The Fossil Record of Tapirs (Mammalia: Perissodactyla: Tapiridae) in Greece

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1 Introduction

Tapirs (Mammalia: Perissodactyla: Tapiridae) are odd-toed ungulates. From the short and robust limbs, the forefoot also preserves the fifth digit, sometimes used, the dental formula is 3-1-4-3 / 3-1-3/4-3 with low-crowned, lophodont cheek teeth and molarized premolars, and possess a short and flexible proboscis (Rustioni and Mazza 2001). Due to their particular lifestyle in forests, significant water sources are required and given that fossil tapirids do not differ significantly from living tapirs (Kurtén 1968) (living fossils), they are considered to be useful indicators of the paleoenvironment. This group is known at least since the Early Eocene of Kyrgyzstan (Asia) and has always been associated with tropical-subtropical forestry environments. Besides the extant genus—which is known by five extant and more than 15 extinct species (Cozzuol et al. 2013 and references therein)—Tapiridae includes several other extinct genera and species whose phylogenetic relationships are not well known. After their appearance in the Ypresian (Eocene), tapirids quickly achieved their maximum diversity in the Lutetian with at least 14 species; since then, the diversity of this group has been gradually declining (PaleoBiology Database 2019). Molecular analyses corroborate the monophyly of crown tapirs and recover them as the sister-group of the rhinoceroses, forming together the perissodactyl clade called Ceratomorpha Wood, 1937 (Steiner and Ryder 2011). The inclusion of extinct tapir species in phylogenetic analyses has been slow, but Cozzuol

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et al. (2013) presented a phylogeny containing all extant tapirs and several extinct species. Based on this analysis, it seems that crown Tapiridae is divided into two main clades, one defined by the extant Baird's and Malayan tapir and the other by the extant Brazilian, Mountain, and Kabomani tapirs (Cozzuol et al. 2013). Extinct tapirs are placed within those clades, as well as along the stem of crown Tapiridae (Cozzuol et al. 2013).

In Europe, the Plio-Pleistocene fossil record is represented by two species of tapirs: *Tapirus arvernensis* Croizet and Jobert, 1828 and *T. jeanpiveteaui* Boeuf, 1991 (Boeuf 1991; Guérin and Eisenmann 1994). The former is much more common than the latter and closer to the extant *T. terrestris* (Linnaeus, 1758) from South America. *Tapirus arvernensis* includes two sub-species: *T. a. minor* Michaux et al., 1976 and *T. a. arvernensis* Croizet and Jobert, 1828.

2 Historical Overview

Tapir fossils are rare in the Greek fossil record (Table 1 and Fig. 1). Paraskevaidis (1977) referred, but without description and measurements, three upper cheek teeth of *Tapirus* sp. found during research in the late Miocene lignite of Servia (Kozani, W Macedonia), and without a known host location of the specimens; as such, this occurrence is cited herein with caution. The only two confirmed occurrences of a tapir are known from the research and the systematic excavations in Milia (Grevena) area in the last 25 years. The Milia association is also unique in Greece and very rare in Europe, defining the MN16a biozone of Late Pliocene. The Milia vertebrate paleo-fauna, besides *Tapirus arvernensis*, consists of mastodons, gomphotheres, rhinoceroses, suids, carnivorans, bovids, cervids, hipparions, micromammals, and turtles (Guérin and Tsoukala 2013; Tsoukala 2000; Tsoukala and Mol 2016; Crégut-Bonnoure and Tsoukala 2017; Vlachos and Tsoukala 2016; Vlachos et al. 2018). The tapir remains from Milia are the southernmost occurrences of the family in the Pliocene of Europe.

Table 1 List of the Greek localities containing tapir fossils. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB)

Localities[PBDB No]	Age (MN)	Taxon
Milia-2[195290]	Late Pliocene (MN16a)	*Tapirus a. arvernensis*[1]
Milia-5[185859]	Late Pliocene (MN16a)	*Tapirus a. arvernensis*[1]
Servia[202257]	Late Miocene	*Tapirus* sp.[2]

MN Mammal Neogene
[1]Guérin and Tsoukala (2013), [2]Paraskevaidis (1977)

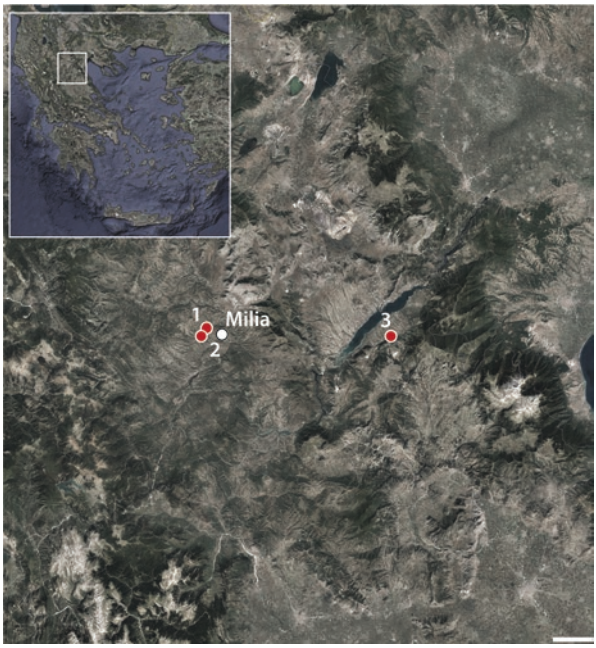

Fig. 1 Map of Greece showing the geographic distribution of the localities with tapir fossils. **1**, Milia-2; **2**, Milia-5; **3**, Servia. See Table 1 for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/ Copernicus. Scale bar equals 10 km, North faces upward

3 Systematic Paleontology

Perissodactyla Owen, 1848

Tapiridae Burnett, 1830

***Tapirus* Brisson, 1762**

Type Species *Hippopotamus terrestris* Linnaeus, 1758.

Included Taxa Extant tapirs comprise five species, distributed in the Central and South America and Southeast Asia (Cozzuol et al. 2013 and references therein). Their fossil record is more extensive and widely distributed, including at least 15 species distributed in Europe, Americas, and Asia.

Remarks The mentioned material from the late Miocene of Servia (W Macedonia) by Paraskevaidis (1977: pl. II.4), comprising three upper cheek teeth, has never been described in detail. As we do not know if and where this material is preserved/ stored, it is not possible to confirm this identification. As such, this material is tentatively included herein with its original identification as *Tapirus* sp.

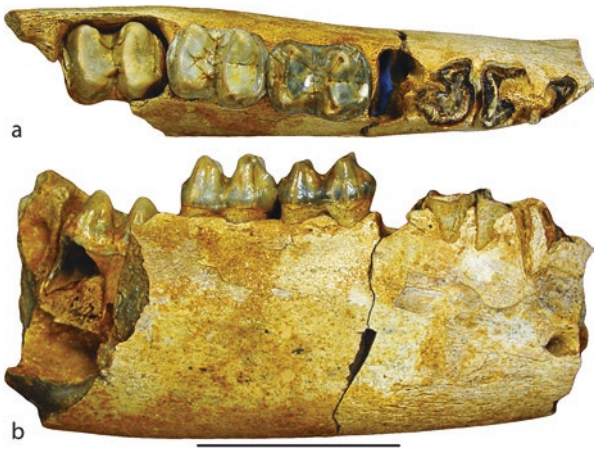

Fig. 2 A selected fossil of tapir from Greece. The right hemi-mandible (LGPUT MIL 649) of *Tapirus a. arvernensis* from the Late Pliocene (MN16a) of Milia, in **a** occlusal, and **b** buccal view. Scale bar equals 5 cm

***Tapirus arvernensis arvernensis* Croizet and Jobert, 1828**

Type Material Mandible with p3–m3, left; mandible with d1–d4, m1; I2 right; upper molar; atlas (Croizet and Jobert 1828:pl. 2, figs. 1, 3, 5 and pl. 12, figs. 4–6).

Type Locality Perrier-les-Étouaires, France, late Pliocene, late Ruscinian, MN16a.

Distribution This species is known from several localities in the Neogene of Europe. In Greece, this species is known only from Milia (N Greece).

Remarks The most complete material of this species is known from the Late Pliocene of Camp del Ninots (Spain; Gómez de Soler et al. 2012), with one complete skeleton of *T. arvernensis* in articulation; this occurrence is roughly coeval with the occurrences of this species in Greece. The referred material from Greece consists of a complete, well-preserved right calcaneum of an adult and a partial right hemi-mandible, with the alveoli of d2 and d3, with d4 and m1; the m2 is unerupted, indicating that this specimen belonged to a juvenile individual (Fig. 2). The Milia fossils are clearly larger than those of *T. a. minor*, and are safely attributed to *T. a. arvernensis* (Guérin and Tsoukala 2013). Based on the known fossils, the estimated size of *T. arvernensis* is similar to the extant Mountain Tapir from South America, with a length between 1.8 and 2.0 m, a shoulder height of 75 and 80 cm, and weight over 200 kg (Guérin and Tsoukala 2013, and references therein).

4 Concluding Remarks

Tapirs are among the least common elements of the Neogene faunas of Greece. Given that earliest report of tapirs in Greece (Paraskevaidis 1977) cannot be evaluated, the two occurrences in Milia (Guérin and Tsoukala 2013) confirm the presence of tapirs in Greece with the species *Tapirus a. arvernensis*. The association of the *Tapirus a.*

arvernensis with the other species from Milia in the Early Villafranchian (~3,5 Ma, MN16a, Late Pliocene), bearing anatomical characteristics similar to those of extant species, suggests paleoecological implications on similar ecology: a warm and humid environment, probably a dense wooded area, and access to sufficient water resources. These are the southernmost occurrences of this species in the Pliocene of Europe.

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