Deep nesting in a lizard, *déjà vu* devil’s corkscrews: first helical reptile burrow and deepest vertebrate nest

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Dating back to 255 Mya, a diversity of vertebrate species have excavated mysterious, deep helical burrows called *Daimonelix* (devil’s corkscrews). The possible functions of such structures are manifold, but their paucity in extant animals has frustrated their adaptive explanation. We recently discovered the first helical reptile burrows, created by the monitor lizard *Varanus panoptes*. The plugged burrows terminated in nest chambers that were the deepest known of any vertebrate, and by far the deepest of any reptile (mean = 2.3 m, range = 1.0–3.6 m, N = 52). A significant positive relationship between soil moisture and nest depth persisted at depths > 1 m, suggesting that deep nesting in *V. panoptes* may be an evolutionary response to egg desiccation during the long (approximately 8 months) dry season incubation period. Alternatively, lizards may avoid shallower nesting because even slight daily temperature fluctuations are detrimental to developing embryos; our data show that this species may have the most stable incubation environment of any reptile and possibly any ectotherm. Soil-filled burrows do not support the hypothesis generated for *Daimonelix* that the helix would provide more consistent temperature and humidity as a result of limited air circulation in dry palaeoclimates. We suggest that *Daimonelix* were used mainly for nesting or rearing young, because helical burrows of extant vertebrates are generally associated with a nest. The extraordinary nesting in this lizard reflects a system in which adaptive hypotheses for the function of fossil helical burrows can be readily tested. © 2015 The Linnean Society of London, Biological Journal of the Linnean Society, 2015, 116, 13–26.


INTRODUCTION

Our underestimation of the diversity of behaviour in extinct organisms is inevitable. Palaeoethologists and palaeoecologists are challenged with inferring behaviour from a fossil record that consists of a minute portion of the original biota and a limited knowledge of the palaeoenvironment (Dodd & Stanton, 1990). Ecologists, ethologists, and behavioural ecologists are not thus limited, and behavioural ecology is a burgeoning discipline that continues to uncover the proximate and ultimate explanations for novel behaviours not imagined just 30 years ago (Parker, 2006; Drickhamer & Dewsbury, 2009).

Despite the behavioural ecology revolution, the basic ecology and behaviour of a great number of extant species remains unknown (Stuart et al., 2004; Greene, 2005; Drickhamer & Dewsbury, 2009). This massive collection of knowledge gaps is further exacerbated by the recent trend away from studying ‘natural history’ (Stuart et al., 2004; McCallum & McCallum, 2006). In the words of Greene (2005), there has been ‘an overemphasis on hypothesis testing and concept building as the defining criteria for allocating resources in biology, to the detriment of

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exploratory field research .’ Despite this trend, many biologists continue to reveal a remarkable diversity in the behaviour, ecology and thus natural history of organisms, often driven by conservation goals under the mantra that ‘we cannot protect what we do not understand’.

In the meantime, the reconstruction of behaviours of long-extinct species remains fraught with difficulties (Benton, 2010). A major issue is the poor understanding of the range and plasticity of the behaviour of extant organisms, coupled with a tendency to generalize and over-interpret the limited fossil information available (Hone & Faulkes, 2014). On the other hand, ecologists, palaeoecologists and palaeoethologists share a common goal (Jackson, 2007; Rull, 2010) and cross-disciplinary research and interactions between the disciplines has increased (Flessa & Jackson, 2005; Willis et al., 2007).

In 1892, Irwin Barbour published his new discovery of remarkable ‘gigantic fossils’ from the Badlands of North America (Barbour, 1892). Owing to their similarity to immense corkscrews, he dubbed these three-meter-high fossils ‘Daimonelix’ or ‘devil’s corkscrews’ (Fig. 1A). After a relatively brief period in which the structures were considered to be giant sponges (as a result of their colloidal silica composition), what followed was a veritable war between two opposing camps over the origin of Daimonelix. The vegetal theorists considered that the spirals were akin to vines such as the large tropical lianas of South America (Barbour, 1895, 1897; Darton, 1903; Riggs, 1909; Lugn, 1941), whereas the animal proponents considered them to be burrows, based on nearby vertebrate skeletons and what appeared to be claw marks in some of the spirals (Cope, 1893; Fuchs, 1893; Peterson, 1904, 1905; Wood & Wood, 1933; Schultz, 1941, 1942).

Nearly nine decades after its discovery, Daimonelix was confirmed as the burrow of Palaeocastor, a late-Oligocene early–Miocene (22–34 Mya) terrestrial beaver that lived in colonies with burrows, much as prairie dogs do today (Martin & Bennett, 1977). Elsewhere, other Daimonelix were discovered, including large burrows possibly excavated by another Miocene mammal (14 Mya; Hembree & Hasiotis, 2008), as well as smaller but very similar burrows excavated by the dicynodont Dictodon, a small herbivorous mammal-like therapsid from the late Permian (255 Mya; Smith, 1987) (Fig. 1B).

Why did Palaeocastor, Dictodon, and other species excavate deep helical burrows? Meyer (1999) calculated that the helical burrows of Palaeocastor required 36–61% more effort than straight burrows with the same incline, suggesting an adaptive function. He argued against the helix as a solution to predation pressure, or to prevent interference between adjacent burrows, instead concluding that helical burrows were more likely a response to dry and hot palaeoclimates. Helical passages, he argued, would limit air circulation as a result of higher subsurface air volume and wall surface area compared to straight burrows, providing a more consistent subsurface temperature and humidity during extreme surface conditions. Others have speculated that helical burrows provide a site for a permanent dwelling, hibernation, aestivation, rearing young, food storage, waste disposal or protection from inundation (Hasiotis et al., 2004; Koch, 1978). A consensus adaptive explanation for deep helical burrows has not been reached.

We recently discovered giant, helical burrows excavated by the (extant) yellow-spotted monitor lizard, Varanus panoptes (Storr, 1980), in north-western Australia (Doody et al., 2014). The burrows of V. panoptes are very similar to those of Palaeocastor and Dictodon, offering an ideal extant system for revealing why some extinct species excavated deep helical burrows. To address this question, we documented the burrow structure of a series of V. panoptes nesting warrens. We tested the hypothesis that abiotic factors explained the deep nesting by quantifying depth gradients in soil temperature and moisture, asking the question: why did lizards not nest at shallower depths? To address why such diverse animals create(d) helices, we compare the lizard burrows with their extinct and extant analogues in an attempt to reduce the number of possible explanations for their creation.
MATERIAL AND METHODS

We studied nesting in *V. panoptes* at two sites in the west Kimberley region, Western Australia (WA). Both study sites were in open savannah woodland in the wet–dry tropics. The main site was along the Margaret River near Fitzroy Crossing (−18.212761 S, 125.861943 E). The second site comprised two areas along the Pentecost River in El Questro Wilderness Park near Kununurra, WA, Australia (−15.7721, 127.873893; −16.010753, 127.976633). The lizards nest during the late wet season and early dry season at the sites (February to June; Doody *et al.*, 2014; J. S. Doody, unpubl. data). The lizards nest in burrows, generally in warrens (groups of up to 30 burrows close to one another). At our site, nesting warrens generally occurred along rivers and creeks in sandy areas with an open canopy and scattered shrubs and grasses. During the dry season, warrens are characterized by areas of bare sandy soil with little vegetation. Nesting warrens were discovered by walking transects along approximately 15 km of the river by two to four individuals, and their locations were recorded using a hand-held Global Positioning System.

Excavation was conducted during April and May 2013, and involved following each surface burrow entrance to its point of termination, whether a nest chamber, another burrow or a dead end as a result of a root, rock or other terminus (see Supporting information, Fig. S1). We excavated each burrow by hand and by shovelling out a platform on which the excavator could stand on at the same time as continuing to follow the burrow. Once the platform was >2 m deep, a bucket on a rope was used to remove soil. Depths, widths, and lengths of straight sections of the burrows were measured, along with the outer diameter and circumference of spiral turns, the angle of incline, the number and direction of turns, and the dimensions of the nest chamber. Nest chambers with eggs were from the present year (2013), whereas those with hatched eggshells were from previous years. Eggs were counted, measured and weighed in the field, and returned to the nest chamber within 24 h. Moist soil was added to the eggs as they were replaced to ensure they would not desiccate prior to the equilibration of moisture to that of the surrounding soil. Two temperature data loggers (DS1921G iButton; Thermochron; accuracy ±0.5°C) were waterproofed with Parafilm M laboratory film (Pechiney Plastic Packaging) and attached at the desired length along the string reflecting depth once in the ground (10 cm, 25 cm, 50 cm, 1 m, 1.5 m, 2 m, 2.5 m, and 3 m). The string was lowered into the column and fastened to the top of the column with tape, and both ends of the column were taped to prevent air flow. Each column was placed into the excavated pit near each nest, and the pit was then backfilled with the soil that had been removed. Data loggers were retrieved by uncapping the columns and pulling the data logger strings up out of the columns; the columns thus provided an efficient way of retrieving the data loggers without re-excavation. The accuracy of the columns was tested in the field by burying a column with paired data loggers attached at different depths (0, 30, 60, and 90 cm) on both the inside and outside of the column. The columns were buried overnight, and the resulting temperatures were the same inside and out within the degree of accuracy (0.5°C) of the data loggers.

To test the hypothesis that deep nesting in *V. panoptes* is related to soil moisture, we quantified the effect of depth on soil moisture. We took soil samples from a gradient of depths near each nest, including 10 cm, 25 cm, 50 cm, 1 m, 1.5 m, 2 m, 2.5 m, and 3 m below the surface (in some cases, the deepest samples were not taken if they were deeper than the adjacent nest). Each sample (500–600 g of soil) was taken from each depth by excavating a hole in the wall of the excavated platform above the nest using a trowel. Care was taken to extract soil that was at least 8 cm into the wall in case drying had occurred in the wall surface. Soil samples were immediately placed into Ziploc bags (S. C. Johnson & Son) (double-bagged) and weighed on an electronic table top balance (accuracy of 0.1 g). Samples were later dehydrated in a drying oven at 105°C at the University of Newcastle for 8 days. Samples were then reweighed, and their weight subtracted from their initial weight and multiplied by 100% to obtain the percentage soil moisture. Although this is a crude measure of soil moisture, measuring water potential...
in the field is problematic because of the need to disturb nests, and our method would be expected to yield reasonable results provided that there was no recent rainfall (which was the case).

**Statistical Analysis**

The variability in temperatures with depth as a result of differences between burrows, as well as day-to-day and seasonal variability, was examined graphically. Three 1-month periods were chosen from the 8-month period to represent the range of seasonal variation experienced throughout incubation period; these included the mid-dry season (15 June to 16 July 2013; coldest temperatures with the least daily variation), early wet season (15 October to 16 November 2013; hottest temperatures with the most daily variation), and the late dry season, which was halfway between the two (15 August to 16 September 2013; intermediate temperatures with intermediate daily variation) (see Supporting information, Fig. S2). Descriptive statistics for the range of temperatures within the three periods and within day were prepared for further analysis. The significance of differences in the mean of the mean daily temperatures between depths was examined using a linear mixed effects model in SAS (SAS Institute Inc.) with fixed effects for depth, period and their interaction. Variation as a result of differences between burrows was modeled as a random effect and a residual covariance matrix was used to model correlation in the residuals as a result of day-to-day differences. The best fitting structure for the covariance matrix (based on the Akaike information criterion) had separate matrices for each period, with the matrices having a first auto-regressive structure over depth and different variances for each depth. This model was used to determine the significance of the differences between mean depths both within a period and among periods and to provide the fitted means and 95% confidence intervals for the depth by period plot. Single-factor analysis of variance was used to test for the effect of site on nest depth. A nonlinear regression was used to test for a relationship between depth and soil moisture and a linear regression was used for temperature range and depth.

**Results**

We found 52 nests in 12 nesting warrens, including 15 nests with eggs from the current year from seven warrens, and 37 old nests with hatched eggshells. Of the 15 current nests, 11 were from Fitzroy Crossing (FX) and four were from El Questro Wilderness Park (ELQ). Mean ± SD nest depth was 2.5 ± 0.696 m for current nests and 2.3 ± 0.650 m (range 0.95–3.6 m, \(N = 52\)) for all nests. Mean ± SD nest depth was 2.6 ± 0.547 m at FX and 2.3 ± 0.912 m at ELQ, and did not differ between sites (\(F_{1,14} = 1.62, P = 0.225\)). Eggshells showed no evidence of predation; aside from four unhatched eggs with dead embryos, all eggshells showed slits that reflected successful hatching (\(N = 24\) nests) or were too broken down to determine whether hatching was successful (\(N = 13\) nests).

Nesting burrows, from top to bottom, consisted of a straight section (sometimes followed by a sharp turn and another straight section), followed by a helix, and then a nest chamber below the helix (Fig. 2; see also Supporting information, Fig. S1; for burrow dimensions, see Table 1). Of 38 helices examined closely, 15 were in the clockwise direction, 10 were counter-clockwise, and three switched from one direction to the other. A *V. panoptes* skeleton (see Supporting information, Fig. S3) was uncovered in the helix of an old burrow at a depth of 1.93 m in a warren at FX. This animal had apparently been entombed in wet soil.
that had set around the body, based on the imprints of the limbs and scales left in the soil (see Supporting information, Fig. S3). Only the bones remained of the animal, which was female-sized.

**NEST TEMPERATURES AND THEIR RELATIONSHIP WITH DEPTH**

Within current nests, temperatures were relatively constant throughout the incubation period (Fig. 3A). The mean ± SD range of nest temperature traces over the entire incubation period was 3.3 ± 1.22°C (range 0.5–5.5°C, N = 15 nests). The mean range of nest temperatures was significantly inversely related to depth ($r^2 = 0.78$, $F_{1,14} = 46.28$, $P < 0.001$) (Fig. 3B). However, mean nest temperatures were not significantly related to depth ($r^2 = 0.06$, $F_{1,14} = 0.83$, $P = 0.380$). The grand mean ± SD nest temperature was 29.4 ± 0.85°C (range 28.2–31.1°C; $N = 15$ nests).

**EFFECT OF DEPTH ON SOIL TEMPERATURE AND MOISTURE: WHY NOT NEST AT SHALLOWER DEPTHS?**

A total of 127 291 soil temperature measurements were analyzed from the depth columns throughout the study period. Mean daily temperatures changed significantly with depth during all three time periods, although their pattern of change varied with time of year ($F_{14,7522} = 778.5$, $P < 0.001$) (Fig. 4A). During the coldest part of the year (mid-dry season), mean soil temperatures were cooler near the surface and significantly warmer with depth (e.g. 10 cm = 24.9°C, 50 cm = 25.8°C, $P = 0.02$) but levelled off after 200 cm (200 cm = 28.6°C, 300 cm = 29.2°C; $P = 0.41$) (Fig. 4A). Conversely, during the hottest time of the year (early wet season), mean soil temperatures were warmest near the surface and significantly cooler with depth (10 cm = 36.4°C, 25 cm = 35.1°C; $P < 0.01$) but levelled off after 250 cm (250 cm = 30.2°C, 300 cm = 29.8°C; $P = 0.20$) (Fig. 4A). The intermediate time period (late dry season) showed relatively stable soil temperatures across the depth gradient; although mean temperatures were significantly warmer near the surface (10 cm = 30.6°C, 25 cm = 29.4°C; $P < 0.01$), they levelled off beyond 100 cm (100 cm = 28.1°C, 300 cm = 28.6°C; $P = 0.16$) (Fig. 4A).

As expected, the daily range in mean daily temperatures was greatest at shallower depths, decreasing with depth for all time periods (Fig. 4B). Within-day temperature range dropped rapidly beyond depths of 10 cm, and did not exceed 1°C at depths beyond

<table>
<thead>
<tr>
<th>Burrow dimension</th>
<th>Mean ± SD (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth to nest</td>
<td>2.6 ± 0.55 m (15)</td>
</tr>
<tr>
<td>Width</td>
<td>10.5 ± 1.61 cm (26)</td>
</tr>
<tr>
<td>Incline</td>
<td>8.4 ± 2.56° (26)</td>
</tr>
<tr>
<td>Distance from entrance to first turn</td>
<td>94.0 ± 45.76 cm (24)</td>
</tr>
<tr>
<td>Depth to top of helix</td>
<td>1.2 ± 0.34 m (39)</td>
</tr>
<tr>
<td>Number of turns</td>
<td>3.1 ± 1.55 (33)</td>
</tr>
<tr>
<td>Turn diameter</td>
<td>35.3 ± 4.75 cm (29)</td>
</tr>
<tr>
<td>Length of complete turn</td>
<td>107.4 ± 9.75 cm (29)</td>
</tr>
<tr>
<td>Chamber height</td>
<td>9.0 ± 1.45 cm (40)</td>
</tr>
<tr>
<td>Chamber width</td>
<td>14.9 ± 2.55 cm (40)</td>
</tr>
<tr>
<td>Chamber length</td>
<td>22.2 ± 7.26 cm (40)</td>
</tr>
</tbody>
</table>

**Table 1.** Summary of *Varanus panoptes* burrow dimensions

![Figure 3. Nest temperatures and their relationship with nest depth. A, continuous nest temperatures throughout incubation from 15 *Varanus panoptes* natural nests ranging from 1.1 to 3.6 m deep. Data were obtained from data loggers employed in each nest. B, the total range of each nest temperature trace in (A) regressed against nest depth.](https://academic.oup.com/biolinnean/article-abstract/116/1/13/2447915)
50 cm (Fig. 4B). The differences in daily range of temperature between depths at 100–300 cm were negligible (Fig. 4B).

Soil moisture data from the FX warrens was compromised by a heavy early dry season rainfall event in late March just prior to our excavation; this led to an inverse relationship between soil moisture and depth, a temporary condition that masks the true moisture–depth gradient during the dry season. At ELQ, however, we obtained soil moisture data that reflected typical dry season conditions early in the incubation period (Fig. 4C). Mean soil moisture early in the incubation period, based on four nesting warrens, was significantly positively related to soil depth ($r^2 = 0.932; F_{2,7} = 59.67, P < 0.001$) (Fig. 4C). Moreover, soil moisture at 3 m depth averaged 37% greater than that at 1 m depth (Fig. 4C). This moisture–depth gradient may be even steeper later in the dry season; during the excavation of an ELQ nest in late December prior to any significant rainfall, the walls of our pit in the topmost metre ‘caved in’ as a result of the very dry sand.

Figure 4. Abiotic influences on deep nesting in Varanus panoptes. A, relationships between mean temperature and soil depth across three time periods (mid dry, late dry, early wet) for eight V. panoptes nesting warrens at two sites. Breaking incubation into these time periods highlights seasonal differences in the direction of the temperature–depth gradient, resulting from a lag between air and soil temperatures. The arbitrary horizontal reference line is at 29.5°C. B, relationships between mean daily temperature range and soil depth across the same three time periods, warrens and sites, as above. C, relationship between mean soil moisture and soil depth for four V. panoptes nesting warrens at El Questro Wilderness Park. Four nests, one in each burrow, are also plotted. Soil moisture was measured early in the incubation period.
DISCUSSION

To our knowledge, *V. panoptes* excavates the deepest nests of any extant vertebrate, and by far the deepest nest of any reptile. Moreover, its burrows are the first known helical burrows created by a reptile, and the first helical burrows (extinct or extant) that are confirmed to be plugged with soil by the excavator. Finally, our data indicate that *V. panoptes* eggs may experience the most stable egg environment of any reptile, and possibly any ectotherm (Fig. 3A). Soil moisture, which increased significantly with increasing depth even beyond 100 cm (Fig. 4C), may have explained deep nesting in the species: eggs at intermediate depths could desiccate in this species with a long incubation period (approximately 8 months), especially when dry seasons are prolonged. Alternatively, lizards may nest at great depths because even slight daily temperature fluctuations at shallower depths are detrimental to developing embryos. The most widely cited hypothesis for why extinct animals excavate helical burrows (i.e. a more consistent subsurface temperature and humidity as a result of limited air circulation during extreme surface conditions) is not applicable to *V. panoptes* burrows. The helical burrows of *V. panoptes* are used exclusively for nesting, and are filled with soil, essentially allowing no air flow. Although the function of the helix in animal burrows remains a mystery, we hypothesize that *Daimonelix* were used mainly for nesting or rearing young because helical burrows of extant vertebrates are generally associated with a nest (Table 2).

Our data support a recent pilot study proposing that *V. panoptes* nests were by far the deepest of any reptile (Doody et al., 2014). In that study, three nest chambers averaged 1.5 m deep; in the present study, 52 nests averaged 2.4 m deep, and ranged up to 3.6 m deep. The majority of the world’s reptile nests within 25 cm of the surface, and even the largest of reptiles such as sea turtles and large crocodilians typically nest < 50 cm deep (Doody et al., 2014). Indeed, we can find no vertebrate that consistently excavates nests at depths > 1 m. To our knowledge, the only subterranean animals that nest deeper than *V. panoptes* are ants (*Prenolepis *= 3.6 m, *Messor* = 4 m, *Atta* = 7 m :Kubota, 1948; Tschinkel, 1987; Farji-Brener & Medina, 2000). Deep nesting in *V. panoptes* thus requires an adaptive explanation.

Perhaps the most cited reason for why an animal excavates a burrow at a particular depth is to provide a refuge for the animal to escape harsh environmental conditions at the surface. Indeed, this was cited as the possible reason for deep nesting in both *Palaeocaster* and *Dictodon*, which lived in hot, dry palaeoclimates (Martin & Bennett, 1977; Smith, 1987, 1993; Meyer, 1999). In support, medieval pocket gophers burrowed to greater depths than modern gophers, associated with a transition from humid to arid conditions triggered by relatively rapid climate change (Schmiesser, Loope & Wedin, 2009). The need for environmental insulation from surface conditions could indeed explain the consistent and great depth of *V. panoptes* burrows, although by what mechanism? The most extreme surface conditions might be related to fires; however, fires in the Australian tropical savannah tend to be ‘cool’ fires that penetrate only a few cm into the soil (Williams et al., 2004). Could helical burrows be excavated at great depths to facilitate behavioural thermoregulation, as suggested for *Dictodon*, *Palaeocaster*, and other extinct excavators (Martin & Bennett, 1977; Koch, 1978; Smith, 1987; Meyer, 1999; Hembree & Hasiotis, 2008; Riese, Hasiotis & Odier, 2011)? Mean soil and nest temperatures were similar at depths of 100–300 cm when considering the entire incubation period (Fig. 4A). However, we cannot rule out temperature as a reason for deep nesting. Cooler soil temperatures nearer the surface in winter were contrasted by warmer soil temperatures near the surface in spring. For example, during the mid-dry season, mean temperature was 3°C and cooler at 100 cm than at 300 cm (27°C vs. 30°C), although the situation was reversed during the early wet season, with mean temperature being 3°C warmer at 100 cm than at 300 cm (33°C vs. 30°C) (Fig. 4A). These contrasting slopes of the temperature–depth gradients among the three time periods were a result of the seasonal lag between air and soil temperatures at greater depths. Although daily fluctuations were non-existent between 100 and 300 cm (Fig. 4B), the range in nest temperatures across the entire incubation period was narrower deeper in the ground (Fig. 3B). Thus, *V. panoptes* mothers may excavate nests deeper in the soil if their embryos are more successful when incubating at temperatures that remain more constant across the entire incubation period. The negligible difference in mean and variance in temperature at depths > 100 cm in the burrows of *V. panoptes* and presumably other species suggests that the ‘harsh’ environmental conditions buffered by deep nesting would be dry conditions, rather than hot conditions. We hypothesize that lower soil moisture at shallow and intermediate depths may have promoted deep burrowing in *Palaeocaster* and *Dictodon*, as well as *V. panoptes*.

Soil moisture not only increased significantly with depth early in incubation (June-July), but also was significantly (37%) greater at 300 cm than at 100 cm (Fig. 4C). Assuming this difference persisted throughout the incubation period (i.e. significant rainfall generally does not occur until November at...
<table>
<thead>
<tr>
<th>Attribute</th>
<th>Diictodon</th>
<th>Unknown</th>
<th>Palaeocastor (3 spp.)</th>
<th>Unknown mammal?</th>
<th>Geomys breviceps, Geomys texensis, Geomys pinetis</th>
<th>Cratogeomys fumosus</th>
<th>Varanus panoptes</th>
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<tbody>
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<td></td>
<td>Nebraska, USA</td>
<td>Colorado, USA</td>
<td>Texas and Florida, USA</td>
<td>Jalisco, Mexico</td>
<td>Western Australia</td>
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<tr>
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<td>Upper</td>
<td>Lower Miocene 22 Mya</td>
<td>Middle Miocene 14 Mya</td>
<td>Extant</td>
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<td></td>
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<td>Alluvium</td>
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<td>Alluvial montane basin</td>
<td>Proximal floodplain</td>
</tr>
<tr>
<td><strong>Climate/palaeoclimate</strong></td>
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<td></td>
<td>Semi-arid to arid, highly seasonal rainfall</td>
<td>Semi-arid to arid, highly seasonal rainfall</td>
<td>Sub-humid to humid, sub-tropical, seasonal rainfall</td>
<td>Tropical, arid to wet, highly seasonal rainfall</td>
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<tr>
<td><strong>Depth (m)</strong></td>
<td>0.5–0.75</td>
<td>0.5–1.5</td>
<td>2.1–2.75</td>
<td>2–3</td>
<td>0.5–1.5</td>
<td>0.5–1.0</td>
<td>1.0–3.6</td>
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<tr>
<td><strong>Number of turns</strong></td>
<td>2–3</td>
<td>5–6?</td>
<td>6–12</td>
<td>3–5</td>
<td>2.5–6, ?, 3–4</td>
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<td>2–7</td>
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<td><strong>Spiral diameter (cm)</strong></td>
<td>16</td>
<td>5–20</td>
<td>12</td>
<td>30–50</td>
<td>12–15, 13–14, 20–36</td>
<td>42.5</td>
<td>35</td>
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<td>?, ?, dextral</td>
<td>Dextral</td>
<td>Sinistral, dextral, both</td>
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<td><strong>Openness</strong></td>
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<td>Open?</td>
<td>Open?</td>
<td>Open</td>
<td>Open</td>
<td>Open</td>
<td>Plugged</td>
</tr>
<tr>
<td><strong>Upper portion</strong></td>
<td>Straight decline</td>
<td>Pit</td>
<td>Amorphous enlarged pit</td>
<td>Straight decline with branches and chambers</td>
<td>Straight decline with branches</td>
<td>Straight decline with branches</td>
<td></td>
</tr>
<tr>
<td><strong>Middle portion</strong></td>
<td>Helix</td>
<td>Helix</td>
<td>Helix</td>
<td>Pair helices, helix</td>
<td>Helix</td>
<td>Helix</td>
<td></td>
</tr>
</tbody>
</table>
the earliest) then nesting at depths > 100 cm could reduce the probability that eggs will desiccate in drying conditions. In support, when we excavated two warrens in late December before any appreciable rain had fallen, the soil in the topmost 100–150 cm was extremely dry and ‘caved in’ as we excavated the nest site. Our data and observations may explain deep nesting in the species; dry conditions late in the dry season may cause eggs to desiccate if they are laid at intermediate depths, especially if the dry season is protracted. Although we cannot discount the effects of temperature, deep nesting in *V. panoptes* may be an evolutionary response that reduces the probability of egg desiccation in this species with a long, dry season incubation period (approximately 8 months).

Turning to the helix itself, although it is possible that *V. panoptes* excavate them for different reasons than did *Palaeocastor* and *Diictodon*, we might expect a common function. Although more stable moisture as a result of increased surface area could be adaptive for the excavators of *Daimonelix*, the plugged nests of *V. panoptes* would allow little or no airflow, apparently precluding the need for a helix. It is of course possible, however, that plugging was a modification of the helical burrow added by *V. panoptes* to facilitate nesting in some other way. The other (non-nesting) burrows of *V. panoptes* appear to lack helices, including those used for aestivation (Doody *et al.*, 2014), suggesting that the extra energy involved in constructing a helix is only justified when nesting. Some species of burrowing mammals plug their burrows during the day or during the dry season to prevent water loss, and this keeps the burrows saturated with humidity (Jarvis & Sale, 1971; Nevo, 1973). If the burrow is completely filled with soil as in *V. panoptes*, a helical structure to maintain high humidity appears to be superfluous. An important distinction here is that, after laying, *V. panoptes* abandons its parchment-shelled eggs to a approximately 8-month incubation period, whereas *Palaeocastor* bore live young. Thus, buffering for *Palaeocastor* would only require adequate water retention for the mother (and her embryos) and for the young when they are born. It is unlikely, given live birth, that the helical burrows of *Palaeocastor* were plugged by their excavators; indeed, there is no direct evidence of *Palaeocastor* plugging its burrows (Martin & Bennett, 1977). However, although very young specimens have been found, it is not known whether *Diictodon* laid eggs or bore live young (King, 1990). If *Diictodon* laid eggs, then it may have plugged its helical burrows. The best evidence for higher humidity or soil moisture as the reason for helical burrows comes from scorpions: the burrows of *Urodacus* in open ground, compared to those under

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Lower portion</th>
<th>Nest?</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Geoemyx breviceps</strong></td>
<td>Horizontal terminal chamber</td>
<td>Yes</td>
<td>Hembree &amp; Hasiotis (2008)</td>
</tr>
<tr>
<td><strong>Geoemyx texensis</strong></td>
<td>Horizontal terminal chamber at or near bottom of spiral, or between paired spirals</td>
<td>Yes</td>
<td>Brown &amp; Wilkins &amp; Wilkins &amp; Roberts (2007)</td>
</tr>
<tr>
<td><strong>Geoemyx pinetis</strong></td>
<td>Horizontal terminal chamber</td>
<td>Yes</td>
<td>Hasiotis (1973); Meyer (1969)</td>
</tr>
<tr>
<td><strong>Diictodon</strong></td>
<td>Mostly horizontal, enlarged terminal chamber</td>
<td>Unknown</td>
<td>Smith (1987)</td>
</tr>
</tbody>
</table>

Table 2. Continued
surface objects, are deeper, have more spiral turns, and occur in the more arid parts of Australia (Hasiotis et al., 2004). Helical burrows are also excavated by some African and North American scorpions in dry climates (Lamoral, 1979; Bradley & Brody, 1984).

Another possible reason for deep helical nesting in V. panoptes, Palaeocastor, Dictodon, and others is predator avoidance. Burrow depth in Palaeocastor may have been an effective predator deterrent (Meyer, 1999); the function of helical burrows of the pocket gopher Geomys pinetis may be to slow down, confuse or stop predators such as weasels or snakes that would chase the gophers in total darkness (Brown & Hickman, 1973). Ironically, helical burrows of scorpions were hypothesized to reduce the probability of predation by Varanus lizards (Hasiotis et al., 2004). Predators of V. panoptes eggs in nature are unknown and we have not observed any potential predators in the nesting burrows. However, perhaps the most likely predator is a conspecific male. Males of the congeneric V. rosenbergi prey upon conspecific eggs, which may be relatively easy to locate because they are laid in termite mounds (Rismiller, McKelvey & Green, 2010). Male V. panoptes, which are adept egg predators (Christian, 2004), visit conspecific nesting warrens (Doody et al., 2014). Although they possess excellent olfactory ability (Cooper, 1988, 1994), perhaps the effect of deep nesting on olfactory detection, combined with obstructions such as back-filled helices, reduces the likelihood of nest predation. Predators that were sufficiently small to fit into Palaeocastor burrows may have been too long and/or not supple enough to follow the beavers down into the tight helical design (Meyer, 1999). In the same way, V. panoptes males, which are considerably larger than females and adept diggers, might find it particularly difficult to excavate through the tight helical design. However, an argument could be made that a deep burrow that is too narrow for a male V. panoptes to navigate would suffice to deter nest predation, precluding the need for a helix. Martin (Martin, 1989, 1994) noted out that predators of Palaeocastor such as snakes and weasels could readily access helical burrows, noting the finding of a predatory relative of the raccoon, Zoodiolestes daimonelixensis, in a Palaeocastor burrow. It is also possible that V. panoptes evolved helix creation as a deterrent to a now extinct predator such as a Thylinace or Megalania (Clode, 2009).

Could a helix reduce the chances of neighbouring burrows interfering with one another? The suggestion that the high density of Palaeocastor burrows may explain their spiral structure (Martin & Bennett, 1977) was tested by Meyer (1999), who analyzed the spatial distribution of a set of Palaeocastor burrows, concluding that the interference potential of both the straight burrow sections and living chambers was negligible (5–8%). Our V. panoptes burrows were very close to one another, and close to nesting burrows from previous years, although we did not observe interference between burrows or nest chambers from the same year. The interference hypothesis could be tested in situ with nesting warrens of V. panoptes, or experimentally with smaller animals amenable to experimentation in the laboratory. For example, Hembree, Johnson & Tenwalde (2012) experimentally determined the effect of horizontal space on burrow complexity in scorpions (Hadrurus). Another way that horizontal space could influence the use of a helix involves the patchiness of some soil property such as hardness, texture or friability. If heterogeneity in the preferred soil property is greater in the horizontal plane than in the vertical plane, the helix could allow the excavator to increase the likelihood of burrowing into the preferred soil patch; the excavator may confirm a sufficient or optimal patch of soil, and then excavate the helix at that point. Conversely, a long straight section may bring the excavator out of the patch of preferred soil, a hypothesis that could be tested in V. panoptes (but not in the extinct species) by quantifying the three-dimensional soil matrix at nesting warrens.

The increased surface area of helical burrows may increase drainage during minor flooding as a result of heavy rainfall. According to Koch (Hasiotis et al., 2004), advantages of the extensive spiralling in burrows of Urodaucus scorpions could include reducing the effects of sheet-flooding. The very fact that Daimonelix exist supports their susceptibility to flooding. They are found in paleosols, either alluvial or proximal floodplains, and thus owe their preservation to being backfilled by crevasse splay sand during catastrophic sheet flood events; the splays in-filled many of the burrows with fine-grained sand and silt and occasionally entombed an aestivating Dictodon (Martin & Bennett, 1977; Schmiesser et al., 2009). Although a V. panoptes burrow is mostly plugged with soil, the first 0.5–1.0 m or so is not, and much of the rest of the burrow varies from tightly-packed to loosely-filled. Because nesting occurs during the wet season and early dry season, flooding of the burrow and nest chamber from heavy rainfall is quite possible, and the combination of backfill and the helix could promote drainage, sparing the eggs from long-term inundation. Survival of reptile eggs is greatly reduced after 24 h of inundation (e.g. Plummer, 1976). As for the helix increasing drainage in Palaeocastor and other live-bearing excavators of Daimonelix, the flooding of resting or nesting chambers could also be disadvantageous (e.g. by causing hypothermia in young).

A review of extant vertebrates that excavate helical burrows (Table 2) suggests that a helix may be invariably associated with a nest (eggs or young). Among extant vertebrates, the pocket gophers (Geomysidae) of North America are best known for excavating helical burrows. For example, three species of pocket gophers (Geomys breviceps, Geomys texensis, and Geomys fumosus) excavated helical burrows, of which most were associated with a nest (Wilkins & Roberts, 2007), and 28 of 40 burrow systems of G. pinetis contained a nest within a short distance of the bottom of the helix (Rismiller et al., 2010). Other studies have reported helical burrows for Geomys attwateri and Cratogeomys tylorhinus (Cameron et al., 1988; Roberts et al., 1997); however, one report mentions helical burrows but not nests for Cratogeomys merriami (Villa-C, 1989). Interestingly, the nests of two pocket gopher species (Table 1) were placed in a lateral tunnel connecting paired helices. Elsewhere among vertebrates, burrows of the prairie dog, Cynomys mexicanus, descend vertically or in a steep spiral for (1 m) or more before becoming horizontal (Ceballos-G & Wilson, 1985). The notion that deep helical nests in extinct forms were also excavated to facilitate nesting is not new; for example, young Palaeocastor fossils have been found in the terminal chambers (Martin & Bennett, 1977). However, nesting is generally given within a list of other possibilities, including permanent dwelling, shelter from extremes and predators, hibernation, aestivation, food storage, waste disposal, and protection from inundation (Koch, 1978). We suggest that helical structures in Daimonelix were associated with nesting in Palaeocastor, Diictodon and other extinct forms, and that other nonhelical sections of the burrow systems (see inclined tunnels in Fig. 1) served other purposes (from the list above).

We have not considered in our discussion burrows of animals that are weakly helical, sinuous or winding. For example, the burrows of gopher tortoises (Gopherus polyphemus) of North America and of the Bilby (Macrotis lagotis) in central Australia twist in a loose fashion for one complete turn (Finlayson 1935 in: Johnson, 1989; Kinlaw & Grasmueck, 2012). There are a number of weakly helical burrows of extinct species that we also did not consider (Koch, 1978). Although the reasons for these burrow types may be similar to those behind helical burrows, their similarity to straight burrows makes them difficult to definitively characterize. We also do not include the mole rat, Cryptomys damarenensis, which can excavate spiral burrows around tubers to eat them (Lovegrove & Painting, 1987). Finally, there are invertebrates other than scorpions that construct (small) helical burrows, such as millipedes and marine invertebrates (Dworschak & Rodrigues, 1997; Hembree, 2009). These burrows were not considered in the present study, despite the possibility that they may contain clues to the ultimate function of helical burrows in vertebrates.

In summary, the present study reports the first helical burrows in a reptile, the first helical burrow that is plugged, and the deepest nesting burrow of any extant (or extinct?) vertebrate. The success of reptilian eggs incubating in nature requires three important environmental factors: adequate temperature, moisture, and gas exchange (Ewert, 1979). If we assume that the availability of oxygen is not limiting in deep nests (the egg chambers in the present study were air-filled rather than soil-filled), we can hypothesize that V. panoptes nests at great depths because nesting at shallower depths would lower egg survival as a result of sub-optimal temperature or moisture regimes. We hypothesize that deep nesting in V. panoptes facilitates the hydric environment for developing eggs: dry conditions during incubation at intermediate depths could lead to egg desiccation, especially after small wet seasons in this species with a very long egg incubation period. Our results, along with observations on deep helical burrows of extant mammals, should force a rethink on hypotheses erected for Daimonelix. For example, the interpretation of Upper Jurassic Morrison Formation burrows excavated by mammals (Koch, 1978) based on (1) similarities with other extinct and extant mammal burrows, including helices, and on (2) the assertion that extant reptiles have not been observed to construct burrows as complex as those of mammals, needs to be reconsidered. The complex helical burrows in the present study were excavated by reptiles, which, as Koch (1978) noted, were abundant during the Upper Jurassic. Our findings prompt other important questions: Were Daimonelix associated with a nest? Were they plugged and with eggs (e.g. Diictodon) and how would this influence the ‘environmental conditions’ hypothesis for the evolution and maintenance of helical burrows? We propose a cautious approach when interpreting deep helical burrows and their tracemakers (Hone & Faulkes, 2014), partly because we know so little about burrowing in secretive, extant groups such as reptiles. For example, the nesting habits are unknown for most reptiles (Dooddy, Freedberg & Keogh, 2009), including 39 of the world’s 53 species of monitor lizards known at that time (Dooddy et al., 2014). Despite the unanswered questions, studying deep helical nesting in V. panoptes has begun to shed light on behaviour in extinct forms by reducing the number of likely explanations for its evolution (e.g. temperature alone cannot explain deep helical burrows in Daimonelix). The deep helical burrows of V. panoptes offer a unique extant system for solving the adaptive function of Daimonelix.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Figure S1.** Excavation of a 3.3 m deep *Varanus panoptes* burrow, showing spirals of the helix (arrows). The burrow entrance was in the foreground (see composite in Fig. S2).

**Figure S2.** Continuous temperatures from eight *Varanus panoptes* nesting warrens, recorded every 3 h at all depths (10–300 cm) during incubation in April to December. Coloured dots indicate data points included in the analysis: red dots = 15 June to 16 July (mid-dry season winter); green dots = 15 August to 16 September (late dry season spring); blue dots = 15 October to 16 November (early wet season leading into summer).

**Figure S3.** Form and skeleton of a *Varanus panoptes* found entombed in the helical structure of a nesting burrow at FX. The impression of scales indicates that the burrow was flooded. Visible are several vertebrae.