

Testicondy and ecological opportunism predict the rapid evolution of elephants

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ABSTRACT: Elephants are generally considered to have surprisingly high evolutionary rates for animals with very long generation times. We propose that these high evolutionary rates are the result of a combination of elevated mutation rates in male elephants and the behavioral flexibility of this group of animals. Elephants have long been known to be testicond, i. e., to have internal testicles located near the kidneys. Since the core body temperature of elephants ($36.8 \pm 0.4^\circ\text{C}$) is similar to that of humans, their testicles function in an ambient temperature higher than would have been the case had they been placed in a scrotum. Such elevated temperatures are associated with elevated mutation rates in a wide variety of animals and we propose that this is true also of elephants. In addition, elephants are highly flexible behaviourally and ecologically, which allows them to adapt to a wide variety of environments and presumably to rapid environmental change as well. This ecological opportunism will enable them to take advantage of the high mutation rates and lead to high evolutionary rates.

Introduction

The Proboscidea, elephants and their kin, have an extensive fossil record (Shoshani and Tassy, 1996). One of the most discussed aspects of this fossil record concerns the high rates of evolution within some lineages of the order, especially the family Elephantidae, to which modern elephants belong (Aguirre, 1969; Beden, 1983; Maglio, 1973; Shoshani and Tassy, 1996; Stanley, 1979; Vrba, 1987) (Fig. 1). These rates have been documented as both taxonomic and morphologic rates. While these two measures clearly are not independent of each other, since fossil taxa are in general based on morphological differences, studies using one or the other measure do tend to corroborate one another. Some studies have shown rates of taxonomic diversification within the

Elephantidae to have been equal to or even greater than those of rapidly speciating groups of rodents such as the Muridae (Stanley, 1979), although such calculations may be somewhat exaggerated due to oversplitting in elephant taxonomy (Roth, 1992; Todd and Roth, 1996). Still, such oversplitting reflects high rates of morphological change and is thus of relevance to the present discussion. In other analyses (e. g., Vrba 1987), rate calculations have been biased by considering only the progenitors of the extant genera and excluding entirely extinct genus-level lineages. This biases against elephants since it excludes the large and speciose *Mammuthus* lineage in much the same way that it would bias calculations comparing hyaenas (a clade with few extant lineages) with felids (a clade with many extant lineages), despite the fact that these lineages probably had similar numbers of species

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Evolutionary Theory 12: 39–45 (December, 1999)

The editors thank three referees for help in evaluating this paper.

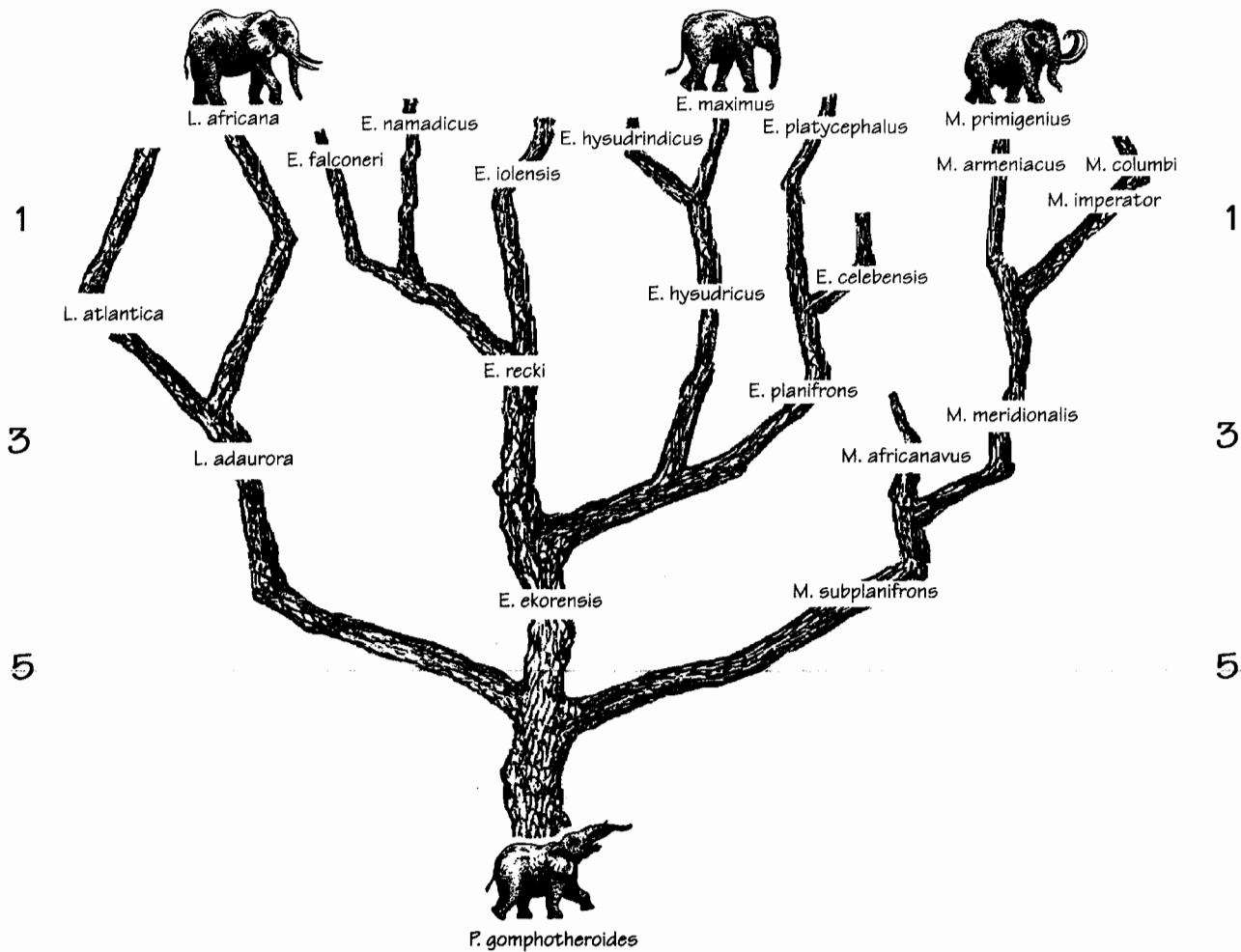


Figure 1: Diagram showing a portion of the phylogeny of the Elephantidae (Maglio, 1973). Only a limited selection of taxa is presented. The numbers indicate millions of years before present. The diagram clearly shows the rapid diversification of this family over the last 5 million years.

over the timespan of their existence. Since it has been suggested by many authorities that evolutionary rates should be expected to correlate with generation length, (e. g., Simpson, 1944, 1953), and since the generation length of elephants is among the longest in mammals, the high evolutionary rates in elephants require some explanation. The most common such explanation has to suggest in relatively vague terms that other factors have been limiting and obscured the effects of generation length (Simpson, 1953; Zeuner, 1931). Vrba (1987) examined a whole suite of more general hypotheses

to account for different evolutionary rates in different lineages. However, she did not consider less general features that may account for anomalies in specific lineages. We believe that we have identified such a factor that is applicable to elephants.

Anatomical background

It has been known since the dawn of comparative anatomy (Smith and Ross, 1910) that elephants are testicond, i. e., that their testes are non-scrotal and located intra-abdominally in the onto-

genetically primary position near the kidneys (Fig. 2) . Intra-abdominal testes also occur in other Paenungulata (Hyracoidea, Sirenia), as well as in a range of other mammals (Carrick and Setchell, 1977; Werdelin and Nilsson, 1999). Most authorities have assumed that the presence of a scrotum is a derived condition within the Mammalia and therefore a number of explanations for its presence (and by inference of testicular descensus) have been proposed. The most often cited explanation, though by no means the only one (Freeman, 1990; Werdelin and Nilsson, 1999), is that it provides a cool environment for spermatogenesis, which is disrupted at the typical core body temperatures of the majority of mammals (Cowles, 1958, 1965). For instance, mean scrotal temperature in healthy human males measured at ambient temperatures of 21°C and 25°C was $34.4 \pm 0.2^\circ\text{C}$, i. e., approximately 2.5°C less than core body temperature (Valeri *et al.*, 1993). Some taxa that have non-scrotal testes have alternative cooling mechanisms. In whales, e. g., the intra-abdominal testes are cooled by venous blood which flows from the extremities through the spermatic arterial plexus (Pabst *et al.*, 1995). A similar mechanism is present in true seals, Phocidae (Rommel *et al.*, 1995). However, no such mechanism is present in the Proboscidea (Short *et al.*, 1967).

We have elsewhere (Werdelin and Nilsson, 1999) presented evidence to show that the scrotum is primitive at least among Eutherian mammals, and that therefore the explanations put forward to account for its presence in various mammalian groups are somewhat off the mark. The feature that requires explanation is instead the derived lack of a scrotum in a few mammalian orders. We suggest that since testicular descent is costly in terms of reproductive success, it should be lost in those mammal groups that have been able to solve the problems related to core body temperature.

Evolutionary consequences of testicondy

It has been assumed by some (Cowles, 1965) that terrestrial testicond mammals compensate for the absence of the cooling device provided by the scrotum by having lower body temperatures. This is, in fact, true of the majority of testicond mammals (e. g., MacDonald, 1984; Werdelin and

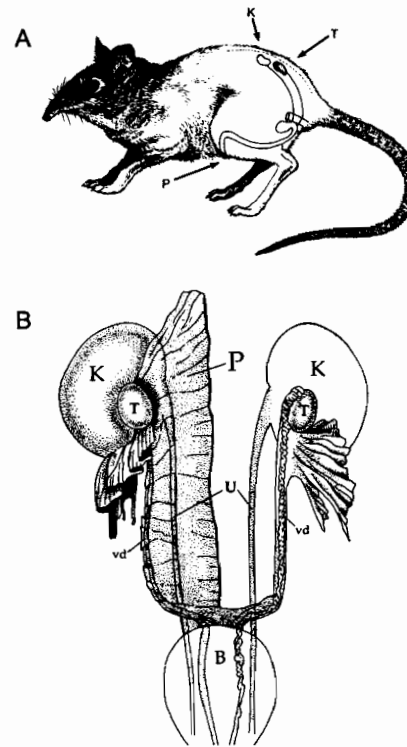


Figure 2: A) The position of the testicles relative to the scrotum on a testicond mammal, the elephant shrew *Elephantulus rufescens*. K = kidney, T = testicle, P = penis. B) Diagram showing the anatomy of the male reproductive tract of the elephant and the position of the testicles ventral to the kidneys. On the right side of the diagram the peritoneum has been removed, on the left side it is in place. K = kidneys, T = testicles, P = peritoneum, U = ureters, vd = vas deferens, B = bladder.

Nilsson, 1999), but not, as far as is known, of Proboscidea. A study of elephants has demonstrated an average intra-abdominal temperature of 36.8 °C (Short *et al.*, 1967), which is in line with core body temperatures of other mammals. Thus, the testes of elephants function in an ambient temperature higher than that in which the testes of scrotal animals function. The significance of this fact lies in the correlation between temperature and mutation rate, which has been demonstrated for a wide range of organisms. In numerous studies, elevated temperatures have shown to be associated with increased mutation rates, e. g., (Cowles, 1965; Ehrenberg *et al.*, 1957; Muller, 1928) up to the

point at which spermatogenesis is completely disrupted (above ca. 38° in mammals). We conclude that male elephants, with their high testicular temperatures, can be expected to have elevated basal mutation rates compared to scrotal mammals or mammals endowed with other testicular cooling mechanisms.

The significance of high mutation rates in male elephants becomes even more evident when coupled with the fact that even in scrotal mammals such as humans and other primates, mutation rates are higher in males than in females (Miyata *et al.*, 1987; Shimmin *et al.*, 1993, 1994). One reason may be that in female mammals all germ cell divisions - except the two meiotic ones - are already completed by the time of birth, whereas in the male there is continuous germ cell division throughout life. In humans it is estimated that an oocyte will have undergone about 22 divisions, while the spermatocytes of a 35-year old man will have undergone about 496 divisions (Vogel and Rathenberg, 1975). The male/female mutation ratio ranges from 3.5 and upwards in various genes (Drake *et al.*, 1998; Shimmin *et al.*, 1994). In the specific case of haemophilia B, e. g., the mutation rate has been shown to be 11 times higher in males than in females (Montandon *et al.*, 1992).

This line of reasoning allows us to conclude that elephants potentially can have very high rates of evolution due to the proposed high mutation rates in the male reproductive system. It may be perceived that this high mutation rate would be potentially hazardous to the organism. The situation where mutations with significant effect increase drastically in frequency does not represent a problem, as these would be selected against in the normal way and if they were too many, the population or species could not survive at all. Hence, these mutations must be sufficiently few to be balanced out by selection for positive traits originating by the same mechanism. The problem of genetic load arising through accumulation of very slightly deleterious mutations (VSDMs) is more difficult to assess. Indeed, the study of VSDMs is one of the central aspects of population genetics (Crow, 1997; Muller, 1950; Ohta, 1992). However, it appears that genomic deleterious mutation rates at least in hominids are more common than has been perceived (Eyre-Walker and Keightley,

1999), suggesting that the effects of VSDMs may not be multiplicative. It is possible that such mutations remain hidden behind modifiers such as heat-shock proteins (Rutherford and Lindquist, 1998). On the other hand, following a suggestion by (Kondrashov, 1995), inspired by, e. g., Crow (1970), VSDMs may act as time bombs limiting the life span of a lineage. Kondrashov (1985) suggests that vertebrate lineages with effective population size, $N_e \leq 10^4$ - 10^5 should be limited to $\sim 10^6$ - 10^7 generations. Elephants probably have N_e less than the specified number, but 10^6 generations is a very long time for organisms with generation times measured in decades, suggesting that a moderate increase in mutation rate may not be a serious problem at least from this perspective.

Under ordinary circumstances an increase in mutation rate may not have any, or only negative, macroevolutionary consequences. However, during times of rapid environmental change and/or habitat fragmentation, mutation rates may be an important factor in the rate of response of mammal species to such change. This is reflected in the varying evolutionary rates of elephants in the Pleistocene (Maglio 1973).

Having established that germ-cell mutation rates in elephants are likely to be higher than in other mammals, it must be emphasized that this only provides the potential for high evolutionary rates. Some adaptational flexibility is also required. Elephants have an inherently flexible behavior and opportunistic ecology (Kingdon, 1979; Shoshani and Eisenberg, 1992). In these features they differ markedly from most other megaherbivores. Thus, elephants live in a wide variety of environments, from savannah to tropical forest, while the rhinoceroses, the hippopotami and the giraffe are each much more restricted in their habitat (Kingdon, 1979; Owen-Smith, 1988). This flexible system has allowed elephants to take advantage of environmental changes in the Tertiary and Quaternary by adapting their ecologies to new habitats. High mutation rates would consequently lead to rapid diversification within these habitats, both morphologically and taxonomically. In this way, the behavioral ecology of elephants provides the bridge between mutation rate and evolutionary rate. Such a combined reproductive-ecological view of elephant evolution derives support from the probos-

cidean fossil record, which fails to show high rates of evolution in strictly lophodont groups, notably deinotheres and mammutids (Shoshani and Tassy, 1996), in which a much less flexible dietary regime must be assumed (Hunter and Fortelius, 1994).

What of other testicond mammals? As noted, most have low body temperatures or some form of testicular cooling mechanism and it is only within Paenungulata that this is not always the case. Therefore we must ask why evolutionary rates of Sirenia and Hyracoidea do not appear to be extremely high. In the case of the former this is, in fact, likely due the existence of specific cooling mechanisms for the testes, much as in seals and dolphins (Rommel *et al.*, 1998). Hyracoids, on the other hand, have poor thermoregulatory ability, particularly in hot temperatures (Bartholomew and Rainey, 1971) and in open, hot environments without significant amounts of shade their core body temperature and by extension their testicular temperature may rise beyond the point at which spermatogenesis is disrupted and aspermia occurs (Cowles, 1965). Thus, an opening of the environment should have put hyracoids at a reproductive disadvantage because of their testicondy. This prediction seems to be supported by the available fossil record. Hyracoids were a highly diverse and rapidly evolving group in the Oligocene (Schwartz *et al.*, 1995) and have gradually diminished in diversity with the evolution of more open habitats, beginning in the early Miocene. The generally large body mass and resultant inertial homeothermy of elephants would have protected them from this problem.

An important point regarding the mechanism of rapid evolutionary change suggested here is that it is the same mechanism that operates to promote rapid within species evolution and rapid lineage diversification, requiring only to be modulated by temporal and geographic variation in the environment. This mechanism is natural selection in a variable environment operating on a high intrinsic mutation rate and mediated by behavioral flexibility. There is no reason to postulate any special features of speciation leading to rapid morphological change or to most morphological change being concentrated to speciation events, as suggested by, e. g., (Eldredge and Gould, 1972; Stanley, 1979).

Javier Herbozo drew figures 1 and 2A. The work of LW is supported by the Swedish Natural Science Research Council and that of MF by the Academy of Finland.

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