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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 species *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 Holarctic scale, a detailed synoptic survey and discussion of the fossil record, taxonomy, and phylogeny of the oldest representatives of Ochotoninae are provided.

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R É S U M É

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-paratéthyenne. 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'Ochotoninés sont ici fournis.

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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 Holarctic 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 *Mastra 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

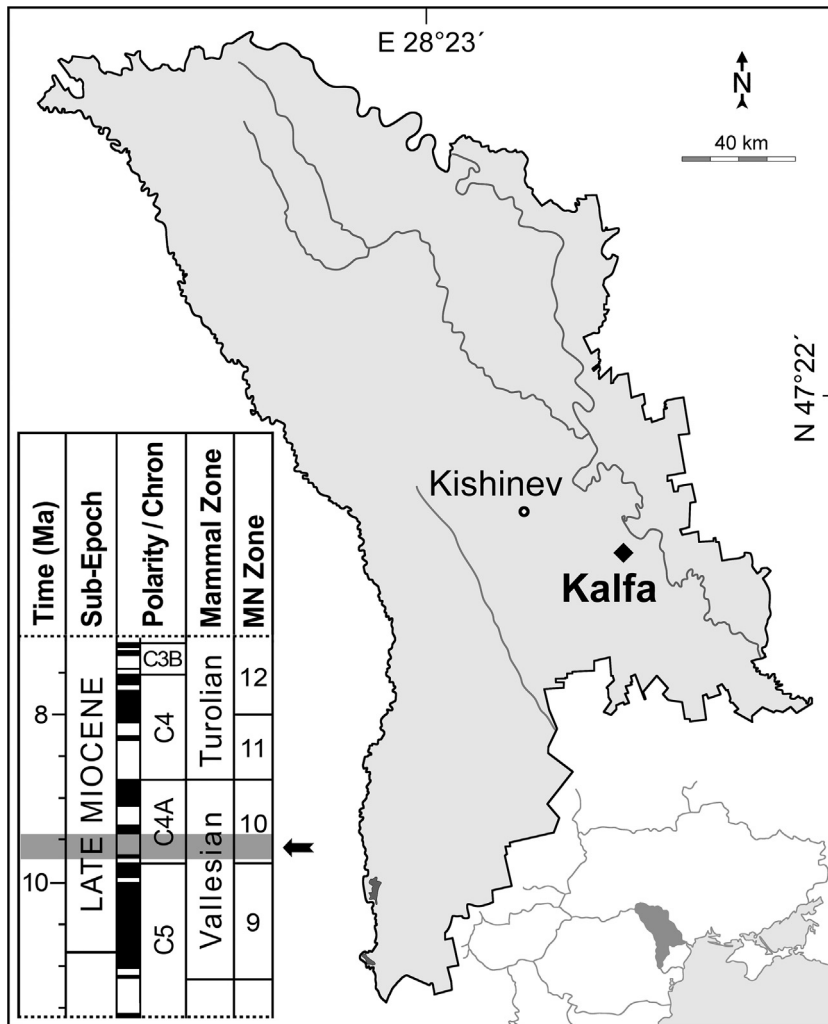


Fig. 1. Geographical localization and age estimation of the Kalfa type locality (Moldova).

Fig. 1. Localisation géographique et âge estimé de la localité type de Kalfa (Moldavie).

correlation of the normal polarity interval of the Khersonian to the younger chron C4An. The reversed intervals with the Bessarabian–Khersonian boundary may consequently correspond to C4Ar. Thus the *Hipparion* sites in Moldova may be significantly younger than suggested by Vangengeim et al. (2006).

The results of Vasiliev et al. (2011) are in a good agreement with the view of M. Sinitsa (Sinitsa, pers. comm. 2014; Sinitsa and Delinschi, in press) who, based on the presence of at least two murid genera and *Spermophilinus turoleensis*, and the absence of *Democricetodon*, *Megacricetodon*, and *Microtocricetus*, correlate the small mammal faunas of Kalfa and Buzhor 1 with the Late Vallesian (early MN10), thus being younger than those of Götzendorf (AT), Rudabánya (HU), and Gritsev (UA). This correlation seems to be most probable and is followed in this paper.

3. Material and methods

The revision of the species *kalfense* is based on the original material by Lungu (1981) from the Kalfa type locality

(Moldova, early MN10) and the material in France published by Sen (2003). The studied material is curated in the collections of the TSU (prefix FTGU Lag/Kfa-) and MNHN (prefix MNHN Lag/Kfa-). The interspecific comparisons, using original material (indicated by “**”) or a bibliographical basis (unless otherwise stated, data were taken from original descriptions of species), were made with:

- *Bellatona forsythmajori* Dawson, 1961 from Tairum Nor of the Tunggur formation [type locality] (Nei Mongol, CN)—Middle Miocene (Early Tunggurian, Early Astaracian, MN6; Qiu Z.-D. et al., 2013);
- *Bellatona yanghuensis* Zhou, 1988 from Yanghu [type locality] (Xinzhou, Shanxi Province, CN)—Middle Miocene;
- *Bellatona kazakhstanica* Erbajeva, 1988 from Ashutas [type locality] (KZ)—Early Miocene;
- **Bellatonoidea eroli* Sen, 2003 from Sinap Tepe, TR (Localities 8A [type locality] and 120)—early Late Miocene (Early Vallesian, MN9); MNHN collections;

- Ochotonids from locality DM01 at Damiao (Nei Mongol, CN)—late Middle Miocene (Late Tunggurian, late MN7/8; Kaakinen et al., 2015; Wang et al., 2013) described by Zhang et al. (2012) as *Bellatona* cf. *B. forsythmajori*, *B. eroli*, and *Ochotona* cf. *Ochotona lagreli* [here referred to as *Ochotona* sp.];
- * *O. ozansoyi* Sen, 2003 from Sinap Tepe, TR (locality 84 [type locality])—early Late Miocene (base of the Late Vallesian, early MN10); MNHN collections;
- * *O. eximia* (Khomenko, 1914) from Tarakliya [type locality] (Keushen region, MD)—Late Miocene (Middle Turolian, MN12); PMONU collections;
- *O. lagreli* Schlosser, 1924 and *O. birgerbohlini* Averianov, 1998 [commonly erroneously referred to as *O. minor* Bohlin, 1942 (= a junior homonym of *O. minor* Link, 1795)] from localities Ertemte 2 (Latest Miocene, Late Turolian, MN13) and Harr Obo 2 (Miocene/Pliocene boundary, Late Turolian/Early Ruscinian, MN13/MN14)—Fahlbusch et al. (1983), Qiu (1987), Qiu Z.-X. et al. (2013), Qiu Z.-D. et al. (2013); data for comparison taken from Qiu (1987);
- * *Ochotona antiqua* Argyropulo and Pidoplichka, 1939 from Novopetrovka [type locality; see Čermák and Rekovets (2010)] and Frunzovka 1 (UA)—Early Pliocene (Early Ruscinian, MN14); NMNHU collections;
- *Ochotona mediterraneanensis* Suata-Alpaslan, 2009 from İğdeli [type locality] (TR)—Early Pliocene (Early Ruscinian, MN14; Suata-Alpaslan (2010));
- *Ochotona ursui* Simionescu, 1930 from Mălușteni [type locality] (RO)—Early Pliocene (Ruscinian, MN 15a); Rădulescu and Samson (1995), Terzea (1997);
- *Ochotona pseudopusilla* Gureev and Schevtschenko, in Gureev (1964) from Ukrainskij Trostinec [type locality] (UA)—Early Pliocene (Early Ruscinian, MN14);
- * Ochotonids from Sinap Tepe (TR) described by Sen (2003) as *Ochotona* sp. cf. *O. ozansoyi* (Inönü area, unpublished locality—Early? Turolian, ?MN11) and *Ochotona* sp. cf. *O. eximia* [here referred to as *Ochotona* sp.] (Inönü, Loc. 45—Middle? Turolian, ?MN12); MNHN collections;
- Ochotonids from Builstyn Khudag at Valley of Lakes (Mongolia)—middle Late Miocene (MN11/12, Early Baodean, the revised correlation by Maridet et al. (2014a, b, 2015) [Note the previous correlations by Daxner-Höck et al. (2013) and Wang et al. (2013) with the late MN9, Early Baodean]) described by Erbjajeva (2003) as *O. lagreli* and *O. minor* [here referred to as *Ochotona* sp.]; the presence of two distinct species cannot be excluded];
- * Ochotonids of Moldova described by Delinschi (2014) as “*Proochotona*” sp. [here referred to as *Ochotona* sp.] from Razeni (Early Turolian, MN11/12; Delinschi (2014)) and “*Proochotona*” cf. *eximia* [here referred to as *Ochotona* ? spp.] from Gradishte (Middle Turolian, MN12; Delinschi [2014]); NMENH collections;
- *Ochotona* sp. from Maritsa I (GR), described by De Bruijn et al. (1970)—near the Miocene/Pliocene boundary, possibly MN13 according to Doukas (2005);
- * *Ochotona* sp. from Frunzovka 1 (UA), described by Čermák and Rekovets (2010)—Early Pliocene (Early Ruscinian, MN14); NMNHU collections;
- * “*Proochotona*” *kirgizica* Gureev, 1964 and “*Proochotona*” *kurdjukovi* Gureev, 1964 from the southern bank of the lake Issyk Kul (KG) [type locality]—probably the

Pliocene (Dmitrieva and Nesmeyanov, 1982); ZIN RAS collections.

All drawings and measurements were taken with the aid of a binocular microscope with camera lucida and ocular micrometer. Dental measurements were taken as maximum anteroposterior or bucco-lingual dimensions of the respective two-dimensional dental structures orthogonal to the prismatic shaft. All measured data are given in millimeters. Dental nomenclature follows Sen (1998), measurements Erbjajeva (1988) and Čermák (2004). Jaw measurements follow Erbjajeva et al. (2001) with several modifications for the lower jaw (heights of mandibular body are measured on the lingual side). The biostratigraphic terminology used in this paper follows Steininger (1999). Outline maps used in Fig. 1 were taken from <http://d-maps.com/>. Country abbreviations follow ISO 3166-1 alpha-2 codes.

3.1. Abbreviations

CV	coefficient of variation
FAD/LAD	first/last appearance datum
L	length
M	mean
MHL	[(height of mandible at m3)/(alveolar length of p3-m3)]*100
MNHN	National Museum of Natural History, Paris, France
N	number of specimens
NMENH	National Museum of Ethnography and Natural History, Kishinev, Moldova
NMNHU	National Museum of Natural History, V. Topachevsky Palaeontological Museum, Kiev, Ukraine
OR	observed range
PMONU	Odessa I.I. Mechnikov National University, Palaeontological Museum, Odessa, Ukraine
PPW	paraflexo-protoconal width
TSU	Faculty of Geography of the Tiraspol State University, Department of General Geography, Kishinev, Moldova
W	width
ZIN RAS	Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia. Upper and lower case letters
P/p	(premolars) and M/m (molars) refer to upper and lower cheek teeth, respectively

4. Systematic palaeontology

Class Mammalia Linnaeus, 1758
 Order Lagomorpha Brandt, 1855
 Family Ochotonidae Thomas, 1897
 Subfamily Ochotoninae Thomas, 1897
 Genus *Ochotona* Link, 1795
Ochotona kalfense (Lungu, 1981)

Name-bearing type, type locality, and age: Holotype (*sensu* Article 73.1 of ICZN, 1999) — left mandible with p3-m3 (Fig. 2A–F), [coll. No. 2 (118)] *sensu* Lungu (1981),

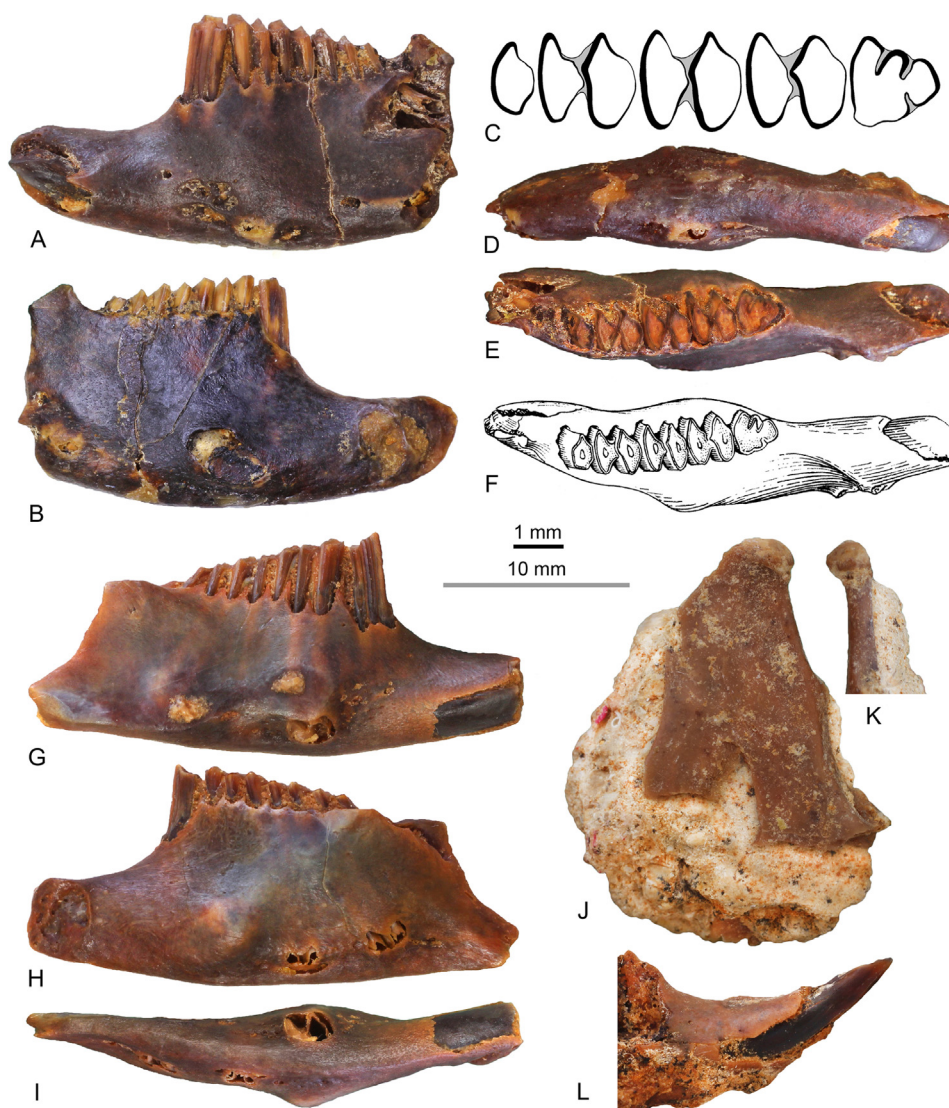


Fig. 2. Lower jaws of *O. kalfense* from Kalfa (Moldova): **A–F.** Left mandible (holotype) with i1, p3–m3 (TSU Lag/Kfa-1; coll. No 2 (118) in Lungu, 1981); **A:** buccal view; **B:** lingual view; **C:** occlusal view of tooth row (p3–m3); **D:** ventral view; **E:** dorsal view; **F:** original illustration of the holotype (Lungu, 1981: pl. 5, fig. 4). **G–I.** Right mandible with i1, p3–m3 (TSU Lag/Kfa-10); **G:** buccal view; **H:** lingual view; **I:** ventral view. **J–K.** Mandibular ramus with articular head of right mandible (TSU Lag/Kfa-15); **J:** buccal view; **K:** rostral view. **L.** Diastema with incisor of right mandible (TSU Lag/Kfa-15). Scale bars: grey (10 mm) for mandibles, black (1 mm) for teeth.

Fig. 2. Mâchoires inférieures de *O. kalfense* de Kalfa (Moldavie) : **A–F.** Mandibule gauche (holotype) avec i1, p3–m3 (TSU Lag/Kfa-1 ; coll. N° 2 (118) in Lungu, 1981) ; **A :** vue buccale ; **B :** vue linguale ; **C :** vue occlusale de la rangée dentaire (p3–m3) ; **D :** vue ventrale ; **E :** vue dorsale ; **F :** illustration originale de l'holotype (Lungu, 1981 : pl. 5, fig. 3). **G–I.** Mandibule droite avec i1, p3–m3 (TSU Lag/Kfa-10) ; **G :** vue buccale ; **H :** vue linguale ; **I :** vue ventrale. **J–K.** Ramus mandibulaire avec tête articulaire de la mandibule droite (TSU Lag/Kfa-15) ; **J :** vue buccale ; **K :** vue rostrale. **L.** Diastème avec incisive de mandibule droite (TSU LAG/Kfa-15). Barres d'échelle : grise (10 mm) pour les mandibules, noire (1 mm) pour les dents.

deposited in the TSU; type locality (*sensu* Article 76.1 of ICFN, 1999) – Kalfa (Late Miocene, Late Vallesian, early MN10). In the original description, Lungu (1981: 46) wrongly referred to the holotype mandible as a right one (cf. Lungu, 1981: pl. 5, fig. 4).

Stratigraphic and geographic distribution: Late Vallesian (early MN10) of Moldova, from localities Kalfa and Buzhor 1.

Material analysed (original material described by Lungu (1981), prefix TSU Lag/Kfa-): Seven mandibular bodies sin with p3–m3: 1, 2; m1–m2: 3; p3–m2: 4; p4–m1: 5;

p4–m3: 6; m1–m3: 7. Seven mandibular bodies dex with p3–m3: 8; p3–p4: 9; i–p3–m3: 10; p3–m2: 11; p4–m2: 12; p4–m3: 13; m2–m3: 14. One mandibular ramus dex: 15. Two p3 sin: 16, 17. Five p3 dex: 18–22. Two maxillae sin with P3–M2: 24; P3–M1: 25. One maxilla dex with P2–M2: 23. One P2 sin: 26. Two P3 sin: 28, 29. One P3 dex: 27. One M2 sin: 30. (prefix MNHN Lag/Kfa-) Four p3 sin: 1–4. One p3 dex: 5.

Measurements: For measurements, see Tables 1 and 2.

Description: Mandible (Fig. 2): In adult individuals – mandibular body relatively robust and high; alveolar

Table 1

Tooth measurements of *O. kalfense* from Kalfa (Moldova).

Tableau 1

Mesures des dents de *O. kalfense* de Kalfa (Moldavie).

Measurements	N	M	OR	CV
<i>p3</i>				
Length	15	1.79	1.54–1.95	5.37
Anteroconid length	15	0.79	0.58–0.92	10.75
Posteroconid length	15	1.19	1.07–1.33	6.96
Anteroconid width	15	0.90	0.74–1.08	9.23
Posteroconid width	15	1.86	1.70–2.06	5.66
Conid confluence distance	16	0.20	0.08–0.31	34.18
<i>P2</i>				
Length	2	–	0.96, 0.96	–
Width	2	–	1.84, 2.01	–
<i>P3</i>				
Length	6	1.54	1.44–1.62	5.45
Width	6	3.07	2.84–3.37	6.20
Paraflexo-protoconal width	6	1.84	1.53–2.10	10.21
Paraflexo-hypoconal width	6	2.00	1.66–2.45	13.62

Table 2

Mandibular and maxilla measurements of *O. kalfense* from Kalfa (Moldova).

Tableau 2

Mesures mandibulaires et maxillaires de *O. kalfense* de Kalfa (Moldavie).

Measurements	N	M	OR	CV
Lingual height of mandible at p3	3	7.49	7.15–7.66	–
Lingual height of mandible at p4	5	9.68	9.15–10.47	5.19
Lingual height of mandible at m3	9	8.60	7.71–9.27	6.44
Length of diastema	4	7.91	7.25–8.37	6.99
Alveolar length of p3–m3	3	10.64	10.28–10.96	–
Mandible width at p4	5	4.84	4.73–5.06	2.65
Mandible width at m2	12	3.52	3.25–3.75	3.70
Alveolar length of P2–M2	1	–	10.86	–

length of p3–m2 distinctly longer than diastema; posterior mental foramen oval and located ventral to the area between the trigonid of m2 and m3, in most cases below the talonid of m2 (ca 56%, N=9); area below p3 richly fenestrated; root end of lower incisor extending in 50% of cases (N=10) below the trigonid of m1; ventral margin

of the mandible variable, predominantly convex; mylohyoid line long, moderately developed, from the ventral view lying in the buccal third of the mandibular body; articular head large; coronoid process weakly developed, dorso-ventrally shortened; mandibular ramus low, antero-posteriorly elongated.

p3 (Fig. 3): Medium to large size (OR=1.54–1.95); in adult individuals—large anteroconid (M of L × W=0.79 × 0.90), typically asymmetric (buccally distinctly widened into semicircular or rectangular buccal outline), often anteriorly with depressions, but never with re-entrant

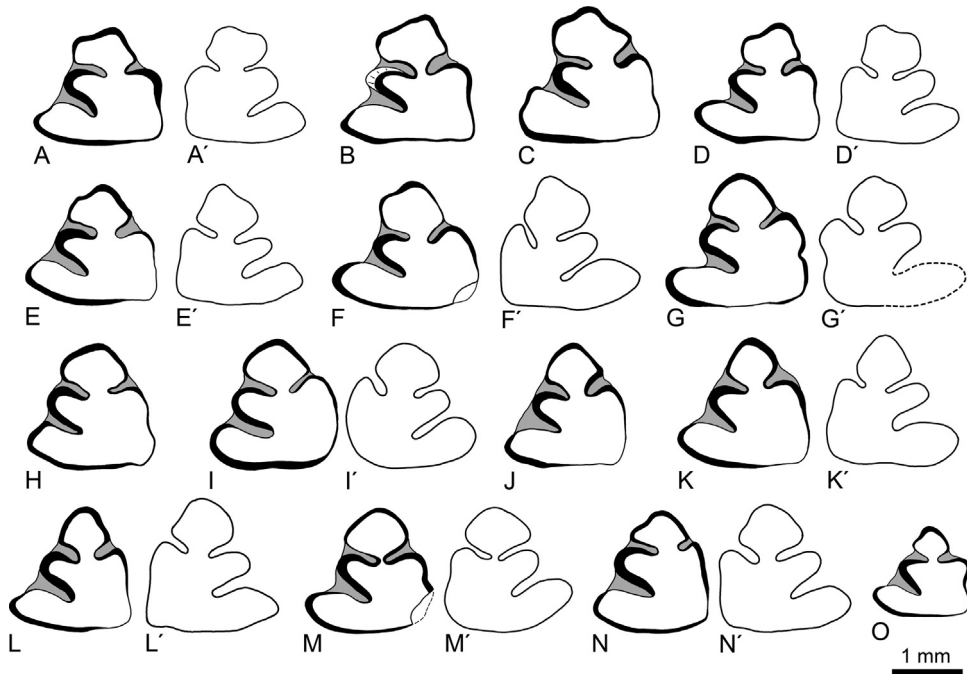


Fig. 3. Lower teeth of *O. kalfense* from Kalfa (Moldova) : **A–A'**. Right p3 (TSU Lag/Kfa-19), occlusal and root views, reversed. **B.** Right p3 (TSU Lag/Kfa-8), occlusal view, reversed. **C.** Left p3 (MNHN Lag/Kfa-1), occlusal view. **D–D'**. Right p3 (TSU Lag/Kfa-18), occlusal and root views, reversed. **E–E'**. Left p3 (TSU Lag/Kfa-17), occlusal and root views. **F–F'**. Right p3 (MNHN Lag/Kfa-5), occlusal and root views, reversed. **G–G'**. Left p3 (MNHN Lag/Kfa-2), occlusal and root views. **H.** Left p3 (TSU Lag/Kfa-1; holotype), occlusal view. **I–I'**. Left p3 (MNHN Lag/Kfa-3), occlusal and root views. **J.** Left p3 (TSU Lag/Kfa-2), occlusal view. **K–K'**. Left p3 (TSU Lag/Kfa-16), occlusal and root views. **L–L'**. Right p3 (TSU Lag/Kfa-20), occlusal and root views, reversed. **M–M'**. Left p3 (MNHN Lag/Kfa-4), occlusal and root views. **N–N'**. Left p3 (TSU Lag/Kfa-21), occlusal and root views. **O.** Right p3 (TSU Lag/Kfa-9), occlusal view, reversed.

Fig. 3. Dents inférieures d'*O. kalfense* de Kalfa (Moldavie). **A–A'**. p3 droite (TSU Lag/Kfa-19), vue occlusale et vue de racine, retournées. **B.** p3 droite (TSU Lag/Kfa-8), vue occlusale retournée. **C.** p3 gauche (MNHN Lag/kfa-1), retournée. **D–D'**. p3 droite (TSU Lag/Kfa-18), vue occlusale et vue de racine, retournées. **E–E'**. p3 gauche (TSU Lag/Kfa-17), vues occlusale et de racine. **F–F'**. p3 droite (MNHN Lag/Kfa-5), vues occlusale et de racine, retournées. **G–G'**. p3 gauche (MNHN Lag/Kfa-2), vues occlusale et de racine. **H.** p3 gauche (TSU Lag/Kfa-1; holotype), vue occlusale. **I–I'**. p3 gauche (MNHN TSU Lag/Kfa-3), vues occlusale et de racine. **J.** p3 gauche (TSU Lag/Kfa-2) vue occlusale. **K–K'**. p3 (TSU Lag/kfa-16), vues occlusale et de racine. **L–L'**. p3 droite (TSU Lag/Kfa-20), vues occlusale et de racine, retournées. **M–M'**. p3 gauche (MNHN Lag/kfa-4), vues occlusale et de racine. **N–N'**. p3 gauche (TSU Lag/Fka-21). **O.** p3 droite (TSU Lag/Kfa-9) vue occlusale retournée.

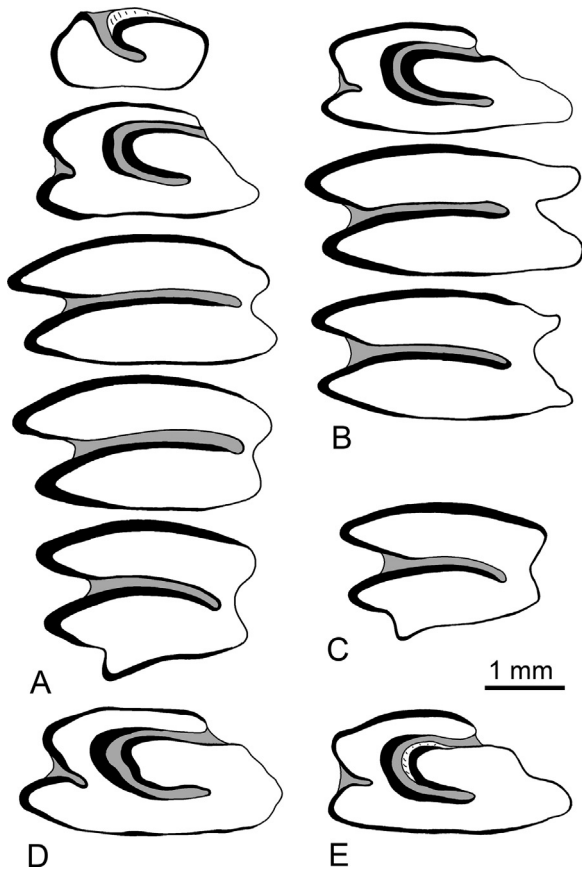


Fig. 4. Upper teeth of *O. kalfense* from Kalfă (Moldova): **A.** Right tooth row with P2–M2 (TSU Lag/Kfa-23), reversed. **B.** Left tooth row with P3–M1 (TSU Lag/Kfa-25). **C.** Left M2 (TSU Lag/Kfa-30). **D.** Right P3 (TSU Lag/Kfa-27), reversed. **E.** Left P3 (TSU Lag/Kfa-29). Occlusal views.

Fig. 4. Dents supérieures d'*O. kalfense* de Kalfă (Moldavie). **A.** Rangée dentaire droite, avec P2–M2 (TSU LagKKfa-23), retournées. **B.** Rangée dentaire gauche, avec P3–M1 (TSU Lag/Kfa-25). **C.** M2 gauche (TSU Lag/Kfa-30). **D.** P3 droite (TSU Lag/Kfa-27), retournée. **E.** P3 gauche (TSU Lag/Kfa-29). Vues occlusales.

folds (anteroflexids); proto- and paraflexid simple without crenulation, the former typically longer than the latter; antero-posteroconid junction moderately wide ($M = 0.20$); hypoflexid short, shorter than the half of W p3.

Maxilla: premolar foramen small-sized, oval, next to the anteroph of P4.

P2 (Fig. 4A): single-lobed tooth of rectangular occlusal outline with anteriorly convex lagiconus and sharpened hyperconus; no enamel hiatus; moderately developed paraflexus.

P3 (Fig. 4A–B, D–E): occlusal morphology and widths quite variable; tooth of trapezoidal occlusal outline with PPW ranging from 52% to 66% of W ; hypoflexus well-developed, distinctly narrowed buccally.

Upper and lower molariforms (Figs. 2C and 4A–C): P4–M2 and p4–m3 with no taxonomically important features discriminating them from the corresponding teeth of other *Ochotona* species; M2 posteroloph with well-developed posterolingual process.

Notes on morphological changes of p3 through ontogeny: In all prismatic teeth (Fig. 3A, A', D–G, I, I') of the studied sample, the general occlusal outline is comparable with that of the root, and no important morphological changes are visible. In young individuals, with conical teeth (Fig. 3K–N'), the root morphologies – representing a stage that appears with wear in more adult ontogenic phases – differ from the occlusal ones and thus several morphological changes through ontogeny can be traced. The anteroconid displays most changes among all p3 structures. In very young individuals (Fig. 3O), i.e. in very early stage of p3 abrasion, the anteroconid is small and almost symmetrical. Through ontogeny, it grows in relative size. In early permanent teeth, both widened and elongated anteroconids can be recognized in the sample; later in the ontogenetic development the anteroconid extends buccally and becomes predominantly more asymmetric. In adult specimens, a degree of anteroconid asymmetry (buccal extension) is very variable in contrast to relatively stable anteroconid length (Fig. 2). At any rate, a tendency to anteroconid asymmetry is possible to recognize in all ontogenic stages of permanent teeth. Concave anterior walls of anteroconid generally appear in largely asymmetric anteroconids. Proto- and paraflexid are very variable with no recognizable trends in their morphologies, deflections, and relative lengths (depending on the asymmetry of anteroconid) through ontogeny. The lingual side is predominantly concave (e.g., Fig. 3B, C), occasionally with incipient mesoflexid (Fig. 3G); the phenomenon seems not to be related to the age of the individual. The relatively small sample from the type locality does not allow a credible quantification of p3 morphotype composition in *O. kalfense*.

Comparisons: *O. kalfense* differs from all available species of *Bellatona* and from *B. eroli* of Sinap Tepe in its larger size (Fig. 5), larger and well-developed p3 anteroconid, and longer and narrower P3 hypoflexus; from the

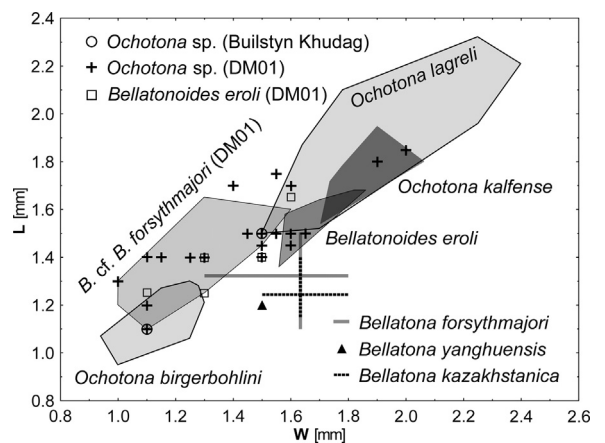


Fig. 5. The p3 length-to-width scatterplot showing the size relationship among studied *O. kalfense* and selected Middle–Late Miocene ochotonids of Asia referred to genera *Belatona*, *Bellatona*, and *Ochotona*.

Fig. 5. Diagramme de dispersion longueur–largeur de p3 montrant la relation de taille parmi les échantillons d'*O. kalfense* étudiés et les ochonidés d'Asie sélectionnés au Miocène moyen–supérieur, rapportés aux genres *Belatona*, *Bellatona* et *Ochotona*.

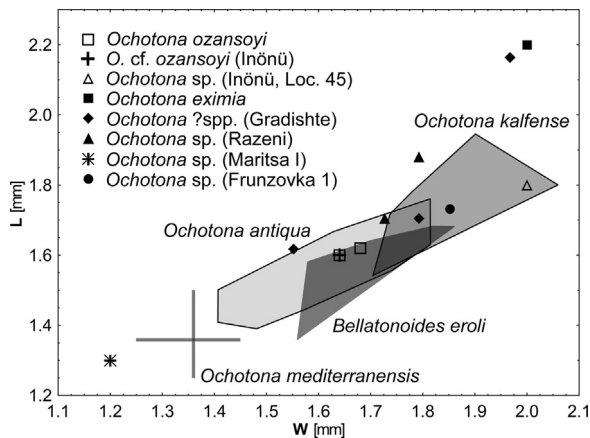


Fig. 6. The p3 length-to-width scatterplot showing the size relationship among the Late Miocene and Early Pliocene ochotonines of the peri-Paratethyan area.

Fig. 6. Diagramme de dispersion longueur-largeur montrant la relation de taille parmi les ochotoninés de la zone péri-paratéthysienne au Miocène supérieur et au Pliocène inférieur.

former also in its well-developed p3 proto- and paraflexid and constant presence of posterolingual process in M2. The majority of p3 specimens from Damiao (DM01) referred to by Zhang et al. (2012) as *Bellatona* cf. *B. forsythmajori*, *B. eroli*, and *Ochotona* cf. *O. lagreli* are generally smaller than those in *O. kalfense* (Fig. 5). Moreover, in contrast to *O. kalfense*, p3s attributed to (1) *Bellatona* cf. *B. forsythmajori* has an incipient or no paraflexid, a smaller anteroconid, and probably an unstable presence of posterolingual process in M2; (2) *B. eroli* has a less developed paraflexid, a wider anteroconid-posteroconid connection, and a shorter and more simple anteroconid; (3) *Ochotona* cf. *O. lagreli* have a more symmetrical anteroconid (developed lingually) and the anteroconid-posteroconid connection is generally narrower. Two p3s from Bulstyn Kudak (MN) are smaller and show similar morphological differences as *Ochotona* cf. *O. lagreli* from DM01. Among the Late Miocene *Ochotona* of the peri-Paratethyan area: (1) *O. ozansoyi* has a smaller p3 with the symmetrical anteroconid and narrower anteroconid-posteroconid connection, a more linguo-buccally oriented p3 paraflexid, a shorter and wider P3 hypoflexus, and a slightly longer and thinner posterolingual process in M2; (2) *O. eximia* has a larger and relatively elongated p3 with the symmetrical anteroconid. The Pliocene species of the peri-Paratethyan area, *Ochotona antiqua*, *O. mediterraneensis*, and *O. ursui*, are smaller than *O. kalfense* (Fig. 6). Moreover, in contrast to *O. kalfense*, *O. antiqua* has a more symmetrical p3 anteroconid (if asymmetrical, its lingual part is generally enlarged), a narrower p3 anteroconid-posteroconid connection, a less robust mandible with posterior mental foramen situated more posteriorly, a relatively lower mandibular body (MHL is 69 for *O. antiqua* vs. 84 for *O. kalfense*), and a more developed condylar process of mandibular ramus. More detailed comparison with *O. mediterraneensis* and *O. ursui* is impossible due to lack of sufficient published data. This is also true for *O. pseudopusilla* (see Čermák and Rekovets, 2010 for details). In the peri-Paratethyan area, there are

several scanty findings with unsure taxonomic attribution. Their p3 size relationship to those of *O. kalfense* is shown in Fig. 6. From a morphological point of view, in contrast to *O. kalfense*: (1) *Ochotona* cf. *ozansoyi* from Inönü (TR) has a narrower p3 anteroconid-posteroconid connection, a smaller symmetrical p3 anteroconid, a shorter and wider P3 hypoflexus, and a more developed mylohyoid line in the mandibular body – from the ventral view situated more medially (positions of the posterior mental foramen and root end of lower incisor in mandibular body are comparable with those of *O. kalfense*); (2) *Ochotona* sp. from Inönü (Loc. 45; TR) has a p3 with symmetrical anteroconid and developed mesoflexid; (3) *Ochotona* sp. from Razeni (MD) has a p3 with the larger and distinctly more triangular anteroconid, a narrower anteroconid-posteroconid connection, and proto- and paraflexid more parallel to linguo-buccal axis; (4) *Ochotona* sp. from Maritsa I (GR) has a p3 with the symmetrical anteroconid of rhombic outline and narrower anteroconid-posteroconid connection; (5) *Ochotona* sp. from Frunzovka 1 (UA) has a triangular outline of p3 with the prolonged and markedly narrow anteroconid, a shorter and wider posteroconid, and a narrower anteroconid-posteroconid connection with notably more posteriorly oriented proto- and paraflexid; (6) three p3s (all prismatic) from Gradiste (MD) show a noticeable morphological variability making comparison difficult; the p3 varies (i) in the anteroconid from large, symmetrical, and triangular to small, asymmetrical, and rounded, (ii) in the anteroconid-posteroconid connection from narrow to very wide.

Emended diagnosis: Medium to large-sized p3 with large buccally widened asymmetric anteroconid of semi-circular or rectangular buccal outline, often anteriorly depressed, anteroconid-posteroconid junction moderately wide; well-developed proto- and paraflexid without crenulation. Mandibular body robust and high; p3-m2 alveolar row distinctly longer than diastema; posterior mental foramen predominantly below the talonid of m2; mylohyoid line long, moderately developed, from the ventral view in the buccal third of the mandibular body. M2 posteroloph with well-developed posterolingual process.

Remarks: The material under study is attributed here to the subfamily Ochotoninae (first unequivocally separated by Sen (2003) as the “*Ochotona* group”), a monophyletic lineage derived from *Bellatona* Dawson, 1961 and comprising here *Bellatonoides* Sen, 2003; *Ochotona*; *Ochotonoma* Sen, 1998; *Pliolagomys* Agadjanian and Erbajeva, 1983; and *Ochotonoides* Teilhard de Chardin and Young, 1931 (Čermák, 2010). This subfamily is characterized by the combination of autapomorphies including: (i) the posterolingual process of M2, (ii) well-defined anteroconid with round or more or less triangular outline on p3, and (iii) the presence of the opposite paraflexid and protoflexid on p3 (Sen, 2003). This subfamily demarcation differs significantly from a taxonomical meaning of Ochotoninae defined by Erbajeva (1986; 1988; 1994; Erbajeva et al., 2011; Erbajeva et al., 2015 [in earlier works she used the name Lagomyinae Lilljeborg, 1866 – see Čermák [2010: 10] for explanation]). In her view Ochotoninae comprises also *Marcuinomys* Lavocat, 1951; *Lagopsis* Schlosser, 1884; *Albertona* López-Martínez, 1986; *Alloptox* Dawson, 1961;

and *Paludotona* Dawson, 1959 [grouped tentatively here in the separate subfamily Lagopsinae], despite assuming that the subfamily was derived from the *Bellatona* stock (Erbajeva, 1994; Erbajeva et al., 2011). Moreover, she places *Bellatonoides* – a presumed direct descendant of *Bellatona* and ancestor of *Ochotona* (Sen, 2003; Zhang et al., 2012) – in different subfamily Sinolagomyinae. Even though the phylogenetic interrelationships among genera of Lagopsinae is still unclear, the phenotypes in the earliest representatives of *Marcuinomys*, *Lagopsis*, or *Alloptox*, all available already in the middle Early Miocene (i.e. MN2–3; Daxner-Höck et al., 2013; Hordijk, 2010; Lavocat, 1951; Tobien, 1963), are distinctly different from those available in, more or less coeval, the earliest records of *Bellatona*. This strongly indicates that these taxa cannot be derived from the *Bellatona* stock. The present state of knowledge rather supports a hypothesis that *Marcuinomys* most likely branched from a European rooted form like *Titanomys* von Meyer, 1843 and subsequently gave rise to *Lagopsis* (Hordijk, 2010 and references therein). *Paludotona* has been suggested as a possible descendant of presumed relict population of *Lagopsis* (Dawson, 1967; Hordijk, 2010; López-Martínez, 1986, 1989). Phylogenetic affinities of *Albertona* and particularly Asian *Alloptox* are less clear and are need of revision. The subfamily Ochotoninae *sensu* Erbajeva (1994; Erbajeva et al., 2011, 2015) is not a monophyletic.

5. Results and discussion

5.1. Generic attribution of the ochotonid from Kalfa

The species *kalfense* was originally attributed by Lungu (1981), without any discussion of the generic validity, to the genus *Proochotona*. The genus was erected by Khomenko (1914) based on the type species *P. eximia* (=originally *P. eximius* in Khomenko (1914) – cf. Article 34.2 of ICZN (1999); =type species designated by monotypy [Article 68.3 of ICZN, 1999]) described from the Middle Turolian (MN12) Moldovan Tarakliya locality. The species description fulfills the mandatory conditions of Article 12.1 of ICZN (1999). *Proochotona* was accepted as a valid genus by Gureev (1964) who included in it three other species – *P. gigas* (Argyropulo and Pidoplichka, 1939); *P. kudjukovi* Gureev, 1964; and *P. kirgizica* Gureev, 1964. *Proochotona* as an independent genus was also accepted by Agadjanian and Erbajeva (1983) as a monospecific genus with *P. eximia* and later by Erbajeva (1986, 1988, 1994) and Erbajeva et al. (2015) as a genus with *P. eximia* and *P. kalfense*. The generic name *Proochotona* was accepted in faunal lists, reviews or in brief descriptions of new material, also in, e.g., Schlosser (1924), Dmitrieva and Nesmeyanov (1982), Agadjanian and Erbajeva (1983), Nesin and Nadachowski (2001), Lungu et al. (2007), Delinschi (2009), Sinitza (2009), Erbajeva et al. (2011), and Lungu and Rzebik-Kowalska (2011).

The main taxonomic argumentation of Gureev (1964: 223) and Erbajeva (in Agadjanian and Erbajeva, 1983: 67; Erbajeva, 1988: 71) for generic discrimination was based particularly on (i) the large size, and (ii) the simple p3 anteroconid without flexids (in Gureev, 1964) or the very large p3 anteroconid of trilobed configuration, symmetric

disposition, and narrow anteroconid–posteroconid junction (in Agadjanian and Erbajeva, 1983, Erbajeva, 1988). I fully agree with Sen (2003) that these characters regarded as diagnostic make *Proochotona* indistinguishable from some species of *Ochotona* (e.g., *O. lagreli* described by Qiu (1987) from Ertemte 2; cf. Figs. 5 and 6). At any rate, the determinative question is: “Is the type species of *Proochotona* distinct at the generic level?”

A direct revision of the holotype of *P. eximia* (fragment of left mandibular body with p3-m1, No. 3193, PMONU collections; cf. Khomenko [1914]) shows that its p3 possesses the medium-sized anteroconid of symmetric disposition (proto- and paraflexid are of similar length, without crenulation), anteriorly with depressions. The p3 antero-posteroconid junction is moderately wide, but narrower than in *O. kalfense*. The tooth size does not exceed the size range observed in large-sized *Ochotona*, e.g., *O. lagreli* (Figs. 5 and 6) – the well-known species of *Ochotona* from the Late Miocene of East Asia. Thus, taking into account these features of the type species of *Proochotona* (represented by the holotype) and the emended generic diagnosis given by Erbajeva (1988), the species *eximia* is referred here to the genus *Ochotona*. Therefore, the genus *Proochotona* Khomenko, 1914 is regarded here as a junior subjective synonym of *Ochotona* Link, 1795; this view was earlier suggested by Argyropulo and Pidoplichka (1939), Qiu (1987), Sen (1991, 1998, 2003), and Čermák (2010).

As for other species previously referred to the genus *Proochotona*; (i) the species *gigas* was later designated by Agadjanian and Erbajeva (1983) as the type species of a new genus *Pliolagomys*. The taxonomic model of *Pliolagomys* as an independent genus has not been questioned and is accepted in this paper. (ii) The species *kurdjukovi* and *kirgizica* were erected by Gureev (1964) based on fragmentary mandibles originating from the type locality (Article 76.1 of ICZN, 1999) specified in the original description as “the southern bank of the lake Issyk Kul (Kirghizia)” (Gureev, 1964: 224–225). Based on data from Dmitrieva and Nesmeyanov (1982: 97) the original material was most probably collected by Kurdjukov in 1959 from the Late Pliocene [?Early Pleistocene] site of Keklikbulak, the stream near the town of Bokonbayevo. Unfortunately, the species identity of the nominal species-group taxa *P. kirgizica* Gureev, 1964 and *P. kurdjukovi* Gureev, 1964 cannot be determined from these name-bearing types (holotypes No. 27553 and 27554; ZIN RAS collections) represented by badly preserved mandibles without p3s. The available large-sized ochotonids allow confident systematic attributions only at the family level Ochotonidae. Thus, in accordance with Sen (2003), the names *P. kirgizica* Gureev, 1964 and *P. kurdjukovi* Gureev, 1964 are regarded here as *nomina dubia*.

Sen (2003) showed some morphological similarities between the ochotonid from Kalfa and *B. eroli* from Sinap Tepe (Locs. 8A and 120; MN9). Based on the rounded labially displaced p3 anteroconid and the shallow p3 paraflexid (cf. Sen, 2003, p. 170, fig. 7.8. D–F), he assigned the former to the genus *Bellatonoides*. Nevertheless, as shown above in “Systematic palaeontology”, the identified cranial and dental features of the Kalfa ochotonid, particularly its large p3 anteroconid without flexids separated by well-developed

proto- and paraflexid without crenulation, are typical for the genus *Ochotona* and fully compatible with the emended generic diagnosis given by Erbajeva (1988: 82; cf. Gureev, 1964: 226; Gromov and Erbajeva, 1995: 34–35). Thus, the species *kalfense* is referred here to the genus *Ochotona*. At any rate, as shown in “Comparisons”, the Early Vallesian taxon from the Sinap Tepe area strongly differs from *Ochotona* from Kalfa.

5.2. *Ochotona kalfense* in the context of the oldest representatives of *Ochotoninae*

5.2.1. Fossil record

The roots of the *Ochotoninae* clade can be traced back to *Bellatona*, probably to the *B. forsythmajori* stock. *Bellatona* is referred to from the early to the late Late Miocene (ca MN3–late MN7–8, Early Shanwagian–Late Tunggurian) of China, Mongolia, and Kazakhstan from localities Gashun-yinadege (CN); Yanghi (CN); Tairum Nor, Moergen, and Tamuqin of Tunggur formation (CN); [?]Damiao–DM01 [distinct from a typical *Bellatona*, see below], DM02 (CN); [?]Balunhalagen (CN); Ulan-Tologoi (MN); Valley of Lakes – biozones D, D1/1 (MN); and Ashutas (KZ) (Dawson, 1961; Daxner-Höck et al., 2013; Deng et al., 2007; Erbajeva, 1981, 1988, 2007; Erbajeva and Daxner-Höck, 2001; Höck et al., 1999; Meng et al., 1996; Qiu and Wang, 1999; Qiu et al., 2006; Qiu Z.-D. et al., 2013; Qiu Z.-X. et al., 2013; Wang et al., 2003, 2009; Zhang et al., 2012; Zhou, 1988). Records from Tamuqin and Damiao (DM01, DM02) indicate that the LAD for *Bellatona* seems to be the Late Tunggurian (Kaakinen et al., 2015; Qiu et al., 2006; Qiu Z.-D. et al., 2013; Qiu Z.-X. et al., 2013; Wang et al., 2013). The presence and exact age of *Bellatona* (and other findings referred to *Ochotona*; Wang et al. (2009)) in Balunhalagen – Late Tunggurian and Early Bahean – are unsure. Findings from the Early Baodean (ca MN12/13) Bilutu locality (CN) referred to by Wang et al. (2009) as *Bellatona* sp. were most probably a product of redeposition from older horizons (Qiu Z.-D. et al., 2013).

Around the Middle/Late Miocene boundary (MN7–8/MN9, Tunggurian/Bahean), morphologically transitional forms between a typical *Bellatona* and *Ochotona* are reported from Inner Mongolian localities Damiao–DM01 (of similar age or slightly younger than Tamuqin; Zhang et al., 2012; Wang et al., 2013), Balunhalagen, and Amuwusu (Qiu and Wang, 1999; Wang et al., 2009; Zhang et al., 2012). The lower part of the Balunhalagen bed appears to be coeval with Damiao (DM01), the upper one with Amuwusu (Wang et al., 2013). Qiu and Wang (1999) and Qiu Z.-D. et al. (2006, 2013) exclude explicitly the presence of *Bellatona* in Amuwusu. These findings are considered by Qiu et al. (2006) to be the oldest record of *Bellatonoides*. At any rate, Amuwusu is of similar age as Sinap Tepe–Locs. 8A, 120 (Sen, 2003; MN9; TR), the type locality of *B. eroli*.

Ochotonids from the basal part of the Bahe Formation – Loc.12, China, Loess Plateau (latest MN9, Early Bahean, 9.95 Ma; Qiu et al., 2003; Zhang et al., 2013) – were generally considered as one of the earliest records of *Ochotona* (Erbajeva et al., 2015; Zhang et al., 2013). This material is represented by a few specimens and was tentatively

referred to *Ochotona* cf. *O. lagreli* (Qiu et al., 2003). A coeval or slightly younger record of *Ochotona* is also referred from Qinghai-Tibetan Plateau (China) from the Shengou (MN9/10, Early Bahean; Qiu and Li, 2008; Wang et al., 2007, 2013; Woodburne et al., 2013). This locality is of similar age as Sinap Tepe – Loc. 84 (Sen, 2003, early MN10; TR), the type locality of *O. ozansoyi*. The possible presence of *Ochotona* in Balunhalagen is unclear, but, at any rate, the upper part of Balunhalagen Fm. is coeval with the lower part of Bahe Fm. (Wang et al., 2013). Nevertheless, recently, Zhang et al. (2012) published undoubted *Ochotona* from Inner Mongolian Damiao locality (DM01). The age attribution of the locality by Zhang et al. (2012) and Kaakinen et al. (2015) pushes back the FAD of *Ochotona* to the late Middle Miocene (12.1 Ma, Late Tunggurian, middle MN7/8). A similar age was suggested by Vangengeim et al. (2006) for Kalfa (see above). Erbajeva (2003; 2007; Erbajeva and Daxner-Höck, 2001) referred *Ochotona* from Builstyn Kudag (Biozone E) of Valley of Lakes (Mongolia). The locality was originally tentatively correlated with the middle Late Miocene (Daxner-Höck and Badamgarav, 2007; Höck et al., 1999), later Daxner-Höck et al. (2013) revised the age to the Early Bahean (*sensu* Zhang et al., 2013; ca late MN9). But subsequent revisions of rodents by Maridet et al. (2014a, b, 2015) implied that the age of Builstyn Khudag is younger than the age proposed by Daxner-Höck et al. (2013); i.e., approximately from the Latest Bahean (*sensu* Zhang et al., 2013; ca MN11/12, Late Tortonian). This age estimation is in my view more plausible and in better accordance with the recorded *Ochotona* phenotype.

O. kalfense from the early Late Miocene (early MN10) locality of Kalfa represents the oldest record of *Ochotona* in Europe (*contra* Erbajeva et al., 2015: 21; cf. Čermák, 2010 and “Material and methods” above). Kalfa seems to be coeval with Sinap Tepe – Loc. 84 (type locality of *O. ozansoyi*). Among the Chinese localities, following Wang et al. (2013), the age of locality under study seems to be comparable with Shengou and lower part (Unit/Biozone BH1) of Bahe Fm., thus younger than Amuwusu and simultaneously older than the Late Bahean *Ochotona* bearing localities Huitenghe and Shala (Qiu and Wang, 1999; Qiu et al., 2006; Qiu Z.-D. et al., 2013).

5.2.2. Taxonomy and phylogeny

Dawson (1961) proposed *Bellatona* as a plausible direct ancestor for *Ochotona* and Sen (2003) as an ancestor for *Bellatonoides*. Zhang et al. (2012) hypothesize a successive linear evolutionary relationship of *Bellatona*–*Bellatonoides*–*Ochotona*; in their view *Ochotona* may have originated directly from *Bellatonoides*. The available findings of this group share the same general dental morphology with a successive development of p3 anteroconid, p3 proto- and paraflexid, and posterior process of M2 posteroloph. The successive linear evolutionary relationship seems to be supported by the time sequence of the phenotype appearances in Asian localities Tunggur (Tairum Nor–Moergen–Tamuqin)/Amuwusu–Sinap Tepe (8A, 120)/Bahe–Shengou; i.e. typical *Bellatona* is recorded from the Early Tunggurian (MN6) and its LAD seems to be in the Late Tunggurian (late MN7–8), the morphologically transitional forms between a typical *Bellatona*

and *Ochotona* are recorded around the Tunggurian/Bahean boundary (MN7–8/MN9), and the clear *Ochotona* is early Bahean (latest MN9) [Dawson, 1961; Qiu and Wang, 1999; Zhang et al., 2013]. Nevertheless, the fragmentary nature of the still relatively scanty fossil material, occurring mostly as isolated teeth, and the lack of its detailed analyses and comparisons prevent any conclusive statements. There is still a disagreement in the generic attribution of findings morphologically intermediate between *Bellatona* and *Ochotona*. Based on the revision of the type material described by Sen (2003) and the data presented here, I am not able to provide at present a conclusive argument to reinforce or undermine the taxonomic model with *Bellatonoides* as a distinct genus. Nevertheless, considering all the available data, including the palaeobiogeographic context and the age of Sinap Tepe localities 8A and 120, I propose here to retain for the moment the original concept of *Bellatonoides* as a distinct genus.

The recently published work by Zhang et al. (2012) provides the first detailed description of ochotonine phenotype from the time period critical for the origination of *Ochotona*. On the other hand, the extensive material of DM01 dated to the middle MN7–8 (12.1 Ma; Kaakinen et al., 2015) complicates the above phylogenetic scenario. Zhang et al. (2012) recognize all three genera at DM01; *Bellatona* cf. *B. forsythmajori*, *B. eroli*, and *Ochotona* cf. *O. lagreli*. Inferring from measurements given in the study, there are no significant metric differences in p3 size among these taxa (Fig. 5). The published tooth sample contains p3s with undoubted *Ochotona* phenotype (cf. Zhang et al., 2012: fig. 2G–K). On the other hand, the majority (42 of 48) of the specimens attributed to *Bellatona* do not show features characteristic of the nominal taxon of *Bellatona* described by Dawson (1961) from Tairum Nor. They possess a very long narrow protoflexid (Zhang et al., 2012: fig. 2B, C); i.e., a considerably derived structure very atypical for this taxon, particularly at such high frequency. In comparison with p3s of *Bellatona* species, those of *Bellatona* cf. *B. forsythmajori* from DM01 also exhibit a different L/W ratio, implying a longer anteroconid part of p3, corresponding rather to the condition in *Ochotona* (Fig. 5). The features available in p3s from DM01 attributed to *Bellatonoides eroli* are compatible with the diagnosis of *Bellatonoides* by Sen (2003: 166), but the specimens differ from the nominal species from Sinap Tepe in their smaller average size (Fig. 5), less slender p3 anteroconid, and wider p3 antero-posteroconid connection. Nevertheless, the morphology of the specimen figured in Zhang et al. (2012: fig. 2F) is attributable to *Ochotona*, morphologically similar to the Kalfa form. Unfortunately, the root sides of remaining specimens with shortened anteroconid (Zhang et al. [2012: fig. 2D–E]) were not described/figured to exclude a possibility of them representing sub-adults; cf. the condition in Kalfa p3 in Fig. 3N–N’.

The p3 of *Ochotona* cf. *O. lagreli* from DM01 expresses the general morphology of *O. lagreli* from Ertemte and Harr Obo (Qiu, 1987; Schlosser, 1924), but it is smaller (of intermediate size between *O. lagreli* and *O. birgerbohlini*, Fig. 5) and has a higher tendency to buccal enlargement of p3 anteroconid, though not as high as in the Kalfa form. Such an advanced p3 phenotype is very surprising for a locality of

this age and a close affinity to *O. lagreli* seems to be very unlikely, thus *Ochotona* from DM01 is tentatively referred to here as *Ochotona* sp. This is also the case for *Ochotona* from Builstyn Khudag in the Valley of Lake and the material with only two p3s described by Erbajeva (2003) is tentatively referred here also as *Ochotona* sp.

Unfortunately, the stratigraphic provenance of particular specimens in DM01 is unclear from the published data (cf. Kaakinen et al., 2015; Zhang et al., 2012). Zhang et al. (2012: 209) admit a secondary depositional process and mixture of fossils from different horizons, but exclude this as a great factor and the material as a whole attributed to horizon DM01. The age of sedimentation is fixed with the chron C5An.1n, i.e. at 12.014–12.116 Ma (Kaakinen et al., 2015). Taking into account the available Tunggurian–Bahean record, the phenotype of available rootless ochotonids from DM01 implies either (i) fossil material originating from a longer period of time (i.e. a mixture of fossils from different horizons) with possible presence of more than one species belonging to one (or more [in my view less probable]) evolutionary lineage(s) or (ii) fossil material originating from a relatively short period of time, but in that case, a presence of three species of one clade is very unlikely. Unfortunately, isolated teeth from DM01 in themselves, with their unsure stratigraphic provenance and/or without additional discriminative parameters in other body parts, do not allow a decision between these alternative variants. At any rate, a mosaic pattern of p3 characters distributed in various proportions within a clade with a successive selection of morphotypes leading to a dominance of selected phenotypes characteristic for particular taxa can be assumed. Thus, if we hypothesize the presence of three successive taxa in DM01, then within the above limits, an unequivocal division into distinct species/genera is impossible. The material also does not show the successive linear evolutionary lineage *Bellatona*–*Bellatonoides*–*Ochotona*. In this context, the locality DM02 dated to the earliest Late Miocene (ca 11.6 Ma, Kaakinen et al., 2015), i.e. at about 0.5 Myr younger than DM01, seems to be very promising. Its fossil ochotonines referred by Kaakinen et al. (2015) to *Bellatona forsythmajori* and *Ochotona* sp. indet. (but surprisingly without *Bellatonoides*) may shed some light on the still poorly understood early evolution of Ochotoninae.

A more conclusive evaluation of the phylogenetic relationships of *Ochotona* from Kalfa with other relevant species discussed in this paper is still impossible. With the exception of Zhang et al. (2012) there is a lack of detailed up-to-date studies dealing with the earliest Ochotoninae. The tendency to lateral displacement of p3 anteroconid documented in taxa from Damiao – DM01, Sinap Tepe – Locs. 8A, 120, and Kalfa may indicate a phylogenetic closeness. This feature has not yet been documented in later European taxa of *Ochotona* recorded from the Late Miocene (MN11–13) of the peri-Paratethyan area (cf. Čermák, 2010 and data herein). Undoubted *Ochotona* findings recorded from DM01, Sinap Tepe (Loc. 84), and Kalfa demonstrate the occurrence of surprisingly advanced p3 phenotype already in the pre-Vallesian (pre-Bahean, pre-MN9) of the Far East Asia and in the pre-Turolian of the peri-Paratethyan area of Europe.

6. Conclusions

I revised the original ochotonid material from the early Late Miocene Kalfa locality (Moldova) described by Lungu (1981) as “*Prochotona*” *kalfense*. The taxonomic analysis of this taxon was supported by a direct examination of type materials of *P. eximia*, *B. eroli*, and *O. ozansoyi*, the relevant Late Miocene ochotonines of the peri-Paratethyan area.

Based on the p3 features in the holotype of *P. eximia* (the type species of the genus *Prochotona*), the species *eximia* undoubtedly belongs to *Ochotona*. Therefore, the genus *Prochotona* Khomenko, 1914 is regarded here as a junior subjective synonym of the genus *Ochotona* Link, 1795. The morphometric analyses of the material from Kalfa confirm the taxonomic validity of the species *kalfense*. Its p3 features are also typical and discriminative for *Ochotona* [cf. the emended generic diagnosis given by Erbajeva (1988: 82; cf. Gureev, 1964: 226, Gromov and Erbajeva, 1995: 34–35)], and thus the species *kalfense* is referred here to that genus. Considering all the available data, I propose here, following Čermák (2010), to retain for now the original concept of *Bellatonoidea* as a distinct genus.

O. kalfense from the early Late Miocene (early MN10) locality of Kalfa represents the oldest record of *Ochotona* in Europe; it seems to be coeval with *O. ozansoyi* described from Sinap Tepe (loc. 84). These species demonstrate the occurrence of surprisingly advanced p3 phenotype already in the pre-Turolian of the peri-Paratethyan area. Among the Chinese localities, the age of Kalfa seems to be comparable with Shengou and lower part (Unit/Biozone BH1) of Bahe Fm., thus younger than Amuwusu and older than the Late Bahean *Ochotona* bearing localities Huitenghe and Shala. The material under study is attributed here to the subfamily Ochotoninae; the monophyletic lineage derived from *Bellatona*. A more conclusive evaluation of phylogenetic relationships of *Ochotona* from Kalfa to other relevant species of the clade discussed in this paper is still impossible. Nevertheless, the lateral displacement of p3 anteroconid documented in taxa from Damiao (DM01), Sinap Tepe (Locs. 8A, 120), and Kalfa may indicate a phylogenetic closeness. This feature has not yet been documented in later European taxa of *Ochotona* recorded from the Late Miocene (MN11–13) of the peri-Paratethyan area.

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