

RESEARCH ARTICLE

Cranial suture complexity in caviomorph rodents (Rodentia; Ctenohystrica)

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Abstract

Due to their flexibility, sutures are regions that experience greater strains than the surrounding rigid cranial bones. Cranial sutures differ in their degree of interdigitation or complexity. There is evidence indicating that a more convoluted suture better enables the absorption of high stresses coming from dynamic masticatory forces, and other functions. The Order Rodentia is an interesting clade to study this because of its taxa with diverse chewing modes. Due to repeated loading resulting from gnawing and grinding, energy absorption by the sutures might be a crucial factor in these mammals. Species within the infraorder Caviomorpha were chosen as a case study because of their ecomorphological and dietary diversity. This study compared five sutures from the rostrum and cranial vault across seven caviomorph families, and assessed their complexity by means of the relative length and fractal dimension. Across these rodents, cranial sutures are morphologically quite diverse. We found that the sutures connecting the rostrum with the vault were relatively more interdigitated than those in the cranial vault itself, especially premaxillofrontal sutures. Suture interdigitation was higher in species that display chisel-tooth digging and burrowing behaviors, especially in the families Ctenomyidae and Octodontidae, than those in families Dasyproctidae and Cuniculidae, which have more gracile masticatory systems. The reconstruction of the ancestral character state, on family and species phylogeny, points toward low suture interdigitation (i.e., low length ratio) as a likely ancestral state for interfrontal, premaxillofrontal and maxillofrontal sutures. Interspecific differences in suture morphology shown here might represent adaptations to different mechanical demands (i.e., soft vs. tough foods) or behaviors (e.g., chisel-tooth digging), which evolved in close association with the diverse environments occupied by caviomorph rodents.

KEYWORDS

bite force, energy absorption, mechanical loading, digging behavior

1 | INTRODUCTION

One of the unique aspects of the tetrapod skull is the presence of sutures, that is, sites of appositional bone growth separating the individual bones, which are crucial for proper skull development (Hanken & Hall, 1993; Opperman, 2000). The persistence of unfused sutures in mature skulls is thought to be related to stress transfer and/or stress dampening (Sun, Lee, & Herring, 2004). Indeed, as part of the cranium, sutures are under mechanical stresses coming from different sources (Hanken & Hall, 1993), such as the static expansion of growing soft tissues (e.g., the expansion of the brain) (Ogle, Tholpady, McGlynn, & Ogle, 2004), dynamic masticatory forces (Herring & Teng, 2000), and

traumatic impacts (Jaslow & Biewener, 1995) which can be quite commonly caused by inter-male aggression in certain taxa (e.g., Cervidae, Caprinae) (Hanken & Hall, 1993; and references therein). Mature craniofacial sutures are composed of an extracellular matrix of collagen fibers, proteoglycans, and water (Opperman, 2000). Sutures are zones of flexibility and energy absorption undergoing greater tensional, compressive or both types of deformation than the nearly rigid bones of the skull (Herring & Mucci, 1991; Rafferty & Herring, 1999). Cranial sutures play a dual role. On the one hand, they are presumed to transmit loads from one bone to another, providing integration and strength to the skull; on the other hand, they are relatively flexible and constitute zones where loads are damped and energy is absorbed.

A striking feature of cranial sutures is their difference in degree of interdigitation, from those whose path is nearly straight and simple to those highly sinuous and complex. From a comparative perspective, it has been shown that increased suture complexity characterizes those species capable of exerting relatively strong bite forces and/or having a diet of hard food items (Byron, Borke, Yu, Pashley, Wingard, & Hamrick, 2004; Monteiro & Lessa, 2000). The capuchin monkey *Sapajus apella*, which consumes foods of higher toughness than other species within the *Sapajus* genus, showed a more robust morphology and more complex sagittal sutures than its congeners (Byron, 2009). After studying a South American genus of alligatorids with differences in hardness of their preferred diets, Monteiro and Lessa (2000) found that *Caiman latirostris* has relatively more complex and interdigitated sutures than *C. sclerops* and *C. yacare*, showing also a major preference for hard shelled gastropods. These authors have suggested that a greater interdigitation of the rostral sutures increases the area for attachment of fibrous connective tissue allowing the absorption of high tensile forces. In addition to dynamic masticatory forces, another source of stress on the skull is the inter-male aggressive encounters usually seen in certain horned or antlered ungulate species. Impact-loading experiments performed on the ungulate *Capra hircus* showed that bone regions with sutures absorb more impact energy than bones without them (Jaslow, 1990). Further, a fivefold increase in energy absorption by the sutures was significantly correlated with increased suture interdigitation. Thus, it was argued that higher suture interdigitations provide larger surface areas for increased extracellular matrix attachment. However, the evidence is not conclusive in this regard. Nicolay and Vaders (2006) studied the suture morphology in the white-tailed deer *Odocoileus virginianus*, the males of which have large antlers that are used during aggressive encounters. Despite the major effect expected due to the weight of the antlers themselves and the impacts during encounters, they did not find a significant sexual dimorphism in suture complexity.

Whereas the aforementioned studies analyzed the sutures considering their ectocranial surface morphology (i.e., their path along the skull's surface), other studies have focused on the internal morphology (i.e., in transverse plane) of the contact zone between two bones of the skull (Rafferty & Herring, 1999; Sun et al., 2004). One striking conclusion from these studies is that suture morphology was related to the strain polarity but not the magnitude of strains. Suture interdigitation is specifically associated with compression, and butt-ended and simple suture morphologies with tension (Rafferty & Herring, 1999; Sun et al., 2004). Also using strain gauges, Markey, Main, and Marshall (2006) analyzed the cross section of three vault sutures in the extant bichir fish *Polypterus*. They found that sutures experiencing compression were more interdigitated than sutures under tension. In a more detailed analysis on the same species, Markey and Marshall (2007) found in the suture between the frontal and parietal bones a complex strain pattern, under both tension and compression. Furthermore, histological evidence suggests that interdigitation facilitates an oblique arrangement of collagen fibers, which would be a good compression-resistance mechanism (Herring & Teng, 2000).

Vertebrates exhibit a great structural diversity in their masticatory apparatus, allowing them to feed on a wide range of items (Feldhamer,

Drickamer, Vessey, & Merritt, 1999). The skulls of different taxa are subjected to dynamic loads coming from contrasting chewing modes. In this regard, Rodentia is an interesting group to study the morphology of cranial sutures because of their distinctive feeding modes (Feldhamer et al., 1999; Olivares, Verzi, & Vassallo, 2004). Rodents can gnaw using their chisel-like incisors, or they can grind foods using the molars in a series of medio-to-lateral and/or antero-to-posterior movements of the jaw (Druzinsky, 2015; Feldhamer et al., 1999). Moreover, several species (e.g., *Ctenomys* spp.; *Nannospalax ehrenbergi*) use the incisors to break down the soil when its mechanical resistance exceeds the foreclaws' capability (Mora, Olivares, & Vassallo, 2003; Vassallo, 1998). When performing this type of digging behavior, the procumbent upper incisors are strongly anchored into the substrate while the lower ones are used for breaking-down the soil into pieces, involving the powerful mandibular adductor and neck muscles as key adaptations (Becerra, Casinos, & Vassallo, 2013; Becerra, Vassallo, Echeverría, & Casinos, 2012). Therefore, as in other mammals, the rodent skull must be able to withstand large reaction forces received both on incisors and molars (Ungar, 2010). However, due to the repetitive gnawing loads, potential energy absorption by sutures becomes a crucial factor in these mammals. The monophyletic South American hystricomorph rodents (i.e., Caviomorpha) were chosen as a case study because of their diverse ecologies, diets, and biting performances (Becerra, Echeverría, Vassallo, & Casinos, 2011; Becerra et al., 2012; Mares & Ojeda, 1982; Ojeda, Novillo, & Ojeda, 2015; Olivares et al., 2004). Their contrasting habits include: semiaquatic, arboreal, epigeal, fossorial (i.e., burrowers who spend a substantial fraction of their lives outside their burrows, with relatively long excursions to collect food; e.g., *Aconaemys*, *Octodon*) or subterranean (i.e., conducting the vast majority of their life underground, with foraging excursions usually limited to the vicinity of burrow openings; e.g., *Ctenomys*) (Lessa, Vassallo, Verzi, & Mora, 2008; Mares & Ojeda, 1982). *Ctenomys*' skeletal adaptations for digging are found in both the postcranium and the masticatory apparatus (Álvarez, Perez, & Verzi, 2011; Becerra, Echeverría, Casinos, & Vassallo, 2014; Becerra et al., 2013; Hautier et al., 2011; Lessa et al., 2008; Olivares et al., 2004; Vassallo, 1998, 2000; Woods, 1972). Species belonging to Caviidae, Dasyproctidae, Echimyidae, and Cuniculidae, which show mainly ground-dwelling habits (with a few exceptions; Rocha-Barbosa, Fiuza de Castro Loguercio, Casinos, Silva Climaco das Chagas, & Abreu dos Santos, 2015) have relatively gracile masticatory systems associated with less mechanically challenging diets (e.g., fruits; leaves). Species belonging to Ctenomyidae and Octodontidae have robust masticatory systems associated with relatively hard foods (e.g., roots, grasses) (Ojeda et al., 2015). A recent study focused on the pattern of cranial suture closure in hystricognath rodents has found that, although small sequential differences take place between species, the overall pattern was conserved across these rodents (Wilson & Sánchez-Villagra, 2009). Sutures located at the cranial base and vault were the first to close whereas the last ones were all located in the facial region of the skull (Wilson & Sánchez-Villagra, 2009). Differing life history and locomotor habits appear to be associated with both differing degrees of suture closure and heterochronic transformations in

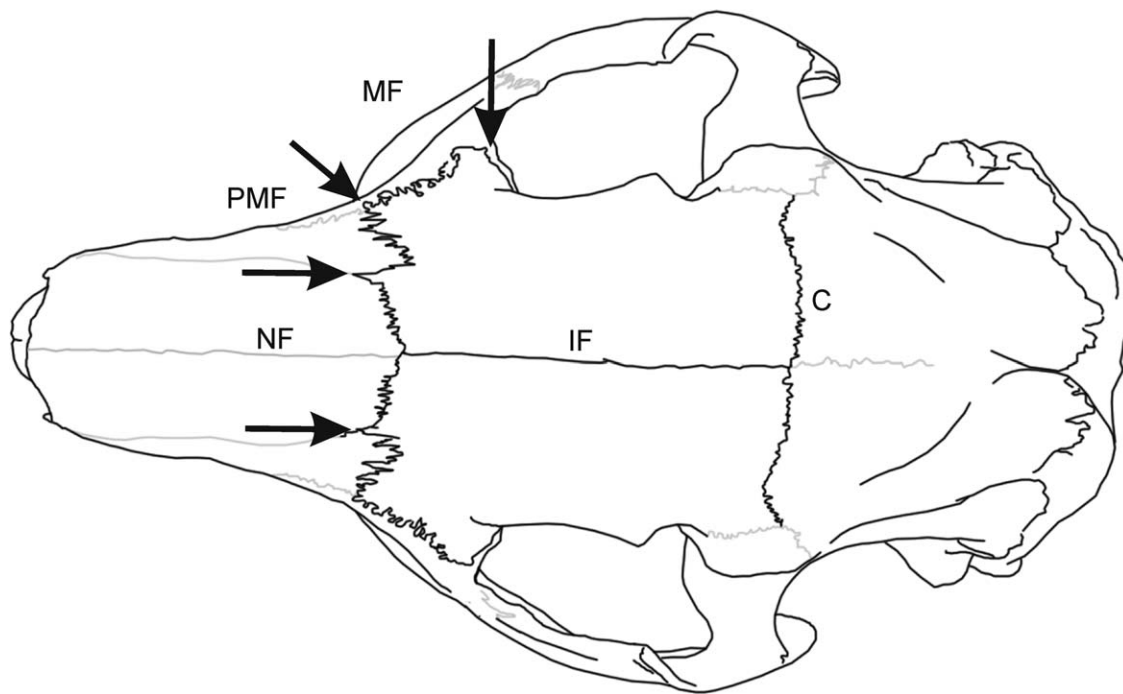


FIGURE 1 Analyzed sutures (in bold) as they appear on a *Myocastor coypus*' skull. References: NF = Nasofrontal suture; MF = Maxillofrontal suture; PMF = Premaxillofrontal suture; IF = Interfrontal suture; C = Coronal suture. Arrows indicate where rostral sutures end

suture patterns. However, the ectocranial surface morphology of sutures (i.e., their degree of interdigitation) and its possible functional significance in caviomorph rodents has not yet been addressed.

The aims of this study were (1) to assess the morphology of five homologous cranial sutures located in different regions of the vault and its boundary with the rostrum in rodents, belonging to different families of Caviomorpha; and (2) to examine the effect of specialized behaviors on suture morphology, particularly the effect of chisel-tooth digging, which presumably exerts considerable loads on the skull.

2 | MATERIALS AND METHODS

2.1 | Sample used

Specimens belonging to 32 species and of seven families within Caviomorpha (Wood, 1955), housed in four different museum collections (Supporting Information Table 1), were studied to assess suture morphology. We focused on adult specimens, defined by the presence of a functional third molar. The sampled species were selected to get a wide representation of: (1) the taxonomic diversity within this infraorder; and (2) the behavioral diversity that reflects differences in diet (hard vs. soft foods) and niche use (e.g., ground dwelling vs. fossorial vs. subterranean and chisel-tooth diggers).

2.2 | Suture morphology and indices

The morphology of five homologous sutures located across the cranial vault and its boundary with the rostrum was assessed (Figure 1). Due

to their presumed role in allowing energy to be absorbed during incisor biting and molar grinding (Herring & Teng, 2000; Rafferty & Herring, 1999), we focused our attention on: the suture between the frontal and parietal bones (coronal; C), suture between the frontal bones (interfrontal; IF), the suture between the nasal and frontal bones (nasofrontal; NF), the suture between the maxilla and the frontal bone (maxillofrontal; MFL and MFR for left and right side, respectively), and the suture between the premaxilla and the frontal bone (premaxillofrontal; PMFL and PMFR for left and right side, respectively; Figure 1). The coronal sutures were considered as a single suture given that they continue one another. Sutures were photographed with a digital camera (Olympus E620, Tokyo, Japan) mounted on a copy stand for large specimens (e.g., *Lagostomus maximus*), or on a stereoscopic microscope (12X magnification; Olympus SZ61, Tokyo, Japan) for small specimens (e.g., *Ctenomys*), and traced from an ectocranial perspective throughout the original image amplified with a 300% digital zoom. Using a 2 pixel thick line on Inkscape v0.91 software (inkscape.org), a vector graphic of each suture was produced (Figure 2). Two dimensional digital image tracings might suffer parallax problems compared to tracing methods that account for cranial curvature, but differences between species are proven to be consistent (Byron, 2009) when using this method.

Two indices were used to study suture ectocranial complexity (i.e., degree of interdigitation): length ratio (LR), and fractal dimension (FD). The length ratio is calculated as the total length of the suture path divided by the linear distance between its two ending points (as originally described by Jaslow, 1989). Lengths were measured using the built-in Measure tool on Inkscape. The fractal dimension has been previously used to analyze suture complexity in mice (Byron et al., 2004),

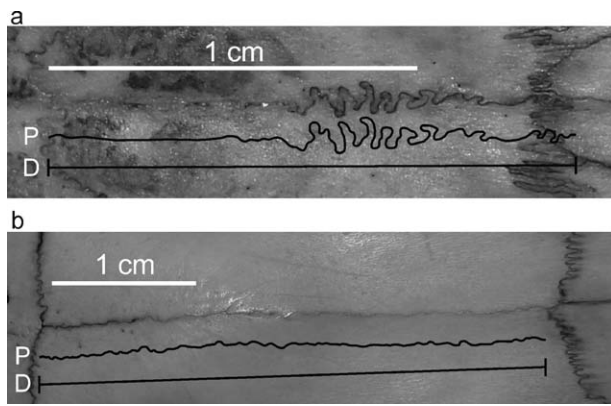


FIGURE 2 Ectocranial shape of the interfrontal suture (IF) in *Ctenomys sociabilis* (a) and *Myocastor coypus* (b). The tracings of suture path (P) and distance between ends (D) were used to calculate FD and LR indices (see Methods)

capuchin monkeys (Byron, 2009), caimans (Monteiro & Lessa, 2000), and the white-tailed deer (Nicolay & Vaders, 2006). This method assesses the space filling properties of an object that repeats itself in different scales, and cannot be analyzed precisely with Euclidean geometry since measurements change with the scale used (Mandelbrot, 1983). Here, we used the box-counting method with the FracLac plugin (Karperien, 1999–2013) for ImageJ software (Abràmoff, Magalhães, & Ram, 2004). This method superimposes grids of different cell size over the suture and counts the number of boxes traversed by the suture path on each grid. Then, the fractal dimension index is calculated as: $FD = \lim_{r \rightarrow 0} (\log Nr / \log r)$; r being the values of box size and Nr the number of boxes occupied by the suture. For 2D-images like a sutures' path, values of FD oscillates between 1 and 2. As the suture becomes more convoluted (i.e., increase in complexity), the index increases its value.

2.3 | Statistical analysis and ancestral character reconstruction

A Pearson correlation test was performed between length ratio (LR) and fractal dimension (FD) indices to assess if they were yielding similar results. Bilateral symmetry of MF and PMF sutures was analyzed using a paired t -test. Given that our data did not met with ANOVA assumptions, and to avoid the use of data transformations, we used a generalized linear model (GLM) to test the effect of Suture Type and Taxonomic Clade: Family (the explanatory variables) on the LR (the response variable) of the analysed sutures. A Gamma error structure with a reciprocal link function (Crawley, 2007) was used for LR. Significance level was set at 0.05. The effect of skull size on suture complexity was analyzed by means of type II regressions, using the naso-occipital length (a skull size proxy) as the independent variable, and each suture's LR as the dependent variable. To address the statistical nonindependence among the studied taxa due to common ancestry, measures were previously converted into phylogenetically independent standardized contrasts using the PDAP module (Midford, Garland, & Maddison, 2005) in the program Mesquite (Maddison & Maddison, 2006). Statistical analyses were conducted using R 3.0.2 software (R

Core Team, 2012). To reconstruct the evolutionary history of suture morphology within the studied caviomorph rodent taxa, values of LR were mapped on a phylogenetic tree using the Phytools package for R (Revell, 2012) for each suture, under a maximum-likelihood criterion. Phylogenetic relationships among taxa and time scales were taken from Parada, D'elía, Bidau, and Lessa (2011), and Upham and Patterson (2012).

3 | RESULTS

3.1 | Length ratio versus fractal dimension

Because no significant differences were found between length ratio values from either side of MF and PMF sutures (paired t -test: $t = 1.02$, $p = 0.31$; $t = 0.09$, $p = 0.93$, respectively), bilateral symmetry in complexity could be confidently assumed for these sutures, and further analyses could be based on the right sided sutures. The similarity between the two indices used to assess suture complexity, as indicated by Pearson's correlations, was highly variable. The correlation between the indices for the interfrontal suture (the only midline suture analyzed here) was high, but it was low for the others (varying from 0.18 to 0.62, see Table 1; Supporting Information Figure 1), at which LR was high (i.e., complex morphology) but FD was low.

3.2 | Sutures' general characteristics

Figure 3 shows some examples of cranial sutures, which highlight the diversity of suture paths within Caviomorph rodents. Differences in path morphology are evident when comparing sutures within a single family or particular sutures among families. For example, it can be seen that the interfrontal suture (i.e., the only midline suture) possesses an elongated straight path that is rather similar among the studied groups (Figure 3.2), whereas other sutures (paired ones, transverse to the midline of the skull) are much more curved, complex and/or variable among families, for example, coronal, maxillofrontal, and nasofrontal sutures (Figure 3.1, 3.3, 3.4, respectively). The complexity of the path depends primarily on the degree of interdigitation, a feature especially demonstrated in certain families such as Octodontidae and Ctenomyidae at the premaxillofrontal and interfrontal sutures, respectively. Interdigitations may show a serrated (e.g., Figure 3.1e,3.4g) or lobed edge (e.g., Figure 3.1c); and may extend over the entire suture

TABLE 1 Pearson's correlations between the proxies of complexity length ratio and fractal dimension

Suture	N	r^2
Combined sutures	471	0.26
Coronal	90	0.59
Interfrontal	91	0.91
Maxillofrontal	97	0.6
Nasofrontal	95	0.18
Premaxillofrontal	98	0.58

All regressions are significant at $p < 0.001$.

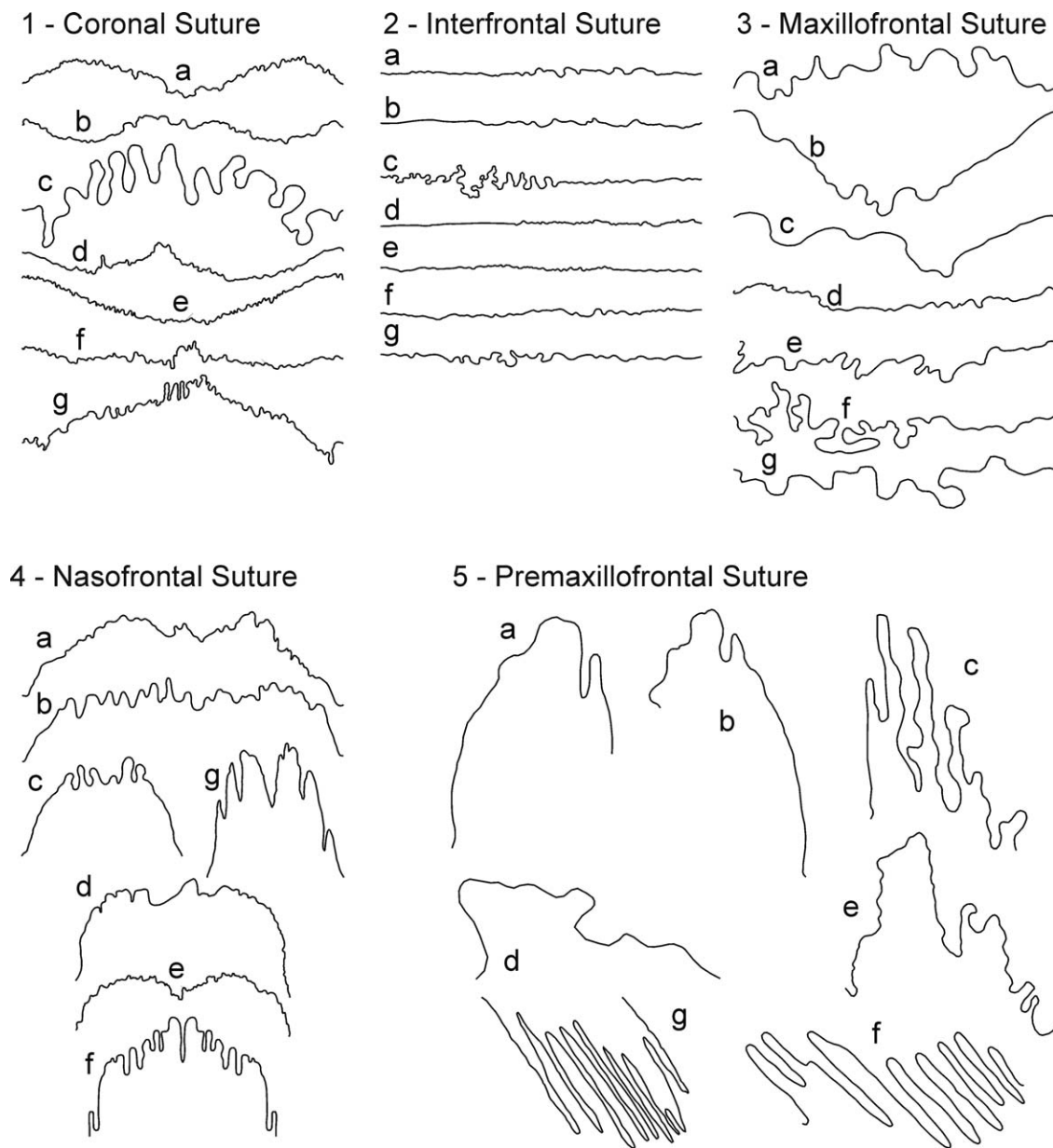


FIGURE 3 Examples of sutural morphology for each caviomorph rodent family analyzed. These are representative examples, but there can be some variation within families. References: Sutures are grouped by suture type (in numbers) and family represented (a- Caviidae; b- Chinchillidae; c- Ctenomyidae; d- Cuniculidae; e- Dasyproctidae; f- Echimyidae; g- Octodontidae). Tracings are not in scale

(e.g., Figure 3.1g), or only in a certain portion of the suture (e.g., Figure 3.2c). Finally, in some cases, the suture itself seems to have fractal geometry in the sense that the tracing exhibits a self-repetitive pattern at different scales, in other words interdigitations within interdigitations (e.g., Figure 3.3f). Supporting Information Table 2 summarizes LR and FD values of all sutures present in Figure 3.

There was no significant relation between the skull size (estimated by the naso-occipital length) and the complexity of the sutures ($R^2 = 0.01$, $p = 0.64$ for the coronal suture; $R^2 > 0.01$, $p = 0.82$ for the interfrontal suture; $R^2 = 0.02$, $p = 0.58$ for the maxillofrontal suture; $R^2 = 0.01$, $p = 0.61$ for the nasofrontal suture; and $R^2 < 0.01$, $p = 0.98$ for premaxillofrontal suture).

3.3 | Intersuture and inter-taxa comparisons

Cranial sutures of caviomorph rodents greatly differ in complexity as measured by their LR values. The GLM revealed significant differences in LR among suture types (Figure 4f). Sutures connecting the rostral region with the cranial vault tended to be more complex and interdigitated than those located in the cranial vault itself (Figure 4f). Premaxillofrontal, and to a lower extent the nasofrontal suture, have the highest LR values (Figure 4f). The family effect was tested separately for each suture series and the overall finding was that it significantly affects them all (Supporting Information Table 3). GLM revealed that ctenomyids had the highest values for sutures in the cranial vault (i.e., coronal and interfrontal sutures; Figure 4a,b) and intermediate values

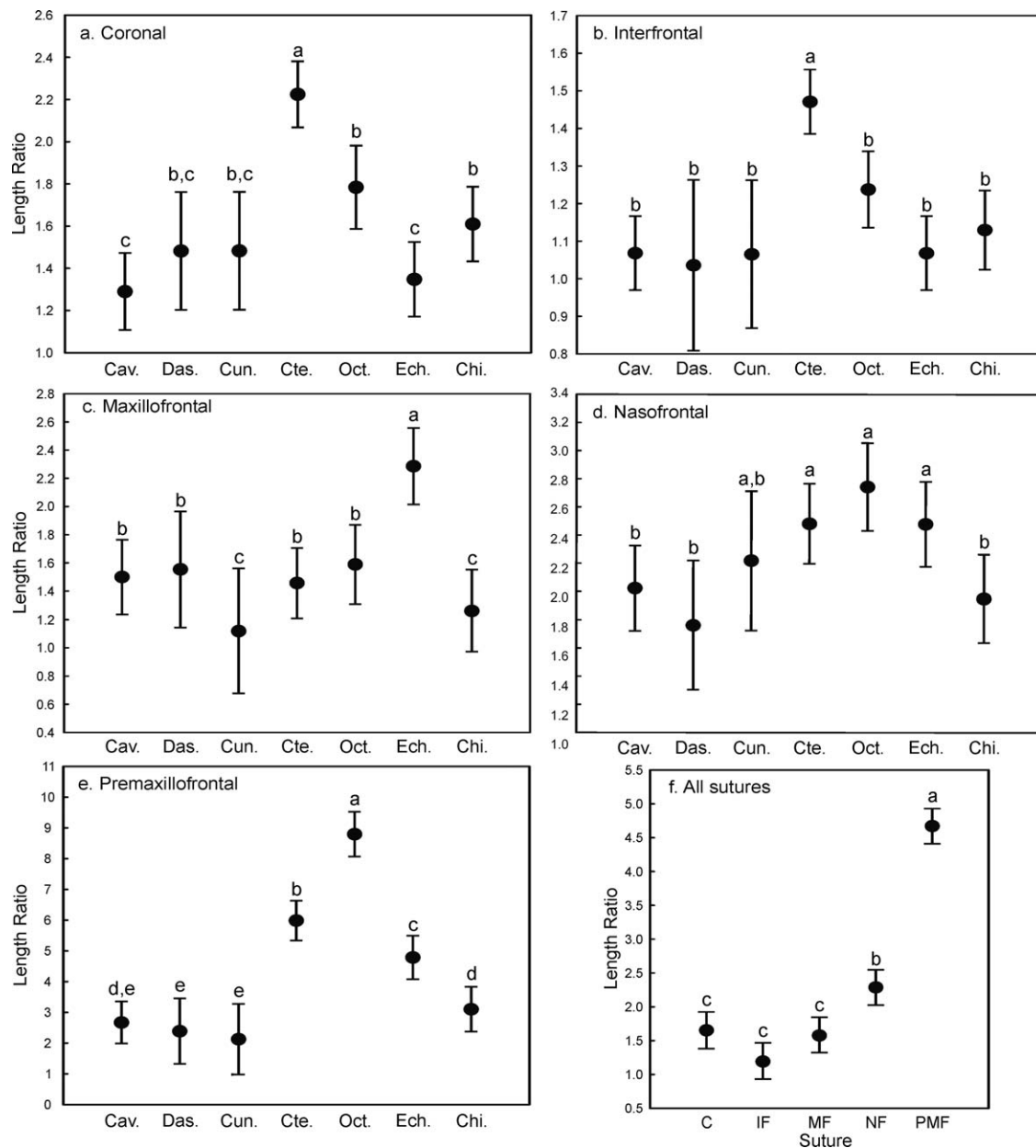


FIGURE 4 Suture complexity comparison between caviomorph families (4a to 4e) and between sutures (all families combined, 4f). Means and 95% confidence intervals for Length Ratio are represented. Letters over the plot indicate significant differences from the post-hoc analyses. Significance level: 0.05. Family references: Cav = Caviidae; Das = Dasyproctidae; Cun = Cuniculidae; Cte = Ctenomyidae; Oct = Octodontidae; Ech = Echimyidae; Chi = Chinchillidae. Suture references: C = coronal; IF = interfrontal; MF = maxillofrontal; NF = nasofrontal; PMF = premaxillofrontal

for two of the three sutures between the rostrum and the vault (i.e., maxillofrontal and nasofrontal sutures; Figure 4c,d). Octodontids exhibited the highest values for the most anteriorly positioned sutures at the rostrum-cranial vault junction and an intermediate value at the transverse suture of the cranial vault (nasofrontal and premaxillofrontal, and coronal sutures; Figure 4d,e,a, respectively). Echimyids, conversely, showed high to intermediate values for the sutures at the rostrum-vault edge (premaxillofrontal, maxillofrontal, and nasofrontal sutures; Figure 4c,d,e). Finally, families Caviidae, Dasyproctidae, Cuniculidae, and Chinchillidae tended to have low sutural complexity for all sutures (Figure 4).

3.4 | Ancestral character reconstruction

The reconstruction of the ancestral character states, on family and species phylogeny, points toward a relatively low suture complexity (i.e., low LR) as the most likely one for the interfrontal and premaxillofrontal (Figure 5), and maxillofrontal sutures (Supporting Information Figure 2). The families Echimyidae, Ctenomyidae, and Octodontidae have evolved the most complex premaxillofrontal sutures, especially the latter family (Figure 5 right). For the maxillofrontal suture, the highest complexity is shown by *Myocastor coypus*. For the case of the coronal and nasofrontal sutures (Supporting Information Figures 3 and 4,

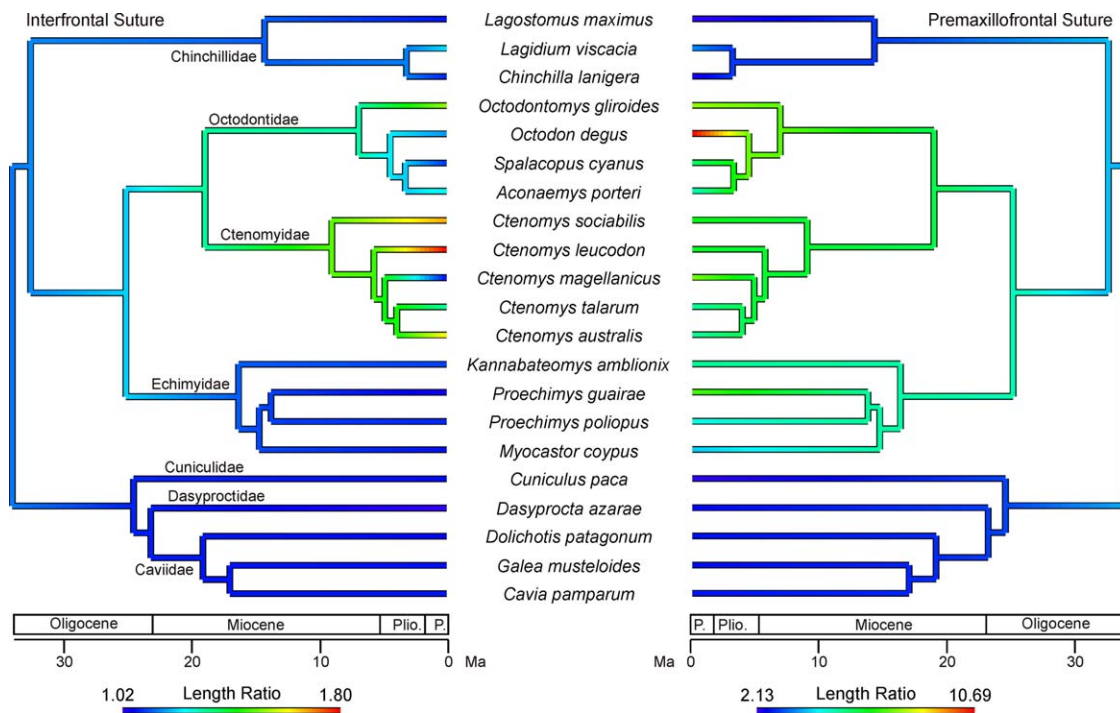


FIGURE 5 Ancestral character state reconstruction for length ratio of interfrontal (left) and premaxillofrontal (right) sutures, mapped on a customized phylogeny of the caviomorph species used in this study. Phylogenetic relationships, distances, and timescales are based on Parada et al. (2011) and Upham and Patterson (2012)

respectively), the possible ancestral state might have been at the approximate average of the measured LR range. Whereas coronal suture increase of complexity seems to be developed throughout the evolution of one clade (*Ctenomys*) and remained stable on the rest, nasofrontal suture seems to have changed several times during the evolution of caviomorph rodents. It is important to point out that a higher complexity of the premaxillofrontal suture's morphology might developed throughout the separation of Octodontoidea superfamily from its sister taxa Chinchilloidea. However, for the interfrontal suture (Figure 5, left) complexity would have increased after the appearance of the Ctenomyidae-Octodontidae clade. Within Dasyproctidae, Chinchillidae, Cuniculidae, Caviidae, and Echimyidae, the complexity remained low for most of the sutures.

4 | DISCUSSION

Whereas previous studies suggested that both length ratio (LR) and fractal dimension (FD) produce similar results regarding suture complexity (Byron, 2009; Nicolay & Vaders, 2006), here it was found that those indices yielded diverse correlation values, depending on the suture's position. The interfrontal suture, the only one in this study that is both at a midline position and mainly under tensile stress naturally demonstrates a more linear morphology. This also shows the highest correlation between the indices (Table 1), a pattern also observed in *Cebus*' sagittal suture (Byron, 2009). For all other sutures, mainly laterally positioned and under compressive stresses, estimation of complexity seems to diverge and correlations between LR and FD indices

are lower (Table 1). As Nicolay and Vaders (2006) have correctly stated LR and FD are not identical measures of the same morphological phenomenon. Also, not all rodent sutures studied need to be "fractal objects" in the sense of having a self-similar pattern (Mandelbrot, 1983). It was clear that a suture may have both a high LR value and a low FD, especially those positioned at the rostrum-vault junction or with serrated or interdigitated edges, lacking of a self-repetitive pattern (e.g., Figure 3.1c and 3.5g). Hence, low correlations between the two indices were obtained in some instances, for example for the nasofrontal suture (Table 1). We consider Length Ratio as more reliable to our sample because of its direct relationship to the surface area along the suture margin available for the attachment of collagen fibers. We consider it a better correlate of a suture's functional morphology, and thus it was used in further analyses.

The results of the present study, focused on several taxa of South American caviomorph rodents, show that cranial sutures are morphologically quite diverse. This diversity in path morphology becomes evident when comparing either sutures from different cranial regions, or particular sutures among specific rodent taxa. Our main findings are that: (a) the most anterior sutures connecting the rostrum and the cranial vault possess higher complexity and interdigitation than those in the cranial vault itself (Figures 3 and 4f); and (b) suture complexity tends to be relatively higher, in general terms, in fossorial and subterranean species from more open and arid environments such as in families Ctenomyidae and Octodontidae, whose masticatory apparatus are under relatively greater mechanical demands (Figures 4 and 5). It should be noted that suture complexity was not affected by skull size.

4.1 | Cranial vault sutures

Sutures in the cranial vault are, in general terms, simpler and less interdigitated than those located at the junction between the rostrum and the vault (Figures 3 and 4f). Although the interfrontal suture complexity is close to 1 (i.e., total absence of interdigitations; Figure 4f) for most of the families, in some cases the interdigitation is present only in a certain portion of the suture's path (Figure 3.2c). This could indicate that actually complex patterns of tensile/compressive stresses are acting on bones and sutures in this region of the skull. Due to the anatomical position of the interfrontal and coronal sutures, they might more likely be affected by chewing rather than by gnawing forces. Moreover, beyond the low complexity in both sutures of the cranial vault, the interfamily comparison shows Ctenomyidae (a family with robust masticatory apparatus) as the only one being statistically different and with the most complex sutures in that region (Figure 4a,b). This fact is better understood when some ecological and behavioral considerations are taken into account. The analyzed species, with the exception of those belonging to the sister family Octodontidae, have relatively softer and less mechanically challenging diets (e.g., fruits; leaves) than Ctenomyidae (e.g., fibrous roots, grasses) (Guichón & Cassini, 1998; Ojeda et al., 2015; Spotorno, Zuleta, Valladares, Deane, & Jimenez, 2004; Woods & Boraker, 1975). This leads to relatively lower loadings on the skull due to muscle forces or reaction forces over the teeth (with concomitant lower energy absorption), which can be expected from the mastication of such foods. Families Octodontidae and Ctenomyidae underwent cladogenesis in the relatively more open and arid south-western portion of South America (i.e., the Andean-Patagonian Subregion, *sensu lato*; Hershkovitz, 1969) since the Late Oligocene-Early Miocene (~9–24 Ma) (Upham & Patterson, 2012). These families evolved special adaptations in their masticatory apparatus such as more robust zygomatic arches, more powerful masseter muscles, and an improved molar grinding capacity to process the less nutritious and more abrasive herbivorous foods in those environments (Becerra et al., 2012; Comparatore, Cid, & Busch, 1995; Verzi, Morgan, & Olivares, 2015; Vieytes, 2003). These diets require high magnitudes of jaw muscle contraction and/or more chewing cycles, which would presumably cause higher strains on sutures and bones (Byron, 2009). If cranial vault sutures are affected by masticatory forces exerted by chewing muscles and reaction forces from molar teeth, more abrasive diets might promote the development of the more complex coronal and interfrontal sutures observed in Ctenomyidae and Octodontidae. It cannot be excluded that loads from the incisor-digging in fossorial and subterranean species within these two families would also affect the sutures of the cranial vault, especially the coronal ones, due to their perpendicular orientation to the direction of biting forces.

Complex patterns of compressive and tensile loadings related to feeding were recorded *in vivo* in vault sutures of miniature swines (*Sus scrofa*) (Sun et al., 2004), and the saddled bichir (*Polypterus endlicherii*) (Markey & Marshall, 2007). It is reasonable to think that given the diverse use of the masticatory apparatus in rodents—which includes incisor gnawing, and either oblique or bilateral molar chewing (Langebach & van Eijden, 2001; Olivares et al., 2004; Ungar, 2010)—the vault

sutures of caviomorphs are subjected to complex loading patterns as well. Oblique unilateral chewing (i.e., antero-mesial jaw displacement with alternate occlusion of left and right molar series) was documented in some octodontid and ctenomyid species (Olivares et al., 2004) and it may cause changes in masticatory stress polarity (i.e., tension vs. compression) on vault sutures. The predominance of compressive or tensile loadings might determine the equivalent predominance of interdigitated or butt-ended morphologies, respectively, in different portions of the suture. The most conspicuous case is the interfrontal suture of Ctenomyidae, which shows an interdigitated pattern and also a straight pattern in the same suture (Figure 3.2c).

4.2 | Sutures between the rostrum and the vault

Since rodent incisors are nearly inelastic (Freeman & Lemen, 2007), the rostrum carries the load to the skull when subjected to a structural load (e.g., a reaction force acting upright on the upper incisors) (Boyle, 1938; Moxham & Berkovitz, 1995). The periodontal ligament covers the non-enameled surface of the incisors' embedded portion and certainly provides an elastic matrix to absorb a substantial fraction of those external loads (Boyle, 1938; Sloan & Carter, 1995; Zajicek, 1976). Additional loading is expected to be absorbed by bones and sutures. Consequently their morphology is remodeled during growth (Burn et al., 2010), giving rise to different patterns of suture morphology. The nature and magnitude of the forces acting on rodent cranial sutures are still unknown. However, *in vivo* studies performed with surface strain gauges in miniature swines have shown that the nasofrontal suture, more posteriorly located when compared with those of caviomorphs, experienced large compression loads during mastication (Herring & Rafferty, 1998; Rafferty & Herring, 1999). Moreover, Thomason and Russell (1986) proposed that, in mammals with a relatively elongated rostrum, compression might get introduced because the rostrum acts like a cantilever beam attached to the front of the skull. We found that sutures located between the rostrum and the cranial vault are more heterogeneous in terms of shape and complexity (Figure 3.3–3.5) than those in the cranial vault itself. Amongst the former group of sutures, the maxillofrontal suture is the least complex (Figure 4f), being mainly elongated and whose central axis can have some degree of curvature. Considering interfamily comparisons, Echimyidae (e.g., spiny tree rats) showed intermediate-to-high LR values for this suture, with *Myocastor coypus* in the highest end, which tended to be higher than the ones observed in the other families (Figure 4c). The coypu (*M. coypus*) forages mainly on hygrophilic and terrestrial monocotyledons (Guichón, Benítez, Abba, Borgnia, & Cassini, 2003). However, some studies have noted that it also incorporates some shelled mollusks in its diet (El-Kouba, Marques, Pilati, & Hamann, 2009; Mares & Ojeda, 1982) which, besides its occasional digging behavior, may contribute with strong forces while chewing that get transmitted to the maxillofrontal sutures.

The nasofrontal suture is significantly more complex than the maxillofrontal one and both others in the cranial vault (Figure 4d). If the nasofrontal suture in rodents is subjected to compression, the greater degree of interdigitation observed in this suture would provide the

space required for a compression-resistant collagen fiber arrangement (Herring & Teng, 2000). The family Octodontidae, which includes from ground dwellers to strict chisel-tooth digging species, showed a naso-frontal suture significantly more complex than the ground dwelling families Caviidae, Dasyproctidae, and Chinchillidae. Families Ctenomyidae (both chisel-tooth and scratch-diggers), Echimyidae and Cuniculidae (ground-dwellers) showed no significant differences with respect to the other families. As suggested by studies that showed an increased sutural complexity as an adaptation for mechanically demanding diets (Byron, 2009; Herring & Rafferty, 1998), a higher complexity should characterize ctenomid and octodontid sutures due to their abrasive diets and digging habits. Our results partly support this prediction because of the high LR values observed in octodontids, but not the expected ones for the ctenomids, suggesting that strain transmission is actually more complex than anticipated.

The premaxillofrontal suture is the most complex one overall (Figure 4f), exhibiting families clustered in three groups: Octodontidae (highest values), Ctenomyidae and Echimyidae (intermediate values), and the remaining four families altogether (lowest values; Figure 4e). The overall complexity of this suture in rodents might be mainly associated to its anatomical position and to the fact that incisors are anchored on the premaxilla. Thus, loading resulting from reaction forces on the incisors tip will propagate directly to this cranial bone and, therefore, they will affect the premaxillofrontal suture by compression. Therefore, our *a priori* hypotheses were partially supported by these results. As it was expected, ground-dwellers in all families Caviidae, Chinchillidae, Cuniculidae, and Dasyproctidae, and the subterranean Ctenomyidae—which perform also the weakest and the strongest relative incisor biting (Becerra, 2015)—showed simple and complex premaxillofrontal sutures, respectively. Nevertheless, this suture's morphology in families Octodontidae and Echimyidae turns out to be much more complex than what it was hypothesized according to their niches and habits.

4.3 | The family Ctenomyidae

In this study, we expected subterranean rodents belonging to the family Ctenomyidae to show the most complex cranial sutures given their relatively more robust and powerful masticatory apparatus, which let them exert relatively strong bite forces (Becerra et al., 2011, 2013, 2014; Vassallo, 1998), and display the chisel-tooth digging behavior. This behavior in particular, which appears early during ontogeny (Echeverría, Biondi, Becerra, & Vassallo, 2015), requires the capacity to exert strong bite forces (Becerra, 2015; Hildebrand, 1985; Samuels, 2009; Van Daele, Herrel, & Adriaens, 2009). Stronger bite forces applied on the foods or the soil when digging would necessarily result in corresponding stronger reaction forces on their teeth. Ultimately, they are expected to generate heavy stresses on the skull, unlike what happens with other taxa that also have an abrasive diet but do not use incisors as digging tools (Lessa et al., 2008). In fact, in the case of the chisel-tooth digger *Nannospalax ehrenbergi*, it has been shown that the continuous mechanical pressure on its oral tissues leads to cell and tissue fatigue, evidenced by palatal perforation by the upper incisors in aged

individuals (Zuri & Terkel, 2001). Moreover, a comparative study by Becerra et al. (2014) showed that incisors bite force in the subterranean species *Ctenomys australis* can reach absolute values three times higher, and relative ones between two and five times higher, than those in *Octodon degu* and *Chinchilla laniger*.

It might be suggested that relatively more interdigitated cranial vault sutures would be a derived condition associated to the acquisition of burrowing and chisel-tooth digging habits, accompanying the emergence of other adaptations to the relatively arid south-western portion of South America such as those affecting incisor enamel microstructure (Vieytes, Morgan, & Verzi, 2007), masseteric musculature (Vassallo & Mora, 2007) and mandible articulation (Verzi & Olivares, 2006). The reconstruction of the ancestral character states in part supports this claim (Figure 5). It is noteworthy that the facial sutures closed last among the subterranean rodents *Bathyergus suillus*, *Rhizomys sumatrensis*, and *N. ehrenbergi* (Wilson & Sánchez-Villagra, 2009). This fact might be related to osteological modifications of the skull in favor of their digging habits and/or a higher requirement of stress transfer or stress dampening. Our results partially support this line of reasoning so that future studies looking at ontogeny of these sutures, among other things, will shed new insights on this issue.

4.4 | Ancestral character reconstruction

For the five sutures analyzed here, the ancestral state is of a relatively low complexity (here, we show two representative trees in Figure 5; the remaining three are available as Figures 2–4 in Supporting Information). The ground dwelling families Caviidae, Chinchillidae, Cuniculidae, and Dasyproctidae, which have relatively gracile masticatory apparatus, might display a morphotype which could have remained stable throughout the evolution of caviomorphs, with a few exceptions of sutures with intermediate complexity (Chinchillidae: *L. maximus*, Coronal and Nasofrontal sutures; Supporting Information Figures 3 and 4, respectively). Conversely, the sister clades Octodontidae and Ctenomyidae evolved more complex sutures starting from the Miocene (about 15 Ma), a fact that may be related to the evolution of burrowing habits (Lessa et al., 2008) and/or the climatic changes produced by the Andes uplifting during the Miocene epoch (Blisniuk, Stern, Chamberlain, Idleman, & Zeitler, 2005). Evolution of interfrontal suture might have taken place after the emergence of Octodontidae–Ctenomyidae clade, suggesting that the increase in complexity of sutures might have been gradual. It is noteworthy that within ctenomids, both of the most basal species (i.e., *C. sociabilis* and *C. leucodon*) showed more complex sutures than the more derived species. In contrast to most ground dwelling species, echimids showed a relatively high complexity in several sutures, a fact that is hard to interpret with the available data.

5 | CONCLUSIONS

Much of the diversification experienced by caviomorph rodents relates to the remarkable environmental differences between the biomes characterizing the north-eastern versus the south-western regions of South America, which were triggered by Cenozoic climatic changes. The

former region mainly includes the Amazon, coastal tropical forests, whereas the latter one includes relatively mesic and arid biomes (e.g., Puna; Pampas' grasslands; Patagonian steppes) characterized by a rather open vegetation. A comprehensive recent study attributes the evolution of morphological disparity concerning the skull and masticatory apparatus, among families Echimyidae vs. Octodontidae-Ctenomyidae, to such a different environmental context (Verzi et al., 2015). Moreover, experimental studies and interspecific comparisons established the important role of suture complexity as stress absorption by the skull (Byron, 2009; Monteiro & Lessa, 2000; Rafferty & Herring, 1999). Therefore, the interspecific differences in suture morphology shown here might represent, in part, adaptations to different mechanically challenging diets (i.e., soft vs. tough foods) or particular behaviors (e.g., chisel-tooth digging), which evolved in close association with the diverse environments occupied by caviomorph rodents.

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