Early Pliocene ochotonids (Mammalia, Lagomorpha) from Southern Ukraine

Stanislav ČERMÁK
Institute of Geology, Academy of Sciences of the Czech Republic,
Rozvojová 269, CZ-16500 Prague 6 - Lysolaje (Czech Republic)
and Department of Zoology, National Museum (Natural History),
Václavské nám. 68, CZ-11579 Prague 1 (Czech Republic)
cermaks@gli.cas.cz

Leonid I. REKOVETS
Department of Zoology and Ecology,
The Faculty of Biology and Animal Science,
Wroclaw University of Environmental and Life Sciences,
ul. Kożuchowska 5B, PL-51631 Wrocław (Poland)
leonid.rekovets@up.wroc.pl

Čermák S. & Rekovets L. I. 2010. — Early Pliocene ochotonids (Mammalia, Lagomorpha) from Southern Ukraine. *Geodiversitas* 32 (1): 107-120.

ABSTRACT
The aim of this paper is to enlarge knowledge about poorly known ochotonids from the Early Pliocene (Ruscinian, MN 14) from southern Ukraine. The abundant new material of *Ochotona antiqua* Argyropulo & Pidoplichko, 1939 from Novopetrovka (type locality) and Frunzovka-1 is analyzed in detail and compared with the type material. The results are expressed in a redescription of the taxon and evaluation of its intraspecific variation, including the outlying and/or aberrant forms closely related to it. *Pseudobellatona relicta* Topachevsky, Nesin & Topachevsky, 1993 confined to the type locality Krasnopol is redescribed and considered herein as a taxon *incertae sedis* within the Ochotonidae clade. Specificities of the Early Pliocene taxa from the Kuchurganian sedimentary series are discussed in the context of phylogeny and systematics of Eurasian ochotonids.

KEY WORDS
Mammalia,
Lagomorpha,
Ochotonidae,
Ochotona antiqua,
Pseudobellatona relicta,
Ukraine,
Early Pliocene,
Ruscinian.

RÉSUMÉ
Ochotonides (Mammalia, Lagomorpha) du Pliocène inférieur du sud de l'Ukraine.
L'objectif de cet article est d'élargir la connaissance, jusqu'alors faible, des ochotonides du Pliocène inférieur (Ruscinien, MN 14) du sud de l'Ukraine. Le nouveau matériel abondant d'*Ochotona antiqua* Argyropulo & Pidoplichko, 1939 de Novopetrovka (localité type) et de Frunzovka-1 est analysé en détail et comparé avec le matériel type. Les résultats proposent une nouvelle description du taxon ainsi qu'une évaluation de sa variation intra-spécifique, en prenant en compte les formes sortant de cette variabilité et/ou aberrantes qui lui sont proches. *Pseudobellatona relicta* Topachevsky, Nesin & Topachevsky, 1993, dont la seule occurrence est la localité type de Krasnopol, est redécrite et considérée comme un taxon *incertae sedis* dans le clade des Ochotonidae. Les spécificités des taxons du Pliocène inférieur des séries sédimentaires du Kuchurganien sont discutées dans le contexte de la phylogénie et de la systématique des ochotonides d'Eurasie.

MOTS CLÉS
Mammalia,
Lagomorpha,
Ochotonidae,
Ochotona antiqua,
Pseudobellatona relicta,
Ukraine,
Pliocène inférieur,
Ruscinien.

INTRODUCTION

The fossil record of medium sized ochotonids from the Kuchurganian (Early Ruscinian, MN 14) sedimentary series in southern Ukraine (Odesskaya Province) represents an important source of information for the Pliocene-Pleistocene evolution of ochotonids in Europe. The first form of these ochotonids from the Early Pliocene gravels of the River Kuchurgan was firstly reported by Pidoplichko (1938). Later, based on the analysis of that material, Argyropulo & Pidoplichko (1939) erected a new species, *Ochotona antiqua*, from the localities Novopetrovka and Grebenniky. Since then, a large number of records from southern Ukrainian localities were referred to that species (see Dubrovo & Kapelist 1979 for details), unfortunately without detailed morphometric description enabling a view of intraspecific variation of this taxon in comparison with other Eurasian ochotonids. Besides this species, there are also two similarly sized ochotonids described from the Kuchurganian of Odesskaya Province. The first one was erected by Gureev & Schevtschenko *in* Gureev (1964) from the Early Ruscinian (MN 14) locality of Ukrainskiy Trostyanec (= Novopetrovka) as *Ochotona pseudopusilla*. The other taxon was erected by Topachevsky *et al.* (1993) from the Early Ruscinian (MN 14) site of Krasnopol as *Pseudobellatona relicta*. To date, both taxa are only known from their type localities.

The remains of the above mentioned ochotonids of southern Ukraine, mostly referred to *Ochotona antiqua*, have not yet been revised in detail within the context of the recent knowledge on European ochotonids. Furthermore, to date, no precise data has been published to demonstrate their morphological and size variation. This paper fills this gap by providing 1) a detailed morphometric redescription of *O. antiqua*, 2) characteristics of intraspecific variation of the species, 3) data on morphology of outlying and/or aberrant forms closely related to this species, and 4) a survey of their systematic relationship to other European ochotonids, based on the available material.

The localities and stratigraphy

The type specimens and new ochotonid material described in this paper come from the Early Ruscinian (Kuchurganian *sensu* Shevchenko (1965), MN 14) localities Novopetrovka, Frunzovka-1, and Krasnopol, all in the Frunzovskiy District (Odesskaya Province, southern Ukraine). The localities are situated along the river system of Kuchurgan (Fig. 1). All the faunas, including the ochotonids under study, come from the alluvial units mostly consisting of gravels and sands. The

most complete profile in the vicinity of Krasnopol village has been designated as the reference locality of the Kuchurganian age (Nesin 1996). The other Kuchurganian localities in Odesskaya Province are Trudomirovka, Velikomikhailovka, Voinichevo, and Yurkovka (Dubrovo & Kapelist 1979; Nesin 1996, 2004; Nesin & Nadachowski 2001).

The above mentioned localities are characterized by the following significant micromammal association of the Early Pliocene (Early Ruscinian) age: *Pliopetaurista* sp., *Tamias* sp., *Prospalax rumanus* Simionescu, 1930, *Nannospalax macoveii* Simionescu, 1930, *Occitanomys* sp., *Apodemus* cf. *dominans* Kretzoi, 1959, *Kowalskia* sp. (LAD), *Odessanomys* sp. (FAD), *Polonomys* sp. (FAD). Among rodents the true spalacid *Nannospalax* is predominant and *Polonomys*, an ancient arvicolid, appears. Among ochotonids *Ochotona* predominates over *Prolagus*, the rodent/lagomorph ratio is low. See also Korotkevich (1988) and Nesin & Nadachowski (2001) for details.

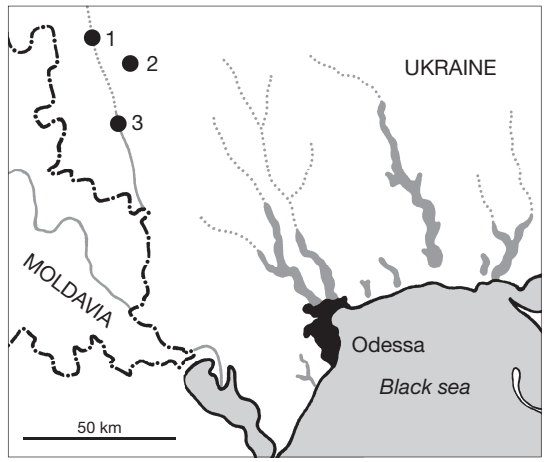

FIG. 1. — The geographical position of the Early Pliocene (Early Ruscinian, MN 14) localities under study: **1**, Funzovka-1; **2**, Krasnopol; **3**, Novopetrovka.

MATERIAL AND METHODS

All drawings and measurements were made using a binocular microscope and ocular micrometer. For purposes of metric analysis, only non-juvenile specimens (according to Lissovsky 2004) were taken into account. The dimensions of the teeth were taken on the occlusal surface, outside of the enamel border, at their maximum length and width. All measured data are given in millimeters and ratios in percentages. The dental terminology and metrics used here to describe dental structures follow López-Martínez (1974), Erbajeva (1988), and Čermák (2004). The meaning of the genera and families are in agreement with the proposal by Sen (2003). All nomenclatural acts presented here conform to the mandatory provisions of the *International Code of Zoological Nomenclature* (ICZN 1999). The biostratigraphic terminology used in this paper follows Fejfar & Heinrich (1983), Semenenko (1987), Nesin (1996, 2004) and Fejfar *et al.* (1998). For comparative purposes, the morphometric data on the relevant taxa were partly provided by authors (collections of National Natural History Museum, Kiev; Natural History Museum, Basel; Geological Institute of Hungary [MÁFI], Budapest; and Zoological Institute, Russian Academy of Sciences, Saint Petersburg) and partly by Khomenko (1914), Simionescu (1930), Argyropulo & Pidoplichko (1939), Dawson (1961), Gureev (1964), Lungu (1981), Agadjanian & Erbajeva (1983), Melik-Adamyan (1986), Qiu (1987), Erbajeva (1988, 2003), Erbajeva & Shushpanov (1988), Zhou (1988), Topachevsky *et al.* (1993), Rădulescu & Samson (1995), Averianov & Tesakov (1998), Sen (1998, 2003), Erbajeva *et al.* (2001, 2006), Erbajeva & Zheng (2005).

The new ochotonid material from the localities Novopetrovka and Frunzovka-1 was collected by the research workers of National Natural History Museum in Kiev (NNHM) during the last four decades of the 20th century. All the material described in this paper is housed in fossil vertebrate collections of the NNHM.

ABBREVIATIONS

AR	p3 anteroconid ratio (p3 anteroconid width×100/ p3 width);
ccd	conid confluence distance;
CV	coefficient of variation (%);
DR	diastema ratio (length of diastema×100/alveolar length of p3-m3);

FAD first appearance datum in the studied area;
L length;
LAD last appearance datum in the studied area;
M mean;
MR mandible ratio (buccal height of mandible at m2×100/alveolar length of p3-m3);
N number of specimens;
OR observed range;
P3R p3 ratio (p3 length×100/p3 width);
W width.

SYSTEMATICS

Order LAGOMORPHA Brandt, 1855
Family OCHOTONIDAE Thomas, 1897
Genus *Ochotona* Link, 1795

TYPE SPECIES. — *Ochotona minor* Link, 1795 (= *Lepus dauuricus* Pallas, 1776) by original designation (see Hoffmann & Smith [2005] for details).

Ochotona antiqua
Argyropulo & Pidoplichko, 1939
(Figs 2A-Q; 3; Tables 1; 2)

Ochotona pusilla antiqua Pidoplichko, 1938: 124 [*nomen nudum*].

LECTOTYPE. — NNHM, no. 2616 (37-239), fragment of left mandibular ramus with p3-m2 (Fig. 2I); designated by Erbajeva (1988), see "Nomenclatural remarks" for details.

TYPE LOCALITY AND AGE. — Novopetrovka (Odessa province, Ukraine); Early Pliocene (Ruscinian, MN 14) (Fig. 1).

MATERIAL EXAMINED. — In addition to the lectotype (no. 2616) and paralectotype (no. 2618), the following specimens of *O. antiqua* from Novopetrovka (NOP, N = 70) and Frunzovka-1 (FRA, N = 18) were examined: 35 mandibles in various conditions with various teeth, or without them (NOP21, 22; NOP27-59), 11 maxilla fragments with various teeth, or without them (NOP60-NOP70), 42 isolated p3 (NOP1-20, NOP23-26; FRA 1-10, FRA 12-19). The fossil remains of ochotonids are well preserved, mostly brownish and/or blackish coloured.

EMENDED DIAGNOSIS. — A medium sized ochotonid; alveolar length of p3-m3 is 8.40-9.41-10.8, length of p3 is 1.39-1.53-1.76. The p3 anteroconid is large and wide, generally with a simple morphology and sharp anterior margin; the anteroconid-posteroconid junction is narrow and placed symmetrically to the tooth. The mandibular ramus is rather long and slight; its ventral margin is convex. The coronoid process is well developed.

MEASUREMENTS. — See Tables 1 and 2.

REDESCRIPTION

Ochotona antiqua is a medium sized ochotonid (Tables 1, 2). The p3 possesses a relatively large and wide anteroconid, generally with a simple morphology and a sharp top. Non-plicated para- and protoflexids are nearly of the same depth, thus the very narrow (M of ccd is 0.06, N = 25) anteroconid-posteroconid junction is placed symmetrically to the tooth. The hypoflexid is rather short, generally less than half of the p3 width. The occlusal outline of P3 is trapezoidal, the mesial hyperloph is narrow (M = 65% of tooth width, N = 7). The p4-m3, as well as P4-M2, do not differ morphologically from the corresponding teeth of *Ochotona* species.

The mandible is relatively long, and in ventral view rather slight; it is higher below the p4 than below the m3. The mandibular diastema is relatively short (DR is M = 60, OR = 51-67, N = 18). The lower incisor extends posteriorly along the ventral border to the level of the area bounded by dividing lines of p4/m1 and m1/m2 alveoli and forms distinct tubercles on both the lingual and buccal sides of the horizontal ramus. The ventral margin of the mandible is convex. At the base of horizontal ramus, a relatively short groove extends anteriorly from the end of the tooth row along the close proximity of the lingual face (Fig. 3B-D). The posterior mental foramen is located ventrally to the area between m2 talonid and m3, or even more posteriorly. The ascending ramus is high, its coronoid process is well developed (Fig. 3A, A'). The dorsal outline of mandibular condyle is triangular in shape, wide in anterior part and sharply narrower posteriorly.

VARIABILITY

The specimens of *O. antiqua* analyzed showed a great variability in some characters, without significant differences between the localities under study. The anteroconid and paraflexid are the most variable

TABLE 1. — Lower and upper teeth (p3 and P3) measurements of *Ochotona antiqua* Argyropulo & Pidoplichko, 1939. Abbreviations: see Material and methods.

Measurements	Novopetrovka				Frunzovka-1			
	N	M	OR	CV	N	M	OR	CV
p3:								
Length	23	1.53	1.39-1.67	5.18	14	1.53	1.41-1.76	6.84
Anteroconid length	24	0.84	0.73-1.00	7.85	13	0.82	0.67-1.00	12.70
Posteroconid length	24	0.93	0.80-1.17	8.27	13	0.90	0.78-1.04	7.33
Anteroconid width	24	0.79	0.67-0.93	8.10	15	0.78	0.69-0.96	11.62
Posteroconid width	22	1.60	1.33-1.78	7.27	12	1.58	1.41-1.81	9.99
Conid confluence distance	25	0.06	0.00-0.15	62.55	15	0.07	0.00-0.15	68.33
P3:								
Length	7	1.26	1.17-1.33	5.30				
Width	7	2.65	2.37-3.19	10.19				
Paraflexo-protoconal width	7	1.70	1.48-2.07	12.35				
Paraflexo-hypoconal width	7	1.91	1.70-2.33	11.20				

TABLE 2. — Mandibular and maxillar measurements of *Ochotona antiqua* Argyropulo & Pidoplichko, 1939. Abbreviations: see Material and methods.

Measurements	Novopetrovka			
	N	M	OR	CV
Total height of mandible	6	19.64	18.29-21.98	6.62
Total length of mandible	4	31.31	29.36-33.52	5.45
Lingual height of mandible at p3	28	5.81	5.30-6.50	5.81
Lingual height of mandible at p4	27	7.42	6.60-8.60	7.65
Lingual height of mandible at m3	29	6.46	5.50-7.55	7.97
Length of diastema	17	5.60	4.50-6.20	7.83
Alveolar length of p3-m3	29	9.41	8.40-10.80	6.21
Mandible width at p4	29	3.89	3.40-4.50	7.83
Mandible width at m2	29	3.51	2.85-4.10	8.58
Length of p3 alveolus	28	1.92	1.70-2.18	8.35
Width of p3 alveolus	28	1.99	1.70-2.27	8.63
Alveolar length of P2-M2	11	9.20	8.20-10.10	7.07

parts of p3 pattern. The former is not plicated (i.e. it is with convex, or concave enamel walls without grooves, or even flexids) in 90.5% of the material under study (N = 42); three specimens (7%) are with non-cemented groove on the antero-lingual side (see e.g., Fig. 2Q) and one specimen (2.5%) with cemented flexid (Fig. 2L). The ratio between symmetrical anteroconid (i.e. antero-buccal and antero-lingual enamel walls are of the similar length; Fig. 2D) and asymmetrical one (Fig. 2E) is 45 vs 54% (N = 19 vs 23). Proto- and paraflexids are of the same length (55%, N = 42), nevertheless in 23% of studied p3s the former is slightly longer. The angle of paraflexid deflection from the longitudinal axis of p3 falls in a range between 43 and 74° with a mean of 59° (N = 42, CV = 14.61). In four specimens (9.5%; see e.g., Fig. 2C, E), there is a slight indication of the "*Pliolagomys*"-like paraflexid (i.e. slightly V-shaped and bent anteriorly in its distal part). The variously developed mesoflexid occurs also in 9.5% (see e.g., Fig. 2H-J); its occurrence seems not to be related to the age of the individual.

In side views, the outline morphology of mandible is not variable; the ventral margin of horizontal ramus is always convex (Fig. 3A, A'). In ventral view (Fig. 3B-D), the buccal and lingual tubercles are developed in varying degree (viz. 57%, 30%, and 13% for morphotypes figured on Figure 3B, C, and D, respectively) and form the thickest part of the mandible. The general outlines of the p3

alveoli show the same structures (Fig. 3E-N) and proportions as the studied p3s; P3R is 97 (N = 28) for alveoli and 96 (N = 33) for related teeth. The posterior mental foramen is located mostly (52%, N = 32) below the m3. The root end of lower incisor extends mostly (41%, N = 32) below the trigonid/talonid boundary of m1.

Because of the overlap of morphological characters between subadults and adults, we were able to reliably distinguish juveniles from adults only. Nevertheless, concerning the size of cheek teeth, values near the lower margin of size variation (see Tables 1, 2) are regarded here as indicative of the size boundary between subadults and adults, although the influence of subadults in measurements is possible. In any case, all specimens smaller than related size ranges (see Tables 1, 2) still retain their conical structure of teeth and were not taken into account in metric analysis.

Comparison

The newly re-described features as well as the variation range of the species allow us to provide here a more detailed comparison with relevant ochotonid taxa. *Ochotona antiqua* under study differs from stratigraphically and geographically close taxa especially in its p3 morphology and/or in its size.

Bellatonoides kalfense (Lungu, 1981) – "*Prochotona kalfense*" *sensu* Lungu 1981; Erbajeva 1988, 1994 – from the Vallesian (MN 9 or 10, Kalfian *sensu* Lungu 1978) from Kalfa (Moldavia) differs from the studied species in its distinctly larger size (L of p3 is OR = 1.65-2.15). The p3 of *Bellatonoides* from Kalfa possesses buccally shifted anteroconid with a more rounded top. The enamel bridge between anteroconid and posteroconid is generally wider. Its paraflexid is less developed. The unique p3 from the Early Pliocene (MN 14) locality Krasnopol (Ukraine) described by Topachevsky *et al.* (1993) as *Pseudobellatona relicta – nomen dubium sensu* Averianov 1998 (see below for details) – differs from *O. antiqua* in lacking paraflexid (only a slight depression is visible). In its size (see below), the taxon falls into the variation range of *O. antiqua* (Table 1). The Early Pliocene (MN 15) *Ochotonoma* Sen, 1998, known from localities of southeastern Europe and the Middle East, differs from *Ochotona antiqua* in its more plicated p3 anteroconid, and in its smaller and more robust mandible (see Sen 1998 and Čermák 2007 for details). All the species of *Pliolagomys* Agadjanian & Erbajeva, 1983, known in the Pliocene localities from an area extending from Moldavia to Prebaikal (Topachevsky & Skorik 1977; Agadjanian & Erbajeva 1983; Erbajeva 1988, 1994; Erbajeva & Shushpanov 1988), differ from *O. antiqua* in their larger size (L × W of p3 is OR = 1.35-2.60 × 1.60-3.00, N = 89 – the range is based mostly on published data, so the influence of juveniles is possible; alveolar length p3-m3: OR = 9.50-11.90, N = 12), more plicated anteroconid, and buccally moved anteroconid-posteroconid junction. The species under study differs from the former in its posteriorly bent paraflexid; only a slight indication of the "*Pliolagomys*"-like paraflexid was observed in 9.5% (N = 42) of the studied *O. antiqua* p3. Some p3s of young individuals of *Pliolagomys* may resemble *O. antiqua* in their occlusal size and pattern (i.e. more smooth and rounded outline of anteroconid, less asymmetric position of anteroconid-posteroconid junction and anteroconid top, as well as shorter and straighter paraflexid), but in these cases their crowns have a markedly conical structure. The shape of p3 alveolus in *O. antiqua* is distinguishable from that of *Pliolagomys* in being symmetrically located top in about half of specimens (Fig. 3E-I); in any case, the alveoli of *O. antiqua* are smaller (Table 2) than those of *Pliolagomys* species.

The oldest species of the genus *Ochotona* in Europe – *O. eximia* (Khomenko, 1914), "*Prochotona eximia*" *sensu* Khomenko 1914; Gureev 1964; Erbajeva 1988, 1994 – was described from the late Miocene (MN 11 or 12) locality Taraklia (Moldavia). This taxon differs from *O. antiqua* in its notably larger size (see Khomenko 1914; Argyropulo & Pidoplichko 1939; Gureev 1964 for details). The species under study most closely resembles the poorly known *Ochotona ursui* Simionescu, 1930, described from the Early Pliocene (Ruscinian, MN 15a; Terzea 1997) locality Măluşteni (Romania). The lectotype, assigned to this species by Rădulescu & Samson

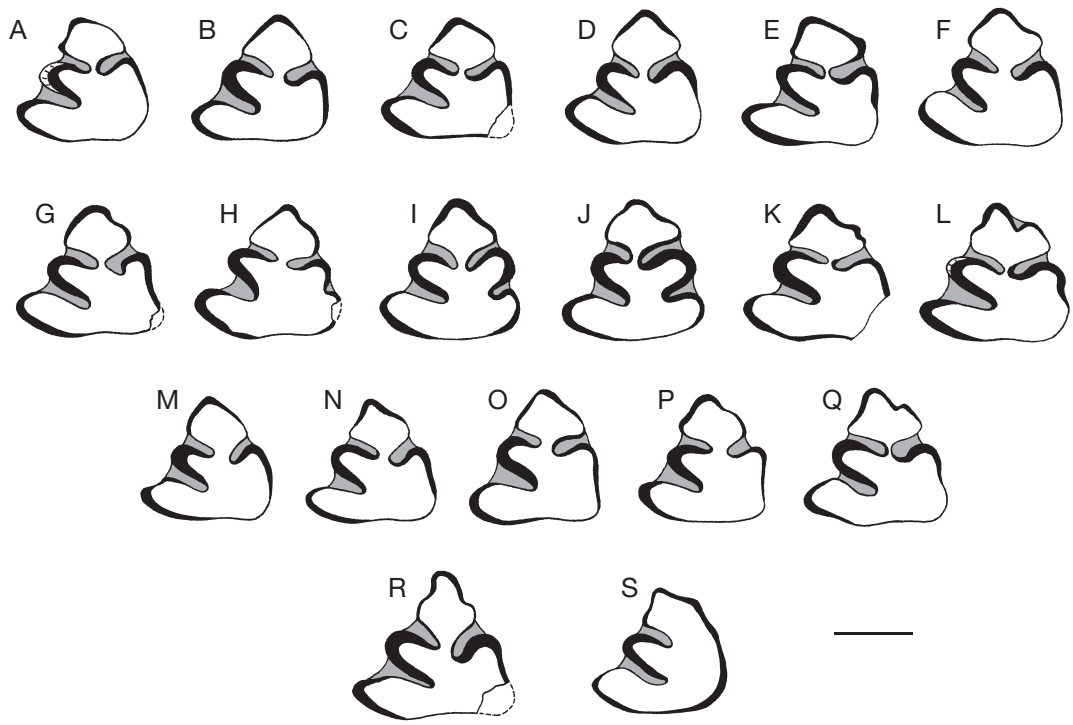

FIG. 2. — Morphology of p3 in studied ochotonids from the Early Pliocene (Early Ruscinian, MN 14) of southern Ukraine (Odesskaya Province): **A**-**L**, *Ochotona antiqua* Argyropulo & Pidoplichko, 1939 from Novopetrovka (**I**, lectotype); **M**-**Q**, *O. antiqua* from Frunzovka-1; **R**, *Ochotona* sp. 1 from Frunzovka-1; **S**, *Pseudobellatona relicta* Topachevsky, Nesin & Topachevsky, 1993 from Krasnopol (holotype). All teeth are figured as left specimens (**A**, **C**, **K**-**M** and **P** are reversed). Scale bar: 1 mm.

(1995), differs from *O. antiqua* under study in its shorter, taller, and more robust horizontal ramus of mandible; MR is 82 in the former in contrast to 66 (M = 66, OR = 62-70, N = 29) in the latter. According to the additional material (three fragmentary mandibles without p3s) from the type locality, housed in the Natural History Museum of Basel, this ochotonid also differs from *O. antiqua* in its slightly elongated p3 alveolus pattern; P3R of alveoli are 103 and 97, respectively. The p3 of the lectotype also possesses a derived morphology of paraflexid (i.e. a slight indication of the "*Pliolagomys*"-like bent). Nevertheless, from the only available p3, without knowledge of morphotypes proportion in a more significant sample, it is difficult to evaluate the actual meaning and/or validity of this character in this species.

The description of *Ochotona pseudopusilla*, conforming Article 13 of ICZN (1999), given by Gureev & Schevtschenko in Gureev (1964), is insufficient to provide a proper comparison with *O. antiqua*. Unfortunately, neither holotype (No. M1-1) nor other ochotonid specimen from Schevtschenko's collection, or at least an additional relevant ochotonid material from the type locality is available in the Institute of Geological Sciences (Gureev 1964) or National Natural History Museum of the National Academy of Sciences of Ukraine in Kiev. Based on measurements given by Gureev & Schevtschenko (in Gureev 1964) in the original description of the species, the mandible of *O. pseudopusilla* should be smaller and slightly more gracile than that of *O. antiqua*; OR of the p3-m3 length and height at m2 is 8.00-9.00 and 5.00-5.70, respectively, in

the former compared to 8.40-10.60 and 6.50-7.00 in the latter (see Gureev 1964: 231 for details). Nevertheless, our measurements (see Table 2) as well as data provided by Argyropulo & Pidoplichko (1939) and Erbajeva & Shushpanov (1988) do not fully support their conclusions. In its size variation, *O. pseudopusilla* closely corresponds with *O. antiqua*. The morphological features of mandible in *O. pseudopusilla* stressed by Gureev & Schevtschenko (in Gureev 1964: 231, 232) do not allow a closer comparison with the relevant taxa. In any case, in our opinion, these characters (as e.g., the position of posterior mental foramen at mandible, etc.) suggest a closer affinity to *O. antiqua* rather than to *O. pusilla.*

The studied *O. antiqua* differs from all Villányian-Biharian species of *Ochotona* known from Central-West Europe in its larger size and/or p3 ratio (see Sych 1980; Erbajeva *et al.* 2001; Čermák 2004).

The other forms, supposedly related to *Ochotona antiqua*, are known from the Ruscinian localities Nurnus, Armenia (MN 14/15, Kuchurganian/Moldavian *sensu* Melik-Adamyan *et al.* 1988), and Kosyakino, Stavropol Region, Russia (MN 14 *sensu* Averianov & Tesakov 1998). The former one was reported by Melik-Adamyan (1986) as *Ochotona* ex gr. *antiqua*, the latter one by Averianov & Tesakov (1998) as *Ochotona* cf. *antiqua*. The p3s reported by Melik-Adamyan (1986: figs 4-7) are notably smaller (L × W of p3 is M = 1.38 × 1.35, OR = 1.24-1.50 × 1.25-1.47, N = 4; inferred from the figures 4-7) than those of typical *O. antiqua*. Moreover, the Armenian ochotonid differs from *O. antiqua* under study in its distinctively more trilobate appearance of p3 anteroconid as well as in its more evolved and wider p3 paraflexid. The ochotonid from Kosyakino is more similar to the studied *O. antiqua* (see Tables 1, 2; Fig. 2) than the Armenian form. Its size (L × W of p3 are 1.50 × 1.60 and 1.75 × 1.90; height of mandibles at p3 is 5.30 and 6.50) and the morphology of p3 (see Averianov & Tesakov 1998: fig. 1a, b) fit with that of *O. antiqua* (see Tables 1, 2; Fig. 2). Nevertheless, it differs slightly from *O. antiqua* in having narrower and more rounded anteroconid; AR is M = 50, OR = 43-56, N = 35 for *O. antiqua* from Novopetrovka and Frunzovka-1 in contrast to 44 and 39 for ochotonids from Kosyakino.

Ochotona antiqua differs from the oldest representatives of *Ochotona* in Asia known from the Latest Miocene to Early Pliocene of the Mongolian Plateau (see e.g., Qiu 1987; Erbajeva 1988, 2003); *O. lagreli* Schlosser, 1924 differs from the species under study in its larger size (L × W of p3 is M = 1.81 × 1.80, N = 106/101) and in having notably higher mandibular body (height at m1 is 9.00), *O. birgerbohlini* Averianov, 1998 – commonly known as *O. minor* Bohlin, 1942 (= a junior homonym of *O. minor* Link, 1795) differs in its notably smaller size (L × W of p3 is M = 1.11 × 1.12 , N = 12; alveolar length p3-m3 is 6.60). Compare with new species described by Erbajeva *et al.* (2006) from the late Miocene of China (Shanxi Province). The following species of *Ochotona* from Asia are generally correlated with the late Pliocene, MN 16 (Erbajeva 1994; Erbajeva & Zheng 2005). *Ochotona antiqua* differs from *O. intermedia* Erbajeva, 1976 and *O. sibirica* Erbajeva, 1988 (Mongolia and Transbaikalia) as well as from *O. gracilis* Erbajeva & Zheng, 2005 and *O. lingtaica* Erbajeva & Zheng, 2005 (North China) in its larger size; from *O. gromovi* Erbajeva, 1976 (Transbaikalia) in its smaller size. Similarly sized *O. plicodenta* Erbajeva & Zheng, 2005 (North China) differs from *O. antiqua* by having a plicated paraflexid of p3.

Nomenclatural remarks

The name "*antiqua*" was firstly used by Pidoplichko (1938: 124). Based on the material from Andriashevka, the new form of *Ochotona* was referred there to a new subspecies of *O. pusilla*. Although many authors, such as Argyropulo & Pidoplichko (1939), Gureev (1964), Agadjanian & Erbajeva (1983), Erbajeva (1988), Erbajeva & Shushpanov (1988), or Čermák (2004), considered this work as a description, this first usage of the name fails to conform to Article 13 of ICZN (1999); therefore it must be regarded as a *nomen nudum*. The name was made available by Argyropulo & Pidoplichko (1939); based on the analysis of the material from Pidoplichko's

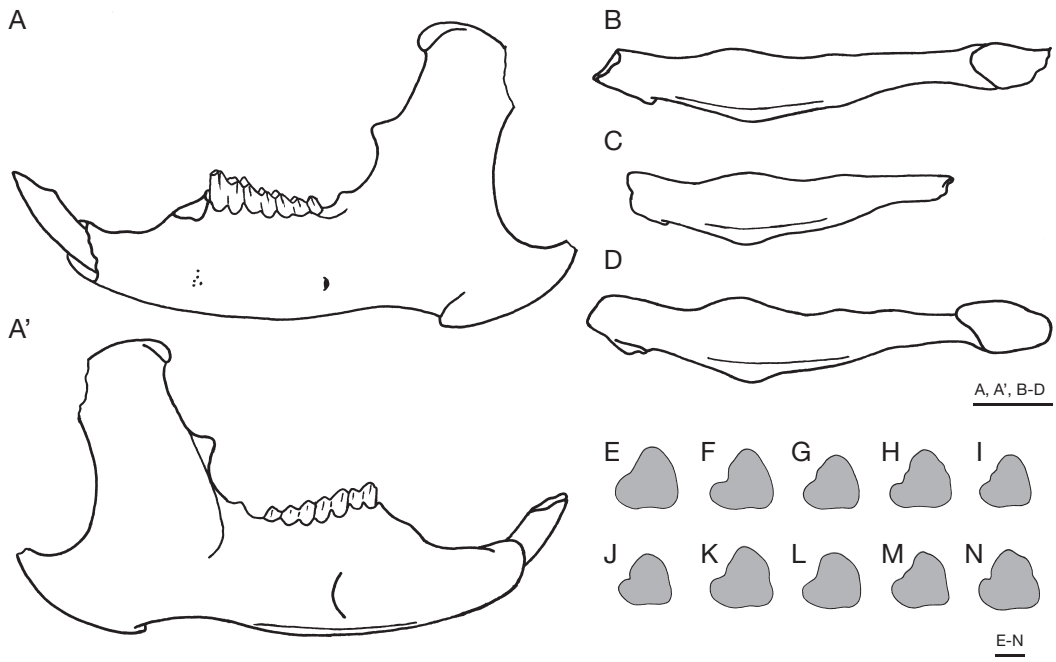

FIG. 3. — Mandibular morphology of *Ochotona antiqua* Argyropulo & Pidoplichko, 1939 from Novopetrovka (Early Ruscinian, MN 14): **A**,**A'**,**B-D**, mandibles; **A**, **A'**, buccal/lingual view; **B-D**, ventral views; **E-N**, alveoli. All mandibles and alveoli are figured as left specimens (**A**,**A'-C**, **E**, **F**, **I**, **K-M** are reversed). Scale bars: A, A', B-D, 5 mm; E-N, 1 mm.

collections (mainly from explorations in 1934, see Pidoplichko [1938] for details), they described a new species – *Ochotona antiqua* and designated syntypes (they used the term "types", see Article 73.2) from Novopetrovka (no. 2616) and Grebenniky (no. 2618).

Unfortunately, from the following relevant publications (i.e. Gureev 1964; Agadjanian & Erbajeva 1983; Erbajeva 1988), it is not fully clear which specimen of the type series was subsequently designated as the single name-bearing type (i.e. lectotype). Agadjanian & Erbajeva (1983: 75) followed the terminology used by Argyropulo & Pidoplichko (1939). Gureev (1964: 231) used the term "type" for the specimen from Grebenniky (mandible without p3, no. 2618), but undoubtedly within the meaning of "holotype" (compare his usage of the terms "type" and "type (lectotype)" in Gureev [1964: 83 and 106], or his subsequent usage of the term "holotype" for the above mentioned specimen [i.e. no. 2618] in Gromov & Baranova [1981: 70], etc.). Since Gureev (1964) did not mention the remaining specimen of the type series (i.e. the act of the explicit indication that he was selecting from the type series the particular specimen to serve as the name-bearing type; Article 74.5), we cannot consider it as a valid designation of the lectotype. In this sense of Article 74.5, we accept the work of Erbajeva (1988) as valid designation of the lectotype, insomuch she also wrongly used the terms, nevertheless, we consider here the strict combination of the terms "type" and "paratype" as the act of the explicit indication of specimens within the type series.

Summing up the above mentioned facts, in agreement with Erbajeva (1988) and Erbajeva & Shushpanov (1988), we consider here the syntype from Novopetrovka (no. 2616) to be the lectotype of the nominal taxon *Ochotona antiqua* and the remaining specimen, from Grebenniky (i.e. no. 2618), to be the paralectotype. The place of origin

of the lectotype (i.e. Novopetrovka) is then the type locality of *Ochotona antiqua* (see Article 76.2).

Ochotona sp. 1
(Fig. 2R)

MATERIAL EXAMINED. — One isolated left p3 (FRA11) of black colour.

LOCALITY. — Frunzovka-1 (Odessa province, Ukraine); Early Pliocene (Ruscinian, MN 14) (Fig. 1).

MEASUREMENTS. — L = 1.73, ccd = 0.11, anteroconid (L = 1.11, W = 0.74), posteroconid (L = 1.00, W = 1.85).

DESCRIPTION

Among the studied ochotonids from Frunzovka-1, there is one p3 which is strongly different from all specimens under study. The related p3 belongs to a medium-large sized ochotonid. The tooth is unique in its long and markedly narrow anteroconid with cement free depressions on its anterior sides. Together with short and wide posteroconid, they form a distinctly triangular appearance of the occlusal outline. The proto- and paraflexid are oriented notably posteriorly; the latter is slightly longer and more curved.

COMPARISON

The specimen under study differs from all the above mentioned taxa in its distinctly narrower p3 anteroconid, and in its para- and protoflexid development. The specimen is smaller than *Bellatonoides kalfense*, *Pliolagomys* species, and *Ochotona eximia*; at the same time, it is larger than *Pseudobellatona relicta*, *Ochotonoma* species, *Ochotona antiqua*, *O. pseudopusilla*, *O. ursui*, and Villányian-Biharian species of *Ochotona* known from Central Europe (see above for the measurements).

It might well be that this individual represents a new species of *Ochotona*. However, the intraspecific variability of p3 in *O. antiqua* is high. Therefore, based on one distinct p3 only, the above mentioned differences may represent an unusual morphologic variation of *O. antiqua*'s p3. In any case, the lack of additional p3s does not allow us to a new species assignment here, thus we assign this p3 tentatively to *Ochotona* sp. 1.

Genus *Pseudobellatona*
Topachevsky, Nesin & Topachevsky, 1993

TYPE SPECIES. — *Pseudobellatona relicta* Topachevsky, Nesin & Topachevsky, 1993 by original designation.

Pseudobellatona relicta Topachevsky, Nesin & Topachevsky, 1993 (Fig. 2S)

MATERIAL EXAMINED. — One isolated left p3 (No. 37-2542) of brownish colour (the holotype and only known specimen).

LOCALITY. — Krasnopol (Odessa province, Ukraine); Early Pliocene (Ruscinian, MN 14) (Fig. 1).

EMENDED MEASUREMENTS. — L × W of p3 is 1.56 × 1.69 (measurements of the specimen taken by the authors) compared with 1.65 × 1.90 after Topachevsky *et al*. (1993).

REDESCRIPTION

The only available hypselodont p3, without traits of conical structure, belongs to a medium-large sized ochotonid. The occlusal surface is wider than long, it is cut by proto- and hypoflexids; the paraflexid is absent – only a slight depression is visible on its anterolingual enamel wall. The top of the anteroconid is sharp and buccally moved. The protoflexid is long, narrow, and curved posteriorly; it reaches the longitudinal axis of the tooth. The hypoflexid is also narrow; it penetrates lingually half of the posteroconid width; in its distal part it is bent anteriorly.

COMPARISON AND REMARKS

In its general occlusal pattern, the tooth is somewhat similar to some advanced (non rooted) representatives of Sinolagomyinae, particularly to the Early-Middle Miocene species of the genus *Bellatona* Dawson, 1961 known from Central and Eastern Asia (Dawson 1961; Erbajeva 1988; Zhou 1988; Qiu 1996). Nevertheless, the studied p3 sharply differs from them in its much longer and cemented protoflexid. The other p3 features (i.e. long and narrow hypoflexid, anteroconid with concave enamel walls and sharp tops) are much more developed and indicate a more advanced degree of evolution typical rather

for the Pliocene species of Ochotoninae than for the Miocene clades of Sinolagomyinae.

In its buccaly situated anteroconid and little developed paraflexid, the specimen from Krasnopol also resembles *Bellatonoides eroli* Sen, 2003 known from the Early Vallesian (MN 9) localities 8A and 120 of the Sinap Tepe area (Turkey) and *B. kalfense* known from the Vallesian (MN 9 or 10) locality Kalfa (see above for details). The former species of *Bellatonoides* differs from the specimen under study in its more developed paraflexid (in two specimens filled with cement, N = 6, loc. 8A of the Sinap Tepe) and in its rounded anteroconid (in two specimens its outline is rather triangular, N = 9, loc. 8A and 120 of the Sinap Tepe). The latter species, *B. kalfense*, differs from the Krasnopol ochotonid (in addition to above mentioned characters for *Bellatonoides* from Turkey) in its notably larger size (L of p3 is 1.65-2.15 *sensu* Lungu 1981).

Among the relevant *Ochotona* species, the studied specimen is the most similar to *O. antiqua*; particularly in its size and anterior morphology of anteroconid. Nevertheless, it distinctively differs from this species in lacking the paraflexid of p3.

Most of the above discussed characteristics fit with those of the ochotonids, although based on the available material, the evaluation of their actual meaning is very difficult. In our opinion, this specimen cannot be attributed to *Hypolagus* (compare with Averianov 1998) because of its much smaller size, its much longer and narrower protoflexid (some extreme p3 morphotypes of *Hypolagus* from the Biharian of the Czech Republic possess similarly developed protoflexid; Čermák unpublished data), and its different morphology of the buccal part of hypoconid (compare with Dawson 1958; Averianov 1996; Fladerer & Reiner 1996; Fladerer & Fiore 2003). It is probable that this only available p3 from Krasnopol belongs to an aberrant individual of *O. antiqua*. In any case, its more precise taxonomic determination is still impossible.

In conclusion, based on the available combination of the all above discussed characters in the only available (type) specimen, it is not possible to unequivocally discriminate it from all other ochotonid genera/species and to attribute it to any taxonomic level lower than Ochotonidae clade *sensu* Sen (2003). Thus, we assign herein taxon *Pseudobellatona relicta* as *incertae sedis* within Ochotonidae clade *sensu* Sen (2003).

DISCUSSION AND CONCLUSIONS

A detailed revision of the complete ochotonid material available from all known Early Pliocene (Early Ruscinian, MN 14) localities of the Kuchurganian sedimentary series is beyond the scope of this paper. Here, we focused on a detailed analysis of the new material of *Ochotona antiqua* from Novopetrovka and Frunzovla-1. We re-analysed the state and variation of diagnostic characters in the species, including the outlying and/or aberrant forms. We provide a redescription of the Early Pliocene ochotonids from the Kuchurganian sedimentary series, including their type material, and propose hypotheses on their systematic relationship within the context of the recent knowledge on the Eurasian ochotonids.

Based on the present analyses, respecting also the recent literary sources (Argyropulo & Pidoplichko 1939; Gureev 1964; Agadjanian & Erbajeva 1983; Erbajeva 1988, 1994; Erbajeva & Shushpanov 1988; Averianov & Tesakov 1998), the taxonomic concept of *Ochotona antiqua* as a separate species from the Early Ruscinian (MN 14) of southeastern Europe is supported in this paper. However, some remarks on the medium sized Early Pliocene taxa are necessary.

As mentioned above, the taxonomic status of the poorly known *O. pseudopusilla*, confined to the type locality Ukrainskiy Trostyanec (Early Ruscinian, MN 14), cannot be solved. This species is poorly described, its type material is not available, and the type locality did not yield any additional relevant material. To date, available material of *O. ursui* from the type locality Maluşteni (late Ruscinian, MN 15a) does not allow us a closer comparison with *O. antiqua*, so it is difficult to evaluate the actual meaning of the above mentioned differences between these species (see "Comparisons" for details). Therefore, their definite taxonomic relation cannot be solved and we tend to express here only the tentative hypotheses on that matter: a) *O. antiqua* and *O. ursui* are either two different species

(the eventuality that the nominal taxon of *O. ursui* represents a sub-adult individual of *Pliolagomys* is also possible of course), or b) nominal taxa of *O. antiqua* and *O. ursui* represent one species. At any rate, until further relevant material is available, we tentatively suggest to retain *O. pseudopusilla* and *O. ursui* as two separate species.

After studying the significant sample of the new material of *O. antiqua*, the characterizing features of this species are quite well expressed and essentially complete. Nevertheless, to which degree such features are taxonomically significant or, in other words, which were actual patterns of variation in the outlying and/or aberrant fossil forms, it remains a task of further research. Without detailed information on this matter and, particularly, without an additional fossil material it seems quite premature to discuss on species content and/or phylogenetic interrelationships within this group of the medium sized ochotonids.

In conclusion, the following results can be inferred and briefly summarized from the above surveyed facts:

1) The Early Ruscinian (MN 14) species *Ochotona antiqua* is characterized by the combination of discriminant features that include: a) the medium size (see Tables 1; 2); b) the large and wide p3 anteroconid, generally with a simple morphology; c) the narrow symmetrically placed anteroconid-posteroconid junction of p3; and d) the rather long and slight mandibular ramus (see Figs 1; 2).

2) The analysis of morphotype frequencies reveals high variability of p3 (see above for details), manifesting itself mainly in morphology of the anteroconid a) with convex or concave anterior enamel walls, without well-developed grooves or even flexids, in more than 90% of cases; b) with the almost equal ratio of the symmetrically to asymmetrically placed tops; and c) paraflexid with the mean angle of deflection from the longitudinal axis of p3 at 59°.

3) The frequency of the p3 anteroconids with cemented and/or non-cemented reentrant folds is significantly lower in *O. antiqua* than those in taxa of *Pliolagomys*, *Ochotonoma*, and *Ochotonoides* (compare e.g., with Agadjanian & Erbajeva 1983 and Čermák 2007). The variation of this anteroconid pattern, together with the above features (1a-c) can be used as a discriminant criterion for this Ruscinian species of *Ochotona*.

4) The peculiar forms from the Ruscinian localities Frunzovka-1 and Krasnopol are tentatively regarded here as outlying and aberrant forms, respectively, probably related to *Ochotona antiqua*; their identification as *Ochotona* sp. 1 and *Pseudobellatona relicta* Topachevsky, Nesin & Topachevsky, 1993 – a taxon *incertae sedis* within Ochotonidae clade *sensu* Sen (2003) proposed in this paper is a provisional solution, and it remains a task of further research.

Acknowledgements

The authors wish to express their warmest thanks to Dr Yuriy Semenov, Dr Dmitry Ivanoff, and Dr Valentin Nesin (all from Natural History Museum, Kiev) for access to study the ochotonid material under their care and for numerous valuable suggestions and assistance. We wish to convey our sincere thanks to Prof. Oldřich Fejfar, Prof. Ivan Horáček (both from Charles University, Prague), and MSc. Jan Wagner (Academy of Sciences of the Czech Republic, Prague) for inspiring discussion and valuable suggestions on the manuscript. The authors are indebted to Dr Burkart Engesser (Natural History Museum, Basel), Prof. László Kordos (Geological Institute of Hungary (MÁFI), Budapest), and Dr Alexander Averianov (Zoological Institute RAN, Saint Petersburg) who kindly enabled us to study the comparative material under their care. Our gratitude also goes to Dr Margarita Erbajeva (Geological Institute, Ulan-Ude) for providing us with important information. We are also very grateful to the referees Prof. Sevket Sen (Muséum national d'Histoire naturelle, Paris) and Prof. Zhuding Qiu (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) for their critical reading and helpful comments on the manuscript. Last but not least, we owe the French translation of the abstract to Dr Loïc Costeur (Natural History Museum, Basel). The study was supported by the Academic Project of the Institute of Geology in Prague No. AV0Z30130516, and by grants from the Grant Agency of the Czech Republic No. 205/09/0184 and from the Grant Agency of the Academy of Sciences of the Czech Republic No. GAAVČR IAA300130701.

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Submitted on 5 March 2008;
accepted on 18 December 2008.