The evolution of lynxes

Lars Werdelin

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The intra- and interspecific variation of certain felid species belonging to, or morphologically related to, the genus *Lynx* is studied with the help of bivariate and multivariate statistical methods. With this as a base, the major evolutionary patterns within *Lynx* are outlined and interpreted.

The genus *Lynx* is considered to be of African origin. Its earliest occurrence is early or mid Pliocene. This species, *L. issiodorensis*, had lynx-like dental features, but skeletally resembled *Felis*. It migrated into the Northern Hemisphere and gave rise to several species.

In Europe, *L. pardina* is a direct descendant of *L. issiodorensis*. This transition is found to have involved a gradual reduction in size and relative lengthening of M_1, through the intermediates *L.i. valdarnensis* (ssp. n.) and *L.p. spelaea*.

In Asia, *L. issiodorensis* gave rise to *L. lynx*. This latter species migrated into Europe and North America, on the latter continent giving rise to *L. canadensis*. The differences between *L. lynx* and its ancestor and descendant are studied and interpreted.

In North America, *L. issiodorensis* gave rise to *L. rufus*.

The first appearance of *Lynx* in North America coincides with a postulated 2.6 Ma. mammalian dispersal event. Other Blancan *Lynx* species are reviewed. *L. compressus* is incorporated into *L. rufus*, while *L. calcaratus* is separated into two groups, one incorporated into *L. rufus*, and the other tentatively into *F. yaguaroundi*.

The caracal differs considerably from *Lynx*, particularly in the relative size of the postorbital constriction. No evidence for a close phylogenetic relationship between *Caracal* and *Lynx* has been found.

Very little sexual dimorphism was found in *Lynx*. Geographical variation was also found to be small, and it is suggested that the subspecies of recent *Lynx* are in need of thorough revision.

Lars Werdelin, Department of Geology, University of Stockholm, Box 6801, S-113 86 Stockholm, Sweden.

1. Introduction

The lynxes are a group of felids distinguished by the following characters: tufted ears, short tail, long legs in relation to body length, and relatively small head. The major dental character used in identifying lynxes has been the absence of P^2 (Teilhard & Leroy 1945, Savage 1960). The value of this character has been lessened, however, by the demonstration by Glass & Todd (1975) that it is polymorphic in several felid species. In this study several species which retain P^2 are considered.

This study has several aims. The first is to throw light on the question of the number of recent species belonging to the genus *Lynx*, about which there has been much debate (True 1887, Ellerman & Morrison-Scott 1951, Kurtén & Rausch 1959, Kurtén 1968). An attempt is also made to trace the phyletic relationships within the

group, investigating the origins and evolution of the recent species. The several species which have been considered by various authors to be related to the group are also considered.

Further relevant comments on lynxes in general will be included in Section 3, in the introduction to each separate species.

2. Material and methods

The material studied in the present paper consists of measurements of the skull, mandible and dentition of recent and fossil specimens either belonging to the genus *Lynx* or morphologically similar to it. The variables are listed below and shown in Figure 1. Table 1 presents a list of the species included in this study, together with their code letters. The bulk of the material was measured by Dr. Björn Kurtén. Additional material was obtained from published mensurations. All measurements are in millimetres. In the original material approximately 8 % of the
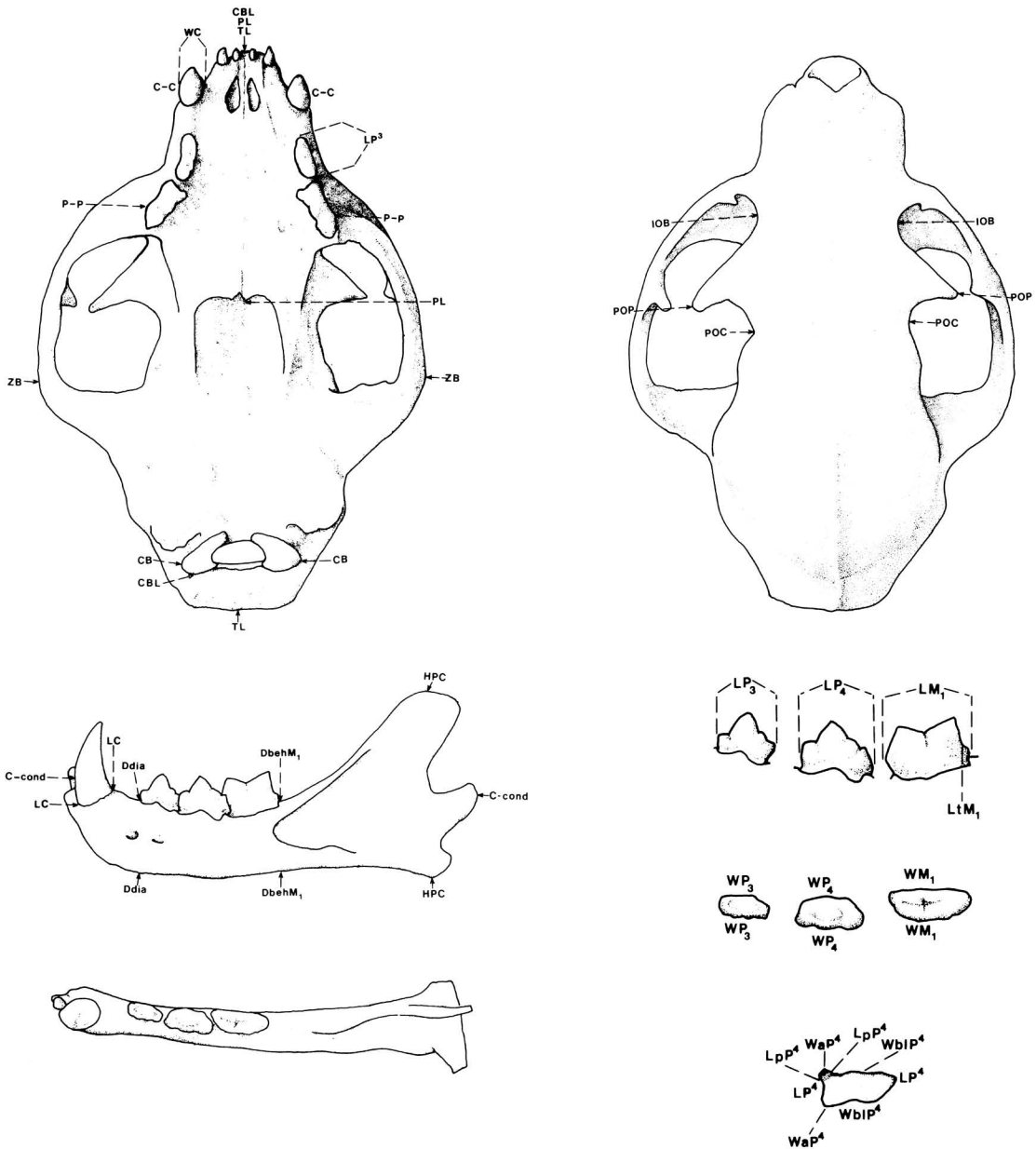
Fig. 1. Generalized skull and mandible of *Lynx*, showing points between which measurements have been made. See text for definition of measurements.

measurements used were missing. These were approximately evenly distributed throughout the material. These missing data have been added through linear regression analysis. No specimens with more than 20 % of data missing were reconstructed in this manner. This method means that the results on intraspecific variation obtained from the multivariate analyses will be slightly, but not seriously, underestimated.

2.1. Variables

Condylobasal length (CBL): Distance from anterior end
   of premaxillae to posterior end of occipital condyles.
Total length (TL): Greatest length of skull.
Palatine length (PL): Distance from prostion to nasion.
Rostral width (C-C): Width of rostrum above canines.
Carnassial width (P-P): Width across upper carnassials.

Table 1: Species studied and their codes.

Lynx lynx, recent	A
Lynx lynx, fossil	a
Lynx pardina, recent	B
Lynx pardina, fossil	b
Lynx canadensis, recent	D
Lynx canadensis, fossil	d
Lynx rufus, recent	E
Lynx rufus, fossil (Wisconsinan)	e
Caracal caracal, recent	F
Caracal caracal, fossil	f
Lynx rufus koakudsi	ek
Lynx rufus, pre-Wisconsinan	er
"*Lynx calcaratus*"	ec
Lynx issiodorensis issiodorensis	g
Lynx issiodorensis valdarnensis	h
Felis rexroadensis	r
Felis lacustris	m
Felis aff. *Felis issiodorensis*[1])	s
Felis obscura	z
Felis aff. *issiodorensis*[2])	w
Felis teilhardii	t
Felis peii	p
"*Lynx* sp. 1"	k_1
"*Lynx* sp. 2"	k_2
Lynx shansius	v
Caracal brevirostris	j
Felis christolii	y

[1]) Savage 1960.   [2]) Hendey 1974.

Zygomatic width (ZB): Width of skull across zygomatic arches.

Interorbital width (IOB): Least width between orbits.

Postorbital width (POP): Width across the postorbital processes.

Postorbital constriction width (POC): Least width across the frontals behind the postorbital processes.

Condylar width (CB): Width across occipital condyles.

Mandibular length (C-cond): Length of mandible from anterior part of canine to posterior part of condyle.

Height of mandible (HPC): Distance from lowermost tip to top of coronoid process.

Ramus depth at diastema (Ddia): Height of ramus at anterior edge of M_1.

Canine length (LCs, LCi): Distance between anterior and posterior edges of canines.

Canine width (WCs, WCi): Transverse width of canines.

Premolar length (LP^3, LP$_3$, LP$_4$): Anteroposterior length of premolars.

Premolar width (WP^3, WP$_3$, WP$_4$): Transverse width of premolars.

Length of upper carnassial (LP^4): Anteroposterior length of P^4.

Anterior width of upper carnassial (WaP^4): Width of P^4 at protocone.

Blade width of upper carnassial (WblP^4): Transverse width of blade of P^4.

Length of protocone of P^4 (LpP^4): Anteroposterior length of protocone.

Length of metastyle of P^4 (LmP^4): Anteroposterior length of metastyle.

Length of lower carnassial (LM$_1$): Anteroposterior length of M$_1$.

Width of lower carnassial (WM$_1$): Transverse width of M$_1$.

Trigonid length of lower carnassial (LtM$_1$): Distance from anterior edge of M$_1$ to posterior edge of protoconid.

2.2. Statistical methods

A number of statistical methods have been used in this paper. Apart from simple univariate t testing, bivariate and multivariate methods have been used. The bivariate regression axes have been calculated by the reduced major axis method (Miller & Kahn 1962). Two different z tests were used to determine whether axes were significantly different. That designated z_1 compares the slopes of two axes (Miller & Kahn 1962: 206, top equation), and z_2 compares the vertical difference between two lines (Miller & Kahn 1962: 206, bottom equation). All significances were taken at the 5 % level.

The multivariate methods used herein are principal components analysis and canonical variates analysis. The object of the former is to reduce a large number of correlated variables to a smaller set of uncorrelated components. After the components were extracted they were rotated, using the varimax criterion (Kaiser 1958). In the present study principal components analysis has been used to study clusters of observations and the differences separating these clusters. The mathematical background to principal components analysis is to be found in specialized texts (Harman 1967, Timm 1975). The object of canonical variates analysis is to find linear combinations of the variables which discriminate between two or more sets of observations. In this study canonical variates analysis has been used to analyse the differences between *a priori* groups of observations. The method of canonical variates analysis is described in Blackith & Reyment (1971).

The following comments are relevant to the statistical analyses. The variables have been standardized in all multivariate analyses. All components with an eigenvalue greater than one have been extracted. In tables listing principal components or canonical variates, decimal points have been omitted.

3. Intraspecific variation

Before comparisons could be made between the different species, it was necessary to determine the extent of variation within each species. Aspects included were sexual dimorphism, geographical variation and differences between fossil and recent specimens of the same species.

3.1. Lynx lynx

The northern lynx, *Lynx lynx* (L.), is a very widespread species, ranging from China in the southeast to Sweden in the northwest. In the recent past, the northern lynx was spread throughout Europe, but as a result of harassment by man its range has become restricted to heavily forested regions in the eastern and northern parts of the continent (Jonsson 1979a).

L. lynx, and in particular the Swedish population, is the largest of the recent lynxes.

Material

There were 71 specimens of *L. lynx* which were complete enough to be used in the principal components analysis. Of these 51 came from Scandinavia, nine from Finland, six from continental Europe, and five from Asia.

Only 15 fossil specimens of *L. lynx* were available for this study. Of these, eight were complete enough to be used in the principal components analysis of recent and fossil *L. lynx* together. Of these eight, three were from the Ipswichian of England, one from the Devensian of England, two from the Weichselian of Northern Europe, and one each from the Postglacial of England and Denmark.

Multivariate analysis

Four components were extracted in the principal components analysis of recent *L. lynx*. These together accounted for 77 % of the total variance. The first component has high loadings for skull and mandible variables, and lower ones for dental variables (see Table 2); this is interpreted as a component describing the size of the skull and mandible. The second component has

Table 2: Rotated component loadings for recent *Lynx lynx*.

Variable	Component			
	1	2	3	4
CBL	940	068	181	−062
TL	940	081	198	−013
PL	878	164	295	−039
C-C	885	224	120	211
P-P	799	344	052	215
ZB	965	032	070	066
IOB	930	051	−002	−016
POP	890	−041	−166	−040
POC	−139	−072	−692	−176
CB	401	161	561	−303
C-cond	924	106	244	057
HPC	891	180	218	181
DbehM$_1$	850	154	267	275
Ddia	540	420	405	146
LCs	379	487	519	361
WCs	294	430	589	401
LP^3	154	627	405	318
WP^3	307	623	223	444
LP^4	173	865	202	−023
WaP^4	224	793	160	266
WblP^4	033	651	053	335
LpP^4	014	666	448	025
LmP^4	128	878	028	−194
LCi	185	572	616	235
WCi	141	431	653	359
LP$_3$	096	482	641	117
WP$_3$	229	423	375	602
LP$_4$	101	492	595	−081
WP$_4$	043	485	175	645
LM$_1$	076	758	258	118
WM$_1$	042	759	199	359
LtM$_1$	129	788	346	209
Percent variance explained	31.2	24.5	13.8	7.3

Table 3: Values of t for groups of *Lynx lynx* which differ from each other in the principal components analysis.

Groups compared	t	df	Component
Cont. Europe/S. Sweden	4.443	18	3
Cont. Europe/C. Sweden	3.978	22	3
Cont. Europe/N. Sweden	3.430	13	3
Cont. Europe/Finland	2.468	13	3
Asia/S. Sweden	6.420	17	3
Asia/C. Sweden	5.639	21	3
Asia/N. Sweden	4.970	12	3
Asia/Finland	4.009	12	3
S. Sweden/C. Sweden	2.385	30	4
S. Sweden/Finland	2.945	21	4
Cont. Europe/C. Sweden	2.878	22	4
Cont. Europe/Finland	3.193	13	4

high loadings for dental variables, and lower ones for skull and mandible variables; this is interpreted as describing the size of the teeth. The third component has high loadings for the length and width of the upper and lower canines, lengths of P^3, P$_3$, P$_4$ and protocone of P^4, CB, Ddia, and a high negative loading for POC. The fourth component has high loadings for the widths of P^3, P$_3$ and P$_4$. This means that specimens with high component scores for the third component will have long teeth and a low value for POC, while specimens with high component scores for the fourth component will have broad teeth.

Specimens from six different geographical regions were compared for differences in the four components. These regions were: northern Sweden, central Sweden, southern Sweden, Finland, continental Europe and Asia.

No differences were found between the different subsamples in the first and second components. In the third component the subsamples from continental Europe and Asia differ significantly from those of Sweden and Finland (Table 3). In the fourth component the subsamples from southern Sweden and continental Europe differ from those of central Sweden and Finland (Table 3). These two components are illustrated in Fig. 2. Morphologically the results indicate that specimens from continental Europe and Asia have shorter teeth and greater POC values than specimens from other regions, while specimens from southern Sweden and continental Europe have broader molars than specimens from other regions. From an evolutionary viewpoint the results corroborate the conclusions of Kurtén (1967). He suggested that the Swedish *L. lynx* population may have immigrated from two regions, from the north via Finland and from the south via Denmark. This conclusion is supported
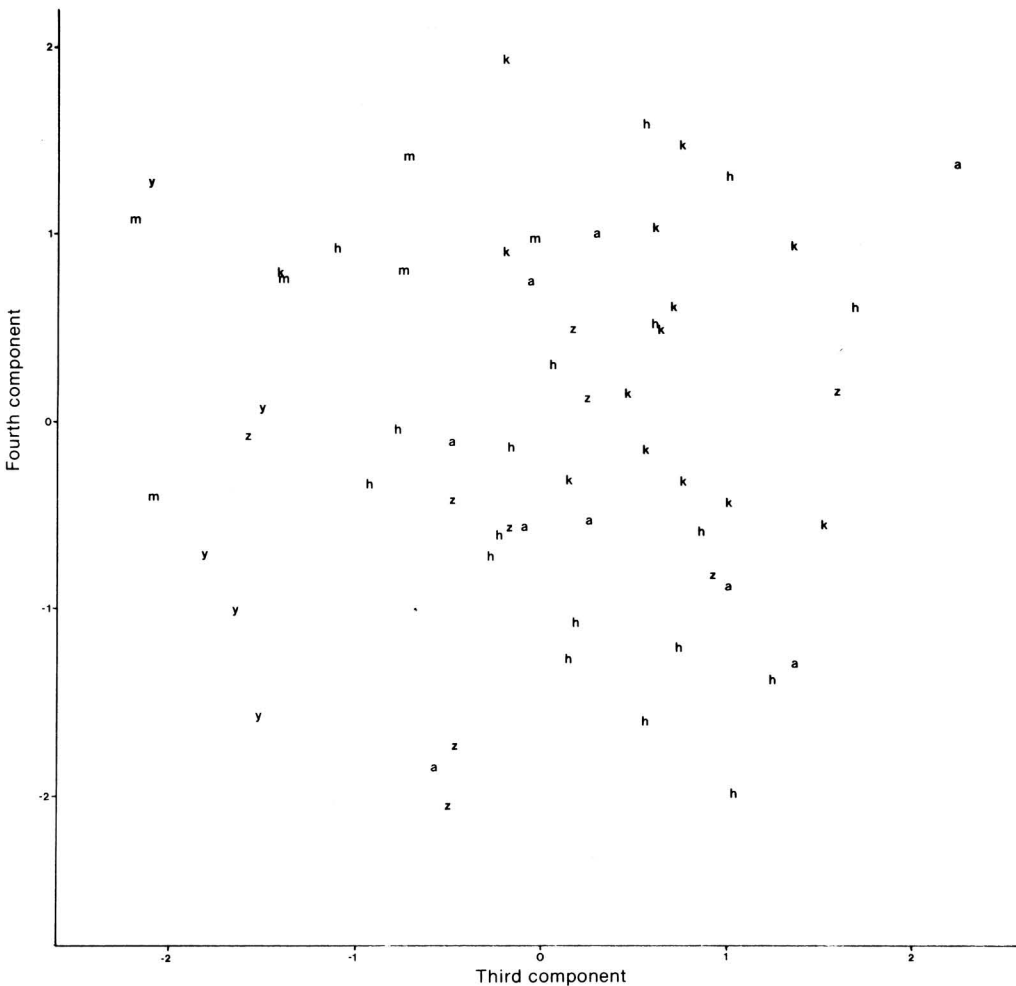
Fig. 2. Principal components analysis of recent *Lynx lynx*, third component against fourth component. a = N. Sweden, h = C. Sweden, k = S. Sweden, m = Cont. Europe, y = Asia, z = Finland.

by the affinities found in this study between Finnish and northern Swedish, on the one hand, and between southern Swedish and continental European lynxes, on the other.

The principal components analysis of recent and fossil *L. lynx* used nine variables, all from the lower dentition. One component was extracted, accounting for 64 % of the total variance. This component has high loadings for all variables, and is therefore interpreted as a general size component. (Table 4). Differences were found between the recent specimens from continental Europe and Asia, on the one hand, and all other subsamples except the Finnish one, on the other. Recent European and Asian specimens tend to have smaller lower teeth than do fossil specimens

Table 4: Rotated component loadings for recent and fossil *Lynx lynx*.

Variable	Component 1
LC_i	874
WC_i	864
LP_3	729
WP_3	743
LP_4	643
WP_4	771
LM_1	821
WM_1	863
LtM_1	853
Percent variance explained	63.7

Table 5: Groups of *Lynx lynx* which differ in the principal components analysis of recent and fossil specimens.

Groups compared	*t*	df
Cont. Europe/N. Sweden	2.160	13
Cont. Europe/S. Sweden	3.776	18
Cont. Europe/Fossil	2.495	13
Asia/N. Sweden	3.534	12
Asia/C. Sweden	2.999	21
Asia/S. Sweden	6.077	17
Asia/Fossil	3.306	12

and recent specimens from Sweden. Results of the *t* tests for difference of means of component scores are presented in Table 5.

Bivariate analysis

L. lynx has already been studied extensively by Kurtén & Rausch (1959), and Kurtén (1967), using bivariate methods. Guided by these studies and by the principal components analysis of the previous section I made a number of bivariate plots, but no new results emerged. For this reason I choose not to elaborate on them, but instead refer the reader to the above-mentioned studies by Kurtén and Rausch, and Kurtén.

Univariate analysis

A few plots were made to see whether any sexual dimorphism existed. These plots showed that males tend to be larger, but in no case was the difference statistically significant. It therefore seems that *L. lynx* is the least sexually differentiated of the lynxes (see sections on sexual dimorphism in the other species studied).

Conclusions

Principal components analysis was used to compare specimens from six different geographical regions. It was found that the specimens from Sweden and Finland differ from those of continental Europe and Asia. Specimens from the two latter regions have smaller and, particularly, shorter lower teeth than specimens from the other regions. Further, the specimens from southern Sweden and continental Europe differ from those of central and northern Sweden, Finland and Asia. These differences support Kurtén's (1967) hypothesis concerning the migratory pattern of *L. lynx* in the

Postglacial. The fossil specimens have larger lower teeth than those from continental Europe and Asia, but do not differ significantly from the Swedish and Finnish specimens.

3.2. Lynx canadensis

Apart from the northern lynx, the Canada lynx, *Lynx canadensis* Kerr, is probably the best known of the lynxes. Many studies have been concerned with the abundance of this species, and its dependence on the snowshoe hare, one of the best-known examples of prey-dependent abundance (see Pianka 1978, and references given by him).

The range of the Canada lynx extends from the northern United States northward through Canada and Alaska. Two subspecies are recognized (Hall & Kelson 1959), *L.c.canadensis* and *L.c.subsolanus*. The latter is known only from the Newfoundland area. The former occupies the rest of the species range. No specimens of *L.c.subsolanus* were available to me, for which reason the status of this subspecies is not further discussed here.

Material

The recent material of *L. canadensis*, 50 specimens, is essentially the same as that used by Kurtén and Rausch (1959). Most of the specimens were collected by them, but 13 specimens were taken from Merriam & Stock (1932). All but five of the specimens measured by Kurtén and Rausch come from Alaska, the remaining five being from the northern United States. Merriam and Stock do not state the provenance of their material, but it is assumed to be from Canada.

Fossil material of *L. canadensis* is very scarce, so scarce that it was not possible to use it in the multivariate analysis. The material at my disposal included only five fragmentary specimens. One of these, a fragmentary P$_4$, was of little use in this study. The remaining four, all of which are incomplete mandibles, come from the Wisconsinan. In view of this scarcity of material it is very difficult to make any definite statements about the fossil history of *L. canadensis*. The comments made below and elsewhere on this topic are tentative.

Multivariate analysis

As stated earlier, no fossil specimens were used in this analysis. In the analysis of recent material, 25 variables were used.

In the principal components analysis, three components were extracted, together accounting for 73 % of the total variance. The first component

Table 6: Rotated component loadings for *Lynx canadensis*.

Variable	Component		
	1	2	3
CBL	923	175	038
PL	827	180	029
C-C	788	362	361
P-P	757	317	314
ZB	945	076	181
IOB	869	103	190
POC	−542	009	355
C-cond	938	178	123
HPC	911	111	110
DbehM$_1$	888	060	104
LCs	477	648	198
WCs	552	505	334
LP^3	274	816	190
WP^3	278	587	544
LP^4	040	861	000
WaP^4	139	786	092
LCi	262	668	393
WCi	378	560	304
LP$_3$	247	723	223
WP$_3$	425	307	747
LP$_4$	−010	879	064
LM$_1$	−085	675	439
WM$_1$	041	490	495
LtM$_1$	124	687	· 273
Percent variance explained	33.6	27.9	11.3

has high loadings for skull and mandible variables and for the length and width of the upper canine. The second component has high loadings for the dental variables, the loadings for the lengths of the lower molars being slightly lower than the rest. The third component has high loadings for the widths of P$_3$, P$_4$ and P^3 (Table 6).

Merriam & Stock do not state where their material came from, and therefore it was not possible to study differences between specimens from different geographical regions. Most of the specimens used in this study were sexed, but no systematic differences between male and female specimens were detected. No other systematic variation has been traced either, and this principal components analysis permits no definite comments on intraspecific variation in *L. canadensis*.

Bivariate analysis

A number of bivariate plots were made of the teeth and other variables. In none of these is there any indication of a difference between the specimens from Alaska and those listed by Merriam & Stock. Nor do the specimens from the northern United States show any systematic differences

from the Alaska material. As far as this analysis goes, *L. canadensis* is a very homogeneous species.

The few fossil specimens available were also included in the bivariate analysis. They display no characteristics to set them apart from the recent specimens. This scanty material thus gives the impression that *L. canadensis* has not changed significantly since its first recorded appearance.

Univariate analysis

Even though multivariate analysis gave no indication of any sexual dimorphism, a few variables were examined for such differences. Because the provenance of Merriam and Stock's material is unknown, this was not used. the material used was that of Kurtén and Rausch from Alaska, which includes 14 males and 21 females. Significant differences between males and females were found for the length of the upper canine ($t = 3.184$, df $= 32$), the width of the upper canine ($t = 3.719$, df $= 32$), and the length of the lower canine ($t = 3.204$, df $= 31$). In all cases males were larger.

Conclusions

L. canadensis seems to be a very homogeneous species, and on the basis of the present evidence does not appear to have changed significantly since its first recorded appearance. No undoubted *L. canadensis* specimens older than the Wisconsinan have been found. This evidence supports the suggestion of Kurtén and Rausch (1959) that *L. canadensis* is the result of immigration from Eurasia during either the Riss of Würm glaciation. More will be said on this matter when the phylogeny of the lynxes is discussed.

3.3. Lynx pardina

The Spanish or pardel lynx, *Lynx pardina* Temminck, is closely related to *L. lynx* in general morphology. It was formerly distributed throughout Spain and southern France, but today it is restricted to the Coto Doñana wildlife reserve in Andalusia, Spain. The ecology of the Coto Doñana lynxes has been studied by Valverde (1959). The number of Spanish lynxes remaining has been estimated as 150—200 (Fitter & Leigh-Pemberton 1968), and more recently as 30—40 (Salvadori & Florio 1978). This small number of specimens (the animal is seriously threatened by

extinction) means that the current population may be subject to genetic drift, as described by Todd (1965) for the Gir lions. My specimens are from the turn of the century, when there was still a sizeable population, so genetic drift should not be a problem here.

In appearance L. pardina resembles L. lynx. It differs chiefly in being smaller and more heavily spotted, and in the shape of the "beard". Doubt as to the exact classification of the Spanish lynx has remained ever since Ellerman & Morrison-Scott (1953) placed it as a subspecies of L. lynx. I hope to show in this paper that the Spanish lynx merits specific distinction.

Material

The recent material of L. pardina consisted of only 14 specimens, all from Spain. Of these, 11 were complete enough to be used in the multivariate analysis. The remaining three were incomplete, and were used only in the bivariate and univariate analyses.

The fossil material was more extensive. Only lower dentition data were complete enough, however, to be used in the multivariate analyses. There are a total of 25 specimens, of which 15 were used in the multivariate analyses. All the specimens are from either the Iberian peninsula or the French Pyrenées. They are all late Pleistocene in age, none being older than the Eemian.

In addition to the above-mentioned specimens, two specimens from the Cromerian of Germany, and four from the Holsteinian of France were studied in the bivariate analysis for comparison with L. pardina. These specimens have been suggested to be intermediate between L. issiodorensis and L. pardina.

Multivariate analysis

A principal components analysis was carried out on recent and fossil L. pardina. Only variables from the lower dentition were used. One component, interpreted as a general size component, was extracted (Table 7). The component shows high loadings for all variables except the width of the lower first molar. As seen from the correlation matrix, this variable shows low correlations with the other variables. Thus the width of the lower molar is only moderately size-correlated.

The fossil specimens of L. pardina tend to have higher component scores than the recent ones. The difference is highly significant ($t = 5.443$, df = 24). This corroborates the opinion of Boule (1910), who placed the fossil specimens of L. pardina in a separate subspecies, L.p.spelaea. This is a temporal subspecies, larger than the recent L.p. pardina, and smaller than L. issiodorensis. Size reduction is characteristic of many animals

Table 7: Rotated component loadings for recent and fossil Lynx pardina.

Variable	Component 1
LC_i	904
WC_i	908
LP_3	926
WP_3	893
LP_4	806
WP_4	881
LM_1	960
WM_1	434
LtM_1	944
Percent variance explained	74.6

during the Holocene, and is very clear in this species.

Bivariate analysis

In all variables studied, L.p.spelaea is larger than L.p.pardina. Owing to the small number of specimens available, very few pairs of variables showed significant correlations for both subsets. This means that very few regression lines could be directly compared. In only two cases is the difference between the regression lines significant. These are LP^4/WaP^4 ($z_2 = 3.551$), which shows that the upper carnassial is relatively wider in the recent specimens, and LM_1/LP_4 ($z_2 = 4.078$), which shows that recent specimens have a relatively shorter M_1 and longer P_4 than the fossil specimens.

The bivariate plots also show that the four Holsteinian specimens are very similar to L.p. spelaea, and I suggest that they may be classified with this species (Figs 3, 4). This makes them the oldest representatives of the species. The two Cromerian specimens, on the other hand, differ clearly from L.p.spelaea. They will be considered further below.

Univariate analysis

Owing to the small number of specimens, the results of a study of sexual dimorphism are highly equivical. Eleven specimens were sexed. Of these, eight were male and only three female. The means of the two groups were compared in t tests. Only two differences were found to be significant: LC_s ($t = 2.844$, df = 9) and LP^4 ($t = 3.288$, df = 9). In both cases the males were larger. In neither case is the difference large enough to warrant any
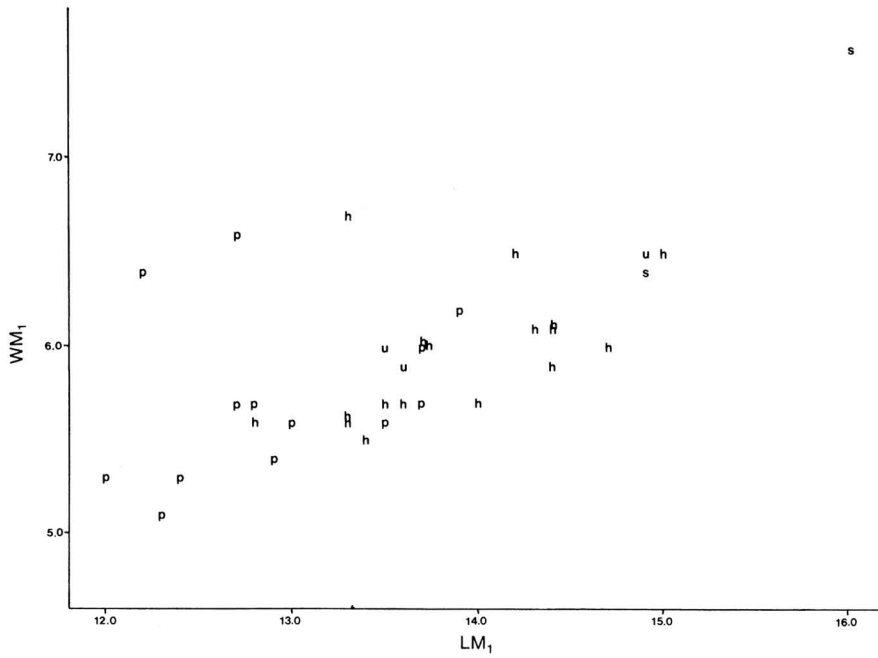
Fig. 3. Plot of length/width relationship of M_1 in *Lynx pardina*. p = recent *L.p. pardina*, h = fossil *L.p. spelaea*, u = Holsteinian specimens, s = Cromerian specimens.
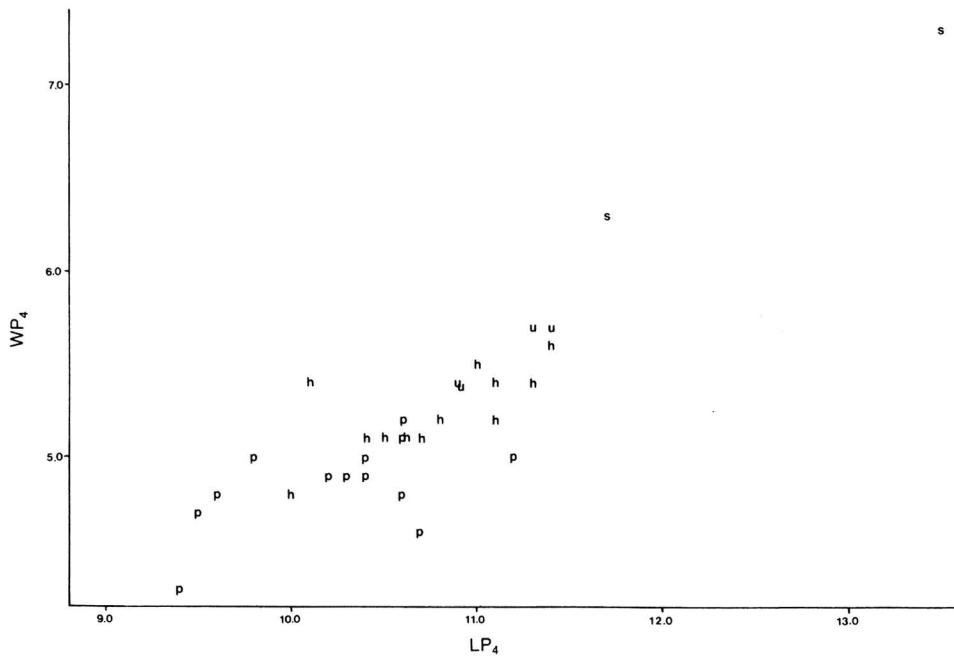

Fig. 4. Plot of length/width relationship of P_4 of *Lynx pardina*. For code, see Fig. 3.

conclusions regarding the sex of the fossil specimens, which in any case are much larger. It appears unlikely, however, that L.p.spelaea could be sexed on the basis of tooth morphology alone.

Conclusions

The significant difference in size found between the recent subspecies, L.p.pardina, and its fossil predecessor, L.p.spelaea, is fully consistent with the creation of a temporal subspecies by Boule (1910). The phyletic importance of this morphological change will be discussed later in this paper.

The dearth of material of this species rules out a study of the variation of the recent populations beyond what has been said in Section 2.3.5. If and when more material becomes available, important areas of study would be sexual dimorphism, habitat-related variation, and the differences between the recent and fossil subspecies.

3.4. Lynx rufus

In skull size the bobcat, Lynx rufus (Schreber), is the smallest of the recent species of lynx. Its present range extends through the United States and northwards into Canada. This large area of distribution shows that L. rufus has adapted to a wide range of environments, from subtropical swamps and forests in Florida to arid areas in the southwest and to temperate forest in the north. L. rufus is the only lynx known to exhibit melanism (Ulmer 1941).

On account of the wide range of L. rufus, the species has been separated into many subspecies. The eastern subspecies were revised by Peterson & Downing (1953) and the Californian ones by Grinnell and Dixon (1926). At present 11 subspecies are recognized (Hall & Kelson 1959). These are: L.r.floridanus, L.r.pallescens, L.r.baileyi, L.r.californicus, L.r.rufus, L.r.gigas, L.r.texensis, L.r. escuinapae, L.r.peninsularis, L.r.fasciatus and L.r. superiorensis. The first four of these are represented in the present study. They will be compared in order to determine whether they deserve subspecific rank on the basis of skull and tooth morphology. Of the four, L.r.floridanus is found in Florida and the neighbouring states, and the other three are found in the California area. From its geographical distribution, L.r.floridanus might be expected to differ most from the others. Besides these four subspecies, one specimen each of L.r.rufus and L.r.escuinapae were available for study. As this is obviously not sufficient for a de-

termination of the status of either of these subspecies, they were omitted from the multivariate analysis. They were, however, included in the bivariate study, in which the patterns of variation between recent and fossil L.rufus were investigated.

Material

A total of 61 specimens of recent L. rufus were available for study. The recent material from Florida comes from various localities in that state. The data on Californian lynxes are from Merriam & Stock (1932). Although the authors do not state the exact provenance of their material, it was subspecifically determined.

The fossil material comes from many different localities in all parts of the United States, and from as far south as Nuevo Léon, Mexico. It varies temporally from the late Blancan to the Postglacial. Most specimens are from the Wisconsinan. In the fossil material only variables from the lower dentition were used in the multivariate analysis. It might have been possible to use the upper dentition as well. but many additional data would then have been missing and estimation of these by regression analysis would have increased the error considerably.

Multivariate analysis

In the principal components analysis of recent L. rufus, 50 specimens were used, each measured for 28 variables. In this analysis four components were extracted, together accounting for 79 % of the total variance (Table 8). The first component reflects the size of the skull and mandible, and the cross-sectional area (defined as length times width) of the upper and lower canines. The second component is related to the size of the teeth, except for the lengths of the upper and lower carnassials. The third component reflects the cross-sectional area of the canines, and the lengths of the carnassials. The fourth component reflects variation in some variables in the orbital region of the scull: POC, POP and IOB.

It should be said that, as the component loading patterns are not very clear, the interpretations of components 2—4 are tentative. I have retained these interpretations partly because they do separate between subspecies.

The results of the principal components analysis do not admit of any ecological interpretation at the present time. L. rufus has been studied too little in this respect to justify such an attempt. When more is known, for example, about the prey preferences of this species in different habitats, such an interpretation may become possible.

Table 8: Rotated component loadings for recent *Lynx rufus*.

Variable	Component			
	1	2	3	4
CBL	844	344	281	—021
TL	863	381	242	005
PL	876	191	282	027
C-C	668	155	514	341
ZB	846	316	226	263
IOB	685	—022	178	566
POP	704	049	127	537
POC	006	089	053	885
CB	556	302	—112	211
C-cond	841	404	278	042
HPC	876	291	172	—007
$DbehM_1$	672	489	242	114
Ddia	626	259	441	050
LCs	500	515	536	037
WCs	569	510	479	019
LP^3	349	640	326	329
WP^3	145	874	198	—007
LP^4	376	290	737	107
WaP^4	155	683	494	131
LpP^4	150	152	826	—058
LCi	476	514	526	048
WCi	616	390	489	065
LP_3	276	719	214	143
WP_3	355	868	072	—019
LP_4	248	710	414	225
WP_4	322	787	306	—135
LM_1	157	271	807	149
WM_1	262	474	—004	382
Percent variance explained	32.0	23.1	16.3	7.3

Principal components analysis shows that *L.r. floridanus* is, in fact, the subspecies which differs most from the others. This is particularly evident from the fourth component, for which *L.r. floridanus* shows significantly lower component scores than either of the other three subspecies ($t = 4.302$, $df = 22$ when compared to *L.r. pallescens*, $t = 4.030$, $df = 23$ when compared to *L.r. baileyi*, and $t = 3.776$, $df = 21$ when compared to *L.r. californicus*). *L.r. floridanus* also differs from *L.r. pallescens* in the first component ($t = 2.866$, $df = 22$). These results are shown in Figure 5. *L.r. pallescens* differs from *L.r. baileyi* and *L.r. californicus* in component two ($t = 2.554$, $df = 25$ and $t = 2.145$, $df = 23$, respectively). This is illustrated in Fig. 6. *L.r. pallescens* also differs from *L.r. californicus* in the first component ($t = 2.560$, $df = 23$). *L.r. baileyi* and *L.r. californicus* do not differ from each other in any of the four components.

In the principal components analysis of both fossil and recent *L. rufus*, only six variables were used. These were measurements of the lower dentition, excluding the lower canine. It is regrettable that so few variables were used, but the specimens, though numerous (50), were mostly fragmentary. The majority included only P_3—M_1, and were broken off anteriorly and posteriorly.

In this analysis only one component was considered useful. This component, which explains 68 % of the total variance, is interpreted as a general size component. The component loadings for the length and width of M_1 are slightly lower than the rest, however (Table 9). This indicates that a larger proportion of the variation in size of M_1 is growth-free than is the case with P_3 and P_4. The recent and fossil specimens differ significantly in their mean component scores ($t = 2.536$, $df = 101$), the fossil specimens being larger.

In the principal components analysis, all fossil *L. rufus* were lumped together. In order to discover whether this was justified, they were separated into two groups in the bivariate analyses described below. The regression axes were calculated from the Wisconsinan specimens, and the pre-Wisconsinan specimens were compared with these axes.

Bivariate analysis

No separate bivariate analysis of the recent subspecies was carried out, as the principal components analysis was felt to be sufficiently detailed in this respect.

There are only three cases in the bivariate analysis in which recent and fossil *L. rufus* differ significantly. In the plot of $LP^4/WblP^4$ ($z_2 = 2.864$) (Fig. 18) the growth patterns differ, small fossil specimens having a narrower blade of P^4, whereas in large specimens the blade widths are nearly equal in the two groups. Secondly, in the plot of LP^3/WP^3 (Fig. 19, $z_2 = 4.189$) fossil *L. rufus* have a wider P^3 than recent specimens. Thirdly, in the plot of C-cond/HPC (Fig. 25, $z_1 = 2.961$) large specimens of fossil *L. rufus* have a relatively higher coronoid process than recent ones.

Table 9: Rotated component loadings for recent and fossil *Lynx rufus*.

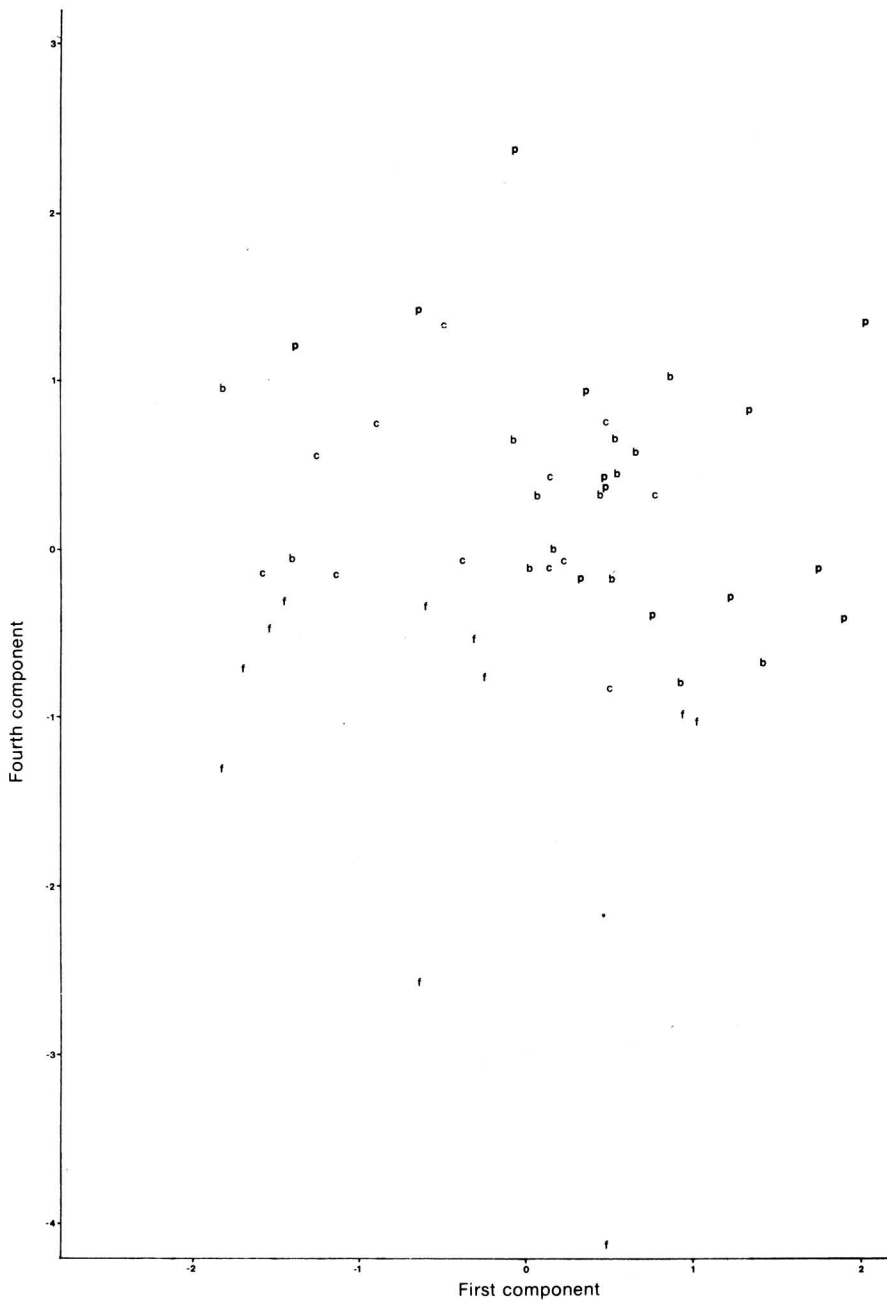| Variable	Component 1
LP_3	866
WP_3	884
LP_4	871
WP_4	899
LM_1	761
WM_1	641
Percent variance explained	68.1

Fig. 5. Principal components analysis of recent *Lynx rufus*, first component against fourth component. f = *L.r. floridanus*, p = *L.r. pallescens*, b = *L.r. baileyi*, c = *L.r. californicus*.

Comparison of the pre-Wisconsinan *L. rufus* with the other fossil specimens and with the recent specimens showed that those specimens which were classified as *L. rufus* by their describers deviate very little from the two comparison groups. Thus, the analysis bore out their taxonomic status. Among these specimens may be noted the *L.* cf. *rufus* of Savage (1960) and the *L.* cf. *rufus* of Brown (1908). Other early specimens which do not differ appreciably from the later fossil or
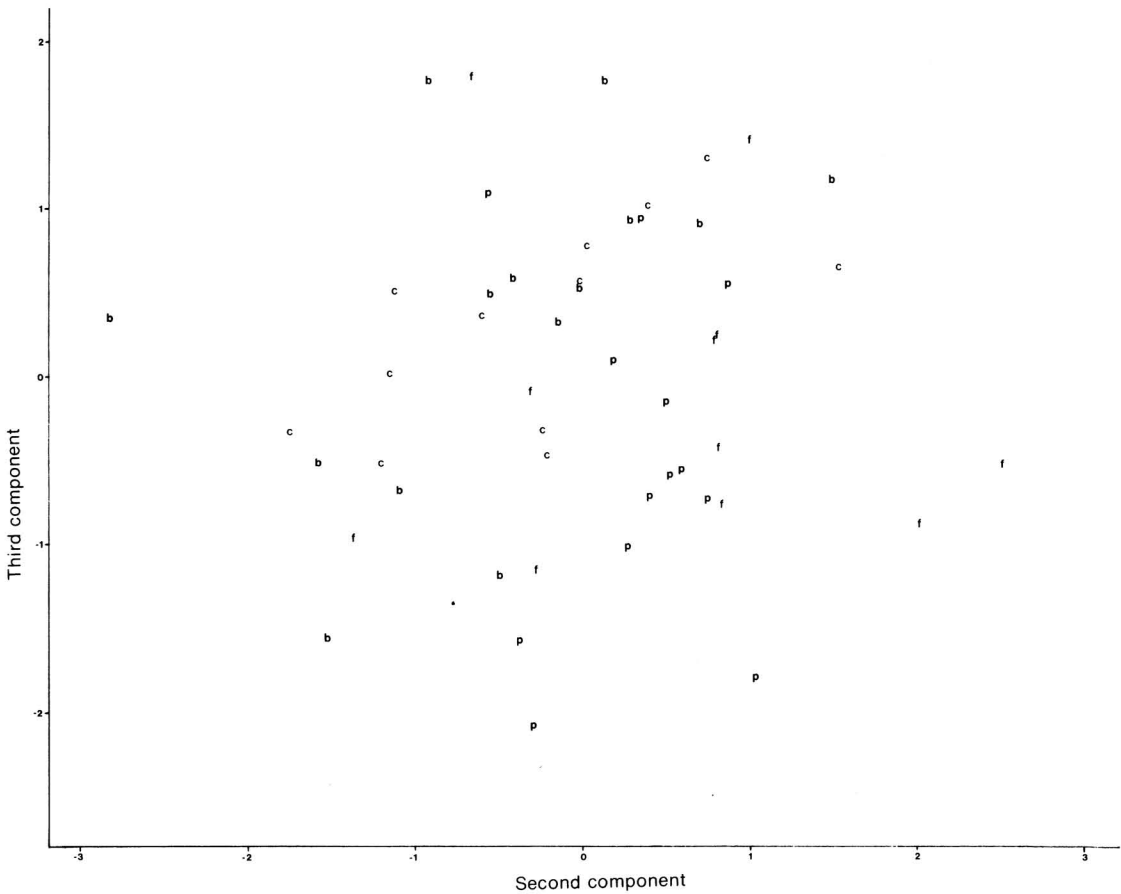
Fig. 6. Principal components analysis of recent *Lynx rufus*, second component against third component. For code, see Fig. 5.

recent *L. rufus* are the specimens described by Brown (1908) as *L. compressus*. Even in the diagnostic feature cited by Brown (WaP⁴) the type specimen of *L. compressus* remains clearly within the range of both recent and fossil *L. rufus* (Fig. 17).

There are, however, at least two groups of specimens which do differ distinctly from the later fossil and recent *L. rufus*. These are *L.r.koakudsi*, described by Kurtén (1965), and the group of specimens described by Cope (1899) as *L. calcaratus*. *L.r.koakudsi* differs in having a very long P⁴, with a very narrow blade (Fig. 18). Other distinctive features of this subspecies are described in Kurtén (1965). This brings us to the problem of *L. calcaratus*. First of all it appears that Cope's material includes two quite different groups of specimens. The two mandibular fragments, of which the type specimen is one, are equal in size to the largest fossil *L. rufus*, while the four maxillary

fragments are equal in size to the smallest fossil specimens of *L. rufus*. Of the two mandibular fragments one (the type specimen) has a long and narrow P₄ but is within the range of fossil *L. rufus* (Fig. 14). In all other variables studied these two specimens lie close to the regression lines calculated for *L. rufus*. The maxillary fragments, on the other hand, have one feature in which they differ markedly from other *L. rufus*: in these specimens the P³ is very short (Fig. 19).

One aspect of the pre-Wisconsinan specimens remains to be discussed, and that is the difference, mentioned above, between the mandibular and maxillary fragments described by Cope. From the discussion above it is clear that they do not belong to the same individuals. Is there, then, any possibility of finding specimens of mandibles and maxillaries which may be more definitely associated than the groupings by Cope? In fact there is. Cope described two mandibular fragments

from Port Kennedy Cave under the name of *Felis eyra*, jaguarundi. These are about the same size as the *L. calcaratus* maxillae, and do not differ noticeably from the *L. rufus* regression lines. I suggest therefore that the *L. calcaratus* maxillae may be associated with the "*F. eyra*" mandibles. Whether these specimens are to be classified as *L. rufus* or *F. yaguaroundi* is a matter which cannot be fruitfully discussed here.

Univariate analysis

No univariate analysis was carried out for *L. rufus*. I felt that the variation between the different subspecies would obscure any sexual dimorphism which might exist. Such an analysis cannot be carried out for each subspecies separately either, as the samples then become too small for statistical analysis.

Conclusions

In the course of many investigations, *L. rufus* has been separated into a number of subspecies, some of which have been studied here. One of them, *L.r.floridanus*, shows clear differences from the others. To a lesser degree, so does another, *L.r. pallescens*. I have failed, however, to find any differences between the two remaining subspecies, *L.r. baileyi* and *L.r.californicus*. This suggests that certain of the subspecies now accepted may be valid, while others are more questionable. Our knowledge of *L. rufus* would benefit greatly from a thorough revision of the currently recognized subspecies.

Analysis of skull and tooth variation in fossil and recent *L. rufus* indicates that the species has undergone a slight but significant size reduction in the Holocene. Apart from this the most noteworthy difference between recent and fossil *L. rufus* lies in the wider P^3 of the latter group. This is interesting, as this trend is the opposite of that seen in *L. lynx*. Comparison of Wisconsinan and pre-Wisconsinan *L. rufus* showed that while some of the early specimens are very similar to the later ones, others differ to a greater or lesser degree. Evidence presented here indicates that *L. compressus* is not a tenable species, but should be subsumed under *L. rufus*. *L.r.koakudsi* appears to be a valid subspecies. The status of *L. calcaratus*, on the other hand, is more equivocal. The type specimen and the other mandibular fragment appear to be normal *L. rufus*. The maxillary fragments may be either a subspecies of *L. rufus*, or

may be *F. yaguaroundi*. At present I do not have enough material of the latter species to settle the matter.

3.5. Caracal caracal

In external appearance the desert lynx, *Caracal caracal* (Schreber) differs strikingly from the other species included in this study. It has a sand-coloured fur lacking spots, and it also lacks the bushy "sideburns" characteristic of the lynxes. Both these differences can probably be explained by the differences in habitat between the caracal and the other species. The caracal inhabits arid and semi-arid regions of Africa and western Asia, where the spotted fur of forest cats is useless as camouflage. A sand-coloured fur, on the other hand, offers excellent camouflage and is seen in another savannah-inhabiting cat, the lion. The "sideburns" may be a disadvantage in the hot savannah climate, and may also be lost. Both of these effects can be seen to a lesser degree in *L. rufus*, where individuals inhabiting hot, dry regions have a less dense and less clearly spotted fur than those of forest regions. In other external characteristics the caracal is similar to the other species considered here. It has ear-tufts, long legs, a small skull and a tail which, though not as short as in the other species, is shorter than in typical felids. The question I shall attempt to answer is whether the caracal is related to the other species included in this study, or whether the above-mentioned characteristics are due to convergence or parallelism.

The caracal is found throughout the semi-arid regions of Africa and the Middle East, as far east as the Kutch region of western India. A number of subspecies have been described within this range, but the material available has not permitted a study of the variation between these subspecies.

Material

The material pertaining to this species consisted of 29 recent and 12 fossil specimens. Of these, 26 recent and 10 fossil specimens were used in the multivariate analysis. All the specimens were measured by Kurtén, except for two taken from Hendey (1974). The fossil material comes from only two localities. That measured by Kurtén comes from Palikao-Ternifine in Algeria, a locality noted for its finds of *Homo erectus*. This locality is Mindelian in age. The other specimens are from Elandsfontein in South Africa. One specimen is of Florisian age, whilst the other is slightly younger (Hendey 1974).

Multivariate analysis

In the principal components analysis of recent *C. caracal* four components were extracted. Together they account for 84 % of the total variance. These components are shown in Table 10. The first component is interpreted as a general size component of skull and mandible. The second component has high loadings for the lengths and widths of P^3, P_3 and P_4, and the width of P^4. The third component has high loadings for the length and width of M_1 and the length of P^4. The fourth component has high loadings for the upper and lower canine and the length of P_4, and a high negative loading for the POC.

As was the case with *L. rufus*, components 2—4 are only tentatively interpreted, and comments about them should be taken as suggestions only. The following points should nevertheless be noted. The POC has a high negative loading in the fourth component (as will become apparent in the discussion of interspecific variation, in Section 3, this is a most important variable in connection with *C. caracal*), and the length and width of P^4 have been disassociated from each other. The width of P^4 in *C. caracal* is also important to the discussion of interspecific variation.

One particular specimen is worth mentioning in connection with the first component. This is the only specimen available of the subspecies *C.c. damarensis*. It has a very high component score for the first component, and thus a very large skull and mandible. The large skull is one of the diagnostic characters of the subspecies (Roberts 1926).

Apart from the species mentioned above, the specimens show no systematic variations, either when grouped into different geographical regions or when grouped according to sex. The main reason is probably that the samples became very small in such groupings. More material is needed before the intraspecific variation of *C. caracal* can be fully elucidated.

In the principal components analysis of recent and fossil *C. caracal*, seven variables were used. These were variables of the lower dentition, excluding the canine. One component was extracted, explaining 71 % of the total variance. This is interpreted as a general size component, as all variables show high loadings. Once again there were no systematic differences within the material. Recent and fossil specimens do not differ significantly from each other ($t = 1.169$, df $= 34$). As the sample of fossil *C. caracal* is small, it is impossible to decide whether this similarity is real or apparent, although if any difference does exist, it cannot be very large.

Table 10: Rotated component loadings for recent *Caracal caracal*.

Variable	Component			
	1	2	3	4
PL	794	223	161	405
C-C	800	281	310	339
P-P	785	362	376	005
ZB	918	248	130	145
IOB	937	—077	—018	—014
POP	943	034	098	—066
POC	101	—395	242	—718
CB	758	224	309	048
C-cond	891	190	194	317
DbehM$_1$	843	372	071	249
Ddia	638	344	266	433
WCs	435	—134	083	748
WP^3	038	878	338	065
LP^4	189	489	707	339
WaP^4	184	698	360	247
WblP^4	360	579	358	316
LpP^4	163	089	895	—054
LmP^4	028	447	721	224
LCi	497	261	438	563
LP$_3$	282	588	284	479
WP$_3$	251	813	363	087
LP$_4$	245	605	274	500
WP$_4$	289	908	117	—003
LM$_1$	325	455	743	—035
WM$_1$	284	434	789	—014
Percent variance explained	32.5	22.2	17.7	11.5

Bivariate analysis

There is nothing in the bivariate analysis to show whether recent and fossil *C. caracal* are in any way different. This suggests that this species has remained unchanged, at least with regard to the variables studied here, since the Mindelian.

Univariate analysis

Univariate analysis of *C. caracal* shows that, yet again, the teeth which differ most between the sexes are the canines. In the length of both the upper canine ($t = 2.896$, df $= 12$) and the lower canine ($t = 2.881$, df $= 11$) the male specimens have a larger average value. In view of the small number of specimens sexed (nine males and six females) no further study was made of sexual dimorphism in *C. caracal*. The above results suggest that when more sexed specimens become available, such a study may be profitable.

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Conclusions

The above results show that the material examined is best considered as one sample. The variation which exists is mainly individual. There are no significant differences between the recent and fossil specimens, nor between specimens from different geographical areas. This is a negative result from the viewpoint of intraspecific variation, but is a highly useful one for the study of interspecific variation in Section 3. In that and subsequent sections, the taxonomic status of the caracal will be discussed.

3.6. Lynx issiodorensis

The great Issoire lynx, *Lynx issiodorensis* (Croizet & Jobert) was first described from Mt.Perrier, France. Since that time it has been found at a number of localities throughout the northern hemisphere, and possibly also in South Africa (Hendey 1974). These localities range from the early Pliocene to the late Villafranchian.

Kurtén (1968, 1978) has shown that *L. issiodorensis* is of prime phyletic importance within the lynx group. He suggests that it is ancestral to *L. lynx* and *L. canadensis*. I will argue in this paper that it is also ancestral to *L. pardina* and *L. rufus*. This makes *L. issiodorensis* the pivotal point in the phylogeny of the lynxes.

Although the present study is not directly concerned with the post-cranial skeleton of the lynxes, a few words about this aspect of *L. issiodorensis* seem appropriate here. The post-cranial skeleton of the lynxes has been studied comprehensively by Kurtén (1978). He has shown that in this respect *L. issiodorensis* differs more from the recent lynxes than it does in the skull and dentition. The fossil species did not have the long legs characteristic of recent lynxes, and therefore resembled the ordinary felids in appearance. The skull is also much larger relative to the body than in recent lynxes. For a reconstruction of *L. issiodorensis*, see Kurtén (1978).

Material

The material used here comes from a number of sites in the northern hemisphere. All the specimens have been measured by Kurtén.

Besides the specimens studied and described as *L. issiodorensis* by previous authors (Schultz & Martin 1972, Glass & Martin 1978, Kurtén 1978), two specimens from the Cromerian of Europe have been included in this study. These are mentioned by Kurtén (1963) as resembling

Table 11: Rotated component loadings for *Lynx issiodorensis*.

Variable	Component 1
LCi	885
WCi	891
LP$_3$	920
WP$_3$	609
LP$_4$	903
WP$_4$	870
LM$_1$	904
WM$_1$	890
LtM$_1$	885
Percent variance explained	75.1

L. pardina, and are included in the present section because of the close phyletic relationship between *L. pardina* and *L. issiodorensis* (see Section 5).

Multivariate analysis

The principal components analysis of *L. issiodorensis* used only measurements of the lower dentition (nine variables). Other variables were measured on too few specimens to be of use here. The above-mentioned Cromerian specimens were not used in the multivariate analysis, only in the bivariate analysis.

Owing to the nature of the material, the only possible distinction is between specimens of late Villafranchian age, and those which are older.

In the principal components analysis, one component was extracted. This accounted for 75 % of the total variance, and was interpreted as a general size component. It shows high loadings for all variables, with only a slightly smaller loading for the length of P$_3$ (Table 11). Comparison showed that the two groups differ significantly ($t = 3.027$, df $= 23$), with the younger specimens being the smaller.

Bivariate analysis

In this section early and late specimens of *L. issiodorensis* have been compared, as well as the Cromerian specimens mentioned earlier.

About the skulls there is nothing to say, as no complete skulls of late Villafranchian specimens were available. Kurtén (1978) has studied the skull of early Villafranchian *L. issiodorensis* from Europe, and made comparisons with *L. lynx*. The same comments apply to the study of mandibular variables.
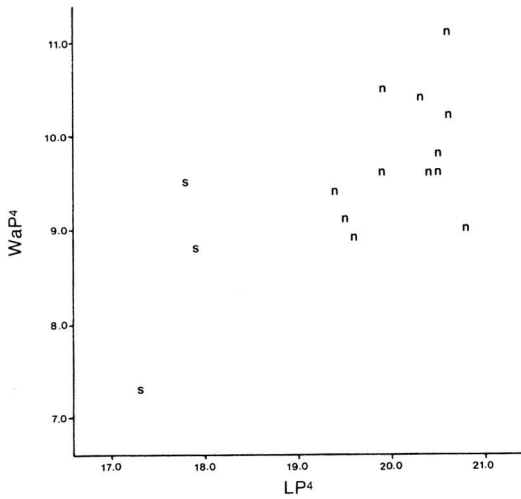
Fig. 7. Plot of length/width relationship of P^4 of *Lynx issiodorensis*. n = Early and Middle Villafranchian, s = Late Villafranchian.
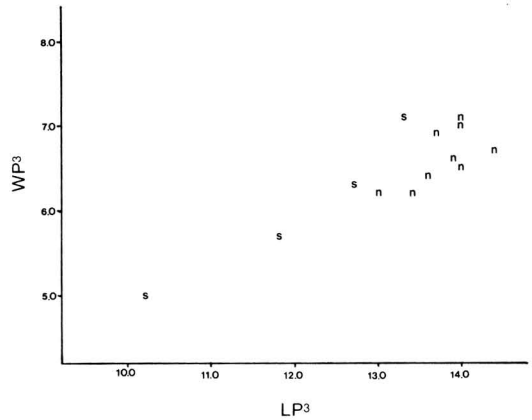

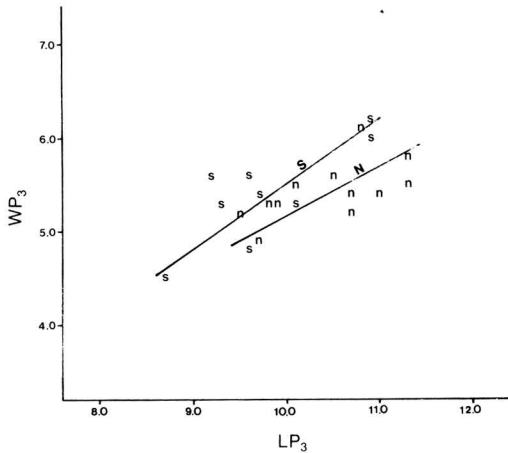Fig. 8. Plot of length/width relationship of P^3 of *Lynx issiodorensis*. For code, see Fig. 7.

Fig. 9. Plot of length/width relationship of P_3 of *Lynx issiodorensis*, N = regression line of Early and Middle Villafranchian specimens, S = regression line of Late Villafranchian specimens, for explanation of other letters, see Fig. 7.
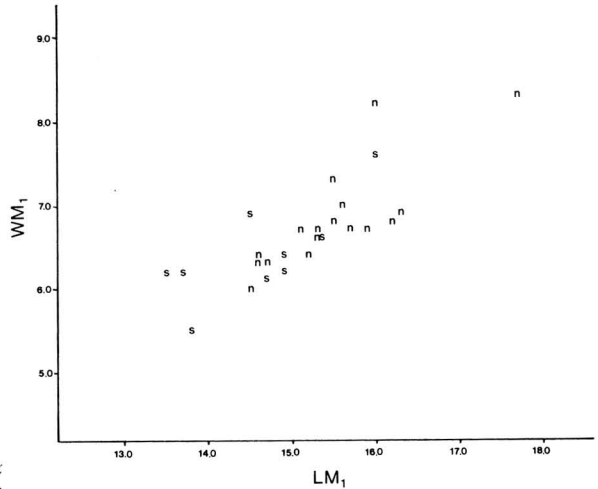

Fig. 10. Plot of length/width relationship of M_1 of *Lynx issiodorensis*. For code, see Fig. 7.

The study of the upper dentition also suffers from a dearth of late Villafranchian material. In this case, however, there were at least some specimens available, and plots were made of those variables for which both early and late specimens were available (Figs 7 and 8). The first of these plots shows the length/width relationship of the P^4. A striking difference in length is apparent between the two subsamples. The width, on the other hand, varies considerably within each sample. The second plot shows the length/width

relationship of P^3. Although the samples are too small to allow a study of regression lines, this plot suggests that P^3 is narrower in earlier specimens of *L. issiodorensis*. The widening of P^3 is considered further in the analysis of interspecific variation in Section 4.

In the plots of the lower dentition variables, it is more difficult to detect any consistent differences. However, the two subsamples differ significantly in the length/width relationship of P_3 $(z_2 = 4.699)$. In this plot (Fig. 9) the late specimens are

wider for a given length of P_3. An interesting pattern of variation emerges in the plot of the length/width relationship of M_1. This plot (Fig. 10) shows that certain specimens have a wider M_1 than do the majority. These specimens are not united by any common denominator as far as is known. They are of different ages and from different localities. When more material becomes available, a further study may be useful in determining whether these specimens share any other traits besides the relatively wide M_1.

In none of the variables studied do the two Cromerian specimens differ significantly from the late Villafranchian specimens. I am therefore led to regard these as belonging to the species *L. issiodorensis*.

Univariate analysis

A univariate test was carried out for only one variable, the length of P^4. A comparison was made between the means for early and late specimens of *L. issiodorensis*. It was found that the late specimens were significantly smaller ($t = 8.385$, df $= 13$). The lower dentition variables were discussed on p. 52, where it was shown that the late specimens were smaller for a component which constituted a composite of these variables.

Conclusions

It is possible to separate *L. issiodorensis* into an early and a late form. The early form ranges from the lower Villafranchian to the middle Villafranchian, while the late form ranges from the late Villafranchian (Val d'Arno stage) to the Cromerian. Of these two types the late one is found only in Europe. In my opinion, the late type represents a subspecies distinct from the early type. This opinion is based in part of the differences outlined above, but also on the fact that the late form of *L. issiodorensis* is intermediate in morphology between the early *L. issiodorensis* and *L. p.spelaea*. This transition from *L. issiodorensis* to *L. pardina*, with intermediate steps, I consider to be an example of phyletic gradualism, in contradistinction the Eldredge-Gould model of punctuated equilibria (Eldredge & Gould 1972, Gould & Eldredge 1977). The erection of a new subspecies of *L. issiodorensis* would serve to express this transition in words.

The type of *L. issiodorensis* belongs to the early form, so this form becomes the nominate subspecies.

Lynx issiodorensis valdarnensis n. ssp.

Holotype: Mandible and fragmentary skull remains, Institute of Geology, Florence, IGF 893 (Fabrini, 1896, Pl.1, Figures 6 and 7).

Type locality: Il Tasso, Val d'Arno, Italy.

Stratigraphic occurrence: Late Villafranchian (Val d'Arno Stage), to Cromerian.

Referred material: Mandible, IGF 894; mandible, IGF 4396; right ramus, IGF 892; right ramus, IGF 898; right ramus, IGF 896; skull fragment, IGF 4399; mandible, VA 1164 (Basel); right ramus, SL 15 (Basel); left ramus, HGU 19201 (Heidelberg).

Diagnosis: A *Lynx issiodorensis* intermediate in size between the nominate subspecies and *L. pardina spelaea*. Both upper and lower dentition smaller than in the nominate subspecies (Figures 7—10).

Comments: The type specimen of *L.i.valdarnensis* is smaller than average. This shows that all three specimens included in Figure 8 are smaller than average.

I indicated earlier that the line *L. issiodorensis issiodorensis* - *L.i. valdarnensis* - *L. pardina spelaea* - *L.p. pardina* represents a phylogenetic lineage. I will argue this more fully in Section 4.

3.7. Other species

Besides the species emphasized in this paper, several others have been described as belonging to the genus *Lynx*, or as closely related to it. The following are considered here.

1. *Lynx shansius* Teilhard de Chardin. Teilhard (in Teilhard & Leroy 1945) describes this species as a lynx of large size, not differing significantly from *L. lynx* in dental characters. The material he describes comes from the mid-Pliocene of Locality 12 of Choukoutien, the Villafranchian of Nihowan, Yushe, and Locality 18 of Choukoutien. Teilhard also states that this material possibly represents two or more forms differing slightly in geological age. Unfortunately, Teilhard presents measurements only for his type specimens, for which reason nothing can be said here about his conclusions.

2. *?Lynx* sp. 1, described in Teilhard and Leroy (1945). This material (two mandibles) comes from Yushe, and is of Villafranchian age. The specimens are slightly smaller than those of *L. shansius*. Teilhard suggests that they may represent the lower dentition of *Felis peii* (see below).

3. *?Lynx* sp. 2, described in Teilhard and Leroy (1945). This form, represented by one mandible from Yushe, is very similar to the preceding one, but lacks the metaconid and talonid of M_1.

4. *Felis teilhardii* Pei. Pei (1934) described this species from Locality 1 of Choukoutien (lower Pleistocene). The specimens differ from those of recent lynxes in retaining P^2. Otherwise, the species is very lynx-like, and Kurtén (1957) suggested affinities with the lynxes.

5. *Felis peii* Teilhard. This species, described in Teilhard & Leroy (1945), is very similar to the preceding one, but is slightly smaller. It is also older, being from the Villafranchian of Yushe.

6. *Felis rexroadensis* Stephens. Kurtén (1963) was the first to suggest affinities between this species and the lynxes. Recently, Glass & Martin (1978) included this species in the genus *Lynx*. The material comes from the upper Pliocene of Kansas.

7. *Felis lacustris* Gazin. This species is found at several localities in the upper Pliocene and lower Pleistocene of North America. Bjork (1970: 44) discussed the relationships of this species and concluded that "affinities with the *Lynx* group are possible, but must be considered with caution."

8. *Felis, ?aff. Felis (Lynx) issiodorensis*, described by Savage (1960) from Cita Canyon, late Blancan, Texas. Savage compared his material with that of several species, and concluded that it most nearly resembled *L. issiodorensis*.

9. *Felis aff. issiodorensis*, described by Hendey (1974) from the early Pliocene of South Africa. This material is very similar to, but smaller than, that of *L. issiodorensis*.

10. *Felis obscura* Hendey. This species, of the same age as the preceding one, was slightly larger than the average *L. issiodorensis*. Hendey (1974) suggested that it may have been ancestral to *C. caracal*, and suggested possible affinities with the genus *Sivafelis*.

11. *Caracal brevirostris* (Croizet and Jobert). This species was described from the Pliocene of Roussillon by Depéret (1893). According to Fabrini (1896), it is a synonym for *Lynx issiodorensis*.

12. *Felis christolii* Gervais. This species has been found in the caves of Lunel-Viel and in the marine sands of Montpellier (Paulus & Tron 1945). Hendey (pers. comm.) states that material of this species deposited in Basel resembles that of his *Felis aff. issiodorensis* (see above).

Very little material was available of any of the above-mentioned species. Any remarks made about them will therefore be tentative. In no case is it possible to state definitely what a species is, but it may nevertheless be possible in some cases to say what it is not.

4. Interspecific variation

This section concerns the variation between species. The results of the principal components analyses are presented first, then the results of the bivariate analyses, and finally the results of the canonical variates analyses. The groups used in this last analysis are based on the findings of the two previous sections, as well as on the findings of Section 3 on intraspecific variation.

4.1. Principal components analysis

Two principal components analyses were carried out using all data, one for the recent specimens, and the other for the recent and fossil specimens together.

The analysis involving only recent specimens included all recent specimens used in principal components analyses in Section 3. This meant that the number of variables used had to be reduced to 23, this being the largest number of variables common to all specimens. A total of 211 specimens were used in this analysis. Three components were extracted, together accounting for 93 % of the total variance. The first component has high loadings for variables of the dentition,

Table 12: Rotated component loadings for recent lynxes.

| Variable	Component		
	1	2	3
CBL	488	850	011
PL	530	811	—036
C-C	573	743	258
ZB	417	879	145
IOB	373	790	361
POC	038	062	982
C-cond	562	815	022
HPC	387	858	—229
DbehM$_1$	610	736	154
LCs	817	528	—059
WCs	785	537	020
LP^3	848	437	143
WP^3	831	456	121
LP^4	881	375	—040
WaP^4	862	410	110
LCi	845	490	038
WC$_1$	798	514	015
LP$_3$	881	404	002
WP$_3$	839	461	121
LP$_4$	884	366	—014
WP$_4$	876	388	029
LM$_1$	882	387	106
WM$_1$	834	413	092
Percent variance explained	52.5	34.9	5.9
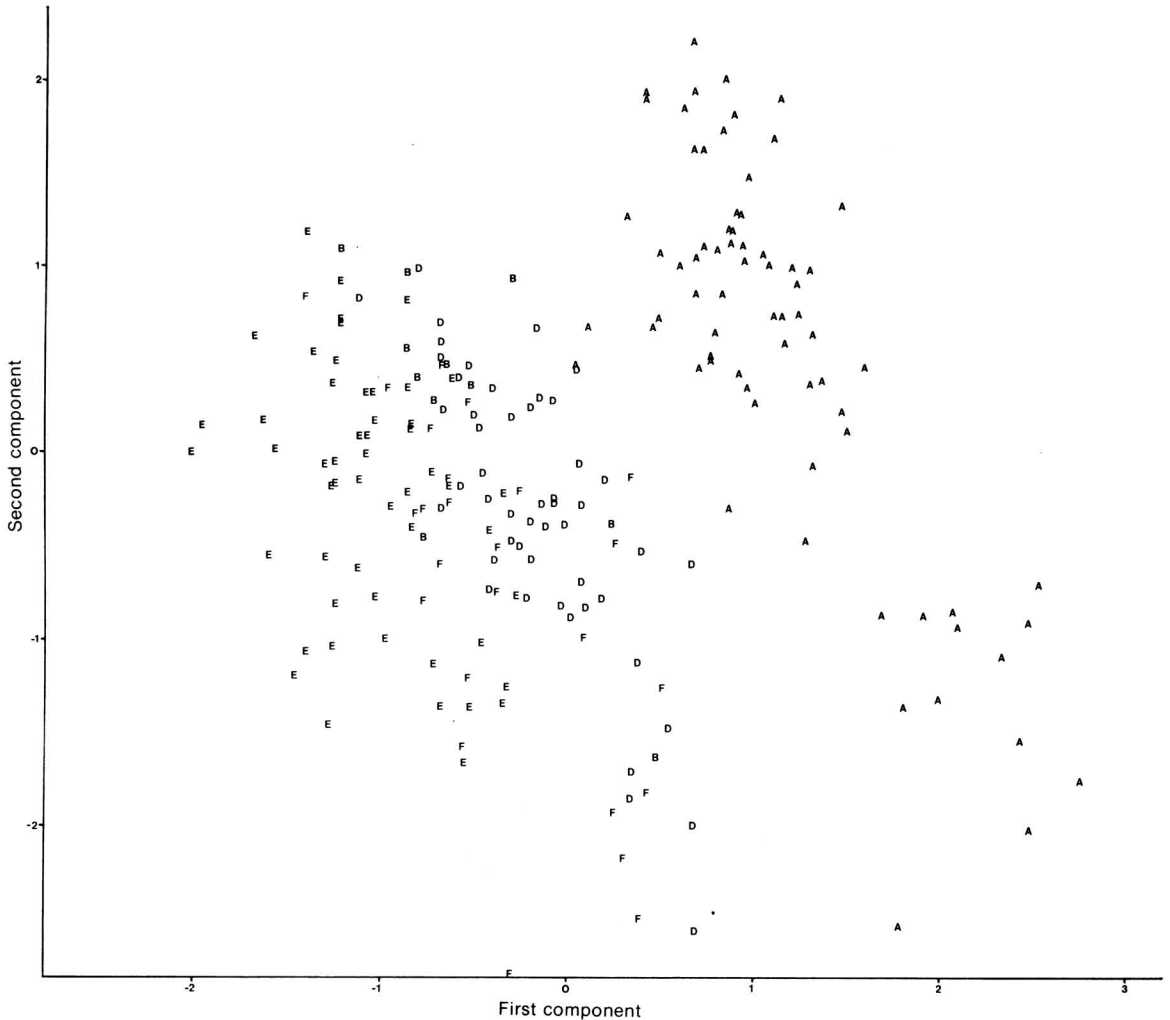
Fig. 11. Principal components analysis of all recent specimens, first component against second component. For code, see Table 1.

and lower ones for those of the skull and mandible; this was interpreted as a component describing the size of the teeth. The second component has high loadings for skull and mandible variables and lower ones for dental variables, and was interpreted as describing the size of the skull and mandible. The third component shows a high loading only for the POC. The three components are shown in Table 12.

The first two components create a scale on which the specimens fall in order of size (Fig. 11). It is seen that *L. lynx* is distinctly separated, whereas the other species show considerable overlap. The small subgroup at the lower right of

Figure 11 contains juvenile specimens of *L. lynx*. These specimens have smaller component scores for the second component (skull and mandible size), but larger scores for the first component (tooth size). This last condition may be due to lack of wear in the teeth of juvenile specimens.

In Fig. 12 the first component is plotted against the third. It is immediately obvious that the latter component separates *C. caracal* from the other species. As this component describes the least width across the postorbital constriction (POC), we see that *C. caracal* has a smaller width across this portion of the skull than the other species. It is also found that two specimens of *L. rufus* fall
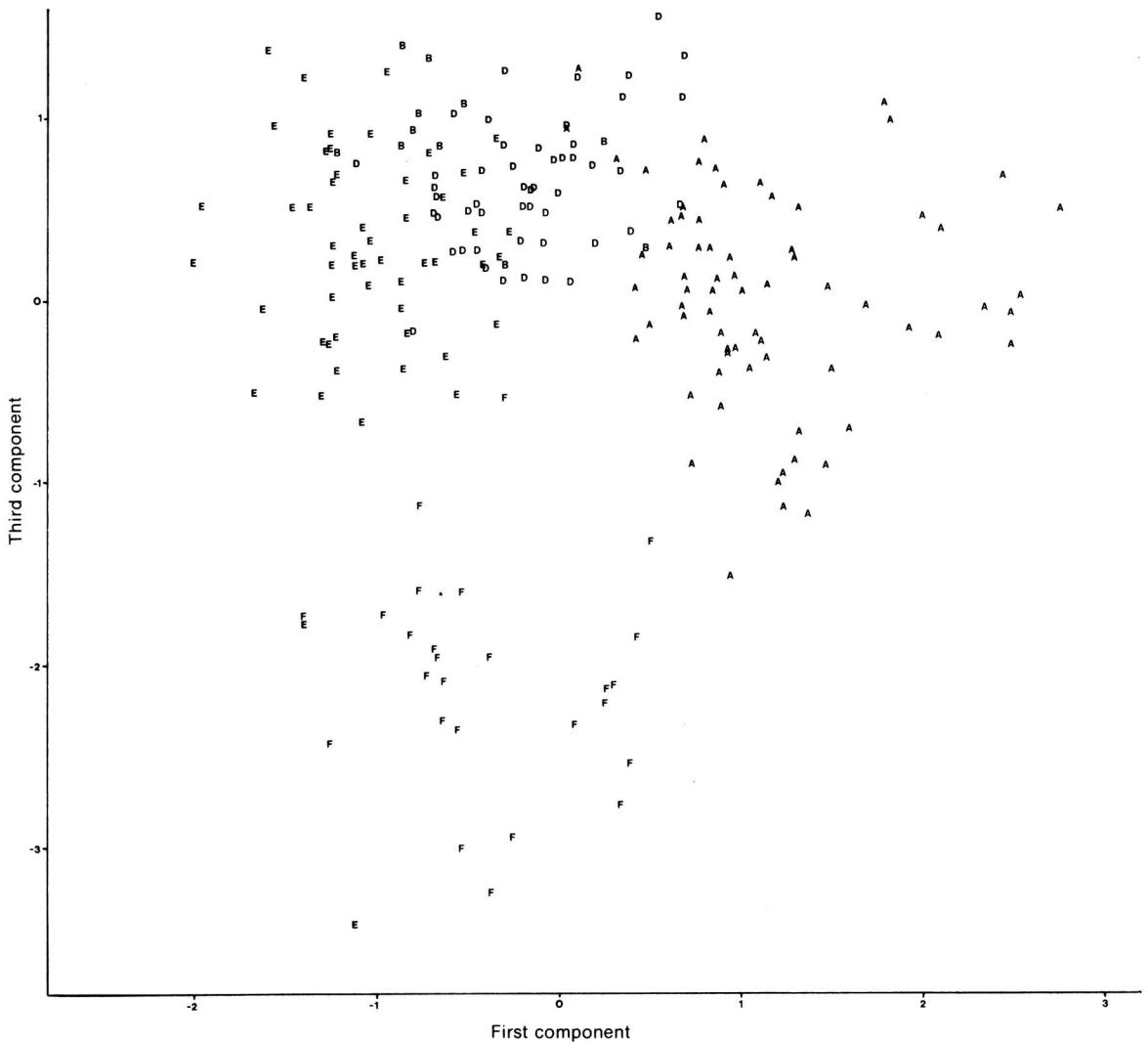
Fig. 12. Principal components analysis of all recent specimens, first component against third component. For code, see Table 1.

within the range of *C. caracal* in this plot. These two specimens have very low values for the POC.

The principal components analysis of recent and fossil specimens used only six variables from the lower dentition. A total of 325 specimens were included. One component was extracted (Table 13), accounting for 92 % of the total variance. This component has high loadings for all variables included, and is interpreted as a general size component. It serves to spread out the specimens along its axis, according to the size of the lower dentition.

Table 13: Rotated component loadings for recent and fossil lynxes.

Variable	Component 1
LP_3	971
WP_3	961
LP_4	957
WP_4	964
LM_1	968
WM_1	942
Percent variance explained	92.3
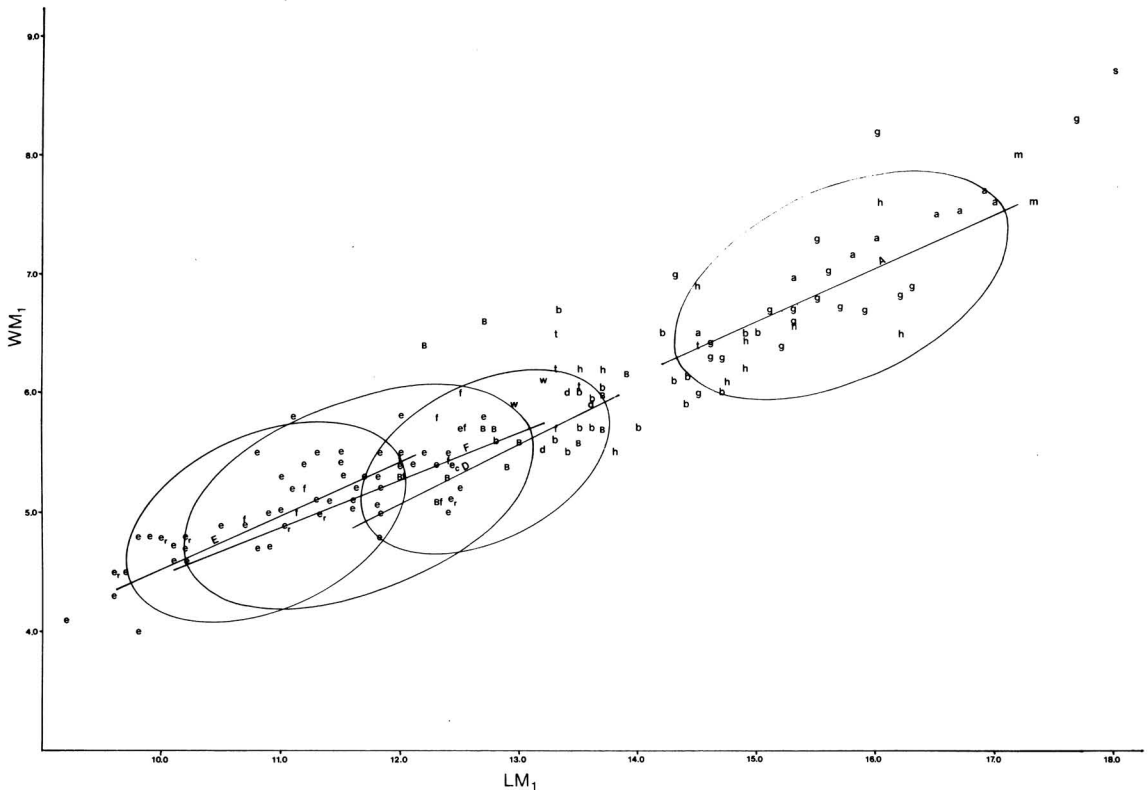
Fig. 13. Plot of length/width relationship of M_1, all specimens. For code, see Table 1. In this and all subsequent bivariate diagrams, recent species are represented when possible by their 95 % probability ellipses and regression lines, other species by individual specimen points.

4.2. Bivariate analysis

In this section we turn our attention from multivariate analysis to a study of individual cranial and dental features.

The species introduced in Section 3.7 are included here. The analyses are presented plot by plot with a commentary for each. The integration of these and other data is deferred to Section 5.

LM_1/WM_1 (Fig. 13): This plot clearly shows the size difference between *L. lynx* and the other recent species. The other species are similar to each other, only *L. rufus* differing in having a relatively wider M_1. *L. issiodorensis* differs in that, for specimens of large size, the M_1 of this species is relatively wider than that of recent species. Of other species, *F. lacustris* resembles *L. issiodorensis*, as does *F.* aff. *F. issiodorensis* of Savage (1960), while *F. teilhardii* and *F.* aff. *issiodorensis* of Hendey (1974) are closer to the condition seen in *L. lynx*.

LP_4/WP_4 (Fig. 14): In this plot *L. lynx* and *L. issiodorensis* differ significantly ($z_2 = 7.687$), *L. lynx*

having a relatively wider P_4. The other recent species are divided into two groups, P_4 being narrow in *L. canadensis* and *C. caracal*, and wide in *L. rufus* and *L. pardina*. This plot separates *F. lacustris* into two groups, P_4 being short and relatively wide in one, and long and relatively narrow in the other. *F.* aff. *issiodorensis* falls into the latter group.

LP_3/WP_3 (Fig. 15): In this plot also, *L. lynx* and *L. issiodorensis* differ, the former having a wider tooth. Here, however, the slopes of the regression lines also differ significantly ($z_1 = 1.983$). This means that the difference in width between the P_3 of *L. lynx* and that of *L. issiodorensis* increases as the teeth compared become longer. The only other significant difference in this plot is that *C. caracal* has a narrower P_3 than the other species. Both *F. lacustris* and *F. teilhardii* are widely spread in this plot, and it is difficult to draw any conclusions from their positions. *F.* aff. *issiodorensis* of Hendey lies close to where the regression lines of *L. lynx* and *L. issiodorensis* would meet if extrapolated.
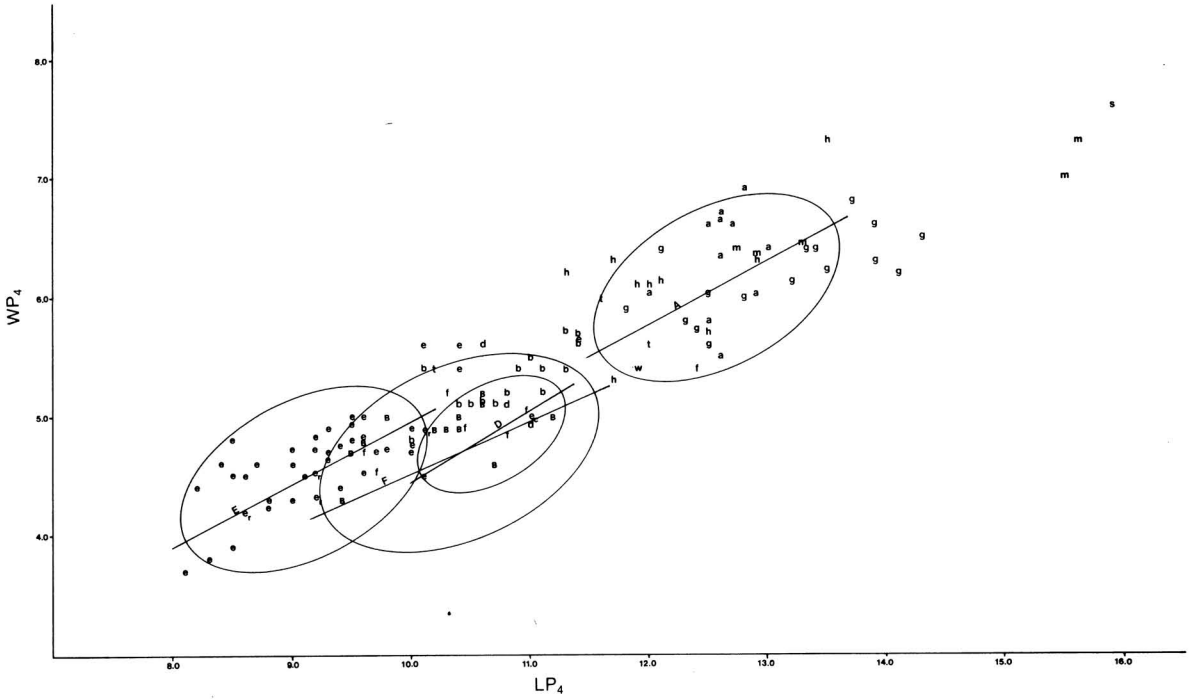
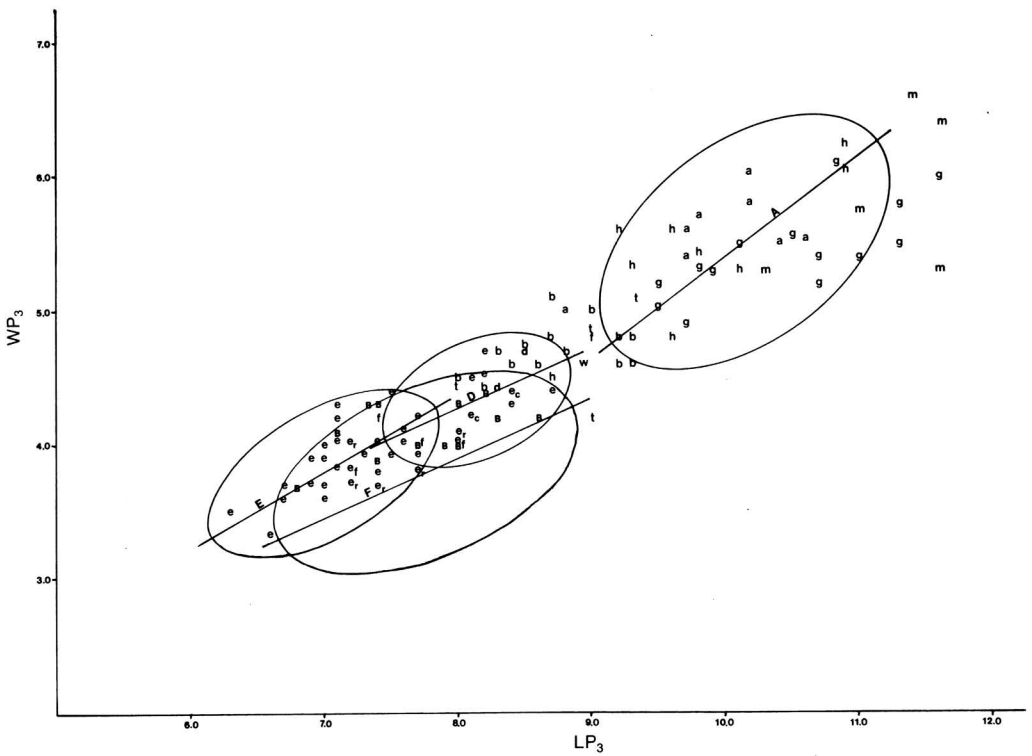Fig. 14. Plot of length/width relationship of P_4, all specimens. For code, see Table 1.

Fig. 15. Plot of length/width relationship of P_3, all specimens. For code, see Table 1.
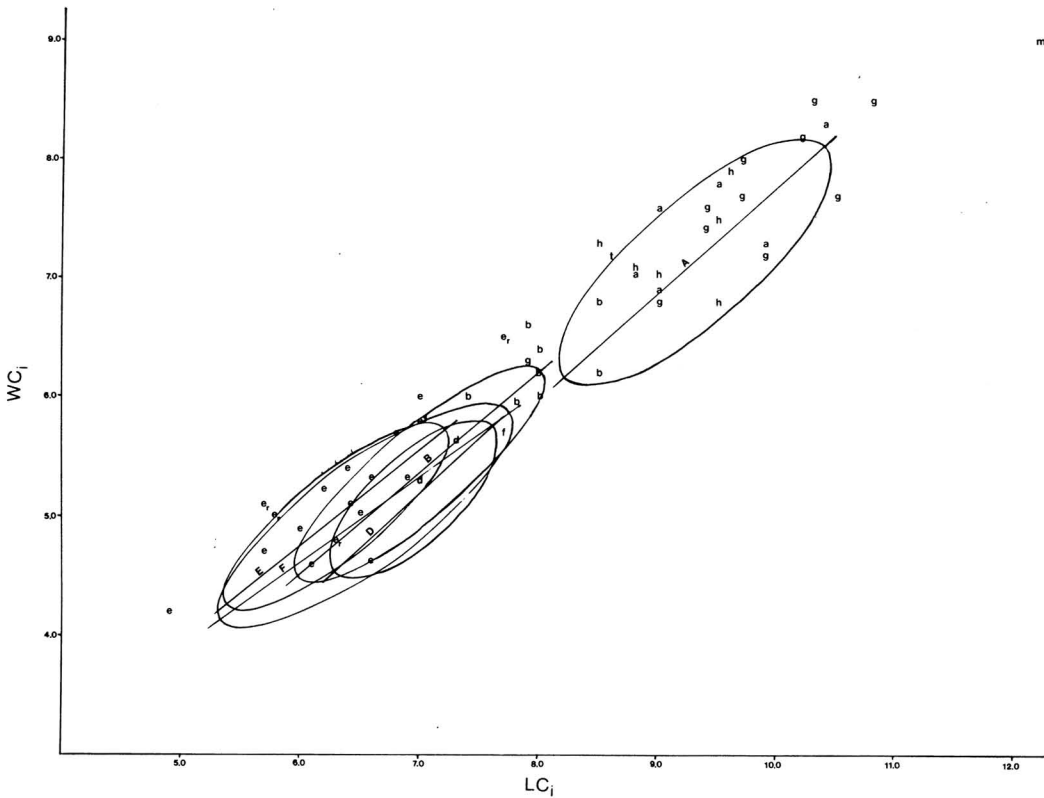
Lars Werdelin

Fig. 16. Plot of length/width relationship of C_i, all specimens. For code, see Table 1.

LC_i/WC_i (Fig. 16): *L. lynx* has a narrower lower canine than *L. issiodorensis*, the difference being small but significant ($z_2 = 4.985$). The regression lines for the other species are all similar in slope, but differ in location. *L. rufus* has the most rounded canine, and *L. canadensis* the narrowest, with *L. pardina* and *C. caracal* being intermediate. *F. lacustris* is represented by only one specimen, which has a narrower canine than the other large species, *L. lynx* and *L. issiodorensis*.

LP^4/WaP^4 (Fig. 17): The correlation between these variables in *L. issiodorensis* was too low for the calculation of a regression line. Of the recent species, *L. lynx* and *C. caracal* are similar (except for the size difference) in having a P^4 which is narrow anteriorly. An interesting point is that recent *L. pardina* have a much wider P^4 than fossil specimens of that species. All the miscellaneous species resemble *L. lynx*.

$LP^4/WblP^4$ (Fig. 18): The blade width of P^4 is a very important character, particularly for the separation of *C. caracal*. Unfortunately, few researchers have measured this variable, for which reason data have been available for only five

species. Of these *L. lynx* and *L. pardina* are similar, except for the size difference. *C. caracal* has a much narrower blade than either of these, a condition also seen in *L.r. koakudsi*, while other *L. rufus* have a P^4 with a very wide blade. All the specimens of *L. issiodorensis* for which this variable was measured lie below the regression line of *L. lynx*, which indicates that *L. issiodorensis* had a P^4 with a narrower blade than did *L. lynx*.

LP^3/WP^3 (Fig. 19): In this variable there is an important difference between *L. lynx* and *L. issiodorensis*. The latter species has a much narrower P^3 than the former. *L. pardina*, *L. canadensis* and *C. caracal* all have a slightly narrower P^3 than *L. lynx*, while in *L. rufus* P^3 is still broader than in *L. lynx*. In this respect *F. obscura* closely resembles *L. issiodorensis*. *F. teilhardi* and *F. rexroadensis* both resemble *L. lynx*, while *F. lacustris* shows a tendency towards a still wider P^3.

LC^s/WC^s (Fig. 20): The only significant difference between any of the groups in this plot is that in *L. rufus* C^s is relatively round, while in *C. caracal* it is more flattened. The upper canines of *F. lacustris* and *F.* aff. *F. issiodorensis* are similar in
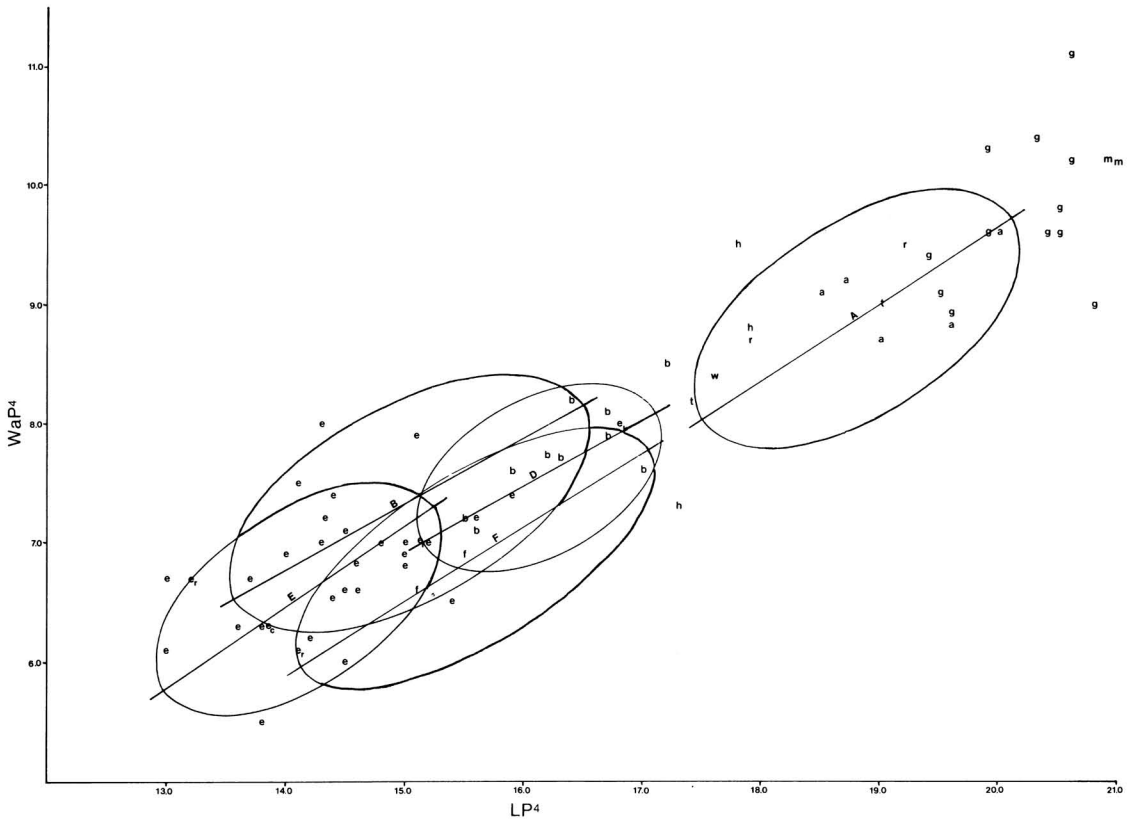
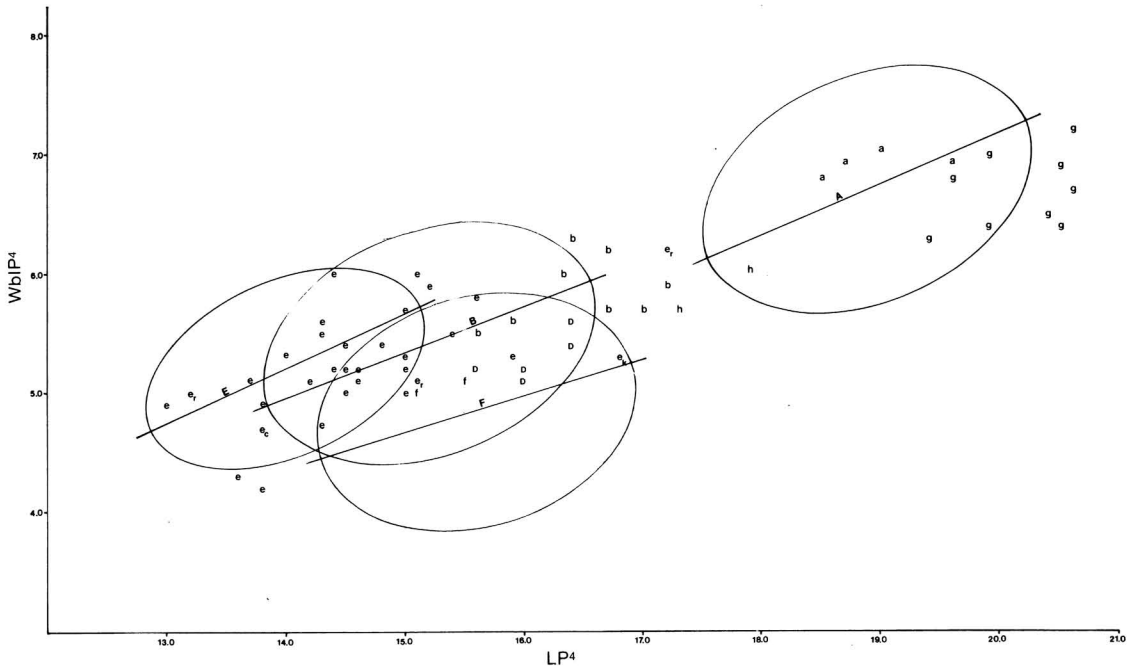Fig. 17. Plot of LP^4/WaP^4 relationship, all specimens. For code, see Table 1.

Fig. 18. Plot of LP^4/WblP^4 relationship, all specimens. For code, see Table 1.
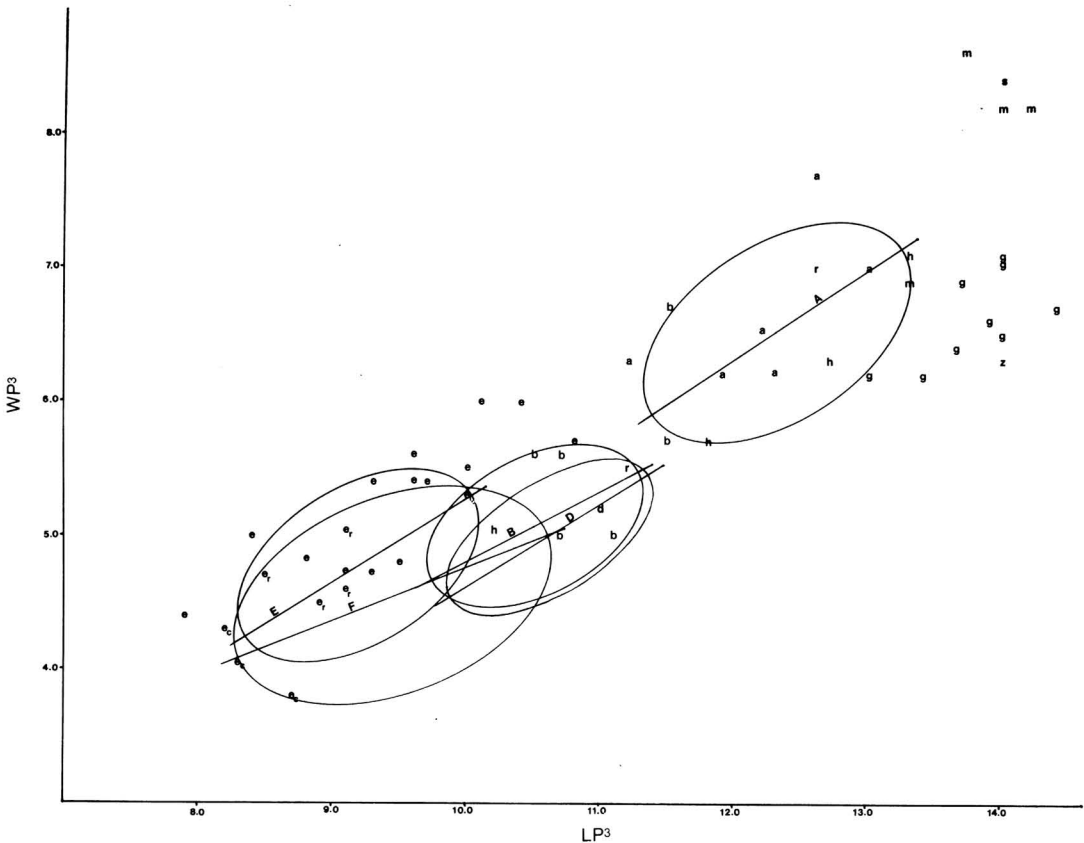
Fig. 19. Plot of length/width relationship of P^3, all specimens. For code, see Table 1.

size, and larger than those of *L. issiodorensis*.

LM_1/LP_4 (Fig. 21): This plot shows clearly that *L. issiodorensis* has a relatively longer P_4 than *L. lynx*. The reason for this difference will be discussed in Section 4. The other species vary considerably in the relationship between the lengths of these two teeth. As compared with the P_4 of *L. lynx*, that of *L. canadensis* is relatively long, whereas the P_4 of *L. pardina*, and particularly *L.p. spelaea*, is relatively short. In *C. caracal* P_4 is relatively longer than in *L. issiodorensis*. It is very difficult to say anything conclusive about the other species included in this plot, because of the considerable variation within each species. Suffice it to say that *F. aff. issiodorensis* of Hendey (1974) shows similarities to *L. issiodorensis* and *C. caracal*, while *L. shansius* shows similarities to *L. lynx*.

LP^4/LP^3 (Fig. 22): *L. lynx* and *L. caracal* resemble each other closely here in having a relatively short P^3, a characteristic shared with *L.r. koakudsi* and *F. rexroadensis*. *L. pardina* has a long P^3, while *L. canadensis* and *L. rufus* are inter-

mediate. *F. obscura* appears to have a very short P^3, but as only one specimen was measured, and as both *L. lynx* and *C. caracal* include aberrant individuals in which the P^3 is very short, this may not be the normal condition in *F. obscura*.

ZB/IOB (Fig. 23): This plot shows that in *L. pardina* and *L. canadensis* the eyes are set relatively far apart as compared with the other recent species. *L. lynx* is intermediate, while *C. caracal* differs in the slope of the regression line. This means that large individuals have eyes more closely set in *C. caracal* than in the other species.

ZB/P-P (Fig. 24): This plot shows that *L. lynx* has a great intercarnassial width in the upper jaw as compared with the zygomatic width. *L. canadensis* shows this characteristic to a lesser degree, while the other recent species are comparatively narrow between the upper carnassials.

C-cond/HPC (Fig. 25): This variable pair separates the species into two groups. One comprises *L. rufus* and *C. caracal*, which have a relatively short mandible and high coronoid
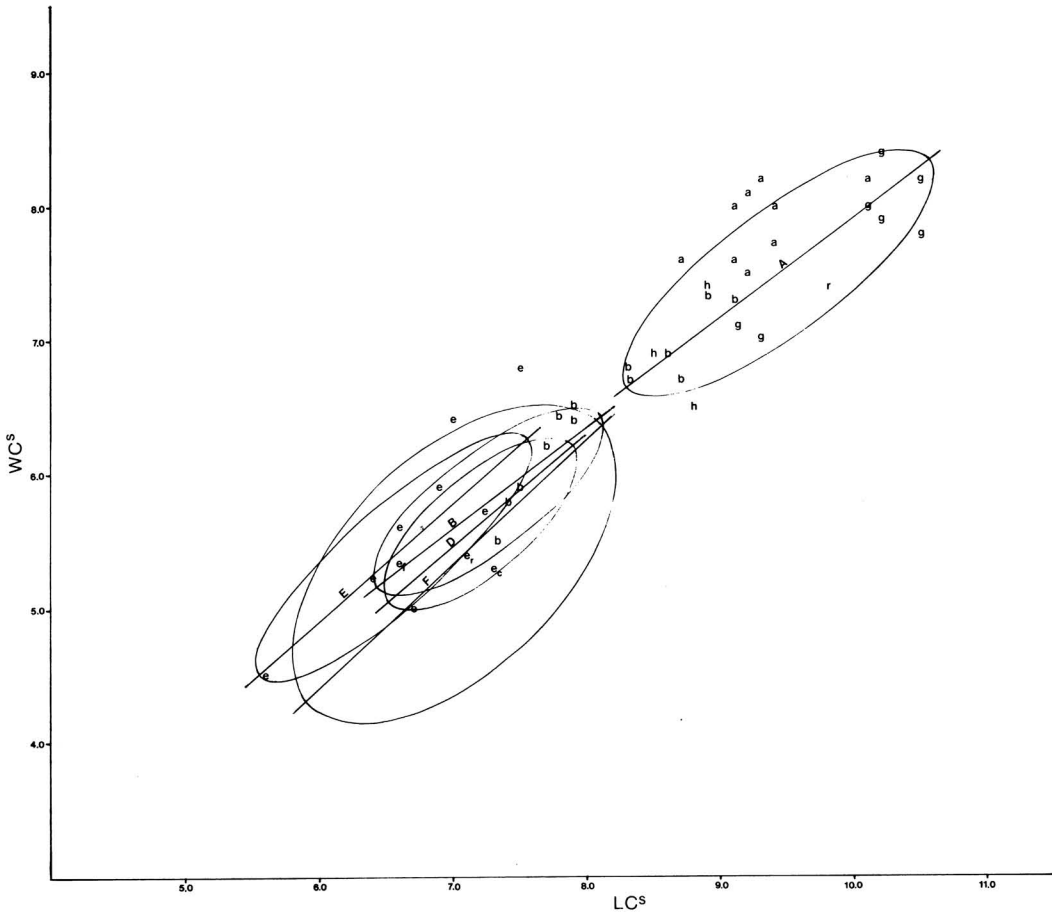
Fig. 20. Plot of length/width relationship of C^s, all specimens. For code, see Table 1.

process. The other group comprises *L. pardina*, *L. canadensis* and *L. lynx*, which have a long mandible with a low coronoid process. A feature of interest is that fossil *L. rufus* resembles *C. caracal* to a greater extent than does recent *L. rufus*.

4.3. Canonical variates analysis

Two canonical variates analyses were carried out, one using only recent specimens, and the other using both recent and fossil specimens.

In the analysis of recent specimens the same variables and specimens were used as in the principal components analysis. Three of the variates extracted were considered useful. These accounted for 97 % of the total variance.

In order to investigate what the extracted variates describe, the correlations between the canonical variates and the original variables were studied. The first variate shows high values for all variables except the POC (Table 14). It is therefore interpreted as a general size variate. It should be noticed that the correlations for tooth variables are higher than those for the skull and mandible variables, and that the tooth variables thus contribute more to the separation of groups along the first axis than do the other variables. The second variate has a high negative correlation for the POC, contrasted with lower positive values for some mandible and tooth variables (Table 14). The separation along this axis is thus mainly due to the variation in the POC, but is also influenced by other variables, such as the HPC. The third
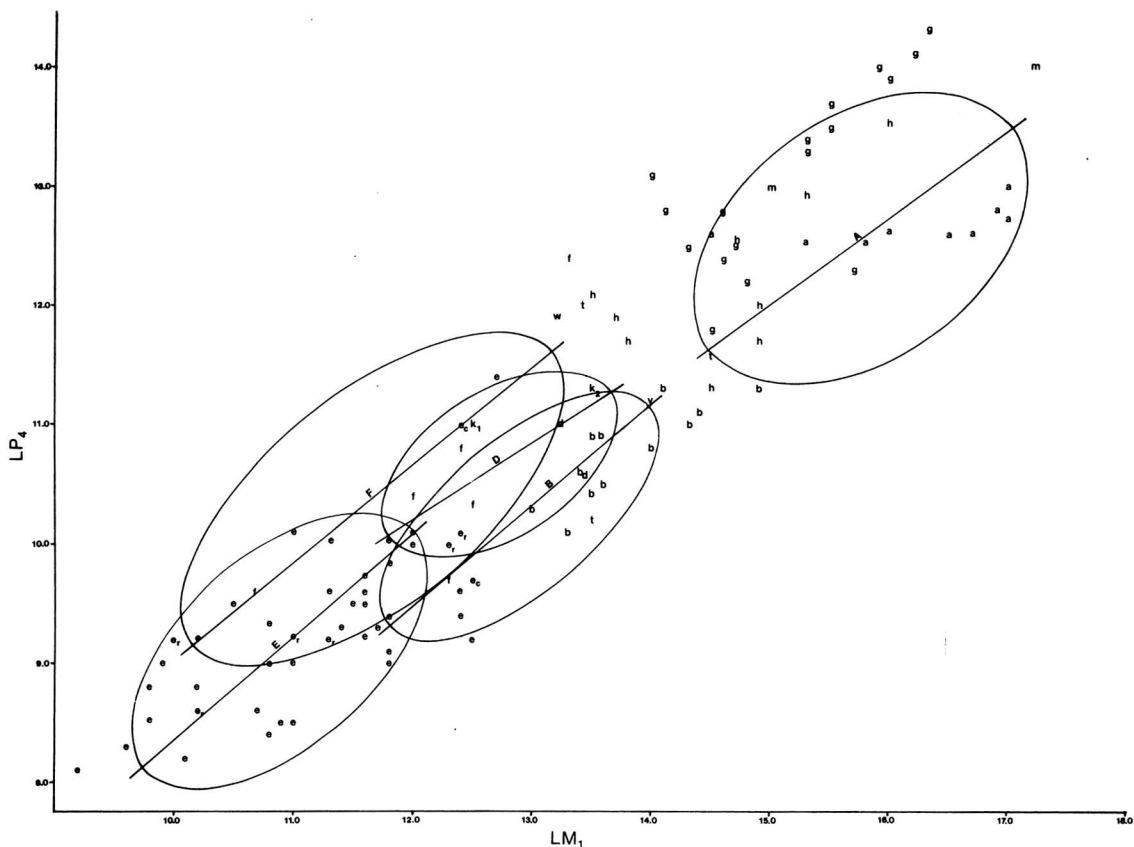
Fig. 21. Plot of LM_1/LP_4 relationship, all specimens. For code, see Table 1.

variate has no very high values for any of the variables (Table 14). It is therefore difficult to give this variate any definite interpretation. It may suffice to say that the variate describes systematic differences between certain species, as discussed below.

Fig. 26 shows the group means and 95 % probability circles for the first and second canonical variates. Here the first axis serves to separate the species according to size. The largest, *L. lynx,* is on the left, and the other species follow in order of decreasing size. The second axis serves chiefly to separate *C. caracal* from the other species. As has been seen in Section 4.2, this species has a lesser width across the postorbital constriction than the other species, and the distribution of species along the second canonical variate illustrates this. The third variate separates the species into three groups (Fig. 27): *L. lynx* and *L. rufus* form one group, *L. pardina* and *C. caracal* a second, and *L. canadensis* lies separately from the other species. Referring back to the original

Table 14: Correlations between original variables and canonical variates: recent lynxes.

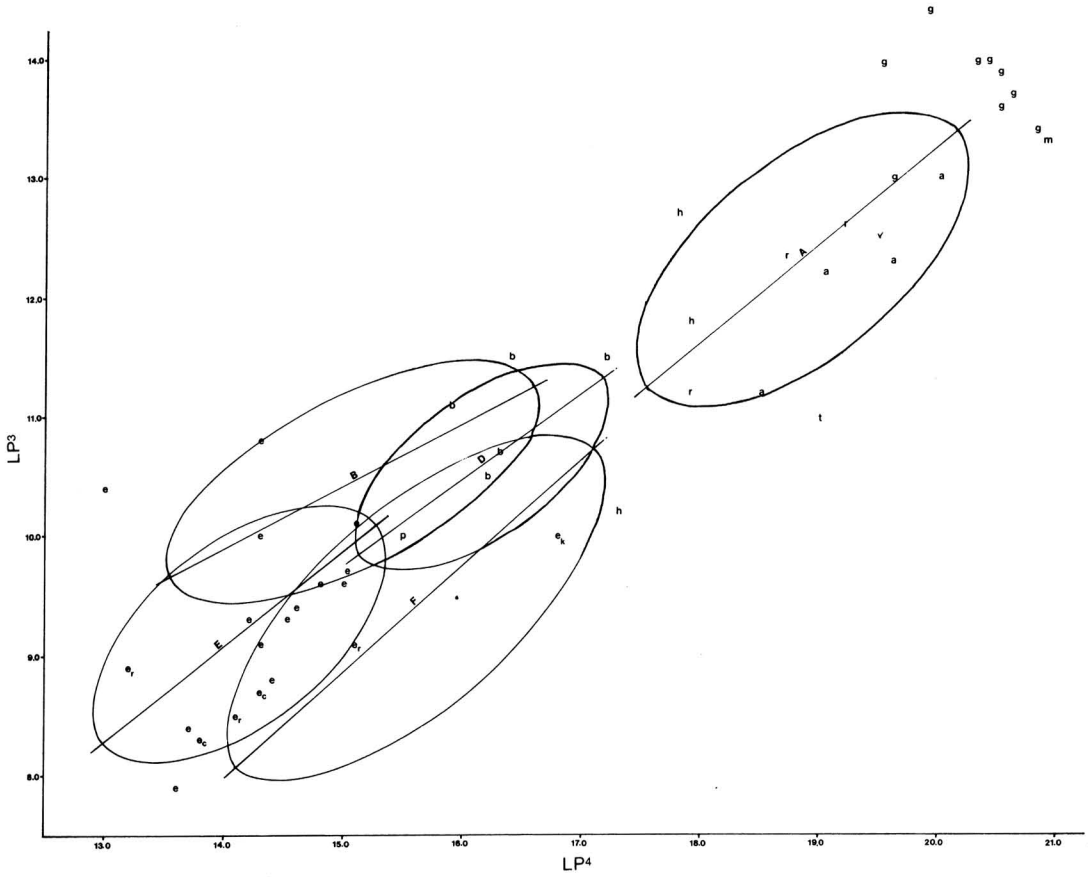| Variable	Variate		
	1	2	3
CBL	764	—096	173
PL	755	—156	286
C-C	838	123	194
ZB	734	027	214
IOB	766	178	—056
POC	297	793	047
C-cond	815	—114	176
HPC	570	—313	302
$DbehM_1$	863	020	131
LCs	874	—289	181
WCs	867	—170	317
LP^3	937	—079	—003
WP^3	905	—080	320
LP^4	910	—320	—018
WaP^4	921	—144	001
LCi	919	—181	215
WCi	865	—179	369
LP_3	924	—249	070
WP_3	942	—074	149
LP_4	913	—314	—058
WP_4	899	—216	214
LM_1	955	—168	046
WM_1	889	—178	235

Fig. 22. Plot of LP⁴/LP³ relationship, all specimens. For code, see Table 1.
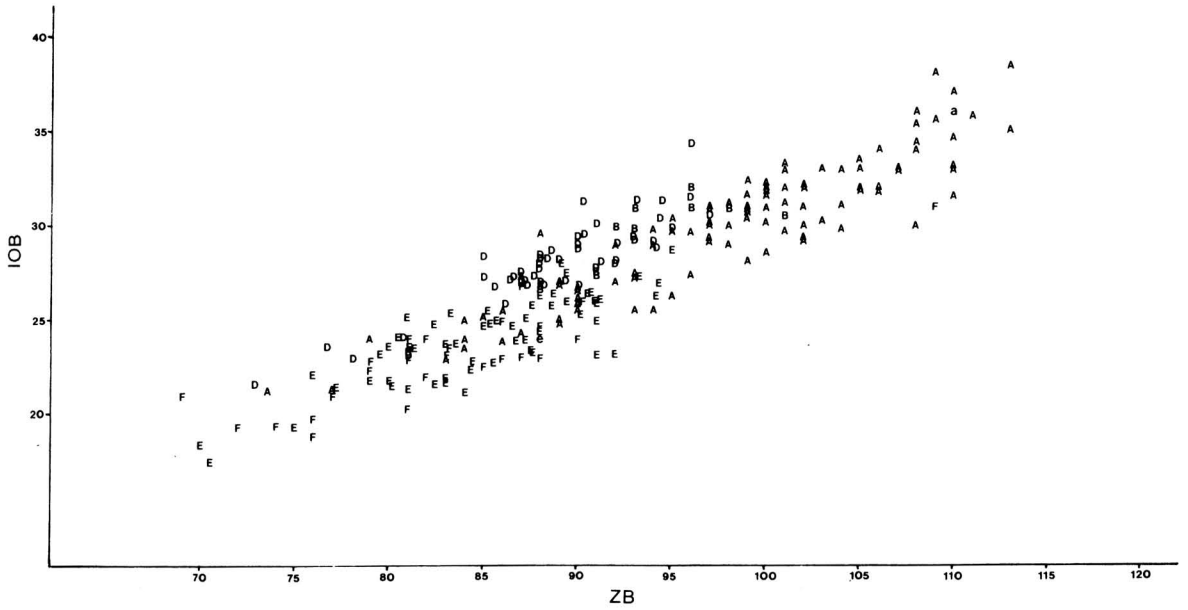

Fig. 23. Plot of ZB/IOB relationship, all specimens. For code, see Table 1.
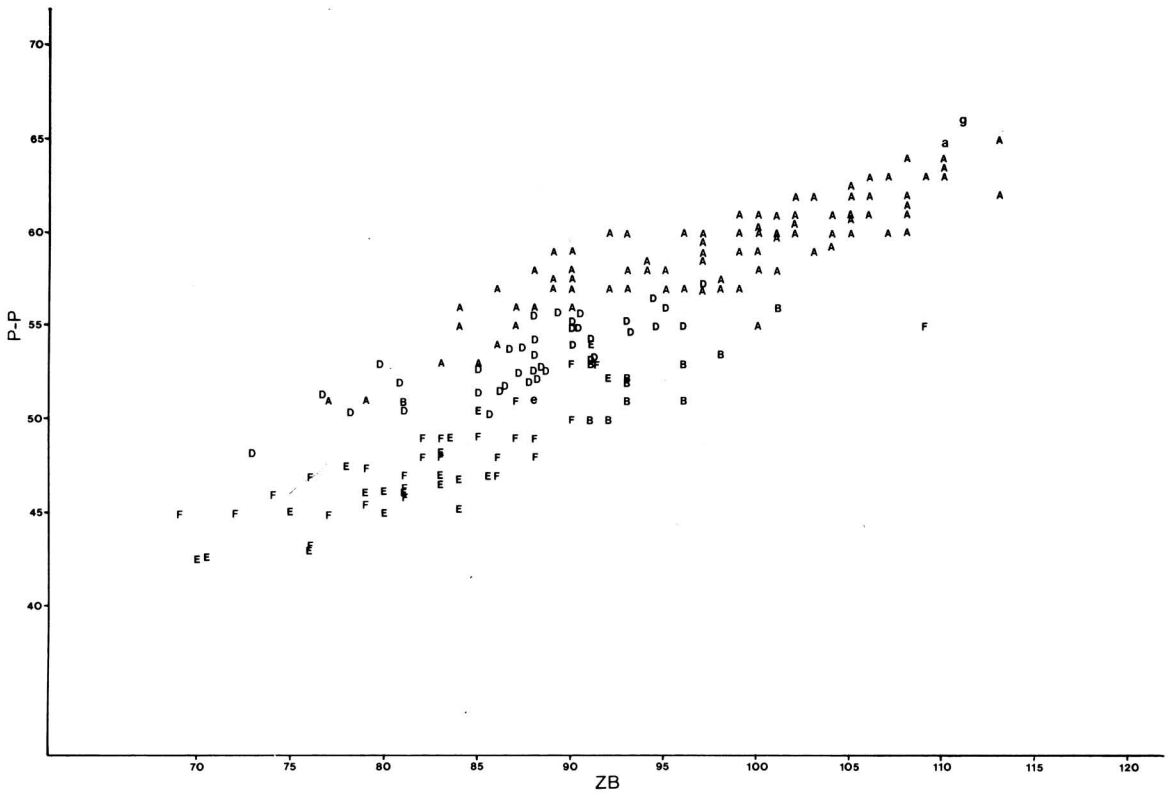
5

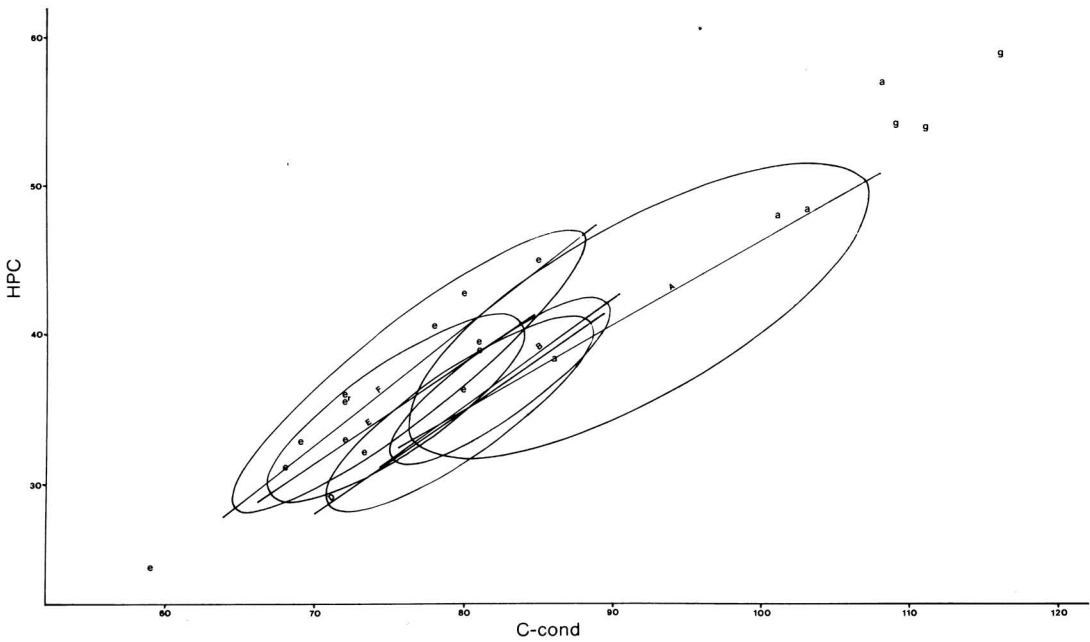Fig. 24. Plot of ZB/P-P relationship, all specimens. For code, see Table 1.

Fig. 25. Plot of C-cond/HPC relationship, all specimens. For code, see Table 1.
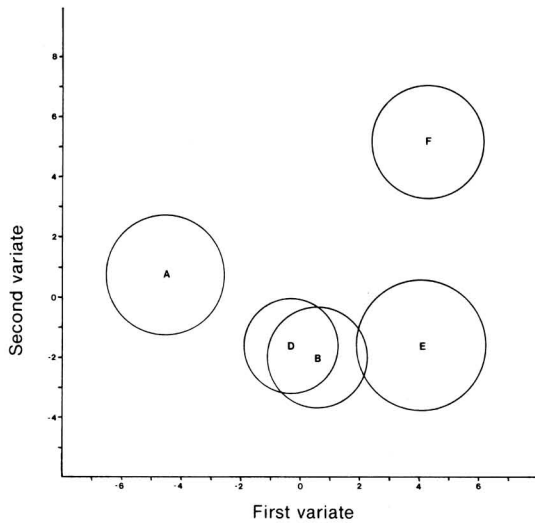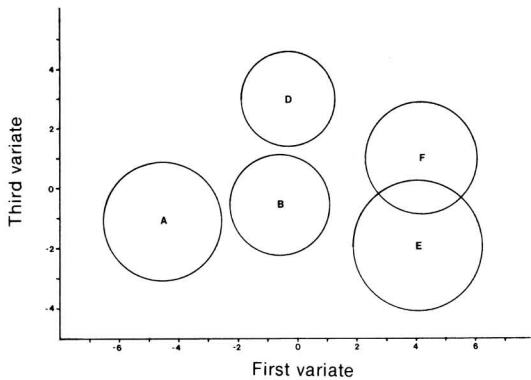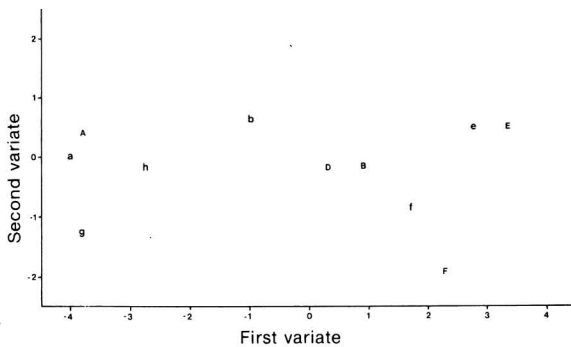
Fig. 26. Canonical variates analysis of recent species, first variate against second variate. For code, see Table 1. In this and the next figure species are represented by their group means and 95 % probability circles.

Fig. 27. Canonical variates analysis of recent species, first variate against third variate. For code, see Table 1.

Fig. 28. Canonical variates analysis of recent and fossil species, first variate against second variate. For code, see Table 1. Species represented by their group means.

Table 15: Correlations between original variables and canonical variates: recent and fossil lynxes.

Variable	Variate	
	1	2
LP_3	964	079
WP_3	961	160
LP_4	938	307
WP_4	929	017
LM_1	981	000
WM_1	917	072

variables and the bivariate analyses of Section 4.2, it is found that the variables having high correlations with canonical variate three are those that unite *L. lynx* with *L. rufus* (particularly WP^3) and *L. pardina* with *C. caracal* (particularly WC_i), and keep *L. canadensis* separate (particularly ZB).

In the second canonical variates analysis, in which both recent and fossil specimens were included, only six variables from the lower dentition were used. Two variates were considered of importance. These explain 94 % of the variance. The first of these has high values for all correlations between the canonical variates and the original variables (Table 15). It is interpreted as a general size variate. The second variate shows only two significant correlations, with LP_4 and WP_3. In the latter case the correlation is negative. This axis should separate species that have a short P_4 and a broad P_3 from those with a long P_4 and a narrow P_3. Looking back at the bivariate analyses, we find that these variables are characteristics that separate *L. lynx* from *L. issiodorensis*. These two species are also widely separated by the second axis in Fig. 28, in which are shown the group means for the first and second canonical variates. As before, the first variate separates the species according to size.

5. Evolutionary interpretation

This section is an attempt to summarize and interpret the data gleaned in the preceding sections.

The earliest species of lynx for which there is unequivocal evidence is *L. issiodorensis* from the early Villafranchian of Southern Europe. It has been seen, however, that the *Felis* aff. *issiodorensis* of Hendey (1974) shares a number of characteristics with the European *L. issiodorensis* (Figs. 14, 15, 21), and differs from the latter chiefly in size. I suggest that the African specimens may be

included in *L. issiodorensis.* The age of the African specimens is approximately 4 Ma. (Hendey 1978), making them the oldest remains of the genus *Lynx* yet found. *Caracal brevirostris* may be of approximately equal age, but the material of this species is not sufficient to allow a definite conclusion regarding its affinities.

The present evidence supports the view that the origins of the lynx group may be sought in Africa. From there the species *L. issiodorensis* spread to other regions, and in the middle Villafranchian was found throughout the northern hemisphere (Kurtén 1963, 1978, Schultz & Martin 1972).

At this stage of development, *L. issiodorensis* was characterized by a relatively short M_1 and a narrow P^3 (Figs 13, 19, 21). These are traits in which *L. issiodorensis* resembled felids of the genus *Felis* rather than the lynxes. Similar differences are seen in the postcranial skeleton, in which *L. issiodorensis* also resembled *Felis* rather than *Lynx* (Kurtén 1978).

In Europe the further evolution of the lynxes was characterized by a gradual decrease in size, and an increase in the relative length of M_1. This trend continued through *L.i. valdarnensis* and *L.p. spelaea* to the recent *L.p. pardina* (Figs 9, 21). I believe that the cause of this trend was twofold: the early stages were initiated through competition with felids that were present in Europe at the time when *L. issiodorensis* reached that continent. One candidate for such a competitive position is *Panthera schaubi* (Viret 1945). The response of *L. issiodorensis* to this competition was a reduction in gross size, whereby the species could exploit smaller prey and consequently avoid competition. The later stages of the trend towards size reduction came about through competition from another felid, *L. lynx,* which immigrated from the east, as described below.

In Asia the situation is more complex. A number of different species have been described from China (see Section 3.7). The three species *L. shansius,* *?Lynx* sp. 1 and *?Lynx* sp. 2 are all of about the same age (Teilhard & Leroy 1945). The available evidence suggests that they are separable into two groups, particularly if Teilhard was correct in believing that *L. shansius* should be separated into two groups. The one group would consist of those *L. shansius* which are similar to the type specimen (which is the only specimen for which Teilhard supplies sufficient measurements) and *?Lynx* sp. 2. These resemble *L. lynx* in the relationship between LM_1 and LP_4 (Fig. 21). The other group would consist of *?Lynx* sp. 1 and (hypothetically) the remaining *L. shansius.* The first of these resembles *L. issiodorensis* in the

relationship between LM_1 and LP_4 (Fig. 21). This still leaves *F. teilhardi* and *F. peii* to consider. These differ in age, the former species being the younger. They may represent a side branch in the evolution of Chinese lynxes. The presence of P^2 does not imply that they cannot be lynxes (Glass & Todd 1977). It should be emphasized that the above statements are highly speculative. In order to determine the true relationships with any degree of accuracy, a re-study of the original material is necessary.

The main line of lynx evolution in China proceeded from *L. issiodorensis* to *L. lynx* (with the two groups mentioned above as possible intermediates) during the Villafranchian. In the late Pleistocene, *L. lynx* spread westward towards Europe, where it began to appear as a member of the fossil communities in the Eemian. Morphologically, the evolution from *L. issiodorensis* to *L. lynx* was characterized by a decrease in the skull size, an increase in the relative size of the extremities (Kurtén 1978), and a broadening of the precarnassial teeth (Figs 14, 15, 21). This last feature, I suggest, is an adaption to a change in the type of prey and the portion consumed. *L. lynx* subsists mainly on a diet of roedeer (*Capreolus*), when possible (Jonsson 1979b). In feeding *L. lynx,* particularly the female with kittens, consumes most of a prey animal, including the long bones (Jonsson pers. comm.). I suggest that the broad precarnassial teeth may be an adaptation for crushing bones, somewhat along the lines of, but on a smaller scale than, the condition observed in hyaenas.

One other feature in the evolution of the lynxes should be mentioned in connection with *L. lynx.* This is the development of the metaconid-talonid complex of the M_1. The evolutionary significance of this feature has been discussed by Kurtén (1963). I wish to comment on the possible function of such a feature.

It has been seen that one of the major differences between *L. lynx* and *L. issiodorensis* is that the former has a smaller skull (Kurtén 1978). This reduction in skull size must have been accompanied by a reduction in the size of the attachment areas of the masticatory muscles and consequently a reduction in the strength of these muscles. This in turn led to a reduction in biting strength. As already mentioned, the preferred prey of *L. lynx* is the roedeer. It seems to me likely that *L. issiodorensis* also preferred prey of about this size; it is at least unlikely that it took prey much larger than roedeer. This means that, despite the reduction in the strength of the bite, *L. lynx* probably brings down prey of the same size

as was brought down by *L. issiodorensis*. I suggest that this reduced strength had to be compensated for, and that the compensatory mechanism was the development of the metaconid-talonid complex and later of M_2, as shown by Kurtén (1963). Through occlusional experiments with clay and analysis of the wear facets, I have found that the development of the metaconid-talonid complex and of M_2 serves to increase the length of the cutting section of the tooth row, and to decrease its distance from the jaw joint. This last feature should serve to increase the shear of the bite, and thus to compensate for the decreased biting strength. It is also possible that the increased cutting region of M_1, and the development of M_2 may serve to compensate for the decrease in cutting length brought about by the broadening of the precarnassial teeth.

In the last 200 000 years, *L. lynx* probably also spread eastwards from central Asia into North America, and gave rise to *L. canadiensis*, the first appearance of which is either Sangamonian or early Wisconsinan (Kurtén & Anderson 1980, and also this paper). The morphological relationships between these species have been discussed elsewhere (Kurtén & Rausch 1959). The most obvious differences between *L. lynx* and *L. canadensis*, however, is that of size. I suggest that the reason for this size difference lies in the types of prey eaten by the two species. *L. lynx* prefers prey the size of roedeer, whereas *L. canadensis* subsists on a diet composed almost exclusively of snowshoe hare. When *L. lynx* reached North America no prey the size of roedeer was available in the areas first colonized. The animal nearest in size to the original prey was the hare. From the viewpoint of bioenergetics the decrease in size must clearly have been advantageous to the lynx, given the smaller size of its prey. Other evidence for the adaptation of *L. canadensis* to hare hunting is that it has a greater percentage of successful attacks on hares than does *L. lynx* (Matjuschkin 1978).

The Blancan of North America presents a highly complex situation in the evolution of the lynxes. The lynxes from the Old World apparently reached North America in the Pliocene. In this connection it is significant that the first recorded appearance of the genus in North America is from Cita Canyon, which lies just below the Gauss-Matuyama geomagnetic event (Lindsay et al. 1974). This would make the age of the Cita Canyon fauna somewhere around 2.4—2.5 Ma. This correlates closely with the postulated 2.6 Ma. dispersal event of Lindsay et al. (1980), thus providing independent evidence for their contention
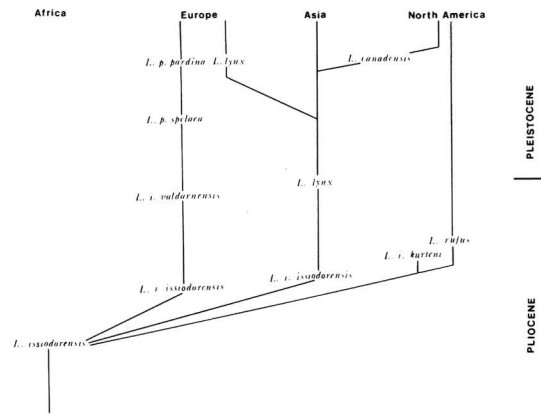

Fig. 29. Suggested phylogeny of *Lynx*.

Leaving aside *Felis lacustris* and *F. rexroadensis* for the moment, lynxes are represented in the Blancan by *L. issiodorensis kurteni* and *L. rufus*. The first species apparently died out rapidly, while the second is still extent in North America today. Once again it is the smaller species that has survived. In this case also I suggest that the mechanism was competition, specifically with felids of the puma group. An intermediate position between the pumas and the lynxes is held by *F. rexroadensis* and *F. lacustris*. Into the later of these species must surely be assimilated the Cita Canyon material (Figures 14, 19) ascribed by Savage (1960) to *F. aff. F. issiodorensis*. From Figure 19 it is also apparent that *F. lacustris* cannot be included in the lynx group. Given the apparently close relationship between *F. lacustris* and *F. rexroadensis* (Savage 1960, Bjork 1970), the latter species would also appear to be excluded from the lynx group, despite certain similarities found by Glass & Martin (1977) and confirmed in this study (Fig. 17).

It remains to discuss the affinities of *C. caracal*. The analyses show that this species differs significantly from the other species discussed here (Figs. 12, 15, 18, 21, 26). I believe that these differences are sufficient to warrant generic distinction. There is no positive evidence for any close phylogenetic affinities between the lynxes and *C. caracal*, either. Indeed, if we accept the suggestion made by Hendey (1974) that *C. caracal* is related to *F. obscura*, this implies that the phylogenetic relationship between *C. caracal* and the lynxes may be very distant. Unfortunately, the available material of *F. obscura* is not sufficient to allow any positive assertions to be made con-

cerning its relationships. The present evidence shows that *F. obscura* differs from the lynxes chiefly in the shorter P³ (Fig. 19).

A summary of the evolution of the genus *Lynx* as interpreted in this paper is presented in Fig. 29.

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