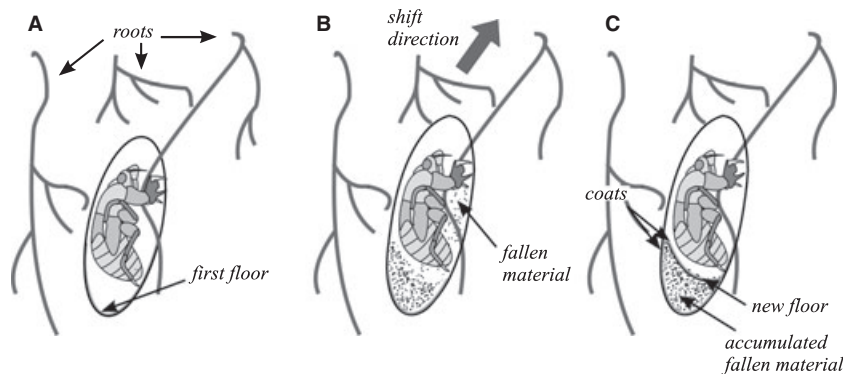
insects. Beetles, cydnid bugs and cicada nymphs are common root-feeding insects. However, only cicada nymphs produce anal excretions such as those mentioned previously. As the diet of the cicada nymphs is based on root xylem (White and Strehl 1978; Williams and Simon 1995), such insects include a segment of a root in the feeding cells that they inhabit (Marlatt 1907; Beamer 1928; Torres 1953; Dybas and Lloyd 1962). Field observations on modern *Dorisiana drewseni* nymph chambers have confirmed that all cells were associated with roots, which are externally attached to the wall and pierce it, penetrating its interior (Text-fig. 7E–F). These root traces resemble the grooves described in *Feoichnus challa*.

## CONCLUSIONS

A new ichnotaxon, *Feoichnus challa*, is created for pan or dish-shaped trace fossils in palaeosols. It was found in the Cenozoic of Central Patagonia, the Cretaceous and Cenozoic of the USA, the Oligocene of Ethiopia, and the Miocene of the United Arab Emirates and Kenya. *F. challa* ranges from the Upper Cretaceous to the Pliocene, supplementing the information yielded by the current body-fossil record to help understand the evolutionary history of cicadas.

*Feoichnus challa* is characterized by: (1) a hemispherical shape and mostly subvertical orientation; (2) a smooth internal surface, with knobby texture; (3) a rough, irregular external surface devoid of ornamentation; (4) a wall consisting of a lining plus a layer of surrounding soil material, or of a superposition of these layers (floors and coats); and (5) subvertical to subhorizontal grooves, with smooth surfaces and longitudinal striations attributable to roots.

*Feoichnus challa* is attributed to cicada nymph chambers (Hemiptera: Sternorrhyncha: Cicadidae) on the basis



**TEXT-FIG. 9.** Origin of floors and coats of *F. challa*. A, original chamber with a single floor and lateral coat. B, excavation of the upper part of the chamber, searching for a new section of the feeding root; fallen material accumulates under and behind the nymph. C, formation of a second floor and coat over the removed soil material, while the nymph feeds again and excretes anal liquid.

of comparisons with extant material. The most significant characters are: (1) differential preservation of the basal part of the original chambers; (2) an interior lining with similar inner surface texture; and (3) the presence of root traces in the wall and in the interior of the chamber.

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## REFERENCES

- AMEGHINO, F. G. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie. *Anales del Museo Nacional de Historia*, **8**, 1–568.
- ANDREIS, R. R., MAZZONI, M. M. and SPALLETTI, L. A. 1975. Estudio estratigráfico y paleoambiental de las sedimentitas terciarias entre Pico Salamanca y Bahía Bustamante, provincia del Chubut, República Argentina. *Revista de la Asociación Geológica Argentina*, **30**, 85–103.
- BEAMER, R. H. 1928. Studies on the biology of Kansas Cicadidae. *The University of Kansas Science Bulletin*, **18**, 155–263.
- BELLOSI, E. S. 2004. Sedimentologic control of the *Coprinisphaera* ichnofacies. *Ichnia 2004. First International Congress on Ichnology, Abstract Book*, p. 19.
- and GENISE, J. F. 2004. Insect trace fossils from paleosols of the Sarmiento Formation (Middle Eocene–Lower Miocene) at Gran Barranca (Chubut Province). 15–29. In BELLOSI, E. S. and MELCHOR, R. N. (eds). *Ichnia 2004. First International Congress on Ichnology. Fieldtrip Guidebook*. Museo Paleontológico Egidio Feruglio, Trelew, Argentina, 81 pp.
- LAZA, J. H. and SANCHEZ, M. V. 2005. Terrestrial trace fossils and ichnostratigraphy of the Sarmiento Formation: implications for the oldest grass-dominated ecosystem. *16° Congreso Geológico Argentino, Resúmenes*, 306 pp.
- GONZÁLEZ, M. G., KAY, R. F. and MADDEN, R. H. 2002. El valle inciso colhuehuapense. *9° Reunión Argentina de Sedimentología*, **1**, 49.
- LAZA, J. H. and GONZÁLEZ, M. G. 2001. Icnofaunas en paleosuelos de la Formación Sarmiento (Eoceno–Mioceno), Patagonia Central. *4° Reunión Argentina de Icnología y 2° Reunión de Icnología del Mercosur*, **1**, 31.
- BOULARD, M. 1965. Notes sur la biologie larvairie des cigales (Hom. Cicadidae). *Annales de la Société Entomologique de France*, **1**, 503–251.
- BOWN, T. M. and LARRIESTRA, C. N. 1990. Sedimentary paleoenvironments of fossil platyrrhine localities, Miocene Pinturas Formation, Santa Cruz Province, Argentina. *Journal of Human Evolution*, **19**, 87–119.
- and LAZA, J. H. 1990. A Miocene fossil termite nest from southern Argentina and its paleoclimatological implications. *Ichnos*, **1**, 73–79.
- and RATCLIFFE, B. C. 1988. The origin of *Chubutolithes* Ihering, ichnofossils from the Eocene and Oligocene of Chubut province, Argentina. *Journal of Paleontology*, **62**, 163–167.
- BRANSON, C. C. 1959. Some problematic fossils. *Oklahoma Geology Notes*, **19**, 82–87.
- CHAMBERLAIN, C. K. 1971. Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma. *Journal of Paleontology*, **45**, 212–246.
- CIFELLI, R. L. 1985. Biostratigraphy of the Casamayoran, early Eocene of Patagonia. *American Museum Novitates*, **2820**, 1–26.
- CRIMES, T. P., LEGG, I., MARCOS, A. and ARBOLEYA, M. 1977. ?Late Precambrian–Lower Cambrian trace fossils from Spain. 91–138. In CRIMES, T. P. and HARPER, J. C. (eds). *Trace fossils 2*. Geological Journal, Special Issue, **9**, 351 pp.
- DYBAS, H. S. and LLOYD, M. 1962. Isolation by habitat in two synchronized species of periodical cicadas (Homoptera: Cicadidae: *Magicicada*). *Ecology*, **43**, 444–459.
- FERUGLIO, E. 1949. *Descripción geológica de la Patagonia 2*. Dirección General de Yacimientos Petrolíferos Fiscales. Coni Press, Buenos Aires, 349 pp.
- FRENGUELLI, J. 1931. Nomenclatura estratigráfica patagónica. *Anales de la Sociedad Científica de Santa Fe*, **3**, 1–117.
- GENISE, J. F. 2004. Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in paleosols attributed to coleopterans, ants and termites. 419–453. In MCILROY, D. (ed.). *The application of ichnology to palaeoenvironmental and stratigraphic analysis*. Geological Society, London, Special Publication, **228**, 496 pp.
- and BOWN, T. M. 1990. The constructor of the ichnofossil *Chubutolithes*. *Journal of Paleontology*, **64**, 482–483.
- — 1994. New Miocene scarabeid and hymenopterous nests and Early Miocene (Santacrucian) paleoenvironments, Patagonian Argentina. *Ichnos*, **3**, 107–117.
- and HAZELDINE, P. L. 1998. The ichnogenus *Palmiraichnus* Roselli for fossil bee cells. *Ichnos*, **6**, 151–166.
- and LAZA, J. H. 1998. *Monesichnus ameghinoi* Roselli: a complex insect trace fossil produced by two distinct trace makers. *Ichnos*, **5**, 213–223.
- and POIRÉ, D. G. 2000. Fluidization in insect constructions in soils. *Ichnos*, **7**, 127–134.
- BELLOSI, E. S. and GONZÁLEZ, M. G. 2004. An approach to the description and interpretation of ichnofabrics in paleosols. 355–382. In MCILROY, D. (ed.). *The application of ichnology to palaeoenvironmental and stratigraphic analysis*. Geological Society, London, Special Publication, **228**, 496 pp.

- CLADERA, G. and TANCOFF, S. 2001. La presencia de *Eatonichnus claronensis* en el Paleoceno del Chubut (Argentina). 4° Reunión Argentina de Icnología y 2° Reunión de Icnología del Mercosur, 1, 45.
- MÁNGANO, M. G., BUATOIS, L. A., LAZA, J. and VERDE, M. 2000. Insect trace fossil associations in paleosols: The *Coprinisphaera* ichnofacies. *Palaaios*, 15, 33–48.
- SCIUTTO, J. C., LAZA, J. H., GONZÁLEZ, M. G. and BELLOSI, E. S. 2002. Fossil bee nests, coleopteran pupal chambers and tuffaceous paleosols from the Late Cretaceous Laguna Palacios Formation, Central Patagonia (Argentina). *Palaeoecology, Palaeoclimatology, Palaeoecology*, 177, 215–235.
- GRIMALDI, D. and ENGEL, M. S. 2005. *Evolution of the insects*. Cambridge University Press, New York, NY, 755 pp.
- KAY, R. F., MADDEN, R. H., BELLOSI, E. S., CARLINI, A. A., HEIZLER, M., RE, G. H., VILAS, J. F. and VUCETICH, M. G. 2001. Puesto Almendra-Colhué Huapí contact at Gran Barranca, Sarmiento Formation, Chubut, Argentina. *Ameghiniana*, 38 (Supplement), 35.
- KRAMARZ, A. G. and BELLOSI, E. S. 2005. Hystricognath rodents from the Pinturas Formation, Early–Middle Miocene of Patagonia, biostratigraphic and paleoenvironmental implications. *Journal of South American Earth Sciences*, 18, 199–212.
- LAZA, J. H. 2006. Dung-beetle fossil brood balls: the ichnogenera *Coprinisphaera* Sauer and *Quirogaichnus* n. igen. (Coprinisphaeridae). *Ichnos*, 13, 217–235.
- LEGARRETA, L. and ULIANA, M. A. 1994. Asociaciones de fósiles y hiatos en el Supracretácico–Neógeno de Patagonia: una perspectiva estratigráfico-secuencial. *Ameghiniana*, 31, 257–281.
- — and TORRES, M. A. 1990. Secuencias deposicionales cenozoicas de Patagonia Central: sus relaciones con las asociaciones de mamíferos terrestres y episodios marinos epicontinentales. Evaluación preliminar. 2° Simposio sobre el Terciario de Chile, 1, 135–176.
- MARLATT, C. L. 1907. The periodical cicada. *Bulletin of the United States Department of Agriculture. Bureau of Entomology (New Series)*, 71, 1–181.
- MAZZONI, M. M. 1979. Contribución al conocimiento petrográfico de la Formación Sarmiento. Barranca sur del lago Colhué Huapí, provincia de Chubut. *Revista de la Asociación Argentina de Mineralogía, Petrología y Sedimentología*, 10, 33–53.
- PASCUAL, R. and ODREMAN RIVAS, O. 1971. Evolución de las comunidades de los vertebrados del Terciario Argentino. Los aspectos paleozoogeográficos y paleoclimáticos relacionados. *Ameghiniana*, 8, 372–412.
- ORTEGA HINAJOSA, E., GODNAR, D. and TONNI, E. 1965. Las edades del Cenozoico mamalífero de la Argentina, con especial atención a aquellas del territorio Bonaerense. *Anales de la Comisión de Investigación Científica*, 6, 165–193.
- PEMBERTON, S. G., FREY, R. W. and BROMLEY, R. G. 1988. The ichnotaxonomy of *Conostichus* and other plug-shaped ichnofossils. *Canadian Journal of Earth Sciences*, 25, 866–892.
- PFEFFERKORN, H. W. 1971. Note on *Conostichus broadheadi* Lesquereux (trace fossil: Pennsylvanian). *Journal of Paleontology*, 45, 888–892.
- SIMPSON, G. G. 1933. Stratigraphic nomenclature of the early Tertiary of Central Patagonia. *American Museum Novitates*, 644, 1–13.
- 1940. Review of the mammal-bearing Tertiary of South America. *Proceedings of the American Philosophical Society*, 83, 649–709.
- SPALLETI, L. A. and MAZZONI, M. M. 1977. Sedimentología del Grupo Sarmiento en un perfil ubicado en el sudeste del Lago Colhué Huapí, provincia del Chubut. *Obra Centenario de La Plata*, 4, 261–283.
- — 1979. Estratigrafía de la Formación Sarmiento en la barranca sur del Lago Colhué Huapí, provincia del Chubut. *Revista de la Asociación Geológica Argentina*, 34, 271–281.
- TORRES, B. A. 1953. Estudio biológico sobre *Fidicina Mannifera* (Fab. 1803) y su importancia económica en la Argentina. *Revista del Museo de la Ciudad Eva Perón (Nueva Serie)*, 6, 285–296.
- WHITE, J. A. and LLOYD, M. 1975. Growth rates of 17 and 13-year periodical cicadas. *American Midland Naturalist*, 94, 127–143.
- — and ZAR, J. H. 1979. Faulty eclosion in crowded suburban periodical cicadas: population out of control. *Ecology*, 60, 305–315.
- — and STREHL, C. E. 1978. Xylem feeding by periodical cicada nymphs on tree roots. *Ecological Entomology*, 3, 323–327.
- WILLIAMS, K. S. and SIMON, C. 1995. The ecology, behavior and evolution of periodical cicadas. *Annual Review of Entomology*, 40, 269–295.