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The Late Miocene species *Ochotona kalfense* (Mammalia, Lagomorpha) of Moldova: The oldest European record of the genus in the context of the earliest Ochotoninae

L'espèce Ochotona kalfense *(Mammifères, Lagomorpha) du Miocène tardif de Moldavie : le plus ancien enregistrement européen du genre dans le contexte du tout premier Ochotoninae*

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ABSTRACT

Although the pika from the Moldovan Kalfa locality (early MN10) — representing the oldest European record of Ochotoninae (the clade derived from *Bellatona*) — is of crucial importance to understand the earliest history of *Ochotona*, its taxonomy has remained unclear until now. The paper fills the gap by providing a detailed revision of the type material from Kalfa, originally referred to *Proochotona kalfense*. The analysis is supported by a direct comparison with type materials of *Proochotona eximia*, *Bellatonoides eroli*, and *Ochotona ozansoyi*, the important early ochotonines of the peri-Paratethyan area. The genus *Proochotona* is regarded here as a junior subjective synonym of *Ochotona*. The specie *kalfense* is confirmed to be valid, undoubtedly belonging to the genus *Ochotona*. It demonstrates an occurrence of a surprisingly advanced p3 phenotype already present in the pre-Turolian of Europe. At the Holoarctic scale, a detailed synoptic survey and discussion of the fossil record, taxonomy, and phylogeny of the oldest representatives of Ochotoninae are provided.

Mots clés :
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RÉSUMÉ

Bien que le pika de la localité moldave de Kalfa (early MN10) – représentant le plus ancien enregistrement européen d'Ochotoninae (le clade dérive de *Bellatona*) – soit d'une importance cruciale pour comprendre le tout début de l'histoire d'Ochotona, sa taxonomie est restée incertaine jusqu'à présent. Cet article comble cette lacune en fournissant une revue détaillée du matériel type de Kalfa, rapporté à l'origine à *Proochotona kalfense*. L'analyse est corroborée par une comparaison directe avec les matériels types de *Proochotona eximia*, *Bellatonoides eroli* et *Ochootona ozansoyi*, les principaux ochotoninés précoces de la zone péri-paratéthysienne. Le genre *Proochotona* est considéré ici comme un synonyme de sujet juvénile. L'espèce *kalfense* est confirmée comme étant valide, appartenant sans aucun doute au genre *Ochotona*, avec l'occurrence étonnamment avancée d'un phénotype de p3 déjà

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présent dans le pré-Turolien d'Europe. À l'échelle de l'Holoarctique, un examen synoptique détaillé, ainsi qu'une discussion sur l'enregistrement fossile, la taxonomie et la phylogénie des plus anciens représentants d'Ochootoninés sont ici fournis.

1. Introduction

Ochotona Link, 1795 represents the sole living genus of the lagomorph family Ochotonidae. The origin of the genus is generally linked to *Bellatona* Dawson, 1961 known from the Middle Miocene of eastern Asia. Nevertheless, the clade derived from *Bellatona* often comprises taxa with remarkable similarity in general morphology. As a result, the number of recognized genera and/or species throughout this lineage is not stable. In the context of *Ochotona* ancestry, two other genera, both described from the Late Miocene of the peri-Paratethyan area, are mentioned in the literature: the genus *Proochotona*, erected by Khomenko (1914) based on the type species *Proochotona eximia* from Tarakliya (Middle Turolian, MN12; MD), and the genus *Bellatonoides*, erected by Sen (2003) based on the type species *Bellatonoides eroli* from Sinap Tepe (Locs. 8A and 120; Early Vallesian, MN9; TR). Unfortunately, taxonomy of these genera is still open. Apart from these taxa, *Ochotona ozansoyi* described by Sen (2003) from Sinap Tepe (Loc. 84) undoubtedly documents early Late Miocene (Late Vallesian, early MN10) *Ochotona* in that area.

The ochotonid from Kalfa (Late Vallesian, early MN10) represents the earliest European record of Ochotoninae (*sensu* Čermák, 2010; discussed also in this paper). The species *kalfense* was originally attributed by Lungu (1981), without any discussion of the generic validity, to the genus *Proochotona*. Later, Sen (2003) showed some morphological similarities between the ochotonid from Kalfa and *B. eroli*, and assigned the former to the genus *Bellatonoides*. At any rate, the taxonomy of the ochotonid species *kalfense* has until now remained unclear. Apart from the original description, no studies have provided detailed data based on direct observation of the type material.

Thus, in the light of the above, the ochotonid from Kalfa is undoubtedly of crucial importance for understanding the earliest history and origination of *Ochotona*. It may also help to clarify the question of taxonomic validity of genera *Bellatonoides* and *Proochotona*. The aim of this paper is to perform:

- a detailed revision and morphometric re-description of original ochotonid material from Kalfa described by Lungu (1981) including a direct comparative analyses of other important type materials of the region, namely *P. eximia*, *B. eroli*, and *O. ozansoyi*;
- a discussion of the taxonomic validity of *Proochotona* and *Bellatonoides*, to determine the generic affiliation of the species *kalfense* and to formulate its emended diagnosis;
- at the Holoarctic scale, a detailed synoptic survey and discussion of the fossil record, taxonomy, and phylogeny of the oldest representatives of Ochotoninae.

2. Kalfa: geological setting and age attribution

The locality is situated in a large outcrop about 700 meters northwest of Kalfa [Calfa, Калфа] village (Anenii Noi district, Moldova) on the southern escarpment of the Byk river valley (Fig. 1). The remains of small vertebrates come from the alluvial deposits consisting of various limestones and clays with shells of mollusks (e.g., marine *Mactra podolica*, *M. fabreana, Plicatiforma fittoni*, *Solen subfragilis*, *Cerithium comperei* and/or freshwater *Lymnea* sp., *Planorbis* sp.). The small extent and thickness of bone-bearing layers, apparently deposited in a short time, suggest an activity of periodical streams in the vicinity of the Sarmatian river (Lungu and Rzebik-Kowalska, 2011). The most detailed studies of the geology, taphonomy, and age of the locality were provided by Lungu (1978, 1981) and Lungu and Rzebik-Kowalska (2011).

Kalfa has yielded about thirty mammalian taxa (see Lungu, 1978, 1981, 1984, 1990; Lungu and Rzebik-Kowalska, 2011 for details), but, apart from ochotonids, small mammals are very scanty and give little information about the mammalian age. The available taxa are comparable to those reported from Buzhor 1 (Khynchesht district) that has yielded a much more diverse small mammal community including a few taxa of high biostratigraphic value. Nevertheless, the exact age of Kalfa and Buzhor 1 still remains unclear. The locality under study was originally referred by Lungu (1981) to the Middle Sarmatian. In the eastern Paratethys, the Sarmatian stage (*sensu* Suess, 1866) is considered to include the Volhynian and (Lower) Bessarabian (Simionescu, 1906) substages; further east to the Caspian Sea, the Sarmatian also includes the Upper Bessarabian and Khersonian (Simionescu, 1906), and is commonly labeled as Sarmatian (s.l.) as proposed by Barbot de Marny (1869). The Middle Sarmatian corresponds approximately to the Early Vallesian (ca MN9). This age for Kalfa was followed by, e.g., Rzebik-Kowalska and Lungu (2009), Lungu and Rzebik-Kowalska (2011), or Delinschi (2014). On the other hand, Topachevski et al. (1997) and Nesin (2004) refer Kalfa, based on the mammals listed by Lungu (1981), tentatively to the Late Vallesian (MN10).

Vangengeim et al. (2006) provided a magnetostratigraphic analysis of Middle Sarmatian deposits in *Hipparion* localities of Moldova and correlated them to an upper part of chron C5An (upper boundary 11.9 Ma) or, less likely, with subchron C5r2n (base 11.5 Ma); it corresponds in their view to the base of the Vallesian. However Vasiliev et al. (2011) question the age by Vangengeim et al. (2006) and argue that it was only based on the correlation of the Khersonian–Meotian boundary to an age of 9.8 Ma and the predominantly normal polarities of the Khersonian to C5n.2n. The new radio-isotopic data by Vasiliev et al. (2011) for the Khersonian–Meotian boundary indicates a