Paleobiological implications of Campanian coprolites

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Abstract

Vertebrate coprolites (153 samples) in association with vertebrate and plant remains in the Upper Cretaceous (Campanian) sediments of the Cerro del Pueblo Formation, in southeastern Coahuila, Mexico, represent at least ten morphotypes, ranging from ca. 1 cm to 3 cm. At least one suggests a carnivore origin due to the presence of abundant bone fragments, but most of the coprolite morphotypes were produced by either omnivores or herbivores. Analysis of inclusions of the coprolites revealed plant remains, such as stems and isolated vascular elements, and papillate and non-papillate cuticles. Two seed types have been recognized within two coprolite morphotypes. The first one has lythraceous affinity, being comparable to members of a morphological complex within Nesaeae. The second seed type, which shows adaptations for water dispersal, belongs to Ranunculaceae, and is described as *Eocaltha zoophila* gen. et sp. nov. Although *Eocaltha* evolved a mechanism for abiotic dispersal, the seeds were apparently occasionally ingested by a vertebrate. The presence of seeds of *E. zoophila* in a coprolite suggests that the organism that produced it was looking for a high-quality diet perhaps represented by the seeds, and served indirectly as a biotic seed dispersal agent. The combination of abiotic and biotic dispersal syndromes, plus the fact that the seeds appear to be scarified suggest a case of diffuse coevolution. Interactions, as herbivory, during the Cretaceous prompted biotic dispersal of angiosperm diaspores as revealed by the presence of seeds of *E. zoophila*. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Upper Cretaceous; coprolites; Coahuila, Mexico; plants; vertebrates

1. Introduction

Several attempts have been made to understand aspects of ancient terrestrial ecosystems from the scope of plant–animal interactions (e.g. Scott, 1977; Scott and Taylor, 1983; Taylor and Scott, 1983; Zavada and Mentis, 1987; Edwards et al., 1995), but these were based mainly on evidence from the Paleozoic. Scott et al. (1992) reviewed plant–animal interactions for the Paleozoic and Mesozoic and plant–insect interactions were also discussed by Scott (1992). However, some authors have dealt with interactions between Mesozoic vertebrates and gymnosperms (e.g. Weishampel, 1984; Chin and Gill, 1996), while few researchers have dealt directly with interactions involving angiosperms (e.g. Bakker, 1978; Coe et al., 1987; Wing and Tiffney, 1987a,b; Collinson and Hooker, 1991; Tiffney, 1992). Although dental morphology, stomach contents and co-

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Coprolites are three sources of information that provide evidence of animal–plant interactions (Weishampel, 1984; Tiffney, 1986), relatively few reports mention coprolites as evidence for these interactions. Furthermore, little strength has been given to the fact that their analysis provides clues about the partial diet of an organism, thus having paleobiological implications (Scott and Taylor, 1983; Hunt et al., 1994; Edwards et al., 1995; Chin and Gill, 1996).

Coprolites, or fossil feces (Ash, 1978), belong to a group of ichnofossils known as bromalites, which also include regurgitalites (gastric residues evacuated anteriorly from the oral cavity) and cololites or gut contents (e.g. Stokes, 1964; Hunt, 1992; Hunt et al., 1994). The analysis of inclusions in different morphotypes of coprolites has shown organic remains which were part of the diet or were ingested accidentally by the organism that produced them. Ostracodes have been found inside vertebrate coprolites (Bradley, 1946; Sohn and Chatterjee, 1979), skeletal elements such as fish scales and teeth, as well as bone fragments and feather impressions also have been found inside coprolites, suggesting carnivorous organisms (e.g. Johnson, 1934; Wetmore, 1943; Jepsen, 1963; Zangerl and Richardson, 1963).

Several plant-bearing coprolites have been reported, but based in their small size these are mainly interpreted as produced by arthropods (e.g. Harris, 1964; Scott, 1977; Baxendale, 1979; Scott and Taylor, 1983; Edwards et al., 1995), and only a few are thought to be from herbivorous vertebrates (e.g. Chin and Gill, 1996). Although vertebrate plant-bearing coprolites seem scarce in the fossil record and some authors suggested that they are rather rare, they have been known for a long time (Hunt et al., 1994). Toschi (1854) was one of the first to mention plant traces within two coprolites based on material from Romania. More recently, some Mesozoic plant-bearing coprolites have been attributed to dinosaurs due to their strong association with skeletal elements of these animals (Hill, 1976; Chin, 1990; Chin et al., 1991a,b; Chin and Gill, 1996). Tertiary and/or Quaternary plant-bearing coprolites from herbivorous mammals are more common in the fossil record (e.g. Eames, 1930; Hansen, 1978). Some plant material has been found inside coprolites that have been attributed to carnivores, but probably only by occasional ingestion (Bradley, 1946; Jepsen, 1963). Although coprolites found in the Upper Cretaceous (Campanian) sediments of the Cerro del Pueblo Formation have been mentioned since the first stratigraphic studies of the area (Hernandez, 1992; Rodríguez-de la Rosa and Cevallos-Ferriz, 1995), this is the first time that they are studied with some detail within the context of a better-understood biotic community, contributing two new taxa of angiosperms previously unknown in the area, and documenting plant–animal interactions such as herbivory and seed dispersal. Inference of the physiological process termed seed scarification, which aids germination in many extant plants, is also documented for the first time in the fossil record. This new evidence is discussed as suggesting a case of diffuse coevolution between a plant and a vertebrate. Diffuse coevolution could be supported as a very important mechanism in angiosperm evolution.

2. Material and methods

Coprolites from three areas (Rincon Colorado, Rancho Altamira and El Pelillal locality, Fig. 1) are considered in this study, being representative of the coprolites collected elsewhere in the Cerro del Pueblo Formation. Some of them have abundant plant material (Rodríguez-de la Rosa and Cevallos-Ferriz, 1995). The Cerro del Pueblo Formation is the lowest formation of the Difunta Group. Its stratigraphic position and correlation indicates a Campanian age for this sedimentary sequence (Murray et al., 1962; McBride et al., 1974; Vega-Vera et al., 1990).

At least ten morphotypes, among 153 coprolites, have been recognized and collected in the Ejidos (the commons or enclosed spaces of public land) Presa San Antonio (Municipio de Parras de la Fuente), Agua de la Mula, La Rosa, Rincon Colorado (Municipio de General Cepeda), Rancho Altamira (Municipio de Saltillo) and in the El Pelillal locality (Municipio de Ramos Arizpe) in southeastern Coahuila, Mexico (Fig. 1). Most of the coprolites are silicified. A chemical analysis (Table 1) was made utilizing a Tracor Northern dispersive energy detector with a JEOL scanning electron microscope (model JSM-35C). Coprolites were studied using standard thin-section techniques. The resulting slides were
Fig. 1. Geographic locations of the studied areas in southeastern Coahuila: A = Presa San Antonio (Municipio de Parras de la Fuente); B = Agua de la Mula; C = La Rosa; D = Rincón Colorado (Municipio de General Cepeda); E = Rancho Altamira (Municipio de Saltillo); F = El Pelillal locality (Municipio de Ramos Arizpe).

Table 1
Chemical analysis of the different coprolite morphotypes

<table>
<thead>
<tr>
<th>Element</th>
<th>Coprolite groups</th>
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<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>SiO₂</td>
<td>27.59</td>
</tr>
<tr>
<td>TiO₂</td>
<td>0.71</td>
</tr>
<tr>
<td>Al₂O₃</td>
<td>11.43</td>
</tr>
<tr>
<td>FeO</td>
<td>18.76</td>
</tr>
<tr>
<td>MnO</td>
<td>0.79</td>
</tr>
<tr>
<td>MgO</td>
<td>2.65</td>
</tr>
<tr>
<td>CaO</td>
<td>13.03</td>
</tr>
<tr>
<td>Na₂O</td>
<td>0.78</td>
</tr>
<tr>
<td>K₂O</td>
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</tr>
<tr>
<td>P₂O₅</td>
<td>0.53</td>
</tr>
<tr>
<td>SO₃</td>
<td>22.11</td>
</tr>
</tbody>
</table>

At least one sample of the coprolites of each morphotype figured in the paper has been examined for the chemical composition. 1a, is a coprolite sample of Group 1 but from those though to be a probable subgroup of concentrically layered coprolites, the result to the left is from the exterior part and to the right is from the central white nucleus. In Group 6 the coprolite examined is that containing the *Eocaltha* seeds; the result to the left is from the coprolite matrix and to the right is from the seeds. In Group 10 the result to the left is from the coprolite matrix and to the right is from the major bone fragment.

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viewed with an Olympus BH-2 light microscope. Microphotographs were taken with an Olympus photographic system (model PM-10ADS) and an Olympus C-35AD-4 camera.

For comparative purposes, the seeds of some extant Ranunculaceae (*Caltha palustris* L. [MEXU-126289]; *Caltha aff. laeta* Schott, Nym. and Kotschy [MEXU-270069]; *Ranunculus ambiguens* Watson [MEXU-180199]; and *Ranunculus abortivus* L. [MEXU-243326]) were prepared using standard histological techniques, stained with toluidine blue, and mounted with Coverbond.

Measurements of the coprolites were taken with the aid of a vernier caliper. Anatomical measurements of the inclusions are based on 25 cells of each type, except for some poorly preserved cellular types. The exceptions are mentioned in the text, with the range of minimum to maximum within parentheses, and where the number of cells measured is preceded by an asterisk.

3. Results

3.1. Coprolite morphology

It is well documented that similar and/or related organisms may produce very dissimilar droppings, that unrelated organisms may produce identical droppings, and that 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). Therefore a morphological classification is useful for the interpretation of biological affinities (Schmitz and Binda, 1991), although not for the identification of the producer. According to morphological characteristics (shape, constrictions, presence of striations or ribs, surface texture, grain-size of the matrix, size, etc.) and type of the inclusions, the coprolites from the Cerro del Pueblo Formation can be organized in at least ten groups.

Group 1 (Fig. 2A–L). These are the most commonly found coprolites (111 samples). They are spheroidal and/or elliptical to sausage-shaped or reniform, with mean diameter of 1.45 cm (0.9–2.0 cm), composed of a fine-grained matrix, have a smooth surface and occasional constrictions due to sphincter action (Fig. 2C, D). Some of these coprolites, which may represent another morphological group, are concentrically layered and have a conspicuous light-coloured nucleus (Fig. 2I–L).

Group 2 (Fig. 3A, B). Five samples of elliptical to cylindrical, coiled coprolites, ranging in diameter from small (1.8 cm) to large (3.0 cm), have a slightly coarse-grained matrix, a smooth surface with occasional rugosities, and occasional glossy patches.

Group 3 (Fig. 3C–E). This group consists of three cylindrical coprolites with tapering ends. In addition, they are longitudinally compressed, 4.0–7.0 cm long, have a mean diameter of 2.4 cm, are composed of a fine-grained matrix, and have a smooth surface that may be slightly coarse in some samples.

Group 4 (Fig. 3F–H). Four cylindrical coprolites, that are longitudinally compressed with tapering and/or rounded ends, and a wrinkled surface are included in this group. They measure 3.5 cm (2.9–4.2 cm) in length and 1.8 cm (1.5–2.1 cm) in their widest diameter.

Group 5 (Fig. 3I–L). The five samples included here are of ovoid to sigmoidal shape. Some have fusiform ends, are usually small in size (ca. 1 cm), and have a fine-grained matrix and a smooth to rugose surface.

Group 6 (Fig. 4A–H). Twenty-one cylindrical and longitudinally ribbed coprolites, with fusiform final ends (Fig. 4G) and ribs radiating from a rounded initial end (Fig. 4C, E), have fine-grained matrix and occasional constrictions due to sphincter action (Fig. 4C). These coprolites measure 2.6 cm (1.2–3.8 cm) in length and 1.9 cm (0.7–2.7 cm) in their widest dimension. The number of longitudinal ribs varies from 8 to 23 depending on the size and preservation of the coprolite. A feature of some of the coprolites in Group 6 is that the fecal matter occasionally had such a consistency to permit the impression of the ribs of the last portion of the dropping over the first produced portion, as seen in Fig. 4F. A small cylindrical coprolite sample with more fine striae (Fig. 4H) was included in this group, although it possibly represents another morphological group.

The following coprolite morphologies are based on a single sample of each.

Group 7 (Fig. 4I). A cylindrical coprolite with a tapering end, transverse striations and slightly coarse-grained matrix. It measures 3.5 cm in length and 2.3 cm in its widest diameter.

Group 8 (Fig. 4J). A cylindrical coprolite with a conspicuous fusiform end, sphincter action marks, smooth surface with glossy patches, slightly coarse-grained matrix and desiccation marks. It measures 3.4 cm in length and 2.1 cm in its widest diameter.

Group 9 (Fig. 4K). A cylindrical spiraled coprolite with a flattened ventral side, fine-grained matrix and surface with desiccation marks. It measures 3.0 cm in length and 2.1 cm in width.
Group 10 (Fig. 4L, M). An ovoid coprolite with a flattened ventral side, fine-grained matrix and coarse surface. This coprolite is thought to belong to a carnivore due to the presence of abundant bone fragments (Fig. 4M). It measures 4.8 cm in length and 3.1 cm in width at its widest part.

3.2. Adhesions

In the course of deposition and burial of the feces other materials naturally found in the surroundings (i.e., pebbles, stems, pollen, etc.) could adhere to the surface of the fecal matter. Pebbles (Fig. 2A)
3.3. Inclusions

Coprolite inclusions are organic components ingested by an animal that contribute to the information of the partial diet of an organism and, in fact, are the best clue to identify coprolites (Hunt et al., 1994). Among the inclusions found inside the coprolites from Coahuila are stems, vascular elements, cuticles, groups of cells (Figs. 5 and 6) and at least...
Fig. 4. Coprolites of Group 6 (A–H), coprolite of Group 7 (I), coprolite of Group 8 (J), coprolite of Group 9 (K), coprolite of Group 10 (L, M). (A) IGMPB-956: longitudinally ribbed coprolite of Group 6. (B) IGMPB-957: longitudinally ribbed coprolite of Group 6 with a rounded end. (C) IGMPB-958: longitudinally ribbed coprolite with a rounded end and a sphincter action mark (arrow). (D) IGMPB-959: longitudinally compressed coprolite of Group 6 with a rounded end (central part of the picture). (E) IGMPB-960: longitudinally ribbed coprolite with the ribs radiating from a pole. (F) IGMPB-961: fecal mass of longitudinally ribbed coprolites with an impression of the ribs of the same coprolitic group (arrow). (G) IGMPB-962: coprolite with a conspicuous fusiform end. (H) IGMPB-963: small cylindrical coprolite with more fine striae. (I) IGMPB-964: cylindrical coprolite of Group 7 with a tapering end and transverse striations. (J) IGMPB-965: cylindrical coprolite of Group 8 with a conspicuous fusiform end, sphincter action and desiccation marks. (K) IGMPB-966: cylindrical spiraled coprolite of Group 9 with desiccation marks. (L) IGMPB-967: coprolite of Group 10 with a bone fragment (arrow). (M) Magnification of the bone fragment shown in (L). Scale bars 1 cm.
two seed types (Figs. 7–9). Most of the plant material described in this paper come from coprolite Groups 1 and 6.

3.3.1. Stems and vascular elements (Fig. 5B–E)

Stem fragments ranging from 108 to 180 μm in width are found in coprolite Groups 1, 2 and 6 (Fig. 5B, C), with a relative density of ten to fifteen stem fragments observed per slide prepared (at least ten slides per coprolite were prepared, and two to four coprolite samples were utilized for each group). One of the stem fragments is observed in cross-section and represents a small branching stem (Fig. 5C), 0.4 mm in diameter. It has a pith with a diameter of 250 μm, a thick cortex 133 μm wide and a cuticle 15 μm thick. Isolated vascular elements (Fig. 5A, D) are also found in the same coprolite groups. One of the inclusions found is interpreted as a meristem fragment with portions of two leaves (Fig. 5E).

Due to the poor preservation of the stem fragments a more precise taxonomical identification is not possible and isolated vascular elements are not identifiable.

3.3.2. Cuticles (Fig. 5F–I, Fig. 6A–D)

Several non-papillate (Fig. 5F–I, Fig. 6A, B) and papillate cuticles (Fig. 6C, D) of at least six types have been found in coprolite Groups 1 and 6. Some cuticle morphologies include the following.

Type 1 (Fig. 5F, G): cuticle with polyhedral to subrectangular cell impressions, each cell 31.8 μm long (28.8–37.7 μm *5) by 23.8 μm wide (20.1–27.8 μm *5), with paracytic stomatal apparatus composed of guard cells, 22 μm long by 12.7 μm wide and irregular deposits, 1.7 μm thick (Fig. 5G).

Type 2 (Fig. 5H, I): cuticles with subrectangular to rhomboidal cell impressions, each cell 34.1 μm (24.9–43.0 μm *5) long by 16.8 μm (12.2–21.3 μm *5) wide. The cells occasionally have thickenings inside the lumen (Fig. 5H).

Type 3 (Fig. 6A): cuticles with impressions of rectangular cells 56.9 μm long (30.0–96.0 μm *8) by 21.5 μm wide (13.0–33.0 μm *15). Circular trichome bases 27.5 μm in diameter (26.0–30.0 μm *4) are present.

Type 4 (Fig. 6B): cuticles that represent pixis of young leaves, with a linear arrangement of the leaves.

Type 5 (Fig. 6C): papillate cuticles with poorly preserved cells, and star-like lobed papillae.

Type 6 (Fig. 6D): papillate cuticles having simple, conical papillae with rounded apexes (Fig. 6D, arrows), 15.4 μm high (12–20 μm *5) by 11.6 μm wide (10–13 μm *5) at the base.

Metcalf and Chalk (1979, p. 148) mentioned that papillae appear to be present more frequently in tropical species; however, there are conifers (and other gymnosperms), and even plants of arid zones, that also have papillate cuticles. It has been also mentioned for angiosperms, but may be also true for gymnosperms, that papillae serve as light-condensers in shaded leaves and/or facilitate the removal of water from the leaf surface in tropical-rain-forest plants (Metcalf and Chalk, 1979, pp. 148–149). The presence of the papillate cuticles in the coprolites of the Cerro del Pueblo Formation suggests that the plants perhaps developed in a humid and warm climate, as is suggested by the presence of Zingiberales, Araceae and Pandanaceae (all represented by fruits) found in association within the studied area (Cevallos-Ferriz et al., 1992; Rodríguez-de la Rosa and Cevallos-Ferriz, 1993, Cevallos-F; Cevallos-Ferriz and Rodríguez-de la Rosa, 1994). Abundance of these cuticles suggests that plant diversity was higher than that suggested by the known macrofossils.

From the scope of animal–plant interactions some authors have mentioned that structures like papillae and trichomes could discourage herbivores (e.g.
Wing and Tiffney, 1987a,b; Howe and Westley, 1988); however, it is interesting that they are frequently found in some coprolite groups (e.g., 1 and 6). Structures such as leaf trichomes and papillae found inside some coprolites beginning in the Carboniferous served against arthropod herbivory (e.g. Scott and Taylor, 1983). The most likely idea regarding the Cretaceous material is that they may have had
two functions, that of a light-condenser as suggested by Metcalfe and Chalk (1979) for extant plants and later of discouraging predation by arthropods and/or vertebrates.

Due to the limited information about the cuticles of extant plants, the taxonomic affinity of these fossil cuticles is not clear, although it is known that cuticles with rectangular cells that are oriented in parallel, as seen in Fig. 6A, are more common in monocotyledons among flowering plants.

3.3.3. Unidentified cell groups (Fig. 6E)

Among these cell groups, the most conspicuous is composed of polyhedral to isodiametric cells, 16.6 μm in diameter (13.4–18.6 μm *5). Intermingled with these cells are others with larger diameter, 28.8 μm (25.1–33.8 μm *5), that in some cases have conspicuous dark contents (Fig. 6E).

Due to the fragmentary nature of the tissue the affinity of these cell groups is not clear.

3.3.4. Type I seed (Fig. 7)

Systematic description
Order: Myrtales.
Family: Lythraceae.
Tribe: Nesaeae.

Description. The following description is based on a single specimen of a valvate, winged seed, with
a roughly triangular shape and rounded corners. It is 465 μm wide at the side of the valve, 470 μm dorsoventrally, and has an embryo sac cavity that is 190 μm wide (Fig. 7). Two integumentary zones can be distinguished on cell characteristics (Fig. 7A, B). The outer and most conspicuous cell layer is composed of polyhedral to isodiametric, thin-walled cells, averaging 22.6 μm (17.0–28.0 μm) in diameter. This layer corresponds to the middle layer of the outer integumentary zone and forms two lateral wings (Fig. 7A). The inner layer is a dark area, 32.5 μm thick. It corresponds to the inner layer of the outer integumentary zone and/or the inner integumentary zone (Fig. 7A). The valve (Fig. 7B) is 165 μm wide and composed of a palisade of rectangular, moderately thick-walled cells, 32.3 μm high by 11.0 μm wide (+3).

Discussion. Members of the Lythraceae are well known from their morphology and anatomy (e.g. Graham, 1964; Graham et al., 1986) as well as palynology (e.g. Graham et al., 1990). According to Corner (1976) Lythraceae have minute to small seeds of subcylindrical to trigonal or pyramidal shape. The fossil record of Lythraceae extends from the Upper Cretaceous to the Recent. For a review of the fossil history of the Family see Sahni (1943), Graham and Graham (1971), Eyde (1972), and Tiffney (1981) for macrofossils, and Muller (1981) for the fossil pollen record. Tiffney (1981) grouped the fossil fruits and seeds of the Lythraceae in three tribes: Lythreae, Nesaeeae, and the carpological remains not assignable to either of the two sections. He compared the lythaceous remains from the Branch Lignite with the members of a morphological complex within the Nesaeeae formed by Decodon, Microdiptera, Mneme and Alatospermum (Tiffney, 1981). The fossil record of this morphological complex ranges from the Middle Eocene to the Recent (Tiffney, 1981; Cevallos-Ferriz and Stockey, 1988). The seeds of Decodon are small (0.8–1.9 mm long and 0.6–1.9 mm wide), they are elongate to pyramidal with angular to sharply rounded corners and no clear lateral wings (Tiffney, 1981; Cevallos-Ferriz and Stockey, 1988). Microdiptera seeds are 0.9–2.0 mm long and 0.5–2.0 mm wide and are flattened dorsoventrally with a concave to flat dorsal surface and a convex ventral surface. The seeds are irregularly subtriangular in shape, varying from small to elongate and to larger and broader forms. The lateral wings are large and flat, but sometimes narrow (Tiffney, 1981). The seed posses two well developed grooves that flank the seed body on the dorsal side of the seed (Tiffney, 1981; Fig. 8A). The seeds of Mneme are 1.0–2.5 mm long and 1.0–2.4 mm wide and are flattened and subcircular to oval, with a convex ventral surface and a flat to convex dorsal surface. The seed has two well developed lateral wings. Mneme possesses two well developed grooves that flank the seed body on the dorsal side of the seed, separating the wings from the central body (Tiffney, 1981; Fig. 8 B). Alatospermum seeds are broadly triangular, 0.08–1.55 mm long to 0.85–1.8 mm wide. They are dorsoventrally flattened, oboval, sub-quadangular or irregular in outline. The wings are narrow and thin and may form a narrow marginal flange or a broader triangular area on each side of the seed body. No flanking grooves are apparent (Chandler, 1962; Tiffney, 1981).

The seed type presented here differs from Decodon mainly in shape and lack of lateral wings. However, this new seed type is comparable to the other members of this morphological complex. It differs in shape with

Fig. 9. Eocaltha zoophila Rodríguez-de la Rosa, Cevallos-Ferriz et Silva-Pineda gen et sp. nov. (A) Seeds in longitudinal section (central portion of the picture), longitudinal–oblique section (upper right portion of the picture) and cross-section (lower right portion of the picture); MI = micropyle, ES = embryo sac cavity, FCH = flotation chamber (IGM-LPB 2926-974). (B) Magnification of the flotation chamber (FCH) of the seed shown in (A) (IGM-LPB 2926-974). (C) Magnification of the seed in longitudinal section shown in (A); polyhedral to isodiametric cells form the inner layer of the outer integumentary zone (IO); arrow points to the inner integumentary zone; FCH = flotation chamber (IGM-LPB 2926-974). (D) Cross-section of a seed through the flotation chamber (FCH, IGM-LPB 2926-974). (E) Group of seeds in cross-section through the flotation chamber suggesting an arrangement in the fruit (IGM-LPB 2926-977). (F) Seeds in longitudinal–oblique section with a characteristic white halo (arrow) of some seeds (IGM-LPB 2926-973). (G) Slightly lateral, cross-section of a group of cells of the outer integumentary zone (IGM-LPB 2926-976). (H) Cross-section of a group of cells of the outer integumentary zone (IGM-LPB 2926-973). (I) Cross-section of a seed showing raphe (arrow) in the inner layer of the outer integumentary zone (IGM-LPB 2926-974). Scale bars: in (B–D, G–I) 100 μm; in (A, E, F) 200 μm.
respect to Microdiptera and Mneme (Fig. 8) which are more flattened dorsoventrally. Nevertheless, this new seed type shares the general shape of the wings and the apparent lack of dorsal flanking grooves with Alatospermum. Although there are some differences between the new fossil seed and those previously reported, anatomical and morphological similarities between the new fossil seed and the members of Nesaeeae (Fig. 8) suggest the presence of a new taxon within this group of lythraceous seeds. Recognition of a new taxon was not made because only a single specimen was found. Thus, it is better to wait until more specimens become available, allowing confirmation of the anatomical interpretations and further understanding of the morphology and variation of the new fossil seed.

3.3.5. Type II seed (Fig. 9)

**Systematic description**

Order: Ranunculales
Family: Ranunculaceae
Genus: *Eocaltha* Rodríguez-de la Rosa, Cevallos-Ferriz et Silva-Pineda gen. nov.
Species: *Eocaltha zoophila* Rodríguez-de la Rosa, Cevallos-Ferriz et Silva-Pineda sp. nov.

**Diagnosis.** Anatropous seeds characterized by the presence of an embryo sac cavity, a fusiform micropyle and a flotation chamber. Inner integumentary zone composed of isodiametric to polyhedral, thick-walled cells. Inner layer of the outer integumentary zone composed of isodiametric to polyhedral, thin-walled cells that surround the flotation chamber; these cells are smaller around the flotation chamber. Outer layer of the outer integumentary zone composed of a palisade of cuboid cells. The raphe is located in the inner layer of the outer integumentary zone.

**Holotype:** IGM-LPB 2926-974.
**Paratypes:** IGM-LPB 2926-973, IGM-LPB 2926-975 to IGM-LPB 2926-977 and IGM-LPB 2926-13361 to IGM-LPB 2926-13370.
**Coprolite sample:** number IGM-PB 2926-13360.

**Etymology.** The generic name is based on Eos (Greek) which means dawn, and alludes the early occurrence (Cretaceous) of a taxon similar to the extant genus *Caltha*; the specific epithet is after zoom, animal, and philos, friend, making reference to the seeds being inside a coprolite, and suggesting a relationship between the plant and the producer of the coprolite.

**Description.** Seeds are elliptical to globose in shape (Fig. 9A), anatropous, 1.17 mm in length and 0.62 mm at the widest dimension. Structurally the seed is characterized by the presence of an embryo sac cavity, a fusiform micropyple and a flotation chamber (Fig. 9A). The integument can be divided into three zones according to cell characteristics (Fig. 9B). The inner integumentary zone is composed of isodiametric to polyhedral, thick-walled cells (Fig. 9C), 9 μm (6–12 μm) in diameter. The inner layer of the outer integumentary zone (Fig. 9B, C) is the most conspicuous and delimits the flotation chamber. It is composed of isodiametric to polyhedral, thin-walled cells, 26 μm (21–30 μm) in diameter that become smaller around the flotation chamber (Fig. 9C–E). In this area, these cells are 27 μm anticlinal (19–35 μm) by 18 μm periclinal (12–24 μm). The outer layer of the outer integumentary zone is composed of a palisade of cuboid cells (Fig. 9G, H), 25 μm (14–34 μm) high, 17 μm (11–24 μm) wide and 45 μm (42±50 μm) long. This layer is not found in direct contact with the seed (Fig. 9F). Instead groups of these cells are found dispersed in the coprolite matrix (Fig. 9G, H). The raphe is located in the inner layer of the outer integumentary zone (Fig. 9I).

**Discussion.** Seeds of extant Ranunculaceae according to Corner (1976) are small (1–5 mm long), albuminaceous and exarillate. Their integument is not or only slightly multiplicative, characterized by having a single layered outer integumentary zone composed of cuboid or tabular cells forming a short palisade. The inner integumentary zone is usually un Specialized or with fine bar-like thickenings on the radial walls. In *Caltha palustris* the seeds possess a flotation chamber formed by the swollen raphe and chaalazal area (Ridley, 1990), and have an integument composed of enlarged and crushed cells, except for the exotesta, which is composed of the characteristic palisade of cuboid cells, with slightly thickened outer wall and cuticle (Corner, 1976; Fig. 10).

The description and reconstruction of the seeds of *E. zoophila* (Fig. 11) as well as its general integumentary features (mainly the palisade of cuboid cells) support well its relationship with the Ranunculaceae. However, the most important feature for
Fig. 10. Seeds of extant Ranunculaceae. (A) Longitudinal section of the seed of *Caltha palustris* L. showing the proliferation of the cells of the inner layer of the outer integumentary zone at the chalazal area (arrows) and micropyle (MI, IGM-LPB 2926-1041). (B) Longitudinal section of the seed of *Caltha palustris* L. showing an invagination at the chalazal area (arrow, IGM-LPB 2926-1042). (C) Longitudinal section of the seed of *Caltha aff. laeta* Schott, Nym. and Kotschyi; *FCH* = flotation chamber, MI = micropyle (IGM-LPB 2926-1043). (D) Longitudinal section of the seed coat of *Caltha palustris*; arrow points to the palisade layer of the outer integumentary zone (IGM-LPB 2926-1044). (E) Longitudinal section of the seed coat of *Caltha aff. laeta*; arrow points to the palisade layer of the outer integumentary zone (IGM-LPB 2926-1043). Scale bars: in (A–C) 250 μm; in (D, E) 100 μm.

taxonomic identification was the flotation chamber (Fig. 9A, B). The genus *Caltha* (Ranunculaceae) is the only reported extant plant having a flotation chamber similar to that found in the fossil. As described by Ridley (1990) for *C. palustris*, it possesses a particular flotation structure formed by the swollen raphe and chalazal area. Delimitation of the flotation chamber is accomplished by the proliferation of cells of the inner layer of the outer integumentary zone (Fig. 10A). However, our own observations for *C. palustris* suggest that such structure is formed by an invagination of the integument in the chalazal area,
Fig. 11. Reconstruction of the seed of *Eocaltha zoophila* Rodríguez-de la Rosa, Cevallos-Ferriz et Silva-Pineda gen et sp. nov. as seen in longitudinal and cross-section views. The arrangement of the cells of the outer integumentary zone is based on fossil and extant evidence; *FCH* = flotation chamber; *ES* = embryo sac cavity; *R* = raphe; *MI* = micropyle. Scale bar 0.25 mm.
where proliferation of the cells of the inner layer of the outer integumentary zone occurs (Fig. 10A, B). Nevertheless, in C. aff. laeta the flotation chamber is formed in a similar way as described by Ridley (1990; Fig. 10C), suggesting that this characteristic feature of the seeds of Calthta may have both origins. In addition, one conspicuous feature that Eocalthta shares with Calthta, is the fusiform micropyle (Fig. 9A, Fig. 10A, C).

The Ranunculaceae are a family recorded only for the Tertiary (see Collinson et al., 1993 and references therein) and specifically Calthta is recorded from the Neogene Beaufort Formation on Banks and Meighen Islands in the District of Franklin (Matthews, 1987), although its presence is not well documented. Thus, the presence of this seed type in a coprolite of Group 6 of the Cerro del Pueblo Formation extends the fossil record of the Ranunculaceae back to the Cretaceous.

3.3.6. Incertae sedis

During the feeding of a vertebrate other materials that differ from those of the principal diet could be accidentally ingested and found as inclusions in the coprolites. Three unidentified inclusions are termed A, B and C.

Object A (Fig. 12A, B) is found as an outline (or ghost) within a coprolite of Group 1 and can be divided in two portions, an abdomen-like portion and a ‘cephalized’ portion (Fig. 12A). The abdomen-like portion measures 1.7 mm and is divided in six more or less hexagonal segments, of which the most distally located decreases in size and has a conspicuous sharp end (Fig. 12A). The cephalized portion is elliptical in shape, 1.05 mm in length and 0.55 mm wide at the widest part. The entire object is bilaterally symmetrical. The cephalized portion has
two lobe-like structures (Fig. 12B) at the same level on both sides. Also in this cephalized portion, two delicate fan-like structures diverge anteriorly from two points in the posterior area (Fig. 12B).

Object B was found within a layered coprolite of Group 1. It is irregularly shaped, 0.13 mm long, and strongly recalls an exuvia of an aquatic arthropod.

Object C (Fig. 2H) appears embedded in the matrix of a coprolite of Group 1. It is a segmented and/or pupa-like object with four segments and an elongate portion (Fig. 2H).

The following peculiarities can be mentioned regarding Object A: (a) the presence of bilateral symmetry suggests a biological origin; (b) this object strongly recalls the shape of an aquatic larva or nympha of an insect; (c) the two lobes on both sides of the cephalized portion and the fan-like structures recall the position of both pairs of insect alar buttons. Object A could represents a juvenile aquatic stadium of an insect. Fig. 13 shows the aquatic larvae of a dipteran (*Aedes* sp., Culicidae; Fig. 13A) and a zygopteran (*Calopteryx* sp., Calopterygidae;}

![Figure 13](image_url)

Fig. 13. Aquatic larvae of a dipteran and a zygopteran. (A) Larva of *Aedes* sp. (Culicidae, Diptera). (B) Larva of *Calopteryx* sp. (Calopterygidae, Zygoptera); marked portion between a and b indicates that not a whole organism could be represented in the inclusion or object A; (A) from Peterson, 1960; (B) from Miller, 1987; not drawn to scale.
Fig. 13B) for comparison. The general shape of *Aedes* sp. strongly recalls the shape of object A, and the portion marked between a and b in the larva of *Calopteryx* suggests that only a part of an organism could be represented in object A. In this way the mesothorax and the caudal or the abdominal region of an aquatic larva of an insect could be represented by object A.

Structures like an appendage and what seems to be an eye are distinguished (Fig. 12C) in object B, suggesting that it may represent the exuvia of a small aquatic arthropod.

With regard to object C, its shape suggests that it represents the mold of a pupa-like object due to the fact that no traces of organic material were found. Object C was found in the fracture surface of a coprolite (Group 1, Fig. 2H) indicating that it was an inclusion of the coprolite. Although the details of object C are not clear, it is possible that it is myriapodal in origin, representing probably a millipede due to the fact that millipedes, unlike other myriapods and insects, have a calcium-impregnated exoskeleton with sclerites that could survive digestion in a coprolite. Coprolites containing millipedes or their remains are known from the Late Carboniferous of Mazon Creek in Illinois (C. Labandeira, pers. commun., 1996).

4. General discussion

During the last few years, paleontological research has documented to some degree the biotic diversity that was present during deposition of the Campanian sediments of the Cerro del Pueblo Formation. Members of this Campanian community include angiosperm fruits of zingiberalean (Rodríguez-de la Rosa and Cevallos-Ferriz, 1993, 1994), Araceae and Pandanaceae affinity, a complex fruit probably related to Phytolaccaceae (Cevallos-Ferriz et al., 1992; Cevallos-Ferriz and Rodríguez-de la Rosa, 1994), an infructescence that initially was thought to be a gymnosperm cone (Rodríguez-de la Rosa and Cevallos-Ferriz, 1994) and angiosperm leaf and flower impressions. Among fossil vertebrates are remains of fishes, reptiles and dinosaurs (Hernandez, 1992; Hernandez and Kirkland, 1993; Kirkland and Aguillon-Martinez, 1995; Rodríguez-de la Rosa, 1996). Unfortunately, no effort has been made to bring these isolated reports into a single discussion within a paleobiological context.

Although geological work was done in the early 60’s and 70’s, new field work by different research groups has extended the distribution of the Cerro del Pueblo Formation. However, no attempt has been made to map and correlate the new localities and outcrops. The localities where the vertebrates, plants and coprolites were collected are synchronous. Although not all of the fossils have been collected from a single locality, their confined presence in the localities strongly suggests that they were deposited within a relatively short interval of time. For example, different types of fruits have been collected along with the same vertebrate remains from different localities. Also, longitudinally ribbed coprolites (Group 6) and at least three turtle taxa and two crocodilians have been found in association in several localities. Thus, from a biostratigraphic point of view, the assumption of discussing a single community seems well supported (Johnson, 1934; Hunt, 1992; Hunt et al., 1994).

Some features of the coprolites from Coahuila, such as ribs or desiccation marks (e.g. Groups 1, 6 and 9), suggest that they were dropped on land; most likely they were hydrodynamically concentrated in some localities of southeastern Coahuila. This situation is seen in some North American sites such as those of the Upper Triassic Bull Canyon Formation in eastern New Mexico or in the Maastrichtian Whitemud Formation in southern Saskatchewan, where coprolites have been concentrated together with the skeletal remains of vertebrates, invertebrates and plants (Nambudiri and Binda, 1989; Hunt et al., 1994). A similar situation is seen at such localities as that of El Pelillal and in Rincon Colorado (Fig. 1) where coprolites of at least two groups (1 and 6) are found in good quantity and in association with disarticulated vertebrate material, invertebrates and fruits of angiosperms.

The association of coprolites with vertebrate remains suggests that the producers of these scats should be found among them. However, it is well documented that correlating a coprolite with a particular type of organism is a very difficult task. For example, Murie (1974, fig. 135) illustrated whitetail-deer droppings with different morphologies due
to the different diet of the animal throughout the year. In a similar way, it has been documented that not related organisms produce similar dropping morphologies (Murie, 1974; Halfpenny and Biesot, 1986). Thus, since the evidence we have, to associate a particular type of coprolite with a vertebrate from the Cerro del Pueblo Formation is still vague, a morphological classification was used to distinguish different types and more precise correlation has to wait until further information is gathered.

4.1. Mode of preservation

The chemical analysis of the coprolites (Table 1) supports that most of them are silicified. Besides, coprolite Group 10 has a high percentage of P$_2$O$_5$ and CaO as compared with the other nine morphotypes. Presence of phosphate and calcium in coprolites has been suggested as indicative of a carnivore and/or omnivore origin (K. Chin, pers. commun., 1997). The fact that bone fragments are found in coprolite morphotype Group 10 further suggest a carnivore relationship. Low percentages of phosphate and/or calcium in the other nine morphotypes suggest either a herbivore or omnivore origin.

Difference in chemical composition plus abundance of plant material in coprolite morphotypes 1, 2 and 6 suggest that they were produced by herbivores. In contrast the other morphotypes may have been produced by omnivores. For example, coprolite morphotype Group 7 has a higher concentration of P$_2$O$_5$ and CaO as compared with those proposed as being produced by herbivores, but the percentages of these chemicals compared to the carnivore morphotype (Group 10) are relatively low.

Although the chemical analysis must be regarded as preliminary since more detailed studies are needed for a better understanding of the origin of these components, the results are congruent with what is expected from their fossil contents.

In only a few previous works it has been possible to relate a coprolite morphotype to a particular vertebrate taxon due to its association with vertebrate skeletal remains (Chin, 1990; Chin et al., 1991a,b; Hunt, 1992; Chin and Gill, 1996). Other taxonomic determinations of coprolites have been mostly inferential. Among the vertebrates that have been found in the sediments of the Cerro del Pueblo Formation are carnivorous, omnivorous and herbivorous organisms. These include: fishes (carnivores) of the families Lepisosteidae and Amiidae; a sawfish has been reported from a marine facies within the Cerro del Pueblo Formation; turtles (carnivores) of the families Trionychidae, Chelydridae, Kinosternidae and the extinct Compsemys victa (incertae sedis); crocodiles (carnivores) are represented by neosuchian remains similar to Goniocepholis and remains of Eusuchia crocodiles; the proximal end of a tibia of a pterosaur has been found; among dinosaurs are remains of ornithopods (herbivores) and theropods (carnivores) (Hernandez, 1992; Hernandez and Kirkland, 1993; Kirkland and Aguillon-Martinez, 1995; Rodriguez-de la Rosa, 1996).

4.2. Animal–plant interactions

Among the reported cases of plant–animal interactions involving Mesozoic plants, Weishampel (1984) suggested a relationship between the cycadeoids and some Mesozoic vertebrate taxon, arguing that the cycadeoid receptacles could represent the diaspores of these plants. Some support to this idea is given by the finding of a coprolite containing cuticles of a receptacle of Ptilophyllum in the Middle Jurassic of North Yorkshire (Hill, 1976). Another example is that of Harris (1964) who reports Jurassic coprolites containing seeds and receptacles of the Mesozoic seed fern Caytonia. The tiny seeds of Caytonia were enclosed in a fleshy receptacle that perhaps served as the diaspora. Thus, this finding also could suggest seed dispersal (Tiffney, 1986). In spite of these examples, it has been suggested that these two Mesozoic plants were abiotically dispersed (Tiffney, 1986).

The presence of plant remains inside coprolites indicates that herbivore or even omnivore vertebrates were feeding on a wide variety of plants of their environment. Their study gives some hints about the partial diet of an organism, and can give clues about the physiology, biology, ecology, etc. of an organism or group of organisms. The presence of a single lythraceous seed in a coprolite could be merely an occasional ingestum (Fig. 7). This is also suggested for the inclusions of probable insects (Fig. 12), since animals having a semiaquatic life-style (e.g. turtles), could accidentally ingest other items such as aquatic
insects and/or aquatic dispersed diaspores. In fact, it is well demonstrated that extant representatives of the fossil Trionychidae, Chelydridae and Kinosternidae found in the sediments of the Cerro del Pueblo Formation are carnivorous and occasionally omnivorous, eating aquatic arthropods, crustaceans, amphibians and plants (Ernst and Barbour, 1989).

Structures like trichomes and papillae are found on leaves of extant plants that are the food source of several reptilian groups (such as turtles). For example, Elodea and Vallisneria of the Hydrocharitaceae are part of the diet of extant kinosternid turtles, and fossil remains of kinosternid turtles are found in localities where the Cerro del Pueblo Formation outcrops. Both genera of plants have leaf margins with hairs. The significance of cuticles with trichomes and papillae inside the coprolites could suggest the presence of generalized herbivores, and/or that these structures in angiosperms were diffusely coevolving with vertebrates as defense mechanisms to avoid herbivory.

In contrast, the presence of many seeds (ca. 200) of Eocaltha zoophila in a coprolite sample (IGM-PB 2926-13360) may suggests seed dispersal. The high number of seeds of E. zoophila found in a coprolite suggests that the organism producing the coprolite was feeding on a high quality diet represented by the seeds, eating perhaps one or more fruits (Fig. 9E), and serving as a biotic seed dispersal agent.

The small amount of nourishment offered by small seeds could be used against the idea of a high quality diet. However, it has been suggested that sometimes foliage serves as the ‘fruit’ of the plant, and that seeds ingested while feeding are dispersed (Janzen, 1984). This could be the situation represented by the seeds of Eocaltha in the coprolite from Coahuila. However, it is well demonstrated that higher animals (e.g. amphibians, reptiles, mammals, etc.) cannot synthesize some types of fatty acids by themselves; these essential fatty acids, necessary for the synthesis of other products in the organism, must be obtained through a diet of plants (Murray et al., 1990; Lehninger et al., 1993, p. 655). It has been also demonstrated that essential fatty acids are found in glandular secretions of some extant reptiles, and that they may have had a dual function as an antipredator mechanism and/or as sex recognition signal (Rose, 1970; Mason, 1992). Either way, they must obtain this supplement by eating plants. One extant plant group that synthesizes essential fatty acids, such as gamma-linolenic, are the Ranunculaceae, and their presence in the genus Caltha has already been demonstrated (Aitzetmueller et al., 1993). The producers of coprolites belonging to Group 6, where the seeds of E. zoophila were found, probably had requirements of fatty acids that can be obtained from plants in their environment. However, if the coprolites belonging to Group 6 were produced by animals such as turtles (Matley, 1939a,b; Bradley, 1946), it is most probable that they were breeding in a similar way as they do today, needing essential fatty acids for the production of pheromones. Therefore, eating plants, in this case of the extinct Ranunculaceae Eocaltha zoophila, could satisfy these nutritional and reproductive requirements.

A considerable proportion of extant plants have seeds adapted for dispersal after ingestion or endozoochory (Fenner, 1985). One of the most classical examples is that of the dodo (Raphus cucullatus L.) and Calvaria major Gaertn in which the dodo served as the dispersal agent of the seeds of Calvaria (Temple, 1977). An important factor in this kind of animal–plant interaction is that a proportion of the consumed seeds needs to pass in viable condition through the disperser’s gut (Fenner, 1985). It is most probable that at the moment of deposition of the coprolite of Group 6 the seeds of E. zoophila were in viable condition to germinate because they are uncrushed. Also a considerable quantity of seeds are present. Sometimes seeds need a special treatment, such as scarification and/or a gastric chemical treatment, to facilitate embryo germination, as in the case of Calvaria (Temple, 1977). The finding of cell groups of the outer layer of the outer integumentary zone of Eocaltha not in contact with the seeds is not a product of the diagenetic process (Fig. 9F–H). The seed by itself shows adaptations for abiotic dispersal such as dispersal by water (as represented by the flotation chamber; Fig. 9A). However, the presence of the outer layer of the outer integumentary zone in the coprolite matrix (Fig. 9G, H) suggests that a physiological factor similar to scarification was acting in the producer of the coprolite in order to facilitate seed germination once the seeds were released from the animal.

Some studies have demonstrated that a particular
feature of some plants has evolved due to the selective pressure of a vertebrate herbivore, as for example, a seed dispersal agent. This has been termed diffuse coevolution (Herrera, 1984; Wing and Tiffney, 1987a,b). Although Eocaltha evolved a mechanism for abiotic dispersion, interaction with a vertebrate herbivore may have provided special treatment of the seeds in the gastric system of the disperser, facilitating germination. This suggests a case of diffuse coevolution.

Coprolites from Coahuila provide an excellent opportunity for the study of plants not represented as macrofossils in the sediments of Cerro del Pueblo Formation. When coprolites have well preserved inclusions, as do the coprolites from Coahuila, a unique opportunity for the study of paleobiological processes exists. Coprolites from Coahuila demonstrate that a wide variety of animals were interacting with the plants of their surrounding environment, mainly utilizing them as food source. It is possible to appreciate that some processes in angiosperms could become selected in many different ways mean biotic interactions and through cases of diffuse coevolution, as suggested by the presence of seeds of Eocaltha.

It has been widely mentioned that biotic mechanisms for dispersal gain importance during the Tertiary, as suggested by the fossil record. However, during the Cretaceous the interactions of plants and animals, such as herbivory, lead to attempts of biotic seed dispersal by vertebrate herbivores as revealed by the treatment and/or scarification suffered by the seeds of Eocaltha zoophila. It could mean a case of diffuse coevolution in which while the seeds show an abiotical dispersal mechanism by themselves, an interaction with a vertebrate herbivore permitted an optimal germination; then with this kind of attempt animal–plant interactions became well-established through time.

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