Vertebrate coprolites from the Triassic of Argentina (Cuyana Basin)

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Abstract. Abundant vertebrate coprolites collected from the Triassic Potrerillos, Cacheuta and Río Blanco formations (Cuyana Basin) are analyzed. The studied material includes both specimens originally described by Rusconi plus many new undescribed materials. Four morphotypes were identified on the basis of the morphological features of the coprolites as shape, surface texture, size and internal structure, among others. Morphotype A is characterized by spiral coprolites with also an internal coiled aspect and they contain numerous ganoid scales. Morphotype B includes coprolites with an amorphous homogeneous phosphatic internal structure, in contrast with those of Morphotype C which present a phosphatic granulate internal aspect. Finally, Morphotype D is characterized by an agglomeration of ganoid scales visible both externally and internally. The four morphotypes show similar sedimentological and taphonomic features that suggest that their producers inhabited the water bodies. Moreover, their phosphatic composition and inclusions of fish scales are considered unequivocal evidence of the carnivore diet of their producers. Aquatic vertebrates known by skeletal remains from the same levels are actinopterigian fishes and temnospondyl amphibians and are the more likely producers of the studied coprolites. Particularly, Morphotype A might be also related to dipnoans or coelacanths though morphotypes B, C and D can not be specifically related to any vertebrate group. Nevertheless, their morphological and compositional differences suggest quite dissimilar producers.

Resumen. COPROLITOS DE VERTEBRADOS DEL TRIÁSICO DE ARGENTINA (CUENCA CUYANA). Abundantes restos de coprolitos de vertebrados coleccionados de las formaciones triásicas de Potrerillos, Cacheuta y Río Blanco (Cuenca Cuyana) son analizados. El material estudiado incluye tanto especímenes originalmente descriptos por Rusconi como nuevos materiales recientemente colectados. Cuatro morfotipos fueron identificados sobre la base de las características morfológicas de los coprolitos como forma, textura superficial, tamaño y estructura interna, entre otros. El Morfotipo A está caracterizado por coprolitos espiralados, externa e internamente, y que contienen numerosas escamas ganoideas. El Morfotipo B incluye coprolitos con una estructura interna fosfática homogénea amorfa, a diferencia de los del Morfotipo C, los cuales presentan un aspecto interno granular fosfático. Finalmente, el Morfotipo D está caracterizado por poseer una estructura formada por la aglomeración de escamas ganoideas, visibles tanto externamente como internamente. Los cuatro morfotipos muestran similares características sedimentológicas y tafonómicas, que sugieren que los productores habitaron el cuerpo de agua. Más aún, la composición fosfática y la inclusión de escamas de peces son consideradas evidencias inequívocas de la dieta carnívora de sus productores. Todos los vertebrados acuáticos conocidos por restos esqueletarios de los mismos niveles son peces actinopterigios y anfibios temnospóndilos, y son considerados los productores más probables de los coprolitos estudiados. Particularmente, el Morfotipo A puede ser también relacionado a dipnoos o celacantos por su estructura espiralada, mientras que los morfotipos B, C, y D no pueden ser específicamente relacionados a ningún grupo de vertebrados. Sin embargo, sus diferencias morfológicas y de composición sugieren productores completamente diferentes.

Key words. Coprolites. Lake deposits. Triassic. Cuyana Basin. Argentina.

Palabras clave. Coprolitos. Depósitos lacustres. Triásico. Cuenca Cuyana. Argentina.

Introduction

Coprolites are trace fossils which represent the fossilized excrement of animals, independently of size, composition, and producer (Sarjeant, 1975; Hunt *et al.*, 1994; Lamboy *et al.*, 1994). They are commonly found in marine and non-marine sequences, and can form important accumulations in some deposits (*e.g.* Johnson, 1934; Rusconi, 1947; Häntzschel *et al.*, 1968; Sarjeant, 1975; Broughton *et al.*, 1978; Hunt *et al.*, 1994; Rodriguez-de la Rosa *et al.*, 1998). Even though coprolites have been recognized for many years, they have been rarely employed in paleobiological analyses (Hunt *et al.*, 1994). Recently, some works have demonstrated that they can be used to provide information on the diet of the producer, the structure of the digestive tracts, the diversity of the biota, the predator-prey or plant-animal relationships (Waldman and Hopkins, 1970; Sarjeant, 1975; Stewart, 1978; Rodriguez-de la Rosa *et al.*,

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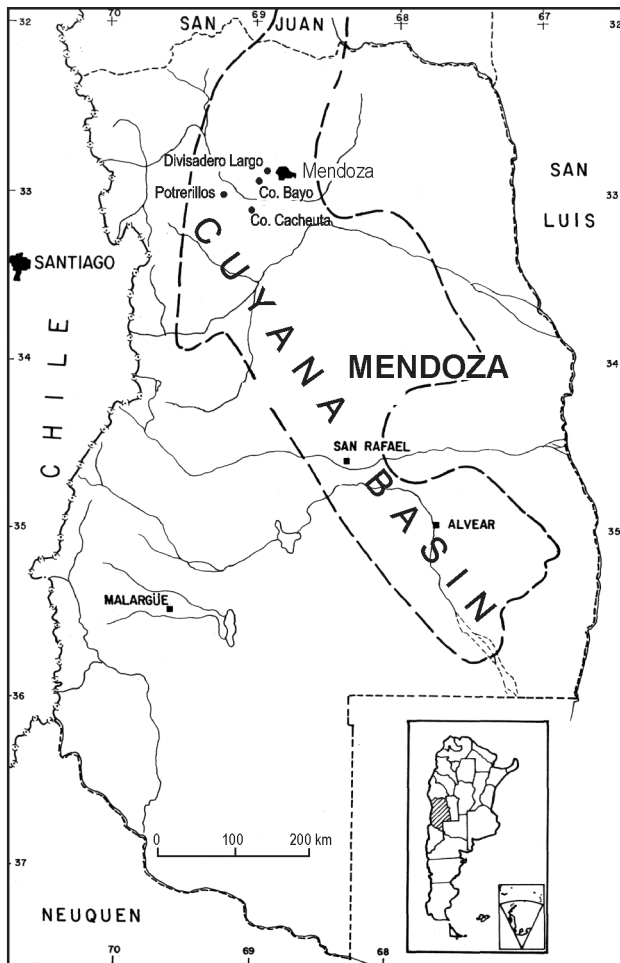
Figure 1. Location Map of the Potrerillos, Cerro Cacheuta, Divisadero Largo (Mina Atala) and Cerro Bayo (Las Heras) localities, Cuyana Basin, Mendoza province, Argentina / *Mapa de ubicación de las localidades Potrerillos, Cerro Cacheuta, Divisadero Largo (Mina Atala) y Cerro Bayo (Las Heras), Cuenca Cuyana, provincia de Mendoza, Argentina.*

1998). In addition, the coprolites can also be indicators in sedimentological analyses of currents, stimation of rates of deposition, degree of compaction, current velocity and as evidence of periods of nondeposition, among others (Hunt, 1992).

Particularly in Argentina, vertebrate coprolites were first described by Rusconi (1947) from levels of the Triassic Cuyana Basin. This author documented the presence of abundant coprolites in the Potrerillos and Cacheuta formations from several localities (Rusconi, 1947, 1950, 1951) and interpreted some of them as fecal material of temnospondyl amphibians (Rusconi, 1950, 1951), whereas other ones as produced by basal archosaurs (Rusconi, 1947, 1951).

In the present contribution, a revision of Rusconi's original material housed in the collections of the Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano" (MCNAM) was performed. Moreover, additional new coprolite material collec-

ted from the Cacheuta and Río Blanco formations at Potrerillos, Cerro Cacheuta, Divisadero Largo (Mina Atala) and Cerro Bayo (Las Heras) localities (figure 1) were also analyzed.

Geological setting

The entirely nonmarine Triassic infilling of the Cuyana Basin (figure 1) starts with coarse clastic facies of the Río Mendoza Formation which interfingers with the sandstones and tuffs of the Cerro de las Cabras Formation; this sequence reflects an initial phase of fast tectonic subsidence (synrift phase) in the basin (Kokogian and Mancilla, 1989; López-Gamundí *et al.*, 1994; Kokogian *et al.*, 2001). Subsequently, the sequence grades up to cross-bedded sandstones, shales, and tuffs, all interpreted as deposited by braided-river systems (Potrerillos Formation). These fluvial deposits pass upward into the widespread euxinic lacustrine bituminous shales of the Cacheuta Formation, which is succeeded by the fluvial red beds of the Río Blanco Formation. The lacustrine Cacheuta Formation and the fluvial Potrerillos and Río Blanco formations represent the phase of thermal subsidence (postrift phase) of the basin (Kokogian and Mancilla, 1989; López-Gamundí *et al.*, 1994)

In the Cacheuta levels, the coprolites were recorded in horizontally laminated black claystones and horizontally laminated-massive dark gray siltstones. These facies were deposited from suspension in distal-lake conditions. The coprolites from the Río Blanco levels were found in the lower part of the unit, characterized by gray to red horizontally laminated and massive claystones, which suggests a shallow distal lake setting. The sequence passes upward into thick deltaic/fluvial red beds (Spalletti and Barrio, 1999; Kokogian *et al.*, 2001). Apparently, Rusconi also collected coprolites from different levels of the Potrerillos Formation without any specification of the exact position in the column (Rusconi, 1949). Even though, it was possible to assert the sedimentological features of the bearing rock of part of Rusconi's material as several specimens are still in blocks. The material is in very fine laminated mudstones suggesting a low energy setting, probably related to flood plain deposits.

Cuyana Basin paleontological content

Fresh water invertebrates (conchostracans, ostracods, insects, and pelecypods) have been reported only from the Potrerillos and Cacheuta formations (e.g. Ballent, 1993; Riccardi *et al.*, 1993; Gallego, 1992, 1997), although vertebrate remains were found in nearly the whole column. Basal actinopterigian fish-
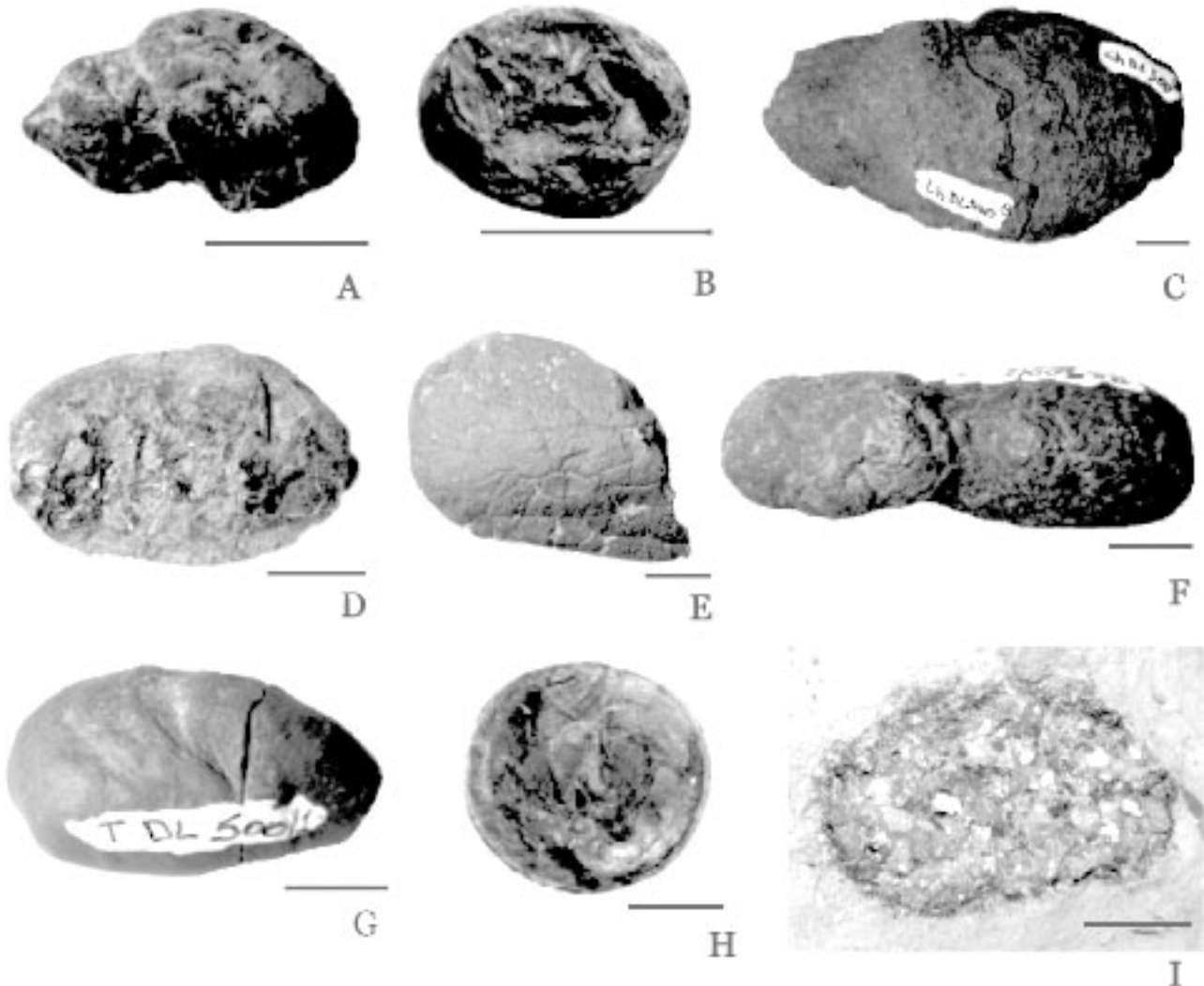
Figure 2. A, Morphotype A (MCNAM 1942), lateral view / *vista lateral*; **B,** Morphotype A (MCNAM 1956), transversal section / *corte transveral*; **C,** Morphotype B (MCNAM 3514), lateral view / *vista lateral*; **D,** Morphotype B (MCNAM 3513), transversal section / *corte transversal*; **E,** Morphotype B (MCNAM 3494), lateral view / *vista lateral*; **F,** Morphotype B (MCNAM 3526), lateral view / *vista lateral*; **G,** Morphotype C (MCNAM 3473), lateral view / *vista lateral*; **H,** Morphotype C (MCNAM 3474), transversal section / *corte tranversal*; **I,** Morphotype / *Morfotipo* D (MCNAM 3472). *Escala = 1 cm /*Scale bar = 1 cm.

es are fairly diverse and were recovered at different localities from the Cerro de las Cabras, Potrerillos, Cacheuta and Río Blanco formations (see Báez *et al.,* 1993). The tetrapod fauna is very scarce and nearly restricted to amphibian temnospondyls collected from the lacustrine facies of the Cacheuta and Río Blanco formations (Marsicano, 1999). Amniote remains are even more rare and are mainly represented by non-mammalian therapsids, exhumed from the lower half of the sequence (Bonaparte, 1969, 1970; Báez *et al.,* 1993), and a unique basal archosaur recorded from the Cacheuta black shales (Desojo *et al.,* 2002).

Macro and microfloral content of the Cuyana Basin infilling is well known and was collected from the Cerro de las Cabras, Potrerillos, Cacheuta and Río Blanco formations. The megaflora assemblage is included in the "*Dicroidium*-type flora" (e.g. Stipanicic and Bonetti, 1969; Stipanicic, 1983; Morel, 1994; Spalletti *et al.,* 1999) whereas the microfloral content of the Potrerillos and Cacheuta formations includes "Ipswich-type Microflora", thus suggesting a "Carnian" age for these units (Zavattieri and Batten, 1996; Zavattieri, 2002).

Coprolite material

In order to recognize coprolites several criteria have been proposed by different authors summarized by Hunt (1992). Particularly, in the present analysis some of these criteria have been used to characterize the material from Mendoza and they
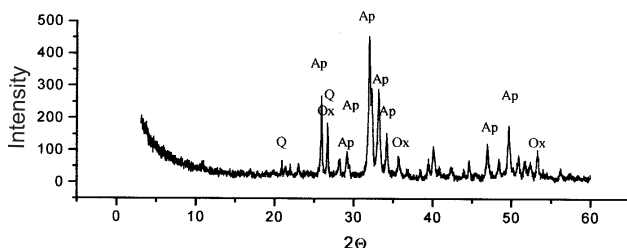
Figure 3. X-Ray diffraction diagram of a specimen of morphotype B. Apatite = Ap, Fe iron oxides = Ox, quartz = Q / *Diagrama de difracción de Rayos-X de un especimen del morfotipo B. Apatita = Ap, óxido de hierro = Ox, cuarzo = Q.*

are: the extrusive external morphology, the internal structure, the presence of longitudinal or spiral striations, the similarity of morphology to animal guts, inclusions of organic matter, the presence of evidences for gas bubbles or gas-escape structures, composition of calcium phosphate, marked vertical relief even in finely laminated shales, and their presence in sedimentary rocks or unconsolidated sediment (Amstutz, 1985; McAllister, 1988; Hunt, 1992).

Material. The specimens collected by Rusconi and Tellechea are housed in the Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano" (MCNAM). MCNAM 1820, 1833, 1836, 1860, 1863, 1865, 1866, 1880, 1888, 1906, 1926, 1931, 1941, 1942-1962, 2223 and one S/N (unnumbered specimen) were collected from levels of the Potrerillos Formation at the Quebrada de los Leones, El Challao locality (figure 1); MCNAM 2665, 2672, 2685, 2686, 2692, 2696 were collected from the Cacheuta Formation in the Cerro Bayo area at Las Heras (figure 1). The new coprolites collected by the authors, MC-NAM 3472- 3513, were recovered from levels of the Cacheuta Formation at the Potrerillos, Cerro Cacheuta and Divisadero Largo (Mina Atala) localities (figure 1) and MCNAM 3514-3573 were exhumed from the Río Blanco Formation at the Potrerillos, Divisadero Largo (Mina Atala) and Cerro Bayo (Las Heras) localities (figure 1).

Description. On the basis of the morphological features mentioned above (shape, constriction, surface texture, size, internal structure, etc.), four morphotypes were identified in the studied material.

Morphotype A: This morphotype (figures 2.A, 2.B) is characterized by spiral coprolites, which are mainly ovoid and occasionally cylindrical in shape. These coprolites range from 10 mm to 45 mm in length, and from 4 mm to 20 mm in maximum diameter. Their surface shows a coiled aspect which is reflected also in the internal structure. Internally, they contain numerous ganoid scales. This morphotype corresponds only to Rusconi´s original material from Potrerillos Formation at the Quebrada de los Leones, El Challao locality (MCNAM 1820, 1833, 1836, 1863, 1865, 1866, 1880, 1888, 1906, 1926, 1931, 1942 - 1962, 2212, 2223).

The morphotype A is moderately abundant in relation to the other morphotypes described in this paper.

Morphotype B: This morphotype (figures 2.C, 2.D, 2.E, 2.F) is characterized by the presence of an amorphous homogeneous internal structure and the coprolites are generally cylindrical or ovoid in shape. They range from 19 mm to 69 mm in length, and from 12 mm to 36 mm in maximum diameter. The surface of the coprolites can be both smooth and somewhat rough, and some of them might show patterns of delicate cracks and/or constrictions. However, the most important feature is the amorphous homogeneous internal structure. In thin section, they show phosphatic composition. Phosphatic material occurs as dark brown and reddish brown ovoid or spherical pellets. Some pellets are very well rounded whereas other pellets have an irregular surface composed of small-size aggregates. X-Ray diffraction analysis (figure 3) was made on a Phillip (X' Pert model) goniometer filled with a sealed proportional detector using Ni-filtered CuKa radiation. Powedered rocks were scanned from 3 to 60° 2ø at 2° 2 ø a scanning speed to identify the dominant minerals comprising the phosphate material of the coprolites. As a result, Fe iron oxides, quartz and feldspar were indicated on the diffractogram, appart from the major constituent (Apatite = Ap) (figure 3).

Specimens of this morphotype (MCNAM 3494-510, 3513 - 3573) were collected from Cacheuta and Río Blanco formations at the Potrerillos, Divisadero Largo (Mina Atala) and Cerro Bayo (Las Heras) localities. Morphotype B is the most abundant morphotype in the sample analyzed herein.

Morphotype C: This morphotype (figure 2.G, 2.H) is characterized by coprolites with a granulate internal structure; all coprolite material is elliptically shaped. They range from 31 mm to 76 mm in length, and from 26 mm to 43 mm in maximum diameter. The material presents both smooth and rough surfaces, and might show constrictions. However, the most important feature is their agglomerated granular internal structure of phosphatic composition. This morphotype includes both part of Rusconi´s original material (MCNAM 2665, 2672, 2685, 2686, 2696) and some of the new collected material (MCNAM 3473-3493, 3511, 3512). Rusconi´s material was recorded in the Cacheuta Formation at the Cerro Bayo area (Las Heras), whereas the new material included in this morphotype comes from the same unit but at the Divisadero Largo (Mina Atala) locality. This morphotype has a moderate abundance, similar to that of Morphotype A.

Morphotype D: This morphotype (figure 2.I) is characterized by coprolites which are composed by an agglomeration of ganoid scales visible both externally
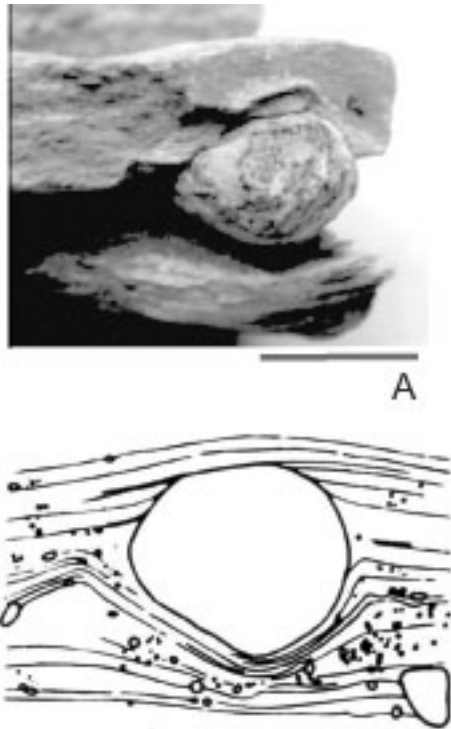
Figure 4. A, coprolite (MCNAM 2212) breaking the lamination of the bearing sediment, **B,** dropstone structure, modified from Miller (1996). Scale bar = 1 cm / *A, coprolito (MCNAM 2212) rompiendo la laminación del sedimento portador,* **B,** *estructura de un cadilito, modificado de Miller (1996). Escala = 1 cm.*

and internally; the shape of the coprolites is cylindrical to ovoid. They range from 41 mm to 38 mm in length, and from 13 mm to 23 mm in maximum diameter. Their surface is rough due to the ganoid scales and internally they also show an agglomerate structure, as mentioned above. In some cases, groups of scales appear to be orientated, but each cluster is in different direction to the others. This type of coprolite corresponds to material exhumed by Rusconi (MCNAM s/n, 1941) from the Potrerillos Formation at the Quebrada de los Leones (El Challao locality), and partially by new material (MCNAM 3472) recovered from the Cacheuta Formation at Cerro Cacheuta locality. Morphotype D has a relatively very poor abundance.

Discussion

Coprolites provide a record of animal activity with the potential to supplement information obtained from body fossils (Chin, 1997). Similar and/or related organisms may produce very dissimilar droppings and unrelated organisms may produce identical droppings. Moreover, even a single animal can produce a variety of different fecal shapes due to changes in its diet through the year (Thulborn, 1991; Hunt *et al.*, 1994), in the water content, and/or ani-

mal age (Verde and Ubilla, 2002). Therefore, a morphological classification is useful for the interpretation of their biological affinities, but not for the precise identification of the producer (Schmitz and Binda, 1991; Rodriguez-de la Rosa *et al.*, 1998).

From a sedimentological point of view, the coprolites are, in general, among the trace fossils that can be transported from the original setting (Hunt *et al.*, 1994). However, in the case studied here, the coprolites form an *in situ* deposit and not a secondary mechanical concentration as could be produced by current transport. This hypothesis is supported by the excellent preservation of the material, without any obvious signs of, for example, abrasion. Moreover, the observed concentration in the studied sequences might be the result of a very low sedimentation rate during deposition in a distal lake environment (Broughton *et al.*, 1978). Another important sedimentological aspect is that the material found *in situ* was breaking the lamination of the bearing sediment (figure 4.A), as occurs with the dropstones (figure 4.B) (Miller, 1996). This suggests that they arrived to the bottom of the water body from the surface or from some point of the water column and were not transported from the margins.

As mentioned above, some features can be used to suggest the biological affinities of the coprolites. Thus, their composition can constrain the number of likely producers by providing clues of the feeding strategies of source animals (Hunt *et al.*, 1994; Chin, 1997). Inclusions of bone fragments, teeth, fish scales, or mollusc shells, for example, give evidence of carnivory (Chin, 1997) however, content is not always discernible in all coprolites because the residues have often been destroyed by digestion and/or diagenesis. Nevertheless, the presence of phosphate and calcium in coprolites might indicate a carnivore and/or omnivore origin (Rodriguez-de la Rosa *et al.*, 1998). Previously, Bradley (1948) noted that most coprolites are phosphatic and that carnivore feces contain relatively high percentages of phosphorous. Thus, this author suggested that carnivore feces are preferentially fossilized because of the availability of dietary calcium phosphate (Bradley, 1948). This is consistent with the observation that permineralized coprolites containing substantial plant material are relatively rare and are almost invariably calcareous or siliceous (Chin, 1997). All material described herein presents phosphatic composition, thus suggesting a carnivore and/or omnivore origin. Moreover, the inclusions of fish scales in morphotypes A and D unequivocally indicate the carnivory of their producers.

Related to the external aspect of the coprolites, the constriction that characterized the surfaces of many specimens might be considered as organic in origin (Häntzschel *et al.*, 1968; Broughton *et al.*, 1978). They

are suggested to be the result of localized squeezing of the excrement attendant upon contraction of the sphincter muscles during defecation (Broughton *et al.*, 1978). Perforations and large cracks on the surfaces of some specimens might be gas-escape features and serve as degassing channels during anaerobic decomposition of the fecal masses (Broughton *et al.*, 1978); also they might be related with desiccation or syneresis (Thulborn, 1991). Constriction and large cracks are observed in the studied material and are mainly found in Morphotypes B and C. The spiral shape of some coprolites is also regarded as a diagnostic feature of an excremental origin. The spiral coprolites frequently exhibit an intricate internal folding that was apparently caused by passage of fecal material through a spiral intestine (Williams, 1972). Thus, spiral configuration is the only distinctive coprolite morphology that can be reliably associated with a type of source animal (Chin, 1997). A range of fish groups (agnathans, basal actinopterygians, dipnoans and coelacanths) have spiral intestinal valves that could affected the egestion of coiled feces (Jain, 1983; Pollard, 1990); spiral intestinal valves have apparently been secondarily lost in teleosts and tetrapods (Romer and Parsons, 1986; Gilmore, 1992; Hunt *et al.*, 1994). In the present case, only the material included in Morphotype A presents a spiral structure thus relating these coprolites to fish producers (basal actinopterygians, dipnoans or coelacanths). Moreover, these coprolites also bear inclusions of fish scales suggesting a carnivore and/or omnivore fish.

Non-spiraled coprolites are more highly variable and distinctive shapes and/or striations could be found in feces produced by many different vertebrate groups (Thulborn, 1991; Hunt *et al.*, 1994). Thus, a secondary evaluation of non-morphological characters is necessary to assess the source animal. For example, it is important that the stratigraphic distribution of potential source animals is consistent with the age, locality and depositional environment of the coprolite material itself. Even so, the co-occurrence of skeletal elements in the same sediments with coprolites might only suggest the same depositional environment for both body and trace fossils.

In the present study, part of the coprolite material was found associated in the same levels with skeletal remains (Rusconi, 1947, 1950, 1951). This situation was interpreted by Rusconi (1947, 1951) as evidence to assign his material from the Potrerillos Formation to "basal archosaurs". This was due to the association of the coprolites with dermal scutes now referred as indeterminate vertebrate material (Desojo, 2001). The coprolites collected in the Cacheuta Formation by Rusconi (1950, 1951) were also related by this author to fecal material of temnospondyl amphibians by the same reasons as discussed above. However, associated postcranial archosaurian bones (Desojo *et al.*, 2002) and fish remains are also found in the same levels. Thus, the co-occurrence in both mentioned cases only suggests that the coprolites and vertebrate body fossils were preserved in the same depositional environment.

As previously discussed, all material described in the present contribution was found related to decantation deposits and, moreover, without any obvious signs of transport. These features strongly suggest that the coprolites were produced by vertebrates which inhabited these water bodies. Morphotype A, due to its spiral shape, can be restricted to a fish producer, as basal actinopterygians, dipnoans or coelacanths; to date, only body-fossil remains of basal actinopterygians are known from the Cuyana Basin (Marsicano *et al.*, 2001). In contrast, the identification of the putative producers of the remaining morphotypes described (B, C, D) is even more doubious. As mentioned above, their phosphatic composition suggests that they were produced by carnivorous animals that inhabited the water bodies. It is not possible to suggest important differences among the phosphatic composition of morphotypes B and C, and also they are found, in many cases, associated in the same levels without any differences in their taphonomic features. Even though Morphotype C is relatively larger than Morphotype B, which is the most abundant type recorded. The apatitogenesis of the inicial feces has been proposed to be produced by microbial processes during early diagenesis and differences in the phosphatic structure might indicate differences in microbe diversity in the digestive tract of the producer (Lamboy *et al.*, 1994). As mentioned above, these morphotypes have large cracks on their surfaces suggesting the presence of degassing channels during microbial anaerobic decomposition. Thus, the differences in the phosphatic internal structure between these two morphotypes (B and C), not related to different taphonomic histories, might suggest the presence of two different types of producers which differ in the environmental conditions in their digestive tracts (see Lamboy *et al.*, 1994).

Morphotype D is fairly different to the others and was collected in a different stratigraphic level. Coprolites of this morphotype are composed by agglomerated ganoids scales that strongly suggest the carnivorous nature of their producers. The lack of phosphatization in these types of coprolites also suggests a different producer. However, different taphonomic conditions to the ones discussed above can not be proposed. The coprolites included in the morphotypes B, C and D do not show differences in their taphonomic characteristics as patterns of arrange-

ment in space, sorting, transport, modifications, among others.

The only groups of carnivorous aquatic vertebrates recorded in the Cuyana Basin are, until now, basal actinopterygian fishes and temnospondyl amphibians, both represented by several different taxa (Báez *et al.*, 1993; Marsicano, 1999; Marsicano *et al.*, 2001). These vertebrate groups are here suggested to be the most likely producers of the coprolites described above although there is not evidence in the studied material that might help to discriminate among the mentioned groups as was previously proposed by Rusconi (1947, 1950, 1951).

Conclusions

The four morphotypes (A, B, C, D) identified among the studied coprolite material, on the basis of their morphological features, show similar sedimentological and taphonomic characteristics. These features suggest that the coprolite producers inhabited the water bodies, and the phosphatic composition and inclusions of fish scales unequivocally evidence their carnivore diet. All aquatic vertebrates known by skeletal remains from the same levels (fishes and temnospondyls) are carnivorous and are the more likely producers of the studied coprolites. Morphotype A can be related to basal actinopterygians, dipnoans or coelacanths even though, the morphotypes B, C and D can not be specifically related to any vertebrate group. However, their morphological and compositional differences suggest quite dissimilar producers.

Acknowledgments

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