

First trace and body fossil evidence of a burrowing, denning dinosaur

David J. Varricchio^{1,*}, Anthony J. Martin² and Yoshihiro Katsura³

¹Earth Sciences, Montana State University, Bozeman, MT 59717, USA

²Department of Environmental Studies, Emory University, Atlanta, GA 30322, USA

³Gifu Prefectural Museum, 1989 Oyana, Seki-shi, Gifu 501-3941, Japan

A fossil discovery in the mid-Cretaceous Blackleaf Formation of southwest Montana, USA, has yielded the first trace and body fossil evidence of burrowing behaviour in a dinosaur. Skeletal remains of an adult and two juveniles of *Oryctodromeus cubicularis* gen. et sp. nov., a new species of hypsilophodont-grade dinosaur, were found in the expanded distal chamber of a sediment-filled burrow. Correspondence between burrow and adult dimensions supports *Oryctodromeus* as the burrow maker. Additionally, *Oryctodromeus* exhibits features of the snout, shoulder girdle and pelvis consistent with digging habits while retaining cursorial hindlimb proportions. Association of adult and young within a terminal chamber provides definitive evidence of extensive parental care in the Dinosauria. As with modern vertebrate cursors that dig, burrowing in *Oryctodromeus* may have been an important adaptation for the rearing of young. Burrowing also represents a mechanism by which small dinosaurs may have exploited the extreme environments of polar latitudes, deserts and high mountain areas. The ability among dinosaurs to find or make shelter may contradict some scenarios of the Cretaceous–Paleogene impact event. Burrowing habits expand the known range of nonavian dinosaur behaviours and suggest that the cursorial ancestry of dinosaurs did not fully preclude the evolution of different functional regimes, such as fossoriality.

Keywords: Dinosauria; Ornithopoda; Ichnology; burrow; parental care; Blackleaf Formation

1. INTRODUCTION

Despite the longevity and predominance of dinosaur lineages throughout the Mesozoic, the radiation of nonavian dinosaurs remained morphologically restricted in comparison with the diversity found among Cenozoic mammals (Sereno 1999). Originating from small bipedal cursors, nonavian dinosaurs maintained primarily terrestrial habits throughout their history (Sereno 1999). Even the climbing capabilities hypothesized for the dinosaurian ancestors of birds remain quite controversial (Zhang *et al.* 2002; Padian 2004). Although skeletal features suggest a digging and tearing habit in the dinosaurs *Heterodontosaurus* and *Mononykus* (Norman *et al.* 2004; Senter 2005) and earthen nest structures represent the products of digging behaviour in the theropod *Troodon* (Varricchio *et al.* 1997) and titanosaur sauropods (Chiappe *et al.* 2004), the nonavian dinosaur radiation has been regarded as devoid of true burrowing forms (Sereno 1999; Robertson *et al.* 2004). A novel discovery (Museum of the Rockies, MOR, 1636) from the mid-Cretaceous of Montana consists of the skeletal remains of an adult and two juvenile dinosaurs preserved within an infilled burrow (figures 1 and 2). Here, we describe this dinosaur, *Oryctodromeus cubicularis*, as a new genus and species of hypsilophodont (here considered a grade of basal ornithopods), and present the first trace and body fossil evidence for fossorial behaviour in a nonavian dinosaur. Recognition of such behaviour has implications for dinosaur ecology, reproduction, distribution, evolution and extinction.

2. SYSTEMATIC PALAEOLOGY

Ornithischia Seeley, 1887

Ornithopoda Marsh 1881

Euornithopoda Sereno 1986

Oryctodromeus cubicularis gen. et sp. nov.

(a) *Etymology*

The generic name comes from the Greek words *orycto* and *dromeus*, meaning the ‘digging runner’. The species name, *cubicularis*, translates to ‘of the lair’, referring to the inferred denning habit of the taxon.

(b) *Holotype*

MOR 1636a consists of the following elements: fused premaxillae; posterior/occipital region of the braincase; three cervical, six dorsal, sacrum and 23 caudal vertebrae; three dorsal ribs; scapulocoracoid; scapula; coracoid; humerus; ulna; radius; tibiae; distal fibula; and metatarsal IV (figures 3 and 4).

(c) *Paratype*

MOR 1636b includes cranial and postcranial materials found in association with the holotype and represents two juveniles with most linear dimensions measuring 55% to 65% those of the adult (figure 4).

(d) *Locality and horizon*

The new specimens come from the upper portion of the mid-Cretaceous Blackleaf Formation near the Lima Peaks, Beaverhead Co., Montana, USA (figure 1). Dyman & Nichols (1988) designate this sequence as the ‘volcaniclastic lithofacies’, a 270 m thick lithologically heterogeneous unit

* Author for correspondence (djv@montana.edu).

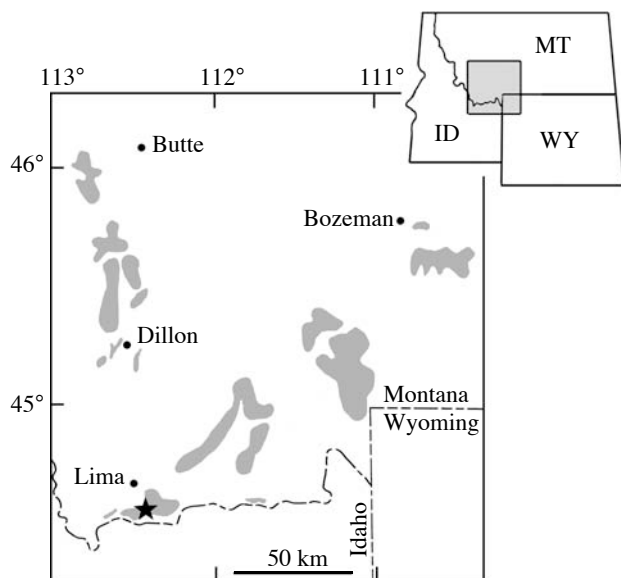


Figure 1. Map of southwestern Montana, USA, showing the distribution of mid-Cretaceous rocks of the Blackleaf and Frontier Formations. Star denotes the location of MOR 1636. Modified from Dyman & Nichols (1988).

consisting of abundant mudstone, siltstone, lithic-rich sandstone and subordinate conglomerate (Zartman *et al.* 1995). Low in this lithofacies, mudstone is olive green to grey, variably calcareous and structureless. Mudstone of the middle and upper portions may be porcelanitic of various colours (red, grey or green), bentonitic with 'popcorn-texture' weathering, or strongly calcareous, non-porcelanitic and grading laterally into micritic limestone (Dyman & Nichols 1988). Siltstone may be tan to grey, rippled, bioturbated and variably calcareous. It occurs as thin discontinuous beds within mudstone or above sandstone in lenticular bodies (Dyman & Nichols 1988). Sandstone is typically fine-grained, variably calcareous and thin to medium bedded. In the Lima Peaks area, sandstone contains a high proportion (as much as 50%) of volcanic and plagioclase grains (Dyman *et al.* 1988).

These sedimentary rocks represent deposition on a broad flood plain with relatively small fluvial channels at the western, proximal edge of the foreland basin (Dyman & Nichols 1988). The high volcanoclastic content reflects the proximity of nearby volcanism associated with the development of the Idaho batholith (Dyman & Nichols 1988; Dyman *et al.* 1988). Bivalves, unidentified reptilian bone fragments, leaves and wood, including the genus *Tempskya*, represent the only macrofossils previously described for the Blackleaf Formation (Cobban *et al.* 1976; Dyman & Nichols 1988). The upper, volcanoclastic lithofacies may correlate with the Vaughn Member described from more northern outcrops near Great Falls, Montana (Cobban *et al.* 1976), the Mowry Shale of Montana and Wyoming and the Aspen Formation of western Wyoming and eastern Idaho (Dyman & Nichols 1988). Palynomorphs and radiometric dates indicate a Cenomanian age for this portion of the formation (Dyman & Nichols 1988; Zartman *et al.* 1995).

The holotype and paratype material occurs within an unusual sedimentary structure consisting of an isolated, sinuous sandstone body sitting within and crosscutting a succession of three mudrock units (figure 2). The lowermost mudstone is greater than 35 cm in thickness,

light greenish grey and weakly calcareous. This unit exhibits extensive dark reddish grey mottling over its uppermost portion. Additionally, carbonate nodules as much as 4.5 cm in diameter form a discontinuous layer of 20–25 cm below the sharp upper contact of the unit. A dark greenish-grey claystone succeeds vertically. This 25 cm thick unit is calcareous with a platy structure and grades upwards into a greenish grey blocky mudstone with some organics. This third unit encloses the upper portion of the sedimentary structure (figure 2*a,d*) and bears a sharp, irregular contact with an overlying burrowed dark red claystone. A thin (approx. 30 cm thick) sandstone and additional mudrocks represent the remaining strata visible at this outcrop.

The lithology of the structure contrasts sharply with the surrounding host mudrock and facilitates recognition of the structure in the field (figure 2). The lower, bone-bearing portion consists of 25–30 cm of medium to fine, calcareous greenish-grey sandstone, moderately sorted with abundant plagioclase and other volcanogenic grains (figure 2*d*). Small (3–6 mm), rounded mud clasts are common in the coarser basal portion. This structureless unit fines upwards with an increasing clay content. A thin, 1–2 cm thick, grey claystone separates this lower sandstone from an upper fine sandstone. The bedding parallels that of the host mudrocks. Reduced clay content, grey colour and larger (approx. 10 mm), platy mud clasts distinguish this unit from the otherwise similar, lower sandstone. A thin (less than 1 cm) rim of tan claystone with abundant calcite veins separates the lower portion of the structure from the host mudrocks.

The preserved portion of the structure measures more than 210 cm long and is sinuous and semi-helical. Throughout most of its length, the structure maintains a fairly constant oval cross-section measuring 30–38 cm high \times 30–32 cm wide before ending abruptly as a partially preserved expansion. From its upper eroded limit, the structure slopes downwards at 6° for 60 cm, turns sharply right and continues down at 18° for another 70 cm (figure 2*a,d*). It then turns sharply left and proceeds a short distance (40 cm) before expanding (figure 2*b,d*). Over its course, the structure drops nearly 50 cm from the horizontal. Erosion had exposed the terminal expansion and its bone content by the time of discovery. Excavation of fossils further destroyed aspects of the structure, particularly the upper portions of the expansion, prior to its recognition and photo documentation (figure 2). Hence, the expansion's preserved dimensions, 40–50 cm long \times 45 cm wide, represents only a portion of its original size. The bone assemblage consisted of a densely packed jumble of adult and juvenile bones concentrated in the basal 7 cm of the lower sandstone just prior to and primarily within the terminal expansion (figure 2*d*). This concentration is greatest a few centimetres above the base of the structure and the coarsest non-bone clasts. A few small juvenile bones, e.g. caudal centra and cranial elements, occurred at a higher level in this unit. Except for one unidentifiable fragment and those truncated by recent erosion, bones were complete prior to fossilization and assignable to *Oryctodromeus*.

Small cylindrical features composed of the same sandstone as the large described structure extend horizontally from the main structure at each of the two right-angle turns (figure 2*a,c,d*). A cluster of five or six

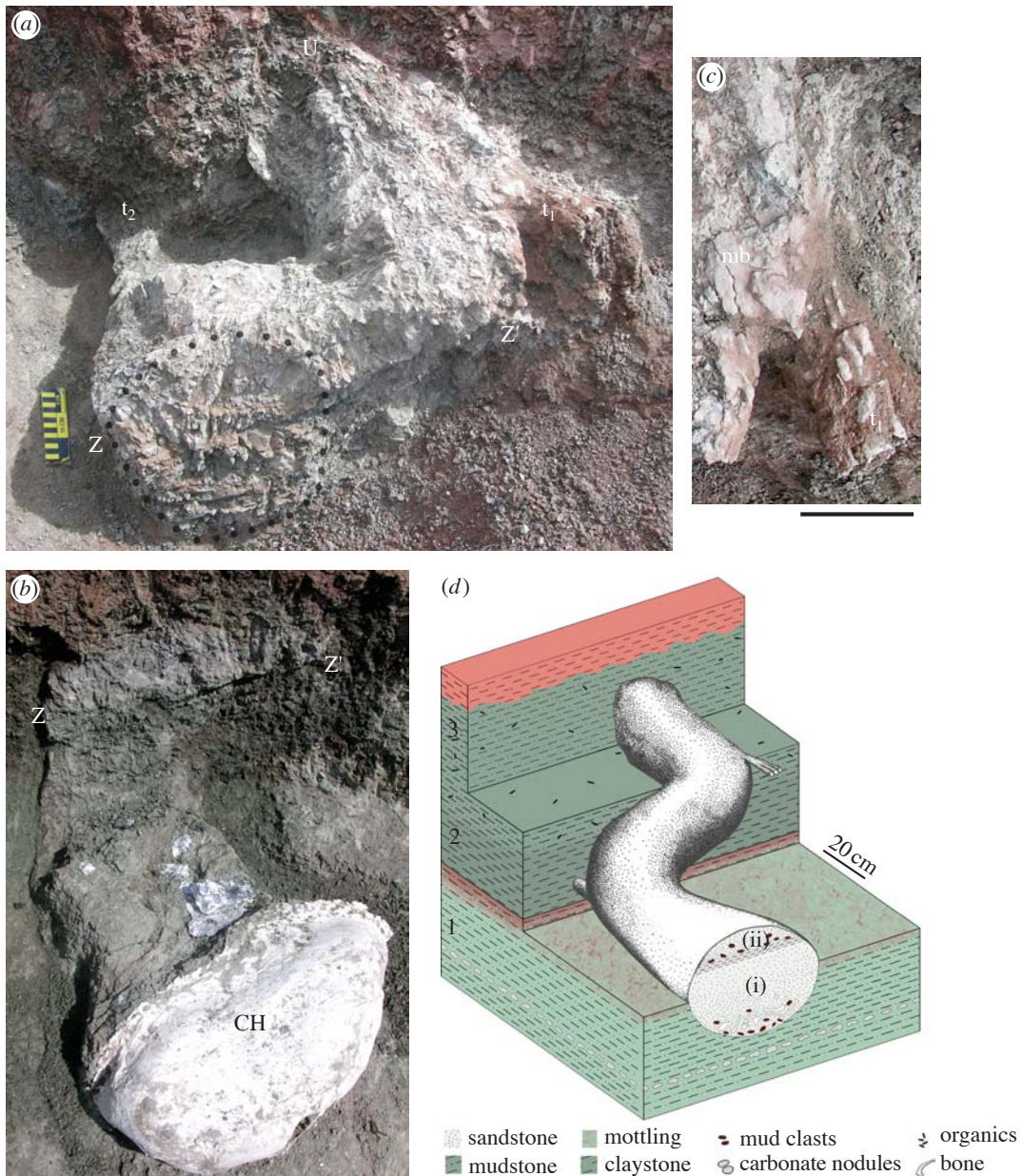


Figure 2. Burrow for *O. cubicularis*. (a) Upper portion of tunnel, which from its upper erosional end, U, slopes down making first a right turn followed by a left turn. The dotted oval represents the cross-section of the tunnel, as it turns left towards the terminal chamber. Smaller tunnels, t_1 and t_2 , of possible commensal burrowers project off either side. Scale bar, 15 cm. (b) Lower portion of burrow showing the last section of tunnel (32 cm wide) expanding into the chamber, CH. View is similar to that of (a), with Z–Z' representing equivalent portions in both the photographs. This edge of the tunnel was damaged during excavation. Bone occurred in the last portion of the tunnel and chamber; plaster now covers the original weathered face. Note the burrow cuts across the contact between the host mudstones. (c) Close-up view from above of the upper set of small accessory burrows (t_1), showing them diverging from the upper aspect of the main burrow (mb). Scale bar, 10 cm. (d) Schematic showing the preserved portion of the MOR 1636 burrow. The sinuous burrow crosscuts a series of mudrocks (units 1–3) before terminating in the exposed chamber. Two episodes of infilling by coarser material (units (i) and (ii)) preserved the main burrow and the smaller subsidiary burrows (t_1 and t_2 in figure 2a) as natural casts. The first episode of infilling buried the bones as a dense concentration near the base of the lower unit (i) with a few small elements occurring higher up. The full extent of the terminal chamber remains unknown, as recent weathering had exposed it and its bony contents prior to discovery.

closely spaced and in some instances doubled cylinders, each 1×2 cm in cross-section and 15 cm long, originate from the upper aspect of the main structure near the outside corner of the uppermost turn. A single, larger feature, 7–9 cm in diameter and at least 10 cm long, likewise extends from the main structure at the outside of the lowermost turn. Unlike the smaller features, this emerges from the lower aspect of the main structure. No external ornamentation or internal structures such as meniscae are evident in these features.

(e) *Diagnosis*

Oryctodromeus cubicularis exhibits the following autapomorphies: long paraoccipital processes indicating a skull with relatively broad proportions; basioccipital with a steeply sided ventral 'box' just rostral to the occipital condyle (figure 3b); sacrum incorporating seven vertebrae, including two posterior dorsals and their ribs; large scapula with a sharply angled and narrow acromion process bearing a thin-edged laterally projecting scapular spine and a distinct posterior bend to the scapular blade; ilium with

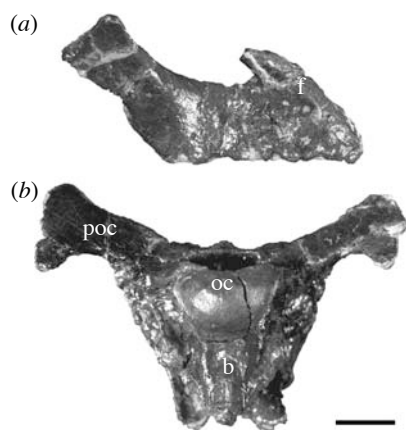


Figure 3. Adult cranial elements for the *O. cubicularis* holotype (MOR 1636a). (a) Fused premaxillae in right lateral view. Premaxillae bears five teeth posterior to a small beak and a transversely expanded and roughened anterior face, f. (b) Ventral view of posterior braincase showing elongate paroccipital processes, poc, and steeply sided ventral 'box', b, just anterior to the occipital condyle, oc. Scale bar, 1 cm.

very short pre-acetabular and long post-acetabular portions; brevis shelf slopes mediolaterally and is visible laterally throughout its length; and long prepubic process with a transversely broad proximal portion possessing an elongate ventral fossa (figure 4).

(f) Description

Medium-sized, hypsilophodont-grade, basal ornithopod; adult humerus length 157 mm and adult tibia 254 mm. Extensive adult fusion (premaxillae, posterior braincase, all neurocentrum sutures, sacrum and scapulocoracoid). Anterior margin and posterior nasal processes of premaxillae angled more posterodorsally (at 45°) than in *Zephyrosaurus* (Sues 1980). Juvenile lacking jugal boss; adult condition unknown. Cervical centra weakly opisthocelous. Transverse processes of anterior dorsal vertebrae steeply angled (figure 4a). Parapophysis and diapophysis not occurring together on horizontal plane until possibly dorsal six or seven, as in more advanced ornithopods such as *Tenontosaurus* and *Iguanodon* (Scheetz 1999). Sacral ribs forming continuous iliac contact surface from the pubic peduncle through length of brevis shelf. Third sacral vertebra with small abutment for bracing of pubis (figure 4b). Caudal centra developing more hexagonal cross-sections distally with transverse processes diminishing rapidly and absent by 20th caudal. Post-zygopophyses by about caudal-14 consisting simply of lateral depressions at the neural spine base. In more distal caudal vertebrae, elongate pre-zygopophyses simply overlap the shortening neural spine. Few ossified tendons and absence of a tendon lattice in tail. Robust scapula longer than humerus (176 versus 157 mm) and with long, narrow acromion running nearly perpendicular away from scapular blade (figure 4c). As in other hypsilophodonts (Norman *et al.* 2004), ilium with bulbous antitrochanter (supracetabular process) on ischial peduncle. Bone completely encircling obturator foramen. Bowed femur with pendant fourth trochanter and small cleft separating the cranial and greater trochanters. Juvenile hindlimb ratios of 1.19 for tibia/femur and 0.58 for metatarsal III/femur, adult ratios probably similar but slightly lower.

3. DISCUSSION

Phylogenetically, *O. cubicularis* groups among basal euornithopods with two other Montana hypsilophodonts: *Zephyrosaurus schaffi* from the Lower Cretaceous Cloverly Formation (Sues 1980) and *Orodromeus makelai* from the Upper Cretaceous Two Medicine Formation (Horner & Weishampel 1988; Scheetz 1999; figure 5). These three taxa share a prominent scapular spine and direct pubosacral articulation. Three features unite *Orodromeus* and *Zephyrosaurus* more closely: inflated postorbital; fossa or groove at the base of pterygoid wing of quadrate; and jugal boss (Scheetz 1999). The adult status of these features in *Oryctodromeus* remains unknown. Additional features shared by *Oryctodromeus* and at least one of the other Montana forms include: fused premaxillae (*Zephyrosaurus*); cranial nerve V passing fully through the prootic; and potentially seven sacral vertebrae (*Orodromeus*). The last two features are not preserved in *Zephyrosaurus* (Sues 1980).

The distinct, stratified fill, crosscutting relationship with surrounding horizons and regular form and dimensions indicate that the *Oryctodromeus*-bearing sedimentary structure represents an infilled burrow (Voorhies 1975; Smith 1987; Groenewald *et al.* 2001; Hasiotis *et al.* 2004). The varied and bedded rock types that comprise the structure are inconsistent with soft-sediment deformation and instead indicate passive filling of an open structure (figure 2). At least two episodes of filling would be required to account for the distinct sandstone units (Groenewald *et al.* 2001). The thin, calcite-veined claystone surrounding the lower portion of the sandstone fill could represent initial deposition within the burrow, but more probably represents secondary clay movement and mineral precipitation along the lithological boundary between the sandstone fill and host mudrocks.

Burrows of both terrestrial and marine taxa often house commensal species. For example, a wide variety of both invertebrates and vertebrates reside in or temporarily occupy the burrows of the gopher tortoise (*Gopherus polyphemus*) and nine-banded armadillo (*Dasyurus novemcinctus*) (Kent *et al.* 1997; Platt *et al.* 2004). These taxa may generate their own associated tunnels intersecting the host burrow (Kent *et al.* 1997; de Gibert *et al.* 2006; Martin 2006). For the Blackleaf specimen, the small, cylindrical structures that extend from near the two major turns (figure 2a,c) possess the same fill as the main burrow structure. This indicates that they were open until the time of burrow filling. These accessory structures are too small to be generated by *Oryctodromeus* and, consequently, may represent the products of commensal cohabitants of the overall burrow structure.

The mudrocks surrounding the burrow are typical of those broadly interpreted as representing flood-plain deposition within the Blackleaf Formation (Cobban *et al.* 1976; Dyman & Nichols 1988). The sharp upper contact, mottled upper zone and carbonate nodule layer clearly indicate that the lower host unit (figure 2d) represents a moderately developed palaeosol (Retallack 1988). They further suggest a calcisol (Mack *et al.* 1993), a moderately alkaline, well-drained soil formed under modest precipitation as in semi-arid to subhumid climates (Retallack 1990). In contrast, the overlying two units exhibit only minimal soil development. Although they share a gradational contact, a sharp upper contact at the top of the third

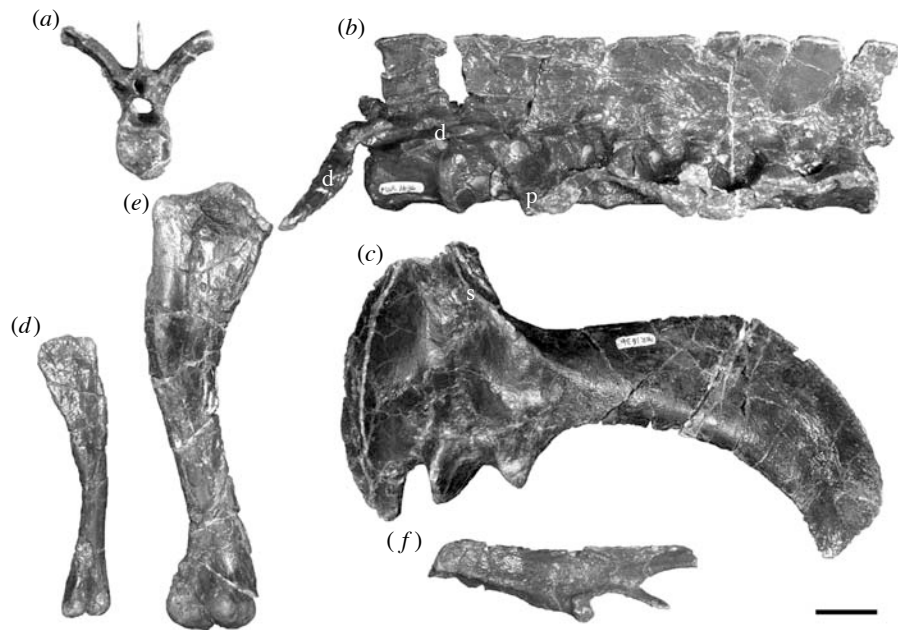


Figure 4. Adult and juvenile postcranial elements for *O. cubicularis* holotype and paratype (MOR 1636a and b, respectively). (a) Anterior dorsal vertebrae in posterior view with steeply inclined transverse processes. (b) Sacrum with seven vertebrae, two pairs of fused dorsal ribs, d, and an articulation for the pubis, p. Note long attachment for ilium. (c) Fused left scapulocoracoid with large acromion process with scapular spine, s, and strong posterior bend of the distal blade. (d,e) Left juvenile and right adult humeri in anterior view. (f) Left juvenile ilium in lateral view with long post- and short pre-acetabular portions. Scale bar, 2 cm.

unit and platy to blocky structures, they lack discrete soil horizons and root traces (figure 2a,d). The grey coloration, alkaline nature and presence of visible organics may link them to relatively immature palaeosols, such as the Haltso and Maksini pedotypes described from the Chinle and Two Medicine Formations, respectively (Retallack 1997). These pedotypes are interpreted as representing young, streamside communities with short soil development histories (Retallack 1997).

Burrow architecture consists of a sloping, sinuous tunnel ending with a terminal chamber (figure 2d) and is similar to those of many extant burrowing vertebrates, e.g. various rodents, striped hyena (*Hyaena hyaena*), aardwolf (*Proteles cristatus*), gopher tortoise and puffin (*Fratercula arctica*) (Voorhies 1975; Rieger 1981; Koehler & Richardson 1990; Doonan & Stout 1994; Terres 1995; Hasiotis *et al.* 2004). The taphonomy, burrow dimensions and anatomic evidence identify *Oryctodromeus* as the burrow maker. Both adult and juvenile fractions include portions of the cranial, axial and appendicular skeleton. Transport of complete carcasses deep within a burrow by either hydraulic processes or scavengers seems unlikely. The hydraulically disparate mixture of large adult limb bones and delicate, juvenile cranial and axial elements argues against fluvial transport. Furthermore, the absence of bite marks and pre-fossilization breaks is inconsistent with carnivore-generated bone assemblages (Brain 1981).

Based on the preserved vertebrae ($n=39$), the adult would measure 2.1 m long with a major portion (approx. 1.25 m) representing tail. Breadth of the trunk as estimated from placement of the scapulocoracoids and dorsal ribs would be 26–30 cm. Tunnel width (approx. 30 cm) and length between turns (approx. 70 cm) thus correspond to torso breadth and length of the adult. Comparable tight fits occur in modern burrowing animals and often serve as a deterrent against predators (Rieger 1981; Koehler & Richardson 1990; Miller *et al.* 2001). For

example, the aardwolf stands 45–50 cm at the shoulder but has tunnels measuring only 20×30 cm (Koehler & Richardson 1990); the striped hyena, 60–94 cm at the shoulders, has tunnel diameters of only 40 cm (Rieger 1981). Furthermore, an allometric equation comparing burrow cross-sectional area and body mass for a variety of modern invertebrate and vertebrate burrowers (White 2005) predicts an animal weighing between 22 and 32 kg for the Blackleaf burrow (figure 2a). These figures correspond to weight estimates of medium-sized hypsilophodonts (Pezkis 1994).

Although its hindlimb proportions compare favourably to other hypsilophodonts and denote cursorial habits (Carrano 1999; Norman *et al.* 2004), *Oryctodromeus* exhibits features of the snout, shoulder girdle and pelvis consistent with digging. Several of these represent derived features of *Oryctodromeus* and its closest sister taxa (figure 5), the two other Montana hypsilophodonts. For example, some extant fossorial vertebrates use their snouts to loosen or move dirt (Hildebrand 1985). The fused premaxillae with expanded anterior face of *Oryctodromeus* could represent such an implement (figure 3a). Among ornithopods, only *Zephyrosaurus* exhibits similar fused premaxillae (Sues 1980).

Despite similar forelimb proportions and morphology, the scapulocoracoid of *Oryctodromeus* differs markedly in comparison with those of other hypsilophodont-grade ornithopods, such as *Thescelosaurus* and *Hypsilophodon* (Norman *et al.* 2004). The robust scapula bears a long, narrow acromion that angles sharply away from the scapular blade (figure 4c). A distinct ventrolaterally projecting spine extends the entire length of the acromion. *Oryctodromeus* and *Zephyrosaurus* also possess scapular spines (Scheetz 1999), but that of *Oryctodromeus* differs, in that the spine projects nearly perpendicular from the flat, lateral surface of the acromion. Further, the anterior margin of the scapular blade bears a small triangular

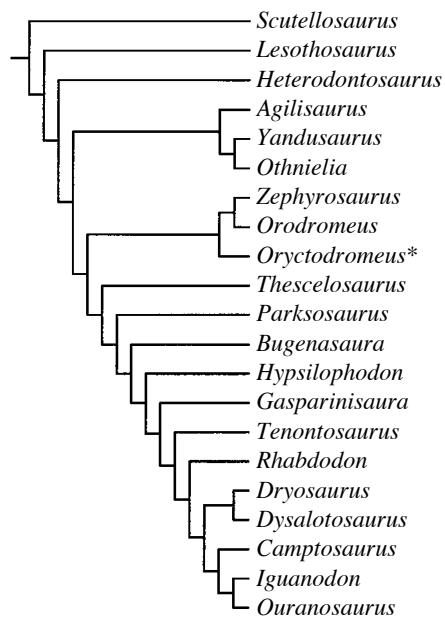


Figure 5. Phylogenetic position of *O. cubicularis* gen. et sp. nov. among ornithopods and some potential basal marginocephalians (Xu *et al.* 2006). This single most parsimonious tree has 377 steps, retention index (RI) of 0.66 and consistency index (CI) of 0.47. Bootstrap analysis with 1000 replicates found greater than 50% support for all nodes, except those among *Agilisaurus*, *Yandusaurus* and *Othnielia* and for *Thescelosaurus* and *Parksosaurus*. The Montana hypsilophodont clade occurred in 60% and *Zephyrosaurus*–*Orodromeus* in 58% of the replicates. Analysis used PAUP v. 4.0b10 (Swofford 1998) and the matrix of Schetzl (1999) with three modifications: (i) adding one character in the absence/presence of fused premaxillae, (ii) altering character 81 (number of sacral vertebrae) to accommodate the presence of seven sacrals, and (iii) correcting two typographic errors for *Orodromeus* in characters 90 and 98. The final matrix consisted of 21 taxa and 125 characters. *Oryctodromeus* was scored as follows: 001?? ?1000/????? ????//????? ?111?/01000 0???0//0?00 1??1?/200?? ?0?00//1?0?? ??001/110?? 11131//41022 ?1112/0?100 ??21?//???10 10110/?1200 100??//????1. Characters and character states as in Schetzl (1999) with fused premaxillae as character 125.

projection. From this point distally, the blade expands markedly and bends sharply posteriorly. In the adult specimen, the left scapula and coracoid are fully fused. Among ornithopods, this condition occurs elsewhere only in the iguanodontian *Ouranosaurus* (Norman 2004).

The enlarged, fused scapulocoracoid with prominent acromion and scapular spine would increase attachment areas for muscles that used to stabilize and operate digging forelimbs (Hildebrand 1985). The armadillo *Dasyurus* possesses a distal expansion and posterior bend in the scapular blade similar to those of *Oryctodromeus*. This modification increases the lever arm for the enlarged teres major muscle and facilitates forelimb retraction (Hildebrand 1985; Pough *et al.* 1999).

In order to effectively apply a force to the ground, a digging animal must counteract the equal opposing force generated. For example, those mammals that dig with their forelimbs brace themselves with their hindlimbs and prop-like tail (Hildebrand 1985). *Oryctodromeus* exhibits several skeletal features that among extant vertebrates are associated with such behaviour (Hildebrand 1985): an

expanded sacrum; greater attachment of pelvis and sacrum; absence of a pelvic symphysis; and expanded proximal caudals (figure 4). The large sacrum has seven vertebrae, including two dorsal vertebrae and their ribs, a long iliac attachment and direct pubosacral contact. *Oryctodromeus* is unusual in possessing seven sacrals, a number more typical of much larger Iguanodontia and other more advanced ornithopods (Norman 2004). Irregular surfaces on unfused posteriormost dorsals of *O. makelai* suggest the possibility of a seven-vertebrae sacrum in this Late Cretaceous form. The pubosacral articulation and the scapular spine represent the two synapomorphies that define the clade of *Zephyrosaurus*, *Oryctodromeus* and *Orodromeus* (figure 5). In the tail, the longest transverse processes occur on the third or fourth caudal vertebrae as in *Hypsilophodon* and more advanced ornithopods (Schetzl 1999). The tallest neural spines of the vertebral column also occur in this region. Together, these features suggest a robust basal portion of the tail.

Oryctodromeus lacks the extreme skeletal modifications found in subterranean vertebrates, such as the golden mole (*Amblysomus* sp.), wombat (*Lasiornhinus* sp.), echidna (*Tachyglossus aculeatus*) and armadillo (*Oryzomys* sp.). Missing traits include an elongate humeral head, transverse expansion of the distal humerus and prominent olecranon (Hildebrand 1985). Given its hindlimb proportions and modest forelimb modifications, *Oryctodromeus* is similar but more specialized than various cursorial, facultative diggers, such as the armadillo (Koehler & Richardson 1990), hyaenids (Rieger 1981), various canids, Patagonian cavy (*Dolichotis patagonum*; Campos *et al.* 2001) and the Old World rabbit (*Oryctolagus cuniculus*; Nowak & Paradiso 1983). The bipedal gait of the dinosaur may have accommodated greater forelimb specializations without compromising terrestrial locomotion.

Although associated burrows are currently unknown for *Zephyrosaurus* and *Orodromeus*, the skeletal features shared by all the three Montana hypsilophodonts suggest that the clade may have been specialized for digging. The three small dinosaurs each occur within proximal portions of the Cretaceous foreland basin and in association with variegated, often red and purple, caliche-bearing mudstones (Retallack 1997). Modern tetrapod burrowers prefer drier, upland soils (Voorhies 1975; Groenewald *et al.* 2001; Hasiotis *et al.* 2004), and these well-drained seasonally arid palaeosols (Retallack 1997) of the Cretaceous would represent favourable substrates. At least two *Orodromeus* specimens (MOR 1136 and 1141) consisted of densely packed, three-dimensional bone assemblages similar to that of *Oryctodromeus*, suggesting within-burrow preservation. Uniformity of sediments may have obscured burrow preservation (Voorhies 1975) in these instances.

Fossorial behaviour represents a marked departure from the strictly cursorial niche envisioned for basal ornithopods (Carrano 1999; Norman *et al.* 2004). Furthermore, despite their bipedal, cursorial ancestry, dinosaurs evolved a variety of functional modes that now include fossorial, arboreal (Zhang *et al.* 2002) and several unrelated quadrupedal forms (Serenio 1999).

Vertebrates burrow for a variety of reasons: to find food; escape predators; and avoid harsh environmental conditions (Voorhies 1975; Hildebrand 1985). Among modern digging cursors, burrows serve primarily as dens for the rearing of

young (Rieger 1981; Nowak & Paradiso 1983; Koehler & Richardson 1990; Campos *et al.* 2001). The occurrence of an adult and two juveniles within the expanded portion of a burrow indicates that *Oryctodromeus* both burrowed and exhibited extensive parental care. The juveniles possess limb element and centra lengths measuring 60% to 65% those of the adult, exhibit no fusion except in the distal most caudals and would have measured 1.3 m in total length. Although growth rates were probably fast (Padian *et al.* 2004), the large size of the juveniles suggests that the parent–young bond persisted for a minimum of several months. Parental care of the young has been proposed for several dinosaur taxa (Horner & Makela 1979; Bakker & Bir 2004; Meng *et al.* 2004), but even the best examples either lack a direct juxtaposition of adult and young (Horner & Makela 1979), consist only of shed teeth (Bakker & Bir 2004) or remain taphonomically ambiguous (Meng *et al.* 2004). Thus, MOR 1636 uniquely preserves both an adult–young association and direct evidence of denning in the form of a dwelling trace. The presence of parental care in a basal ornithomimid supports the hypothesis that such behaviour was ancestral for Dinosauria and, possibly, Archosauria (Meng *et al.* 2004).

Burrowing behaviour allows vertebrates to escape harsh environmental conditions by taking advantage of equable burrow microclimates (Voorhies 1975; Hildebrand 1985; Miller *et al.* 2001; Platt *et al.* 2004). By denning, small dinosaurs could have potentially withstood severe conditions, such as aridity, drought and daily or seasonal temperature extremes. Such behaviour would have allowed dinosaurs to occupy high mountains, desert environments (Loope 2006a) and polar regions and may explain the presence of hypsilophodonts in high-latitude areas, such as the Early Cretaceous of Australia (Rich & Rich 1989). The most similar Mesozoic traces to the one described here include a collection of burrows from the Middle Jurassic Entrada Sandstone (Loope 2006b). Although these burrows lack the sinuosity of the Blackleaf specimen, they share comparable tunnel lengths, slopes and diameters. One even possesses a terminal chamber (Loope 2006b). These taxonomically unassignable traces represent the only other burrows suitably sized to be the product of nonavian dinosaurs. Regardless of the trace maker, these burrows probably represented temporary shelters from harsh desert and dune field conditions of the Middle Jurassic (Loope 2006b).

Survivability of terrestrial vertebrates at the end-Cretaceous event has been attributed to sheltering behaviour, with the extinction of nonavian dinosaurs resulting from their inability to find an appropriate cover (Robertson *et al.* 2004). Burrowing dinosaurs would challenge this argument, but these are yet to be found in the latest Cretaceous formations. Much of the research on the Cretaceous–Paleogene extinction event has focused on the Hell Creek Formation and similar equivalent units of North America (Hartman *et al.* 2002). If burrowing dinosaurs existed in the latest Cretaceous, they would more probably be found not in coastal settings like the Hell Creek Formation (Hartman *et al.* 2002) but rather in more upland environments with better-drained palaeosols.

We thank C. Ancell for the excellent preparation; F. Jackson, M. Brown, Dead Lizard Society (MSU), M. Gardner and

M. Ivie for their helpful comments and discussion; L. Hall for the illustration; M. Drool for inspiration; and M. Holland, R. Kambic, J. Li, E. Morschhauser, C. Wong and Project Exploration. A. Rindsberg is thanked for his assistance with etymology and taxonomy. We especially appreciate the support of J. Horner, Museum of the Rockies and the Dillon Ranger District, US Forest Service. The Jurassic Foundation and the Department of Earth Sciences, MSU supported this research. The manuscript benefited greatly from the comments of D. Eberth and D. Fastovsky.

REFERENCES

- Bakker, R. T. & Bir, G. 2004 Dinosaur crime scene investigations: theropod behavior at Como Bluff, Wyoming and the evolution of birdness. In *Feathered dragons* (eds P. J. Currie, E. B. Koppelhus, M. A. Shugar & J. L. Wright), pp. 301–342. Bloomington, IN: Indiana University Press.
- Brain, C. K. 1981 *The hunters or the hunted? An introduction to African cave taphonomy*. Chicago, IL: University of Chicago Press.
- Campos, C. M., Tognelli, M. F. & Ojeda, R. A. 2001 *Dolichotis patagonum*. *Mamm. Species* **652**, 1–5. (doi:10.1644/1545-1410(2001)652<0001:DP>2.0.CO;2)
- Carrano, M. T. 1999 What, if anything, is a cursor? Categories versus continua for determining locomotor habit in mammals and dinosaurs. *J. Zool. Lond.* **247**, 29–42.
- Chiappe, L. M., Schmitt, J. G., Jackson, F. D., Garrido, A., Dingus, L. & Grellet-Tinner, G. 2004 Nest structure for sauropods: sedimentary criteria for recognition of dinosaur nesting traces. *Palaeos* **19**, 89–95.
- Cobban, W. A., Erdmann, C. E., Lemke, R. W. & Maughan, E. K. 1976 Types sections and stratigraphy of the members of the Blackleaf and Marias River Formations (Cretaceous) of the Sweetgrass Arch, Montana. *USGS Prof. Pap.* **974**, 1–66.
- de Gibert, J. M., Netto, R. G., Tognoli, F. M. W. & Grangeiro, M. E. 2006 Commensal worm traces and possible juvenile thalassinidean burrows associated with *Ophiomorpha nodosa*, Pleistocene, southern Brazil. *Palaeoogeogr. Palaeoclimatol. Palaeoecol.* **230**, 70–84. (doi:10.1016/j.palaeo.2005.07.008)
- Doonan, T. J. & Stout, I. J. 1994 Effects of gopher tortoise (*Gopherus polyphemus*) body size on burrow structure. *Am. Midl. Nat.* **131**, 273–280. (doi:10.2307/2426253)
- Dyman, T. S. & Nichols, D. J. 1988 Stratigraphy of mid-Cretaceous Blackleaf and lower part of the Frontier Formations in parts of Beaverhead and Madison Counties, Montana. *USGS Bull.* **1773**, 1–27.
- Dyman, T. S., Perry Jr, W. J. & Nichols, D. J. 1988 Stratigraphy, petrology, and provenance of the Albian Blackleaf Formation and the Cenomanian to Turonian lower part of the Frontier Formation in part of the Beaverhead and Madison Counties, Montana. *Mt. Geol.* **25**, 113–128.
- Groenewald, G. H., Welman, J. & MacEachern, J. A. 2001 Vertebrate burrow complexes from the Early Triassic *Cynognathus* zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaeos* **16**, 148–160.
- Hartman, J. H., Johnson, K. R. & Nichols, D. J. 2002 *The Hell Creek Formation and Cretaceous–Tertiary boundary in the Northern Great Plains*. Geological Society of America, Special Paper 361
- Hasiotis, S. T., Wellner, R. W., Martin, A. J. & Demko, T. M. 2004 Vertebrate burrows from Triassic and Jurassic continental deposits of North America and Antarctica: their paleoenvironmental and paleoecological significance. *Ichnos* **11**, 103–124. (doi:10.1080/10420940490428760)

- Hildebrand, M. 1985 Digging in quadrupeds. In *Functional vertebrate morphology* (eds M. Hildebrand, D. M. Bramble, K. F. Liem & D. B. Wake), pp. 89–109. Cambridge, MA: Bellknap Press.
- Horner, J. R. & Makela, R. 1979 Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* **282**, 296–298. (doi:10.1038/282296a0)
- Horner, J. R. & Weishampel, D. B. 1988 A comparative embryological study of two ornithischian dinosaurs. *Nature* **332**, 256–257. (doi:10.1038/332256a0)
- Kent, D. M., Langston, M. A., Hanf, D. W. & Wallace, P. M. 1997 Utility of a camera system for investigating gopher tortoise burrows. *Fl. Sci.* **60**, 193–196.
- Koehler, C. E. & Richardson, P. R. K. 1990 *Proteles cristatus*. *Mamm. Species* **363**, 1–6.
- Loope, D. B. 2006a Burrows dug by large vertebrates into rain-moistened, Middle Jurassic dune sand. *J. Geol.* **114**, 753–762. (doi:10.1086/507618)
- Loope, D. B. 2006b Dry-season tracks in dinosaur-triggered grainflows. *Palaios* **21**, 132–142. (doi:10.2110/palo.2005.p05-55)
- Mack, G. H., James, W. C. & Monger, H. C. 1993 Classification of paleosols. *GSA Bull.* **105**, 129–136.
- Martin, A. J. 2006 A composite trace fossil of decapod and hymenopteran origin from the Rice Bay Formation (Holocene), San Salvador, Bahamas. In *12th Symp. Geology of the Bahamas and Other Carbonate Regions* (eds D. Gamble & R. L. Davis), pp. 99–112. San Salvador, Bahamas: Gerace Research Center.
- Meng, Q., Liu, J., Varricchio, D. J., Huang, T. & Gao, C. 2004 Parental care in an ornithischian dinosaur. *Nature* **431**, 145–146. (doi:10.1038/431145a)
- Miller, M. F., Hasiotis, S. T., Babcock, L. E., Isbell, J. L. & Collinson, J. W. 2001 Tetrapod and large burrows of uncertain origin in Triassic high paleolatitude floodplain deposits, Antarctica. *Palaios* **16**, 218–232.
- Norman, D. B. 2004 Basal Iguanodontia. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson & H. Osmolska), pp. 413–437. 2nd edn. Berkeley, CA: University of California Press.
- Norman, D. B., Sues, H.-D., Witmer, L. M. & Coria, R. A. 2004 Basal Ornithopoda. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson & H. Osmolska), pp. 393–412. 2nd edn. Berkeley, CA: University of California Press.
- Nowak, R. M. & Paradiso, J. L. 1983 *Walker's mammals of the world*. Baltimore, MD: Johns Hopkins University Press.
- Padian, K. 2004 Basal Avialae. In *The Dinosauria* (eds D. B. Weishampel, P. Dodson & H. Osmolska), pp. 210–231. 2nd edn. Berkeley, CA: University of California Press.
- Padian, K., Horner, J. R. & De Ricqles, A. 2004 Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. *J. Vert. Paleontol.* **24**, 555–571. (doi:10.1671/0272-4634(2004)024[0555:GISDAP]2.0.CO;2)
- Pezkis, J. 1994 Implications of body-mass estimates for dinosaurs. *J. Vert. Paleontol.* **14**, 520–533.
- Platt, S. G., Rainwater, T. R. & Brewer, S. W. 2004 Aspects of the burrowing ecology of the nine-banded armadillos in northern Belize. *Mamm. Biol.* **69**, 217–224.
- Pough, F. H., Janis, C. M. & Heiser, J. B. 1999 *Vertebrate life*. Prentice Hall: Upper Saddle River, NJ.
- Retallack, G. J. 1988 Field recognition of paleosols. *GSA Spec. Pap.* **216**, 1–20.
- Retallack, G. J. 1990 *Soils of the past: an introduction to paleopedology*. Boston, MA: Unwin Hyman.
- Retallack, G. J. 1997 Dinosaurs and dirt. In *DinoFest international* (eds D. L. Wolberg, E. Stump & G. D. Rosenberg), pp. 345–359. Philadelphia, PA: Academy of Natural Sciences.
- Rich, T. H. V. & Rich, P. V. 1989 Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *Natl Geogr. Res.* **5**, 15–53.
- Rieger, I. 1981 *Hyaena hyaena*. *Mamm. Species* **150**, 1–5.
- Robertson, D. S., McKenna, M. C., Toon, O. B., Hope, S. & Lillegraven, J. A. 2004 Survival in the first hours of the Cenozoic. *GSA Bull.* **116**, 760–768.
- Scheetz, R. D. 1999 Osteology of *Orodromeus makelai* and the phylogeny of basal ornithopod dinosaurs. Montana State University, Bozeman, Ph.D. dissertation.
- Senter, P. 2005 Function in the stunted forelimbs of *Mononykus olecranus* (Theropoda), a dinosaur anteater. *Paleobiology* **31**, 373–381. (doi:10.1666/0094-8373(2005)031[0373:FITSFO]2.0.CO;2)
- Sereno, P. C. 1999 The evolution of dinosaurs. *Science* **284**, 2137–2147. (doi:10.1126/science.284.5423.2137)
- Smith, R. M. H. 1987 Helical burrow casts of therapsid origin from the Beaufort Group (Permian) of South Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **60**, 155–170. (doi:10.1016/0031-0182(87)90030-7)
- Sues, H.-D. 1980 Anatomy and relationships of a new hypsilophodontid dinosaur from the Lower Cretaceous of North America. *Palaeontographica Abt. A* **169**, 51–72.
- Swofford, D. L. 1998 *PAUP*. Phylogenetic analysis using parsimony (*and other methods). version 4*. Sunderland, MA: Sinauer Associates.
- Terres, T. K. 1995 *The Audubon Society encyclopedia of North American birds*. New York, NY: Wings Books.
- Varricchio, D. J., Jackson, F., Borkowski, J. J. & Horner, J. R. 1997 Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* **385**, 247–250. (doi:10.1038/385247a0)
- Voorhies, M. R. 1975 Vertebrate burrows. In *The study of trace fossils* (ed. R. W. Frey), pp. 325–350. New York, NY: Springer.
- White, C. R. 2005 The allometry of burrow geometry. *J. Zool. Lond.* **265**, 395–403.
- Xu, X., Forster, K., Clark, J. M. & Mo, J. 2006 A basal ceratopsian with transitional features from the Late Jurassic of northwestern China. *Proc. R. Soc. B* **273**, 2135–2140. (doi:10.1098/rspb.2006.3566)
- Zartman, R. E., Dyman, T. S., Tysdal, R. G. & Pearson, R. C. 1995 U-Pb ages of volcanogenic zircon from porcellanite beds in the Vaughn Member of the mid-Cretaceous Blackleaf Formation, southwestern Montana. *USGS Bull.* **2113-B**
- Zhang, F., Zhou, Z., Xu, X. & Wang, X. 2002 A juvenile coelurosaurian theropod from China indicates arboreal habits. *Naturwissenschaften* **89**, 394–398. (doi:10.1007/s00114-002-0353-8)