“Proboscidean agent” of some Tertiary megafaunal extinctions

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SUMMARY: Proboscideans constantly and strongly modified Tertiary ecosystems. Their impact was mostly beneficial for herbivores, but not for the other elephant-sized mammals. So, proboscideans superseded arsinoitheres in Africa (Late Oligocene) and indricotheres in Asia (Early Miocene). Indricotheres efficiently browsed only at considerable height of standing trees. Gomphotheres, like modern elephants, were mixed browsers/grazers able to take food from different storeys owing to their long trunked snout and to tree-felling habits. They destroyed many trees. Still more trees were converted to a state inappropriate for the indricothere feeding. The Plio-Pleistocene contact of proboscideans with giant sloths did not result in either group extinction. Both were equally protected from predators and equally adapted for the efficient feeding on tree vegetation of different type.

1. Introduction

The outstanding ecosystem impact of modern elephants and other pachyderms helped to unravel the puzzle of Pleistocene ecosystem functioning and that of the Wurm mass extinctions (e.g. Owen-Smith 1988; Putshkov 1989, 1994, 1997; Schule 1990). This impact may help to understand certain previous events too.

2. Proboscideans and non-Human predators

Various proboscideans evolved competing with each other under the pressure of formidable creodonts and, later, of large carnivorans (mainly saber-toothed cats), killing calves, subadult and old individuals. In response, proboscideans not only increased in size, but became very ‘clever’ beasts too (Gabunia 1969). They withstood foes efficiently and their population density stabilized just below their niche capacity level. Hence, proboscideans could constantly exert a potent ecosystem-shaping impact.

3. Proboscideans, vegetation and other herbivores

Both modern elephants despite their differences in dentition are mixed browsers/grazers that feed in any storey using trunk, tusks and felling trees (e.g. Kingdon 1979). In most cases the extinct proboscideans were ecologically flexible and basically polyphagous too. Their trophic and landscape preferences seem to be formed more by the competition and by the accessibility of one or another kind of food than by morphological differences (e.g. Putshkov 1989, 1997; Lambert 1992; Putshkov & Kulczicki 1995).

Already early Miocene gomphotheres, true mastodonts, and dinotheres ranging from rhino to Asian elephant size increased drastically the nutrient recycling rates and vegetation cover mosaicity. They destroyed many trees both by felling and by barking them. Also many damaged trees perished from diseases, fires, wood-boring insects. Thus giants created clearings and then maintained them by the repeated browsing over regrowth. Gomphotheres shaved the bark with their pointed upper and pointed or chisel-like lower tusks aided with trunk (Lambert 1992; Putshkov & Kulczicki 1995). The long trunked snout permitted them to browse efficiently on low, medium and quite tall trees (these were often uprooted), bushes, herbs and grasses (Lambert 1992; Putshkov & Kulczicki 1995). Due to such mixed 'all-storeys' feeding habits these strong and 'clever' gregarious creatures not only lived in savannas, but created them too in seasonally dry regions, like modern elephants do.

The still large later proboscideans exerted even more strong impact on Old and New World ecosystems. This impact usually was beneficial for smaller megafauna (up to the modern black rhino size) (e.g. Owen-Smith 1988; Putshkov 1989, 1997, Schule 1990) but not for the elephant-sized mammals. Only the last aspect is considered here.

4. Indricothere 'Demise': Drought or Gomphotheres 'Accession'?

The sudden final Early Miocene extinction of impressive indricotheres (baluchitheres) (*Indricotheriidae*) has been ascribed to the fact that they were simply too big. Hence, they could not exist for a long time due to their slow generation turnover (Janis & Carrano 1991). Yet, indricotheres were taller but not heavier than large elephants (e.g. Gromova 1959) and thrived for more than 15 million years (e.g. Savage & Russell 1983).

Other version blames the increase in aridity caused by rain shadow effect of the uplift of mountain ranges from Himalayas to Dinarids (e.g. Gromova 1959; Gabunia 1969). However, open steppes have occupied most of the Inner Eurasia more than 10 million years after the indricothere extinction. At the time of extinction mountains were low and caused only moderate-scaled increase in aridity. As a result, the indricothere life zone (parklands and savannas of warm-temperate, subtropical and tropical types) expanded while closed forests contracted in range (e.g. Yassamanov 1985).

Indricotheres disappeared from the geological record soon after the gomphothere invasion from Africa (e.g. Savage & Russell 1983). Is it possible that gomphotheres with a shoulder height of 1.7-2.5 m and a weight of 1.5-3.5 tons outcompeted the indricotheres with a shoulder height of 4-6 m, head height of 6-9 m and a weight of 3-15 tons? The unravel of the puzzle seems to be just there.

Indricotheres ate twigs and stripped the bark upwards mostly at height near 4.0-8.5 m with their strong lower incisors (Putshkov & Kulczicki 1995). Earlier *Indricotherium* also used large upper incisors for the bending of high branches. Later *Paraceratherium* had small or no upper incisors while the lower ones became even larger. Gromova (1959) supposed that the former was more leaf-eating and less bark-eating than the latter. Yet, these changes reflect perhaps the giants-driven changes of tree-form rather than trophic changes (Putshkov & Kulczicki 1995). Due to the upward barking with lower incisors some trees perished, but other died back only above the leisured zone. Beneath it, trees reacted by abundant trunk-shooting. Giants, attracted by the shoots, browsed upon them repeatedly. Due to the compensatory growth the dense 'brush' of shoots appeared. Some trees, whose terminal buds were repeatedly browsed could never reach their normal height. They formed dense distorted crowns at the height convenient for the indricothere feeding. Such distorted trees made up the considerable part of all trees in the 'indricothere' savannas and parklands. The beasts found enough of leaved twigs at 3.5-8 m height (Putshkov & Kulczicki 1995). It became unnecessary to bend the branches of the remaining higher trees that were, however, more convenient for the upward barking than trees distorted as yet. These indricothere-driven changes of tree-form became the selective agent causing the mentioned changes in the indricothere dentition. Huge indricotheres damaged trees more than the modern giraffes, but far less than the elephants do. Unlike proboscideans, indricotheres could not inhabit both temperate and tropical forests. Like giraffes, they remained exclusively parkland and savanna-dwellers (Putshkov & Kulczicki 1995).

Gomphotheres came to Eurasia through the new-established land bridge. They felled trees or barked them upwards and downwards at the far lower level than indricotheres did. Neither plants nor carnivores of Asian ecosystems were adapted to gomphotheres. It is probable that at first the latter increased in number explosively (as recently elephants in Tsavo Park: e.g. Beard 1989) and occupied the indricothere range rapidly not only geologically but ecologically speaking as well (Putshkov & Kulczicki 1995). They soon destroyed many trees (both undistorted and distorted by indricotheres) in savannas, parklands and riparian forests or converted them into the non-climax state of low regrowth, bushes, scrub, dense stool-shoots, etc. Such changes were adverse neither for gomphotheres with their mixed browsing-grazing 'all-storeys' feeding nor for the most of smaller herbivores (Putshkov & Kulczicki 1995). For indricotheres the changes were disastrous. Similar to modern giraffes that can not cover their energy losses while being forced to browse upon vegetation lower than 2 m, giraffe-like indricotheres could not find enough food in tree-stands transformed by gomphotheres. Indricotheres as hindgut fermenters needed more food than the foregut fermenting and much smaller giraffes need. Probably, only small indricothere herds near forest edges did not starve to death (Putshkov & Kulczicki 1995).

After several generations gomphothere numbers should have arrived to the dynamic equilibrium with their environment. The interaction between their natality rates and mortality factors may have resulted in fluctuations of gomphothere density just below the level permitted by their trophic resources. Besides other mortality agents (diseases, periodic attrition, etc.), predators that previously killed indricothere calves had to switch to subadult gomphotheres. Certain formidable foes, as probably *Hyainailouros*, may have arrived from Africa following on their proboscidean prey 'heels'. Yet, indricothere populations could not recover. Gomphotheres with their far more developed brain (Gabunia 1969) and more flexible feeding strategy withstood the hostile factors more efficiently than indricotheres did. Hence, they constantly remained 'too numerous' and went on converting many trees to the state inappropriate for the indricothere feeding. The 'ill-fed' indricotheres brought feeble calves and often could not protect them from predators. The small residual indricothere populations were doomed to the extinction by stochastic events, although they could linger in some regions till more proboscidean species appeared due to migration and speciation processes (Putshkov & Kulczicki 1995).

5. Proboscideans and other elephant sized Mammals

Probably the small-brained arsinoitheres of African Oligocene were superseded by 'clever' proboscideans that defended their calves against creodonts more efficiently. On the other hand, the gomphotheres (and partially mastodonts and mammoths as well) coexisted with elephant sized sloths (eremotheres and megatheres) in America during late Pliocene and Quaternary times. These sloths were difficult prey for any predator due to their monstrous claws combined with exceptional strength and thick skin. Also, unlike indricotheres, they could live in both savannas and heavily wooded regions and feed efficiently on trees broken or fallen by proboscideans or by sloths themselves.

6. Conclusions

Since late Oligocene proboscideans were both giant and 'clever' creatures. Predators and other adverse agents could only confine their population density just below their niche capacity level. Hence, they strongly modified ecosystems. These changes were usually useful for smaller megafauna. For the other elephant-sized giants they may be harmful, especially if these giants were less able to withstand predators. Therefore, proboscideans superseded arsinoitheres in Africa (Late Oligocene) and indricotheres in Asia (Early Miocene). Indricotheres efficiently browsed only on trees that were tall enough. Trees distorted by their repeated browsing had abundant shoots and/or ramifications at the height of 3.5-8.0 m. Gomphotheres were mixed browsers/grazers taking food from different storeys owing to their long trunked snout and to tree-felling habits. They destroyed many trees and converted still more trees to the state inappropriate for the indricothere feeding. The Plio-Pleistocene contact of proboscideans with giant sloths in Americas did not result in either group extinction. Both were equally well protected from predators and equally well 'equipped' for the efficient feeding on tree vegetation of different type; both were mighty 'tree fellers'.

7. References

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