

How old are subspecies? A tiger's eye-view of human evolution

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Abstract

'Replacement' and 'Regional Continuity' models of *Homo sapiens* evolution are still subject to lively debate, but the human case has been discussed without reference to what happens in other animals. It happens that some large mammal species have fossil records that are good enough to permit, to some degree, the history of their subspeciation and of their mode of origin. With one rather dubious exception, there is no case of Regional Continuity. Some can be demonstrated to originate from their parent species and then subspeciate; subspecies may evolve and continue *in situ*, or there may be a complicated pattern of intra-species replacements.

Many of the species concerned are rare or endangered, and have been subject to genetic studies directed towards captive management. Genetic distances tend to correlate poorly with known or inferred fossil information; except for the White Rhinoceros the separation time of the two living subspecies as calculated from mtDNA is consistent with the fossil record.

The implications of this for human evolution are discussed.

Introduction

In the debate about human origins, whether by Regional Continuity (multiregional evolution) or by Replacement, the question has not yet been asked, what has happened in other species? Is it justified to use other species as models for our own evolution, and if so what have they to tell us about evolutionary norms?

The crux of the problem is the evolution of subspecies. While it can be debated whether human 'races' are actually subspecies (i.e. 90% different from each other), there is no question but that they are geographic variants in the same way as are acknowledged subspecies in other large mammals. The claim that characters distinctive of a given human 'racial' group can be detected in an anatomically archaic taxon (*Homo erectus*, or whatever) from the same general area, i.e. that subspecific character states preceded the anatomically modern form of the human species, is the essence of the Regional Continuity model; so it is worth asking whether subspecific characters in any other mammal can be demonstrated to have preceded the appearance of the species in its modern form. If they can, then Regional Continuity is a known mode of evolution in large mammals and

it becomes that much more likely that it occurred in human evolution too; if they can not, then any claim for regional continuity in humans must be examined very carefully indeed.

The notion that we are unique in the way we have evolved — that we alone, of all large mammals, have kept our quasi-subspecific character states over eons, irrespective of species-wide anatomical change and even across what most (not all) anthropologists see as species boundaries — is an arresting one; in a biological context, even bizarre. It is certainly true that we *are* in many ways unique; but so is every other species, as Foley (1987) has recently pointed out. The question is, are the ways in which we are unique — language, culture, degree of cognitive development, and associated features — sufficient to ensure that we have evolved by modes which are unusual or even unknown in other animals? It is possible that they might be, but the case would need to be carefully argued; in general, the insight that human beings are animals like any other is perhaps the most important message of the Darwinian revolution.

A word about taxonomic categories is in order before beginning the survey. Even in living animals it is often not possible to determine whether two populations represent the same or different species. We can deduce that they are different species if their ranges overlap with no signs that there are interbreeding, or if their chromosomes are strongly different; we can deduce that they are conspecific if they have large separate ranges but intergrade where these ranges meet. It is much more difficult in the case of fossils; usually, complete morphological discontinuity is used as rule-of-thumb. Thus, species rank in palaeontology is often more a matter of convenience than anything else; a change of species over time equates with some large morphological change, and divergence of two species from a common ancestor may, if geography is involved, be merely a well-marked separation of subspecies.

The aim of this paper, then, is to examine what is known of the evolution and origin of geographic diversity of some other mammal subspecies, using fossil, molecular and morphometric evidence. Large mammals often have a rather good fossil record, and clear-cut geographic variation, so this is the area we will concentrate on. With this database, we can turn to human evolution and assess the relative likelihoods of regional continuity and replacement.

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Replacement or Continuity?

Cases from the mammalian fossil record with no genetic information

1 Family Felidae. Werdelin (1981) compared recent lynxes (*Lynx lynx*) with Pleistocene and early Holocene specimens from England, Denmark and elsewhere in northern Europe (northern Asia being unknown in this respect). The only modern lynxes to resemble the fossil and subfossil type are those from northern Sweden and Finland; other European (and Asian) lynxes are rather different. We do not find distinctive regional features in fossil lynxes being continued into their modern geographic successors; instead, replacement has evidently taken place over most of Europe.

The earliest leopards (*Panthera pardus*) are from the Pinjor zone in the Siwaliks, from Jeruk in Java, and also from Sterkfontein (Hemmer, 1973). Middle Pleistocene specimens from Java, southern China and Europe are derived in such features as the shortened carnassials. The living Java leopard, *P.p. melas*, retains primitive features from the Middle Pleistocene Asian forms, whereas the modern South China leopard (*P.p. sinensis*), while very like its fossil precursor, is more derived. In Europe, the Middle Pleistocene leopard was replaced in the Upper Pleistocene by an immigrant African type, which survives as the Caucasian *P.t. tulliana* (Hemmer, 1972). No regional continuity here.

2 Family Mustelidae. The modern North American wolverine, *Gulo gulo luscus*, is nearly identical to the Pleistocene wolverine from both North America and Europe, though the length/breadth relationship of M¹ is a little changed. On the other hand the modern European *G.g.gulo* is considerably different, the shape of M¹ being the only character in which it has not changed (Kurten and Rausch, 1959). Modern wolverines would therefore seem to have diverged — European more than North American — from generalised widespread ancestral stock. We cannot claim that one subspecies has replaced another, but no regional continuity is evident either.

3 Family Canidae. The wolf, *Canis lupus*, is an example of a species where a replacement event has actually occurred (demonstrably within the one species) in modern times. In 1914-16, Banks Island in the Canadian Arctic was inhabited by *C.l. bernardi*, but since that time it has been replaced, curiously, by a more primitive wolf, of a type more widespread in the Arctic, resembling *C.l. furlongi* from Rancho La Brea (late Pleistocene) (Nowak, 1979). Subspecies, then, do replace one another, and can do so within a strikingly short period of time.

4 Family Cervidae. Some members of the Deer family (Cervidae) have a fairly good fossil record in Eurasia, in particular the genera *Alces* (Moose or Elk) and *Cervus* (Red Deer and Wapiti).

Living moose (*Alces alces*) divide readily into two subspecies or groups of subspecies: *A.a. alces* of Europe and western Siberia, and *A.a. americana* (more likely a cluster of closely related subspecies) from eastern Siberia and North America. Moose of the *americana* group have wider antlers with longer beams, constructed on a four-point plan; in the largest subspecies, *A.a. gigas* of Alaska, the mature antler span varies from 140 up to 197cm. In *A.a. alces*, the antlers are constructed on a three-point plan (Geist, 1987).

In the Middle Pleistocene the ancestral moose, *A. latifrons*, spread into North America and speciated (or subspeciated), giving rise to the highly distinctive *A. scotti*. Modern *A. alces* appeared probably in the late Middle Pleistocene; the last occurrence of the precursor taxon, *Alces latifrons postremus*, is at Ehringsdorf, about 200,000 B.P. (Heintz and Poplin, 1981). The antlers of *A. latifrons* had very long beams (some 40-50cm long), but were constructed on a three-point plan; all *A. alces* have a shortened beam (<20cm), but the *americana*-group have undergone less beam shortening than *A.a. alces*, which on the other hand retains the primitive plane of three points.

A. alces evidently evolved somewhere in Eurasia, perhaps even in Europe; it replaced unchanged *A. latifrons* in Alaska in the early Upper Pleistocene, and at the end of the Pleistocene (with the opening-up of ice-free corridors) spread further south and replaced *A. scotti*. Thus, modern moose subspecies have clearly sprung from a common origin and owe nothing, genetically, to their regional precursors; instead, subspecies of the *americana* group replaced first a remnant of the ancestral taxon, then a near relative. *Alces* evolution is outlined in Fig.1.

Modern *Cervus elaphus* has many subspecies which, however, divide into three groups: the *elaphus* or Red Deer group of Europe, the *wallichi* or Shou group of Central Asia, and the *canadensis* or Wapiti group of northeastern Asia and North America (Groves and Grubb, 1981). The species is known in modern form in the early Middle Pleistocene, and the division into the three subspecies-groups appears to be late Middle Pleistocene, so that these subspecies-groups are as old as is the entire species *Alces alces*. The Red Deer and Wapiti groups can be shown developing in their present ranges from Shou-like ancestors; the earliest development of typical Red Deer 'crowned' antlers is seen at Swanscombe and Steinheim.

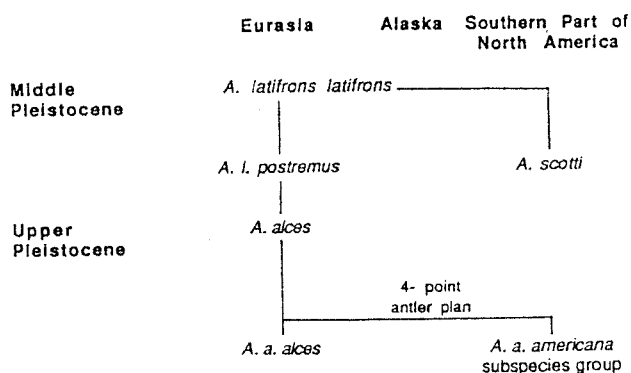


Fig.1. Summary of evolution of *Alces alces*.

There is no regional continuity; instead, there is simple *in situ* evolution of modern intraspecific groups.

5 Family Bovidae. Modern African buffalo (*Syncerus caffer*) fall into three subspecies-groups (Grubb, 1972): the small rain-forest buffaloes of the nanus-group, with a horn span of <50cm; *S.c. brachyceros* of the West African savannah, with a span of 50-70cm; and the Cape Buffalo (*S.c. caffer*) group, of Sudan, Ethiopia, and East and South Africa, with a span of >70, often >90cm. In *S.c. caffer* the horns are downswept and develop a large basal boss.

The ancestral species, *S. acoelotus*, occurs throughout the Olduvai sequence (Gentry and Gentry, 1978). The horns are less hollowed and less dorsoventrally flattened than in the modern species *S. caffer*, but in their simple form they resemble a larger version of *S.c. brachyceros*; there is no resemblance to *S.c. caffer*, which lives in the Olduvai region today. An *acoelotus/caffer* transitional specimen is known from the Kibish Formation at Omo, which is likewise within the range of *S.c. caffer*; it is again large in size, but has *brachyceros*-like horns. *S.c. caffer* first appears in the Upper Pleistocene, at Melkbos, South Africa, but even this lacks the extreme development of the frontal boss and downswept horns of the true Cape Buffalo; consequently the modern morphology of this subspecies is very recently evolved indeed. The modern subspecific characters do not precede the appearance of the anatomically modern stage of the lineage, as would be required by Regional Continuity; instead, we see a typical speciation (perhaps phyletic) followed by diversification sequence; despite the fact that the sites which offer good evidence of the sequence are all within the modern range of *S.c. caffer*, none shows any trace of the latter's subspecific characters. The evolution of *Syncerus* is outlined in Fig.2.

6 Family Rhinocerotidae. The maxillary teeth of the modern subspecies of Black Rhinoceros, *Diceros bicornis*, offer distinguishing characters concerned with a small process attached to the metaloph, the crochet (Rookmaaker and Groves, 1978). In both East and South African subspecies, the crochet is often bifid on the premolars (a highly derived condition); it never is in those subspecies living in West Africa and the Horn of Africa. A regional continuity model would expect bifid crochets in archaic Black Rhinos from the Middle or Lower Pleistocene.

In a specimen from between the KBS tuff and the KF complex at Koobi Fora, cranially more primitive than the

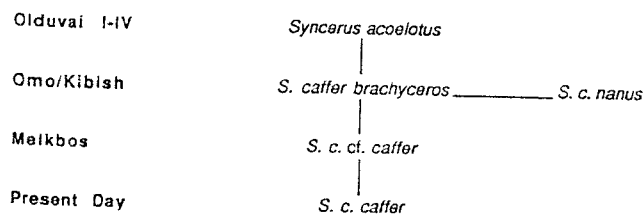


Fig.2. Summary of evolution of *Syncerus* spp.

living species (Harris, 1983), the crochet on the premolars is simple, the primitive condition. The same simple form is seen in a specimen of unknown cranial morphology from Olduvai Bed IV (see Hooijer, 1969, pl.3). There is, consequently, no evidence for the regionally characteristic bifid crochet even by the early Middle Pleistocene.

Groves and Guérin (1980) have however noted a possible regional resemblance between living and fossil subspecies of the Javan Rhinoceros (*Rhinoceros sondaicus*) from the Indochinese region. In the living Vietnam form, *R.s. annamiticus*, a crista, a small process emerging from the lingual aspect of the ectoloph, is present on the molars of two out of four available skulls (on M¹ alone in one case, on all three molars in the other). It is absent from living *R. sondaicus* subspecies from Java, Sumatra, the Malay peninsula and Bengal, and from the Middle Pleistocene form (*R.s. sivasondaicus*) from Java; but a small crista is present on the left M³, but on no other molars, of the type of *R.s. guthi* from the Pleistocene of Cambodia. All modern subspecies are more graviportal than their Pleistocene precursors, so if confirmed this would be a case of a regional character state (presence of crista) persisting from an archaic to a modern morphological grade. The case is somewhat weak because of small sample sizes, and the erratic occurrence along the molar row of the crista; nonetheless the occurrence of a crista on some molar or other in both modern and fossil Indochinese representatives (or its absence in fossil and modern Javanese ones, if its presence is primitive) could be taken as suggestive of regional continuity. This is the only case so far that is even remotely suggestive of regional continuity.

Testing the molecular clock from the fossil record

1 Family Felidae: lions. According to Hemmer (1974), the Asian lion, *Panthera leo persica*, and the Barbary lion, *P.l. leo*, are 'only slightly varied relict forms' of Lower and Middle Pleistocene lions. These fossil forms include not only the European *P.l. fossilis* (known from sites such as Mauer, Vertesszöllos and Petralona) but also the African *P.l. shawi*, known from Sterkfontein Mbr.5, Swartkrans and Olduvai Bed II, sites that are all within the range of the highly derived modern subsaharan subspecies *P.l. massaicus* and *P.l. krugeri*. There is no trace of *massaicus/krugeri* features in the fossil record until the Upper Pleistocene.

O'Brien *et al.* (1987) examined a number of blood proteins in several subspecies of living lions and calculated Nei's Distances between them, although the small sample sizes in some cases render these more like estimations. Distances of subsaharan lions from *P.l. persica* varied from 0.007 to 0.033 (mean, 0.016); from *P.l. leo*, from 0.012 to 0.023 (mean, 0.018). Nei (1987) gives the formula

$$t = 5 \times 10^6 D$$

where t is the time in years since two lineages diverged and D is the genetic distance between them. The Asian lion

dens). At Wanxien, Lyakhov Island and Jana River, Zhoukoudian type recurs but is extremely large, and resembles both Siberian (*Pt. altaica*) and Indian (*Pt. tigris*) modern subspecies. This suggests where the big Ngandong tiger came from, although the narrow occiput of the latter is idiosyncratically Javanese (Hemmer, 1971, 1972).

The record of tiger evolution tells us a lot about modes of change within a restricted lineage. There has been replacement after replacement, as well as *in situ* change, but there is absolutely no sign of multiregional evolution. The primitive stock spread from northeastern Asia down into Java by about a million years ago, where it underwent change and, by half a million years ago, had spread back north into China where it replaced the archaic form. The new northern tiger underwent further evolution, and by about 100,000 years ago had spread back south, replacing the old Javanese type and evolving into the modern Java tiger.

Among modern subspecies, the Sumatran *Pt. sumatrae* is the plesiomorphic sister taxon of *Pt. sondaica* of Java, which it resembles in stripe pattern while lacking the derived occiput shape. Tigers are not known from Sri Lanka (whereas a fossil lion has been found there); this suggests that they are post-Pleistocene (post-sea level rise) immigrants into India. The Indian *Pt. tigris* strikingly resembles the Siberian *Pt. altaica*, while the geographically intervening South China *Pt. amoyensis* and *corbetti* are somewhat different, which might suggest a post-Pleistocene differentiation for them too. The Indonesian tigers would, if this scenario is correct, be much the most divergent subspecies. This rather complicated scenario is summarised in Fig.3.

What of the genetic data? The Java tiger is extinct, the other subspecies all endangered, so they have been the subjects of genetic studies. O'Brien *et al.* (1987) calculated Nei's Distances between *tigris*, *altaica* and *sumatrae* as follows:

	<i>altaica</i>	<i>tigris</i>
<i>sumatrae</i>	0.003	0.010
<i>altaica</i>		0.007

(On the other hand, Goebel & Whitmore (1987) give a Distance between *tigris* and *altaica* of 0.0098). Using the formula given above, we calculate the following separation times:

	<i>altaica</i>	<i>tigris</i>
<i>sumatrae</i>	15,000	50,000
<i>altaica</i>		35,000 (O'Brien <i>et al.</i>)
		49,000 (Goebel & Whitmore)

It must be admitted that these figures are not in agreement with the fossil record, if the interpretation of *sumatrae* as the plesiomorphic sister-group of *sondaica* is

correct. As discussed above, it is likely that the drift in gene frequencies depends much more on demographic bottlenecks than on elapsed time, and that such indices as Nei's Distance tell us more about past population size fluctuations than about time since separation.

2 Family Rhinocerotidae. The fossil record of the White Rhinoceros, *Ceratotherium simum*, is better than that of the Black Rhinoceros, *Diceros bicornis*, despite the fact that within historic times the Black Rhino has been almost continuously distributed over its wide range while the White Rhino has been restricted to two widely separated areas: south of the Zambezi, and between the Nile and Lake Chad. The two subspecies of White Rhino, the southern *C.s. simum* and the northern *C.s. cottoni*, are distinguished by tooth size and skull shape (Groves, 1975). The toothrow length averages 281mm (41% of basal skull length) in the southern subspecies, 263mm (39%) in the northern. The depth of the dorsal concavity of the skull averages 66mm (9.6% of basal length) in the southern form, 44mm (6.4%) in the northern. The ancestral species, *C. praecox*, had large teeth (42%) and a deep dorsal concavity (10%), so it is the northern subspecies, *C.s. cottoni*, which is the more derived in both characters. On the other hand, the metaloph on the upper molars is on average more transverse, less oblique (i.e. less plagiolophodont) in *C.s. cottoni* than in *C.s. simum* (see Heller 1913: pl.21. fig.1; pl.22, figs.1,2; pl.23; compare pl.21, figs.2-4, pl.22, fig.4), and this is a primitive condition.

A number of nearly complete fossil crania are known for this species (Hooijer 1969; Groves 1975; Harris 1983). The oldest are from the Koobi Fora Formation at Ileret (exact stratigraphy unclear, but presumably 1.5 to 1.9 million years old). The concavity depth in the nearly complete, adult cranium, ER 328C, is 55mm, or 7.4% of the basal length; the toothrow is about 285mm long, or 38.3% of basal length. Both these values are within the range of *C.s. cottoni*; in fact, the only difference, on the available evidence, is its large size. Harris (1983) had identified this cranium as *C.s. germanoaffricanum*, a fossil subspecies, on the basis of its more transverse metaloph; but, as we have seen above, *C.s. cottoni* is, in fact, less plagiolophodont in any case. The modern subspecies of White Rhino, then, may have already begun to differentiate nearly two million years ago — the oldest still surviving subspecies of which we have knowledge (though it must be noted that, in a multivariate analysis, the Koobi Fora skull does not fall precisely within the dispersion of *cottoni*).

The White Rhinos of Olduvai are described and figured by Hooijer (1969). Maxillary cheekteeth from Upper Bed II vary from nearly transverse to fairly oblique. A cranium, OLD 62 from Rhino Korongo, Bed IV, is fully plagiolophodont; its dorsal concavity is about 81mm, or 10.7% of basal length, and its toothrow is 335mm or 44.4% of basal length. It is, again except for its large size, apparently indistinguishable from *C.s. simum*.

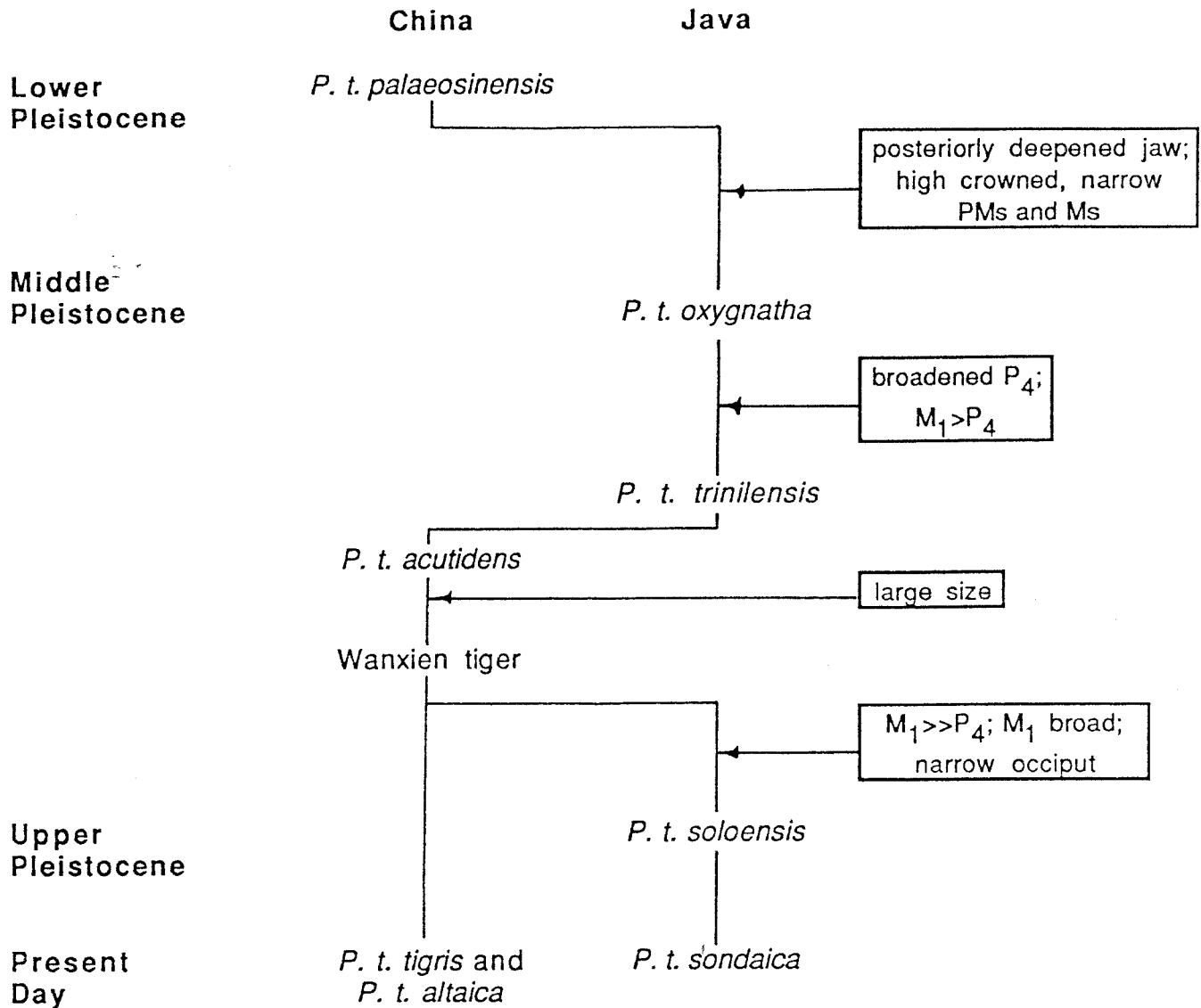


Fig.3. Summary of evolution of *Panthera tigris*.

would then have diverged 5×0.016 million = 80,000 and the Barbary lion 5×0.018 million = 90,000 years ago. As modern subsaharan features had not appeared by about 1 million years ago, these figures are at least not wrong by as much as an order of magnitude!

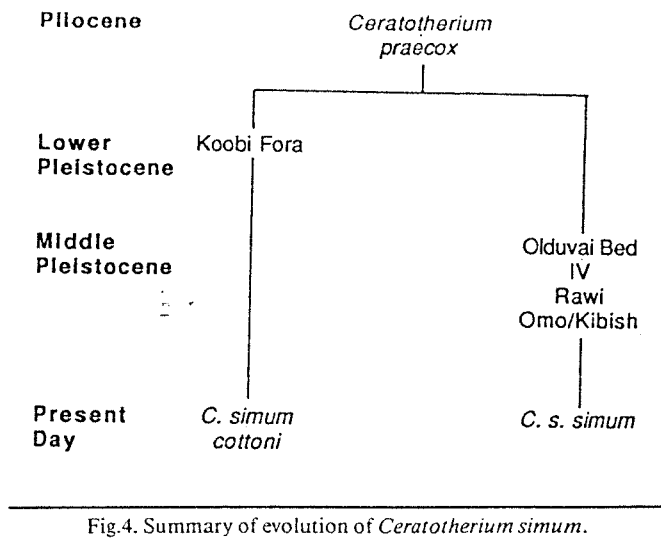
It should be added, however, that Nei's Distances between *P.l. krugeri* and two populations of *massaicus*, members of the highly derived subsaharan subspecies group, are .024 and .031 — greater than most of the distances between them and Barbary or Asian lions. In effect, therefore, this distance measure is in conflict with the cladistic and, inferentially, the fossil data. I have suggested, above, some possible reasons why such gene-frequency distances may not accurately reflect separation dates at least over long periods of time.

Family Felidae: tigers. The most primitive known tiger is *Panthera tigris palaeosinensis* from the Lower Pleistocene of northern China (which, curiously, survived in Japan

into the Upper Pleistocene). It was a small tiger which retained primitive, jaguarlike features such as the thick, massive metapodials, low-crowned and broad cheekteeth, M₁ shorter than P₄, and a mandibular corpus that was deeper below P₃ than behind M₁ (Hemmer, 1967).

The earliest Java tiger, *Pt. oxygnatha* from Sangiran and Kedung Brubus, had a posteriorly deepened mandible, and higher-crowned and narrower cheekteeth. The Trinil tiger, *Pt. trinilensis*, had a broad P₄ and, like all subsequent taxa, had M₁ longer than P₄. The tiger from Punung and Ngandong, *Pt. soloensis*, was abruptly different: very much larger (the size of modern Indian and Siberian tigers), different cusp development, even longer M₁, narrow P₄ but broad M₁, and, for the first time, the typical narrow occiput of the small recent Java tiger, *Pt. sondaica* (Hemmer, 1971).

On the mainland, a primitive tiger still occurred at Lantien, contemporary with, or even later than, Sangiran; the long M₁ first appeared as late as Zhoukoudian (*Pt.*



Two other useful fossil crania are from Rawi, Kavirondo (presumed Middle Pleistocene) and Rhino Canyon, Kibish Formation, Omo (130,000 BP); these are briefly described by Groves (1975). Both are strongly plagiolophodont. The dorsal concavity depth cannot be measured, but the toothrow length of the Omo skull is 46.7% of basal length, and of the Rawi skull probably much the same. This is unexpected, especially in the case of the Omo skull, and suggests replacement of *cottoni* by *simum* in the Turkana basin in the Upper Pleistocene (Fig.4).

Very evidently there is no regional continuity; merely, a divergence in the Lower Pleistocene which has been maintained ever since, with some reshuffling of their distributions from time to time (which is, after all, what replacement is all about).

In this case, mitochondrial DNA data exist. George *et al.* (1983) studied the mtDNA of both living subspecies by means of Restriction Fragment Enzymes, and calculated that they differ by 4%, which according to the authors would mean a divergence time of two million years (actually 1 to 2; according to whether rate of change is 2 or 4% per million years). This agrees strikingly well with the fossil evidence.

Morphometric distances in the light of divergence times

I calculated Mahalanobis Distances on the basis of craniometric data, collected by myself and the late Dr V.Mazak, and used data on human crania kindly made available by Prof.W.W.Howells. These distances should give some idea of the degree of correlation, if any, of morphological change with divergence time, as well as with genetic distance (Table 1). (Although no fossil record is available for Great Apes, they are included in the table because genetic distances are also available for them). The inclusion of human data is for purposes of comparison; looking at the genetic data for subspecies of other species, can we propose correlations with fossil separation times, and so by comparison predict fossil separation times for human geographic variants?

subspecies	Separation dates from:			Mahalanobis	
	Nei's D	mtDNA	Fossil	Distance F	Distance M
<i>Pongo pygmaeus pygmaeus/abeli</i>	¹ 125k ² 85k	1.25-2.5m	—	2.42	2.59
<i>Pan troglodytes/paniscus</i>	¹ 375k ² 100k	.93-1.85m	—	4.14	3.92
<i>Ceratotherium simum simum/cottoni</i>	—	1-2m	>1.5m	4.97	4.54
<i>Panthera tigris altaica/tigris</i>	³ 49k ⁴ 35k	—	10k	5.28	6.68
<i>altaica/sumatrae</i>	⁴ 15k	—	100k	4.81	7.57
<i>Panthera leo massaica/persica</i>	80-90	—	100k	7.58	3.90
<i>Homo sapiens</i>					
Afr/Europe and China	⁵ 135-145k ⁶ 149-314k	90-180k	c.100k	6.08	5.13
Europe/China	⁵ 50k	—	⁷ 67k	4.74	5.24

Table 1. Molecular and fossil separation dates, and Mahalanobis Generalised Distances, of large mammal subspecies. ¹isozymes; ²3DE; ³Goebel and Whitmore, 1987; ⁴Janczewski *et al.*, 1990; ⁵Nei and Roychoudhury, 1982; ⁶Groves, 1990; ⁷Liujiang

People and tigers are about equally differentiated morphometrically; lions and orang utans rather less so. Curiously, the two distinct *species* of chimpanzees are as poorly differentiated craniometrically as are lions and orang utans. In all cases, however, over 90% of skulls were correctly sorted by this procedure (except for male orangs, where the percentage was 88.3%).

Discussion

Table 2 summarises the modes of evolution of the large mammals treated in this paper: Replacement, Regional Continuity, or *In Situ* evolution. There is a single, questionable, case of Regional Continuity; there are at least five, perhaps seven examples of Replacement. The *In Situ* cases are also of great interest in showing the origin of the most apomorphic modern representatives of a species — in one case (African Buffalo), from a more plesiomorphic subspecies which happens still to be extant.

How have these replacements occurred? We need not envisage literal 'struggles for existence', though there may well have been actual conflict, such as is known to occur between competing species of large carnivores today. Quite simply, one species (or subspecies, if the taxonomy is correctly assessed) was slightly more efficient at resource exploitation than the other, and acquired a gradual demographic advantage. There may even have been a certain amount of interbreeding: in the case of subspecies, of course, there must have been, although gene-flow would have been sufficiently limited that no

Subspecies	First appearance	Ancestor	Mode of origin
<i>Lynx lynx</i> spp	late Holocene	?	
<i>P.pardus melas</i>	Mid. Pleistocene	?	Replacement?
<i>P.p.tulliana</i>	U. Pleistocene		Replacement?
<i>G.gulo gulo</i>	Holocene	Afr. spp.	Replacement
<i>A.alces</i> spp	U. Pleistocene	cf. <i>luscus</i>	Replacement
<i>C.e.elaphus</i> gp	220,000 B.P.	<i>postremus</i>	Replacement
<i>S.c.brachyceros</i>	130,000 B.P.	<i>acoronatus</i>	Replacement
<i>S.c.caffer</i>	U. Pleistocene	<i>acoelotus</i>	<i>In situ</i>
<i>D.b.minor</i>	<750,000	<i>brachyceros</i>	<i>In situ</i>
<i>R.s.annamiticus</i>	?	subsp.	<i>In situ</i>
<i>P.l.massaicus</i>	<1 million	<i>guthi</i>	Continuity?
<i>P.t.sondaica</i>	100,000	<i>shawi</i>	<i>In situ</i>
<i>P.t.altaica</i>	Mid. Pleistocene	<i>soloensis</i>	<i>In situ</i>
<i>P.t.tigris</i>	Holocene	<i>acutidens</i>	<i>In situ</i>
<i>C.s.cottoni</i>	1-2 million	<i>altaica</i>	Range extension
<i>C.s.simum</i>	750,000	subsp.	<i>In situ?</i>
		<i>germano-africanum</i>	<i>In situ</i>

Table 2. Evolutionary modes of subspecies of large mammals.

character continuity was evident. Why need it have been different between *Homo sapiens* and *Homo erectus* or *H. neanderthalensis*?

Table 1 compares separation dates of large mammal species as shown by fossil data (where these are available) and those calculated from two sorts of molecular evidence, Mitochondrial DNA and allelic frequencies (Nei's Distances). The agreement of the fossil and mtDNA dates, in the two cases where these are both available, is excellent; Nei's D, however, agrees with neither fossil nor mitochondrial evidence except in the human case. Nei's distances for chimpanzees and orang utans, for example, are given by Janczewski *et al.* (1990) as: *Pongo pygmaeus pygmaeus* vs. *abeli*, 85,000 and 125,000 by two different methods, and *Pan troglodytes* vs. *paniscus*, 375,000 and 100,000 years. These figures flatly disagree with those calculated from mtDNA. As we have already seen, the lion and tiger splitting times calculated by this means are likewise far too young. It would seem, therefore, that it may be only chance that the human separation times calculated by the two methods seem to agree so well; or it may be the inferred recency of the split. (It may be recalled, however, that Groves and Stott (1979) found the plasma protein date for the split of *Gorilla gorilla gorilla* and *G.g. graueri* (1.6-1.7 ma) to be not incompatible with the inferred minimum geological date for the separation of *G.g. beringei* from *graueri* of <1.2 ma).

The Mahalanobis Generalised Distances (Table 1) likewise do not reflect apparent splitting times. Nor do they correlate with Nei's Distance; the Orang Utan subspecies, with among the longest separation times as calculated from Nei's formula, have the smallest Generalised Distance values. The conclusion seems to be that degree of morphological differentiation, as represented by craniometrics, is not highly correlated with inferred divergence time at least within species or close-knit genera. This conclusion, acknowledging the

possibility of long-lasting morphological stasis (and of episodes of very rapid change), is well illustrated by the White Rhino fossil record.

Summary

1. Subspecies divergence has occurred almost as long ago as the Plio-Pleistocene boundary (White Rhino) and as recently as the late Upper Pleistocene (in both recently evolved species like Moose, and longer-established species like Cape Buffalo).
2. Even within the same species (Tiger), evidence suggests that some subspecies may have emerged by the beginning of the Upper Pleistocene, others after the beginning of the Holocene.
3. Only one possible (and that not very convincing) case of multiregional evolution may have occurred in the species surveyed (Javan Rhino); replacement, of one subspecies by another or of one species by another, is the usual occurrence.
4. The only mtDNA separation date (for the subspecies of White Rhino) agrees well with the evidence from the fossil record.
5. Nei's distances, when converted to divergence times by the proposed formula, do not agree with either the fossil record or the mtDNA separation times.
6. There is no consistent relationship between morphological differentiation, as measured by craniometric Generalised Distance, and time since divergence.

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