



## FOSSIL COCOONS ASSOCIATED WITH A DINOSAUR EGG FROM PATAGONIA, ARGENTINA

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Typescript received 31 August 2009; accepted in revised form 6 September 2010

**Abstract:** Eight fossil (Cretaceous) insect cocoons were discovered within the infillings of a broken dinosaur egg of a clutch from a Patagonian locality. Cocoons are considered to be *in situ* based on detailed preservation of thin, delicate walls with surface texture, infillings that are similar to the surrounding rock matrix and the clustered distribution of cocoons in only one egg out of the clutch of five eggs. According to the shape, size, and thin wall with surface texture, the cocoons are interpreted as having been produced by wasps. The wasps may have been attracted to the egg because of the presence of scavenging insects feeding on the decaying

organic matter, or they may have been attracted to spiders feeding on the scavenging insects. In either scenario, after attacking the insects or spiders inside the sand infillings of the egg, the wasp larvae produced the cocoons described herein. The presence of wasps, which are at the top of the scavenging food webs, suggests that a complex community of invertebrates would have developed around rotten dinosaur eggs.

**Key words:** wasp fossil cocoons, dinosaur egg, scavenging, Patagonia, Argentina.

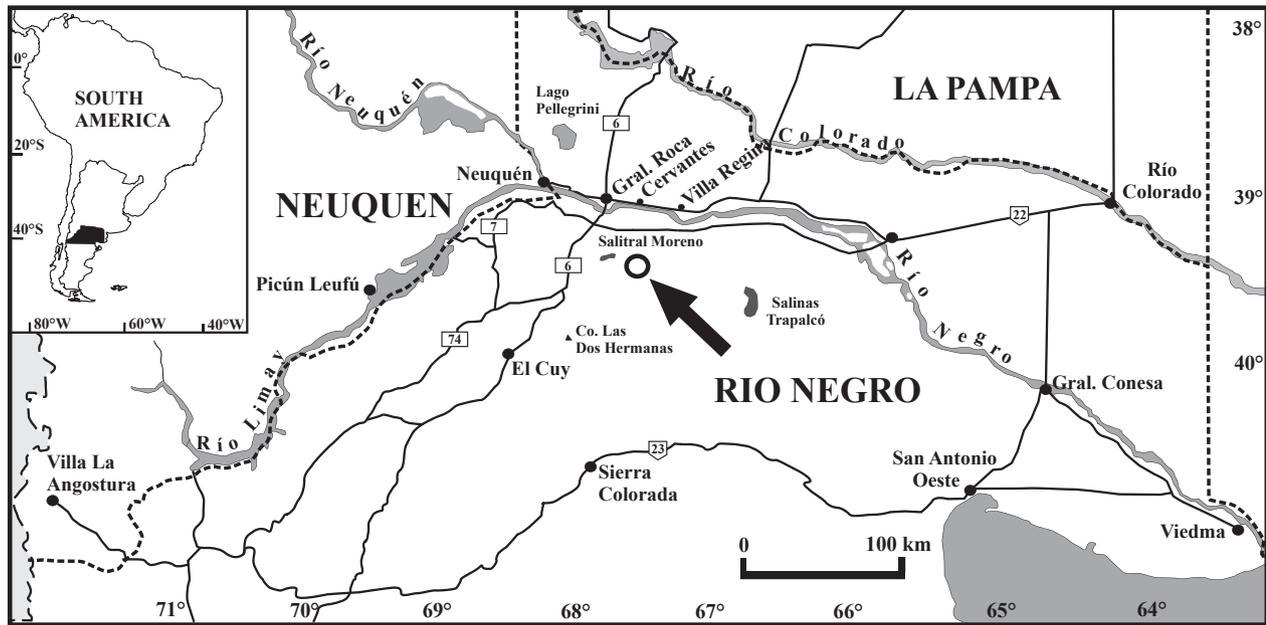
TRACE fossils are the physical evidence of the behaviour of extinct animals in the fossil record (Seilacher 1967). As such, they provide data on nesting, foraging, predation and a large repertoire of animal behaviours including scavenging. Burrows, pits, scratch marks and other trace fossils record a range of scavenging behaviours in dinosaur bones (Paik 2000; Roberts *et al.* 2007). In addition to carcasses, dinosaur eggs, broken by trampling or hatching (Powell 1992; Cousin *et al.* 1994; Hirsch 1994; Sander *et al.* 1998), would have produced a large amount of decaying organic matter in nesting sites that could affect or even preclude subsequent nesting if not removed by scavengers. However, no direct evidence of invertebrate scavenging on dinosaur eggs has previously been reported, even when similar cocoons to those described herein were found near nests of the theropod *Troodon formosus* from the Two Medicine Formation (USA) (Horner 1984, 2000; Martin and Varricchio 2001).

Here, cocoons are reported in a broken dinosaur egg from Patagonia, a region that has already yielded critical evidence on dinosaur eggs, nests, embryos and juveniles (Bonaparte and Vince 1979; Powell 1992; Chiappe *et al.* 1998, 2001). The clutch of dinosaur eggs was collected during a field expedition of the Museo Paleontológico Egidio Feruglio (MPEF) (Trelew, Chubut) in 1989, to the Río Negro Province (Patagonia, Argentina) headed by the technician Pablo Puerta, and after preparation, it was

exhibited at the museum. The presence of the cocoons inside one egg was noted in 2007, after the discovery and study of similar ones from other Patagonian localities (Genise *et al.* 2007). The fossil cocoons, attributed herein to wasps, shed new light on scavenging and decaying processes in dinosaur nesting sites and suggest that wasps could be more related with carrion food communities than forensic entomology has recorded until now.

### GEOLOGICAL SETTING

The egg studied here comes from the Allen Formation (middle Campanian – lower Maastrichtian) at Bajo de Arriagada, northern Patagonia (Río Negro Province), Argentina (Text-fig. 1). The Allen Formation contains some of the main dinosaur egg-bearing deposits of the Río Negro Province (Powell 1992; Salgado *et al.* 2007). It is included in the basal part of the Malargüe Group (Groeber 1946; Riccardi 1988) and along with the Loncoche and Huantraico Formations represents the upper strata of the Neuquina Basin, which were deposited in a sedimentary environment with marine influence (Legarreta and Uliana 1999). The lower section of the Malargüe Group is mainly composed of clastic deposits with associated limestone and anhydrite beds (Legarreta and Uliana 1999). Salgado *et al.* (2007) recognized two subunits for



**TEXT-FIG. 1.** Location map. Circle shows the ichnofossiliferous locality.

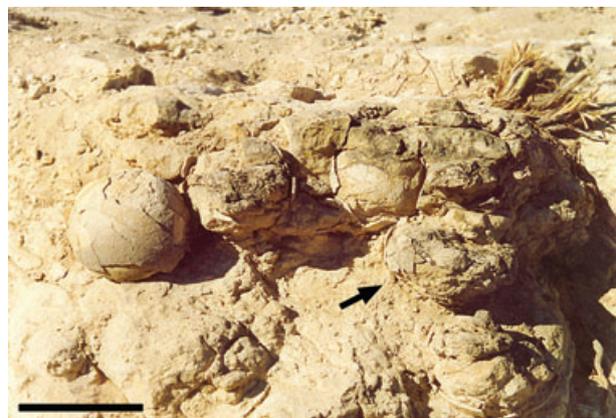
the Allen Formation. The lower one is composed of sandy deposits, subordinate muddy layers and evaporitic levels, interpreted as lagoonal and supratidal environments and associated with aeolian sands and deposits of ephemeral rivers. The thick upper subunit is composed of siltstones and mudstones with intercalation of ostracod-rich limestones and sandy levels. The clutch of dinosaur eggs treated herein was found at the top of a palaeosol developed in a very pale orange (10 YR 8/2), medium-size grained, sandstone with carbonate cement, probably from the lower subunit of Salgado *et al.* (2007), as this subunit is the only one containing dinosaur eggs and palaeosols.

## DESCRIPTION

**Repository.** The specimens described herein are deposited in the Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina, in the palaeovertebrate (MPEF-PV, eggs) and ichnological (MPEF-IC, cocoons) collections.

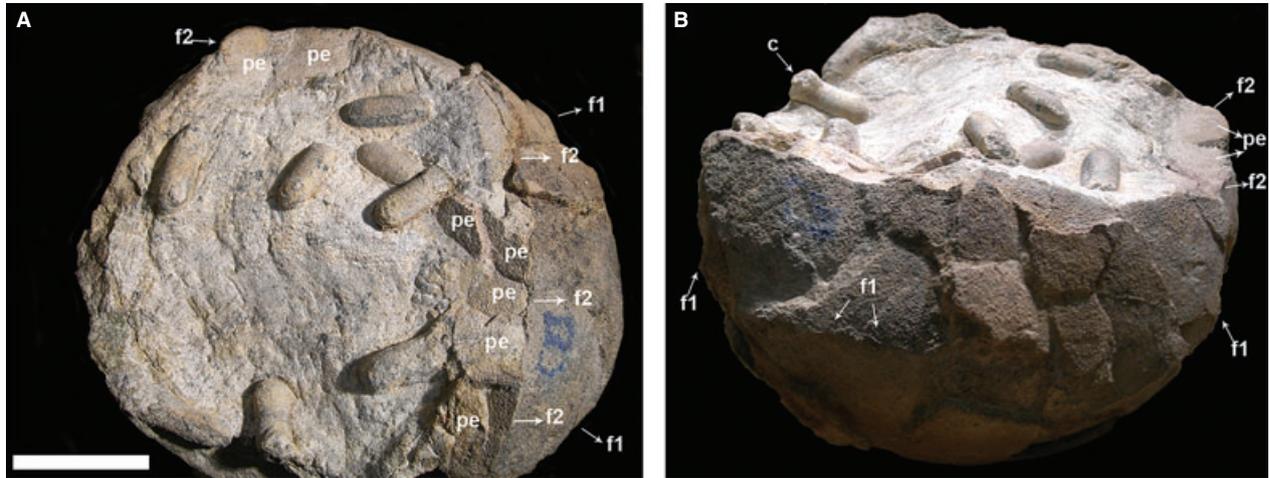
### Eggs

The five eggs in the clutch are spherical, ranging from 19 to 20 cm in diameter (Text-fig. 2). As the original location of each egg in the clutch was lost during preparation, because it was collected only for museum exhibition, the position of the cocoon-bearing egg was inferred by comparing the prepared eggs with the original picture of the clutch taken in the field. The three upper eggs from the clutch could be disregarded as being those bearing the



**TEXT-FIG. 2.** Dinosaur egg clutch showing five eggs at the top of a palaeosol from the Allen Formation (Río Negro, Argentina). Arrow shows the cocoon-bearing egg. Scale bar represents 20 cm.

cocoons because they show rounded fillings in the upper hemispheres, with eggshells mostly lost by weathering in two of the examples. At a lower level in the palaeosol, the other two eggs are characterized by mostly missing their upper halves, like the cocoon-bearing one, but additionally the one indicated by an arrow (MPEF-PV 3137; Text-fig. 2) shows evidence of broken and hinged eggshell – like the egg with the cocoons studied herein – a feature that is absent in the other egg. Differences between the egg with the cocoons, illustrated herein, and the field specimen are as a result of subsequent laboratory preparation, during which the cocoons became exposed. After taking the pictures shown in Text-figure 3, part of the fill-



**TEXT-FIG. 3.** Dinosaur egg (MPEF-PV 3137) with the eight cocoons (c) (MPEF-IC 517-524). A, Top view showing fracture 1 (f1) along the right border and fracture 2 (f2) with horizontal pieces of broken eggshell (pe). Note contact among some cocoons. B, Lateral view showing (f1) with pieces of eggshell at both sides articulated in angle and pieces of eggshell (pe) horizontally oriented along (f2). Scale bar represents 5 cm.

ings of this egg, and of the other four, were removed in the laboratory to look for more cocoons, albeit with negative results.

The eggshell of the studied specimen is cracked mostly in the midline and the lower half, whereas inside the infillings, it shows eight cocoons (Text-fig. 3A, B) around the equator at the equatorial plane. In lateral view, one side of the eggshell follows the original rounded shape, whereas the opposite one shows a horizontal fracture with pieces of eggshell at both sides articulated at an angle. A second horizontal fracture is evidenced by small pieces of eggshell, oriented horizontally or towards the interior of the egg, surrounding the missing part with the cocoons (Text-fig. 3B). Their size, shape, surface ornamentation and eggshell microstructure correspond to Megaloolithidae, an egg type attributed to Sauropoda and particularly to titanosaurs (Powell 1992; Chiappe *et al.* 1998).

#### Cocoons

Eight cocoons (MPEF-IC 517-524) were revealed after laboratory preparation (compare Text-figs 2, 3) inside the infill of the dinosaur egg MPEF-PV 3137. They range in length from 22 to 30 mm and in width from 10 to 12 mm (mean  $26.6 \times 11.5$  mm) and are horizontally arranged, separated up to 2 cm in vertical section and randomly oriented (Text-fig. 3A). Two of them are in contact at almost a right angle. One cocoon shows both ends rounded, whereas in the remaining ones, one of the ends is truncated. They show a thin (0.1 mm) outer wall (Text-fig. 4B) and infill similar to the rock matrix. One of the cocoons (MPEF-IC 524) was removed to prepare

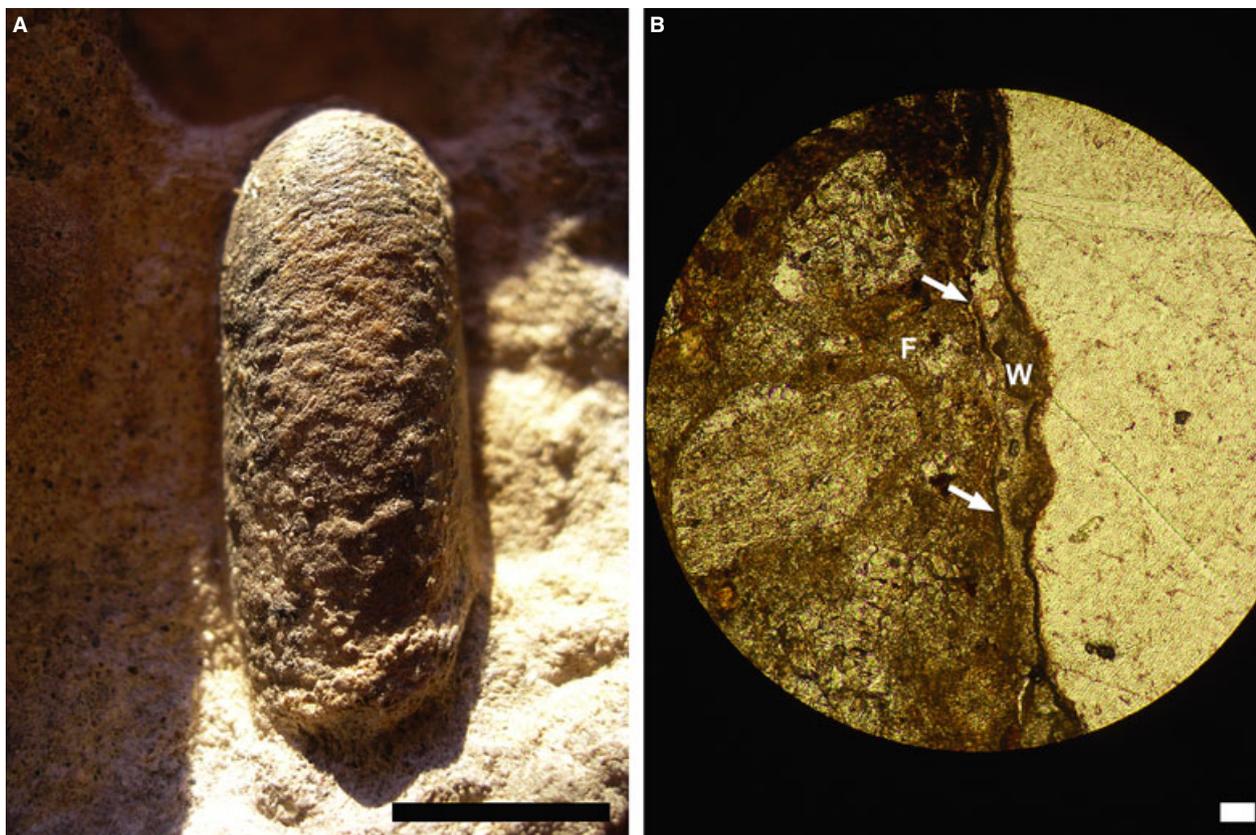
thin sections of wall. Thin section shows that the wall is separated from the infill by a dark line of oxides and that it has higher porosity than the infill. Its surface texture is smoother than the rock matrix in all cases, and some of them preserve gridded textures showing lobes resulting from the intersection of a double helical arrangement of ridges (Text-fig. 4B).

#### DISCUSSION

Three questions should be addressed to understand the relationship between the cocoons and the dinosaur egg: (1) are the cocoons *in situ*, (2) could they be related to the organic matter present in the egg and (3) can the producer and its role within the rotten egg community be determined?

Evidence for considering that the cocoons are *in situ* is the preservation of a 0.1-mm wall showing a delicate surface texture reflecting the original presence of woven, silky walls that could not be transported without severe damage or destruction, their infill similar to the rock matrix, and their number and clustered distribution in only one egg within the clutch.

The second question to address is whether the cocoons were part of the scavenging community or were located there by chance. The presence of multiple cocoons within only a single egg in the clutch supports the former assumption. Harrison (2005) utilized the number of dipteran cases in a Pliocene bird egg to support the hypothesis that an adult fly had probably laid eggs inside the broken bird egg before its burial, as opposed to the alternative scenario involving fly larvae, which had burrowed



**TEXT-FIG. 4.** A, Detail of a cocoon (MPEF-IC 523) showing the helical surface texture, particularly on top. Scale bar represents 1 cm. B, thin section of a cocoon (MPEF-IC 524) showing the fillings (F), the wall (W) and the boundary (arrows) between both, outlined by a thin oxidized layer. Scale bar represents 0.1 mm.

down randomly through the sediment to reach the egg. In our case, if the cocoons were independent of the egg contents, they would have a random distribution in the clutch and be present in the palaeosol, which is not the case. Their relationship with the egg contents is also supported by the record of similar cocoons in fossil vertebrate carcasses from two different localities (Kitching 1980). Additional examples from fossil and modern ground nesting birds also support the hypothesis that the cocoons were part of the scavenging community. The Pliocene bird egg reported by Harrison (2005) is particularly

important because its infillings contained a number of fly maggots and burrows derived from the larvae. If the most likely scenario is that the fly laid eggs (Harrison 2005), the presence of maggots indicates that larvae completed their development probably feeding on the egg contents. Moreover, Hayward *et al.* (1989) reported the occurrence of fly larvae feeding on dried organic matter inside a bird egg that had been buried for nearly a year (prior to being scavenged) by an ashfall. These examples demonstrate that in some cases, the complete decay of egg contents may be a slow process that allows scavengers to feed on

#### EXPLANATION OF PLATE 1

Fig. 1. Wasp cocoon of *Pepsis* sp. (Pompilidae) showing the constructed wall and the helical surface texture. Scale bar represents 1 cm.

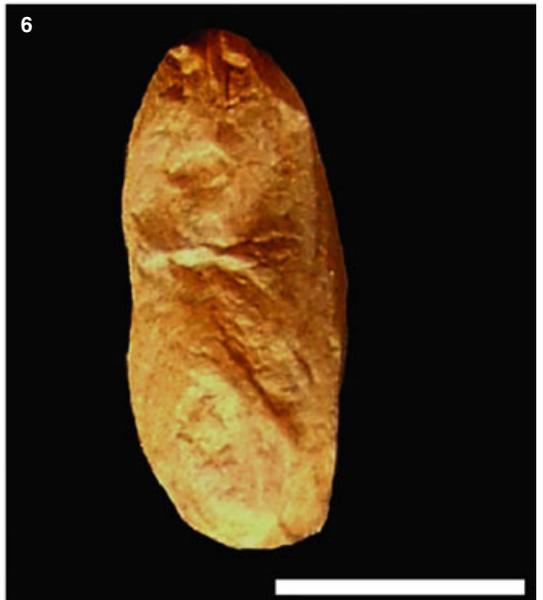
Fig. 2. An adult of Trogidae (Coleoptera) inside a soil chamber beneath a cow carcass from La Pampa Province. Scale bar represents 1 cm.

Fig. 3. The same chamber of the previous figure without the adult. Note the absence of constructed wall and helical surface texture. Scale bar represents 1 cm.

Fig. 4. *Tiquadra pircuniae* (Tineidae, Lepidoptera) cocoon and larva. Scale: 1 cm. Picture courtesy of Juan Farina.

Fig. 5. Cocoons in a nest of *Camponotus rufipes* (Hymenoptera and Formicidae).

Fig. 6. Detail of one cocoon showing the weak, wrinkled and silky wall. Scale bar represents 0.5 cm.



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dried organic matter for a long time, as well as pupating or dwelling within the sediment that filled the empty space inside the egg. This was probably the case in the cocoon-bearing egg treated herein. The asymmetrical outline and horizontal fractures, in contrast to the other eggs of the clutch, suggest that this egg in particular was broken by a force applied specifically on this specimen such that it did not affect the other eggs within the clutch, as would be the case of compression by burial. The presence of original egg contents (i.e. organic membranes and embryonic remains) may have prevented the detachment of the fractured and hinged pieces of eggshell when the egg was broken. The filling of the egg with sediments, therefore, probably occurred when these organic remains were still present, preserving the crushed pieces in their original position. Once broken, the egg contents became first an important source of fresh organic matter for colonizing scavengers, and then, while the interior was filling with sediment, a suitable environment for insects feeding on dried organic matter and their predators.

#### *Cocoon producers?*

What were the producers of the cocoons? From the standpoint of ichnology, the cocoons documented here are comparable with the Cretaceous insect trace fossil *Rebuffoichnus sciuttoi* (Genise *et al.* 2007) based on size, ovoid shape with a truncated end and particularly by the thin wall showing a helicoidal grid of ridges and lobes (Text-fig. 4A). Some of these characters were used previously to attribute ovoid trace fossils to wasp cocoons (Ritchie 1987; Bown *et al.* 1997; Edwards *et al.* 1998; Hasiotis 2003; Genise and Cladera 2004; Genise *et al.* 2007). Characters such as size and shape are, on first appearances, typical for hymenopteran and particularly wasp cocoons (Pl. 1, fig. 1). Both ends may be rounded or may show a particular structure at one end. This can be made by the last instar wasp larva causing it to become truncated at one end later when the adult emerges (Evans 1966; Evans and West Eberhard 1970). Both cocoon types have been described as trace fossils (Ritchie 1987; Bown *et al.* 1997; Edwards *et al.* 1998; Hasiotis 2003; Genise *et al.* 2007) and are recorded in the dinosaur egg shown herein. In addition to size and shape, specific characters particularly in the wall structure distinguish wasp cocoons from pupation chambers of other insects, like coleopterans and lepidopterans (Genise and Cladera 2004) (Pl. 1, figs 2–6). In wasp cocoons, the presence of a constructed wall and its helicoidal surface texture is the most important characters to identify them (Genise *et al.* 2007). The extant wasp cocoon wall is thin and may show different surface textures produced by the arrangement of the weave, such as longitudinal and sinu-

ous ridges or grided textures showing lobes resulting from the intersection of a double helical arrangement of ridges (Genise *et al.* 2007) (Pl. 1, fig. 1). Such a particular surface texture can be observed in the cocoons presented herein (Text-fig. 4A).

Similar cocoons, densely grouped, have been recorded from fossil carcasses from an African Plio-Pleistocene locality and a North American Oligocene one (Kitching 1980). They were attributed to carrion beetles, particularly to Trogidae by Kitching (1980, p. x), in his own words: 'based on a colleague expert advice, and my own observations and deductions'. They were also found near a nest of the Cretaceous theropod *Troodon formosus* from the Two Medicine Formation (USA) and also interpreted as produced by carrion beetles (Horner 1984, 2000). Later, these cocoons were found inside individual burrows and attributed to hymenopterans (Martin and Varricchio 2001; Hasiotis 2003). We concur with the conclusion of the latter authors, interpreting the cocoons described in this study as having been produced by wasps. Even when carrion beetles cannot be disregarded completely as producers, ichnological evidence on coleopteran pupation chambers does not provide any support for this attribution. Chambers occupied by Trogidae under an extant cow carcass studied in La Pampa Province (Argentina) showed neither constructed wall nor helicoidal surface textures (Pl. 1, figs 2–3), like those described herein. Detailed discussions on the attribution on ovoid structures to coleopteran pupation chambers were presented by Johnston *et al.* (1996) when analysing the affinities of *Fictovichnus* and by Genise *et al.* (2002) and by Genise (2004), when analysing those of *Rebuffoichnus casamiquelai*. The walls of these chambers are very different from those of wasps. Coleopterans make pupation chambers that may show thick linings of soil material easily detachable from the soil or rock matrix when fossilized (*Rebuffoichnus casamiquelai*) or may produce thin linings fused with the surrounding soil. The latter chambers, when fossilized, are preserved as empty chambers or casts in palaeosols (*Fictovichnus gobiensis*) (Johnston *et al.* 1996; Genise 2004). In summary, recorded coleopteran pupation chambers are different to the cocoons in the dinosaur egg. It is also known that many carrion beetles pupate directly in bones (i.e. Roberts *et al.* 2007 and references therein).

#### *Forensic entomology*

Succession in modern carrion communities has been extensively studied in the field of forensic entomology (Smith 1986; Gennard 2007; Byrd and Castner 2009). In addition, eggs and ground nests of turtles, lizards, crocodiles and birds are known to be attacked by a similar

community of scavengers (Bell *et al.* 2004; Katilmiscedil and Urhan 2007; Maros *et al.* 2003; Pfrommer and Krell 2004). Surprisingly, cocoons like those described herein are apparently not known from extant vertebrate carcasses nor from modern eggs, despite this extensive literature on the entomology of carrion and rotten eggs. Among insects known to construct silken cocoons (Chapman 1982), representatives of Lepidoptera and Hymenoptera are the only ones associated with decaying organic matter (Smith 1986). Scavenging Lepidoptera, belonging to the families Pyralidae and Tineidae, constructs cocoons very different from those found in the dinosaur egg, which are reinforced with bits of food material or waste (Smith 1986). Plate 1, figure 4 shows a cocoon composed of weaved bits of wood made by *Tiquadra pircuniae* (Tineidae), which feeds on rotting wood in trunks. Among scavenging Hymenoptera, bees are attracted when fluids are present, social wasps and ants may be scavengers or predators, predatory wasps are opportunistic feeders on other carrion insects or spiders, and parasitic wasps are known to attack fly maggots (Payne and Mason 1971; Smith 1986). Furthermore, bees and social wasps construct nests away from their food sources. Parasitic wasps recorded from carrion are mostly small-sized parasites of flies and moths (Smith 1986). Some ants construct cocoons that are generally similar to those documented in this contribution and are common components of the carrion community (Payne and Mason 1971; Smith 1986) (Pl. 1, figs 5–6). However, their cocoons are not recorded from carcasses (Payne and Mason 1971), and in comparison with wasp cocoons, their size is smaller, their silky wall is weaker and in many cases wrinkled, and their surface texture is not clearly helical (Pl., fig. 6). In addition, cocoons with similar characters to the ones shown herein were found isolated in palaeosols (Genise *et al.* 2007) and even associated with individual burrows (Martin and Varricchio 2001), which is unlikely for social insects. Sphecidae and pompilid wasps construct this type of cocoon (Evans 1966; Genise *et al.* 2007) and have been recorded occasionally from carrion (Smith 1986).

The close distribution of cocoons, particularly the contact between two individual cocoons, suggests that they were not located in nests excavated from the soil surface like those of most predatory wasps included in Pompilidae and Sphecidae. Even those predatory wasps that dig nests in close proximity to one another recognize some kind of underground signals that avoids cell contact (Evans 1966). In contrast, many Pompilidae and some Sphecidae show parasitoid behaviour paralysing and laying eggs on other arthropods such as spiders, crickets or mole crickets underground the moment they find them, but after that they do not construct nests (Iwata 1976). Incidentally, there is a record of the mole cricket, *Scapter-*

*iscus didactylus*, attacking leatherback turtle eggs (Maros *et al.* 2003). Thus, the most likely interpretation of the association of the dinosaur egg and cocoons from the standpoint of forensic entomology is that the cocoons were made by the larvae of wasps that attacked other insects feeding on dried organic matter (or spiders feeding on these) in their own burrows.

The record of fossil wasp cocoons associated with vertebrate carcasses (Kitching 1980) and eggs (this study) is interesting, particularly because this association has not been apparently recorded in the forensic entomological literature (Smith 1986), probably because wasps pupate after feeding on the very last components of the carrion community, when all other activity stopped time ago.

## CONCLUSIONS

Ichthyology and forensic entomology point towards the same producer for the cocoons associated with the dinosaur egg: wasps. The presence of wasps, which are at the top of carrion food web (Payne and Mason 1971; Smith 1986), suggests that a complex community of invertebrates would have developed around rotting dinosaur eggs. This community, along with vertebrate scavengers and inorganic processes, would have been responsible for cleaning up the soil or material potentially hosting pathogenic microorganisms, allowing the nest site fidelity by dinosaurs (Horner 1982).

*Acknowledgements.* We thank Duncan McIlroy, Adriana Oliva, Ricardo Melchor, Diego Pol, Pablo Puerta, Mirta González, Mariano Caffa, Daniel Rojas Lanús and Daniel Speranza for different assistance during manuscript preparation. Juan Farina provided the picture and identification of the Tineidae. We also thank the anonymous reviewers for improvement of the manuscript. Research was funded by grant PICT 13286 and PICT 1972 of the Agencia Nacional de Promoción Científica y Tecnológica from Argentina.

*Editor.* Jason Dunlop

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