



## Short communication

## Aquatic adaptations in the four limbs of the snake-like reptile *Tetrapodophis* from the Lower Cretaceous of Brazil



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## ABSTRACT

The exquisite transitional fossil *Tetrapodophis* – described as a stem-snake with four small legs from the Lower Cretaceous of Brazil – has been widely considered a burrowing animal, consistent with recent studies arguing that snakes had fossorial ancestors. We reevaluate the ecomorphology of this important taxon using a multivariate morphometric analysis and a reexamination of the limb anatomy. Our analysis shows that the body proportions are unusual and similar to both burrowing and surface-active squamates. We also show that it exhibits striking and compelling features of limb anatomy, including enlarged first metapodials and reduced tarsal/carpal ossification – that conversely are highly suggestive of aquatic habits, and are found in marine squamates. The morphology and inferred ecology of *Tetrapodophis* therefore does not clearly favour fossorial over aquatic origins of snakes.

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The ecology of snake origins remains highly debated, with most recent studies favouring a burrowing (Longrich et al., 2012; Hsiang et al., 2015; Yi and Norell, 2015) rather than an aquatic (Caldwell and Lee, 1997; Lee, 2005) origin. Intriguingly, however, the most comprehensive study of the external relationships of snakes has reinstated marine lizards (dolichosaurs, mosasaurs, etc.) as their nearest relatives (Reeder et al., 2015); while this can still be consistent with fossorial habits in the common ancestor of snakes, it reveals that aquatic habits at least characterised the closest snake relatives. *Tetrapodophis*, a candidate stem-snake retaining all four limbs, from the Lower Cretaceous of Brazil, is exceptionally complete and provides important and unexpected insights into this debate, as well as snake origins in general (Martill et al., 2015). *Tetrapodophis* is much more complete than other recognised or putative stem-snakes so far identified (Caldwell et al., 2015), and

was interpreted as a burrower with limbs potentially used for seizing and holding prey, thus supporting a fossorial origin of snakes (Martill et al., 2015).

Burrowing habits of *Tetrapodophis* were proposed on the basis of its elongate body, small limbs, and “short” tail (Martill et al., 2015), but while morphometric measurements were presented, no quantitative analysis was performed. Here, we place *Tetrapodophis* in a multivariate morphometric analysis expanded from earlier work (Wiens et al., 2006; Müller et al., 2011), which reveals that *Tetrapodophis* occupies an unusual, thinly-populated region of morphospace. While the body shape of *Tetrapodophis* is consistent with fossorial habits, it also closely resembles certain (surface-active) terrestrial lizards; in addition, our quantitative analysis reveals that non-fossorial lifestyles cannot be excluded. We also highlight a suite of highly distinctive traits in the limbs that are consistent with aquatic adaptation, as well as affinities with marine lizards; these traits were mentioned and/or illustrated in the original description, but their significance was not discussed. *Tetrapodophis*, like many elongate limb-reduced tetrapods, therefore represents an enigmatic mélange of characters that can be

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interpreted as either aquatic or fossorial. These ecomorphological results also have potential implications for both the phylogenetic affinities of *Tetrapodophis* and for the ecology of snake origins.

## 1. Materials and methods

We expanded a multivariate morphometric analysis of lepidosaurs (lizards, snakes, tuataras) of known ecology (Wiens et al., 2006; Müller et al., 2011) by adding *Tetrapodophis* and fossil marine squamates (pleurosaurs, dolichosaurs, mosasauroids). The original habitat divisions were reduced by combining three overlapping categories (cryptic, saxicolous, terrestrial) into one category (terrestrial); a new category (fully aquatic) was added to accommodate the additional taxa included, leading to 5 habitat groups (terrestrial *sensu lato*, arboreal, fossorial, semi-aquatic, fully aquatic).

The added taxa were scored for seven variables by direct observation or from the primary literature (sources listed in Supplementary File 1): snout-vent length (SVL), snout-eye length (SEL), tail length (TL), forelimb length (FLL), hind limb length (HLL), number of forelimb digits (FING), number of hind limb digits (TOES). Principal component analysis (PCA) was performed to visualise the distribution of the 5 ecomorphs and *Tetrapodophis*. In the focal PCA analysis, all linear variables were scaled by dividing by head length (as indexed by snout-eye length, SE), giving *rel\_SVL*, *rel\_TL*, *rel\_FLL* and *rel\_HLL* (plus FING and TOES). A second PCA analysis was also performed where linear variables were scaled by dividing by SVL, giving *rel\_SEL*, *rel\_TL*, *rel\_FLL* and *rel\_HLL* (plus FING and TOES). Head width could also have theoretically been measured and used to scale for size, but this dimension cannot be estimated in the crushed skull of *Tetrapodophis*, so employing this as a size index would have meant deleting the main taxon of interest from the analysis.

In each PCA analysis all six variables were log-transformed (after the addition of 1 to eliminate unloggable zero values: Wiens et al., 2006). PCA was performed in R (package Rcmdr: Fox, 2005) and employed the correlation matrix since the variables were not all to the same scale and spanned very different ranges. PC1 and PC2 were each regressed against SEL, in the first analysis, and against SVL, in the second analysis. Both SEL and SVL were loosely correlated with PC1 ( $R^2 = 0.25^*$  and  $0.12^*$  respectively), but SEL had a much weaker correlation with PC2 ( $R^2 0.02$  vs  $0.56^*$ ) [ $* = \text{significant at } P = 0.05$ ]. Subsequent analyses, and the Discussion, focus on the datasets that were transformed by scaling to SEL; however, analyses using data scaled to SVL were performed and gave similar results as discussed below. Scaling by SVL might be less effective at correcting for body size in reptiles because body length is poorly correlated with mass in reptiles of very different shapes (tetrapodal versus serpentine), and using SVL as a size index potentially overestimates the size of elongate, narrow reptiles (Lee et al., 2013).

A non-phylogenetic multivariate analysis of variance (MANOVA) using PAST (Hammer et al., 2001) was used to test for differences in the multivariate means of the 5 known ecomorphs considered together (Wilks lambda, Pillai trace), and in pairs (Hotelling's  $T^2$  with Bonferroni correction for multiple tests). As these revealed significant differences, linear discriminant analysis (LDA) was carried out using R (package Vegan: Oksanen et al., 2016) and PAST to determine how accurately the morphometric traits predicted the (known) habitat of each living species, and also what habitat(s) these traits predicted for *Tetrapodophis*.

We also re-evaluated the limb morphology of *Tetrapodophis*, highlighting several important features (evident in the original description but not discussed), which are relevant to inferring the ecology of this taxon. Examination of *Tetrapodophis* (by MC and RR) confirmed the general accuracy of the original description and

illustrations for the traits considered here (morphometric and meristic measurements, limb morphology).

## 2. Results and discussion

The PCA analysis (data scaled to SEL; Fig. 1, File 1) revealed that most (82%) of the variance was captured by the first 2 principal components, with loadings suggesting that PC1 represents shape change associated with body elongation, and PC2 relative tail length. The bivariate plot of the first 2 PCs confirms that *Tetrapodophis* falls near fossorial forms, close to long-bodied but tetrapodal skinks that burrow through loose sediments and leaf litter, such as *Sepsina angolensis* and *Chalcides (Sphenops) sphenopsiformis*. However, *Tetrapodophis* lies only slightly outside the concave hull of surface-active terrestrial forms: notably, the nearest point is not a fossorial taxon, but the cryptozoic anguimorph *Celestus (Sauresia) agasepsoides* (Fig. 1) which has slightly longer limbs and a slightly shorter body. Furthermore, the central region of morphospace occupied by *Tetrapodophis* is sparsely populated: very few living squamates exhibit similar body proportions, suggesting that similar transitional fossils will be exceptionally rare.

PCA with data scaled to SVL gave similar results (Fig. S1); *Tetrapodophis* falls closest to (but outside) the fossorial forms, in a thinly occupied region of morphospace. Here, however, it plots quite distinctly outside of the terrestrial (*sensu lato*) forms.

The MANOVA, using the data scaled by SEL, revealed that the 5 ecomorphs considered simultaneously had significantly different multivariate means (Pillai  $F = 5.32^*$ ). Pairwise tests (Table S1) revealed that this result is largely driven by two of the ecomorphs, the burrowing ecomorph (which differs from each of the 4 other ecomorphs), and the aquatic ecomorph (which differs significantly from the terrestrial and fossorial ecomorphs). All other paired comparisons were not significantly different. MANOVA using the data scaled to SVL gave very similar results (Table S2).

These results were consistent with the LDA analysis (Fig. 2), which revealed that while all ecomorphs overlapped to some degree, the fossorial and aquatic ecomorphs also partly occupied unique regions of ecospace. 100% of the terrestrial ecomorph cloud, however, overlapped with one or more of the other ecomorphs. Because of this overlap, the LDA was especially poor at predicting the habitat of terrestrial species (18% accurately), but all other habitat groups were predicted with >47% accuracy (Table S3). When *Tetrapodophis* was added to the LDA analysis, it did not neatly fit any of the groupings (Fig. 2), but was predicted to most likely be fossorial (84%; Table S5); however, aquatic (10.3%) and terrestrial (5.5%) habits could not be excluded at  $P = 0.05$ . The caveat must be made, though, that the LDA was relatively poor at predicting the habitat of living species. LDA using the morphometric data scaled by SVL gave similar results (Fig. S2, Tables S4 and S6).

The analyses of the morphometric data suggest that *Tetrapodophis* may have exhibited some degree of burrowing habit, although the success rate of the LDA for inference of a fossorial lifestyle was only around 50%. Skeletal traits as reported by Martill et al. (2015), such as low neural spines, and inferred presence of accessory vertebral articulations, are also consistent with fossoriality, though the latter are present in many non-burrowing and even aquatic taxa (Romer, 1956; Russell, 1967; Caldwell, 2002; Caldwell and Palci, 2010; Gauthier et al., 2012). However, the position of *Tetrapodophis* close to terrestrial, non-burrowing forms in at least some analyses (Fig. 1) suggests that it wasn't highly committed to a burrowing lifestyle. The relatively gracile skull of *Tetrapodophis* is typical of squamates that move through soft sediments such as loose sand, and lacks the robustness found in squamates (e.g. blindsnakes and amphisbaenians) that burrow in

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