

The Lower Pleistocene Primate-Bearing Fossil Site of Dafnero (W. Macedonia, Greece): New Data from classic and Innovative Approaches

D. S. Kostopoulos¹, E. Aidona¹, M., Benammi², A.Gkeme¹, L. Grasset², F. Guy², G. Koufos¹, Z. Kynigopoulou^{1,3}, A. Le Maitre^{2,4}, A. Novello⁵, Ch.-A. Plastiras^{1,2}, G. Merceron²

(1)School of Geology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece, dkostop@geo.auth.gr

(2) PALEVOPRIM, University of Poitiers, France

(3) School of GeoSciences, Grant Institute, University of Edinburgh, UK

(4) Department of Theoretical Biology, University of Vienna, Austria,

(5) CEREGE, Europole Mediterraneen de l'Arbois BP80 - 13545 Aix-en-Provence Cedex 4, France

Introduction

Well hidden in an intricate system of deep ravines crossing the Aliakmon River Valley -one of the most beautiful and wildest landscapes in NW Greece- is the fossil locality of Dafnero (Dafnero-1), nearby the homonymous village (Fig. 1A). Discovered in 1990 and originally explored between 1990 and 1994 (Koufos *et al.*, 1991), the locality has yielded a limited but significant Early Pleistocene fossil mammal assemblage.

A Greek-French partnership between the Aristotle University of Thessaloniki (Lab of Palaeontology) and the University of Poitiers (PALEVOPRIM), came back to this area in 2010 and started a new field campaign that soon allowed locating two additional fossil sites. Dafnero-3 has proven to be extremely promising in terms of quality and density of fossils (Fig. 1C) and four years later (summer 2014) a fairly complete skull of a large baboon-like monkey was unearthed (Fig; 1C), upgrading the locality to a primate-bearing one. After seven years of intense field and lab work new data on the Dafnero fauna, flora, stratigraphy, and age picture altogether an astonishing mammal palaeocommunity at the gates of Europe.



Figure 1. Overall view of Dafnero fossil locality (A); discovery of primate cranium (B) and fossil preparation on field (C).

The Dafnero Fauna and Age

Earlier works allowed identifying within the Dafnero fauna the carnivores Chasmaporthetes lunensis, Baranogale cf. helbingi, Nyctereutes megamastoides, Vulpes alopecoides, and Ursus cf. etruscus, the equid Equus stenonis cf. vireti, the giraffid Palaeotragus inexspectatus, the cervids Metacervoceros ex gr. rhenanus, and Eucladoceros tegulensis, and the bovids Gallogoral meneghinii, Gazella bouvrainae, and Gazellospira torticornis. The 2011-2018 mission in Dafnero-3 allows us to add at the moment the hysticid Hystrix sp., the rhino Stephanorhinus sp., the machairodontine felid Homotherium latidens (Koufos et al., in press), and the cercopothecid Paradolichopithecus aff. arvernensis (Kostopoulos et al. 2018; Fig. 2A). This mammal assemblage as a whole match perfectly those recovered previously from Volakas (Drama), Vatera (Lesvos Island), and Sesklo (Thessaly), keeping strong affinities with contemporaneous mammal communities from SW Europe and W Asia, and suggesting the establishment across this latitudinal belt of a rather homogeneous and characteristic South Alpine mammal palaeocoenosis.

Preliminary data based on mammal biochronology allow suggesting for Dafnero mammal assemblage a middle-late Villafranchian age, European Land Mammal zone MN 17b. An extensive magnetostratigraphic sampling conducted in 2016 and 2017 from 31 horizons in two partially overlapping lithostratigraphic sections allowed reconstructing the local

magnetostratigraphy, which includes two long reverse units interrupted by a short normal one. Correlation with GPTS is still in progress but preliminary data suggest a better match within C2r (i.e., within post-Olduvai Matuyama Chron) (Benami et al. in progress).

Innovative Palaeoecological Approaches

In order to further address phylogenetic and ecological questions related to the cercopithecid Paradolichopithecus aff. arvernensis based mainly on the characteristics of the internal structure of the cranium LGPUT DFN3-150 from Dafnero-3 we applied micro-CT scan imaging analysis i) the inner ear anatomy (Fig. 2B), ii) the development of maxillary sinuses and iii) the enamel thickness (Fig. 2C). These approaches are combined by dental microwear texture analysis (DMTA; Fig. 2D) which provides a glance on its dietary preferences. The results allow us to propose Paradolichopithecus as a terrestrial omnivore "opportunist", a European Early Pleistocene analogue of extant baboons, and to call into question the traditional hypothesis of a Macaca-Paradolichopithecus relationship (Le Maitre et al., submitted).

Investigation for palynomorphs/phytoliths within the sedimentary sequence of Dafnero has provided poor results. Instead, we applied botanical palaeochemotaxonomy as a complementary proxy for palaeoflora and palaeoclimate reconstruction. According to our preliminary results, the overall extractable lipid distribution from Dafnero fossil horizon is characterized by n-alkan-1-ols, phytosterols, fatty acids, series of aromatics typical of charred wood residues and an important amount waxy nalkanes in the C15-C37 range (Grasset et al., in progress).



Figure 2. Digital reconstruction of outer (A) and inner (B, C, D) features of Paradolichopithecus from Dafnero 3.

Discussion

Planned field work over the next few years at Dafnero focuses on the improvement of the local fossil record in order to identify with the utmost precision and safety the taxinomic content and the composition of the fauna and its paleozoogeographic relations with adjacent areas. At the same time the forthcoming magnetochronology and updated biochronology will provide accurate dating of the fauna allowing an important review of the local-scale biostratigraphy and a refinement of regional to continental-scale correlations. The per species analysis of the dietary preferences of the mammals recorded in the Dafnero fauna along with independent paleoecological approaches will finally lead to the reconstitution of the local palaeoenvironment, triggering further discussions about temporal and spatial oscillations of environmental factors controlling primate distribution.

Acknowledgements

Excavations at Dafnero were supported by the Lab of Paleontology, AUTh, the CNRS, France [grant number PICS5185; 2010-2013]; and the National Geographic Society [grant 9903-16; 2016-2017]. ALM studies were partly supported by the Austrian Science Fund [FWF grant number P29397] and ChAP studies by Eiffel scholarship program of excellence.

References

- Kostopoulos D.S., Guy, F., Kynigopoulou, Z., Koufos, G., Valentin, X., Merveron, G. 2018. A 2Ma old baboon-like monkey from Northern Greece and new evidence to support the *Paradolichopithecus – Procynocephalus* synonymy (Primates: Cercopithecidae). Journal of Human Evolution 121, 178-192.
- Koufos, G.D., Kostopoulos, D.S., Merceron, G., The saber-toothed cat *Homotherium latidens* (Owen, 1864) from the Lower Pleistocene locality Dafnero, Western Macedonia, Greece. Geodiversitas (in press).
- Koufos, G.D., Kostopoulos, D.S., Koliadimou, K., 1991. Un nouveau gisement de mammiferes dans le Villafranchien de Macedoine occidentale (Grèce). Comptes Rendus de l'Académie des Sciences de Paris 313, 831-836.
- Le Maitre, A., Kynigopoulou, Z., Plastiras Ch.-A., Guy, F., Merceron, G. Kostopoulos, D.S. (submitted). Inner cranial anatomy of *Paradolichopithecus* aff. *arvernensis* from Dafnero 3 (Lower Pleistocene, Greece) as inferred from microCT-scan imaging analyses. Journal of Anatomy (submitted).