

## Patterns of Postnatal Development in Skulls of Lynxes, Genus *Lynx* (Mammalia: Carnivora)

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**ABSTRACT** Studies on ossification patterns and other ontogenetic events associated with postnatal cranial growth of wild felids are scarce. An analysis of developmental processes undergone by several cranial structures (presphenoidal and sphenoccipital synchondroses, temporal and sagittal crests, and deciduous and permanent teeth) during postnatal growth has been conducted on a sample of 336 specimens belonging to the four Recent species of lynxes (*Lynx pardinus*, *Lynx lynx*, *Lynx rufus*, and *Lynx canadensis*). Age has been estimated based on tooth replacement, skull size, and by counting the annual lines of cementum growth. Comparison of the results obtained for each of the four species reveal (1) a single pattern for both tooth replacement and ossification of the sphenoccipital synchondrosis, (2) two ossification patterns for the presphenoidal synchondrosis, (3) a common pattern for development of temporal ridges and sagittal crest showing different degrees of morphological expression, and (4) evidence suggesting the involvement of a heterochronic process, neoteny, in the morphological differentiation of several populations and species of the genus *Lynx*. These data also support the hypothesis that processes involved in the replacement of carnassials are based on functional requirements. © 1996 Wiley-Liss, Inc.

In felids, postnatal growth occurs mostly during the first two years of life, and has been described by several investigators for lynxes (bobcat—Kritzman and Dudley, '86; Eurasian lynx—Andersen and Wiig, '84; Iberian lynx—García-Perea, '91; Beltrán and Delibes, '93; Canadian lynx—Saunders, '61). Most papers emphasize allometric changes of cranial dimensions, and little attention has been paid to ossification patterns and changes of other structures that may continue their development after the global growth has ceased.

Postnatal patterns of skull growth in mammals are influenced by changes in size and orientation of the cranial base during ontogeny, due to the growth provided by basicranial synchondroses (Moore, '81). Important skull changes also occur in carnivores by development of superstructures related to the masticatory apparatus: e.g., temporal ridges and sagittal crests. Feeding habits of carnivores are associated with specific patterns of tooth replacement. Developmental mechanisms underlying these structures are well documented for domestic animals (e.g.,

domestic cat—Jayne, 1898; Gaunt, '59; Beer, '85), mostly during the embryonic stage. Other studies conducted on wild populations have focused mainly on age estimation (e.g., Eurasian lynx—Kvam, '82; bobcat—Tumlinson and McDaniel, '84; caracal—Stuart and Stuart, '85).

The comparative study of ontogenetic variation in cranial structures helps in the understanding of evolutionary processes (e.g., Williams et al., '93), providing insight into the structural composition and origin of derived complex functional units (e.g., Hunt and Tedford, '93). Developmental information may also be an important source for phylogenetic inference (e.g., Hunt, '74, '87, '89; Tedford, '76).

In this study, I analyze the morphological changes that occur in the two basicranial synchondroses, temporal ridges, sagittal

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crest, and tooth replacement during the post-natal period of growth in the four species of Recent lynxes. The main objectives are (1) to identify potential shared developmental patterns, and (2) to provide insight into evolutionary processes that have occurred in the genus *Lynx*.

#### MATERIALS AND METHODS

A total of 336 skulls belonging to the four living species of lynxes were analyzed: 138 *Lynx lynx* (Eurasian lynx), 81 *L. pardinus* (Iberian lynx), 82 *L. rufus* (bobcat), and 35 *L. canadensis* (Canadian lynx). Specimens came from the scientific collections of 26 European and American institutions (see Appendix).

I estimated age in the following manner. To determine whether juvenile specimens were in their first or second year of life, tooth characteristics were examined, relying on previously published data (Saunders, '61; Crowe, '75; O'Connor, '84; Tumilson and McDaniel, '84). Individuals showing milk dentition or signs of tooth replacement were considered in their first year; those with full permanent dentition but still not adult size were considered in their second year.

Juvenile specimens are arranged in seven classes of relative age based on tooth replacement and tooth growth (Fig. 1). Classes J0 to J4 represent progressive stages of tooth replacement, starting from individuals with all the milk dentition erupted and ending with individuals that have just acquired all permanent teeth, including intermediate cases. When the permanent dentition is recently erupted, the apical foramen of canine root is still open (class J5), but it closes shortly later (class J6; this group includes specimens still undergoing cranial growth; Saunders, '61; Andersen and Wiig, '84; Kritzman and Dudley, '86; García-Perea, '91; Beltrán and Delibes, '93). Each stage of tooth replacement and growth is attained at approximately the same age by individuals of the four species (García-Perea, '91). Forty specimens of *Lynx pardinus*, 68 *L. lynx*, 13 *L. rufus*, and 3 *L. canadensis* were classified as juveniles.

Adults are specimens older than two years. Absolute age in years was estimated in 78 individuals by counting the annual lines of cementum growth from tooth sections (Crowe, '72; Kvam, '84; O'Connor, '84). I examined 34 adult specimens of *Lynx pardinus*, and 35 of *L. lynx*. The adult condition of the remaining specimens ( $n = 159$ ) was determined based on their skull size and other

morphological characteristics (García-Perea, '91).

To analyze the ossification pattern of the two basicranial synchondroses (presphenoidal and sphenoccipital), I considered four degrees of ossification (Fig. 2A–D) based on observation of collection material (cleaning processes usually destroy cartilages): (A) borders of adjacent bones separated; (B) borders of adjacent bones contacting; (C) active ossification occurring in the synchondrosis; (D) ossification of synchondrosis complete.

The following metrical variables were measured on the specimens with a digital caliper, to the nearest 0.02 mm (Fig. 3): lyre width at the coronal suture (LW), length of sagittal crest (LSC), and basicranial axis length (BAL) (measured from the midventral border of the foramen magnum to the presphenoidal synchondrosis).

Statistical tests consisted of regression analyses and *t*-tests. Regressions were used to estimate the variation of LW with age and the correlation between LSC-LW and LSC-BAL. I used the ratios LSC/BAL and LW/BAL for comparisons among species, as suggested by Radinsky ('84).

#### RESULTS

##### *Tooth replacement*

The permanent tooth formula for all representatives of the genus *Lynx* is I3/3, C1/1, P2/2, M1/1; i.e., each hemimaxilla and hemimandible has three incisors (I), one canine (C), two premolars (P), and one molar (M). The deciduous tooth formula is dI3/3, dC1/1, dP2/2. In *L. lynx*, supernumerary P2 and m2 may appear at low frequency (8–27% P2, 7–20% m2; García-Perea, '91).

A comparison of all the replacement sequences observed (Table 1) reveals considerable homogeneity within the genus: the first teeth to erupt are incisors; canines and molars start to erupt immediately after; the next teeth replaced are dP4 and dp4, followed by dP3 and dp3. M1 and m1 are not replaced. Upper and lower homologous incisors erupt simultaneously, but as with molars, the lower dentition starts to erupt one tooth delayed in relation to the upper series. Upper and lower

Fig. 1. Characteristics of tooth replacement in six age classes (J0–J5) of *Lynx pardinus*. Left and right photographs of a row correspond to upper and lower dental series of the same individual.

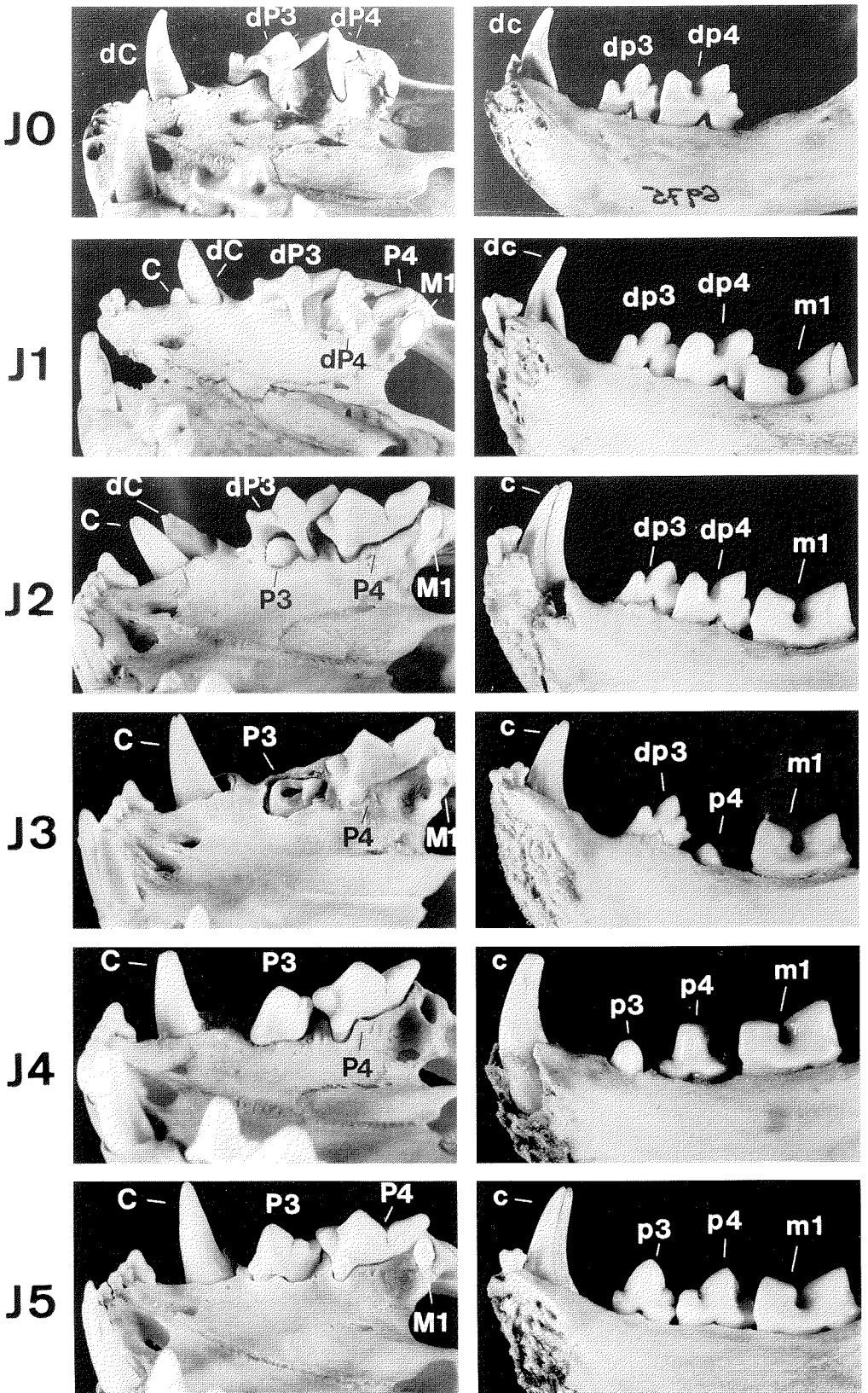


Figure 1

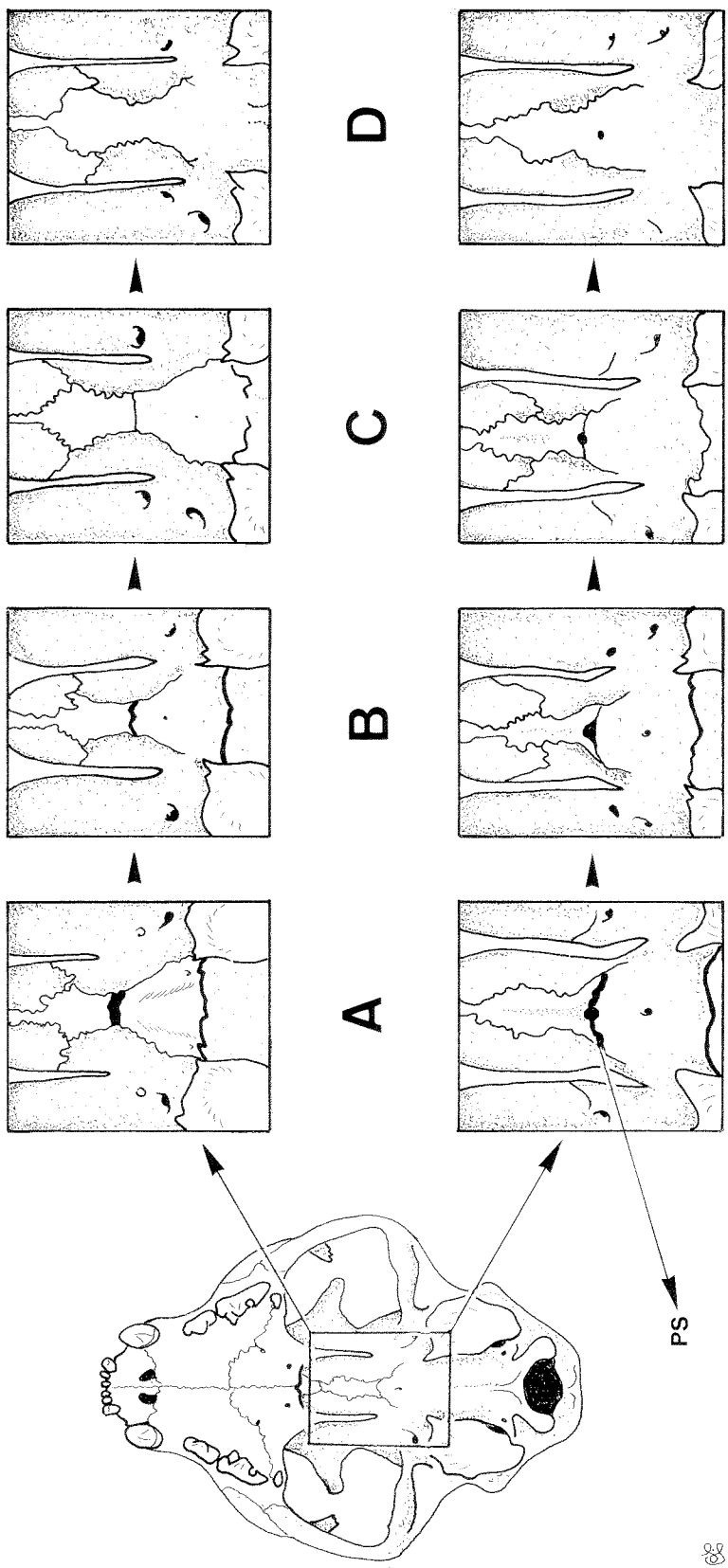


Fig. 2. Ossification patterns of presphenoidal synchondrosis (PS) for *Lynx pardinus* (upper series) and *L. lynx* (lower series). A, B, C, D represent progressive ossification degrees, different for the two patterns observed (see text).

canines start to erupt simultaneously with I3/i3, and are the last teeth to complete eruption.

#### *Sphenooccipital synchondrosis*

In *Lynx pardinus*, the earliest ossification stages of the sphenooccipital synchondrosis (degrees A and B) occur during the first year of life. Degree C is reached when specimens are 1–3 years old. Most specimens (86%,  $n = 7$ ) between 3 and 4 years old show degree D, i.e., ossification is completed. All specimens 5 years or older have the synchondrosis totally ossified. In *L. lynx*, the sphenooccipital synchondrosis performs a similar ossification process, although the youngest specimen showing degree D in my sample is 4 years old.

Data on *Lynx rufus* specimens up to 3 years of age suggest a similar timing for the process to that observed for *L. lynx* and *L. pardinus*. In *L. canadensis*, the ossification process seems to be similar to that of the other three species, although I have no data to establish timing.

#### *Presphenoidal synchondrosis*

Data for *Lynx pardinus* indicate that the earliest ossification stages (degrees A and B) of the presphenoidal synchondrosis occur during the first two years of life. The synchondrosis ossifies between two and eight years, appearing totally ossified in most specimens after nine years (Fig. 2D, upper). I have named this sequence "pattern A," and it is present in most Iberian specimens (81%,  $n = 45$ ), although a small percentage (19%,  $n = 11$ ) of the sample shows stages that could resemble the second pattern, described below.

For *Lynx lynx*, the ossification process is somewhat different (Fig. 2, lower series). Briefly, after the earliest stage (degree A), ossification proceeds from lateral to medial zones of synchondrosis. A central hole can be observed in collection specimens (Fig. 2B, lower). This progressively diminishes in size (Fig. 2C, lower), reaching a minimum size in oldest specimens, with the lateral zones of the synchondrosis totally ossified (Fig. 2D, lower). However, I have not found specimens with the entire synchondrosis ossified (adult  $n = 50$ ). I have named this "pattern B."

Timing and ossification stages for the presphenoidal synchondrosis in *Lynx rufus* specimens up to three years old resemble those

found in *L. lynx*. Most adults exhibit the same stage shown in Figure 2B,C lower (72%,  $n = 36$ ).

I have no data for establishing timing in *Lynx canadensis*, but ossification of this synchondrosis seems to follow the same pattern of *L. lynx* and *L. rufus*; the stage shown in Figure 2B,C lower is the most common among adults (80%,  $n = 27$ ).

Although the three latter species mostly show pattern B (*Lynx lynx* 89%,  $n = 107$ ; *L. rufus* 77%,  $n = 43$ ; and *L. canadensis* 87%,  $n = 30$ ), a small percentage of the samples show stages assignable to pattern A (*L. lynx* 11%,  $n = 13$ ; *L. rufus* 23%,  $n = 10$ ; *L. canadensis* 13%,  $n = 4$ ).

#### *Temporal ridges and sagittal crest*

Analysis of aged skulls shows the following morphological changes for temporal ridges and sagittal crest during the postnatal period. Juvenile lynxes present a pair of temporal lines, two symmetric ridges running almost parallel along the parietal surface. During postnatal development, these temporal ridges move medially toward each other, and eventually meet at the interparietal region, in the midline of the skull. The surface delimited by these temporal ridges is usually lyre-shaped, and I refer to this condition simply as "lyre." The sagittal crest starts to develop posterior to the intersection of the temporal ridges. The crest becomes more prominent with age (in some cases it also lengthens anteriorly), and the lyre surface becomes reduced in length and breadth. I have evaluated these changes with the variables Lyre width (LW, Fig. 3), length of sagittal crest (LSC, Fig. 3), and type of sagittal crest (TSC, Fig. 4).

In *Lynx pardinus*, juvenile specimens assigned to age classes J0 to J3 have weakly or undefined temporal ridges, therefore I have not measured LW. The values for the other juvenile age classes and adults are in Table 2. In general, the pattern is a decrease of LW (Fig. 3, upper series, Table 2) with age ( $r = -0.71$ ,  $P \ll 0.001$ ,  $n = 21$ ), which seems to stop at the age of two years. Adults show well defined ridges, the lyre becoming higher on the parietal surface with ageing, but never exceeding 2 mm high. The youngest specimens with sagittal crest developing belong to age class J6 (age < two years). Because only two specimens of this age class show a developing crest ( $n = 7$ ), it has been not possible

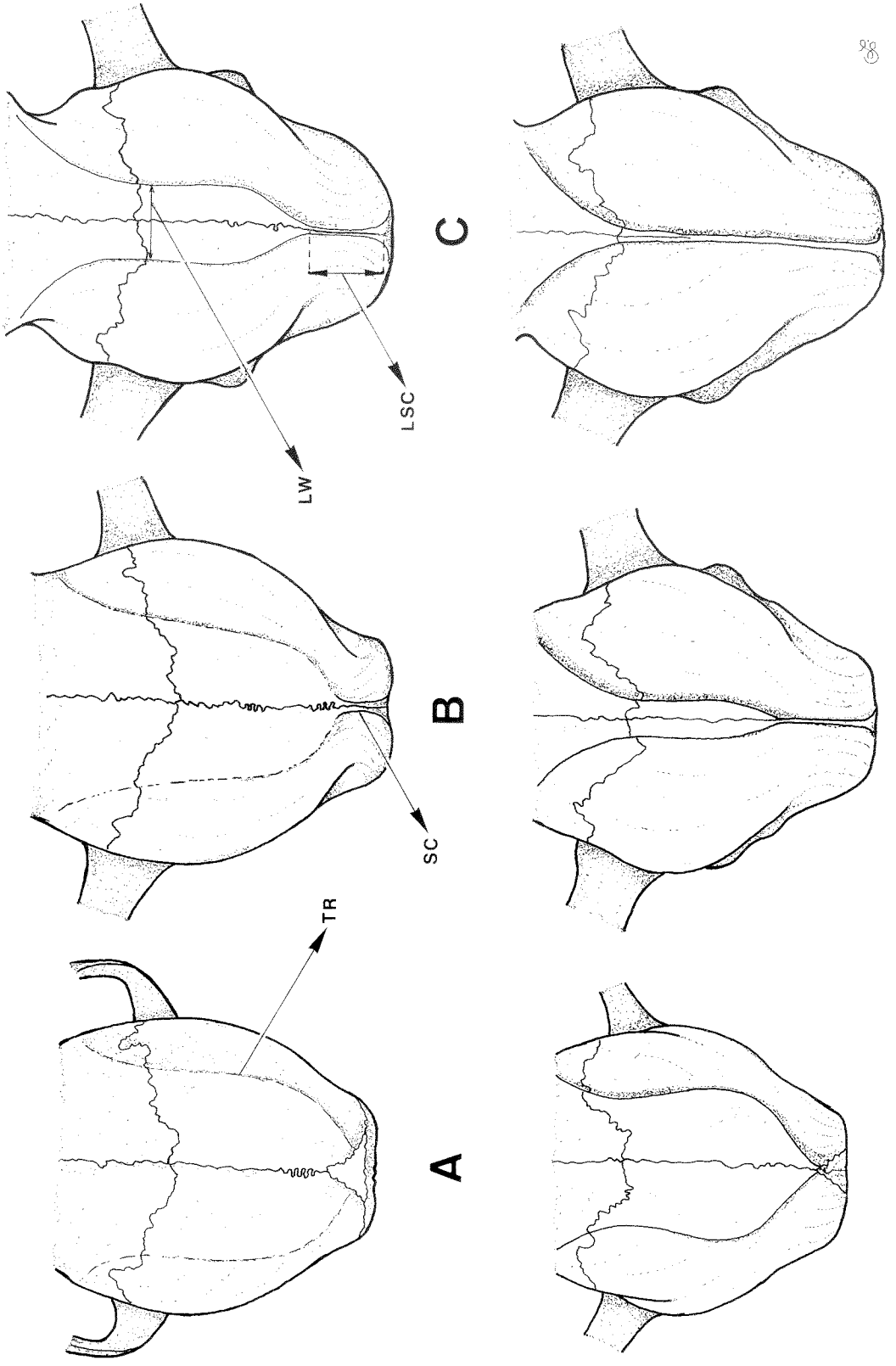


Figure 3

TABLE 1. Inferred tooth replacement sequences in the four *Lynx* species, and sequence estimated for the genus<sup>1</sup>

Deciduous teeth formula:	dI3/3	dC1/1	dP2/2	
Permanent teeth formula:	I3/3	C1/1	P2/2	M1/1
Tooth replacement sequences:				
<i>Lynx pardinus</i>				
current data (n = 22)	I1 - I2 - I3 + M1 +	C1 +	P4 - P3	
	i1 - i2 - i3 + m1 +	c1 -	p4 - p3	
<i>Lynx lynx</i>				
current data (n = 20)	I1 - I2 - I3 + M1 +	C1 -	P4 - P3	
(Matjuschkin, '78)	i1, i2 - i3 + m1 +	c1 -	p4 - p3	
	I1 + I2 + I3 + M1 +	C1 -	P4 - P3	
	i1 + i2 + i3 + m1 +	c1 -	p4 - p3	
<i>Lynx rufus</i>				
current data (n = 6)	I1, I2 + I3 + M1 +	C1 -	P4 - P3	
	i1, i2, i3, m1 +	c1 -	p4 - p3	
(Crowe, '75)	I1 - I2 - I3 + C1 + M1 -		P4 - P3	
	i1 - i2 - i3 + c1 + m1 -		p4 - p3	
<i>Lynx canadensis</i>				
current data (n = 1)	I1, I2 - I3 + M1,	C1,	P4, P3	
and Saunders ('64)	i1, i2 - i3 + m1,	c1 -	p4 - p3	
Estimated sequence for genus <i>Lynx</i> :				
	I1 - I2 - I3 + M1 -	C1	P4 -	P3
	i1 - i2 - i3		+ m1 -	p4 - p3

<sup>1</sup>Each sequence consists of two series of permanent teeth (upper = maxillary teeth, lower = mandible teeth) arranged from left to right by chronological order of eruption. Teeth erupting simultaneously are grouped by (+), and are separated by (-) from teeth erupting earlier (left) or later (right). When relative order is unknown, teeth are separated by a comma.

to estimate the difference in LSC values between J6 and adults.

In *Lynx lynx*, the values of LW are significantly different from those found in *L. pardinus* (J5,  $t = 2.547$ ,  $P = 0.04$ ,  $n = 9$ ; J6,  $t = 4.779$ ,  $P \ll 0.001$ ,  $n = 12$ ). However, the pattern of variation for LW is similar in both species, decreasing with age (*L. lynx*  $r = -0.80$ ,  $P = 0$ ,  $n = 40$ ; Fig. 3 lower series). In *L. lynx*, the sagittal crest starts to develop in some specimens of class J5, and is observed in almost all specimens of class J6. Contrary to LW, LSC values increase with age (Fig. 3, lower series; Table 2): significant differences are found between LSC values of individuals J6 and adults ( $t = -4.973$ ,

$P \ll 0.001$ ,  $n = 82$ ). Decreasing of LW and increasing of LSC seem to stop at the age of 2 years.

Because I have no data on the juvenile classes of *Lynx rufus* and *L. canadensis*, I cannot determine at what age the sagittal crest starts to develop in these species, although specimens of J6 class show sagittal crests. Values of LW and LSC are given in Table 2. For both variables, no significant differences seem to exist, although the small size of the samples prevents adequate analyses.

Analyses of LSC versus LW within species indicate that long sagittal crests are associated with narrow lyres, and vice versa ( $r = -0.918$ ,  $P = 0$ ,  $n = 82$  for *Lynx lynx*;  $r = -0.634$ ,  $P \ll 0.001$ ,  $n = 36$  for *L. pardinus*;  $r = -0.763$ ,  $P = 0$ ,  $n = 45$  for *L. rufus*;  $r = -0.809$ ,  $P = 0$ ,  $n = 28$  for *L. canadensis*).

For each of the four species, significant and positive correlations were found between LSC and BAL (*Lynx lynx*  $r = 0.72$ ,  $P \ll 0.001$ ,  $n = 73$ ; *L. rufus*  $r = 0.56$ ,  $P < 0.001$ ,  $n = 41$ ; *L. pardinus*  $r = 0.46$ ,  $P = 0.034$ ,  $n = 21$ ; and *L. canadensis*  $r = 0.47$ ,  $P = 0.016$ ,  $n = 26$ ).

From a qualitative approach, I identified several types of sagittal crest (variable TSC) and classified them in four morphotypes (Fig. 4):

- A—*Juvenile stage*, temporal ridges present, but no sagittal crest
- B—*Sagittal crest poorly developed*, restricted to interparietal region
- C—*Sagittal crest moderately developed*, occupying posterior half of suture between parietals
- D—*Sagittal crest well developed*, occupying total length of parietal suture, no lyre present

Type D is typical of *Lynx lynx*, although it can be found occasionally in *L. rufus* (7%,  $n = 3$ ) and *L. canadensis* (4%,  $n = 1$ ); it has never been observed in *L. pardinus*. Type A is exclusively in juvenile specimens, although types B and C may also appear in juveniles J5 or older (Table 3). In species showing the four types of sagittal crest, the ontogenetic sequence is A-B-C-D. Some populations and species only show the sequences A-B or A-B-C.

## DISCUSSION

This study of ontogenetic variation in lynx skulls supports the hypothesis of a functional significance of the carnassial teeth replace-

Fig. 3. Postnatal development of temporal ridges (TR) and sagittal crest (SC) in *Lynx pardinus* (upper series) and *L. lynx* from Northern Europe (lower series). A, specimens of class J1; B, specimens of class J6; C, adults; LW, Lyre width; LSC, Length of sagittal crest.

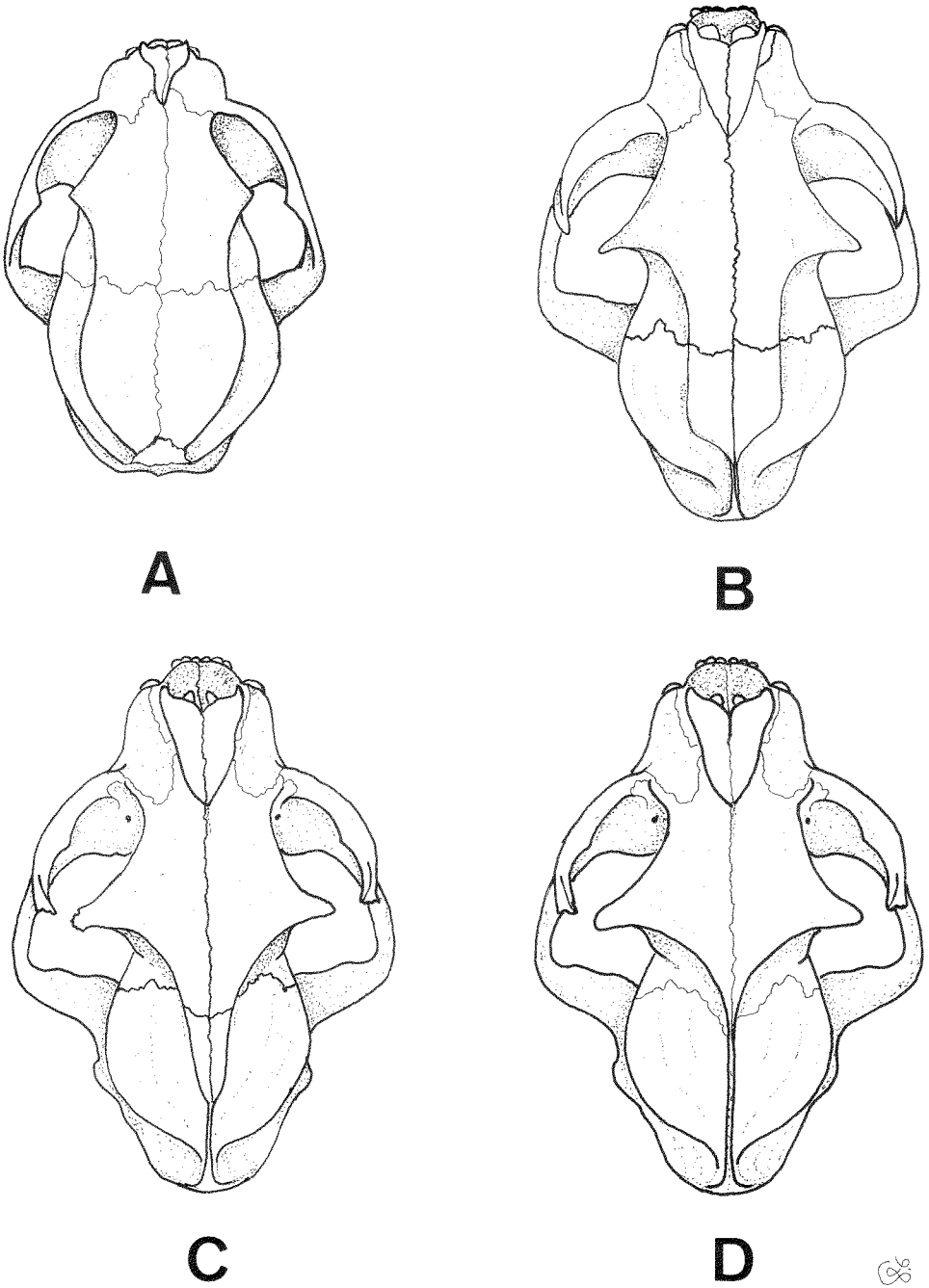


Fig. 4. The four morphotypes (types A–D) found in lynxes related to the degree of development of sagittal crest.



TABLE 2. Variation with age of LW and LSC values (in mm), as well as of morphological types of temporal ridges and sagittal crest (TSC) among recent *Lynx* species<sup>1</sup>

Species	Age	LW			LSC			TSC
		R	$\bar{x}$	n	R	$\bar{x}$	n	
<i>Lynx pardinus</i> (BAL = 38)	J4	25-29	27.5	4	—	—	0	A
	J5	27-34	27.3	6	—	—	0	A
	J6	17-30	21.6	5	16-17	16.5	2	B
	AD	6-25	16.6	33	14-28	21.1	29	B, C
<i>Lynx lynx</i> (BAL = 43)	J4	18-25	20.7	7	—	—	0	A
	J5	8-28	18.3	13	16-26	21	2	B, C
	J6	6-18	10.7	19	12-62	28.5	21	B, C, D
	AD	3-15	8.7	26	22-73	49.5	59	B, C, D
<i>Lynx rufus</i> (BAL = 37)	< J6	ND	—	0	ND	—	0	ND
	J6	13-20	17.8	5	16-22	18.7	5	B
	AD	5-27	17.9	37	14-35	20.9	37	B, C
<i>Lynx canadensis</i> (BAL = 37)	< J6	ND	—	0	ND	—	0	ND
	J6	21-27	23.3	3	10-16	13	2	B
	AD	13-28	20.3	27	11-24	16.8	25	B, C

<sup>1</sup>Average adult skull size of each species is represented by BAL. J4-J6, juvenile age classes; AD, adults. ND, not data; R, range of values;  $\bar{x}$ , mean value; n, sample size.

ment sequence, and suggests the existence of a genus-level developmental pattern for the sagittal crest, regulated by a heterochronic process. I consider here heterochronies as evolutionary shifts in the rate of developmental change, or in the timing of their onset, in the ontogeny of a descendant species relative to its ancestor (Wiltshire et al., '94).

#### Tooth replacement

The tooth replacement sequences described above are similar to those described by Tumlison and McDaniel ('84) for *Lynx rufus*. They

TABLE 3. Ontogenetic sequences (A-B-C-D) observed in lynxes from different geographic origin in relation to the morphological expression of sagittal crest<sup>1</sup>

	BAL	J3	J4	J5	J6	AD
<i>Lynx rufus</i> NW USA	37	A	—	—	B	B
<i>Lynx canadensis</i>	37	A	—	—	B	B, C
<i>Lynx pardinus</i>	38	A	A	A	A, B	B, C
<i>Lynx rufus</i> Maine-Nova Scotia	39	—	—	—	—	B, D
<i>Lynx rufus</i> Lake Superior	39	—	—	—	—	B, D
<i>Lynx lynx</i> Caucasus	41	—	—	—	B, C	B, C, D
<i>Lynx lynx</i> N and E Europe	43	A	A	B	B, C, D	C, D
<i>Lynx lynx</i> Carpathian Mts.	45	—	A	B	C	D

<sup>1</sup>Populations are arranged by cranial size (BAL). J3-J6, juvenile age classes; AD, adults; BAL, average values for basicranial axis length in the samples (adults).

reveal a common pattern for the Recent representatives of the genus *Lynx*, and a complex system of progressive replacement for carnassials. The lack of synchrony in eruption of upper and lower homologous premolars is apparently a response to a functional need related to carnassial biting. Carnassial function in young lynxes is assumed by dP3 and dp4, but this function shifts to P4 and m1 in adults, the morphology of dP3 and dp4 being similar to that of P4 and m1 (Tumlison and McDaniel, '84; personal observations). Only after P4 and m1 have erupted enough to be functional, are dP3 and dp4 lost and replaced by P3 and p4, which have no carnassial morphology. Since weaning and replacement of carnassials occur when lynxes are two- (Ewer, '73) and five to six months old (García-Perea, '91) respectively, they only feed on solid food during the replacement period. The replacement process described above is therefore fundamental, because it allows lynxes to have a functional pair of carnassials even during the replacement of milk dentition by permanent teeth. Similar processes involved in the replacement of carnassials have been reported for other carnivores, such as domestic cats (Gaunt, '59), *Felis silvestris* (García-Perea et al., in press), *Mustela vison*, *Vulpes vulpes*, and *Paradoxurus hermaphroditus* (Ewer, '73).

#### Sphenooccipital synchondrosis

*Lynx lynx* and *L. pardinus* show the same ossification pattern for the sphenooccipital

synchondrosis. This is consistent with data offered by Schmidly and Read ('86) for bobcats from Texas. Because the youngest specimens showing a totally ossified sphenooccipital synchondrosis are three years old, this characteristic may be considered as a useful criterion to distinguish adult lynx specimens from juveniles.

#### *Presphenoidal synchondrosis*

The presphenoidal synchondrosis shows two ossification patterns, one typical of *Lynx pardinus* (pattern A), and other common to the three remaining species (pattern B). Pattern B has been found in all species but two (personal observations) of the "Panthera group" (*Pardofelis marmorata*, *Panthera tigris*, *P. leo*, *P. pardus*, *P. onca*, *Neofelis nebulosa*, and *Uncia uncia*) of Wayne et al. ('89), the proposed sister group of lynxes. This fact suggests a close relationship between lynxes and large cats, but additional information on other felid species is required for an adequate phylogenetic assessment.

#### *Temporal ridges and sagittal crest*

Age-related morphological changes observed in temporal ridges and sagittal crests are similar to those reported by Kvam ('82) for Norwegian lynxes, and by Saunders ('61) for Canadian lynxes. These changes seem to be related to the development of the main jaw-closing muscle, the temporalis, which originates on the temporal ridges, temporal fossa and sagittal crest and inserts on the mandible. During postnatal growth, the temporalis muscle grows, as the temporal ridges migrate to the top of the skull, decreasing LW with age. The sagittal crest provides additional attachment surface by lengthening itself and becoming higher, showing a pattern of morphological change opposite to that of temporal ridges, i.e., LSC increases with age.

Although temporal ridges and sagittal crest show opposite patterns of change, their consequences are similar from the functional point of view. The migration and expansion of the origin margins of the temporalis muscle with age would allow an increase of the muscle mass implying an increase in the number of fibers (the temporalis is bipennate; Moore, '81) very likely resulting in a more powerful action (Bock, '74). This may be fundamental for success in killing prey using the lethal bite technique (Leyhausen, '65), an activity often practiced by young lynxes on prey provided by their mothers, while they

learn their predatory skills. In fact, development of the sagittal crest begins at the end of the first year (age classes J5, J6), when young lynxes adopt an independent way of life and must capture prey without help.

A common ontogenetic pattern emerges when these developmental changes are analyzed on a qualitative morphological basis, expressed in a developmental sequence A-B-C-D (Fig. 4) of discrete nature (*sensu* Alberch, '85). In order to identify potential heterochronic processes, the following assumptions were considered. Stages A-D present in each one of the four species are considered homologous. Because *Lynx lynx* is considered to have derived directly from the common ancestor of the Recent lynxes, *Lynx issiodorensis* (Kurtén, '78), and its skull morphology and size are similar, I considered the ancestral timing of this developmental sequence to be similar to that of one of the largest representatives of *L. lynx*, the Carpathian population (Table 3).

Starting from these premises, my results reveal differences in timing of homologous developmental stages among different populations and species of lynxes (Table 3). These deviations from the hypothetical ancestral pattern support the hypothesis of a heterochronic process regulating this system within the genus *Lynx*, neoteny—using the terminology proposed by Alberch et al. ('79). Neoteny would be represented by a slower rate of morphological change in certain populations of lynxes (e.g., *L. rufus* from NW USA, Table 3) relative to the hypothetical ancestral timing, resulting in adult morphologies (type B) resembling juveniles (J5) of the population considered similar to the ancestor (Carpathian *L. lynx*). The result is that lynx populations with developmental timing altered are paedomorphic in relation to their common ancestor.

On the other hand, data offered in Table 3 also suggest that populations and species with larger skulls (higher BAL values) attain more advanced stages of the developmental sequence A-B-C-D. This is consistent with the results of the analysis of LSC versus BAL, showing a significant correlation in the four species. These facts suggest the existence of a common ontogenetic pattern that can modify its phenotypic expression depending, at least partially, on skull size. However, this allometric pattern is true only within the generic limits, and does not hold when *Lynx* is com-

pared to other felid genera with different skull sizes. For example, *Prionailurus planiceps*, a smaller cat (BAL = 33 mm, n = 14), has a well developed sagittal crest, corresponding to type D, and even more developed than that of large lynxes (higher on the braincase surface). However, *Lynchailurus pajeros* (*sensu* García-Perea, '94), a cat of similar skull size (BAL = 32 mm, n = 21), never shows type D of sagittal crest.

The developmental system described for temporal ridges and sagittal crest resembles the general structure of dynamic developmental models outlined by Alberch ('85). This assumes the existence of the same underlying ontogenetic program producing different intermediate morphologies that are regulated by a combination of heterochronic mechanisms and variation of parameters such as skull size. Further studies are desirable to identify other epigenetic (*sensu* Hall, '83) parameters regulating the system, e.g., functional factors such as mechanical loads (Herring, '93).

Lynxes are considered to be highly efficient predators due to several morphological specializations achieved on teeth, limb proportions, and predatory behavior (Ewer, '73). Since heterochronies are considered means of rapid phenotypic evolution with minor alterations to the genome (Wiltshire et al., '94), it is possible to hypothesize that neotenic processes have been involved in the differentiation of several lynx populations, allowing changes in overall body size without striking alterations of primary morphology—highly successful for this genus. Differences in body size among lynx populations could be related to the size of the main prey available. Further studies are required to test these hypotheses.

The morphological expression of the ontogenetic program described above seems to be limited by genus-level constraints of a phylogenetic nature. Other developmental patterns have been identified in this study (tooth replacement, ossification of sphenoccipital shynchondrosis) shared by Recent representatives of genus *Lynx*. Further studies are warranted to find whether these patterns are shared by other felids, or are also restricted by genus-level phylogenetic constraints.

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## APPENDIX

## List of collections consulted and specimens studied.

AMNH (American Museum of Natural History, New York), BM (Natural History Museum, London), CM (Carnegie Museum of Natural History, Pittsburgh), DBUC (Departamento de Biología Animal I, Universidad Complutense, Madrid), DVF (Direktoratet for Vilt og Fersvannsfisk, Trondheim), EBD (Estación Biológica de Doñana, Seville), FS (Forschungsinstitut Senckenberg, Frankfurt), ISEZ (Institute of Systematic and Experimental Zoology, Krakow), MHNG (Muséum d'Histoire Naturelle, Geneva), MHNGA (Musée d'Histoire Naturelle "Grigore Antipa," Bucharest), MNCN (Museo Nacional de Ciencias Naturales, Madrid), MRI (Mammals Research Institute, Bialowieza), MZUF (Museo Zoologico de "La Speccola," Firenze), MZUM (Museum of Zoology of the University of Michigan, Ann Arbor), MZUS (Musée Zoologique de l'Université d'Estrasbourg, Strasbourg), MNH (Termesztudományi Múzeum Allattára, Budapest), NBM (New Brunswick Museum, Saint John), NHMB (Naturhistorisches Museum Basel, Basel), NHRM (Naturhistoriska Riksmuseet, Stockholm), NMP (Národní Muzeum v Praze, Prague), NNHM (National Natural History Museum, Sofia), USNM (National Museum of Natural History, Washington D.C.), UZA (Unidad de Zoología Aplicada, Madrid), ZMH (Zoological Museum of Helsinki University, Helsinki), ZMM (Zoological Museum of Moscow State University, Moscow), ZSM (Zoologische Staatssammlung München, Munich).

*Lynx pardinus*

AMNH 169.492, BM 4.12.12.2, BM 4.12.12.1, BM 72.10.26.1, BM 3.3.16.1, BM 94.6.11.1, BM 42.2.26.1, BM 89.8.27.1, BM 7.6.4.2, BM 8.3.8.2, BM 7.12.10.1, BM 95.9.4.1, BM

39.3664, DBUC 1R, EBD 1376, EBD 6975, EBD 7099, EBD 17938, EBD 19283, EBD 19322, MNCN 1R, MNCN 3R, NHMB 8865, NHMB 8800, NHRM A59/5864, NHRM A58/5291, USNM 152618, USNM 152619, UZA 1960.00.00.01-07, UZA 60.00.00.09, UZA 1960.00.00.11, UZA 1970.00.00.01-04, UZA 1970.00.00.06, UZA 1970.00.00.08, UZA 1970.00.00.10, UZA 1970.00.00.18-21, UZA 1971.10.07.01, UZA 1972.00.00.01-05, UZA 1972.00.00.13-14, UZA 1973.00.00.01-03, UZA 1974.00.00.01, UZA 1974.00.00.03, UZA 1974.00.00.13, UZA 1974.00.00.22, UZA 1974.10.00.01, UZA 1974.12.00.01, UZA 1975.11.00.01, UZA 1975.12.15.01, UZA 1976.00.00.01-02, UZA 1977.00.00.01, UZA 1977.05.00.01, UZA 1978.00.00.06, UZA 1979.00.00.06, UZA 1979.06.00.01, UZA 1980.04.13.01, UZA 1984.02.25.01, UZA 1985.11.14.05-09.

*Lynx lynx*

AMNH 41337, BM 51.11.8.16, BM 58.5.4.63a, BM 55.12.26.176, BM 69.10.19.16, BM 42.41, BM 58.5.4.63b, BM 2.3.9.1, BM 30.5.1.1, BM 81.12.7.2, BM 83.4.21.1, BM 98.8.5.1, BM 85.803, DVF 27/76, DVF 12/76, DVF 14/76, DVF 17/76, DVF 118/76, DVF 10/76, DVF 41/76, DVF 13/76, DVF 59/76, DVF 18/76, DVF 121/76, FS 15711, FS 16253, ISEZ M/1099/59, ISEZ M/1109/59, ISEZ M/2108/61, ISEZ M/4658/70, ISEZ M/1108/59, MHNG 223.37, MHNG 618.58, MHNG 668.32, MHNG 603.64, MHNGA 3473, MHNGA 3475, MNH 2470/1, MNH 2470/2, MNH 2495, MNH 2506/1, MNH 2507, MNH 2636, MNH 2966, MNH 3790, MNH 4171/1, MNH 4173, MNH 4359, MNH 4395, MNH 4455/1, MNH 4455/2, MNH 53.42.1, MNH 57.6.1, MNH 63.12.1, MNH 84.19.1, MRI 118, MRI 1119, MRI 617, MRI 618, MZUF 11428, MZUF 11429, MZUS i.177, MZUS 1.154, NHMB 1250, NHMB 8864, NHMB 8634, NHMB 8158, NHMB 8362, NHRM 583726, NHRM 583730, NHRM 582868, NHRM 581275, NHRM 583729, NHRM 583047, NHRM 582949, NHRM 583046, NHRM 585260, NHRM 584923, NHRM 595141, NHRM 589654, NMP 11811, NMP 11812, NMP 21887, USNM 84.090, USNM 198.468, ZMH 963, ZMH 1387, ZMH 556, ZMH 1388, ZMH 1389, ZMH 1391, ZMH 1392, ZMH 1393, ZMH 1394, ZMH 1395, ZMH 1396, ZMG 1397, ZMH 3849, ZMH 4947, ZMH 5709, ZMH 6729, ZMH 6749, ZMH 14193, ZMH 14558, ZMH 23103, ZMH 31503, ZMH 31588, ZMH 21/1960, ZMH 48/1960, ZMH 61/1960, ZMH 151/1960, ZMM 3073, ZMM 14193, ZMM 14233, ZMM 14263, ZMM 36915, ZMM 52259, ZMM 55079, ZMM 55081, ZMM 55082, ZMM 55086, ZMM 55088, ZMM 106524, ZMM 14260, ZMM 22352, ZMM 22353, ZMM 40435, ZMM 75081, ZMM 75082, ZMM 75083, ZMM 75084, ZMM 75085, ZSM 1914/1196, ZSM 1913/418, ZSM 1914/1142, ZSM 1914/1143, ZSM 1954/225, ZSM 1964/59.

*Lynx rufus*

BM 55.12.24.275, BM 57.6.22.6, BM 13.8.2.1, BM 94.5.9.1, BM 94.5.9.2, BM 77.12.10.4, BM 55.11.26.4, BM 82.10.26.10, BM 1227a, BM 46.5.13.3, BM 19.4.2.1, BM 98.3.1.52, BM 46.11.19.8, BM 19.7.7.2755, BM 88.11.25.1, BM 46.11.29.7, BM 46.10.27.12, BM 43.5.27.5, BM 85.816, CM 40412, CM 2593, CM 3224, CM 3231, CM 8585, CM 10151, CM 11309, CM 20704, CM 51998, CM 10711, CM 21796, CM 16511, CM 16512, CM 12369, CM 12368, CM 18103, CM 11307, CM 11308, CM 18104, CM 30449, CM 48897, CM 8693, CM 8694, CM 8696, CM 8695, CM 8692, CM 4246, CM 8598, CM 8591, CM 8592, CM 13167, CM 21943, CM 22603, CM 21944, CM 21941, CM 61309, CM 21947, CM 21949, CM 61307, CM 61311, CM 21372, CM 61312, CM 61306, CM 61304, CM 45230, CM 30451, CM 61308, CM 21933, CM 61310, CM 21934, CM 8691, CM 21946, CM 21940, CM 21948, CM 21945 NBM 456, NBM 123, UMMZ 157.212, UMMZ 157.231, UMMZ 157.292, UMMZ 157.219, UMMZ 157.246, UMMZ 157.269.

*Lynx canadensis*:

BM 52.1249, BM 62.12.12.29, BM 92.4.19.1, BM 45.7.4.15, BM 63.2.24.20, BM 68.12.29.34, BM 85.804, BM 16.29.1, BM 89.377, BM 4.2.39, BM 42.20, CM 3.208, CM 3.209, CM 4.273, CM 13.312, CM 21.936, CM 21.942, CM 22.295, CM 22.296, CM 61.286, CM 61.288, CM 61.380, CM 61.381, CM 61.382, CM 61.384, CM 61.385, UMMZ 98.121, UMMZ 98.122, UMMZ 98.123, UMMZ 98.124, UMMZ 98.125, UMMZ 98.126, UMMZ 98.127, UMMZ 98.128, UMMZ 98.129.

*Prionailurus planiceps:*

USNM 144119, USNM 145591, USNM 145592, USNM 145594, USNM 196604, USNM 196605, USN 196607, USNM 489422, USNM 489424, USNM 489425, USNM 489426, USNM 489427, USNM 489428, USNM 49973.

*Lynchailurus pajeros:*

AMNH 76150, AMNH 16695, BM 27.11.1.67, BM 34.9.2.31, BM 34.11.4.5, BM 12.7.12.4, BM 21.6.7.5, BM 55.12.24.261, BM 3.2.24.1, FMNH 68318, FMNH 80994, FMNH 43291, FMNH 52488, MACN 16489, MACN 17816, MACN 30103, MVZ 114777, MVZ 139613, MVZ 114942, MVZ 114943, USNM 172786.