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1 **Foraging mode constrains the evolution of cephalic horns in lizards and** 2 **snakes**

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17 methods; squamates

18

19 **Abstract**

20 A phylogenetically diverse minority of snake and lizard species exhibit rostral and ocular
21 appendages that substantially modify the shape of their heads. These cephalic horns have
22 evolved multiple times in diverse squamate lineages, enabling comparative tests of
23 hypotheses on the benefits and costs of these distinctive traits. Here, we demonstrate
24 correlated evolution between the occurrence of horns and foraging mode. We argue that
25 although horns may be beneficial for various functions (e.g., camouflage, defence) in
26 animals that move infrequently, they make active foragers more conspicuous to prey and
27 predators, and hence are maladaptive. We therefore expected horns to be more common in
28 species that ambush prey (entailing low movement rates) rather than in actively searching
29 (frequently moving) species. Consistent with that hypothesis, our phylogenetic comparative
30 analysis of published data on 1939 species reveals that cephalic horns occur almost
31 exclusively in sit-and-wait predators. This finding underlines how foraging mode constrains

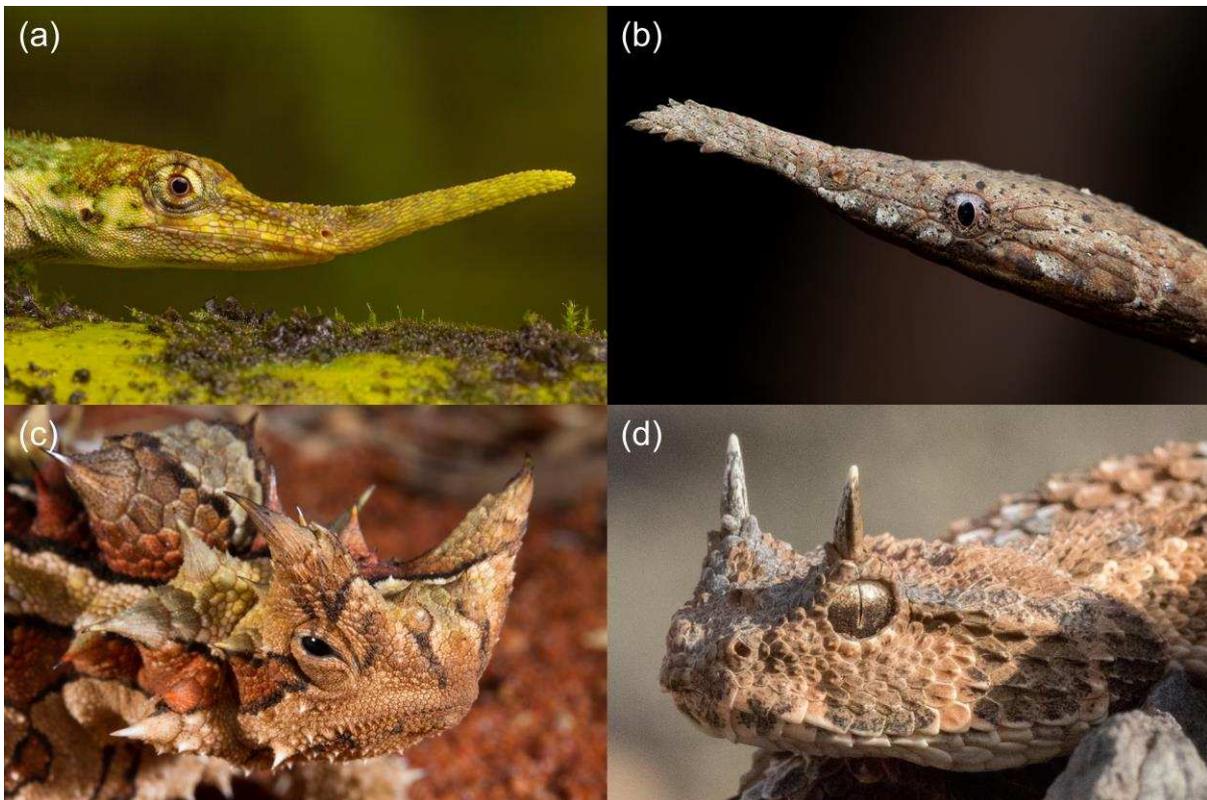
32 the morphology of squamates and provides a compelling starting point for similar studies in
33 other animal groups.

34

351. BACKGROUND

36 The heads of many animals support eye-catching appendages. Such species range from
37 hose-nosed weevils to rhinoceroses, and from angler fish to narwhals. The functions of
38 these protruding cephalic structures are well understood in some groups (e.g., dung beetles
39 and ungulates [1]), but less so in others, including squamate reptiles. The heads of
40 numerous species of lizards and snakes are adorned with crests, spines, spikes, or other
41 projections (which we refer to as 'horns' - Figure 1). These spectacular appendages may play
42 a role in aspects such as foraging [2,3], enhancement of camouflage (by disrupting the
43 outline of the head) [4–6], protection [7–11], and intraspecific interactions including combat
44 and courtship [12–15]. Phylogenetic associations between horns and species' morphology,
45 ecology, and habitat have been used to infer fitness advantages of horns (e.g., [10,16–19]).
46 In contrast, the potential costs of possessing such structures have rarely been mentioned.

47



48

49 Figure 1. Examples of the diversity of cephalic horns in squamates. Rostral appendages in
50 *Anolis proboscis* (a) and *Langaha madagascariensis* (b); squamosal-parietal and supra-ocular
51 horns in *Moloch horridus* (c) and supra-ocular horns in *Cerastes cerastes* (d). Photo credits:
52 Javier Ábalos Álvarez (a); Frank Deschandol (b); Stephen Zozaya (c); Laura Ruysseveldt (d).

53

54 Morphological traits entail both benefits and costs, and the evolution of any trait is driven
55 by the balance between those two sides of the equation. For example, body armour in
56 cordylid lizards provides protection (e.g., in *Ouroborus cataphractus* [20]) but restricts
57 locomotion and flexibility, and thus is most evident in sedentary heavy-bodied species [21].
58 Costs for cephalic horns might include hindering locomotion and rendering an individual
59 more visible when it moves. In general, camouflage works best when an animal is immobile
60 [22,23]. We posit that protruding structures on the head may render a moving reptile more
61 easily discernible from the background, hence more obvious to both predators and prey, or
62 even hinder movements [24]. This hypothesis predicts that the benefit-to-cost ratio for
63 cephalic horns is higher in sedentary individuals than in more active ones.

64

65 Many squamate species can be classified as either sit-and-wait foragers or actively foraging
66 species [25,26]. Foraging style in squamates is associated with a suite of behavioural,
67 physiological, morphological and life history characteristics, supporting the existence of a
68 ‘foraging syndrome’ [27,28]. If horns are more conspicuous when animals are moving, we
69 expect that these structures should occur more often in sit-and-wait predators than in
70 widely foraging species. Here we test this hypothesis through phylogenetically informed
71 comparative analyses.

72

732. MATERIALS AND METHODS

74

75 (a) DATA COLLECTION

76 We retrieved data on foraging mode from an updated version of the dataset of Meiri [29]
77 and other published studies (see electronic supplementary material, Table S1 for full list of
78 references), for a total of 1939 squamate species classified either as active or sit-and-wait
79 foragers. Species with mixed foraging modes, and those lacking data on foraging mode,

80 were excluded. For each of these 1939 species, we then collected data on the presence and
81 absence of horns, visually assessed from images on ReptileDatabase [30] and ‘research
82 grade’ observations from iNaturalist [31]. When images of a species were not available from
83 those sources, we consulted recent publications on the taxon or original descriptions (see
84 electronic supplementary material, Table S1 for full list of references).

85

86 We defined as ‘horns’ any protruding structure present in the rostral, ocular or occipital
87 area of the head (Figure 1). Some of these structures fall into the category of ‘true horns’,
88 being bony protrusions covered by a keratin sheath (e.g., in some chameleons [32]),
89 whereas others are protuberant bony cranial processes and/or soft projections composed of
90 connective tissue covered by one or multiple keratinous scales. Rostral horns were usually
91 composed of either enlarged nasal (sub-, post-, supra-, inter-), rostral and/or fronto-nasal
92 scales (e.g., in *Anolis proboscis*, *Langaha madagascariensis*, *Cyclura cornuta*). Ocular horns
93 were either protruding ocular (supra-, post-) or supraciliary scales (e.g., in *Moloch horridus*,
94 *Cerastes cerastes*, *Correlophus ciliatus*), whereas occipital horns included all overgrowths of
95 parietal (e.g., crests, processes) and squamosal (e.g., tufts, spines, horns, casques) scales
96 (e.g., in *Basiliscus basiliscus*, *Phrynosoma cornutum*, *Anolis chamaeleonides*). Species with
97 any of those structures were considered horned. Species exhibiting appendages only in the
98 adult stage (e.g., *Ceratophora stoddartii*), or in only one sex (e.g., *Anolis proboscis*), or
99 species showing horn polymorphism (e.g., *Cerastes cerastes*), were also classified as horned.
100 If horns were not evident from either images or descriptions, the species was classified as
101 hornless. Species with elongated snouts (e.g., *Oxybelis fulgidus*) and/or specialised rostral
102 scales (e.g., ‘hog-nose’, ‘shovel-nose’, ‘leaf-nosed’, and ‘quill-snouted’ snakes) were also
103 classified as hornless because they lack protruding structures. We mapped our data on a
104 time-calibrated phylogeny for squamates [33] for phylogenetic analyses.

105

106 (b) ANALYSES

107 Prior to phylogenetically informed data analysis, we explored associations between cephalic
108 horns and foraging mode using chi-square (χ^2) statistics. After pruning the phylogenetic tree
109 to include only the 1939 species covered in this study, we tested for phylogenetic signal in
110 both variables by calculating Fritz and Purvis’ D [34] (10 000 permutations; ‘phylo.d’
111 function; ‘caper’ package [35]). We then ran phylogenetic generalized linear models (PGLM

112 logistic regression; 'phyloglm' function; 2000 bootstraps; 'phylolm' package [36]) to quantify
113 the predictive power of foraging mode on the presence of cephalic horns (binomial variable:
114 horned = 1; hornless = 0). We used Pagel's [37] PGLS method ('fitPagel' function; 'phytools'
115 package [38]) to test for a phylogenetic correlation between horns and foraging mode. We
116 conducted such tests under both 'equal rates' (ER) and 'all rates different' (ARD)
117 evolutionary models, exploring different dependency relationships between the two
118 variables. Next, we performed ancestral state reconstructions via stochastic character
119 mapping (1000 simulations; 'make.simmap' function [38]) to estimate the number of
120 transitions from hornless to horned in squamate evolutionary history. We ran
121 reconstructions under both ER and ARD scenarios and retained the most parsimonious
122 model (i.e., lowest number of transitions).

123

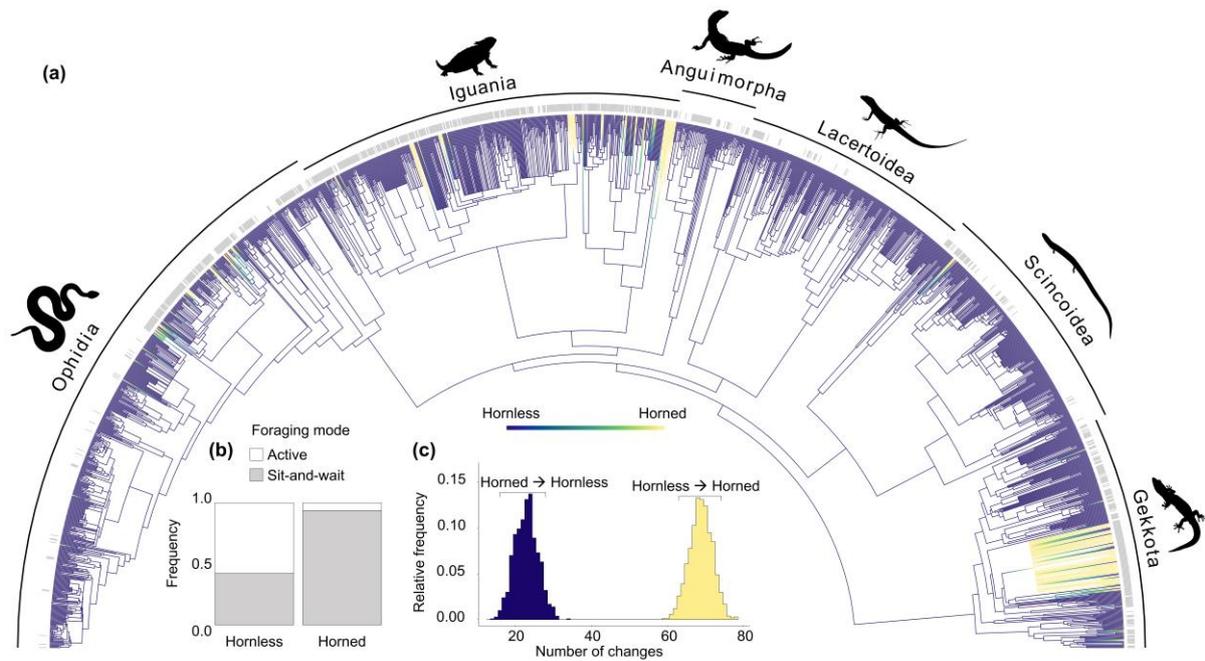
124 To test the robustness of our results with respect to phylogenetic uncertainty, we repeated
125 the PGLM test on a set of 1000 trees, randomly sampled from the 10 000 trees used to
126 generate our adopted phylogeny [39] via the 'tree_phyglm' function of the 'sensiPhy'
127 package [40].

128

1293. RESULTS

130 Of the 1939 squamate species in this study, 53% were reported to be active foragers (n =
131 1031) and 47% to be sit-and-wait foragers (n = 908). Nine percent (n = 175) of all species
132 were horned and 91% were hornless (n = 1764) (electronic supplementary material, Table
133 S2a). The vast majority of horned squamates were sit-and-wait foragers (94%; n = 164; vs
134 active foragers 6%, n = 11; $\chi^2 = 167.77$, d.f. = 1, $p < 0.001$) (Figure 2b; electronic
135 supplementary material, Table S2b). Phylogenetically informed analyses corroborated the
136 relationship between foraging mode and cephalic horns ($\beta \pm SE: 0.810 \pm 0.3$, pseudo- $R^2 =$
137 0.5 , $z = 2.7$, $p < 0.01$) (electronic supplementary material, Table S3a). Also, all Pagel's tests
138 supported correlated evolution between horns and sit-and-wait foraging ($p < 0.001$)
139 (electronic supplementary material, Table S4a).

140



141

142 Figure 2. Horn expression across the adopted squamate phylogeny (a), with proportion of
 143 foraging mode (b) and frequency of trait gains and losses (c). Squamate phylogeny (1939
 144 species) indicating the posterior probability of cephalic horns, obtained via stochasticity
 145 mapping along branches (ER model; 1000 replicates), with sit-and-wait foragers indicated at
 146 the branch tips of the tree (a). Frequencies of horn losses (from horned to hornless state)
 147 and gains (from hornless to horned state) across the 1000 replicates are also shown (c),
 148 together with the proportion of active and sit-and-wait foragers amongst hornless and
 149 horned squamates considered in this study (b). Silhouettes images from PhyloPic
 150 (<https://www.phylopic.org/>).

151

152 Fritz and Purvis' phylogenetic signal test revealed that horn presence exhibited moderately
 153 strong phylogenetic clumping ($D < 0$, $p_0 = 0.65$, $p_1 = 0$), as expected under a Brownian
 154 motion model of trait evolution ($D = 0$) (electronic supplementary material, Table S5).
 155 Stochastic character mapping over 1000 reconstructions (model = ER) revealed an average
 156 of 92 transitions (Figure 2a), of which 69 were independent gains (range = 63-74) and 23
 157 were losses (range = 17-29) of horns across squamate phylogeny (Figure 2c; electronic
 158 supplementary material, Table S6a).

159

160 Furthermore, the evolutionary models considering interdependent evolution between the
161 two variables scored best (lower AIC), suggesting that foraging mode had a role in horn
162 evolution, but also that cephalic appendages (when present) influenced the species'
163 foraging habits (electronic supplementary material, Table S4b). Results from the sensitivity
164 analysis ($\beta \pm SE: 0.855 \pm 0.3, z = 2.9, p < 0.01$ - electronic supplementary material, Table S3b)
165 furtherly supported our initial PGLM results (electronic supplementary material, Table S3a),
166 suggesting that they are not influenced by phylogenetic uncertainty.

167

1684. DISCUSSION

169 Consistent with our predictions, cephalic horns occur mostly in sit-and-wait predators. This
170 result is unlikely to be due to chance, as correlated evolutionary changes between horns
171 and sit-and-wait foraging have occurred several times in squamate phylogeny (Figure 2).
172 Furthermore, our analyses show not only that shifts between states in both horns and
173 foraging mode are common in squamates (electronic supplementary material, Table S6-7),
174 but also that these shifts have happened together - or in tandem, in many cases (electronic
175 supplementary material, Figure S1). This pattern suggests that our significant results are
176 not driven by phylogenetic inertia, where a few clades happen to retain both traits [41].

177

178 Previous research has identified multiple plausible functions (benefits) of horns. For
179 example, cephalic ornaments in many lizards are more developed in adult males than in
180 females, and are used in territorial displays, courtship and/or male-male combat bouts (e.g.,
181 [8,14]). Where present in both sexes, horns may also serve in species recognition (e.g., in
182 chameleons [12]). Other plausible functions of cephalic horns include foraging: for example,
183 rostral projections of the tentacled snake (*Erpeton tentaculatum*) are mechanosensory
184 structures that aid this sit-and-wait predator to capture fish [3]. Plausibly, sharp rigid spines
185 on the head also may discourage a predator from seizing the animal (e.g., in *Phrynosoma*
186 spp. [10] and *Moloch horridus* [11]). Lastly, cephalic horns may enhance the effectiveness of
187 camouflage for a more sedentary reptile by disrupting the outline of the head [6]. Except for
188 the latter hypothesis, all these functions should apply equally to active-foragers as to sit-
189 and-wait predators, and thus cannot explain the strong association between cephalic horns
190 and foraging mode revealed by our analyses.

191

192 Turning to the costs of cephalic horns, we suggest that complex protruding structures on an
193 animal's head render it more detectable against the background while moving. Thus, a trait
194 that enhances camouflage when the animal is immobile may have the reverse effect when
195 the animal moves rapidly [22,42]. Theoretical and empirical studies on camouflage
196 consistently demonstrate that detection of a complex outline is dependent on movement
197 [43,44], but more direct experimental tests would be valuable. Ideally, such studies would
198 incorporate rates of movement. Some chameleons, for example, move slowly but
199 consistently through the habitat despite their overall reliance on sit-and-wait foraging [45].
200 At such slow rates of movement, cephalic horns may still help in camouflage.

201

202 Some of the most interesting cases of cephalic horns involve horned species that are active
203 foragers rather than sit-and-wait predators: that is, exceptions to the general rule. If
204 cephalic horns are a disadvantage to a fast-moving animal (by rendering it more
205 conspicuous), why do some active foragers have cephalic horns? The answer may lie in
206 features either of the horns, or of the movement patterns of the species involved. For
207 example, males of the sea snake *Emydocephalus annulatus* develop pronounced rostral
208 spines only during the mating season and use them to prod females during courtship
209 [13,46]. In that case, the small (and temporary) forward-projecting spine would have little
210 impact on the snake's visibility to predators, especially given the low movement rates of this
211 species and the scarcity of predators in shallow-water habitats [47]. Small forward-
212 projecting rostral spines are also seen in some of the other 'exceptions to the rule', such as
213 the arboreal snakes *Ahaetulla nasuta* and *Philodryas baroni*. For these active foragers,
214 however, horns may be more beneficial (e.g., for camouflage) than detrimental.

215

216 The functional relationships between cephalic ornamentation and foraging mode seen in
217 our broadscale comparisons could be explored in more detail within clades that exhibit
218 variation in these traits. An interspecific link between body shape (often associated with
219 foraging mode) and investment into defensive and offensive structures (e.g., spines and
220 horns) has been documented in several lizard lineages, whereby stockily built species have
221 larger structures [21,48]. In phrynosomatid lizards, horn size appears to depend on
222 predation pressure [10], and species with larger cephalic horns are slower and more

223 specialised sit-and-wait foragers than are congeners with smaller horns [48]. Correlations
224 between habitat type and horn morphology in vipers [17], and ornamentation
225 conspicuousness (including horns) in agamid lizards [6], further support the idea that
226 variation in habitat and, consequently in exposure to predators, may affect a species'
227 investment into cephalic horns.

228

229 Intraspecific variation in horn elaboration also provides exciting research opportunities. For
230 example, a single population of vipers can contain individuals with horns and others
231 without, sometimes in the same litter (e.g., *Cerastes cerastes* [49]). It would be fascinating
232 to see if the correlation between foraging mode and cephalic horns occurs within, as well as
233 among, populations. Studying finer-scale variation in foraging behaviour (e.g., movement
234 rates [26,50]) and degrees of horn development, rather than treating both as binary
235 variables, may also prove insightful.

236

237 Cephalic structures often differ between the sexes (e.g., in *Langaha* spp. [51] and
238 *Ceratophora* spp. [16]) and/or are developed in one sex only (e.g., *Anolis proboscis* [15,52]).
239 In agamid lizards, the evolution of sexually dimorphic cephalic and body ornamentations
240 occurred either in one sex independently or in both sexes contemporarily, with subsequent
241 transition to male-biased dimorphism [53]. We hypothesise that in such cases, sex
242 differences in horn size may be associated with sex differences in movement patterns (and
243 perhaps in foraging mode), as commonly occur in squamates (e.g., *Acrochordus arafurae*
244 [54,55]).

245

246 Our results reinforce suggestions that cephalic horns in lizards and snakes have evolved for
247 a range of functions, and have arisen independently multiple times. This leaves many
248 possibilities open for future studies on the significance and function of such enigmatic
249 structures. Importantly, our analyses suggest that the evolution of horns in squamate
250 reptiles may have been influenced more heavily by constraints (i.e., failure of camouflage
251 when the animal moves frequently) than by advantages.

252 While we tested only squamates, our hypothesis may apply to additional taxa. Cephalic
253 appendages are found in many other species, from arthropods to vertebrates including fish,
254 amphibians, and mammals [1]. In all those groups, there are examples of foraging modes

255 that range from ambush to active searching [56–60]. We predict that the association
256 between foraging mode and cephalic horns will apply to such groups as it does to lizards and
257 snakes. Analyses of selective forces for trait elaboration must consider costs as well as
258 benefits when interpreting diversity in organismal morphology.

259

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267 **Data Accessibility.** Data and codes are available from the Dryad Digital Repository:
268 <https://doi.org/10.5061/dryad.fqz612jzm> [61].

269 The data are also provided as table S1 in electronic supplementary material [62].

270

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