STRIGILITES (FOSSILIZED OWL PELLETS) FROM THE OLIGOCENE OF WYOMING

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Abstract—We document an extensive (at least 1 x 0.3 m) mass of a purgolite composed of strigilites (fossilized owl pellets) from the lower Oligocene (Orellan, ~32-33 Ma) Orella Member of the White River Formation near Douglas in eastern Wyoming, USA. These pellets are preserved as calcareous nodules full of fossil mammal bones that are either discrete, bordered by green claystone matrix, or coalesced flattened masses that likely represent coalesced strigilites. The Orellan owl pellet locality has yielded the type specimens of the sciurid rodent *Cedromus wilsoni* and the todid bird *Palaeotodus emryi*. The owl pellet assemblage also includes the skeletons, bearing skulls, of at least three individual owls, which strongly reinforces the interpretation of these small masses of bone as owl pellets. These owls were not prey items and are large enough to have preyed on the mouse-sized rodents (eomyids and heteromyids) and on the mouse-sized marsupials, which together constitute the overwhelming number (more than 90%) of prey individuals in the owl pellet assemblage. The strigilites in the assemblage display many of the features deemed characteristic of recent owl pellets based on actualistic studies, including abundant and high quality bone preservation, extreme inequitability of species distribution, intact skulls, numerous mandibles and femora and good representation of all skeletal parts. Further preparation of the bones in the Orellan strigilites is needed to quantify species abundance, bone element frequencies and the statistics of element breakage and completeness, among other data. Nevertheless, the Orellan strigilites are apparently the oldest and one of the few unambiguous published records of fossil owl pellets. Indeed, despite repeated claims that owl pellets are important contributors to the Tertiary microvertebrate fossil record, very few fossil owl pellets have been documented. We conclude that owl pellets are not a significant component of the Tertiary fossil record despite their abundance in some Quaternary deposits.

INTRODUCTION

The bone-rich pellets regurgitated by extant owls are well studied by modern biologists. They not only provide evidence of the presence of owls, but they also can be used to assess their predatory behaviors and the composition of their prey population. Indeed, a diverse literature exists on these topics (e.g., Andrews, 1990; Elbroch et al., 2001, and references cited therein). The recognition of the "scatological origin" of some vertebrate microfossil assemblages by Mellett (1974) ignited interest in the identification of fossil owl pellets (e.g., Dodson and Wexlar, 1979; Kusmer, 1990; Terry, 2004). Yet, in the last 30 plus years, very few fossil owl pellets have been documented in the paleontological literature (Gawne, 1975; Andrews, 1990; Kusmer, 1990; Terry, 2004, 2007, 2008; Hunt and Lucas, 2007; Myhrvold, 2011; Czaplewski, 2011). Here, we document an owl pellet fossil assemblage from the lower Oligocene of Wyoming (Fig. 1). This is apparently the oldest documented record of fossil owl pellets and well illustrates the identification of such an assemblage and the challenges and opportunities it poses for paleobiological interpretation.

Hunt and Lucas (2012) refined the terminology associated with fossils that represent regurgitated material. Regurgitalites (*sensu* Hunt, 1992) are trace fossils that include all manipulated or digested/partially digested food material egested via the oral cavity. Regurgitalites that derive from the stomach, such as owl pellets, are ekrhexalites (*sensu* Hunt and Lucas, 2012). Regurgitalites of birds are ornithoregurgitalites, and those produced by owls, specifically, are strigilites (Hunt and Lucas, 2012). Purgolites are accumulations of regurgitalites and include accretionary purgolites that result from accumulation due to physical, rather than biological, processes, and ethological purgolites are those that result from behavior of an organism (Hunt and Lucas, 2012). In this paper, USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.

PROVENANCE

Korth and Emry (1991, p. 991) described the strigilite occurrence (which is the type locality of the sciurid rodent *Cedromus wilsoni* Korth and Emry, 1991 and the todid bird *Palaeotodus emryi* Olson, 1976) as a "very dense concentration of bones 5.5 m (18 feet) above the base of a channel fill within the White River Formation. The channel appears to be cut from at least 39.6 m (130 feet) above the base of the Orella Member of the White River Formation, SE1/4, sec. 27, T32N, R71W, Converse County, Wyoming." The "dense concentration of bones" noted by Korth and Emry (1991) was discovered and collected by one of us (RJE) in 1972 at a locality referred to as "owl pocket" (RJE field number WYO 72-246) (Fig. 1). This stratigraphic horizon is of middle or late Orellan age, ~32- 33 Ma, and therefore of early Oligocene age (Larson and Evanoff, 1998; Prothero and Emry, 2004).

DESCRIPTION

At the owl pocket locality, thousands of bones of fossil mammals were found packed into round to ovoid calcareous nodules, mainly amalgamated into an irregular mass about 1 m long x 0.3 m wide (Figs. 2-7). These nodules, all apparently originally discrete, are in some places bounded by a green mudstone matrix, but are mostly amalgamated into the mass. Similar calcareous nodules around the mass were also collected. The most concentrated part of the mass was collected in a single plaster jacket ~83 cm x 29 cm x 10 cm (Fig. 2). However, the size of this plaster jacket is much less than the total size of the original deposit.

The deposit was in a channel fill. The pinkish gray to white nodular masses have a calcareous matrix, and many display fossil bones on their external surfaces. Some of the nodules are discrete and have a flattened (in the vertical dimension) and rounded to ovoid (in the horizontal dimension) shape. However, others are not discrete. In these, there are very large, platy pieces of the calcareous matrix – likely parts of

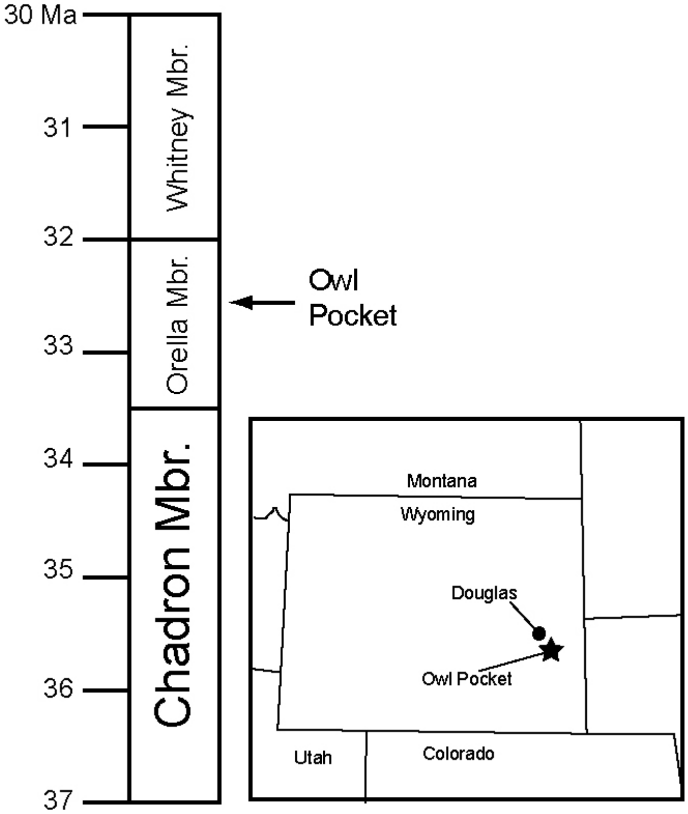

FIGURE 1. Index map and stratigraphic diagram locating the Oligocene owl pocket purgolite.

the deposit where the discrete nodules coalesced, probably after maceration or partial disaggregation and subsequent compaction, or an agglomeration of bones derived from macerated and disaggregated pellets, and subsequently cemented into a calcareous nodule or concretion.

We divide the objects from the owl pocket deposit into three categories: nodular masses, discrete pellets, and the bones partially or wholly prepared from the deposit. Here, we describe the different classes of objects, all of which are in the USNM collection.

Nodular Masses

Many of the owl pellets are preserved as discrete ovoid objects. Indeed, there are many areas in the jacketed material where the pellets are united to form large, coalesced masses that probably reflects either pre-fossilization disaggregation/maceration or diagenetic compression of once discrete pellets, or where the mass is an accumulation of bones from one or more pellets cemented together (Figs. 2B-C, 3, 6A-C, 7A-B). Stated simply, these are discrete masses or nodules with many bones, held together in potato-shaped masses by carbonate cement. In our opinion, each of these masses most likely has the bony content of many actual owl pellets. We conclude this largely because if these larger masses actually represent owl pellets, then the owl that made them would have been much larger than any living owl.

The coalesced masses range from about 6 to 18 cm in maximum dimension, and most are 7-11 cm long. A typical mass is one with a large rodent skull, ribs and foot bones that has dimensions of 7 x 4.5 x 4 cm (Fig. 3A-C). However, this large rodent skull seems likely to not have been regurgitated by an owl, but instead the skull was a prey item that was too large to be swallowed whole, and instead the rodent was picked apart and eaten in pieces. Indeed, few of the *Cedromus* skulls in the assemblage are preserved in the close association with their postcranial elements that would indicate that they were packaged together in a pellet. Instead, a single regurgitated pellet (see below) typically contains one, sometimes two, skulls and associated bones of much smaller rodents and marsupials. Indeed, this is usually the case in modern owl and hawk pellets, in which a single pellet normally contains the remains of part of one, one entire, or parts of two to three prey animals (e.g., Czaplewski, 2011).

Another partially prepared mass (Fig. 3G-H) is 6 x 5.5 x 4.5 cm and is full of rodent bones, especially vertebrae and ribs. A larger mass (11 x 7 x 4 cm) is similar, and also includes complete rodent limb bones (Fig. 3I-J).

Many of the masses (and pellets) contain bones of mammals other than rodents. A small mass (5 x 3.5 x 1 cm) has marsupial mandibles (Fig. 6A), and bones of a small, mouse-sized marsupial are very common. Our subjective impression is that this marsupial occurs in about the same frequency as the smaller rodents, though perhaps not as common as the eomyid taxon, but more common than the heteromyid. Also, the crushed, anterior portion of a juvenile carnivore skull (*Hesperocyon*) with only the deciduous dentition is in a 30 mm long and 31 mm wide pellet (Fig. 6B-C). Other masses contain bird skulls and bones – as Olson (1976, p. 111) noted, "the beautifully preserved skeletons of at least four small owls, possibly of two species." One of the large masses (11 x 7.5 x 3 cm) with owl bones includes a skull that is 35 mm long (Fig. 7A-B). However, the owl skull illustrated in Figure 7A-B was preserved with the long axis vertical, and the skull is distorted—shortened—the bill is pushed backward into the skull. Another less distorted skull is 50 mm long, and we think this is a more accurate measure of skull length.

Discrete Pellets

Many discrete pellets are preserved in the owl pellet assemblage (e.g., Fig. 4). Discrete pellets have an irregular surface texture, brecciated exteriors with green claystone filling and are packed with bones. The external texture and bone content of these discrete pellets is the same as that of the masses, but the discrete pellets are much smaller, with a maximum length of about 5 cm.

Three discrete pellets (Fig. 4B-E) are characteristic. They contain skull and mandible parts of rodents as well as other rodent postcranial bones. One (Fig. 4C) has the skull of a small geomyoid (most likely an eomyid). Another (Fig. 4D) contains the skull and jaws, essentially articulated, of two small rodents, as well as many postcranial elements, undoubtedly of the same two individuals. A third pellet (Fig. 4E) has skull parts and a jaw of the sciurid rodent *Cedromus*. These pellets occur as compacted masses of bones in a whitish, calcareous matrix, surrounded by greenish claystone (Fig. 4B). The maximum dimension of these pellets is about 2 cm. Intact preservation of delicate mandibular elements--the thin mandibular angle and ascending ramus--as well as the intact incisors are striking features of the rodent remains in these pellets.

Perhaps the most unique pellet with rodent bones is a long, thin and small pellet (6 x 2.5 x 1.4 cm) that has a partially articulated but much compressed, anterior portion of a small rodent skeleton from the maxilla at one end, through disarticulated skull parts, the vertebral column, ribs and parts of the fore limbs, including a semi-articulated manus with delicate metacarpals and phalanges (Fig. 4A). In contrast, a large (18 x 11 x 3.5 cm) flattened mass shows few bones on its unprepared surface (Fig. 3D-F). All of the pellets and masses of amalgamated pellets contain small rodent and marsupial bones, particularly evident upon preparation.

Prepared Fossil Bones

Only a few of the many fossil bones in the owl pocket deposit have been prepared free from matrix (e.g., Figs. 5, 6D-E, 7C-E). The prepared material consists mainly of five skulls of the sciurid rodent *Cedromus*, some of them with associated or articulated mandibles. These specimens were described by Korth and Emry (1991), who made one of the skulls with mandibles (USNM 256584) the type of *Cedromus wilsoni*, and referred the other skulls to the species. In the same paper, Korth and Emry (1991) described and illustrated a skull of the small aplodontid

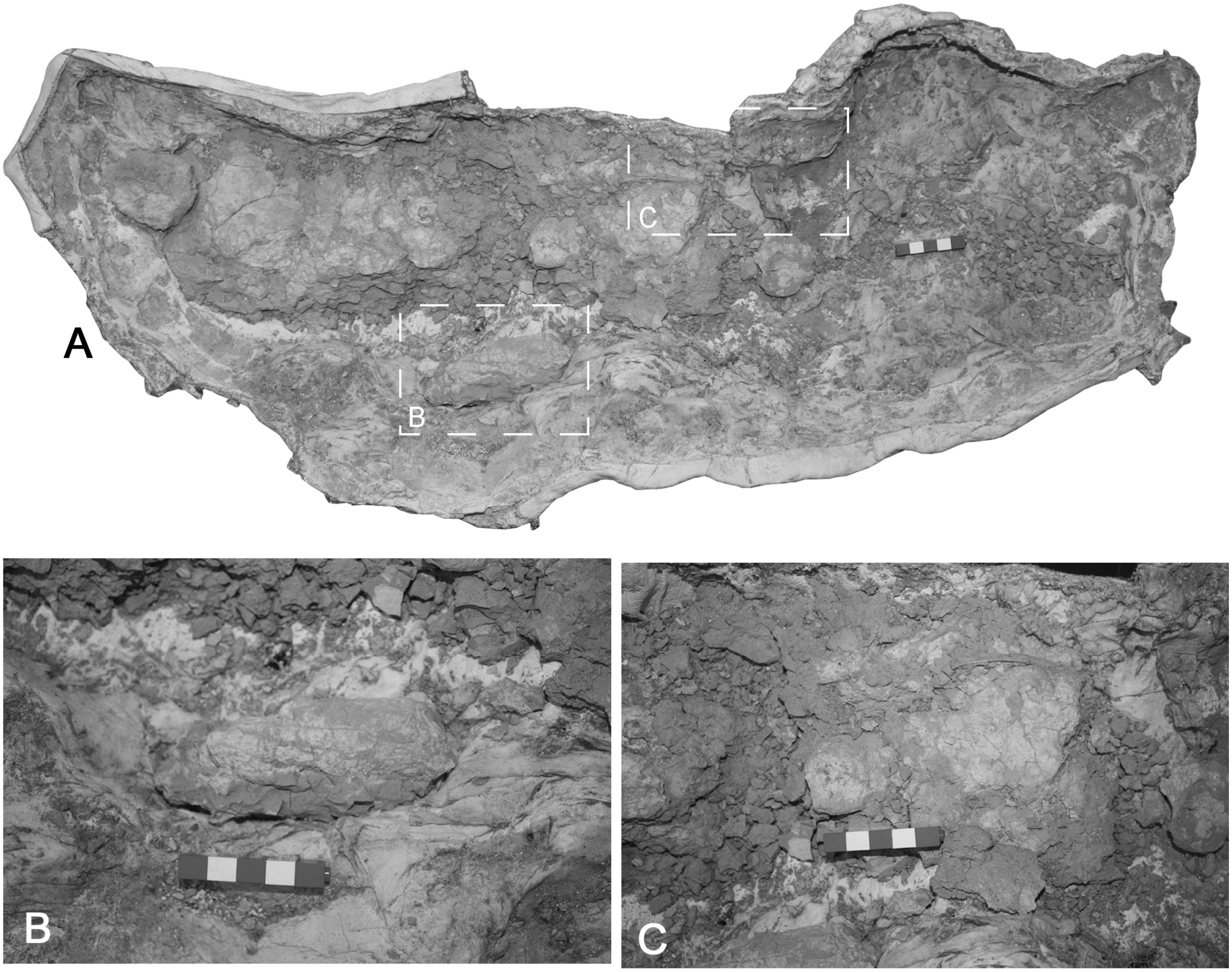

FIGURE 2. **A**, Overview of partially prepared plaster jacket containing strigilites collected at owl pocket locality. **B-C**, Close up of select areas of strigilite block showing **B**, characteristic coalesced mass and **C**, bones protruding from coalesced mass. Scale bars in cm.

rodent *Prosciurus relictus* from the assemblage. Olson (1976) described and illustrated USNM 205608, the holotype skull of the todid bird *Palaeotodus emryi*. These are the only bones prepared from the pellets that have been previously published. The bones that have been prepared are remarkably complete and well preserved, showing no evidence of abrasion or breakage (Fig. 5).

No more than 5% of the fossilized pellets have had the bones completely prepared. This makes it impossible to compile the prey species represented by the bones, bone element frequency and damage (modification) of the bones. A subjective assessment based on the prepared bones and a survey of unprepared (or partially prepared) pellets indicates that bones of small rodents (eomyids and heteromyids) dominate the assemblage, and a small mouse-sized marsupial is almost equally common. Less common are larger rodents – the sciurid *Cedromus* mentioned above, plus a single specimen of *Protosciurus*, and the small aplodontid *Prosciurus*. Other mammals are present but very rare – an insectivore (cf. *Centetodon*) and a carnivore (*Hesperocyon*). A few birds are also present – a tody and owls. A single gastropod shell is in one pellet (Fig. 6F).

We conclude that all the bones in the pellets, except those of the owls, are those of prey items, though it is possible that some bones represent animals that died in or around the pellet assemblage (purgolite). One of the owl skeletons is articulated or semi articulated and shows none of the damage that would be expected had it been eaten, and we know of no evidence that owls eat each other. However, we note the complete and pristine preservation of almost all of the bones in the owl pellet assemblage, and their presence *inside* pellets or coalesced pellets. These observations strongly support our conclusion that virtually all of the bones in the pellet assemblage are those of prey items.

However, the juvenile carnivore (*Hesperocyon*) palate in the assemblage (Fig. 6B-C) may be from an animal too large to have been a prey item of the owls that produced the vast majority of the owl pellet assemblage (N. Czaplewski, written commun., 2012). It is either the prey item of a much larger owl, the remains of an animal that became preserved in the assemblage without being consumed by an owl, or most likely part of the skull of an animal killed by an owl that discarded this skull fragment and ate part or all of the reminder of the *Hesperocyon*.

Thin Sections

We cut thin sections of two masses of amalgamated pellets for petrographic examination (Fig. 8). The first is 4.8 x 3.0 cm and composed of gray to dark gray, irregular micritic to pelmicritic matrix containing small irregular vugs and fissures filled with coarse blocky calcite cement and silica. A few small quartz grains are present in the matrix. Locally,

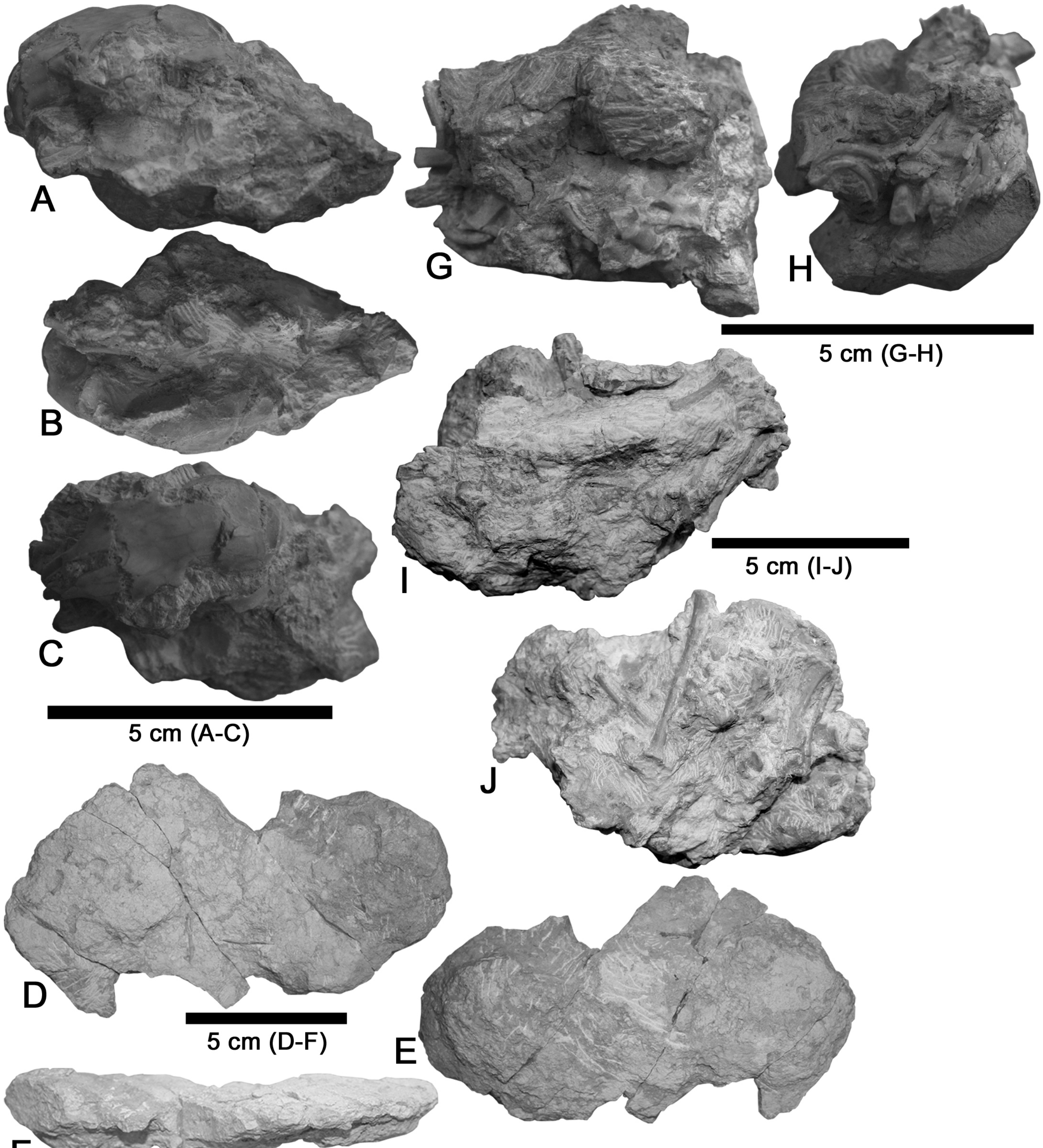

FIGURE 3. Selected strigilites from the owl pocket locality. **A-C**, Rodent skull in part of coalesced mass in three views. **D-F**, Large, flattened mass in **D-E**, topside, bottomside and **F**, edge view. **G-H**, Mass with skeletal elements in two views. **I-J**, Matrix block with skeletal elements in two views.

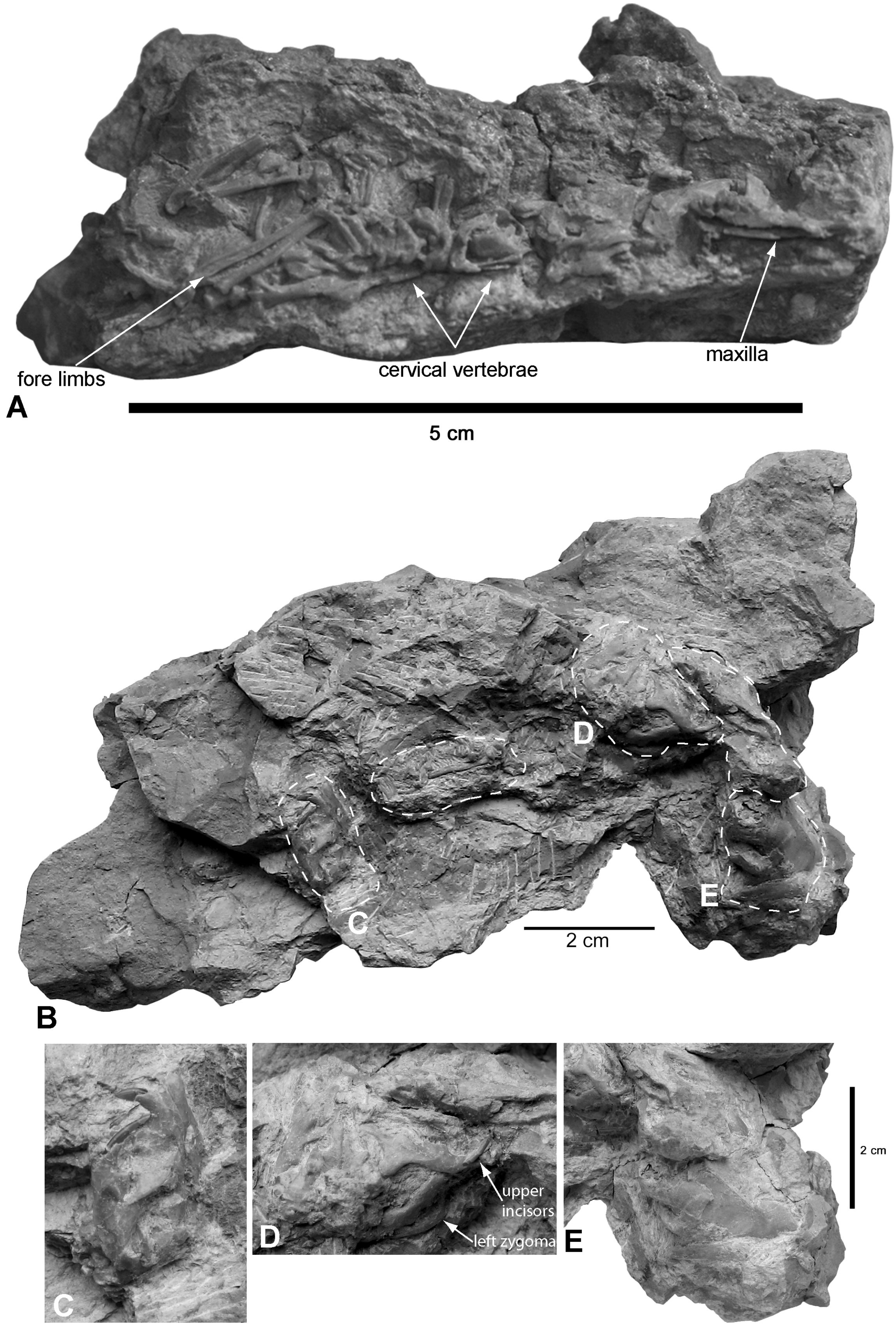

FIGURE 4. **A**, Strigilite with anterior portion of skeleton of a small rodent. **B**, Block of host rock with five discrete pellets (dashed outlines); labeled pellets are detailed in **C**-**E**. **C**, Discrete pellet with small eomyid rodent skull and mandible and other bones. **D**, Discrete pellet with two small eomyid rodent skulls with mandibles and postcranial elements. **E**, Discrete pellet with dentary and skull fragments of the sciurid rodent *Cedromus*.

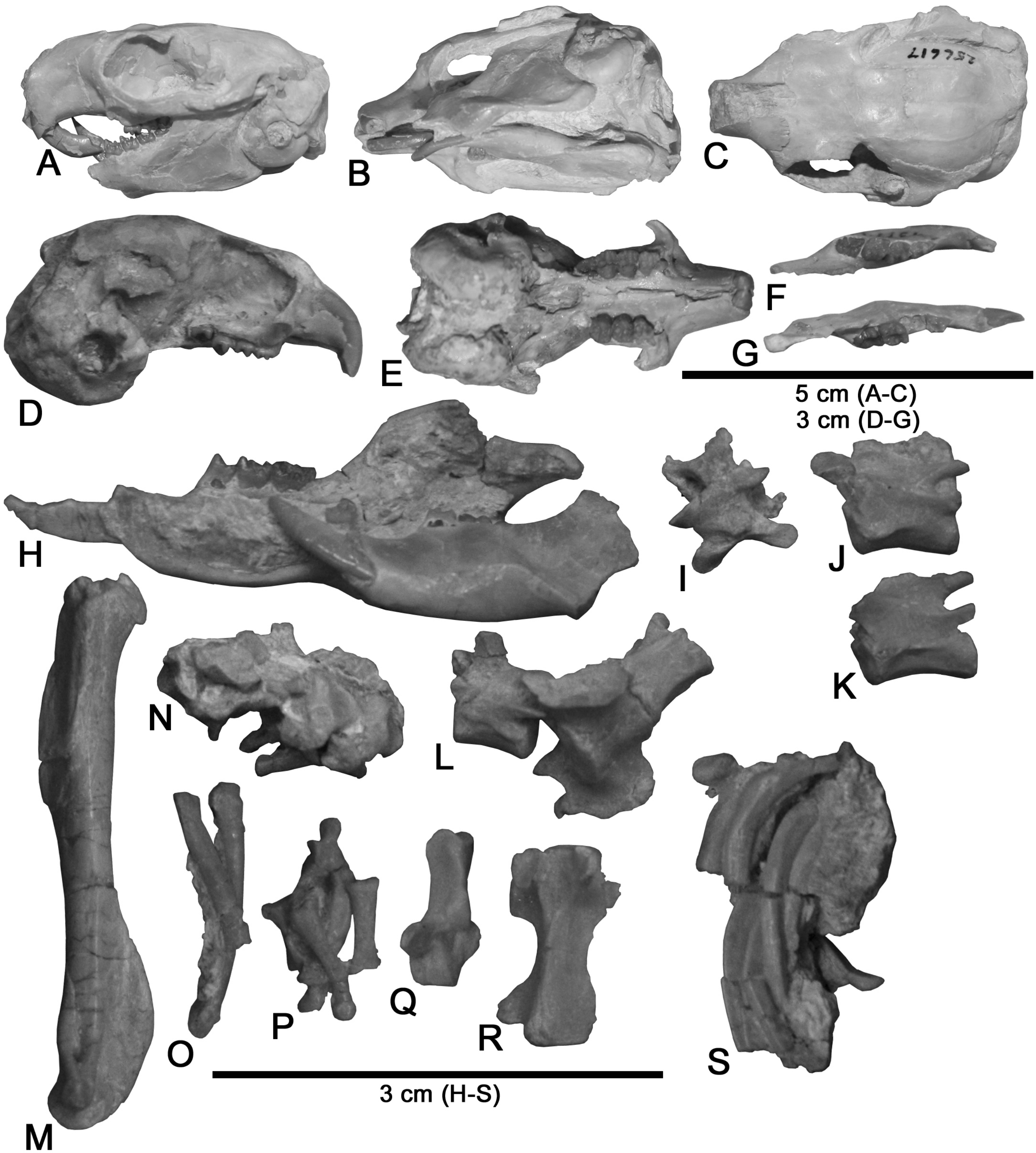

FIGURE 5. Bones fully prepared from the Owl Pocket purgolite. **A-C**, *Cedromus wilsoni*, USNM 256617, skull and lower jaws in **A**, left lateral, **B**, ventral and **C**, dorsal views. **D-G**, *Prosciurus relictus*, USNM 437793, skull in **D**, right lateral and **E**, ventral views and **F-G**, mandibles in occlusal view. **H-S**, Associated rodent skeletal elements prepared from one coalesced mass, **H**, paired mandibles, **I-L**, **R**, vertebrae, **M**, humerus, **N-P**, associated manual/pedal elements, **Q**, calcaneum, **S**, associated ribs.

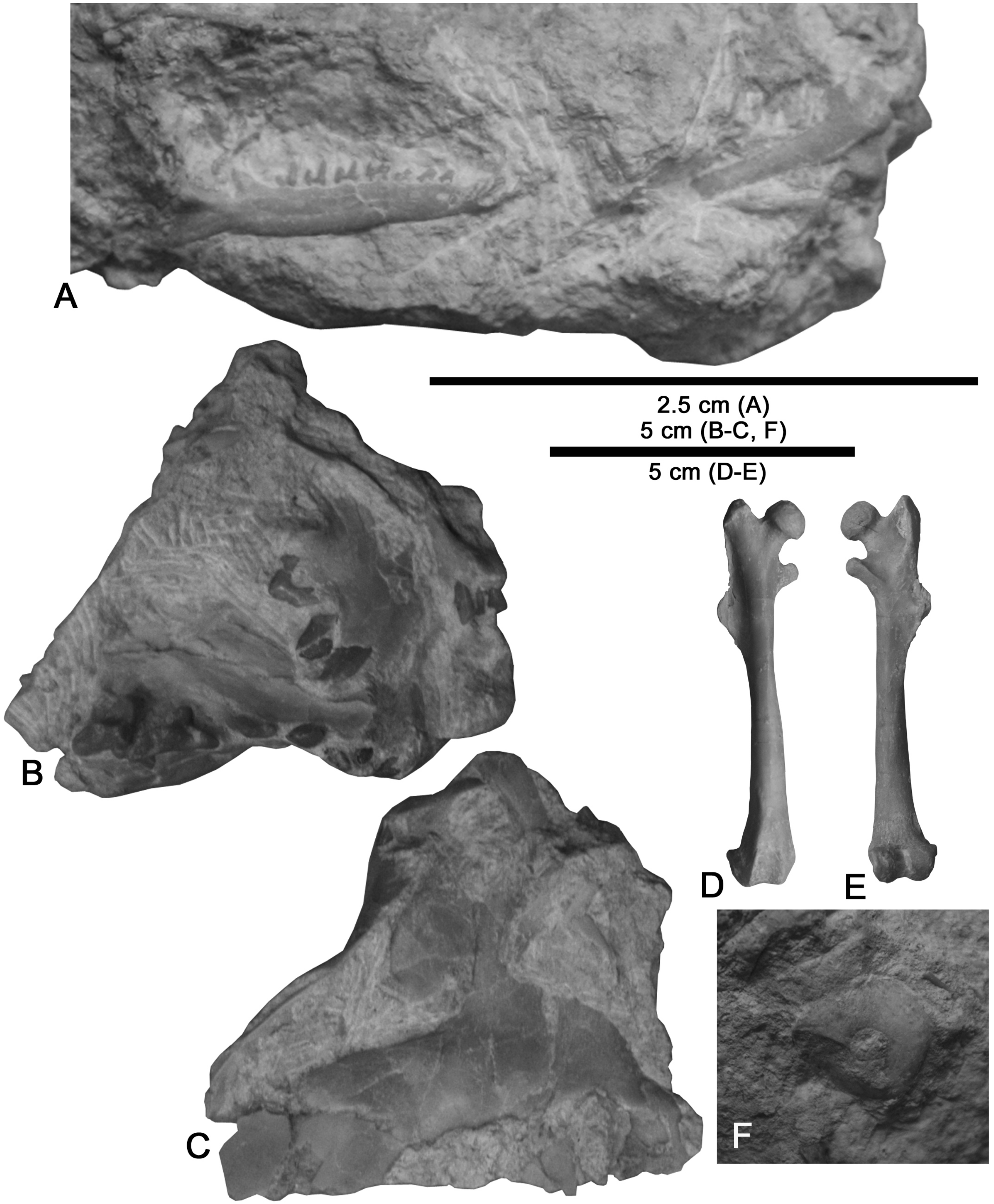

FIGURE 6. Selected elements of the Owl Pocket purgolite. **A**, Marsupial jaw fragments in pellet. **B-C**, Incomplete carnivore (*Hesperocyon*) skull in pellet **B**, occlusal and **C**, dorsal views. **D-E**, Prepared rodent femur in **D**, anterior and **E**, posterior views. Note that this is the longest bone collected from the strigilite assemblage. **F**, Gastropod in pellet.

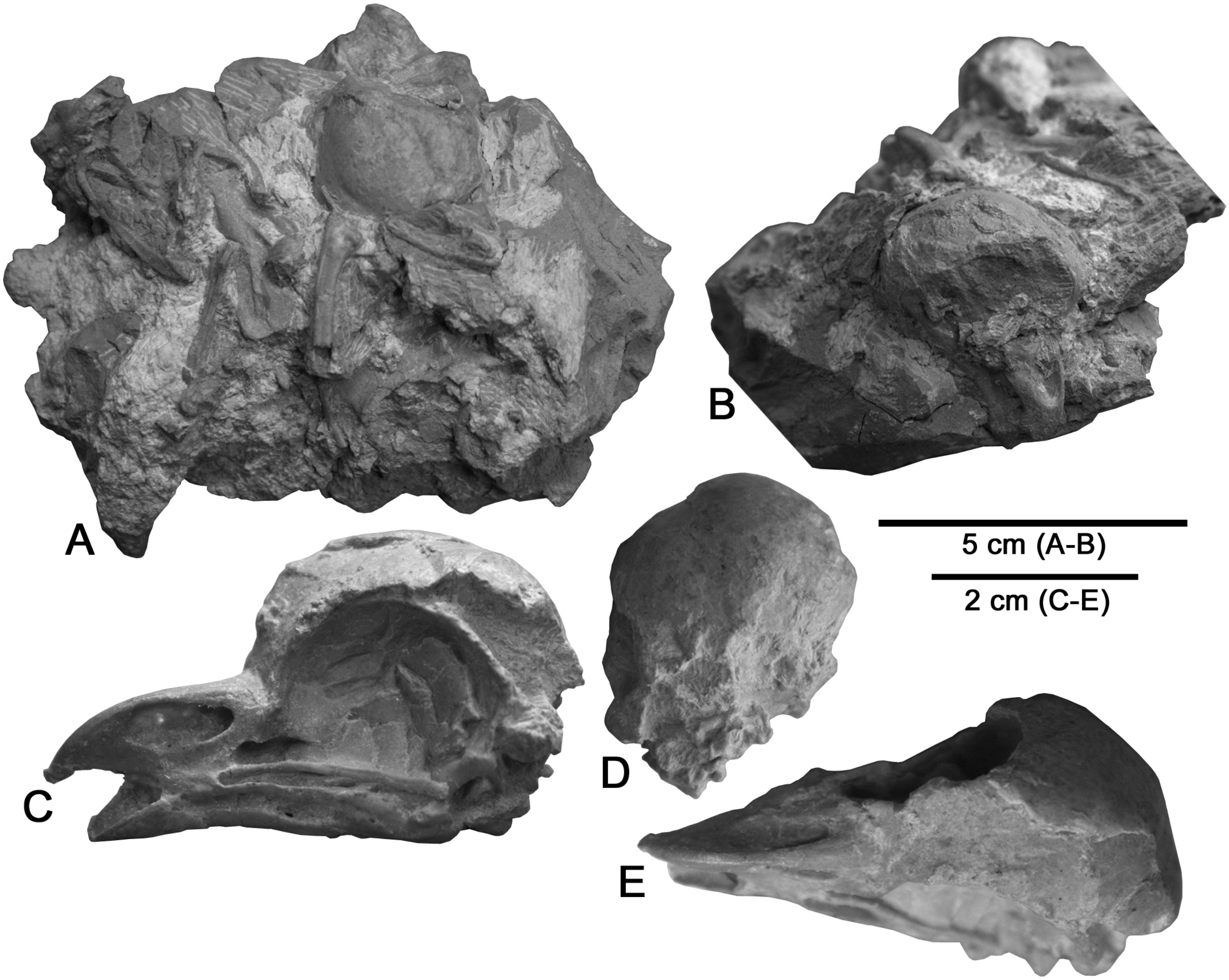

FIGURE 7. Owl bones from the Owl Pocket purgolite. **A-B**, Owl skull and bones in coalesced mass, **A**, overview of mass and **B**, closeup of owl skull. **C-E**, Prepared owl skull in **C**, left lateral, **D**, occipital and **E**, dorsal views.

irregular lamination is observed. Tubular structures are present, representing cyanobacteria. Mostly, these tubular structures are overprinted and therefore not visible. Floating in the matrix are many bone fragments, which are well preserved and up to 36 mm long (mostly a few mm long). This pellet also contains brownish silty material (probably part of the host rock in which the pellet occurs) in fissures. The siltstone is composed of abundant small quartz grains embedded in silty carbonate. Pores are filled with coarse blocky calcite and mostly with radial-fibrous silica (probably chalcedony).

The second mass studied petrographically is 4.4 x 2.5 cm and is composed of irregular, dark gray, peloidal micrite locally containing well-preserved tubular structures (cyanobacteria) and irregular voids and fissures filled with calcite cement and silica (chalcedony?). Pellet 2 contains a few small bone fragments. Rare tubular structures (cyanobacteria) are also silicified.

The presence of cyanobacteria in the Oligocene pellets from Wyoming is noteworthy. It may be characteristic of fossil owl pellets. However, in modern owl pellets, much of the volume of the pellets is hair. This raises the question of whether some of the fine tubular structures seen here in thin section (Fig. 8) are remnants (imprints) of hair. Farlow et al. (2010) reported probable hairs in coprolites, mostly as encrusted cylindrical hollows. This suggests to us that some of the tubular structures seen here in the thin sections may represent some kind of trace remnants of hairs instead of cyanobacteria. Particularly striking are the tubular filaments seen in Figure 8G, which resemble the texture of matted mammalian hair. However, further study under higher magnification will be needed to determine if any of these tubular structures have microtexture that unambiguously identifies them as the imprints of hair.

DISCUSSION

Given the presence of the strigilites within a channel-form body we interpret this concentration as an accretionary purgolite. The ecology of Recent owls suggests that ethological purgolites composed of strigilites might be expected in palaeosols or other deposits that represent points on ancient land surfaces below roosts or cliffs.

Only a small number of the fossil bones in the Orellan purgolite have been prepared. Because of this, it is not possible to provide a census of the bones or of all the prey taxa represented in the assemblage. We estimate that full preparation of all the bones in the purgolite would take at least two person-years. Until this extensive preparation job is completed, we can only make a subjective assessment of the bones present in the strigilites. Such an assessment indicates the following:

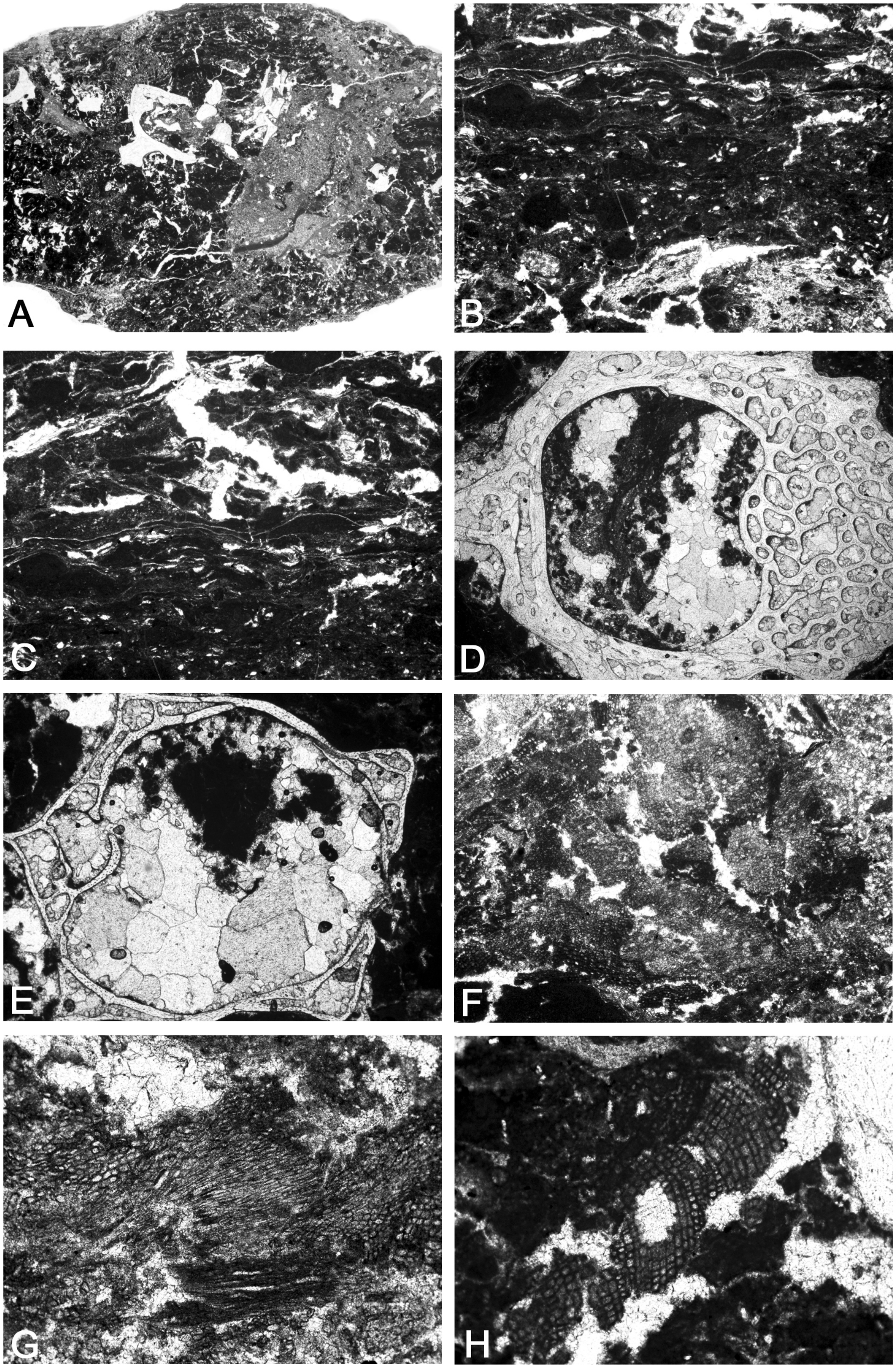

FIGURE 8. Thin section photographs of strigilites from the owl pocket assemblage (all under plane light). **A**, Overview of the composition and internal structure of an owl pellet composed of inhomogeneous micritic sediment containing a few bone fragments and many fissures and vugs filled with calcite cement and silica. Width of photograph is 35 mm. **B-C**, Detail of an owl pellet showing laminated micritic sediment (probably formed by cyanobacteria) and many fissures and vugs filled with calcite and silica cement. **D-E**, Well-preserved bone fragments embedded in an owl pellet. Interior of the bones is partly filled with pelmicritic sediment, partly with coarse blocky calcite cement. Width of **D** is 6.3 mm, of **E** 3.2 mm. **F**, Detail of an owl pellet composed of micritic sediment displaying tubular structures representing cyanobacteria colonies. Width is 3.2 mm. **G-H**, Well-preserved tubular structures (cyanobacteria) within an owl pellet. Width of photographs is 1.2 mm.

1. The vast majority of bones belong to one or more species of small mouse-sized rodents, and a small marsupial of the same approximate size. Other mammal taxa – an insectivore, a small hesperocyonid carnivore, sciurids and other relatively large rodents – are relatively uncommon. Thus, one (or a few) species of small rodent dominate the bone assemblage.

2. Virtually all bones of the skeleton of the rodents are present, including complete (or nearly complete) skulls and mandibles, vertebrae and associated (articulated to semi-articulated) bone material (e.g., Fig. 5). The quality of bone preservation is very high – there is little breakage and no abrasion, and what there is appears to be largely post-depositional.

The strigilite deposit described here thus well meets most of the criteria Dodson and Wexlar (1979, p. 283) first established as "important general characteristics" of owl pellet accumulations:

1. Abundant and high quality preservation of bone.
2. An extreme inequitability of species distribution – small rodents and marsupials dominate the assemblage, whereas other mammal species are relatively rare.
3. Good representation of all skeletal parts, including mandibles and vertebrae.
4. High representation of mandibles and complete femora.
5. Intact (or largely intact) skulls.

Extant and geologically relatively young (mostly Pleistocene) bird pellets provide diverse information on the mechanism and effects of predation, on the predators as bone collectors, on the size of the predator's territory, on predators as prey, on the size and availability of prey, and on species representation in the prey assemblages, among other things (e.g., Andrews, 1990; Elbroch et al., 2001). However, detailed analyses require complete disaggregation of pellets or other means of extracting all the bones in the pellets so they can be identified, counted and classified with regard to nature of breakage and other forms of bone modification.

As stated above, all the bones in the owl pocket assemblage are reasonably inferred to be those of prey eaten and regurgitated by the owls. The taxonomic identity of the owl species that produced the assemblage is unknown. The owl skeletons that occur in the pellet assemblage have not been described, but based on skull measurements these fossil owls are very close to the size of the extant Burrowing Owl, *Athene cunicularia*, and thus are of appropriate size to have preyed on at least the smaller rodents and marsupials that occur in the discrete pellets, and which make up the overwhelming majority of prey individuals in the strigilite deposit. It is possible that the owl skeletons in the deposit are of individuals that fell from a nest (or maybe the whole nest collapsed) and became integrated into the deposit of pellets.

In extant North American owls, maximum prey size increases with overall owl body size (Earhart and Johnson, 1970). This relationship was further quantified by Czaplewski (2011, fig. 14) by providing a figure charting the relationship between owl predator body mass and approximate mass of the largest recorded prey. Thus, by examining and estimating the maximum prey size we can extrapolate the size of the owls that generated the strigilites that form the owl pocket assemblage. The largest and most complete skeletal element for which total body size can be extrapolated is a *Cedromus wilsoni* skull, USNM 256617, which is 44 mm in condylobassal length (Fig. 5A-C). This fits well within the lower size range of the extant American red squirrel (*Tamiasciurus hudsonicus*), which has a condylobassal length of 42-50 mm (Steele, 1998, p. 2), making a small individual of *T. hudsonicus* a reasonable size analog for *C. wilsoni*. The overall size of *T. hudsonicus* is 200-250 g, suggesting that the *C. wilsoni* specimen from the owl pocket assemblage was ~215 g in overall size. When applying this estimated body mass to the predator/prey chart of Czaplewski (2011, fig. 14) the result is the predator was likely 150 to 300 g in overall size, actually quite similar in size to the Verde fossil owl reported by Czaplewski (2011). As mentioned above, the extant Burrowing Owl, *Athene cunicularia* is a close size analog for the fossil owl occurring in the owl pellet assemblage; an internet source gives 170 to 214 g as the weight range of Burrowing Owls. Thus, the fossil owls associated with the pellets are within the size range estimated from Czaplewski's (2011, fig. 14) chart for a predator capable of preying on the squirrel *Cedromus*, although a predator of this size would have to consume *Cedromus* in bite-size pieces rather than swallowing it whole.

Various workers have claimed that owl pellets are an important source of fossilized microvertebrate bones (e.g., Dodson and Wexlar, 1979; Kusmer, 1990; Andrews 1990; Terry, 2004). As Andrews (1990, p. 34) succinctly put it "owls are probably the major contributors to fossil bone assemblages." Nevertheless, very few bona fide Tertiary strigilites have been published in the paleontological literature (Hunt and Lucas, 2007; Mhyrvold, 2011). Indeed, other than Czaplewski (2011) and the Orellan pellets documented here, there is little prima facie evidence of a North American Tertiary owl-pellet-produced accumulation of fossil bones, even though the body fossil record of owls extends back over more than 50 million years to the late Paleocene (Rich and Bohaska, 1981; Mourer-Chauvire, 1994).

Most Tertiary microvertebrate assemblages are not characterized by complete, well-preserved bones, especially "pristine" skulls and mandibles. Instead, isolated teeth and a selection of complete compact bones (such as vertebral centra and foot bones) and fragments of other bones is typical, indicative of hydraulic sorting and concentration (e.g., Korth, 1979). In some geologically-young settings, such as Pleistocene-Holocene caves, owl pellets are an important component in fossil/subfossil bone accumulation (Andrews, 1990). However, the importance of owl pellets to the accumulation of Tertiary microvertebrate fossil assemblages has clearly been overstated for decades.

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