

# Why Animals Construct Helical Burrows: Construction vs. Post-Construction Benefits

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## Abstract

The extended phenotype of helical burrowing behavior in animals has evolved independently many times since first appearing after the Cambrian explosion (~540 million years ago). A number of hypotheses have been proposed to explain the evolution of helical burrowing in certain taxa, but no study has searched for a general explanation encompassing all taxa. We reviewed helical burrowing in both extant and extinct animals and from the trace fossil record and compiled from the literature 10 possible hypotheses for why animals construct helical burrows, including our own ideas. Of these, six were post-construction hypotheses—benefits to the creator or offspring, realized after burrow construction—and four were construction hypotheses reflecting direct benefits to the creator during construction. We examined the fit of these hypotheses to a total of 21 extant taxa and ichnotaxa representing 59–184 spp. Only two hypotheses—antipredator, biomechanical advantage—could not be rejected for any species (possible in 100% of spp.), but six of the hypotheses could not be rejected for most species (possible in 86–100 % of spp.): microclimate buffer, reduced falling sediment (soil), anticrowding, vertical patch, and the above two hypotheses. Four of these six were construction hypotheses, raising the possibility that helical burrowing might have evolved without providing post-construction benefits. Our analysis showed that increased drainage, deposit feeding, microbial farming, and offspring escape could not explain helical burrowing behavior in the majority of taxa (5–48%). Overall, the evidence does not support a general explanation for the evolution of helical burrowing in animals. The function and evolution of the helix as an extended phenotype would seem, at least in some cases, to provide different advantages for different taxa. Although direct tests of many of the hypotheses would be difficult, we nevertheless offer ways to test some of the hypotheses for selected taxa.

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Construction vs. Post-Construction Benefits

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and from the trace fossil record and compiled from the literature 10 possible hypotheses for why animals construct helical burrows, including our own ideas. Of these, six were post-construction hypotheses—benefits to the creator or offspring, realized after burrow construction—and four were construction hypotheses reflecting direct benefits to the creator during construction. We examined the fit of these hypotheses to a total of 21 extant taxa and ichnotaxa representing 59–184 *spp.* Only two hypotheses—antipredator, biomechanical advantage—could not be rejected for any species (possible in 100% of *spp.*), but six of the hypotheses could not be rejected for most species (possible in 86–100 % of *spp.*): microclimate buffer, reduced falling sediment (soil), anticrowding, vertical patch, and the above two hypotheses. Four of these six were construction hypotheses, raising the possibility that helical burrowing might have evolved without providing post-construction benefits. Our analysis showed that increased drainage, deposit feeding, microbial farming, and offspring escape could not explain helical burrowing behavior in the majority of taxa (5–48%). Overall, the evidence does not support a general explanation for the evolution of helical burrowing in animals. The function and evolution of the helix as an extended phenotype would seem, at least in some cases, to provide different advantages for different taxa. Although direct tests of many of the hypotheses would be difficult, we nevertheless offer ways to test some of the hypotheses for selected taxa.

Key words: behavior; extended phenotype; costs-benefit; spiral burrow; helix; ichnotaxa

## Introduction

An extended phenotype, when referring to a single species, includes some architecture or entity (e.g., beaver dam, termite mound) in which the phenotype is the fitness of the construction for survival and reproduction (Dawkins, 1982, 2004). Scientific interest in extended phenotypes has been widespread and sustained, encompassing diverse areas ranging from parasite manipulation of hosts (Hughes and Libersat, 2019) to relationships between genomes and phenotypes (Hunter, 2018) to human sexual selection theory (Luoto, 2019).

Burrow architectures are classic extended phenotypes that show great diversity and complexity and can reflect important fitness-related traits (Hansell, 2005). In a classic example, the old-field mouse, *Peromyscus polionotus*, constructs complex burrows with a long entrance tunnel that leads into a nest cavity and a secondary escape tunnel, while its sister species, the deer mouse (*P. maniculatus*) builds shorter, single-tunnel burrows (Weber et al., 2013). The complex burrowing behavior of *P. polionotus* is derived, has a strong genetic component, and its putative adaptive function is to facilitate escape in an open, exposed habitat (Wolfe and Esher, 1977; Weber and Hoekstra, 2009; Weber et al., 2013).

A diversity of terrestrial and aquatic animals excavates mysterious helical burrows that comprise multiple, symmetrical spirals descending into a medium (i.e., substrate, sediment). The first of these kinds of burrows appeared with the Cambrian explosion ~540 million years ago (e.g., Goldring and Jensen, 1996; Hasiotis, 2012; Sappenfield et al., 2012; Zhang et al., 2015) and many others are known only from fossils, including the remarkable 3-meter-deep burrows assigned to the ichnotaxon *Daimonelix* that were constructed by the terrestrial beaver *Palaeocaster* from the Miocene (Barbour, 1892; Martin and Bennett, 1977). Various forms of *Daimonelix* are now known to have been constructed by a variety of terrestrial vertebrates since the Late Permian, approximately 260 million years ago (Smith, 1987; Fischer and Hasiotis, 2018; Raisanen and Hasiotis, 2018). Living examples of species that construct helical burrows include terrestrial taxa, such as some pocket gophers, monitor lizards, and scorpions, and marine forms such as some shrimp and some polychaetes (e.g., Powell, 1977; Koch, 1978; Löwemark and Schäfer, 2003; Hasiotis and Bourke 2006; Netto et al., 2007; Wilkins and Roberts, 2007; Doody et al., 2015).

The relentless, independent evolution of helical burrowing behavior across disparate unrelated taxa dating back hundreds of millions of years attests to its apparent utility. Yet, the reason(s) for the evolution of the helix from more simple burrows remains largely speculative and unresolved. One problem is that little is known of the natural history of the tracemakers of the fossil burrows or trace fossils (e.g., Bromley, 1996; Hasiotis 2007). Another problem is no study has considered all taxa in the search for a general explanation, although a diversity of functions is certainly possible and is sometimes suggested. To illustrate, collectively,

helical burrows have been proposed to have evolved to buffer microclimate of the burrow from harsher outside conditions (e.g., temperature, aridity, salinity), promote drainage during flooding, thwart predators, reduce burrow interference with conspecifics, increase surface area to expose more sediment for deposit-feeding, or promote bacterial farming (e.g., Martin and Bennett, 1977; Koch, 1978; Dworschak & Rodriguez, 1997; Myer, 1999; Netto et al., 2007; de Gibert et al., 2012; Doody et al., 2015; Raisanen and Hasiotis, 2018; Muñiz and Belaústegui, 2019). Moreover, some have hypothesized that helical burrows could serve multiple functions (behavioral category polychresichnia; Hasiotis, 2003) (Koch, 1978; Netto et al., 2007; Carvalho and Baucon, 2010; deGibert et al., 2012; Raisanen and Hasiotis, 2018).

These hypotheses offered to explain helical burrowing behavior generally invoke adaptation in the form of ‘post-construction’ benefits to the creator. Indeed, an adaptive function(s) of helical burrows seems plausible, given its multiple origins and the increased effort required to create a helix compared to a simpler (straight) burrow of the same incline (volumetric calculations by Meyer, 1999). Much less attention has been given to ‘construction’ costs-benefits of helical burrows, or those that provide no benefit to the occupant after burrow construction, but rather are restricted to cost-benefits of burrowing behavior itself. In an exception, White (2001) estimated the total cost of helical burrow construction in scorpions by calculating the net cost of soil transport and the costs of the animal moving itself and soil horizontally, and vertically against gravity. Helical burrowing scorpions minimized both (i) the energy used during burrow excavation by descending as steeply as possible, and (ii) the energy required for burrow maintenance, by constructing an entrance run that is shallower than the angle of repose (rest) of dune sand (White, 2001).

Recently, two species of monitor lizards were found to excavate deep, helical burrows for the sole purpose of nesting and the authors discussed the fit of some post-construction (adaptive) hypotheses for the function of the helix in these lizards (Doody et al., 2014, 2015, 2018a, b, 2021). The communal nests of the yellow-spotted monitor (*Varanus panoptes*) and Gould’s monitor (*V. gouldii*) are by far the deepest extant vertebrate ground nests known (averaging 2–3 m deep and reaching 4 m deep). The burrows are soil-filled, and consist of an incline to a depth > 1m, followed by 2–7 tight descending spirals that terminate in a slightly enlarged nest chamber (Fig.1a,b). Mothers excavate the burrows, lay their eggs, and then abandon the burrows. Unlike scorpions, the lizards do not transport the soil out from the burrows—they remain soil-filled and the lizards ‘swim’ through the excavated soil after laying eggs. Thus, White’s (2001) calculations and conclusions for scorpions and potentially other animals do not apply to the lizards. Although a few of the post-construction hypotheses might apply to the lizard burrows (e.g., the helix potentially reducing egg predation), ‘construction’ benefits may provide a more parsimonious explanation than ‘post-construction’ benefits; e.g., the helix preventing soil from falling back into the burrow as it’s removed; falling soil might make burrow creation impossible or extremely difficult in a steep and straight inclined burrow.

Herein we generate and review the major ‘construction’ and ‘post-construction’ hypotheses for why animals evolve the extended phenotype of helical burrows. We address 10 hypotheses including those extracted from the literature and our own. We ask if any of the hypotheses could be general for all taxa. If not, we ask the opposite question: Why did helical burrowing evolve for different reasons in different taxa? To address these two overarching questions, we examined the fit of each hypothesis to each of 21 taxa representing 77–188 spp., based on natural history, behavior, and deductive reasoning, from published sources. We outline potential future tests of hypotheses for selected taxa.

## Materials and Methods

We surveyed the scientific literature for evidence of helical burrows in invertebrates and vertebrates using two-way searches on Google Scholar and Google (general web search). We excluded species for which there was only one (or less) spiral turn (e.g., Linsenmair, 1967; Basan and Frey, 1977; Hembree, 2009; Carvalho and Baucon, 2010; Kinlaw and Grasmueck, 2012; Hembree, 2014; Mikus and Uchman, 2013; Vazirianzadeh et al., 2017; Paul et al., 2019). We also excluded studies describing burrows that were weakly helical, weakly sinusoidal or ‘loosely spiraling’ (e.g., Finlayson 1935 in Johnson, 1989; Koch, 1978; Coelho et al., 2000; Kinlaw and Grasmueck, 2012). Although there is likely a continuum of sinuosity, we found a somewhat dichotomous grouping of burrows that were slightly curved vs. repeatedly or regularly spiral or helical. We thus only

included species with burrows described as ‘tortuous’ or ‘possessing regularly descending spiral coils,’ or a ‘helix’ (e.g., Powell, 1977; Koch, 1978). Although the behavior of constructing weakly helical burrows could be important in understanding the evolution of helical burrowing behavior (indeed *Urodacus* scorpions do both), the number of taxa exhibiting weakly spiral burrowing are too numerous to consider here. Moreover, the degree of burrow sinuosity has not been quantified for most taxa, making interspecific comparisons difficult. We included papers on both extant and extinct helical burrows produced by animals, although the producers of helical burrows—trace fossils reported as ichnotaxa or described in open nomenclature—in the fossil record are often unknown. For trace fossils, several tracemakers from different species as well as different phyla can produce a similar type of trace fossil morphology (ichnotaxon), for example *Daimonelix* (Raisanen and Hasiotis, 2018). Thus, our data rows in Table 1 often reflected more than one species. We also do not consider burrows that occurred in one horizontal plane, including sinusoidal traces (e.g., *Sinusichnus* ; Belaústegui et al., 2014; Soares et al., 2020) and the spiral feeding traces that occur in soft sediment in one surface plane (e.g., the polychaete *Paraonis fulgens* ; Risk and Tunnicliffe, 1978).

We compiled hypotheses offered for the function of the helix, against which we could assign the likelihood that the hypothesis fit a particular taxon or ichnotaxon. For this we used ‘possible’, ‘not likely’ or ‘n/a’ (not applicable); ‘n/a’ indicated that there was virtually no chance of a fit, based on deductive reasoning. For example, the hatchling escape hypothesis developed for lizards, which proposes that the helix loosens the soil to facilitate hatchlings escaping the burrow through meters of resistant soil, would not be applicable to aquatic species with open burrows. We subjectively assigned ‘not likely’ if a good fit was unlikely, and we explained our reasoning in the text. Unlike with ‘n/a’, ‘not likely’ could change with the addition of new information or if our reasoning or that of others, was less informed. The assignment of ‘possible’ indicated a good fit or potential fit, based on the available evidence, context, and our reasoning or that of other authors. In many cases, however, designation of ‘possible’ reflects that difficulty in testing hypotheses—for example, directly testing the antipredator hypothesis for most extinct species is not possible. Thus, we could not conclusively claim that a hypothesis was general even if it scored ‘100% possible’ for all taxa. However, by eliminating some taxa for each hypothesis (by assigning ‘n/a or ‘not likely’) we could potentially conclude that some or all of the hypotheses *could* be general for all taxa.

## Results

Table 1 shows the results of the fit of hypotheses for the function of helical burrows to 21 taxa representing 59–184 species. The wide range in the potential number of species reflects both our lack of knowledge of the burrow types in extant and extinct conspecifics and the uncertainty of the species richness of ichnotaxa.

Of the 10 hypotheses, six are post-construction hypotheses and four are construction hypotheses. Of the 21 taxa, 12 (57%) are extant, eight (38%) are ichnotaxa and one includes both (5%; Table 1).

Two of the hypotheses, antipredator and biomechanical advantage, were designated as ‘possible’ for all taxa (score of 100%; Table 1). Other high-scoring hypotheses were the anticrowding (95%), vertical patch (95%), falling sediment (soil) (95%), and microclimate buffer hypotheses (86%). Two hypotheses, deposit feeding and increase drainage, received moderate scores (both 48%), mainly due to the fit of each to only terrestrial or only aquatic animals (Table 1). The remaining two hypotheses, microbial farming and offspring escape, received low scores (24% and 5%, respectively).

Although the hypothesis sample sizes precluded statistical comparison, the mean score for construction hypotheses ( $91.5 \pm 2.99\%$  SE;  $N=4$ ) was higher than the mean score for post-construction hypotheses ( $49.3 \pm 14.06\%$  SE;  $N=6$ ).

## Discussion

Our review revealed that six of the 10 hypotheses for why animal construct helical burrows could not be confidently rejected for most of the taxa (86–100% possible; Table 1). These hypotheses range from ‘indirectly testable’ (falling sediment, vertical patch, biomechanical) to ‘extremely difficult or impossible to test’ (antipredator, anticrowding). Interestingly, four of those six hypotheses are ‘construction’ hypotheses,

raising the possibility that helical burrowing could save on energy costs associated with constructing a helix without implicating post-construction adaptive benefits. Our analysis also eliminated some hypotheses as general explanations for the behavior; hypotheses involving increased drainage, deposit feeding, microbial farming, and hatchling escape could not explain helical burrowing behavior in the majority of the animals (5–48%, Table 1). The function and evolution of the helix as an extended phenotype remain unknown but would seem, in some cases, to provide different advantages for different taxa. In the following sections we discuss the fit of each hypothesis to selected taxa.

#### 4.1. Post-construction hypotheses

##### 4.1.1. Antipredator hypothesis

Perhaps the most obvious reason to construct a more complex, helical burrow is to reduce the threat of predation of the inhabitant(s) (Martin, 1994; Doody et al., 2015). Accordingly, we could not rule out this explanation for helical burrows of any species (Table 1). Any burrow refuge could decrease predation, but a spiral could slow or confuse a predator in pursuit of the inhabitant as it attempts to escape down the burrow. The helical burrow could also, depending on size and mobility of the predator, prohibit the predator from reaching the inhabitant, its eggs, or offspring. For example, the helical burrows of the pocket gopher *Geomys pinetis* may slow down or confuse predators such as weasels or snakes (Brown and Hickman, 1973). Myer (1999), however, noted that while predators that could fit into *Palaeocaster* burrows may have been too long and/or not flexible enough to follow the beavers down into the tight helix, snakes and weasels could easily access helical burrows, and such predator fossils as *Zodiolestes daimonelixensis* (a prehistoric weasel) have been found in *Palaeocaster* burrows (Martin, 1989; 1994). Elsewhere, helical burrows have been speculated to help thwart monitor lizard and fish predators of scorpions (*Urodacus*) and shrimp (*Axianassa*), respectively (Koch, 1978; Felder, 2001). According to Adams et al. (2016), the cost of predator excavation may increase disproportionately the deeper and more tortuous the burrow, as sand caves in and the tunnel becomes increasingly harder to follow.

In the case of monitor lizards (*Varanus panoptes* and *V. gouldii*) that construct helical burrows solely to lay eggs, the helix could thwart egg predators. In support of predator exclusion geometry, monitor helical burrows are very tight and regular. No egg predators have been identified for these lizards, but the most likely predator would be conspecific males (Doody et al., 2015). The monitor eggs at the burrow terminus would be difficult to detect and reach by any predator because the burrows are 2–4 m deep and soil-filled (Doody et al., 2015; 2018a, b; 2020), but perhaps the addition of a helix would further frustrate a predatory monitor lizard. Alternatively, Doody et al. (2015) speculated that perhaps the helix in monitor lizards evolved as a deterrent to a now-extinct predator, such as *Thylacinus* or *Megalanina* (Clode, 2009).

There is no real evidence for an antipredator function of helical burrows, but testing this hypothesis would be difficult for most species, especially *in situ*, and not possible for ichnotaxa with no modern homologs. In the monitor lizards, field experiments comparing nest predation rates between natural nests and artificial nests without a helix could be a useful indirect test, as could creating baited, artificial helical burrows to see if (marauding) male monitor lizards could navigate the burrows.

##### 4.1.2. Microclimate buffer hypothesis

An often-cited potential function of helical burrows is to buffer the burrow microclimate from the outside environment; microclimate factors discussed include temperature, humidity, and salinity. Indeed, in our review, the hypothesis could not be rejected for most taxa (86%, Table 1). Koch (1978) showed that scorpion (*Urodacus*) species in more open areas in more arid parts of Australia construct deeper burrows with more spirals than those that construct burrows under cover objects in more mesic areas, concluding “It is clear that deep spiral burrow construction has evolved as an adaptation for the avoidance of harsh surface conditions, and has enabled species of the genus *Urodacusto* spread to otherwise inhospitable arid environments.” While animals constructing deeper burrows in more arid environments to buffer against extreme temperatures and low humidity is logical—Koch successfully leverages the literature on arthropods in this argument—this apparent relationship does not necessarily have a direct bearing on the presence of, or number of spirals in,

a helix, which may simply be a correlate of depth, without implicating microclimate buffering.

The ichnogenus *Daimonelix* has been interpreted as multi-purpose burrows (i.e., polychresichnia; Hasiotis, 2003) in which the helix functions to buffer inhabitants from surface extremes. Noting the seasonally hot and dry paleoclimate inhabited by *Palaeocaster*, the Miocene terrestrial beaver tracemaker of some *Daimonelix*, Martin and Bennett (1977) proposed that the helix would contribute to keeping burrow humidity high. Myer (1999), after calculating the comparative volumes and surface areas of helical vs. straight burrows, concluded that the *Daimonelix* helical design would have resulted in a more consistent temperature and humidity when extreme variations were experienced at the surface. In support, Smith (1987, 1993, see also Smith et al., 2021) hypothesized that the helical burrows of *Diictodon*, a mammal-like therapsid from the Permian of South Africa and another *Daimonelix* tracemaker, offered climate control (cool, moist conditions) during extremely hot and dry atmospheric conditions; limited air flow of the helix would allow the humidity of the terminal chamber to rise, especially if near the water table. *Daimonelix* burrows in Triassic (therapsids) and Jurassic (mammals) continental deposits also occur in floodplain and alluvial plain settings formed under megamonsoonal and tropical wet-dry climates, respectively (Fischer and Hasiotis, 2018; Raisanen and Hasiotis, 2018). Thus, the hypotheses of microclimate mediation and predator avoidance would apply to these Mesozoic burrows as well.

According to Adams et al. (2016), Koch's (1978) assertion that scorpion burrows are more helical and deeper in more arid areas is supported by exposure to more wind and eddies in a turbulent boundary layer on plains and sand dunes (Stull, 1988; Turner and Pinshaw, 2015) and higher rates of water loss in burrowing scorpions than in non-burrowing species (Gefen and Ar, 2004). Scorpions typically have very low rates of evaporative water loss through their cuticle, however (Hadley 1970, 1990; Toolson and Hadley 1977). Thus, helical burrows as an adaptation to sustain high relative humidity, thereby reducing the evaporative water loss of scorpion inhabitants, is plausible.

Interestingly, deep and shallow helical scorpion burrows were found to occur together in the same area in central Australia (Hasiotis and Bourke, 2006; Hembree and Hasiotis, 2006). This association indicates that there may be other factors at work, such as: (1) the occurrence of different species with slightly different burrow morphologies; or (2) ontogenetic variation in burrow size, with older and larger scorpions having larger diameter, deeper, and more levels of helices in the burrow. Also, perhaps, the orientation of the dune slope on which the burrow is constructed may play a role in the burrow depth, with deeper burrows on north-facing slopes because of the greater amount of solar insolation.

Some monitor lizards (*Varanus*) construct helical burrows solely for nesting; the 2–4 m deep burrows are unique among helical burrows in that they are soil-filled (Doody et al., 2014, 2015, 2018a, b, 2021). This places some doubt on microclimate buffering as an explanation for helical burrowing in the lizards (Doody et al., 2015). If climate control is the chief function of the helix, why add soil to the helix, or why not construct a soil-filled straight burrow? The answer is not clear. Since the soil-filled monitor burrows are not inhabited by the lizards themselves, the removal of soil would not be considered when calculating the relative costs of straight vs. helical burrows. Most other nesting monitor lizards construct shallower (<0.5 m deep) burrows in which they remove and then back-fill the soil (Pianka and King, 2004); thus, the habit of leaving the soil in the burrow exhibited by the deep-helical-nesting monitor lizards would likely be a derived behavior. Although the deep-nesting, helical burrowing monitor lizards do remove soil from the first ~0.5 m of the burrow length, the remaining soil is not removed. Although it is possible that monitor lizards evolved helical burrow construction in response to dry conditions, and then subsequently evolved leaving the soil in the burrow to further insulate it or to thwart predators, this sequence of evolutionary events is less parsimonious.

The aquatic helical burrows of the ichnogenus *Gyrolithes*, constructed from the Permian to the present-day, have been interpreted as a refuge from extreme salinity fluctuations in transitional environments between the continental and marine realms (Beynon and Pemberton, 1992; Buatois et al., 2005; Netto et al., 2007; Hasiotis et al., 2013). Theoretically, the effect of salinity fluctuations would be diminished because fine sediment of infaunal habitats slows down the exchange of pore water (Rhoads, 1975; Saunders et al., 1965). This

hypothesis was based on the idea that *Gyrolithes* was restricted to shallow marine environments (Gernant, 1972). However, some (e.g., all Cambrian) *Gyrolithes* are found in open-marine environments, which is suggestive of normal salinity conditions, shedding considerable doubt on salinity buffering as the primary function of the helix (Netto et al., 2007; de Gibert et al., 2012; Laing et al., 2018). Moosavizadeh and Knaust (2021) similarly questioned the modulation of salinity as the principal function of *Gyrolithes* due to their apparent high-salinity paleoenvironments. Similarly, *Lapispira* has been found in fully marine deposits (Lanes et al., 2008), shedding doubt on the salinity buffering hypothesis for that ichnotaxon (de Gibert et al., 2012).

There are several important caveats to consider when interpreting behavior and purpose of burrow construction. One of the basic principals in ichnology is that any one particular burrow architecture—in this case, helical burrow *Gyrolithes*—can be used under different conditions for different purposes (e.g., Ekdale et al., 1984; Bromley, 1996). Some *Gyrolithes* occur in the transitional zone where salinities vary between marine, brackish, and fresh water, whereas others occur in normal marine settings. There are also helical burrows assigned to *Gyrolithes* that reflect parts of larger burrow systems, such as *Ophiomorpha* and *Thalassinoides* (Mayoral and Muñiz, 1995, 1998; Dworschak and Rordrigues, 1997). The occurrence of *Gyrolithes* has been attributed to brackish water conditions but not necessarily extreme in fluctuations, but more like mesohaline or polyhaline salinities. For example, Jackson et al. (2016) and Oligmueller and Hasiotis (2022) described *Gyrolithes* from Lower Permian river-dominated delta deposits in Antarctica and Upper Cretaceous intertidal deposits in Colorado (USA), respectively. Both of these occurrences are in the transitional zone where salinity fluctuations were a daily phenomenon. Perhaps the helical burrow was a way for the constructor to limit the amount of water in the burrow exchanged with the flow and mixing of freshwater with marine water or the changing tides. Also, the helical structure of *Gyrolithes* might have been an advantage to the constructor so as not to be hydrodynamically removed from the burrow by changing water currents, or as predator avoidance as the tracemaker withdraws itself into the burrow.

Evidence for the microclimate buffering hypothesis is indirect at best for most taxa. In particular, the unique soil-filled burrows of the monitor lizards raises doubts. Addressing this hypothesis requires understanding which extended phenotype evolved first—the helix or the soil-filled aspect of the burrow. The two known helical-burrowing monitor lizards are sister taxa, and most other species construct simple, inclined soil-filled nesting burrows (Pianka and King, 2008). The ancestral burrow morphology for the helical nesters is thus soil-filled (back-filling or leaving the soil in place). The helical burrows are also extremely deep (Doody et al., 2014, 2015, 2018a, b, 2021)—another derived trait. The most parsimonious evolutionary sequence of burrow construction for the deep-nesting monitor lizards is thus, soil-filled first, deep next, and then the helix. Why construct a helix when the deep, plugged burrow would already provide buffering between the burrow and the outside environment? The hypothesis appears to be a poor fit to the monitor lizards.

#### *Increased drainage hypothesis*

A third hypothesis for helical burrows in terrestrial taxa proposes that the helix provides improved drainage in flood conditions via increased surface area, thereby preventing or reducing burrow flooding that could, for example, cause mortality or expulsion of scorpions or failure of lizard eggs (Koch, 1978; Doody et al., 2015). This explanation was rejected for a majority of taxa (possible in 48% of taxa, Table 1). Koch (1978) proposed that the extensive spiraling of *Urodacusscorpion* burrows would reduce the effect of sheet flooding during the wet season. This idea may be supported by seasonal flash flooding apparently experienced by *Diictodon* (the constructor of *Daimonelix*; King, 1996), although this hypothesis was not explicitly discussed (Smith, 1987; Smith et al., 2021). Indeed, somewhat ironically, the taphonomy of helical burrows relies on flooding in alluvial environments (e.g., Smith et al., 2021).

Although the helix itself may not be beneficial for drainage after flooding, the upturned terminal chambers on many of the Miocene and some of the Jurassic *Daimonelix* burrows (Martin and Bennett, 1977; Raisanen and Hasiotis, 2018) have been thought to trap air in the burrow chamber so that during flooding, the burrower would not drown in its burrow (Hasiotis et al., 2004).

Nesting in both *V. panoptes* and *V. gouldii* in northern Australia is during the late wet season and early

dry season, and there can be substantial rainfall including ‘sheet’ flooding during the first two months of incubation for the earlier nests (Australia Bureau of Meteorology). Although the lizard burrows are soil-filled, the soil is somewhat loose early in incubation. The loose soil combined with the increased surface area of the helix could improve drainage above the nest thereby preventing egg inundation, or reducing the amount of time eggs are inundated. Lizard eggs can withstand inundation for up to six hours based on previous experiments (Heger and Fox, 1992; Losos et al., 2003).

#### *Deposit-feeding hypothesis*

Some marine forms such as *Gyrolithes* (e.g., Dworschak and Rodriguez, 1997; Pervesler and Hohenegger, 2006; Carvalho and Baucon, 2010) may construct helical burrows for deposit feeding in shallow to deep-water marine settings. Specifically, the increased surface area of the helix compared to a straight burrow would enhance deposit feeding by optimizing the utilization of nutrients in a given sediment volume in animals, such as shrimp, polychaetes, and other vermiform animals. For example, the helices found in the burrows of the thalassinid shrimp *Axiانassa australis* may allow the animals to burrow to greater depths with gentle slopes in order to exploit deeper sediment layers rich in organic matter (Dworschak and Rodriguez, 1997; see also Atkinson and Nash, 1990; Nickell and Atkinson, 1995 for similar conclusions for the shrimp *Callianassa subterranea*). Although deposit feeding in *A. australis* burrows needs confirmation, the poor fit of the diameter of the shrimp to the burrow diameter suggests deposit feeding, because suspension feeders tend to fit closely into their burrows (Dworschak and Pervesler, 1997; see also Pervesler and Dworschak, 1985); a close fit is necessary for effective ventilation of the burrow for respiration and feeding in suspension feeders (Dworschak, 1981, 1987). Wetzal et al. (2010) considered deposit feeding as likely in *Gyrolithes*, partly based on the finding of an abundance of plant material in the vicinity of the burrows (Dworschak and Rodriguez, 1997). Laing et al. (2018), however, considered deposit feeding unlikely in *Gyrolithes*, whether made by polychaetes or decapod crustaceans, based on the lack of evidence of active infill or fecal pellets. However, the presence or absence of backfill menisci and/or fecal pellets are not necessary to determine if a burrow is used for deposit-feeding. There are many callianassid and thalassinid shrimp that produce fecal pellets while in their burrows and either used them to construct burrow walls or expel them from the burrow by recirculating the water (e.g., Kennedy et al., 1969; Curran and Seike, 2016; Netto et al., 2017).

Helical burrows in terrestrial animals are likely not involved in feeding, based on the lack of food resources deep in the ground (with the exception of roots and tubers, which are shallow and close to the surface), and based on the lack of frequent branching and fecal fillings (Toots, 1963). The common mole rat does construct complex, shallow burrows to feed on roots and tubers, but apparently does not construct helical burrows (e.g., Spinks et al., 2000). Analogous burrow morphologies to these modern burrowers have been found in Lower Jurassic continental erg deposits of the Navajo Sandstone in Utah (Riese et al., 2011).

#### *4.1.5. Microbial farming hypothesis*

In a variation of the deposit feeding hypothesis, marine burrowers have been hypothesized to create a helix to optimize feeding by increasing the sediment-to-burrow ratio; this is referred to as microbial farming or gardening (Felder, 2001; Moosavizadeh & Knaust, 2001; Netto et al., 2007). Netto et al (2007) argued that Permian *Gyrolithes* were created by crustaceans (rather than by polychaetes, as proposed by Powell, 1977; see also Gingras et al., 2008), possibly implicating microbial feeding since the Paleozoic. Moosavizadeh & Knaust (2021) considered microbial farming as the most likely function of *Gyrolithes* from Iran, which occurred in soft, low-energy sediments. Microbial farming has also been hypothesized as a potential function of helical burrows of trace fossil *Helicodromites* in oligotrophic conditions in a well-oxygenated environment (Poschmann, 2015). The possibility of microbial gardening in *Gyrolithes* was discussed by several authors (e.g., Seilacher, 2007; Wetzal et al., 2010); however, the burrow morphology is not a good candidate for such a behavior as it is also part of other burrow systems that are boxwork structures (Mayoral and Muñiz, 1995, 1998; Dworschak and Rodriguez, 1997; Carvalho and Baucon, 2010). Furthermore, microbial farming is indeed a trait of such marine trace fossils as *Chondrites* and *Paleodictyon*, which have much more complex morphologies, like downward and outward dendritic branching patterns and intricate horizontal tubular patterns with vertical tubes (similar in pattern to a chain-linked fence), respectively (Ekdale et al., 1984;

Bromley, 1996). Direct observations in extant marine helical-burrowing species *in situ* or in a laboratory setting are needed to provide indirect support for this hypothesis.

#### 4.1.6. Offspring escape hypothesis

The sole (new) hypothesis involving postnatal parental care proposes that the helix, by loosening the soil above the nest, facilitates hatchling escape of neonate monitor lizards (this hypothesis is new and may not apply to any other taxon). There is little doubt that the soil is less resistant in the excavated helix compared to the surrounding soil, which is often compact and firm. In fact, some helices were filled with very loose soils and in some the core of the helix even collapsed, leaving a cylinder-shaped section filled with loose soil (JSD, pers. obs.). Hatchling emergence or escape burrows were found for both deep-nesting species (Doody et al., 2018a, b). Hatchlings excavated escape burrows nearly straight upwards from the nest 2–4 m to the surface, rather than following their mother’s soil-filled burrow. Such deep nesting would challenge hatchlings to emerge considerable distances through resistant soils. Although emergence burrows were not carefully mapped, at least some of these burrows partly emanated through the helix (JSD, pers. comm.); burrowing through the helix would involve traversing ~1–3 m of softer soil than the surrounding firm soils (given that the helix begins at ~1.2–1.5 m below the surface). In short, the helix increases the probability of escaping by reducing the effort required by hatchlings.

Perhaps in support of this hypothesis, the low clutch size (e.g., 3–8 eggs; Doody et al., 2020) of an animal nesting very deep might indeed select for parental effort for careful nest excavation to facilitate hatchling escape. While most ground-nesting reptiles deposit eggs <30 cm below the surface, these lizards nest 2–4 m deep in firm soils, seemingly requiring considerable energy for a small group of hatchlings to excavate one emergence burrow. In only one of many nests did we observe multiple emergence burrows emanating from the same nest—there were two. The position of the helix directly above the nest supports a useful function, but one could ask why the entire burrow is not a helix (although perhaps loosening the soil for half the emergence distance is enough to facilitate successful excavation and escape). No other species can shed light on this hypothesis because none are known to lay eggs or possess emergence burrows excavated by hatchlings.

The recent finding of fossilized neonate *Diictodon* skeletons with adults in burrows assigned to *Daimonelix* suggest that they could have served as brood chambers; whether *Diictodon* bore live young or laid eggs is still under debate (Smith et al., 2021). Pocket Gopher (*Geomys*) nests have also been found associated with helical burrows (Brown and Hickman, 1973; Wilkins and Roberts, 2007). Although the helix could be associated with brooding or eggs in some species other than monitor lizards, the open *Daimonelix* burrows of *Paleocaster* and *Diictodon* do not support the idea of the helix loosening the soil for neonates as posited by the hatchling escape hypothesis.

Otherwise, there is little support for hatchling escape as a general explanation for helical burrows. This hypothesis could be directly tested by carefully excavating hatchling escape burrows to determine if they typically emanate through the helical portion of the mother’s burrow. If they do, measuring the energetic costs of the hatchling escape through resistant (no helix) soil vs. less-resistant soil (helix) in the laboratory would be ideal. Measuring the energetic cost of the mother’s excavation of a helical nesting burrow would also provide context for understanding any energetic benefit to hatchlings (see Rusli et al., 2016 for a relevant example with sea turtle hatchlings).

### 4.2. Construction hypotheses

#### 4.2.1. Falling soil hypothesis

Burrow structure can reflect the energetic cost of burrowing (Vleck, 1981; White, 2001). A new hypothesis, but partly based on previous observations on helical burrowing in scorpions and evidence from vertical burrows in pocket gophers, is that the spirals may allow the animals to excavate a steep descent without much soil falling back into the burrow during excavation; that is, the spirals would serve to hold much of the newly excavated soil that would otherwise fall back into the burrow terminus as its being removed, preventing

or impeding further excavation.

The first line of evidence supporting this hypothesis is found in the relationship between climate-soil type-soil moisture and burrow depth-number of spirals in scorpions. Scorpions occupying dry climates with sandy dry soils construct deeper burrows with more spirals than those in wetter climates. Polis (1990) hypothesized that by attenuating the burrow angles the spirals would facilitate the vertical movements of scorpions in burrows that are required to be deep enough to reach optimal temperature and humidity. Adams et al. (2016) countered that several species of scorpions construct simple vertical burrows without spirals that descend 70–90° from the horizontal to 15–10 cm deep. This comparison is confounded by soil type and moisture, however. Compared to those in more mesic environments, scorpion burrows in more arid climates are deeper and possess more spirals (references in Adams et al., 2010). For example, burrows of the scorpion *Urodacus yaschenkoi* in loose sandy soil with little clay content were significantly shallower in depth and angle, and with more spirals, compared to those in damp, low-lying areas subject to flooding (Koch, 1977, 1978; Shorthouse and Marple, 1980). Similarly, the deepest scorpion burrows with the most spirals in South Africa were found in soils with high sand content and low content of silt, clay, and organic matter, as well as low soil moisture, compared to scorpion burrows in other areas (Abdel-Nabi et al., 2004).

A second piece of related evidence comes from burrows of the pocket gopher, *Thomomys bottae*, which excavates lateral tunnels running parallel to the surface but must push excavated soil to the surface to clear the burrows. According to Vleck (1981), “*Thomomys* in cohesive soils often dig nearly vertical laterals and have little difficulty pushing lumps of excavated soil out or plugging the lateral afterward (unpublished data). However, in cohesionless sands like those in the study area, pocket gophers’ efficiency in pushing soil declines as slope increases. At steep angles of ascent, much of a load of sand may fall back down the tunnel, increasing the number of trips necessary to push a given amount out. Laboratory observations indicate that *T. bottae* may also have difficulty in plugging the surface openings of vertical tunnels in cohesionless soils. The slope of laterals is probably dictated by soil characteristics and the differential efficiency of pushing soil with changes in slope. Laterals that ascend at shallow angles may be the most efficient solution in sandy soil.”

White (2001) demonstrated that the energetically cheapest method of reaching an appropriate depth is to burrow the shortest possible distance, which would be straight down (a vertical burrow). However, they also noted that burrow structure may not be determined solely by energetic concerns, and constructing a burrow from the surface at 90° may not be possible. The burrow entrance constructed by the scorpion *U. yaschenkoi* is angled at about 25–30° (Koch 1978; Shorthouse and Marples 1980), only marginally shallower than the angle of repose of dune sand (32°: Robinson and Seely 1980). Thus, if burrows were constructed at angles > 32°, sand would fall into, and fill the burrow (White, 2001). Beyond the entrance run, the burrows begin to spiral and descend steeply, as the soil becomes moister and more cohesive with increasing depth. Burrows constructed by *U. yaschenkoi*, thus, minimize both the energy used during burrow construction by descending as steeply as possible, and the energy required for burrow maintenance by constructing an entrance run that is shallower than the angle of repose of dune sand (White, 2001).

As with scorpions, helical burrows of deep-nesting monitor lizards also exhibit a straight, gently sloping entrance run followed by a deeply descending helix (Doody et al., 2015; 2018). The major difference is that the lizard burrows are soil-filled—the soil is not removed during construction. Thus, White’s (2001) calculations of energy expended moving soil out of the burrow would not apply to the lizard burrows because the lizards do not remove the soil (except for the first ~0.5 m straight run). This focuses attention on the digging action by asking: why not excavate straight down or straight at a steep angle of incline? The answer may lie in the ability of the spiral, combined with the lizard’s body, in preventing loose, excavated soil from falling back into the burrow terminus. Resisting the effects of gravity by repeatedly removing falling soil would not only incur extra costs, but could prohibit burrow construction.

Meyer (1999) used volumetric calculations to conclude that a helix would cost 36–61% more effort than a straight burrow. We do not challenge the calculations or logic used by Meyer (1999); rather, we note that those calculations did not consider the cost of repeatedly moving the same soil that falls into the (shifting) burrow terminus during construction. Thus, the need for constructing deep burrows—which apparently evolved to

provide moist conditions during the long dry season incubation period in *Varanus* lizards (see Doody et al., 2015, 2018)—may have ‘prompted’ helical construction to reduce the energetic cost of repeatedly removing falling soil, or the falling soil could have prohibited construction altogether. Another factor to consider is the degree of firmness or cohesiveness of the soil in which *Daimonelix* was excavated. If the burrow walls contain scratch marks (*sensu* Zonneveld et al., 2022), then the sediment was cohesive and much less likely to collapse in on itself. This would limit the amount of effort in moving excavated material as long as the matrix did not collapse in on it. Vertical burrows in stiff or firm, cohesive sediment would also stay open; however, the biomechanics of the organism would determine if a vertical burrow was a constructable and/or livable situation (*c.f.*, Hasiotis and Mitchell, 1993).

Could the falling soil hypothesis explain helical burrows in other animals? The challenge of constructing a burrow vertically while resisting the effects of gravity on both the body and loosened soil could be general. Even in aquatic burrows the excavated soil must be removed upwards against gravity, and a straight vertical shaft could inhibit or prohibit this. Consider the amount of effort an organism expends in maintaining its position in a vertical burrow excavated in soil, 1–5 m deep, with appendages sprawled while excavating or maintaining the burrow and removing the material to the surface. An arthropod (e.g., arachnid, crustacean, or hexapod) with 6, 8, or 10 pairs of appendages could accomplish this feat (e.g., Hasiotis and Mitchell, 1993; Hasiotis et al., 1993). Such burrow construction by a tetrapod would be extremely difficult for carrying material while removing it from the bottom or maintaining its position in the burrow to maintain the burrow walls (Hasiotis et al., 1999).

A gently inclined, long burrow might incur a lower energetic cost to construct depending on the degree of inclination and distance between the burrow entrance and terminus. Soil profiles have surface and subsurface horizons from top to bottom with distinct composition and firmness (e.g., Kraus, 1999; Brady and Weil, 2002). A gently inclined burrow would increase the probability of spending more time within a horizon with similar composition and firmness, whereas a vertical burrow would have a higher probability of passing more quickly through multiple horizons with different composition and firmness. If an inclined burrow passes from a surface horizon that is relatively loose and contains organics (*i.e.*, A horizon) into a subsurface horizon (E, B, or C horizon) that is more cohesive and firmer, than a higher energetic cost might be incurred. The degree of energetic costs depends on the development and thickness of each horizon, which reflects overall soil formation.

The solution to conserve energy expenditure during construction would seem to be a zigzag or switchback pattern which could eventually ‘tighten’ into a helix. However, some marine organisms construct(ed) helical burrows in the horizontal direction (e.g., Dworschak and Rodrigues, 1997; Minter et al., 2008); the falling soil hypothesis is not a good fit as an explanation for helical burrows in these species. Similarly, some helical sections in the burrows of the shrimp *Callianassa bowvier* may be excavated in the upwards direction (Dworschak and Pervesler, 1988).

Some skinks construct a switchback style of burrow that mimics a spiral (Hembree and Hasiotis, 2006). These switchbacks come from the main part of the inclined burrow, which is flattened, elliptical in cross-section, and resembles an upside-down U or reniform-shape (Hasiotis et al., 2004; Hembree and Hasiotis, 2006). A possible function of this switchback structure, which is not visible from the surface of the soil, is to escape the burrow if a predator enters. Likewise, if the hidden switchback burrow opening is discovered, a potential predator might not be able to follow the tortuous path into the main part of the burrow.

Testing the falling soil hypothesis in monitor lizards could involve observing nesting females in a captive situation to determine how well mothers prevent soil from reaching the burrow terminus; alternatively, recreating a helix in the laboratory with a model lizard could shed insights into this ability, as would experiments with humans attempting to construct a helical burrow.

#### 4.2.2. *Anticrowding hypothesis*

Many investigators have mentioned or addressed the possibility that helical burrowing could reduce crowding and subsequent interference that might otherwise occur if there were multiple burrows with straight runs or

ramps within a discreet area (Martin and Bennett, 1977; Koch, 1978; Shorthouse and Marples, 1980; Myer, 1999; Gingras et al., 2008; Adams et al., 2016; Doody et al., 2015). For example, Martin and Bennett (1977) supposed that helical burrows in *Paleocaster* could save horizontal space and avoid neighboring burrows while maintaining a shallow incline, great depth and close packing of burrows. For scorpions, Koch (1978) mentions the avoidance of neighboring burrows under crowded conditions as a possible function, and Shorthouse and Marples (1980) hypothesized that helical burrows might decrease the risk of antagonism or cannibalism by reducing the encounters probability between scorpions from neighboring burrows. When discussing the function of *Gyrolithes*, Gingras et al. (2008) considered it likely that the similar helical burrows of thalassinid shrimps were a response to high population densities.

Myer (1999) used field data from *Paleocaster*-constructed *Daimonelix* to calculate that burrow interference with straight ramps or runs would lead to a low probability of a burrow interfering with another (5–8%). Adams et al. (2016) suggested that this hypothesis leads to the prediction that burrows in dense populations are more spiral than those in sparse populations; yet they noted that hormurid scorpions that construct simple, vertical burrows, occur in similar densities to those constructing burrows with spirals (Harington, 1978). Cambrian *Gyrolithes* examined by Laing et al. (2018) were relatively sparse, which may be due to them being part of larger burrow systems of *Thalassinoides*.

The anticrowding hypothesis is logical and supported by some evidence of high densities of burrows, but is extremely difficult, if not impossible, to directly test. An indirect test would be to characterize burrow types at different densities, but this would assume that the inclusion of spirals is a phenotypically plastic behavior, or that there has been behavioral evolution among populations leading to disparate burrow morphology.

#### 4.2.3. Vertical patch hypothesis

A third new hypothesis reflects potential heterogeneity in media stiffness in the vertical vs. horizontal planes. Each soil horizon tends to be more homogeneous in composition compared to overlying and underlying in a particular area due to the abiotic and biotic processes that form them (Kraus, 1999; Brady and Weil, 2002; Hasiotis, 2007). Overall, there is greater heterogeneity vertically in a soil profile than laterally, where the tendency is for the surface horizon (i.e., A horizon) is looser with a greater amount of organic matter compared to the subsurface horizon (e.g., B horizon), which is the zone of accumulation of clays and other minerals that make it firmer and more compact. Thus, deep burrowing in the form of a vertical burrow or tightly helical burrow will incur a higher energetic cost to construct the burrow. However, this cost is offset with the benefit of (1) greater relative humidity and soil moisture (microclimate amelioration) combined with (2) greater soil density (firmness and consistency) to ensure a lower chance of soil collapse (i.e., escape of hatchlings) that also doubles as better burrow construction in that sediment-filled burrows result in predator avoidance.

In the case that shallower optimal or suitable sediment layers predict similar layers directly below, it could benefit creators to construct helical burrows once those shallower sediment conditions have been discovered, rather than chance burrowing into suboptimal or unsuitable conditions by excavating angular burrows. Relevant conditions could be sediment or soil friability, hardness, or some biotic factor such related to food or farming. In the case of deposit feeding or microbial farming here could be post-construction benefits (see details for those hypotheses). With the monitor lizards, most nesting areas are communal and traditional, possibly due to the reduction in excavating costs associated with constructing burrows in soil already loosed by conspecifics (Doody et al., 2015; 2018).

#### 4.2.4. Biomechanical advantage

A fourth new hypothesis for helical burrows relates to biomechanical advantage. As a burrower excavates, it may be better able, leverage-wise, to remove or rework sediment (soil) with a lateral (side) stroke that results in the burrow bending left or right. This could result in a savings in energy or better efficiency in excavation that could offset the increased effort required, mathematically, to excavate a helical burrow rather than a straight burrow (as calculated by Meyer, 1999 for *Palaecaster* constructing *Daimonelix*; but see previous section on falling soil hypothesis). This pattern would also result in easier removal of excavated material

from the burrow for many tetrapods and arthropods. Also, helical burrowing in stiffer, more cohesive media (sediment, soil) appears to be a tendency observed by one of us (STH) in during burrow construction by spiders and crayfish (also see Hasiotis and Bourke, 2006). Such a result might also be expected for tetrapods that construct helical burrows in stiff or firm, cohesive soils (also see Hembree and Hasiotis, 2006; Riese et al., 2011).

There is currently no evidence for this hypothesis in any taxon. However, Monod et al. (2013) hypothesized that different burrow architecture between taxonomic groups of scorpions was due to behaviors related to morphology: fossorial hormurids are pedipalp burrowers that use the large, often rounded pedipalpal chelae to loosen the soil and carry it out of the burrow, whereas the closely related scorpionoid families are cheliceral burrowers that use their enlarged chelicerae to loosen the soil and then scrape it out of the burrow using the legs and/or metasoma (see references in Monod et al., 2013). Barrass (1963) found the direction of the spiral was related to the asymmetry of the crab's claws such that the males with the major claw on the right exit from the burrows spiralling counterclockwise, and vice-versa.

Testing the biomechanical hypothesis would minimally require observing the digging strokes and understanding the biomechanics of burrow excavation and preferably involve a comparison of energy required and the efficiency of strokes that would create helical vs. straight burrows. Toots (1963) provided an insightful treatment of the fundamental biomechanical requirements of helical burrow construction by considering the need for asymmetrical digging along the horizontal axis and geotaxis and transverse gravity orientation (Toots, 1963). This represents a good starting point for exploring the biomechanical underpinnings of constructing a helical burrow, which may provide insights into energetics and construction costs-benefits.

#### 4.2.5. Additional hypotheses

There were a few hypotheses mentioned in the literature that warranted less attention based on their obvious lack of support or generality. Koch (1978) proposed that extensive spiraling in scorpion burrows could reduce the effects of wind-blown debris entering the burrow. This is logical, but scorpions and other terrestrial animals often clear their burrows of debris including blown sand, cave-in sand and vegetation (Shorthouse and Marples, 1980). Spiral burrows produced by marine organisms may help keep the burrow free of sediment debris. Another hypothesis, raised for *Gyrolithes*, suggests that the helical burrow promotes anchoring of the tracemaker in the burrow in a high-energy environment (Gingras et al., 2008; see also Laing et al., 2018). However, the *Gyrolithes* studied by Moosavizadeh and Knaust (2021) reflected a low-energy environment. Finally, some male ghost crabs (*Ocyopde*) may construct spiral burrows for courtship (Schober & Christy, 1993; Clayton, 2005). However, only one species has been shown to construct burrows with more than one spiral: at least some of the burrows of *Ocyopde ceratophthalmus* exhibit two spirals (Parenzan, 1931, in: Eshky, 1985; Fellows, 1966, in: Vannini, 1980). Some authors have included the hypothesis that helical burrows serve(d) as domiciles (domichnia) that protect the burrows inhabitants (e.g., Laing et al., 2018). We did not consider this hypothesis because it cannot in itself explain the evolution, benefits, or function of helical structure above and beyond what the aforementioned hypotheses (e.g., antipredator) attempt to explain.

#### 4.3. Potential evolutionary sequence of deep, helical burrowing behavior in some monitor lizards

We can reconstruct the putative evolution of nesting behavior in these species using the discussions in previous sections. Large monitor lizards that lay large eggs that require long incubation periods (6–9 months; Horn and Visser 1989; 1997) that must stretch over dry seasons in species inhabiting arid areas, at least in Australia (Doody et al., 2015; 2018). These species have evolved the behavior of nesting much deeper than any other reptile (Doody et al., 2014; 2015; 2018). The cheapest way, energetically, *with regards to distance only*, for a monitor lizard to nest 2, 3, or 4 m deep is to construct a vertical tunnel straight below the site they have chosen (White, 2001, referring to scorpions). However, a lizard cannot excavate a burrow straight down because the soil continues to fall in on itself. For the lizard to remove the soil from the burrow once they are deeper than 1 m is effectively impossible because the soil would need to be thrown upwards out of the burrow a considerable distance with efficiency. To our knowledge, monitor lizards cannot carry or transport

soil other than kicking or dragging it on the surface with their limbs, head, and neck. So, a deep, straight vertical burrow is physically impossible because the creator could not get the loose soil out of the way to allow continued burrow construction.

A physically manageable but more energetically expensive (distance-wise) approach would be to excavate an inclined (straight) burrow run at an angle that would prevent soil from falling back down once loosened. The mean incline for *V. panoptes* entrance burrows was 8° (Doody et al., 2015). If the burrow is to be 3 m deep, with an angle of 8°, solving for the opposite side of a right triangle yields a horizontal distance of the nest from the burrow entrance of 19 m (13 m if 2 m deep, 26 m if 4 m deep). This is a considerable distance from where the mother selected a suitable patch of soil, creating risk that she might encounter more resistant soils that would be more costly to burrow through. In support, both *V. panoptes* and *V. gouldii* nest communally and traditionally, apparently taking advantage of soil loosened by conspecifics by nesting in a discreet area of soil that is softer than the surrounding area (Doody et al., 2015). Increasing the angle of incline (steeper) would decrease the horizontal distance of the nest from the burrow entrance, but at some point, the incline allows soil to fall back into the burrow. As noted earlier, continually removing soil that is falling back into the burrow is energetically expensive and probably impossible at depths greater than one meter. This cost could be large enough to offset or even outweigh the cost of constructing a helix (calculated by Myer, 1999). Steeper inclines would at some point be prohibitive (as with the vertical burrow above).

The possible solution was the construction of a helix, which is physically manageable, and possibly energetically equivalent or superior to a straight incline and would bring the creator straight down into the intended nesting area with loosened soil. Perhaps there were intermediates that resembled a zigzag or switchback pattern; these could eventually ‘tighten’ into a helix. Stopping the falling soil might be especially needed useful for monitor lizards because they do not remove the soil from the burrow, except for the first 0.5 m of the entrance run.

## Conclusions

Our near-exhaustive review was the first to consider all taxa when addressing the evolution and function of, and costs and benefits to, helical burrowing in animals. Our examination of the fit of 10 hypotheses to numerous living and extinct taxa failed to find compelling evidence for one general hypothesis for why animals construct helical burrows. Only two hypotheses—antipredator and biomechanical advantage—could not be rejected for any species, although six of the hypotheses could not be rejected for most species (possible in 86–100 % of *spp.*). Thus, one or more of these could explain the behavior of helical burrowing in most species. Four of these six were construction hypotheses, raising the possibility that helical burrowing might have evolved without providing post-construction benefits. Our analysis did eliminate four hypotheses - increased drainage, deposit feeding, microbial farming, and offspring escape - as explanations for helical burrowing behavior in the majority of taxa (possible in 5–48% of *spp.*). The extended phenotype of helical burrowing may have evolved for a diversity of reasons. Further observations of helical burrowing in different biotic and abiotic contexts, and in particular, experiments, could in some cases eliminate or provide support for some of the hypotheses, while other hypotheses are difficult to test, or not directly testable.

## Tables

See attached file.

## Figures

See attached file.

## Data Accessibility

All data are contained within this manuscript and its associated tables.

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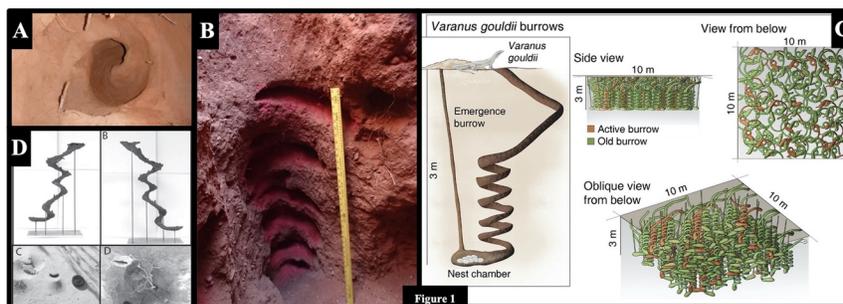


Fig. 1. Helical burrows in extant taxa. (A) Top-down view of a *Varanus panoptes* nesting burrow from Australia (J. S. Doody). (B) Side view of a *Varanus gouldii* nesting burrow from Australia (J. S. Doody). (C) Diagram depicting *Varanus gouldii* nesting burrows (Doody et al., 2018). (D) Casts of scorpion burrows (top panels) and entrances (bottom panels) from Australia (Hasiotis and Bourke, 2006).

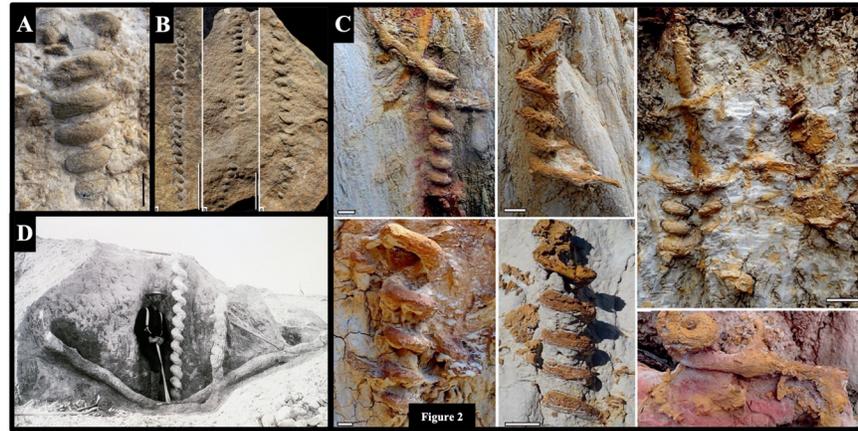


Fig. 2. Helical burrows in extinct taxa. (A) *Gyrolithes* probably created by Crustaceans during the Miocene from the Cacela Formation, Portugal (Cachao et al., 2009). (B) *Helicodromites* probably created by vermiform animals during the Devonian from the Hohenrein and Laubach Formations, Germany (Poschmann 2015). (C) *Gyrolithes* created by shrimp during the Pliocene from the Guadlquivir Basin, Spain (Muniz and Belaustegui, 2019). (D) *Daimonelix* burrows created by *Paleocaster* during the late Oligocene-early Miocene in the Harrison Formation, United States (Martin, 1977; Permission granted to use, see Doody et al., 2015).

## 6. Tables

Table 1. Hypotheses for helical or spiral burrows across 21 extant and extinct genera and ichnogenera representing 59–184 *spp* .

Genus/ Ichnogenus (# spp.)	Post- construction bene- fits	Post- construction bene- fits	Post- construction bene- fits	Post- construction bene- fits	Post- construction bene- fits	Post- construction bene- fits	Construction bene- fits	Construction bene- fits	Construction bene- fits
	Micro- climate Buffer	Increased drainage	Deposit feeding	Microbial farming	Offspring escape	Reduced falling soil	Anti- crowding <sup>y</sup>	Vertical patch <sup>y</sup>	
<i>Anuroctonus</i> (2)	Poss.	Poss.	n/a	n/a	n/a	Poss.	Poss.	Poss.	
<i>Axianassa</i> (13)	Poss.	Poss.	n/a	Poss.	n/a	Poss.	Poss.	Poss.	
<i>Axiopsis</i> (1)	Poss.	Poss.	n/a	Poss.	n/a	Poss.	Poss.	Poss.	
<i>Callianassa</i> (2-47)	Poss.	Poss.	n/a	Poss.	n/a	Poss.	Poss.	Poss.	
<i>Cratogeomys</i> (1)	Poss.	Poss.	unlikely	n/a	n/a	Poss.	Poss.	Poss.	
<i>Cylindrichnus</i> (2)	Poss.	Poss.	n/a	Poss.	Poss.	n/a	Poss.	Poss.	Poss.

	Post- construction bene- fits										
<i>Cynomys</i> <sup>x</sup> (1)	Poss.	Poss.	Poss.	unlikely	n/a	n/a	Poss.	Poss.	Poss.	Poss.	
<i>Daimonelix</i> (2-4)	Poss.	Poss.	Poss.	unlikely	n/a	n/a	Poss.	Poss.	Poss.	Poss.	
<i>Diictodon</i> (1-7)	Poss.	Poss.	Poss.	unlikely	n/a	n/a	Poss.	Poss.	Poss.	Poss.	
<i>Geomys</i> (3)	Poss.	Poss.	Poss.	unlikely	n/a	n/a	Poss.	Poss.	Poss.	Poss.	
<i>Gyrolithes</i> (15)	Poss.	Poss.	n/a	Poss.	Poss.	n/a	Poss.	Poss.	Poss.	Poss.	
<i>Helicodromites</i> (2)	Poss.	unlikely	n/a	Poss.	Poss.	n/a	n/a	unlikely	n/a	n/a	
<i>Lapispira</i> (1)	Poss.	unlikely	n/a	Poss.	Poss.	n/a	Poss.	Poss.	Poss.	Poss.	
<i>Notomastus</i> (1)	Poss.	Poss.	n/a	Poss.	n/a	n/a	Poss.	Poss.	Poss.	Poss.	
<hr/>											
<i>Ocypode</i> (1)		Poss.	Poss.	n/a	Poss.	n/a	n/a	Poss.	Poss.	Poss.	Poss.
<i>Ophiomorpha</i> (1-3)		<b>Poss.</b>	<b>Poss.</b>	<b>n/a</b>	<b>Poss.</b>	<b>Poss.</b>	<b>n/a</b>	<b>Poss.</b>	<b>Poss.</b>	<b>Poss.</b>	<b>Poss.</b>
<i>Opisthophthalmus</i> (1-61)		Poss.	Poss.	Poss.	n/a	n/a	n/a	Poss.	Poss.	Poss.	Poss.
<i>Paleocaster</i> (1-4)		<b>Poss.</b>	<b>Poss.</b>	<b>Poss.</b>	<b>unlikely</b>	<b>n/a</b>	<b>n/a</b>	<b>Poss.</b>	<b>Poss.</b>	<b>Poss.</b>	<b>Poss.</b>
<i>Paruroctonus</i> (1-8)		Poss.	Poss.	Poss.	n/a	n/a	n/a	Poss.	Poss.	Poss.	Poss.
<i>Urodacus</i> (5)		Poss.	Poss.	Poss.	n/a	n/a	n/a	Poss.	Poss.	Poss.	Poss.
<i>Varanus</i> (2)		Poss.	unlikely	unlikely	n/a	n/a	Poss.	Poss.	Poss.	Poss.	Poss.
SCORE:		100%	86%	48%	48%	24%	5%	95%	95%	95%	100%

Table 1. Hypotheses for helical or spiral burrows across 21 extant and extinct genera and ichnogenera representing 59–184 *spp*. (see text for explanation of why there is a range in the number of species). Designations include ‘poss.’ (possible), ‘unlikely’, or ‘n/a’ (not applicable, not possible, or highly unlikely). Scores = the proportion (%) possible for each taxon. <sup>x</sup> = ichnotaxa & modern taxa; y = could also result in post-construction benefits. Data based on deductive reasoning and the following sources: *Anuroctonus* (Williams, 1966); *Axianassa* (Dworschak and Rodriguez, 1997; Felder, 2001; Netto et al., 2007); *Axiopsis* (Dworschak and Ott, 1993); *Callianassa* (Dworschak and Pervesler, 1988; Atkinson and Nash, 1990; James et al., 1990; Nickell and Atkinson, 1995); *Cratogeomys* (Villa, 1989; Roberts et al., 1997; Wilkins and Roberts, 2007); *Cylindrichnus* (de Gibert et al., 2006); *Cynomys* (Wood & Wood, 1933; Schultz, 1942; Ceballos-G and Wilson, 1985); *Daimonelix* (Fischer and Hasiotis, 2018; Raisanen and Hasiotis, 2018); *Diictodon* (Smith, 1987; Smith, 1993; King, 1996; Smith et al., 2021); *Geomys* (Brown and Hickman, 1973; Cameron et al., 1988; Wilkins and Roberts, 2007); *Gyrolithes* (Gernant, 1972; Bromley and Frey, 1974; Powell, 1977; Ekdale et al., 1984; Beynon and Pemberton, 1992; Mayoral and Muñiz, 1995; Bromley, 1996; Dworschak and Rordrigues, 1997; Mayoral and Muñiz, 1998; Buatois et al., 2005; Netto et al., 2007; Wetzal et al., 2010; de Gibert et al., 2012; Hasiotis et al., 2013; Jackson et al., 2016; Laing et al., 2018; Muniz and Belastegui, 2019; Moosavizadeh and Knaust, 2021; Oligmueller and Hasiotis, 2022); *Helicodromites* (Poschmann, 2015); *Lapispira* (Lanes et al., 2007; de Gibert et al., 2012); *Notomastus* (Powell, 1977); *Ocypode* (Parenzan, 1931, in: Eshky, 1985; Fellows, 1966, in: Vannini, 1980; Schober and Christy, 1993; Clayton, 2005); *Ophiomorpha* (Loope and Dingus,

1999; de Gibert et al., 2012); *Opisthophthalmus* (Lamoral, 1978); *Paleocaster* (Martin and Bennett, 1977; Meyer, 1999); *Paruroctonus* (Bradley, 1988); *Urodacus* (Koch, 1977; 1978; Shorthouse and Marples, 1980; White, 2001; Adams et al., 2016); *Varanus* (Doody et al., 2014; Doody et al., 2015; Doody et al., 2018a,b; Doody et al., 2020).

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