New insect pupation chambers (Pupichnia) from the Upper Cretaceous of Patagonia, Argentina

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Abstract

Three new records of insect pupation chambers are reported from two localities in the Cretaceous Chubut Group of Patagonia, Argentina: from Sierra Nevada, a new and older ichnospecies of *Rebuffoichnus, R. sciuttoi* isp. nov. (Coprinisphaeridae), and the first Cretaceous and South American specimens of *Pallichnus dakotensis* Retallack (Pallichnidae), known until now from a single North American Oligocene locality; from Cañadón Puerta del Diablo, a new type of *Rebuffoichnus casamiquelai* Roselli that shows some differences from known material of the ichnospecies from the same locality, suggesting a different trace maker. Affinities of *P. dakotensis*, interpreted originally as a cast of a lined pupation chamber, remain unknown in the light of the new material. Its micromorphology is quite simple, with no constructed wall. *R. sciuttoi* has a very thinly constructed wall, showing an external texture composed of lobes and fine, helically arranged ridges. Such characters are compatible with those of wasp cocoons. *R. casamiquelai*, interpreted originally as a coleopteran pupation chamber, has a thickly constructed wall composed of two layers of soil material, showing redistribution of clay and orientation of long grains. Macro- and micromorphology of palaeosols indicate that in both localities pupation occurred in vitric entisols developed on pyroclastic ash-fall deposits on a fluvial floodplain. These new records double the number of the few Cretaceous insect pupation chambers. This is a critical period for understanding the origin and early evolution of building behaviour in insects. Three types of Cretaceous pupation chambers can now be recognized: (1) excavated and lined, e.g. *Fictovichnus* and *Pallichnus* (Pallichnidae); (2) constructed mostly with silk, resulting in thin-walled cocoons, e.g. *R. sciuttoi* (Coprinisphaeridae); (3) constructed mostly with soil material, resulting in thick-walled chambers, e.g., *R. casamiquelai* (Coprinisphaeridae). A new ethological category, Pupichnia, is proposed for grouping ichnotaxa representing pupation chambers, which, with Calichnia representing nests, comprises the two major types of insect trace fossils in palaeosols.
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1. Introduction

The Cretaceous is a critical period for insects because it records the appearance of key ecological groups, such as termites, phytophagan beetles, aculeate Hymenoptera, cyclorrhapan Diptera, and glossatan Lepidoptera (Grimaldi and Engel, 2005). Such a radiation seems to be mostly related to the appearance of angiosperms. This early Cretaceous event is paralleled in the ichnofossil record with the first unequivocal evidence of insect constructions in palaeosols during the Late Cretaceous (Genise, 2004). This is explained by the behaviour of some of these new groups of insects that constructed nests and pupation chambers in soils instead of merely excavating

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them (Genise and Bown, 1994). The known ichnofossil record of insects shows a few examples of insect constructions in Cretaceous strata followed by increasing diversity and abundance during the Cenozoic Era (Genise, 2004). At present, two examples of Cretaceous insect nests are known, one from the USA and the other from Argentina (Elliott and Nations, 1998; Genise et al., 2002b), and three records of pupation chambers (Johnston et al., 1996; Martin, 2001; Martin and Varrichio, 2001; Genise et al., 2002a,b).

The Cretaceous system is also critical from the viewpoint of searching for the early stages of the construction of pupation chambers in soils. Even when the history of holometaboly can be traced to the Palaeozoic (Labandeira and Phillips, 1996; Grimaldi and Engel, 2005), representatives of some holometabolous orders pupate in water, in wood, inside the last larval cuticle, or attached to plants, whereas others have mobile pupae or construct fragile cocoons. Of the remaining taxa whose pupation chambers would be expected in palaeosols, some appear in the Cretaceous or the Cenozoic. Definite terrestrial groups of beetles such as Carabidae and Staphylinoidea arose in the Triassic, but only during the Late Jurassic did most polyphagan families diversify significantly (Grimaldi and Engel, 2005). Considering that many of them might have simple excavated pupation chambers, with low preservation potential, the Cretaceous is still a critical period for understanding the evolution of insect building behaviour.

The three new examples of pupation chambers described here from two Cretaceous localities in Patagonia, Argentina (Fig. 1) double the number of previously known examples for this period. Sciutto and Martínez (1996) briefly mentioned as undetermined fossil insect nests, two of the pupation chambers described here from Sierra Nevada. These constitute the first record of a new ichnospecies of *Rebuffoichnus*, *R. sciuttoi* isp. nov., and the first Cretaceous and South American record for *Pallichnus dakotensis* Retallack, 1984, known hitherto from only a single North American Oligocene locality. In addition, a new type of *Rebuffoichnus casamiquelai* Roselli, 1987 showing some differences from the previously known material, was found at Cañadón Puerta del Diablo, from where other insect trace fossils were already known (Genise et al., 2002b).

2. Geological setting

The Chubut Group (Hauterivian−Maastrichtian), in which the trace fossils were found, is a thick succession of continental deposits that constitutes the main fill of the San Jorge Basin, Patagonia. The Bajo Barreal Formation, bearing *Pallichnus dakotensis* and *Rebuffoichnus sciuttoi* isp. nov., and the Laguna Palacios Formation, yielding *Rebuffoichnus casamiquelai*, comprise the upper part of the Chubut Group. The Bajo Barreal Formation is characterized by the presence of greyish sandstones or gravelly sandstones interbedded with tuffaceous fine-grained sandstones and mudstones. This 200−1200-m-thick succession accumulated in a fluvial system with permanent, moderate- to low-sinuosity channels, and in subordinate small, shallow lakes (Bridge et al.,

2000). Floodplain facies include scarce, weakly developed palaeosols, such as andic entisols and andisols (Bellosi et al., 2002). Dinosaur fossils have been found at several localities, but plant remains are very scarce. The Bajo Barreal Formation has been considered to be Cenomanian−Coniacian in age on the basis of sequence stratigraphy, palynology, and radiometric dating (Fitzgerald et al., 1990; Archangelsky et al., 1994; Bridge et al., 2000; Bellosi et al., 2002). Bridge et al. (2000) reported an Ar/Ar date from an ignimbrite considered to belong to the lowermost part of the Laguna Palacios Formation at Cerro Colorado de Galveniz (45°25′42″ S; 69°46′59″ W), which yielded an age of 85.1 ± 0.79 Ma (late Coniacian−early Santonian). However, the ignimbrite occurs in a mudstone-dominated succession several metres above the section with frequent fluvial channel sand bodies studied by Bridge et al. (2000) (G. Jalfin, pers. comm., 2001), which are typical of the lower member of the Bajo Barreal Formation (Figari et al., 1990). The sedimentological evidence suggests that the interval from which the dated ignimbrite was obtained actually belongs to the Upper Member of the Bajo Barreal Formation (Figari et al., 1990). Consequently, a late Coniacian−early Santonian is considered a reliable age estimate for the Upper Member of Bajo Barreal Formation and the trace fossils described here, which were collected at Cañadón de las Horquetas, Sierra Nevada (44°52′30″ S; 69°24′40″ W) (Fig. 1).

The uppermost unit of the Chubut Group is the Laguna Palacios Formation, 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). Its stratigraphic relationships suggest a Santonian−early Maastrichtian age (Sciutto, 1981; Fitzgerald et al., 1990; Bridge et al., 2000). *Rebuffoichnus casamiquelai* was collected from the Upper Member of the Laguna Palacios Formation exposed at Cañadón Puerta del Diablo (45°30′36″ S, 69°45′33″ W), southwest San Bernardo Range (Fig. 1). At Cañadón Puerta del Diablo the formation reaches its maximum thickness (330 m) and is overlain by the Palaeogene Peñas Coloradas Formation. The stratigraphic relationship with the underlying formation, Bajo Barreal, is transitional and conformable (Di Persia, 1953). Towards the centre of the basin, the Upper Member of the Bajo Barreal Formation replaces laterally the Laguna Palacios Formation (Sciutto, 1981), indicating that they are approximately coeval (Fig. 2). The lowest, light brown−yellowish palaeosol is commonly taken as the lower boundary of the Laguna Palacios Formation (Sciutto, 1981).

2.1. Sedimentary facies and palaeoenvironments

The sedimentary facies and micromorphology of palaeosols of the trace fossil-bearing sections are described below, and the palaeoenvironmental conditions during deposition are inferred. The nomenclature for thin section descriptions of palaeosols is after Bullock et al. (1985).
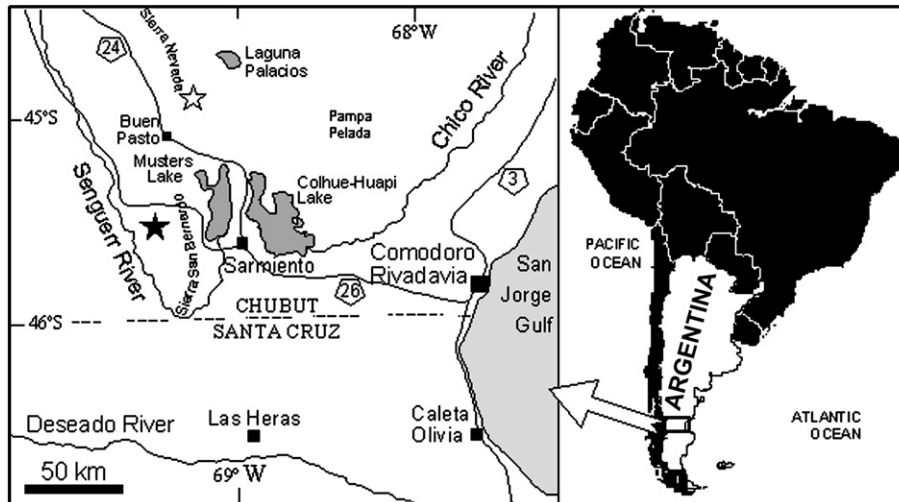
Fig. 1. Location of the material studied. White star: Cañadon de las Horquetas, Sierra Nevada. Black star: Cañadon Puerta del Diablo.

2.1.1. Bajo Barreal Formation

The outcrops of the upper part of the Bajo Barreal Formation at Cañadón de las Horquetas (Sierra Nevada) are about 103 m thick, including a 40-m-thick lower section showing channel sandbodies interbedded with finer-grained sediments (Lower Member of the formation) and a siltstone-dominated upper section (Figs. 2, 3A). The lower section is composed of fining-upward cycles 8−10 m thick that include fine- to medium-grained sandstones 2.0−8.5 m thick showing trough cross-bedding and parallel bedding (channel sandbodies) and overlying massive siltstone and mudstone with interbedded fine-grained cross-laminated sandstone, interpreted as floodplain deposits. The finer grained part of the cycles also includes thinly laminated brown claystones bearing sparse rootlets, and an interval showing abundant fine rootlets and burrows 0.5−1.5 cm in diameter. The upper section of the Bajo Barreal Formation is characterized by massive olive-green tuffaceous siltstones with sparse rootlets interbedded with 1−2-m-thick, massive, fine grained sandstones with mud clasts and thin (0.2−0.6 m) fine-grained, pale orange vitric tuffs. The tuff beds are massive and display some features suggestive of pedogenic modification. The fossil pupation chambers were found in three poorly developed tuffaceous palaeosols (Fig. 2, SN 1−SN 3) located in the middle part of the Upper Member of the Bajo Barreal Formation. The thicker and slightly more developed palaeosol underlies a sharp non-erosive surface and is developed in fining-upward tuff beds 80 cm thick. It includes two horizons of different colour, structure, and bioturbation. The upper horizon is a massive and very pale orange (10YR8/2) fine-grained tuff, 20 cm thick, showing a coarse subangular blocky structure (Fig. 3E). The sparse to low bioturbation is restricted to the presence of *Rebuffoichnus sciuttoi* isp. nov. and *Pallichnus dakotensis*. Under the microscope, the structure is massive and non-porous (Fig. 3E). The coarse fraction (50%) is poorly sorted, fine-grained sand. It is composed of strongly weathered glass shards and pumice replaced by zeolites, scarce altered plagioclase, and slightly corroded quartz grains. The fine fraction is

a brownish non-recrystallized clay. The more common pedofeatures are Fe-Mn nodules and a system of subparallel tapered cracks that resemble root traces (Fig. 3E). The lower horizon is a fine-to medium-grained tuff 60 cm thick. It is mottled and reddened (moderate orange pink, 10YR7/4) in the upper part and includes sub-vertical, slightly curved burrows 1 cm in diameter. Micromorphologically, it is also massive and dense (ca.1% porosity). The outstanding differences from the upper horizon are a slightly coarser grain size, more abundant coarse fraction (70%), higher proportion of Fe oxides, and the absence of cracks.

According to mineral composition and described characteristics, this palaeosol is considered a vitric entisol (Soil Survey Staff, 1975). A weakly to very weakly pedogenic development is interpreted from the little evidence of soil processes. The high proportion of non-recrystallized clay would have been derived from diagenetic alteration of the volcanic material. The incipient pedogenesis precludes its designation as an andisol (Retallack, 2001). It would have originally been a pyroclastic ash fall deposit, later pedogenized, as revealed by insect traces and shallow root penetration in the surface horizon (A horizon) above a massive C horizon. Shallow-penetrating root traces are common in well-drained soils. The Fe-Mn nodules and mottling are compatible with some seasonal waterlogging. Concurrently, the rate of weathering of volcanic glass shards is more rapid in humid climatic conditions (e.g. Chamley, 1989), although the poor development of the palaeosol precludes any climatic interpretation. The upper section of the Bajo Barreal Formation at Cañadón de las Horquetas is considered to reflect a floodplain setting with important pyroclastic input where deposition took place mostly in a subaerial environment. The tuffaceous sediments were reworked by gravity flows, and partially modified by pedogenesis, probably, under a sub-humid or humid climate.

2.1.2. Laguna Palacios Formation

The trace fossil-bearing pyroclastic succession at Cañadón Puerta del Diablo belongs to the Upper Member of the Laguna
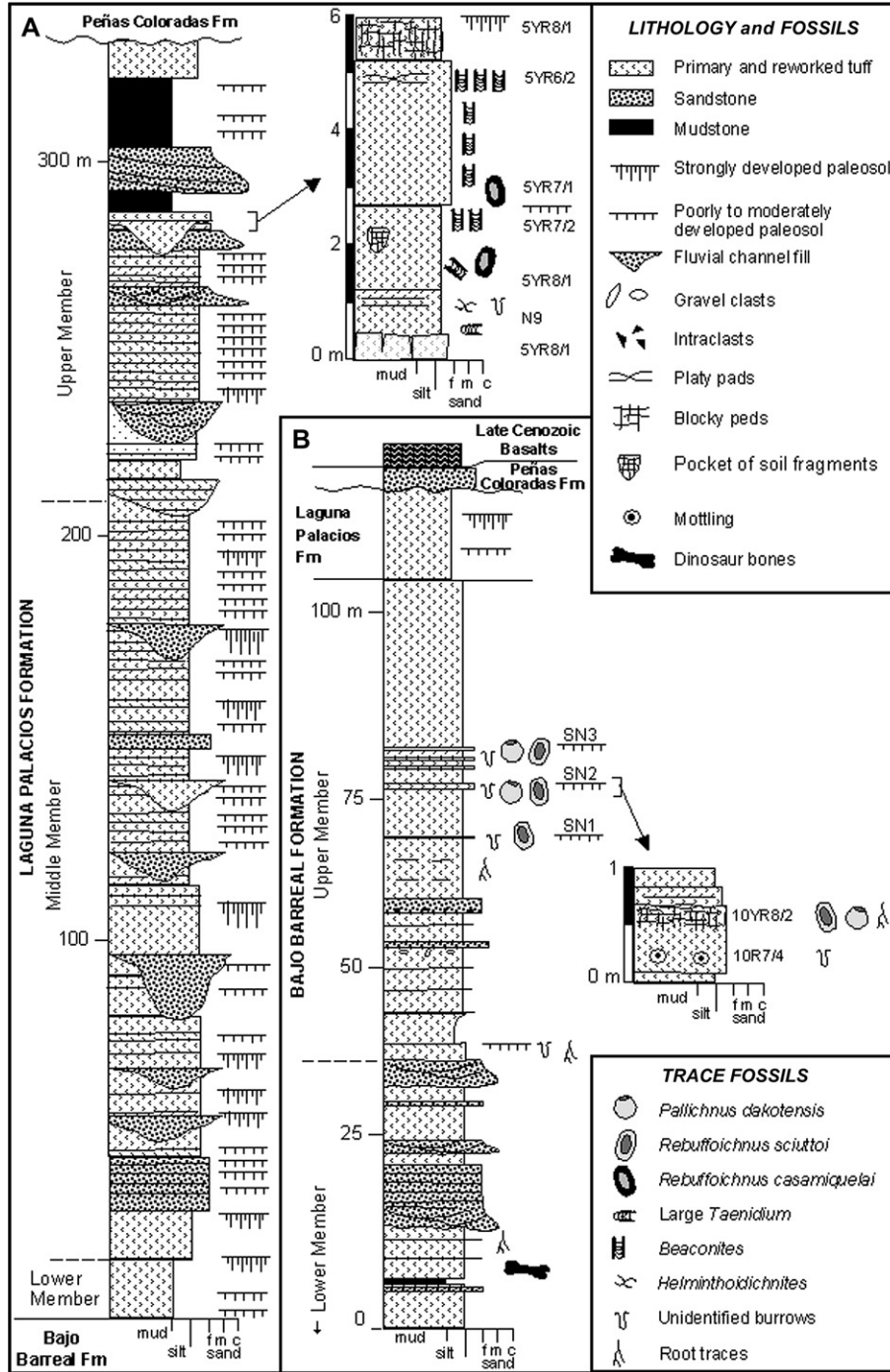
Fig. 2. Sedimentological logs showing the stratigraphic levels bearing the insect pupation chambers.

Palacios Formation, which is composed of ash-fall tuffs, cross-bedded sandstones, scarce pyroclastic flow deposits, and subordinate intraformational conglomerates (Genise et al., 2002a). The most frequent facies of the Upper Member are primary and reworked tuffs with different degrees of pedogenesis and bioturbation (Fig. 2). Stacked, moderately- to well-developed palaeosols with abundant meniscate burrows and rhizoliths, clay cutans, slickensides, blocky peds, and Fe-Mn nodules are common. In addition, there are rare ribbon channel-fill deposits composed of a thin lag of intraclasts,

fine-grained tuff with large trough cross-bedding, and a capping tuffaceous palaeosol. The Laguna Palacios Formation is envisaged as reflecting low-relief loess plains traversed by a few rivers and containing ponds (Bellosi and Sciutto, 2002; Genise et al., 2002b).

The pupation chambers studied were found in a 1.4-m-thick massive tuff bed, which is considered roughly correlative with the tuff bed that yielded the bee nests described by Genise et al. (2002b) (Fig. 3B, D). This tuff overlies a 0.7-m-thick laminated tuff bed with invertebrate trails (Helminthoidichnites tenuis)
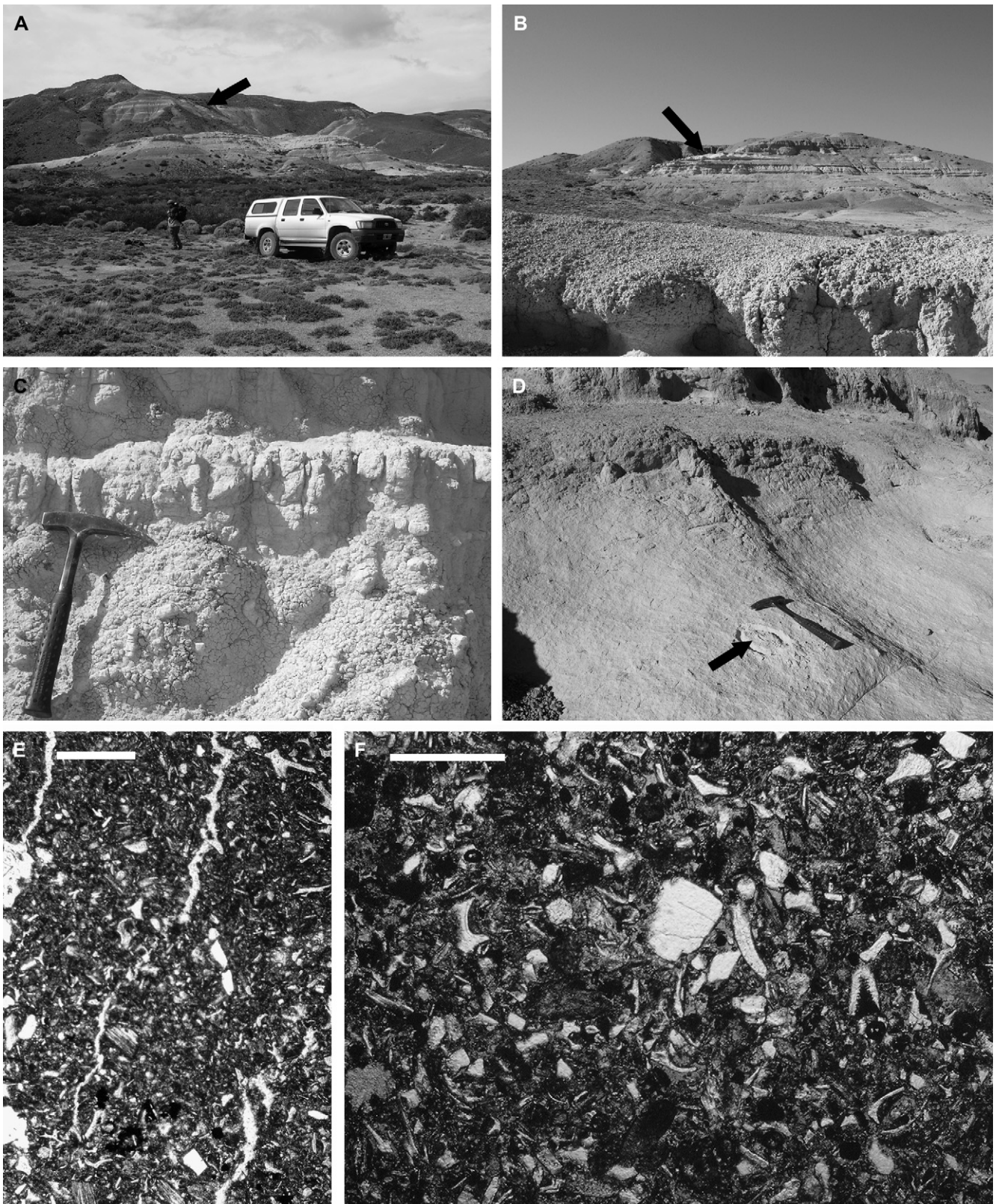
Fig. 3. A, Sierra Nevada: arrow shows the stratigraphic level bearing *P. dakotensis* and *R. sciuttoi*. B, Cañadon Puerta del Diablo: arrow shows the stratigraphic level bearing *R. casamiquelai*. C, palaeosol from Sierra Nevada. D, palaeosol from Cañadon Puerta del Diablo: arrow shows location of one specimen (MPEF-IC 1365) of *R. casamiquelai*. E, micromorphology of palaeosol from Sierra Nevada; note the fissures resembling rootlets. F, micromorphology of palaeosol from Cañadon Puerta del Diablo. Scale bars represent 500 μm.

and large meniscate unwalled burrows, 2 cm in diameter (*Taenidium* isp.). The upper tuff bed, which yielded the pupation chambers, displays a vertical and gradual change in colour from light grey (5YR8/1) to greyish orange pink (5YR7/2). The lower part of the bed contains scattered pupation chambers and *Beaconites* filled with darker material similar in colour to those at the top of the bed. The darker, upper third of the tuff bed shows a marked increase in the amount of bioturbation in the form of vertical *Beaconites*, as well as horizontal, planar clay cutans. In different parts of the bed, subspherical to ellipsoidal, 0.10–0.15-m-wide pockets filled with soil fragments, 0.5–1.0 cm in diameter, were identified. Micromorphological observations in a sample from the lower part of this tuff bed suggest an apedal, single-grain to bridged microstructure (Fig. 3E). Estimated total void space is 30% and there are also packing voids. The grain size of the coarse fraction (upper 80%) is between coarse silt and fine sand, and is mostly composed of fresh to weakly altered volcanic glass shards and pumice, and subordinate tabular plagioclase grains and subrounded rock fragments. The fine fraction is light yellowish brown clay. The groundmass presents a very weakly developed, punctuated-undifferentiated b-fabric and shows a gefuric to enaulic coarse/fine distribution. The only recognizable pedofeatures are small Fe-Mn nodules. The parent material and the limited evidence of pedogenic modification indicate that this weakly developed palaeosol corresponds to a vitric entisol. The probable correlative palaeosol that yielded the bee nests described by Genise et al. (2002b) is located 1.5 km to the south. In comparison with the palaeosol described here, the bee nest-bearing palaeosol is similar in mineral composition and microstructure, but is lighter-coloured, displays less total void space (15%), has a less abundant (45%) and slightly finer coarse fraction, includes scarce pedotubules surrounded by clays, shows a less diverse ichnofabric, and lacks Fe-Mn nodules. This latter palaeosol is regarded as an andic entisol (Genise et al., 2002b). The absence of Fe-Mn nodules in the palaeosol with bee nests would indicate drier conditions than for the palaeosol described here.

The tuff bed described is overlain by a 2-m-thick reworked tuff bed that displays no primary sedimentary structures, abundant vertical *Beaconites*, and a single pupation chamber near its base. The density of burrows increases from the base to the top of the bed; their average lateral separation is 5 cm in the lower part of the bed and less than 1 cm (commonly burrows in contact) in the upper part. The upward increase in bioturbation is accompanied by a change in colour from greyish orange pink (5YR7/2) to light brown (5YR6/2). The upper 0.25 m of the bed contains platy peds. Sedimentation of the section with pupation chambers occurred on a surface with subdued relief, frequently covered by thick, distal, and mostly subaerial ash fall deposits, modified by pedogenesis. The occurrence of a laminated tuff with invertebrate trails in the lower part of the section studied suggests that tuff deposition was probably subaquatic. Pedogenesis was commonly incipient and differences in pedofeatures of correlative intervals were probably linked to topographic differences in a palaeocatena. The postulated higher moisture content of the palaeosol in which pupation chambers occur (this study), and that of the

probable correlative palaeosol with bee nests (Genise et al., 2002b), is also suggested by the occurrence of possible subaquatic deposits underlying the former palaeosol. This suggests that the palaeosols with pupation chambers developed in low-lying areas.

3. Systematic ichnology

The specimens described here are housed at the Museo Desiderio Torres, Sarmiento, Chubut (MDT); ichnological collection of the Universidad de la Patagonia San Juan Bosco, Comodoro Rivadavia, Chubut (UNPSJB-IC); Museo Paleontológico Egidio Feruglio, Trelew, Chubut (MPEF-IC); and División Icnología, Museo Argentino de Ciencias Naturales, Buenos Aires (MACN-Icn).

Ichnofamily: Pallichnidae Genise, 2004
Ichnogenus *Pallichnus* Retallack, 1984

Pallichnus dakotensis Retallack, 1984
Fig. 4

Material. Eleven specimens from the Upper Member of the Late Cretaceous Bajo Barreal Formation (Coniacian–Santonian) at Cañadón de las Horquetas, Sierra Nevada, Chubut province, Argentina: MDT 478, UNPSJB-IC 33, MEPF-IC 1343–1349; MACN-Icn 2313–2314.

Description. Isolated, spherical to subspherical casts of chambers, showing no discrete wall, and a rounded irregular scar, about half the diameter of the chamber, at one pole (Fig. 4A). The structures were found mostly detached from the rock matrix, among weathered debris. Some found in situ in vertical exposures were easily removed from the host rock. Equatorial diameter ranges from 14 to 23 mm (N = 12) and height from 13 to 22 mm (N = 7). Diameter of scar ranges from 7 to 12 mm (N = 8). One specimen (MPEF-IC 1346) is very flattened, its equatorial diameter being 20 mm and its height 13 mm. In this specimen the scar is visible at one pole as a smoother rounded area. Retallack (1984) considered that flattening of specimens resulting from compaction of the sediments. In specimens that are attached to fragments of the rock matrix, no discrete wall can be observed between the chamber and the host rock. In some specimens, raised, irregular rims surround the rounded scar, which is slightly concave. The external aspect of the chambers is irregularly lumpy. Two specimens (MPEF-IC 1343, 1344) show at the pole opposite the scar a pointed protuberance with three radiating ridges arising from it (Fig. 4B).

The filling of the chambers is a homogeneous clayey matrix stained by Fe oxides, with scarce and very weathered floating grains (10%), similar in composition to the host palaeosol (Fig. 4C). Abundant circular and ovoid microgranules (mean size 300 μm) consisting of soil material, with a thin, dark rim, were recognized within the filling. The external layer of the cast is a discontinuous, darker, thin band (50–70 μm) with a higher clay content and showing a gradual passage to the filling material (Fig. 4C). The lack of a sharp discontinuity between
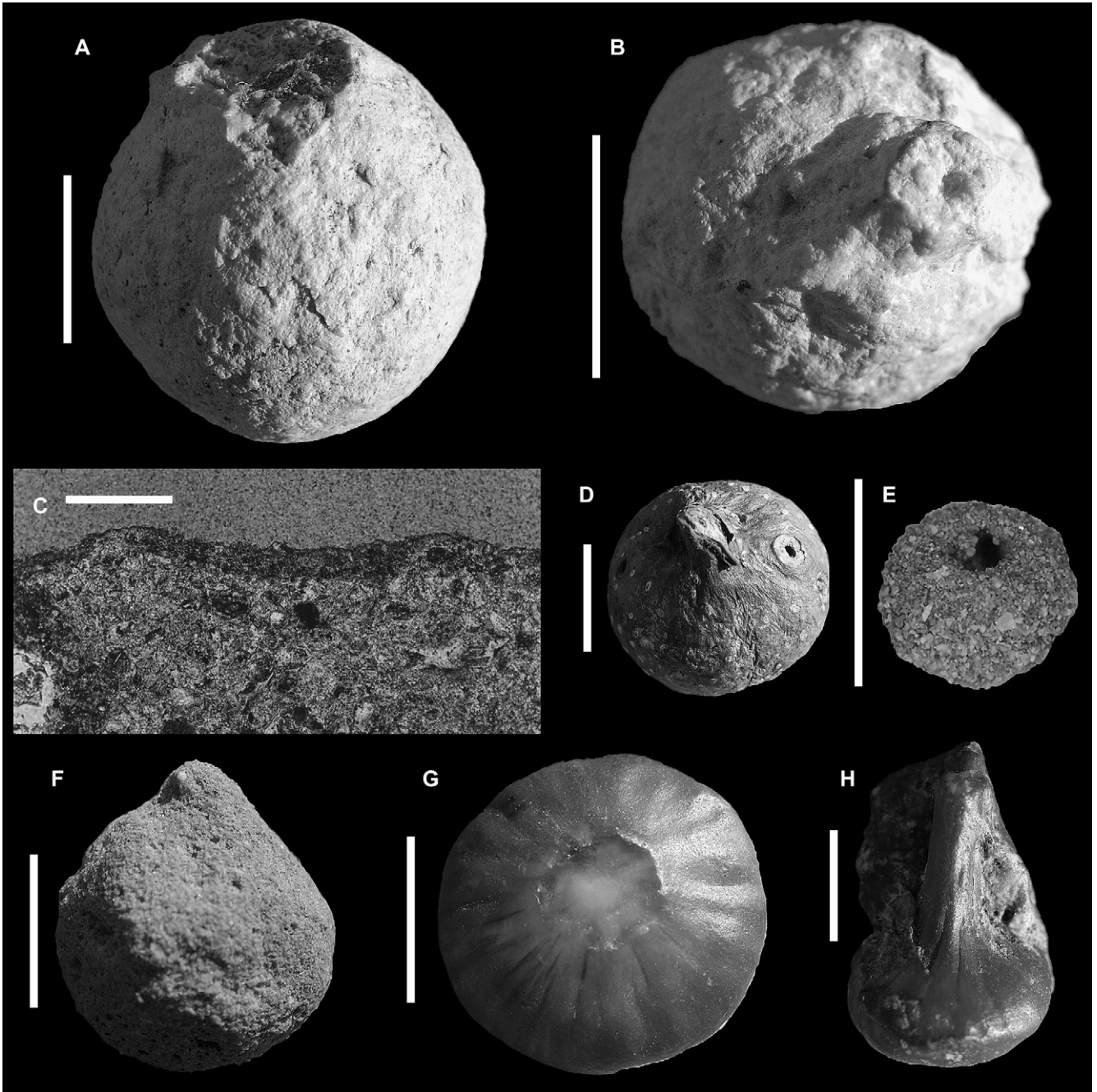
Fig. 4. A, *Pallichnus dakotensis*, specimen UNPSJB-IC 33 showing scar. B, *P. dakotensis*, specimen MPEF-IC 1343 showing the radiating protuberance opposite the scar. C, micromorphology of *P. dakotensis*, crossed nichols, specimen MACN-Icn 2313; note the birefringent outer layer. D, fruit of extant *Nothofagus* sp.; note the radiating protuberance. E, pupation chamber of Myrmeleontidae; note the rounded emergence hole. F, possible fruit cast from Peñas Coloradas Formation (Paleocene); note the protuberance. G, H, Jurassic araucarian seed showing the seedling and the scar corresponding to its detachment point. Scale bars represent 1 cm in A, B, D–H; 250 μm in C.

this layer and the filling indicates that it is neither a discrete wall nor a well-defined lining. This external layer is also present in the palaeosol fragment adhering to the filling, displaying a gradual passage between palaeosol and filling. It may be interpreted as an inorganic pedogenic/diagenetic feature.

Remarks. The specimens from the Oligocene Brule Formation in the USA are covered with a clay rind that is detachable from the cast, and which is part of a distinct lining between the cast and the rock matrix (Retallack, 1984). In other aspects, the material described here shows minor differences from the type material. Size, overall shape, presence and shape of the scar, flattened specimens, and lumpy aspect are common to both the Cretaceous and Oligocene material. The material described here constitutes the second record of the ichnogenus, and implies an expansion of its age range from the Oligocene to the Late Cretaceous, and also of its geographical range, from North America to southern South America.

Ichnofamily: Coprinisphaeridae Genise, 2004
Ichnogenus *Rebuffoichnus* Roselli, 1987

Rebuffoichnus sciuttoi isp. nov.
Figs. 5, 6

2004 *Fictovichnus* isp; Genise p. 435.

Derivation of name. After geologist Dr. Juan Carlos Sciutto, who discovered the first specimens.

Holotype. Specimen MPEF-IC 1352 is here designated because it preserves the flat oval area and scar (Fig. 5A). The surface texture is better preserved in the paratypes.

Paratypes. UNPSJB-IC 34, MACN-Icn 2315, MPEF-IC 1353, MDT 479; same locality and stratigraphic level as the holotype.

Material. Twenty-seven specimens from the same locality and stratigraphic level as the type material: MDT 480–485; UNPSJB 35–37, MEPF-IC 1350, 1351, 1354–1363; MACN-Icn 2316–2319.

Type locality and stratigraphic level. Cañadón de las Horquetas, Sierra Nevada, Chubut Province, Argentina; Upper Member of the Late Cretaceous Bajo Barreal Formation (Coniacian–Santonian).

Diagnosis. *Rebuffoichnus* with an ovoid shape and a very thinly constructed wall that preserves a helical surface texture composed of fine, dense ridges impressed over wide, flattened lobes (Fig. 5D, G). The best-preserved specimens show a slightly depressed cross-section, a rounded scar near one end, and a flat, oval, smoothed area near the other end (Fig. 5A, B, E, F). Other specimens show a truncated, flat, irregular end instead of the scar (Fig. 5B, E, F).

Description. Isolated, completely ovoid or truncated chambers that show patterned surfaces and a thin but discrete wall. The wall displays a helical pattern of fine ridges, tightly grouped (Fig. 5D), faintly impressed over wide and flattened lobes that are also helically arranged (Fig. 5G), observable in the best-preserved specimens. In cross-section, many specimens have a slightly depressed outline. Some specimens show a rounded, irregular, sub-terminal scar (Fig. 5A, F). This has an irregular surface and a surrounding rim. In truncated specimens it is lacking (Fig. 5B, E, F). Opposite the scar or truncation, and at the other end of the chamber, there is a sub-terminal, flat, smooth, oval area (Fig. 5B, E).

The completely ovoid specimens are considered to be the closed ones from which the trace makers never emerged. In them, length ranges from 26 to 33 mm (N = 11), width from 13 to 16 mm (N = 16), and height from 11 to 13 mm (N = 13). In specimens showing a rounded cross-section, the maximum diameter ranges from 12 to 16 mm (N = 11). The scar is 6–8 mm in diameter (N = 9). Other specimens are truncated at one end, showing a flat, irregular, rounded surface. These are considered to be the open ones from which the trace makers emerged. Length ranges from 23 to 29 mm (N = 9) and the truncation from 9 to 12 mm in diameter (N = 16). The chambers were mostly detached from the rock matrix on the palaeosol surface, surrounded by other weathered material. Some specimens are broken, others show deformation, and still others show attached pieces of rock matrix. Among the last of these, one specimen (MPEF-IC 1351) shows a large, irregular, protuberant, rounded area in the middle, suggesting equatorial emergence (Fig. 5C). In some specimens remains of the wall can be seen with the naked eye; this appears as a smooth outer layer with a helical surface texture composed of lobes and fine ridges.

The micromorphology of two specimens was analysed, one of which preserves a discrete wall (MACN-Icn 2317). This wall is separated by a sharp discontinuity from the filling and is preserved around most of the cross-section (Fig. 6A). Its thickness ranges from 100 to 750 μm, the latter width corresponding to lobes. It is mostly composed of clay, the b-fabric of which is weakly developed and punctuated-undifferentiated. Isolated crystals of plagioclase and volcanic shards, similar to those of the filling, compose the coarse fraction. There are also some small Fe-Mn nodules. In addition, the wall shows the same porphyric coarse/fine distribution as the palaeosol host, suggesting that the trace maker did not sort the coarse grains. The filling of the specimens studied is similar to the surrounding palaeosol, although the coarse fraction is considerably reduced. It consists of a dark greyish brown, non-recrystallized clay matrix deeply stained by Fe oxides, and subordinate coarser grains (30%). Circular and ovoid microgranules (average size 300 μm) composed of soil material were also identified as in *Pallichnus* casts, although the clay rim of the microgranules is slightly thicker. The specimen that lacks the discrete wall (MACN-Icn 2316) shows an external discontinuous and poorly defined layer 125–200 μm wide, which has a higher authigenic clay content than the remaining filling. This layer displays a gradual passage to the filling, as for specimens of *Pallichnus dakotensis* described previously. The specimen with a discrete wall lacks this layer.

Remarks. Differences between *R. casamiquelai* and *R. sciuttoi* are based mainly on the wall. The former has a thicker wall lacking any regular pattern externally, whereas the latter has a very thin wall with a complex helical surface texture. The material described from the Eocene Bembridge Limestone Formation by Edwards et al. (1998) is similar to *R. sciuttoi*. The Cretaceous and Eocene material share the size, shape (completely ovoid and truncated specimens), and helical surface texture, although the structure of this texture differs. The Eocene material also lacks the scar and flat area of the Cretaceous form, and sometimes preserves part of an associated burrow, which is lacking in the latter. However, the main difference to analyse is the presence of a discrete wall. The best-preserved Cretaceous specimens show a thin, though well-defined discrete wall, which is clearly separate from the fill of the chamber (Fig. 6A, C). In contrast, some of the Eocene specimens
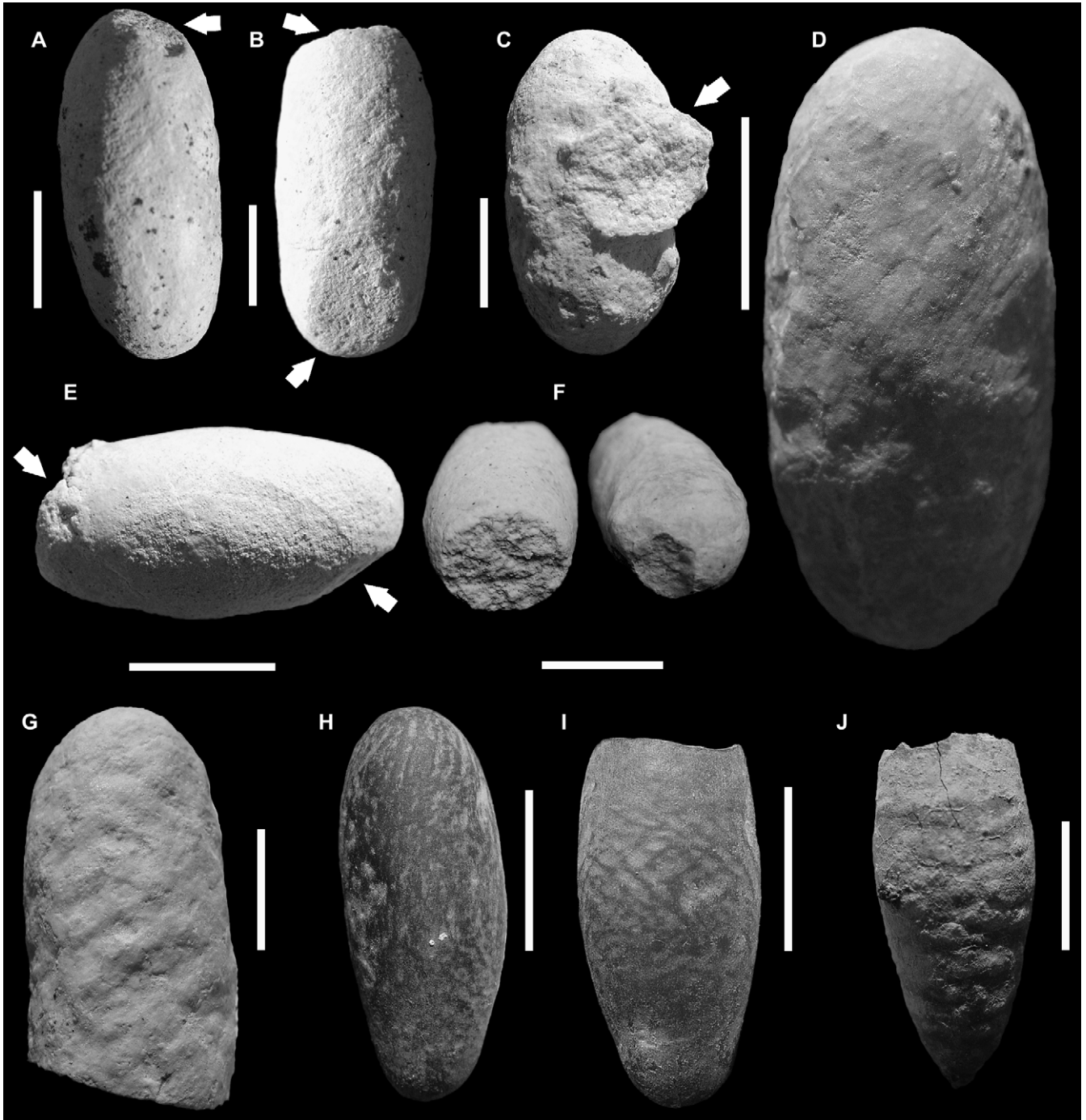
Fig. 5. *Rebuffoichnus sciuttoi* isp. nov. A, holotype, MPEF-Ic 1352 showing the rounded scar at one end (arrow). B, paratype MPEF-IC 1353 showing the truncation (top, arrow) and the flat oval area at the other end (bottom, arrow). C, specimen MPEF-Ic 1351 showing an equatorial emergence tunnel (arrow). D, paratype MACN-Icn 2315 showing the upper half the helical texture of fine ridges. E, lateral view of paratype MDT 478 showing truncation (left, arrow) and the flat area at the other end (right, arrow). F, specimens showing differences between truncation (left, MPEF-IC 1353) and scar (right, MPEF-IC 1363). G, MACN-Icn 2320 showing lobes arranged helically; fine ridges are faintly impressed over them. H, I, modern cocoons of *Tachypompilus* sp. showing different arrangements of silk weave. J, modern cocoon of *Rubrica gravida* showing a texture of wide flattened lobes. Scale bars represent 1 cm.

preserve an external wall, clearly defined micromorphologi-cally, but fused internally with the sedimentary fill (Edwards et al., 1998, fig. 3). One possibility is to consider the Eocene specimens as taphonomic variants of the best-preserved Creta-ceous material. The lack of a clear distinction between the wall and the filling may be a result of the re-crystallization of calcite

in the former. Genise (2004) formerly attributed the Bembridge specimens to *Fictovichnus* isp. (Pallichnidae) because of the lack of a discrete wall. This is still another possibility, if only considering those specimens. The data presented here on *R. sciuttoi* indicate that the most complete morphology involves the presence of a discrete wall. The wall, even when very
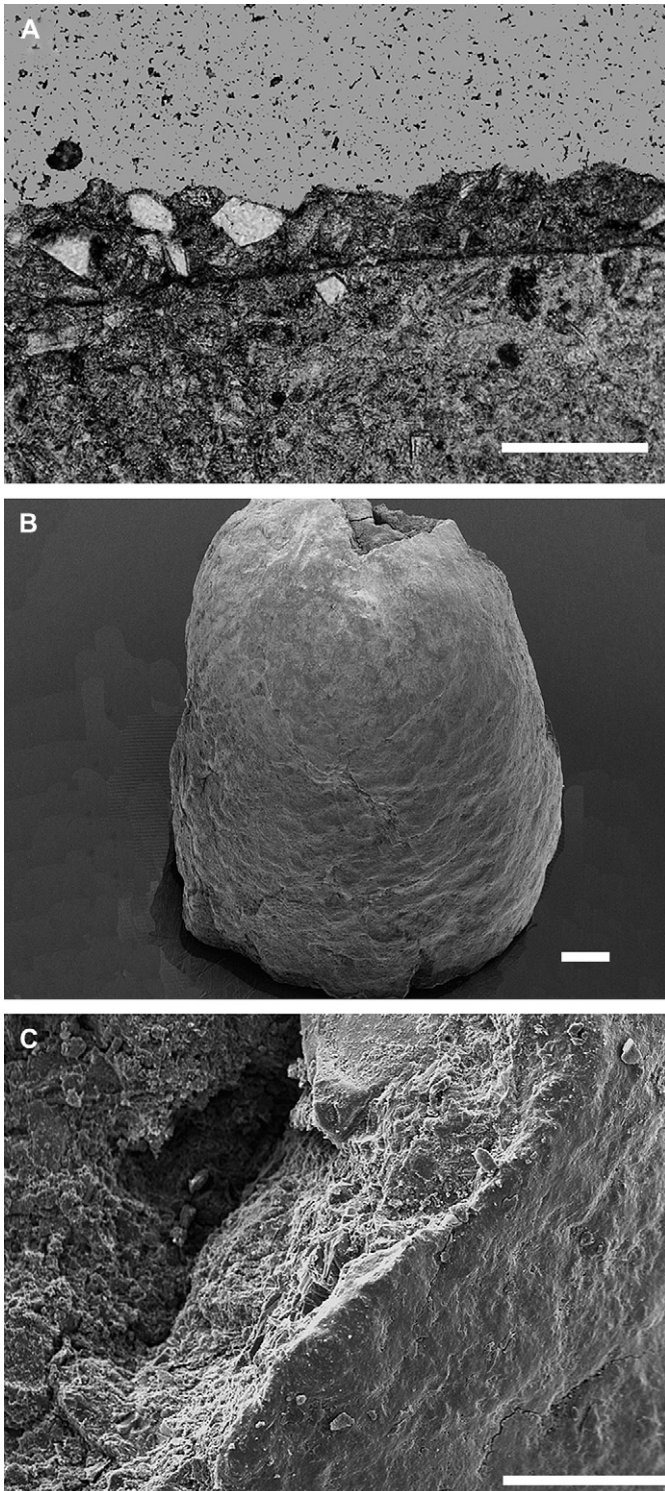
Fig. 6. *Rebuffoichnus sciuttoi* isp. nov. A, thin section of MACN-Icn 2317 showing the wall containing coarse grains and separated from the filling by a darker line. B, SEM image of MACN-Icn 2319 showing the lobes. C, same specimen showing micromorphological differences between the wall and the filling, which are separated by a gap. Scale bars represent 500 μm in A; 1 mm in B; 200 μm in C.

thin, has an external surface texture that indicates that the trace maker interacted with the inner and outer surfaces, resulting in a discrete constructed wall sensu Genise (2004). In addition, thin sections and SEM images show a clear discontinuity between the wall and the filling (Fig. 6A, C). The latter character leaves no doubt about its inclusion in *Rebuffoichnus* (Coprinisphaeridae).

Rebuffoichnus casamiquelai Roselli, 1987
Figs. 7, 8

Material. Three specimens from the Upper Member of the Upper Cretaceous Laguna Palacios Formation (Campanian−early Maastrichtian) from Cañadón Puerta del Diablo, Chubut Province, Argentina: MPEF-IC 1364−1365; MACN-Icn 2321. Further material was observed and photographed in the field.

Description. Isolated, subovoid chambers showing a discrete wall with a rugose external surface and a smooth inner surface. The internal cavity is ovoid and has a circular cross-section. In one specimen (MPEF-IC 1365; Fig. 7A) and a second observed in the field (Fig. 7D), the chamber is prolonged as a short meniscate-walled burrow, comparable with specimens of *Beaconites* from the same level, showing the concavity of menisci towards the chamber (Fig. 7A). Walls of both *Rebuffoichnus* and *Beaconites* merge, indicating that the trace maker burrowed down to a depth at which it constructed the chamber, and following construction, failed to emerge. This is an example of a compound trace fossil sensu Pickerill (1994). The external length of the chamber ranges from 22 to 38 mm (N = 3) whereas the maximum diameter ranges from 14 to 20 mm (N = 3); the mean L/D ratio is about 1.4 (N = 3). The internal length ranges from 20 to 30 mm (N = 3) whereas the maximum diameter ranges from 11 to 13 mm; the mean L/D ratio is 2.22 (N = 3). The wall thickness ranges from 2 to 6.5 mm (N = 3). The associated walled burrows are up to 15 mm long, the wall thickness is about 2 mm, and the menisci are 2−5 mm wide. Chambers were found in situ in the palaeosol, in a horizontal to subhorizontal position, showing a darker colouration than the other associated trace fossils, which are mostly *Beaconites* (Fig. 7A−D). The chamber wall is almost welded to the matrix, precluding their easy removal, unlike the other chambers described here.

Micromorphologically, the wall consists of two layers 4.75 and 1.5 mm thick respectively, showing the same composition as the soil material, and with transitional boundaries. Each layer has an internal less porous band 2.25 and 0.5 mm thick respectively, with a higher clay content than the soil, and an outer more porous band, 2.5 and 1 mm thick respectively. This contains less clay than the soil, resulting in a redistribution of soil porosity (Figs. 7E, F, 8). Such redistribution was probably produced by the fluidisation of wall material during its construction (Genise and Poiré, 2000). The trace maker constructed the wall with moistened soil pellets. Water became expelled from the pores, owing to the pressure produced by moulding. Thus, the clay accumulated in the inner zone from where the pressure was applied,
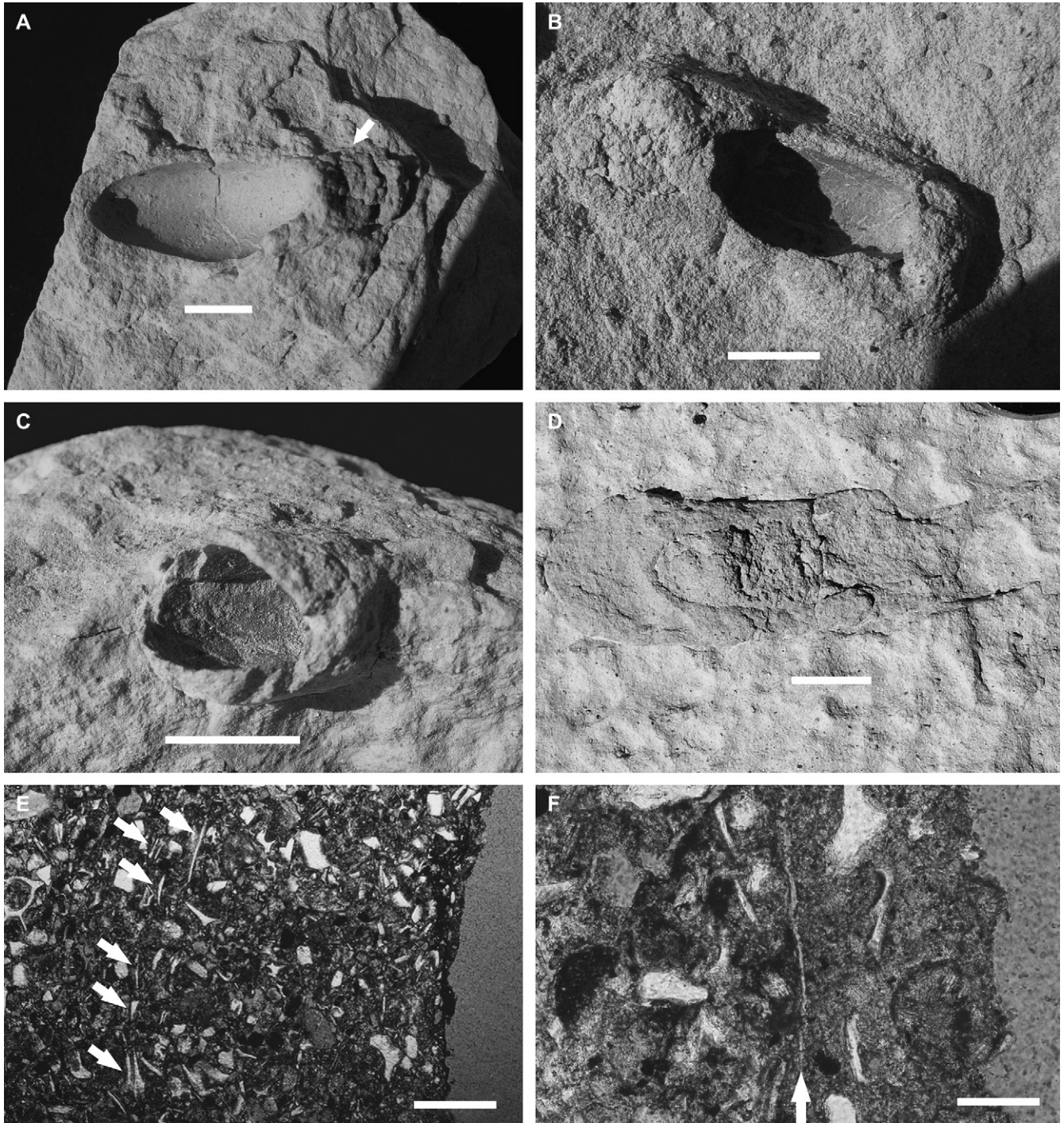
Fig. 7. *Rebuffoichnus casamiquelai*. A, MPEF-IC 1365 showing internal smooth lining and associated *Beaconites* burrow (arrow). B, MACN-Icn 2321. C, MPEF-IC 1364. D, specimen in the field showing a thick wall at the rear and association with *Beaconites*. E, thin section of wall showing the orientation of long grains (arrows). F, thin section of the wall showing an internal lining separated by a gap from the wall (arrow). Scale bars represent 1 cm in A–D; 500 μm in E; 100 μm in F.

whereas in the outer zone the clay content is greatly reduced. The same moulding produced the orientation of long grains (Genise and Hazeldine, 1998) seen in the internal layer (Fig. 7E). A third, innermost layer, 100–250 μm thick, has the highest clay content, very low porosity, only a few coarse grains, and a very fine spongy structure. This layer partially covers the internal cavity (Fig. 7F) and probably resulted from mixing selected fine soil material with an organic

secretion of the trace maker. The secretion may be inferred from the presence of the fine spongy structure, which would have resulted from the degradation of the original organic secretion. The specimens of *Rebuffoichnus casamiquelai*, described previously from other stratigraphic levels at this locality, show different micromorphological attributes (Genise et al., 2002b). The wall of these specimens lacks the two-layered structure, the differential concentration of clay,
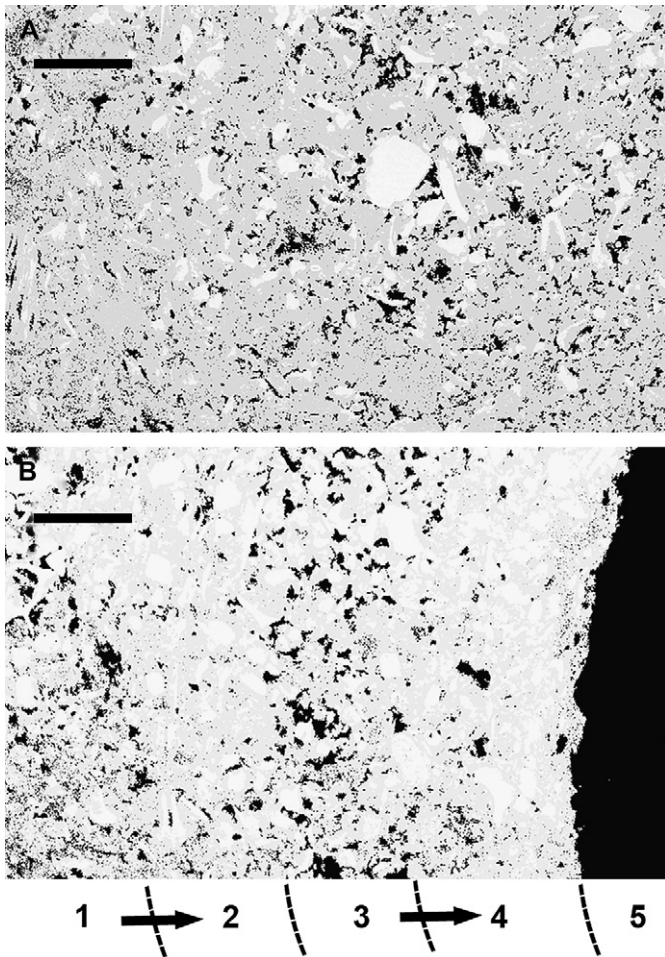
Fig. 8. A, contrasted image from Fig. 3F showing the distribution of porosity (black areas) in the palaeosol. B, contrasted image from Fig. 8E showing the redistribution of soil porosity. Arrows indicate that clay migrated from 1 to 2, and from 3 to 4, whereas 5 is the internal cavity of the chamber. Scale bars represent 500 μm.

and the inner lining, showing instead a high concentration of organic pigment towards the cavity.

In addition, the specimens described here are more slender (mean L/D ratio: 2.22) than previously known material of *R. casamiquelai* (mean L/D: 1.68), and the walls are thinner, indicating different trace makers. Even when these chambers can be distinguished from previously known forms, based on their more slender outlines and three-layered walls, the potential occurrence of intermediate sizes and ratios of further material, preclude any ichnotaxonomical distinction. In contrast, these differences suggest that the trace makers of both types of *R. casamiquelai* from this locality were either very closely related species or both sexes of the same species.

4. Discussion

Palaeoichnology can contribute significantly to knowledge of the evolutionary history of insects when the fossil constructions studied are complex enough to be attributed unequivocally to particular taxa (Genise, 2004). With the exception of

earthworm aestivation chambers, which show particular features (Verde et al., 2004), and large-chambered vertebrate caves (Voorhies, 1975), chambered trace fossils in palaeosols can mainly be attributed to breeding (Calichnia: Genise and Bown, 1994) and pupation structures of insects (Genise, 2004). The latter, which in contrast may be termed Pupichnia, can be distinguished by their passive fillings, or by being empty, and particularly by their mode of construction from the inside, resulting usually in structures having walls that are completely smooth on the inside (Edwards et al., 1998; Genise, 2004). Although adult insects of some groups (e.g., bees, dung beetles, termites, ants) produce Calichnia for the production of offspring, the larvae of other insects, mostly living freely in soils or in vegetation, produce Pupichnia for their protection during pupation. Whereas in Pupichnia, the same individual, although in different developmental stages, makes the structure and then emerges from it, in Calichnia the larvae are concealed in chambers in nests constructed and provisioned by adults. Calichnia result from the behaviour of two or more individuals, the constructors and the emergent adult. The structures described here, Pupichnia attributed to the ichnogenera *Pallichnus*, and *Rebuffoichnus*, show sizes and shapes that are compatible with modern insect pupation chambers. The attribution of pupation chambers to modern insect taxa is difficult because they are rather simple structures and neoichnological descriptions are scarce and scattered in the entomological literature.

Retallack (1984) tentatively attributed *Pallichnus* to pupation chambers of dung beetles: Geotrupinae or Scarabaeinae. Such an attribution, not discussed since, was based on: (1) circumstantial evidence for the presence of dung, such as the fibrous nature of the wall material, its high phosphorous content, and the remains of large mammals at the same locality; (2) the absence of a thick constructed wall and a cavity around it, which is typical of dung beetle brood chambers, instead of pupation chambers; and (3) the presence of associated, though irregular, burrows similar to those of dung beetles. Retallack (1984) pointed out that, compared to *Pallichnus*, modern species of Geotrupinae and Scarabaeinae have more ellipsoidal pupation chambers, even though some of them may be almost spherical, or some deformation of the fossil forms may be involved. The body fossil record of Geotrupinae extends to the Upper Jurassic–Lower Cretaceous, whereas that of Scarabaeinae is mostly Cenozoic, with a single record from the Upper Cretaceous of China (Krell, 2000). True coprophagous beetles have been recorded from the Upper Cretaceous (Chin and Gill, 1996; Ponomarenko, 2002). However, evidence for the attribution of *Pallichnus* to coprophagous beetles until now has been circumstantial, as Retallack (1984) indicated. Subspherical pupation chambers, such as those described here, are also present in other orders of insects having stout-bodied larvae, such as ant lions (Genise and Archangelsky, unpublished data) (Fig. 4E). The aestivation chambers of earthworms are also spherical, although the known fossil examples show a pelletal wall and fillings that are very different from those described here (Verde et al., 2004). In addition, two specimens of *P. dakotensis* show

a pointed pole and three radiating ridges, like those described from the casts of Palaeocene fruits (Somoza et al., 1995, figs. 8, 9) (Fig. 4F), and which are also present in some fruits today(Fig. 4D). Some of these fruits also show a flat area roughly resembling the scar at the opposite pole. Germinated conifer seeds from the Jurassic of Argentina show similar shapes and scars, which resulted from the detachment of the seedling (Fig. 4G, H). The attribution of the rather simple morphology of *Pallichnus* to a particular taxon of insects is, therefore, still debatable.

Edwards et al. (1998) analysed the attribution of the ovoid Bembridge trace fossils, which are similar to *Rebuffoichnus sciuttoi*, to a particular group of insects. They ruled out wasps as producers because of the lack of a tapering end. Genise and Cladera (2004), reviewing wasp ichnofossils, concluded that shape is insufficient for recognition of wasp cocoons, and that additional structures should be identified. One end may be capped and the opposite end bear a nipple-like protuberance (Evans, 1966, table 46a, fig. 207a), they may show equatorial protuberances or pores (Evans, 1966; Evans and West Eberhard, 1970), or one end may have a particular shape owing to the presence of a meconium (Evans, 1966; Evans and West Eberhard, 1970). The scar in closed, ovoid specimens of *R. sciuttoi* may be comparable to the cap of some wasp cocoons (Evans, 1966, fig. 207a). It can be readily distinguished from the rounded irregular rupture at one end produced by the emergence of an adult in open examples, which resulted in truncated specimens (Fig. 5F; but see also open modern examples in figure 5I, J). Truncated specimens bear no scar, thus revealing that it is located at the end from which the adult emerged, as in wasp cocoons. The flat area, another important character of *R. sciuttoi*, is always at the opposite end of the scar or truncation, and also in the opposite hemi-ovoid. It can be distinguished by its smoothness and lack of any surrounding rim, indicating that it is not a sectioned or broken area (an interruption of the wall) but part of it. It may be the area of attachment to the floor of the surrounding cavity, where, for instance, wasp larvae deposited a bundle of silk (Evans, 1966, p. 456). The suggestion that the cocoon might be in a horizontal position, the flat area against the floor, is also supported by the fact that the emergence truncation is on the opposite side (Fig. 5E).

Wasp cocoons are mainly constructed using silk and different amounts and types of soil material depending on the species involved (Evans, 1966; Evans and West Eberhard, 1970) (Fig. 5H-J). They are thin-walled and show different surface textures, ranging from completely silky (Fig. 5H, I) to clayey (Fig. 5J) or sandy, when different soil material is added. The silkier textures may show the arrangement of the weave as a surface composed of ridges or lobes. The two examples of cocoons of *Tachypompilus* sp. (Pompilidae) illustrated here show different arrangements of the silk threads, ranging from tight, almost longitudinal and sinuous ridges (Fig. 5H), to grilled textures resulting from a double helical arrangement (Fig. 5I). The cocoon of *Rubrica gravida* (Sphecidae) (Fig. 5J) shows the same texture of wide and flattened lobes as one specimen of *Rebuffoichnus sciuttoi* (MACN-Icn 2320) (Fig. 5G). These lobes may have

resulted from the incorporation of more soil material to the construction. The paratype MACN-Icn 2315 illustrated in Fig. 5D and the modern cocoon in Fig. 5H show a sinuous arrangement of silk threads. The SEM image of specimen MACN-Icn 2319 shows a texture of small lobes resulting from the intersection of two helicoids of ridges like those shown by the wasp cocoon in Fig. 5I. Some Lepidoptera also build underground pupation chambers that have a constructed wall, some with an exit valve for the adult at one end (Chapman, 1982, fig. 304b), or a capped end and a surface texture composed of lobes (Genise and Cladera, 2004, fig. 4), but in the latter case the wall is thicker and no silky weave is visible if constructed mostly with moulded soil material. To summarise, the characters of *R. sciuttoi* are compatible with those of cocoons made by aculeate wasps, whose body fossils have been recorded from deposits of Late Cretaceous age (Grimaldi and Engel, 2005).

The previously described *R. casamiquelai* was attributed to pupation chambers of beetles, and particularly to weevils, on account of its rounded emergence hole (Genise et al., 2002a,b). The specimens described here are more slender than previously described specimens from the same locality. The walls are thinner, and some ecological preferences of both trace makers seem to have differed, considering the more immature palaeosol in which the new specimens were found. The emergence hole is lacking, precluding a further analysis of the body outline. The scarce material lacks any evidence of caps, pores, lobate texture, or other characters attributed to wasp or lepidopteran cocoons. In conclusion, the new chambers of *R. casamiquelai* described here can be attributed to a trace maker slightly different from that pertaining to the previously described forms (Genise et al., 2002a,b), either a very closely related species or the other sex of the same species. Considering their association with meniscate-walled burrows, it should be possible to analyse the origin of chambers based on the putative producers of the burrows. However, although a few modern invertebrates are known to make meniscate burrows in soils, including insects and earthworms (Frey et al., 1984; Retallack, 2001; O'Geen and Busacca, 2001; Verde et al., 2004), none combines the walled meniscate burrow and chamber recorded here.

5. Conclusions

The new information presented here contributes to knowledge of the earliest stages in production of insect pupation chambers in Cretaceous soils. The ichnofossil record now involves three types. The first is composed of excavated and lined chambers (Pallichnidae), such as *Fictovichnus gobiensis* from the Campanian of Mongolia (Johnston et al., 1996), and *Pallichnus dakotensis,* recorded here from the Coniacian–Santonian of Argentina, even though the affinities of the latter are doubtful. The second type was basically constructed of silk, with the addition of a little soil material, such as *Rebuffoichnus sciuttoi* (Coprinisphaeridae), described here from the Coniacian–Santonian of Argentina. It resulted in thin-walled chambers attributable to wasp cocoons. The presence of a silk weave is indicated by a helical surface texture of

fine ridges. Cocoons described by Martin and Varrichio (2001) from the Campanian Two Medicine Formation in the USA, can also probably be included in this type. The third type, represented by *R. casamiquelai* from the Campanian–early Maastrichtian of Patagonia, was basically constructed of moulded soil material, probably cemented by secretions, and resembles coleopteran pupation chambers (Genise et al., 2002b). Two types of wall have been recorded for *R. casamiquelai*: one is more massive, showing organic pigment towards the inner cavity, and the other, described here, is composed of two layers of soil material. These were probably made from moulded soil pellets, considering their micromorphological characters, such as the orientation of long grains and evidence for fluidisation. Present data show that the oldest pupation chamber in palaeosols, *R. sciuttoi* and *P. dakotensis*, involving thin constructed walls or linings respectively, are recorded from deposits as old as Coniacian–Santonian, whereas the third type, involving a thick wall and extensive moulding of soil pellets, are from deposits that are about 15 myr younger, within the Campanian–Maastrichtian. The record of thicker walls, mostly constructed with soil material cemented by silk, may reflect the appearance of new groups of trace makers. In addition, the increasing number of pupation chambers described from palaeosols encouraged the creation of the new ethological category, Pupichna, proposed here for grouping ichnotaxa representing pupation chambers. Calichnia, representing nests, and Pupichnia, constitute the two major types of insect trace fossils in palaeosols.

Acknowledgements

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