



## SYMPOSIUM

# Heterochronic Shifts Mediate Ecomorphological Convergence in Skull Shape of Microcephalic Sea Snakes

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**Synopsis** Morphological variation among the viviparous sea snakes (Hydrophiinae), a clade of fully aquatic elapid snakes, includes an extreme “microcephalic” ecomorph that has a very small head atop a narrow forebody, while the hind body is much thicker (up to three times the forebody girth). Previous research has demonstrated that this morphology has evolved at least nine times as a consequence of dietary specialization on burrowing eels, and has also examined morphological changes to the vertebral column underlying this body shape. The question addressed in this study is what happens to the skull during this extreme evolutionary change? Here we use X-ray micro-computed tomography and geometric morphometric methods to characterize cranial shape variation in 30 species of sea snakes. We investigate ontogenetic and evolutionary patterns of cranial shape diversity to understand whether cranial shape is predicted by dietary specialization, and examine whether cranial shape of microcephalic species may be a result of heterochronic processes. We show that the diminutive cranial size of microcephalic species has a convergent shape that is correlated with trophic specialization to burrowing prey. Furthermore, their cranial shape is predictable for their size and very similar to that of juvenile individuals of closely related but non-microcephalic sea snakes. Our findings suggest that heterochronic changes (resulting in pedomorphosis) have driven cranial shape convergence in response to dietary specializations in sea snakes.

## Introduction

Viviparous sea snakes are a prolific radiation comprising more than 60 highly marine species that share a common ancestor with the Australasian terrestrial elapids (taipans, death adders, tiger snakes) only 8–18 million years ago (Sanders and Lee 2008; Lee et al. 2016). In particular, the *Hydrophis* clade of sea snakes has anomalously fast speciation rates and is ecologically very diverse, with a wide range of head and body sizes and proportions (Voris and Voris 1983; Lee et al. 2016). The most extreme shape changes are linked to highly specialized diets of burrowing eel prey (Voris and Voris 1983; Sherratt et al. 2018), the so-called “microcephalic” sea snakes, which have tiny heads and narrow forebodies used to probe burrows on the seafloor, while their

hindbodies can be three times the girth of their forebodies. Previous studies have shown that the evolution of this ecomorph has occurred at least nine times in *Hydrophis* sea snakes and involves a complex interplay of heterochronic shifts in embryonic and postnatal development (Sanders et al. 2013b; Sherratt et al. 2018, 2019). Microcephalic species develop higher pre-cloacal vertebral counts than most other sea snakes (implicating changes in somitogenesis during embryonic development), and their hindbodies grow too much greater sizes than their forebodies during the postnatal stage (which is suggestive of a Hox gene transition) (Sherratt et al. 2019). Although head and forebody size appear to be coupled during development, the cranial shape changes that have accompanied the reduced head/

forebody sizes in these species have yet to be examined.

Snake skulls are well known for having a derived, highly kinetic morphology that allows ingestion of large prey. As is typical for vertebrates, snake heads grow with negative allometry relative to body length, so that juvenile snakes have larger heads relative to their bodies while adults have smaller heads relative to their bodies (e.g., King 2002; Vincent et al. 2006). Microcephalic sea snakes are an extreme in this respect because they can attain a large adult body size while having a relatively tiny head (Fig. 1A). Moreover, minimum prey size and overall snake size (i.e., body length) have a positive allometric relationship, indicating that large snakes eat even larger prey and generally drop small prey from their diets (e.g., Shine 1991; King 2002).

Here we investigate the potential selective pressures and developmental mechanisms responsible for the diminutive head of microcephalic sea snakes. Building upon previous studies (Sherratt et al. 2018, 2019) we examine evolutionary and ontogenetic patterns of cranial shape diversity in sea snakes to understand the extent that morphology is predicted by dietary specialization and examine whether cranial shape of microcephalic species may be a result of heterochronic processes. Specifically, we first assessed whether the dietary specialization on burrowing eel prey, which is known to promote convergent evolution in body shape (Sherratt et al. 2018), also promotes convergent evolution in cranial shape. Given that we found convergent evolution, we then addressed whether this convergence is explained by similar developmental processes by investigating evolutionary and ontogenetic allometry. We tested whether the diminutive head is explained by phylogenetic patterns of allometric scaling (evolutionary allometry, derived from the species-averaged adult data). Then we examined patterns of ontogenetic allometry across species to deduce whether the head shape of adult microcephalic species is similar to that of juveniles of other non-microcephalic species. If evolutionary allometry is underpinned by ontogenetic allometry, this would suggest that small heads are the result of heterochronic processes such as pedomorphosis, that is the retention of juvenile head size (and thus shape) into adulthood.

## Materials and methods

### Samples and CT scans

We sampled 123 adult specimens from 30 species of sea snakes from the genera *Hydrophis*, *Microcephalophis*, *Hydrelaps*, *Parahydrophis*, and

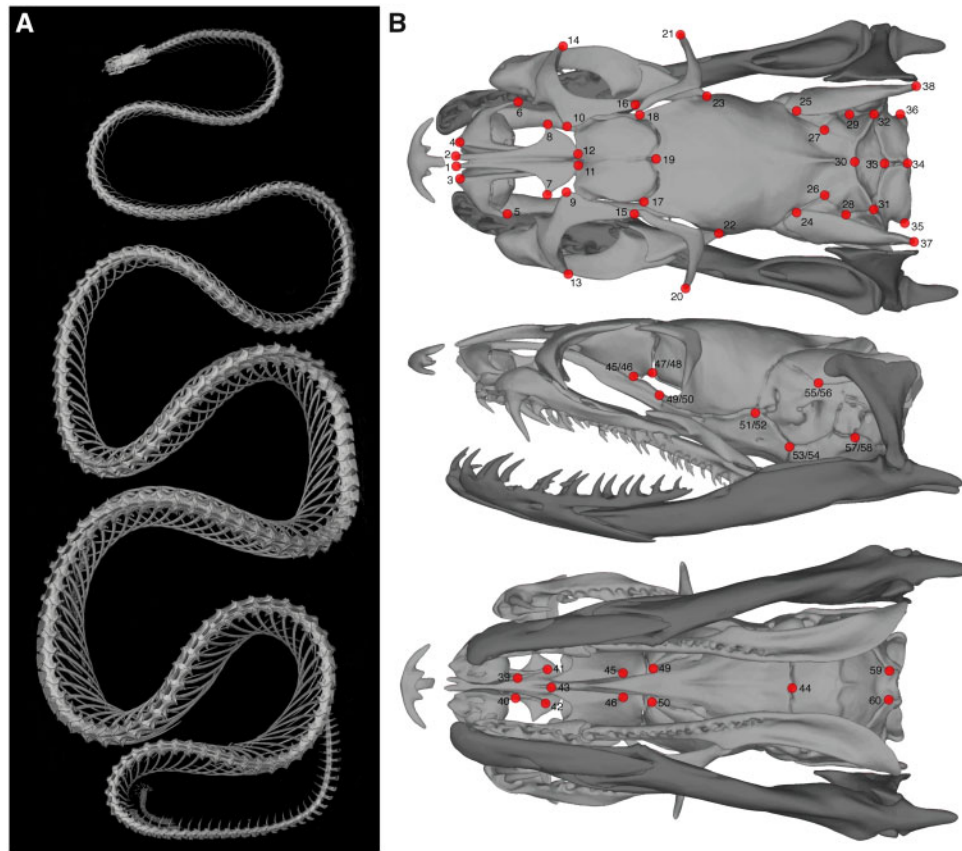
*Ephalophis*, which together form a monophyletic group (Sanders et al. 2013a). We also sampled 14 neonates or young juvenile specimens from 10 species across the phylogeny and known body form diversity (*Hydrophis curtus*, *H. stokesii*, *H. major*, *H. elegans*, *H. donaldi*, *H. ocellatus*, *H. peronii*, *H. fasciatus*, *H. macdowelli*, *Hydrelaps darwiniensis*). Specimens were sampled primarily from the herpetology collection at the South Australian Museum, Adelaide, and supplemented by loans from other institutions (Supplementary Table S1). Digital representations of the skulls of these specimens were obtained using X-ray micro-computed tomography ( $\mu$ CT) data acquired through Skyscan 1076 and Skyscan 1276 high-resolution  $\mu$ CT-scanners at Adelaide Microscopy, University of Adelaide. The skulls were digitally segmented by applying a threshold for bone using Avizo v.9.0 (Visualization Sciences Group 2013). After digitally removing the vertebrae, the skull was exported as a 3D isosurface model (a triangular mesh of approximately 1 million faces).

### Landmarking and geometric morphometric analysis

To characterize cranial shape, the 3D models were digitized with 60 landmarks (27 paired and 6 along the midline) (Fig. 1B and Supplementary Table S2) placed on all of the relatively-immovable bones of the cranium using IDAV Landmark Editor v.3.6 (Wiley et al. 2007), to reduce shape variation due to preservation. Landmark coordinates were subjected to generalized Procrustes superimposition (Rohlf and Slice 1990) to remove the effects of translation, rotation, and scale while taking into account object symmetry (Klingenberg et al. 2002) using the R package *geomorph* v.3.0.7 (Adams et al. 2018). The resulting Procrustes residuals were used as shape coordinates in the statistical analyses described below, all performed in R statistical environment v.3.5.2 (R Development Core Team 2018). Cranial size was estimated as centroid size of the landmark configurations, which is the square root of the sum of squared distances of a set of landmarks from their centroid.

### Statistical analysis

To examine the influence of trophic ecology on cranial shape, species averages of cranial shape were tested for correlation with the proportion of burrowing prey in the diet (following Sherratt et al. 2018) using a phylogenetic generalized least squares (PGLS) analysis for highly-multidimensional data (Adams 2014) implemented with the “procD.pgls” function in *geomorph*. Comprehensive dietary information is



**Fig. 1** A) A digital rendering of a microcephalic sea snake skeleton (*Microcephalophis gracilis* FMNH 178673), demonstrating the small skull atop a narrow forebody with a wide hindbody that is three times the girth of the forebody. **B)** The 60 landmarks capturing cranial shape on a representative skull (*Hydrophis ocellatus* WAM R174522). Landmarks shown on skull in dorsal (top), lateral (middle), and ventral views (bottom). Numbers refer to [Supplementary Table S2](#). Images obtained by  $\mu$ CT.

available on Dryad digital repository (<https://doi.org/10.5061/dryad.48r5h.1>); the proportion of prey known to have a burrowing life habit was calculated from the diet sources for each species. The proportion is a continuous variable ranging from 0 to 1, where 1 equals 100% of the prey items having a burrowing life habit. The phylogenetic hypothesis used is a maximum clade credibility tree from a dated Bayesian analysis, details of which are given in [Sherratt et al. \(2018\)](#). To visualize this relationship in a phylogenetic context, we used a phylomorphospace approach, whereby the phylogeny was projected into a scatterplot of the first two principal axes of a principal components analysis of average cranial shape and estimated internal nodes (estimated as phylogenetic independent contrasts, using the “pic” function in *ape* v. 5.0 [[Paradis et al. 2004](#)]).

We then tested whether microcephalic species, known to have convergently evolved a similar body shape and size, have also convergently evolved similar cranial shapes. We used the test for convergent evolution implemented in the R package *convevol* v.

1.3 ([Stayton 2015](#)). The statistic  $C_1$  was calculated, which measures whether the putative convergent taxa occupy a smaller area of morphospace than would be expected under Brownian motion and their estimated ancestral positions in morphospace. Morphospace was defined as the first six PC axes of the shape space, that together explain 75% of the variance; subsequent PC axes each contribute <5% of the variance. Statistical significance was evaluated using phylogenetic simulation: the variables were simulated along the phylogeny using Brownian motion, using the “sim.char” function in *geiger* v. 2.0.6 ([Harmon et al. 2008](#)), and the observed test measure  $C_1$  was compared with a distribution of 1000 simulated values using the maximum clade credibility tree.

The allometric framework was used to investigate whether the shape of the small crania of microcephalic species is predictable based on their size. Allometry, the relationship between biological traits and size, can be considered at three biological levels: during ontogeny (ontogenetic allometry), among

individuals of the same age class (static allometry), and among species (evolutionary allometry) (Klingenberg 1996). Finding relationships between these levels allows us to understand the role that allometry plays, either as a contributor or a constraint, on morphological diversity (Gould 1966; Cheverud 1982; Klingenberg and Zimmermann 1992).

Broadly there are two ways in which morphological diversity can arise from the ancestral developmental trajectory, which can be assessed in the allometric framework (e.g., Mitteroecker et al. 2004; Strelin et al. 2016): (1) by maintaining the ancestral developmental trajectory but changing the stage at maturity via changes in the time or rate of development (heterochrony), as predicted by the ontogenetic scaling hypothesis, or (2) by departures from the ancestral developmental trajectory by changes in either the intercept and/or the slope of the shape–size relationship. Although allometry does not explicitly examine morphological changes with time, some inferences about heterochronic changes can be made from studies of allometric scaling at different levels (Klingenberg 1998; see also Esquerré et al. 2017).

We examined evolutionary and ontogenetic allometry in the cranial shape data to see whether ontogenetic trajectories were following a global trajectory defined by all sampled species (supporting the ontogenetic scaling hypothesis) or were diverse in their slopes and falling outside of the evolutionary trajectory. Allometric patterns were visualized using a multivariate regression approach (Klingenberg 2016) of the shape data on log-transformed centroid size, and the regression score (a univariate summary of multivariate regression coefficients, Drake and Klingenberg 2008) was calculated for visualization purposes. An alternative approach is to use the size–shape space visualized with principal components analysis (Mitteroecker et al. 2004), which we found to yield visually identical results; thus we only present the regression approach.

Evolutionary allometry is the correlated shape change with size along branches of the phylogeny (Klingenberg 1996) and was statistically assessed by calculating the species averages of cranial shape and size for adult specimens and evaluating the relationship with a PGLS. For ontogenetic allometry, a multivariate regression of all specimens (adult and juvenile) was performed to visualize the ontogenetic trajectories for individual species within the evolutionary space. Due to the low sample sizes for each species, the ontogenetic trajectories could not be compared statistically using a standard ANOVA.

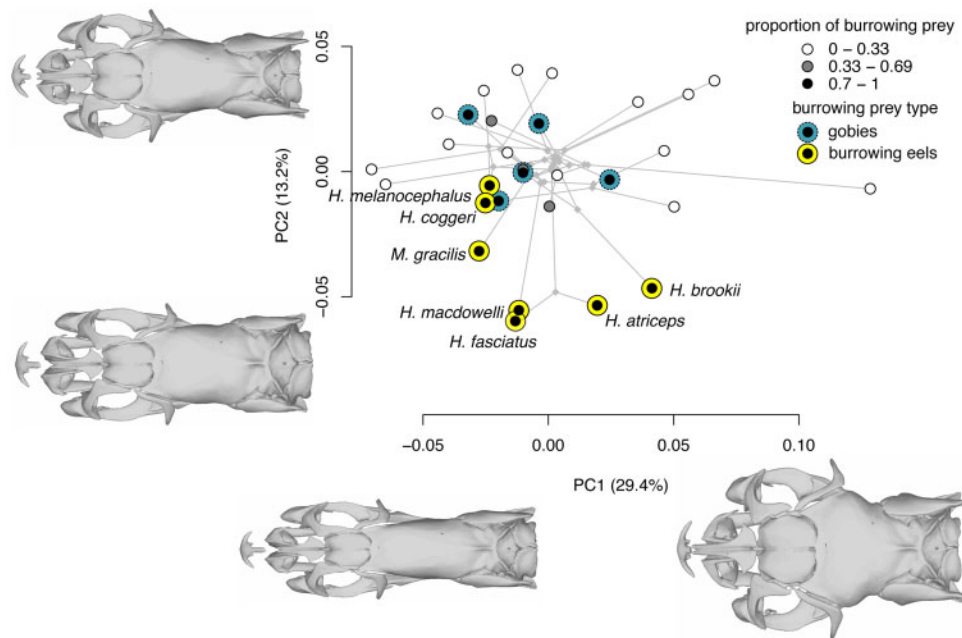
## Results and discussion

Sea snake cranial shape is diverse among species but strongly correlated with trophic ecology, specifically the proportion of burrowing prey, which predicts 13% of cranial shape variation (PGLS,  $R^2 = 0.134$ ,  $F_{(1,28)} = 4.32$ ,  $P = 0.001$ ), and 64% of cranial size variation (PGLS,  $R^2 = 0.64$ ,  $F_{(1,28)} = 49.7$ ,  $P = 0.001$ ). These results are driven by convergent evolution in seven microcephalic species that are more similar to one another than would be expected under a Brownian motion model of evolution ( $C_1 = 0.14$ ,  $P = 0.0089$ ), and clearly occupy a distinct region of cranial morphospace compared with other species (all microcephalic species have negative values of PC2; Fig. 2). Hence, the convergent body shape changes previously reported for these burrowing eel specialists (Sherratt et al. 2018) appear to be accompanied by convergent changes in cranial shape. It is notable, however, that the value of  $C_1$  indicates that evolution has closed only 14% of the distance in cranial shape among these species relative to their estimated ancestral positions in morphospace, compared with the  $C_1$  value of 55% reported for these species' body shape in the previous study (Sherratt et al. 2018).

Given that microcephalic sea snakes appear to have repeatedly evolved similar cranial shapes, we assessed whether these convergent changes are driven by similar developmental processes by analyzing patterns of evolutionary and ontogenetic allometry. Analyses of evolutionary allometry show that interspecific variation in cranial shape is significantly correlated with cranial size (PGLS,  $R^2 = 0.164$ ,  $F_{(1,28)} = 5.49$ ,  $P = 0.001$ ). Cranial size explains 16% of the shape variance among sea snake species, which is a relatively low proportion but is within the range reported for other vertebrate clades (e.g., Sanger et al. 2012; Sherratt et al. 2014; Marcy et al. 2016; Mitchell et al. 2018). The strong correlation between diet and head form reported above is evident in the allometric trajectory (Fig. 3A), where the burrowing eel specialists occupy the lower end of the allometric trajectory, goby specialists have an intermediate position, and species with negligible burrowing prey in their diet occupy the higher end. The evolution of a smaller head thus appears to be related to specialization on burrowing prey. Relatively small heads are also found in goby specialists (Fig. 3A), but these species have a low relative girth and have evolved a smaller body size overall (Sherratt et al. 2018).

The pattern of evolutionary allometry in cranial shape aligns broadly with ontogenetic allometry. The individual ontogenetic allometric trajectories of





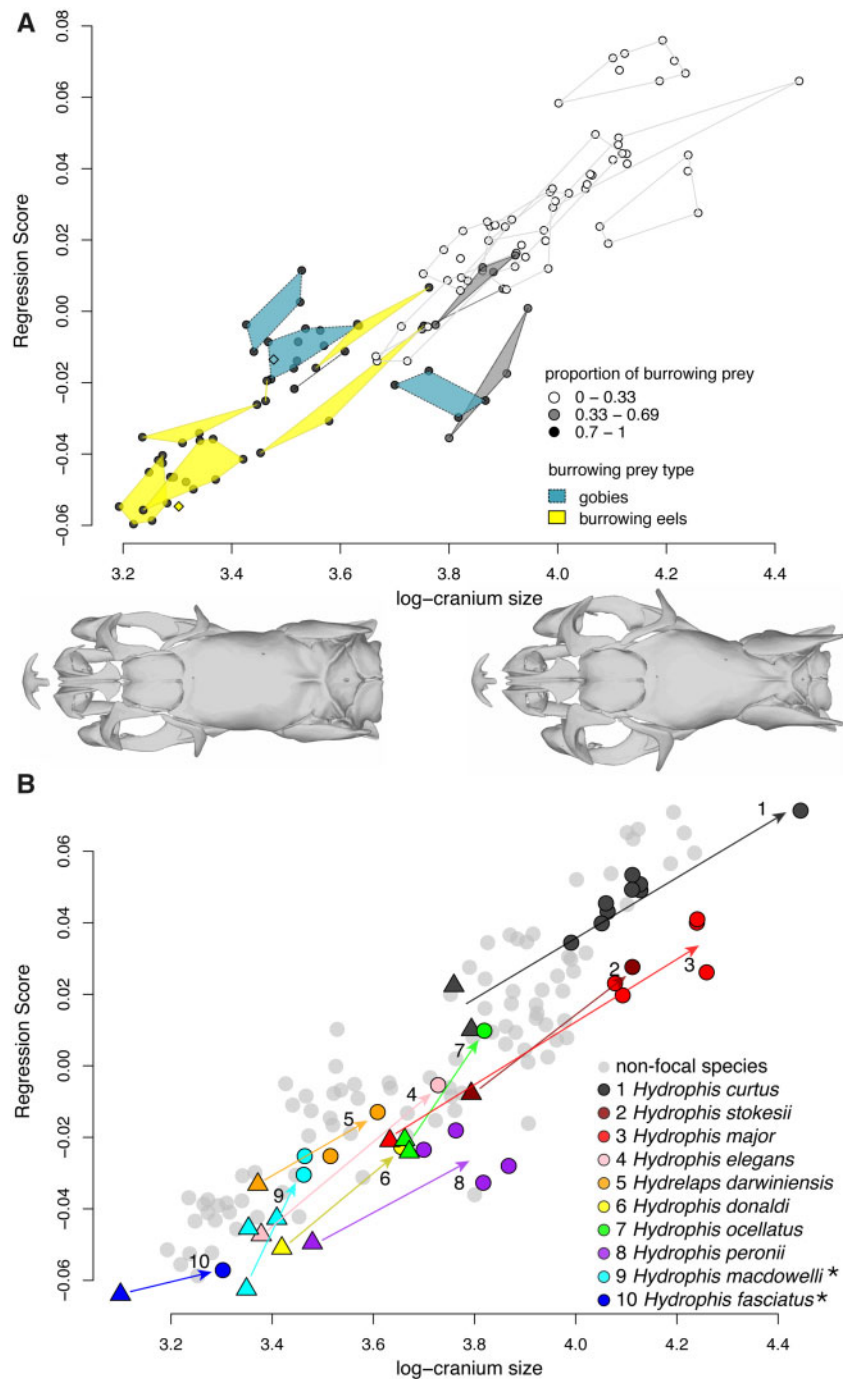
**Fig. 2** Phylomorphospace of average adult cranial shape for 30 species, with representative shapes of the extremes of PC1 and PC2 shown as a skull model (from Fig. 1B) warped to the landmark configurations using the thin-plate spline approach. PC2 is the axis that best captures the shift towards microcephalic morphotypes (negative values of PC2). Points are overlaid with species dietary information following Sherratt et al. (2018). The microcephalic species, those that feed on burrowing eels, are labeled.

the 10 species fall along the global trajectory made up of adults of all species (Fig. 3B). These results indicate that adult crania of some species show broadly similar morphology for their size to juveniles of other species. For example, among non-microcephalic forms, adult specimens of *H. donaldi* resemble juvenile *H. major* and *H. ocellatus* (Fig. 3B). Notably, the small heads of microcephalic species are not only predictably shaped for their size but resemble the juveniles of non-microcephalic species (Fig. 3). This is particularly evident in the close proximity of adult *H. maddowelli* (microcephalic) and juvenile *Hydrelaps darwiniensis* (non-microcephalic) in Fig. 3B. Based on these results, we suggest that the evolution of microcephalic sea snakes involved heterochronic developmental changes resulting in a pedomorphic skull morphology compared with non-microcephalic sea snakes.

Figure 2 shows that the second principal component (PC2) approximates the direction of evolutionary change toward microcephalic species. The “microcephalic” direction of this axis is associated with a proportionally larger braincase and orbit, a short, wide basisphenoid, and a shorter supratemporal. Interestingly, the same morphological changes observed in microcephalic forms are also typical of neonate/juvenile macrostomatan snakes in general, as shown in a previous study that compared juvenile and adult snakes representative of various lineages

(Palci et al. 2016), and one that examined ontogenetic change in a single xenodontine species (Murta-Fonseca and Fernandes 2016). This lends further support to the hypothesis that microcephalic skull form in sea snakes is the result of pedomorphosis. Furthermore, these results are consistent with recent findings from the postcranial skeleton (Sherratt et al. 2019) that demonstrate the narrow forebody is achieved through heterochronic shifts during ontogeny. Further work is required in order to discern how the head and forebody are coordinated during development and decoupled from the hindbody, particularly the mechanisms of such implicit “mosaic heterochrony” or “dissociated heterochrony” (David 1990; McKinney and McNamara 1991), and the mechanisms responsible for this morphology (Alberch et al. 1979; Raff and Wray 1989).

Although our results suggest convergent evolution of cranial shape in microcephalic sea snakes, we also find notable cranial shape diversity among the seven microcephalic species. This variation is visible in Fig. 2 as a spread of points along both PC axes and is not correlated with differences in relative fore- versus hindbody girth among microcephalic species (PGLS,  $R^2 = 0.186$ ,  $F_{(1,5)} = 1.14$ ,  $P = 0.336$ ), implying that microcephalic species are not just more or less extreme pedomorphic variants of the adult cranial shape. A contribution of novel, taxon-specific features are indicated particularly along PC1,



**Fig. 3** The allometric relationship of cranial shape and size for 123 adult specimens of 30 species of sea snake. Cranium size (log-transformed centroid size) is plotted against the regression score of cranial shape, where points represent a single individual specimen. The shape change associated with the regression score is shown as a skull model (from Fig. 1B) warped to the landmark configuration of the minimum (left) and maximum size (right) using the thin-plate spline approach. **A**) Within-species variation shown as convex hulls (or line for two specimens, or diamond for one). Points are colored with species dietary information following Sherratt et al. (2018), see legend. The microcephalic species, those that feed on burrowing eels, are clustered at the bottom left of the graph. **B**) Ontogenetic series for 10 species, numbered according to legend; asterisks indicate microcephalic forms. Triangles indicate neonate/juvenile specimens, circles indicate adults. Arrows overlaid for illustrative purposes to demonstrate the approximate ontogenetic trajectory for each species. Transparent points are adult specimens of other species to illustrate global evolutionary allometry trajectory.

which is associated with relative head width and separates narrow (*M. gracilis*) versus broader head shapes (*H. brookii*). This disparity among microcephalic species is not unexpected given the phylogenetic distance between of these species, but also given that burrowing eels constitute a very broad dietary resource comprising several highly speciose and morphologically diverse families (Nelson 2006). Most diet data for sea snakes are records of semi-digested stomach contents that are rarely identified beyond family level, yet these indicate divergent dietary specializations among microcephalic species. For example, the microcephalic species *H. atriceps*, *H. brookii*, and *H. melanocephalus* often occur in sympatry and specialize, respectively, on false moray eels (Chlopsidae), worm/spaghetti eels (Moringuidae), and snake eels (Ophichthidae) (Voris and Voris 1983; Sanders et al. 2013b; Sherratt et al. 2018).

The diminutive size of the head coupled with a narrow forebody comprising many small vertebrae seen in microcephalic sea snakes raises questions regarding the biomechanical constraints on a head feeding in a crevice. The hypothesis that microcephalic species have a limited gape remains to be tested using approaches that integrate the elastic properties of soft-tissue with dimensions of skeletal elements (e.g., Jayne et al. 2018). Morphological traits associated with the microcephalic sea snake cranial shape such as large orbits and short jaws are found in fossorial terrestrial elapid snakes (e.g., *Simoselaps*, *Neelaps*) and fossorial xenodontine snakes that specialize on caecilian and amphisbaenian prey (Klaczko et al. 2016). This may suggest that these traits have adaptive significance related to feeding in space-limited environs, but this needs to be tested against the alternative hypothesis that these traits are simply a consequence of miniaturization and allometry (e.g., Hanken 1984; Wake 1986; Vallejo-Pareja et al. 2019).

## Conclusion

We have provided further evidence that trophic specialization has had a strong influence on whole body morphology in microcephalic sea snake species that feed upon burrowing prey. This study adds to the growing body of evidence that trophic diversification needs to be considered as a key influencer of snake skull morphology (e.g., Vincent et al. 2009; Hampton 2011; Klaczko et al. 2016) in addition to other ecological factors when estimating the evolutionary history of snakes (e.g., Da Silva et al. 2018). This study also found evidence that skull form in

microcephalic species appears to be the result of heterochronic shifts in postnatal development, where adult microcephalic snakes resemble neonates or juveniles of non-microcephalic species (i.e., pedomorphosis). Thus, it appears that heterochronic changes in skull development drive predictable morphological changes that are linked to dietary specialization in these species.

## Ethical statement

Not applicable.

## Data accessibility

Diet data and phylogenetic tree are available on Dryad (<http://dx.doi.org/10.5061/dryad.48r5h.2>), morphological data and R scripts are available on Figshare (<http://dx.doi.org/10.25909/5cb523d6c6e52>). The  $\mu$ CT slice data are stored in the digital archives of the South Australian Museum and also archived on MorphoSource ([www.morphosource.org](http://www.morphosource.org)) project ID P744.

## Author contributions

K.L.S., A.W., and E.S. conceived the study; A.P., E.S., A.W., and M.N.H. collected the data; E.S. and A.P. performed the statistical analyses; E.S., K.L.S., and A.P. wrote the manuscript with input from M.N.H. and M.S.Y.L.; all authors read and approved the final manuscript.

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## Supplementary data

Supplementary data are available at *ICB* online.

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