Beneath the surface: physiology, behaviour, and performance of fossorial amphibians and reptiles

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Abstract

Fossoriality has evolved recurrently in amphibians and reptiles, exposing organisms to a distinctive physical environment that has favoured diverse morphological, physiological, behavioural, and biomechanical adaptations to enable life beneath the surface. Despite substantial progress over recent decades, research has largely examined these traits

independently, limiting our understanding of how fossorial ectotherms function as integrated organisms. Here, we synthesise current knowledge on the mechanisms underlying fossoriality in amphibians and reptiles, focusing on the interactions among morphology, functional performance, thermoregulation, water balance, respiration, energetics, and seasonal dormancy. We show that physiological and behavioural responses reflect continuous trade-offs among temperature, water availability, respiratory gases, and substrate properties, highlighting the multidimensional nature of the subterranean environment. Likewise, many features commonly associated with fossoriality, including body elongation, limb reduction, cranial reinforcement, and sensory reorganisation, have evolved repeatedly but through lineage-specific combinations of traits rather than a single adaptive syndrome. We argue that understanding fossoriality requires moving beyond descriptive accounts of individual traits towards an integrative framework that connects organismal function with environmental conditions. We identify key knowledge gaps and propose future research priorities centred on comparative studies, experimental approaches that manipulate multiple environmental variables simultaneously, and the integration of empirical data with mechanistic biophysical models. Together, these approaches offer a predictive framework for understanding how fossorial amphibians and reptiles interact with heterogeneous subterranean environments and provide a foundation for a more mechanistic understanding of one of the most remarkable lifestyles among terrestrial vertebrates.

Keywords: burrow, gas exchange, humidity, hydroregulation, locomotor performance, morphology, temperature, thermoregulation

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I. Introduction

Fossoriality has evolved repeatedly and independently across amphibians and reptiles, placing distinct lineages under a common set of environmental and mechanical constraints. Approximately 11% of amphibians and 18% of reptiles spend the majority of their lives beneath the surface (Measey, 2006; Oliveira *et al.*, 2017), making subterranean life a recurrent ecological strategy in these groups (**Figure 1**). Life underground may confer advantages such as protection from predation and shelter from climatic extremes (Scheffers *et al.*, 2014). At the same time, subterranean environments impose constraints on locomotion, sensory perception, gas exchange, and resource acquisition (Abe & Johansen, 1987; de Barros *et al.*, 2021; Giacometti, Moldowan & Tattersall, 2024). As a result, fossorial amphibians and reptiles have evolved suites of morphological, physiological, and behavioural adaptations that mitigate these constraints. For example, fossorial caecilians (Amphibia: Gymnophiona) have respiratory and circulatory properties that favour life in conditions with limited access to the free atmosphere, like an increased reliance on cutaneous respiration and blood with high oxygen affinity (Wood *et al.*, 1975; Smits & Flanagin, 1994). Moreover, amphisbaenians (Squamata: Amphisbaenia) possess highly specialised morphological and muscular traits that aid in burrowing and moving in the

88 subsoil (Navas *et al.*, 2004). These examples underscore the capacity of amphibians and reptiles
89 to persist underground, yet the mechanistic foundations of their success remain only partly
90 understood.

91 Despite the longstanding interest in studying the physiology and behaviour of amphibians
92 and reptiles, research focus has typically concerned species that live aboveground as study
93 systems (Feder & Burggren, 1992; Angilletta, 2009). Consequently, most of the current
94 knowledge available may not be representative of fossorial species. There are at least two non-
95 mutually exclusive reasons for this dearth of knowledge. The first stems from the largely
96 untested assumption that fossorial animals are buffered from climatic fluctuations because the
97 underground conditions they experience are more stable than those aboveground (Kinlaw, 1999).
98 Although such buffering may hold over short timescales (e.g., hours), underground climates vary
99 substantially over longer periods (e.g., months) (Cui *et al.*, 2011; Moldowan, Tattersall &
100 Rollinson, 2022), suggesting that fossorial ectotherms may not be as buffered as assumed and
101 that these species may be subject to selection acting on physiological and behavioural processes.
102 The second reason relates to the innately cryptic nature of fossorial species. Indeed, fossorial
103 amphibians and reptiles spend most of their time underground, with short periods of
104 aboveground activity that are associated with breeding or foraging (Faccio, 2003; Encarnación-
105 Luévano, Rojas-Soto & Sigala-Rodríguez, 2013). Because of this, research into fossorial species
106 has been hampered both by the difficulty of finding individuals in the wild and by the challenges
107 of maintaining them under controlled laboratory conditions. Thus, fossorial ectotherms remain
108 understudied relative to their epigeal counterparts (Henderson *et al.*, 2016).

109 Nonetheless, studies with fossorial amphibians and reptiles exist, although the
110 ecophysiological and behavioural literature remains fragmented (Bars-Closel & Kohlsdorf,

2012). Studies typically focus on individual taxa or specific traits, like morphology (Rieppel, 1984), locomotor performance (Martín *et al.*, 2021b), hydroregulation (Cartledge *et al.*, 2006), or thermal tolerance (Claussen, 1977), rather than combining multiple axes of response (but see Navas *et al.*, 2004; Camacho *et al.*, 2015; Giacometti & Tattersall, 2023). A framework that integrates and compares these perspectives is thus necessary to understand the mechanisms that connect environmental conditions with organismal responses, predict physiological and behavioural outcomes, and infer vulnerability under changing climates (Camacho *et al.*, 2015; Bars-Closel, Camacho & Kohlsdorf, 2018). The main goal of this review is to provide a comprehensive synthesis of the current knowledge of physiological and behavioural responses to a fossorial lifestyle in amphibians and reptiles. We begin our review by outlining the unique ecological opportunities and constraints that fossorial ectotherms face in subterranean habitats. Next, we address the physiological and behavioural strategies that allow survival in underground environments, as well as the morphological syndromes often observed in fossorial species. Then, we discuss theoretical frameworks that can help predict species' responses to environmental change. Finally, we highlight current knowledge gaps and suggest directions for future research aimed at fostering a more integrative and mechanistic understanding of fossorial life.

II. Opportunities and constraints of subterranean environments

(1) The underground as a refuge

The underground environment has repeatedly offered vertebrates a refuge from ecological and climatic disturbances, ultimately promoting the evolution of fossorial lineages that still persist among amphibians, reptiles, and other taxa (Olson & Bolles, 1975). In early

tetrapods, fossoriality likely evolved as a means to avoid predation, desiccation, and thermal stress, offering selective advantages during periods of climatic instability aboveground (Kinlaw, 1999). In extant ectotherms, fossoriality still functions as a defensive and regulatory strategy that reduces exposure to predators and modulates the physiological costs of environmental variation (Wu, Parker & Thompson, 2009; Raya-Garcia, Alvarado-Diaz & Martín Rueda, 2019). This buffering function may also provide protection from acute environmental disturbances such as wildfire (Pilliod *et al.*, 2003). However, the climatic buffering observed in underground environments is neither absolute nor cost-free. Soil temperature, moisture, and gas composition still follow daily and seasonal cycles, all of which also vary with soil depth, soil type, and broader environmental context (Boynton & Compton, 1944; Illston, Basara & Crawford, 2004; Alves & Schmid, 2015). Thus, fossorial species must either continually adjust their physiology and behaviour, or be able to sustain performance across a wide range of changing conditions.

(2) The thermal and hydric landscapes

Temperature and water availability are among the most pervasive environmental variables influencing ectotherms (Feder & Burggren, 1992; Angilletta, 2009), defining both the challenges and opportunities of underground life. The thermal landscape experienced by fossorial species is markedly different from the one experienced by species that live aboveground. The soil acts as a physical buffer, reducing the amplitude of daily thermal fluctuations and mitigating warm and cold extremes (Cui *et al.*, 2011; Scheffers *et al.*, 2014). The extent of thermal buffering, however, depends on both soil depth and composition. Deeper burrows experience small diel temperature fluctuations, but may lag behind surface temperatures over longer timescales, such as seasonal transitions (Moldowan *et al.*, 2022). Soil composition

156 also modulates thermal conductivity, with sandy or dry soils allowing faster heating and cooling
157 than clay-rich or humid soil (Smits *et al.*, 2013; Mu *et al.*, 2019). Moreover, the strength of
158 thermal buffering varies across microhabitats, with surface shading and vegetation cover
159 influencing how heat flows into the subsoil (Alves & Schmid, 2015). As a result, shifts in air
160 temperature may be transmitted underground with a considerable delay, meaning that
161 underground temperatures may peak or trough days or even weeks after those aboveground
162 (Moldowan *et al.*, 2022) (**Figure 2**). From an ecological standpoint, such thermal inertia can
163 decouple surface environmental cues from the physiological or behavioural timing of fossorial
164 organisms, potentially influencing emergence or reproductive phenology (Moldowan *et al.*,
165 2022; Giacometti *et al.*, 2024).

166 These facets demonstrate that underground thermal environments are both temporally and
167 spatially heterogeneous, challenging the longstanding assumption that burrows provide a
168 uniform thermal refuge (Camacho *et al.*, 2015; Forget-Klein & Green, 2021; Moldowan *et al.*,
169 2022). For amphibians and reptiles, whose biology is highly sensitive to temperature (Tattersall
170 *et al.*, 2012), underground thermal variation can impact a variety of biological processes. For
171 example, work in the Fowler's toad (*Anaxyrus fowleri*) demonstrated that individuals responded
172 to daily thermal fluctuations in the soil by adjusting the depth to which they were buried. In
173 doing so, toads maintained body temperatures (T_bs) around 30ºC (**Figure 3**), which possibly
174 facilitated the digestion of food items obtained while foraging aboveground in the previous night
175 (Forget-Klein & Green, 2021). Long-term observations likewise indicate that underground
176 positions are not fixed. Hibernating common toads (*Bufo bufo*) moved vertically in the soil as
177 temperature gradients changed, with individuals occupying different depths over the course of
178 winter (van Gelder *et al.*, 1986). Thus, while the subsoil can buffer short-term thermal extremes,

179 fossorial ectotherms may track temporal changes in underground thermal conditions by adjusting
180 their position within the soil profile.

181 Besides temperature, water availability also has a fundamental influence on fossorial
182 amphibians and reptiles. Relative to the surface, the subsoil generally maintains higher and more
183 stable moisture levels due to reduced evaporation and limited exposure to wind and solar
184 radiation (Hanks, Gardner & Fairbourn, 1967). Because of this, underground environments are
185 also interpreted to provide shelter from desiccation (Rothermel & Luhring, 2005; Martín *et al.*,
186 2025). Similar to temperature, however, this apparent hydric stability masks spatiotemporal
187 variability in soil water content. Indeed, soil water dynamics are driven by complex interactions
188 among precipitation, drainage, evaporation, and capillary action, which in turn vary with soil
189 texture, compaction, organic matter content, and temperature (Hanks *et al.*, 1967; Bittelli, 2011;
190 Li *et al.*, 2024). Within the scope of this review, the relationship between temperature and
191 humidity is of particular importance. Soil water content influences thermal conductivity, such
192 that wetter soils buffer temperature fluctuations more effectively than dry soils (Mu *et al.*, 2019).
193 Conversely, warming increases evaporative demand (Anderson, 1936), and may create sharp,
194 vertical hydric and thermal (hereafter "hydrothermal") gradients in relatively shallow soil (Hanks
195 *et al.*, 1967). These interacting gradients define the hydrothermal niche available to fossorial
196 organisms, which consists of a dynamic axis along which behavioural and physiological
197 regulation must occur.

198 This combination of factors results in an underground hydrothermal mosaic (Hanks *et al.*,
199 1967), suggesting that the thermal and hydric optima of a given species rarely occur at the same
200 depth. Based on this, one may hypothesise that the presence of hydrothermal gradients should
201 drive decision-making with respect to the maintenance of homeostasis, thereby influencing

202 fossorial species to move through the subsoil to seek favourable conditions. A central tenet of
203 this view is that fossorial ectotherms should face a fundamental trade-off between maintaining
204 thermal balance and conserving body water (Giacometti & Tattersall, 2025). However, the drive
205 to conserve body water should be disproportionately greater in fossorial amphibians than
206 reptiles. Amphibians possess highly permeable and vascularised skin and are particularly
207 sensitive to drying conditions, whereas reptiles have evolved keratinised integuments that confer
208 an enhanced resistance to evaporative water loss (Lillywhite, 2006). Preliminary evidence
209 supports this notion: under mild hydric and thermal stress, European toads (*Bufotes viridis*) and
210 Pacific horned frogs (*Ceratophrys stolzmanni*) rapidly sought deeper layers in the soil and
211 decreased emergence to the surface to minimise evaporative water loss (Hoffman & Katz, 1989;
212 Székely *et al.*, 2018). By contrast, simulated drought only caused a transient increase in
213 glucocorticoid levels in the Iberian worm lizard (*Blanus cinereus*) that was mitigated by
214 behavioural selection of soil with favourable water content (Martín *et al.*, 2025). Together, these
215 data suggest that the ability to detect changes in soil temperature and soil water content is
216 integral to burrow-depth selection and to maintain hydrothermal balance.

217

218 *(3) Gas composition and metabolic constraints*

219 The gaseous properties of underground environments impose additional constraints on
220 fossorial ectotherms, influencing their respiratory and metabolic strategies. In burrows, restricted
221 diffusion and low air turnover lead to the progressive depletion of oxygen and the accumulation
222 of carbon dioxide, therefore creating potentially hypoxic and hypercarbic conditions for a
223 resident animal (Withers, 1978; Boutilier, 1990). The detrimental effects of prolonged exposure
224 to hypoxia and hypercarbia are myriad, ranging from changes in thermoregulatory set-points

(Tattersall & Boutilier, 1997; Tattersall & Milsom, 2009) to augmented breathing and respiratory acidosis (Ar, Arieli & Shkolnik, 1977; Jackson, 2007). Importantly, our understanding of how fossorial animals deal with hypoxia and hypercarbia under natural conditions is still limited and largely biased toward endotherms, whose elevated metabolism leads to situations which can outpace the rate of gas diffusion through soil. For example, measurements from burrows of the Middle East blind mole rat (*Spalax ehrenbergi*) and Botta's pocket gopher (*Thomomys bottae*) found minimum oxygen concentrations of 7.2–15.5% and maximum carbon dioxide concentrations of 3.8–6.1% (Darden, 1972; Shams, Avivi & Nevo, 2005). In comparison, measurements from burrows of the Gopher tortoise (*Gopherus polyphemus*) and nests of green sea turtles (*Chelonia mydas*) found the lowest oxygen concentrations to be 18% (Prange & Ackerman, 1974; Ultsch & Anderson, 1988), and data from burrows of spotted salamanders (*Ambystoma maculatum*) suggest maximum carbon dioxide to be around 1.3% (**Figure 4**). Thus, it is possible that fossorial endotherms and ectotherms encounter different respiratory pressures, shaped in part by their divergent metabolic demands (i.e., greater in endotherms than in ectotherms).

One interpretation of these gas dynamics is grounded in the hypothesis that the occupation of hypoxic and hypercarbic burrows favours the evolution of reduced metabolic rates, which would enable fossorial species to conserve energy in habitats with limited access to the free atmosphere (hereafter "energetic-savings hypothesis") (McNab, 1966). Support for the energetic-savings hypothesis comes primarily from work in fossorial mammals, which appear to have a reduced oxygen demand as well as blunted sensitivity to high carbon dioxide levels (Nevo, 1979; Milsom & Jackson, 2011). This hypothesis was later extended from mammals to reptiles, with the intent to explain metabolic differences between fossorial species and those that

live aboveground (**Figure 5**). For example, the California legless lizard (*Anniella pulchra*), the eastern glass lizard (*Ophisaurus ventralis*), and the checkerboard worm lizard (*Trogonophis wiegmanni*) were shown to maintain metabolic rates 34–67% lower than lizards of similar sizes that do not have a fossorial habit (i.e., hereafter "epigeal") (Kamel & Gatten, 1983). Although similar results were reported in additional species (Andrews & Pough, 1985), the hypothesis that fossoriality selects for chronically reduced metabolic rates in reptiles has received mixed empirical support. For example, metabolic rates in fossorial skinks were broadly consistent with allometric expectations (Withers, 1981), while fossorial tortoises and snakes did not consistently exhibit lower metabolism than epigeal or semi-fossorial counterparts after accounting for body mass (Ultsch & Anderson, 1988; Wang & Abe, 1994). Central to this counterargument is the fact that reptiles function at intrinsically lower metabolic levels than mammals, so further metabolic reductions caused by fossoriality would be evolutionarily implausible because of a relatively small energetic benefit (Wang & Abe, 1994).

A formal phylogenetically controlled test of the energetic-savings hypothesis has yet to be conducted in reptiles. However, comparative data from 185 species support the idea that fossoriality alone is an unlikely selective pressure on amphibian metabolism. Indeed, after controlling for temperature and body mass effects, metabolic rates were similar between fossorial and epigeal amphibians (**Figure 5**) (Giacometti & Tattersall, 2023). Thus, while many amphibians tolerate hypoxic and hypercarbic conditions (Tattersall & Boutilier, 1997; Bícego-Nahas & Branco, 1999; Sheafor, Wood & Tattersall, 2000; Ultsch, 2012), current evidence does not suggest a systematic metabolic depression in response to the colonisation of environments with periodically or chronically low oxygen and high carbon dioxide levels. Besides their low energetic requirements (Pough, 1983), fossorial amphibians may also demonstrate an enhanced

reliance on cutaneous respiration, which allows gas exchange to occur across the integument under conditions where pulmonary ventilation may be constrained, including prolonged exposure to water-saturated substrates (Smits & Flanagin, 1994). Cutaneous respiration may therefore provide an additional pathway for O_2 uptake and carbon dioxide excretion in underground environments, potentially reducing the dependence on pulmonary ventilation under hypoxic or waterlogged conditions (Boutilier & Toews, 1981; Sheafor *et al.*, 2000). Alternatively, behavioural adjustments like exploiting well-ventilated soil layers or periodically emerging to the surface could help restore oxygen and carbon dioxide balance and avoid hypoxia and hypercarbia. To our knowledge, direct observations of such behaviours remain undocumented. Taken together, these pieces of evidence suggest that underground gas composition may reinforce existing physiological strategies rather than impose a single convergent solution. Whereas some mammals and reptiles respond to hypoxic and hypercarbic conditions through a reduction of metabolic demand and expenditure, amphibians may be able to maintain relatively stable metabolic performance through physiological (and possibly behavioural) buffering.

(4) Mechanical and structural constraints

Fossorial animals also face mechanical and structural challenges that influence how they navigate underground environments. Unlike air or water, soil is a dense medium whose physical properties (e.g., compaction, moisture content, particle size) determine resistance to penetration and the costs of locomotion (de Barros *et al.*, 2021). For fossorial ectotherms, these properties also dictate the extent to which individuals can reposition themselves to access favourable hydrothermal or respiratory conditions (Jared, Navas & Toledo, 1999; Navas *et al.*, 2004).

Therefore, soil characteristics may not only constrain movement, but also contribute to the hydrothermal and energetic constraints highlighted in earlier sections.

A key aspect of these mechanical constraints is the interplay between soil density and moisture, which collectively shape the energetic costs of burrowing. Compacted and clay-rich soils offer great resistance to forward motion, meaning that substantial muscular effort is necessary to push or displace the substrate (Gans, 1978). Conversely, loose and sandy soil offer little support and may collapse during excavation, requiring animals to invest additional effort to stabilise tunnels and burrows (Camacho *et al.*, 2015). Moisture content further modulates these dynamics: wetter soils can reduce friction and lower resistance to digging; however, excavation may be impeded when the soil becomes saturated due to loss of structural integrity (Bittelli, 2011; Doody *et al.*, 2015). As a result, fossorial amphibians and reptiles often exhibit preferences for specific soil textures and moisture levels (Cartledge *et al.*, 2006; Greenville & Dickman, 2009; Martín *et al.*, 2021a), and may time their above- and below-ground movement to coincide with periods when mechanical resistance is minimised, such as following rainfall. By effectively tracking shifts in soil mechanics, fossorial animals capitalise on windows of opportunity that present lower costs for movement (Traeholt, 1995).

Because digging is energetically demanding (Wu *et al.*, 2015), fossorial species either adopt locomotor strategies that reduce the need for sustained excavation, or display morphophysiological adaptations that maximise digging and burrowing performance. For example, fossorial amphibians with limited morphological specialisation, like some mole salamanders (*Ambystoma* spp.), exploit pre-existing burrows or soil fissures to minimise the cost of movement (Semlitsch, 1983; Dzenowski & Hembree, 2014). Other species with more specialised morphologies, like amphisbaenians, limb-reduced skinks, and some anurans, display

distinct modes of burrowing (hindlimb- or head-first), “sand-swimming”, or concertina locomotion that facilitate travel through narrow spaces with minimal excavation (Gans, 1978; Navas *et al.*, 2004; Nomura, Rossa-Feres & Langeani, 2009). These coordinated behavioural and biomechanical strategies illustrate that fossorial amphibians and reptiles do not depend solely on digging ability to persist underground. Rather, animals combine active excavation with exploitation of natural soil architecture to sustain mobility in mechanically complex substrates. From an evolutionary perspective, such locomotor specialisations reflect traits that were selected in response to the burden of displacing dense or unstable substrates (Navas *et al.*, 2004; de Barros *et al.*, 2021).

Soil properties also impact burrow architecture and stability, which in turn affect microclimate exposure and refuge quality (Laundré & Reynolds, 1993). Appropriate tunnel diameter, curvature, and depth result from a balance between mechanical stability and the need for ventilation, drainage, and movement (Traeholt, 1995; Doody *et al.*, 2015). One may hypothesise, thus, that amphibians that rely heavily on cutaneous respiration may favour wider or more humid chambers that favour gas exchange and the maintenance of water balance (Wu *et al.*, 2025). In contrast, reptiles may be less constrained by dry subterranean microhabitats due to their reduced risk of evaporative water loss (Abe & Johansen, 1987; Martín *et al.*, 2025). These contrasting requirements imply that burrow architecture may differ between fossorial amphibians and reptiles, although evidence in this context comes primarily from work in extinct, rather than extant, species (Hembree, Martin & Hasiotis, 2004; Dzenowski & Hembree, 2014; Doody *et al.*, 2015). Furthermore, burrow stability is influenced by seasonal changes in soil moisture and freeze-thaw cycles, which can collapse tunnels and force animals to relocate or reconstruct refuges (Traeholt, 1995; Shenbrot *et al.*, 2002; Doody *et al.*, 2015). Such structural dynamics

likely interact with hydrothermal and respiratory demands and constraints, ultimately influencing which microhabitats remain accessible to fossorial animals throughout the year.

Finally, it is worth emphasising that mechanical constraints are rarely examined in concert with behavioural and physiological responses, despite representing an important aspect of fossorial life (Jared *et al.*, 1999; Navas *et al.*, 2004). By modulating the energetic costs of movement, the possibility of accessing viable microclimates, and the stability of underground refuges, soil mechanics help determine the extent to which fossorial amphibians and reptiles can deal with environmental variability. Thus, mechanical properties of the soil interact with hydrothermal and respiratory demands, shaping not only movement but also when, where, and how animals utilise subterranean habitats.

(5) Sensory constraints

Compared with the surface, underground environments present a radically altered sensory landscape. Because light is virtually absent and sound transmission is muffled, fossorial animals are reliant on mechanosensation and chemosensation to sense their surroundings and communicate with one another (Mason & Narins, 2001; Martín *et al.*, 2020). As a result, fossorial taxa often display neuroanatomical configurations that differ markedly from those of their surface-dwelling counterparts, including enlarged somatosensory regions and reduced processing centres, reflecting both adaptive specialisation and relaxation of unused sensory structures (Madison, 1977; Wake, 1985). Visual constraints are the most immediately apparent. Several fossorial lineages possess reduced eyes and visual acuity, or even complete eye regression (Gans, 1978; Wake, 1985). In caecilians (Amphibia: Gymnophiona), the reduction of

ocular structures has long been interpreted as a consequence of fossorial life, with vision playing little to no role in underground navigation, individual recognition, or foraging (Wake, 1985; Martín *et al.*, 2020). Similarly, many fossorial reptiles possess eyelid-protected eyes that only allow for a crude detection of light intensity, likely assisting in orientation or diel timing but not in spatial discrimination (Foureaux *et al.*, 2010; Guerra-Fuentes *et al.*, 2014). Thus, the relaxation of visual demands suggests the predominance of other sensory axes in fossorial taxa.

Vibration appears to be an important orientational cue in fossorial species. Soil transmits low-frequency vibrations while attenuating high-frequency signals, creating a sensory environment in which seismic disturbances provide crucial information about predators or prey (Mason & Narins, 2001; Young & Morain, 2002). Worm-lizards (Squamata: Amphisbaenia), for example, possess a highly specialised inner ear morphology that enhances the detection of substrate vibrations, allowing them to interpret the direction and intensity of mechanical cues as they navigate the soil (Gans & Wever, 1972; Clark *et al.*, 2024). While some amphibians also appear to rely on seismic signals as a means of communication (Narins, 1990), such data come from epigeal instead of fossorial species. Nonetheless, it is plausible to expect that fossorial amphibians that possess broad cutaneous mechanoreceptors may be particularly suited to detect underground vibrations (Catton, 1958). Unlike reptiles (e.g., Young & Morain, 2002), empirical tests of vibration sensitivity in fossorial amphibians are notably lacking.

Chemical sensing and olfaction may also be modified underground. The diffusion and degradation of odorants through the soil depends on pore size, moisture content, and mass flow of air (Som, Willett & Alborn, 2017). Consequently, fossorial animals often experience reduced access to airborne chemical cues. Reptiles that rely on lingual-vomeronasal sampling, like skinks and amphisbaenians, may compensate through an enhanced sensitivity to odorants or an increase

in sampling behaviour, thus permitting the detection of conspecifics and favourable microhabitats (Martín *et al.*, 2020, 2021a). Data from aquatic and epigeal amphibians suggest that chemoreception plays an important role in predator avoidance, habitat selection, and reproduction (Reiss & Eisthen, 2008; Woodley, 2015). Plethodontid salamanders provide a particularly well-characterised example of substrate-borne chemoreception, as their nasolabial grooves can transport chemicals from the substrate to the vomeronasal organ during nose-tapping, facilitating the detection of non-volatile chemical cues (Dawley & Bass, 1988). It is therefore likely that fossorial amphibians similarly exploit chemical gradients to detect conspecifics, navigate microhabitats, or locate prey, although explicit assessments have yet to be conducted.

Given the unique sensory landscape presented by underground environments, the sensory hierarchies of fossorial amphibians and reptiles appear to be reorganised: vibration, mechanosensory and chemosensory cues may dominate over vision and airborne cues. How these inputs are processed remains poorly understood, but available evidence suggests substantial neural and behavioural modifications relative to species that live above the surface (Wahnschaffe, Fritzsch & Himstedt, 1985; Fritzsch & Wake, 1988). Despite this, sensory constraints remain of the least studied aspects of fossorial life, especially in amphibians. Integrating sensory studies with the hydrothermal, respiratory, and mechanical perspectives outlined above will be crucial for understanding how fossorial animals perceive and respond to subterranean environments.

III. Physiological and behavioural strategies of fossorial taxa

(1) Hydroregulation and osmoregulation

In fossorial ectotherms, hydroregulation is fundamentally governed by the physics of water exchange between the animal and its surrounding environment. Net water flux is determined by gradients in water potential, which integrate effects of temperature, substrate water content, and solute concentration (Shoemaker *et al.*, 1992). When the water potential of the surrounding soil falls below that of the animal's body fluids, water is lost passively; conversely, when the gradient is reversed, water uptake from the substrate becomes possible (Spight, 1967). Given that soil water potential can vary sharply over small spatial scales, especially in drying surface layers, fossorial species are presumed to be exposed to steep and dynamic hydric gradients. Consequently, the capacity to either resist water loss or exploit specific zones of higher water availability is central to the maintenance of hydric and osmotic balance underground (Székely *et al.*, 2018). The extent to which these gradients translate into water loss or gain is contingent on organismal traits, such as integument structure and osmoregulatory capacity, which ultimately govern how water flux is regulated in amphibians and reptiles (Lillywhite, 2006). Importantly, much of the empirical foundation for these mechanisms derives from epigeal or semi-aquatic species, and direct tests in strictly fossorial amphibians and reptiles remain scarce.

The structure and permeability of the integument represent a key point of divergence between amphibians and reptiles. Amphibians possess a thin and highly vascularised skin that is permeable to both water and dissolved gases (Tattersall, 2007). These characteristics enable efficient cutaneous water uptake in moist conditions, but simultaneously predispose amphibians to substantial evaporative water loss when exposed to drier conditions (Giacometti & Tattersall, 2025). In contrast, reptiles possess a stratified epidermis with a well-developed stratum corneum

that is composed of keratinised scales and lipid layers that collectively reduce cutaneous permeability to water, ultimately allowing reptiles to maintain internal water balance even in relatively dry conditions (Lillywhite & Maderson, 1988; Lillywhite, 2006). However, this reduced permeability also limits the potential for direct water uptake through the skin, thereby rendering reptiles more reliant on drinking environmental water or producing it metabolically (Shoemaker & Nagy, 1977; Lillywhite, 2017).

Beyond these structural differences, fossorial amphibians and reptiles also diverge in the mechanisms that regulate water balance. In amphibians, specialised regions of the integument enhance hydroregulatory capacity. The pelvic patch is a highly vascularised area of ventral skin that is particularly important for water absorption, allowing individuals to rehydrate rapidly when in contact with moist substrates (Parsons & Mobin, 1991). Water uptake across the pelvic patch is facilitated by its dense vascularisation and the presence of aquaporins, whose activity is regulated by arginine vasotocin, a hormone that increases skin permeability and promotes water absorption (Lemenager *et al.*, 2022). In addition to regulating water uptake, amphibians may also exert control over water loss. Recent work suggests that the fossorial *A. maculatum* can maintain a relatively constant vapour pressure deficit (i.e., the driving force for evaporative water loss) across contrasting thermal conditions via selection of favourable microhabitats. This indicates an ability to sense and process environmental water content, as well as engage regulatory mechanisms that stabilise rates of dehydration under variable environments (Giacometti & Tattersall, 2025). Together, the capacity to regulate both water uptake and loss likely enables amphibians to exploit fine-scale hydric heterogeneity in the soil, effectively using behavioural and physiological adjustments to maintain hydric balance (Spotila, 1972). In fossorial contexts,

where direct access to free-standing water may be limited, such integrative control of water flux may be critical for sustaining hydration without frequent surface emergence.

In reptiles, hydroregulation appears to rely less on a dynamic modulation of cutaneous exchange and more on minimising water loss and conserving internal water stores. Indeed, due to their integumentary characteristics, reptiles possess markedly lower rates of cutaneous permeability compared to amphibians (Lillywhite & Maderson, 1988; Lillywhite, 2006). To maintain water balance, reptiles depend on the integration between behavioural strategies (e.g., microhabitat selection) and physiological mechanisms. Central to this is the regulation of renal function and nitrogen excretion. Most reptiles are uricotelic, excreting nitrogenous wastes that precipitate with minimal water loss, thus enhancing water conservation (Shoemaker & Nagy, 1977). Although some reptiles possess urinary bladders capable of temporary water storage and reabsorption (Jørgensen, 1998), this mechanism is generally less crucial to water balance than in amphibians. Hormonal regulation also modulates renal water reabsorption and urine concentration in reptiles, contributing to the maintenance of osmotic balance under dry conditions (Bradshaw, 1972). As with amphibians, much of this understanding is derived from epigeal species. Nonetheless, hydroregulation in fossorial reptiles is likely centred on minimising water loss and maximising retention, which may render them more tolerant of drier and more variable soils than amphibians, albeit with a reduced capacity for direct water uptake from the substrate (Jared *et al.*, 1999; Martín *et al.*, 2025).

Osmoregulatory strategies also differ between amphibians and reptiles in terms of internal water storage and endocrine control. Many amphibians possess a urinary bladder that serves as a reservoir for water storage, allowing individuals to buffer short-term fluctuations in hydration state (Shoemaker *et al.*, 1992). When necessary, water stored in the bladder can be

reabsorbed into circulation, a process that is hormonally regulated and contributes substantially to the maintenance of osmotic balance (Bentley, 1966). In contrast, reptiles are more reliant on renal regulation and nitrogen excretion strategies to conserve water, primarily through the production of uric acid, which minimises water loss during excretion (Dantzler & Bradshaw, 2008). At the endocrine level, both amphibians and reptiles regulate water balance through neurohypophysial hormones, particularly arginine vasotocin. In amphibians, vasotocin influences kidney function, bladder permeability, and cutaneous water uptake, whereas in reptiles its role is largely restricted to modulating renal water reabsorption and urine concentration (Bentley, 1966; Dantzler & Bradshaw, 2008). These physiological pathways provide a mechanism through which the internal state of an organism can be coordinated with external environmental conditions, thereby enabling adjustments in water balance under fluctuating moisture regimes.

Collectively, the differences highlighted in this section reinforce two contrasting hydroregulatory strategies: amphibians operate as highly permeable systems that depend on environmental water availability and behavioural modulations, whereas reptiles function as more conservative systems that minimise water loss through structural and physiological barriers. In the spatially heterogeneous and often rapidly shifting hydric environment of the subsoil, these contrasting strategies are likely to shape how fossorial species access, exploit, and remain within suitable microhabitats, ultimately influencing patterns of vertical movement, refuge use, and surface emergence (Székely *et al.*, 2018; Martín *et al.*, 2025).

493 *(2) Thermal physiology*

494 Traditionally, the thermal physiology of fossorial ectotherms has been interpreted through
495 the lens of a syndrome that includes: i) relatively low T_bs, ii) reduced thermal preference (T_{pref})
496 and selected temperatures (T_{sel}), iii) and limited thermoregulatory performance compared to
497 epigeal species (Andrews, 1994; Camacho *et al.*, 2015). The fossorial syndrome of thermal
498 physiology is generally attributed to the thermal properties of the subsoil, where diel fluctuations
499 are dampened and thermal extremes are attenuated. Under these conditions, both the opportunity
500 and necessity for active thermoregulation are presumed to be reduced (Bury & Balgooyen, 1976;
501 López, Civantos & Martín, 2002). As a result, fossorial ectotherms are often interpreted as
502 thermal generalists that have not been naturally selected for overt behavioural thermoregulation
503 and just passively track underground temperatures (Camacho *et al.*, 2015; Giacometti *et al.*,
504 2021). However, this interpretation remains only partially supported, and may oversimplify the
505 thermal biology of fossorial taxa.

506 Although reduced thermal variability in the soil may limit the range of temperatures
507 available at a given depth, vertical thermal gradients can still be pronounced in the subsoil
508 (Forget-Klein & Green, 2021). As a result, fossorial ectotherms may retain the capacity for
509 behavioural thermoregulation by adjusting their position within the soil column. Indeed, recent
510 studies suggest that some fossorial amphibians make thermally-oriented decisions in both natural
511 and laboratory settings. For instance, Fowler's toads (*Anaxyrus fowleri*) have been shown to
512 move vertically along underground thermal gradients, which ensures that their T_b stays within
513 their T_{sel} range (Brattstrom, 1963; Forget-Klein & Green, 2021) (**Figure 3**). Similarly, *A.*
514 *maculatum* has been demonstrated to behaviourally adjust T_{sel} in response to seasonally-changing
515 acclimation conditions (Giacometti & Tattersall, 2024). In fossorial reptiles, the available

evidence suggests that thermoregulatory behaviour may be constrained by the thermal properties of the subsoil. Fossorial skinks exhibit T_{pref} that exceed their field-measured T_bs, indicating that while positive thermotaxis may be retained in fossorial taxa, the opportunity to realise these preferences may be limited by restricted access to suitable thermal microhabitats underground (Withers, 1981). Thus, while fossorial ectotherms may not be predominantly thermoconformers, behavioural thermoregulation may be constrained.

A related and largely unresolved question concerns the efficiency of thermoregulation in fossorial environments. Indeed, despite the widespread use of thermoregulatory indices in surface-active ectotherms (Hertz, Huey & Stevenson, 1993; Blouin-Demers & Nadeau, 2005), their use has yet to be applied to fossorial species. Possibly, this is due to the difficulty of quantifying the operative thermal environment (Bakken, 1992) and behavioural access to thermal microhabitats underground. Consequently, the extent to which fossorial ectotherms achieve a narrow control over T_b remains unclear. In systems where thermal gradients are shallow or temporally lagged, behavioural adjustments may result in less precise thermoregulation relative to epigeal species (Bogert, 1949; Camacho *et al.*, 2015). Alternatively, the predictability and temporal lag of underground thermal regimes may allow fossorial ectotherms to control T_b through depth and activity adjustments rather than continuous tracking of local thermal conditions (van Gelder *et al.*, 1986; Forget-Klein & Green, 2021). Resolving this issue will require integrating fine-scale measurements of soil temperature profiles with continuous records of T_b and movement patterns (Forget-Klein & Green, 2021).

The mechanisms that underly thermal perception in fossorial environments are also poorly understood. In the absence of radiative heat flux, heat exchange underground occurs primarily through conduction (Jameson, 1981). This suggests that fossorial ectotherms rely

primarily on thigmothermy; that is, the detection of temperature through direct contact with the substrate (Black *et al.*, 2019). Because conductive heat transfer operates over short spatial scales, thermal gradients in soil may be shallow and highly localised, potentially reducing the spatial resolution of thermal cues available to fossorial animals. Under such conditions, the spatial distribution and sensitivity of cutaneous thermoreceptors may play an important role in thermal orientation. If thermosensitive units are unevenly distributed across the body surface, as has been suggested in some vertebrates, this could bias how animals sample thermal information (Cabanac, Hammel & Hardy, 1967; Romanovsky, 2014), ultimately impacting their ability to detect the directionality of thermal gradients. In this context, anterior body regions like the head may function as primary sampling interfaces, allowing animals to detect thermal discontinuities during forward displacement through the substrate. If thermal perception is indeed constrained by contact-based sensing, thermoregulatory behaviour in fossorial ectotherms may depend on iterative sampling and short-distance movements, rather than directed navigation along continuous gradients (Giacometti *et al.*, 2021). However, empirical data on the neurophysiology of thermosensation in fossorial amphibians and reptiles are virtually absent, representing a major gap in our understanding of how these animals perceive and respond to thermal heterogeneity underground.

(3) Seasonal dormancy

The remarkable adaptability of ectothermic tetrapods is nowhere more evident than in seasonally fluctuating environments, where a diverse set of amphibians and reptiles not only survive but thrive under temporal changes in biotic and abiotic features. As previously established, fossoriality is closely tied to the ability to survive prolonged dry spells or severe

562 temperature, with many species relying on subsurface refugia to buffer environmental extremes
563 (Little & Seebacher, 2016). This rationale is supported by fossil evidence indicating that fossorial
564 habits emerged early in the evolutionary history of various ectothermic lineages, thereby
565 representing an ancient state that allows animals to persist in changing environments (Hembree
566 *et al.*, 2004; Nomura *et al.*, 2009). Often, species that spend long portions of the year
567 underground present hypometabolic adjustments that reduce their energy demand while buried in
568 the soil. This reduced energetic demand is not merely a short-term survival mechanism; it also
569 promotes an increase in overall lifespan. By simultaneously lowering metabolic rates,
570 minimising activity, and slowing down physiological processes, seasonal dormancy conserves
571 vital energy reserves and reduces oxidative damage, which collectively contribute to extended
572 longevity (Storey & Storey, 2012).

573 In general, seasonal metabolic depression entails a marked decrease of physiological
574 functions across multiple organismal systems in response to environmental cues and, in some
575 cases, due to the action of endogenous rhythms (Dark, 2005; Storey & Storey, 2010). In
576 amphibians and reptiles that undergo seasonal dormancy like aestivation (inactivity associated
577 with water deficit) or hibernation (inactivity associated with low body temperatures), voluntary
578 locomotion ceases and feeding along with digestive processes comes to a halt (Sanders *et al.*,
579 2015; Zena *et al.*, 2016). Concomitantly, cardiac and respiratory rates decline, and cerebral
580 electrical activity becomes notably slower (Storey & Storey, 1990). The controlling events
581 associated with these processes must therefore promote a new state of equilibrium, which
582 involves a reduction in the rates of all cellular processes, along with specific biochemical
583 adjustments such as shifts in the type of energy substrate used and changes in the accumulation
584 of catabolites (Hochachka & Guppy, 1987; Wang & Wolowyk, 1988). For example, in animals

585 that exhibit profound metabolic depression under hypoxic conditions, there is an inhibition of
586 enzymatic steps in the glycolytic pathway and of pathways that regulate carbohydrate entry into
587 the Krebs cycle, thereby limiting ATP production from this substrate (Storey & Kelly, 1995;
588 Hochachka & Somero, 2002). On the other hand, it is known that aestivation in most anuran
589 species is predominantly an aerobic phenomenon, although in some species it occurs under
590 mildly hypoxic conditions (Storey & Storey, 2012). Thus, aestivating animals can utilise
591 oxidative pathways for ATP production albeit at lower rates. In such cases, the mechanisms
592 underlying metabolic depression are potentially more complex, since the control of the
593 hypometabolic state involves multiple cellular pathways and operates differently across various
594 organs and systems (Storey & Storey, 1990; Carvalho, Navas & Pereira, 2010; Storey & Storey,
595 2012; Staples, 2016). Metabolic homeostasis during the hypometabolic period is then ensured by
596 lipid stores, which are oxidised at rates compatible with the depressed oxygen consumption and
597 overall activity levels of the animals (Florant, 1998; Dark, 2005; Chazarin *et al.*, 2019).

598 Beyond the mechanistic processes of biochemical and physiological control, seasonal
599 variation in energy metabolism constitutes a fundamental ecophysiological challenge for
600 amphibians and reptiles, as the observed metabolic adjustments arise from the integration of
601 microhabitat selection, behavioural plasticity, and physiological responses. Microhabitat
602 selection carries profound physiological implications for these animals, particularly regarding
603 exposure to environmental extremes (Huey, 1991). Through behavioural strategies, individuals
604 can mitigate such extremes by seeking thermal and hydric refugia from harsh seasonal conditions
605 (Carvalho *et al.*, 2010; Oromí, Sanuy & Sinsch, 2010). For instance, tegu lizards (*Salvator*
606 *merianae*), one of the largest lizards in South America, usually alternate between moments spent
607 inside and outside burrows to thermoregulate during the active season despite their enhanced

ability to produce endogenous body heat (Abe, 1995; Tattersall *et al.*, 2016). With approaching winter, shorter photoperiods and cooler temperatures, tegus increase the proportion of time spent inside burrows and exhibit spontaneous hypophagia (Abe, 1983). These lizards are known to hibernate throughout austral autumn and winter, exhibiting a profound depression of aerobic metabolism, ventilation and heart rate independent of environmental and body temperatures (Abe, 1995; Andrade & Abe, 1999; Sanders *et al.*, 2015). Therefore, for tegus, burrows serve not merely as refugia from harsh weather, but as a critical resource that provides the protective conditions essential for survival during prolonged inactivity.

The degree of reliance on burrows, however, differs markedly across species based on their ecological traits. For instance, among aestivating anurans, spadefoot toads (*Scaphiopus couchii*) avoid exposed areas by burrowing into shaded, vegetated sites where temperature fluctuations are reduced and moisture persists longer, a microhabitat preference that mirrors its broader selection of grassland over more arid scrub habitats during the active season (Mayhew, 1965; McClanahan Jr, 1972). Likewise, Australian green-striped frogs (*Cyclorana alboguttata*) show clear selectivity for sandy soil when allowed to choose from different substrates in controlled settings (Booth, 2006). Conversely, some frogs adopt strategies that do not necessarily mitigate stress. The African reed frog (*Hyperolius viridiflavus*) undergoes seasonal dormancy while clinging to sunlit vegetation, while being fully exposed to heat and desiccation (Kobelt & Linsenmair, 1995). Despite numerous reports in the literature on seasonal changes in behavioural and physiological aspects of aestivation in anurans, many subtle features concerning site selection are not yet understood. This issue warrants particular attention, as it bears directly on understanding how burrowing strategies and physiological adjustments are integrated to ensure survival.

For example, aestivating *C. alboguttata* create small air chambers when burrowed, likely through limb movements that compact the soil, which may ultimately reduce cutaneous contact with dry substrates and limit water loss (Booth, 2006). In contrast, spadefoot toads (*Scaphiopus hammondii*) lie fully enveloped by sand during aestivation (Ruibal, Tevis Jr & Roig, 1969). Other aspects of aestivation in these anurans must be considered. For example, *C. alboguttata* form cocoons (i.e., accumulated layers of shed epidermal cells) that promote a reduction in water conductance across the skin (Withers, 1998), while *Scaphiopus* spp. do not form cocoons but instead accumulate large amounts of urea that serve as an organic solute to minimise the osmotic gradient with the environment (Jones, 1980). Moreover, there are clear physicochemical differences between the substrates in which organisms burrow (e.g., sandy soils or drying mud), each presenting distinct challenges for gas exchange and water balance. In the case of *Scaphiopus* spp., individuals buried in sand typically leave no openings to the surface, relying entirely on oxygen diffusion through the substrate, which remains near atmospheric levels even beneath the ground (Seymour, 1973; Carvalho *et al.*, 2010) . Sandy environments thus rarely impose gas exchange limitations for seasonally dormant animals. In contrast, muddy substrates, especially when dry, are likely far less permeable to respiratory gases, though this issue remains understudied (Carvalho *et al.*, 2010). Regarding water availability, the granular structure of sand influences how easily burrowing anurans can extract environmental moisture; water uptake depends not merely on soil water content but also on tension (Ruibal *et al.*, 1969). Together, these examples illustrate that seasonal dormancy underground is an integrated response to the physical and ecological conditions of the subterranean environment. The capacity to remain inactive for prolonged periods depends on the interaction between metabolic depression, water conservation, respiratory physiology, and behavioural selection of suitable microhabitats, with

654 the relative importance of each mechanism varying among dormancy contexts. Consequently,
655 understanding seasonal dormancy in fossorial amphibians and reptiles requires considering how
656 physiological adjustments are coordinated with the properties of the burrow itself.

657

658 *(4) Emergence and activity patterns*

659 For fossorial species that periodically access the surface, emergence represents a critical
660 behavioural transition between two markedly different environments. While the subsoil provides
661 protection from predators and environmental extremes, the surface offers access to food
662 resources, mates, dispersal opportunities, and suitable sites for reproduction (Semlitsch, 1983;
663 Kinlaw, 1999). Consequently, emergence reflects a trade-off between the benefits of remaining
664 underground and the ecological opportunities available aboveground. Rather than occurring
665 randomly, periods of surface activity are typically concentrated within relatively narrow temporal
666 windows during which environmental conditions minimise physiological costs while maximising
667 fitness benefits (Traeholt, 1995; Madison, 1997; Encarnación-Luévano *et al.*, 2013).
668 Temperature and water availability are the main environmental cues that induce emergence. In
669 amphibians, rainfall frequently triggers synchronised emergence by simultaneously minimising
670 rates of evaporative water loss and facilitating locomotion through moist soil (Faccio, 2003;
671 Rothermel & Luhring, 2005). Likewise, soil temperature contributes to emergence timing, either
672 by directly influencing physiological performance or indirectly through its effects on
673 reproductive phenology and prey availability (Forget-Klein & Green, 2021; Moldowan, 2023).
674 Reptiles also exhibit weather-dependent emergence patterns, although most species studied to
675 date appear to respond more strongly to temperature than moisture alone (Greenville &
676 Dickman, 2009; Raya-Garcia *et al.*, 2019; Martín *et al.*, 2021b). Importantly, because

underground temperatures often lag behind those at the surface, environmental cues perceived within burrows may be substantially different than those experienced immediately after emergence (Giacometti *et al.*, 2024).

Emergence decisions are also state-dependent. Hydration status, energetic reserves, reproductive condition, and thermal state may all influence whether the potential benefits of surface activity outweigh its physiological costs (Madison, 1997; Székely *et al.*, 2018; Martín *et al.*, 2025). For example, dehydrated individuals must remain underground until favourable hydric conditions are restored, whereas reproductive migration may necessitate emergence despite increased desiccation, thermal, or predation risks (Semlitsch, 1983; Rothermel & Luhring, 2005; Giacometti, Moldowan & Tattersall, 2025). Similarly, individuals recovering from seasonal dormancy often emerge only after environmental conditions allow for sustained locomotion and positive energy balance (Carvalho *et al.*, 2010; Holden *et al.*, 2021).

Recent advances have further emphasised that fossorial life is characterised by continual movement between subterranean and surface environments rather than permanent residence belowground (Giacometti *et al.*, 2024). Within this framework, emergence is best viewed as an integrative decision-making process in which animals simultaneously evaluate multiple external cues (e.g., temperature, soil moisture, gravitational orientation, and seasonal information) alongside their internal physiological state to optimise the timing of surface activity. Such a perspective shifts the emphasis from single environmental drivers toward a mechanistic understanding of how multiple sensory and physiological pathways interact to regulate transitions between subterranean and surface habitats. Thus, this perspective recognises that underground and aboveground habitats provide complementary ecological functions: the subsoil

699 primarily serves as a refuge, whereas the surface provides opportunities for resource acquisition,
700 reproduction, and dispersal.

701

702 IV. Morphology and locomotion

703 *(1) Morphological syndromes associated with fossoriality*

704 Fossoriality imposes a distinctive set of mechanical demands on amphibians and reptiles,
705 including the need to access subterranean environments, displace resistant substrates, generate
706 propulsion within confined spaces, and withstand frictional and compressive forces acting across
707 the body (Gans, 1974; Ebel *et al.*, 2020). Movement underground therefore requires sufficient
708 force production and the efficient transmission of that force while negotiating frictional
709 resistance and maintaining stability within narrow spaces (Gans, 1974; Navas *et al.*, 2004; Lowie
710 *et al.*, 2022). Consequently, the functional demands of fossoriality are distributed across multiple
711 anatomical systems, including the body axis, cranium, limbs, musculature, and integument,
712 which operate together rather than as independent traits. Although fossoriality has repeatedly
713 favoured changes in body shape, cranial architecture, limb morphology, and muscular
714 organisation, no single anatomical configuration characterises all fossorial taxa (**Figure 1**).
715 Instead, comparable functions have evolved through distinct and phylogenetically contingent
716 combinations of traits (Gans, 1975; Wiens, Brandley & Reeder, 2006; Keeffe & Blackburn,
717 2020; Morinaga & Bergmann, 2020).

718 This diversity is further compounded by variation in the extent to which species depend
719 on subterranean environments. Whereas obligately fossorial taxa conduct most activities below
720 ground and often exhibit extensive morphological specialisation, semi-fossorial or seasonally

721 burrowing species may retain traits associated with surface locomotion, feeding, and dispersal
722 (Kinlaw, 1999; Wu *et al.*, 2015). These contrasting ecological demands are likely to constrain the
723 extent to which morphology can become specialised for subterranean locomotion without
724 compromising performance in other functional contexts. Consequently, the degree and nature of
725 morphological modification are expected to reflect the mechanical demands of burrowing, as
726 well as the frequency, duration, and ecological context of subterranean activity (Buttimer,
727 Stepanova & Womack, 2020; Keeffe & Blackburn, 2020; Giacometti *et al.*, 2024). Among the
728 morphological responses to these combined demands, body elongation and associated axial
729 specialisation represent recurrent, although not universal, patterns across fossorial amphibians
730 and reptiles (Gans, 1975; Wiens *et al.*, 2006).

731 Body elongation and axial specialisation have evolved independently in multiple
732 amphibian and reptile lineages, but similar external forms may arise through distinct anatomical
733 and evolutionary pathways (Brandley, Huelsenbeck & Wiens, 2008; Bergmann *et al.*, 2020). In
734 elongate tetrapods, axial specialisation can involve changes in vertebral numbers and
735 proportions, and regional differentiation along the spine (Bergmann & Irschick, 2012; Lowie *et*
736 *al.*, 2022). These components do not necessarily evolve in parallel with limb reduction in
737 squamates, whereas caecilians combine extreme elongation and limblessness with marked
738 regional variation in vertebral form (Sanger & Gibson-Brown, 2004; Brandley *et al.*, 2008;
739 Bergmann & Irschick, 2012; Lowie *et al.*, 2022). These axial configurations provide the
740 structural basis for propulsion and force transmission within confined spaces. Conversely, many
741 fossorial anurans retain a compact body plan and rely primarily on specialised forelimbs or
742 hindlimbs for excavation, illustrating that elongation is only one of several evolutionary
743 solutions to subterranean locomotion (Emerson, 1976; Vidal-García & Keogh, 2015; Vidal-

744 García & Scott Keogh, 2017; Keeffe & Blackburn, 2020). Thus, the locomotor significance of
745 elongation depends partly on whether the limbs remain important for propulsion, become
746 specialised for excavation, or are reduced or lost.

747 Limb reduction and limb specialisation represent alternative evolutionary responses to
748 fossoriality rather than successive stages along a single adaptive trajectory. In elongate lineages
749 that rely predominantly on axial or head-first propulsion, the limbs may become reduced or lost,
750 although body elongation and appendicular reduction can evolve at different rates and through
751 partially independent pathways (Brandley *et al.*, 2008; Camaiti *et al.*, 2021). By contrast,
752 appendicular diggers retain the limbs as the primary structures for substrate displacement and
753 commonly exhibit increased robustness of the associated bones and girdles, enlarged areas for
754 muscle attachment, and modifications of the distal limb that enhance force transmission during
755 excavation (Vidal-García & Keogh, 2015). Among anurans, these configurations vary with
756 digging mode: forward burrowers show recurrent specialisation of the forelimbs and pectoral
757 apparatus, whereas the more widespread backward-burrowing condition relies primarily on the
758 hindlimbs, pelvis, and metatarsal structures (Emerson, 1976; Vidal-García & Scott Keogh, 2017;
759 Keeffe & Blackburn, 2020). Comparative analyses further indicate that appendicular morphology
760 can be evolutionarily labile in relation to locomotion and burrowing, even when other anatomical
761 regions remain more strongly constrained by phylogenetic history (Vidal-García & Scott Keogh,
762 2017). Reptiles likewise span a continuum from taxa retaining functional limbs for excavation to
763 lineages increasingly dependent on axial and cranial propulsion, emphasising that limb loss is
764 neither an inevitable nor a universally advantageous outcome of fossorial evolution (Camaiti *et*
765 *al.*, 2021). Rather, the retention, specialisation, reduction, or loss of appendages reflect lineage-
766 specific interactions among ancestral body plan, digging behaviour, and ecological context.

(2) Cranial, integumentary, and sensory adaptations for subterranean locomotion

During head-first burrowing, the cranium forms the leading mechanical interface with the substrate, transmitting forces generated by the axial musculature while resisting loads imposed during substrate displacement (Gans, 1974; Bergmann & Berry, 2021; Lowie *et al.*, 2021). Across caecilians and fossorial squamates, recurrent modifications include compact, strongly ossified skulls, consolidation of cranial elements, interlocking sutures, and changes in snout geometry that influence force transmission (Kearney, Maisano & Rowe, 2005; Kazi & Hipsley, 2018; Lowie *et al.*, 2021). These modifications, however, do not converge on a single cranial configuration. Amphisbaenians include rounded, shovel, keel, and spade-headed forms associated with distinct digging movements, whereas comparative analyses of fossorial lizards indicate that convergence remains constrained by phylogenetic history and substrate properties (Kearney *et al.*, 2005; Kazi & Hipsley, 2018; Stepanova & Bauer, 2021). Indeed, lizards occupying moist and dry soils have evolved towards distinct adaptive optima in head shape, suggesting that fossoriality can favour alternative morphological solutions to the same functional challenge under different substrate conditions (Anelli *et al.*, 2024). Caecilians likewise possess generally compact skulls but vary in temporal closure, mandibular architecture, and regions associated with jaw-muscle attachment (Sherratt *et al.*, 2014; Lowie *et al.*, 2021). Such variation cannot be arranged along a simple continuum of specialisation. Cranial architecture must also accommodate feeding, muscle attachment, and sensory functions, potentially imposing competing functional demands. Cranial morphologies therefore represent lineage-specific solutions shaped jointly by ancestry, substrate, and digging behaviour, rather than successive degrees of fossorial specialisation. Once a burrow has been initiated, continued progression also

depends on how the body surface manages friction and abrasion against the surrounding substrate.

The integument constitutes not merely a physiological barrier but also the continuous mechanical interface between the animal and the substrate, a role particularly pronounced in elongate, limb-reduced forms, in which much of the body surface contacts the burrow walls during locomotion (Gans, 1978; Allam, Daza & Abo-Eleneen, 2016). Across fossorial squamates, smooth or reinforced integumentary surfaces and variation in scale arrangement can reduce abrasion and regulate friction against the substrate (Gans, 1978; Baumgartner *et al.*, 2007). Importantly, these surfaces do not simply minimise friction: scale overlap and orientation can generate direction-dependent resistance, facilitating forward sliding while providing purchase against backward displacement (Gans, 1978). Such properties are especially pronounced in sand-swimming skinks, whose scales combine low friction with high resistance to abrasion by granular substrates (Baumgartner *et al.*, 2007). However, integumentary structure also varies among limbless squamates occupying different environmental conditions, suggesting that the mechanical demands of subterranean locomotion interact with lineage-specific anatomy and broader habitat constraints (Allam *et al.*, 2016). Relatedly, the skin of fossorial amphibians must retain its roles in water and gas exchange while remaining exposed to friction and abrasion (Lillywhite, 2006). In caecilians, abundant mucous glands provide a potential solution by maintaining a lubricated body surface, while the concentration of enlarged mucous glands near the head may facilitate its movement through the substrate (Jared *et al.*, 2018). Thus, the integument contributes to performance through different structural and secretory mechanisms, reflecting a balance among mechanical protection, frictional control and cutaneous exchange rather than a single convergent modification.

Subterranean conditions are also associated with a reorganisation of craniofacial sensory structures, although this does not entail their uniform reduction or loss. In amphisbaenians, the eyes are generally small and covered by skin or scales, and external ear openings are absent, contributing to a continuous head surface while limiting the external exposure of sensory organs (Gans, 1978). Caecilians exhibit even greater variation, with eyes ranging from externally visible to concealed beneath skin or cranial bones; nevertheless, the retention of a differentiated retina and optic nerve in most examined species indicates that external reduction does not necessarily imply the complete loss of photoreceptive capacity (Wake, 1985). Visual reduction should therefore be interpreted as part of a broader reorganisation of the craniofacial surface rather than as a uniform progression towards blindness. Other sensory structures may be retained or elaborated within this modified architecture. The caecilian tentacle, for example, incorporates muscles, glands, and nerves associated developmentally with the orbital region and connects to the vomeronasal system, providing a distinctive chemosensory interface near the anterior surface of the head (Billo & Wake, 1987; Himstedt & Simon, 1995). The position of the tentacular aperture also varies among caecilian lineages and remains taxonomically informative, although its distribution reflects both phylogenetic inheritance and homoplasy (Nussbaum & Wilkinson, 1989; Wilkinson & Nussbaum, 2006). In snakes, scale organs, or sensilla, constitute mechanosensory structures whose size and distribution vary among lineages, with enlarged organs or greater densities reported in some fossorial taxa, although their function has been examined directly in only a limited range of ecological contexts (Crowe-Riddell *et al.*, 2019). The repeated occurrence of ocular reduction or coverage alongside alternative sensory structures suggests broad functional convergence across independent fossorial lineages, but its anatomical

835 expression remains contingent on ancestry, cranial architecture and the sensory demands
836 associated with different substrates and digging modes.

837 One can thus infer that fossoriality is associated with recurrent modifications in body
838 proportions, limb development, cranial architecture, integumentary surfaces and sensory
839 structures. These traits, however, neither evolve as an invariant suite nor converge towards a
840 single morphological optimum. Repeated transitions towards elongate, limb-reduced forms in
841 squamates illustrate convergence at the level of the overall body plan, yet fossorial locomotion
842 may also involve the retention or specialisation of limbs and distinct combinations of axial and
843 cranial traits (Wiens *et al.*, 2006). Likewise, variation in head shape and body proportions across
844 substrates and lineages indicates that similar subterranean demands can produce different
845 morphological configurations depending on phylogenetic history and the physical properties of
846 the environment (Stepanova & Bauer, 2021; Anelli *et al.*, 2024). These alternative configurations
847 may also entail context-dependent trade-offs with feeding, surface locomotion and microhabitat
848 use, preventing fossorial specialisation from being arranged along a single linear continuum.
849 Morphological similarity among fossorial taxa should therefore be treated as a hypothesis of
850 functional equivalence rather than evidence of it, requiring direct tests of how alternative trait
851 combinations affect burrowing and surface locomotor performance across substrates. This
852 context dependence can be conceptualised as a functional landscape in which alternative
853 morphological configurations may achieve similar performance, while substrate properties alter
854 the distribution and accessibility of performance optima (**Figure 6**).

855

(3) Environmental determinants of locomotor performance

Locomotor performance represents the functional expression of how a whole-organism phenotype interacts with its mechanical environment, thereby linking morphology to the execution of biologically relevant tasks (Arnold, 1983; Irschick & Garland, 2001). In fossorial amphibians and reptiles, performance is inherently multidimensional, encompassing force production, the rate and endurance of progression, and the capacity to initiate or extend a burrow (Irschick & Garland, 2001). These components may vary independently, such that similar morphologies can produce different functional outcomes, whereas distinct anatomical configurations can achieve comparable levels of performance (Irschick & Garland, 2001; Bergmann & Berry, 2021). Moreover, the expression and ecological significance of each component depend on the physical properties of the substrate against which performance is generated (Bergmann & Berry, 2021).

The mechanical challenge imposed by the substrate varies not only in magnitude but also in kind, as particle size and shape, compaction, moisture, and cohesion influence the resistance encountered during underground movement (Sharpe, Kuckuk & Goldman, 2015). In caecilians, increasing soil compaction reduced the proportion of individuals able to burrow and increased the time required to do so (**Figure 7**), while animals consistently preferred less compact soils and existing tunnels over the construction of new ones (Ducey *et al.*, 1993). These conditions differ fundamentally from locomotion through loose granular media, in which specialised sand-swimming lizards advance by propagating axial undulations through the surrounding substrate (Maladen *et al.*, 2009). Even within granular substrates, performance can vary with particle properties. For example, two *Calyptommatus* (Squamata: Gymnophthalmidae) species burrowed faster in fine, homogeneous sand, and associations between morphology and performance

879 emerged only under this lower-resistance condition (de Barros *et al.*, 2021). Variation in
880 moisture and compaction can further constrain burial depth and alter the effectiveness of a given
881 locomotor strategy (Sharpe *et al.*, 2015). Performance measured during sand-swimming
882 therefore cannot be generalised to active excavation through compact or cohesive soils, or to
883 movement within pre-existing tunnels. Consistent with this distinction, fossorial lizards
884 associated with dry and moist substrates exhibit different evolutionary regimes of morphological
885 diversification (Anelli *et al.*, 2024), suggesting that substrate-specific mechanical demands may
886 contribute to lineage-specific relationships between form and performance.

887 Underground progression can be achieved through different combinations of
888 appendicular, cranial, and axial force, whose relative contributions vary among lineages and
889 locomotor modes. Among burrowing anurans, most species excavate backwards through
890 alternating movements of the hindlimbs, with force production and transmission involving the
891 hindlimb–pelvic complex and mobility of the iliosacral articulation; a smaller number of species
892 burrow forwards using the forelimbs, sometimes in combination with the head (Emerson, 1976;
893 Jorgensen & Reilly, 2013). These contrasting modes are embedded within broader, repeatedly
894 evolved fossorial morphotypes across distantly related anuran lineages (Vidal-García *et al.*,
895 2014; Vidal-García & Keogh, 2015). Head-first burrowing predominates in many fossorial
896 squamates, but the cranium generally applies forces generated elsewhere in the body. In
897 *Leposternon microcephalum* (Squamata: Amphisbaenidae), for example, the axial musculature
898 powers upward head strokes that compress soil against the roof of the developing tunnel (Navas
899 *et al.*, 2004). Terrestrial caecilians rely entirely on the axial system and may use internal
900 concertina locomotion, in which portions of the body wall brace against the burrow while the
901 vertebral column and associated musculature advance partly independently within it (O'Reilly,

902 Ritter & Carrier, 1997; Herrel & Measey, 2010). Elongate squamates likewise make extensive
903 use of axial propulsion, but transitional forms may combine body undulation with residual limb
904 movements, and similar external proportions do not necessarily correspond to convergent
905 locomotor kinematics (Bergmann *et al.*, 2020). Nevertheless, comparisons across *Lerista*
906 (Squamata: Scincidae) species indicate that more snake-like species can enter sand faster than
907 more lizard-like forms, demonstrating that shifts in the relative contributions of axial and
908 appendicular systems can have measurable consequences for fossorial performance (Morinaga &
909 Bergmann, 2020). These contrasting mechanisms show that underground progression is not a
910 single functional task and that its evaluation requires performance measures matched to the
911 particular way in which force is generated and applied.

912

913 *(4) Functional consequences of morphological variation*

914 Fossorial performance cannot be represented by a single measurement, because force,
915 speed, and endurance capture distinct aspects of whole-organism capacity (Irschick & Garland,
916 2001). This limitation is evident in caecilians: biomechanical models indicate that complete
917 temporal closure does not confer greater cranial performance under simulated burrowing loads,
918 while comparative measurements show that overall cranial shape does not predict maximal in
919 vivo push force, although other attributes such as head angle or burrowing speed may still be
920 functionally relevant (Kleinteich *et al.*, 2012; Lowie *et al.*, 2021). Potential trade-offs also
921 depend on the performance traits and taxonomic scale under study. Within *Acontias percivali*
922 (Squamata: Scincidae), individuals with relatively wider heads produced stronger bites but
923 burrowed more slowly, suggesting a possible trade-off between bite force and burrowing speed
924 (Vanhooydonck *et al.*, 2011). Importantly, this intraspecific relationship does not demonstrate an

antagonism between biting and pushing capacity. Indeed, a broader comparison across fossorial and leaf-litter skinks found no trade-off between maximal bite and push forces: species capable of pushing harder also tended to bite harder (Le Guilloux *et al.*, 2020). Similarly, snake-like *Lerista* entered sand faster than lizard-like species, without a detectable reduction in surface or leaf-litter locomotor performance (Morinaga & Bergmann, 2020). Trade-offs among burrowing force, speed, endurance, biting, and surface locomotion should therefore be tested directly rather than inferred from morphology, with comparisons accounting for body size, phylogenetic history, substrate, and experimental methodology.

Collectively, the available evidence indicates that the ecological significance of fossorial morphology cannot be inferred from the presence of particular traits alone but depends on the performance those traits enable under specific environmental conditions (Arnold, 1983; Irschick & Garland, 2001). Relationships between form and performance need not be one-to-one: distinct morphological configurations may produce comparable functional outcomes, whereas similar external forms may differ in performance when multiple traits and tasks are considered (Wainwright, 2007; Bergmann & McElroy, 2014). In fossorial taxa, substrate-dependent associations between head morphology and movement, together with the differing effects of body form across locomotor contexts, illustrate why morphological similarity alone cannot establish functional equivalence (Morinaga & Bergmann, 2020; Bergmann & Berry, 2021). Phylogenetically informed comparisons using standardised performance measures across ecologically representative substrates are therefore needed to determine whether recurrent morphologies confer similar performance capacities. Placing these capacities within the physiological and physical context of underground movement represents the next step towards a mechanistic understanding of fossoriality.

V. Future directions

Although research on fossorial amphibians and reptiles has progressed substantially over the past decades, most studies continue to examine physiology, behaviour, and performance in isolation. The synthesis presented here argues that the next stage of this field lies not simply in accumulating additional descriptive data, but in integrating complementary perspectives to understand how organisms interact with the dynamism of the subsoil. Such an approach requires shifting from trait-based descriptions toward mechanistic approaches that explicitly link environmental conditions, organismal traits, and whole-organism performance. Several promising avenues emerge from this context (**Table 1**). For instance, comparative studies may extend beyond documenting morphological convergence to testing whether and how similar morphologies produce equivalent functional outcomes across diverse phylogenetic lineages (Bergmann *et al.*, 2020; Morinaga & Bergmann, 2020; Anelli *et al.*, 2024). Standardised measurements of burrowing and locomotor performance, thermal and hydric physiology, respiratory function, and sensory capabilities across representative clades would provide a robust basis for evaluating the repeated evolution of fossoriality (Camacho *et al.*, 2015; Giacometti & Tattersall, 2023). These comparisons should span biologically relevant scenarios, considering differences in substrate composition, soil compaction, moisture, temperature, and gas composition, all of which are expected to influence organismal performance. From an experimental perspective, laboratory systems capable of manipulating hydrothermal gradients, substrate mechanics, and oxygen and carbon dioxide levels make it possible to investigate how fossorial ectotherms respond physiologically and behaviourally to multiple environmental cues (Ultsch & Anderson, 1988; Booth, 2006; de Barros *et al.*, 2021; Giacometti & Tattersall, 2025).

Experiments of these kinds should move beyond single-factor designs and instead evaluate how interacting environmental parameters influence the maintenance of homeostasis. At the same time, technological advances like miniaturised biologgers, automated tracking systems, environmental sensors, and high-resolution imaging techniques offer unprecedented opportunities to study fossorial ectotherms under both natural and laboratory conditions (Martín *et al.*, 2020; Forget-Klein & Green, 2021; Giacometti *et al.*, 2025).

Perhaps the greatest opportunity lies in combining empirical data with mechanistic biophysical models. Mechanistic models that explicitly incorporate heat transfer, water balance, gas exchange, and substrate mechanics can provide quantitative, trait-based predictions of how fossorial ectotherms respond to current and future climatic conditions (Encarnación-Luévano *et al.*, 2013; Huey *et al.*, 2021). Unlike correlative approaches, these models are grounded in first principles and can thus be extrapolated beyond the environmental conditions under which experimental data were initially collected (Kearney & Porter, 2020). The integration of empirical data with biophysical modeling may help researchers simulate, for instance, how fossorial animals navigate complex hydrothermal landscapes, identify critical environmental thresholds, or predict how altered climatic regimes influence fitness. Evidently, these predictive frameworks also have direct implications for conservation. Fossorial species are likely to be affected by climatic changes that alter the physical properties of the subsoil. However, subterranean environments remain largely absent from most assessments of habitat quality and species vulnerability (Encarnación-Luévano *et al.*, 2013). As such, mechanistic models informed by empirical physiological and behavioural data may provide a means for identifying climatic refugia, forecasting shifts in suitable subterranean conditions, and prioritising conservation actions (Lara-Reséndiz *et al.*, 2021; Moreno-Lara, Becerra-López & Ramírez-Bautista, 2023).

VI. Conclusions

(1) The subsoil is heterogeneous and dynamic, with thermal, hydric, respiratory, and mechanical conditions varying across space and time.

(2) Fossoriality thus emerges from the continuous interaction between organismal traits and an abiotic landscape in which animals continually balance competing functional demands.

(3) The functional consequences of fossorial morphology are context dependent, because the relationship between form and performance depends on substrate properties, locomotor mode and phylogenetic history.

(4) Future progress will depend on integrating physiology, behaviour, morphology, biomechanics, and environmental physics in a common framework.

(5) Adopting this mechanistic perspective will advance our understanding of life underground, and help establish fossorial animals as powerful model systems for investigating how organisms interact with complex and dynamic environments.

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IX. Author contribution

DG and GJT conceived the study. DG led the writing of the manuscript, with critical input from MBC, JEC, and GJT.

X. Data availability

The data and code necessary to reproduce our figures can be accessed from: https://doi.org/10.5281/zenodo.22209333.

XI. Conflict of interest

None.

XII. References

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XIII. Tables

Table 1. Open questions about the physiology, behaviour, and performance of fossorial amphibians and reptiles, along with potential approaches to answer them, and their broader biological significance.

Open question	Proposed approach	Relevance
How do fossorial amphibians and reptiles integrate thermal and hydric information when selecting underground microhabitats?	Use laboratory hydrothermal gradients in which temperature and soil moisture are manipulated independently or simultaneously while continuously recording body temperature, hydration state, movement, and microhabitat selection	Reveals behavioural decision rules underlying hydrothermal trade-offs and identifies environmental thresholds governing subterranean habitat selection
How do underground respiratory environments influence physiology and behaviour?	Expose animals to ecologically realistic combinations of oxygen and carbon dioxide while measuring metabolic rate, ventilation, and body temperature selection	Determines whether respiratory constraints directly influence energy balance, and thermoregulation

How do multiple environmental variables interact to influence underground decisions?	Conduct factorial experiments manipulating temperature, moisture, respiratory gases, and soil mechanics simultaneously.	Identifies interactions and trade-offs among environmental drivers, providing a mechanistic understanding of subterranean behaviour
How do fossorial animals regulate seasonal dormancy?	Combine environmental manipulations with automated underground tracking or telemetry across simulated seasonal cycles	Clarifies the mechanisms governing overwintering, aestivation, and seasonal energy conservation
How do substrate properties influence burrowing performance?	Measure burrowing speed, force production, energy expenditure, and endurance across soils differing in compaction, moisture, texture, and particle size	Determines how soil mechanics constrain locomotion, habitat use, and underground performance
Do repeated morphological adaptations lead to convergent functional performance?	Compare morphology and standardised performance metrics across species occupying similar and contrasting substrates	Reveals whether repeated morphological evolution results in predictable functional convergence
Which fossorial species are most vulnerable to environmental change?	Combine physiological, behavioural and environmental data within mechanistic biophysical and species distribution models	Predicts range shifts, identifies vulnerable species, and informs

conservation planning under future climate scenarios

1565

XIV. Figures

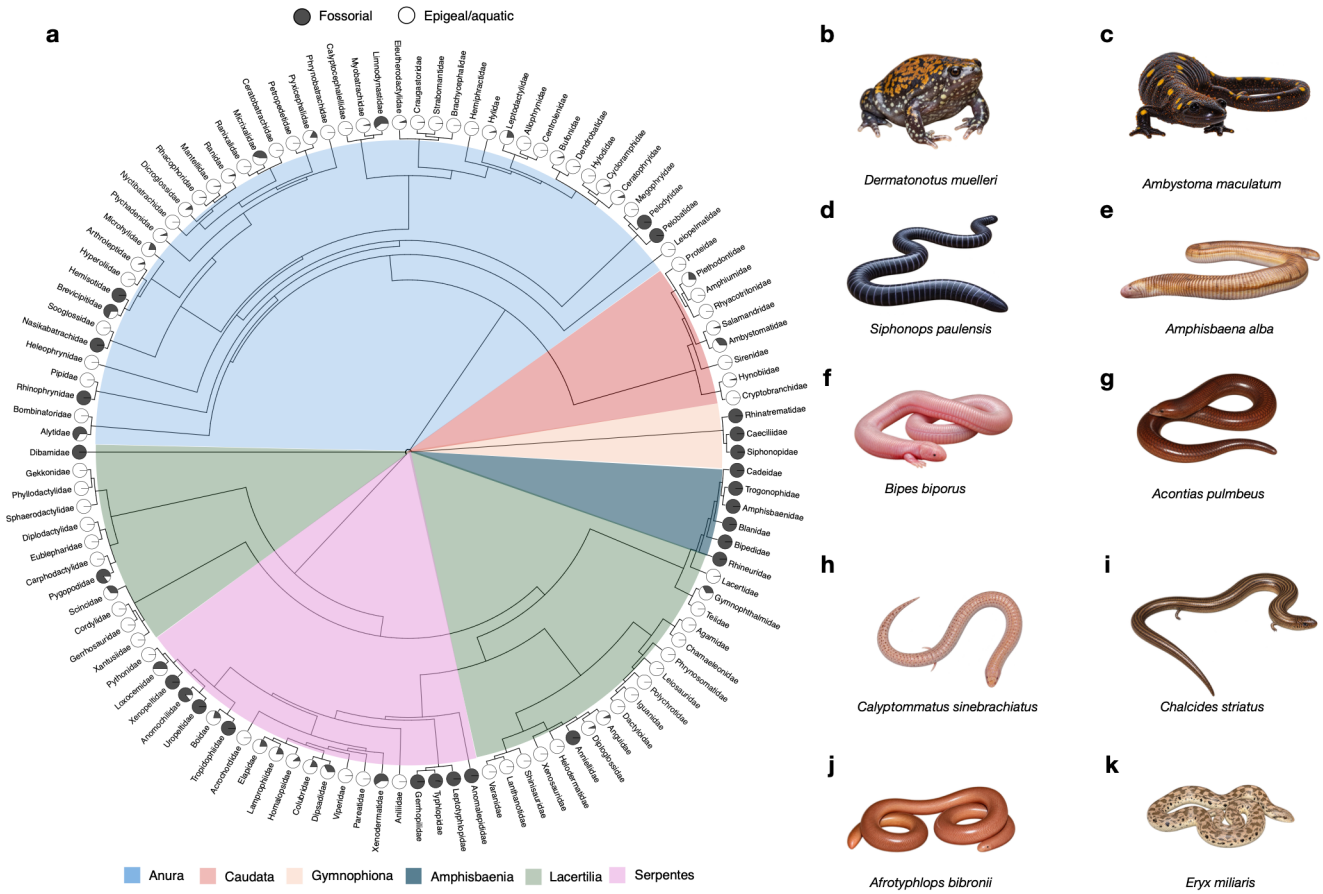
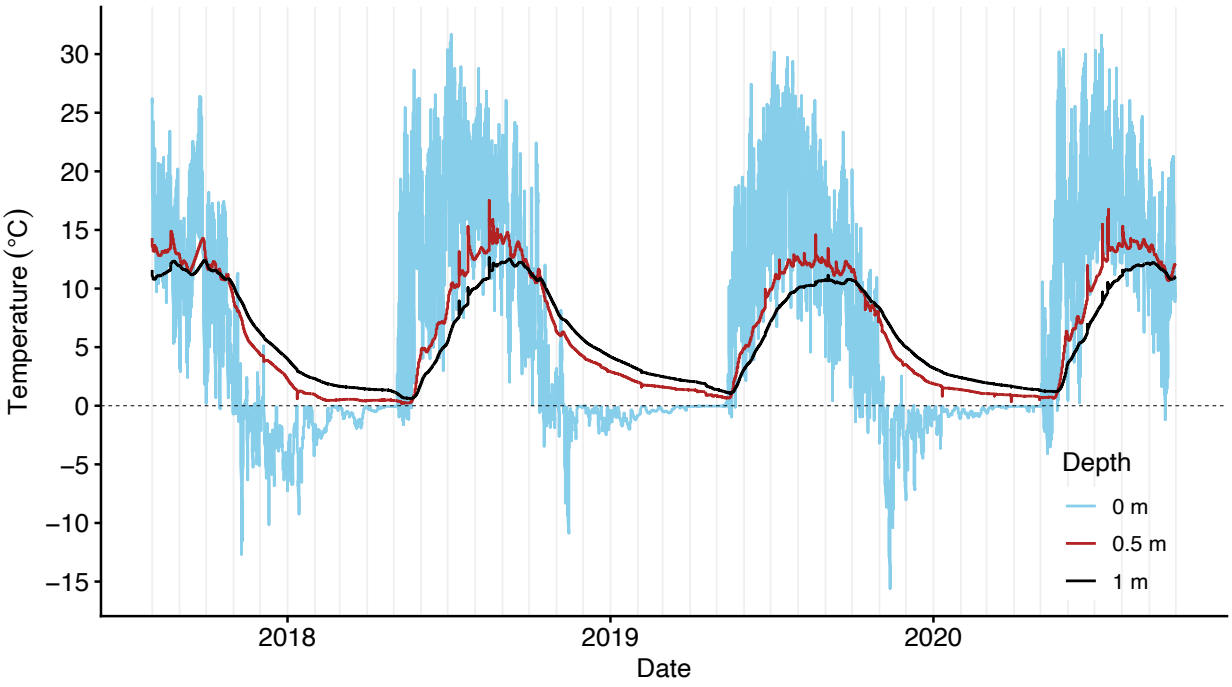
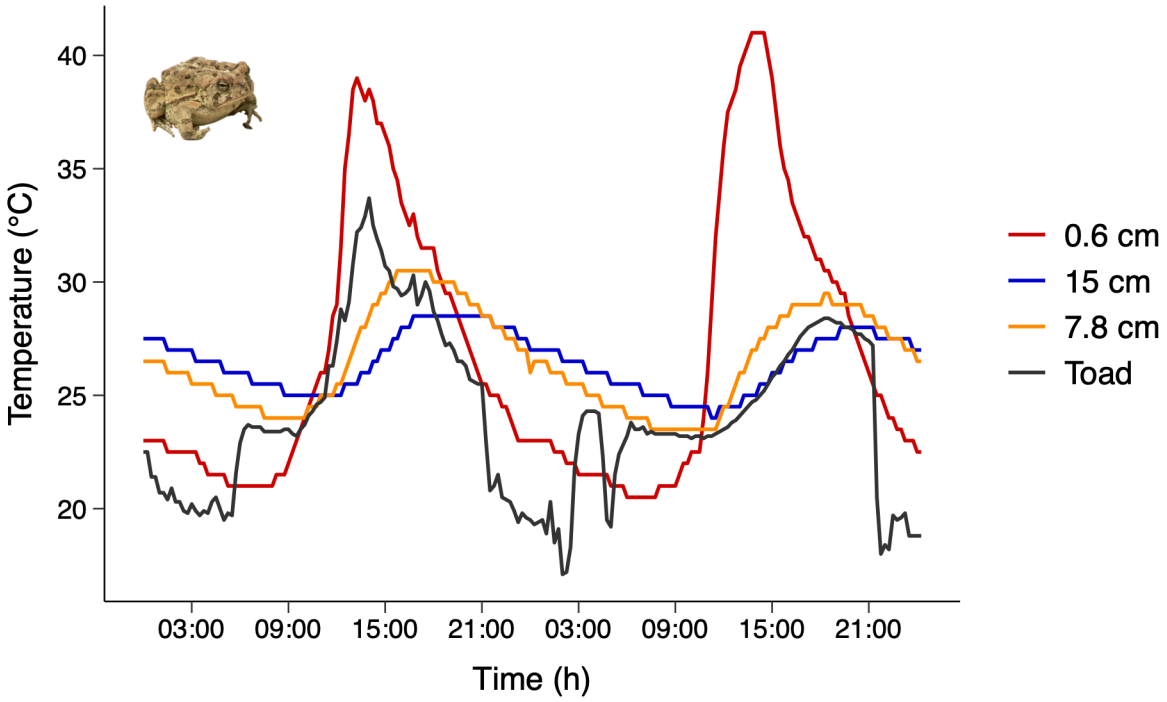


Figure 1. Phylogenetic distribution and morphological diversity of fossorial amphibians and squamates. (**a**) Family-level phylogeny of Amphibia and Squamata, with circles representing the proportion of species classified as fossorial or epigeal/aquatic based on data from Bars-Closel *et al*. (2017) and Oliveira *et al*. (2017). (**b–k**) Representative taxa illustrating the diverse morphology of fossorial species. Photos (**b**, **d**, and **e**) are courtesy of Lucas Botelho; photo (**c**) by Danilo Giacometti. The remaining photos were obtained from iNaturalist under CC BY-NC licenses.



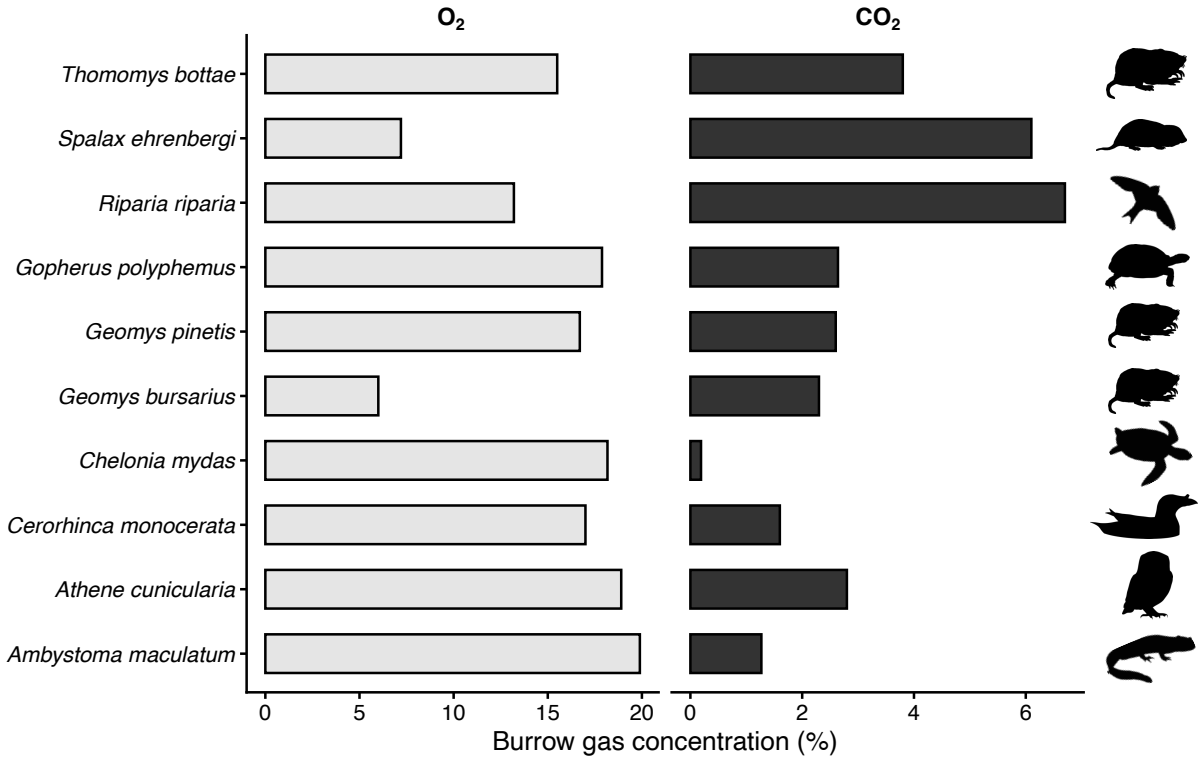
1575

1576 **Figure 2.** Thermal profile at different depths in Bat Lake, Algonquin Provincial Park, ON,
1577 Canada, highlighting how shallow depths may experience greater thermal fluctuations than
1578 deeper layers. Depths are representative of the underground environments occupied by mole
1579 salamanders (*Ambystoma* spp.) that live in the forest surrounding the lake. Redrawn from
1580 Moldowan *et al*. (2022).



1581

1582 **Figure 3.** Temporal changes in operative temperatures measured at three soil depths and body
1583 temperatures of free-ranging Fowler's toad (*Anaxyrus fowleri*). Shallow soil exhibited the
1584 greatest diel thermal fluctuations, whereas deeper layers buffered temperature variation. Toads
1585 adjusted the depth at which they were buried in response to thermal variation in the soil.
1586 Redrawn from Forget-Klein & Green (2021). Inset photo by Laura Perlick (U.S. Fish and
1587 Wildlife Service; public domain).



1588

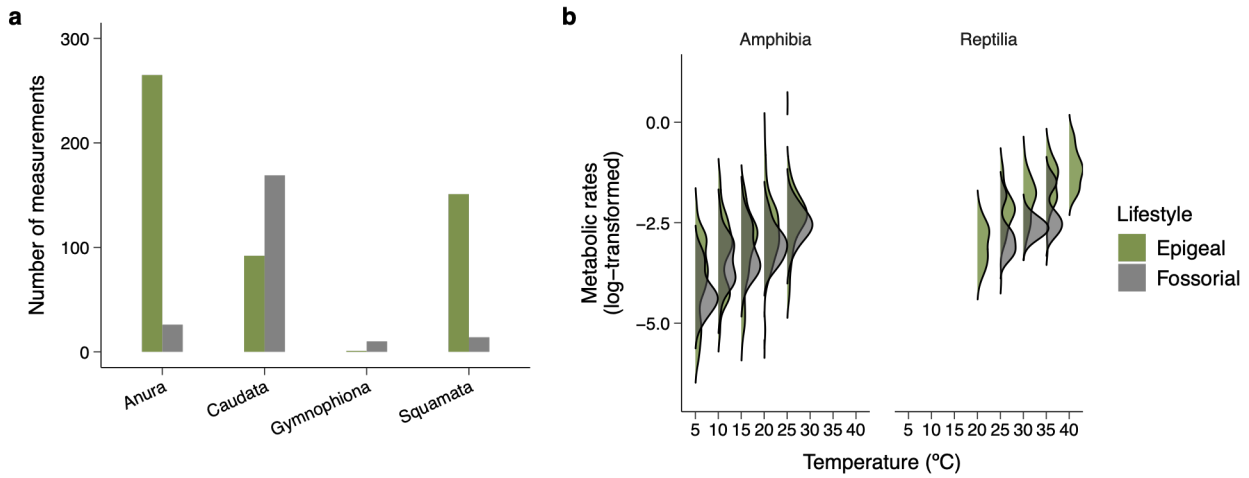
1589 **Figure 4.** Minimum oxygen and maximum carbon dioxide concentration (%) measured from

1590 burrows of different species of fossorial vertebrates. The extent to which burrows remain

1591 normoxic and normocarbic, or become hypoxic and hypercarbic varies across species. Data for

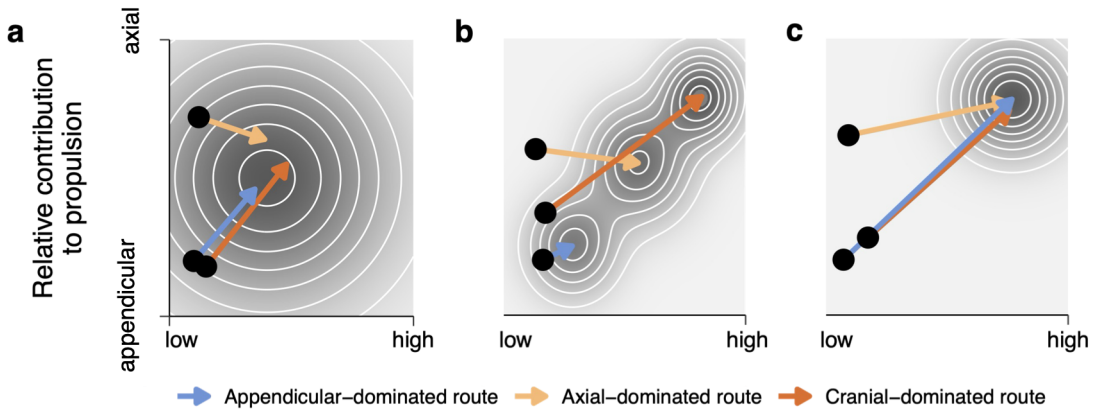
1592 all species were obtained from the literature, except for *Ambystoma maculatum* (D.G. & G.J.T.,

1593 unpublished observations). Silhouettes were obtained from PhyloPic's public domain.



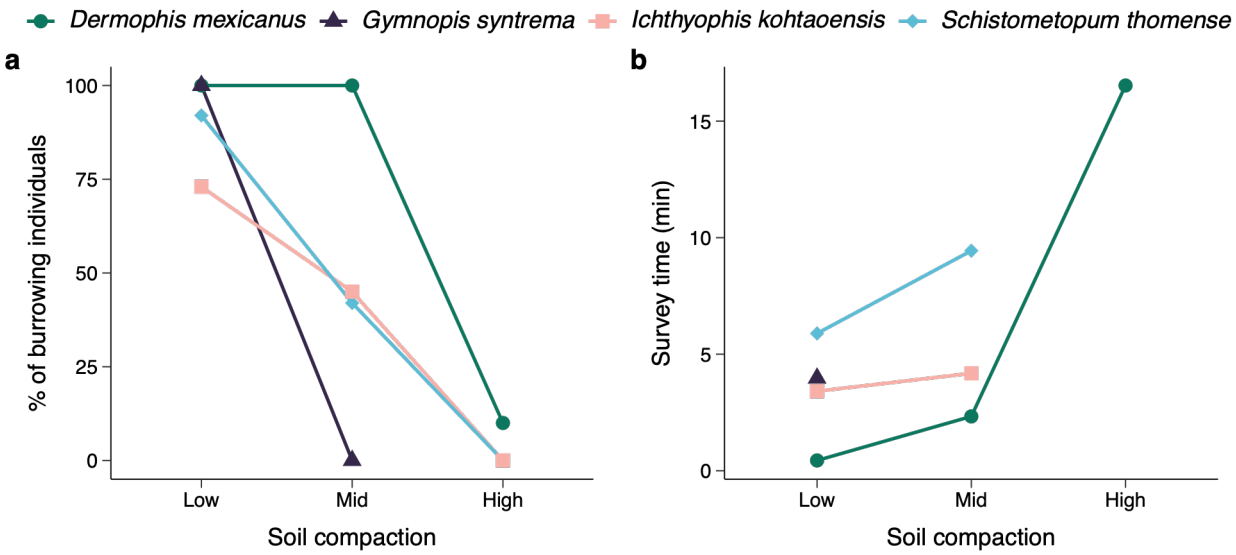
1594

1595 **Figure 5.** Metabolic rate measurements across fossorial and epigeal amphibians and reptiles. (**a**)
1596 Number of metabolic rate measurements available for each taxonomic order and lifestyle
1597 category. (**b**) Density distributions of mass-specific metabolic rates (log-transformed) across
1598 experimental temperatures for fossorial and epigeal amphibians and reptiles. Data from Andrews
1599 & Pough (1985) and Giacometti & Tattersall (2023).



1600

1601 **Figure 6.** Conceptual depiction of context-dependent landscapes of fossorial ecomorphology. (**a**)
1602 Pre-existing tunnels generate a broad performance plateau, allowing distinct morphological
1603 combinations to achieve similar performance. (**b**) Cohesive substrates generate multiple local
1604 optima associated with alternative locomotor strategies. (**c**) Loose and granular substrates
1605 produce a narrower optimum toward an integrated, highly derived phenotype, predicting
1606 convergence among lineages with different ancestral morphologies. In all panels, shading
1607 represents predicted performance, from lower (light) to higher (dark), across variation in cranial
1608 specialisation and the relative contribution of appendicular versus axial propulsion. Black circles
1609 indicate lineage-specific ancestral phenotypes.



1610

1611 **Figure 7.** Effects of soil compaction on the burrowing behaviour of four caecilian species. (**a**)
1612 Percentage of individuals that successfully burrowed under each level of soil compaction. (**b**)
1613 Mean time required for individuals to disappear into the substrate, illustrating the increasing
1614 difficulty of burrowing as soil compaction increased. Soil compaction was measured as the force
1615 required for soil penetration. Low < 0.0078 kg cm^{-2}, Mid = 0.078 kg cm^{-2}, and High = 0.250 kg
1616 cm^{-2}. Redrawn from Ducey *et al.* (1993).