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## Quasi-continuous variation of the second upper premolar in *Felis bengalensis* Kerr, 1792 and its significance for some fossil lynxes

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### Introduction

*Felis (Prionailurus) bengalensis*, the leopard cat, is distributed throughout the Far East, in the Amur Basin and along the coast of the Sea of Japan northward to approximately 51° N latitude, westward to Blagoveschensk in the USSR, and southward in Korea, China, Tibet, Indochina, Burma, Nepal, India, northwestern Pakistan, Sumatra, Bali, Java, Borneo, and the Philippine Islands (NOVIKOV 1962; ALWIS 1973). This wide distribution makes the species ideal for studies of geographic variation, especially in regard to those characters which have been important in felid systematics.

The absence of P2 in *Lynx* has generally been regarded as diagnostic for distinguishing *Lynx* from *Felis* (TEILHARD DE CHARDIN and LEROY 1945; SAVAGE 1960; KURTÉN 1963). POCKOCK (1917) forcefully suggested, however, that this was a dubious character on which to separate the two taxa. Instead, he preferred to raise them to the generic level on the basis of the presence, in *Lynx*, of the relatively slender nasal branch of the premaxillae, and the thinner, less depressed and sharper postorbital processes, as well as the shape of the palate and the more anterior placement of the first large upper premolar (P3). The dubious nature of P2 as a diagnostic character is supported by the universal absence of P2 in *F. (Otocolobus) manul* (POCKOCK 1951). In addition, SEARLE (1959) reported that P2 was absent in 21.9 per cent ( $n = 32$ ) of *Felis catus* from Singapore, which is not significantly different from the value of 22.6 per cent ( $n = 31$ ) obtained by TODD et al. (1974) for *F. catus* in Caracas, Venezuela and 23.6 percent ( $n = 89$ ) for *F. catus* from northern Mexico (TODD and GLASS, MS) but much higher than the 3.4 per cent ( $n = 290$ ) reported by BATESON (1894) in England.

This paper is, apparently, the first report of relatively frequent polymorphism of P2 in any other wild felid excepting *Felis caracal*, where the absence of P2 is the

normal condition (POCOCK 1917; GLASS, unpub.). At the present time, we are studying other species of Recent Felidae to determine the extent of P<sup>2</sup> polymorphism. This paper discusses the validity of P<sup>2</sup> as a diagnostic character in the fossil record.

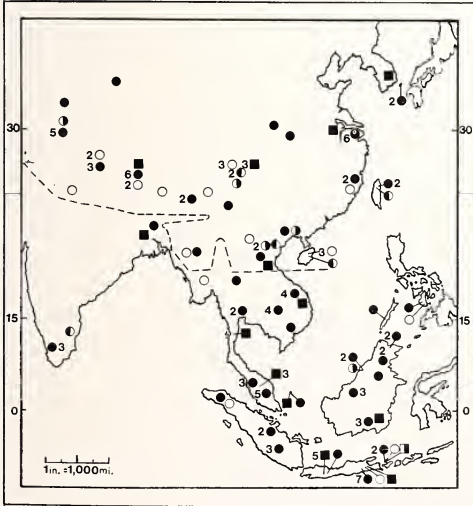
## Material and methods

One hundred and sixty skulls of *F. bengalensis* were examined for the presence or absence of P<sup>2</sup>. The sample consisted of 112 specimens from the British Museum of Natural History (BMNH; 97 adults, 15 juveniles), nine from the Museum of Comparative Zoology (MCZ; 5 adults, 4 juveniles), 36 from the National Museum of Natural History (USNM; 28 adults, 8 juveniles), and one adult from the American Museum of Natural History (AMNH) and two adults from the Field Museum of Natural History (FMNH).

In examining the skulls, care was taken to separate those individuals that had lost the second upper premolar during life from those which had never developed the tooth. This was usually not very difficult, since the alveoli in the former tend to be obvious. Any skulls for which the absence of the tooth was questionable were assumed to have possessed P<sup>2</sup> during life.

The museum number, sex and collecting locality of each individual were recorded from the museum tag and the specimens were aged as adult or juvenile. Juveniles were defined by the presence of deciduous dentition. Adults were further subdivided into young and mature adults. The two groups were classified on the basis of the relative width of the postorbital constriction, which KURTÉN and RAUSCH (1959) showed to be wider in younger lynxes and narrower in older individuals. This tendency for relative, as well as absolute, narrowing of the postorbital constriction also seems to be an ontogenetic trait of the entire family. Other characteristics considered in placing an individual in an age category were the degree of ossification of the cranial sutures and the development of the temporal and sagittal crests. This was done to test null hypothesis that the absence of P<sup>2</sup> was due to accidental loss during life rather than representing ontogenetic development. In the former case, older adults might be expected to show a greater absence of P<sup>2</sup> than younger adults.

The locality from which each specimen was collected was plotted on a map (Fig. 1) and the occurrence of P<sup>2</sup> noted in relation to presumed geographic barriers. Six specimens, including one lacking P<sup>2</sup> bilaterally, were not plotted because of insufficient locality data.



Map showing the locality of the specimens of *Felis bengalensis* which were examined for the presence or absence of P<sup>2</sup>. Circles indicate adults, squares represent juveniles. A solid symbol represents a specimen having P<sup>2</sup> bilaterally, open symbols indicate the lack of P<sup>2</sup> bilaterally. Halfclosed symbols represent the unilateral presence of P<sup>2</sup> on the darkened side. The dotted line indicates the border between the northern and southern samples as defined in the text

The test for homogeneity of a binomial distribution (SNEDECOR and COCHRAN 1971) was used to compare the frequency of P<sup>2</sup> in various populations sampled. Results were considered significant at  $P < 0.05$  for one degree of freedom in all calculations. The frequency of P<sup>2</sup> in the juveniles from south of the Himalayas, the Chin Hills, the Thangla Range and the northern border of the Annam Cordillera (referred to collectively as the southern sample)

was compared with the frequency of the character in the remainder of the juvenile sample (referred to as the northern sample). In addition, the following samples were also tested: The northern adult sample and the southern adult sample, the southern adult sample and the entire juvenile sample, and the northern adult and the entire juvenile sample.

## Results

One hundred and thirty-three individuals were classified as adults. Thirty-nine were females, 50 were males and 44 were undetermined. Twenty adults were considered young (7 females, 6 males, 7 undetermined). There was no significant difference for

Table 1

### Specimens of *Felis bengalensis* showing absence of P2

Presence of P2 indicated by +, absence by —. M = Male, F = Female, ? = Sex not determined. P2 is absent in 25.6 % of the adult females, 23.4 % of the adult males, and 25.0 % of those where sex could not be determined

Museum Number	Sex	Age	Locality	P2	
				Right	Left
BMNH 48.8.14.6	?	Adult	India	-	-
BMNH 58.11.13.4	?	Young	Nepal	-	-
BMNH 50.528	?	Adult	Upper Burma	-	-
BMNH 33.3.1.21	M	Adult	Tigu-Shola, Palni Hills	+	-
BMNH 32.3.1.7	?	Adult	Hain Gyan, Chin Hills	-	-
BMNH 26.50.8.28	M	Adult	Jannsar, United Provinces	-	-
BMNH 32.3.1.25	F	Adult	Kumaon, United Provinces	-	-
BMNH 42.44	?	Adult	Bhutan	-	-
BMNH 63.358	M	Adult	Hatia, Arun River	-	-
BMNH 79.11.21.626	M	Adult	Kumaon	-	-
BMNH 18.2.2.2	?	Adult	Kashmir	+	-
BMNH 51.186	M	Adult	Baram, Sarawak	-	+
BMNH 40.381	F	Young	Surabaya, Java	-	-
BMNH 36.5.18.4	M	Juvenile	Gilimanoek, N.W. Bali	-	+
BMNH 36.5.18.5	M	Young	Prapatagoeng, N.W. Bali	-	-
BMNH 97.5.2.11	?	Adult	Negros, Philippines	-	-
BMNH 99.6.12.1	?	Adult	Deli, Sumatra	-	-
BMNH 32.3.1.12	M	Adult	N. of Toungoo, Burma	-	-
BMNH 25.1.1.30	F	Adult	Ngai-Tio, Tonkin	-	+
BMNH 27.12.1.70	F	Adult	Backan, Tonkin	+	-
BMNH 27.12.1.66	M	Adult	Backan, Tonkin	+	-
BMNH 70.7.18.25	?	Adult	Formosa	-	+
BMNH 54.31	F	Adult	Kouang-Tcheou-Wan, China	+	-
BMNH 55.585	?	Adult	Kuanhsien, Szechuan	-	+
BMNH 10.4.25.5	F	Adult	Mt. Wuchi, Hainan	-	-
USNM 254687	F	Young	Tseo Kiago, Szechuan	+	-
USNM 240484	F	Young	Lai Chau, French Indochina	-	-
USNM 241191	M	Adult	Suifu, Szechuan	-	-
USNM 252590	F	Young	Huang Jia Keo, Szechuan	-	+
USNM 252589	F	Adult	Huang Jia Keo, Szechuan	-	-
USNM 254352	?	Young	Suifu, Szechuan	-	-
MCZ 24846	M	Adult	Yenping, China	-	-
AMNH 27589	M	Adult	Mt. Wuchi, Hainan	-	-
FMNH 39338	M	Adult	Nodoa, Hainan	-	+
FMNH 39339	M	Adult	Nodoa, Hainan	-	-

the frequency of P2 between young and mature adults ( $X^2 = 0.18$ ,  $P < 0.5$ ) so the two populations were pooled and the null hypothesis that the absence of P2 is due to accidental loss during life was tentatively rejected.

Thirty-four adults (25.6%) displayed absence of one or both P2's (Table 1); twenty-two (16.5% of the 133) lacked P2 bilaterally, five (3.8%) lacked P2 on the right side only, and seven (5.3%) lacked P2 on the left side only.

The northern juvenile sample consisted of nine individuals. None lacked P2. A sample of 17 individuals represented the southern juvenile population, of which only one (BMNH 36.5.18.4) lacked P2. This individual lacked P2 unilaterally. There was no significant difference between the juvenile samples ( $X^2 = 0.55$ ,  $P < 0.1$ ), therefore, due to the high degree of homogeneity throughout the juvenile sample, juveniles were excluded from calculations of geographic variation of P2 and they were combined for calculations comparing adult and juvenile samples.

Sixty-five adults comprised the sample representing the northern adult sample and one or both P2's were absent in 26 specimens (40%). The southern adult sample contained 62 skulls, with seven individuals lacking one or both P2's (11%). There is a highly significant difference between the two samples for the absence of P2 ( $X^2 = 11.86$ ,  $P < 0.005$ ).

There was no significant difference for the frequency of P2 when the southern adults were compared to the total juvenile sample ( $X^2 = 1.23$ ,  $P < 0.1$ ). A highly significant difference was found, however, when northern adult and total juvenile samples were compared ( $X^2 = 11.63$ ,  $P < 0.005$ ).

## Discussion

Many characters of an organism are manifested in discontinuous patterns (e. g., resistance to disease, litter size, presence or absence of organs). Most such characters show a polygenic inheritance like that of a continuously varying character with the exception that there is a physiological threshold level below which the character does not develop and above which it is manifested (FALCONER 1960). This pattern, known as quasi-continuous variation, was described by GRÜNEBERG (1952) in a study of variation found within inbred strains of laboratory mice. One of the characters examined was the variable absence of the third molars (GRÜNEBERG 1951). He hypothesized that if the tooth germ size was below the threshold level at some critical stage of development the tooth failed to develop any further (GRÜNEBERG 1951; SEARLE 1954a, 1959).

GRÜNEBERG (1952) found a number of characteristics which most quasi-continuous characters shared. Among these were: 1. The character affects both sexes about equally, 2. it may be symmetrical or present on only one side, and 3. when the character is present it is capable of graded expression. Both GRÜNEBERG (1952) and SEARLE (1954a, 1959) stressed that the environment "... in the widest sense of that word ..." (GRÜNEBERG 1952), plays an important role in the manifestation of the character. GRÜNEBERG (1951) found a strong tendency for "bunching" of the abnormal character within litters of the same mother, suggesting that a variable prenatal environment was responsible for the absence of the third molars. It was later shown (SEARLE 1954b) that postnatal factors could also influence the development of these characters. This suggests that microenvironment, prenatal and postnatal nutrition, and other highly variable factors may influence the presence or absence of some particular character.

The present data seem to fit the observations of quasi-continuous characters discussed by GRÜNEBERG (1952): Approximately equal sex ratios and variable expres-



sion (Table 1). Although the size of each P2 was not measured, each was ranked as rudimentary (present as a disorganized piece of enamel), very small (single rooted with a simple crown), small (suggestion of double root or crown), and medium (double root and/or double cusp). These data, summarized in Table 2, show a graded expression of P2. They are in agreement with GRÜNEBERG's (1952) observations that as the character approaches the hypothetical physiological threshold (i. e., rudimentary size class) the frequency becomes very low. While the absence of P2 in *F. bengalensis* cannot be positively considered a case of quasi-continuous variation without experimental breeding results, we believe that the hypothesis is consistent with the available data.

The interactions of genetic and environmental factors on the presence or absence of P2 are unknown in *F. bengalensis*, although GRÜNEBERG's (1951, 1952) and SEARLE's (1954a) studies suggest that the role of genes is to determine the approximate size of the germ tooth which is then subject to strong modification by prenatal and postnatal development of the individual. The lack of replacement of the deciduous second premolar (DP2) by P2 in the northern sample suggests that postnatal environmental influences may be particularly strong. SLAUGHTER et al. (1974)

report that *Galicitis* has an unreplaced DP1/dp1, the loss being concomitant with the shortening of the face. If the same is true for northern *F. bengalensis* (i. e., shortening of the muzzle), it may be that there is a selective advantage to reduced surface area in that extremity to slow heat loss in the colder northern climate (Allan's Rule). This would explain the significant differences found between the frequencies of P2 in the northern adult sample and the southern adult sample and juvenile samples.

Insufficient data are available from the northern portion of the range to determine whether the P2 frequency decreases with increasing latitude or whether its manifestation in the Himalayas represents a large, but isolated, gene pool. The high frequency of P2 in cats from around the mouth of the Yangtze River (Figure 1) does not equivocate the former hypothesis. This is a lowland area whose climate is ameliorated by close proximity to the East China Sea. In support of the former hypothesis, NOVIKOV (1962, Fig. 167) illustrates a skull of *Felis euphilura* (= *F. bengalensis*) with P2 absent and STROGANOV (1969) reports that, "In adults this tooth usually disappears . . .", which suggests that the loss of P2 is not restricted to the Himalayan region.

The localities of the seven individuals of the southern sample which lack P2 can be grouped into three, nonexclusive categories: Those associated with mountainous regions (e. g., Palni Hills of India, the Philippine island of Negros, and the Iran Mountains of Sarawak), island populations, and large trading cities where specimens may have been purchased from professional collectors.

While environmental extremes in tropical montane regions may not be as adverse,

Table 2

Frequencies of ranked size classes of P2 in adult  
*Felis bengalensis*

Low frequencies in rudimentary size class suggests the presence of a threshold effect for the character (See text)

Degree of Development	Number of Teeth
Absent	58
Rudimentary	4
Very Small	53
Small	97
Medium	56

in terms of absolute variation, as those found in temperate regions, JANZEN (1967) suggests that their relative force on the animals which have evolved in a tropical region may be particularly strong. Thus, presumably, tropical mountain environments could provide sufficient stimulus for the loss of P<sub>2</sub> in the portions of the southern population which inhabit montane areas, if postnatal environment plays a major role in the expression of P<sub>2</sub>.

IMAIZUMI (1967) describes eight specimens (skins and skulls) from Iriomote Island 200 km east of Formosa for which he proposes a new genus and species, *Mayailurus iriomotensis*. LEYHAUSEN does not consider this population generically distinct from *Prionailurus* (= *Felis*) but recognizes it as distinct at the species level (IMAIZUMI, pers. comm.). While IMAIZUMI (1967) emphasizes the strong resemblance of the Iriomote Island form to the Korean or Tsushima race of *F. bengalensis*, neither he nor LEYHAUSEN consider the conditions of the environment in which the animals live. Iriomote Island is small, less than 300 km sq. The cat is taken, not infrequently, by natives in traps and was subjected to extreme doses of DDT after 1945 which exterminated the entire population of domestic cats on the island (IMAIZUMI 1967). In all probability, what was originally a small population has been subjected to extreme selective pressures with the attendant possibility of genetic drift. TODD (1966) and TODD and BOSSERT (1969) discuss the genetic drift of metrical and nonmetrical characteristics (including lack of development of permanent dentition) that has accompanied the decrease in the population of Indian lions. It does not seem unreasonable to suspect that island populations of *F. bengalensis* may show similar tendencies toward genetic drift with the possible decrease from the mainland P<sub>2</sub> frequencies as in the 4 adult specimens from Hainan island where seven of the possible eight (87.5%) P<sub>2</sub>'s are absent, or even fixation for the absence of P<sub>2</sub>, as is found in the "Iriomote cat".

While the validity of the presence or absence of P<sub>2</sub> as a diagnostic character is questionable it is not of considerable importance to the systematics of modern felids because of the presence of other systematic characters. However, the range variability present in the Felidae have posed problems in interpreting fossil records (BRONGERSMA 1935) and it is only after series of fossil specimens have been collected that characters can be chosen as diagnostic.

The occurrence of P<sub>2</sub> to distinguish between *Felis* and *Lynx* has been of particular use in classifying the Chinese fossil material of *Felis issiodorensis*. KURTÉN (1963, 1968) has proposed that *F. issiodorensis* is the most recent common ancestor of the Old World lynxes. It has been found in Europe (KURTÉN 1963), China (TEILHARD DE CHARDIN and LEROY 1945), Africa (HENDEY 1973, 1974) and North America (SCHULTZ and MARTIN 1972). A closely related form (*Felis* ?aff. *issiodorensis*) is also reported from North America (SAVAGE 1960). The two Chinese forms of special interest are *Felis shansius* (= *F. issiodorensis*) and *Felis peii*. The distinguishing characteristic is the presence of P<sub>2</sub> in *F. peii* (TEILHARD DE CHARDIN and LEROY 1945; KURTÉN 1963). We suggest that *F. peii* and *F. shansius* represent a case of intra-specific variation in the same manner as found in *F. bengalensis*. It is known that P<sub>2</sub> was polymorphic in *Felis rexroadensis* (STEPHENS 1959) which was, presumably, ancestral to *F. issiodorensis* (KURTÉN, 1963, 1968) and that P<sub>2</sub> is sometimes retained in *F. caracal* (POCOCK 1917). It would be difficult to accept that *F. issiodorensis* would completely lack a character (P<sub>2</sub>) which is present in both its ancestors and its descendants.

*Felis rexroadensis* is known from three specimens taken from the type locality in Meade County, Kansas. The upper tooth rows are present in all three specimens; although the condition of one (UMMP 34196) makes it difficult to determine the presence or absence of P<sub>2</sub>. UMMP 29644 clearly shows the presence of the P<sub>2</sub> alve-

olus which is single rooted as in most of the *Prionailurus* specimens; UMMP 34195, the holotype, shows no trace of an alveolus or any porosity in the region which is normally occupied by P2. While the condition of UMMP 34196 is equivocal, P2 also seems absent. STEPHENS (1959) originally stated that P2 had been present in UMMP 34195, but had been lost with closure of the alveolus taking place. No evidence is cited (STEPHENS 1959) to support this interpretation of the data. Keeping in mind the quasi-continuous nature of P2 we suggest, that *F. rexroadensis* shows the same polymorphism for P2 that is exhibited by *F. catus*, *F. bengalensis* and *F. caracal* and that UMMP 34195 never developed P2.

To retain *F. peii* as a species distinct from *F. shansius* on the basis of such a polymorphic character seems to be of dubious merit. We suggest that the taxonomic status of *F. peii* be reviewed with consideration given to the view that *F. peii* is a synonym of *F. shansius* (= *F. issiodorensis*) and that the presence or absence of P2 represents a long standing polymorphism in *Felis rexroadensis*, as well as its derivative species.

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#### Summary

*Felis (Prionailurus) bengalensis* is distributed throughout much of the Far East from the Equator to 51° N latitude. Throughout its range this species shows geographic variation for the presence or absence of the second upper premolar (P2), the absence of which is often considered diagnostic for the subgenus *Lynx*. Examination of 160 specimens shows the average frequency of occurrence of P2 to be 74.4 per cent, but significant differences in the occurrence of P2 were found between samples from south of the Himalayas and associated mountain ranges and samples from north of this zone. Significant differences were also found when northern adult and juvenile samples were compared but no difference was found when southern samples of adults and juveniles were compared. The presence or absence of P2 in individuals appears to be an example of quasi-continuous variation, a phenomenon which is strongly dependent upon environmental factors. As a result, the use of P2 as a diagnostic character is suspect. The occurrence of P2 has been of significance for the interpretation of the Early Pleistocene fossil material from China associated with *Felis issiodorensis*. The distinguishing characteristic separating *Felis peii* from *Felis shansius* (= *F. issiodorensis*) has been the presence of P2 in *F. peii*. The material described as *Felis rexroadensis*, the ancestor of *F. issiodorensis*, also exhibits polymorphism for P2, which is interpreted as quasi-continuous variation, casting further doubt on the validity of distinguishing *F. peii* from *F. shansius* solely on the basis of the presence of P2.

#### Zusammenfassung

Quasi-kontinuierliche Variation des zweiten oberen Prämolaren von *Felis bengalensis* Kerr, 1792 und zur Bedeutung dieser Variabilität für die Klassifikation einiger chinesischer Feliden  
*Felis (Prionailurus) bengalensis* ist in ganz Ostasien vom Äquator bis 51° nördlicher Breite verbreitet. Im gesamten Verbreitungsgebiet dieser Art fehlt der zweite obere Prämolare (P2)



in geographisch unterschiedlicher Häufigkeit. Das Fehlen des  $P^2$  wird oft als diagnostisches Merkmal für die Untergattung *Lynx* angesehen. An 74,4 % von 160 Schädeln der Leopardkatze war der  $P^2$  vorhanden, die mittlere Häufigkeit variierte jedoch signifikant zwischen Schädeln aus der Gegend südlich des Himalajas und benachbarten Gebirgszügen von Schädeln nördlicher dieser Zone. Signifikante Häufigkeitsunterschiede traten auch zwischen Altersklassen im nördlichen Verbreitungsgebiet auf, doch konnten solche Unterschiede bei südlichen Vertretern der Art nicht nachgewiesen werden. Das Vorhandensein oder Fehlen des  $P^2$  bei verschiedenen Individuen scheint ein quasi-kontinuierliches Variationsmerkmal zu sein, das möglicherweise stark von Umweltfaktoren abhängt. Eine solche Umweltabhängigkeit kann die geographische Variation der  $P^2$ -Häufigkeit erklären. Dank dieser Variation verliert das fragliche Merkmal an diagnostischem Wert. Das Vorhandensein des  $P^2$  war für die Interpretation früher pleistozäner chinesischer mit *Felis issiodorensis* assoziierter Fossilien von Bedeutung. In diesem Material wurden Schädel mit  $P^2$  als *Felis peii* von solchen ohne  $P^2$  als *Felis shansius* (= *F. issiodorensis*) abgetrennt. Fundmaterial von *Felis rexroadensis*, dem Vorläufer von *F. issiodorensis*, zeigt ebenfalls Polymorphismus für das Vorhandensein von  $P^2$ , was auch als quasi-kontinuierliche Variation betrachtet wird. Dieser Befund verstärkt die Zweifel an der Berechtigung *F. peii* von *F. shansius* allein auf der Basis fehlender  $P^2$  zu differenzieren.

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## The ovary of the Thomson's Gazelle

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### Introduction

Thomson's gazelle, *Gazella thomsoni* Guenther, 1884, is a small wild ungulate within the group of antelopes (BROOKS 1961). The female weighss approximately 23 kg., while the male weighs 29 kg. It is abundant in open grasslands of Kenya.

Breeding in Thomson's gazelle occurs throughout the year, but the highest number of pregnancies noted occurred between August and October during the short rains. This, however, coincided with the period during which most of the specimens were collected. BROOKS (1961) and HOPCRAFT (1970) reported biannual breeding. ROBINETTE and ARCHER (1971) observed two lambing peaks in May and November, while BROOKS (1961) noted a peak in April.

At present, little information is available on the duration of gestation and on the birth weight of Thomson's gazelle. HOPCRAFT (1970) recorded a gestation period of three months and three weeks. WEHR (1971) observed a period of 222—224 days. The Thomson's gazelle is monotocous bearing only one offspring per gestation.

### Materials and methods

The animals used in this study were collected from Kekopey Ranch 36°E, 1°S, Kajiado 37°E, 2°S and Maralal 37°E, 1.5°N in Kenya:

Ovaries used for histology were measured, weighed and fixed in Bouin's fluid, dehydrated, and embedded in paraffin wax. The reproductive tracts for gross anatomy were

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