Evolutionary Biology (2019) 46:239–248
https://doi.org/10.1007/s11692-019-09477-7

RESEARCH ARTICLE

Craniofacial Allometry is a Rule in Evolutionary Radiations of Placentals

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Received: 4 February 2019 / Accepted: 4 May 2019 / Published online: 27 May 2019
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Abstract

It has been suggested that larger species of mammals tend to become long-faced when they diverge in size during an evolutionary radiation. However, whether this allometric pattern, reminiscent of ontogenetic changes in skull proportions, is indeed a rule has yet to be thoroughly tested. Using ~6000 adult specimens from 14 phylogenetically well separated and ecomorphologically distinctive lineages, 11 orders, and all superorders of the placentals, I tested each group for positive craniofacial allometry (CREA). The evidence supporting CREA is overwhelming, with virtually all analyses showing proportionally longer faces in bigger species. This corroborates previous studies in other groups, consolidates CREA as a pervasive morphological trend in placental evolution and opens important research avenues for connecting micro- and macro-evolution. If found in even more lineages of non-placental mammals, confirmed in birds, and possibly discovered in other tetrapods, CREA could become one of the most general rules of morphological evolution in land vertebrates.

Keywords Braincase · Evolutionary trend · Face · Mammals · Morphology · Prognathism

Pervasiveness of Scale, Allometry and Mammalian Disparity

Scale has a vast range of consequences on a variety of aspects of biology including body proportions and the shape of specific anatomical regions (Gould 2002; Thompson n.d.; West 2017). In morphology, allometry refers to size-related variation in ontogeny and evolution (Klingenberg 1998), and can either reveal constraints to change or be a promoter of novelty along lines of least evolutionary resistance (Cardini and Polly 2013; Gould 2002; Marroig and Cheverud 2005; Renaud and Auffray 2013). Mammals offer particularly interesting examples to explore the role of size and allometry in evolution, as they vary in body mass more than any other class of vertebrates: the smallest shrew or bat weighs just a few grams, while the blue whale may exceed 150 tons and is the largest animal of all times. Mammals also tend to have larger brains compared to other tetrapods, and are defined by a large number of derived traits in head anatomy (heterodont dentition, secondary bony palate, complex turbinates, paired occipital condyles etc.). Thus, the origin of craniofacial differences and allometric variation is central to the study of mammalian biology and evolution.

Cranial Evolutionary Allometry (CREA) and 'Rules' of Morphological Evolution

Adults of larger species, in a group of closely related mammals, tend to have relatively longer faces and smaller braincases (Cardini and Polly 2013; Radinsky 1985). This macroevolutionary pattern of cranial evolutionary allometry (CREA (Cardini et al. 2015)) was first described as a mammalian trend by Radinsky (1985) and has later been hypothesized to be a rule of morphological evolution (Cardini et al. 2015; Cardini and Polly 2013). CREA has been mainly explored in placentals (Cardini and Polly 2013; Tamagnini et al. 2017), but occurs also in marsupials, such

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11692-019-09477-7) contains supplementary material, which is available to authorized users.

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as didelphids (Radinsky 1985) and kangaroos (Cardini et al. 2015), and more recently, but less conclusively, has been supported even in birds (Bright et al. 2016; Linde-Medina 2016; Tokita Masayoshi et al. 2017). However, before it can join the list of established evolutionary 'rules', stronger evidence from a larger number of species and lineages must be obtained.

In this context, it is important to bear in mind that the term "rule" is used in a loose sense to refer to broad patterns, that are common in a group of organisms but may vary in magnitude and can have exceptions (Raerinne 2011). Despite possible differences and exceptions, however, they represent consistent evolutionary trends across a large number, or even the majority of taxa, in a lineage. Thus, Bergmann's, Allen's, Rensch's and other rules, including CREA, are not strict laws describable by constants of nature (Raerinne 2011), but general patterns, whose taxonomically contingent occurrence in a vast number of cases suggests commonalities in the mechanisms behind them. Causal processes are seen by some as a fundamental requirement for proposing a rule (Watt et al. 2010). Indeed, that may be true in specific historical contexts, such as the original formulation of Bergmann's rule (Watt et al. 2010), but does not apply to the vast majority of evolutionary rules, that are best described as *explananda* rather than *explanantia* (Raerinne 2011). In fact, mechanisms tend to be often speculative and based on correlational evidence. Even in the case of Bergmann, possibly the best known evolutionary rule in mammals, its explanation is often presented as a fact, but is largely still debated (Meiri 2011).

Documenting Rules: Overwhelming Evidence for CREA in Mammalian Radiations?

Before proposing any explanation for the seemingly pervasiveness of a pattern, that pervasiveness must be first verified to establish whether it is a rule or not. Thus, focusing on placentals, the first and main lineage in which CREA has been described, and using a sample of almost six thousands specimens and 235 species (Table S1), I will examine whether this pattern is supported in 14 phylogenetically well separated and ecomorphologically disparate lineages from 11 different orders, representing all four superorders of placentals. The study follows the traditional allometric school of Huxley and Teissier (Gayon 2000; Klingenberg 1998), and employs major axis (MA) regressions and comparative methods on species average measures of facial and braincase overall size, as well as ventral and dorsal lengths. In total, more than 2000 allometric slopes will be estimated to explore the sensitivity of results to: the choice of the morphometric descriptor; the taxonomic level (with both supra- and, whenever enough species are available, infrageneric analyses); sexual dimorphism, if present and large; the inclusion or exclusion of species with very small samples ($N \leq 5$); and differences in branch lengths in phylogenetic trees (corresponding to models varying from star radiation and early diversification to intermediate and late diversification, as in Tamagnini et al. 2017).

The anatomical points used to compute (a) facial and braincase centroid size are shown in Fig. 1 together with (b) the lengths of the nasals and cranial vault (dorsal view), and (c) those of the palate and cranial base (ventral view). The specific boundaries between the two anatomical regions follow the subdivisions proposed by Hallgrímsson et al. (2006), with the braincase being made of neurocranial and basicranial modules. This subdivision reflects the developmental organization of the cranium and allows for precise boundary landmarks to be identified. Alternative definitions are possible (e.g., with part of the frontal bone and the orbit belonging to the face), which may reflect different hypotheses in relation to function (e.g., masticatory region together

Fig. 1 Measures. Anatomical landmarks and linear distances used to measure the size and length of the face and braincase

with sensory organs) instead of development, but they are less suitable in the evolutionary-developmental context of CREA.

Support for CREA is found when the increase in facial size during an evolutionary radiation is faster than that of the braincase, which is indicated by slopes > 1 in MA regressions of facial onto braincase measurements. The main results are summarized in Table S2 and slopes are shown in Figs. 2, 3, 4 and 5. The vast majority of analyses and taxa support the prediction that the face is characterized by positive allometry (slope > 1) relative to the braincase. The relationship between facial and braincase measurements is strong with almost 80% of regressions accounting on average for more than 2/3 of variance (R2) in the data. The average of slopes across evolutionary models in each set of analyses (Table S2) is > 1 in 96% of cases, > 1.2 in 75% and > 1.5 in 34%. Some groups have stronger patterns and steeper slopes (e.g., most primates and sometimes the African megabats), and others show weaker trends with shallower slopes (e.g., often armadillos or, sometimes, canids and ungulates). However, virtually all lineages, regardless of the type of measure of craniofacial proportions and the inclusion or exclusion of smaller samples, indicate that, among closely related species, the size-related trend of facial elongation and braincase reduction is clear and consistent. Thus, as for Bergmann's rule (Meiri 2011), the strength of the trend varies from case to case, but the pattern is overwhelmingly supported.

Exceptions to CREA?

There are some exceptions to CREA, and they mostly occur in a very limited number of lineages using lengths in ventral view. In ungulates, African antelopes and equids, the palate and cranial base lengths can increase isometrically in bigger species or sometimes even with a slight shortening of the face in relation to the cranial base. Radinsky (1985) also analysed equids, as well as the whole bovid family, but did not find them to depart from the general trend of positive allometry. However, he could only use ordinary least square models (that do not take the non-independence due to phylogeny into account), employed a slightly different measure of braincase size, and only analysed the ventral view of the cranium. He also sampled different species, presumably including fossils in the high-crowned equids and using 18 species to represent the whole diversity and disparity of the bovids. His study was based on a single individual for each species and did not take possible sex differences into account. Thus, the difference between my results and Radinsky's findings only concerns a minority of cases using ventral lengths in two groups, that did not fully overlap across our analyses and may have different issues in terms of sampling error and statistical inaccuracies.

Besides ungulates, and again only using ventral lengths, also canids [as in Radinsky (1985)], hyraxes, *Cercopithecus* monkeys and male macaques support CREA less strongly, as positive allometry is on average very moderate in these groups and sometimes isometry is found. However, results that might contradict CREA represent overall less than 10% of the total, with in fact dorsal lengths as well as analyses of centroid size consistently confirming positive allometry of the face in all taxa, including ungulates, hyraxes, canids and all monkeys.

'Flexible Constraints' and Generality of CREA

The main conclusion of an overwhelming support for CREA is therefore robust. However, potential exceptions to the rule, such as ventral lengths in ungulates and few other groups, provide interesting examples of how different taxa, and cranial regions, may have departed from the general trend. This, and the variability of slopes, suggests that CREA acts as a widespread constraint (in terms of direction but not necessarily of speed) of changes in craniofacial proportions during evolutionary radiations. The constraint is of moderate strength, and the rule is flexible, so that it can be modified, or even reversed, by natural selection. For instance, in ungulates, the pressure for breaking the rule in ventral cranial proportions could have been the need of housing large hypsodont teeth, whose size might be relatively larger in small herbivores, forcing the palate to be proportionally long despite a modest cranial size. Tamagnini et al. (2017) also speculated that teeth might be important in modifying the rule, as the main exception among pantherines was the proportionally long palate of the relatively small clouded leopard, a species with exceptionally long canines and therefore very deep and long dental roots. In human evolution, in contrast, selective pressures for evolving large brains, together with tool use, cooking, and other forms of food processing, made large teeth unnecessary and probably contributed to revert CREA (Cardini and Polly 2013). That thus led to the distinctive morphology of modern humans, with their disproportionately large braincase and orthognathic face.

The robust support for CREA in 14 distantly related, and ecomorphologically disparate, placental lineages makes it unlikely that the pattern arose independently so many times. In fact, this analysis, the largest until now in terms of samples and taxonomic groups, together with Radinsky's (1985) pioneering work, and a number of studies reporting similar craniofacial allometric patterns within one or or another specific lineage of mammals, provide evidence for CREA in: four large taxa of primates (Radinsky 1985), as well as four families of carnivores (Cardini et al. 2015; Radinsky 1985; Tamagnini et al. 2017); several groups of rodents (Cardini and Polly 2013; Lessa and Patton 1989;

SLOPES
all species
species with N>5
centroid size
dorsal
ventral
SLOPE
Afr_colob_F
Afr_colob_M
Afr_colob_M*
Piliocolobus_F
Piliocolobus_M
Piliocolobus_M*
guenons_F
guenons_M
Cercopithecus_F
Cercopithecus_M
papionins_F
papionins_M
Macaca_F
Macaca _M
leporids
Lepus
squirrels
megabats_F
megabats _M
Erinaceinae
antelopes_F
antelopes_M
antelopes_M*
equids
herpestids
canids
canids_F
canids_M
Vulpes
hyraxes
armadillos
sloths

◂**Fig. 2** Summary of slopes. Profile plots of average slopes (red lines) using all species or the reduced dataset with larger species samples (N > 5); the light blue shaded area shows the range of variation (10th and 90th percentiles) of slopes estimated using regressions with different branch lengths; the horizontal dotted line indicates isometry (slope = 1). Abbreviations: *Afr_col* African colobines, *F* females, *M* males (Color figure online)

McIntosh and Cox 2016; Mora et al. 2003), and the main living family of the lagomorphs, the leporids (Radinsky 1985); three lineages of arctiodactyls (Cardini and Polly 2013; Radinsky 1985; van der Geer et al. 2018), and at least one of perissiodactyls (Radinsky 1985); one of the main lineages of erinaceomorphs (Radinsky 1985) and one of bats (Cardini and Polly 2013); two families of Afrotheria (the tenrecs (Radinsky 1985), besides the hyraxes analysed here); two out three of the main xenarthran clades; and at least two families of marsupials (Cardini et al. 2015; Radinsky 1985). Thus, parsimony suggests that most other placentals might follow CREA, that, if found in even more lineages of marsupials (and maybe also in the echidnas), confirmed in birds (Bright et al. 2016; Linde-Medina 2016; Tokita Masayoshi et al. 2017) and possibly discovered in other land vertebrates, could become one of the most general rules of morphological evolution in the tetrapods.

Taxonomic Level for Testing the Rule

Probably the most important aspect not to forget in future studies of CREA concerns the choice of an appropriate taxonomic level for the analysis. Radinsky (Radinsky 1985) largely focused on families. That has the advantage of apparent consistency and might seem more objective. However, neither taxonomy nor evolutionary time can provide on their own a simple criterion to select the level at which CREA should be tested. Some families may be more conservative in cranial form and others show larger disparity. And even closely related lineages may evolve along different morphological trajectories. Cercopithecines and colobines are both members of the family Cercopithecidae, but cercopithecines, and especially papionins, are mostly omnivorous and tend to have on average long snouts, whereas the predominantly folivorous colobines are typically orthognathic. Such large differences in ecology and average cranial proportions between subfamilies or tribes of Old World monkeys make the cercopithecid family as a whole an unlikely target for testing CREA. Tests within its subclades, in contrast, are appropriate and have until now produced support for the rule. Similarily, CREA occurs both within the felids (Tamagnini et al. 2017) and the viverrids (Radinsky 1985), whereas a test performed after pooling the generally larger but short-faced hypercarnivorous cats and the smaller long-faced omnivorous genets would not make much sense despite their close phylogenetic relationship. This is not only because, as the Bermann's rule (Meiri 2011), CREA is defined as a trend found in closely related species and populations (Cardini and Polly 2013). It is also, and more importantly, because pooling lineages that diverged so much in ecology, that their formerly common cranial bauplan becomes different in terms of typical craniofacial proportions, would produce a meaningless test of CREA, clearly outside the realm in which the rule has been proposed and described (Cardini and Polly 2013). Indeed, a sharp drop in the fit of a single regression line in a larger lineage, compared to separate regressions within its sub-clades, might often be a clue that differences have become too large for pooling the clades.

In contrast, within a group sharing a common cranial bauplan, CREA might be tested and supported (with more or less strength) or rejected. If CREA is supported, that will be as an average trend in that group, despite possible and potentially interesting exceptions. Among big cats (subfamily Pantherinae), as mentioned, the clouded leopard is relatively long-faced despite being smaller than other species (Tamagnini et al. 2017), thus deviating from the general trend probably because of its very long canines (proportionally longer than in any other living felid). In the case of simple bivariate regressions, as in this study, the magnitude of the deviation from the main regression line can be taken as an estimate of how unusual a species is for craniofacial proportions compared to its closest relatives, exactly in the same way as one uses the encephalization quotient to infer unusually large (or small) brains relative to body mass (Boddy et al. 2012). Indeed, as the pace of evolution varies across groups and structures, there will not be a simple unique taxonomic level for testing CREA, that fits all taxa. To make the taxonomic level less approximate, one could try to relate the strength of CREA (and its likely refutation above a certain degree of variation) to morphological disparity across groups within a larger clade.

Guessing the Processes behind the Pattern

As anticipated, for now, one can only speculate about the processes behind CREA. The resemblance to an almost universal mammalian trend of within species post-natal ontogenetic change (Cardini and Polly 2013), in which the rate of facial growth is faster than that of the braincase, making the face of adults proportionally longer, is evident and intriguing. One might assume that, if this similarity is based on homologies, it could provide an evolutionary developmental link between micro- and macro-evolutionary mechanisms of morphological variation. That adults of domestic mammals, selected to be smaller than their wild counterparts, in general originally tended also to be somewhat paedomorphic and short-faced seems consistent with a relationship between

Fig. 3 Slopes for centroid size. Scatterplots of slopes using different branch lengths in comparative analyses. Slopes from analyses of the full dataset are on the horizontal axes and those of the reduced dataset (including only species with N > 5) are on the vertical axes. Dotted lines indicate isometry. Scatterplots are grouped by taxa. Abbreviations use the first three letters of the genus name; for African colobines, guenons and papionins the abbreviations are respectively Afr_col, gue and pap. F and M indicate respectively females and males in analyses with separate sex

growth and the origin of evolutionary change (Cardini and Polly 2013). Also, a genetic correlation between craniofacial variation and body mass has been demonstrated in primates and suggested to provide a potential mechanistic explanation for CREA (Joganic et al. 2018). Nevertheless, as we and others discussed in previous papers (Cardini and Polly 2013; Lessa and Patton 1989; Radinsky 1985), dietary pressures and biomechanical adaptations might provide alternative and non-mutually exclusive explanations of CREA. In this respect, showing that facial elongation in larger species is adaptive to, for instance, climate (Milne and O'Higgins 2002) does not refute CREA, as CREA is purely about the

Fig. 4 Slopes for dorsal lengths. Scatterplots of slopes based on different datasets, models and taxa. See Fig. 3 for full legends

pattern and does not assume any specific mechanism. It does not even rule out an hypothetical explanation in terms of genetic and developmental architecture (Joganic et al. 2018; Usui and Tokita 2018), which might on one hand constrain to a larger or smaller degree evolvability (Minelli 2009), but, within this narrower range of potential directions of variation, can also provide a simple 'evolutionary trick' to speed up change and produce adaptations along an allometric line of least evolutionary resistance (Marroig and Cheverud 2005; Renaud and Auffray 2013).

Evolution tinkers with available mechanisms and often exploits already existing developmental processes

Fig. 5 Slopes for ventral lengths. Scatterplots of slopes based on different datasets, models and taxa. See Fig. 3 for full legends

to produce morphological variation (Hallgrimsson et al. 2007). Both brain and metabolism scale negatively with body mass in mammals, thus making negative allometry of the braincase somewhat expected (Cardini and Polly 2013). However, ontogenetic trajectories usually diverge progressively across species as they radiate, as shown in a variety of mammals from rodents (Tavares et al. 2018) to hominins (Bastir et al. 2006). Therefore, interspecific allometries may share aspects of a common ontogenetic pattern but are unlikely to be produced by simple extension or truncation of size-related developmental trajectories. To make the picture more complicated, epigenetic factors, such as hormone levels, muscle development and dietary change, act upon bone shape during growth, adding

a layer of plasticity to the phenotypic output of regulatory networks and the potential constraints set by gene linkage and pleiotropy (Cardini and Polly 2013; Joganic et al. 2018). Discovering the process (or the multiplicity of processes) behind evolutionary rules is clearly a challenge, but lacking an explanation does not diminish the importance of robustly documenting patterns (Meiri 2011). In this respect, CREA is now a big step closer to becoming a well supported evolutionary rule of morphological change in placentals and probably other groups of mammals and vertebrates.

Acknowledgements New data, which are published for the first time in this paper, were collected at Museo Civico di Storia Naturale di Milano, Natural History Museum Vienna, National Museum Prague, Museum für Naturkunde, Museum National d'Histoire Naturelle, Hungarian Natural History Museum, Naturhistoriskariksmuseet. I owe a huge thank to all curators, collection managers and staff, including the SYNTHESYS administrators, whose help and support was fundamental. I am also deeply grateful to a number of colleagues who provided technical help and advice. With anticipated apologies for certainly forgetting to explicitly mention several of the many people whom I am in debt with, as well as for listing names in quasi-random order, I would like to thank a lot: Wim Wendelin, Emmanuel Gilissen, Giorgio Bardelli, Görföl Tamás, Gabor Csorba, Virginie Bouetel, Aurelie Verguin, Frank Zachos, Alex Bibl, Krapf Andrea, Petr Benda, Karel Kaderàbek, František Vacek, Manja Voss, Christiane Funk, Detlef Willborn, Mayer Frieder, Daniela Kaltoff, Irene Bisang, Emily Dock Åkerman, Jessica Joganic, Aurélie Siberchicot, David Katz, Mike Collyer, David Warton, Sara Taskinen, Paul O'Higgins, Sarah Elton, David Polly, Krish Seetah, Dan Franklin, Carlo Meloro, Diego Fontaneto and Alessandro Minelli. A special thank also to the greatly missed Colin Groves, for his fundamental contribution to interpreting the preliminary analyses of wild asses, and to Anderson Feijó, who helped with species identification of some of the armadillos. My gratitude goes also to the American Society of Mammalogists, for inviting me to present the preliminary results of this study at their annual conference and for covering all the costs of my trip to the US. This paper is dedicated to the memory of Mario Zambarbieri and Paolo Tongiorgi, my greatest mentors and friends, as well as to that of Colin Groves, a most extraordinary mammalogist, and of Leonard Radinsky, first discoverer of CREA, whose important role I would have acknowledged well before, had I found earlier his surprisingly little cited and yet fundamental contribution on patterns in mammalian morphological evolution. Finally, I am greatly in debt to Julien Claude, an anonymous reviewer and the Editor-in-Chief Benedikt Hallgrimsson, for their most helpful review and appreciation of my work.

Author contributions This study was designed, all data were collected, analyses done, and the paper written by CA.

Funding Data collection was funded by SYTHESYS (BE-TAF-2861, SE-TAF-4409, AT-TAF-4816, CZ-TAF-4817, HU-TAF-4818, DE-TAF-4819, FR-TAF-4820) for all lineages except most primates, that were measured for a previous project with Sarah Elton, funded by the Leverhulme Trust (F/00128/T).

Compliance with ethical standards

Conflict of interest I declare no competing interests or conflict of interest.

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