Phylogenetic relationships and biogeographical history of the large, extinct European testudinids

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Background. Large-sized testudinids had a long evolutionary history in Europe during the last 50 million years before becoming extinct in the beginning of the Pleistocene. Despite a 150-year long history in research and a decent fossil record, the European large testudinids have received limited attention so far.

Methods. New excavations, descriptions of new specimens from Greece, Spain and Germany, revisions of previously published European taxa and comparative studies with extant testudinids now provide a major advancement in understanding the anatomy and evolutionary history of these turtles. This contribution aims to provide an updated summary of the accumulated knowledge on European large tortoises and to explore in detail their phylogenetic relationships in a global context (including small-sized extinct and extant taxa). The phylogenetic analysis is based on a new character/taxon matrix of morphological characters. Parsimony analysis was performed both with and without molecular backbone constraints.

Results. We describe new material of large testudinids from Greece, Spain and Germany and revise most of the available material that has been previously published. Our morphology-based results are promising since they are consistent with recent molecular studies in identifying large testudinids traditionally referred to the *Geochelone* complex as polyphyletic. Furthermore, we were able to reproduce the molecular phylogeny of Mediterranean tortoises (Testudona).

Discussion. The phylogenetic framework presented here allows addressing several open questions of the history of testudinids. First of all, it hints to a more complex biogeographic

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history of European testudinids than previously recognized. Although the early Paleogene history of testudinids cannot be accurately traced at the moment it seems probable that, besides Asia and North America, Europe also played a major role in the early diversification of Testudinidae. We demonstrate that large European testudinids do not form a monophyletic lineage. The widely recognized genus *Cheirogaster* should only include the Eocene type species, and exclude other large Paleogene or giant Neogene taxa so far known. Our analysis reveals that large size evolved independently in several clades and in several continents during warmer parts of the Cenozoic. Besides this general scheme other factors might have played a role regionally (e.g. changes in vegetation, island isolation).

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