

# First Lower Jurassic vertebrate burrow from southern Africa (upper Elliot Formation, Karoo Basin, South Africa)



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## ABSTRACT

Vertebrate burrows are common ichnofossils in the Permo-Triassic of the main Karoo Basin in South Africa. They are generally attributable to one of several lineages of therapsid, including the derived clade known as cynodonts. Despite the presence of cynodont species in the Upper Triassic and Lower Jurassic of the Karoo Supergroup, vertebrate burrows have never been reported from this part of the succession. Recent fieldwork recovered a semi-elliptical burrow cast in the Lower Jurassic upper Elliot Formation (Stormberg Group) on the farm Edelweiss 698 (Free State). The horizontal and vertical diameters of the burrow cast are ~18 and ~7 cm, respectively. This semi-horizontal, straight to slightly sinuous tunnel is ~50 cm long with a ramp angle of <5°. The tunnel lacks branching, terminal chambers, and associated fossil bones. The burrow cast consists of medium, massive sandstone and very rare, faint, horizontal to slightly inclined lamination. The burrow cast is hosted in fine-grained, palaeo-pedogenically altered, crevasse splay sandstone that is 10–20 cm thick and is under- and overlain by a massive, red, bioturbated floodplain mudstone unit with large-scale (>20 cm deep) desiccation cracks, invertebrate trace fossils, calcareous rhizoconcretions, and spherical-to-elongated carbonate nodules. These and other associated sedimentary features provide evidence for a semi-arid, fluvio-lacustrine palaeoenvironment during the burrowing activity. Based on comparisons to fossil and modern burrows, this burrow cast is interpreted as a vertebrate burrow, and is the first record of vertebrate fossorial activity within the Lower Jurassic of southern Africa. The ancient burrow architect has yet to be positively identified. However, given the size and morphology of the burrow and the occurrence of similar sized fossil cynodont therapsids that inhabited the main Karoo Basin in the earliest Jurassic, the potential burrow-maker may be tentatively linked to the Cynodontia (e.g., *Pachygenelus* - an advanced tritheledontid).

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## 1. Introduction

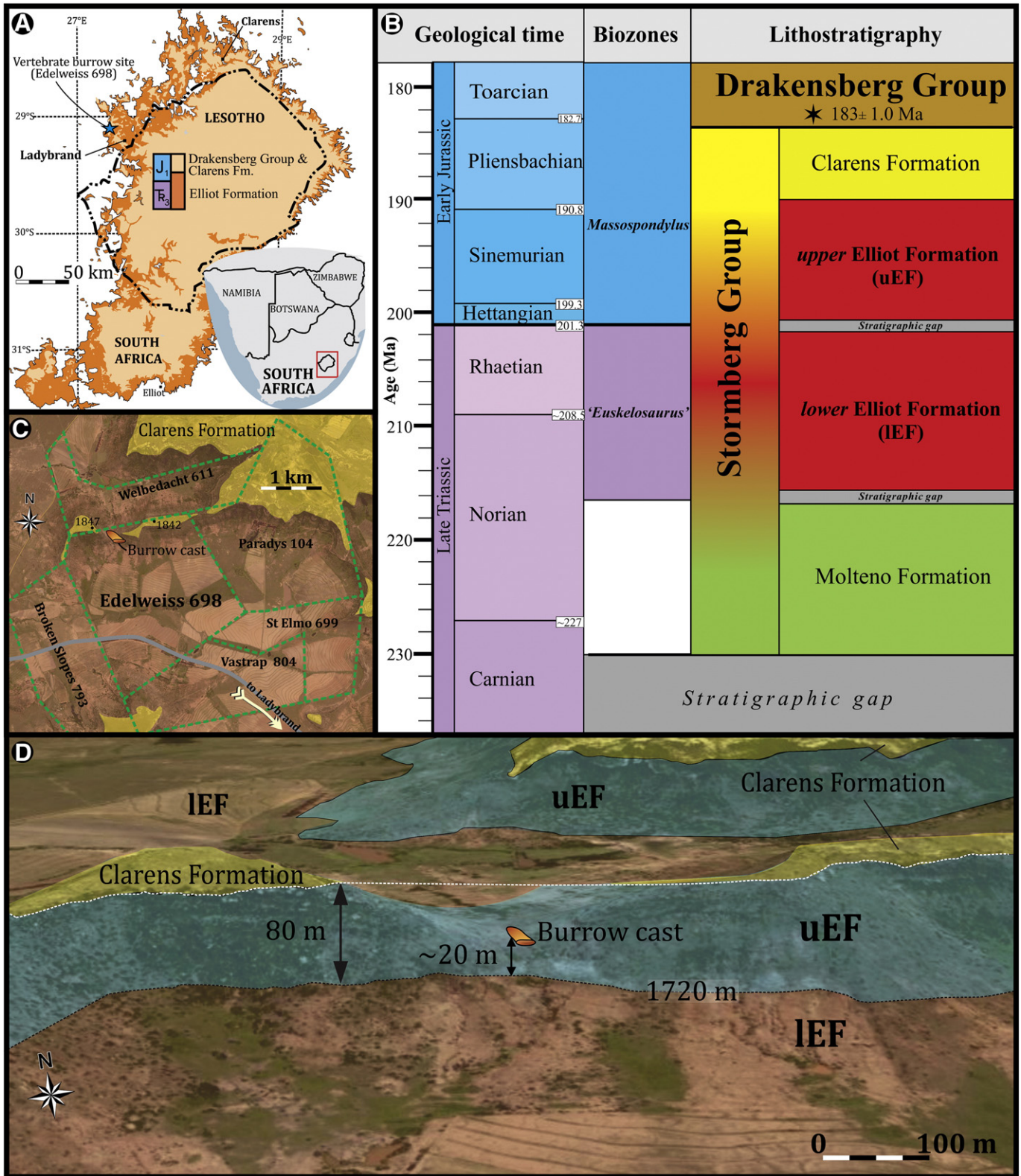
Vertebrate burrows are relatively common in the Permo-Triassic Beaufort Group of the Karoo Supergroup of South Africa. Generally, these vertebrate burrows have been tentatively attributed to cynodonts (*Langbergia*, *Thrinaxodon*) and dicynodonts (*Diictodon*, *Lystrosaurus*) whose complete skeletons or isolated bones are preserved inside these structures (e.g., Smith, 1987; Groenewald, 1991; Groenewald et al., 2001; Damiani et al., 2003; Abdala et al., 2006; Sidor et al., 2008; Bordy et al., 2011; Bordy and Krummeck, 2016; Krummeck and Bordy, 2017). However, the Lower Jurassic rocks of southern Africa, which preserve abundant tetrapod footprint assemblages (e.g., Ellenberger, 1970,

1972, 1974; Olsen and Galton, 1984; Wilson et al., 2009; Sciscio et al., 2016), have never produced a vertebrate burrow. The lack of vertebrate burrows within the Elliot Formation is even more perplexing when considering that: 1) the formation is a fluvio-lacustrine succession suitable for burrow preservation, and 2) the body-fossil record of potential vertebrate burrow-makers, such as tritheledontid and tritylodontid cynodonts (Smith and Kitching, 1997; Gow, 2001; Botha, 2002), have been described from within the upper part of the Elliot Formation. In addition to non-mammaliaform cynodonts, the Elliot Formation is well-known for its high diversity and size disparity of vertebrate body fossils, which include tiny early mammaliaforms, small crocodylians, and enormous sauropodomorph dinosaurs and amphibians, as well as turtles, fish, conchostracans, petrified wood and root traces (Jenkins and Parrington, 1976; Kitching and Raath, 1984; MacPhee et al., 2014; Bordy and Eriksson, 2015).

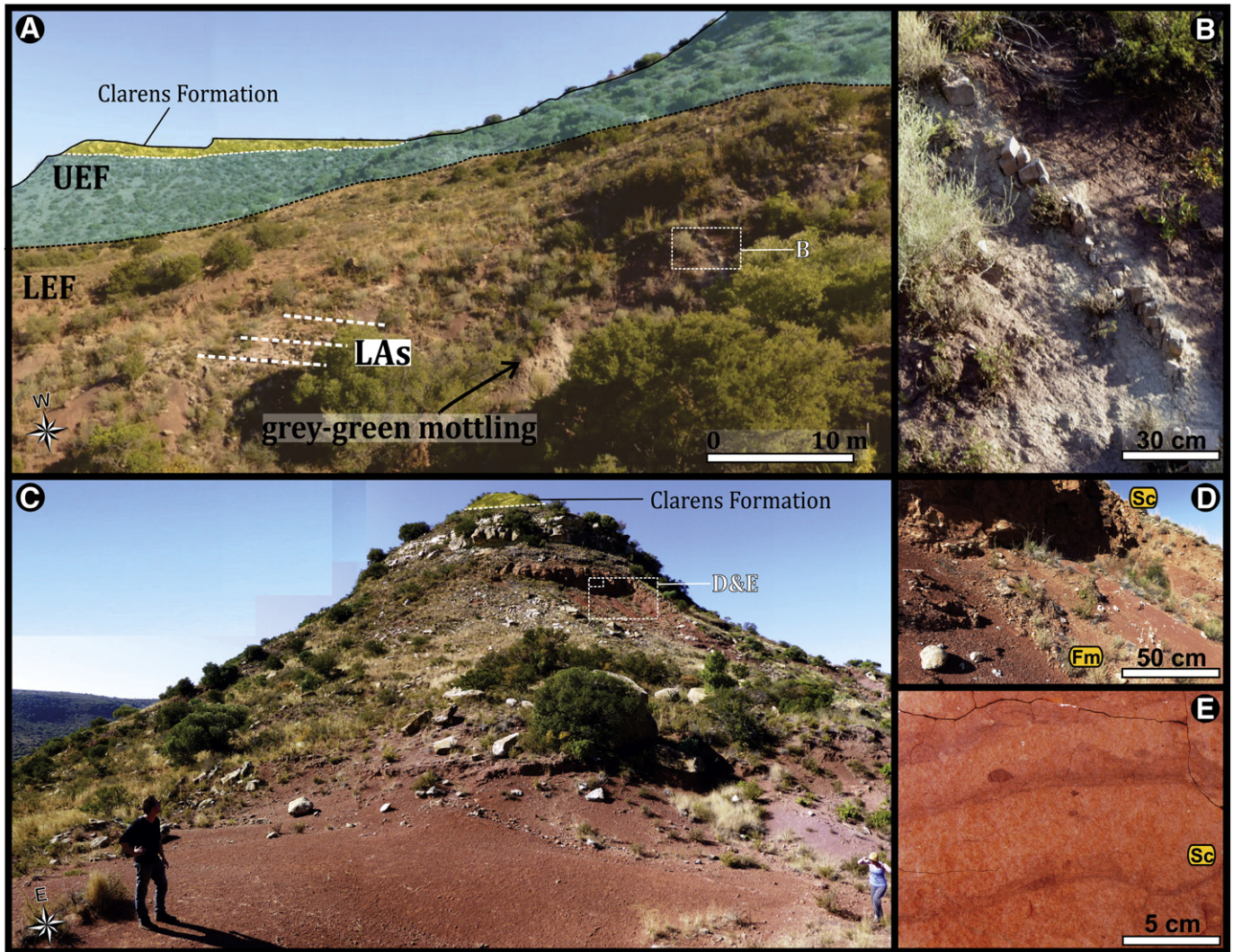
Our recent palaeontological fieldwork in the Elliot Formation (Free State province, South Africa - Fig. 1) recovered an ichnofossil that we

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**Fig. 1.** Location and stratigraphy of the burrow site in the Elliot Formation (on farm Edelweiss 698, Ladybrand District, Free State Province, South Africa). **A:** simplified geological map of the Elliot Formation in the Republic of South Africa and Lesotho indicating the location of farm Edelweiss 698 (red star) and aerial extent of the Elliot Formation outcrop area (map modified after the 1:1,000,000 Geological map of RSA and Lesotho, 1984). The grey inset is the outline of the southern African countries with the study area marked with a red rectangle; blue star denotes the study area (see C for close up). **B:** the litho- and biostratigraphy of the upper Karoo Supergroup in the main Karoo Basin (modified after Lucas and Hancox, 2001; Bordy et al., 2004). Drakensberg Group radiometric date ( $183 \pm 1.0$  Ma) is from Duncan et al. (1997). Geological time scale based on Cohen et al. (2013). **C:** in the immediate vicinity of the burrow site (green star in A), only the Elliot and Clarendon Formations (light yellow) are exposed. Intrusive mafic dyke of the Drakensberg Group are omitted. **D:** landscape view of the study site showing aspects of the local stratigraphy. Note that the contact between the IEF and uEF has been identified at 1720 m above sea level, thus the uEF here is ~80 m thick. The vertebrate burrow cast and spatially closely associated, in situ vertebrate fossils (*Antetonitrus*, ?cynodont remains) were collected in the uEF, ~60 m below the base of the Clarendon Formation. IEF - lower Elliot Formation; uEF - upper Elliot Formation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** A: sedimentological aspects of the Elliot Formations at Edelweiss. IEF - lower Elliot Formation; uEF - upper Elliot Formation A: although very poorly exposed, the IEF shows features (e.g., grey-green mottling, lateral accretion surfaces - LAS) that are typical in the lower part of the formation regionally; here they are found ~25 m below the upper contact of the IEF. B: a deeply penetrating and up to 15 cm wide desiccation crack in the IEF (see inset in A for location). C: the uEF above the logged section (see Fig. 3) is dominated by deep red, maroon to deep pink massive mudstones with well-developed palaeo-pedogenic alteration features (e.g., in situ carbonate nodules). Furthermore, clast-rich very fine-grained sandstone, a recurring and unique facies in the uEF, is also common. Laterally persistent, sheet-like, fine-grained, massive to laminated sandstone beds occur in the uppermost part of the uEF. D: note the clusters of in situ pedogenic nodules in facies Fm (massive mudstone) indicative of palaeo-pedogenic overprinting. E: deep red to maroon, clast-rich very fine-grained sandstone (facies Sc) with poorly sorted, 1–4 cm angular, rip-up mudstone clasts and localized, faint lamination that defines a crude bedding. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

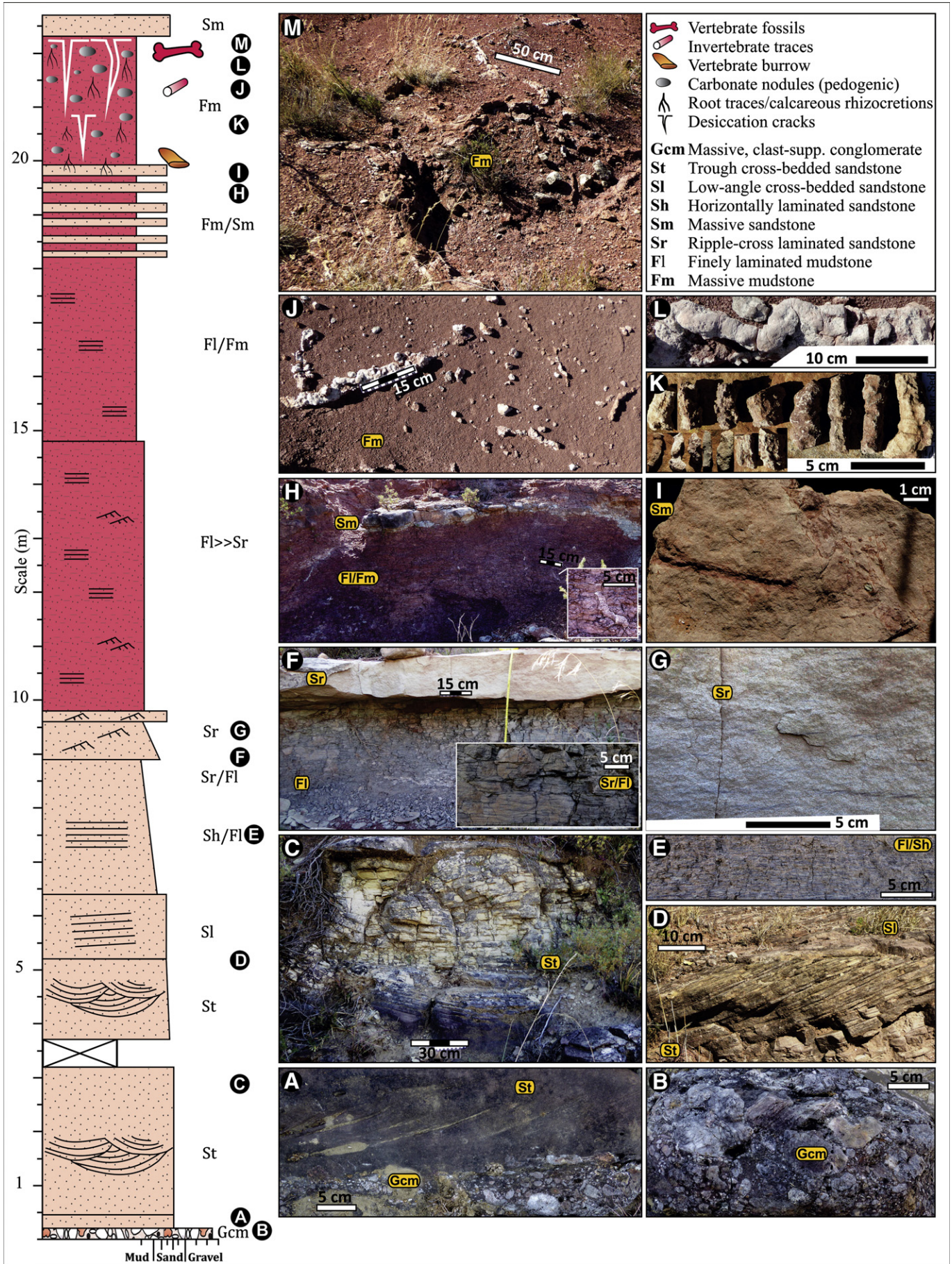
interpret here as a vertebrate burrow. We describe the morphology of the burrow and the sedimentology of the Lower Jurassic host rock, and provide a palaeoecological interpretation of the site.

## 2. Geological background

The Elliot Formation (Fig. 1) was deposited from the Late Triassic to the Early Jurassic in a fluvio-lacustrine setting, and has an unconformable, sharp, regionally traceable lower contact with the coal-bearing,

fluvio-lacustrine Molteno Formation and a conformable, chiefly gradational upper contact with the mainly aeolian Clarens Formation (Bordy et al., 2004). Presently, the Elliot Formation crops out in South Africa and Lesotho as a ring-shaped belt surrounding the Drakensberg Plateau. It has a maximum thickness of almost 500 m in the south, declining to <30 m in the north (Botha, 1968; Smith and Kitching, 1997). Within the Elliot Formation, there are major sedimentary facies differences that allow the subdivision of the formation into two informal units, namely the lower and upper Elliot Formations (hereafter

**Fig. 3.** Sedimentology of the lowermost 22.5 m in the upper Elliot Formation at Edelweiss 698. The typical features of the coarse-grained facies association are shown in A to G. The coarser grained facies (facies Gcm, St, Sl - A, B, C & D) in the lower part of the log give way to finer grained facies (facies Sh, Sr, Fl - E, F & G), and together form ~10 m thick upward-fining succession, which lacks evidence for lateral accretion processes. The succession is abruptly overlain by the fine-grained facies association (facies Fm, Fl and Sm - H to M), which is >12 m thick at Edelweiss. Note that the fossiliferous zone, which yielded the in situ sauropodomorph and ?cynodont remains as well as the vertebrate burrow cast, is well above the diagnostic massive, clast-supported carbonate nodule conglomerate (facies Gcm) that marks the base of the uEF at this locality. Contrast log with the Fig. 1 in Abdala et al. (2007, p. 18). A to D: Diagnostic, massive, clast-supported carbonate nodule conglomerate (facies Gcm - A & B) immediately overlain by trough cross-bedded sandstones (A, C & D). E to G: in the upper part of the coarse-grained facies association, finer grained rocks comprise sandstones with horizontal and ripple cross-lamination (facies Sr, Sh, and minor Fl). H to M: Typical features in the fine-grained facies association included interbedding of massive to laminated mudstones (facies Fm, Fl - H) and ripple cross-laminated to massive sandstones (facies Sr, Sm - I), in situ carbonate nodules (J), root traces and calcareous rhizoconcretions (I, J, K), smooth-sided, cylindrical invertebrate traces (J, L, inset in H) and desiccation cracks (M) that are deeply penetrating and up to 10 cm wide in the upper part of the fossiliferous zone.



IEF and uEF; Bordy et al., 2004). These informal lithostratigraphic units of the Elliot Formation coincide with informal biostratigraphic units of Kitching and Raath (1984), namely the 'Euskelosaurus' and *Massospondylus* Range Zones, respectively (Fig. 1B).

Because the Edelweiss burrow cast is located within the uEF, the following description only concerns the uEF and is based on Bordy et al. (2004), which should be consulted for the general background on the IEF. Regionally, the uEF consists of silty mudstones with intermittent sandstones that have a distinctive deep red to maroon colour with erratic light grey mottles and other features indicative of pervasive pedogenic overprinting in a semi-arid climate (Bordy et al., 2004; Sciscio et al., 2016). The uEF mudstones are 0.5–10 m thick and range from pure claystone to fine-sandy siltstone layers which are mainly massive and less commonly horizontally laminated. The mudstones contain in situ pedogenic carbonate nodules, irregular mottles that are white or light grey, desiccation cracks and mud drapes. These palaeo-pedogenic alteration features are more abundant in the uEF mudstones than in those of the IEF.

The sandstones of uEF are sheet-like, tabular and multi-storied bodies, tens of metres wide and up to 6 m thick. The individual sandstone beds within the sandstone bodies have a thickness ranging between 0.2 and 1 m and are separated by flat, internal erosional surfaces with geometries similar to the basal bounding surface of the multi-storied sandstone bodies. The bounding surfaces are laterally continuous and parallel, devoid of topographical irregularities > 50 cm. Internally, the tabular, very fine to fine-grained sandstones of the uEF are dominated by massive beds, horizontal lamination, low-angle cross-bedding, parting lineations, ripple cross-lamination, flaser and wavy bedding, mud-draped surfaces, small-scale soft sediment deformations and bioturbation. Mainly common in the upper uEF, deep red to maroon, clast-rich very fine-grained sandstones contain poorly sorted, up to 4 cm long, angular, rip-up mudstone or very fine-grained sandstone clasts. At the base of the sandstone bodies, channel lags consisting of bone-bearing carbonate nodule conglomerates are frequent and denote one of the diagnostic lithologies of the uEF. In addition to the carbonate nodule conglomerates, mud pebble conglomerates may also form stringers at the bases of the upward fining successions. Taken together, the bone-bearing, reworked carbonate nodule conglomerates, the clast-rich very fine-grained sandstone, the tabular geometry of the strata, and the well-developed palaeo-pedogenic alterations are diagnostic to the uEF, and thus are of key stratigraphic importance in differentiating the uEF from other stratigraphic units.

### 3. Material and methods

Two in situ vertebrate burrow casts were found spaced laterally ~1 m apart from each other in a sandstone layer of the Elliot Formation on the farm Edelweiss 698 (29° 6'36.95"S 27° 19'17.02"E; ~1740 m asl – Fig. 1). The burrow casts were recorded in detail via photographs, photomosaics and sketches in the field. The better exposed cast was also measured and then removed for further laboratory investigation. This specimen was deposited and accessioned in the Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg, South Africa under BP/6/736 (field number EW/15/2). The description only refers to the collected specimen, because the morphology of the second burrow cast is obscured due to poor exposure.

Field evidence for the sedimentological context of the burrow casts was collected in the form of macroscopic observations of the ichnofossil-bearing sedimentary rocks as well as by documenting the vertical and lateral distributions of the sedimentary characteristics at farm Edelweiss and its vicinity. More specifically, the outcrop was photographed and described with enough detail to produce an in-depth characterization of the sedimentary facies, which entailed the documenting of the lithology, geometry, sedimentary structures, palaeocurrents and fossil content at centimetre-scale resolution.

## 4. Results

### 4.1. Sedimentology of the Edelweiss site

The Elliot Formation at the Edelweiss locality is ~150 m thick of which ~70 m is IEF and ~80 m is uEF (Figs. 1, 2, 3). The former is exclusively exposed in patchy outcrops that are below the level of diagnostic carbonate nodule conglomerates (facies Gcm) of the uEF (i.e., below ~1720 m contour line – Figs. 1, 2). The chief sedimentary characteristics in the poorly exposed IEF (e.g., grey-green mottling, lateral accretion surfaces) are shown in Fig. 2A and B.

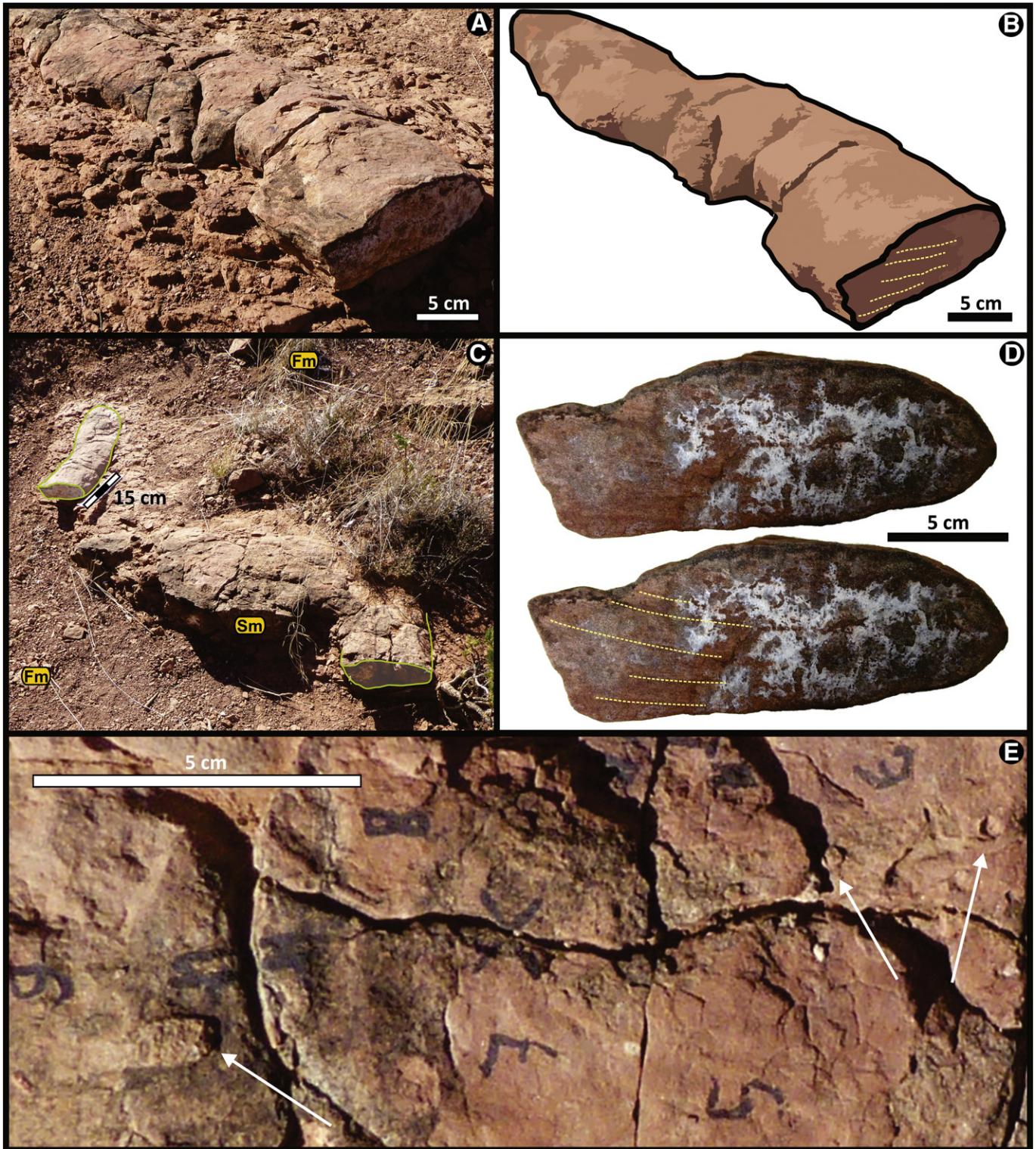
The uEF at Edelweiss can be subdivided into two major facies associations based on their shared characteristics of sedimentary features, geometries, lithology and grain size. The fine-grained facies association (Figs. 2, 3) is dominated by deep red, maroon to deep pink laminated and massive mudstones (facies Fl, Fm) that are palaeo-pedogenically overprinted (e.g., large, in situ carbonate nodules, rhizoconcretions – Fig. 3J, K), contain desiccation cracks (Fig. 3M) and are interbedded with massive, very fine-grained sandstone beds (facies Sm) (Fig. 3H, I, and log). These massive sandstones (see upper part of log in Fig. 3) become progressively thicker and slightly coarser upward and are also palaeo-pedogenically overprinted as they display rootlets (Fig. 3I) and desiccation cracks. The interbedding of mudstone and sandstones is especially common in the upper part of the uEF (Fig. 2C). Here, the massive mudstones with well-developed palaeo-pedogenic alteration features (Fig. 2D) are interbedded with sandstone beds that are either: 1) laterally persistent, sheet-like, fine-grained, massive to laminated or 2) irregularly-based, massive to crudely bedded, very fine-grained and clast-rich (Fig. 2C). The latter, a regionally recurring and unique rock type (facies Sc) in the uEF (Bordy et al., 2004, 2005), is deep red to maroon and contains poorly sorted, 1–4 cm angular, rip-up mudstone clasts and localized, faint laminations (Fig. 2E).

The burrow cast was found in the fine-grained facies association within a fossiliferous stratigraphic interval, which contains in situ sauropodomorph and cynodont remains (Figs. 1, 3). This fossil-rich interval shows features of palaeo-pedogenic alteration and is associated with large-scale desiccation cracks, root traces, calcareous rhizoconcretions, spherical-to-elongated carbonate nodules and smooth-sided, cylindrical invertebrate traces (Fig. 3I–M). In addition, the in situ carbonate nodules and desiccation cracks show an up-section increase in abundance and size. Root traces and calcareous rhizoconcretions are chiefly vertical structures that taper and branch downwards. Their diameters vary from 0.1 to 50 mm, and the main structures may terminate in multiple branching filamentous root-hairs (see Fig. 3I which are rootlets in an interbedded, massive sandstone). The typical invertebrate traces in the fine-grained facies association are slightly curving to straight, vertical or horizontal, non-branching, unlined, unornamented, cylindrical tubes that range in diameter from 0.5 to <3 cm (Fig. 3H, J, L). They are filled with massive very fine-grained sandstone and typically occur in isolation as separate tubes (i.e., not as clusters) in the massive mudstones (Fig. 3H, I) or on top of casts of desiccation cracks (Fig. 3J, L).

The exposed coarse-grained facies association at Edelweiss is ~10 m thick and is based by a ~25 cm thick, massive, poorly sorted, bone-bearing, reworked carbonate nodule conglomerate (facies Gcm – Fig. 3A, B) that is laterally traceable in excess of 100 m. The nodules range from rounded to sub-angular, are poorly to moderately sorted and are grey, white-to-red in colour. They commonly form a clast-supported fabric (Fig. 3A, B). The rest of the coarse-grained facies association is dominated by very fine- and fine-grained sandstones (with subordinate medium-grained sandstones – Figs. 2C–E, 3C–D). The conglomerate, as well as the trough- and low-angle cross-bedded sandstones (facies St, Sl – Fig. 3C, D), are overlain by mud-draped, horizontally laminated and ripple-cross laminated sandstones (facies Sh, Sr – Fig. 3E, H), and collectively form a well-defined fining-upward succession (log in Fig. 3). The overall geometry (i.e., lenticular or not) of the coarse-grained facies association is

impossible to establish with certainty. However, the limited, patchy outcrops on Edelweiss and better-exposed sandstones on the adjacent farm Vastrap (Fig. 1) are suggestive of vertically stacked strata

that are confined to tabular bodies with lateral continuity of a few hundreds of meters. In the course of our fieldwork, no lateral accretion surfaces were found in any of the sandstone bodies within the



**Fig. 4.** Architectural morphology of the vertebrate burrow cast. **A & B:** photograph and interpretative drawing of the straight-to-slightly-sinuous, tunnel-like overall morphology of the burrow cast (cross-sectional width of ~18 cm; total height of ~7 cm; length of ~50 cm; ramp angle of  $<5^\circ$ ). Note that the width remains the same along the length of the burrow cast, except for one, ~5 cm long section (cast fragment numbered 2), which appears to have been broken off due to recent weathering. **C:** The burrow cast is hosted in maroon, fine-grained sandstone (facies Sm). Note that the second, poorly-exposed burrow cast on the right is barely distinguishable from the host sandstone, hence this description only concerns the burrow cast on the left. **D:** The semi-elliptical cross-section of the burrow casts with a flat floor and a slightly arched ceiling. Internally, the cast consists of medium-grained sandstone which is mostly massive and rarely shows faint horizontal (to slightly inclined) lamination. **E:** Horizontal and vertical invertebrate traces in the uppermost  $<2\text{ cm}$  of the burrow cast. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**  
Palaeontological context for the uEF vertebrate burrow site and stratigraphic distribution of vertebrate taxa on farm Edelweiss 698. Stratigraphic abbreviations are IEF: lower Elliot Formation; mEF: middle Elliot Formation; uEF: upper Elliot Formation. Note that mEF is the lower part of uEF of Bordy et al., 2004.

Group	Taxon	Element/s	Stratigraphic position within the Elliot Formation	ESI Catalogue number	Notes	Source(s)
Sauropodomorpha	cf. <i>Massospondylus</i> sp.	Sacrum fragment	Unspecified, tentatively uEF (mEF)	BP/1/6579		Kitching and Raath, 1984
	<i>Antetonitrus ingeniipes</i>	In situ bonebed: disarticulated but closely associated postcrania	IEF prior to this paper; reassessed as uEF in this contribution	BP/1/4952 (holotype) BP/1/4952b, c (referred specimens)	Found 20 m above the unique carbonate nodule conglomerate beds, which are hallmarks of the uEF	Yates and Kitching, 2003; McPhee et al., 2014
	cf. <i>Melanorosaurus</i> sp.	Femora, a tibia, pubis-ischium and some vertebrae	Unspecified, tentatively IEF	BP/1/5090	Large-bodied, heavy-set sauropodomorph but smaller than <i>Antetonitrus</i>	Kitching and Raath, 1984; Abdala et al., 2007; ESI Catalogue
Theropoda	<i>Coelophysis</i> (= <i>Syntarsus</i> ) <i>rhodesiensis</i>	Pelvic fragment (partial sacrum)	uEF: within or near the <i>Tritylodon</i> Acme Zone	BP/1/5246	Mature individual; significantly smaller than the holotype; collected by J W Kitching in 1985; could be the predator of the burrow-maker	Munyikwa and Raath, 1999
Cynodontia	?Diademodontidae	Jaw fragment	IEF prior to 2016; reassessed as uEF in this contribution	BP/1/5724	Not a potential burrow-maker as the skull size is too large for the burrow diameter	Abdala et al., 2007

facies association typified by the unique carbonate nodule conglomerate beds.

#### 4.2. Palaeontology of the Edelweiss site

In situ fossils of the sauropodomorph *Antetonitrus ingeniipes* (Yates and Kitching, 2003; see Kitching and Raath, 1984: Fig. 4) as well as a fragmentary cynodont jaw (tentatively assigned to the Diademodontidae by Abdala et al., 2007) were collected previously within 2 m of the Edelweiss burrow cast (e.g., at least one *Antetonitrus* fragment by EMB in 2002 – Fig. 3). Other fragmentary postcranial fossil remains with an uncertain stratigraphic provenance that were reported from Edelweiss belong to sauropodomorph and basal theropod ('coelophysid') dinosaurs (Table 1). <4 km from the Edelweiss study site (Fig. 1; Table 2), fossils of the following taxa have been reported by Kitching and Raath (1984): dinosaurs [cf. '*Euskelosaurus*' sp., *Massospondylus* sp., *Coelophysis* (= *Syntarsus*) sp.]; cynodonts (*Tritylodon* sp.; *Pachygenelus* sp.); basal archosaurian reptiles ('thecodont'); brachyopid amphibians (skull and jaw fragments), lungfish and conchostracans.

**Table 2**  
Stratigraphic distribution of vertebrate taxa in the immediate vicinity of farm Edelweiss 698 based on Kitching and Raath (1984). See Table 1 for stratigraphic abbreviations. For farm locations, see Fig. 1.

Fossil taxa	Stratigraphy	Farm name and distance from the burrow site
<i>Pachygenelus</i> sp., cf. <i>Massospondylus</i> sp., ?Thecodont	uEF	St Elmo 699, ~4 km to ESE
<i>Pachygenelus</i> sp.	uEF	Paradys 104, ~3 km to E
<i>Tritylodon</i> sp., cf. <i>Massospondylus</i> sp.	uEF (mEF)	E
Brachyopid amphibian, cf. <i>Ceratodus</i> sp. (lungfish tooth plates plus partial skeletons), conchostracans	uEF	Vastrap 804, <3 km to ~S
<i>Tritylodon</i> sp., <i>Coelophysis</i> (= <i>Syntarsus</i> ) sp., cf. <i>Massospondylus</i> sp.	uEF (mEF)	
cf. <i>Ceratodus</i> sp. (lungfish), conchostracans	uEF	Broken Slopes 793, <3 km to ~S
Brachyopid amphibian, cf. <i>Massospondylus</i> sp., conchostracans	uEF (mEF)	
cf. <i>Massospondylus</i> sp. cf. ' <i>Euskelosaurus</i> ' sp.	uEF (mEF) IEF	Welbedacht 611, <1 km to N

#### 4.3. Description of the burrow cast

The burrow is confined, at a <5° ramp angle, to a dark red, maroon, massive fine-grained sandstone (Figs. 3, 4). The sandstone is ~3 m wide, ~10–20 cm thick and under- and overlain by red, massive, bioturbated mudstones (facies Fm) with large-scale desiccation cracks, calcareous rhizoconcretions and spherical-to-elongate carbonate nodules (Figs. 3, 4). The host sandstone, which is interlayered with palaeopedogenically altered floodplain mudstones, is interpreted as a crevasse splay deposit on a fluvial floodplain (see previous section on Sedimentology of the Edelweiss site).

The burrow cast is a ~50 cm long, straight-to-slightly-sinuuous tunnel with a flat floor and slightly arched ceiling (Fig. 4A, B). The cross-section of the burrow is semi-elliptical, with a horizontal diameter of ~18 cm (width) and a vertical diameter of ~7 cm (height). The width and height of the tunnel and the overall morphology remain constant along its length (except for one, ~5 cm section that seems to have been affected by recent weathering – see cast fragment numbered 2 in Fig. 4A). The burrow cast does not include branches or a terminal chamber. No fossil bone material has been found in the burrow cast.

Internally, the burrow cast consists of mostly massive, fine-grained sandstone, identical to the host sandstone; however, some horizontal (to slightly inclined) laminations are present in the basal part of the burrow cast (fragments numbered 1 to 4; Fig. 4B, D). Furthermore, rip up mud clasts and carbonate nodules of <0.5 cm diameter are present within the burrow fill (in cast fragments 9 and 10). Numerous invertebrate traces (arrows in Fig. 4E), which are straight, horizontal or vertical, non-branching, unlined, unornamented, cylindrical tubes with diameters of ~0.3–0.5 cm, appear to exploit the uppermost <2 cm of the burrow cast. The burrow cast has a granular surface texture along its base and top, resulting from inorganic carbonate mineral precipitation during palaeo-pedogenic alternation, which is common in the host rock and surrounding beds.

## 5. Discussion

### 5.1. Sedimentological interpretation of the uEF at Edelweiss

The sedimentary facies association of the uEF at Edelweiss (Figs. 2, 3) suggests that the sediments were mainly deposited in a vegetated floodplain (e.g., abundance of palaeo-pedogenic alteration features such as in situ carbonate nodules, root traces), where sheet flooding and sediment gravity flows were common events, especially during

episodic flash floods in a seasonally dry fluvio-lacustrine environment (e.g., Stear, 1985; Reid and Frostick, 1997; Bordy et al., 2004). After the initial (and rapid) abandonment of a moderate size channel (see middle part of the log in Fig. 3), evidence for increasingly well-drained soils and higher energy depositional conditions suggests that the floodplain environment was positioned progressively closer to an area of persistent sheet flooding. This is supported by the increasing abundance of interbedded sandstones in the fine-grained facies association (Fig. 2C–E, upper part of the log in Fig. 3). Those interbedded sandstones that are tabular are interpreted as ancient crevasse splay sand bodies (facies Sm and Sr) that underwent dying and pedogenic alteration, including calcretization (desiccation cracks, carbonate nodules). The latter is typical in semi-arid environments with episodic and severe moisture deficiency periods (e.g., Blodgett, 1988; Spötl and Wright, 1992; Alonso-Zarza and Wright, 2010). Those interbedded sandstones that have irregular lower contacts are interpreted as gully-infilling sediments (facies Sc) associated with sediment gravity flows that filled smaller, rainstorm-eroded gullies and other irregular depressions of the floodplain area (also see Bordy and Catuneanu, 2001: p. 616, 624; Bordy et al., 2004: p. 393, 395, 397 and references therein).

In summary, the uEF at Edelweiss is characterized by sedimentary features that are common in the uEF on a regional scale and contains facies that, to date, have not been found in the sedimentary associations of IEF in southern Africa (Bordy et al., 2004, 2005). In particular, two of the unique and reliable stratigraphic markers of the uEF, namely the bone-bearing, reworked carbonate nodule conglomerate beds and the clast-rich very fine-grained sandstone, are present at Edelweiss. The regional stratigraphic value of the bone-bearing, reworked carbonate nodule conglomerate beds as one of the most striking features of the upper parts of the Elliot Formation was first recognized by Ellenberger et al. (1964; p. 323, 324).

## 5.2. Stratigraphic position and inferred age of the burrow cast

At the study site, the upper contact of the Elliot Formation is ~1800 m above sea level, whereas the lower contact is not exposed, but has been identified at ~1650 m above sea level <1.5 km west of the burrow site (Fig. 1B). The burrow cast is ~60 m below the base of the Clarens Formation (Fig. 1C), and stratigraphically above the transition from the lower to the upper Elliot Formation, a zone traditionally considered to represent the divide between the Late Triassic and Early Jurassic (Fig. 1). The primary sedimentological evidence for the burrow site being located well within the uEF is that the burrow-bearing layer is between two diagnostic sedimentary facies of the uEF: 1) a massive, clast-supported carbonate nodule conglomerate (facies Gcm); and 2) a deep red to maroon, clast-rich very fine-grained sandstone (facies Sc) (Figs. 1, 2, 3). Furthermore, other features of the host sediment, such as the fine-grained, palaeo-pedogenically altered, crevasse splay sandstone under- and overlain by massive, bioturbated, floodplain mudstone with large-scale desiccation cracks, invertebrate trace fossils, calcareous rhizoconcretions, and spherical to elongated carbonate nodules are, especially when co-occurring, typical features of uEF (Figs. 1, 2, 3). Accepting that the burrow site is stratigraphically in the uEF, a succession widely accepted to be Lower Jurassic (e.g., Olsen and Galton, 1984; Lucas and Hancox, 2001; Sidor and Hancox, 2006), the burrowing activity can be interpreted to have occurred in the Early Jurassic. The revised interpretation of the sedimentology and stratigraphic relationships within the Elliot Formation at Edelweiss (i.e., the uEF starting at ~1720 m above sea level – Figs. 1, 3) has direct bearing on the temporal relationships of several taxa that were found there. A primary corollary is that the important sauropodomorph *Antetonitrus* can now be shown to have been collected from the Lower Jurassic uEF (Figs. 1, 3), suggesting that this taxon is younger than previously thought (Yates and Kitching, 2003; McPhee et al., 2014).

## 5.3. Genesis of the burrow

The infill texture of the burrow (mainly massive, rarely laminated sandstone) and lack of recognisable scratch marks may reflect an open, subaerially exposed burrow, which was excavated in a semi-firm substrate (i.e., pedogenically altered crevasse splay sand) that was not susceptible to collapse, but also not cohesive enough for preserving digging/scratching marks. Given the laminated fill, the burrow was likely filled passively by sand, potentially in a subsequent crevasse splay formation or other high energy mass movement event that delivered sediment, not only into the open burrow, but also the desiccation cracks on the surface of the host sediment (Fig. 3F). This subsequent sandy fill of the desiccation cracks and vertebrate burrows was exploited by invertebrates, most likely due to the higher nutrient content of the infilling, moist sediment that was brought in by flash floods (cf. Buatois and Mángano, 2011). In conjunction with the other proxies from the uEF (e.g., sedimentary structures indicative of episodic and severe moisture deficiency periods), the burrow morphology, passive fill, and position within a crevasse splay sandstone may suggest that the burrow represents the simple, horizontal, subterranean tunnel of a facultative burrower that was primarily used for (?short term) shelter from predators or harsh climatic conditions (Reichman and Smith, 1990). Furthermore, the scarcity of similar structures in the uEF implies that this burrow probably did not function as temporary feeding tunnel or as a permanent aestivating, breeding or nesting structure.

## 5.4. Possible burrow-maker

A close correlation between burrower body mass and excavated burrow cross-sectional area has been observed, and this relationship presumably serves to limit excavation costs and to exclude predators from entering the burrow (e.g., Anderson, 1982; Miller et al., 2001; White, 2005). If considered an ellipse, BP/6/736 has a cross-sectional area of 93.9 cm<sup>2</sup>. Following White's (2005) allometric equation, the burrow-maker has an estimated body mass of 691 g (Fig. 5):

$$A_b = 1.34M^{0.65} \quad (1)$$

$$93.9 \text{ cm}^2 = 1.34M^{0.65} \quad (2)$$

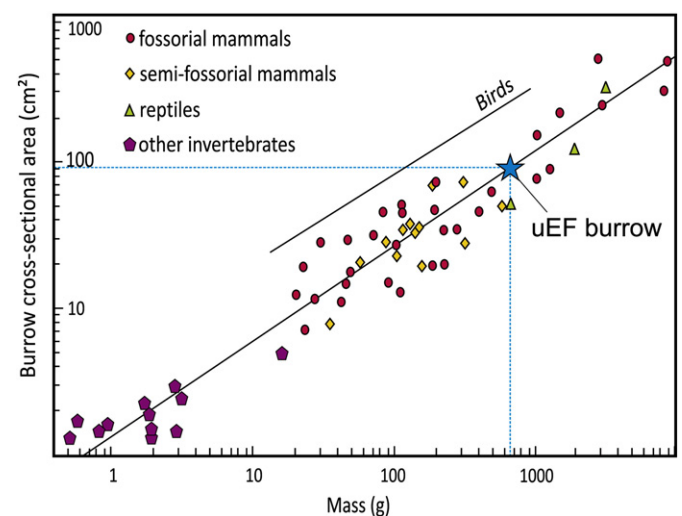
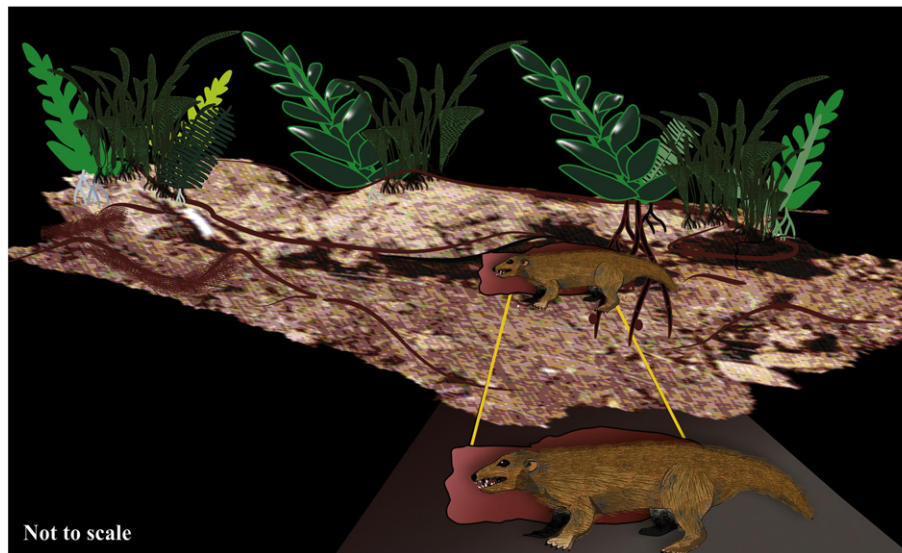


Fig. 5. Graph of burrower body mass estimation from the cross-sectional area of burrows, based on the equation  $A_b = 1.34M^{0.65}$  from White (2005). With a 93.9 cm<sup>2</sup> cross-sectional area of the Edelweiss burrow cast, the estimated body mass of the burrow-maker is 690 g. Edelweiss burrow data marked with a blue star; all other data points are from White (2005). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)





**Fig. 6.** Reconstruction of the vegetated and burrowed crevasse splay deposit of the upper Elliot Formation. The firm, pedogenically altered crevasse splay sand body acted as a suitable substrate for burrowing by vertebrates and invertebrates. A likely burrow-maker candidate, e.g., *Pachygenelus*, an advanced synapsid, is shown in the foreground at the mouth of the burrow.

$$M = 690.76 \text{ g} \quad (3)$$

where:  $A_b$ : burrow cross-sectional area and  $M$ : body mass.

Known sizes and burrowing styles of continental invertebrates (Hasiotis et al., 2002) are, respectively, well below and architecturally dissimilar to our observations on the Edelweiss burrow cast. In combination with the estimated body mass of the inhabitant, these differences exclude invertebrates (e.g., earthworms, crayfish, scorpions, large spiders) from the list of potential burrow-makers. The Edelweiss burrow cast is instead more consistent with fossil and modern vertebrate burrows, an interpretation we explore in more depth below.

Fossilized bone remains are not directly associated with the Edelweiss burrow cast, but a number of fossorial vertebrates are known to have lived in uEF palaeoenvironments, including lungfish, amphibians and cynodonts (Kitching and Raath, 1984; Tables 1 and 2). Among these candidate burrow-makers, lungfish are disqualified as they exclusively produce vertical burrows (Hembree, 2010). Brachyopid and chigutisaurid amphibians in the uEF (Damiani and Rubidge, 2003; Steyer and Damiani, 2005) are excluded because their size is incompatible with the dimensions of the current burrow. Cynodont therapsids include both species with fossorial adaptations of the postcranial skeleton (e.g., broad proximal and distal humeral articulations, long olecranon processes) and species known to inhabit burrows (e.g., Groenewald et al., 2001; Damiani et al., 2003; Abdala et al., 2006). Cynodonts are of the appropriate size-class to have produced and/or inhabited the Edelweiss burrow, and the group is represented by body fossils in the uEF (Tables 1 and 2). Finally, the morphology of the Edelweiss burrow cast

is similar to that of burrow casts from the Lower Triassic of South Africa attributed to cynodonts (e.g., Damiani et al., 2003).

Cynodont therapsids known from body fossils in the Elliot Formation include: traversodontid cynodonts (e.g., *Scalenodontoides macrodotes*), tritheledontid cynodonts (e.g., *Pachygenelus monus*, *Tritheledon riconoi*, *Diarthrognathus broomi*, *Elliotherium kersteni*) and tritylodontid cynodonts (e.g., *Tritylodon longaevus*) (Sidor and Hancox, 2006; Abdala et al., 2007). Of these, *Pachygenelus*, *Tritheledon*, *Diarthrognathus* and *Tritylodon* have been found in the upper Elliot Formation (Sidor and Hancox, 2006). Tritylodontids, the most common non-mammaliaform cynodonts in the uEF (Smith and Kitching, 1997), have been hypothesized to be burrowers based on anatomical features such as an ulna with an elongated olecranon process and sigmoid notch (Sues, 1986; Gow, 2001), as well as thick bone walls in postcranial histology samples (Botha, 2002). This group can be ruled out as the candidate burrow-maker in this instance because the diameter of the Edelweiss burrow cast does not compare well to the skull (and body) size of adults of these taxa. This is particularly evident given the large skull dimensions of adult *Tritylodon* (basal skull length: 130 mm; estimated corporal weight: 10.6 kg; Gaetano et al., 2016), even if the vertical diameter (height) of the burrow (~7 cm) was somewhat larger before sediment compaction.

Known tritheledontids from the uEF are small animals, with adult skull length between 50 and 60 mm (personal observation). Extinct mammalian skulls of this length have been estimated to correspond to live body masses of between 530 and 940 g (Van Valkenburgh, 1990; Fariña et al., 1998). These values bracket the 690 g estimated from the

**Table 3**  
Body size dimensions for *Pachygenelus* based on specimens in the ESI collection. All measurements are in mm.

ESI Catalogue number	Skull length	Skull width	Skull height	Mandible		Humerus	Ulna	Radius
				Height	Length			
BP/1/4982	40	25	N/A	N/A	N/A	N/A	N/A	N/A
BP/1/5110	33	22	17 (with mandible)	N/A	N/A	N/A	N/A	N/A
BP/1/5691	41	30	10 (deformed, not including mandible)	14	N/A	N/A	N/A	N/A
BP/1/4761	41	26	19 (incomplete)	N/A	N/A	N/A	N/A	N/A
BP/1/4381	N/A	N/A	N/A	N/A	77	N/A	N/A	N/A
BP/1/5623	N/A	N/A	N/A	N/A	N/A	33	32	28

cross-sectional area of the Edelweiss burrow cast and indicate that only tritheledontids are represented by taxa small enough to occupy a burrow of this size.

*Pachygenelus*, an advanced tritheledontid (Gow, 1980, 1981, 1994, 2001; Bonaparte et al., 2003; Sidor and Hancox, 2006) is considered here as the most probable burrowing candidate (Fig. 6; Table 3), because: 1) the largest skull size of *Pachygenelus* is 60 mm (with the majority of known specimens being below that value); and 2) it is closely related to *Irajatherium* a Brazilian tritheledontid with possible fossorial adaptations in the humerus (e.g., a proximally deep bicipital groove, prominent lesser tuberosity, and well-developed deltopectoral crest; Martinelli et al., 2005). *Pachygenelus* is the only tritheledontid that has a worldwide distribution, being known from the uEF, where it is the most common member of this family, and also from the McCoy Brook Formation in Canada (Shubin et al., 1991). Tritheledontids are represented by at least five taxa and are considered, in some phylogenies, as the sister group to mammaliaforms (e.g., Bonaparte, 2012). They are best represented in South Africa, but are also known from Argentina and, more recently, from Brazil (Gow, 2001; Martinelli et al., 2005; Martinelli and Rougier, 2007).

Although the current uEF burrow cast is the first description of this kind of vertebrate trace fossil in the Lower Jurassic of southern Africa, similar aged burrows have been previously, and very tentatively, attributed to Early Jurassic herbivorous tritylodontid cynodonts (Navajo Sandstone – Lucas et al., 2006; Moenave Formation – Tanner and Lucas, 2008) and therapsids (Navajo Sandstone – Riese et al., 2011) in the Glen Canyon Group (USA). Research on fossoriality (e.g., Groenewald et al., 2001; Hasiotis et al., 2004; Abdala et al., 2006; Bordy and Krummeck, 2016) has firmly established that the behaviour appeared in non-mammalian cynodonts at least by the earliest Triassic. The Edelweiss burrow cast is suggesting that fossoriality persisted for >50 million years in some of the closest relatives of mammals.

## 6. Conclusions

This study reports the first record of vertebrate burrowing activity in the Lower Jurassic upper Elliot Formation of southern Africa. The section containing the vertebrate burrow cast is interpreted to have formed under semi-arid climatic conditions with seasonal flash flooding, after which the water-saturated sediment was colonized by plants and other soil biota during the process of drying and pedogenesis (e.g., bio- and pedoturbation features: invertebrate traces, calcareous rhizoconcretions, pedogenic carbonate nodules, desiccation cracks). As a firm substrate, the vegetated crevasse splay deposits may have been burrowed by vertebrates, potentially as a form of shelter (temporary dwelling). The size and morphology of the burrow cast indicate that the burrow-maker was a vertebrate. A likely candidate would be a member of the Cynodontia, a therapsid vertebrate group well-represented in the fossil record of the upper Elliot Formation. Of the potential burrowing cynodont candidates, the body size of the locally abundant *Tritylodon* is too large for the burrow structure, however, tritheledontids have the right size to have been the makers of the burrow cast described here.

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