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Björn Kurtén: On the evolution of the European Wild Cat,
Felis silvestris Schreber

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ON THE EVOLUTION OF THE EUROPEAN WILD CAT,
FELIS SILVESTRIS SCHREBER

BY

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Introduction

Remains of small cats are very rare in lower and middle Pleistocene deposits in Europe. A travel and research grant during the years 1961—1963 from the University of Helsinki/Helsingfors made it possible for me to study some of these fossils. All of the material turned out to be related to the living European Wild Cat (*Felis silvestris*¹), and the suggestion is that the species evolved *in situ* in Europe (and probably neighbouring parts of Asia and Africa). The ancestral species appears to be the Villafranchian *Felis lunensis*.

In order to make the comparisons as detailed as possible, it was found necessary to study representatives of several local populations or subspecies of the recent form. Data on the differentiation within the living species are thus included in the present work, and this aspect seems to me quite necessary for the understanding of its fossil history. Furthermore, a number of fossil samples from the late Pleistocene and Postglacial throw light on the intra-specific differentiation in earlier times and on the histories of local populations.

¹ The sole exception is some Polish material related to the Steppe Cat (*Felis manul*), on which a separate report is being planned.

On this basis, the present paper attempts to give an outline of the descent of the species *Felis silvestris* as known in Europe and neighbouring southwest Asia.

Apart from some incomplete postcranial material, the only small cat fossils that have been available to me from the lower and middle Pleistocene consist of lower jaws or isolated lower teeth. Hence, for the present purpose, the study has been limited to the mandible and mandibular dentition.

Material

Felis lunensis Martelli.

1. The type specimen, a right lower jaw with C and P_3-M_1 , from the late Villafranchian of Olivola, is preserved in Florence under the number IGF 4298 (MARTELLI, 1906, pl. VIII, fig. 3; this paper, fig. 1, pl. 1, fig. A—B).

2. B.M. M 18444, a right P_4 of a small cat in the Savin Collection of fossil mammals from the Forest Bed of East Anglia, is tentatively referred to this species (pl. 1, fig. C). (Under the same number there is also a premolar of a mustelid, at present unidentified.) It comes from the Upper Freshwater Bed at West Runton and thus dates from the Cromerian Interglacial *sensu stricto*.

Felis silvestris Schreber.

Fossil material.

3. Heppenloch Cave, Württemberg. Cast of the original specimen, a left mandible, in the Basel Museum, no. D 338. It carries P_3-P_4 and is broken before and behind these teeth. The fauna of Heppenloch Cave dates from the Holsteinian Interglacial (ADAM, 1959).

4. Lunel-Viel Cave, Hérault. Specimens in the Institute of Geology, University of Montpellier: Nos. 256—258, two right and one left mandibles respectively (see pl. 2, fig. A—B). Unnumbered, front end of left mandible (same as 258?) with C_1 . The age of this fauna seems also to be Holsteinian (see HARLÉ, 1910; personal communication from E. BONIFAY, engaged in new excavations at the site).

5. A sample of late Pleistocene fossils from Germany and Switzerland, referred to below as «Late Pleistocene, Continent». It consists of the following material.

5 a. Freudenthalhöhle at Schaffhausen. Basel Museum B 6354, cast (original in private collection JOOS, Schaffhausen), mandible with P_3-M_1 , described and figured by HELBING (1935). Magdalenian.

5 b. Vogelherd, Württemberg. Geological Institute of the University of Tübingen, right mandible with $C-M_1$, described by LEHMANN (1954). Aurignacian (cave level IV).

5 c. Wolfshöhle: Geological Institute of the University of Bonn, left mandible with P_3-M_1 ; right mandible with $C-M_1$.

6. A sample of late Pleistocene fossils from Great Britain, probably dating mainly from the Würm, as follows.

6 a. Creswell Caves, Derbyshire. Manchester Museum, four right and one left mandibles, all from different individuals; most specimens evidently from Pin Hole Cave. $C-M_1$ present in three mandibles; P_3 absent in one, and only P_3 and M_1 present in one. In one of the specimens there is a hole bored through the hind part of the jaw.

6 b. Ravencliff Cave, Derbyshire. B.M. M 9577—9578, two left mandibles with C-M₁ (pl. 3). The first-mentioned is very much smaller than the other and almost certainly represents a domestic cat, and has been excluded from the statistical computations.

6 c. Kent's Cavern, Torquay. O.M. Q 2067, right mandible with P₃-M₁. B.M. 16710, right mandible with C-M₁ (OWEN, 1946, fig. 67).

6 d. Kinsey Cave, Yorkshire. The Pigyard Club Museum at Settle, left mandible with C-M₁.

6 e. Cat's Hole, Gower. B.M. M 95, right and left mandibles with M₁ and C-M₁ respectively.

6 f. Elsay »Brock«, Caithness. B.M. M 8781, mandible with P₃ and M₁.

7. Fossil material from Palestine, described in KURTÉN (1965). For the present purpose, the sample from the earlier part of the Main Würm has been selected.

8. Subfossil Wild Cat from Denmark, described by DEGERBØL (1933). Although I have not examined this material, the detailed measurements given in DEGERBØL's paper are invaluable for quantitative studies. Two samples have been used:

8 a. Mesolithic (»Azilian«), Sværdborg and Holmegaard.

8 b. Neolithic (»Campignian«), Kassemose, Solager, Vejleby, Klintesø, Faarevejle, Nivaa, Ertebølle, Mejlgaard, Fannerup, Aamølle, and Gjessinggaard. †

Recent material.

9. Scotland, Zoological Museum, Cambridge, 6 specimens; British Museum (Natural History), about 60 specimens (see HALTENORTH, 1953, for specification of most of the material of this and other recent populations). Since this sample is by far the largest homogeneous one available to me, it has been used as a standard of comparison in various respects, although, of course, it represents a marginal population with some traits of its own.

This sample is referred to in table 2 under the subspecific trivial name »*grampia*«, although this does not imply unreserved acceptance of that subspecies.

10. Continental Europe, representing the main population of the nominate subspecies, and distributed as follows.

10 a. Institut für Haustierkunde, University of Kiel. 445 ♂, Bükk-Gebirge, north-east Hungary. 81 (mandible only), no locality.

10 b. Zoological Institute, University of Hamburg. 3211 ♀, 3345 ♂, both from Euskirchen, Rheinland.

10 c. Natural History Museum, Leiden. Württemberg ♀, Siebenbürgen ♂.

10 d. Senckenberg Museum, Frankfurt. 37, Germany; 4802 ♀, Gross Gerau; 4808 ♂, Langen, Hessen; 5651 ♀, Hausen, Taunus; 5837, St. Goar; 9613, Karlsruhe; 9961 ♂, Lorchhausen, Rhein; 11359 ♂, Kammerfort, Rheingau; 16243, Niedensteiner Kopf, Gudensberg, Kurhessen.

10 e. B.M. 1143 d ♀, 1143f ♂, S. Germany; 20.7.4.3. ♂, Kirnbergwald near Tübingen; 11.1.2.104, Ingelheim, Rheinhessen; 19.7.7.2901, 19.7.7.3645 ♂, near Moulins, Mouladin, Allier; 95.11.9.1. ♂ Manonville, M.-et-M.; 95.11.9.2, Salavon, Haute Maine.

11. Southern part of Iberian Peninsula. Natural History Museum, Leiden, Mafra, Portugal. B.M. 2.6.3.3. ♀, Andalusia; 7.12.5.1. ♂, Sierra Morena, Palma del Rio. (Two other skulls, from Andalusia and Coto Doñana, unfortunately lack the lower jaw.) Specimens from Burgos and the Pyrenees lack the characters of the southern population, which is cited in table 2 under the subspecific trivial name »*startessia*«.

12. Palestine and neighbouring area, a sample described in KURTÉN (1965).

Measurements

In general the length of a tooth denotes the greatest length of the crown in an antero-posterior direction, while the breadth is measured at the broadest place of the crown. The length of canine is measured from the base of the enamel on the anterior face of the tooth to the base on the posterior face; the width from the base on the external face in a line at right angles to the length, and also to the long axis of the tooth. The height of the premolars is measured externally, from the incurvation of the enamel at the base. On the carnassial, the height of the paraconid is measured on the anterior face of the tooth, and that of the protoconid externally, from the basal incurvation. The width of M_1 is measured at the broadest point of the crown, not by placing calipers tangential to the external and internal faces along the tooth, which would give a higher value in most cases (because of the curvature of the carnassial blade).

The length of the jaw is measured from the anterior face of the canine to the middle of the posterior face of the condyle. The height of the coronoid process is taken from the ventral side of the jaw vertically from the highest point of the coronoid. The depth of the ramus behind M_1 and at the diastema is always taken at the shallowest place. The length of the diastema is alveolar; that of P_3-M_1 coronal.

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Abbreviations

Abbreviations used to identify collections:

B.M., the British Museum (Natural History).

I.G.F., the Institute of Geology, University of Florence.

O.M., the Oxford Museum.

Abbreviations in the tables:

M, mean

N, number of specimens

O.R., observed range of variation

S.D., standard deviation

V, Pearsonian coefficient of variation

Description of fossil material

Felis lunensis Martelli, 1906

The type specimen of *Felis lunensis* (fig. 1, pl. 1. figs. A—B) comes from Olivola, Val di Magra, and thus dates from the later part of the Villafranchian. The associated fauna includes late elements such as *Hyaena brevirostris* Aymard and a large form of *Ursus etruscus* Cuvier (see KURTÉN, 1963 a). The specimen differs from modern Wild Cat in a number of characters, which taken together warrant fully the specific distinction made by MARTELLI.

Among the characters mentioned in MARTELLI's description is the great length of P_3-M_1 in relation to $C-M_1$. In other words, the diastema between the canine and the premolars is quite short. It is, in fact, shorter than in any specimen of *F. silvestris* in my sample (tables 1—2). The diastema may be short in juvenile individuals, but the type of *F. lunensis* is fully adult, even though the teeth are unworn.

P_3 is characterized by the complete absence of an accessory posterior cusp, a condition that is very rare, if not unknown, in *F. silvestris*. However, as may be noted in pl. 1, fig. A, the hind edge of the protoconid has a slight curvature seemingly foreshadowing the cusp. The aspect may be somewhat similar in certain specimens of M_1 in *F. issiodorensis*, for instance the one figured in KURTÉN, 1963 b, fig. 1 B. There is here a slight deformation of the hind edge of the protoconid, which may foreshadow the metaconid that arose later in the sequence.

The main cusp of P_4 has been broken at the base but appears to be correctly rejoined on to the crown. The relatively great height and short anteroposterior diameter of this cusp, together with the weak development of the anterior and posterior accessory cusps, give this tooth a striking appearance differing from the norm in *F. silvestris*. The small size of the posterior cusp is especially notable.

The canine and carnassial do not differ markedly from the pattern in modern Wild Cat; and the jawbone, as far as preserved, exhibits no distinctive characters. But the teeth seem exceptionally big in relation to the size of the mandible, and this character is not easy to match in fossil or recent *F. silvestris*.

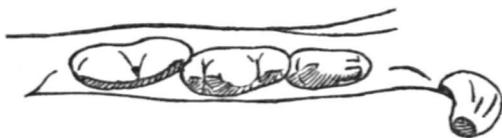


FIG. 1. IGF 4298, *Felis lunensis*, type. Right lower dentition, crown view.
2 times natural size.

TABLE 1. Measurements of lower dentition and mandible in fossil samples of Wildcat (*Felis silvestris* and *F. lunensis*).

	N	O.R.	M	S.D.	V
Length, C ₁					
Late Pleistocene, Britain	8	4.0— 5.8	4.88 ± 0.23	0.64	13.2
» Continent	2	3.9— 5.5	4.7	—	—
Holsteinian, Lunel-Viel	3	4.3— 4.8	4.57 ± 0.15	—	—
Villafranchian, Olivola	1	—	4.5	—	—
Width, C ₁					
Late Pleistocene, Britain	7	2.9— 4.0	3.57 ± 0.15	0.39	10.9
» Continent	2	3.1— 4.1	3.6	—	—
Holsteinian, Lunel-Viel	3	3.4— 3.7	3.60 ± 0.10	—	—
Villafranchian, Olivola	1	—	3.3	—	—
Length, P ₃					
Neolithic, Denmark	24	5.4— 7.2	6.27 ± 0.08	0.39	6.2
Mesolithic, Denmark	3	5.8— 6.7	6.23 ± 0.26	—	—
Late Pleistocene, Britain	10	4.6— 6.9	5.88 ± 0.22	0.68	11.6
» Continent	4	5.5— 7.1	6.15 ± 0.34	—	—
Holsteinian, Lunel-Viel	2	6.4— 6.5	6.45	—	—
» Heppenloch	1	—	7.4	—	—
Villafranchian, Olivola	1	—	5.7	—	—
Width, P ₃					
Late Pleistocene, Britain	10	2.3— 3.3	2.78 ± 0.09	0.30	10.7
» Continent	4	2.5— 3.2	2.88 ± 0.17	—	—
Holsteinian, Lunel-Viel	2	2.8— 3.2	3.0	—	—
» Heppenloch	1	—	3.2	—	—
Villafranchian, Olivola	1	—	2.9	—	—
Height, P ₃					
Neolithic, Denmark	18	4.0— 4.7	4.36 ± 0.05	0.20	4.7
Mesolithic, Denmark	1	—	4.5	—	—
Late Pleistocene, Britain	9	3.3— 4.5	4.06 ± 0.12	0.35	8.6
» Continent	3	4.1— 4.5	4.30 ± 0.12	—	—
Holsteinian, Heppenloch	1	—	4.8	—	—
Villafranchian, Olivola	1	—	3.8	—	—
Length, P ₄					
Neolithic, Denmark	28	6.8— 8.2	7.52 ± 0.08	0.42	5.6
Mesolithic, Denmark	3	7.3— 7.6	7.40 ± 0.10	—	—
Late Pleistocene, Britain	9	6.1— 8.0	7.17 ± 0.19	0.58	8.1
» Continent	4	6.7— 8.8	7.8 ± 0.4	—	—
Holsteinian, Lunel-Viel	3	7.3— 7.7	7.50 ± 0.12	—	—
» Heppenloch	1	—	8.8	—	—
Cromerian, West Runton	1	—	7.9	—	—
Villafranchian, Olivola	1	—	6.9	—	—

	N	O.R.	M	S.D.	V
Width, P ₄					
Late Pleistocene, Britain	9	2.7— 3.9	3.28 ± 0.13	0.39	11.8
» Continent	4	3.1— 4.0	3.55 ± 0.18	—	—
Holsteinian, Lunel-Viel	3	3.4— 3.6	3.50 ± 0.06	—	—
» Heppenloch	1	—	3.8	—	—
Cromerian, West Runton	1	—	3.6	—	—
Villafranchian, Olivola	1	—	3.2	—	—
Protoconid length, P ₄					
Late Pleistocene, Britain	8	3.2— 4.1	3.69 ± 0.11	0.31	8.5
» Continent	4	3.7— 4.5	4.18 ± 0.18	—	—
Holsteinian, Lunel-Viel	3	3.9— 4.0	3.97 ± 0.04	—	—
» Heppenloch	1	—	4.4	—	—
Cromerian, West Runton	1	—	3.9	—	—
Villafranchian, Olivola	1	—	3.4	—	—
Height, P ₄					
Neolithic, Denmark	19	4.4— 5.5	5.12 ± 0.07	0.32	6.3
Mesolithic, Denmark	1	—	5.2	—	—
Late Pleistocene, Britain	7	4.0— 5.3	4.83 ± 0.18	0.47	9.7
» Continent	3	4.5— 5.1	4.83 ± 0.18	—	—
Holsteinian, Heppenloch	1	—	5.7	—	—
Cromerian, West Runton	1	—	5.6	—	—
Villafranchian, Olivola	1	—	5.5	—	—
Length, M ₁					
Neolithic, Denmark	33	7.5—10.0	8.76 ± 0.11	0.62	7.0
Mesolithic, Denmark	5	8.7—10.0	9.30 ± 0.26	0.57	6.1
Late Pleistocene, Britain	12	7.0— 9.5	8.44 ± 0.19	0.65	7.7
» Continent	4	7.9—10.0	8.9 ± 0.4	—	—
Holsteinian, Lunel-Viel	3	8.0— 8.6	8.37 ± 0.19	—	—
Villafranchian, Olivola	1	—	8.2	—	—
Width, M ₁					
Late Pleistocene, Britain	12	2.7— 4.2	3.68 ± 0.11	0.38	10.4
» Continent	4	3.6— 4.3	3.88 ± 0.16	—	—
Holsteinian, Lunel-Viel	3	3.8— 3.8	3.8	—	—
Villafranchian, Olivola	1	—	3.5	—	—
Paraconid height, M ₁					
Neolithic, Denmark	25	3.6— 5.0	4.28 ± 0.08	0.40	9.4
Mesolithic, Denmark	1	—	4.0	—	—
Late Pleistocene, Britain	4	3.5— 4.3	3.90 ± 0.17	—	—
» Continent	3	4.2— 4.7	4.40 ± 0.15	—	—
Villafranchian, Olivola	1	—	a3.7	—	—

	N	O.R.	M	S.D.	V
Protoconid height, M_1					
Late Pleistocene, Britain	4	4.7—5.3	4.98 ± 0.14	—	—
» Continent	3	5.0—5.9	5.47 ± 0.26	—	—
Villafranchian, Olivola	1	—	5.1	—	—
Jaw length, C-condyle					
Neolithic, Denmark	3	58—66	61.3 ± 2.4	—	—
Late Pleistocene, Britain	9	49—68	55.5 ± 1.9	5.8	10.4
» Continent	1	—	62	—	—
Depth at coronoid process					
Neolithic, Denmark	3	24.5—31.3	28.7 ± 2.1	—	—
Late Pleistocene, Britain	6	22.3—27.1	24.7 ± 1.0	2.4	9.6
» Continent	1	—	30.8	—	—
Ramus depth behind M_1					
Neolithic, Denmark	24	9.7—14.0	11.82 ± 0.24	1.18	10.0
Mesolithic, Denmark	4	10.5—14.2	11.9 ± 0.8	—	—
Late Pleistocene, Britain	11	9.3—14.5	11.0 ± 0.4	1.4	12.6
» Continent	4	11.9—14.7	13.0 ± 0.6	—	—
Holsteinian, Lunel-Viel	3	12.8—13.3	13.03 ± 0.15	—	—
Villafranchian, Olivola	1	—	11.0	—	—
Ramus depth at diastema					
Neolithic, Denmark	15	9.8—12.6	11.07 ± 0.23	0.88	7.9
Mesolithic, Denmark	4	10.5—14.2	11.9 ± 0.8	—	—
Late Pleistocene, Britain	12	8.5—13.4	10.3 ± 0.4	1.3	12.5
» Continent	4	10.1—14.0	11.6 ± 0.9	—	—
Holsteinian, Lunel-Viel	3	10.5—11.0	10.77 ± 0.15	—	—
» Heppenloch	1	—	12.2	—	—
Villafranchian, Olivola	1	—	9.5	—	—
Length, diastema					
Neolithic, Denmark	12	5.2—7.0	6.05 ± 0.14	0.49	8.2
Mesolithic, Denmark	2	5.1—6.5	5.8	—	—
Late Pleistocene, Britain	12	4.8—6.7	5.78 ± 0.16	0.54	9.3
» Continent	4	6.1—6.7	6.35 ± 0.13	—	—
Holsteinian, Lunel-Viel	2	6.8—8.2	7.5	—	—
Villafranchian, Olivola	1	—	4.1	—	—
Length, P_3-M_1					
Neolithic, Denmark	24	19.7—24.8	21.75 ± 0.25	1.20	5.5
Mesolithic, Denmark	5	21.2—24.2	22.8 ± 0.6	1.3	5.8
Late Pleistocene, Britain	12	18.0—24.4	21.2 ± 0.4	1.5	7.1
» Continent	4	20.0—25.4	22.4 ± 1.1	—	—
Holsteinian, Lunel-Viel	2	21.4—22.2	21.8	—	—
Villafranchian, Olivola	1	—	20.2	—	—

While the type of *F. lunensis* differs from the living species in many details, its main characters still appear to range it closer to that species than to any other living small cat, which raises the question whether it may in fact represent the ancestry of *F. silvestris*. The intermediate character of the middle Pleistocene material indicates that this may be so.

The Cromerian material available to me consists of a single tooth, the P_4 . Fortunately this tooth is highly distinctive in *F. lunensis*. In the tooth from West Runton (see pl. 1, fig. C) the anterior cusp is well developed and set off from the main cusp by a large notch. The main cusp or protoconid is very high, with a short anteroposterior diameter. The posterior cusp is small, hardly at all higher than the anterior. In all these characters the specimen shows close resemblance to *F. lunensis*, and deviates from the usual pattern in *F. silvestris*, although the deviation is less extreme than in the type from Olivola.

The resemblance may justify a tentative reference of the Forest Bed specimen to MARTELLI's species, subject to such qualification as study of other Cromerian material may suggest.

Felis silvestris Schreber, 1777

Our next glimpse of the evolving line comes with the Holsteinian sample. The single specimen from the Heppenloch represents a very large individual, surpassing the Cromerian form as well as most recent Wild Cats in size. The small sample from Lunel-Viel also represents a large form, though not as large as the Heppenloch specimen. Unfortunately the specimens from Lunel-Viel have worn teeth which do not show the dental characters as well as might be wished for. P_3 has a small accessory cusp and thus agrees with *F. silvestris*, and the characters of P_4 , M_1 , and the mandibular ramus resemble the modern form. The diastema is indeed unusually long in both the specimens showing the character (see pl. 2, figs. A—B). No. 257 shows a fairly well developed metaconid in M_1 , a character occasionally seen in modern Wild Cat. The elongation of the jawbone and the relatively small canine tooth combine to bring about a certain resemblance to steppe races of *F. silvestris* (*F. lybica* of authors).

The Heppenloch P_4 is of special interest, for it shows some peculiarities reminiscent of *F. lunensis*: unusual height of the protoconid, in relation to the anteroposterior diameter, and a relatively weak posterior cusp.

There seems thus to be some evidence of a transition from *F. lunensis* to *F. silvestris*. It seems clear enough that the modern species had appeared by Holsteinian times. If, as it tentatively done here, the Cromerian form is referred to *F. lunensis*, the actual transition would be localized within the Mindel/Elster. More definite conclusions must await the study of additional material.

TABLE 2. Measurements of lower dentition and mandible in recent samples of Wildcat
(*Felis silvestris*).

	N	O.R.	M	S.D.	V
Length, Ci					
»grampia»	48	3.8— 5.4	4.53 ± 0.06	0.44	9.6
»silvestris»	22	3.6— 5.6	4.52 ± 0.10	0.48	10.7
»tartessia»	3	5.3— 5.6	5.50 ± 0.10	—	—
Width, Ci					
»grampia»	51	2.9— 4.1	3.45 ± 0.05	0.33	9.7
»silvestris»	18	3.1— 4.3	3.51 ± 0.08	0.38	10.7
»tartessia»	3	4.2— 4.4	4.33 ± 0.07	—	—
Length, P ₃					
»grampia»	49	5.0— 6.3	5.62 ± 0.05	0.34	6.1
»silvestris»	22	5.3— 6.2	5.73 ± 0.06	0.30	5.3
»tartessia»	3	6.1— 6.8	6.37 ± 0.22	—	—
Width, P ₃					
»grampia»	49	2.5— 3.3	2.81 ± 0.03	0.18	6.3
»silvestris»	22	2.5— 3.1	2.83 ± 0.03	0.16	5.6
»tartessia»	3	3.0— 3.1	3.07 ± 0.03	—	—
Height, P ₃					
»grampia»	36	3.6— 4.4	3.98 ± 0.03	0.19	4.9
»silvestris»	18	3.8— 4.5	4.17 ± 0.05	0.19	4.7
»tartessia»	3	4.3— 4.4	4.33 ± 0.03	—	—
Length, P ₄					
»grampia»	51	5.7— 7.5	6.78 ± 0.05	0.36	5.3
»silvestris»	22	6.2— 8.2	7.10 ± 0.09	0.44	6.2
»tartessia»	3	7.3— 7.9	7.57 ± 0.18	—	—
Width, P ₄					
»grampia»	51	2.9— 3.6	3.18 ± 0.03	0.18	5.6
»silvestris»	22	2.9— 3.5	3.26 ± 0.03	0.16	5.0
»tartessia»	3	3.5— 3.9	3.67 ± 0.12	—	—
Protoconid length, P ₄					
»grampia»	37	3.2— 4.1	3.63 ± 0.04	0.21	5.9
»silvestris»	16	3.5— 4.0	3.71 ± 0.05	0.18	4.9
»tartessia»	3	3.7— 4.2	3.97 ± 0.15	—	—
Height, P ₄					
»grampia»	32	4.3— 5.1	4.68 ± 0.03	0.19	4.0
»silvestris»	18	4.4— 5.2	4.83 ± 0.05	0.23	4.7
»tartessia»	3	4.9— 5.2	5.07 ± 0.09	—	—

	N	O.R.	M	S.D.	V
Length, M ₁					
»grampia»	51	6.7— 8.9	7.92±0.06	0.45	5.6
»silvestris»	23	7.4— 9.0	8.26±0.09	0.45	5.5
»tartessia»	2	8.4— 9.7	9.05	—	—
Width, M ₁					
»grampia»	51	3.2— 4.0	3.56±0.026	0.19	5.2
»silvestris»	23	3.2— 3.9	3.54±0.04	0.20	5.6
»tartessia»	2	3.9— 4.5	4.2	—	—
Paraconid height, M ₁					
»grampia»	29	3.2— 5.0	3.93±0.07	0.37	9.5
»silvestris»	15	3.2— 4.4	4.03±0.08	0.32	7.9
»tartessia»	2	4.2— 4.7	4.45	—	—
Protoconid height, M ₁					
»grampia»	29	4.9— 6.0	5.33±0.07	0.38	7.1
»silvestris»	15	4.7— 5.7	5.25±0.08	0.32	6.0
»tartessia»	2	5.8— 6.1	5.95	—	—
Jaw length, C-condyle					
»grampia»	51	53—66	58.2 ± 0.5	3.5	6.0
»silvestris»	23	52—64	57.5 ± 0.6	3.0	5.2
»tartessia»	3	57—62	59.7 ± 1.5	—	—
Depth at coronoid process					
»grampia»	50	24.0—34.5	28.5 ± 0.4	2.6	9.3
»silvestris»	23	22.5—31.5	26.3 ± 0.5	2.4	9.1
»tartessia»	3	24.4—29.1	26.8 ± 1.4	—	—
Ramus depth behind M ₁					
»grampia»	51	9.9—13.5	11.33±0.12	0.88	7.7
»silvestris»	23	9.2—13.2	11.07±0.19	0.91	8.2
»tartessia»	3	10.7—11.4	11.10±0.21	—	—
Ramus depth at diastema					
»grampia»	51	8.8—11.2	9.88±0.10	0.70	7.1
»silvestris»	23	8.5—11.4	10.06±0.16	0.77	7.7
»tartessia»	3	10.5—11.5	10.93±0.30	—	—
Length, diastema					
»grampia»	51	4.2— 8.0	5.78±0.13	0.90	15.6
»silvestris»	19	5.1— 7.1	6.26±0.15	0.64	10.2
»tartessia»	3	4.6— 6.4	5.6 ± 0.5	—	—
Length, P ₃ -M ₁					
»grampia»	51	18.8—22.0	20.42±0.12	0.85	4.1
»silvestris»	23	18.5—22.4	20.64±0.20	0.98	4.7
»tartessia»	3	21.3—23.3	22.4 ± 0.6	—	—

The late Pleistocene populations of Wild Cat in Europe show little morphological distinction from the living form, and their position is best elucidated by means of biometric analysis.

Analysis of evolutionary trends

The statistics of the samples that have been available to me are summarized in tables 1—2. On the basis of the mean values recorded here a series of ratio diagrams (see SIMPSON, 1941) has been constructed to visualize the evolution and differentiation from the Villafranchian to the present day. The standard of comparison is, in each case, the modern Scottish population, »*grampia*».

Fourth lower premolar

This tooth has a particularly instructive history. The upper graph in fig. 2 sets forth a sequence of temporal samples leading from the *F. lunensis* of Olivola to the modern form. The lower graph attempts to depict late Pleistocene and modern differentiation in the species *F. silvestris*. Let us first consider the earlier sequence.

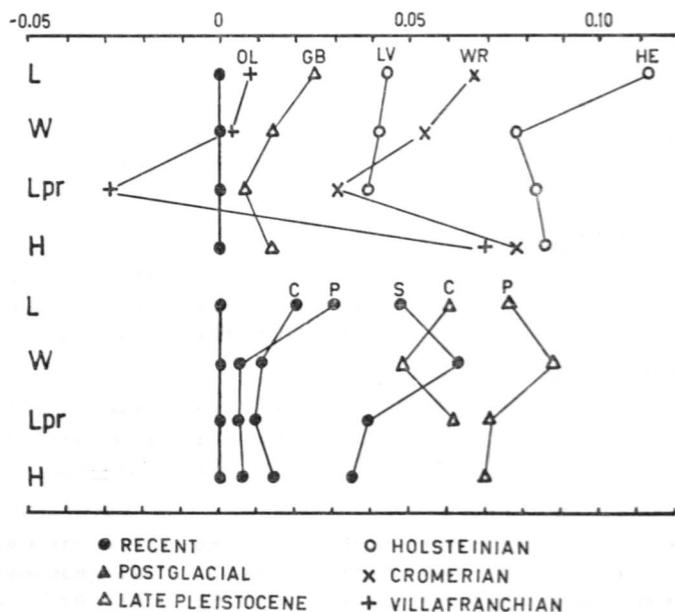


FIG. 2. Ratio diagram of mean dimensions of P_4 in fossil and recent Wild Cat. L, Length; W, width; Lpr, length of protoconid; H, height. Standard of comparison, recent Scottish sample. C, European continent; D, Denmark; GB, Great Britain; HE, Heppenloch; LV, Lunel-Viel; OL, Olivola; P, Palestine; S, southern Spain and Portugal; WR, East Runton. Symbols indicate geological age as shown at bottom of diagram.

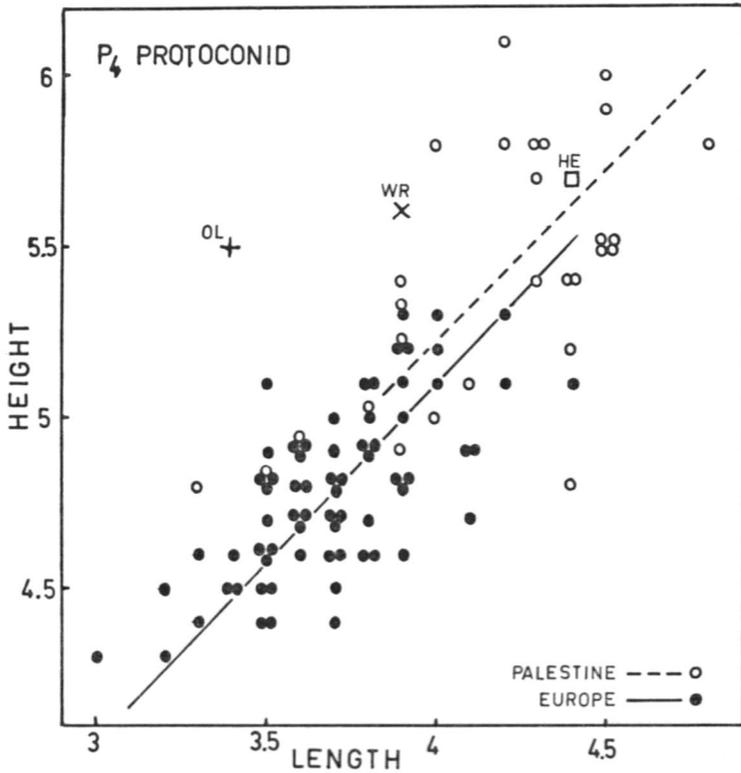


FIG. 3. Relationship between height and anteroposterior length of the protoconid in P_4 , with axes for (a) recent and late Pleistocene Wild Cat from Palestine, (b) recent and late Pleistocene material from Europe. Symbols for Olivola, West Runton and Heppenloch as in fig. 2. The regressions for Palestine and Europe are significantly different ($P < 0.001$).

The Villafranchian *F. lunensis* departs strongly from the straight vertical. While the absolute length and width of the tooth are nearly the same as the «grampia» averages, the protoconid is extremely short anteroposteriorly, and high-crowned. The pattern for the West Runton specimen is somewhat similar but less extreme, or in other words intermediate between the type of *F. lunensis* and the modern form. At the same time, it represents a size increase of about ten per cent.

The Heppenloch specimen represents a form in which the protoconid is still short (anteroposteriorly) relative to the crown length, but now has the reduced height typical of modern Wild Cat. The size trend appears to culminate in this form; however, the specimen may be an unusually large one. The approximately contemporaneous form of Lunel-Viel is somewhat smaller, or about as large as the Cromerian (West Runton) cat. The Lunel-Viel pattern

approaches a straight vertical, indicating relative proportions similar to those in the modern form; however, the protoconid height is not known.

The transition to the modern form is indicated by the late Pleistocene British sample, showing size reduction and gradual approach to the modern Scottish Wild Cat.

Evidently the great height of the protoconid in *F. lunensis* is a significant character. As shown in fig. 3, it is outside of the variation range in *F. silvestris*. Both the Olivola and West Runton specimens are displaced relative to the scatter diagram for *F. silvestris*.

The lower graph in fig. 2 depicts the differentiation in the modern species. Late Pleistocene forms both in Europe (C) and Palestine (P) are much larger than their living descendants; the latter differ only slightly in size from the modern Scottish «*grampia*». (The story in Palestine has been discussed in more detail in KURTÉN, 1965). The only exception to this general story of dwarfing is the Spanish *F. silvestris tartessia*, which retains the large size of its Pleistocene ancestors. The agreement between this form and the large Palestinian Wild Cat that lived during the Main Würm is especially striking and has been previously noted (KURTÉN, *op.cit.*). As far as P_4 is concerned, the only difference is a very slight one in mean absolute size.

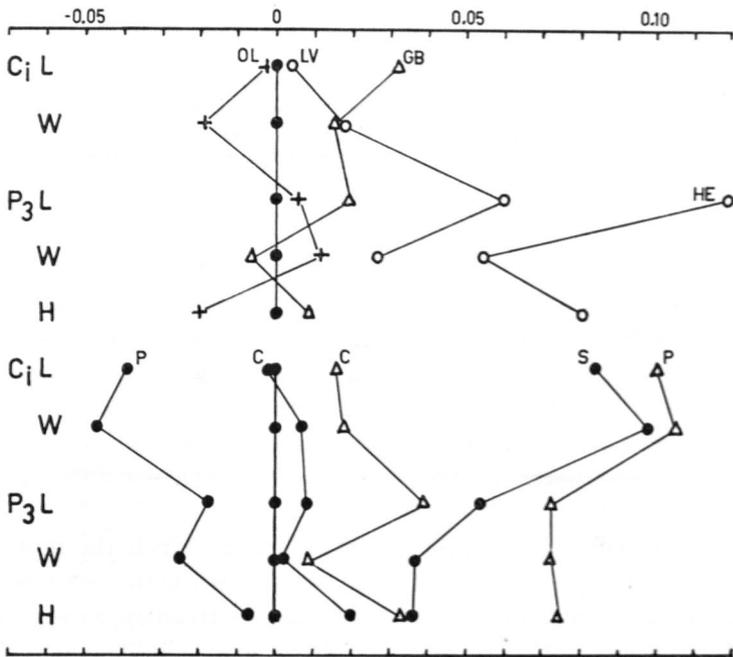


FIG. 4. Ratio diagram of mean dimensions of C_1 and P_3 in fossil and recent Wild Cat. Symbols and abbreviations as in fig. 2.

Lower canine and third premolar

The proportions of C_1 and P_3 are represented in fig. 4, which has been constructed in the same way as fig. 2. The Villafranchian form is mainly characterized by its low-crowned P_3 . This condition would seem to persist in the Heppenloch specimen, but in addition the Holsteinian Wild Cats (Lunel-Viel and Heppenloch) have much narrower P_3 , relative to length. This latter trait persists in the late Pleistocene samples from Great Britain and the Continent, although these are now as high-crowned in P_3 as *»grampia»*.

Among the late Pleistocene and recent populations, the Iberian form (SP) and that from the Würm of Palestine have strikingly large canine teeth; the similarity between these two is again apparent. In contrast, the late Pleistocene form on the European continent has relatively small canines. In the modern Palestinian Wild Cat the canines are especially small.

Carnassial

Differentiation in the carnassial teeth is represented in fig. 5. The M_1 of the Villafranchian specimen is relatively narrow and low-crowned, but almost the same pattern recurs in the late Pleistocene Wild Cat from Great Britain, while the Lunel-Viel form had a slightly broader tooth. Late Pleistocene and recent forms show some variation in size and relative breadth, the indication being that the standard of comparison, the Scottish *»grampia»*, may have an unusually broad M_1 ; it is surpassed in this respect only by the Spanish form.

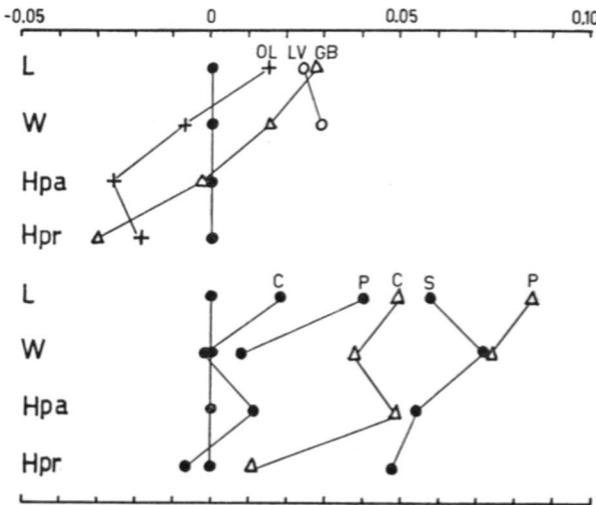


FIG. 5. Ratio diagram of mean dimensions of M_1 in fossil and recent Wild Cat. Hpa, height of paraconid; Hpr, height of protoconid. Other symbols and abbreviations as in fig. 2.

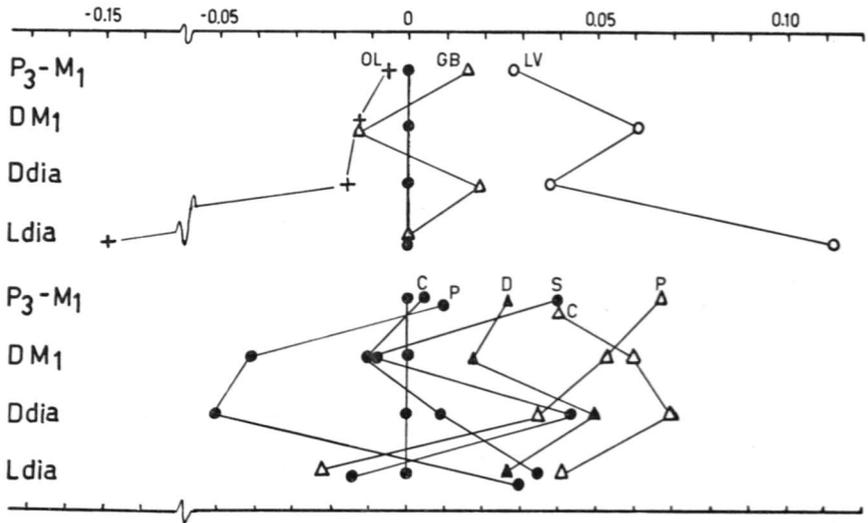


FIG. 6. Ratio diagram of mean dimensions of lower jaw in fossil and recent Wild Cat. DM₁, ramus depth behind M₁; Ddia, ramus depth at diastema C-P₃; Ldia, length of diastema. Other symbols and abbreviations as in fig. 2.

The latter again stands out as the largest of the living Wild Cats, and is only slightly smaller than the great Palestinian Würm form.

Mandible

Proportions of the jawbone are represented in fig. 6. They tend generally to be more variable than those of the teeth, and less reliable in taxonomy. In the present case it appears that a form with very short diastema (Olivola) was succeeded by one with a very long (Lunel-Viel), whereas later Wild Cats have diastema lengths falling between these two extremes. Actually the length of the diastema is greatly influenced by relatively slight changes in the length of the mandible and the size of the teeth. The Olivola jaw is of about the same size as the modern Scottish average, while the middle Pleistocene specimens from Lunel-Viel belonged to larger animals.

In the late Pleistocene and early Postglacial, the British form was already somewhat smaller than the Continental; the Neolithic Danish Wild Cat is transitional in size between the Late Pleistocene and modern Continental ones.

The late Pleistocene form in Palestine, which exceeded all the others in total size, is also characterized by a very short diastema. The same character is also seen in *F. silvestris tartessia*, which again shows characters resembling the fossil cat of Palestine. On the other hand, the recent Palestinian Wild Cat has a long diastema and a relatively shallow jaw.

Indices of size and shape

It would be useful to be able to express morphological differences, like those represented in the ratio diagrams, by simple numerical values. The use of the ratio diagram suggests a possible method.

This is to compute the mean and the standard deviation of the log differences between two sets of means. The closer to a straight vertical that a series of observations will fall in a ratio diagram, the lower is the standard deviation of the log differences; when the relative proportions of the two specimens or sample means are identical, the standard deviation becomes 0. It will thus be proportional to the degree of differentiation in shape. McCrady *et al.* (1951) demonstrate amusingly how the order of structures in a ratio diagram may be shuffled to change the visual impression of resemblance. This emphasizes the need for an objective measure of shape differentiation. It is suggested that the standard deviation of the log differences may serve as such a *shape index*.

At the same time, the mean of the log differences, positive or negative as the case may be, is an expression of the *size* difference between the two forms. This value may then serve as a *size index*.

For the present kind of work, the method outlined here seems to hold more promise than the use of such measures as, for instance, the »generalized distance» of MAHALANOBIS (1936), which does not discriminate between the effects of size and shape. An attempt to use the »generalized distance» in an analogous case (evolution of Red Fox in Palestine, in KURTÉN, 1964) gave indifferent results.

An analogous pair of indices, though not based on log differences, was proposed by PENROSE (1954).

Indices found in two sequences of comparisons, using »*grampia*» and the Olivola specimen respectively as standards of comparison, are recorded in table 3. The size and shape columns under »*grampia*» may thus be taken as a summary of the graphic comparisons set forth in figs. 2, 4, and 5. (Data on mandibular dimensions, except the length of P₃-M₁, have been excluded to avoid the influence of individual age.)

It is now possible to assess the trends of evolution in size and shape in terms of the new indices. The patterns of evolution and differentiation found may then, in future, be directly compared to analogous patterns worked out for other, unrelated forms.

Trends in size

The size indices make it easy to visualize the size trends in the successive populations of Wild Cat. This has been done in fig. 7, where size indices are plotted against a time scale. The unequal fossil representation made it neces-

TABLE 3. Values of size and shape indices in comparison between various recent and fossil Wildcat samples. Based on sample means for dental dimensions.

	Standard of comparison			
	Recent »grampia»		Olivola	
	Size	Shape	Size	Shape
Recent:				
»grampia»	0	0	0.0010	0.0250
»silvestris»	0.0082	0.0083	0.0092	0.0242
»tartessia»	0.0547	0.0190	0.0557	0.0350
Palestine	-0.0027	0.0259	0.0026	0.0363
Fossil:				
Neolithic, Denmark	0.0397	0.0067	0.0329	0.0310
Late Pleistocene, Britain	0.0110	0.0157	0.0120	0.0252
» Continent	0.0346	0.0181	0.0356	0.0346
» Palestine	0.0793	0.0124	0.0768	0.0306
Holsteinian, Lunel-Viel	0.0315	0.0155	0.0334	0.0192
» Heppenloch	0.0879	0.0218	0.0836	0.0404
Cromerian, West Runton	0.0575	0.0202	0.0445	0.0247
Villafranchian, Olivola	-0.0010	0.0250	0	0

sary to use two different time scales. One of the charts gives a generalized curve of size evolution from the Villafranchian to the present day, while the other gives a more detailed representation of local size trends and differentiation in the late Pleistocene and Postglacial.

The generalized curve suggests that the size of the species increased gradually from the Villafranchian, to culminate in the middle Pleistocene; it has since tended to decrease, though some forms continue to be large.

The other chart indicates the great complexity of the changes that have taken place in late Pleistocene and Postglacial times, and suggests that the »general curve» is greatly oversimplified. The set of curves represents (1) evolution in Great Britain, based on the late Pleistocene sample and the recent »grampia», (2) the European Continent, represented by the Late Pleistocene, Mesolithic Danish, Neolithic Danish, and modern »silvestris» samples, in the given order; and (3) Palestine, based on data in KURTÉN (1965).

Judging from this, the size of the Wild Cat of continental Europe increased in the late Würm and early Postglacial to reach a maximum at some time in the Allerød or later Dryas. Since then it has decreased rapidly. Whether there was any increase of this kind in Britain is uncertain; the data suggest that the British Wild Cat was but little larger in the Late Pleistocene than now. There must then have been a cline in size, for the two populations should have been in contact at that time, before the flooding of the Channel.

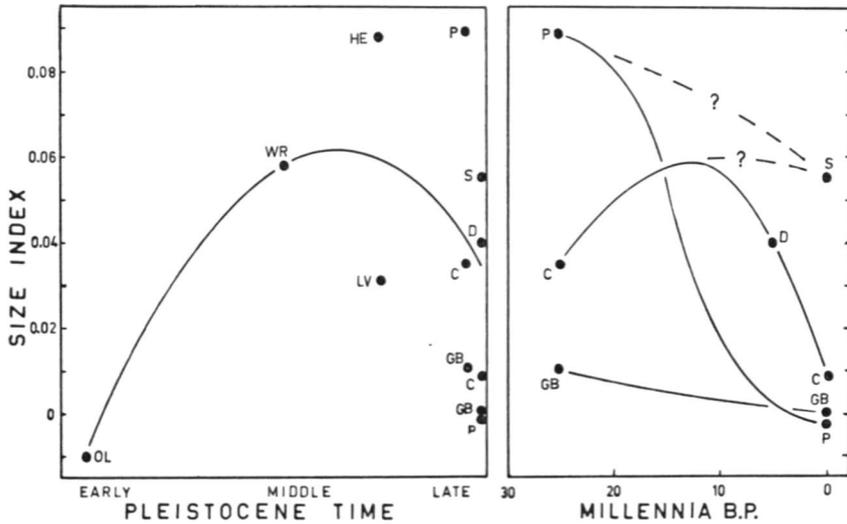


FIG. 7. Evolution of size in Wild Cat. Left, long-range changes in the Pleistocene; no absolute time scale. Right, changes during the latest Pleistocene and Postglacial. Abbreviations as in fig. 2.

The history in Palestine was even more dramatic. The early form here was very large, but in the Mesolithic it underwent a radical dwarfing, so that it is now slightly smaller than its European ally.

The descent of the Spanish form is uncertain. As far as sheer size goes it could represent a holdover of the large Continental type of early Postglacial times. This, however, fails to take into account its remarkable similarity in morphological details to the early form in Palestine. Perhaps it represents the relict of the Western flank of a Mediterranean population of very large Wild Cats existing during the last glaciation. However, this must remain hypothetical until other Mediterranean fossils, for instance in North Africa, have been studied in the same way.

Trends in shape

So far only the size differences have been taken into account. If the differences in shape are considered, a diagram may be constructed in an analogous way, with time on one axis and the shape index on the other (fig. 8).

The long-range curve shows a gradual approach towards the modern type. There is an apparent acceleration in the trend at the end of the sequence, but this does not reflect an acceleration in the rate of evolution. The shape may change considerably without this being reflected in the index, as long as these changes are random in relation to the standard of comparison. For this reason the index is not a good measure of the rate of evolution.

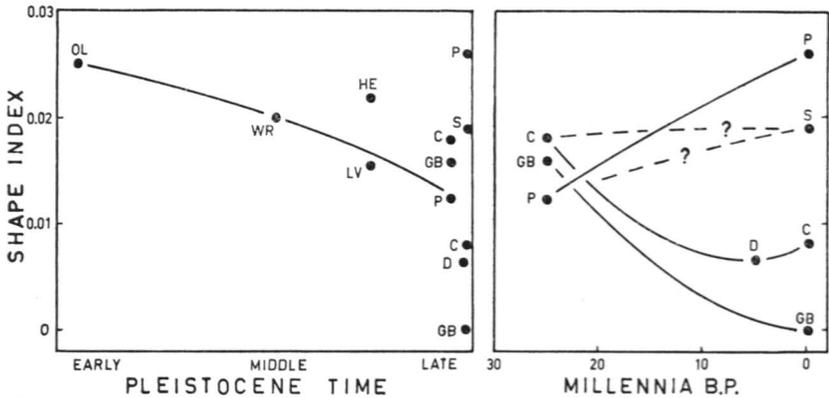


FIG. 8. Changes in the shape index of Wild Cat, using recent Scottish sample as a standard of comparison. Time scales as in fig. 7; abbreviations as in fig. 2.

Finally, by leaving out the time dimension, size and shape indices may be combined in the same diagram. The amount of differentiation is then shown by the displacement of the observations in relation to the standard of comparison, which is located at the point of intersection of the two axes. The arrangement of the observations depends on the selection of a standard of comparison, as shown in fig. 9, based on the two groups of values in table 3. It should be noted that relative position of two observations not including the standard has no bearing on their degree of differentiation from each other. (Note, for instance, the relative positions of the observations for Olivola and the recent Palestine sample in the two cases.) A complete evaluation necessitates the calculation of the total matrix of indices, using each sample in turn as standard of comparison.

The arrows in fig. 9 indicate probable evolutionary changes, the continuous lines denoting those late Pleistocene and Postglacial changes for which the evidence is especially good. As a consequence of the properties of the indices, arrows located close to the standard of comparison tend to be centripetal or centrifugal in direction, whereas tangential directions are more common at a greater distance.

The index values cannot be used directly for a numerical taxonomy. Still, they may help in the formulating of taxonomic conclusions. This is particularly true for the shape index, which tends to have a higher value in interspecific comparisons than in intraspecific. Table 3 contains ten intraspecific and eleven interspecific comparisons. The distribution of shape index values in these comparisons is summarized in table 4. The mean for the interspecific indices, 0.0292, is considerably higher than that for the intraspecific, only 0.0168.

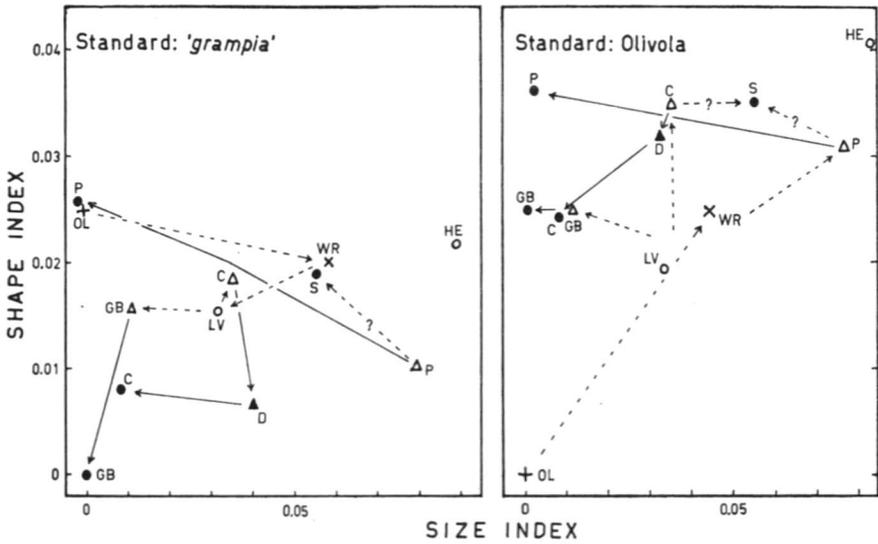


FIG. 9. Differentiation in size and shape among recent and fossil Wild Cat, based on two different standards of comparison, as labelled. Data from table 3. Symbols and abbreviations as in fig. 2. Arrows indicate probable descent.

However, there is a considerable variation in both cases, the standard deviation being about the same for both. It follows that there is a wide overlap between the values found in intraspecific and interspecific comparisons. This invalidates any purely numerical taxonomy based on such data.

TABLE 4. Values of shape index in intra- and interspecific comparisons. Data from table 3.

Index values	Frequencies	
	Intraspecific	Interspecific
0 — 0.0049	—	—
0.0050 — 0.0099	2	—
0.0100 — 0.0149	1	—
0.0150 — 0.0199	4	1
0.0200 — 0.0249	2	2
0.0250 — 0.0299	1	2
0.0300 — 0.0349	—	3
0.0350 — 0.0399	—	2
0.0400 — 0.0449	—	1
Mean	0.0168	0.0292
Observed Range	0.0067—0.0259	0.0192—0.0404
Standard Deviation	0.0064	0.0070

On a more modest level, however, the shape index may well be a valuable taxonomic tool. With a sufficient number of judiciously selected characters, it will express faithfully the amount of morphological differentiation between two forms. Surely this must be a valuable support for further taxonomic judgments. Furthermore, study of distributions like those in table 4, but based on a greater number of data, will make it possible to assess the probabilities of a single observation belonging to one distribution or the other — another contribution bearing on the taxonomic conclusion.

Conclusions

The modern *Felis silvestris* probably descended from the Villafranchian *F. lunensis*. The geographic range of the latter is not known, but there is no reason to assume that it was limited to Europe, any more than that of the modern species.

The stratigraphic range of *F. lunensis* may go back to early Villafranchian times, but the available material (various postcranial fragments, the earliest from Mt. Perrier) is not identifiable to species. It extends upward probably to the Cromerian, for the characters of a small felid specimen from the Cromer Forest Bed at West Runton resemble *F. lunensis* more than they do *F. silvestris*.

The transition to the modern species was completed by Holsteinian times, for specimens of this date from the caves of Lunel-Viel and Heppenloch are referable to *F. silvestris*.

Local late Pleistocene samples show great spatial differentiation within the species, and further change, mostly consisting of a decrease in size but at locally varying rates, occurred in the Postglacial. The form of Wild Cat living in Palestine in the Würm shows detailed similarity to the present-day *F. silvestris tartessia* from the southern part of the Iberian peninsula, and may apparently be referred to the same subspecies.

In his revision of the subspecies of *F. silvestris*, HALTENORTH (1953) suggests that a large number of supposed subspecies from various parts of the range, both in Europe, Asia, and Africa, should be rejected. I fully agree with his procedure on most points. In one or two cases, however, somewhat different conclusions are suggested.

HALTENORTH suggests that the subspecies *F. silvestris tartessia* should be rejected, since the size of the skull does not exceed that in other areas. I wish to emphasize that this subspecies appears to me to be one of the few that are readily identifiable on osteological characters, and that its separation is much clearer than, for instance, that of *F. s. grampia* — which HALTENORTH is

disposed to retain. The teeth of the south Iberian form average much larger than in any other recent population known to me, and this is particularly true for the canines. Again, although the skull is not very long, its broad, powerful build, with a particularly broad rostrum, does indeed set it off clearly from the average type found elsewhere.

On the basis of the present analysis, the late Pleistocene and modern material treated here may perhaps be allocated as follows.

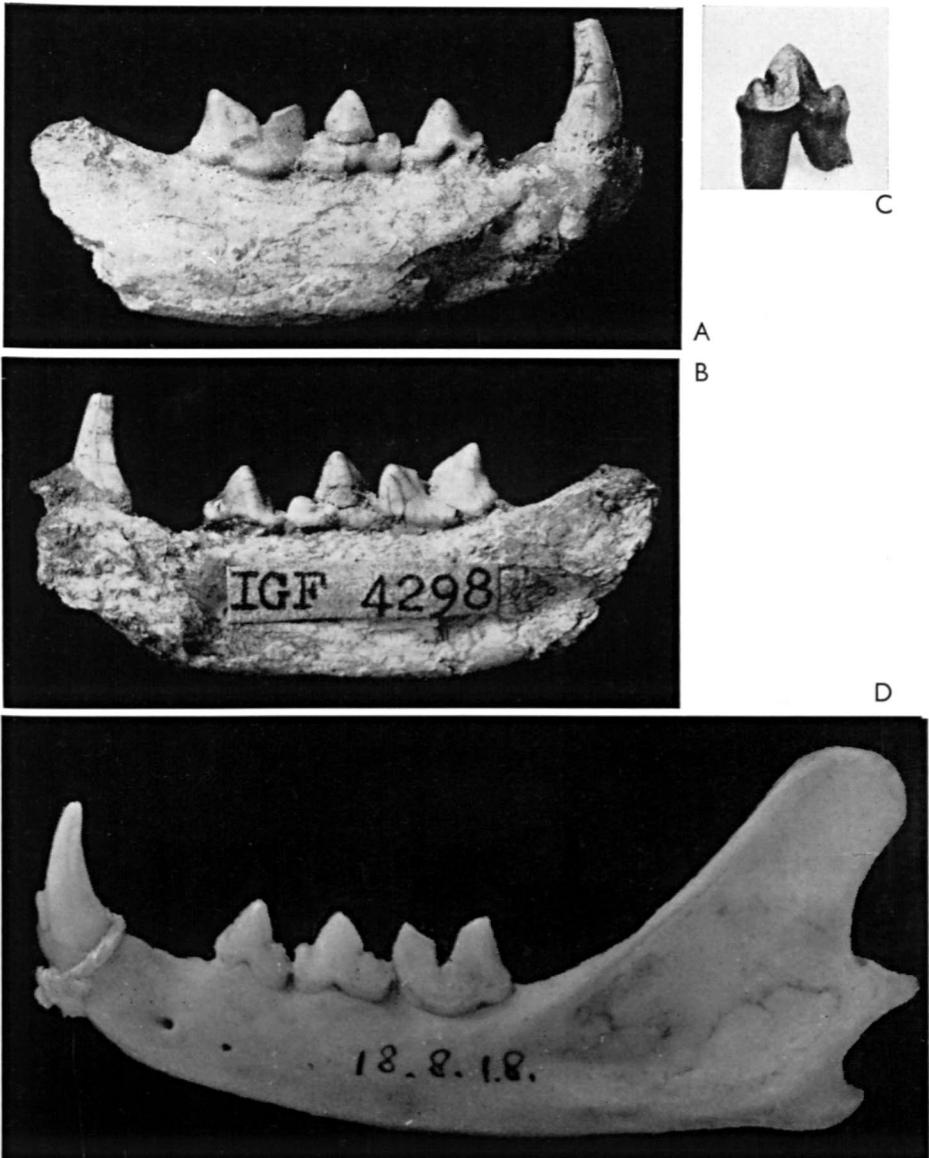
Felis s. silvestris. Recent form of Continental Europe and Scotland; late Pleistocene form of Great Britain.

Felis s. tartessia. Recent form of Iberian Peninsula south of the Ebro and Douro; late Pleistocene form in Palestine; possibly also late Pleistocene form of central and northern Europe, up to and including early Postglacial cats of Denmark. The later Danish material would then represent a transition (chronocline) to *F. s. silvestris*.

Felis s. lybica (or *iraki*, if valid). Recent and Postglacial cats in Palestine (see KURTÉN, 1965). Their evolution from ancestral forms of *tartessia* type probably occurred by massive gene flow from adjoining areas, perhaps further to the south or east.

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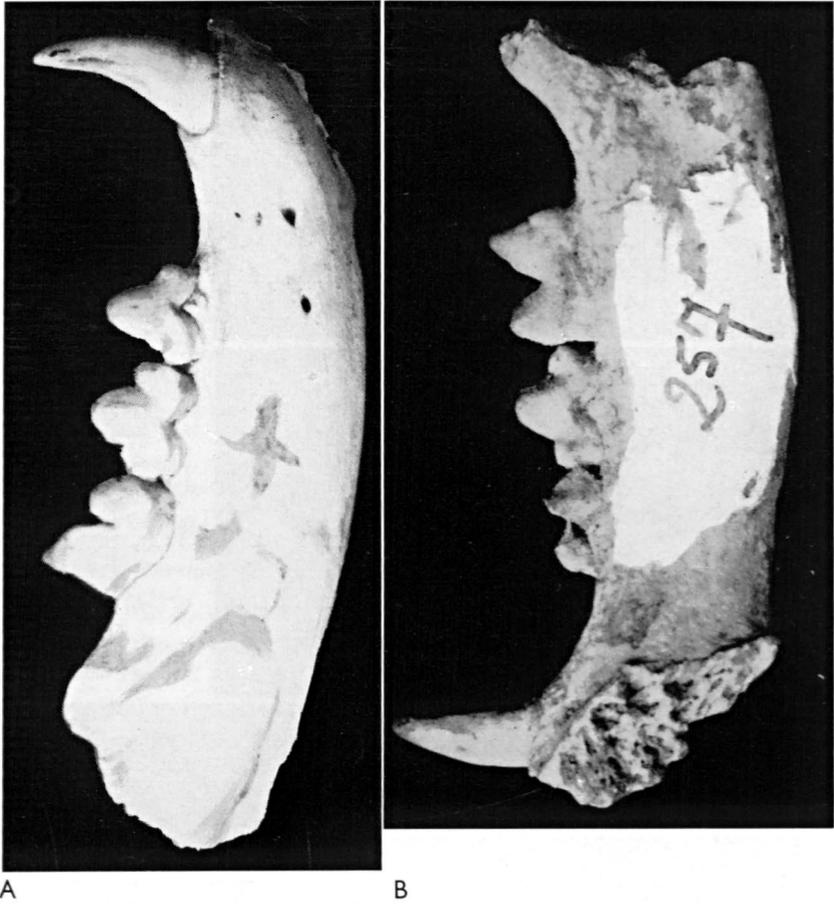
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All figures 2 times natural size.

- A—B. IGF 4298, *Felis lunensis*, type, right mandible. Late Villafranchian, Olivola, Val di Magra, Tuscany.
- C. B.M. M 18444, *Felis cf. lunensis*, right P₄. Cromerian, Upper Freshwater Bed at West Runton, Norfolk.
- D. B.M. 18.8.1.8, *Felis silvestris lybica* or *F. s. iraki*, left mandible. Recent, Jerusalem.

PLATE 2.



All figures 2 times natural size.

- A. Univ. Montpellier 256, *Felis silvestris*, right mandible. Late Middle Pleistocene, Lunel-Viel, Hérault.
- B. Univ. Montpellier 257, *Felis silvestris*, right mandible. Late Middle Pleistocene, Lunel-Viel, Hérault.



2 times natural size.

Left, B.M. M 9577, Domestic Cat, left mandible. Probably Postglacial. Right, B.M. M 9578, *Felis silvestris*, left mandible. Late Pleistocene or Postglacial. Both from Ravencliffe Cave, Derbyshire.

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