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# Dinosaur burrows in the Otway Group (Albian) of Victoria, Australia, and their relation to Cretaceous polar environments

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## ABSTRACT

Three enigmatic structures in an outcrop of the Otway Group (Albian) of Victoria, Australia, compose the first known evidence suggestive of dinosaur burrows outside of North America and the oldest from the fossil record. The most complete of the Otway structures nearly matches the size and morphology of a burrow attributed to the only known burrowing dinosaur, *Oryctodromeus cubicularis* from the Upper Cretaceous (Cenomanian) of Montana (USA). The suspected burrows cross-cut alluvial facies and overlie nearby strata containing dinosaur tracks. The structures contain identical sand fills in their upper portions, implying a near-synchronous origin and filling; graded bedding in the most complete structure also indicates passive filling of an originally open structure. This probable burrow is a 2.1 m long, gently descending, semi-helical tunnel, with a near-constant diameter (about 30 cm) that connects with an enlarged terminal chamber. The structures are unlikely to have been caused by physical or chemical sedimentary processes, and hence are considered as biogenic structures; moreover, their size and morphology imply tetrapod tracemakers. Burrow allometry indicates tracemakers with a mass of 10–20 kg, matching size estimates for small ornithopods from the Otway Group. Burrowing behavior in hypsilophodontid-grade dinosaurs, which compose most of the dinosaurian assemblage in the Lower Cretaceous of Victoria, was proposed previously as an adaptation for surviving formerly polar conditions in southeastern Australia. This paradigm is explored in detail, particularly through actualistic examples of tetrapod burrowing in cold climates. These structures may provide the first clues of ornithopod burrowing in these extreme environments, while also establishing search images for similar structures in other Lower Cretaceous outcrops in Victoria.

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## 1. Introduction

The recent interpretation of a Lower Cretaceous species of burrowing dinosaur, the basal ornithopod *Oryctodromeus cubicularis* in the Blackleaf Formation (Cenomanian) of Montana (USA), provided an additional explanation for some large, enigmatic sedimentary structures in Mesozoic terrestrial deposits (Varricchio et al., 2007). Just before then, Loope (2006) also proposed that large structures in the Entrada Sandstone (Middle Jurassic) of Utah were tetrapod-made, although he lacked sufficient evidence to attribute these specifically to dinosaurs. Varricchio et al. (2007), in contrast, were fortunate enough to have skeletal remains of *O. cubicularis* and two of its probable offspring entombed in the burrow structure.

This circumstance, in addition to anatomical traits in the adult specimen that suggested adaptations for burrowing, composed evidence for the first known burrowing and denning behaviors in dinosaurs. In that study, the authors also proposed that burrowing might have conferred an advantage to small ornithopod dinosaurs living in environments with challenging conditions, such as deserts and polar environments (Varricchio et al., 2007), which had been proposed for large tetrapod burrowing in general (Loope, 2006).

In this report, three closely associated sedimentary structures are described from the Lower Cretaceous (Albian) Otway Group of Victoria, Australia, that are also likely the result of tetrapod burrowing. Moreover, the geometry and size of one structure nearly matches that of the burrow attributed to *Oryctodromeus* (Varricchio et al., 2007) and the other two partially resemble the first; hence these structures are attributed to small dinosaurian tracemakers, such as hypsilophodontid-grade dinosaurs. The Otway Group and slightly older Strzelecki Group (Aptian) of this part of Victoria are well known for their remains of small hypsilophodontids, such as

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*Leaellynasaura*, *Atlascoposaurus*, and *Qantassaurus* (Rich et al., 1988; Rich and Rich, 1989; Rich et al., 2002), thus the structures can be linked with potential tracemakers in the same region and strata. The circumpolar setting of this part of Australia during the Early Cretaceous (Veevers et al., 1991; Gregory et al., 1989; Wagstaff and McEwen-Mason, 1989; Constantine et al., 1998) also supports previous suggestions that some small ornithopods burrowed as an adaptation to extreme environments (Varricchio et al., 2007; Bell and Snively, 2008).

Assuming these structures are dinosaur burrows, they would represent the first known outside of North America and the oldest in the geologic record. Regardless of the identity of the Otway structures, a more detailed consideration of dinosaur burrowing as a behavioral strategy for overwintering in polar environments is further explored, including suggested search images for trace fossil evidence that would support such interpretations in the future.

## 2. Study area and previous research

The Otway Group crop outs in extensive cliff-face and marine-platform exposures along the southern coast of Victoria and west of Melbourne (Fig. 1). The Otway Group is well known for its fossil vertebrates, e.g., fish, amphibians, turtles, dinosaurs, and mammals, most of which were recovered from Dinosaur Cove (Rich et al., 1988; Currie et al., 1996; Rich et al., 1997, 2002, 2005), but also contains a well-documented assemblage of terrestrial plants (Wagstaff and McEwen-Mason, 1989; Cantrill, 1991; Dettmann et al., 1992). Dinosaurs in the Otway Group and nearby Strzelecki Group are dominated by hypsilophodontid-grade ornithopods, which is unusual among dinosaur assemblages worldwide (Rich and Vickers-Rich, 1999; Vickers-Rich et al., 1999; Rich et al., 2002), although a few theropods and representatives of other clades have been identified as well (Rich et al., 1988; Rich and Rich, 1989; Currie et al., 1996; Smith et al., 2008). Invertebrate body fossils in the Otway Group are relatively uncommon, but include parastacid crayfish (also recovered from Dinosaur Cove), the oldest known from the Southern Hemisphere (Martin et al., 2008). Insect body fossils are, however, abundantly represented in the Koonwarra fossil deposit of the Strzelecki Group (Jell and Duncan, 1986). Invertebrate trace fossils in the Otway Group are likewise rarely reported, but burrow systems at several localities have been

attributed to crayfish or similar fresh-water decapods (Martin et al., 2008).

Rock types of the Otway Group include mudstones, cross-bedded sandstones, and intraclast conglomerates and breccias; most clastic facies are composed of reworked volcanoclastic sediments (Bryan et al., 1997; Tosolini et al., 1999; Miller et al., 2002). Otway Group sediments were deposited in the Otway Basin, a rift basin that formed with the divergence of Australia and Antarctica in the Early Cretaceous (Tosolini et al., 1999; Miller et al., 2002; Veevers, 2006). Sedimentary environments of the Otway Group were primarily braided fresh-water braided streams, forming multistorey lithic sandstones with coarser-grained channel-fill and finer-grained sheetflow or overbank deposits (Bryan et al., 1997). In the nearby Strzelecki Group, poorly sorted conglomerates are interpreted as braided stream-dominated alluvial-fan deposits (Tosolini et al., 1999); this diagnosis is probably also applicable to coarse-grained lithofacies in the Otway Group. Sediments were derived from nearby volcanic uplands or reworked from within the basin (Rich et al., 1988; Bryan et al., 1997). Flooding associated with spring and summer thaws, as well as occasional pulses of volcanoclastic sediments, likely caused high-energy flow regimes in seasonally active streams or alluvial channels (Rich et al., 1988; Tosolini et al., 1999). Paleolatitudes are estimated to have been  $78 \pm 5^\circ\text{S}$ , and mean annual air temperatures were in the range of  $-6^\circ$  to  $+8^\circ\text{C}$ , based on a combination of paleogeography, oxygen isotopes, paleobotany, cryoturbation structures, and oxygen isotopes (Veevers et al., 1991; Gregory et al., 1989; Wagstaff and McEwen-Mason, 1989; Constantine et al., 1998). As a result, Otway Group strata are assumed to have formed in periglacial environments, with freezing conditions and prolonged periods of darkness during winters (Constantine et al., 1998; Rich and Vickers-Rich, 2000; Rich et al., 2002).

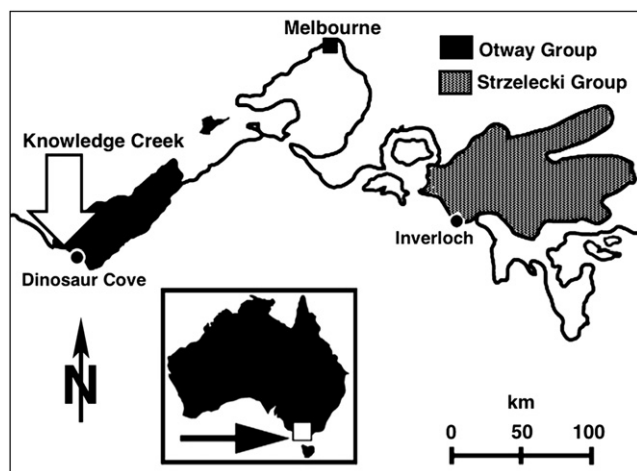
## 3. Diagnosis of Otway Structures

### 3.1. Geologic context and description

The three structures of interest in this study are located in a coastal outcrop of conglomeratic sandstone in the Otway Group (Albian) at a locality dubbed Knowledge Creek, named after the drainage within the ravine (hanging valley) that divides the exposure (Rich and Vickers-Rich, 2000). This small cove is about 240 km southwest of Melbourne, Victoria, and 6–6.5 km northwest of Dinosaur Cove (Fig. 1). The stratigraphic sequence at Knowledge Creek has not been measured or otherwise described, although some lithofacies are described here.

Despite numerous finds of vertebrate material in the Otway Group at other localities, no body fossils have been discerned at this site, and the only significant paleontological find reported there previously was a single dinosaur footprint, discovered in 1980 (Rich et al., 1988; Rich and Vickers-Rich, 2000). This footprint was later confirmed as a small ornithopod track; more recently, other partial, poorly preserved dinosaur tracks have been found at this site (Martin et al., 2007). Since 1980, paleontological researchers (including the author of this study) have visited the site three times, in May 2006, July 2007, and May 2009. During the first of those visits, the author observed and photographed the structures, noting the remarkable similarity of one to a Lower Cretaceous dinosaur burrow he had seen in Montana (research that was, at the time, still in process), but he did not describe it in detail. Follow-up visits by the author in 2007 and 2009 provided the opportunity to make a more thorough description and diagnosis of the structures, related further herein.

The outcrop displays significant exposures of Otway Group lithofacies, including planar-bedded mudstones and siltstones,



**Fig. 1.** Location of Knowledge Creek outcrop and structures (this study), Otway Group (Albian), Victoria, Australia; Latitude-longitude coordinates are  $S38^\circ 45.27'$ ,  $E143^\circ 20.85'$ . Location is indicated relative to the two most productive dinosaur sites in Victoria, Dinosaur Cove (Otway Group) and Inverloch ("Dinosaur Dreaming," Strzelecki Group).

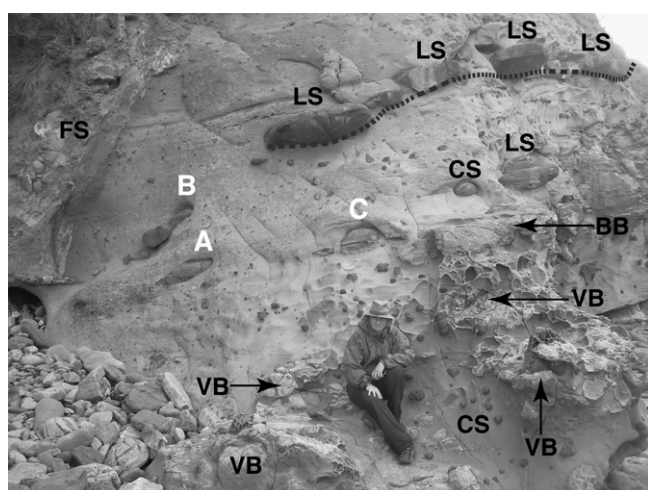
cross-bedded and rippled sandstones, and conglomerates or breccias. More specifically, coarser-grained lithofacies here, i.e., conglomeratic sandstones, conglomerates, and breccias (some containing boulders) are better termed lithic arenites, composed of significant amounts of reworked volcanoclastic sediments. Based on a quick survey of the area, some of the finer-grained lithofacies (mudstones, siltstones, fine-grained sandstones) at Knowledge Creek also contain abundant invertebrate trace fossils (e.g., *Arenicolites*, *Skolithos*). Invertebrate trace fossils were not detected in coarser-grained lithofacies, although an exhaustive search of these has not yet been conducted.

In this study, the lithology surrounding the structures of interest is a very thick (>20 m) planar- to cross-bedded, conglomeratic lithic arenite with rounded or angular pebbles, cobbles, and boulders oriented parallel to bedding (Fig. 2). The lithology is well indurated, but eroded by shoreline processes. Laterally adjacent to and just above (1.5–2.0 m) the structures are a few medium- to very thick-bedded (0.2–1.5 m) lenticular sandstones of limited lateral extent (<5 m). Some of these sandstones follow concave bedding planes, hinting at channel bedforms. Sorting in the main lithology is moderate to poor, and the framework is primarily composed of medium- to coarse-grained sand composed of varying proportions of quartz, feldspars, and lithic clasts. Angular cobbles and boulders of lithic clasts are common in the basal 2–3 m of the outcrop, decrease in size and frequency for most of the succeeding section, and are common again in the upper part of the outcrop. A discontinuous breccia bed, about 30–40 cm thick, is lateral to (east of) the three structures and stratigraphically just above one of the structures, as explained later. Low-angle cross-bedding and horizontal, planar bedding is defined in places by aligned pebbles, cobbles, and a few bedding planes, but otherwise internal stratification is difficult to define, and the overall lithology is somewhat massive. Spherical to semispherical concretions, most of which are 2–15 cm in diameter, are evident in places; fractured examples of these reveal lithic clasts as nuclei.

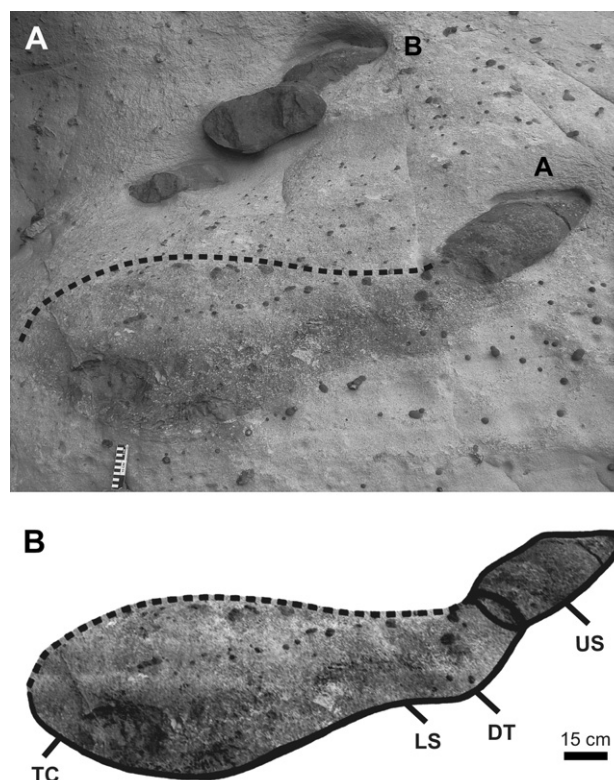
With one exception (noted later), body fossils, such as plants, invertebrates, vertebrates, are apparently absent in this section of the outcrop, although other lithofacies in the Knowledge Creek exposure contain abundant evidence of carbonized material that

is probably plant debris, which commonly occurs in both the Otway and Strzelecki Groups (Rich et al., 1988; Wagstaff and McEwen-Mason, 1989). Other than the structures described in this study, no obvious trace fossils, such as invertebrate burrows or cross-sections of dinosaur tracks, are evident in the surrounding lithology. Beds dip at about 15–20° N-NW, and a prominent high-angle normal fault (with accompanying scarp) is evident about 10 m southwest of the structures; the structures are within a downthrown block immediately east of the fault, and just west of the ravine formed by the Knowledge Creek drainage. The previously mentioned dinosaur tracks are difficult to identify ichnotaxonomically, but are tridactyl (and thus attributable to either ornithopods or theropods), and are evident as positive-relief epichnia in a horizon on the marine platform to the east of the ravine, 50–100 m away from and approximately 5 m below the subjects of this study.

The three enigmatic structures are grouped closely together in the outcrop and are separated from one another by less than 3 m. These structures differ in completeness, but are united by their similar sediment fill, cross-sectional dimensions, and south-southwestern orientation of long axes. They are described here in order of relative completeness, and for the sake of expediency are designated as Structures A, B, and C; Structure A is located stratigraphically below and to the east (or to the right, when facing the outcrop) of Structure B (Fig. 3A), whereas the tops of Structures A and C are on the same datum, but with C about 2 m east of A.



**Fig. 2.** Outcrop context of structures in Otway Group at Knowledge Creek, showing: relative locations of structures (A–C) described in this study; main lithofacies containing volcanoclastic boulders (VB), concretionary structures (CS), discontinuous breccia bed (BB), and lenticular sandstones (LS), with lower boundary of one channel bedform indicated by dashed line (also note planar bedding to left of channel bedform); fault scarp (FS) to the left. Beds are dipping away from the viewer, to the north-northwest.

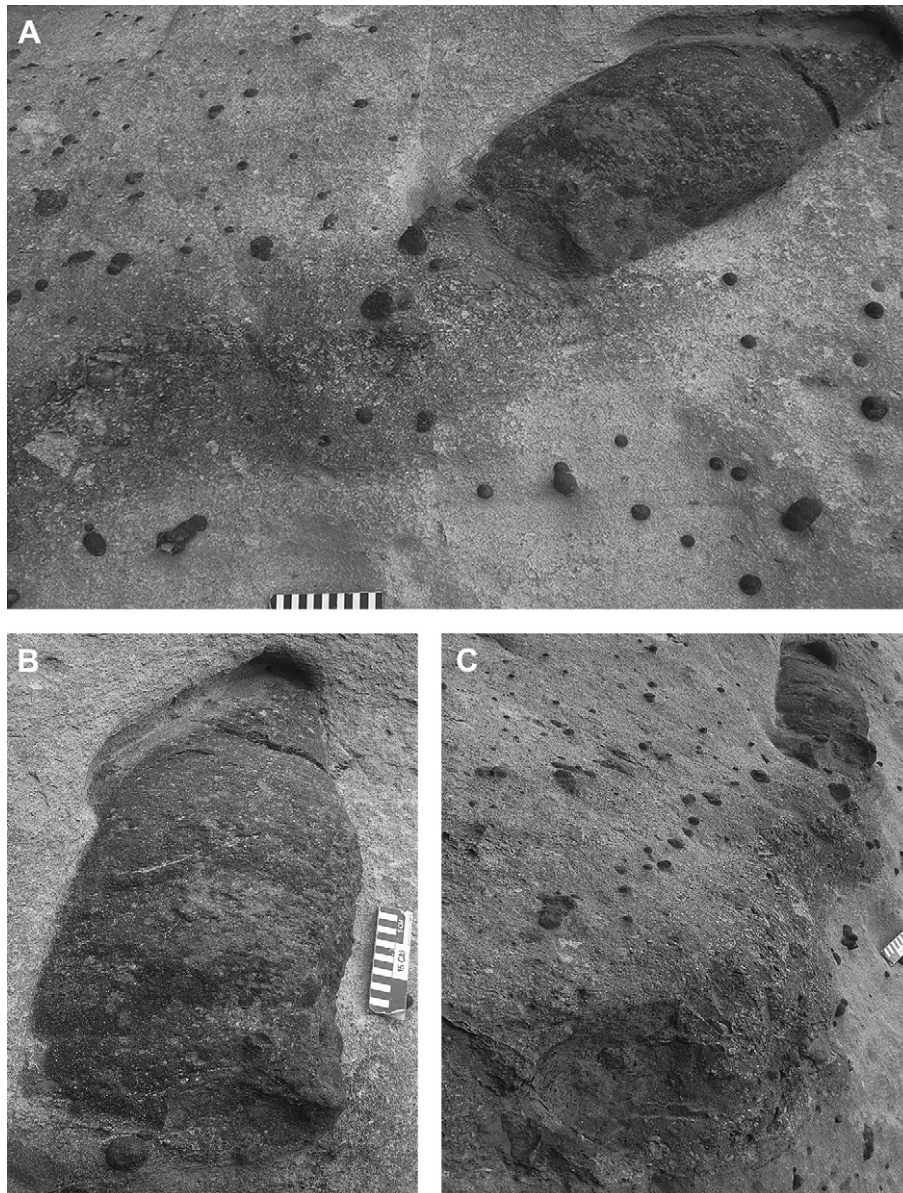


**Fig. 3.** Lateral views of Structures A and B from Otway Group (Knowledge Creek). A, Relative positions of Structures A and B within context of host lithology, photo scale (lower left) = 15 cm; B, Structure A in isolation, showing main aspects of geometry; key: US = upper segment; DT = dextral turn; LS = lower segment; TC = terminal chamber. Dashed line indicates maximum probable extent of upper boundary, inferred on basis of coarser-grained and differently colored sediment fill. Refer also to the text and Fig. 7 for interpreted geometry of the structure.

### 3.1.1. Description of Structure A

This is the most fully expressed structure, and hence the most significant of the three. The smooth, slightly convex face of the outcrop, with a slope of about 50–60°, cuts obliquely across Structure A, but most of its three-dimensional geometry is still discernable (Figs. 3B, 4). Its uppermost portion is weathered out in positive relief, showing a sharp contact with respect to the surrounding conglomeratic lithic arenite (Fig. 4A,B). This relief is imparted by a medium-grained hematitic lithic sandstone, which also shares a well-defined lower contact with a breccia (primarily composed of mudstone clasts of varying composition) in the remainder of the structure. This upper sandstone segment of Structure A is tubular, very slightly curved to straight, 66 cm long, 27–29 cm wide, and 24 cm thick, flattened parallel to bedding (Fig. 4B). Some slight variation in relief (1–2 cm) is evident along the outer boundary of this segment, lending a subtle “pinch and swell” appearance. Slightly further along its length, at about 80–85 cm (below the contact with the breccia), the outer

boundary of this segment bends at a near-right angle dextrally (as viewed from above), although this transition is eroded and incomplete (Fig. 4C). The length of the next segment is likewise difficult to resolve because of its projection into the outcrop and lack of full exposure, but is minimally 40 cm long, and probably longer. This segment turns sinistrally toward its downward end and connects with an expansive, ovoid cross-sectional area that is 100–105 cm long and minimally 35 cm high, although its indistinct upper boundary allows for a thickness of as much as 45 cm. Although eroded, this area is circular to elliptical in end-on view, and its maximum width is about 40 cm. The downward angle (with respect to bedding) of the upper sandstone segment is 23°, whereas the lower segment leading into the expanded part is at an angle of 14°, discernable from where the structure cross-cuts bedding. The vertical drop of the upper segment (to the dextral turn) is 38 cm, and the total vertical drop of the structure is about 50–52 cm, with both distances measured from the lower boundary of the structure.



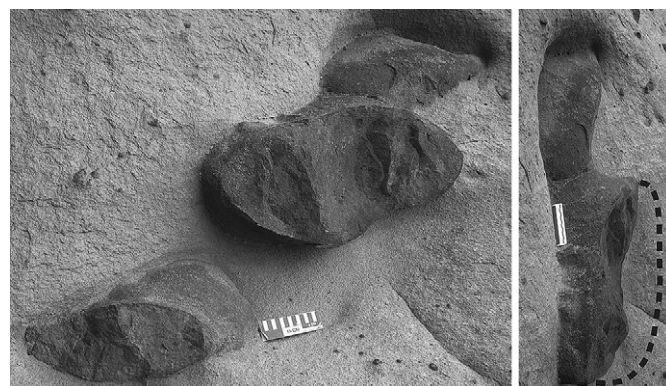
**Fig. 4.** Structure A in several views. A, lateral view, displaying descending tunnels separated by dextral turn (hint of semi-helical form), and uniformity of width; B, top view of descending hematitic sandstone fill, exhibiting tubular morphology (flattened parallel to bedding) and slight dextral curve before segment; C, end-on view (looking up axis), showing torsion in upper portion, approximate width of terminal chamber, and breccia fill in chamber. Scale in each photo = 15 cm.

The bottom boundary of the lowermost portion of the structure is well defined by horizontally aligned and large (3–10 cm long) mudstone clasts and underlying bedding, which is slightly concave and follows a contour defined by the clasts. The uppermost boundary, however, is more vaguely defined. Nonetheless, the breccia and slightly darker hue of this sediment is texturally and compositionally distinct from the surrounding sediment, which helps to define the overall geometry of the structure. Moreover, a line of rounded pebbles, similar in lithology to the hematitic sandstone at the top of the structure, also outlines the upper boundary and is consistent in trend with the underlying color and textural differences; a 15–20 cm thick zone above this line shows a similar influence on bedding formed above the structure. Sediment in the ovoid area of Structure A shows normal graded bedding, from a breccia in the basal 30 cm containing angular clasts as large as 6–10 cm, to a finer-grained pebble conglomerate in the upper 10 cm. The breccia is very similar to the lithology of a discontinuous breccia bed about 3 m east of the structure; the base of this bed is stratigraphically about 20–30 cm above the breccia fill of Structure A, implying that this bed may be related to the original source of sediment. Normal graded bedding is also evident in the upper part of the structure above the ovoid part; this bedding is harmonious with the lower boundary of the structure and is definable as a 20-cm thick zone that continues upward until interrupted by the abrupt contact with the overlying sandstone within the structure. Bedding within the structure is concordant with bedding in the host rock outside of it. No smaller, directly connected or otherwise closely associated structures, such as obvious invertebrate burrows, are evident on the periphery or in the interior of the structure. None of the clasts are identifiable as vertebrate coprolites, although such trace fossils have not yet been interpreted from the Otway and Strzelecki Groups (Rich et al., 1988; Rich and Vickers-Rich, 2000). Additionally, no skeletal material or other body fossils are amid the sediment within the structure.

The overall plan view of Structure A is of a gently descending, tunnel-like, semi-helical, sinuous structure that turns dextrally, then sinistrally before expanding into an ellipsoidal terminal chamber. The structure is minimally 2.1 m along its axial length and maintains a near-constant diameter of about 27–30 cm along 60–65% of its straight-line length until it connects with the wider terminal chamber.

### 3.1.2. Description of Structure B

Structure B is quite similar to the upper part of Structure A in terms of size, initial geometry, lithology, and attitude with respect to bedding (Fig. 5). It is likewise weathered less than the surrounding lithic arenite, rendering it in positive relief. The tubular structure is composed of hematitic medium- to coarse-grained lithic sandstone and is apparently homogeneous throughout, showing no obvious bedding or other internal structures, such as trace fossils (i.e., invertebrate burrows). It is 29 cm wide, 27–29 cm thick, and 59–60 cm long. Structure B also shows torsion similar to that in Structure A, in which a straight, descending segment (about 35–40 cm long) turns dextrally; this turn is more completely expressed than that in Structure A (Fig. 5A, B). The elbow (junction) of the turn is truncated obliquely, resulting in a misleadingly wide cross-section (57 cm) that nearly doubles its actual width, but while maintaining nearly the same thickness. Because of this truncation, however, the outer elbow of the turn is inferred; accordingly, this widened part cannot be discounted entirely as a branch junction, either. The downward angle of the upper segment is slightly steeper than that of Structure A (27°), showing a vertical drop of its lower surface of 31 cm within a shorter length, measurable from the surrounding planar bedding, which the structure cross-cuts. Its long axis, like that of Structure A, is oriented to the southwest.



**Fig. 5.** Structure B in several views. A, lateral view, showing angle of descent, partial spiral, doubled area in cross-section, and smaller (perhaps connected) structure below, scale = 15 cm; B, top view, with fracture across turn and outer edge of turn inferred (dashed line), scale = 10 cm.

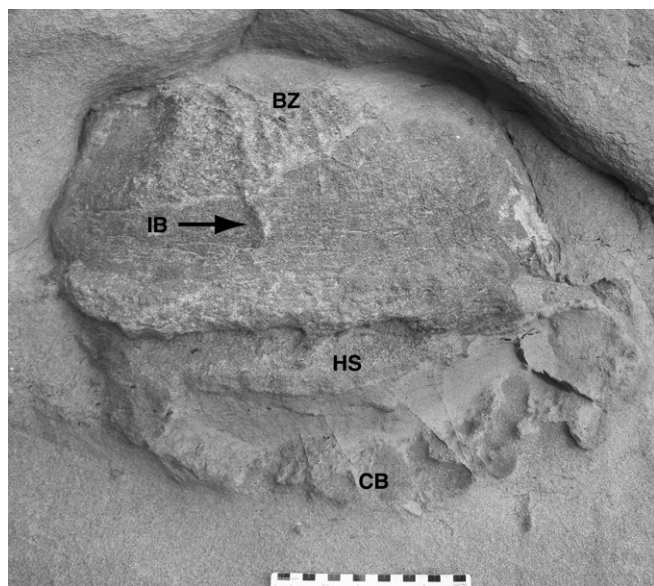
A smaller structure, similar in its positive-relief expression and lithology, is proximal to (20 cm below and west, or left of) Structure B (Fig. 5A). This tubular structure is 29 cm wide, 15 cm thick (oval in cross-section, flattened parallel to bedding), and 28 cm long. Like the other two structures, its long axis is oriented to the southwest, and it follows the descending axis of Structure B at an 18° angle. Its lowermost boundary is 43 cm below that of the uppermost part of Structure B. This structure is so closely associated with Structure B that it may be connected to and part of it, with its distal (down-slope) portion since eroded and the direct linkage hidden by the outcrop. The most likely way for these to be connected would be as a single, downwardly spiraling, sand-filled tube, of which only part is expressed outwardly (Fig. 5C). If connected, these two structures would account for a minimal downslope axial length of 90 cm. Nonetheless, lacking further evidence, the two structures also may be separate, and with different origins.

### 3.1.3. Description of Structure C

As mentioned earlier, the top of Structure C is on the same horizon as that of Structure A. This tubular structure, however, is much shorter than Structure A (about 25 cm long) and is 37–38 cm wide, and 27–29 cm thick, flattened parallel to bedding (Fig. 6). Like the other two structures, it is expressed as positive relief relative to the surrounding host lithology. It also has graded bedding, with its basal 4–7 cm composed of rounded and angular clasts (conglomeratic), which is overlain by a hematitic medium- to coarse-grained lithic sandstone, identical to that in Structure A. This hematitic sandstone shows internal, planar bedding that laps onto the underlying conglomerate, and scattered, black carbonized plant debris is evident in its lower 5 cm. The top few centimeters of the sandstone is slightly mixed (probably bioturbated), and a single, small-diameter (8 mm) meandering burrow, expressed in positive relief, extends along the top surface of the structure. Despite its shorter length, the structure also shows a definite downward trend relative to the surrounding host lithology, although its angle is difficult to discern. Torsion is not discernable in the specimen; its lengthwise trend is slightly different from that of Structures A and B and points more due south, rather than southwest.

## 3.2. Interpretation of Otway structures

The Otway structures are interpreted as biogenic structures, and are most likely attributable to burrows made by relatively large (10–20 kg mass) tetrapods, such as ornithomimid dinosaurs. This interpretation is based on a diagnosis of the following criteria: (1) facies setting; (2) preservational mode; (3) size (dimensions); (4)



**Fig. 6.** Structure C in frontal view. Conglomeratic base (CB), hematitic sandstone (HS), and probable burrowed zone, including invertebrate burrow (BZ and IB, respectively) indicated. Scale = 15 cm.

overall morphology; (5) spatial relationship to one another; (6) resemblance to known tetrapod burrows, specifically one identified previously as a small-ornithopod burrow from the Lower Cretaceous of Montana (USA); (7) occurrence in and proximity to strata with known body and trace fossil evidence of small ornithopod dinosaurs; and (8) paleoenvironmental context. Such a specific designation of a tracemaker may seem tenuous in the absence of accompanying body fossil evidence, and any one of the given criteria is potentially falsifiable or otherwise subject to modification. Nevertheless, it is a reasonable hypothesis when taking into consideration the combination of the given evidence and previous research, elaborated subsequently.

### 3.2.1. Facies setting

Facies at Knowledge Creek are typical for much of the Otway Group reported at other localities, consisting of cross- to planar-bedded fluvial channel-fill sandstones, conglomerates, and breccias, along with overbank deposits of finer-grained ripple-bedded and thinly bedded sandstones and siltstones (Rich et al., 1988; Bryan et al., 1997). At Knowledge Creek, the latter strata also contain small invertebrate burrows (*Arenicolites*, *Skolithos*), as well as tridactyl dinosaur tracks (Rich and Vickers-Rich, 2000; Martin et al., 2007). Facies of the Otway and Strzelecki Groups have been interpreted as the result of high-energy discharge related to seasonal input of reworked intrabasinal volcanoclastic sediments and clasts, but conglomerates and breccias in particular are attributed to braided rivers and alluvial fans (Bryan et al., 1997; Tosolini et al., 1999). Alluvium or abandoned braided fluvial channels would be consistent with tetrapod burrowing during emergent conditions, especially if timed seasonally (discussed in detail later), and the presence of dinosaur tracks in underlying strata at Knowledge Creek points toward the availability of nearby subaerial surfaces within the depositional basin.

The structures cut across a planar-bedded conglomeratic lithic arenite, which is interpreted here as an abandoned braided fluvial or alluvial channel fill that was occasionally cross-cut by subsequent sheet flows and small, shallow, and temporary channels. The latter are evidenced by ephemeral lenticular sandstones above the structures; these were probably deposited into surfaces eroded into

underlying alluvial deposits. Although the outcrop limits the lateral and vertical extent of the main host lithology, it is minimally 20 m thick, pointing toward a continual source of these sediments, albeit with some interruptions in coarse-grained deposition indicated by the lenticular sandstones. Erosion of former bedding surfaces is suggested by the possibility of concealed bed junctions, which is indicated by the lack of a sand body contributing to the sandstone filling the upper portions of Structures A and B, but also the presence of a discontinuous breccia bed stratigraphically just above Structure A, which contains a similar breccia fill (Figs. 2–4).

Evidence for development of paleosols is lacking, such as those associated with cryoturbation structures (formed by the melting of permafrost) in the Strzelecki Group (Constantine et al., 1998; Vickers-Rich et al., 1999). Nonetheless, the sediments containing the structures feasibly could have been emergent long enough (after cessation of seasonal flooding) for burrowing to have occurred before sediment filling and erosion by later discharge within the same alluvial-fluvial drainage. Additionally, if the three structures were formed at the same time (discussed further in the next section), their slight differences in stratigraphic height may be attributable to formation on the slope of a channel bank that was temporarily above the local water table. Unfortunately, such a surface, if preserved, would be hidden from view, as the uppermost parts of the structures (which would intersect with such a surface) are within the outcrop.

### 3.2.2. Preservational mode

Based on the available evidence, Structures A–C were originally open (hollow), tubular concavities and passively filled. Graded bedding in the lower parts of Structures A and C is consistent with deposition by a waning flow, and the slight inclination of both structures would have been amenable to passive filling on a channel margin. Moreover, the two different rock types composing the fill, breccia and hematitic sandstone in the lower and upper sections (respectively) of Structures A and C, reflect two separate episodes of filling. The sharp contact between the two fills shows that a short time elapsed between their deposition: the lower fill had sufficiently compacted so that its top surface was more-or-less planar, and there is no evidence of the second sediment fill mixing with the first, nor erosion of a lithified breccia. Structures A and C may have been slightly compacted (partially collapsed) prior to filling, which is suggested by bedding-parallel flattening, although this flattening is minor in the similarly sized Structure B. Some depositional loading in the lower, terminal chamber of Structure A is also indicated by slight deformation of bedding underneath its lower boundary, which indicates that both the host lithology and the sediment fill were still unconsolidated and probably had some interstitial moisture. Some erosion (and perhaps liquefaction caused by ground water) of Structure A is also suggested by its vague upper boundary, which would be consistent with multiple flooding events that provided at least two pulses of sedimentation. The top portion of Structure A also may have been partially breached by erosion before its final burial and lithification.

Structures B and C are considered as nearly identical to the upper part of Structure A on the basis of size, partially expressed geometry, and sediment fill. Their proximity to Structure A is also intriguing, as it implies they may have been open at the same time, followed by filling from the same sedimentary source. These identical sandstone fills, lacking an obvious overlying sand source, also suggests a concealed bed junction, in which an overlying sand bed that served as the source of the fill was eroded after passive filling of the structures; hence this stratum is missing from the overlying stratigraphic section. Such preservation of fossil burrows is commonly reported in invertebrate ichnology (Savrdra, 2007), although it may not be recognized as often with regard to

vertebrate burrows, which also, despite their oftentimes-larger sizes, may be more elusive to identify compared to invertebrate trace fossils (Hasiotis et al., 2007). Regardless, both the breccia and sandstone fills in each structure are anomalous with the surrounding host lithology, indicating a preservational mode that involved the later transport and deposition of sediment from a source outside of the structures. This proposed situation is bolstered by the presence of a discontinuous breccia bed (Fig. 2) about 3 m east of and 20–30 cm above the breccia fill of Structure A, which may represent the original source of the fill. The possible continuation of Structure B, indicated by a sandy tube with the same lithology and of the same width (but shorter thickness) just below and downslope of it, is explainable here as part of a descending segment following a sinistral turn hidden within the outcrop (Fig. 5C). Furthermore, the bedding-plane parallel flattening in all three structures may be attributable to: post-depositional compaction; a decreased amount of sediment filling an originally hollow structure; an incompletely formed structure at its distal end; or any combination of any of these factors.

The preservational mode for Structure A was similarly interpreted for the burrow and den structure associated with the Lower Cretaceous ornithopod *Oryctodromeus cubicularis* in Montana: a lithic arenite that was conglomeratic at its base (with normal graded bedding) in the lower part of the structure, which included skeletal material of an adult *O. cubicularis* and two juveniles; a sharp contact between it and the overlying sediment (denoted by a 1–2 cm thick claystone); and a finer-grained sandstone in the upper part of the structure (Varricchio et al., 2007). Those researchers also interpreted two episodes of sedimentation that filled the originally open (hollow) structure, which aided in preservation of both the bones and the original structure.

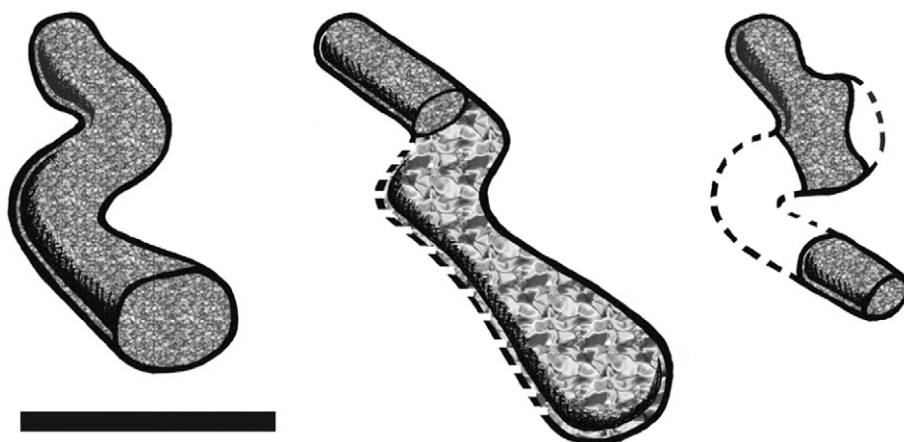
### 3.2.3. Dimensions, morphology, and spatial relationships

The size, morphology, and spatial relationships of the structures to one another are grouped together in this section to better convey their interrelatedness as evidence supporting their biogenic affinity. For example, the size and morphology of Structure A matched the author's search image for a dinosaur burrow (that attributed to *Oryctodromeus*, specifically) and thus constituted the initial basis for a hypothesized dinosaurian tracemaker (Fig. 7). The close proximity of these three unusual yet similar structures, two of which were semi-helical, and each having consistently sized,

cylindrical, descending, and inclined tunnels, is another interesting coincidence, and implies a similar origin, which is more easily explained by their identity as trace fossils, rather than random physical sedimentary structures (i.e., load casts, scour-and-fill structures). Furthermore, their bedded, clastic sedimentary fills (breccia, sandstone) belie any diagenetic origin or other post-depositional chemical structure (i.e., concretions), discussed in more detail later. Structure A shows two turns (dextral and sinistral) of a descending tunnel that leads into an expanded terminal chamber, which cross-cuts pre-existing bedding and is passively filled; its total length is minimally 2.1 m, which represents a significant excavation of the surrounding host sediment that remained open before subsequent filling by sediments. Structure B also may have dextral and sinistral turns, and an inferred downslope axial length of 90 cm is nearly half that of Structure A that nearly coincides with the same upper part of the latter. In short, certain parameters of the structures are more indicative of trace fossils (i.e., burrows) than non-biogenic structures.

The cross-sectional areas for Structures A–C are similar, although Structures A and C are slightly more ovoid compared to the circularity of Structure B, probably as a result of bedding-parallel compaction. Using the two measured perpendicular widths for each structure and calculating for the area of an ellipse (where  $\text{area} = \pi \times \text{radius}_1 \times \text{radius}_2$ ), the upper inclined portion of Structure A has a cross-sectional area of 509–547 cm<sup>2</sup>. Structure B has a cross-sectional area of 615–660 cm<sup>2</sup>, whereas that for Structure C is 770–840 cm<sup>2</sup>. (The calculated ranges account for slight variability in each dimension along the lengths of the structures.) The cross-sectional area of the inferred torsion on Structure B is 1250–1300 cm<sup>2</sup>, which is effectively twice that of the cylindrical portion above. This measurement supports the interpretation that an oblique section through a dextral turn of this sand-filled tunnel resulted in doubling the area because of the two segments meeting at the turn.

Using the assumption that these structures are burrows, the cross-sectional areas of the upper portions of Structures A–C were compared to a regression plot and formula for burrow cross-sections versus body masses of fossorial animals, developed by White (2005). Accounting for little compaction, the cross-sectional area of each structure corresponds with tracemaker body masses of about 9.5–10 kg (Structure A), 12.5–14 kg (Structure B), and 18–20 kg (Structure C). These ranges are consistent with estimated



**Fig. 7.** Diagrammatic comparison of overall geometry between documented ornithopod (*Oryctodromeus cubicularis*) burrow from Blackleaf Formation (Cenomanian) of Montana (USA), Varricchio et al. (2007), and Otway Structures A and B (this study). From left to right, geometry of Blackleaf burrow, Otway Structure A, Otway Structure B; sandstone fill is shown as fine stippling, breccia fill as coarse texture (Structure A). Drawn to the same scale and using a horizontal datum for their uppermost extents; solid lines are based on outward (outcrop) expression, dashed lines are inferred boundaries. Scale bar = 1.0 m.



masses for small ornithopod (hypsilophodontid-grade) dinosaurs of the Otway Group from nearby Dinosaur Cove, such as *Leaellynasaura amicagraphica* and *Atlascopcosaurus loadsi*, and various unclassified specimens comparable to *Fulgurotherium* (Rich and Rich, 1989; Rich and Vickers-Rich, 1999, 2000; Peczikis, 1995). These sizes, however, are also significantly larger than those of any known mammals from either the Otway or Strzelecki Groups (Rich and Vickers-Rich, 2004; Pridmore et al., 2005), yet much smaller than mass estimates for known theropod dinosaurs (*Timimus hermani*), labyrinthodonts (e.g., *Koolasuchus cleelandi*, estimated to have weighed nearly 500 kg), and crocodylians from either the Otway or Strzelecki Groups (Warren et al., 1997; Gaffney et al., 1998; Rich and Vickers-Rich, 2000). The only two non-dinosaurian tetrapods with body widths approaching that estimated from the Otway structures is the chelonian *Otwayemys cunicularius*, with a reconstructed width of about 20 cm (Gaffney et al., 1998), and the largest mammal known from the Lower Cretaceous of Victoria, *Kryoryctes cadburyi* (Pridmore et al., 2005), both of which are too small for the three burrow diameters. With regard to *K. cadburyi*, its size estimate was based on a single humerus that compares well to that of the extant monotreme, *Tachyglossus aculeatus*; the later species varies in adult mass from 3.0 to 7.0 kg (Beard et al., 1992; Rismiller and McKelvey, 2003). Interestingly, Pridmore et al. (2005) also speculated that *B. cadburyi* might have been adapted for burrowing on the basis of expanded distal and proximal ends in its humerus; hence it might be postulated as a tracemaker for other burrow-like structures.

Regular lengths of tunnel segments in a semi-helical structure, as well as the total length of such a structure, also may be applicable to discerning their biogenic origin and tracemaker size. For example, the burrow interpreted for *Oryctodromeus* possessed two segments of nearly equal length (60–70 cm), which corresponded to the approximate torso length of the adult dinosaur (Varricchio et al., 2007): this minimum length was needed for the tracemaker to have turned corners while moving up or down in the burrow (allowing for a flexible tail). In this study, that criterion is not easily applied because the second segment projects into the outcrop and can only be discerned as a minimal length of about 40 cm. The upper segment, however, is more completely expressed, and is minimally 70 cm long before turning dextrally, completing the turn on its outside margin at about 80 cm down its length. Similarly, Structure B has a descending tunnel segment about 60 cm long, although its inferred dextral turn is incompletely expressed. The minimum length of the terminal chamber (100–105 cm) in Structure A also restricts that space to tracemakers of certain sizes, allowing for room to turn around in such a chamber. With these general dimensions in mind, either a tracemaker or secondary occupier of the structure would have had a torso length of less than 70 cm and a total length (including tail) of less than 2.1 m for it to effectively contain an animal using it for concealment. The burrow of *Oryctodromeus* was also 2.1 m long, and the total length of the adult dinosaur was estimated as the same, most of which (60%) was its tail (Varricchio et al., 2007).

Lastly, the close proximity of such conspicuous structures (with only 3 m separation) is viewed here as more than mere happenstance. Two of the structures were rather large, hollow, sinuous, tube-like excavations in the host sediment with similar form, sediment fill, orientation, and outward expression; two other structures are on the same bedding plane. Yet all three occur next to one another in an expansive coastal exposure that contained no other structures matching these descriptions. Although these similar structures may have been made separately by an identical set of unknown physical sedimentary processes, the more likely alternative explanation is that they are trace fossils (burrows) made by the same or comparable tracemakers living in the same place.

### 3.2.4. Resemblance to known tetrapod burrows

As mentioned in the previous section, the overall dimensions and forms of Structure A, and in part Structures B and C, resemble the only well-described dinosaur burrow from the Upper Cretaceous of Montana (Varricchio et al., 2007), but more generally they also match criteria used to identify tetrapod burrows. Tetrapod burrows tend to have elliptical to circular cross-sections, spirals, ramps, enlarged terminal chambers, scratch marks consistent with tetrapod limbs, and other morphological details that reveal their origins, versus burrows made by fish or similarly sized invertebrates (Miller et al., 2001; Groenewald et al., 2001; Hasiotis et al., 2004, 2007; Loope, 2006; Martin et al., 2008; Sidor et al., 2008). Some tetrapod burrows are relatively simple in their overall architecture, such as those made by amphibians, which have a single, straight, vertical shaft or slightly inclined tunnel, and may or may not lead to an enlarged terminal chamber (Hembree et al., 2004, 2005). Spiraling, however, is seemingly a recurring trait of amniote burrows, once all other identifying characteristics are taken into consideration (Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2007; Martin et al., 2008). For example, even the relatively simple burrows of modern gopher tortoises (*Gopherus polyphemus*) show some spiraling: most of their burrows commonly turn sinistrally or dextrally before ending in an enlarged terminal chamber (Doonan and Stout, 1994). Although less studied than burrows and dens made by other tetrapods, structures of the American alligator (*Alligator mississippiensis*) of coastal Georgia (USA) also show near-right angle bends, with each segment of the burrow corresponding to slightly more than the length of the largest adult alligator occupying the structure (Royce Hayes, personal communication 2008). Yangtze alligators (*Alligator sinensis*) of China make similar dens, some of which are quite large (>20 m long) and complicated (Chen et al., 1990). In the fossil record, perhaps the most famous of spiraling amniote burrows are those of the Miocene beaver *Palaeocastor*, body fossils of which have been found in their burrows (Meyer, 1999). Nonetheless, therapsid burrows from the Permian of South Africa (Smith, 1987) and inferred mammal burrows from the Jurassic of Utah (Hasiotis et al., 2004) also exhibit spiraling, indicating that this characteristic has been present in tetrapod burrows for more than 250 million years.

Two of the Otway structures (A and B) are semi-helical and are sloping, turning tunnels, although these traits are only partially expressed in Structure B; one (Structure A) is also connected to an enlarged terminal chamber. As noted previously, and by Loope (2006), Hasiotis et al. (2007), and Varricchio et al. (2007, and references therein), burrows with such a form are made by a large number of modern tetrapods: aardwolves (*Proteles cristatus*), alligators (*Alligator mississippiensis*, *A. sinensis*), coyotes (*Canis latrans*), gopher tortoises (*Gopherus polyphemus*), puffins (*Fratercula arctica*), striped hyenas (*Hyaena hyaena*), and numerous rodents, to name a few. Torsion in these burrows serves multiple purposes, such as: slowing the entry of potential predators (particularly if the burrow is also being used as a den); decreasing the rate of humidity and heat loss from the burrow; or maintaining an equitable microhabitat while shielding its occupants from harsh atmospheric conditions outside of the burrow (Voorhies, 1975; Rieger, 1981; Hildebrand, 1985; Koehler and Richardson, 1990; Willmer et al., 2000). The downward angle shown by two of the Otway structures (A = 22° and B = 27°) is also consistent with declinations measured in extant gopher tortoise burrows, which in one sample showed a median of 30° (Doonan and Stout, 1994).

Lungfish body fossils are in the Otway Group (Rich et al., 1988), and lungfish burrows have been interpreted from the geologic record, hence these are also considered as possible tracemakers for the Otway structures. Lungfish burrows, however, differ considerably

from the Otway structures described here: they are vertically oriented, straight (non-spiraling), and have much smaller average diameters; in fact, lungfish burrows are potentially confused with crayfish burrows (Hasiotis et al., 1993, 1999; Kowalewski et al., 1998; Gobetz et al., 2006; Martin et al., 2008). The only notable feature they share with most tetrapod burrows is an enlarged terminal chamber, which allows for the lungfish to turn around in the burrow (Gobetz et al., 2006).

Given the evidence that the Otway structures are burrows, and more specifically tetrapod burrows, their list of potential tetrapod tracemakers can be further narrowed on the basis of burrow dimensions, as discussed previously. The only known tetrapods within the Otway Group that fall within the size range indicated by the structures (less than 2.1 m long, torso width of about 30 cm, and 10–20 kg mass) would have been small ornithomimid dinosaurs, such as *Leaellynasaura* and *Atlascopcosaurus*. Hence the Otway structures are interpreted as dinosaur burrows, while allowing for the possibility that some yet unknown tetrapod tracemaker may also have been responsible. There is insufficient evidence that these burrows were denning structures (*sensu* Varricchio et al., 2007), although multiple purposes for such burrows are not negated, either.

### 3.2.5. Occurrence in strata with fossil evidence of small ornithomimids

The structures co-occur in the Otway Group with a well-documented dinosaur assemblage, replete with an unusually high proportion of relatively small ornithomimids (Rich et al., 1988; Rich and Vickers-Rich, 1999; Rich et al., 2002), some of which may have been amenable to burrowing. In North America, other than *Oryctodromeus*, Varricchio et al. (2007) proposed that similarly small and closely related Cretaceous hypsilophodontids in Montana, such as *Orodromeus* and *Zephyrosaurus*, also might have burrowed. Part of this hypothesis was based on taphonomy of *Orodromeus*, in which specimens often occur as compacted masses of nearly complete skeletons in concretions, implying their preservation in burrow chambers (Varricchio et al., 2007). Owing to this convergence of similar, small ornithomimids in each area (Montana and Victoria), with one of those areas having probable burrowing abilities, this study proposes that the Victorian assemblage may also contain burrowing forms.

Unfortunately, a direct comparison between Lower Cretaceous hypsilophodontids of the Otway and Strzelecki Groups to those of the Upper Cretaceous of Montana is problematic because of the incompleteness of the Victorian specimens. The Otway and Strzelecki hypsilophodontids, for instance, have not yet been tested for anatomical adaptations related to fossorial behaviors, such as those interpreted in *Oryctodromeus*. Indeed, this hypothesis may not be testable with the given skeletal material gathered thus far. For example, the holotype of *Oryctodromeus* is an adult specimen with three well-defined traits indicating burrowing ability: (1) a fused premaxilla (snout modified for shoveling); (2) enlarged and fused scapulocoracoids with major scapular spines and acromions (for attachment of strong digging muscles); and a modified hip, including seven sacral vertebrae (used for bracing as a counter when burrowing with forelimbs). In contrast, the holotype of *Leaellynasaura amicagraphica* is a single partial skull; moreover, it is suspected as a juvenile specimen (Rich et al., 1988; Rich and Vickers-Rich, 1999). Other small ornithomimid material, such as those from *Atlascopcosaurus*, *Qantassaurus*, and unidentified species allied with *Fulgurotherium*, although abundant, is likewise fragmentary and consists primarily of limb elements, jaw fragments, and teeth (Rich and Vickers-Rich, 1999). As a result, it does not lend well to a detailed diagnosis of functional morphology related to digging ability.

No body fossil evidence of hypsilophodontids or other dinosaurs are known in the Otway Group exposed at Knowledge Creek.

However, strata at Knowledge Creek, just below (about 5 m) and adjacent to (100 m east) the Otway structures, contain dinosaur tracks, including an undoubted small ornithomimid track (Rich et al., 1988; Rich and Vickers-Rich, 2000; Martin et al., 2007). This trace fossil evidence places potential tracemakers in the same area and just before deposition of sediments composing the host lithology for the Otway structures. A dinosaurian presence in and near paleoenvironments of the Otway Group at Knowledge Creek (i.e., within the Otway Basin: Tosolini et al., 1999; Miller et al., 2002) is also assumed on the basis of their abundant representation at Dinosaur Cove, only 6.0–6.5 km to the southeast, although the relative stratigraphic position of the Dinosaur Cove bone bed to strata at Knowledge Creek is currently undetermined.

Regardless, the sheer relative abundance of small ornithomimids in Lower Cretaceous strata of Victoria, Australia, also provokes a simple question: “Why?”. At least part of the answer has been linked to paleogeographic proximity of this area to the South Pole during the Cretaceous (Veevers et al., 1991; Veevers, 2006), and thus is tied into climatic conditions that would have selected for small size and other specialized adaptations in polar dinosaurs, such as burrowing.

### 3.2.6. Paleoenvironmental context

The paleogeography, sediments, and paleontological information provided by the Otway and Strzelecki Groups reflect circumpolar and periglacial conditions in this part of Australia during the Early Cretaceous, in which prolonged periods of darkness and cold would have occurred annually (Vickers-Rich et al., 1999; Rich and Vickers-Rich, 2000; Rich et al., 2002). As a result, such conditions would have encouraged adaptations that allowed for better survival of overwintering animals. Among the adaptations of modern terrestrial tetrapods overwintering in polar environments, burrowing is one of the most common means used to alleviate heat deprivation in polar or otherwise cold environments (Davenport, 1992; Willmer et al., 2000). Thus fossil evidence of such burrows might be expected in ancient terrestrial facies formed in circumpolar environments, particularly if these burrows are interpretable as shelters from extreme environmental conditions (*sensu* Loope, 2006).

Furthermore, Allen's Rule, which states that appendages tend to be shorter in endothermic tetrapods (Nudds and Oswald, 2007, and references therein), may be applicable to the Victorian dinosaurs. The shortening of extremities, such as limbs, decrease heat loss; consequently, cold climates may favor selection for smaller body size in some endothermic tetrapods, or otherwise trigger phenotypic responses to cold temperatures that decrease limb size (Serrat et al., 2008). Accordingly, the circumpolar settings for the Otway and Strzelecki Groups may explain why their dinosaur assemblages are composed predominantly of smaller-sized (i.e., shorter-limbed) ornithomimids. Moreover, the energy expended in association with burrowing (“burrowing cost,” which is proportional to the volume of excavated sediment) limits the sizes of burrowing animals; additionally, shorter-limbed tetrapods within a given lineage, such as in reptiles, are more likely to be burrowers (White, 2005). Again, smaller-sized dinosaurs would have been favorably selected as burrowers, and their trace fossils (e.g., tracks, burrows) would reflect these smaller sizes as well. A corollary to Allen's Rule, however, is Bergmann's Rule, in which large body mass within a species or lineage is favored as a result of surface-area/volume ratios related to heat conservation in cold environments (Blackburn et al., 1999; Blackburn and Hawkins, 2004; Queiroz de and Ashton, 2004). Exceptions to this principle have resulted in its modification as a “rule,” though (Mousseau et al., 1997; Blackburn et al., 1999; Ashton and Feldman, 2003), and its application to the Victorian polar dinosaur assemblage would likely require more knowledge of

the same or closely related dinosaur species from lower paleolatitudes.

In short, the paleoenvironmental setting of the Otway Group should have favored: (1) smaller body sizes in fossorial dinosaurs; (2) burrowing behavior, especially for overwintering dinosaurs (discussed in detail later); and (3) a combination of these two traits, which would be reflected in dimensions and morphology of a fossil burrow. The Otway structures are consistent with this larger-scale setting.

### 3.3. *Alternative hypotheses for Otway structures*

The structures described here are possibly of non-biogenic origin, although their close spacing, similar diameters, and identical preservation imply a common origin, regardless of whether it was through biogenic or physical processes. The similar orientation of the structures (south-southwest) is probably the only quality that may argue for current-aligned structures formed by erosion, which were then filled by sediment differing from the surrounding host lithology. For example, scour-and-fill structures typically: are common in fluvial and alluvial environments; are oriented down-current, with sloping surfaces that are steeper in the upward parts and less steep in their lower parts; can be filled with sediment either finer or coarser than the surrounding host sediment; and can be proximal to one another (Boggs, 1995). Such erosive structures, however, are more like small channels, forming well-defined troughs (Rossetti et al., 2000), and are not known to form semi-helical and tubular structures that act as concavities for collecting sediment. Furthermore, the distinctive sediment fill of Structures A and B, with no clear connection to an overlying bed, argues against their formation through soft-sediment deformation (load casts), even when accounting for unusual sedimentary structures formed in polar environments, such as cryoturbation and frost-heaving structures (Constantine et al., 1998; Vickers-Rich et al., 1999; Rich and Vickers-Rich, 2000; Rich et al., 2002).

The structures also might be initially identified as chemical sedimentary structures (e.g., concretions), and abundant concretions are indeed within the outcrop and near the structures, seen as 2–15 cm wide spherical bodies within the conglomeratic lithic arenite. Nevertheless, the presence of clearly defined bedding within Structures A and C (including lithic clasts and graded bedding), an obvious sandstone fill of Structures A–C, and invertebrate burrowing in Structure C, all dispute a diagenetic origin for the structures. Further evidence disagreeing with a “concretion” identification for the given structures include: (1) consistent widths and lengths, as well as similar cross-sectional areas, of the upper parts of the structures, whereas concretions are more randomly sized, normally formed by chemical precipitation around a nucleus, such as a body fossil or lithic clast (Boggs, 1995; Burley and Worden, 2003); (2) spiraled geometry in two of the structures, which is more typical of biogenic structures (Smith, 1987; Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2007; Martin et al., 2008); and (3) their clastic composition, which contrasts with concretions composed primarily of calcite, dolomite, chert, siderite, hematite, or gypsum (Boggs, 1995; Burley and Worden, 2003, and references therein). Lastly, “concretion” is a commonly used, all-purpose designation historically applied to any oddly shaped structures in the Otway and Strzelecki Groups (Patricia Vickers-Rich and Thomas H. Rich, personal communication, 2009), but at least some of these previously identified “concretions” in both groups were later interpreted as fossil crayfish burrows (Martin et al., 2008). This discovery, along with the results of this study, will hopefully prompt future researchers to take a more cautious approach before similarly labeling enigmatic sedimentary structures in the Otway and Strzelecki Groups.

Testing of the hypothesis presented here is challenging, but possible. Unfortunately, unlike the sediments surrounding the burrow interpreted for *Oryctodromeus* in Montana (Varricchio et al., 2007), the rock within and surrounding the structures is well indurated, hence none of it is easily excavated, which would help to further examine the full expression of the structures. Additionally, like the large structures in the Middle Jurassic of Utah (USA) interpreted by Loope (2006) as tetrapod burrows, no skeletal material or other body fossil evidence that might be linked to a potential tracemaker were in the structures. In fact, during the second visit to Knowledge Creek by the author of this study in July 2007, he asked two accompanying people who were well experienced with identifying bone fragments in the Otway and Strzelecki Groups (Lesley Kool and Michael Cleeland) to examine the structures for such evidence; they confirmed that each seemed devoid of body fossils in their surface expressions.

Oval cross sections, shortened parallel to bedding, may either indicate partial compaction of sediments in and around structures, or if closer to its original cross-sectional profile, which would argue against a dinosaurian tracemaker, and more for a flat-bodied amphibian (labyrinthodont) or chelonian. Collapse of hibernation structures, however, would be more likely for a seasonally occupied burrow that flattened and then filled with spring runoff and deposition. Accordingly, such structures would have been unoccupied during seasonal flooding and filling with sediments. This preservational scenario and possible variations of it within the context of the paleoenvironmental setting are explained further later.

## 4. Discussion: burrowing dinosaurs in polar environments

### 4.1. *Overview of polar dinosaurs*

Polar dinosaurs have long presented challenges to paleontologists in terms of explaining dinosaurian adaptations to seasonally cold and dark environments (Hotton, 1980; Brouwers et al., 1987; Parrish et al., 1987; Paul, 1988; Rich et al., 1988; Rich and Vickers-Rich, 1999; Rich and Rich, 1989; Benton, 1991; Clemens and Nelms, 1993; Chinsamy et al., 1998; Fiorillo and Gangloff, 2001a,b; Rich et al., 2002; Buffetaut, 2004; Hurum et al., 2006; Fiorillo, 2008; Bell and Snively, 2008; Godefroit et al., 2009; Fanti and Miyashita, 2009). For example, Parrish et al. (1987) and Currie (1989) thought that polar dinosaurs might have used seasonal migration to cope with such environments, whereas others hypothesized that some polar dinosaurs lived in these environments year-round, and thus hibernated or were otherwise physiologically adapted for winter conditions (Clemens and Nelms, 1993; Chinsamy et al., 1998; Vickers-Rich et al., 1999; Rich and Vickers-Rich, 2000; Fiorillo and Gangloff, 2001a,b; Fiorillo, 2008; Bell and Snively, 2008). Buffetaut (2004) and Godefroit et al. (2009) also opined that the paucity of ecothermic animals in association with most polar dinosaur assemblages implied that dinosaurs, in general, were better adapted to such cool environments. The likelihood of permanent-resident dinosaurs is supported in part by the presence of relatively small dinosaurs (e.g., hyspilophodontids) that were probably not capable of long migrations (Vickers-Rich et al., 1999; Bell and Snively, 2008). With the Otway Group dinosaurs, this conclusion is supported further by the dominance of juvenile animals in the assemblage, which would have been less likely to survive long migrations to and from polar areas (Rich et al., 1988; Rich and Vickers-Rich, 1999). Fiorillo and Gangloff (2001b) and Fanti and Miyashita (2009) came to the same conclusion with regard to hadrosaur juveniles from Upper Cretaceous strata of Alaska and Alberta, respectively. Furthermore, the lack of LAGs (lines of arrested growth) in limb bones of at least three polar dinosaurs

(*Leaellynasaura amicagraphica* and two unidentified small ornithomimids) from the Otway and Strzelecki Groups of southeastern Australia, as well as enlarged orbits and optic lobes in *L. amicagraphica*, suggest year-round activity in those animals, even during times of prolonged cold and darkness (Chinsamy et al., 1998; Constantine et al., 1998; Vickers-Rich et al., 1999). Bell and Snively (2008) also examined energy requirements for long-distance migrations in Cretaceous polar dinosaurs and concluded that most of these, especially the smaller forms (e.g., *Troodon* and hypsilophodontids), must have overwintered, rather than migrated. The recent discovery of hadrosaurid and non-avian theropod eggshell material in the Maastrichtian of Siberia (Godefroit et al., 2009), as well as hadrosaurid hatchlings and nestlings in the Campanian of west-central Alberta (Fanti and Miyashita, 2009) also confirms dinosaur nesting in circumpolar environments, again implying year-round activity by those dinosaurs.

How year-round residents dealt with polar winters is, perhaps the most intriguing question associated with polar dinosaurs. Using actualism as a guide, behavioral strategies of terrestrial vertebrates living in modern polar environments include (minimally) the following: (1) use of microhabitats, such as burrows; (2) migration; (3) adaptations to reproduction and life cycles; (4) gregariousness (aggregation and huddling); (5) protective insulation; (6) decreasing heat loss at extremities, and heat production in general; (7) hibernation, achieved through hypothermia or torpor; and (8) food caching and other specialized forms of food selection (Davenport, 1992; Willmer et al., 2000). Of these, one of the recurring strategies proposed for dinosaurs coping with polar winters (mentioned earlier) was seasonal migration, which was critically reviewed by Bell and Snively (2008, and references therein). Another commonly proposed strategy was some form of hibernation, or dinosaurs otherwise seeking protection against severe environmental conditions, which of course also may have involved microhabitats (burrows or other forms of shelter), adaptations in life cycles, heat production, and other listed factors. For example, hibernation was interpreted for the ornithomimid *Timimus hermani* on the basis of its possessing well-developed LAGs, which indicated slow periods of bone growth consistent with times of decreased metabolic rates (Chinsamy et al., 1998; Constantine et al., 1998; Rich and Vickers-Rich, 1999).

Nonetheless, perhaps the most common strategy used by modern overwintering terrestrial tetrapods in polar environments, whether they hibernate or not, is burrowing (Davenport, 1992; Willmer et al., 2000). In fact, Rich et al. (1988) first suggested that most animals in the Otway Group (based on evidence then) could have eased overwintering by burrowing; most recently, Bell and Snively (2008) suggested the same strategy as a possibility for smaller polar dinosaurs, rather than long-distance migrations. Hence this paradigm will be explored in the most detail here and applied to the polar dinosaurs of Victoria, Australia.

#### 4.2. Burrowing behaviors in modern polar tetrapods

Numerous modern terrestrial tetrapods, both ectotherms and endotherms, provide actualistic examples of fossorial behavior in coping with cold conditions, whether these animals live in temperate, high-altitude (montane), or circumpolar environments. For example, in the western U.S., desert tortoises (*Gopherus agassizii*) use huge, multigenerational burrows and dens for surviving freezing temperatures during winters (Davenport, 1992; Rautenstrauch et al., 1998). Various species of crocodylians will burrow in response to temperatures approaching 0 °C (Brisbin et al., 1982; Hagan et al., 1983; Brandt and Mazzotti, 1990); the Chinese alligator (*Alligator sinensis*) constructs bank burrows as dens used for overwintering, which are dug seasonally (May to August) and

separately in accordance with hibernation needs of mothers with young or males (Chen et al., 1990; Ding et al., 2003). The Atlantic puffin (*Fratercula arctica*), a shorebird that lives in high northern latitudes, makes burrows as long as 3 m, with a vertical depth of 1 m; these burrows are also used for nesting (Hornung, 1982, and references therein). Rock ptarmigans (*Lagopus mutus*), a bird that (unlike most) overwinters above the Arctic Circle, burrow into the snow to avoid hypothermia and predators (Davenport, 1992). Bank burrows made by the monotreme *Ornithorhynchus anatinus* in alpine lakes of Tasmania provide temperatures as much as 18 °C higher than outside air temperatures during winters (Bethge et al., 2004). Additionally, polar bears (*Ursos maritimus*) are well known for burrowing in snow to better survive winters (or give birth, in maternal dens); brown bears (*Ursos arctos*) also will dig into soil to construct dens before winter (McLoughlin et al., 2002; Ciarniello et al., 2005; Durner et al., 2006). Smaller mammals living in the Arctic Circle, such as lemmings (numerous species of *Lemmus* and *Dicrostonyx*), are active year-round by living in burrow systems, whether these are dug in sediment or snow (Davenport, 1992; Willmer et al., 2000). Interestingly, behaviors denoted by lemming burrows are seasonally dependent: summer burrows in soil are mainly used for avoiding predation, whereas winter burrows in snow are for maintaining a hospitable microclimate (Davenport, 1992). Similarly, moderate-sized mammals, such as muskrats and marmots, use burrows combined with aggregation to survive winters (MacArthur and Aleksyuk, 1979; Arnold, 1988; Bazin and MacArthur, 1992), although one species of marmot (*Marmota monax*) hibernates solitarily in its burrow throughout winter (Feron, 1996).

All in all, burrowing in cold climates is a widespread strategy in a large number of phylogenetically unrelated tetrapods (some with lineages reaching well into the Mesozoic), regardless of ectothermy or endothermy, and in animals sized from mice to bears. As a result, burrowing behaviors for Cretaceous tetrapods living in polar environments may have been typical, and its absence exceptional. Although the beginning of tetrapod burrowing for shelter in cold climates is currently unknown, tetrapod burrows have been interpreted from high paleolatitudes in Triassic deposits (Miller et al., 2001; Hasiotis et al., 2004; Sidor et al., 2008), which provides a minimum time for its start.

#### 4.3. Considerations of burrowing in polar dinosaurs

Burrowing as an adaptive strategy for dinosaurs in polar environments could have been augmented by other adaptations observed in modern terrestrial tetrapods, such as: basking; aggregation (huddling); decreased metabolism of torpor or hibernation; and inclusion of insulating materials in the burrow (e.g., vegetation), which also could represent food storage (Hornung, 1982; Davenport, 1992; Marchand and Walker, 1996; Willmer et al., 2000; McNab, 2002; Andersson, 2003; Espinoza and Quinteros, 2008). The dinosaur burrows interpreted in this study lack sufficient evidence to propose whether any of these additional behaviors may have been employed, but these could be considered in future studies.

For example, the Otway burrows described here show a similar orientation; a larger sample size would allow for testing whether preferred orientations are attributable to alignment of burrow openings, which could be attributable to basking. Preferred orientations of burrow openings for the purposes of basking or other means of thermoregulation (e.g., protection against cold prevailing winds) are well documented for a large number of ectothermic and endothermic tetrapods in cold climates (Davenport, 1992; Willmer et al., 2000; McNab, 2002; Torres et al., 2003; Wu et al., 2003; Schwaibold and Pillay, 2006).

Burrow chambers containing body fossils of the purported tracemakers might provide evidence of aggregation for warmth, which occurs in both ectotherms and endotherms in cold climates (Arnold, 1988; Bazin and MacArthur, 1992; Davenport, 1992; Andersson, 2003; Espinoza and Quinteros, 2008), although aggregation (combined with burrow chambers) is also used in warmer climates to conserve heat in young offspring (Haim et al., 1992). Intraspecific aggregation is indicated by several fossil examples of synapsids and dinosaurs, although these behaviors could also overlap with parental care (Smith and Evans, 1996; Groenewald et al., 2001; Meng et al., 2004; Abdala et al., 2006; Botha-Brink and Modesto, 2007; Varricchio et al., 2007).

Further study of the presence or absence of LAGs in polar dinosaur bones will also assist in pinpointing whether certain dinosaurs identified as potential burrowers (i.e., small ornithopods) were indeed active year-round, as proposed by Chinsamy et al. (1998). Burrows could have aided such activity by lending equable microhabitats during polar winters. On the other hand, burrows that eased overwintering in species capable of periods of torpor also could explain the presence of LAGs in dinosaurs identified in the future as burrowers. In modern tetrapods, subterranean or subniveal overwintering dens assist in survival rates during times of decreased metabolic rates and periods of torpor, dormancy, or hibernation (Davenport, 1992; Willmer et al., 2000; McLoughlin et al., 2002; Ciarniello et al., 2005; Durner et al., 2006).

The presence of fossil plant debris within a terminal chamber or directly associated with the burrow wall would imply the addition of insulating materials in the burrow, or, if the dinosaurs were herbivores, food storage. For example, a Miocene rodent burrow in Germany contained a cache of more than 1,000 nuts, which was interpreted as the probable result of seasonal hoarding (Gee et al., 2003). Skeletal material (particularly with toothmarks) or other body fossils of animals too small for the same type of burrow also might be interpreted as the remains of food caching (i.e., potential prey items), although burrow-commensal species are yet another possibility to consider (Varricchio et al., 2007).

Other trace fossils that would aid in interpreting fossil tetrapod burrows in Cretaceous strata of Victoria include coprolites. Some tetrapod burrows in polar environments include side pockets or tunnels that are used specifically as latrines (Hornung, 1982; Davenport, 1992); this strategy also deters predation, as waste products outside of a burrow are often detectable by some predators (Boonstra et al., 1996). Regardless, a concentration of coprolitic material in a suspected burrow structure may correlate with such a behavior and strengthen the hypothesis. Unfortunately, though, vertebrate coprolites have not yet been interpreted from either the Otway or Strzelecki Groups.

With reference to the fossil record of tetrapod burrows and dinosaurian adaptations, Loope (2006) and Varricchio et al. (2007) suggested that some Mesozoic tetrapods, such as dinosaurs, might have burrowed as a means of escaping severe conditions, such as heat in equatorial deserts or cold winters coupled with prolonged darkness in polar environments. Similarly, Miller et al. (2001) and Sidor et al. (2008) pointed toward burrowing as an adaptation for tetrapods in Triassic polar environments. Varricchio et al. (2007) also proposed specifically that the high relative abundance of small hypsilophodontid-grade dinosaurs in the Lower Cretaceous of Victoria, Australia, and burrowing ability in another Lower Cretaceous ornithopod, *Oryctodromeus*, as a possible adaptation for such small ornithopods in circumpolar environments. As mentioned earlier, *Leaellynasaura amicagraphica* was already proposed as an ornithopod adapted to low-light conditions and year-round activity, based on: disproportionately large orbits; prominent optic lobes; and the absence of LAGs (Rich and Rich, 1989; Chinsamy et al., 1998; Constantine et al., 1998), the latter of which was also

interpreted as evidence of endothermy. Even with such adaptations, burrowing would have added to its behavioral repertoire as an added advantage in polar environments.

Considerations of burrowing ability in small ornithopod (hypsilophodontid-grade) dinosaurs, however, should include whether these behaviors are phylogenetically linked, or, like many behaviors, are simply convergent as a result of selection pressures that resulted in the behavior on a case-by-case basis. For example, Varricchio et al. (2007) suggested that the phylogenetic closeness of the Cretaceous ornithopods *Oryctodromeus*, *Orodromeus* and *Zephyrosaurus* might imply that all three taxa were capable of burrowing. Nonetheless, burrowing abilities also may have evolved in independent lineages of dinosaurs according to local paleoenvironmental selection pressures. Given that the present study is proposing the oldest known dinosaur burrows in the geologic record, as well as their occurrence in circumpolar environments, it is tempting to claim this behavior originated in polar environments and was modified in more temperate climates. Such a statement, however, would be presumptuous without further fossil evidence from Cretaceous paleoenvironments, as well as a comprehensive review of functional morphology in ornithopods related to burrowing versus paleolatitude.

#### 4.4. Seasonality of polar dinosaur burrowing and burrow taphonomy

If any polar dinosaurs burrowed and used burrows for temporary protection from the elements or for hibernation, such structures likely would have been dug and occupied seasonally. Permafrosts, indicated in the Lower Cretaceous of Victoria by cryoturbation structures in the Strzelecki Group (Constantine et al., 1998; Vickers-Rich et al., 1999), certainly would have impeded depth of burrowing in places, a challenge that would have been exacerbated as near-surface sediments also froze with the onset of winter. Modern tetrapods, such as some species of tortoises (e.g., *Terrapene carolina* and *Gopherus agassizii*), will cease burrowing once they encounter subsurface frost (Davenport, 1992), and Atlantic puffins (*Fratercula arctica*) will change their burrowing locations to nest in rock crevices, rather than dig into permafrost (Hornung, 1982; Robards et al., 2000). Additionally, spring thaws and subsequent runoff near drainages also would have necessitated evacuation of burrows before late spring. This sort of adjustment has been documented in a few burrowing mammals living next to water bodies that undergo seasonal flooding (Powers and Mitchell, 1993; Andersen et al., 2000; Jacob, 2003).

Hence burrows adjacent to and affected directly by alluvial and fluvial environments, such as the ones described here, also would have been filled, collapsed, and eroded on a seasonal basis. Spring thaws, accompanied by increased discharge in streams in the Otway Basin (Bryan et al., 1997), likely would have heightened water tables. This in turn would have saturated sediments surrounding any given terrestrial tetrapod burrow and initiated partial or complete collapse of originally open structures. On the other hand, sediment-filled burrows would have avoided complete collapse; moreover, the contrast between sediment fill and the surrounding host sediment better enables their identification in the field (Voorhies, 1975; Hasiotis et al., 2007). With all of these seasonal biological and sedimentological factors in mind, the most apt times for a dinosaur to have formed a burrow, especially for the purposes of overwintering, would have been in the autumn, with abandonment of the burrow by the start of spring. Accordingly, preservation of such structures, filled with intrabasinal clastic sediments that would have contrasted with surrounding host sediments, probably would have happened in the spring, coinciding with increased melt-water run-off and sedimentation.

Future investigators examining the Otway and Strzelecki Groups for dinosaur burrows or similar tetrapod-made trace fossils should keep in mind these factors in burrow formation and preservation.

#### 4.5. The limits of actualism applied to polar dinosaur burrows

A final admonition should be made about actualism of modern tetrapod burrowing in polar environments, and the limits of applying these behaviors to this study. The Lower Cretaceous polar dinosaur assemblage of Victoria, Australia, is representative of an unusual set of paleoecosystems. The fossil flora and lithofacies of the Otway and Strzelecki Groups indicate humid, temperate forests (Wagstaff and McEwen-Mason, 1989; Dettmann et al., 1992), along with braided streams complexes and fresh-water lakes that experienced seasonal flooding (Bryan et al., 1997), all within rift basins associated with plate divergence (Miller et al., 2002; Veevers, 2006) and in a circumpolar setting. Moreover, the fauna included not just small ornithopod dinosaurs, but large labyrinthodonts, the geologically youngest known in the world (Warren et al., 1991, 1997), turtles (Gaffney et al., 1998), the oldest known Gondwanan crayfish (Martin et al., 2008), a diverse assemblage of insects (Jell and Duncan, 1986), and large theropods (Molnar et al., 1981; Martin et al., 2007; Smith et al., 2008), among many other denizens. In other words, as cautioned by Rich et al. (2002), there may be no modern analog for these Cretaceous polar environments, their biota, and by extension, the adaptations of organisms living within and shaping such environments. Hence this study acknowledges that burrowing behaviors in these environments may have been much less, much more, or very different from what is observed today. Accordingly, future researchers testing the hypotheses presented here should keep these cautionary notes in mind while searching for similar trace and body fossil evidence of burrowing dinosaurs.

In summary, the evidence presented here supporting an interpretation of dinosaur burrows is not as robust as that for burrowing in *Oryctodromeus* from the Lower Cretaceous of Montana (Varricchio et al., 2007). Nonetheless, the near-coincident morphology of an Otway structure with a burrow attributed to *Oryctodromeus*, along with two partially preserved and nearby structures, and other supporting geological, biological (actualistic) and paleontological evidence presented here, provide a starting point for considering such structures as probable dinosaur burrows. Furthermore, the description and analysis of these large, enigmatic sedimentary structures may aid in establishing search images for similar such structures, which will serve to test the primary hypothesis proposed here: the predicted presence of dinosaur burrows in polar environments represented by the Lower Cretaceous strata of Victoria, Australia. Indeed, this hypothesis should relate well to the assertion made by Vickers-Rich et al. (1999) that, "...there were cold places on earth during this period [Cretaceous]...and that these areas were inhabited by some dinosaurian groups which had more than one strategy that allowed them to live in such environments."

## 5. Conclusions

Polar dinosaurs have presented many challenges to paleontologists who have speculated as to whether dinosaurs overwintered in circumpolar environments or migrated, and what adaptations they may have used with overwintering. Results of this study indicate that burrowing was one strategy available for overwintering polar dinosaurs of Victoria, Australia; this strategy is also quite common in modern ectothermic and endothermic tetrapods. At least part of the evidence supporting this hypothesis is represented by three structures from the Knowledge Creek outcrop of

the Otway Group (Albian) of Victoria, Australia; the Otway Group is composed of strata formed at about 78°S and with mean air temperatures of –6 to +8 °C during the Early Cretaceous (Veevers et al., 1991; Gregory et al., 1989; Wagstaff and McEwen-Mason, 1989; Constantine et al., 1998). These structures, one of which is strikingly similar to a burrow and den structure interpreted for *Oryctodromeus cubicularis* from the Upper Cretaceous (Cenomanian) of Montana (Varricchio et al., 2007), would compose the first known evidence of dinosaur burrows outside of North America, and the oldest examples of such trace fossils from the geologic record. The size and morphology of these trace fossils, along with other sedimentological, taphonomic, geological, and paleontological evidence from the outcrop and other localities in the Otway Group, lend to the hypothesis that the most likely tracemakers of these burrows were small (10–20 kg) ornithopods, such as the hypsilophodontid-grade dinosaurs (e.g., *Leaellynasaura*, *Atlascopcosaurus*). Hypsilophodontids compose the majority of the polar dinosaur assemblage in the Otway Group and the slightly older Strzelecki Group (Aptian) in Victoria (Rich and Vickers-Rich, 1999; Rich et al., 2002). Hence the given hypothesis helps to explain how small dinosaurs and their juveniles may have coped with circumpolar conditions without migrating, and agrees with assessments that such dinosaurs were not capable of migrating and thus must have overwintered (Rich et al., 1988; Bell and Snively, 2008).

Tetrapod burrows from formerly polar environments have been interpreted from the geologic record before this study (Hasiotis et al., 1999, 2004; Miller et al., 2001; Sidor et al., 2008), but because the trace fossils reported here are the first dinosaur burrows interpreted from formerly polar environments, a list of suggested additional criteria for predicting, testing, and interpreting future identifications is also provided. Hopefully the results of this study will generate search images for similar structures in other Lower Cretaceous outcrops in Victoria, and stimulate searches for more dinosaur trace fossils in strata formed in formerly circumpolar environments.

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