



A new talpid from the late Eocene of North America

KAREN J. LLOYD and JAELYN J. EBERLE

The origin and early evolution of talpids (moles, shrew-moles, and desmans) is not well understood, in large part due to the poor fossil record of early talpids. Here we report the oldest known talpid from North America, *Oreotalpa florissantensis* gen. et sp. nov., based upon a tiny dentary with m1–m3 discovered in upper Eocene (Chadronian) strata of the Florissant Formation, Florissant Fossil Beds National Monument, Colorado. *Oreotalpa* extends the North American record of talpids back by some six Ma and appears temporally correlative with the oldest documented talpids from the late Eocene of Europe. While others have postulated a Eurasian origin for talpids, discovery of *Oreotalpa* suggests that the evolution of the group was underway in North America by late Eocene time and raises the possibility of a North American origin.

Introduction

The Talpidae (moles, shrew-moles, and desmans) comprise some 17 living genera and 42 species of small-bodied, semi-aquatic and subterranean burrowers that are widely distributed throughout temperate regions of Europe, Asia, and North America (Nowak 1991; Sánchez-Villagra et al. 2006). Given their small size and cryptic lifestyles, talpids have been challenging to study.

Most authors (e.g., Hutchison 1968; Yates and Moore 1990; Whidden 2000; Sánchez-Villagra et al. 2006) agree that talpids form a monophyletic group, although evolutionary affinities within the family are controversial and the few published phylogenetic studies focus on modern genera. While talpids traditionally were placed with hedgehogs, shrews, tenrecs, golden moles, and solenodons in the Lipotyphla, this grouping appears to be paraphyletic. Based upon more recent molecular (e.g., Roca et al. 2004) and combined molecular-morphology (e.g., Asher 2007) studies, talpids have been allied only with shrews (soricids) and hedgehogs (erinaceids) in the Eulipotyphla (Waddell et al. 1999; Murphy et al. 2001; Douady and Douzery 2003). McKenna and Bell (1997) placed talpids in the order Erinaceomorpha within the grandorder Lipotyphla, while Hutterer (2005) placed them within the Order Soricomorpha. The origin of talpids is poorly understood, due in large part to the sparseness and fragmentary nature of early talpid fossils.

Here we describe a new fossil talpid based upon a right dentary discovered in uppermost Eocene (Chadronian) strata of the Florissant Formation, central Colorado, USA. The Florissant fossil extends the North American record of Talpidae back by at least six Ma. Up until this discovery, the oldest documented North American talpids were late Oligocene in age (Macdonald

1970; McKenna and Bell 1997). The Florissant talpid appears to correlate in age with the oldest known talpid, *Eotalpa*, from latest Eocene (upper Ludian) strata of the London Basin on the Isle of Wight (Sigé et al. 1977). The Ludian is correlative to the Priabonian age (Savage and Russell 1983) and Headonian European Land Mammal Age, which, in turn, is correlated to the Chadronian North American Land Mammal Age (McKenna and Bell 1997). There is also an undetermined genus and species of Talpinae reported from the terminal Eocene of eastern Kazakhstan (Gabunia and Gabunia 1987; Lopatin 2002a).

The talpid reported here (FLFO 5813) was discovered at University of Colorado Museum of Natural History (UCM) locality 92179 in the Florissant Formation, Florissant Fossil Beds National Monument, central Colorado, USA (Fig. 1). Comprised of lake shales, volcanic sediments, and fluvial deposits, the Florissant Formation was defined by Evanoff et al. (2001), who recognized six informal subdivisions. UCM locality 92179 is within the lower mudstone unit, directly below the famous petrified forest area of the National Monument at the 29-meter level of the stratigraphic section measured by Evanoff et al. (2001: fig. 4). The lower mudstone unit is interpreted as representing stream deposits, and in its top few meters, a lahar deposit that buried the petrified forest (Evanoff et al. 2001). Mammalian biostratigraphy (Worley-Georg and Eberle 2006), paleomagnetic analyses (Prothero and Sanchez 2004), and a weighted mean age of 34.07 ± 0.10 Ma from $^{40}\text{Ar}/^{39}\text{Ar}$ analyses of pumice (Evanoff et al. 2001) indicate a latest Eocene (Chadronian) age for the Florissant Formation.

Institutional abbreviations.—CMNH, Carnegie Museum of Natural History, Pittsburgh, USA; FLFO, Florissant Fossil Beds National Monument, Florissant, USA; UCM, University of Colorado Museum of Natural History, Boulder, USA.

Other abbreviations.—Lowercase letters (e.g., m1) designate teeth from lower jaws; L, left tooth (e.g., Lm1); R, right tooth (e.g., Rm1); M/m, molar; A-P length, anteroposterior length; WT_{ri}, width of trigonid; WT_{al}, width of talonid.

Material and methods

The Florissant talpid was recovered through dry-screening and sorting under magnification of loose sediment recovered from UCM locality 92179. The Florissant talpid is catalogued in the FLFO collection, but deposited in the Fossil Vertebrate Collection at the UCM; consequently, it has a UCM catalog number as

well. Detailed locality information is on file at FLFO and in the Paleontology Section at UCM. The fossil was compared with specimens and casts at the UCM, the American Museum of Natural History, the Field Museum of Natural History, and with descriptions in the literature. Measurements were done via a SpotTM camera attached to a microscope and calibrated SpotTM version 3.5.8 for Windows XPTM software, and are in millimeters (mm). Cusp terminology and measurements follow Hutchison (1974: fig. 1). The classification follows McKenna and Bell (1997).

Systematic paleontology

Grandorder Lipotyphla Haeckel, 1866

Order Erinaceomorpha Gregory, 1910

Family Talpidae Fischer von Waldheim, 1817

Genus *Oreotalpa* nov.

Etymology: *Oreo* (Greek): mountain, in reference to Colorado's Rocky Mountains where the talpid was discovered; *talpa* (Latin): mole.

Type species: *Oreotalpa florissantensis* gen. et sp. nov., by monotypy.

Diagnosis.—As for the type species.

Oreotalpa florissantensis sp. nov.

Fig. 2, Table 1.

Etymology: *Florissantensis*, named for Florissant Fossil Beds National Monument.

Holotype: FLFO 5813 (UCM 99553), a right dentary fragment with m1–m3.

Type locality: UCM locality 92179, Florissant Fossil Beds National Monument, Florissant, Colorado, USA.

Type horizon: Florissant Formation, latest Eocene (Chadronian).

Diagnosis.—Small talpid with m2>m1>m3. Differs from most derived talpids, but similar to some Oligocene talpids, in having m1 with metaconid taller than entoconid. Similar in size and morphology to European *Myxomygale* (Oligocene–Miocene) and Asian *Mongolopala* (Oligocene). Differs from Oligocene *Myxomygale antiqua* and *M. vauclusensis* in more anteriorly-placed posterior mental foramen (under middle of m1). Differs from *M. antiqua*, but as in *M. vauclusensis* and Miocene *M. gracilis*, m1<m2. Differs from *M. gracilis* in more posteriorly-placed mental foramen and cristid obliqua does not join metacristid. Differs from *M. vauclusensis* and Asian Oligocene *Mongoloscapter* in absence of metastyliid and more labial placement of cristid obliqua on posterior wall of metaconid. Differs

Table 1. Dental measurements (in mm) of *Oreotalpa florissantensis* gen. et sp. nov., FLFO 5813 (holotype), right dentary fragment with m1–m3 from UCM locality 92179, Florissant Formation, Florissant Fossil Beds National Monument, Colorado, USA.

| Specimen | Tooth position | A-P length | WTri | WTal |
|-----------|----------------|------------|-------|-------|
| FLFO 5813 | m1 | 1.54 | 0.97 | 1.08 |
| | m2 | 1.61 | 1.01* | 1.06* |
| | m3 | 1.35 | 0.85 | 0.70 |

* estimated widths due to damage along lingual margin.

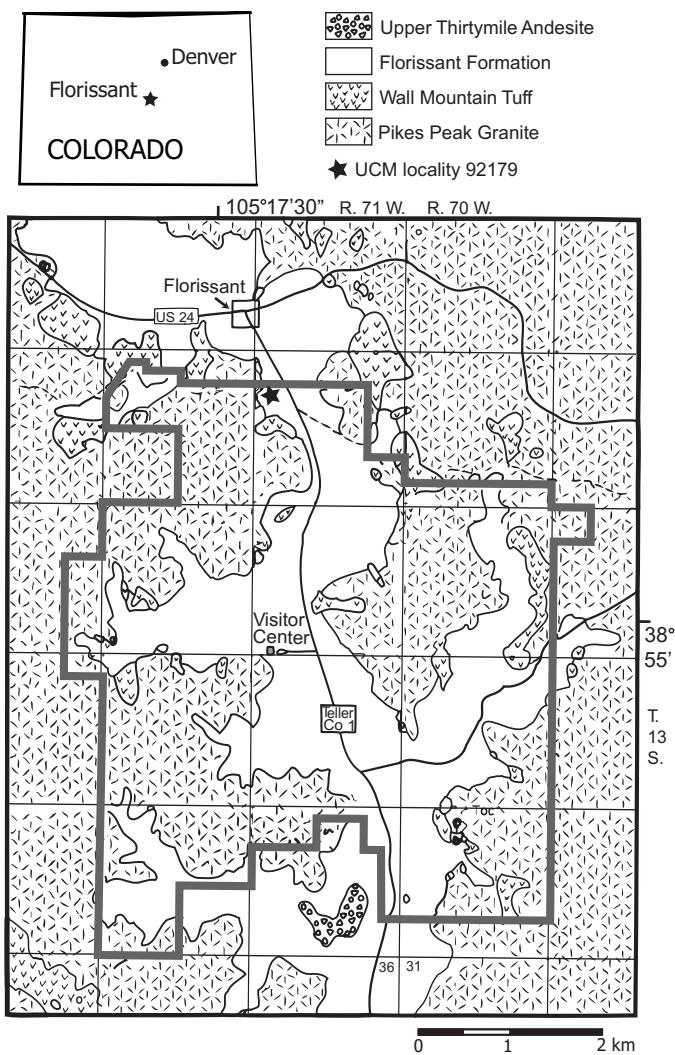


Fig. 1. Geologic map of Florissant Fossil Beds National Monument in central Colorado, USA, modified from Evanoff et al. (2001: fig. 1). Areal extent of the Monument is outlined by thick gray line.

from Asian Oligocene *Mongolopala* in m1<m2 and absence of lingual cingulid below paraconid. Differs from late Oligocene North American *Quadrudens wilsoni* in its smaller size (~50%), discontinuous labial cingulid, and a smaller, narrower m1 that lacks a rectangular trigonid.

Description.—FLFO 5813 (UCM 99553) is a right dentary fragment with m1–m3 (Fig. 2). The posterior mental foramen is positioned under the middle of m1. The apices of several cusps on m1–m2 are broken, but the cusps on m3 are intact and unworn, and consequently we used this tooth as the basis for discussing relative cusp height differences below. The m2 is slightly longer than m1, which, in turn, is longer than m3, as is characteristic of most talpids (Sánchez-Villagra et al. 2006), although in some Oligocene talpids such as *Myxomygale antiqua* (Crochet 1974) and *Mongolopala tathue* (Ziegler et al. 2007), m1>m2. On m1, the trigonid is noticeably narrower than the talonid, while they are closer in width on m2 (Table 1). On m3, the trigonid is wider than the talonid, although they are similar

in length. The protoconid is the tallest molar cusp, the paraconid is considerably smaller and lower than the proto- and metaconids, and the hypo- and entoconids are similar in height. The metaconid is taller than the entoconid. A postcristid runs between the hypoconid and entoconid, and the hypoconulid is separate. A long cristid obliqua extends from the hypoconid diagonally to the posterior wall of the trigonid lingual to the midline of the tooth and ascending the wall of the metaconid, although not to its apex. A V-shaped talonid notch occurs on m1–m2, as in most living talpids (Sánchez-Villagra et al. 2006), although the meta- and entocristids are high enough to lingually close off a relatively deep talonid basin. The m1 and m2 bear a tiny hypoconulid (= entostyloid of Hutchison 1974) that is situated directly posterior to and below the entoconid. The m3 has an unreduced talonid that lacks a hypoconulid. The labial cingulid is not continuous around the hypoconid and protoconid. There is no lingual cingulid. An anterior cingulid is present on m1–m3. Although m1–m2 bear a posterior cingulid, m3 lacks one.

Discussion.—*Oreotalpa* appears morphologically most similar to Oligocene–Miocene *Myxomygale* from Europe and lower Oligocene *Mongolopala* from Asia. Incidentally, Ziegler et al. (2007) noted that *Mongolopala* is morphologically most similar to *Myxomygale*. Oligocene *Myxomygale antiqua* and *M. vauclusensis* differ from *Oreotalpa* in having a more posteriorly-placed mental foramen (under posterior root of m1). Additionally, *M. vauclusensis* differs from *Oreotalpa* in bearing a metastyloid and more lingually-placed cristid obliqua (Crochet 1995). Late Oligocene *Mongoloscapter* also bears a metastyloid (Lopatin 2002a). Early Oligocene *Mongolopala* differs from *Oreotalpa* in having m1>m2 and a weak lingual cingulid on the paraconid (Ziegler et al. 2007).

Up until discovery of *Oreotalpa*, the earliest documented North American talpid was the late Oligocene (Arikareean) *Quadrodens wilsoni* from the Sharps Formation, South Dakota, which was originally described as an erinaceid (Macdonald 1970). *Q. wilsoni* is about 50% larger than *Oreotalpa* and bears a relatively larger m1 that is wider than m2, with a broad, flattened, rectangular trigonid that comprises almost two-thirds of the tooth. Lower molars of *Q. wilsoni* have continuous labial cingulids (Macdonald 1970), unlike *Oreotalpa*, and appear to be more inflated, perhaps adapted to a more durophagous diet.

Because talpid molars are morphologically similar to those of soricids (shrews), chiropterans (bats), and proscalopids, a comparison of *Oreotalpa* to representatives of these groups is given below.

Soricidae was traditionally considered the sister group to talpids (e.g., Butler 1988). *Domnina*, the dominant North American sorcid during Chadronian time, bears a mental foramen beneath m1 and molars that look superficially quite similar to *Oreotalpa*. However, sorcids are more primitive than talpids in having m1>m2>m3 (Sánchez-Villagra et al. 2006). Sorcid molars are differentiated from *Oreotalpa* by having an entoconid that is noticeably taller than the hypoconid and a shallow hypoflexid (Tejedor et al. 2005). Additionally, in sorcids, the molar trigonid is longer due to an anteriorly-expanded paracristid and paraconid. Mo-

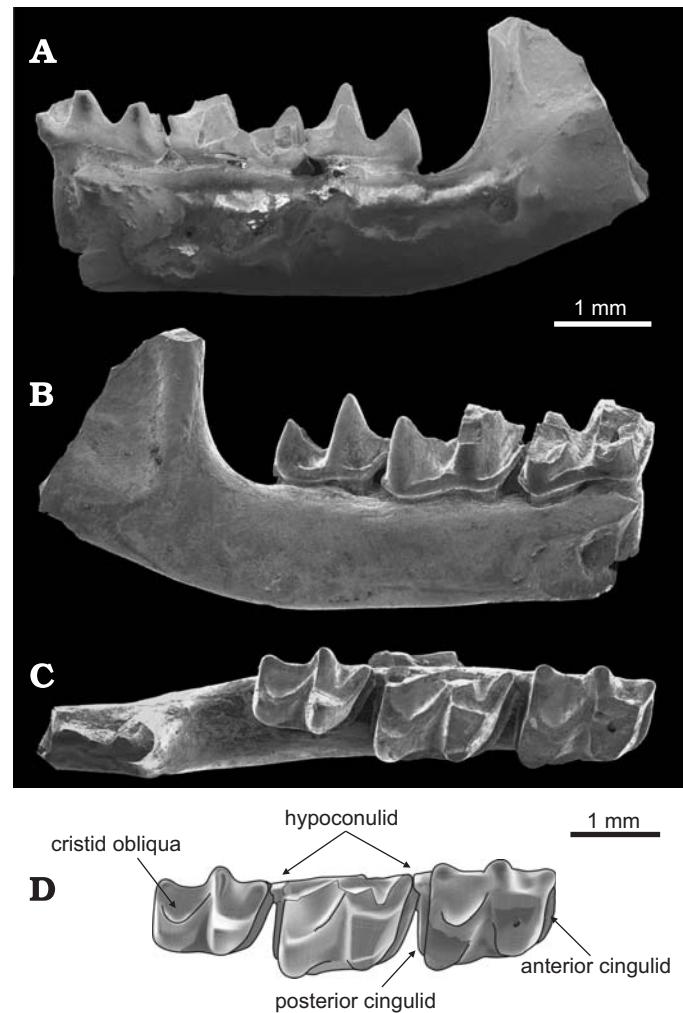


Fig. 2. Talpid mammal *Oreotalpa florissantensis* gen. et sp. nov., FLFO 5813 (holotype), right dentary with m1–m3 from UCM locality 92179, Florissant Formation, Florissant Fossil Beds National Monument, Colorado, USA; latest Eocene (Chadronian). SEM micrographs; in lingual (A), labial (B), and occlusal (C) views, and explanatory drawing of occlusal view (D). Anterior is to the right. Original drawing by Leigh Anne McConaughey. For B, C, and D, anterior is to the right.

Iars bear continuous lingual and labial cingulids, and m3 has a reduced talonid (Repenning 1967; personal observations).

Chiropterans have dilambodont molars similar to those of several insectivorans, including talpids. However, chiropteran molars are characterized by presence of a complete, continuous labial cingulid (Hand et al. 1994), as well as a hypoconid that is taller than the entoconid, straight entocristid, and a cristid obliqua that terminates on the trigonid wall slightly labial to the midline (Tejedor et al. 2005). Unlike talpids, the posterior mental foramen is more anteriorly placed and under the premolars in bats.

Proscalopids, appearing in the Chadronian with talpid-like teeth, traditionally were placed within Talpidae, although differences in the functional morphology of the skull and forelimb support placement in a separate family (Barnosky 1981). Lower molars of early proscalopids, typified by those of early Oligocene (Orellan) *Oligoscalops* and Oligocene–Miocene (Whitneyan–Arikareean) *Proscalops*, bear W-shaped cristids and relatively

narrow talonids, especially on m3 where the talonid is considerably narrower than the trigonid (Reed 1961; Barnosky 1981). In contrast to *Oreotalpa*, *Oligoscalops* molars lack a distinct anterior cingulid. Lower molars on the holotype of *Oligoscalops whitmannensis* (CMNH P25800) are worn and incomplete, and their lengths could not be measured. However, in *Proscalops*, m1 is longer than m2 (Reed 1961), in contrast to talpids where the opposite occurs.

Discovery of *Oreotalpa* implies that the talpid lineage extends back at least to late Eocene time in North America, which is consistent with some molecular estimates of divergence times that suggest eulipotyphlan subfamilies originated during the Eocene (Douady and Douzery 2003). Phylogenetic analysis based primarily upon nuclear DNA (Roca et al. 2004) suggests that soricids (shrews) and erinaceids (hedgehogs) form a clade that is the sister group to talpids. If correct, this implies that a talpid ghost lineage extends back at least into the Paleocene, based upon the earliest erinaceid, *Litolestes*, from North America (McKenna and Bell 1997).

From a biogeographic standpoint, appearance of three morphologically similar talpids, *Oreotalpa* (latest Eocene, North America), *Myxomygale* (early Oligocene, Europe), and *Mongolopala* (early Oligocene, Asia) suggests Holarctic intercontinental dispersal of talpids prior to latest Eocene and raises the question of talpid origins. To date, most workers have favored a Eurasian origin primarily because isolated teeth of the earliest Talpidae were found in the Upper Eocene of Europe and assigned to *Eotalpa* and *Geotrypus* (Sigé et al. 1977; McKenna and Bell 1997; Whidden 2000), and an undetermined genus and species of Talpinae is known from the latest Eocene of eastern Kazakhstan (Gabunia and Gabunia 1987). Within the biostratigraphic resolution, all appear roughly coeval. Although *Oreotalpa* does not preclude a Eurasian origin for the Talpidae, it raises the possibility of a North American origin for the group. Proscalopidae, which first appeared in the latest Eocene of North America, has been tentatively considered the sister group to Talpidae by some workers (e.g., Reed 1961; McKenna and Bell 1997). In addition, soricids and erinaceids may form a clade that is the sister group to talpids (Roca et al. 2004). In any event, presence of talpids in the late Eocene of North America, when considered alongside the assumption that sister taxa originate in the same geographic area, provides support for a North American origin for talpids given the antiquity of proscalopids and erinaceids in North America. Biogeography of the oldest soricids is more uncertain. While *Domnina* from the middle Eocene (Uintan) of North America was long considered the oldest, basal soricid, recent discovery of an Asian middle Eocene soricid may predate *Domnina* (Lopatin 2002b). The age of these early soricids ultimately rests on refinement of biostratigraphic correlations between Asia and North America.

The Eocene talpid record is currently based upon *Oreotalpa* from North America (this report), the European genera *Eotalpa* and *Geotrypus* (Sigé et al. 1977; McKenna and Bell 1997; Whidden 2000), and an undetermined genus and species from eastern Kazakhstan (Gabunia and Gabunia 1987). *Eotalpa* is known from two isolated upper molars (RM1 and M2; Sigé et al. 1977) and the

holotype of *Geotrypus* includes a partial mandible with premolars (Hugueney 1972), precluding their direct comparison with the lower molars of *Oreotalpa* and making it challenging at best to include these taxa in recent talpid phylogenies based mostly on cranial and postcranial characters (Sánchez-Villagra et al. 2006), musculature (Whidden 2000), and molecular sequences (e.g., Shinohara et al. 2003). Our understanding of the geographic origins of talpids requires discovery of many more (and complete) fossils combined with comprehensive phylogenetic analyses that include both fossil and living talpid taxa. Nevertheless, discovery of *Oreotalpa* indicates that talpids had dispersed between North America and Eurasia by late Eocene time.

Acknowledgments.—Paleontological fieldwork was conducted in 2003–2005 within the boundaries of Florissant Fossil Beds National Monument thanks to a permit issued to us by the National Park Service. We thank Herbert Meyer (FLFO) for assistance with the permitting process, and Emmett Evanoff (University of Northern Colorado, Greeley, Colorado, USA) for sharing valuable information concerning the fossil locality. Marie Worley-Georg (Chicago, Illinois, USA) recovered the talpid specimen via sorting sedimentary matrix under magnification. Peter Robinson (UCM) and the late Malcolm McKenna (American Museum of Natural History, New York, New York, USA and UCM) provided valuable advice concerning taxonomic identification. James Honey, Mariko Kageyama, and Toni Culver (UCM), Darrin Lunde (American Museum of Natural History, New York, New York, USA), and William Simpson (Field Museum of Natural History, Chicago, Illinois, USA) loaned specimens and casts for comparative purposes. Sara Olesiak (University of Colorado, Boulder, Colorado, USA) produced SEM images of the talpid specimen. We benefited considerably from the comments of anonymous reviewers on an earlier draft of the manuscript. We especially thank Richard Cifelli (Oklahoma Museum of Natural History, Norman, Oklahoma, USA), Robert Asher (Museum of Zoology, Cambridge University, Cambridge, UK), Alexei Lopatin (Paleontological Institute, Russian Academy of Sciences, Moscow, Russia), and Reinhard Ziegler (Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany) for their constructive comments and advice.

References

- Asher, R.J. 2007. A web-database of mammalian morphology and a reanalysis of Placental phylogeny. *BMC Evolutionary Biology* 7: 108.
- Barnosky, A.D. 1981. A skeleton of *Mesoscalops* (Mammalia: Insectivora) from the Miocene Deep River Formation, Montana, and a review of proscalopid moles: Evolutionary, functional, and stratigraphic relationships. *Journal of Vertebrate Paleontology* 1: 285–339.
- Butler, P.M. 1988. Phylogeny of the insectivores. In: M.J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods, Vol. 2, Mammals*, 117–141. Clarendon Press, Oxford.
- Crochet, J.Y. 1974. Les Insectivores des Phosphorites du Quercy. *Palaeovertebrata* 6: 109–159.
- Crochet, J.Y. 1995. Le Garouilles et les sites contemporains (Oligocène, MP 25) des Phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertébrés. 4. Marsupiaux et Insectivores. *Palaeontographica A* 236 (1–6): 39–75.
- Douady, C.J. and Douzery, E.J.P. 2003. Molecular estimation of eulipotyphlan divergence times and the evolution of “Insectivora.” *Molecular Phylogenetics and Evolution* 28: 285–296.
- Evanoff, E., McIntosh, W.C., and Murphey, P.C. 2001. Stratigraphic summary and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology of the Florissant Formation, Colorado. In: E. Evanoff, K.M. Gregory-Wodzicki, and K.R. Johnson (eds.), *Fossil Flora*

- and Stratigraphy of the Florissant Formation, Colorado. *Proceedings of the Denver Museum of Nature and Science, Series 4* 1: 1–16.
- Fischer von Waldheim, G. 1817. Adversaria zoologica. *Mémoires de la Société Impériale des Naturalistes Moscou* 5: 357–472.
- Gabunia, L.K. and Gabunia, V.J. 1987. On the question of the origin of the Talpinae [in Russian]. *Soobščenija Akademii Nauk Gruzinskoy SSR* 125 (3): 649–651.
- Gregory, W.K. 1910. The orders of mammals. *Bulletin of American Museum of Natural History* 27: 1–524.
- Haeckel, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie. Band I: Allgemeine Anatomie der Organismen. Kritische Grundzüge der mechanischen Wissenschaft von den entwickelten Formen der Organismen, begründet durch die Descendenz-Theorie.* xxxii + 574 pp. Georg Reimer, Berlin.
- Hand, S.J., Novacek, M., Godthelp, H., and Archer, M. 1994. First Eocene bat from Australia. *Journal of Vertebrate Paleontology* 14: 375–381.
- Hugueney, M. 1972. Les Talpidés (Mammalia, Insectivora) de Coderet-Bansat (Allier) et l'évolution de cette famille au cours de l'Oligocène supérieur et du Miocène inférieur d'Europe. *Documents des Laboratoires de géologie de la Faculté des Sciences de Lyon, Notes et Mémoires* 50: 1–81.
- Hutchison, J.H. 1968. Fossil Talpidae (Insectivora, Mammalia) from the later Tertiary of Oregon. *Bulletin of the Museum of Natural History, University of Oregon* 11: 1–117.
- Hutchison, J.H. 1974. Notes on type specimens of European Miocene Talpidae and a tentative classification of Old World Tertiary Talpidae (Insectivora:Mammalia). *Géobios* 7: 211–256.
- Hutterer, R. 2005. Order Soricomorpha. In: D.E. Wilson and D.M. Reeder (eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd edition, 220–311. Johns Hopkins University Press, Baltimore, Maryland.
- Lopatin, A.V. 2002a. An Oligocene mole (Talpidae, Insectivora, Mammalia) from Mongolia. *Paleontological Journal* 36: 531–534.
- Lopatin, A.V. 2002b. The earliest shrew (Soricidae, Mammalia) from the middle Eocene of Mongolia. *Paleontological Journal* 36: 650–659.
- Lopatin, A.V. 2006. Early Paleogene insectivore mammals of Asia and establishment of the major groups of Insectivora. *Paleontological Journal* 40: (Supplement to No. 3), S205–S405.
- Macdonald, J.R. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. *Bulletin of the Los Angeles County Museum of Natural History* 8: 1–82.
- McKenna, M.C. and Bell, S.K. 1997. *Classification of Mammals Above the Species Level*. 631 pp. Columbia University Press, New York.
- Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang, Y.P., Ryder, O.A., and O'Brien, S.J. 2001. Molecular phylogenetics and the origins of placental mammals. *Nature* 409: 614–618.
- Nowak, R.M. 1991. *Walker's Mammals of the World*, 5th edition. 642 pp. Johns Hopkins University Press, Baltimore, Maryland.
- Prothero, D.R. and Sanchez, F. 2004. Magnetic stratigraphy of the upper Eocene Florissant Formation, Teller County, Colorado. In: S.G. Lucas, K.E. Zeigler, and P.E. Kondashov (eds.), *Paleogene Mammals. New Mexico Museum of Natural History and Science Bulletin* 26: 129–135.
- Reed, K.M. 1961. The Proscalopinae, a new subfamily of talpid insectivores. *Bulletin of the Museum of Comparative Zoology* 125: 473–494.
- Repennig, C.A. 1967. Subfamilies and genera of the Soricidae. *United States Geological Survey Professional Paper* 565: 1–74.
- Roca, A.L., Bar-Gal, G.K., Eizirik, E., Helgen, K.M., Maria, R., Springer, M.S., O'Brien, S.J., and Murphy, W.J. 2004. Mesozoic origin for West Indian insectivores. *Nature* 429: 649–651.
- Sánchez-Villagra, M.R., Horovitz, I., and Motokawa M. 2006. A comprehensive morphological analysis of talpid moles (Mammalia) phylogenetic relationships. *Cladistics* 22: 59–88.
- Savage, D.E. and Russell, D.E. 1983. *Mammalian Paleofaunas of the World*. 432 pp. Addison-Wesley Publishing Company, Reading, Massachusetts.
- Shinohara, A., Campbell, K.L., and Suzuki, H. 2003. Molecular phylogenetic relationships of moles, shrew moles, and desmans from the new and old worlds. *Molecular Phylogenetics and Evolution* 27: 247–258.
- Sigé, B., Crochet, J., and Insole, A. 1977. Les plus vieilles taupes. *Géobios Mémoire Spécial* 1: 141–157.
- Tejedor, M.F., Czaplewski, N.J., Goin, F.J., and Aragón, E. 2005. The oldest record of South American bats. *Journal of Vertebrate Paleontology* 25: 990–993.
- Waddell, P.J., Okada, N., and Hasegawa, M. 1999. Towards resolving the interordinal relationships of placental mammals. *Systematic Biology* 48:1–5.
- Whidden, H.P. 2000. Comparative myology of moles and the phylogeny of the Talpidae (Mammalia, Lipotyphla). *American Museum Novitates* 3294: 2–53.
- Worley-Georg, M.P. and Eberle, J.J. 2006. Additions to the Chadronian mammalian fauna of the Florissant Formation, Florissant Fossil Beds National Monument, Colorado. *Journal of Vertebrate Paleontology* 26: 685–696.
- Yates, T.L. and Moore, D.W. 1990. Speciation and evolution in the family Talpidae (Mammalia: Insectivora). In: E. Nevo and O.A. Reig (eds.), *Evolution of Subterranean Mammals at the Organismal and Molecular Levels*, 1–22. Wiley-Liss, New York, New York.
- Ziegler, R., Dahlmann, T., and Storch, G. 2007. Oligocene–Miocene Vertebrates from the Valley of Lakes (Central Mongolia): Morphology, phylogenetic and stratigraphic implications. 4. Maruspialia, Erinaceomorpha and Soricomorpha (Mammalia). *Annalen des Naturhistorischen Museums in Wien* 108A: 53–164.

Karen J. Lloyd [klloyd@twexp.org], University of Colorado Museum of Natural History, University of Colorado at Boulder, 265 UCB, Boulder, Colorado, 80309, USA; current address: The Wildlife Experience, 10035 South Peoria Street, Parker, Colorado, 80134, USA;
Jaelyn J. Eberle [Jaelyn.Eberle@colorado.edu], University of Colorado Museum of Natural History and Department of Geological Sciences, University of Colorado at Boulder, 265 UCB, Boulder, Colorado, 80309, USA (corresponding author).