RESEARCH ARTICLE

Evolution of Cranial Shape in Caecilians (Amphibia: Gymnophiona)

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Abstract Insights into morphological diversification can be obtained from the ways the species of a clade occupy morphospace. Projecting a phylogeny into morphospace provides estimates of evolutionary trajectories as lineages diversified information that can be used to infer the dynamics of evolutionary processes that produced patterns of morphospace occupation. We present here a large-scale investigation into evolution of morphological variation in the skull of caecilian amphibians, a major clade of vertebrates. Because caecilians are limbless, predominantly fossorial animals, diversification of their skull has occurred within a framework imposed by the functional demands of head-first burrowing. We examined cranial shape in 141 species, over half of known species, using X-ray computed tomography and geometric morphometrics. Mapping an existing phylogeny into the cranial morphospace to estimate the history of morphological change (phylomorphospace), we find a striking pattern: most species occupy distinct clusters in cranial morphospace that closely correspond to the main caecilian clades, and each cluster is separated by unoccupied morphospace. The empty spaces in shape space are unlikely to be caused entirely by extinction or incomplete sampling. The main caecilian clades have different amounts of morphological disparity, but neither clade age nor number of species account for this variation. Cranial shape variation is clearly linked to phyletic divergence, but there is also homoplasy, which is attributed to extrinsic factors associated with head-first digging: features of caecilian crania that have been previously argued to correlate with differential microhabitat use and burrowing ability, such as subterminal and terminal mouths, degree of temporal fenestration (stegokrotaphy/zygokrotaphy), and eyes covered by bone, have evolved and many combinations occur in modern species. We find evidence of morphological convergence in cranial shape, among species that have eyes covered by bone, resulting in a narrow bullet-shaped head. These results reveal a complex history, including early expansion of morphospace and both divergent and convergent evolution resulting in the diversity we observe today.

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Introduction

One major aim in evolutionary biology is to understand the history and causes of morphological diversification. Because fossils are not widely available for all groups, one way to retrace the history is with a top-down approach, surveying modern biological diversity and using statistical methods to infer the historical events leading to this diversity (Felsenstein 2004; Pennell and Harmon 2013).

Among the current array of comparative methods, two main approaches are traditionally used to pursue this goal: examining the distribution of species in a morphological space (morphospace) across successive time slices (Ciampaglio et al. 2001; Pie and Weitz 2005; Erwin 2007), and mapping phenotypic characters onto a phylogeny (e.g. Brooks and McLennan 1991). By synthesizing these, it is possible to simultaneously explore the structure of morphological variation among species and infer aspects of the evolutionary history of morphological traits (Rohlf 2001, 2002; Sidlauskas 2008; Klingenberg 2010; Klingenberg and Marugán-Lobón 2013; Monteiro 2013). Macroevolutionary patterns examined in this framework have revealed substantial insights into the origins and maintenance of biological diversity (e.g. Clabaut et al. 2007; Figueirido et al. 2010; Dornburg et al. 2011; Monteiro and Nogueira 2011; Klingenberg et al. 2012). One advantage of this approach is that patterns of morphospace occupation inferred within a phylogenetic context can give insights into the patterns (mode), and magnitude (tempo) of evolution (sensu Simpson 1944), even in the absence of a fully-resolved and time-calibrated phylogenetic hypothesis (e.g. Sidlauskas 2008). This is important, because even in the age of molecular phylogenetic data, phylogenies for few major clades are densely sampled, well resolved, and time calibrated.
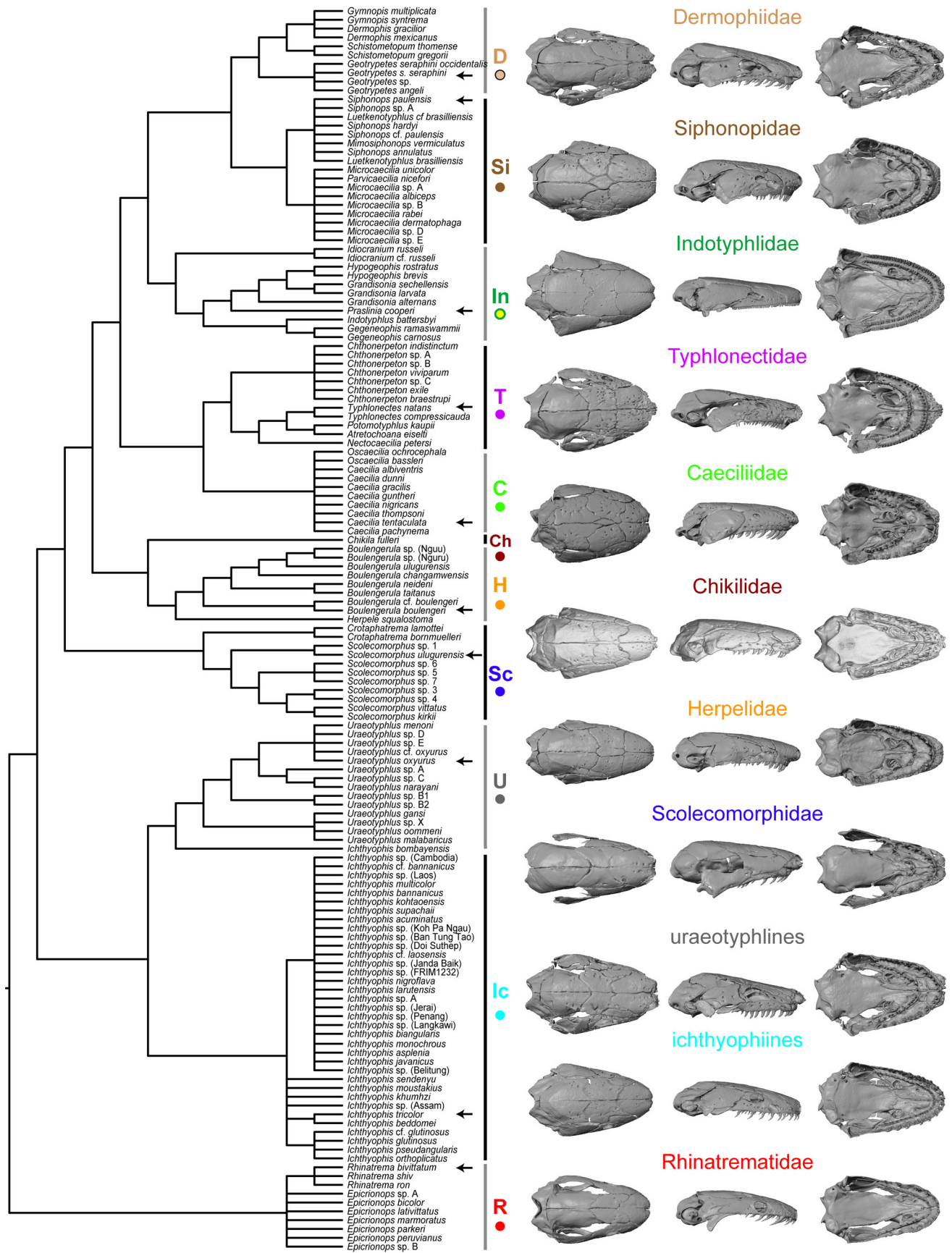
Within the vertebrate radiation, one intriguing aspect of biological diversity lies in the fossorial niche. By their very nature, fossorial vertebrates are cryptic, and so their diversity is often underdocumented and/or underappreciated. Many vertebrate lineages have independently evolved into and speciated within this niche (Gans 1974; Nevo 1979; Wake 1993). Among them are multiple elongate and limb-reduced or limbless lineages, such as amphisbaenian lizards, scolecophidian snakes and caecilian amphibians, that in the absence of limbs use their head to burrow in sand, soil, and leaf litter (Gans 1974; Wake 1993). While diet and feeding ecology are significant factors driving morphological diversification of the skull in many vertebrates (e.g. Stayton 2003; Nogueira et al. 2009; Figueirido et al. 2010), in many fossorial vertebrates these factors have operated within a framework imposed by the functional demands of head-first burrowing. What is not understood is how speciation within the fossorial niche influences the resulting diversity of morphological forms (macroevolutionary patterns of morphology).
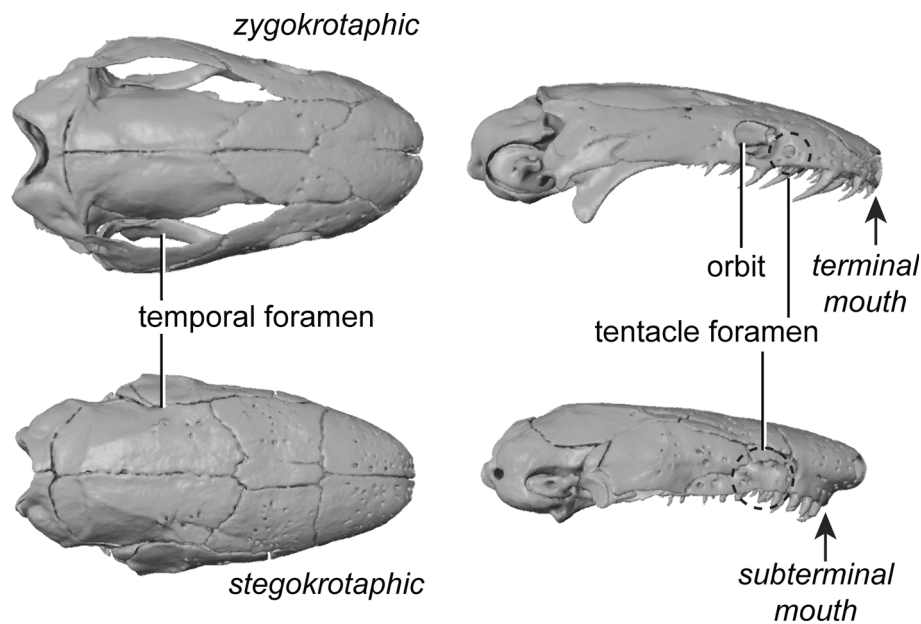
Caecilian amphibians (Gymnophiona) are a moderately speciose (approximately 200 extant species), monophyletic group of limbless, fossorial vertebrates. They are one of the three orders of modern amphibians, likely originating in the Permian or early Triassic (Roelants et al. 2007; Gower and Wilkinson 2009; San Mauro 2010). Estimates of divergence times from molecular data suggest all ten families of

Fig. 1 A consensus tree constructed from multiple sources of the 141 ▶ caecilian 'species' used here. See "Methods" section of text for details and Table S1. Polytomies represent unresolved nodes. *Arrows* denote the species depicted on the *right*, one for each of the clades used in this study

modern caecilians were present by the mid Cretaceous (Roelants et al. 2007; Zhang and Wake 2009). Caecilians have a wide geographic distribution with a Gondwanan signature: Central and South America, Sub-Saharan Africa, the Seychelles, South and Southeast Asia. In many cases, families are restricted to a single continent (Wilkinson et al. 2011). The majority of caecilians are terrestrial, with adults inhabiting soil or leaf litter in tropical forests and agricultural land (e.g. Gower and Wilkinson 2008), with the exception of one clade (Typhlonectidae, Fig. 1) that includes secondarily aquatic or semi-aquatic species (e.g. Taylor 1968; Nussbaum and Wilkinson 1995), including the largest lungless tetrapod, *Atretochoana eiselti* (Wilkinson et al. 1998; Hoogmoed et al. 2011). Field observations suggest that adults of terrestrial caecilians vary from dedicated burrowers to more surface-active animals (e.g. Burger et al. 2004; Gower et al. 2004, 2010), although detailed ecological studies are lacking for most species. As far as is known, all adult caecilians practice some head-first burrowing, even the aquatic and semi-aquatic species (Moodie 1978), but burrowing ability differs among species (Ducey et al. 1993; Herrel and Measey 2010).

Head-first burrowing behaviour is apparent in the form of the caecilian cranium; robust and heavily ossified, their skulls are very different from the crania of frogs or salamanders (Trueb 1993). Yet despite the constraints that head-first burrowing may impose on its form, the caecilian skull is variable in shape and composition of elements across the order (e.g. Fig. 1). Three notable features that vary among species are have been argued to correlate with differential microhabitat use and burrowing ability (Gans 1974; Nussbaum and Gans 1980; Nussbaum 1983; Wake 1993; Gower et al. 2004) (Fig. 2): (1) mouth position may be terminal or subterminal, where the lower jaw is countersunk and the nasal region projects forward of the upper tooth row (e.g. Wilkinson et al. 2011). More subterminal mouths are expected in dedicated burrowers due to biomechanical trade-offs with narrowing the skull (e.g. Gans 1974, 1994). (2) All caecilians have reduced eyes (e.g. Mohun and Wilkinson 2014), but some have the orbit completely closed such that the eye is covered by bone (e.g. Wilkinson et al. 2011). Reduction of the eyes is a common phenomenon in animals that rarely goes aboveground or live in dark environments (reviewed in Pipan and Culver 2012). (3) Fenestration of the temporal region, in which the skull is either fenestrated ('open-roof', *zygokrotaphy*), where the squamosal and parietal bones are widely separated and the adductors are visible externally,

Fig. 2 Caecilians have robust, heavily ossified crania. The cranium is often characterised by three features of particular interest here: temporal region may be open (*top*; 'stegokrotaphic') or closed (*bottom*; 'zygokrotaphic'); orbit closure, although there are always paired foramina for the tentacles, only some species have an open orbit, which may be distinct from or share an edge with the tentacular foramen; the mouth can be terminal, where the teeth are in line with the anterior of the snout, or subterminal, where the jaws are underslung (*right*). Lower jaw is not shown. Species illustrated are the typhlonectid *Potomotyphlus kaupii* (*top*), rhinatrematid *Rhinatrema bivittatum* (*middle*) and herpelid *Boulengerula boulengeri* (*bottom*)

or closed (*stegokrotaphy*), with the squamosal and parietal bones in contact and covering the jaw adductor muscles, the latter form is argued to be structurally stronger for head-first burrowing (Nussbaum 1983). All three characters are known to exhibit homoplasy within caecilians (Wake 2003; Wilkinson and Nussbaum 2006), but the extent of the variation in these features across the order, and how they have evolved in relation to each other has not previously been evaluated. Understanding how these characters have evolved, and characterising overall shape variation across modern caecilians will provide an understanding of how fossoriality influences macroevolutionary patterns of morphology.

The main aim of this paper is to address the question, how have caecilians evolved in cranial morphospace? To accomplish this we use high-resolution X-ray computed tomography and landmark-based geometric morphometric methods to quantify and characterise skull shape. We infer aspects of the history of cranial shape diversification by mapping the phylogeny into morphospace (sometimes called a phylomorphospace, Sidlauskas 2008). Using the phylomorphospace, we infer the mode of evolution and evaluate the following predictions. Firstly, if limblessness and head-first burrowing imposes restrictions on cranial shape or if ecological factors have played an important role in caecilian cranial evolution, we expect there will be substantial homoplasy. Alternatively, if morphological

variation is associated with divergence, we expect to find strong phylogenetic structure to the morphospace. Additionally, we predict that if the three features in Fig. 2—eye covered by bone, subterminal mouth, and stegokrotaphic skull—are adaptations to dedicated burrowing, then they will be found in association in phylomorphospace. Finally, we quantify morphological diversity (disparity) among the main caecilian groups (Fig. 1) to test whether the amount of shape space occupied by each clade is a factor of clade age and/or number of species. These results together will provide insights into caecilian evolution in the absence of a fully-resolved and time-calibrated phylogenetic hypothesis.

Materials and Methods

Study Samples and Phylogeny

We sampled 524 intact, alcohol-preserved specimens representing 141 caecilian "species-level" taxa: 95 named species and an additional 46 populations that possibly represent undescribed species (Fig. 1; Table 1). Caecilian taxonomy is an active field, with the number of species is growing rapidly each year, for example at least nine species were described in the last year (Agarwal et al. 2013; Kamei et al. 2013; Maciel and Hoogmoed 2013; Nishikawa et al. 2013;Wilkinson et al. 2013, 2014). Specimens were

Table 1 Details of the number of caecilian specimens and taxa per major clade included in this study to provide information on completeness of sampling numbers from AmphibiaWeb (2014)

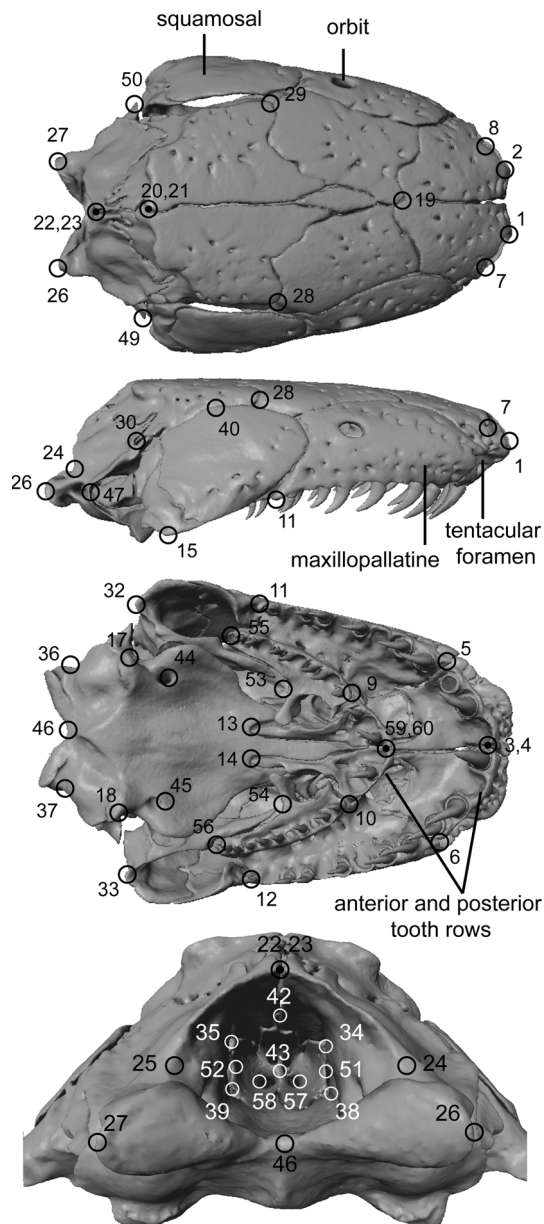| Clade	Specimens included	Total species included	Nominal species included	Potentially undescribed species included	Nominal species not included	Total nominal species
Rhinatrematidae	18	10	8	2	3	11
ichthyophiines	85	35	21	14	27	47
uraeotyphlines	56	15	7	8	1	8
Scolecomorphidae	69	11	5	6	1	6
Herpelidae	65	9	6	3	3	9
Chikilidae	3	1	1	0	3	4
Typhlonectidae	36	12	9	3	4	13
Caeciliidae	44	10	10	0	32	42
Indotyphlidae	42	11	10	1	12	21
Siphonopidae	62	17	9	8	16	25
Dermophiidae	44	10	9	1	5	14
Total	524	141	93	48	107	200

Details of each specimen in Table S1

sampled primarily from the collections of the Natural History Museum, London UK, and supplemented by loans from other collections (Table S1). This study used only alcohol-preserved museum specimens.

Sampling covered almost half of the currently recognised species of caecilians and included all families and all genera except the two monotypic genera *Brasilotyphlus*, and *Sylvacaecilia*, whose phylogenetic positions are unclear but which have cranial shapes similar to those of species in the families Siphonopidae, and Indotyphlidae to which they have been assigned (Wilkinson et al. 2011), and as such we expect that their omission does not considerably bias the results presented here. Sample size per species was limited primarily by time and by availability of material but, where possible, included up to 10 specimens of generally equal sex ratio. We recognise that sexual size and shape dimorphism occurs in caecilians (Teodecki et al. 1998; Kupfer 2009), but preliminary examination of the data showed that among-species variation exceeds intraspecific differences between the sexes. Only adults were sampled in order to avoid substantial confounding effects of ontogenetic variation. Adults were identified on the basis of having identifiable ova or testis, and in some species by the absence of non-adult characters such as spiracles, lateral line systems, deciduous juvenile or foetal teeth, and external gills (Wilkinson and Nussbaum 1998; Kupfer et al. 2006b).

The phylogenetic hypothesis used in this study (Fig. 1) is a topological synthesis (i.e. one without estimated branch lengths) constructed from well-supported relationships in the most recent relevant phylogenetic studies (Wilkinson and Nussbaum 1999; Gower unpublished; Loader 2005; Gower et al. 2011; Loader et al. 2011; San Mauro et al. 2014; Wilkinson et al. 2014) and some specific assumptions of monophyly. Assumptions of monophyly, based

primarily on caecilian taxonomy, are required because a substantial proportion of the included taxa have never been included in any explicit phylogenetic analyses. For the same reason, formal supertree methods are not applicable here and we have essentially produced the tree using "judicious grafting of clades" (Beaulieu et al. 2012) following Wilkinson et al.'s (2001) analysis of what assumption underpin this procedure. The tree is logically implied by the combination of relevant phylogenetic results and limited assumptions of monophyly but many clades are poorly resolved because of the uncertainty of the precise relationships the phylogenetically understudied taxa they are assumed to include. A complete summary of the supporting evidence or assumptions underpinning each of the 67 nodes is given in the supplementary information and Table S2).

To investigate broad patterns across the order, we focus upon 10 clades of caecilians. Seven of these clades correspond directly with monophyletic families recognised by Wilkinson et al. (2011). Two reflect the basal split within the Ichthyophiidae (Gower et al. 2002) and correspond roughly to groups that have often been treated separately in higher classification because they are morphologically very distinct (e.g. Nussbaum and Wilkinson 1989; Wilkinson and Nussbaum 2006) and which we refer to informally here as the ichthyophiines, comprising all but one species of *Ichthyophis* (including species of the recently synonymised *Caudacaecilia* (Nishikawa et al. 2012)) and the uraeotyphlines (comprising *Ichthyophis bombayensis* and all *Uraeotyphlus* spp.). Because only one species of the newly discovered family Chikilidae (Kamei et al. 2012) was available for inclusion in this study, it is included in these analyses with its sister group Herpelidae (Kamei et al. 2012). The number of specimens and species sampled for each of these clades are given in Table 1.

Fig. 3 The 60 3D landmarks used in this study to characterise cranial shape. Landmarks digitzed on cranium surface in dorsal view, lateral view, palatal view and posterior view of internal features (from *top* to *bottom*). Numbers refer to detailed definitions in Table S4. *Double circles* with single numbers indicate paired midline landmarks either side of a wide suture. *White circles* indicate landmarks inside the braincase. Bony elements and cranial features referred to in the text are labelled

X-ray Computed Tomography

We obtained skull data by using non-destructive, high-resolution X-ray computed tomography (HRXCT) to examine bone in situ from the heads of whole, alcohol-preserved specimens. All HRXCT scans were made with the Nikon (Metris) X-Tek HMX ST 225 System at the Natural History Museum, London, using a molybdenum

target that generates low energy X-rays well suited for this type of material. Specimens were scanned using a routine whereby three or four animals are scanned at once, maximizing scan productivity with no discernable detriment to resolution. Details of the individual scans are available from the corresponding author, and in Sherratt (2011).

HRXCT scan data were segmented by applying a threshold for bone and rendered as 3D volumes using VG Studio MAX v.2.0 (Volume Graphics 2001). Non-cranial bony elements (lower jaws and vertebrae) were digitally removed, and the volume of the cranium was converted into an isosurface, a triangular mesh of approximately one million vertices, demarcating the contours of the outer surface of bone. Isosurface models (herein referred to as surfaces, for example Fig. 3) are highly detailed, containing information on both the outside and inside of the cranium.

Landmarks and Shape Analysis

Cranial shape was characterised using landmark-based geometric morphometrics (Bookstein 1996; Dryden and Mardia 1998; Klingenberg 2010). We digitized 60 landmarks in 3D over the cranium (Fig. 3; Table S3), representing likely homologous points on bones at sutures, boundaries of foramina, and at extremes of curvature of structures (e.g. the external naris and foramen magnum), using Landmark Editor v.3.6 (Wiley et al. 2007). Each specimen was digitized once because preliminary analyses revealed that variation due to measurement error was negligible (<2 %, results not shown). Landmark data were subjected to a full Procrustes fit and projection into tangent space with the MorphoJ software (Klingenberg 2011). The Procrustes fit accounted for object symmetry; shape variables for the symmetric component of shape were extracted (Klingenberg et al. 2002). We then calculated the species mean of the symmetric component for use in all subsequent analyses, which were all performed in MorphoJ, except where stated.

Evolutionary Allometry

To determine the degree to which skull shape variation among species was evolutionarily associated with size variation (evolutionary allometry, Klingenberg 1996), we performed a multivariate regression of shape on size (Monteiro 1999) while accounting for the phylogenetic relationships among species. This was accomplished using the set of phylogenetically independent contrasts (Felsenstein 1985) for the symmetric component of shape and the independent contrasts for log centroid size (Klingenberg and Marugán-Lobón 2013). Centroid size is a measure of size that is extracted from the 3D landmarks, calculated as the square root of the sum of squared distances of a set of

landmarks from their centroid (Dryden and Mardia 1998). Cranial size was used rather than body length because the latter is affected by vertebral duplications, which causes substantial variation in overall body length among species.

For all subsequent analyses of cranial shape we used allometry-corrected shape variables for each species in order to examine shape variation not attributable to allometry (Monteiro 1999; Sidlauskas et al. 2011). To obtain values of allometry-corrected shape variables, we used the method described in detail Klingenberg and Marugán-Lobón (Klingenberg and Marugán-Lobón 2013), which is a multivariate adaptation for geometric morphometrics of the phylogenetic size-correction method (Garland Jr and Ives 2000; reviewed in Revell 2009). First, a regression of shape on size was performed using the independent contrasts as described above, and the vector of regression coefficients was obtained. This was then used to compute residual shape scores for the symmetric component of skull shape of each species. Note that this procedure results in a dataset that has species values, not contrasts.

Phylomorphospace

To characterise the evolutionary patterns of cranial shape diversity, we obtained a low-dimensional representation of the caecilian cranial morphospace using principal component analysis of the allometry-corrected shape data. Then we projected the phylogenetic tree in Fig. 1 onto the morphospace (Sidlauskas 2008). This was done by mapping principal component (PC) scores of the species to the phylogeny using squared-change parsimony and computing the PC scores at internal nodes (Maddison 1991; McArdle and Rodrigo 1994), and subsequently projecting the branches of the phylogenetic tree onto the morphospace (e.g., Klingenberg and Ekau 1996; Rohlf 2002; Sidlauskas 2008). The phylomorphospace provides insights into the evolutionary history of morphospace occupation.

The evolutionary history of the three key cranial features illustrated in Fig. 2 was investigated using the principal components analysis and phylomorphospace. Feature 1, the position of the mouth, although described discretely (subterminal/terminal) is a continuously varying trait, consisting of opposite directional shifts of landmarks 1/2 and 3/4 (Fig. 3). We used the shape change graphs (which are visual representations of the PC loadings) to identify which PC axes had proportionally high coefficients for these landmarks while having coincident and opposing directionality (e.g. negative for landmarks 1/2 and positive for 3/4, indicating a terminal mouth). Features 2 and 3, the open or closed orbit, and temporal fenestration of the cranium, were treated discretely because we were not able to place with confidence landmarks around the orbit in all species, nor could homologous landmarks be placed along

the medial edge of either the squamosal or parietal. Therefore, for these two features, we coloured the taxa in phylomorphospace by these binary traits in order to visualise the evolutionary incidence of these characters in the context of whole cranial shape change.
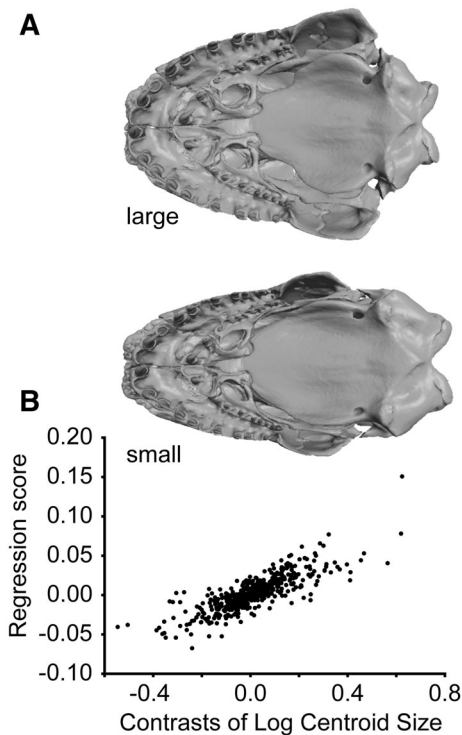
Disparity

We examined how morphological disparity varies among the 10 clades and in association with clade age and the number of sampled species. Disparity was quantified as Procrustes variance, which measures the dispersion of all observations around the mean shape. Procrustes variance is the mean squared Procrustes distance of each specimen from the mean shape of the respective clade, and can be calculated as the sum of the diagonal elements of the covariance matrix of that clade (Zelditch et al. 2012). The association of clade disparity estimates with clade age and the number of sampled species was measured using Pearsons correlation coefficient, r. Clade ages were taken as the averages estimated in Roelants et al. (2007), supplemented with ages for Caeciliidae from Zhang and Wake (2009), and Herpelidae and Chikilidae from Kamei et al. (2012). Scolecomorphidae is excluded from the analysis of disparity versus clade age because no published dated phylogeny includes representatives of both of its two constituent genera.

We then assessed how morphological disparity differs between the species with closed or open orbits, as well as between species with stegokrotaphic or zygokrotaphic skulls. To statistically evaluate the difference between each state (i.e. open vs closed) for both of these characters, we used the group Procrustes variances as test statistics, and evaluated through permutation the difference between groups. 250 permutations were performed for each test, shuffling the species relative to the shape data, and the observed test statistic was compared to the random permutations (e.g. Drake and Klingenberg 2010). Procrustes variances and permutation tests were implemented in R (McKenna et al. 2003; R Development Core Team 2014) using package geomorph (Adams et al. 2014).

Results

Evolutionary Allometry

Evolutionary allometry of the caecilian skull accounts for an appreciable and significant portion of cranial shape variation among species: a multivariate regression of independent contrasts of shape on independent contrasts of log-transformed centroid size reveals that 14 % of the total variance of shape contrasts is associated with size variation, and the permutation test is significant ($P < 0.0001$). From the multivariate regression, we find that greater cranium size in
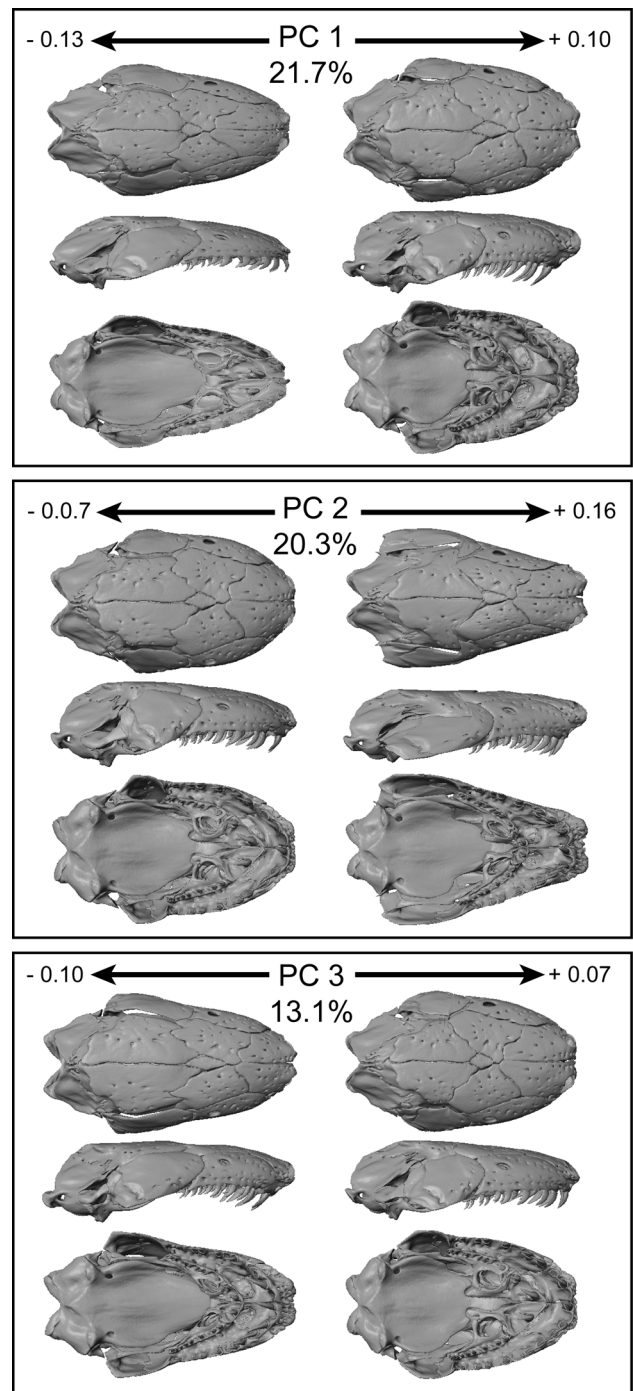
Fig. 4 Evolutionary allometry of the caecilian cranium. Evolutionary allometry of cranial shape was examined by a multivariate regression of the independent contrasts of symmetric shape and of log centroid size. Here, warped surfaces represent the large and small extremes of skull size; evolutionary increase in skull size is associated with a widening of the skull, particularly at the back of the mouth, while reducing centroid size is associated with a narrowing of the skull (**a**). The regression reveals that size accounts for 13.6 % of cranial shape variation among species, and that the contrasts fall fairly close to a straight line of cranial shape change (**b**)

caecilians is associated with a relative wider cranium, particularly at the back of the mouth, producing a more broadly triangular shaped mouth, while smaller size is associated with a relatively narrower cranium producing a more bullet-shaped head and more parallel sides of the mouth (Fig. 4a). All contrasts fall fairly close to a straight line of cranial shape with log size of caecilian species (Fig. 4b). A principal components analysis of the raw (i.e. not allometry corrected) shape variables, with the species points scaled to centroid size reveals that size variation across species is not attributed to any one PC axis, but rather distributed across the morphospace (Figure S1).

Principal Axes of Caecilian Cranial Variation

Cranial shape among caecilians appears to be characterised by somewhat limited variation in limited directions: principal component (PC) analysis reveals that most (69.8 %) of the allometry-corrected shape variation among species is concentrated in only five dimensions (out of 88), with subsequent PCs each contributing small or negligible
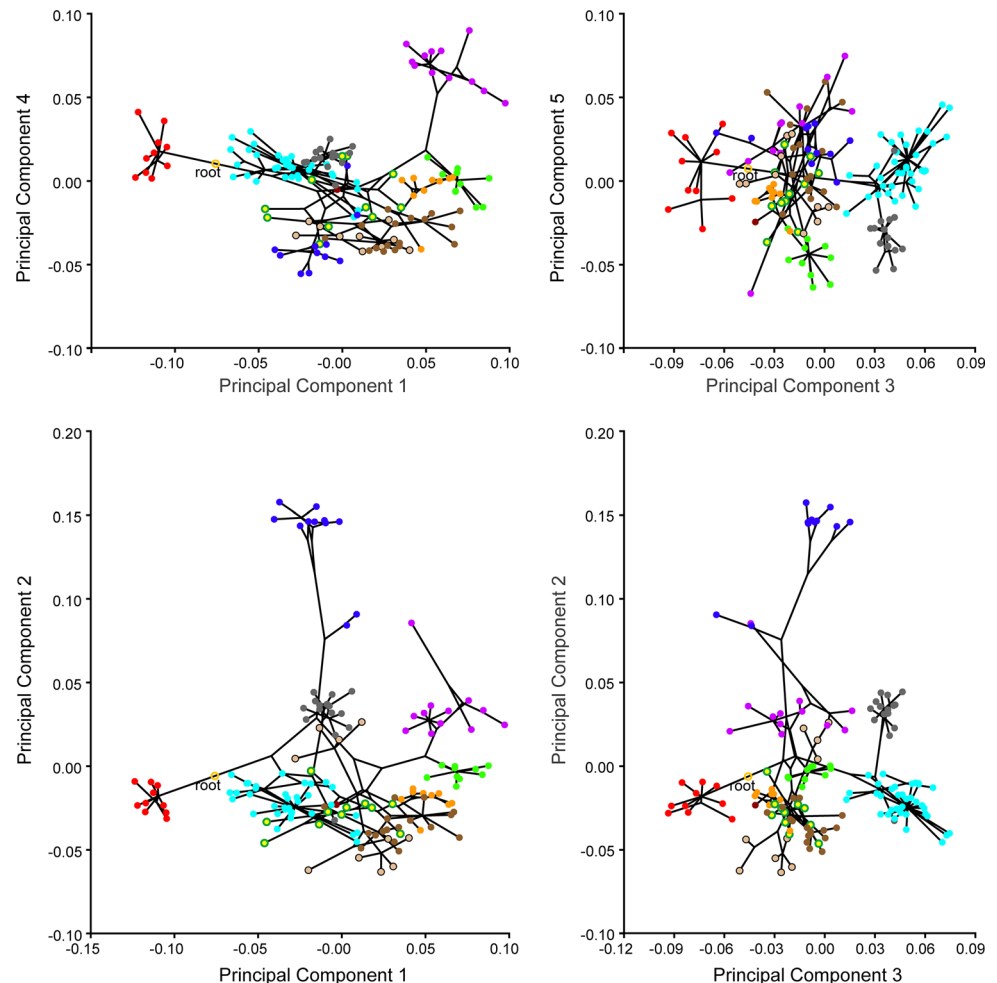
Fig. 5 Three principal axes of cranial shape variation, visualised as warped crania surfaces. PC axes are from a PCA of species means, corrected for evolutionary allometry (Fig. 4). Shape changes associated with the PCs are shown as extreme cranial shapes representing the positive and negative end of each axis. In each case, the magnitude of shape change from the mean corresponds to PC scores in Fig. 6

amounts (<5 %). Shape changes associated with the first five PCs are illustrated in Fig. 5. The primary axis of variation (PC1) contributes 21.7 % of the total variation

Fig. 6 Phylomorphospace of species means made using principal components analysis, coloured by clade. PC scores for the mean shape of each species (corrected for evolutionary allometry) were mapped to the phylogenetic tree from Fig. 1, using unweighted squared-change parsimony. *Each point* represents one species, *coloured* by clade membership (Color figure online)

and mainly describes changes in relative positions of landmarks on the tooth rows. This axis corresponds to the variation in the terminal/subterminal mouth feature highlighted in Fig. 2. A negative change from the mean shifts these outer and inner tooth row landmarks together and moves them inline with the anterior limits of the snout, resulting in a more terminal mouth (with the most extreme being Rhinatrematidae). A positive change from the mean shape describes a posterior shift of the landmarks on the outer and inner tooth rows resulting in a more subterminal mouth (e.g. Caeciliidae and Typhlonectidae).

The second axis of variation, describing almost the same amount of variation as the first (PC2, 20.3 %), pertains to morphological differences between the crania of scolecomorphids and the remaining species (Fig. 6). This axis also describes the variation in the terminal/subterminal mouth of Fig. 2, with terminal mouths in the negative direction, and subterminal in the positive (Fig. 5). Additionally, the shape change towards the positive end of the axis describes a narrower, V-shaped skull, primarily by

relative medial shifts of landmarks on the front of the cranium compared to the back. The rest of the species at the negative end of PC2 have a broader, more U-shaped skull.

Cranium relative width and length is described by the third axis of variation. PC3 (13.1 %) mostly describes variation in the relative lengths of the front of the cranium versus the back (braincase), which give rise to a visually striking difference in overall relative head width. A change in the negative direction corresponds to a relatively longer braincase, and a narrower, longer head, whereas a positive change describes a shorter and more rounded head, with a relatively shorter braincase. Long slender crania are found almost exclusively in Rhinatrematidae (Fig. 6), and the most extreme, almost round, crania occur in Ichthyophiidae (ichthyophiines and uraeotyphlines). All other species occupy intermediate positions along this spectrum.

Shape changes associated with PC4 and PC5 are given in Figure S2. All other PCs contribute negligible amounts of variation (<5 %) and are not considered further.
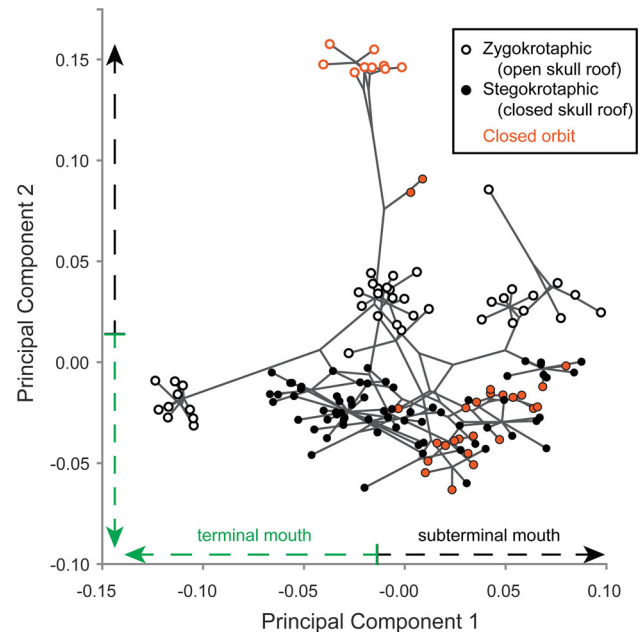
Phylomorphospace

Our data show that extant caecilians form a multi-star-burst pattern in cranial morphospace, comprising a series of very distinct clusters that closely correspond to the 10 main clades (Fig. 6). The phylomorphospace reveals that species of the same clade generally cluster together, and most of the clades are well separated from each other, with notable exceptions: first, two clades (Dermophiidae and Scolecomorphidae) are not unified clusters, but instead each is divided into two clusters (representing different genera); second, three major clades (Dermophiidae, Siphonopidae and Indotyphlidae, which together are monophyletic) overlap in the PC plots (Fig. 6). In the phylomorphospace, clusters at the ends of single branches suggest that ancestral lineages traversed morphospace and evolved novel cranial shapes and subsequently underwent more local shape evolution. There is some criss-crossing of branches within major clades in the phylomorphospace, consistent with mostly local homoplastic shape evolution.

Some clades form tight clusters along PC1 axis, indicating that all members of the clade share a similar mouth type (e.g. Rhinatrematidae all have terminal mouths, Typhlonectidae all subterminal). Criss-crossing of terminal branches along this axis clearly illustrates that several taxa have evolved a more terminal mouth from within clades of predominantly subterminal mouthed species (e.g., *Praslinia cooperi* and *Schistometopum thomense*; Fig. 6).

Species with stegokrotaphic crania are all more similar in overall cranial shape than species with zygokrotaphic crania, which are more widely distributed, and instead cluster in the morphospace by clade (Fig. 7). The Procrustes variance of all zygokrotaphic species is 0.0147, which is double that of all stegokrotaphic species (0.0077), and significantly different ($P = 0.001$). In the phylomorphospace, when zygokrotaphic crania evolve from within predominantly stegokrotaphic clades—*Geotrypetes*, Typhlonectidae, *Uraeotyphlus*—they each shift to occupy a novel region of morphospace (but note that *Geotrypetes* and *Uraeotyphlus* share some features and overlay in a plot of PC1 and PC2, Fig. 6). The scolecomorphid *Crotaphatrema* (stegokrotaphic) lies between zygokrotaphic scolecomorphids (*Scolecomorphus*) and the other stegokrotaphic species. Although stegokrotaphic caecilian crania are more similar in shape than zygokrotaphic crania, they are widely distributed along PC1 indicating substantial variation in mouth position (Fig. 5).

Species with a closed-orbit form two distinct groups in the phylomorphospace, those belonging to Scolecomorphidae and those of five other clades (Fig. 7). The non-scolecomorphid closed-orbit taxa occupy a small area of morphospace at the positive end of PC1 and negative end

Fig. 7 Phylomorphospace illustrating the distribution of the three main features in the cranial shape space. Zygokrotaphic (*hollow circles*) species are widely dispersed in morphospace, due to variation in the shape of the mouth. Stegokrotaphic (*filled circles*) species are mainly clustered on the negative extreme of PC2, except for two species (*Crotaphatrema* spp.) that are weakly stegokrotaphic. Species with eyes covered by bone (*orange*) mostly share very similar cranial shapes, with the exception of Scolecomorphidae at the top of the figure. PCs 1 and 2 both describe subterminal to terminal mouth variation, shown by the *arrows*. Most species have a subterminal mouth, while those in the *bottom left* have a terminal mouth (Color figure online)

of PC2. The Procrustes variance of all species with a closed orbit is 0.0114, which is statistically no different to that of all open-orbit species (Procrustes variance = 0.0106). However, excluding the Scolecomorphidae, the Procrustes variance of all closed-orbit species reduces to a third of that of the open-orbit species (0.0039), and significantly different ($P = 0.001$). Variation among the closed-orbit species comes from different positions of the two tooth rows and the position of landmarks 5 and 6 (suture between maxilla and nasal-premaxilla) as well as in the breadth of the snout.

Evolutionary Dynamics of Disparity

The clades differ substantially in terms of their disparity: the Procrustes variances for the major clades vary by orders of magnitude (Figure S3). There is no significant correlation between clade disparity and clade age (Procrustes variance $r = 0.035$ $P = 0.959$), nor a relationship between clade disparity and the number of species sampled in each clade (Procrustes variance $r = 0.02$ $P = 0.630$). Moreover, there is no significant correlation between clade age and the number of species sampled ($r = 0.41$ $P = 0.232$).

Discussion

Evaluating morphospace and phylomorphospace provides insights into the history of morphological diversification for complex traits and allows some inferences to be made of the tempo and mode of evolution. Applying this approach we find that caecilians have a striking and complex evolutionary history: most species in cranial morphospace occupy very distinct clusters that closely correspond to major clades that, when viewed with the phylogenetic relationships, appear as multiple starbursts or fireworks-like pattern. This pattern supports our prediction that cranial shape variation is associated with species divergence. However, we also find homoplasy among some clades, which is consistent with the hypothesis that extrinsic pressures, such as head-first burrowing or ecological factors, have also played an important role in caecilian cranial evolution. We find that a subterminal mouth, closed orbit and stegokrotaphic skull characteristics are found in association in some species. However, stegokrotaphy is not always found in taxa with closed orbits, and not all taxa with subterminal mouths have orbits covered by bone, suggesting these traits are not highly integrated in evolution. This complexity in the evolutionary history of the caecilian morphospace is also reflected in clade disparity; the phylogenetic clades of caecilians each vary greatly in morphological disparity, but neither the age of the clade nor number of species account for this variation.

History of Morphological Diversification

The pattern for extant caecilian cranial shape of discontinuous morphospace occupation with distinct, clumped monophyletic groups contrasts with the findings from large-scale morphometric studies of other taxa, which have found species to be more evenly dispersed in shape space, often with overlapping clades (Neige 2003; Stayton 2005; Clabaut et al. 2007; Cooper et al. 2010; Drake and Klingenberg 2010; Friedman 2010; Monteiro and Nogueira 2011; Angielczyk and Ruta 2012; Prevosti et al. 2012; Sallan and Friedman 2012; Klingenberg and Marugán-Lobón 2013). Instances of discontinuous morphospace occupation in other taxa are largely restricted to the most distinct, morphologically outlying clades, as is the case for cetaceans among mammals (Marcus et al. 2000), gharials among crocodilians (Pierce et al. 2008), and oviraptorosaurs among therapod dinosaurs (Brusatte et al. 2012). However, some caution is necessary because discontinuity may be caused by sampling artefacts, such as the marked discontinuity found in a study of mammal skulls that included species from two distinct clades, carnivores and marsupials, each of which were continuously distributed in the morphospace (Wroe and Milne 2007; note that

mandible shape appears to be more continuously distributed, Prevosti et al. 2012). Morphometric studies of skull shape in fossil temnospondyls, tetrapods probably more closely related to caecilians and other modern amphibians than to any other living vertebrates, also show mostly evenly dispersed taxa in shape space with a modest degree of clustering of phylogenetic groups and considerable overlap between them (Stayton and Ruta 2006; Fortuny et al. 2011; Angielczyk and Ruta 2012). Judged against the available comparative empirical studies, the starburst pattern with very distinct clusters corresponding to main clades appears to be an unusual feature of caecilian crania.

The pattern of strong phylogenetic structure in the caecilian phylomorphospace, as revealed by distinct clustering of the main clades, is also rather unusual. Several studies using the phylomorphospace approach have uncovered patterns with substantial criss-crossing of branches along multiple axes among closely-related taxa, indicating relatively more evolutionary plasticity in those measured traits (Clabaut et al. 2007; Pierce et al. 2008; Kimmel et al. 2009; Stayton 2011; Sakamoto and Ruta 2012; Casanovas-Vilar and van Dam 2013; Klingenberg and Marugán-Lobón 2013). In several examples, this is taken to the extreme, where different lineages have traversed major areas of morphospace to occupy space otherwise occupied by relatively distantly related species, illustrating strikingly convergent evolution of shape in often ecologically similar taxa (Figueirido et al. 2010; Price et al. 2011; Sanger et al. 2012). A number of studies of other taxa (Nicola et al. 2003; Sidlauskas 2008; Figueirido et al. 2010; Klingenberg and Gidaszewski 2010; Fortuny et al. 2011; Klingenberg et al. 2012; Meloro and Jones 2012) using similar methods to ours have insufficient taxonomic sampling to offer good comparison.

The pattern in morphospace indicates that early in caecilian evolution ancestral lineages moved to new regions of the shape space, and subsequent taxonomic diversification populated those regions (rather than created new regions), suggesting that expansion to much of present-day morphospace occupation occurred relatively early in caecilian evolution. Early expansion of morphospace is a phenomenon found often in the fossil record and has also been detected among modern taxa (Schluter 2000; Streelman and Danley 2003; Uyeda et al. 2011), though the commonality of this phenomenon has recently been challenged (Harmon et al. 2010). Such a pattern has been associated with early filling of major ecological niches (e.g. Sidlauskas 2008). An alternative explanation is that adaptive peaks shifted over time and that evolving clades tracked the moving peaks (Felsenstein 1988). The fossil record for caecilians is too sparse for a direct evaluation of these possible explanations. While it is likely that the distinct position in morphospace of Typhlonectidae is the result of a niche-shift from terrestrial

to more aquatic environments and lifestyles, the situation for other clades is unclear because, although some ecological niche separation has been reported (Gower et al. 2004), the microhabitats occupied by most caecilians species are simply unknown. Further work must be done to quantify caecilian habitat preference and tolerance, diet, and other ecological parameters in order to test the hypothesis that differences in cranial morphology relate to ecological differences among clades.

Caecilians originated in the Permian or early Triassic and the modern major clades are all estimated to be relatively ancient (Roelants et al. 2007; Gower and Wilkinson 2009; San Mauro 2010), with the 10 currently recognised families all older than 50 myr (Wilkinson et al. 2011; Kamei et al. 2012). The strong phylogenetic structure of the cranial morphospace, with mostly discrete clustering of the main clades, is perhaps surprising given that other, substantially younger, vertebrate radiations that are very speciose exhibit great morphological diversity with substantial homoplasy (Meyer 1993; Losos 2009). Although caecilian clades differ substantially in terms of their cranial disparity, there appears to be no particular evolutionary trend. Predictions about the tempo and mode of morphological diversification have historically invoked two factors that may influence clade disparity: clade age and clade diversity (the number of species) (e.g. Simpson 1944; Eldredge and Gould 1972; Purvis 2004; Ricklefs 2004). The lack of correlation between clade disparity and clade age or number of species sampled in each caecilian group is in striking discordance with studies of other major taxa (e.g., Purvis 2004; Ricklefs 2004; Stayton 2005; Pagel et al. 2006; Clabaut et al. 2007; Mattila and Bokma 2008; Adams et al. 2009; Rabosky and Adams 2012). We hypothesise that differences in cranial disparity among major clades of caecilians are more likely the result of biological differences, such as reproductive mode and life-history variation, which differ substantially across the order (San Mauro et al. 2014). More data on the biology of caecilians are needed to test this hypothesis.

Implications for Caecilian Biology and Understanding Fossoriality

Caecilian biology has become an active and fruitful field of research: the last 15 years has seen a remarkable advancement in our knowledge of aspects including development (e.g. Müller et al. 2005; Müller 2006a; Müller et al. 2009), life-history (e.g. Kupfer et al. 2005; Kupfer et al. 2006b; Wilkinson et al. 2008; Kuehnel and Kupfer 2012; Gomes et al. 2013), phylogeny (e.g. Gower et al. 2002; San Mauro et al. 2004; Roelants et al. 2007; Loader et al. 2011; Maddin et al. 2012b) and ecology (e.g. Oommen et al. 2000; Gower et al. 2004; Measey et al. 2004; Kupfer et al. 2006a). There are currently 200 described

species—a number that is increasing rapidly with many new taxa very recently described (Agarwal et al. 2013; Kamei et al. 2013; Maciel and Hoogmoed 2013; Nishikawa et al. 2013; Wilkinson et al. 2013, 2014). Historically, caecilian skull variation has been qualitatively documented in terms of element composition and form (Taylor 1969; Nussbaum 1983; Trueb 1993; Wilkinson et al. 2011), except for an early morphometric study by Renous (1990) that understood the importance of quantifying this variation. The three features in Fig. 2, openness of orbit, mouth position and skull fenestration, have been frequently discussed because they are thought to be associated with differential burrowing ability (Gans 1974; Nussbaum and Gans 1980; Nussbaum 1983; Wake 1993; Gower et al. 2004). What do our quantitative findings suggest are important cranial shape changes during caecilian evolution and how have they contributed to modern diversity?

Eyes covered by bone, a subterminal mouth, and stegokrotaphic skull are found in association in many species, but most importantly, there are not all always found in association. Our results clearly show that all four combinations of terminal/subterminal mouth and stegokrotaphy/zygokrotaphy occur in caecilians. This has important implications for the functional interpretation of these characters; stegokrotaphy and a strongly subterminal mouth, both features presumed to be better for burrowing, occur together, but not exclusively. Characters that are important for a particular function are predicted to be internally coordinated and evolve together (Olson and Miller 1958; Cheverud 1982; Klingenberg 2008). Our findings suggest that the subterminal mouth and a stegokrotaphic cranium have evolved, for the most part, independently.

The closed-orbit phenotype appears to be an important contributor to the homoplasy (criss-crossing of branches within and among several clades observed in the main phylomorphospace) observed. A closed orbit (eyes covered by bone) is perhaps the most suggestive of the three features of the caecilian cranium to be closely associated with a dedicated subterranean lifestyle, with scolecomorphids as an exception—these species have a closed orbit but the eye can emerge through the tentacular aperture (Nussbaum 1985). Species position and branch direction in the phylomorphospace shows that there is some convergence in cranial shape among caecilians with closed orbits (excluding scolecomorphids, Fig. 7). The convergent cranial morphology in these closed-orbit species has clear features that would be useful in head-first burrowing: narrow, bullet-shaped and compact (including stegokrotaphy) with a subterminal mouth. However caution should be made in interpreting these as adaptive features until explicit hypotheses are tested using behavioural and burrowing performance data.

Our analyses showed that variation of mouth position (terminal/subterminal) is very important in caecilian cranial shape variation, contributing to the first two axes. A subterminal mouth in terrestrial vertebrates is often associated with head-first excavation of the substrate (e.g. Wake 1993), and thus the presence of more subterminal mouths, in general, in teresomatans has been interpreted as a general trend within caecilians positively correlated with a more dedicated burrowing lifestyle. Yet attributing a direct, causal relationship is advised against at this time because the scanty available data do not demonstrate a clear correlation. For example, although comparative and experimental evidence suggest that *Schistometopum thomense* (with a relatively terminal mouth, perhaps secondarily) is a relatively poor burrower that prefers to use existing tunnels (Ducey et al. 1993; Nussbaum and Pfrender 1998; Wollenberg and Measey 2009; Herrel and Measey 2010), many caecilians with strongly countersunk mouths (e.g. *Scolecomorphus*, *Geotrypetes*, *Uraeotyphlus*, *Caecilia*) have also been found in leaf litter rather than deeper soil (Burger et al. 2004; Gower et al. 2004; pers. obs.). Although we observe an evolutionary trend from terminal to subterminal mouth in caecilians, the apparent 'reversals' suggest that this is a homoplastic trait that may have evolved under selective pressures other than only those imposed by head-first burrowing.

Variation in skull fenestration (stegokrotaphy/zygokrotaphy) is also revealed by our analyses to be a major part of the cranial shape variation, because the second principal axis defines this feature. The evolutionary and functional implications of zygokrotaphic and stegokrotaphic crania have long been debated. Zygokrotaphy is reasoned to be the ancestral condition for caecilians because this occurs in rhinatrematids (sister group to all other living caecilians) and because frogs and salamanders have fully open-roofed crania (gymnokrotaphy) (reviewed in Kleinteich et al. 2012; Maddin et al. 2012a). While our findings cannot further resolve the ancestral condition in caecilians, the position of zygo- and stegokrotaphic crania in morphospace (Fig. 7) demonstrates multiple transitions between these states during caecilian evolution. Caecilian crania with a closed temporal region are reasoned to be mechanically stronger and better suited for the high-stresses of soil compaction (Nussbaum 1983). Conversely, zygokrotaphic crania are expected to be more kinetic (at least passively) and therefore less suited for burrowing, but perhaps better for handling larger and/or more muscular prey (Nussbaum 1983). Functional models examining patterns of stress and strain across the cranium during different loading regimes suggest however that there is no mechanical disadvantage to zygokrotaphy (Kleinteich et al. 2012). Instead, Kleinteich et al. (Kleinteich et al. 2012)

suggest that burrowing performance may be related to another factor, head angle during soil penetration. Given that zygokrotaphy is not only retained but likely re-evolved within extant caecilians, it seems unlikely that it represents simply the absence of a possible adaptation to improved burrowing. Alternative explanations for variation in caecilian temporal fenestration include cranial kinesis and feeding mechanics (Gower et al. 2004) and protection of soft tissues against potentially harmful organisms (Wilkinson et al. 2013). More empirical data are needed to test functional models and adaptive hypotheses.

Understanding the evolutionary mechanisms that generated the patterns of caecilian cranial phylomorphospace occupation requires that these results are integrated with developmental, functional, and ecological information to test adaptive factors and possible constraints (Breuker et al. 2006; Olson 2012). Some of this information is becoming more available for caecilians (Müller 2006b; Kleinteich et al. 2012) and also for fossil temnospondyls, an extinct group closely related to modern amphibians (Stayton and Ruta 2006; Fortuny et al. 2011; Angielczyk and Ruta 2012). Such studies will also become increasingly feasible as caecilian phylogeny becomes even better resolved. Because skull shape is related to phylogenetic, ecological, biomechanical and developmental aspects of evolution, morphometrics can play the role of a common framework for integrating these different aspects into a comprehensive understanding of evolutionary processes.

Conclusions

Because their head serves as a tool for burrowing in addition to its more usual (feeding and sensory) functions, caecilian amphibians are presented as an informative system with which to study the interplay of multiple, possibly antagonistic selective pressures in shaping morphological diversity. Caecilians are well suited to detailed study because they are a speciose, but not too large, clade, with an increasingly well-understood taxonomy, and active research on their phylogeny and biology. We have reported intriguing and unique patterns of cranial evolution across this major clade of vertebrates, revealing a deep and complex history. The findings presented here indicate that the evolution of the caecilian cranium has much to offer to general understanding of how major taxa evolve. Finally, this study of shape variation across a major clade of non-amniotes serves as a long overdue case for comparison with the much more abundant examples of macroevolutionary patterns in amniotes and fishes that serve in our understanding of how evolutionary processes created diversity in vertebrates.

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