



## CURVED FOSSIL BEE CELLS AS TOOLS FOR RECONSTRUCTING THE EVOLUTIONARY HISTORY AND PALAEOGEOGRAPHICAL DISTRIBUTION OF DIPHAGLOSSINAE (APOIDEA, COLLETIDAE)

by LAURA C. SARZETTI<sup>1\*</sup>, PABLO A. DINGHI<sup>2</sup>, JORGE F. GENISE<sup>1</sup>, EMILIO BEDATOU<sup>3</sup> and MARIANO VERDE<sup>4</sup>

<sup>1</sup>CONICET, División Icnología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Angel Gallardo 470, 1405, Buenos Aires, Argentina; e-mails: lsarzetti@macn.gov.ar, jgenise@macn.gov.ar

<sup>2</sup>Grupo de Investigación en Filogenias Moleculares y Filogeografía (Fac. de Ciencias Exactas y Naturales, UBA), Ciudad Universitaria, CP1428, Buenos Aires, Argentina; e-mail: pablosinghi@ege.fcen.uba.ar

<sup>3</sup>CONICET, INCITAP, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Av. Uruguay 151, 6300, Santa Rosa, La Pampa Argentina; e-mail: emilibedatou@exactas.unlpam.edu.ar

<sup>4</sup>SNI-ANII, Departamento de Evolución de Cuencas de la Facultad de Ciencias, Universidad de la República, Igua 4225, CP 11400, Montevideo, Uruguay; e-mail: verde@fcien.edu.uy

\*Corresponding author

Typescript received 9 April 2013; accepted in revised form 29 July 2013

**Abstract:** The new ichnospecies *Celliforma curvata* is described to include curved fossil bee cells from Argentina, Uruguay and the USA. The upper part of the cell (neck) of the new ichnospecies is curved, and accordingly, it can be attributed to bees of the subfamily Diphaglossinae (Colletidae). The oldest record of *C. curvata*, from the early Eocene of North America (52–49 Ma), provides a minimum age for the appearance of this subfamily, in accordance with an already proposed calibrated phylogeny. It is also proposed that these fossil cells could be used for

future calibrations of molecular clocks. *C. curvata* indicates that Diphaglossinae had a widespread distribution, from southern Utah to extra-Andean Patagonia at 42°S. In contrast, extant representatives reach only 38°S in this region. Diphaglossinae were more extended southwards in the past thanks to better environmental conditions in extra-Andean Patagonia.

**Key words:** *Celliforma curvata* isp. n., curved bee cells, Diphaglossinae, minimum age, palaeodistribution.

BECAUSE of their unique morphology, fossil bee cells can be unequivocally recognized and provide important information for reconstructing the evolutionary history of bees. Furthermore, bee cells are one of the most common trace fossils in palaeosols. Their ichnotaxonomy was reviewed by Genise (2000), who grouped them in the ichnofamily Celliformidae. Several ichnotaxa have been defined for fossil bee cells and nests in the literature (Brown 1934; Roselli 1939; Genise and Bown 1996; Genise 2000; Genise and Verde 2000; and references therein). The ichnogenus *Celliforma* Brown, 1934 redefined by Genise (2000) includes isolated chambers or moulds of cells, having rounded rears and flat tops, with different shapes (subcylindrical, tear, flask, urn, vase, barrel). One of the shared features of all described ichnospecies until now is that the upper part of the cell is straight and truncated or capped by a spiral closure.

New specimens of fossil bee cells found in Patagonia (Argentina), Uruguay and the USA have the upper part of the cell curved. Curved cells in soils are exclusive to Diphaglossinae (Rozen 1984; Sarzetti *et al.* 2013), a superfamily that includes the largest sized Colletidae distributed principally in subtropical regions of America (Michener 2007). Bertling *et al.* (2006) proposed that the knowledge of inferred producer's biology may support ichnotaxonomical arrangements. Accordingly, curved necks, being representative of cells of a whole subfamily of bees, are considered herein a character diagnostic enough to support the creation of a new ichnospecies of *Celliforma*.

The accurate identification of trace makers is a difficult task as body fossils are mostly not preserved within the traces. Identification is only possible when trace fossils are complex enough to preserve unequivocal diagnostic characters of a particular taxon. In bees, the combination of

characters of their cells, such as shape, smooth walls and spiral closures, is very diagnostic. When trace fossils can be attributed to a particular group, as in the case of bees, they provide the physical evidence to complete and improve our knowledge of the trace maker's evolutionary history (Genise and Engel 2000).

The objectives of this paper are as follows: (1) to define a new ichnospecies of *Celliforma* with curved necks, attributable to Diphaglossinae; (2) to analyse their palaeoenvironmental significance; (3) to propose a minimum age and location for the appearance of Diphaglossinae; and (4) to use the record of curved bee cells to infer the palaeogeographical distribution of Diphaglossinae.

## GEOLOGICAL SETTING

The specimens of *Celliforma curvata* came from the middle Miocene Collón-Curá Formation of Argentina, the Palaeogene Queguay Formation of Uruguay and the Paleocene–Eocene Claron Formation [Correction added on 11 March, after first online publication: in references to the Claron Formation throughout the article,

beginning in the preceding sentence, Palaeogene–Eocene has been corrected to Paleocene–Eocene] of the USA (Fig. 1).

### *The Collón-Curá Formation (middle Miocene)*

This formation, composed of both primary and reworked pyroclastic rocks, crops out in a wide area of Northern Patagonia, both in Argentina and Chile (González Bonorino 1979). In Argentina, it represents the final stage of the filling of the Ñirihuau Basin (Spalletti and Dalla Salda 1996; Ramos 1999). Likewise, this formation spreads out of the basin limits and extends to nearby areas (Vucetich *et al.* 1993). The Collón-Curá Formation was deposited over a previous palaeotopography developed on the crystalline basement and the Cretaceous Angostura Colorada Formation (Nullo 1979; Bondesio *et al.* 1980).

In outcrops at Pilcaniyeu (S 41°06'11"; W 70°45'20"), the formation can be recorded in almost its entirety. It is usually separated into:

1. A lower member, composed of light brown to white, massive, fine tuffs and grey clastic tuffs with abundant carbonatic nodules (Nullo 1979; Bondesio *et al.* 1980).



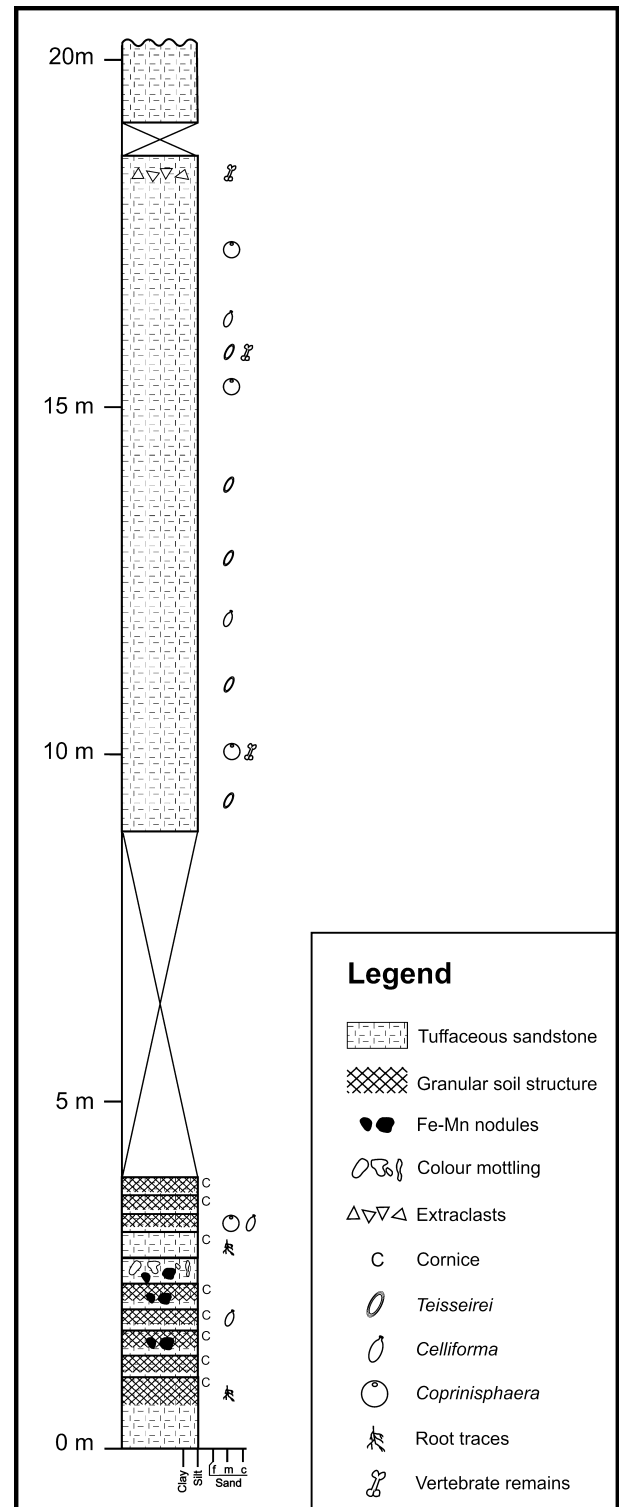
FIG. 1. Location map with the records of *Celliforma curvata*.

These rocks show evidence of soil formation such as crumbly structure, clay coatings, nodules, root traces and insect trace fossils (Vucetich *et al.* 1993). This member has been cited as the La Pava Member (Coira 1979), Carhué Member (Rabassa 1978) or La Pava Formation (Nullo 1979; González Díaz and Nullo 1980).

2. A Pilcaniyeu Ignimbritic Member, composed of white to light blue dacitic to rhyodacitic ignimbrites up to 60 m thick, concordant with the lower member beds (Bondesio *et al.* 1980). Ages from 15.4 to 10.7 Ma were obtained from samples of these ignimbrites (Rabassa 1974, 1978; Marshall *et al.* 1977; González Díaz and Valvano 1979; Cazau *et al.* 1989; Mazzoni and Benvenuto 1990).
3. An upper member, mainly concordant but in some cases eroding the underlying beds (Vucetich *et al.* 1993). It is very similar to the lower member, composed of reworked fine dacitic tuffs with soil horizons. Near the top of the member, there are some fluvial facies composed of sandy tuffs and conglomerates. This member was deposited mostly by ashfalls, but with occasional subaqueous contribution (Bondesio *et al.* 1980). The upper member has yielded important vertebrate fossil remains (Bondesio *et al.* 1980; Vucetich *et al.* 1993), which enabled the definition of the Colloncuran Land Mammal Age (Bondesio *et al.* 1980; Marshall 1990; Marshall and Salinas 1990).

Radiometric ages and mammal fossil remains (Bondesio *et al.* 1980; Pascual *et al.* 1984; Vucetich *et al.* 1993) date the Collón-Curá as Middle Miocene. Lower and upper members are genetically very similar, reflecting wind and, to a lesser extent, water reworking of primary pyroclastic deposits commonly pedogenized. The bee cells from Pilcaniyeu are housed at the Ichnological Collection of the Museo Argentino de Ciencias Naturales, recorded as coming from the Collón-Curá Formation, but without further stratigraphical information. They may belong to the lower or upper member.

At El Petiso (S 42°25'52"; W 69°57'22"), the Collón-Curá Formation is represented only by its lower member, and it lies on Cretaceous conglomeratic sandstones (Fig. 2). At the base, there are some stacked palaeosols with abundant Fe–Mn nodules, root traces and scarce *Coprinisphaera* spp., *Celliforma* isp., and a possible *Cellicalichnus*. The upper part of the succession is composed of a 10-m thick bed of a light grey, to light brown on top, massive silty tuff. *Celliforma curvata* comes from this bed, along with numerous specimens of *Celliforma rosellii*, *Celliforma germanica*, *Teisseirei barattinia*, *Rebuffoichnus sciuttoii* and *Coprinisphaera* spp. These beds would have been formed as ashfall deposits which, especially in the upper part of the succession, are comparable to loess deposits. The lower beds, according to development and stacking of palaeosols, suggest slower sedimentation rates



**FIG. 2.** Sedimentary log of Collón-Curá Formation at El Petiso. For sedimentary logs of the other units, see Alonso-Zarza *et al.* (2011) and Bown *et al.* (1997).

compared with the upper bed and/or major gaps between sedimentation events. The upper bed reflects an increasing sedimentation rate showing greater thickness and lower palaeosol development.

*The Queguay Formation (middle Eocene – middle Oligocene)*

The middle Eocene – middle Oligocene Queguay Formation is part of the sedimentary record of the Chaco-Paranaense and Santa Lucia basins and crops out in several localities from W and S Uruguay. It comprises palustrine and lacustrine limestone units formed under arid to semiarid climates (Alonso-Zarza *et al.* 2011). Recently, Alonso-Zarza *et al.* (2011) proposed a new stratigraphic framework and interpretation of the palaeoenvironments. According to these authors, the Queguay Formation overlies the Asencio Formation and would be middle Eocene – middle Oligocene in age. It is about 10 m thick and consists of two units. The basal unit is composed of coarse to fine sands with sparse larger clasts, some of which are sourced from the Asencio Formation. It is partially silicified and contains carbonate as both matrix and cements. The upper unit consists of a lower part with sandy limestone containing partially silicified carbonate laminae and an upper part with micritic limestone desiccation features and less prominent silicification (Alonso-Zarza *et al.* 2011). The Queguay Formation contains a diversity of insect trace fossils, rhizoliths and fossil invertebrates. The specimens of curved cells come from the upper unit and were found in a railroad cut near Quebracho Town (Paysandú County; S 31°55'19.6"; W 57°54'24.4") associated with *C. germanica* and *Celliforma spirifer* (Verde 2012).

*The Claron Formation (upper Paleocene – Eocene)*

The upper Paleocene – Eocene Claron Formation is extensively developed throughout most of the Colorado Plateau Province, in parts of the Basin and Range province, and in intermediate areas between them (Bown *et al.* 1997). It is late Paleocene – Eocene in age and it is divided into a lower red member and an upper grey or white member (Mackin 1960). The lower member contains the fossil bee cells and consists predominantly of poorly to moderately resistant sandstones intercalated with variegated mudstones, limestones and conglomerates, with some participation of pyroclastic material. It is interpreted as mixed fluvial and lacustrine deposits developed in a semiarid to subhumid climate with soils of fluctuating water tables (Bown *et al.* 1997). The insect trace fossils are abundant and occur in sandstones, mudstones

and volcanoclastic mudstones that have undergone significant pedogenetic alteration (Bown *et al.* 1997). The overlying white member is composed of white limestones, mudstones, sandstones and conglomerates. Pedogenic alteration is common in several deposits of this formation (Mullet *et al.* 1988; Mullet 1989).

## SYSTEMATIC ICHNOLOGY

This published work and the nomenclatural act it contains, have been registered in Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:69873058-4481-4BA6-93DD-314A6A1DB33D>

Ichnofamily CELLIFORMIDAE Genise, 2000  
Ichnogenus CELLIFORMA Brown, 1934

*Type ichnospecies.* *Celliforma spirifer* Brown, 1934.

*Diagnosis.* Chambers or internal moulds of chambers of different shapes (subcylindrical, tear, flask, urn, vase, barrel), having one end rounded and the other either truncated or capped by a flat or conical closure, bearing spiral grooves on its inner surface; walls having a smooth lining (Genise 2000).

*Celliforma curvata* isp. Nov.  
Figures 3A–G

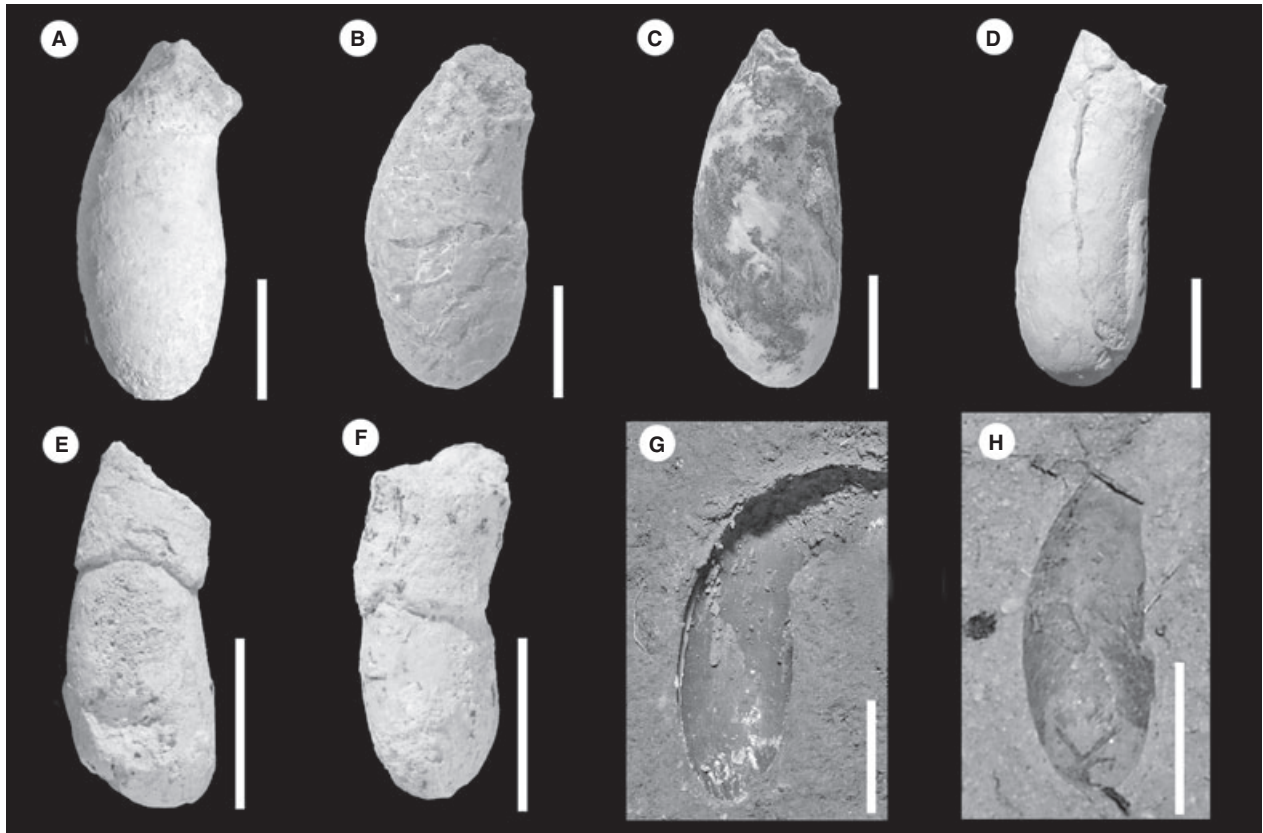
LSID. urn:lsid:zoobank.org:act:FCFC3258-BD67-4504-9AC7-15DF5777D18D.

*Derivation of name.* From the Latin *curvus*, which means bent, without angles.

*Holotype.* One specimen (MACN-Icn 79) from the middle Miocene Collón-Curá Formation of Estancia Criado, Pilcaniyeu, Río Negro Province, Argentina. It is housed in the Ichnological Collection of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires (Fig. 3A).

*Paratype.* One specimen (MPEF-IC 748-1) from the middle Miocene Collón-Curá Formation of El Petiso, Chubut Province, Argentina. It is housed in the Ichnological Collection of the Museo Paleontológico Egidio Feruglio, Trelew, Chubut (Fig. 3B).

*Examined material.* One specimen (MPEF-IC 748-2) from the middle Miocene Collón-Curá Formation of El Petiso, Chubut Province, Argentina (Fig. 3C). One specimen (MACN-Icn 1041) from the Paleocene–Eocene Claron Formation of Utah, USA (Fig. 3D). Two specimens (FCDP 5905 and 5907) from the Palaeogene Queguay Formation of Uruguay housed in the Palaeontological Collection of the Facultad de Ciencias, Montevideo, Uruguay (Fig. 3E–F).



**FIG. 3.** Specimens of *Celliforma curvata* isp nov. and extant cells of Diphaglossinae. A, holotype MACN-Icn 79. B, paratype MPEF-IC 748-1. C, specimen MACN-Icn 1041. D, specimen MPEF-IC 748-2. E, specimen FCDP 5905. F, specimen FCDP 5907. G, extant cell of *Priloglossa tarsata* and H, extant cell of *Cadequala albopilosa*. Note the different curvature of cells. Scale bars represent 1 cm.

**Diagnosis.** Internal moulds of vertical chambers, having rounded bottoms and curved necks finishing with a truncated flat closure. In some cases, the neck is slightly constricted. The wall has a smooth surface.

**Remarks.** This ichnospecies is clearly distinguishable from the other described ones because of its curved neck.

**Description.** The specimens of *C. curvata* were found isolated in palaeosols or detached from them without any connection to tunnels. The cells are vertical, showing a rounded bottom and a curved neck at the other extreme. The neck is curved downward less than 90 degrees from the longitudinal axis. The wall surface is smooth. Examined specimens of *C. curvata* lack a spiral closure. The holotype (MACN-Icn 79) is 3.70 cm high and 1.50 cm in maximum diameter. The neck is 1.10 cm in diameter (Fig. 3A). The paratype (MPEF-IC 748-1) is 2.25 cm high and 0.96 cm in maximum diameter (Fig. 3B). The neck is 0.66 cm in diameter. The specimen from Quebracho FCDP N° 5905 is 2.36 cm high, 0.95 cm in maximum diameter and the neck is 0.82 cm in diameter (Fig. 3E). Specimen FCDP 5907 is 1.84 cm high, 0.76 cm in maximum diameter and the neck is 0.8 cm in diameter (Fig. 3F). These specimens from Uruguay share a structure around the neck like a hood of unknown origin (Fig. 3E–F). The specimen from the Claron

Formation (MACN-Icn 1041) is 2.60 cm high, 1.10 cm in maximum diameter and the neck is 1 cm in diameter (Fig. 3D).

## DISCUSSION

Fossil bee cells grouped in *Celliforma* are one of the most common and simple trace fossils in palaeosols. A great diversity of digging bees may be the trace makers of *Celliforma*, and there is almost no way to positively relate most ichnospecies with a particular taxon of bees (Genise 2000). The case of *C. curvata* is an exceptional one because its curvature enables its attribution to a particular subfamily of bees, the Diphaglossinae. This particular character also justifies the creation of a new ichnospecies, even when the ichnotaxonomy of *Celliforma* is unclear.

The nest architecture and cell morphology of many Diphaglossinae (Colletidae) were described by Claude-Joseph (1926), Janvier (1933, 1955), Roberts (1971), Otis *et al.* (1983), Rozen (1984), Almeida (2008) and Sarzetti *et al.* (2013). Rozen (1984) reviewed previous information on Diphaglossinae and Almeida (2008) on Colletidae. All Diphaglossinae are solitary, ground-nesting bees. The

nests comprise a more or less vertical main tunnel and horizontal lateral ones, which end in one or two vertical, curved cells. As in other colletids, females line the cells with a cellophane-like lining (Michener 2007), which is probably responsible for the smooth surface of fossil cells. Diphaglossinae construct essentially two types of curved cells (Rozen 1984; Sarzetti *et al.* 2013). Species of the genus *Ptiloglossa* and *Crawfordapis* construct cells with the neck highly curved (90 degrees or more; Fig. 3G), whereas those of *Caupolicana*, *Policana* and *Cadeguala* construct less curved necks (<90 degrees; Fig. 3H; Rozen 1984; Sarzetti *et al.* 2013). The specimens of *C. curvata* show the latter type of curved neck. Consequently, the ichnospecies could be attributed more probably to some species of the genera *Caupolicana*, *Policana* or *Cadeguala*. In addition, from the topology shown in Almeida *et al.* (2012), it can be inferred that the less curved bee cell necks might be the ancestral condition for Diphaglossinae. The lack of spiral closure in *C. curvata* is also compatible with Diphaglossinae cells. Spiral closures were recorded for *Ptiloglossa tarsata* (Sarzetti *et al.* 2013), *Ptiloglossa arizonensis*, *Ptiloglossa fulvopilosa*, *Caupolicana gaullei*, *Caupolicana albiventris*, *Cadeguala albopilosa* (Rozen 1984) and *Cadeguala occidentalis* (Torchio and Burwell, 1987). However, spiral closure is not commonly observed in most Diphaglossinae (Roberts 1971; Rozen 1984; Sarzetti *et al.* 2013).

In many cases, insect trace fossils provide valuable information for interpreting palaeoclimatic or palaeoenvironmental conditions based on the ecological preferences of their supposed producers. For instance, the curvature of cell necks was proposed as an advantage to face floodings (Roberts 1971). However, *C. curvata* may not be indicative of any particular climatic condition (Rozen, 1984; Sarzetti *et al.* 2013). The climate in the nesting sites of Diphaglossinae is highly diverse with mean annual temperature (MAT) ranging from 8 to 20°C and mean annual precipitation (MAP) ranging from 250 to 3000 mm (Sarzetti *et al.* 2013).

According to Rozen (1984), cells with curved necks could be considered as a synapomorphy for Diphaglossinae. The record of *C. curvata* from the upper part of Claron Formation (52–49 Ma) provides a minimum age for the appearance of this major lineage of colletid bees in the early Eocene. This record is in concordance with the chronogram for Colletidae shown in Almeida *et al.* (2012), which presents a time range for this ancestral node from 67 to 42 Ma. This case proves that trace fossils can be useful (and regrettably underutilized) tools to calibrate phylogenies. These authors used a relaxed molecular clock, which was calibrated using three *a priori* age distributions assigned to different nodes of a tree with 123 terminals and 22 out-group taxa. Two of them based on body fossils from Dominican amber (Michener and Poinar 1996; Engel 1999) and a third, based on previous age

estimations, using data and patterns of multiple lineage exchanges between South America and Africa for the family Halictidae in its early stages of diversification (Danforth *et al.* 2004). In that analysis, Halictinae trace fossils (Elliot and Nations 1998; Genise *et al.* 2002) were dismissed as calibration points because authors doubted this type of evidence, despite their detailed morphology and specificity to particular tribes of Halictinae. However, well-documented fossil bee nests are usually accepted as reliable evidence (Genise and Engel 2000; J. Rozen Jr, pers. comm. 2004; Michener 2007, p. 101), and the evidence of Halictinae was incorporated in a bee chronogram shortly after (Grimaldi and Engel 2005). Undoubtedly, bee trace fossils could be a fourth set of data to be considered in further analysis (e.g. for Diphaglossinae and Halictinae).

Reliable trace fossils provide not only more calibration points, but a confident source of data that could add more support to topologies, providing extra characters for nonmolecular or mixed matrices. Their information, associated with behaviour, can be followed through time and evolution.

In historical biogeography, the fossils are usually used to corroborate hypotheses tested by algorithms, which are based on extant species. In modern palaeobiogeography, fossils are incorporated into the algorithms themselves (Lieberman 2000). Whether we are facing a biogeographical or a palaeobiogeographical problem, the literature usually refers to body fossils. Once again, trace fossils are not taken into account. However, they are probably the most reliable physical evidence for the past distribution of organisms, to some extent better than body fossils that could be transported. Trace fossils found in palaeosols give the exact geographic location of the producers and as they are *in situ*, they also provide much palaeoecological information, which it is frequently impossible to retrieve from body fossils.

*Celliforma curvata* shows that Diphaglossinae were widespread, ranging from southern Utah to extra-Andean Patagonia at 42°S, and from early Eocene to middle Miocene. Although the oldest record is from the Neartic region, it is not in conflict with the Gondwanan origin of colletids or the Diphaglossinae. Almeida *et al.* (2012) considered the South American continent (for the purposes of biogeographical analysis) as the junction of the Neotropical + Neotemperate regions (*sensu* Amorim and Pires 1996) and also including a narrow portion of the Neartic region (Central America and the southern part of USA). Secondly, the fact that the extant sister group of Diphaglossinae, *Paracolletes crassipes*, occurs in Australia reinforces the hypothesis of a Gondwanan origin for this stem group.

The distribution of extant Diphaglossinae shows that the subfamily is present from USA to Chile at 41°S

(Urban and Moure 2001), excluding the extra-Andean Patagonia. According to the present geographic distribution of Diphaglossinae, all the extant genera present in the Neotropical region have a distribution that mostly overlaps with its ancestral allocation shown by the record of *C. curvata*. In addition, the Miocene record of this ichnospecies in northern Chubut and southern Río Negro in the extra-Andean Patagonia (42°S) shows that Diphaglossinae had a more extended range in the past thanks to better environmental conditions in extra-Andean Patagonia. The southern limit of the extra-Andean distribution of extant Diphaglossinae is around 38°S (Urban and Moure 2001). There is a single record of *Caupolicana funebris* collected by Daguerre in 1901 in Carmen de Patagones (Buenos Aires Province) at 39°S (L. Compagnucci, pers. comm. 2013).

Comparisons between trace fossils of other groups of invertebrates in southern South American palaeosols and extant representatives show similar changes in distribution pattern, although the Diphaglossinae are more extended. Trace fossils of crayfishes dominate Jurassic and Cretaceous palaeosols of extra-Andean Patagonia, whereas extant crayfishes inhabiting soils are presently distributed in southern Chile and southern Brasil (Bedatou *et al.* 2008). Fossil brood balls of dung beetles that dominate middle Cenozoic palaeosols of extra-Andean Patagonia (Sánchez *et al.* 2010) were probably produced by the lineage of *Homocopris torulosus*, also presently distributed in southern Chile and southern Brasil (Dinghi *et al.* 2012).

The rise of the Andes originated in the late Cretaceous, albeit with the peak of uplifting rate at c. 15 Ma (Somoza 1998; Blisniuk *et al.* 2005; Guillaume *et al.* 2009), progressively forming a barrier to moisture-laden South Pacific winds (Riccardi and Rollieri 1980) forming an orographic rain shadow over Patagonia. Along with other factors and climate changes, the rain shadow starts the process of desertification in extra-Andean Patagonia (Bellosi 1995; Blisniuk *et al.* 2005; Ortiz-Jaureguizar and Cladera 2006, le Roux 2012). During the Palaeogene, the climate conditions in extra-Andean Patagonia were more favourable for the development of Diphaglossinae (among other taxa), having a climate and flora more comparable with those of northern localities (Bellosi 1995, 2010; Bellosi and González 2010, le Roux 2012) where they are distributed at present.

**Acknowledgements.** We thank Luis Compagnucci for assistance with entomological collection data and to Marcelo Krause for assistance with photography. This is a contribution of PICT 1972 from the Agencia Nacional de Promoción Científica y Tecnológica of Argentina to Jorge F. Genise. Funds from project ANII FCE 2007/44 to M. Verde made possible fieldwork in Uruguay.

**Editor.** Jason Dunlop

## REFERENCES

- ALMEIDA, E. A. B. 2008. Colletidae nesting biology (Hymenoptera: Apoidea). *Apidologie*, **29**, 16–29.
- ALMEIDA, E., PIE, M., BRADY, S. and DANFORTH, B. 2012. Biogeography and diversification of colletid bees (Hymenoptera: Colletidae): emerging patterns from the southern end of the world. *Journal of Biogeography*, **39**, 526–544.
- ALONSO-ZARZA, A. M., GENISE, J. F. and VERDE, M. 2011. Sedimentology, diagenesis and ichnology of Cretaceous and Paleogene calcretes and palustrine carbonates from Uruguay. *Sedimentary Geology*, **236**, 45–61.
- AMORIM, D. S. and PIRES, M. R. S. 1996. Neotropical biogeography and a method for maximum biodiversity estimation. 183–219. In BICUDO, C. E. M. and MENEZES, N. A. (eds). *Biodiversity in Brazil: a first approach*. Proceedings of the Workshop on Methods for the Assessment of Biodiversity in Plants and Animals, CNPq, Campos do Jordão, SP, Brazil, 326 pp.
- BEDATOU, E., MELCHOR, R. N., BELLOSI, E. and GENISE, J. F. 2008. Crayfish burrows from Late Jurassic–Late Cretaceous continental deposits of Patagonia: Argentina. Their palaeoecological, palaeoclimatic and palaeobiogeographical significance. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **257**, 169–184.
- BELLOSI, E. 1995. Paleogeografía y cambios ambientales de la Patagonia central durante el Terciario medio. *Boletín de Informaciones Petroleras*, **44**, 50–83.
- 2010. Climas y ambientes fluctuantes en la Patagonia central (Argentina) durante el Cenozoico medio. *Libro de Resúmenes del X Congreso Argentino de Paleontología y Bioestratigrafía y VII Congreso Latinoamericano de Paleontología*, p. 59.
- and GONZÁLEZ M. 2010. Paleosols of the middle Cenozoic Sarmiento Formation, central Patagonia. 293–305. In MADDEN, R., CARLINI, A., VUCETICH, M. G. and KAY, R. (eds). *The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia*. Cambridge University Press, Cambridge, 448 pp.
- BERTLING, M., BRADY, S., BROMLEY, R. G., DEMATHIEU, G., GENISE, J. F., MIKULÁŠ, R., NIELSEN, J. K., NIELSEN, K. S. S., RINDSBERG, A., SCHLIRF, M. and UCHMAN, A. 2006. Names for trace fossils: a uniform approach. *Lethaia*, **39**, 265–286.
- BLISNIUK, P. M., STERN, L. A., CHAMBERLAIN, C. P., IDLEMAN, B. and ZEITLER, P. K. 2005. Climatic and ecologic changes during Miocene surface uplift in the Southern Patagonian Andes. *Earth and Planetary Science Letters*, **230**, 125–142.
- BONDESIO, P., RABASSA, J., PASCUAL, R., VUCETICH, M. G. and SCILLATO YAN, G. E. 1980. La Formación Collón Cura de Pilcaniyeu Viejo y sus alrededores (Río Negro, Republica Argentina). Su antigüedad y las condiciones ambientales según su distribución, su litogénesis y sus vertebrados. *Actas II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología*, 2–6 April 1978 Buenos Aires, Argentina, Asociacion Paleontologica Argentina, **3**, 85–99.

- BOWN, T. M., HASIOTIS, S. T., GENISE, J. F., MALDONADO, F. and BROUWERS, E. M. 1997. Trace fossils of Hymenoptera and other insects, and paleoenvironments of the Claron Formation (Paleocene and Eocene), Southwestern, Utah. *US Geological Survey Bulletin*, **2153**, 41–58.
- BROWN, R. W. 1934. *Celliforma spirifer*, the fossil larval chambers of mining bees. *Journal of the Washington Academy of Sciences*, **24**, 532–539.
- CAZAU, L., MANCINI, D., CANGINI, J. and SPALLETTI, L. 1989. Cuenca Ñirihuau. 299–318. In CHEBLI, G. and Y SPALLETTI, L. (eds). *Cuencas sedimentarias Argentinas*. Universidad Nacional de Tucumán, Tucumán. Serie Correlación Geológica, 6, 512 pp.
- CLAUDE-JOSEPH, F. 1926. Reserches biologiques sur les Hyménoptères du Chili (Mellifères). *Annales des Sciences Naturelles, Zoologie series*, **10** (9), 113–268.
- COIRA, B. 1979. Descripción de la Hoja 40d, Ingeniero Jacobacci, Provincia del Río Negro. *Servicio Geológico Nacional, Buenos Aires, Boletín*, **168**, 101 pp.
- DANFORTH, B., BRADY, S., SIPES, S. and PEARSON, A. 2004. Single-copy nuclear genes recover Cretaceous-age divergences in bees. *Systematic Biology*, **55**, 309–326.
- DINGHI, P. A., SÁNCHEZ, M. V. and GENISE, J. F. 2012. Aproximación preliminar de la posición filogenética de *Homocopris torulosus* (Coprini). *Bondades y problemas en la búsqueda. Significancia evolutiva a partir de su comportamiento de nidificación*. Libro de Resúmenes de la IX Reunión Latinoamericana de Scarabaeoidología, Buenos Aires, Argentina, p. 34.
- ELLIOT, D. K. and NATIONS, J. D. 1998. Bee burrows in the Late Cretaceous (Late Cenomanian) Dakota Formation, Northeastern Arizona. *Ichnos*, **5**, 243–253.
- ENGEL, M. 1999. A new xeromelissinae bee in Tertiary amber of the Dominican Republic (Hymenoptera: Colletidae). *Entomologica Scandinavica*, **30**, 453–458.
- GENISE, J. F. 2000. The ichnofamily Celliformidae for Celliforma and allied ichnogenera. *Ichnos*, **7**, 267–282.
- and BOWN T. 1996. *Uruguay Roselli* 1938 and *Rosellichnus*, n. ichnogenus: two ichnogenera for clusters of fossil bee cells. *Ichnos*, **4**, 199–217.
- and ENGEL M. S. 2000. The evolutionary history of sweat bees (Hymenoptera, Halictidae): integration of paleoentomology, paleoichnology and phylogeny. *Abstracts of the I International Meeting on Palearthropodology*. Riberao Preto, Brazil, pp. 116–117.
- and VERDE M. 2000. *Corimbatichnus fernandesi*: a cluster of fossil bee cells from the Late Cretaceous–Early Tertiary of Uruguay. *Ichnos*, **7**, 115–125.
- SCIUTTO, J. C., LAZA, J. H., GONZÁLEZ, M. G. and BELLOSI, E. S. 2002. Fossil bee nests, coleopteran pupal chambers and tuffaceous paleosols from the Late Cretaceous Laguna Palacios Formation, Central Patagonia (Argentina). *Palaogeography, Palaeoclimatology, Palaeoecology*, **177**, 215–235.
- GONZÁLEZ BONORINO, F. 1979. Esquema de la evolución geológica de la Cordillera Norpatagónica. *Revista Asociación Geológica Argentina*, **3**, 184–202.
- GONZÁLEZ DÍAZ, E. F. and NULLO, F. E. 1980. Cordillera Neuquina. 1099–1148. In TORNER, J. C. M. (ed.). *Segundo Simposio de Geología Regional Argentina*, Córdoba, Argentina, 8–9 September 1976. Academia Nacional de Ciencias de Córdoba, tomo II, 1717 pp.
- and VALVANO J. 1979. Plutonitas graníticas cretácicas y Neoterciarias entre el sector norte del lago Nahuel Huapi y el lago Traful (Provincia del Neuquén). *Actas 7º Congreso Geológico Argentino*, **1**, 227–242.
- GRIMALDI, D. A. and ENGEL, M. S. 2005. *Evolution of the insects*. Cambridge University Press, New York, 755 pp.
- GUILLAUME, B., MARTINOD, J., HUSSON, L., RODDAZ, M. and RIQUELME, R. 2009. Neogene uplift of central eastern Patagonia: dynamic response to active spreading ridge subduction? *Tectonics*, **28**, 1–19.
- JANVIER, H. 1933. Etude biologique de quelques Hyménoptères du Chili. *Annales des Sciences Naturelles, Zoologie séries*, **10** (16), 209–346.
- 1955. Le nid et la nidification chez quelques abeilles des Andes tropicales. *Annales des Sciences Naturelles, Zoologie séries*, **11** (17), 311–349.
- LE ROUX, J. P. 2012. A review of Tertiary climate changes in southern South America and the Antarctic Peninsula. Part 2: continental conditions. *Sedimentary Geology*, **247–248**, 21–38.
- LIEBERMAN, B. S. 2000. *Paleobiogeography: using fossils to study global change, plate tectonics, and evolution*. Kluwer Academic/Plenum Publishers, New York, 208 pp.
- MACKIN, J. H. 1960. Structural significance of Tertiary volcanic rocks in southwestern Utah. *US Geological Survey Bulletin*, **338**, 102 pp.
- MARSHALL, L. G. 1990. Fossil marsupials from the type Friasian land mammal age (Miocene), Alto Río Cisnes, Aisén, Chile. *Revista Geológica de Chile*, **17**, 19–55.
- and SALINAS P. 1990. Stratigraphy of the Río Frías Formation (Miocene), along the Alto Río Cisnes, Aisén, Chile. *Revista Geológica de Chile*, **17**, 57–87.
- PASCUAL, R., CURTIS, G. H. and DRAKE, R. E. 1977. South American geochronology: radiometric time scale for middle to late Tertiary mammal-bearing horizons in Patagonia. *Science*, **195**, 1325–1328.
- MAZZONI, M. and BENVENUTO, A. 1990. Radiometric ages of Tertiary ignimbrites and the Collón Cura Formation, Northwestern Patagonia. *XI Congreso Geológico Argentino, San Juan, Argentina, Actas*, **2**, 87–90.
- MICHENER, C. D. 2007. *The bees of the world*, Second edition. The John Hopkins University Press, Baltimore 992 pp.
- and POINAR G. 1996. The known bee fauna of the Dominican amber. *Journal of the Kansas Entomological Society*, **69**, 353–361.
- MULLETT, D. J. 1989. Interpreting the early Tertiary Claron Formation. *Geological Society of America Abstracts with Programs*, **2**, p. 120.
- WELLS, N. A. and ANDERSON, J. J. 1988. Unusually intense pedogenic modification of the Paleocene–Eocene Claron Formation of southwestern Utah. *Geological Society of America Abstracts with Programs*, **20**, p. 382.
- NULLO, F. E. 1979. Descripción geológica de la Hoja 41d, Lipetrén. *Servicio Geológico Nacional, Boletín*, **158**, 1–88.



- OTIS, G. W., MCGINLEY, R. J., GARLING, L. and MALARET, L. 1983. Biology and systematics of the bee genus *Crawfordapis* (Colletidae, Diphaglossinae). *Psyche*, **89**, 279–296.
- ORTIZ-JAUREGUIZAR, E. and CLADERA, G. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments*, **66**, 498–532.
- PASCUAL, R., BONDESIO, P., VUCETICH, M. G., SCILLATO-YANE, G. J., BOND, M. and TONNI, E. P. 1984. Vertebrados fósiles Cenozoicos. 9º Congreso Geológico Argentino, Relatorio 2, **9**, 439–461.
- RABASSA, J. 1974. Geología superficial en la región de Pilcaniyeu-Comallo, provincia de Río Negro. Argentina. Thesis 331. Facultad de Ciencias Naturales y Museo de La Plata, Inédito, 119 pp.
- 1978. Estratigrafía de la región de Pilcaniyeu-Comallo, provincia de Río Negro. 7º Congreso Geológico Argentino. Actas, **1**, 731–746.
- RAMOS, V. A. 1999. Los depósitos sinorogénicos terciarios de la región andina. 651–682. In CAMINOS, R. (ed.). *Geología Argentina*. Instituto de Geología y Recursos Minerales, Buenos Aires, Anales **29**, 796 pp.
- RICCARDI, A. and ROLLERI, E. 1980. Cordillera Patagónica Austral. *Academia Nacional de Ciencias*, **2**, 1173–1306.
- ROBERTS, R. B. 1971. Biology of the crepuscular bee *Ptiloglossa guinnae* n. sp. with notes on the associated bees, mites and yeasts. *Journal of the Kansas Entomological Society*, **44**, 283–294.
- ROSELLI, F. L. 1939. Apuntes de geología y paleontología uruguaya. Sobre insectos del Cretácico del Uruguay o descubrimiento de admirables instintos constructivos de esa época. *Boletín de la Sociedad Amigos de las Ciencias Naturales 'Kraglievich-Fontana'*, **1**, 72–102.
- ROZEN, J. G. 1984. Nesting biology of Diphaglossinae bees (Hymenoptera, Colletidae). *American Museum Novitates*, **2786**, 1–33.
- SÁNCHEZ, M. V., LAZA, J. H., BELLOSI, E. S. and GENISE, J. F. 2010. Ichnostratigraphy of middle Cenozoic *Coprinisphaera* from central Patagonia: insights into the evolution of dung beetles, herbivores and grass-dominated habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **297**, 633–648.
- SARZETTI, L. C., GENISE, J. F., SÁNCHEZ, M. V., FARINA, J. L. and MOLINA, M. A. 2013. Nesting behavior and ecological preferences of five Diphaglossinae species (Hymenoptera, Apoidea, Colletidae) from Argentina and Chile. *Journal of Hymenoptera Research*, **33**, 63–82.
- SOMOZA, R. 1998. Updated Nazca (Farallon) – South America relative motions during the last 40 Myr: implications for mountain building in the central Andean region. *Journal of South American Earth Sciences*, **11**, 211–215.
- SPALLETTI, L. and DALLA SALDA, L. 1996. A pull apart volcanic related Tertiary basin, an example from the Patagonian Andes. *Journal of South American Earth Sciences*, **9**, 197–206.
- TORCHIO, P. F. and BURWELL, B. 1987. Notes on the biology of *Cadeguala occidentalis* (Hymenoptera: Colletidae), and a review of colletid pupae. *Annals of the Entomological Society of America*, **80**, 781–789.
- URBAN, D. and MOURE, J. S. 2001. Catálogo de Apoidea da Região Netropical (Hymenoptera, Colletidae). II. Diphaglossinae. *Revista Brasileira de Zoologia*, **18**, 1–34.
- VERDE, M. 2012. Icnología de la Formación Asencio y las 'Calizas del Queguay' (Cretácico tardío – Terciario temprano) del Uruguay. Unpublished PhD thesis, Universidad de la República, Montevideo, 207 pp.
- VUCETICH, M. G., MAZZONI, M. M. and PARDIÑAS, U. F. J. 1993. Los roedores de la Formación Collón Cura (Mioceno Medio) y la Ignimbrita Pilcaniyeu, Cañadón del Tordillo, Neuquén. *Ameghiniana*, **30**, 361–381.