Valentina Segura*

Skull ontogeny of *Lycalopex culpaeus* (Carnivora: Canidae): description of cranial traits and craniofacial sutures

Abstract: Ontogenetic changes in the skull of *Lycalopex culpaeus* were studied in relation to feeding function and performance at different age classes. Most cranial changes occurred in the orbitotemporal region and consisted of the visible appearance of structures that were later found to be absent in juveniles. These changes were related to the development of the adult skull in order to capture, kill, and process prey. In general, fusion occurred earlier in neurocranial sutures than in the splachnocranium, although rostral sutures never became fused. The cranial sutures of culpeo are conservative, displaying few changes in suture type but some in suture fusion sequence. These modifications occur during the first year, from the late juvenile stages, when individuals are similar to adults in general appearance and body size as well as in skull size. However, it was noted that basicranial synchondroses became fused in the adult stages, indicating that longitudinal growth could extend until this latter time. This could be indicative not only of size change in adult specimens but also of shape change.

Keywords: anatomy; development; ontogeny; skull; suture morphology.

*Corresponding author: Valentina Segura, División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470, CP 1405, Ciudad Autónoma de Buenos Aires, Argentina, e-mail: valu_z@yahoo.com.ar; vsegura@macn.gov.ar; and CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Av. Rivadavia 1917, CP 1033, Ciudad Autónoma de Buenos Aires, Argentina

Introduction

Lycalopex culpaeus (Molina 1782), the culpeo fox, is the largest (≈10 kg) in its genus, and the second largest among South American canids (Novaro 1997). The culpeo fox is distributed along the Andes and hilly regions of South America, from Colombia to southern Chile and Argentina (Jiménez and Novaro 2004). Culpeos are born with their eyes closed and at 2 days they weigh about 168 g and are about 163 mm in length. The pups nurse until they are 2 months old and continue to depend on their parents during a relatively short postweaning period; in this time, they learn to hunt until they are strong enough to fend for themselves. Juveniles reach adult size at 7 months, and sexual maturity is attained during the first year (Crespo and De Carlo 1963, Ewer 1973).

The patterns of cranial ontogeny in canids have been studied from diverse perspectives and using different approaches. Wayne (1986) studied ontogenetic trajectories of skull growth in the domestic dog, using bivariate and multivariate analyses. More recently, La Croix et al. (2011a,b) examined the cranial growth and development of the coyote through two-dimensional geometric morphometric analyses and analyzed the ontogenetic relations between feeding performance, dentition, and feeding biomechanics. Drake (2011) studied heterochronic patterns in the skull morphology of domestic dogs by using three-dimensional geometric morphometrics. In a recently published work, Segura and Prevosti (2012) quantitatively analyzed the ontogenetic pattern of the skull of *Lycalopex culpaeus*, using traditional and geometric morphometric analyses. Although such works represent important contributions to the knowledge of cranial ontogeny for canids in general and *L. culpaeus* in particular, several structural transformations and changes in sutural morphology have not yet been discussed or detected using either geometric or linear morphometric analyses. These changes (some of which have high functional meaning) may be difficult to study using quantitative analyses. For instance, the structural morphology of craniofacial sutures is linked to the mechanical strain caused by tensile and compressive forces (Henderson et al. 2005). Such sutures, formed by collagenous connective tissue fibers that connect mineralized bones, allow deformation and minor displacements, thus absorbing and transmitting mechanical stresses, and play an important role as growth sites in the growing skull (Wagemans et al. 1988, Jaslow 1990, Herring and Teng 2000, Mao 2002, Rice 2008, Jasinoski et al. 2010).

In carnivores and other mammals, several morphometric changes along ontogeny have been related to the

optimization of feeding and biting (e.g., Abdala et al. 2001, Flores et al. 2006, Segura and Flores 2009, Flores et al. 2010, Segura and Prevosti 2012), and similar changes have been detected in phylogenetically distant species. Such patterns have been observed in published works that deal with the structural-descriptive morphology of the skull and sutural changes along ontogeny in carnivorans and other mammals (e.g., García-Perea 1996, Giannini et al. 2006, Segura and Flores 2009, Flores and Barone 2012); however, these studies are limited to only a few species.

In this work, I studied changes in the skull morphology and pattern of sutural change (i.e., type, degree of fusion) in an ontogenetic series of *Lycalopex culpaeus*, exploring the relation of these changes with life history events that took place during the development of individuals. Despite some knowledge of the ontogeny of *L. culpaeus* (e.g., Crespo and De Carlo 1963, Novaro 1997, Segura and Prevosti 2012), several skull characteristics with functional meaning (e.g., development of processes, crests, and suture morphology) have not yet been assessed. Thus, in this widespread South American canid, this approach will contribute to the knowledge and understanding of the development of the skull as a whole.

Materials and methods

I studied a sample of 101 specimens of *Lycalopex culpaeus* collected in 1963 by Crespo and De Carlo in Argentina, Neuquén Province, Catán-Lil (39°33′ S, 70°35′ W), and deposited in the mammal collection of Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, see Appendix 1).

In the sample, individuals ranged in age from 2 months to 11 years (Crespo and De Carlo 1963, Zapata et al. 1997). Twenty-nine of the specimens did not show fully erupted teeth. Using the scheme followed by Segura and Prevosti (2012), I defined seven age classes based on tooth eruption and wear (Figures 1A–D and 2):

J1: complete deciduous dentition present; permanent P1 and p1 erupting

J2: permanent I1, i1, and i2 erupted; I2, M1, and m1 erupting

J3: permanent incisors and canines erupted; M1 and p2 erupted; P4, M2, and m2 erupting

J4: permanent incisors, canines, and molars fully erupted; P3, p3, p4, and m3 erupting

A1: complete permanent dentition with no wear

A2: complete permanent dentition with slight wear; incisors, canines, premolars, and molars with blunt cusps

A3: complete permanent dentition with dentine horns exposed on the cusps of premolars and molars; I3 at the same level of development as I1 and I2

Although previous works have shown the existence of some sexual dimorphism involving cranial and external measurements in *Lycalopex culpaeus* (Crespo and De Carlo 1963, Johnson and Franklin 1994, Travaini et al. 2000), no such dimorphism was observed in the characters or sutures discussed here (i.e., males and females showed the same ontogenetic pattern).

For the qualitative analysis, skull characters were compared across specimens in different ontogenetic stages; the type and degree of fusion in sutures and synchondroses were examined, and the observed differences were described using the anatomical terminology defined by Evans (1993), García-Perea (1996), and Gilbert (1997). Although the anatomy of the whole skull has been explored in a functional context (e.g., Van Valkenburgh 1991, Van Valkenburgh and Koepfli 1993, Slater et al. 2009), in this work I focused only on those characters that presented variation along the ontogeny of *Lycalopex culpaeus*. Depending on the shape of the apposed edges, sutures were classified following Evans' proposal for canid skulls (1993): plane suture, in which bones meet at a right-angled edge or surface; squamous suture, which articulates by overlapping of reciprocally beveled edges; serrated suture, which articulates by means of reciprocally alternating processes and depressions; and foliate suture, in which the edge of one bone fits into a fissure or recess of an adjacent bone. A suture was considered fused when it was no longer visible.

Results

Thirty morphological characters were identified that changed along the ontogenetic series and did not show intra-age class variation (Table 1, Figures 1 and 2). Most changes occurred in the orbitotemporal region (10 characters), followed by the mandible (9), basicranial and auditory regions (4), rostrum (3), and palatal and occipital regions (both with 2 characters). Twelve of them consisted of the appearance of structures absent in juveniles (characters 4, 6, 8, 9, 11, 13, 18, 19, 20, 21, 27, and 30 in Table 1), while almost a third of those changes implied growth or enlargement of structures already present in juveniles (characters 12, 14, 15, 16, 17, 23, 24, 26, 28, and 29); a few changes implied a relative decrease in size or disappearance of structures with advancing age (characters 2, 3, 7, and 10), while some
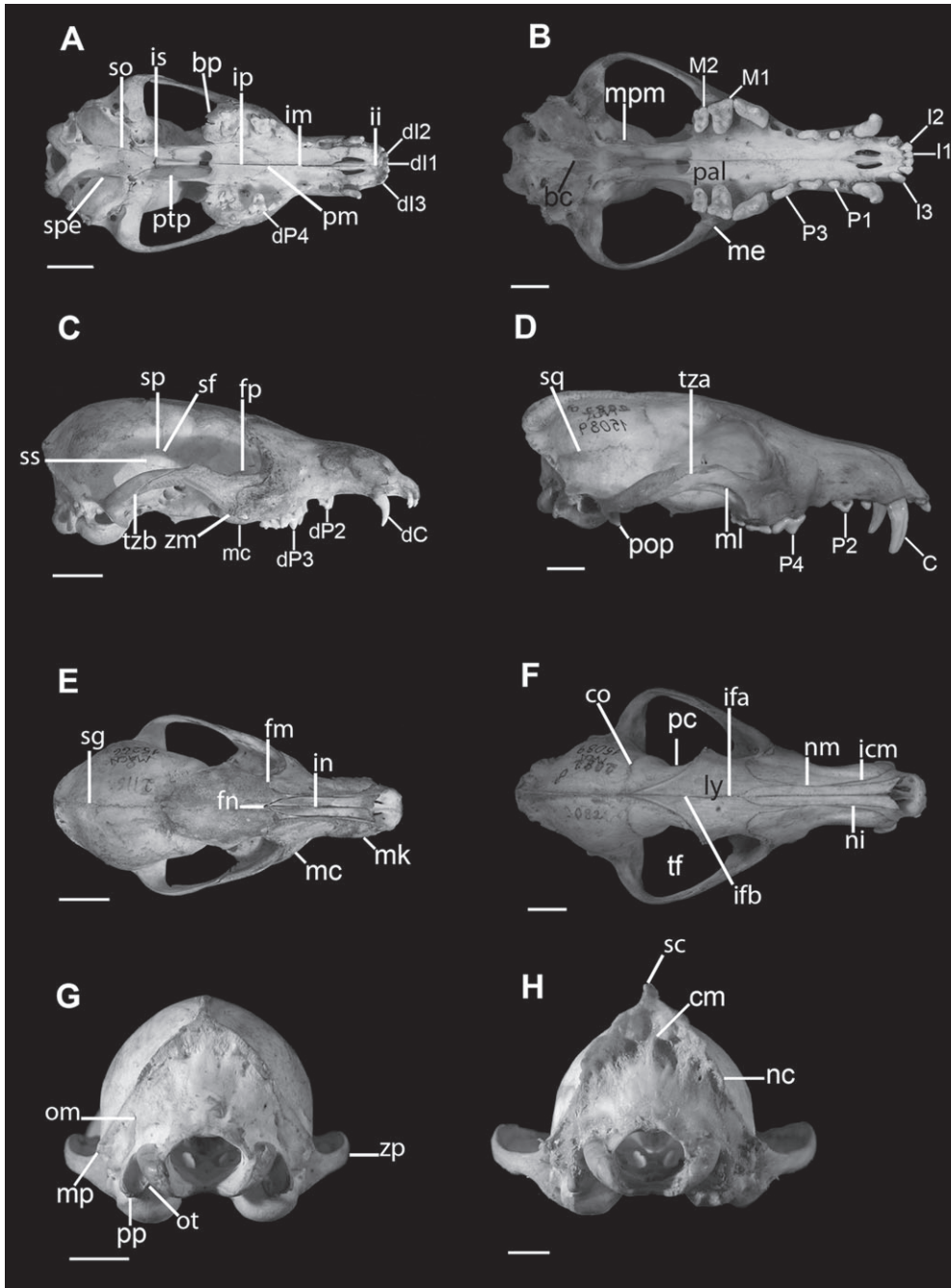
Figure 1 Ventral, lateral, dorsal, and occipital view of young (A-C-E-G, MACN 15266) and adult (B-D-F-H, MACN 15089) *Lycalopex culpaeus*. bc, basioccipital crest; bp, laterocaudal border of palatine; C, permanent canine; cm, scar for cervical musculature; co, suture coronalis; dC, deciduous canine; dI1, deciduous incisor 1; dI2, deciduous incisor 2; dI3, deciduous incisor 3; dP2, deciduous premolar 2; dP3, deciduous premolar 3; dP4, deciduous premolar 4; fm, suture frontomaxillaris; fn, suture frontonasalis; fp, suture frontopalatina; I1, permanent incisor 1; I2, permanent incisor 2; I3, permanent incisor 3; icm, suture incisivomaxillaris; ifa, suture interfrontalis cranial; ifb, suture interfrontalis caudal; ii, suture interincisiva; im, suture intermaxillaris; in, suture internasalis; ip, suture interpalatina; is, synchondrosis intersphenoidalis; ly, lyre width; M1, molar 1; M2, molar 2; mc, molar convexity (molar root); me, maxillary edge; mk, maxillary knob (canine root); ml, masseteric line of the jugal; mp, mastoid process; mpm, scar for medial pterygoid muscle; nc, nuchal crest; ni, suture nasoincisiva; nm, suture nasomaxillaris; om, suture occipitomastoidea; ot, suture occipitotympanica; P1, permanent premolar 1; P2, permanent premolar 2; P3, permanent premolar 3; P4, permanent premolar 4; pal, palatine; pc, postorbital constriction; pm, suture palatomaxillaris mesial; pop, postglenoid process; pp, paraoccipital process; ptp, suture pterygopalatina; sc, sagittal crest; sf, suture sphenofrontalis; sg, suture sagittalis; so, synchondrosis spheno-occipitalis; sp, suture sphenoparietalis; spe, synchondrosis sphenopetrosa; sq, suture squamosa; ss, suture sphenosquamosa; tf, temporal fossa; tza, suture temporozygomatica anterior; tzb, suture temporozygomatica posterior; zm, suture zygomaticomaxillaris; zp, zygomatic process. Scale bars, 2 cm.
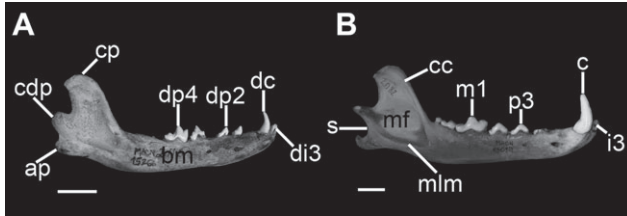
Figure 2 Mandibular view of young (A, MACN 15266) and adult (B, MACN 15089) *Lycalopex culpaeus*.
ap, angular process; bm, body of mandible; c, permanent canine; cc, coronoid crest; cdp, condyloid process; cp, coronoid process; dc, deciduous canine; di3, deciduous incisor 3; dp2, deciduous premolar 2; dp4, deciduous premolar 4; i3, permanent incisor 3; m1, molar 1; mf, masseteric fossa; mlm, masseteric line of mandible; p3, permanent premolar 3; s, separation between condyloid and angular process. Scale bars, 2 cm.

reorganizations occurred (characters 1, 5, 22, and 25). Most of these characters reached their definitive morphology in A1 adults. However, some characters such as molar convexity (character 3), shape of the latero-caudal border of the palatine (5), postorbital constriction (9), development of the paraoccipital process (17), and nuchal crest (20) reached their definitive condition early in the J4 age class, whereas the scar for the medial pterygoid muscle (4), development of the postglenoid process (15), and hardness of the mandibular body (29) occurred late in the A2 age class.

Regarding the patterns of change in cranial sutures, ontogenetic changes were detected in most of the 40 sutures and synchondroses identified in *Lycalopex culpaeus* (Table 2). Two synchondroses associated with the occipital plate (numbered 1 and 2 in Table 2) were completely fused early in juvenile stages (J1 and J2, respectively), while a premaxillary suture (21) became partially fused in age class J3. Eighteen sutures and synchondroses (3–20) were completely fused only in adult stages (A1, A2, and A3). The sutures numbered from 28 to 40, mostly related to the rostrum and zygomatic arches, remained unfused and visible in adult stages. Some sutures (21–27) were partially fused in adults. Only three sutures changed their shape: two of them, related to the palatine (19, palatomaxillaris; 36, palatolacrimalis), changed from plane to squamous or serrated, whereas the third one (23, interfrontalis caudal) changed from serrated to plane.

Discussion

Cranial traits

A series of conspicuous morphological changes were detected in both cranial characters and sutures of

Lycalopex culpaeus. These included strengthening of the rostrum, cranial vault, zygomatic arches, and mandible, and the development of attachment sites for masticatory muscles. In adults, the temporal fossa became wider by lateral flaring of the zygoma and deeper by the development of the postorbital constriction (Figure 1E,F), providing additional space for the temporal and masseteric muscles, both of which elevate the mandible in closing the mouth (Evans 1993); this information has been quantified in a recently published report (Segura and Prevosti 2012). Associated to these changes, the development of the sagittal crest (Figure 1C,D) reflects not only the expansion of the area for attachment of the temporal muscle, the most important jaw adductor in carnivores (Van Valkenburgh 2007), but also the increased strength of the skull to better withstand the deforming forces generated during jaw closure (Moore 1981). Because the temporal muscle in canids is attached to the cranium over a large area (Evans 1993), an increase in the number of fibers results in a more powerful bite (García-Perea 1996, Slater et al. 2009). These acquisitions are related to the success of killing strategies used by most carnivores (Leyhausen 1979). The development of the sagittal crest and enlargement of the temporal fossa began in the first year (A1 class), when culpeo foxes had become sexually mature and were independent individuals. The nuchal crest (Figure 1G,H) experienced the most extreme change between juveniles and adults, likely because it is here that muscles related to biting (temporal) and head movements (e.g., splenius) originated. The development of the nuchal crest also enhanced bite at the level of the canine teeth, given that the posterior temporal fibers (originated on this crest) are more important than the anterior temporal fibers (originated on the sagittal crest) used for generating canine force (Flores et al. 2006, 2010).

From the first year of life, i.e., A1 age class, the origin of the masseteric muscle along the masseteric line of the jugal became strongly marked, and the robustness of the zygomatic process became noticeable (Figure 1C–F). Its insertion in the mandible is indicated by a deep masseteric fossa, reinforced by a coronoid crest and the masseteric line of the mandible (Figure 2) that later became prominent in adults. The same development was observed for the maxillary margin, the site of insertion of the anterior portion of the masseteric muscle. Likewise, the pterygoid and the angular process, the origin and insertion of the medial pterygoid muscle, respectively (Figures 1A,B and 2), were widened and more extended in adults, thus enlarging the attachment surfaces of this muscle that elevates the mandible.

The increased sculpturation of the surface of the occipital plate (Figure 1G,H) and the well-developed

Characters	J1 (n=7)	J2 (n=3)	J3 (n=5)	J4 (n=14)	A1 (n=30)	A2 (n=26)	A3 (n=16)
Rostrum							
1. Anterior portion of the nasals	U shape	U shape	U shape	U shape	W shape	W shape	W shape
2. Maxillary knob (canines root)	Present	Present	Present	Present	Absent	Absent	Absent
3. Molar convexity (molars root)	Present	Present	Present	Absent	Absent	Absent	Absent
Palatine region							
4. Scar for the medial pterygoid muscle	Absent	Absent	Absent	Absent	Absent	Present	Present
5. Laterocaudal border of palatine	Rounded	Rounded	Rounded	Straight	Straight	Straight	Straight
Orbitotemporal region							
6. Maxillary edge	Absent	Absent	Absent	Absent	Present	Present	Present
7. Lyre width	Wide	Wide	Wide	Wide	Narrow	Narrow	Narrow
8. Sagittal crest	Absent	Absent	Absent	Absent	Present	Present	Present
9. Postorbital constriction	Absent	Absent	Absent	Present	Present	Present	Present
10. Fossa for the ventral obliquous muscle	Large	Large	Large	Large	Small	Small	Small
11. Scar for the lateral pterygoid muscle	Absent	Absent	Absent	Absent	Present	Present	Present
12. Temporal fossa	Narrow	Narrow	Narrow	Narrow	Wide	Wide	Wide
13. Masseteric line of the jugal	Absent	Absent	Absent	Absent	Present	Present	Present
14. Zygomatic process	Thin	Thin	Thin	Thin	Robust	Robust	Robust
15. Postglenoid process	Extended to the same level of external acoustic meatus	Extended to the same level of external acoustic meatus	Extended to the same level of external acoustic meatus	Extended to the same level of external acoustic meatus	Extended to the same level of external acoustic meatus	Extended to a level lower than of tympanic bulla	Extended to a level lower than of tympanic bulla
Basicranial and auditory regions							
16. Mastoid process	Poorly developed	Poorly developed	Poorly developed	Poorly developed	Well developed	Well developed	Well developed
17. Paraoccipital process	Poorly developed	Poorly developed	Poorly developed	Well developed Reaching the low level of tympanic bulla	Well developed Reaching the low level of tympanic bulla	Well developed Reaching the low level of tympanic bulla	Well developed Reaching the low level of tympanic bulla
18. Basioccipital crest	Absent	Absent	Absent	Absent	Present	Present	Present
19. Muscular tubercles on basicranium	Absent	Absent	Absent	Absent	Present	Present	Present
Occipital region							
20. Nuchal crest	Absent	Absent	Absent	Present	Present	Present	Present
21. Scar for the cervical musculature	Absent	Absent	Absent	Absent	Present	Present	Present
Mandible							
22. Coronoid process	Tip rounded, caudally oriented	Tip rounded, caudally oriented	Tip rounded, caudally oriented	Tip rounded, caudally oriented	Tip squared, dorsally oriented	Tip squared, dorsally oriented	Tip squared, dorsally oriented
23. Coronoid crest	Inconspicuous	Inconspicuous	Inconspicuous	Inconspicuous	Well developed	Well developed	Well developed
24. Condyloid process	Not lingually extended	Not lingually extended	Not lingually extended	Not lingually extended	Lingually extended beyond of the internal border of the dentary	Lingually extended beyond of the internal border of the dentary	Lingually extended beyond of the internal border of the dentary

(Table 1　Continued)

Characters	J1 (n=7)	J2 (n=3)	J3 (n=5)	J4 (n=14)	A1 (n=30)	A2 (n=26)	A3 (n=16)
25. Separation between condyloid and angular process	Slightly separated	Slightly separated	Slightly separated	Slightly separated	Separated by a deep notch	Separated by a deep notch	Separated by a deep notch
26. Angular process	Short	Short	Short	Short	Caudo-dorsally extended	Caudo-dorsally extended	Caudo-dorsally extended
27. Masseteric line of mandible	Absent	Absent	Absent	Absent	Present	Present	Present
28. Masseteric fossa	Slightly deep	Slightly deep	Slightly deep	Slightly deep	Notably deep	Notably deep	Notably deep
29. Body of mandible	Thin	Thin	Thin	Thin	Thin	Robust	Robust
30. Inner masseteric notch	Absent	Absent	Absent	Absent	Present	Present	Present

Table 1　List of morphological changes detected in a comparison of skull region in all age classes of *Lycalopex culpaeus*.

mastoid and paraoccipital processes of adults (Figure 1C,D,G,H) suggest the importance of the insertion of cervical muscles such as the rectus capitis dorsalis, spinalis capitis, obliquus capitis cranialis, and splenius (related to the first two characters), and provide a marked attachment for the digastricus muscle (i.e., the paraoccipital process). Neck musculature is associated with specific head movements (Wickland et al. 1991, Richmond et al. 1992, Duckler 1998, Antón et al. 2004) and the m. digastricus opens the mandible (Biknevicius and Van Valkenburgh 1996, Antón et al. 2004). These changes took place at the A1 age class and inclusive up to the late juvenile stage (J4 age class), when the culpeos were similar to adults in both general appearance and body size (≈10 kg: Crespo and De Carlo 1963), as well as in skull size, a character that is attained before the acquisition of the adult skull shape (Segura and Prevosti 2012).

The incurving and strengthening of the glenoid fossa (Figure 1C,D), a character reached after the onset of sexual maturity, in the A2 age class, is associated with the limitation of the rostral-caudal displacement of the jaw, emphasizing the vertical jaw movements typical of carnivores (Biknevicius and Van Valkenburgh 1996), and providing greater stability at the temporo-mandibular joint to resist mechanical stresses during the active bite (Mao and Nah 2004, Segura and Flores 2009).

Craniofacial sutures

Generally, sutures are relatively simple (plane, squamous) at birth and during the first age stages, thus allowing a slight degree of compressibility and deformation necessary for the young to pass through the birth canal (Evans 1993, Herring et al. 1996). Although the sample studied here did not include preweaning classes, individuals in the J1 class (2 months, postweaning) presented complex morphology in only two sutures, namely, the interfrontalis caudal and sagittalis. Accordingly, the ontogenetic sample may be considered representative of a complete ontogenetic series. The synchondroses related to the occipital plate (i.e., intraoccipitalis-squamolateralis, intraoccipitalis-basilateralis, and spheno-occipitalis) became fused early in growth (Table 2), reflecting early strengthening of this region, which is a requirement for cephalic support. Such fusions occurred in the J1 (2 months) and J2 age classes when culpeo foxes have recently been weaned and their diet has changed by incorporation of meat and other solid food items. This early fusion of occipital plate bones is highly common among mammals (Wagemans et al. 1988, Jaslow 1990, Herring and Teng 2000, Herring et al.

Sutures/synchondroses	J1	J2	J3	J4	A1	A2	A3
1. Syn. intraoccipitalis-squamolateralis	F	F	F	F	F	F	F
2. Syn. intraoccipitalis basilateralis	Uf	F	F	F	F	F	F
3. Syn. spheno-occipitalis	Uf	Uf	Uf	Uf	F	F	F
4. Sut. occipitomastoidea	Plane	Plane	Plane	Plane	Pf/Plane	F	F
5. Sut. occipitotympanica	Plane	Plane	Plane	Plane	Pf/Plane	F	F
6. Sut. sphenoparietalis	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	F	F
7. Sut. sphenosquamosa	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	F	F
8. Sut. vomeropalatina	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	F	F
9. Syn. intersphenoidalis	Uf	Uf	Uf	Uf	Uf	F	F
10. Syn. sphenopetrosa	Uf	Uf	Uf	Uf	Pf	Pf	F
11. Sut. coronalis	Squamous	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	F
12. Sut. occipitoparietalis	Squamous	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	F
13. Sut. frontopalatina	Squamous/serrated	Squamous/serrated	Squamous/serrated	Squamous/serrated	Squamous/serrated	Pf/Squamous/serrated	F
14. Sut. sphenopalatina	Squamous	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	F
15. Sut. sphenofrontalis	Squamous/serrated	Squamous/serrated	Squamous/serrated	Squamous/serrated	Squamous/serrated	Pf/Squamous/serrated	F
16. Sut. intermaxillaris	Plane	Plane	Plane	Plane	Plane	Pf/Plane	F
17. Sut. interpalatina	Plane	Plane	Plane	Plane	Plane	Pf/Plane	F
18. Sut. palatomaxillaris (mesial)	Squamous/serrated	Squamous/serrated	Squamous/serrated	Squamous/serrated	Squamous/serrated	Pf/Squamous/serrated	F
19. Sut. palatomaxillaris (lateral)	Plane	Squamous/serrated	Squamous/serrated	Squamous/Serrated	Squamous/serrated	Pf/Squamous/serrated	F
20. Sut. pterygosphenoidalis	Squamous	Squamous	Squamous	Squamous	Squamous	Pf/Squamous/serrated	F
21. Sut. interincisiva	Plane	Plane	Pf/Plane	Pf/Plane	Pf/Plane	Pf/Plane	Pf/Plane
22. Sut. squamosa	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	Pf/Squamous	Pf/Squamous
23. Sut. interfrontalis (caudal)	Serrated	Serrated	Serrated	Serrated	Plane	Pf/Plane	Pf/Plane
24. Sut. pterygopalatina	Squamous	Squamous	Squamous	Squamous	Squamous	Pf/Squamous	Pf/Squamous
25. Sut. incisivomaxillaris	Foliate	Foliate	Foliate	Foliate	Foliate	Foliate	Pf/Foliate
26. Sut. interfrontalis (cranial)	Plane	Plane	Plane	Plane	Plane	Plane	Pf/Plane
27. Sut. zygomaticomaxillaris	Foliate	Foliate	Foliate	Foliate	Foliate	Foliate	Pf/Foliate
28. Sut. nasoincisiva	Plane	Plane	Plane	Plane	Plane	Plane	Plane
29. Sut. internasalis	Plane	Plane	Plane	Plane	Plane	Plane	Plane
30. Sut. nasomaxillaris	Plane	Plane	Plane	Plane	Plane	Plane	Plane
31. Sut. frontonasalis	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous
32. Sut. frontomaxillaris	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous
33. Sut. lacrimomaxillaris	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous
34. Sut. frontolacrimalis	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous
35. Sut. zygomaticolacrimalis	Plane	Plane	Plane	Plane	Plane	Plane	Plane
36. Sut. palatolacrimalis	Plane	Plane	Plane	Plane	Squamous	Squamous	Squamous
37. Sut. temporozygomatica (anterior)	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous	Squamous
38. Sut. temporozygomatica (posterior)	Plane	Plane	Plane	Plane	Plane	Plane	Plane
39. Sut. sagittalis	Serrated	Serrated	Serrated	Serrated	NE	NE	NE
40. Syn. intermandibularis	Uf	Uf	Uf	Uf	Uf	Uf	Uf

Table 2 List of changes in sutures and synchondroses in *Lycalopex culpaeus*.
Uf, unfused; f, fused; Pf, partially fused.

2001, Flores and Barone 2012). The basicranial synchondroses are the main growth sites that allow increase of the linear dimensions of the basicranial axis (Moore 1981, Mao and Nah 2004), as well as providing support for the stress accumulated in the basicranium by muscle activity (Slater et al. 2009). According to Mao and Nah (2004), such mechanical stimuli enhance growth at the basicranial synchondroses. Such synchondroses, including also the spheno-occipitalis and intersphenoidalis, are fused at the A1 and A2 age stages, respectively, indicating that most of the longitudinal growth of this area ends at these stages.

The braincase also showed fusion or partial fusion of several sutures and synchondroses in older adults (A3). This fusion reflects the fact that the role of such sutures in absorbing impact and force seems reduced, and is also less responsive to tensile forces (Wagemans et al. 1988), this being possibly related to the decrease in feeding performance detected in this advanced age class (Segura and Prevosti 2012). The presence of visible sutures in the rostral area that remain during the whole ontogeny indicate that marginal bone deposition keeps taking place in this region, in relation to increased kinesis and absorption of mechanical stresses generated by mastication or suckling (Herring et al. 2001). In general, fusion in culpeos occurs earlier in neurocranial sutures than in those of the splachnocranium (Table 2), although rostral sutures were never fused. This finding is also in agreement with observations about skull stress in other canids, indicating that under intrinsic loads, stress accumulates mainly in the rostrum (Slater et al. 2009, Tseng and Wang 2010). Such persistence of rostral sutures during life has also been observed in the felid *Puma concolor* (Linnaeus, 1771) (Segura and Flores 2009). It is noteworthy that whereas growth of the occipital plate and the cranial base ceases early in ontogeny (before reaching adulthood and in the younger adult class A1), the facial skeleton continues to grow well into adulthood (Holton et al. 2010). This condition allows a broad degree of morphological variation of the facial skeleton during growth, reflected in the different morphologies of the rostral area in canids and felids (i.e., canids have an elongated rostral area, while felids have a short rostrum; Biknevicius and Van Valkenburgh 1996).

It was also noteworthy that the culpeo skull was conservative, displaying few changes in suture type and only a slight increase of complexity. Most changes were observed in the sequence of suture fusions. Two sutures increased their complexity (interdigitation and overlap) and resistance, changing from plane to squamous/serrated (palatomaxillaris lateral, Table 2) and from plane to squamous (palatolacrimalis, Table 2). Increasing interdigitation of a suture implies an increase in the area of bone surfaces

and in the number of collagen fibers crossing the suture, thus allowing greater absorption of energy than simple plane sutures (Jaslow 1990, Jasinoski et al. 2010).

Evidence in the literature suggests that *Lycalopex culpaeus* reaches adult size before its first year of age (7 months according to Crespo and De Carlo 1963; J4 age stage according to Segura and Prevosti 2012). However, the basicranial synchondroses, where the linear dimensions of the basicranial axis increase (Moore 1981, Mao and Nah 2004), only become fused in the A1 and A2 age stages, suggesting that longitudinal growth extends until this time and thus contradicting the results of the previous quantitative analysis by Segura and Prevosti (2012). It is possible that the evident basicranial synchondroses are indicative not only of size changes but also of shape changes, which occur until the A2 age stage (Segura and Prevosti 2012).

The suture pattern detected in *Lycalopex culpaeus* (this report) and *Puma concolor* (Segura and Flores 2009) indicates that both species share changes in most sutures. For instance, the sutures of the rostrum (e.g., nasoincisiva, internasalis, nasomaxillaris, and frontonasalis) remain unfused throughout life, and the synchondroses of the occipital region (e.g., intraoccipitalis-squamolateralis and intraoccipitalis basilateralis) become fused early in life. However, in the felid *P. concolor*, 82.2% of the sutures were completely fused in older specimens, while in the canid *L. culpaeus* only 50% of the sutures were fused, and 17.5% were partially fused. Such findings suggest the existence of some conservative patterns in both families, probably constrained due to functional demands (e.g., evident rostral sutures related to bite activity of the muzzle throughout life, and early fusion of the occipital plate for head support and movement). However, the strong differences in the number of fused sutures at older age classes also suggest divergences in the cranial biomechanical pattern of each group.

Conclusion

Although most cranial traits changed their condition in the A1 class, some of them (molar convexity, laterocaudal border of palatine, postorbital constriction, and paraoccipital process and nuchal crest) achieved their final state earlier, in the J4 class, while others (scar for the medial pterygoid muscle and postglenoid process) reached their final state in the A2 class. Regarding the sutures and synchondroses, the largest change in fusion occurred very late in ontogeny, in the A3 class. However, some of these structures were fused in the A2 class (occipitomastoidea,

occipitotympanica, sphenoparietalis, sphenosquamosa, vomeropalatina, and intersphenoidalis), only one in the A1 class (spheno-occipitalis), and two important synchondroses in the early stages of development.

Both cranial traits and craniofacial sutures allow achievement and maintenance of adequate trophic function in adults, increasing bite force and stress support during prey apprehension (Slater et al. 2009, Tseng 2009, Tseng and Wang 2010). The morphological changes described here were expected, given that the growth pattern coincides with sequential changes in feeding habits and with the acquisition of behavior for hunting and killing prey crucial for the individual to achieve an independent existence as a predator (Ewer 1973, Binder and Van Valkenburgh 2000). Agreement between life history and morphology seems to be common in carnivores, as it has also been reported for other groups such as felids (*Puma concolor*; Segura and Flores 2009), hyenas [*Crocuta crocuta* (Erxleben, 1777); Tanner et al. 2010], and other canids [*Canis latrans* (Say, 1823); La Croix et al. 2011a,b].

Appendix

Appendix 1   Specimens of *Lycalopex culpaeus* of MACN used in this study.

15022; 15024; 15025; 15028; 15033; 15037; 15040; 15044; 15045; 15049; 15050; 15055; 15062; 15063; 15064; 15073; 15078; 15081; 15082; 15083; 15089; 15093; 15096; 15101; 15106; 15112; 15119; 15121; 15122; 15123; 15124; 15127; 15129; 15130; 15131; 15132; 15133; 15138; 15140; 15149; 15151; 15154; 15158; 15163; 15168; 15172; 15173; 15177; 15180; 15181; 15182; 15190; 15194; 15196; 15197; 15199; 15200; 15201; 15202; 15203; 15208; 15212; 15220; 15223; 15224; 15226; 15227; 15228; 15229; 15232; 15233; 15240; 15243; 15246; 15248; 15258; 15259; 15260; 15261; 15266; 15267; 15268; 23072; 23076; 23077; 23093; 23095; 23098; 23099; 23100; 23101; 23102; 23103; 23104; 23108; 23119; 23123; 23125; 23143; 23148; 23152.

References

Abdala, F., D.A. Flores and N.P. Giannini. 2001. Postweaning ontogeny of the skull of *Didelphis albiventris*. J. Mammal. 82: 190–200.

Antón, M., M.J. Salesa, J.F. Pastor, I.M. Sánchez, S. Fraile and J. Morales. 2004. Implications of the mastoid anatomy of larger extant felids for the evolution and predatory behaviour of sabretoothed cats (Mammalia, Carnivora, Felidae). Zool. J. Linn. Soc. 140: 207–221.

Biknevicius, A.R. and B. Van Valkenburgh. 1996. Design for killing: craniodental adaptations of predators. In: (J.L. Gittleman, ed.) Carnivore behavior, ecology, and evolution. Cornell University Press, New York. pp. 393–428.

Binder, W.J. and B. Van Valkenburgh. 2000. Development of bite strength and feeding behavior in juvenile spotted hyenas (*Crocuta crocuta*). J. Zool. 252: 273–283.

Crespo, J.A. and J.M. De Carlo. 1963. Estudio ecológico de una población de zorros colorados *Dusicyon culpaeus*. Rev. Mus. Argent. Cienc. Nat. 1: 1–55.

Drake, A.G. 2011. Dispelling dog dogma: an investigation of heterochrony in dogs using 3D geometric morphometric analysis of skull shape. Evol. Dev. 13: 204–213.

Duckler, G.L. 1998. An unusual osteological formation in the posterior skulls of captive tigers (*Panthera tigris*). Zoo Biol. 17: 135–142.

Evans, H.E. 1993. Miller's anatomy of the dog, 3rd edition. W.B. Saunders Company, Philadelphia, PA. pp. 1113.

Ewer, R. 1973. The carnivores. Cornell University Press, Ithaca, NY. pp. 500.

Flores, D.A. and L. Barone. 2012. Cranio-facial sutures of the black-capped squirrel monkey *Saimiri boliviensis* (Primates: Cebidae): gross morphology and postnatal ontogeny. Mammalia 76: 91–98.

Flores, D.A., N.P. Giannini and F. Abdala. 2006. Comparative postnatal ontogeny of the skull in an Australidelphian Metatherian *Dasyurus albopunctatus* (Marsupialia: Dasyuromorpha: Dasyuridae). J. Morphol. 267: 426–440.

Flores, D.A., N.P. Giannini and F. Abdala. 2010. Cranial ontogeny of *Caluromys philander* (Didelphidae: Caluromyinae): a qualitative and quantitative approach. J. Mammal. 91: 539–550.

García-Perea, R. 1996. Patterns of postnatal development in skull of lynxes, genus *Lynx* (Mammalia: Carnivora). J. Morphol. 229: 241–254.

Giannini, N.P., J.R. Wible and N.B. Simmons. 2006. On the cranial osteology of Chiroptera. I. *Pteropus* (Megachiroptera: Pteropodidae). Bull. Am. Mus. Nat. Hist. 295: 1–134.

Gilbert, S.G. 1997. Pictorial anatomy of the cat. University of Washington Press, Seattle, WA. pp. 120.

Henderson, J.H., L.Y. Chang, H.M. Song, M.T. Longaker and D.R. Carter. 2005. Age-dependent properties and quasi-static strain in the rat sagittal suture. J. Biomech. 38: 2294–2301.

Herring, S.W. and S. Teng. 2000. Strain in the braincase and its sutures during function. Am. J. Phys. Anthrop. 112: 575–593.

Herring, S.W., S. Teng, X. Huang, R.J. Mucci and J. Freeman. 1996. Patterns of bone strain in the zygomatic arch. Anat. Rec. 246: 446–457.

Herring, S.W., K.L. Rafferty, Z J. Liu and C.D. Marshall. 2001. Jaw muscles and the skull in mammals: the biomechanics of mastication. Comp. Biochem. Physiol. 131: 207–219.

Holton, N.E., R.G. Franciscus, M.A. Nieves, S.D. Marshall, S.B. Reimer, T.E. Southard, J.C. Keller and S.D. Maddux. 2010. Sutural growth restriction and modern human facial evolution: an experimental study in a pig model. J. Anat. 216: 48–61.

Jasinoski, S.C., B.D. Reddy, K.K Louw and A. Chinsamy. 2010. Mechanics of cranial sutures using the finite element method. J. Biomech. 43: 3104–3111.

Jaslow, C.R. 1990. Mechanical properties of cranial sutures. J. Biomech. 23: 313–321.

Jiménez, J.E. and A.J. Novaro. 2004. *Pseudalopex culpaeus* (Molina, 1782). In: (C. Sillero-Zubiri, M. Hoffmann and D.W. Macdonald, eds.) Canids: foxes, wolves, jackals and dogs. Status Survey and Conservation Action Plan, IUCN/SSC Canid Specialist Group, Gland, Switzerland. pp. 44–49.

Johnson, W.E. and W.L. Franklin. 1994. Role of body size in the diets of sympatric gray and culpeo foxes. J. Mammal. 75: 163–174.

La Croix, S., K.E. Holekamp, J.A. Shivik, B.L. Lundrigan and M.L. Zelditch. 2011a. Ontogenetic relationships between cranium and mandible in coyotes and hyenas. J. Morphol. 272: 662–674.

La Croix, S., M.L. Zelditch, J.A. Shivik, B.L. Lundrigan and K.E. Holekamp. 2011b. Ontogeny of feeding performance and biomechanics in coyotes. J. Zool. 285: 301–315.

Leyhausen, P. 1979. Cat behaviour: the predatory and social behaviour of domestic and wild cats. Garland STPM Press, New York. pp. 340.

Mao, J.J. 2002. Mechanobiology of craniofacial sutures. J. Dent. Res. 81: 810–816.

Mao, J.J. and H.D. Nah. 2004. Growth and development: hereditary and mechanical modulations. Am. J. Orthod. Dentofac. 125: 676–89.

Moore, W.J. 1981. The mammalian skull. Cambridge University Press, Cambridge, UK. pp. 369.

Novaro, A.J. 1997. *Pseudalopex culpaeus*. Mamm. Species 558: 1–8.

Rice, D.P. 2008. Craniofacial sutures: development, disease, and treatment. Frontiers of oral biology. Karger, London. pp. 236.

Richmond, F.J.R., D. Thomson and G. Loeb. 1992. Electromyographic studies of neck muscles in the intact cat. Exp. Brain Res. 88: 41–58.

Segura, V. and D. Flores. 2009. Aproximación cualitativa y aspectos funcionales en la ontogenia craneana de *Puma concolor* (felidae). Mastozool. Neotrop. 16: 169–182.

Segura, V. and F. Prevosti. 2012. A quantitative approach to the cranial ontogeny of *Lycalopex culpaeus* (Carnivora: Canidae). Zoomorphology 131: 79–92.

Slater, G.J., E. Dumont and B. Van Valkenburgh. 2009. Implications of predatory specialization for cranial form and function in canids. J. Zool. 278: 181–188.

Tanner, J.B., M.L. Zelditch, B.L. Lundrigan, K.E. Holekamp. 2010. Ontogenetic change in skull morphology and mechanical advantage in the spotted hyena (*Crocuta crocuta*). J. Morphol. 271: 353–365.

Travaini, A., J. Juste, A. Novaro and A. Capurro. 2000. Sexual dimorphism and sex identification in the South American culpeo fox, *Pseudalopex culpaeus* (Carnivora: Canidae). Wildl. Res. 27: 669–674.

Tseng, Z.J. 2009. Cranial function in a late Miocene *Dinocrocuta gigantea* (Mammalia: Carnivora) revealed by comparative finite element analysis. Biol. J. Linn. Soc. 96: 51–67.

Tseng, Z.J. and X. Wang. 2010. Cranial functional morphology of fossil dogs and adaptation for durophagy in *Borophagus* and *Epicyon* (Carnivora, Mammalia). J. Morphol. 271: 1386–1398.

Van Valkenburgh, B.1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. Paleobiology 17: 340–362.

Van Valkenburgh, B. 2007. Déjà vu: the evolution of feeding morphologies in the Carnivora. Integr. Comp. Biol. 47: 147–163.

Van Valkenburgh, B. and K.P. Koepfli. 1993. Cranial and dental adaptations to predation in canids. Symp. Zool. Soc. Lond. 65: 15–37.

Wagemans, P.A., J. Van de Velde, and A. Kuijpers-Jagtman. 1988. Sutures and forces: a review. Am. J. Orthod. Dentofac. 94: 129–141.

Wayne, R.K. 1986. Cranial morphology of domestic and wild canids: the influence of development on morphological change. Evolution 40: 243–261.

Wickland, C.R., J. Baker and B. Paterson. 1991. Torque vectors of neck muscles in the cat. Exp. Brain Res. 84: 64–659.

Zapata, S.C., M. Funes, A. Novaro. 1997. Estimación de la edad en el zorro colorado patagónico (*Pseudalopex culpaeus*). Mastozool. Neotrop. 4: 145–150.