

A NOTE ON THE SYSTEMATIC AND EVOLUTIONARY RELATIONSHIPS OF *FELIS TEILHARDI* PEI

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In 1934, a number of lynx-like fossils (several lower jaws, one maxilla, and some limb bones) were described by Pei from the *Sinanthropus* deposits of Choukoutien. He noted the generally lynx-like characters of the dentition, but the presence of a small alveolus for P² in the maxilla (this tooth is absent in lynxes) caused him to refer the form to a new species, *Felis teilhardi*.

One of the most interesting features of this species is the variation seen in the lower carnassial. According to Pei (op. cit., p. 141), the development of the talonid is quite variable. Some specimens have practically no talonid at all, most appear to have a small talonid distinctly set off by a notch from the blade, and furthermore a type with a small metaconid intervening between talonid and protoconid is represented. This last-mentioned condition is similar to that invariably seen in the living *Felis lynx*, but the metaconid-talonid complex seems to be somewhat more strongly developed in the modern form. Perhaps this variant of *Felis teilhardi* might be most closely compared with types like *Felis rufus* and *Felis caracal*, in which the complex is relatively weaker than in *Felis lynx*.

In the European Pleistocene there appears to have existed one population which shows precisely the same type of variation in the lower carnassial. This is the Cromerian "lynx", of which I have had an opportunity to study two specimens, one from Mauer (Germany), previously described by Voelcker (1930) and preserved in the Geological Institute of Heidelberg University, and another from Blanzac-Solilhac (France), now in the Natural History Museum, Basel. Apart from these, a good Villafranchian sample of *Felis issiodorensis* was studied in the Basel Museum, and a large sample of Recent Northern lynx was available in museums in Helsingfors (Finland) and Lund (Sweden).

The specimen from Mauer, a lower jaw, has the metaconid-talonid complex fully developed, though weaker than in the living *Felis lynx* and about similar to that seen in *Felis rufus*. The other Cromerian jaw from Europe has no trace of a metaconid, but there is a talonid which is somewhat indistinctly set off from the blade. The conditions in the sample of *Felis teilhardi* shows that such a variation could be realized within a single population, and hence there is nothing to preclude reference of the Mauer and Blanzac-Solilhac jaws to one species.

Now we cannot expect only two specimens to reveal the full range of variation in a population, but the Mauer jaw resembles one of the extreme types in *Felis teilhardi* and

the Blanzac-Solilhac jaw is similar to the modal type of the Choukoutien species. It seems probable that the variation range of the European Cromerian "lynx" was about the same as in *Felis teilhardi*. Further comparison with the variation ranges found in pre- and post-Cromerian samples in Europe strengthens the view that *Felis teilhardi* resembles the Cromer "lynx" particularly closely.

The very early Villafranchian *Felis issiodorensis* from Etouaires (Mt. Perrier), of which there is an excellent sample in the Basel collection, exhibits only one type of M_1 , without distinctly demarcated talonid and no trace of a metaconid. As this character is similar in all the six specimens seen, this may surely be taken as the modal type represented in the population, and perhaps the only type. In the later Villafranchian samples known to me (from the Pardines stage of Mt. Perrier, from Saint Vallier and Val d'Arno), there is a variation from this type to the type with a distinct talonid, but no specimen with a metaconid like the Mauer and extreme *Felis teilhardi* type occurs in the material available to me (see also Viret, 1954).

Finally, in modern and late Pleistocene *Felis lynx* known to me, both metaconid and talonid are always well developed.

We may thus arrange the successive populations in a temporal series which shows that the evolution of the population variation proceeded step by step in the direction of a

METACONID-TALONID VARIATION AND EVOLUTION

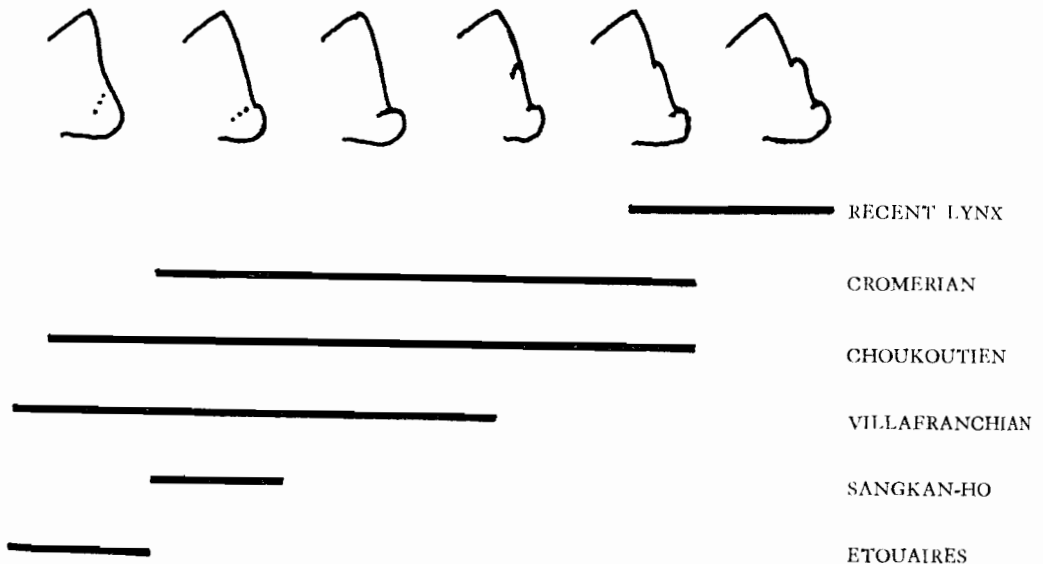


Fig. 1. Diagrammatic representation of the hind edge of the protoconid in M_1 of Pleistocene and Recent lynxes, and the variation range in different populations. "Villafranchian" here signifies the later Villafranchian of Europe; Etouaires is considered as basal Villafranchian.

larger metaconid-talonid complex (fig. 1). In this series, the population of *Felis teilhardi* agrees better with the Cromerian population of Europe than with any other. Furthermore the specimen from Sangkan-ho, described by Teilhard and Piveteau (1930), agrees with the modal type in the Villafranchian *Felis issiodorensis* of Europe.

These results are in accordance with the correlation of Sangkan-ho with the Villafranchian, generally accepted, and also with the correlation of Choukoutien with the Cromerian suggested by Pei (1939) and later by Kurtén (1956, 1957).

In view of the graded series of steps leading from the condition in the Villafranchian *Felis issiodorensis* to that in the Recent lynx, which is also supported by other transitions of a similarly gradual nature (a detailed report on the European succession will be published elsewhere), it would seem difficult to avoid the conclusion that this is actually a phyletic series and that the modern lynx, with a well-developed metaconid-talonid complex, arose from ancestors lacking these characters. This is in conflict with Dollo's law, which states that characters once lost cannot reappear in their earlier form; yet this is just what happens in the present sequence, for the end result in *Felis lynx* is reminiscent of the condition seen in such early Pliocene cats as *Metailurus*. But Dollo's law is an empirical principle and not a fiat, and hence is subject to revision based on further empirical findings.

The position of *Felis teilhardi* in this evolutionary sequence is identical with that of the lynx from Mauer and Blanzac-Solilhac. The differences between the Chinese and

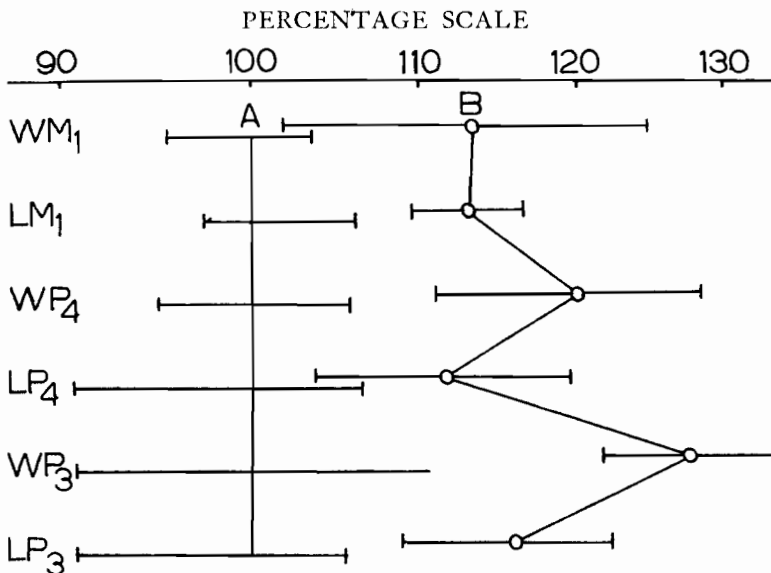


Fig. 2. Ratio diagram (for the method, see Simpson, 1941) comparing means and observed ranges of variation in dimensions of lower check teeth of (A) *Felis teilhardi*, Choukoutien; (B) Cromerian lynx in Europe. Standard of comparison (100 per cent), *F. teilhardi* means, W, width; L, length.

European samples are: Firstly, the Chinese form is somewhat smaller (fig. 2); and secondly, the single known maxilla has a second premolar in *Felis teilhardi*. To be sure, I have seen no maxillae of the European Cromerian form, but P² is lacking both in *Felis issiodorensis* and *Felis lynx*, and may reasonably be expected to have been absent in the Cromerian form as well.

The difference in size is not greater than that between different populations of the living species *Felis lynx*. A "cline" with progressively diminishing size from Northern Europe eastward exists in the living form, for the Canadian subspecies is considerably smaller than the Fennoscandian. An even steeper cline extends from the Fennoscandian to the southern European populations. Choukoutien is further south and east than Europe, and hence a smaller size is just the character to be expected if the two samples are conspecific.

The presence of P² is most likely to be accidental, because the other dental characters seem to suggest a very close relationship between the two samples. Perhaps P² occurred in exceptional specimens of the early Pleistocene lynx populations, as a vestige of ancestral conditions, though no such specimen is so far known to me from Europe. Similar occurrences of supernumerary premolars are known for instance in hyaenas (Kurtén, 1956).

I think it most reasonable to conclude that *Felis teilhardi* is conspecific with the European lynx of the Cromerian, and that this species had a wide Palaearctic distribution on that interglacial, just as *Felis issiodorensis* had earlier and *Felis lynx* has in the present day.

It remains to be considered whether *Felis teilhardi* should be recognized as a distinct species or perhaps merged into either *Felis issiodorensis* or *Felis lynx*, the ancestral and descendant forms respectively. Its intermediate position (e. g.: M₁ intermediate; P³ like *F. lynx*; numerus apparently more like *F. issiodorensis*, judging from Pei's description, "shaft stouter and distal end less expanded than in *Lynx*") is perhaps best signalized by the status of a distinct species. The available name of this species is *Felis teilhardi* Pei, and I hereby place it on record also from Mauer and Blanzac-Solilhac. Further discoveries may necessitate a modification of these views.

If the evolutionary sequence suggested here is taken to be correct, it may also shed some light on the relationships between *Felis teilhardi* and other living members of the subgenus *Felis* (*Lynx*) than the type species. Unfortunately my material is incomplete, but from the stage of development of the metaconid-talonid complexes in *Felis rufus* and *Felis caracal* these would be comparable with the most advanced variants in *Felis teilhardi*. It is therefore possible that these forms arose from *Felis teilhardi* at some time after the Cromerian. Typical *Felis rufus* specimens are known from the American Sangamon (Rancho la Brea, Merriam and Stock, 1932), and the time of speciation (and migration) would therefore lie between the Cromerian and Fемian interglacials.

In concluding, I should wish to express my very sincere gratitude to Dr. Samuel Schaub, Basel, for the generous and invaluable assistance given me in my study of the Basel material.

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德氏林猯 (*Felis teilhardi* Pei) 在分類系統與 進化上的關係

(摘要)

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裴文中 1934 年記述了周口店的許多近似於林猯的化石。由於這種動物在上顎上有一個在林猯上沒有的第二前臼齒的齒槽；因此定為一個新種 *Felis teilhardi*。

這種動物的牙齒的特徵之一是下裂齒的變異。牙齒的齒座 (taloid) 的變化很大。有的沒有齒座，大多數標本都有很清楚的齒座；而且有一些在齒座和原下尖 (protoconid) 間有一小的後下尖 (metaconid)。最後一種與在現生林猯中常可見到的相似，而且發育得更強一些。

在歐洲更新世克魯茂 (Cromer) “林猯”的種羣內，下裂齒也有相似的變異。關於這類林猯，我曾經觀察了德國莫爾 (Mauer) 的和法國白朗薩-砂立海 (Blanzac-Solilhac) 的標本以及維拉方期的 *Felis issiodorensis* 大量的現生北方的林猯標本。

莫爾的標本有很發育的後下尖和齒座，比 *Felis lynx* 的小，大致與 *Felis rufus* 的相似。另一個克魯茂的下顎沒有後下尖的痕跡，有不顯著的齒座。德氏林猯標本中的情形表示這樣的變異在種羣內是存在的。因此莫爾和白朗薩-砂立海的標本屬於同一種是沒有疑問的。

莫爾這個標本與德氏林猯中的極端類型相似，而白朗薩-砂立海的與德氏林猯中一般類型相似。歐洲克魯茂林猯的變異範圍可能與德氏林猯的類似。

愛多埃 (Etouaires) 的 *Felis issiodorensis* 沒有清楚的齒座及後下尖的痕跡。維拉方晚期的標本中有一從這種類型到有一顯著齒座的類型的中間變異。

這連續的種羣的初步排列表示種羣進化的變異逐步向着比較大的後下尖和齒座方向發展 (圖 1)。

從 *Felis issiodorensis* 到現生的林猯之間的等級排列，表示這是一個進化的系統，而且具有很發育的後下尖和齒座的現生林猯是從缺乏這些性質的祖先進化來的。這個與 Dollo 定律相衝突，現生林猯重演了上新世初期貓類 (如 *Metailurus*) 的性質，Dollo 定律只是一個經驗的概括。

德氏林猯與克魯茂的林猯在進化中的位置是相同的，德氏林猯個體較小，多一個第二前臼齒。兩者大小的差別小於現生林猯各種種羣之間的差別。現生種之間有一支從北歐向東個體漸減小的“梯度種” (“Cline”)。在芬蘭斯基的那維亞到南歐的種羣有一支更尖銳的梯度種 (Steeper Cline)。周口店比歐洲更靠東和南，因此，如果是同種的話，較小的個體的性質正可以預料的。第二前臼齒的出現可能是偶然的。類似的額外的前臼齒的出現在鬣狗 (*Hyaena*) 中也有 (Kurtén, 1956)。

根據以上的事實可以得出德氏林猯和克魯茂林猯屬於同種。

還要考慮的問題是 *Felis teilhardi* 應該是一個單獨的種呢？還是歸併到 *Felis issiodorensis* 或歸到 *Felis lynx* 中去？根據它的中間位置， M_1 中等， P^3 與 *F. lynx* 的相似，肱骨與 *F. issiodorensis* 的相似等性質列為一個獨立的種更合適一些，種名就用 *Felis teilhardi* Pei。

如果這個進化順序正確的話，對於 *Felis teilhardi* 和其他除原型以外的 *Felis (lynx)* 亞屬的現生種類之間的關係也提供了些資料。(胡長康節譯)