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Source: Journal of the Kansas Entomological Society, 77(4):626-638. 2004.

Published By: Kansas Entomological Society

DOI: <http://dx.doi.org/10.2317/E-25.1>

URL: <http://www.bioone.org/doi/full/10.2317/E-25.1>

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***Chubutolithes gaimanensis* and Other Wasp Trace Fossils: Breaking through the Taphonomic Barrier**

JORGE F. GENISE^{1,3} AND GERARDO CLADERA²

ABSTRACT: Wasp ichnofossils are scarce in the record because of their low preservational potential. Evidence comprises perforations in bee cells, cocoons, and paper and mud nests, whose preservation may involve the most unusual taphonomic processes. The record includes trace fossils preserved in other trace fossils; paper nests preserved in amber, ironstones and caves; and fragile trace fossils preserved in conglomerates. Evidence for wasps is weak in some cases and more reliable in others. Perforations in bee cells can be attributed to other insects; likewise cocoons can be attributed to other insects and other organic and inorganic processes. Some fossil paper and mud nests are the most reliable wasp ichnofossils. *Brownichnus favosites* preserved in ironstone and in Dominican amber, provide the oldest records of polistines known. One of the best-known examples of wasp ichnofossils is *Chubutolithes gaimanensis*, preserved in intraclast conglomerates. New ichnological and sedimentological evidence suggests that cells were constructed around plant stems from which they could have dropped to the soil, been covered with sediments, impregnated with carbonate, and then reworked by fluvial action along with other carbonate nodules.

KEY WORDS: Wasp ichnofossils, parasitoidism, cocoons, paper nests, mud nests, *Chubutolithes*

The record of wasp trace fossils is sparse in comparison with that of bees, comprising exceptional taphonomic processes. Genise and Bown (1994) noted that bee cells, dung-beetle brood masses, and termite nests were the most frequently recorded insect trace fossils in paleosols and argued that constructed structures have a greater preservation potential than those merely excavated, like most underground wasp nests. In constructed nests, soil material is mixed with secretions or organic matter, resulting in structures that, being stronger than the surrounding soil, are preserved until soil diagenesis acts on the organic matter used in nest construction. Genise and Bown (1994) utilized the differences between wasp and bee nests to explain that, although both hymenopterans nest in the same sites, fossil wasp nests are exceptional, in contrast to fossil bee cells. In soil bee nests, excessive moisture may cause the liquefaction or diffusion of semiliquid provisions and thus, the cell wall is usually lined with water-repellent secretions (Michener, 1979; Cane, 1991). Most cells of wasps, however are provisioned with prey and lack any organic lining on the walls, resulting in simple excavated structures that have a low potential of preservation.

However, there are important exceptions to this rule so that a sparse record of wasp paleonesting behavior exists. This record includes perforations in bee cells, cocoons tentatively attributed to wasps, as well as paper and mud nests. Their preservation involves the most unusual taphonomic processes, such as trace fossils preserved within trace fossils, trace fossils preserved in amber, trace fossils preserved in caves, and fragile fossil nests constructed above the ground in plants and now preserved in conglomerates. One of the best known examples of the last is *Chubutolithes gaimanensis* Bown and Ratcliffe (1988) (Hymenoptera: Pompilidae), a mud nest whose preservation will be analyzed herein after a review of other possible wasp ichnofossils.

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Parasitoidism

Tentative evidence of wasp behavior in the ichnological record is the presence of complete and incomplete holes in the walls of fossil bee cells (e.g., Houston, 1987; Ellis and Ellis-Adam, 1993; Genise and Bown, 1996; Genise and Hazeldine, 1998; Edwards and Meco, 2000; Mikulas and Genise, 2003) (Fig. 1). These trace fossils were interpreted as the work of parasitoids, cleptoparasites or scavengers entering the cells from the outside, as suggested by the presence of incomplete perforations in the outer surfaces of cell walls (e.g., Houston, 1987; Ellis and Ellis-Adam, 1993; Mikulas and Genise, 2003). Ellis and Ellis-Adam (1993) mentioned Meloidae (Coleoptera), Bombyliidae (Diptera) and Mutillidae as possible trace makers, only the last are wasps. The Mutillidae are known to attack larvae in cells by digging through the soil or boring through walls (Evans and Eberhard, 1970), thus they are one of the possible producers of perforations in underground bee cells.

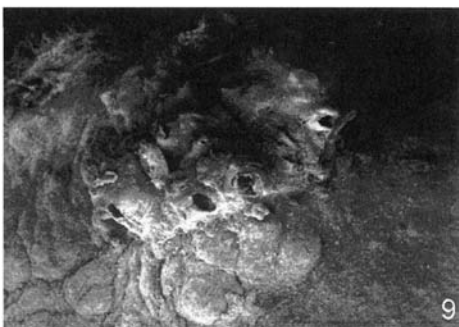
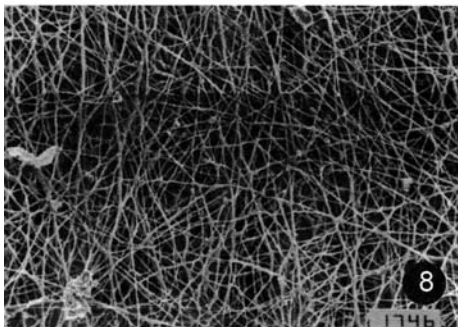
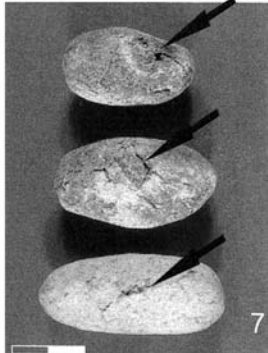
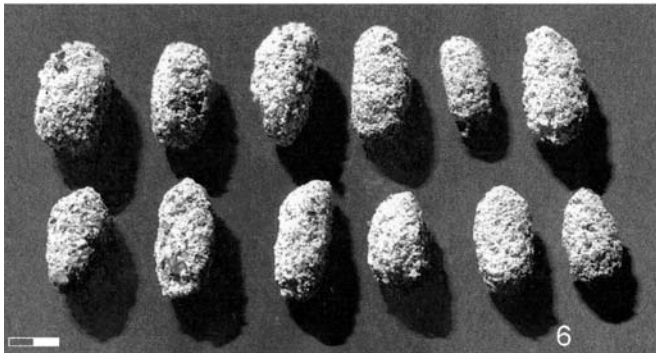
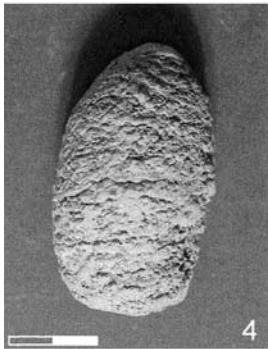
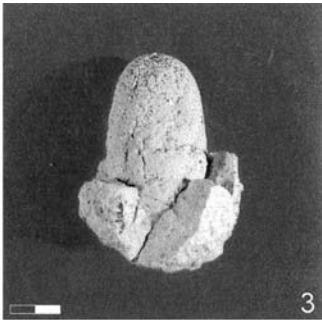
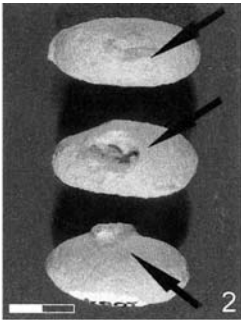
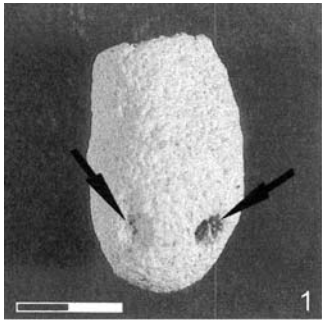
Another possible evidence of wasp parasitoidism was recorded by Bown *et al.* (1997), who studied possible wasp cocoons from the Paleocene-Eocene Claron and Colter Formations of Utah. These authors found four size-groups of ovoid cocoons, the smaller ones frequently contained in the larger ones (Bown *et al.*, 1997). The smaller ovoid structures inside larger ones were interpreted as cocoons of parasitoid wasps inside other wasp cocoons. The reliability of this evidence is subject to the interpretation of these ovoid casts as wasp cocoons, as analyzed in a section below.

Bown *et al.* (1997) also found that some larger cocoons show round or oblong holes laterally, and interpreted them as the work of parasites. This evidence is different from that mentioned above involving fossil bee cells. The latter are cells with thick constructed walls perforated by complete or incomplete, rounded, holes, whereas the former involves only casts in which the holes are suggested by irregular scars produced by detached material (Bown *et al.*, 1997, fig. 8A) (Fig. 2).

These records, which range from the Paleocene to the Holocene, can be attributed tentatively to wasps or other insects, and their preservation is unusual: they represent traces within traces, a still unexplored field of ichnological research with its own particular ichnotaxonomy (Mikulas and Genise, 2003).

Cocoons

Frequently trace fossils consist of ovoid casts in paleosols. Such casts have been described or mentioned as insect or wasp cocoons (e.g., Ritchie, 1987; Thackray, 1994; Bown *et al.*, 1997; Edwards *et al.*, 1998; Melchor *et al.*, 2002). Ritchie (1987) was the first to compare ovoid structures, from the Pliocene of Tanzania, with wasp cocoons. The shape, texture and aggregated distribution in the paleosol suggested to this author their affinities with sphecoid wasp cocoons. Ritchie (1987) also compared the mean ratio of length/diameter from those structures with sphecoid cocoons figured by Evans (1966), concluding that sphecoids usually construct more elongated cocoons, but at least in some genera they were as compact as those found in Tanzania. In contrast, Edwards *et al.* (1998) ruled out wasps as the producers of cocoon-like trace fossils from the Eocene Bembridge Formation of England, because of the lack of a tapering end. Bown *et al.* (1997) also analyzed the affinities of ovoid structures from the Paleocene-Eocene Claron Formation of Utah, concluding that they were wasp cocoons (Fig. 2). The shape, although not tapering, was the main character to support this attribution. In addition, remains of a constructed wall, having an external bioglyph consisting of faint parallel ridges oriented transversely, surrounded a few specimens. These wall remains were interpreted as belonging to the cells



that contained the cocoons (Bown *et al.*, 1997, fig. 6C, E). Other specimens show rounded protuberances that seem to represent the casts of exit tunnels perforated through this wall (Bown *et al.*, 1997, fig. 8A, B).

The interpretation of ovoid casts, as isolated structures or associated with constructed outer walls, was discussed elsewhere (e.g., Johnston *et al.*, 1996; Genise *et al.*, 2002). There are two described ichnogenera that may be related to ovoid casts. *Fictovichnus* Johnston *et al.* (1996) (Coleoptera) occurs as egg-shaped casts or oval chambers enveloped by a thin clay-rich zone showing a subterminal, or medial, exit hole. *Rebuffoichnus* Roselli (1987) (Coleoptera) comprises sub-ovoid to sub-cylindrical structures composed of a constructed wall and an internal ovoid chamber that may be connected to the exterior by a rounded hole (Genise *et al.*, 2002). Specimens of *Fictovichnus* resemble the internal casts of *Rebuffoichnus* and the possible wasp cocoons described by Ritchie (1987) and Bown *et al.* (1997) (Fig. 3). However, *Fictovichnus* was attributed to pupation chambers of Curculionidae, Scarabaeidae, or Tenebrionidae (Coleoptera) (Johnston *et al.*, 1996), whereas *Rebuffoichnus* was attributed particularly to Curculionidae because of its rounded hole (Genise *et al.*, 2002) and the finding of an adult weevil preserved inside one of the specimens from Australia (Lea, 1925).

Ovoid cocoons can be produced not only by wasps and coleopterans, but also by lepidopterans (Fig. 4). In addition, other kind of ovoid structures can be also considered. Frequently ovoid structures have been interpreted as vertebrate eggs or pseudoeegs (Hirsch, 1994). Some mammal droppings have oval shape and may show also similar kind of scars to those illustrated by Bown *et al.* (1997). These scars are produced when droppings that are originally stuck together are later separated by weathering or mechanical factors, resulting in some material from one dropping remaining with another, leaving protuberances and pits respectively (Fig. 7). Inorganic structures such as elliptical armored clay balls (e.g., Ojakangas and Thompson, 1977), herein illustrated with specimens composed of reworked material from the Triassic Ischigualasto Formation of Argentina, may resemble cocoons (Fig. 6). However, they actually show a large range of shapes and sizes as is usual for inorganic structures (Fig. 5).

The incorporation of organic matter mixed with soil material that wasp larvae produce when they construct cocoons can be envisaged as a similar process to that made by adult bees to line cells. As such, wasp cocoons would be as capable as bee cells to pass the taphonomic barrier. However different examples presented herein show that shape is not enough to recognize wasp cocoons, and that some characters like some evidence of the internal silk net (Fig. 8), or external pores (Fig. 9) should be recognized to support their wasp affinities.

Paper Nests

Brown (1941a) described for the first time what he interpreted as a fossil paper nest from the Upper Cretaceous of Utah. Such an interpretation, at that time, produced criticisms and

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Figs. 1–9. 1, A fossil bee cell from the Quaternary of the Canary Islands showing a complete perforation and an incomplete one (arrows). 2, Possible wasp cocoons from the Paleocene-Eocene Claron Formation, USA (arrows show scars). 3, Internal ovoid cast of *Rebuffoichnus casamiquelai* from the Late Cretaceous Laguna Palacios Formation of Argentina (note the wall remains in the lower end). 4, Mud cocoon of a Noctuidae. 5, Armored clay balls showing a wide spectrum of shapes. 6, Selected armored clay balls from 5 resembling ovoid cocoons. 7, Mammal droppings showing ovoid shape and equatorial scars (arrows). 8, Silk net of a sphecoid cocoon (350×). 9, Pore of a sphecoid cocoon (75×). Scale bars: 1 cm.

discussions (Bequaert and Carpenter, 1941; Brown, 1941b). The case was forgotten until Wenzel (1990) definitively confirmed the affinities of this trace fossil, recently renamed as *Brownichnus favosites* (Genise, 2000). Wenzel (1990) extracted important biogeographical and paleoentomological inferences from that nest, but also devoted many paragraphs to explaining its unusual preservation. Incidentally, its preservation was one of the arguments utilized by Bequaert and Carpenter (1941) to reject it as a wasp paper nest.

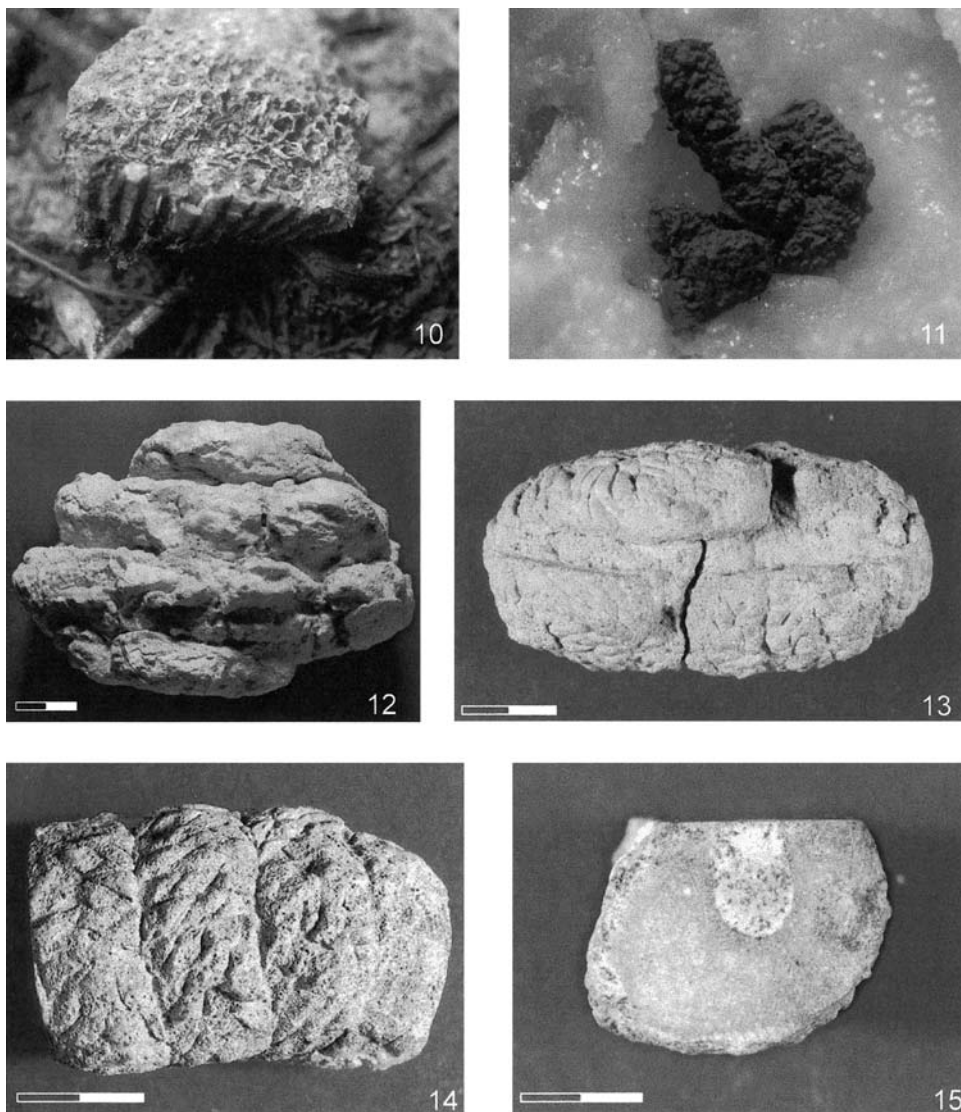
Wenzel (1990) proposed that the preserved domes represented the silk cocoons instead of the paper cells, which would remain united despite the loss of the cell walls. He reconstructed the taphonomic process with a modern paper nest as if it fell on a forest soil and then was washed by a turbid, sandy, stream. Later, the cocoons, filled with sand and mud, would have been buried and definitively preserved in the stream bed (Wenzel, 1990). This process is illustrated herein with a nest of *Polistes* sp. which was found naturally dropped in a stream bed from an overhanging bank and partially buried by sediments (Fig. 10).

An unnamed paper nest attributed to *Stelopolybia* was recorded from a karstic cave in Minas Gerais, Brazil (Rodrigues *et al.*, 1987). The nest was embedded in carbonate and considered to be of recent age. More recently, Poinar (1998) described for the first time a diverse collection of trace fossils preserved in amber. As that author stated, fossilized resin had never been considered a medium for trace fossils until his work was published. From that collection, which is preserved in Oligocene-Miocene Dominican amber, he described and illustrated a piece of a wasp paper nest. Poinar (1998) explained that resin, extruded from a tree, might have engulfed a portion of a nest in its path. Another possibility, although not recorded in amber until now, is that of mud nests constructed directly in crevices of resin extruded by a tree, as depicted in Fig. 11 for the sphecid wasp *Pison*.

Masrichnus issawii Bown (1982, figs. 9B, C and 10) (Fig. 12) from the Eocene-Oligocene Jebel Qatrani of Egypt, is a very particular trace fossil of uncertain affinities composed of tiered, circular, cavities connected by a vertical shaft. Bown (1982) speculated about a termitic origin for this nest but found no similar modern termite nest. In contrast, Sands (pers. comm., in Bown, 1982) believed that *Masrichnus* might be a bee or wasp nest. Genise (1999) tentatively proposed that it could be a paper wasp nest according to certain resemblance to some underground vespine nests, like those of *Vespula germanica* (Fabricius) constructed inside mammal burrows (Evans and Eberhard, 1970, fig. 97). Incidentally, *Masrichnus* occurs in a deposit where fossil mammal burrows are abundant (Bown, 1982; JFG, pers. obs.); they could have offered suitable nesting sites and later, would have favored burial and preservation. However, the resemblance between *Masrichnus* and underground Vespinae nests is not very close: evidence of an external envelope, connecting pedicels, and cells is lacking in the ichnofossil, whereas only the tiered cavities decreasing in size towards the ends, resemble the arrangement of combs of vespine nests. The vertical shaft could be interpreted as the access tunnel to the nesting cavity.

Mud Nests

Apart from *Chubutolithes*, there are three recorded fossil, possibly wasp, mud nests. Handlirsch (1910) described what he considered eumenine mud cells from the Oligocene of Germany. The structures were preserved with land snails, insect larvae(?), lizard eggs and mammal remains, but nothing is said about the deposit in which these fossils occur. The general resemblance to opened cells of eumenines is clear, and the possibility of preservation of aerial mud nests in sedimentary rocks is demonstrated by *Chubutolithes*. However, the structures are also similar to common trace fossils in South American paleosols included in the ichnogenus *Coprinisphaera*, attributed to dung beetle brood



Figs. 10–15. 10, *Polistes* paper nest filled with sediments in a stream bed. 11, *Pison* mud cells in pine resin. 12, *Masrichnus isawii*, from the Eocene-Oligocene Jebel Qatrani Formation in Egypt. 13, A possible wasp mud nest from the Oligocene Fray Bentos Formation (Uruguay), note the pellets and the central groove corresponding to its original attachment. 14, *Chubutolithes gaimanensis* from the Eocene-Miocene Sarmiento Formation (Argentina). 15, A cross-section of the same specimen showing an arched cell around a central rounded structure. Scale bars: 1 cm.

masses. They are also spherical structures, having a constructed wall, an internal cavity that may be empty, and an emergence hole. Further examination of this material, and particularly the possible ornamentation of the walls, is necessary to ascertain its affinities.

A second record of mud nests involves a very particular environment in recent times: a tunnel constructed during the Bronze Age, and sealed about 1000 years B.C. in Megiddo, Palestine (Buxton, 1932). This author found two types of nests and originally assigned both to bees. However, those mentioned here resemble more likely wasp nests. During the

opening of the tunnel in 1931, workers found small, cylindrical mud nests (sphecoid?) supposed to be constructed before the sealing of the tunnel because it was completely closed “also for insects” according to Buxton (1932). This is the second record, with that of Brazil, of sub-fossil nests preserved in caves.

Recently, Genise *et al.* (1998) recorded the presence, in the Oligocene Fray Bentos Formation of Uruguay, of a structure that they attributed to *Monesichnus ameghinoi*, interpreted as a dung-beetle brood mass. The shape, internal chamber and presence of a longitudinal groove suggested that tentative attribution. However, the external ornamentation of the wall, composed of elongated and sharply defined pellets (Fig. 13) (compare with the mud nest illustrated by Evans and Shimizu (1996, fig. 6), constitutes an important difference from *Monesichnus*, as already mentioned by Genise *et al.* (1998). Such sharp relief is also incompatible with a mud wall constructed against the wall of an excavated cavity. Pellets are more pronounced and regularly arranged in aerial nests or when a space is present between the constructed wall and the excavated chamber, (i.e., when cells are constructed from the outside); otherwise, pellets are flattened against a wall and may be more irregularly distributed. Accordingly, this specimen probably represents a hymenopteran (bee or wasp) aerial nest originally attached to a branch or to an exposed root, considering the longitudinal groove that may represent the scar of such attachment. The nest would have fallen, been buried and preserved in a soil as other examples mentioned herein. In other details, the nest is not comparable to any modern example known to us.

Chubutolithes gaimanensis Bown and Ratcliffe, 1988

Chubutolithes gaimanensis is a fossil wasp mud nest that has a long history of discussions about its origin and preservation. Bown and Ratcliffe (1988) stated for the first time its wasp affinities, created its ichnospecific name, and reviewed part of its history. Ihering (1922) created the ichnogeneric name based on material collected by Roth. However, Ihering and other researchers of the first half of that century did not interpret the origin of this ichnofossil (e.g., Schiller, 1919, 1925; Windhausen, 1921; Frenguelli, 1927; Simpson, 1935; Bordas, 1937). Most of those geological publications reviewed by Bown and Ratcliffe (1988), only briefly mentioned *Chubutolithes*, with this name or unnamed, as a fossil of doubtful origin ranging from vertebrate coprolites to casts of coelenterates or tunicates. Having recognized *Chubutolithes* as a wasp mud nest, further discussions after the publication of Bown and Ratcliffe's contribution (1988), dealt with a refinement of its affinities (Genise and Bown, 1990) and particularly with its unusual preservation (Freeman and Donovan, 1991; Genise and Bown, 1991). However, there are still pending points to be addressed about the geographical distribution, origin and preservation of *C. gaimanensis*.

Ihering (1922) described *Chubutolithes* from material collected near Trelew, Chubut, Argentina, in 1891–1895 by Roth's expeditions. Recent observations for this study confirmed its presence on the northern margin of the Chubut River at the Pan de Azúcar locality near Gaiman (20 km from Trelew) from where it was mentioned by former authors (43°16'41"S; 65°31'19"W) (Windhausen, 1921; Frenguelli, 1927; Simpson, 1935; Bown and Ratcliffe, 1988; and probably Ihering, 1922), and also about 500 meters eastwards in the same cliff (Bordas, 1937) (43°16'34"S; 65°30'21"W) (Fig. 16). In addition, its presence in the Chubut River's southern cliff was also confirmed in the Bryn Gwyn Paleontological Park (43°21'18"S; 65°27'20"W), probably the same locality that was mentioned by Bown and Ratcliffe (1988) as “...on south side of Rio Chubut, opposite Bryn Gwyn, Chubut (Bown and Powers, in press, figs. 3, 8)”. Regrettably, Bown and Ratcliffe (1988) for

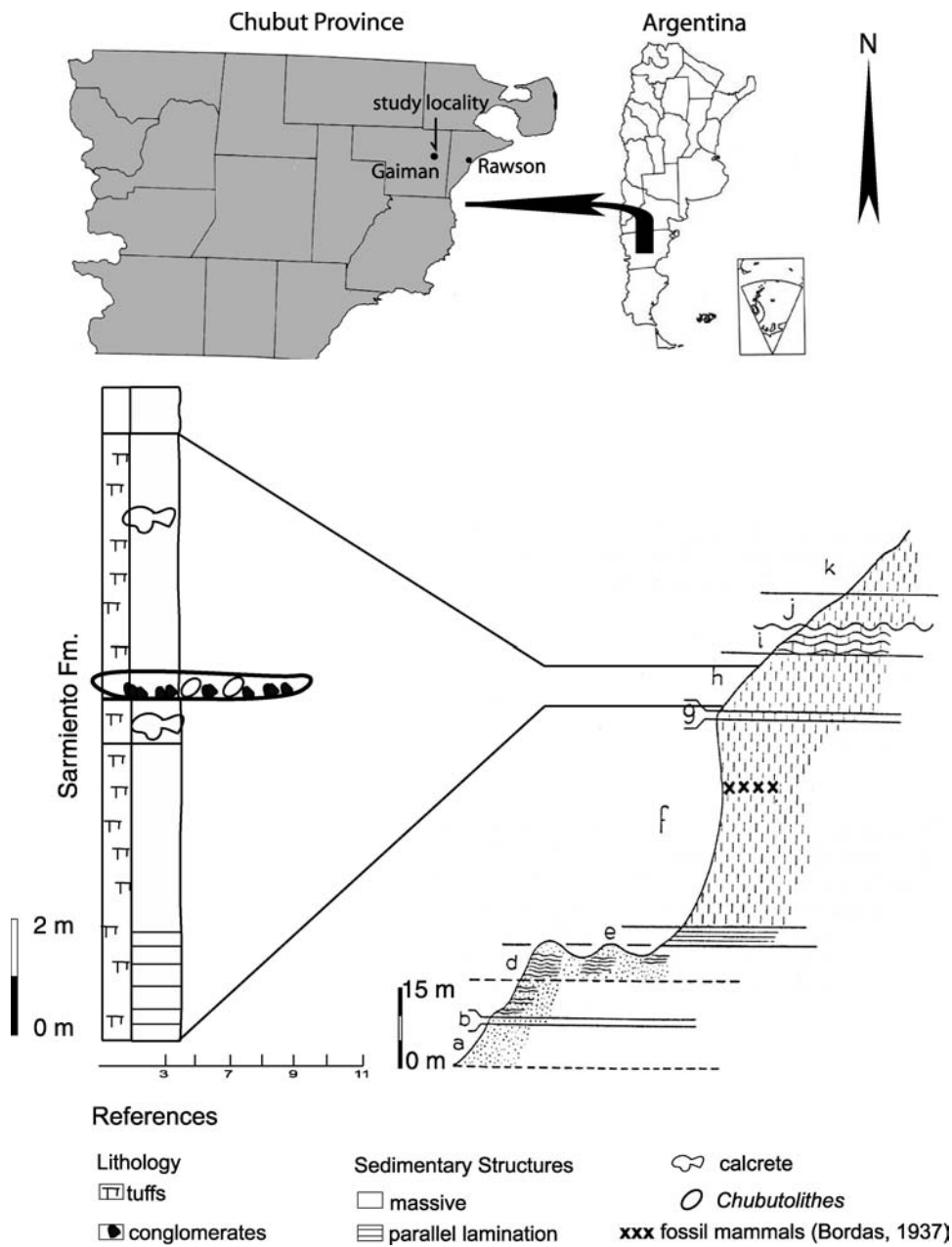


Fig. 16. Geographical location of the Gaiman area. Drawing of the cliff taken from Bordas (1937) at the classical locality near Pan de Azúcar. Detailed section bearing *Chubutolithes*.

localities and stratigraphy, referred mostly to a manuscript by Bown and Powers that was never published (T. M. Bown, pers. comm.). The localities in the Gaiman area, all of them from the same stratigraphical level in the Pan de Azúcar Member of the Sarmiento Formation, are by now the more reliable ones for *C. gaimanensis*. Bown and Ratcliffe (1988) also cited a single specimen from the suprajacent Trelew Member of the Sarmiento

Formation near Bryn Gwyn. This specimen was the only one that shows evidence of abrasion (Genise and Bown, 1991), suggesting that it was transported from the subjacent Pan de Azúcar Member.

All occurrences from other areas apart from Gaiman arose in Schiller's (1925) contribution and require further confirmation. Schiller (1925) stated that Roth mentioned it in 1892 from a locality south of Trelew (Chubut Province) and from the Rio Deseado (Santa Cruz Province). However, there is no contribution published by Roth in 1892 and later ones include no mention of comparable structures (Roth, 1898; J. H. Laza, pers. comm.). Schiller (1925) also mentioned *Chubutolithes* from Bahía Solano (near Comodoro Rivadavia, in Chubut Province), but he only illustrated material that was collected along with remains of marine invertebrates by Lahille in 1895 near Isla Escondida, south of Trelew. However, in Isla Escondida there are no outcrops of the Sarmiento Formation, suggesting that the material came from another locality or was transported. In addition, near Comodoro Rivadavia, was recently found *Eatonichnus claronensis*, in the Peñas Coloradas Formation (Genise *et al.*, 2001); its external appearance roughly resembles *Chubutolithes*. The poor knowledge of these ichnofossils in the first half of the past century might have resulted in misidentifications. Regrettably Schiller's specimens are now unavailable and Lahille's collection is not housed at the Museo de La Plata as stated by Schiller (1925) (A. Pagani, pers. comm.).

Although the Sarmiento Formation extends over 200,000 km² in central and northern Patagonia showing a relative uniform lithology, locally it shows diverse stratigraphy and members (Simpson, 1941; Spalletti and Mazzoni, 1979; Mendía and Bayarsky, 1981). Accordingly, the deposits of the Pan de Azúcar Member bearing *Chubutolithes*, are restricted to the Gaiman area. The uncertainty of the records by Schiller (1925), the particular circumstances of *Chubutolithes* preservation, and its restriction to a certain stratigraphical level in the Pan de Azúcar Member argue against the occurrence of this ichnofossil outside the Gaiman area.

Considering the biology of modern mud-daubers, Bown and Ratcliffe (1988) originally suggested that *Chubutolithes* might have been constructed on overhanging banks along a stream, falling into the stream bed through weathering and/or periodic bank collapse. This idea was followed by Freeman and Donovan (1991) and Genise and Bown (1991). Freeman and Donovan (1991), however, considered questionable that mud nests fallen in water of a stream, as Bown and Ratcliffe (1988) suggested, could survive unless they had undergone early cementation or were strengthened. They stated that modern mud nests disintegrate in water or at least, that ornamentation becomes unrecognizable; moreover the ichnofossils would have been transported with associated intraclasts. As some transport had to be inferred, Freeman and Donovan (1991) proposed that the high percentage of carbonate more probably reflected the early cementation of the nests, which would have favored their preservation. Genise and Bown (1991) replied that probably specimens of *Chubutolithes* accumulated at the base of the bank of a dry stream where they were buried after little fluvial transport, and that subsequently, a soil developed in these deposits (Genise and Bown, 1991).

For these interpretations, the attachment of nests to stream banks was essential to explain the further taphonomic process. However, new observations on the material revealed that nests present no flat surface, which would have resulted if they had been attached to vertical banks. Instead, cells are strongly arched around a central cylinder producing the typical rounded to oval cross section of the whole structure (Figs. 14, 15). The central cylinder, completely replaced by carbonate, may be interpreted as a root or

a stem, considering the habit of some mud-daubers of attaching their nests to such structures. The attachment to a stem suggests the possibility that *Chubutolithes* was constructed outside stream banks. To analyze whether they were constructed around a stem or an overhanging exposed root, or a root in the soil, it is necessary to further discuss the affinities of *Chubutolithes*. The distribution of the pellets suggested that the nests were similar to those of *Auplopus* (Pompilidae, Ajeniellini) (Genise and Bown, 1991), an interpretation that was later accepted by Freeman and Donovan (1991) and Evans and Shimizu (1998). Evans and Shimizu (1996, 1998), who reviewed the nesting behavior of Ajeniellini, stated that there are no representatives of this group that construct mud cells within the soil. Some of them excavate cells from open holes in the soil, others directly are ground or twig nesters, others construct mud cells in protected or in exposed places. The latter group comprises mud nests attached to trunks, stems and leaves constructed by different Oriental species, but are unknown for the Neotropical region (Evans and Shimizu, 1996, 1998). The arrangement of pellets is not only similar to that of aerial *Auplopus* nests, but also their regular design and sharp and protuberant outline are typical of aerial wasp nests constructed from the outside. Thus, the nests might have been attached to overhanging roots or stems, instead of being constructed in the soil even though they are found along with intraclasts of pedogenic origin. Within the group of Ajeniellini that nest in exposed situations, some species construct nests attached to rootlets beneath overhanging banks, whereas others, attach them to leaves or stems covered by other leaves, and still others lack any protective covering (Evans and Shimizu, 1996). In sum, *Chubutolithes* might have been constructed not only around overhanging roots from which they fell to a stream, but also around plant stems, from where they would have fallen directly to the soil.

In the Pan de Azúcar area, *C. gaimanensis* occurs in intraformational conglomerates located in an extended stratigraphical level, which is about 4 meters below the top of the Pan de Azúcar Member between two moderately developed paleosols. The Pan de Azúcar member is mostly composed of fine, light grey to yellowish, massive tuffs probably deposited in wide and shallow streams and adjacent floodplains (Mendía and Bayarsky, 1981). The member is capped by a well developed, reddish-brown paleosol bearing abundant coleopteran pupal chambers (*Teisseirei barattinia*).

The conglomerate bodies that bear *Chubutolithes* are mostly lenticular. However, their width/thickness ratio (44) indicates a trend to a tabular geometry. These deposits are restricted to a definite stratigraphical level extended laterally, which composes a facies that is clearly recognizable. A detailed study of one of these conglomerates, exposed perpendicular to the cliff, showed the largest number of specimens of *Chubutolithes*. This conglomerate is 22 m wide and 0.5 m thick, and its base is erosive. It is clast-supported, with a sandy matrix, showing well sorted, rounded, up to 7 cm intraclasts composed of tuffs, carbonate nodules similar to those of the subjacent paleosol, and specimens of *Chubutolithes*. It contained 34 specimens of randomly oriented *Chubutolithes*, grouped in its central part.

The level with conglomerates overlies a moderately developed tuffaceous paleosol bearing a nodular calcrete with nodules up to 30 cm in size, which probably produced the suprajacent conglomerate intraclasts. However, no specimen of *Chubutolithes* was found in the subjacent paleosol. The absence of nests in the underlying paleosol would suggest (1) different paleoenvironmental conditions in distal areas, or (2) that fallen nests were probably deposited in a superficial soil horizon completely removed by fluvial action. The diverse preservation of the wall relief of different specimens from the same conglomerate, indicates that they were probably transported from different distances.

The lack of orientation of the nests is another evidence of their transported condition. As Freeman and Donovan (1991) stated it is very unlikely that mud nests could resist a long subaquatic transport. However, evidence presented herein shows that they occur in high energy fluvial channels. Accordingly, in the most probable taphonomic scenario, the nests were buried in its original locality, where they underwent a fossildiagenetic process (Fernández López, 2000) before the transport. This process is only possible during a period of stability that would be reflected by the underlying paleosol. A later reactivation of the fluvial system, evidenced by the channels, would have eroded distal areas of this paleosol, removing from different locations specimens of *Chubutolithes* buried in the floodplain from where nests and other clasts of the conglomerate came. The evidence shows that nests would have undergone a biostratinomic stage when fallen to the soil and included in it and a fossildiagenetic stage when cementation took place in the soil. Taphonomically, the nests may be classified as alloctonous and transported.

There are examples of fossil insect nests from the Tertiary of Patagonia constructed in soils that were later transported from their original locations and deposited in intraformational conglomerates (Andreis, 1972, 1981; Genise *et al.*, in press; Cladera *et al.*, in press). Andreis (1981) stated that nests like *Coprinisphaera*, a dung beetle brood mass, may be removed from its original location in soils developed in the floodplains by fluvial erosion, and later deposited in intraformational conglomerates. In sum, new ichnological and sedimentological evidence suggests that mud nests that became *Chubutolithes* were attached to plants from which they fell to the soil and later, covered by sediments, impregnated by carbonate, were removed by fluvial action along with other carbonate nodules.

However the taphonomic process of *Chubutolithes* is interpreted, the data presented herein, along with those available for other wasp ichnofossils, show that known trace fossils that can be reliably attributed to wasps represent cases in which the taphonomic barrier was broken through complicated processes.

Acknowledgments

This article is written in memoriam of Dr Howard Evans, who encouraged J. F. G. with his former research on wasp behavior and later discussions on *Chubutolithes*. The authors thank Dr. Charles Michener and Dr. Mary Jane West-Eberhard for the invitation to participate in this memorial issue, Dr. Markus Bertling for his help with the German bibliography, Dr. Thomas Bown for his comments on *Chubutolithes*, and Dr. Eduardo Bellosi, Dr. Charles Michener and an anonymous reviewer for the critical reading of the manuscript. The grant PICT 99 6156 from the Agency of Scientific Promotion of Argentina and Fundación Egidio Feruglio partially supported this research and publication.

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