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COPROLITES ACROSS THE CRETACEOUS/TERTIARY BOUNDARY, SAN JUAN BASIN, NEW MEXICO

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Abstract—We document Late Cretaceous (Kirtlandian and Edmontonian) through early Cenozoic (Puercan, Torrejonian and Wasatchian) vertebrate coprolites from the San Juan Basin in San Juan and Sandoval counties, New Mexico. A minimum of four morphotypes are present (spindle-shaped, elongated cylinders, cylindrical segments and conglomerated masses) that exhibit various surface textures (worn, smooth, pitted, striated) and other features (constriction marks and inclusions). This includes one specimen assignable to *Alococopros triassicus*, extending the chronological distribution of the ichnotaxon into the Late Cretaceous. Most of these coprolites can be confidently assigned to carnivorous producers based on morphology, composition and inclusions. Many have inclusions (such as bones or gar scales) that are easily identifiable. Plant fossils and herbivorous vertebrate body fossils, are some of the most prevalent found in the Late Cretaceous-Eocene strata of the San Juan Basin, so an explanation is warranted of the lack of plant-bearing coprolites from the area. The fact that the more durable, phosphatic fecal remains of carnivores are more readily fossilized than the feces of herbivores due to accelerated bacterial mineralization seems a likely explanation. Another possible explanation for the lack of coprolites produced by herbivores lies in the relatively small number of coprolites documented from the San Juan Basin, despite collection and study of vertebrate assemblages in the area for over 100 years. A similar issue arises when we consider the relatively small size (<10 cm long) of all coprolite specimens (and assumed producers) from the Late Cretaceous Fruitland, Kirtland, and Ojo Alamo formations in the San Juan Basin, despite the relatively large size of many of the known vertebrates. It is difficult to determine with certainty if this is due to preservational or collection bias. Despite the inherent biases and uncertainties, we find that coprolite morphologies (size, shape and surface texture) and inclusions (bone fragments, fish scales, and gas bubbles) do not change significantly across the K/T boundary in the San Juan Basin. This suggests that either none of the preserved coprolites are dinosaurian, or that dinosaurian coprolites are homeomorphic with those of some other vertebrates, such as crocodyles.

INTRODUCTION

The record of extinction and re-radiation of many vertebrate groups across the K/T boundary is well documented. This record is based primarily on body fossils with relatively little attention paid to the collection and study of trace fossils. Vertebrate coprolites can provide a unique perspective on the anatomy, physiology, feeding and behavior of the producer, and they can potentially be useful as biochronological indices (Hunt et al., 2007). Here we describe and compare Late Cretaceous through Cenozoic vertebrate coprolites curated in the geosciences collection of the New Mexico Museum of Natural History and Science (NMMNH). These coprolites come from the strata of the San Juan Basin in San Juan and Sandoval counties, northwestern New Mexico (Fig. 1); specifically from the Late Cretaceous (Campanian and Masstricthian) Fruitland (Figs. 2A-G, 3A-B, 5J-N), Kirtland (Figs. 2H-M, 3C-D) and Ojo Alamo formations, the Paleocene (Puercan and Torrejonian) Nacimiento Formation (Figs. 2N-T, 4, 5A-I, O-V) and the early Eocene (Wasatchian) San Jose Formation (Fig. 6A-L). These coprolite specimens display a variety of morphologies (size, shape and surface texture) and inclusions (bone fragments, fish scales, plant material and gas bubbles) but do not differ drastically from the Late Cretaceous through the early Cenozoic. We presume that coprolite morphotypes that go unchanged across the K/T boundary were produced by (in this case carnivorous vertebrate) groups that did not go extinct, i.e. crocodyles, turtles, fish, mammals, birds, snakes, lizards, and/or amphibians. However, we are unable, as is most often the case in paleoscatology, to definitively assign producers to most of the coprolites. In this manuscript, NMMNH stands for the New Mexico Museum of Natural History and Science, Albuquerque, New Mexico.

LATE CRETACEOUS (CAMPANIAN) FRUITLAND FORMATION COPROLITES

Referred specimens: NMMNH P-32805 (Fig. 5J-N), P-41721 (Fig. 2A-G), coprolite fragments.

Description: NMMNH P-32805 is a slightly ovoid cylindrical segment that is concave on both ends and is presumed to have been part of a larger fecal mass (Fig. 5J-N). The surface is slightly weathered and pitted, with no visible inclusions. It measures 38.7 mm long, with a maximum diameter of 35.6 mm and a minimum diameter of 28.9 mm.

NMMNH P-41721 is the largest coprolite specimen from the Fruitland Formation in the NMMNH collection, and one of the largest coprolites discussed here, despite consisting of only incomplete fragments (Fig. 2A-G). One of the more complete fragments appears to be the conical terminal end, and another cylindrical segment has a layered or coiled structure. The largest fragment measures 42.3mm long, 61.6 mm wide and 50.9 mm thick.

Discussion: The sample size of coprolites from the Late Cretaceous Fruitland Formation is very small, making it difficult to do a meaningful assessment of any potential implications. Nevertheless, NMMNH P-41721 is notably large and seems to resemble NMMNH P-27431from the Kirtland Formation as well as a coprolite specimen from the Smithsonian collected from the Fruitland Formation (Fig. 3A-B). While neither NMMNH P-32805 or P-41721 contain any visible inclusions that would indicate having been produced by a carnivore, they both share morphological similarities to coprolites from other formations that can be identified as such.

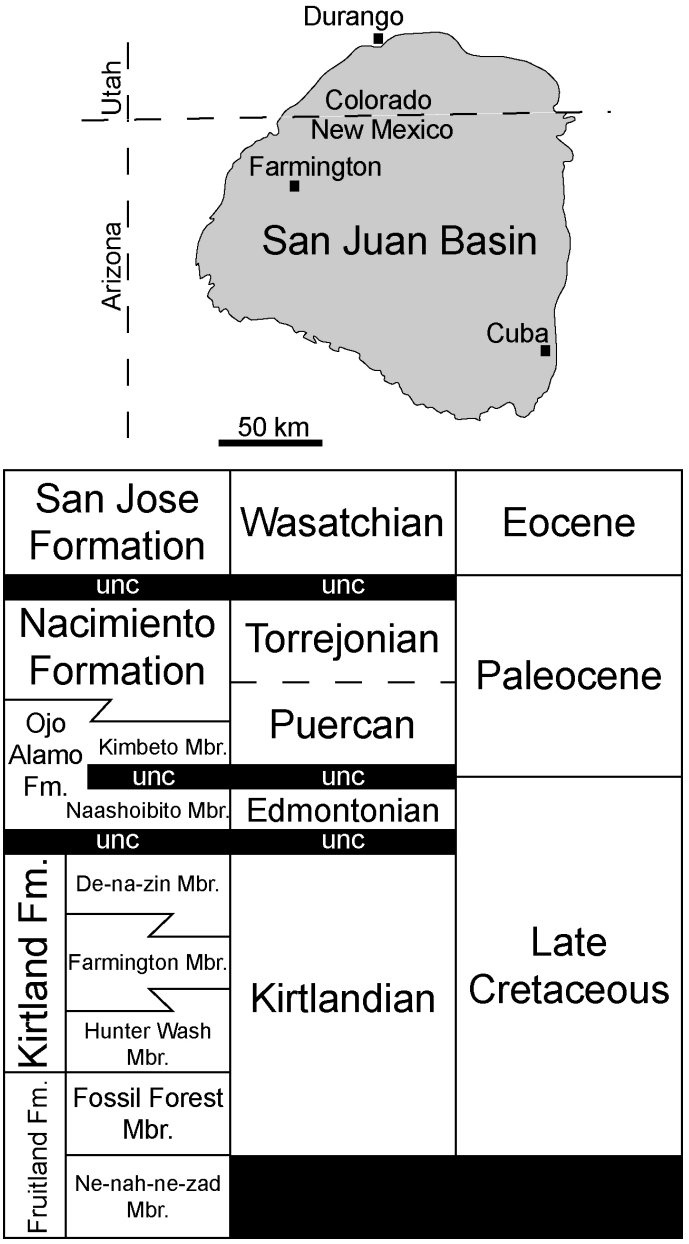

FIGURE 1. Location of San Juan Basin in the Four Corners region and summary of stratigraphy and chronology of coprolite-producing strata across the K/T boundary.

LATE CRETACEOUS (CAMPANIAN) KIRTLAND FORMATION (HUNTER WASH MEMBER) COPROLITES

Referred specimens: NMMNH P-27431 (Fig. 2U), P-30200 (Fig. 2K-M), P-64424 (Fig. 2H-J), coprolite fragments.

Description: NMMNH P-27431 consists of a relatively large, well preserved and nearly complete cylindrical segmented coprolite as well as four small associated coprolite fragments. Two of the pieces contain fragmentary fish scales and are thus attributable to a carnivorous producer. The large coprolite possesses no visible inclusions and measures 92.6 mm long with a maximum diameter of 42 mm.

NMMNH P-30200 is a single terminal cylindrical segment with a tapered tip (Fig. 2K-M). It has a relatively smooth surface texture with constriction marks. There is a single visible fish scale inclusion. The coprolite measures 27.0 mm long, 16.5 mm wide and 15.2 mm thick.

NMMNH P-64424 is the largest coprolite from the Kirtland Formation and one of the largest coprolites examined (Fig. 2H-J). It consists of the conical terminal end of a cylindrical segmented coprolite. It is highly friable, and much of the specimen consists of fragments. Many inclusions are easily identifiable and include bone fragments, fish scales and plant remains. This is the only specimen we document that may have been produced by an omnivore. It is 66.3 mm long, 50.5 mm wide and 40.2 mm thick.

Discussion: As in the Fruitland Formation, the sample size of coprolites from the Hunter Wash Member of the Kirtland Formation is small. NMMNH P-64424 is not only one of the largest coprolites examined, it also has the greatest number of identifiable inclusions. In addition to fish scales (Fig. 3C) and bone fragments, there are carbonaceous plant remains (Fig. 3D). This is the only specimen with identifiable plant remains and possibly attributable to an omnivorous producer, although the relatively small amount of plant material leaves open the possibility of unintentional ingestion. More importantly however, NMMNH P-64424 demonstrates that plant remains can be preserved in coprolites in the Late Cretaceous Hunter Wash member of the Kirtland Formation. So it seems unusual that NMMNH P-64424 is the only coprolite in the collection that has recognizable plant remains, given that fossil plant remains are common in the Hunter Wash Member of the Kirtland Formation.

LATE CRETACEOUS (CAMPANIAN) KIRTLAND FORMATION (DE-NA-ZIN MEMBER) COPROLITES

Referred specimens: NMMNH P-22632, P-27409, P-28861 (Fig. 7C-E), P-28914, P-28950, P-32602, P-37808 (Fig. 6M-Q), P-64473 (Fig. 7I-L), coprolite fragments and segments.

Description: NMMNH P-22632 is composed of numerous small pieces of coprolite(s), some of which contain fragments of bone.

NMMNH P-27409 is a tapered terminal end, similar in shape and texture to P-30200. It does not display any inclusions. It measures 29.5 mm long, 17.9 mm wide and 15.5 mm thick.

NMMNH P-28861 is the terminal end of a coprolite with unusual sinusoidal striations on the surface (Fig. 7C-E). The only visible inclusions are small pits, presumably caused by gases produced from bacterial action. It is 25.1 mm long with a maximum diameter of 16.3 mm.

NMMNH P-28914 is a cylindrical segment and several small pieces. One end of the cylinder is flattened, and the other has two small, concave depressions. The surface is pitted, presumably from gas bubbles. The segment is 29.8 mm long and has a diameter of 17.7 mm.

NMMNH P-28950 is a slightly arcuate, elongated cylinder that has a relatively worn surface and no visible inclusions. It is 29.8 mm long, 24.3 mm wide and 21.6 mm thick.

NMMNH P-32602 is highly fragmented and contains no visible inclusions.

NMMNH P-37808 consists of two long, mostly cylindrical coprolite fragments with no visible inclusions (Fig. 6M-Q). The largest fragment is 83.4 mm long with a diameter of 24.5 mm.

NMMNH P-64473 consists of the coiled and tapered terminus of a coprolite with a concave depression at the opposite end (Fig. 7I-L). It measures 31.0 mm long, 23.2 mm wide and 20.6 mm thick.

Discussion: Vertebrate coprolites appear to be more common from the De-Na-Zin Member than in the other members of the Kirtland and Fruitland formations, but this may be due to collection or preservation bias. Indeed, strata of the De-na-zin Member are not carbonaceous and include prominent red, purple and blue muddy beds, which suggest relatively oxidizing conditions of diagenesis and lithification, if not deposition. In contrast, the Fruitland Formation and the Hunter Wash Member are drab-colored and include beds of coal and carbonaceous shale, representing reducing conditions. We posit that coprolites are preferentially preserved in the oxidizing beds, and this explains their relative abundance in the De-na-zin Member and relative rarity in the Fruitland Formation and the Hunter Wash Member.

The majority of the specimens appear to have been produced by carnivores, a conclusion reached because the coprolites contain animal

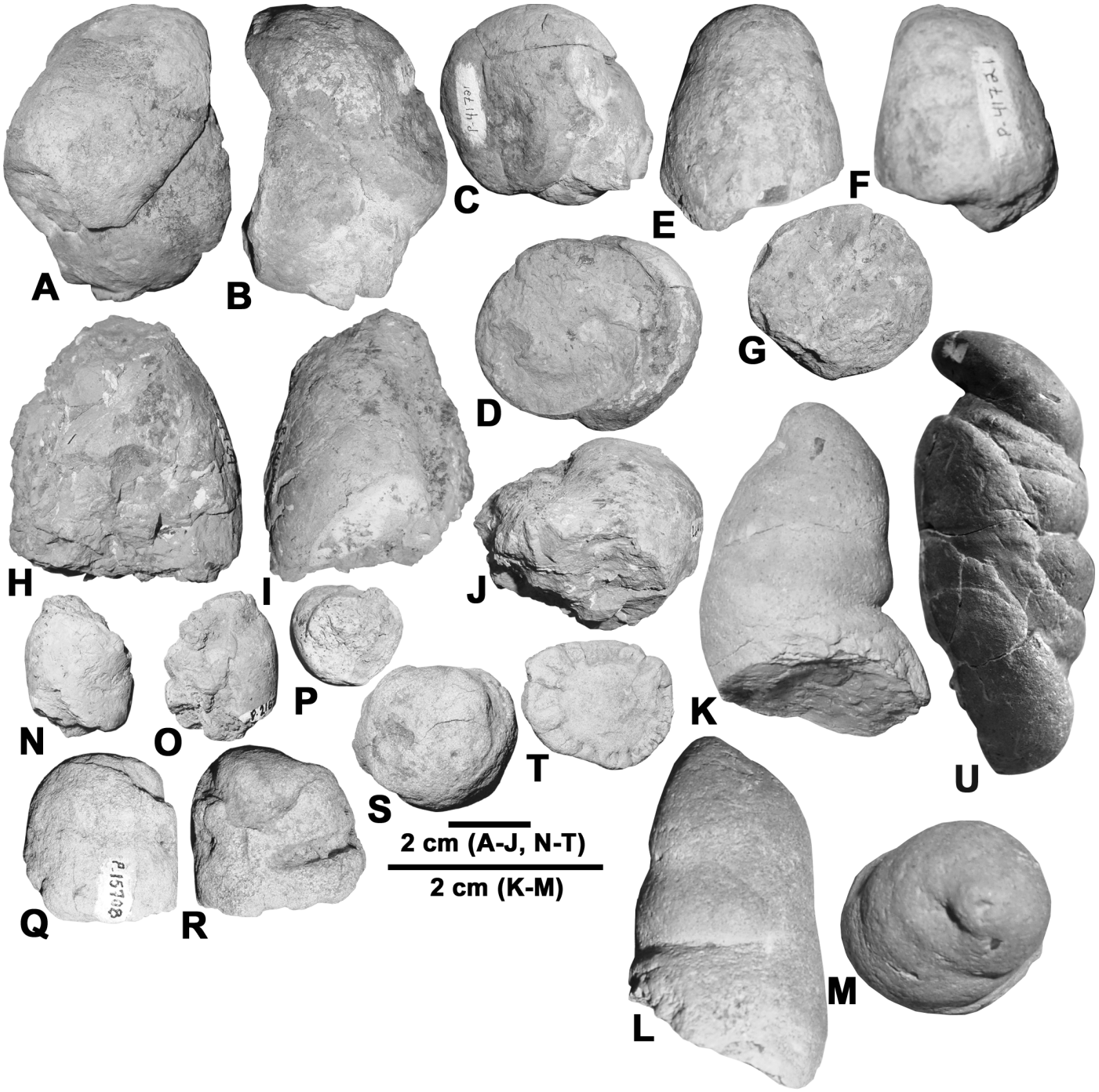

FIGURE 2. Late Cretaceous (**A-G**, Fruitland Formation and **H-M**, Kirtland Formation) and Paleocene (**N-T**) coprolites. **A-G**, NMMNH P-41721, two coprolites in **A-B**, **E-F**, axial and **C-D**, **G**, polar views. **H-J**, NMMNH P-64424, coprolite in **H-I**, axial and **J**, polar views. **K-M**, NMMNH P-30200, coprolite in **K-L**, axial and **M**, polar views. **N-P**, NMMNH P-21629, coprolite in **N-O**, axial and **P**, polar views. **Q-T**, NMMNH P-15708, coprolite in **Q-R**, axial and **S-T**, polar views. **U**, NMMNH P-27431, coprolite in axial view, not to scale.

remains or because they share morphological similarities to other specimens that can be confidently attributed to carnivores. It is unlikely that any of the Campanian coprolites from the Kirtland or Fruitland formations were produced by large adult dinosaurs, given the relatively small size of the specimens.

LATE CRETACEOUS (MAASTRICHTHIAN) OJO ALAMO FORMATION (NAASHOIBITO MEMBER) COPROLITES

Referred specimens: NMMNH P-32799 (Fig. 6F-H), P-32977 (Fig. 7A-B), P-37815, coprolite and coprolite fragments. NMMNH P-27336 (Fig. 3E-G), *Alococopros triassicus*.

Description: NMMNH P-32799 consists of a slightly tapered, mostly cylindrical coprolite fragment (Fig. 6F-H). It measures 32.7 mm long, 19.3 mm wide and 17.5 mm thick.

NMMNH P-32977 is the terminal end of a coprolite that has a small zone of striations at the end that seems to be a separate piece attached to the larger mass. It is 36.9 mm long, with a maximum diameter of 22.1 mm.

NMMNH P-37815 is a single coprolite fragment that is broken longitudinally. The surface has unusual, distinct areas with striations

that run perpendicular to each other. It is 25.1 mm long, 17.7 mm wide and 9.9 mm thick.

NMMNH P-27336 is a complete coprolite that is arcuate or "cashew"-shaped and rounded on both ends with a mostly circular cross section (Fig. 3E-G). Longitudinal striations run the length of the outer surface and wrap around the rounded ends. It is referable to *Alococopros triassicus*. The rest of the coprolite has a smooth surface texture, and there are no visible inclusions. It is 30.3 mm long, 11.8 mm wide and 11.6 mm thick.

Discussion: Most of the coprolites from the Naashoibito Member of the Ojo Alamo Formation have striations present on the surface. Many of the specimens display non-longitudinal striations, and it is unclear how they may have been generated. Longitudinally-striated coprolites have been ascribed to archosaurs (Young, 1964; Northwood, 2005) and turtles (Mately, 1939) based on the presence of intestinal rugae in extant members of each group. Recently, however, workers have cast doubt on the assertion that longitudinally-striated coprolites are diagnostic of archosaurs (Hunt and Lucas, 2010; Cantrell et al., this bulletin), and, as Sharma et al. (2005) point out, Thulborn (1991) found that longitudinal striations are not exclusive to the feces of turtles. Nevertheless, some longitudinally striated coprolites have been assigned an ichnotaxonomic name, namely *Alococopros triassicus* Hunt et al., 2007 and *A. indicus* Hunt et al., 2007. P-27336 matches very closely the diagnosis of *A. triassicus* and clearly pertains to the ichnotaxon (Fig. 3E-G). While the ichnogenus is known from the Cretaceous of India, *A. triassicus* has only previously been reported from Permian-Triassic strata in North America. These records are not only the first reported from the San Juan Basin, but they also greatly extend the upper bound of the chronological distribution of *A. triassicus* from the Late Triassic to the Late Cretaceous. Given the long chronological distribution and ambiguity of possible producers pertaining to *A. triassicus*, it seems unlikely that it would be useful as a biostratigraphic index.

EARLY PALEOCENE (PUERCAN) NACIMIENTO FORMATION COPROLITES

Referred specimens: NMMNH P-8750, P-8663, P-8879 (Fig. 6A-B), P-8997, P-15708, P-16174 (Fig. 5E-I), P-19332, P-21629, complete coprolites and coprolite fragments.

Description: NMMNH P-8750 consists of a small cylindrical coprolite fragment and the flattened, rounded end of a coprolite. The surface of both is pitted, presumably from gas bubbles. The cylinder is 15.2 mm long with a maximum diameter of 8.0 mm. The rounded end is 29.9 mm long and has a maximum diameter of 13.7 mm.

NMMNH P-8663 is a rough cylinder with pits from gas bubbles. It is 34.6 mm long, 18.1 mm wide and 13.2 mm thick.

NMMNH P-8879 consists of a relatively long, thin cylindrical coprolite with accreted pieces of sediment, the rounded end of a coprolite as well as many small pieces (Fig. 6A-B). The thin cylinder is 39.0 mm long and has a maximum diameter of 9.5 mm. The rounded end is 22.8 mm long with a maximum diameter of 17.3 mm.

NMMNH P-8997 is a poorly preserved piece of a cylinder that has no visible inclusions, a length of 30.2 mm and a maximum diameter of 19.7 mm.

NMMNH P-15708 consists of a partial coprolite and a complete coprolite. The complete coprolite is spindle shaped and is slightly arcuate in lateral view, with a length of 38.2 mm and a maximum diameter of 15.5 mm. The surface texture is mostly smooth, with irregular ridges.

NMMNH P-16174 is a partial cylinder that is slightly arcuate and has constriction marks on its surface (Fig. 5E-I). It is 50.5 mm long and has a maximum diameter of 29.6 mm.

NMMNH P-19332 is the flattened end of a coprolite that has constriction marks on its surface and bone fragment inclusions. It has a length of 30.9 mm, a width of 16.5 mm and a thickness of 10.8 mm.

NMMNH P-21629 is composed of four coprolite fragments. The most notable fragment has striations that run perpendicular to its axis as well as bone inclusions. Its surface is marked by furrows or canals, possibly burrows. The largest cylinder measures 29.8 mm long and has a maximum diameter of 22.9 mm. The striated fragment is 21.5 mm long and has maximum diameter of 13.2 mm.

Discussion: One of the Puercan age specimens catalogued as P-15708 is a cylindrical segment that has radiating grooves on the end that are somewhat similar to grooves on the terminal end of another partial coprolite, P-21987, from the Torrejonian of the Nacimiento Formation. While these two specimens do not share many other characteristics, they are the only two that display radiating grooves on the terminal end and may have been excreted by a similar producer. Besides the above mentioned specimens, the coprolites from the Puercan of the Nacimiento Formation do not show any significant difference in size or overall morphological characteristics from other coprolites collected from the San Juan Basin.

EARLY PALEOCENE (TORREJONIAN) NACIMIENTO FORMATION COPROLITES

Referred specimens: NMMNH P-8966, P-12309, P-12315, P-15198, P-15629, P-15650 (Fig. 5A-D), P-15716, P-15730, P-15783, P-15906, P-18894, P-19236, P-19352, P-20782, P-21987, P-27316 (Fig. 4J-M), P-27789, P-29223, P-29432, P-30542, P-39044, P-39614 (Fig. 5O-V), P-42919, P-48031 (Fig. 7M-Q), P-48396, P-51674, P-54103 (Fig. 4F-I), P-54338, P-56907 (Fig. 6I-L), complete and fragmentary coprolites

Description: NMMNH P-8966 is a poorly preserved coprolite, but it clearly has pits possibly from gas bubbles.

NMMNH P-12309 is a poorly preserved cylinder that is slightly arcuate, 31.4 mm long and has a maximum diameter of 17.2 mm.

NMMNH P-12315 is a complete coprolite that is spindle shaped with a surface that has faint constriction marks. It is 26.0 mm long with a maximum diameter of 10.9 mm.

NMMNH P-15198 is the conical end of a coprolite that has a maximum diameter of 18.9 mm and a length of 33.4 mm.

NMMNH P-15629 is a poorly preserved partial coprolite with fragmentary bone inclusions. It is 34.1 mm long and has a maximum diameter of 19.8 mm.

NMMNH P-15650 consists of four cylindrical coprolite fragments, all of which contain bone fragment/fish scale inclusions and gas bubbles (Fig. 5A-D). The largest cylinder is 30.1 mm long and has a maximum diameter of 15.8 mm. The shortest cylinder is 21.9 mm long with a maximum diameter of 14.5 mm.

NMMNH P-15716 is the fragmented apex of a coprolite that has a rounded cross section and constriction marks on its relatively smooth surface. It is 15.3 mm long with a maximum diameter of 15.3 mm.

NMMNH P-15730 is composed of three coprolite fragments, two with rounded ends and the third being a cylinder. The larger, rounded end has a very worn and pitted surface texture, is 40.5 mm long and has a maximum diameter of 17.7 mm. The second rounded end is 22.2 mm long with a maximum diameter of 12.6 mm. The cylinder has constriction marks on its surface, is 32.6 mm long, 16.6 mm wide and 10.9 mm thick.

NMMNH P-15783 is made up of two sub-rounded cylindrical segments, one with a rounded apex and both with bone fragment/fish scale inclusions. The segment with the rounded end is 43.2 mm long and has a maximum diameter of 22.3 mm. The cylindrical segment is 43.9 mm long with a maximum diameter of 18.0 mm.

NMMNH P-15906 is a sub-rounded cylinder with a gastropod inclusion. It is 33.9 mm long with a maximum diameter of 13.2 mm.

NMMNH P-18894 is a partial flattened cylinder with one end having a pyramidal terminus. It is 60.2 mm long and has a maximum diameter of 28.9 mm.

NMMNH P-19236 is a poorly preserved partial coprolite that has sub-rounded cross section and a rough surface texture. It is 35.5 mm long and has a maximum diameter of 20.9 mm.

NMMNH P-19352 is the tip of a coprolite that displays a coiled

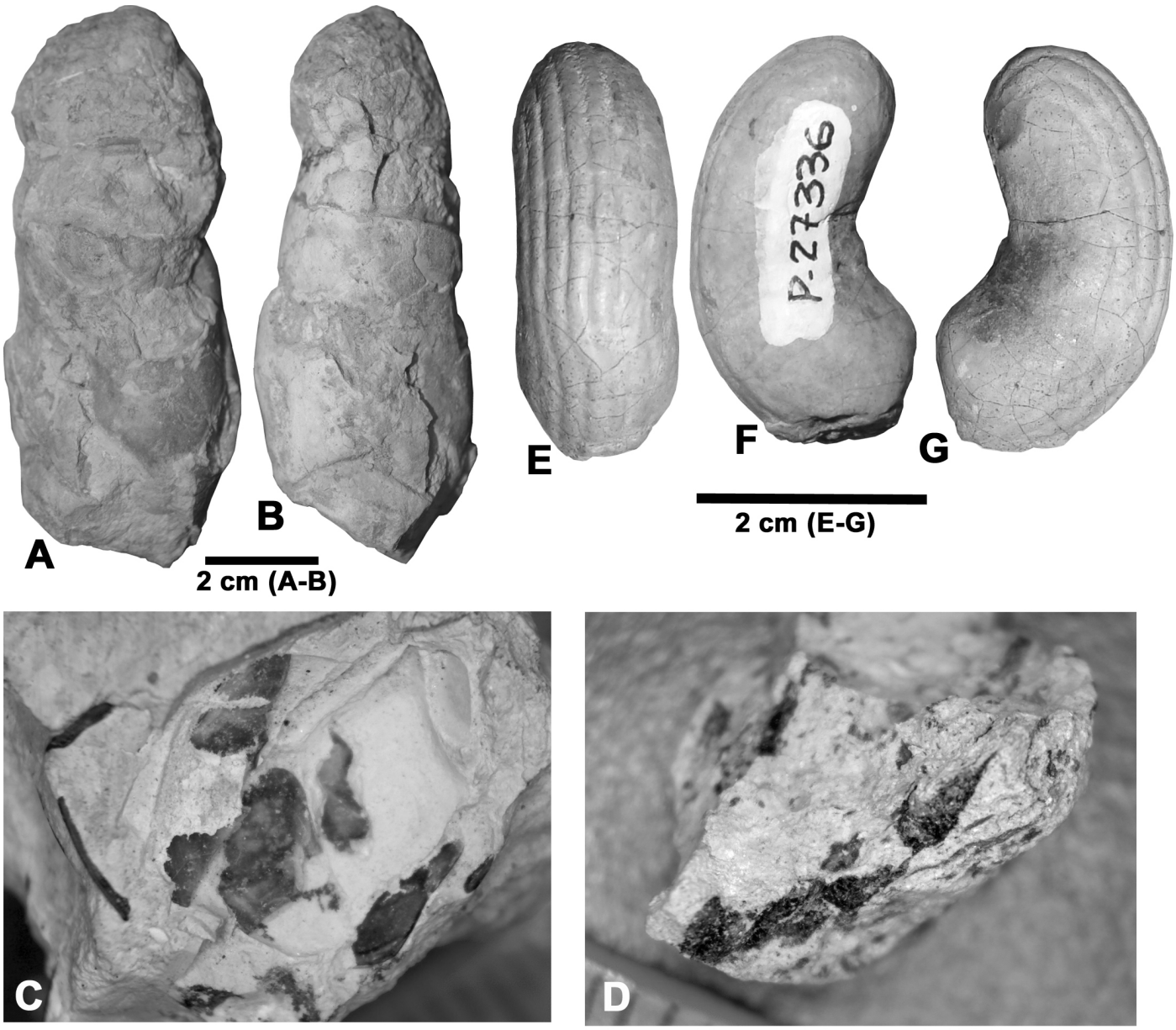

FIGURE 3. Late Cretaceous (**A-D**, Campanian and **E-G**, Maastrichtian) coprolites **A-B**, NMNH uncatalogued, coprolite from the Fruitland Formation. **C-D**, NMMNH P-64424, close up of coprolite from the Kirtland Formation with **C**, gar scale and **D**, carbonaceous plant inclusions. **E-G**, *Alococopros triassicus*, NMMNH P-27336 in **E-G**, axial views.

structure with a folded apex at one end. The other end has a prominent concavity. It has a maximum diameter of 33.1 mm and a length of 23.2 mm.

NMMNH P-20782 is composed of a complete coprolite that is slightly arcuate with a round cross section and an incomplete cylinder with constriction marks. The complete coprolite is 26.1 mm long and has a maximum diameter of 8.5 mm. The cylinder is 20.8 mm long with a maximum diameter of 9.9 mm.

NMMNH P-21987 is a cylindrical coprolite fragment that has a small protuberance with radiating striations at one end and constriction marks on the surface. It is 22.7 mm long with a maximum diameter of 25.4 mm.

NMMNH P-27316 consists of a nearly complete coprolite with many bone fragment and fish scale inclusions as well as gas bubble pits (Fig. 4J-M). It is 28.8 mm long with a maximum diameter of 16.9 mm.

NMMNH P-27789 is made up of four cylindrical coprolite fragments that have worn and pitted surface textures. The largest fragment is 35.4 mm long with a maximum diameter of 20.3 mm. The smallest fragment is 31.3 mm long and has a maximum diameter of 15.6 mm.

NMMNH P-29223 consists of two coprolite fragments – one is a roughly cylindrical section and the other is cylinder with a rounded end. Both fragments contain pits from gas bubbles. The roughly cylindrical coprolite fragment measures 28.1 mm long with a maximum diameter of 12.9 mm. The rounded end is 29.7 mm long with a maximum diameter of 12.3 mm.

NMMNH P-29432 consists of three coprolite fragments, one of which is a tapering terminal end, and the other two are cylinders. The terminal end is 44.8 mm long and has a maximum diameter of 24.0 mm. The larger cylinder is 52.0 mm long with a maximum diameter of 22.9 mm. The smaller cylinder is 34.7 mm long and has a maximum diameter of 20.9 mm.

NMMNH P-30542 is a fragmented segment of a coprolite. The maximum diameter is 16.5 mm and the length is 27.4 mm.

NMMNH P-39044 is a partial coprolite and has a rounded end

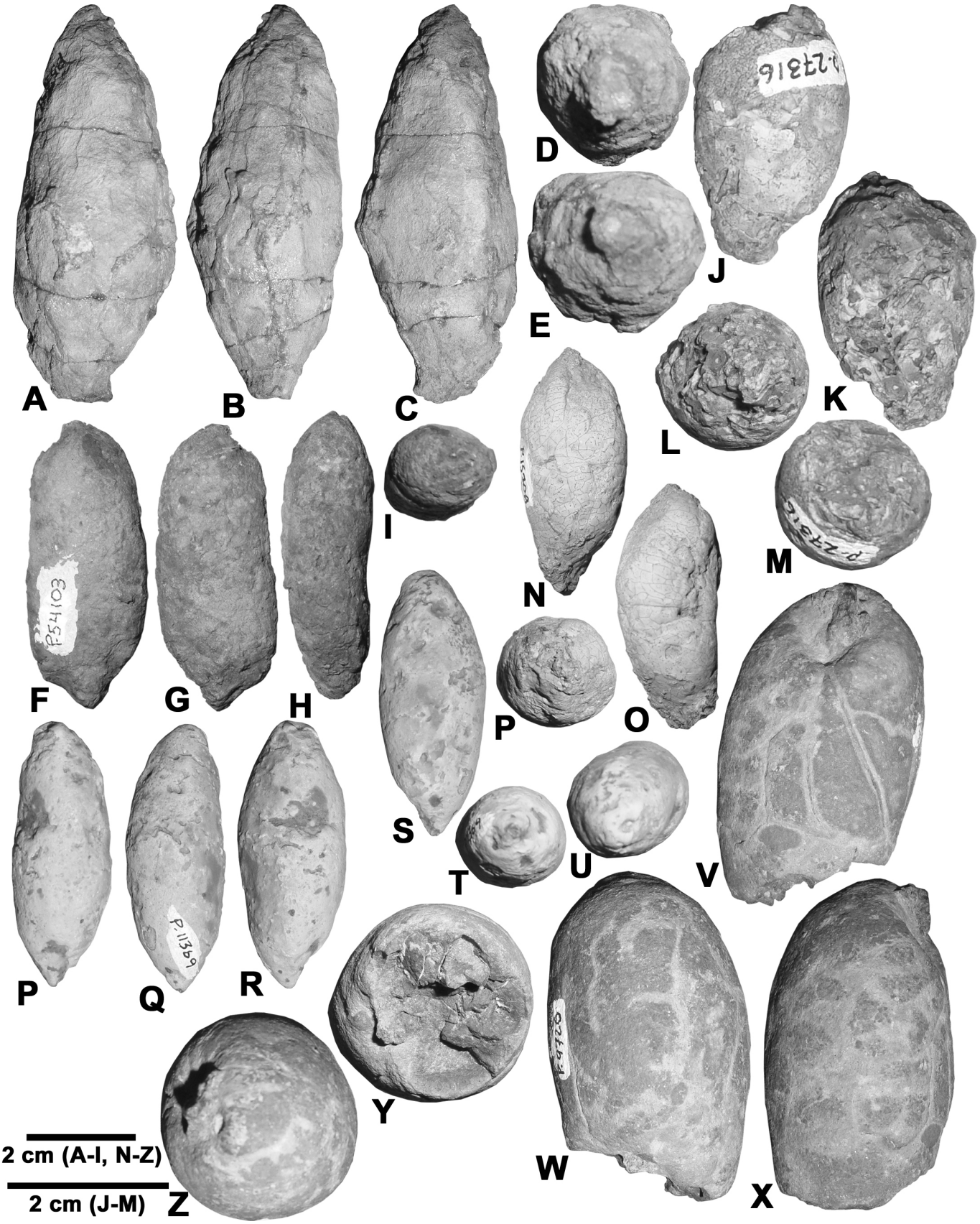

FIGURE 4. Paleocene and Eocene spindle-shaped coprolites. **A-E**, NMMNH P-5751, Wasatchian coprolite in **A-C**, axial and **D-E**, polar views. **F-I**, NMMNH P-54103, Torrejonian coprolite in **F-H**, axial and **I**, polar views. **J-M**, NMMNH P-27316, Torrejonian coprolite in **J-K**, axial and **L-M**, polar views. **N-P**, NMMNH P-15708, Puercan coprolite in **N-O**, axial and **P**, polar views. **Q-U**, NMMNH P-11369, Wasatchian coprolite in **Q-S**, axial and **T-U**, polar views. **V-Z**, NMMNH P-9726, Wasatchian coprolite in **V-X**, axial, **Y,** cross-sectional and **Z**, polar views.

with a slight point. The maximum diameter is 16.1 mm and the length is 26.9 mm.

NMMNH P-39614 is a large cylindrical segment with a sub-rounded cross section and the tapering terminal end of the large cylinder that is also sub-rounded in cross section (Fig. 5O-V). Both display constriction marks and gas bubbles. The tip is 63.3 mm long and has a maximum diameter of 36.4 mm. The large cylinder is 41.3 mm long and has a maximum diameter of 37.1 mm.

NMMNH P-42919 is the rounded tip of a coprolite with a highly pitted surface. Its length is 35.2 mm and its maximum diameter is 15.8 mm.

NMMNH P-48031 is a convoluted mass of what appear to be individual pellets that are rounded in cross section (Fig. 7M-Q). One pellet near the end is striated perpendicular to the long axis of the larger mass. The specimen is 54.3 mm long with a maximum diameter of 22.0 mm.

NMMNH P-48396 is a complete coprolite with a rounded cross section. One end is rounded and slightly broken, and the other end narrows. The surface is marked by pits. Its length is 40.5 mm and its maximum diameter is 25.1 mm.

NMMNH P-51674 is composed of several coprolite fragments that make up a nearly complete cylindrical coprolite that is 39.8 mm long and has a maximum diameter of 15.5 mm. There are no visible inclusions.

NMMNH P-54103 is a complete coprolite that is ovoid in shape, slightly flattened, with a slight protrusion at one apex (Fig. 4F-I). It has no visible inclusions, is 47.3 mm long, 18.6 mm wide and 14.3 mm thick.

NMMNH P-54338 is the broken end of a rounded cylinder that contains fish scale inclusions. It has a maximum diameter of 18.9 mm and a length of 26.0 mm.

NMMNH P-56907 is yet another sub-rounded cylinder, but with constriction marks and bone fragment inclusions (Fig. 6I-L). It measures 28.6 mm long with a maximum diameter of 11.0 mm.

Discussion: The coprolites from the Torrejonian interval of the Nacimiento Formation are typical of most specimens discussed in this manuscript. Most specimens consist of partial or complete cylindrical coprolites with bone inclusions, fish scales, gas bubbles and/or constriction marks on the surface. The relatively large number of specimens from the Torrejonian of the Nacimiento Formation can be at least partially equated with a more vigilant attempt to collect coprolites. Despite this, there are no specimens that can confidently be attributed to herbivorous producers.

EOCENE (WASATCHIAN) SAN JOSE FORMATION (REGINA MEMBER) COPROLITES

Referred specimens: NMMNH P-5749, P-5751 (Fig. 4A-E), P-8600, P-9704, P-9726 (Fig. 4V-Z), P-11369 (Fig. 3Q-U), P-11370, P-33724 (Fig. 6C-E), coprolites and coprolite fragments.

Description: NMMNH P-5749 is a partial segment of a coprolite that is 19.0 mm long and has a maximum diameter of 19.8 mm.

NMMNH P-5751 is a complete coprolite that has an asymmetrical spindle shape and a rounded cross section (Fig. 4A-E). It has a surface texture that is similar to the surface texture of both P-34966 and P-15708. It measures 62.4 mm long and has a maximum diameter 23.2 mm.

NMMNH P-8600 is a small, poorly preserved segment of a coprolite with fish scale inclusions. The length is 14.4 mm and the maximum diameter is 9.0 mm.

NMMNH P-9704 is a poorly rounded cylinder with a sub-rounded end and deep constriction marks on its surface. It is 25.2 mm long and has a maximum diameter of 11.5 mm.

NMMNH P-9726 is a relatively large, nearly complete coprolite that tapers at both ends (Fig. 4V-Z). The more complete end has a fragment of bone protruding from the tip. The specimen is 52.8 mm long with a maximum diameter of 30.6 mm.

NMMNH P-11369 is a complete coprolite with a rounded cross section and slightly pitted surface (Fig. 4Q-U). It is 44.1 mm long and has a maximum diameter of 17.7 mm.

NMMNH P-11370 is a poorly preserved cylindrical fragment that is 34.1 mm long and has a maximum diameter of 21.0 mm.

NMMNH P-33724 is the rounded cylindrical end of a coprolite that has constriction marks on its surface (Fig. 6C-E). It has a length of 19.2 mm and a maximum diameter of 11.6 mm.

Discussion: The San Jose Formation has a diverse vertebrate assemblage, although coprolites have largely been ignored. It is no surprise then that the number of coprolites from the San Jose Formation in the collection at the NMMNHS is small and all appear to be assignable to carnivorous producers. The small number of coprolites and apparent lack of producer diversity is likely the result of the same limitations associated with the other groups of coprolites discussed here.

MORPHOTYPES

Many of the characteristics used here for the description of coprolites overlap one another and do not seem to coincide in any predictable manner. Given the relative variability within each morphotype recognized and discussed here, it seems unlikely that any represent a single group of producers. Nevertheless, a minimum of four morphotypes are present (spindle shaped, elongated cylinders, cylindrical segments and conglomerated masses) that exhibit various surface textures (worn, smooth, pitted and striated) and other features (constriction marks and inclusions).

Spindle-Shaped Coprolites (Fig. 4)

Spindle-shaped coprolites tend to be mostly circular in cross section with tapered or pointed ends (Fig. 4). They also tend to be complete or mostly complete as per the recognition of both ends being tapered. Constriction marks are absent from specimens considered to be spindle-shaped, probably a product of the expulsion process. They exhibit a range of surface textures, presumably due to differences in exposure, preservation and composition. Oddly, there are only spindle-shaped coprolite specimens in the collection of the NMMNH from after the K/T boundary, in the Paleocene and Eocene. Most can be confidently assigned to carnivorous producers. Coprolite specimens discussed here that fall into this category are NMMNH P-15708 from the Puercan (Fig. 2Q-T), NMMNH P-12315, P-27316 and P-54103 (Fig. 4F-I) from the Torrejonian (Fig. 4J-M), and NMMNH P-5751 (Fig. 4A-E) and P-9726 (Fig. 4V-Z) from the Wasatchian.

Cylindrical Segmented Coprolites (Fig. 5)

Cylindrical segmented coprolites (Fig. 5) can be characterized as having concave/convex termini that would have fit together with the concave/convex termini of other segments in a larger fecal mass. A few specimens possess a tapered or pointed end in addition to a concave/convex terminus and presumably represent the terminal end of a larger fecal mass. Still other specimens are complete or nearly complete and display the manner in which segments can be linked together. Inclusions are common and consistent with the inclusions present in the other groups discussed here. Surface texture varies and constriction marks are common. Coprolites that can be characterized as cylindrical segments are some of the most common in the collection of the NMMNH from the San Juan Basin and include NMMNH P-27431 (Fig. 2U), P-28914, P-32805 (Fig. 5J-N), P-41721 (Fig. 2A-G), and P-64424 (Fig. 2H-J) from the Campamian, NMMNH P-16174 from the Puercan (Fig. 5E-I), and NMMNH P-15650 (Fig. 5A-D), P-15708 (Fig. 2Q-T), P-15716, P-15783, P-16198, P-19352, P-21987, P-29432, P-39614 (Fig. 5O-V), P-39644, P-42919, P-48396 and P-54338 from the Torrejoniam.

Elongated Cylindrical Coprolites (Fig. 6)

Elongated cylindrical coprolites (Fig. 6) lack obvious segmentation and thus the convex/concave terminal ends associated with cylindrical segmented coprolites. They also tend to have a greater length to

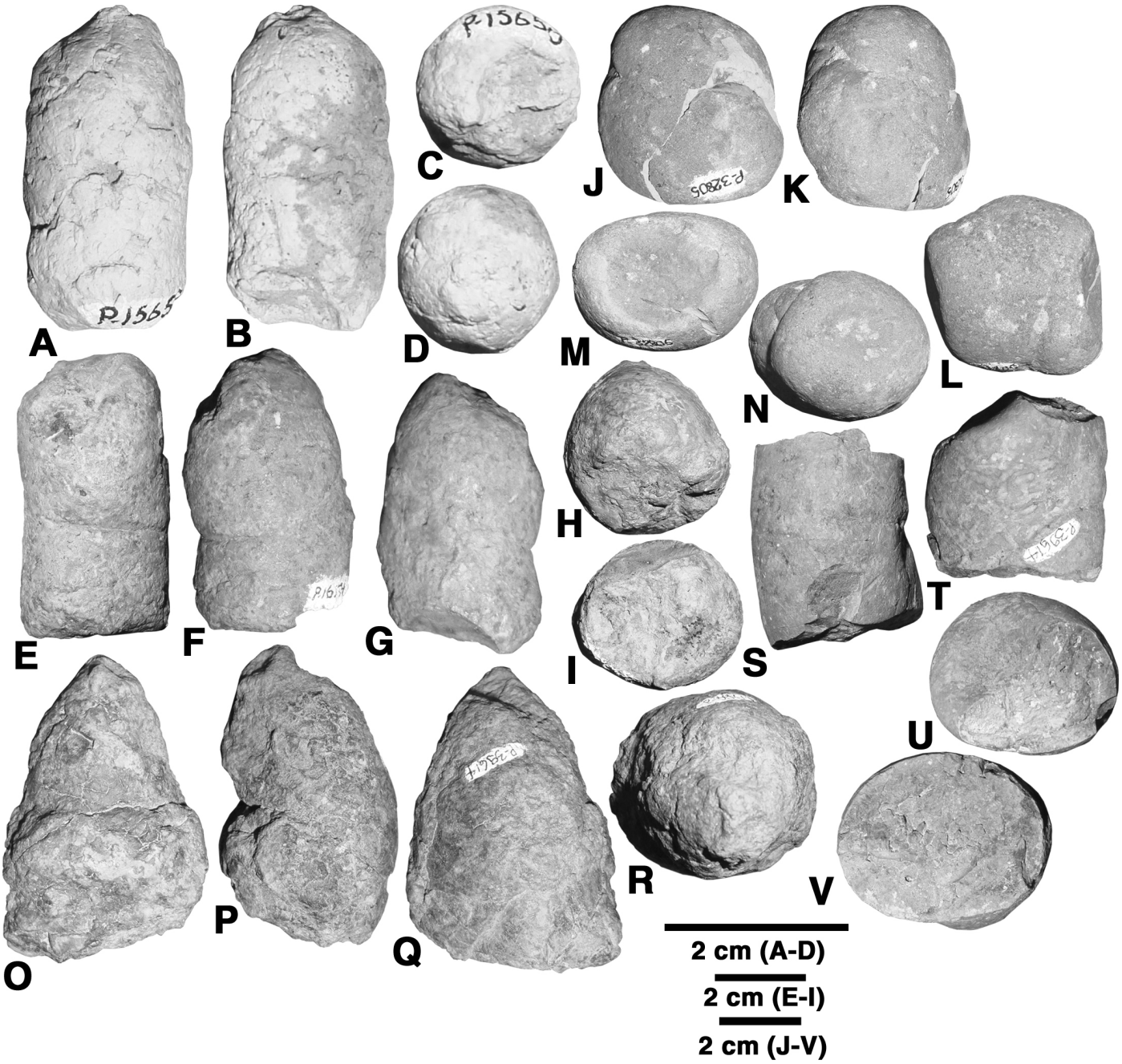

FIGURE 5. Cretaceous-Paleocene cylindrical segmented coprolites. **A-D**, NMMNH P-15650, Torrejonian coprolite in **A-B**, axial and **C-D**, polar views. **E-I**, NMMNH P-16174, Puercan coprolite in **E-G**, axial and **H-I**, polar views. **J-N**, NMMNH P-32805, Campanian coprolite in **J-L**, axial and **M-N**, polar views. **O-V**, NMMNH P-39614, Torrejonian coprolites in **O-Q**, **S-T**, axial, **R**, polar and **U-V**, cross-sectional views.

diameter ratio than cylindrical segmented coprolites and thus many specimens are fragmented in cross section. The terminal ends can be either rounded or pointed and constriction marks are common. Inclusions in elongated cylinders are typical of the other morphologies described here. Specimens classified as elongated cylinders are NMMNH P-28950 and P-37808 (Fig. 6M-Q) from the Campanian, NMMNH P-32799 from the Maastrichthian (Fig. 6F-H), NMMNH P-8879 from the Puercan (Fig. 6A-B), NMMNH P-15730, P-15906, P-19236, P-20782, P-27789, P-29223, P-51674 and P-56907 (Fig. 6I-L) from the Torrejonian as well as NMMNH P-33724 from the Wasatchian (Fig. 6C-E).

Conglomerated Mass Coprolites (Fig. 7)

Conglomerated mass coprolites (Fig. 7) appear to be composed of multiple units or pellets that were expelled in a single mass, fused together. Many have striations that run in directions other than longitudinal and that begin and end abruptly. It seems likely that the areas of unusual striations present on many specimens represent single pellets that were disoriented with respect to the long axis of the larger fecal mass as well as whatever intestinal feature was responsible for the striations, prior to expulsion from the producer. NMMNH P-28861 (Fig. 7C-E) and P-64473 (Fig. 7I-L) from the Campanian, NMMNH P-27409 and P-32977 (Fig. 7A-B) from the Maastrichthian, NMMNH P-21629 from the Puercan (Fig. 7F-H), as well as P-48031 from the Torrejonian (Fig. 7M-Q) can all be designated as conglomerated masses.

DISCUSSION

Most of the Late Cretaceous through Cenozoic coprolites we document here can be confidently assigned to carnivorous producers

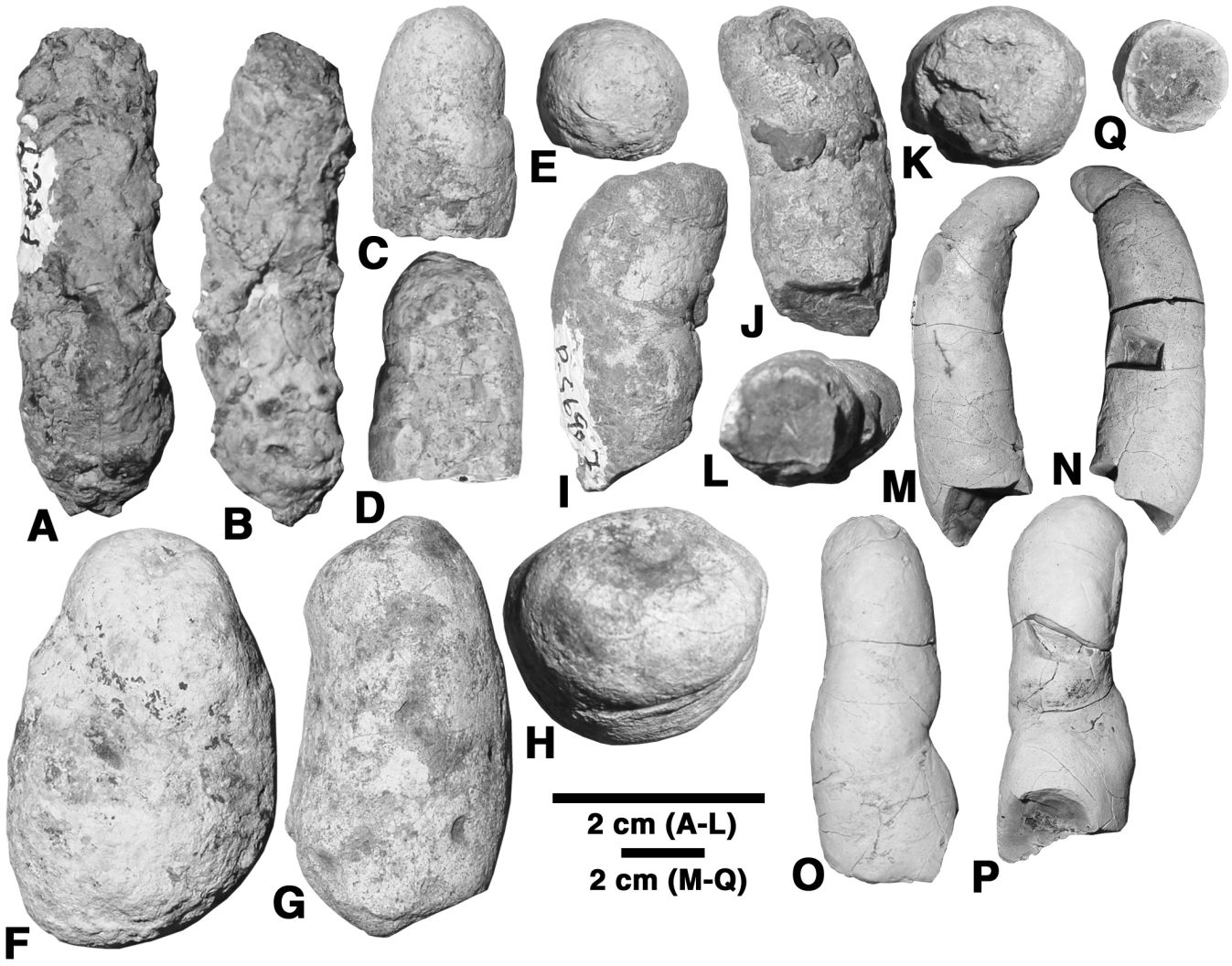

FIGURE 6. Cretaceous-Eocene elongated cylindrical coprolites. **A-B**, NMMNH P-8879, Puercan coprolite in axial views. **C-E**, NMMNH P-33724, Wasatchian coprolite in **C-D**, axial and **E**, polar views. **F-H**, NMMNH P-32799, Wasatchian coprolite in **F-G**, axial and **H**, polar views. **I-L**, NMMNH P-56907, Torrejonian coprolite in **I-J**, axial and **K-L**, polar views. **M-Q**, NMMNH P-37808, Campanian coprolite in **M-P**, axial and **Q**, polar views.

based on morphological and inclusional evidence. This is also the case with vertebrate coprolites from the San Juan Basin curated in the collections of other institutions. The Smithsonian has in its collection a relatively large coprolite specimen from the Fruitland Formation that is very similar in overall morphology to NMMNH P-41721 from the Fruitland Formation and NMMNH P-27431 from the Hunter Wash Member of the Kirtland Formation. Here, due to their small number and overall morphological similarity to other coprolites, these specimens have been designated as cylindrical segmented coprolites. However, with the further collection and analysis of vertebrate coprolites from the San Juan Basin, it may be the case that they constitute a definable ichnotaxon.

Sullivan and Jasinski (2012) describe and discuss the Late Cretaceous vertebrate coprolites collected from the San Juan Basin curated in the vertebrate paleontology collection of the State Museum of Pennsylvania. As might be expected, many of the specimens they examine share numerous similarities with the coprolites discussed here. In particular, what they refer to as 'morphotype C' is most certainly what we have designated as cylindrical segments. It seems likely that coprolites with this type of morphology, which are relatively common, pertain to similar producers and possibly another definable ichnotaxon. Sullivan and Jasinski also examine coprolites they refer to as 'morphotype G.' These coprolites are very similar to P-27336, which we have designated as *Alococopros triassicus*. They are similar in relative size and possess longitudinal striations; however, while P-27336 is arcuate in lateral view, there is no evidence for the coiling characteristic of 'morphotype G.'

With plant fossils and herbivorous vertebrate body fossils being some of the most prevalent found in the Late Cretaceous-Eocene strata of the San Juan Basin, an explanation is warranted for the nearly complete lack of plant-bearing coprolites from the area. The fact that the more durable, phosphatic fecal remains of carnivores are more readily fossilized than the feces of herbivores due to accelerated bacterial mineralization seems a likely explanation (Hunt et al., 1994). However, some workers have found that the fecal remains of herbivorous producers can undergo a similar mode of preservation (Hollocher et al., 2001). In addition to this, one of the specimens discussed here, NMMNH P-64424, demonstrates the possibility of plant remains being preserved in the Hunter Wash Member of the Kirtland Formation. Fecal remains of a herbivorous producer would likely be recognized by the presence of a large amount of undigested plant material. Evidence to support this is provided by Hollocher et al (2001) and Chin (2007). Because the identification, collection and study of coprolites in general have not been ideal, it may be logical to conclude that coprolites from omnivorous or herbivorous producers in the San Juan Basin have simply gone unrecognized.

Another possible explanation for the lack of coprolites produced by herbivores lies in the relatively small number of coprolites documented from the San Juan Basin, despite collection and study of verte-

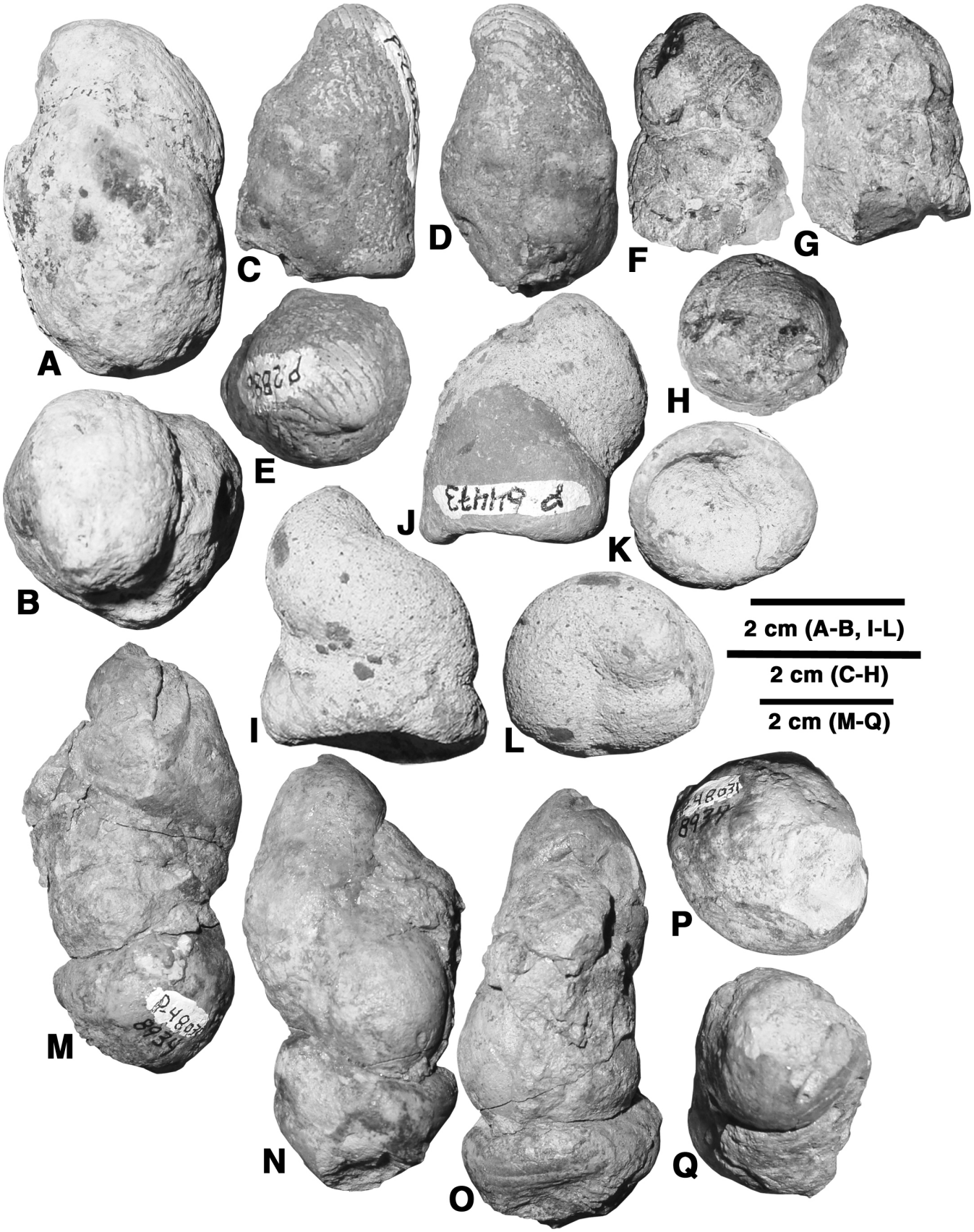

FIGURE 7. Cretaceous-Paleocene conglomerated mass coprolites. **A-B**, NMMNH P-32977, Maastrichtian coprolite in **A**, axial and **B**, polar views. **C-E**, NMMNH P-28861, Campanian coprolite in **C-D**, axial and **E**, polar views. **F-H**, NMMNH P-21629, Puercan coprolite in **F-G**, axial and **H**, polar views. **I-L**, NMMNH P-64473, Campanian coprolite in **I-J**, axial and **K-L**, polar views. **M-Q**, NMMNH P-48031, Torrejonian coprolite in **M-O**, axial and **P-Q**, polar views.

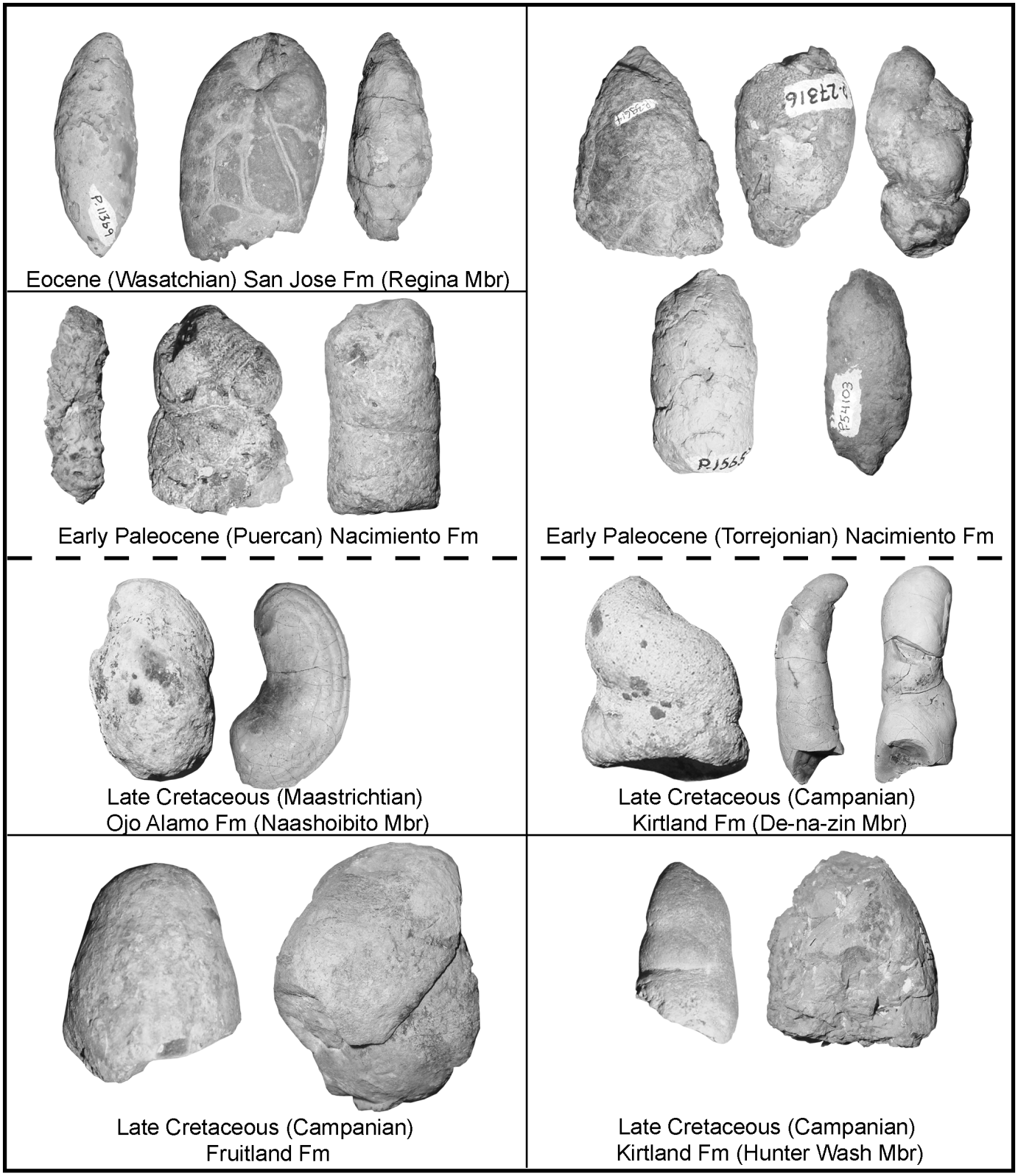

FIGURE 8. Coprolite morphologies across the Cretaceous-Tertiary boundary of the San Juan Basin. Coprolites not to scale.

brate assemblages in the area for over one hundred years (Hunt et al., 1992). Most of these Late Cretaceous-Eocene carnivorous vertebrate coprolites have inclusions (such as bones or gar scales) that are easily identifiable and also have morphological features very obviously pertaining to fossil feces, making recognition of the coprolite more likely. Unfortunately, the extent to which collection bias and preservational bias are factors cannot be definitively concluded without a greater emphasis on recording relevant data and recognizing and collecting different coprolite morphotypes.

A similar issue arises when we consider the relatively small size (<10 cm) of all coprolite specimens (and assumed producers) from the Late Cretaceous Fruitland, Kirtland, and Ojo Alamo Formations in the San Juan Basin, despite the relatively large size of many of the known vertebrates (Sullivan and Lucas, 2006). This suggests that either none of the preserved coprolites are dinosaurian, or that dinosaurian coprolites are homeomorphic with those of some other vertebrates, such as crocodyles.

CONCLUSION

Despite the inherent biases and uncertainties, we find that coprolite morphologies (size, shape and surface texture) and inclusions (bone fragments, fish scales, and gas bubbles) do not change significantly across the K/T boundary in the San Juan Basin (Fig. 8). The apparent uniformity of coprolite morphologies and inclusions is not easily explained given the shift in vertebrate diversity across the boundary. Presumably those coprolite morphotypes that go unchanged across the K/T boundary were produced by (in this case carnivorous vertebrate) groups that did not go extinct, i.e. crocodyles, turtles, fish, mammals, birds, snakes, lizards, and/or amphibians. Determining the producer of any coprolite is difficult and the coprolites from the San Juan Basin demonstrate the strong likely-hood of homeomorphy among the fecal remains of many vertebrate groups. As Hunt and Lucas (2005) point out, the need for systematic collection of coprolite samples is necessary for further development of the field of vertebrate paleoscatology.

ACKNOWLEDGMENTS

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