Fossil bee nests, coleopteran pupal chambers and tuffaceous paleosols from the Late Cretaceous Laguna Palacios Formation, Central Patagonia (Argentina)

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Abstract

The Late Cretaceous Laguna Palacios Formation in Central Patagonia (San Jorge Basin), southern South America, is composed of tuffaceous deposits supplied by periodical volcanic ash falls partly reworked by rivers, on broad plains. Variations in ash-fall rates allowed the formation of stacked, mature paleosols, which are one of the most characteristic features of this formation. The mature paleosols show well-developed horizons, ped structure and bear an intricate network of trace fossils mostly produced by small roots and invertebrates. Two different insect trace fossils could be recognized in this formation: sweat bee nests and coleopteran pupal chambers. Fossil bee nests are composed of inclined tunnels with cells attached to them by means of short necks, a typical construction of bees of the subfamily Halictinae. Similar halictine constructions were reported from the Cretaceous of the USA. Coleopteran pupal chambers are discrete, ovoid structures, having an internal cavity with a smooth surface, and an outer wall of lumpy appearance composed of different layers of soil material. They are commonly constructed by the larvae of different families of Coleoptera. Similar trace fossils were previously reported from the Asencio Formation (Late Cretaceous–Early Tertiary) of Uruguay and from the Djadokhta Formation of Mongolia (Late Cretaceous). These trace fossils constitute some of the only paleontological data from the Laguna Palacios Formation, allowing inferences about its paleoecology, paleoclimatology and paleogeography. Ecological preferences of Halictinae, as well as some features of the nests, suggest a temperate, seasonal climate and an environment dominated by low vegetation for the Laguna Palacios Formation, which is also compatible with sedimentologic and pedogenic evidence. The morphology of the nests, typical of North American halictinae, adds more evidence to the hypothesis of the existence of faunal interchange between North and South America by the Late Cretaceous. The fossil nests constitute some of the oldest evidence of bees in the fossil record, the third known record of bees of Cretaceous age and the first for the Southern Hemisphere. The two traces described are, together with those of Dakota and the Gobi Desert, the only trace fossils from paleosols of Cretaceous age that can be certainly attributed to insects. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: trace fossils; bees; beetles; paleosols; Cretaceous; Patagonia

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1. Introduction

Insect fossil nests have been well known for more than 60 years from Tertiary continental deposits of Patagonia (Genise, 1999 and references herein); however, they have been scarcely mentioned from the well-exposed Patagonian Cretaceous sequences. Sciutto (1981, 1995) first mentioned fossil insect nests from the Late Cretaceous Laguna Palacios Formation at the San Bernardo Range, from a locality known as Lote 37. However, these trace fossils believed to be insect nests were another kind of trace fossil of unknown affinity. Later, Sciutto and Martínez (1996) mentioned fossil insect nests from the subjacent Bajo Barreal Formation at Sierra Nevada, describing them as oval and spherical structures. Part of the material collected by these authors possibly corresponds to internal molds of the coleopteran pupal chambers described herein. The worldwide record of trace fossils that can certainly be attributed to insect nests or pupal chambers in Cretaceous paleosols is also scarce. Aside from those of the Asencio Formation of Uruguay, whose age is a matter of discussion (Genise and Bown, 1996), there are only two other occurrences both published recently. Johnston et al. (1996) described coleopteran pupal chambers from the Late Cretaceous Djadokhta Formation of Mongolia, and Elliott and Nations (1998) described fossil bee nests from the Late Cretaceous Dakota Formation of the USA. Such trace fossils are similar to those recorded herein from a single locality of the Laguna Palacios Formation (Genise et al., 1999). The lack of information on Cretaceous insect nests contrasts with the fact that insects, such as termites, bees, dung beetles and ants, which construct the most preservable nests, had already diversified by the Late Cretaceous (Genise and Bown, 1994). On the other hand, records of insect nests from Jurassic and Triassic age (e.g. Hasiotis and Dubiel, 1995; Hasiotis et al., 1995; Hasiotis and Demko, 1996) would require more detailed descriptions and documentation to confirm their true affinities (Labandeira, 1998; Grimaldi, 1999; Genise, 2000).

The bee nests and coleopteran pupal chambers described herein were collected from the Upper Member of the Late Cretaceous Laguna Palacios Formation (Sciutto, 1981), about 50 m below its eroded top, at the locality of Cañadón Puerta del Diablo (45°31′S, 69°46′W). It is situated in the San Bernardo Range southwest of the town of Sarmiento and near the intersection of the provincial route 20 with the Senguerr River (Figs. 1 and 3A). It may be significant that, although many good exposures of the Laguna Palacios Formation were visited during the field research, both insect trace fossils occur only at this locality, where the formation reaches its greatest thickness and exhibits composite paleosols.

2. Geologic setting

The Laguna Palacios Formation is a continental sedimentary succession belonging to the youngest part of the Chubut Group deposited from Santonian to Maastrichtian times (Sciutto, 1981; Fitzgerald et al., 1990; Bridge et al., 2000) (Fig. 2). The formation is developed only near the west border of the sedimentary basin, where subsidence was relatively minor and tectonic stability and diastems prevailed. It is exposed at the San Bernardo Range, but it becomes a subsurface unit westward of the Senguerr river. Its maximum thickness, 300 m, is at Cañadón Puerta del Diablo, and corresponds with the minimum thickness of the subjacent Bajo Barreal Formation, which is about 70 m at this locality (Di Persia, 1953; Bellosi and Sciutto, in preparation). However, thickness varies greatly within the basin because of the primary conditions of sedimentation and also because the angular unconformity at the top, with the Paleocene Río Chico Formation.

The stratigraphical relationship with the subjacent formation, Bajo Barreal, is transitional and conformable (Di Persia, 1953). The upper member of the Bajo Barreal Formation replaces laterally the Laguna Palacios Formation, indicating that both are approximately equivalent. Usually, the lowest mature paleosol of light brown-yellowish color is taken as the lower boundary of the Laguna Palacios Formation, which is variegated in appearance, due to the alternation of light and dark colors, owing to different proportion of
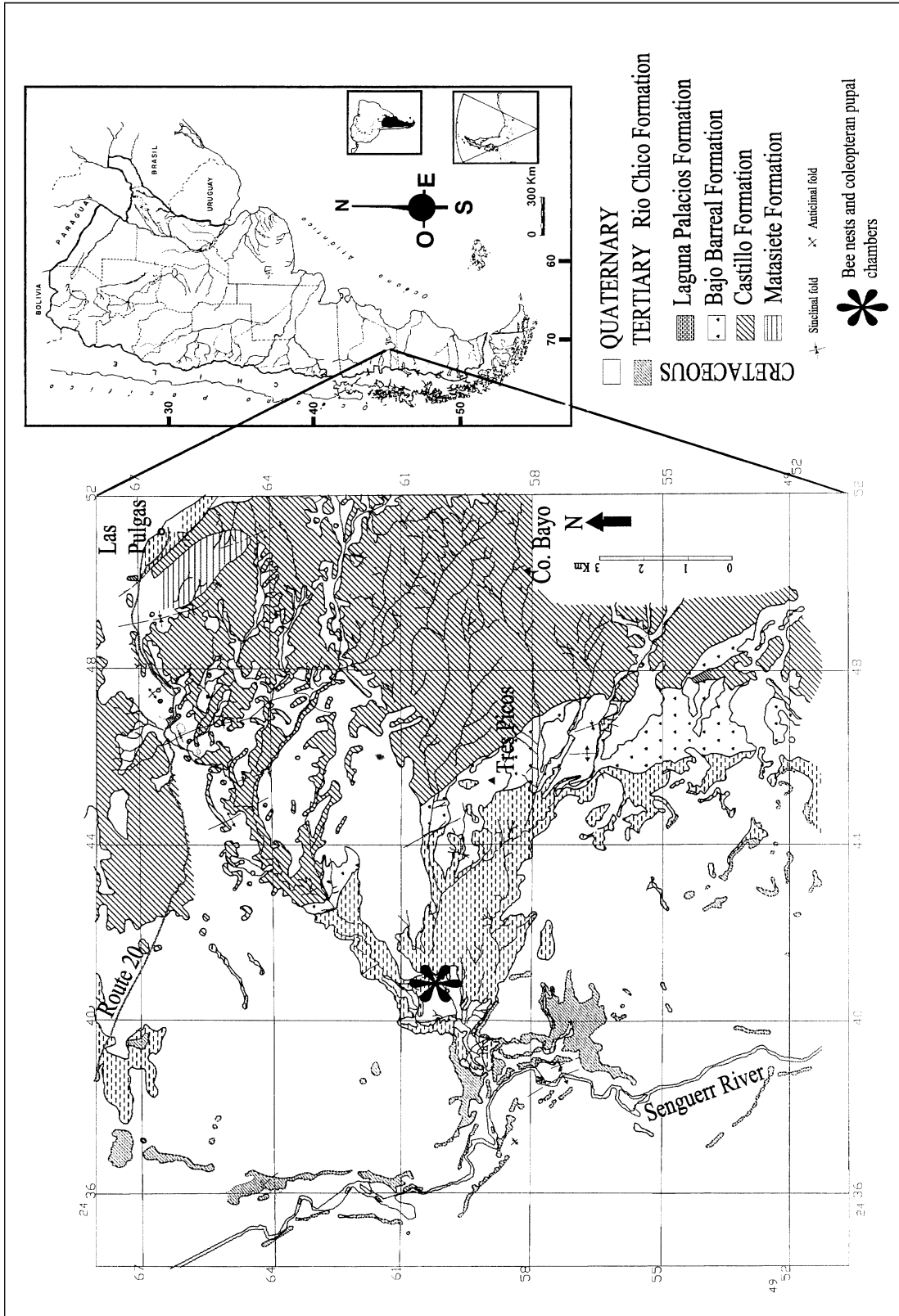
Fig. 1. Location and geologic map of the Cañadón Puerta del Diablo, where the trace fossils were found. (Modified from Di Persia, 1953.)

Paleocene		Río Chico Fm.		
C R E T A C E O U S	Maastrichtian	C H U B U T G R O U P	Laguna Palacios	
	Campanian			
	Santonian			π 85.1
	Coniacian		Bajo Barreal	π 91.0
	Turonian			π 94.2
	Cenomanian			π 95.8
				π 97.1
	Albian		Castillo	π 97.9
	Aptian			π 104.8
	Barremian		Matasiete	
	Hauterivian			

Fig. 2. Stratigraphic position of the Laguna Palacios Formation in the San Bernardo Range, Central Patagonia, and radiometric ages (Ar/Ar) of selected pyroclastic beds in the Chubut Group (taken from Bridge et al., 2000).

iron compounds. These rocks were termed 'Tobas Amarillas' (yellow tuffs) by earlier geologists (i.e. Feruglio, 1949; Ferello, 1951; Di Persia, 1953; González, 1971). In general, the Laguna Palacios Formation is composed of tuffs, sandy and argillaceous tuffs, tuffites, sandstones, and intraformational conglomerates and mudstones. Tuffites are reworked and mixed sedimentary rocks with more than 50% of pyroclastic fragments (Fisher, 1978). Three members are distinguished. The lower exhibits a typical 'badlands' appearance, and is largely eolian in origin. The middle member is generally characterized by conspicuous paleosols forming hard beds (cornices) of tabular morphologies exposed in vertical cliffs. Paleosols were formed on parent material ranging from tuffites, tuffs, and tuffaceous mudstones. The upper member is composed of similar tuffs, tuffites, sandstones and conglomerates and a lesser development of paleosols. In the middle and upper members the eolian facies also predominate but fluvial and lacustrine deposits can be recognized as well.

The pyroclastic succession at Cañadón Puerta del Diablo, bearing the paleosols and the trace fossils, is composed of ash-fall tuffs, scarce pyroclastic flows (Hechem et al., 1990), and crossbedded sandstones and conglomerates. The tuff facies are associated with pyroclastic sandstones and fine intraformational conglomerates, conforming channel fills having high-relief erosive bases. These lenticular bodies are finning upward and show planar and trough cross-bedding. Extrabasinal clasts in the conglomerates are few or absent, whereas tops are pedogenetically altered showing low bioturbation. Laterally, the studied section is associated with an incised ribbon channel body, which is filled by a distinct facies: a well-sorted and pure tuff showing ripple, large-scale trough cross-bedding and convolute bedding. The characteristics of the fine pyroclastic filling suggest an eolian origin, indicating that this fluvial channel was probably not permanent.

The low fragmentation of the tephra of the tuff beds suggests primary deposition. However, eolian reworking cannot be discarded considering the well-sorted sediment and the long distance from a volcanic source (probably from the Patagonian volcanic arc, approximately 150 km to the west of the San Bernardo Range). Additionally, scarce pyroclastic flows and complete absence of surge deposits, coarse-grained pyroclastic rocks and lavas, normally frequent in near-vent areas, also support the distal condition of these deposits. Uniform thickness, mantle bedding, well-sorted grain size and great areal extent are frequent features of fallout accumulations. Fine felsitic ash-fall deposits normally came from the plinian stages of explosive eruptions producing high buoyant plumes of tephra and gas having a relatively great areal dispersal (Fischer and

Fig. 3. (A) General view of the Cañadón Puerta del Diablo showing the paleochannel (a) and the position of the outcrops where the coleopteran pupal chambers (b) and the fossil bee nests (c) where found. (B) Detail of the outcrop bearing the fossil bee cells. (C) Eluvial and illuvial horizons of the mature paleosols where the coleopteran pupal chambers occur. (D) Meniscate tube in mature paleosols. (E) Detached bee cells. (F) Mature paleosols showing an intricate network of trace fossils. Scale bar: 1 cm.
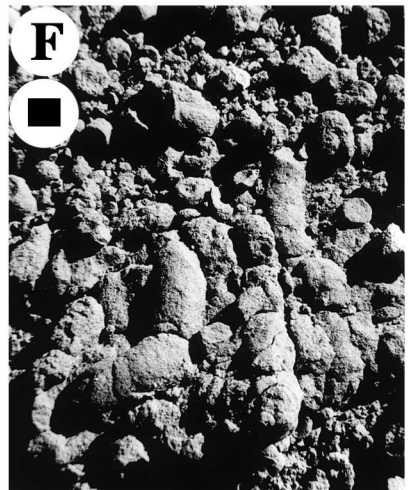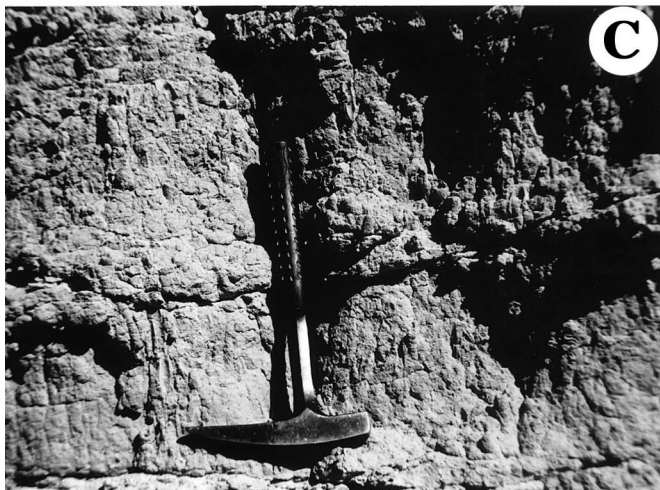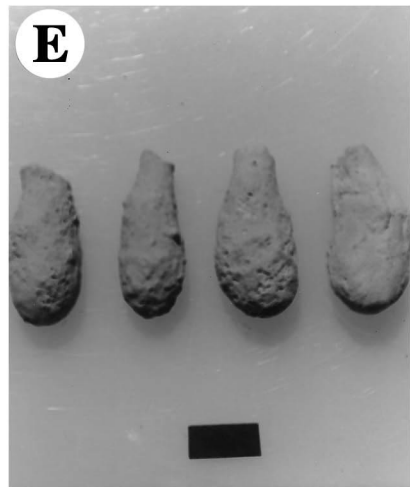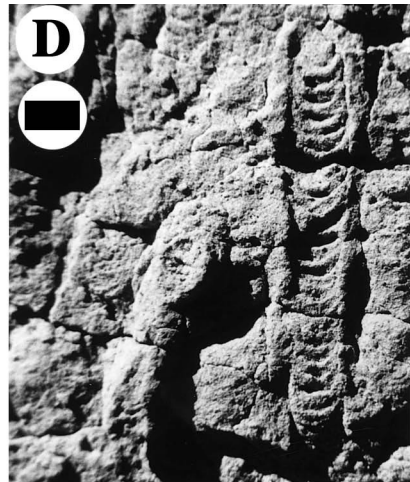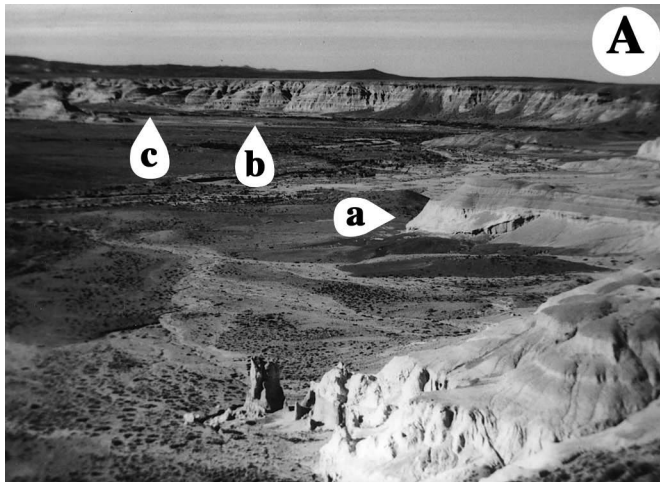
Schmincke, 1984; Cas and Wright, 1987; Lajoie and Stix, 1992). Massive sequences suggest sustained eruptions, whereas stratified or laminated parts indicate fluctuations in eruptive intensity or wind direction. In the Laguna Palacios tuff beds, soil-forming processes are likely responsible for the sharper and more extensive bedding planes. Fine tuffs, originated as distant-source subaerial airfall tephra, deposited on relatively flat surfaces (plains) at a relatively high instantaneous sedimentation rate. Fluvial action and reworking is represented by sandstone and conglomerate channel bodies, which record the presence of bed load low-sinuosity streams.

Environmental conditions in Central Patagonia underwent episodic changes during the Late Cretaceous due to periodic and intensive ash falls. Large explosive volcanic eruptions might have promoted short-term climatic alterations, such as cooling (Cas and Wright, 1987; Rampino, 1991), drying (Bown and Larriestra, 1990; Genise and Bown, 1994; Archangelsky et al., 1995) and the reduction of the plant cover (Genise and Bown, 1994). Such conditions aid the colonization of ashy substrates by small herbaceous forms including lichens, mosses, and grasses (Kimmins, 1987). Accordingly, some of the effects of the recent eruption of the Patagonian Volcano Hudson was the drying up of small water sources (Pearson, 1994); the loss of original vegetation (Saba and de Lamo, 1994); and the increase of annual and rhizomatous grasses (Oliva et al., 1993).

There are almost no paleobotanical data for the Laguna Palacios Formation (Romero and Arguijo, 1981) with the exception of some trunk and stem remains mentioned by Sciutto (1981, 1999). In addition, Andreis (2001) found siliceous phytoliths and poorly preserved angiosperm pollen in some paleosols he studied, which indicates the presence of herbaceous vegetation. The only paleozoological data correspond to those of the supposed fossil insect nests discussed previously (Sciutto, 1981, 1995; Sciutto and Martínez, 1996), whereas the few dinosaur remains mentioned (Bonaparte, 1978) came from localities where the Laguna Palacios Formation is not exposed.

3. Paleosols

3.1. Description

Many outcrops exhibit compound soils (Morrison, 1978), in which the thickness of the ash deposits is greater than the thickness of the soil profile. In such cases, the tops of each deposit show a well-developed paleosol that is separated from the next by another relatively unaltered ash deposit, which might be considered as the C horizon of the overlying paleosol. On the other hand, the deposits bearing the coleopteran pupal chambers described herein exhibit composite soils (Morrison, 1978). In these soils, the thickness of the soil profile is greater than the thickness of the ash deposits, producing the overprinting of paleosol features and a stacked pattern of eluvial and illuvial horizons.

The section studied shows slightly and highly bioturbated tuffs, the former showing the paleosols in which the fossil bee nests occur and the latter those in which the fossil pupal chambers were found. The slightly bioturbated tuffs are fine- to medium-grained, whitish to light brown (10 YR 8/2) (Rock Color Chart, GSA) showing crude stratification (Figs. 3B and 4). The tuff beds are tabular to slightly undulating and continuous (mantle bedding), poorly consolidated, 0.5–3.0 m thick, internally, they are massive or finely laminated. The parent material is scarcely altered by soil processes and bioturbation is restricted to the presence of a few root and invertebrate traces. Volcanic ash is mainly vitric, mesosilicic to silicic in composition, well to moderately sorted, and contains complete glass shards. Accretionary lapilli are common in these beds. Spheroids are very regular and hollow with a muddy rim, 1–4 mm in diameter, spherical, unflattened and uncoated, without evidence of mineral dissolution either inside them or in the matrix. The paleosol developed on these tuffs shows no evidence of horizons, peds, mottling or clay-lined cavities. Macromorphologically it shows only a subtle reddening near the top, where *Taenidium barretti* is more abundant, the fossil bee nests, and few root traces.

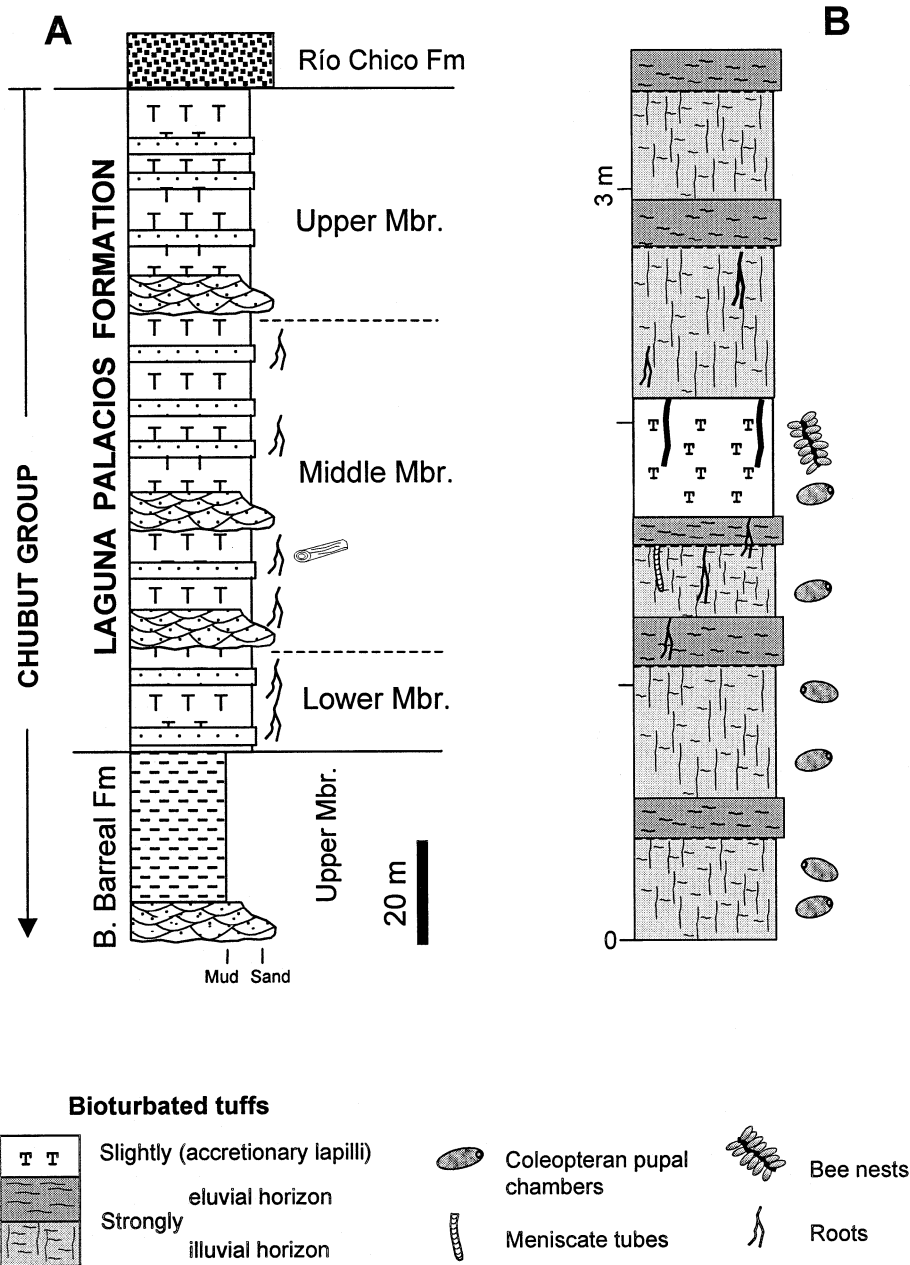This paleosol shows mostly a single-grain to

Fig. 4. (A) Generalized stratigraphic section of the upper Chubut Group in the west flank of the San Bernardo Range (from Sciutto, 1999). (B) Detailed lithologic profile of the Laguna Palacios Formation paleosols in Cañadón Puerta del Diablo.

very weak subangular blocky microstructure. The interpedal space is very small and the intrapedal one is greater but less than 15%. Spaces are mostly irregular vugs. The size of the coarse fraction (40–45%) is silt (Fig. 5F), and is composed

mainly of fresh volcanic glass and, secondarily, of tabular plagioclase and rock fragments. The rock fragments are large and subrounded. The fine fraction (55–60%) consists of very fine, unaltered volcanic glass. The single pedofeatures recognized
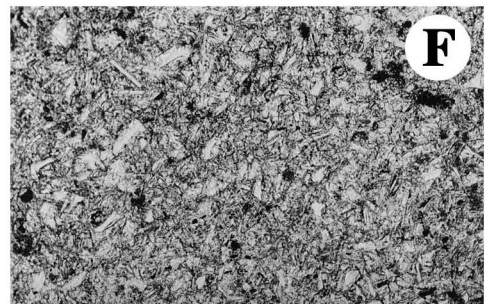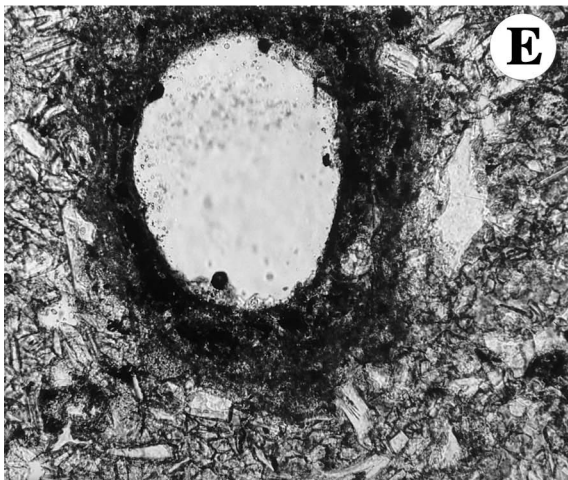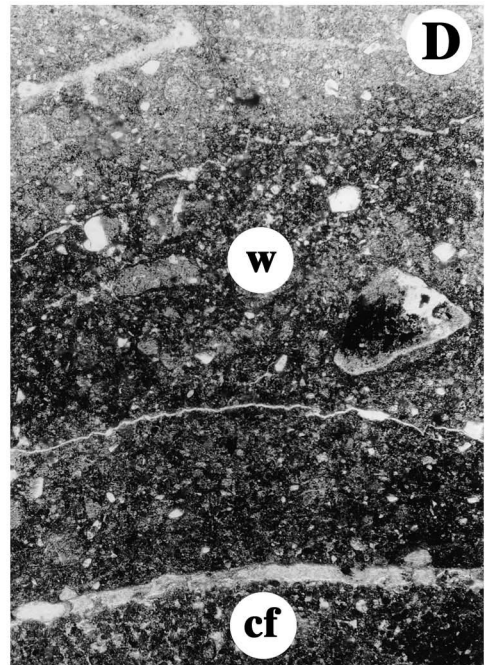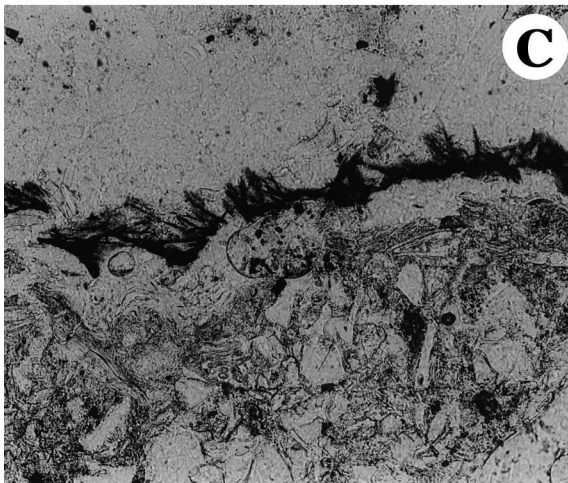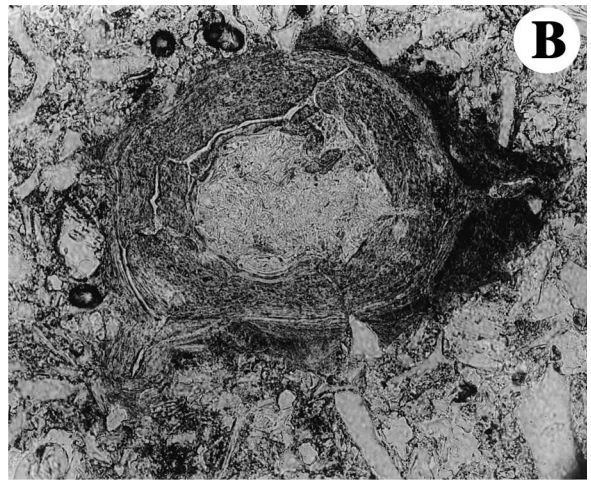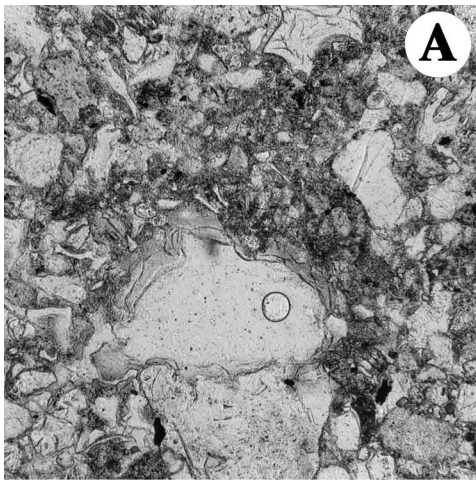
are tubes of unknown origin in which the fine material is concentrated around the pores and coarse grains are partially oriented (Fig. 5E). The nomenclature for thin section descriptions is taken from Bullock et al. (1985).

The highly bioturbated tuffs are yellowish to light brown (5 YR 6/4) and form characteristic paleosols that stand out in relief from the vertical cliffs. Two horizons are recognized in these paleosols: an upper platy eluvial horizon and a lower illuvial horizon, with angular to subangular blocky structure; both horizons are highly bioturbated (Fig. 3C). Commonly, below these horizons there is a deposit of paler, yellowish brown color (10 YR 8/2), scarcely bioturbated and less consolidated, compatible with a C horizon. The top of the mature paleosols is always sharp with overlying units, but the boundary between the blocky horizon and the underlying deposit (C horizon) is gradational. In contrast, some exposures of the Laguna Palacios Formation in Cañadón Puerta del Diablo lack a C horizon, showing instead a succession of up to five discrete eluvial and illuvial horizons (Figs. 3B and 4B). These horizons are bioturbated by abundant small root and invertebrate traces (Fig. 3D,F). Peds and vugs exhibit clay coatings produced by leaching. The lithological attributes are similar to those of the slightly bioturbated tuffs, but accretionary lapilli are absent.

Thin section analyses of these paleosols show a weak blocky to single-grain microstructure. Interpedal voids are scarce, whereas intrapedal ones are abundant and irregular, consisting of unoriented single packed voids, vugs and channels (Fig. 5A). The coarse fraction (40%) is poorly sorted medium sand, and is composed mainly of volcanic glass and, in decreasing order of importance, of rock fragments, plagioclase, and quartz. The individual grains are tabular elongate to equidimensional, and subangular to subrounded. The fine fraction (55–60%) is composed of yellowish to light brown clay, having a well-developed b-fabric, grano, poro and random striated (Fig. 5A,B). The c/f distribution is partly citonic–gefuric and partly porphyric. The principal microscopic pedofeatures that characterize these paleosols are textural. Abundant multilayered clay coatings on grains and wall pores are composed of well-oriented material, which commonly covers or fills them completely (Fig. 5B). The coatings are produced by abundant translocation of illuvial clay. Other important features are the pilose pore coatings and irregular glebules of Fe and Mn compounds (Fig. 5C) and the presence of *Taenidium barretti* that exhibits an alternation of dark and light menisci.

3.2. Interpretation

The slightly bioturbated tuffs are interpreted as entisols because of their very weak development reflected in the absence of horizonation, peds, mottling and clay translocation (Bown and Kraus, 1987; Retallack, 1990; Nettleton et al., 2000). The few root and invertebrate traces are the scarce pedogenic features that indicate the subaerial exposure of these deposits. Entisols can be formed under different climates and usually they support herbs and shrubs (Retallack, 1990).

The highly bioturbated tuffs show a textural Bt horizon, subangular–angular blocky peds, clay coatings and abundant bioturbation, characters that are compatible with the development of alfisols or mollisols (Retallack, 1990; González, 1999; Nettleton et al., 2000). Gradations between alfisols and mollisols are common (Boul et al., 1990) precluding a more definite identification for the paleosols described herein. In addition, paleomollisols are difficult to identify because of the loss of organic content of the mollic epipedon

Fig. 5. Micromorphology of paleosols. (A) Mature paleosol showing a pore coated by well-oriented clays. 72×. (B) Detail of a pore showing a multilayered clay coating. 144×. (C) Mature paleosol showing a pilose pore coating of Fe and Mn compounds. 144×. (D) Coleopteran pupal chamber showing the wall (w) and the chamber filling (cf). Note the darkening of the wall toward the internal cavity. 29×. (E) Immature paleosol showing clays concentrated around a pore. 144×. (F) Micromorphology of the immature paleosol where the fossil bee nests were found. 72×.

upon burial (Retallack, 1990; Nettleton et al., 2000). The abundance of burrows and small root traces in these tuffs would be indicative of mollisols (Retallack, 1990). However, the subangular to angular peds instead of crumb to granular ones and the close relationship of mollisols to post-Paleocene grasslands (Retallack, 1990) would suggest alfisols. Another type of soils, the andisols, are distinguished basically by their parent material, which is volcanic ash (Birkeland, 1984; Retallack, 1990), the same as the Laguna Palacios paleosols. However, andisols are defined for particular environments dominated by sloping surfaces, abundant forest vegetation and considerable rainfall (Retallack, 1990; Soil Survey Staff, 1998), whereas ash falls may occur in a wide range of climates and biomes, forming different soils, such as both shown herein, inceptisols (Melchor et al., 2001) and mollisols (Bown and Larriestra, 1990; Bown and Fleagle, 1993).

Mollisols indicate subhumid to semiarid climates and grassland vegetation, whereas alfisols indicate the same climates and vegetation ranging from wooded grassland to open forest (Retallack, 1990). The small diameters of roots in the highly bioturbated tuffs indicate an environment dominated by herbaceous plants, with scattered trees, regarding the presence of trunk and stem remains (Sciutto, 1981, 1999). Micromorphologically, abundant multilayered coatings on grains and wall pores, composed of well-oriented clay minerals, would be indicative of well-drained soils formed under successive periods of dry and more humid conditions typical of seasonal climates, a similar case to the concentric layers of soil concretions, which are the result of discontinuous, seasonal, growth (Retallack, 1990). On the other hand, the Fe and Mn nodules and pore coatings of Mn+Fe (hydromorphic features of soils) suggest fluctuations of the water table. The presence of Fe and Mn nodules in combination with argillans is common in well-drained mollisols (Boul et al., 1990).

Development of mature alfisols/mollisols, having sharp top contacts, as well as the presence of composite soils would have required long periods of quiescence between each ash-fall event, which would have allowed the development of stacked horizons. Nevertheless, such cycles might be shorter considering that the parent material is fine tephra. In volcanic ash accumulations, weathering proceeds rapidly because of the high surface area, loose packing, high porosity, low bulk density (0.5–0.9 g/cm^3), high water content, phosphate and organic matter retention and the trapped gas, facilitating water circulation (Retallack, 1990). The high porosity and loosely packed parent material also suggest that mature paleosols were well drained. Such soils are very suitable for the nesting activities of insects (Genise, 1999).

The different maturities of the paleosols bearing the trace fossils may be identified following the pedofacies model proposed by Bown and Kraus (1987) for alluvial deposits. Bown and Larriestra (1990) also utilized this model for pyroclastic deposits. In the Laguna Palacios Formation two pyroclastic pedofacies are recognized. One, immature, is characterized by drab paleosols having no horizon formation, no mottling or clay-lined cavities, and very low bioturbation, bearing the fossil bee nests and few root and invertebrate traces (entisols). The other, mature, is characterized by darker paleosols with well-developed horizon formation, abundant clay leaching and bearing the coleopteran pupal chambers and abundant root and other invertebrate traces (alfisols/mollisols).

4. Fossil bee nests

4.1. Description

The fossil bee nests are restricted to an isolated, small outcrop of slightly bioturbated tuffs surrounded by Quaternary deposits forming part of the floor of Cañadón Puerta del Diablo (Fig. 3A,B). The exposed nesting site is 9.50 m long and 5.20 m wide; however, the large number of detached cells and portions of tunnels found in float surrounding the outcrop reveals that the nesting area was originally somewhat larger (Fig. 3E).

The nests were grouped 30 cm or less from each other. In some cases tunnels are separated by less than 2 cm and cells by only a very thin layer of rock. Nests are natural casts covered by a more

resistant layer that allows, in some cases, the preservation of subvertical tunnels with cells in relief on the exposed horizontal surface of the outcrop. It was impossible to obtain a complete nest because the upper part of tunnels was truncated by erosion. However, the distance from the top of the deposit to the uppermost tunnel observed was about 5 cm. Tunnels do not penetrate the subjacent bed, in turn, near the contact, they become more inclined, ending subhorizontally in the contact, and devoid of cells in the last 12 cm. Thus, the complete length of tunnels can be estimated to be 70 cm and the number of cells per nest to be about 120. There is no evidence of tunnel branching. Cells, which are attached by short necks to the main tunnel, are mostly horizontal. However, some of them show the rear ends slightly inclined upwards, an uncommon character for bee cells. This fact indicates that provisions were more or less solid, otherwise they would spill into the tunnel, suggesting that they contained mostly pollen or at least more pollen than nectar. Tunnels also show a relatively small number of knobs that probably correspond to closed or incomplete cells.

The diameter of tunnels ranges from 9 to 11 mm and the teardrop-shaped cells, arranged in closely packed whorls, are 15–30 mm long and 6–13 mm in maximum diameter (Genise, 2000). The variability in cell size does not show important discontinuities that might be related to sexual dimorphism or caste differentiation, when either the whole sample or each nest individually is considered (Fig. 6).

The ichnotaxonomy of these traces was treated in a separate contribution (Genise, 2000), whereas herein are presented complementary data on further material examined, as well as paleoethological, paleoecological and paleogeographical inferences, and trace maker discussion. These trace fossils were included in the new ichnogenus *Cellicalichnus*, which was created to group the fossil nests described herein, named *Cellicalichnus chubutensis*, and other known ichnospecies formerly attributed to *Celliforma*. These ichnospecies, namely *Celliforma ficoides* (Retallack, 1984), *Celliforma habari* (Thackray, 1994), and *Celliforma dakotensis* (Elliott and Nations, 1998) – the latter

also from rocks of the late Cretaceous, share with *C. chubutensis* the presence of rows or whorls of cells attached by means of short necks to main tunnels (Genise, 2000).

4.2. Trace makers

Whorls of cells attached directly or by means of short laterals to vertical tunnels are common nest architectures for the sweat bees (Halictinae) (e.g. Sakagami and Michener, 1962; Eickwort and Sakagami, 1979). This subfamily is currently divided into five tribes, the Old World Nomiodini, the Neotropical Augochlorini and Caenohalictini, and the cosmopolitan Halictini and Gastrohalictini (Engel, 2000). These taxa cannot be distinguished by means of the nest architecture of their species, but Eickwort and Sakagami (1979) observed that in the Augochlorini the arrangement of cells in clusters is predominant. In addition, Eickwort (1969) noted that cells directly attached to tunnels are present in nests of all Augochlorini, whereas in other nests, with the single exception of those of the genus *Ruizantheda*, cells are always connected to main tunnels by a lateral, albeit sometimes very short and inconspicuous (Engel, personal communication). It is impossible to ascertain the original position of the cell closure in the fossil nests of the Laguna Palacios Formation and, hence, whether the narrow passage between the cell and the main tunnel represents a true cell neck or a short lateral. In any case, nests of the Augochlorini that lack cell clusters (Claude-Joseph, 1926; Michener and Lange, 1958a) differ from those of the Laguna Palacios Formation in other important characters. Moreover, being a derived type of nest for augochlorines, its presence in the Late Cretaceous, when this tribe probably arose, is doubtful (Engel, 1996, 2000). Species included in the other neotropical tribe, Caenohalictini, construct nests having cells at the end of long laterals that do not resemble the fossil ones described herein (Eickwort, 1969; Roberts, 1969). In addition, the Neotropical Sphecodina (Halictini) include parasitic species that do not construct any nest (Moure and Hurd, 1987).

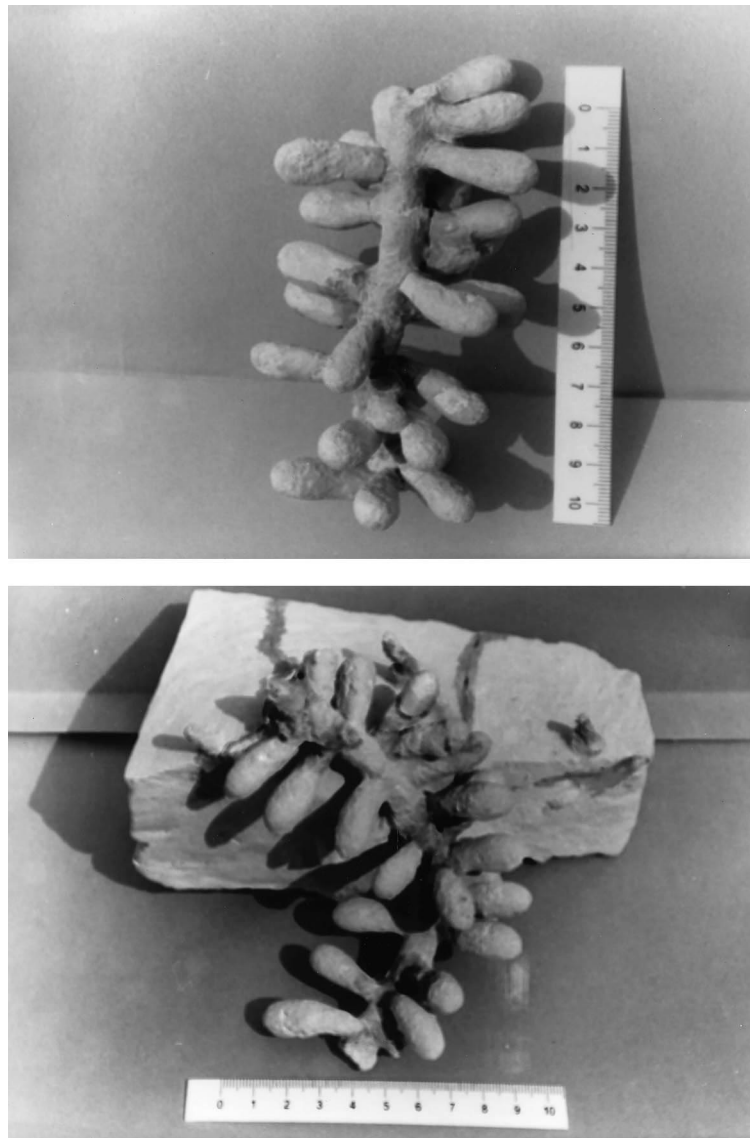In contrast, representatives of Gastrohalictini

Fig. 6. General aspect of two remains of fossil bee nests. Scale bar: 10 cm.

and Halictina (Halictini) construct nests that closely resemble the fossil ones from the Laguna Palacios Formation. All show a similar bauplan: tunnels penetrating vertical banks, or flat ground, bearing horizontal cells attached to them by means of short laterals (Sakagami and Michener, 1962; Batra, 1966, 1987; Michener, 1966, 1974; Michener and Wille, 1961; Michener et al., 1979; Wille and Orozco, 1970; Eickwort and Eickwort, 1971; Breed, 1975; Eickwort, 1986; Packer et al.,

1989; Packer, 1992; Wcislo et al., 1993). However, the Gastrohalictini are not present in South America (McGinley, 1986; Moure and Hurd, 1987) and the South American representatives of Halictina possibly arrived only after the emergence of the Central American land bridge, during Pliocene–Pleistocene times, like other groups of bees (Michener, 1979; Simpson and Neff, 1985), a fact that is suggested by the large number of species of North American Halictina in compar-

ison with the few Neotropical ones (Moure and Hurd, 1987). In addition modern species of Neotropical Halictina, such as *Dialictus*, are too small in body size to be the constructors of the fossil cells (Knerer and Atwood, 1962; McGinley, 1986; Engel, personal communication). These, in turn, correspond more closely to the body sizes of Gastrohalictini, such as *Lasioglossum* or *Evylaeus* (McGinley, 1986).

In summary, the architecture of the fossil bee nests of the Laguna Palacios Formation suggests that they could be constructed by an unknown species of the Halictina (Halictini) not necessarily related to the modern South American representatives of this subtribe, or more likely, a Gastrohalictini, in any case lineages that are no longer represented in the Southamerican fauna.

4.3. Paleogeographical implications

The presence of Halictina or Gastrohalictini in the Late Cretaceous of southern South America supports the hypothesis of its connection with North America by means of chains of islands (Seyfried and Sprechmann, 1985; Bonaparte, 1986; Marshall et al., 1997; Pascual, 1996, 1998). The isolation of South America from other continents began from early to mid-Cretaceous times (Harrington, 1962; Ramos, 1989; Pascual, 1996, 1998), along with the differentiation of bee families and halictid subfamilies triggered by the radiation of angiosperms (Michener, 1979; Engel, 1996). By the Late Cretaceous, when the nests were constructed, South America was completely separated from Africa but would have been connected to North America and Australia (via Antarctica) by means of chains of islands (Pascual, 1998). The colonization from Australia, through cool temperate Antarctica, for warm-temperate bees like halictids, was considered unlikely (Michener, 1979). Thus, leaving aside possible constructors of the nests from African or Australian lineages, and extinct Halictinae from the South American original stock, from which there is no evidence, a North American Halictina or Gastrohalictini seems the most probable constructor.

Michener (1979) postulated the island-hopping bee interchange between South and North Amer-ica during the Tertiary evidenced by a large number of island colonizations by these insects. Similarly, this interchange could have existed as well during Late Cretaceous times if chains of islands connected both continents. The faunal interchange between both Americas during the Last Cretaceous is also supported by dinosaurs (Bonaparte, 1984a,b, 1986 and references herein); by mammals (Pascual and Ortiz Jaureguizar, 1990; Pascual et al., 1992; Marshall et al., 1997); and by ichnological evidence. An insect trace fossil, *Brownichnus favosites*, a comb of a social wasp, poses the opposite case of the fossil bee nests: the presence in the Late Cretaceous of the Nearctic region of a trace fossil of wasps of possible Gondwanan origin (Wenzel, 1990).

4.4. Paleoethological implications

Paleoichnology yields physical evidence on the evolution of behavior of Halictinae from even earlier times than do body fossils, allowing us to calculate minimum dates for the origin of some behaviors and to test phylogenetic hypotheses (Genise and Engel, 2000). The fossil nests described herein, and those described for the Late Cretaceous of Dakota (Elliott and Nations, 1998), do not show the hypothetical features of the most primitive halictine nests proposed in previous papers (Sakagami and Michener, 1962; Eickwort and Sakagami, 1979; Engel, 2000). They show a more derived design, composed of cells without laterals and densely packed along the tunnels. This demonstrates that, by the Late Cretaceous, either the Halictinae had already developed highly derived nest architecture (more likely) or the most primitive type was similar to that described herein.

The fossil nests also yield important data on the degree of sociality that their constructors had developed. Breed (1976) and Packer (1992) thought that nests of *Dialictus*, having a high density of cells, contained a large number of bees per nest and that this was indicative of more advanced sociality. Kukuk and Eickwort (1987) proposed that a low ratio of lateral tunnel length to brood cell length forced close contact among related individuals, thereby fostering the development of

eusociality. Thus, the density of cells and short laterals of the Laguna Palacios fossil nests suggest that the trace makers had developed some degree of sociality.

4.5. Paleoecological implications

Bees, as a whole, are more abundant and diversified in the warm-temperate xeric regions of the world, a fact that is explained by damage (fungal attack, hygroscopic liquefaction) that may be caused by a humid environment to the larval provisions (pollen and nectar) and to the larvae themselves, in soil nests (Michener, 1979). Halictinae that nest in flat ground prefer a bare soil surface, sufficient insolation and firm soil (irrespective of soil types) – conditions common in desert, steppe, or related environments (Sakagami and Michener, 1962). Even so, these authors recognized exceptions for all of these conditions. For example, some species nest in moist tropical forest soils (albeit most of them nest in vertical banks), whereas other species nest in grassy areas with dense root systems, and still others prefer loose sandy soils. Some species nesting in tropical forest soils prefer patches or trails with grassy vegetation or bare soil (Jörgensen, 1912; Wille and Orozco, 1970).

Some structures of halictine nests are interpreted as devices to protect larvae and provisions from excessive moisture, and their presence or absence in fossil nests can be important in obtaining paleoecological data. Entrance turrets, rarely preserved, are constructed to prevent nests from flooding (Sakagami and Michener, 1962). Similarly, cavities around clusters, tunnel constrictions, or tunnels of small diameter are supposed to be devices to prevent larvae from waterlogging (Packer et al., 1989; Packer, 1991 and references therein). None of these features were found in the fossil nests suggesting that flooding and waterlogging were not common processes.

Sakagami and Michener (1962) stated that texture, humidity, and temperature of soil could control burrow depth. Breed (1975) and Eickwort and Eickwort (1971) recorded species of *Dialictus* in which the depth of nests was controlled by soil horizons. In addition, shallow nests and/or non-extended tunnels constructed by some Halictini indicate rainy areas (Michener and Lange, 1958b), rainy and cold environments (Packer et al., 1989) or a relatively long season of activity (Michener et al., 1979). In contrast, in most cases, long tunnels with densely packed cells indicate dry environments, seasonal climate, overwintering adults and/or large societies (Michener and Wille, 1961; Batra, 1966, 1987; Michener, 1966; Wille and Orozco, 1970; Eickwort and Eickwort, 1971; Eickwort, 1986; Packer, 1991; Wcislo et al., 1993).

Fossil nests finished just in the contact of the subjacent bed revealing that its depth was controlled by soil texture and that they were deepened as much as possible. Despite this restriction, the tunnels were 70 cm long, contained densely packed cells and were not constricted suggesting a seasonal climate and a relatively dry environment. The ecological preferences of most Halictinae suggest, in addition, an environment dominated by low or sparse vegetation that provide well-insolated soils.

5. Fossil coleopteran pupal chambers

5.1. Description

The coleopteran pupal chambers occur as scattered, isolated ovoid structures, along the horizontal and sloping surfaces of several outcrops of highly bioturbated tuffs surrounded by the Quaternary deposits forming part of the floor of Cañadón Puerta del Diablo. They occur in situ in a succession of two discrete eluvial and illuvial

Fig. 7. Coleopteran pupal chambers. (A) Different general aspects. (B) Specimens showing the emergence holes. (C) Broken specimen showing the wall composed of two layers of soil material. (D) Specimen showing a faint microrelief impressed on the chamber filling. Scale bar: 1 cm.
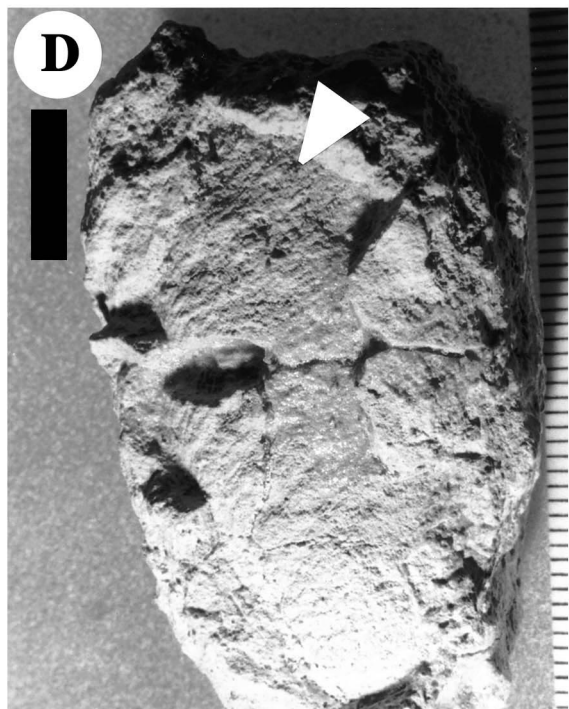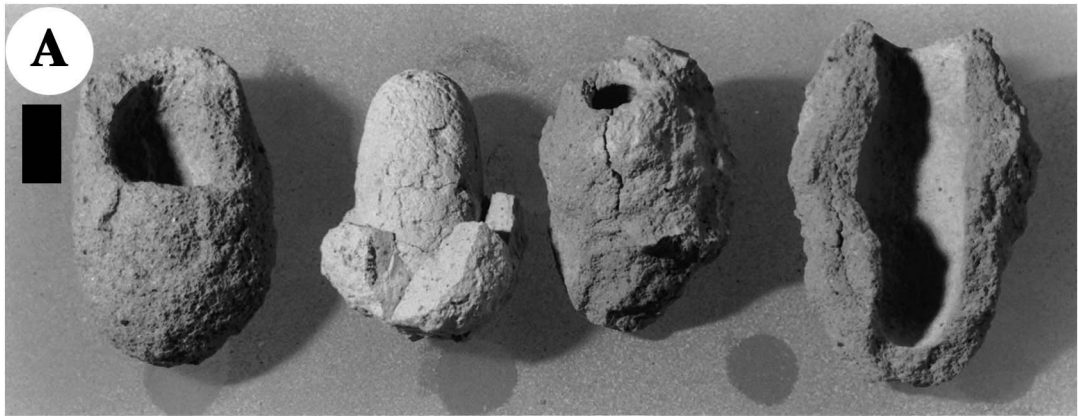
horizons, lying in positions from horizontal to vertical, together with trace fossils of roots and invertebrate burrows (Figs. 3B and 4B). Only 17 specimens, from the 104 collected, were complete; the remainder have one of the ends broken (Fig. 7A). The smallest specimens measure 31.6 mm in length and 20 mm in maximum diameter, whereas the largest ones measure 49 mm in length and 32 mm in maximum diameter. These structures are ovoid, and they have an external lumpy surface. Some of the complete specimens have a well-rounded emergence hole at the top or on the side, 9 mm in diameter (Fig. 7B). Broken specimens demonstrate that they possessed an internal, empty, ovoid, chamber with smooth walls, ranging in length from 25 mm to 36 mm, and in maximum diameter from 13 mm to 17.6 mm (Fig. 7). The dispersion of external and internal diameters as well as external lengths in complete specimens shows no discontinuities suggesting the presence of either different species of trace makers or intraspecific differences in size related to sexual dimorphism or larval feeding. The chamber walls are composed of two layers of soil material that can be distinguished in some broken specimens (Fig. 7C). One specimen exhibits a faint microrelief impressed on the chamber filling, indicating that the trace maker produced it while constructing the chamber (Fig. 7D). A thin section of the wall shows that the ground mass becomes darker towards the internal cavity of the pupal chamber (Fig. 5D). Genise and Hazeldine (1998) found a similar micromorphology in *Palmiraichnus pinturensis*, a fossil bee cell constructed in tuffs. In both cases, the darkening may be attributed to the work of the trace maker. However, it is not produced by a high concentration of clays as in *Fictovichnus gobiensis* (Johnston et al., 1996) and therefore it cannot be attributed to fluidization (Genise and Poiré, 2000).

Similar trace fossils were described from the Late Cretaceous–Early Tertiary Asencio Formation of Uruguay by Roselli (1987) who named them *Rebuffoichnus casamiquelai* and attributed them to constructions of dung beetles. Later, Johnston et al. (1996) described the ichnogenus *Fictovichnus* to include two ichnospecies: *Fictovichnus gobiensis* and *Fictovichnus parvus*, from the Late Cretaceous Djadokhta Formation of Mongolia and other unnamed traces from the Quaternary of Australia (Lea, 1925), similar to those described herein. *Fictovichnus* was attributed to Curculionidae and other families of Coleoptera. Lea (1925) found the trace maker, a large weevil (Curculionidae), preserved inside some of the Quaternary trace fossils of Australia, leaving no doubt as to its origin and affinities. *Fictovichnus* lacks a constructed wall, whereas *Rebuffoichnus* and the traces described herein share a similar morphology, suggesting, more likely, that they can be included in the latter ichnogenus.

5.2. Trace makers

The morphology of coleopteran pupal chambers lacks any comprehensive treatment, the information being scattered over a number of papers and revisions. The following account is fragmentary and only based on a limited number of contributions available to us. Pupal chambers constructed by different families of Coleoptera are impossible to separate macromorphologically, precluding any accuracy in the identification of the trace maker and, consequently, paleoecological inferences that can be obtained from these trace fossils. The scarcity of information precludes a broad comparative study and hence, the similarities between the fossil material described herein and pupal chambers of curculionids, melolonthines and dytiscids are the result of a biased comparison.

Lawrence (1991) recorded 53 families of beetles having representatives that pupate in the soil, although only species of 13 of them have soil-dwelling larvae, feeding on humus, plant roots, and other invertebrates. Silphids and hydrophilids construct subspherical pupal chambers from soil material by rotation of their bodies (Balduf, 1935; Wilson, 1923a). The chambers of some species of Lampyridae are also subspherical, but the construction involves a more complex mud-daubing behavior (Balduf, 1935). Gyrinids construct the pupal cell with a variety of materials apart from soil. Some of them are oval-shaped, but in all cases they are small in size (Balduf, 1935). The

pupal chambers of Cicindelidae are oval-shaped, and are excavated in the soil in connection with larval tunnels, and lack any discrete wall (Shelford, 1909). A similar condition is found in the related Carabidae (Sturani, 1964), and in the Cerambycidae (Leech, 1963). Some pupal chambers of Staphylinidae are elongated, excavated and lined with plant material (Farina, personal communication), whereas the Dytiscidae construct spherical, oval, and pyriform pupal chambers, utilizing mud pellets (Balduf, 1935). One of the largest species studied, *Cybister fimbriolatus*, constructs an oval chamber of similar size to those found in the Laguna Palacios Formation (Wilson, 1923b). Among Scarabaeidae, dung beetles commonly pupate inside the brood masses constructed by the adults (Halffter and Edmonds, 1982). Dynastines, such as *Diloboderus abderus*, construct a pupal chamber with soil material (Frana, personal communication), but cetonines make rounded cells having pellet-like outer surfaces (Johnston et al., 1996; Genise, unpublished) or with a sand-grained texture (Lea, 1925; Skelley, 1991). Melolonthines, like *Sparrmannia flava*, construct elongated pupal cells (Scholtz, 1988) like the fossil forms. The Laguna Palacios fossils also closely resemble curculionid pupal chambers illustrated by Lea (1925, figs. 8 and 9) from Australia. Weevil pupal chambers from Argentina were illustrated by Lanteri et al. (1994), but the general outline differs from the fossil material in being stouter and smaller. Finally, Lawrence (in Johnston et al., 1996) also suggested that members of the Tenebrionidae might construct pupal chambers of this shape and size.

Comparisons involve the size, shape and smooth inner walls, but also they can be extended to the emergence holes. Lea (1925) illustrated chambers with round emergence holes located at the top or laterally, near one extreme. The fossil chambers described herein show well-rounded emergence holes that closely resemble those illustrated by Lea (1925) from weevil pupal cells.

When the trace maker cannot be identified accurately it is impossible to extract important paleoecological implications. Coleopteran pupal chambers were found in only two of the several stacked paleosols, meaning that environmental conditions must have changed through time. They were absent from the bee nesting site, probably because they preferred different, perhaps more humid, soil conditions. Although coleopteran pupal chambers are not indicators by themselves, the similar *Rebuffoichnus casamiquelai* is associated with dung beetle and bee nests in the Asencio Formation of Uruguay, a classic example of the Coprinisphaera ichnofacies (Genise et al., 2000). The data are still sparse but the trace fossils described herein related to herbaceous plant communities could be the first record of the continental Coprinisphaera ichnofacies (Genise et al., 2000) from pre-Tertiary times.

6. Concluding remarks

During Laguna Palacios time, most sediments originated as ash-fall deposits, blown downwind from distant volcanic vents and deposited subaerially on relatively flat plains, where they were pedogenetically altered or reworked by rivers. Sustained eruptions, which allow the formation only of immature soils (entisols), were interrupted by quiescent periods, during which relatively mature soils were formed (alfisols/mollisols). The prevailing climate was seasonal and temperate, showing somewhat drier conditions during sustained eruptions and more humid ones during quiescent periods. The dominant vegetation was herbaceous, with scattered trees.

During this period of time a species of halictine bees, which had developed a certain degree of sociality and a derived architecture, excavated their nests in entisols, favored by drier conditions, whereas beetles constructed pupal cells in the mature alfisols/mollisols under a more humid environment. The halictines, probably related to the North American Halictina or Gastrohalictini, would have invaded South America favored by the presence of chains of islands connecting both continents.

The fossil bee nests described herein represent the third evidence of the presence of bees in the Cretaceous, one of the oldest for this group of insects, and the oldest fossil nests recorded from the Southern Hemisphere.

Acknowledgements

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