Palaeoloxodon cypriotes, the dwarf elephant of Cyprus: size and scaling comparisons with *P. falconeri* (Sicily-Malta) and mainland *P. antiquus*

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SUMMARY: We provide the first detailed biometric study of *Palaeoloxodon cypriotes*, the dwarf elephant of Cyprus, based on the Bate collection from Imbohary. Molar morphology indicates derivation from *P. antiquus*, while molar proportions are unchanged from that species, paradoxically implying an allometric shift. To maintain function, enamel is relatively thick and plates have been lost, producing a molar lamellar frequency analogous to *P. antiquus* milk molars of the same size. Body size was similar to or slightly larger than *P. falconeri*, but the teeth were even smaller. Perhaps as a result, plate loss was more extreme than in that species. Sparse material of slightly larger dwarf elephants from Achna are of uncertain status.

The dwarf elephants of Cyprus were first described by Bate (1904), but have been little-studied since that time. The Bate collection in the Natural History Museum, London, formed the basis of our study. Elephant remains comprise 44 dwarf molars from Imbohary, in the north of the country west of Nicosia, and seven larger (but still dwarf) molars from Achna in the south-east of the country. Very sparse post-cranial and tusk material was also examined.

The molars strongly support derivation from *P. antiquus*, the mainland straight-tusked elephant. They share features such as median expansions of the enamel loops; the division of the loop in early wear into a long central portion flanked by small rings on each side; the tight folding of the enamel; and the narrow shape of the crown.

The single measurable long bone of *P. cypriotes* in the Bate collection – a femur – provides an estimated body weight – using the scaling formula derived by Roth (1990) – of approximately 200 kg. This represents a weight reduction of 98% from the 10-tonne ancestor. A single preserved tusk shows a degree of curvature greater than that seen in *P. antiquus*.

Molars are reduced to approximately 40% the linear size of mainland *P. antiquus*.

Remarkably, given the extreme degree of dwarfing, the length/width/height proportions, i.e. the gross shape of the tooth, are indistinguishable from those of *P. antiquus*. Clearly any changes in skull morphology (e.g. the paedomorphic effects found in *P. falconeri*: Palombo, this volume) have not impinged on molar shape, including crown height. In retaining the same shape as the ancestral *P. antiquus*, the dwarf teeth in fact depart from the intraspecific allometric trend within that species. This suggests that natural selection may have been required to maintain the same (presumably optimal) shape.

Other features have changed, however: molar enamel is thicker, relative to the size of the tooth, than in *P. antiquus*, and plate number has decreased. Both of these, presumably, help maintain shearing function in the much smaller tooth: isometrically reduced enamel might be too thin for mechanical function or even stability, and plates are lost to retain optimal separation between them (cf. Maglio 1973, Lister & Joysey 1992, Lister 1996). In third molars, mean plate number has dropped from c. 18 to c. 11, representing a 40% loss, while in earlier tooth generations between one and three plates have been lost. A very interesting finding is that

P. cypriotes molars (e.g. M3) have exactly the same lamellar frequency as earlier *P. antiquus* tooth generations (e.g. dP3, dP4) of the same crown width. In other words, plates have been lost to just the degree that maintains optimal function for a tooth of that size.

Although limited by small sample sizes, an interesting comparison can be made between *P. cypriotes* and *P. falconeri* from Malta and Sicily. The individual represented by the Imbohary femur was above the range for Sicilan *P. falconeri* based on limb-bone dimensions given by Ambrosetti (1968), suggesting a somewhat larger body size. On the other hand, the molar teeth are clearly smaller in the Cypriot animal, by as much as 40% in mean M3 lengths. Relative to *P. antiquus, P. cypriotes* has a tooth: body ratio closer to isometry, whereas *P. falconeri* shows more strongly the commonly observed relatively larger teeth of dwarfed forms (Ambrosetti 1968; Lister 1996). The reduction in plate number is relatively modest in *P. falconeri* (typically 15 plates remain in M3) compared to *P. cypriotes*. This may indicate that the functional need to shed plates accelerates as the tooth becomes progressively smaller. Alternatively, the degree of plate reduction, as well as the tooth: body size ratio, might reflect greater genetic entrenchment of the dwarfing process in *P. cypriotes* than in *P. falconeri* (cf. Lister 1995).

Finally, the remains from Achna, of unknown age, are too sparse and fragmentary to allow detailed analysis, but indicate a dwarf palaeoloxodont elephant probably about 10-20% larger in dental dimensions than *P. cypriotes.* The work of Simmons (1999) and colleagues at the Akrotiri Aetokremnos locality demonstrates survival of *P. cypriotes* until at least 11 ka BP. Given this very late age, it is tempting to suppose that the Achna population is older and its antecedent. However, until more material becomes available, including an estimate of the age of the larger form, it is impossible to say whether are dealing with two points of a single evolving lineage, or separate dwarfing events, nor whether a taxonomic separation is justified.

In conclusion, the independent dwarfing of *Palaeoloxodon antiquus* on several Mediter-ranean islands provides an exciting experiment for testing evolutionary patterns and processes. The comparison here between *P. cypriotes* and *P. falconeri* is a small beginning of such a study. In the case of *P. cypriotes*, the analysis of new material from Akrotiri Aetokremnos should provide further data contributing to its fuller characterisation.

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