New ochotonids (Lagomorpha) from the Pleistocene of France

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ABSTRACT
The mammalian fauna of insectivores, rodents and lagomorphs found at Les Valerots (Nuits-Saint-Georges, Côte-d'Or) dated as early Pleistocene based on the association of *Hypolagus* Dice, 1917, *Mimomys savini* Hinton, 1926, *Allophaiomys* Kormos, 1932 and *Dicrostonyx* Gloger, 1841 includes only two species of lagomorphs belonging to the families Leporidae and Ochotonidae. Examination of the ochotonid remains shows that the pika from the Les Valerots site is a new taxon, *Ochotona valerotae* n. sp. Study of the representative fossil material of *Ochotona pusilla* Pallas, 1768 found at the localities of La Fage (Corrèze) and of Baume de Gigny (Jura) in France reveals that the small late Pleistocene pika can be described as a new subspecies of *Ochotona pusilla*: *Ochotona pusilla occidentalis* n. ssp. The history of *Ochotona pusilla* in Eurasia is reviewed.

KEY WORDS
Mammalia,
Lagomorpha,
Ochotonidae,
Pleistocene,
France,
new species,
new subspecies.

RÉSUMÉ
Nouveaux ochotonidés (Lagomorpha) du Pléistocène de France.
La faune d'insectivores, rongeurs et lagomorphes de l'aven des Valerots à Nuits-Saint-Georges (Côte-d'Or) datée du Pléistocène inférieur sur la base de l'association de *Hypolagus* Dice, 1917, *Mimomys savini* Hinton, 1926, *Allophaiomys* Kormos, 1932 et *Dicrostonyx* Gloger, 1841 contient seulement deux espèces de lagomorphes appartenant aux Leporidae et aux Ochotonidae. L'étude des Ochotonidae montre que le pika des Valerots correspond à une nouvelle espèce, *Ochotona valerotae* n. sp. L'analyse du matériel quaternaire d'*Ochotona pusilla* Pallas, 1768 de La Fage (Corrèze) et de la Baume de Gigny (Jura) en France montre que le petit pika du Pléistocène supérieur peut être considéré comme une sous-espèce (*Ochotona pusilla occidentalis* n. ssp) de la forme eurasiatique *Ochotona pusilla* dont l'histoire est révisée à cette occasion.

MOTS CLÉS
Mammalia,
Lagomorpha,
Ochotonidae,
Pléistocène,
France,
nouvelle espèce,
nouvelle sous-espèce.

INTRODUCTION

Excavations at more than two hundred Pleistocene sites in France which have yielded associations of rodents (Chaline 1972a, 1987) have also allowed the collection of lagomorph, ochotonid and leporid remains.
This paper is a systematic revision of the Pleistocene Ochotonidae in Europe and Asia and describes a new species and a new subspecies.
The terminology used here to describe tooth structures is that in Erbajeva (1988: fig. 1). The terms "conid", "anteroconid" and "posteroconid" are used for p3 and "talonid" and "trigonid" for p4, m1 and m2. The posteroconid of p3 consists of a paraconid, protoconid, entoconid and hypoconid with inner folds (flexids). They are collectively termed the posteroconid.
External dimensions of teeth are measured on the occlusal surface from enamel to enamel and the maximum lengths and widths are given in millimetres.

ABBREVIATIONS USED

P/p	premolars, upper cheek-teeth;
M/m	molars, lower cheek-teeth;
Val	the Valerot locality;
F	the La Fage locality;
G	the Gigny site.

LOWER PLEISTOCENE OCHOTONIDS

The Les Valerots karst filling at Nuits-Saint-Georges (Côte-d'Or) provides a record of lower Pleistocene climatic fluctuations (Chaline *et al.* 1985). Three stages have been recognized:
– les Valerots 1: speleothem;
– les Valerots 2: breccia with fauna characteristic of cold climates;
– les Valerots 3: stratified silt-clay beds with thermophilous, moisture-seeking flora (with *Ostrya*).
Les Valerots level 2 has yielded a rich fauna of mammals with:
– rodents (Chaline 1969, 1972a; Laplana *et al.* 2000): *Citellus* sp., *Glis minor*, *Eliomys intermedius*, *Glirulus pusillus*, *Cricetus cricetus*, *Sicista praeloriger*, *Mimomys savini*, *Mimomys blanci*, *Pliomys episcopalis*, *Pliomys lenki*, *Ungaromys nanus*, *Allophaiomys nutiensis*, *Microtus burgondiae*, *Allophaiomys valerotensis*, *Dicrostonyx antiquitatis*, *Apodemus sylvaticus*.
Two of these species are intriguing. *Dicrostonyx antiquitatis* is very similar although not identical to *Predicrostonyx hopkinsi* from Cape Deceit (Alaska) described by Guthrie & Mathews (1971), and yet no identical fossil is known from any intermediate site in Europe or Asia. Similarly *Glirulus pusillus* is a common lower Pleistocene fossil in western Europe and survives as an isolated relic in Japan!;

– insectivores (Jammot 1977): *Desmana* sp., *Talpa* cf. *caeca*, *Talpa* cf. *europaea*, *Beremendia fissidens*, *Blarinoides chalinei*, *Drepanosorex margaritodon*, *Sorex savini*, *Sorex runtonensis*, *Sorex minutus*, *Soriculus* sp.;
– carnivores: *Ursus* cf. *deningeri* (after Cordier), *Mustela* sp.;
– perissodactyls: *Dicerorhinus* cf. *etruscus* (after C. Guerin).
Level 2 also contains an amphibian, *Rana* cf. *esculenta* (after J.-C. Rage), and birds: *Falco tinnunculus atavus*, *Lagopus lagopus*, cf. *Alauda arvensis*, cf. *Turdus viscivorus*, *Corvus* cf. *antecorax* (after C. Mourer).
This faunal association can be dated to the Bavelian or the Linge cold phase of Zagwijn and De Jong (Zagwijn & De Jong 1984; Chaline *et al.* 1985).
Of the small mammal fauna, insectivores and rodents predominate while lagomorphs are scarce, which is characteristic of the late Pliocene-early Pleistocene faunas of Europe.
A few taxa of the genus *Ochotona* Link, 1795 of that time are known in Europe: *Ochotona polonica* Sych (Sych 1980) from Poland, *Ochotona* sp. (near to *Ochotona pusilla* Pallas, 1768) from Schernfeld (Germany) (Dehm 1962), *Ochotona* sp. from Maritsa 1 (Greece) (De Bruijn *et al.* 1970) and Püspökfürdö, Beremend, Brasso (Hungary) (Kretzoi 1938).
The species found at Les Valerots is different from these and should be described as a new taxon of small pika for which we propose the name *Ochotona valerotae* n. sp.

SYSTEMATICS

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

Ochotona valerotae n. sp.
(Figs 1; 2; Table 1)

HOLOTYPE. — Left mandibular ramus with p3-m3, without incisor, angular process and condyle, University of Burgundy (Val-8226) (Figs 1A-D; 2).

TYPE LOCALITY. — Les Valerots, level 2, Côte-d'Or, France.

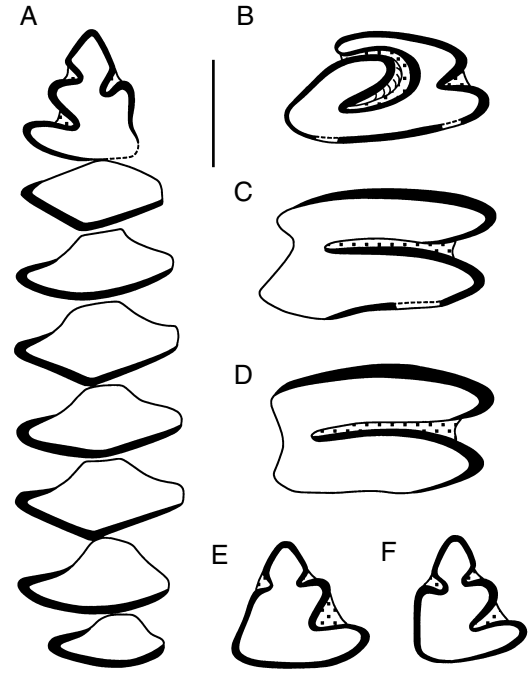

FIG. 1. — Ochotonid tooth structure (occlusal view); **A**-**D**, *Ochotona valerotae* n. sp.; **A**, p3-m3 sin. (Val-8226); **B**, P3 dex (Val-8014); **C**, P4 dex (Val-8013a); **D**, M1 dex (Val-8013b); **E**, *Ochotona pusilla angustifrons* Argyropulo, p3 dex; **F**, *Ochotona* sp., p3 dex (Chembakchino, western Siberia). Scale bar: 1 mm.

ETYMOLOGY. — *valerotae*: found in the Les Valerots karst filling, Côte-d'Or, France.

HYPODIGM. — In addition to holotype: 1 fragment of right mandibular ramus with m1-m3 (Val-8013); 1 fragment of right maxilla with P3 (Val-8014); isolated teeth dex: P4-1 and M1-1 (Val-8013a,b).

HORIZON, LOCALITY AND GEOLOGICAL AGE. — Les Valerots, breccia, level 2, lower Pleistocene, Bavelian age.

DIAGNOSIS. — A small ochotonid. The occlusal surface of p3 is triangular (Fig. 1A), pm3 is distinctly longer than it is wide (length 1.2, width 1.1), its anteroconid is relatively narrow and elongate with a rather sharp anterior margin; the posteroconid is wide, having a straightened lingual margin with a shallow, cement-free groove. The confluence between the anteroconid and posteroconid of this tooth is smaller (Table 1). The alveolar length of the lower cheek teeth (p3-m3) is 7.2.

DIFFERENTIAL DIAGNOSIS. — A relatively small ochotonid similar to the pikas of the "*pusilla*" group. It differs from all fossil taxa of *Ochotona pusilla* in its p3

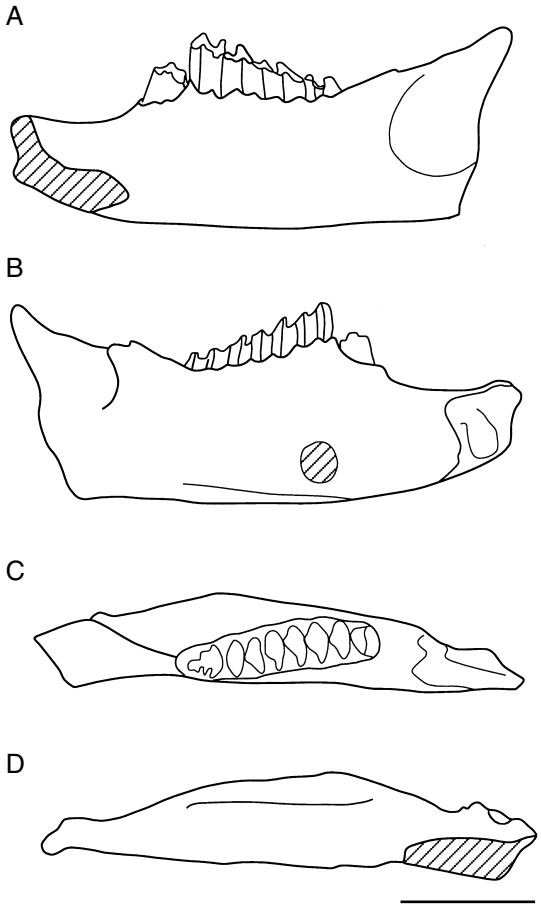

FIG. 2. — *Ochotona valerotae* n. sp., mandible dex (Val-8226), incomplete mandible views; **A**, labial view; **B**, lingual view; **C**, occlusal surface; **D**, under side. Scale bar: 5 mm.

structure: in its elongate anteroconid and narrower posteroconid than in all extinct pikas of the "*pusilla*" group. It differs from extant *Ochotona pusilla* in its distinctively small size, in its somewhat shorter and mandibular ramus and in its p3 structure being slightly longer and narrower than the p3 of *Ochotona pusilla*. *Ochotona valerotae* n. sp. differs from all European pikas: from *Ochotona polonica* Sych, 1980 (Zamkowa Dolna, Poland) and *Ochotona* sp. from Maritsa (Greece) in the smaller p3 and in its narrower and elongate anteroconid which has a small confluence with the posteroconid in contrast to those of the above-mentioned pikas (Table 1).

MORPHOLOGICAL DESCRIPTION

The studied specimens are housed in the collections of the University of Burgundy, UMR CNRS BIOGEOSCIENCES 5561. The mandibular ramus is low and rather robust while the diastema is short (Table 1). The lower incisor extends posteriorly along the ventral border approximately in a line below p4 with a rather well-developed tubercle on the lingual side of the mandibular ramus at the root end of the incisor (Fig. 2A, B). The outer surface of lower jaw is flattened. Almost all of the teeth are well-preserved in the specimens. The first lower premolar (p3) has a relatively large anteroconid with the antero-internal side being longer than the antero-external one; its postero-internal and postero-external sides are of the same length (Fig. 1A). It has two persistent external folds and one internal fold (flexids). The latter is directed towards the longitudinal axis of the tooth and turned backward (posteriorly). The lower molariform teeth are similar in shape to those of all *Ochotona* species. P4 is shorter than m1 and m2. Its trigonid is narrower than the talonid. However m1 and m2 have different proportions: their trigonids are distinctly wider than the talonids. m3 consists of a single narrow column. The enamel of p4-m3 is thicker on the outer and on the posterior walls of the trigonids and talonids.

The occlusal outline of P3 is trapezoidal. It is about two thirds narrower anteriorly than posteriorly (Fig. 1B; Table 1). Its deep, cement-filled, antero-labial fold begins and end at almost the same level of tooth width. The hypostria is short and filled with thin cement. P4 and M1 are similar in shape, the enamel is thicker on the anterior and outer walls of the teeth. Their hypostriae are deep but are not distinguishable on the outer margin of the tooth (Fig. 1C, D).

COMPARISONS

The size and general structures of the teeth and mandibles allow us to compare *Ochotona valerotae* n. sp. with all small extant species of *Ochotona* and with extinct pikas from Europe and Asia. *Ochotona valerotae* n. sp. is slightly larger than extant *Ochotona hyperborea* Pallas, 1811 (all small subspecies), as well as *Ochotona thomasi* and different species of the "*thibetana*" group: alveolar and coronar lengths of p3-m3 of *Ochotona*

TABLE 1. — Measurements of *Ochotona* mandibles and teeth.

Feature measured	*O. valerotae* n. sp. n = 2		*O. pusilla* (Extant) n = 25		*O. polonica* (Zamkowa-Dolna) n = 5		*O.* sp. (Maritsa)
	x	lim	x	lim	x	lim	
Diastema length	4.2		4.7	4.1-5.4	4.3	3.7-4.8	
Mandible width at p4	3.1	3.0-3.2	3.5	3.2-3.8			
Mandible height at p4	4.4		4.8	4.7-5.0	4.6	4.3-4.8	
p3: total length	1.2		1.0	0.95-1.2	1.43		1.3
Anteroconid length	0.6		0.4	0.3-0.5			
Anteroconid width	0.54		0.4	0.35-0.6			
Posteroconid length	0.7		0.67	0.6-0.75			
Posteroconid width	1.1		1.25	1.0-1.5	1.27		1.2
Conid confluence distance	0.15		0.25	0.2-0.3			
p3: length	1.0		1.09	0.95-1.25			
p3: width	1.9		2.15	1.65-2.5			

valerotae n. sp. are respectively 7.2 and 6.5 compared with 7.0 and 6.0 (mean value) for *Ochotona hyperborea hyperborea* from Kolyma (Russia), 6.4 and 5.6 for *Ochotona thibetana* Milne-Edwards, 1871, and 6.3 and 5.6 for *Ochotona thomasi* Argyropoulo, 1948. The new taxon described here differs from the species referred to above in its rather robust lower jaw and its slightly narrower p3 anteroconid, of which the average length and width are respectively 0.6×0.65 for *O. hyperborea*; 0.6×0.57 for *O. thomasi*; 0.65×0.6 for *O. thibetana* and 0.6×0.54 for *Ochotona valerotae* n. sp. Moreover, *O. thibetana* and *O. thomasi* are characterized by the anteroconid of p3 being completely separated from the posteroconid. As a rule *O. hyperborea* has a p3 with almost completely separated antero- and posteroconids, but some specimens from Kamchatka, the extreme East of Russia, have p3 teeth with wide confluences between these conids.

The mandibular rami of the extant species mentioned above are slighter than that of *Ochotona* from Les Valerots: average mandibular width and height at p4 are 3.2 and 4.4 for *Ochotona valerotae* n. sp.; 3.0 and 4.3 for *O. hyperborea*; 2.1 and 3.6 for *O. thomasi*; 2.3 and 3.9 for *O. thibetana*. The other recent species of *Ochotona*, known mainly from Asia, are much larger than the Les Valerots pika.

Ochotona valerotae n. sp. more closely resembles *Ochotona pusilla* in its small size and in having wide confluences between the anteroconid and posteroconid of p3. However it is distinguished from extant *Ochotona pusilla* in its smaller size, its mandibular ramus and its p3 structures (Table 1; Fig. 1A). p3 of *Ochotona pusilla* is characterized by a small anteroconid and wide posteroconid, the internal margin of the latter sloping backwards and outwards. The occlusal outline of this tooth is trapezoidal, its antero-internal and antero-external folds are not as deep as those of *Ochotona valerotae* n. sp (Fig. 1E).

All extinct taxa of *Ochotona pusilla* and of *Ochotona* near to *Ochotona pusilla* differ from *Ochotona valerotae* n. sp. in the structure of p3 having a wide confluence between anteroconid and posteroconid as well as in the wider posteroconid. *Ochotona* from Les Valerots is almost the same size as *Ochotona* sp. from Schernfeld in Germany (Dehm 1962), which was defined as a pika near to *Ochotona pusilla*. The latter is poorly documented, no figures of teeth are given, and it is impossible to compare it with pika from France. *Ochotona valerotae* n. sp. differs from the small pika of Emirkaya (Turkey) (Montuire *et al.* 1994) in its large anteroconid and in the narrower posteroconid of p3. The pika from the Les Valerots site differs from *Ochotona polonica* known from the Zamkowa Dolna locality both

in its smaller size and the persistent confluence of the anteroconid and posteroconid of p3. Moreover, the p3 anteroconid of *Ochotona polonica* is rhombus-shaped which is quite different from the p3 of *Ochotona valerotae* n. sp. The rhombus feature is characteristic of the p3 of the pika from the Maritsa 1 locality. These latter two localities are geologically older than the Les Valerots site. The p3 structure of *Ochotona valerotae* n. sp. resembles the p3 of *Ochotona* sp. from the Chembakchino locality in Western Siberia and is probably of the same geological age. According to Smirnov *et al*. (1986), the Chembakchino locality contains small mammalian fauna similar to the fauna from Les Valerots. However, pikas from these two localities differ slightly in having another type of p3. The West Siberian pika differs from the Les Valerots species in that its p3 has narrower confluences between its anteroconid and posteroconid, as well as in having a slightly smaller anteroconid on this tooth (Fig. 1F).

Systematic remarks

The small ochotonid from the Les Valerots karst filling at Nuits-Saint-Georges, Côte-d'Or, differs from all extant and extinct pikas of the world in the morphological peculiarities of its lower third premolar and in its mandible ramus structures and its size. The morphological features given above in the diagnosis and in the comparative sections allow us to represent the new taxon of small pika – *Ochotona valerotae* n. sp. It is characterized by apomorphic characters: small size; shorter confluences than *Ochotona pusilla* between the anteroconid and posteroconid of p3 (Table 1); straight inner margin of the posteroconid of p3. The following features are plesiomorphic: elongate anteroconid and posteroconid; rather deep antero-external and antero-internal folds on p3; presence of enamel on the inner and posterior walls of trigonids and talonids of p4-m2.

The phylogeny and relationships of small Eurasian ochotonids are still unclearly known because of the paucity of data on fossil taxa. From analysis of the morphology of fossil taxa from Europe and Asia, the main evolutionary trend of ochotonids can be characterized as an increase in size, development of different types of p3 anteroconid and considerable variability in the p3 anteroconid and posteroconid confluence.

On the strength of the related morphological characters mentioned above, it may be suggested that *Ochotona valerotae* n. sp., *Ochotona* sp. from Chembakchino (western Siberia) and ancient fossil taxa of *Ochotona pusilla* could be derived from the ancestral form distributed in Asia at the end of the Pliocene, and it may be assumed that the ancestors of these species bore greater resemblance to pikas from Les Valerots and Chembakchino.

Middle and late Pleistocene *Ochotona pusilla*

Fossil remains of *Ochotona pusilla* Pallas are quite well known in France (Chaline 1969, 1972). The first information about this species arose in the last century when Desnoyers (1842) described a small mammalian fauna from Montmorency including *Ochotona pusilla* and *Lemmus lemmus*. Excavations by archaeologists in the localities of La Fage (upper middle Pleistocene) and Baume de Gigny (Upper Pleistocene) in the last decades have yielded a large number of well-preserved, small mammal remains (Chaline & Brochet 1989) including numerous fossil remnants of ochotonids.

The La Fage karst filling

The La Fage karst filling near Noailles (Corrèze) has yielded a very rich mammal fauna:

– rhinoceroses and proboscideans (Guérin 1973; Beden & Guérin 1975): *Coelodonta antiquitatis*, *Dicerorhinus hemitoechus*, *Dicerorhinus mercki*, *Mammuthus* aff. *Trogontherii*;

– deer, cattle, goats, mountain goats, pigs and horses (Bouchud 1972): *Cervus* cf. *elaphus*, *Dama* cf. *clactoniana*, *Capreolus capreolus*, *Rangifer* sp., *Megaceros giganteus*, *Equus* cf. *steinheimensis*, *Bison* cf. *shoetensacki*, *Sus scrofa*, *Capra ibex*, *Rupicapra rupicapra*;

– carnivores (Ballésio 1975; Bonifay 1975; Hugueney 1975; Martin 1975): *Canis lupus*, *Vulpes vulpes*, *Ursus deningeri*, *Mustela nivalis*,

Mustela erminea, *Meles meles*, *Gulo gulo*, *Mustela (Putorius) eversmanni*, *Panthera (Leo) spelaea*;
– insectivores (Jammot 1973): *Erinaceus davidi*, *Talpa* cf. *europaea*, *Sorex kennardi*, *Sorex minutus*, *Neomys fodiens*, *Crocidura zorzii*, *Crocidura* sp., *Macroneomys* cf. *brachygnathus*;
- bats (Mein 1975): *Myotis bechsteini*, *Myotis myotis*, *Plecotus auritus*;
– rodents (Chaline 1972b): *Citellus major*, *Marmota marmota mesostyla*, *Eliomys quercinus*, *Glis glis*, *Allocricetus bursae correzensis*, *Microtus arvalis-agrestis*, *Microtus gregalis martelensis*, *Microtus malei noaillensis*, *Terricola subterraneus*, *Arvicola terrestris*, *Clethrionomys glareolus*, *Dicrostonyx torquatus*, *Lemmus lemmus*, *Pliomys lenki*, *Apodemus sylvaticus*;
– hares and rabbits (Petter 1973; Chaline 1975a, b): *Lepus capensis*, *Oryctolagus cuniculus*, *Ochotona pusilla*.
To these must be added amphibians, reptiles (Rage 1972) and 104 species of birds (Mourer-Chauviré 1975). The stratigraphy was resumed by Debard (1973).

Gigny cave

The Gigny site is located on a limestone plateau on the western side of the Jura range (France). The Würm glaciation halted some 10 km East of Gigny. Throughout the glacial cycle, the Gigny site was subjected to a highly disruptive periglacial environment (Campy 1982; Campy *et al.* 1989; Campy & Chaline 1993).

The Gigny sequence

Excavation of the Gigny cave filling yielded a 28-level stratigraphic record, divided into five sedimentary units (Campy *et al.* 1989, 1990; Campy & Chaline 1993).
The site has been the focus of much research into stratigraphy, chronology, palaeontology and archaeology. The sequence has yielded plentiful fossil remains: 69 species of birds (Mourer-Chauviré 1989); large mammals – 15 species of carnivores, 12 species of artiodactyls, two species of perissodactyls, one species of proboscidian – and micromammals – two species of lagomorphs, seven species of insectivores (Jammot 1989) and 12 species of rodents (Chaline & Brochet 1989; Brunet-Lecomte *et al.* 1994).

Ochotona pusilla occidentalis n. ssp.
(Figs 3; 4A-H, Q)

Holotype. — Right mandibular ramus with p3-m3, with incisor, without angular process and condyle, University of Burgundy (F-3414) (Figs 3; 4A).

Type locality. — La Fage, level 4, Corrèze, France.

Etymology. — *occidentalis*: found in France, western Europe.

Hypodigm. — In addition to the holotype, a large number of specimens are known: 1) La Fage (Corrèze): 1 fragment of dex mandible with p4-m3 (F-3414bis); 1 fragment of sin mandible with p3-m3 without incisor, angular process and condyle (F-3444); 1 fragment without teeth (F-3444a); 5 fragments of mandible in various conditions with teeth and without teeth (F-3444bis); 3 fragments of mandible without teeth (F-3001, F-3001a, F-3001bis); 2 fragments of dex mandible with p4-m2 (F-1244, F-1244a); 1 fragment of sin mandible with p3-m3 (F-4862) and 1 fragment of dex mandible with p4-m3 (F-4862a); 3 fragments of maxilla with various teeth (F-4862bis).
2) Baume de Gigny or Loisia cave (Jura): 1 fragment of dex mandible with p3-m3 with incisor, without angular process and condyle (G-61000); dex mandibles with various teeth (G-61002-61008); dex mandibles without teeth (G-61009-61016); sin mandibles with various teeth (G-61017-61020); sin mandibles without teeth (G-61021-61023); fragments of maxilla dex with various teeth (G-61024-61025); fragments of maxilla sin with various teeth and without teeth (G-61026-61032); isolated teeth: p3 (G-61001); p4 (G-61033-61047); m1 (G-61048-61051); m2 (G-61052-61061); m3 (G-61062-61066); P3 (G-61067-61081); P4 (G-61082-61101); M1 (G-61102-61123); M2 (G-61124-61135); upper incisors (G-61136-61162); lower incisor (G-61163); fragments of postcranial skeleton (G-61164-61169).

Horizon, locality and geological age. — La Fage, level 4, middle and late Pleistocene.

Diagnosis. — The mandibular ramus is rather short, comparatively low and robust. P2 is oval, its inner part is flattened anteriorly and the inner-posterior wall of the tooth is rounded.

Differential diagnosis. — A small sized pika of the "*pusilla*" group. It differs from extant *Ochotona pusilla* Pallas in its short mandibular ramus, the mandible being almost the same height as that of the Recent

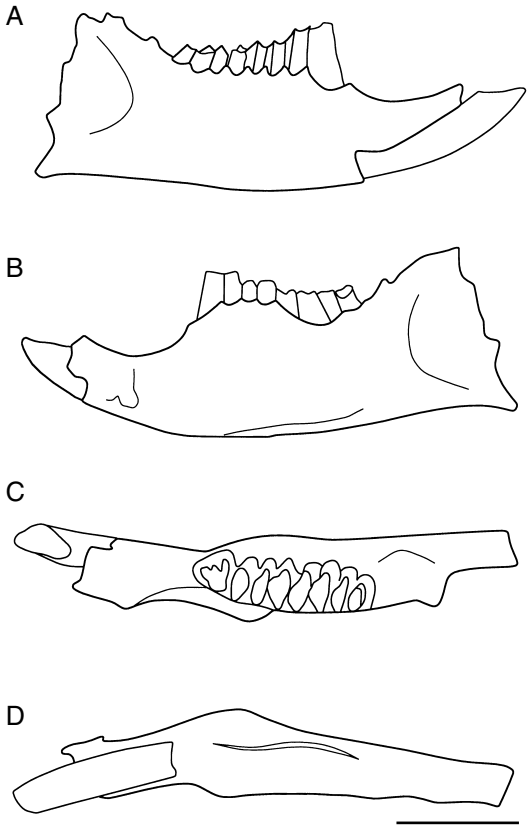

FIG. 3. — *Ochotona pusilla occidentalis* n. ssp., holotype (F-3414), dex mandible with p3-m3; **A**, labial view; **B**, lingual view; **C**, occlusal surface; **D**, under side. Scale bar: 5 mm.

form (Figs 3A; 6A). Moreover, these two ochotonids differ in the slightly smaller size of p3 in the extant pika, in P2 having a shorter anterior fold and in the more rounded shape of the inner-anterior part in *O. p. pusilla* (Fig. 4A-H, N, Q, T). The pika from France differs from the second extant subspecies *O. p. angustifrons* Argyropulo in its smaller size. Average alveolar lengths of P2-M2 and p3-m3 of extinct pika are respectively 7.4 and 7.3 compared with 7.8 and 7.8 for the extant subspecies. They differ also in the distinctively high and narrower mandibular ramus of the latter at p4 (Table 3). *Ochotona pusilla occidentalis* n. ssp. differs from *O. p. angustifrons* in that its P2 has only one anterior fold, the P2 of the latter, apart from a deep anterior fold, having a shallow, cement-free depression on the antero-labial face (Fig. 4V). *Ochotona pusilla* from France differs from all extinct taxa of the "*pusilla*" group in its size: being somewhat smaller than pikas from Emirkaya (Turkey) and from Barakaevo Cave (Russia) (p3 length is equal to or greater than 1.2) and being larger on average than ochotonids from the Aktogai locality (Kazakhstan), and the Malta, Yar and Razdolinskaya localities (eastern Siberia, Russia) (p3 length ranges from 0.9 to 1.05).

REMARKS

More than 200 remains of at least 24 individuals from Gigny and 25 remains of not fewer than six individuals from La Fage can be attributed to a small *Ochotona* species. Considering the number of mandibles, the total material belongs to no fewer than 30 individuals. Judging by the main characters and the proportions of skull remains and mandibles, the ochotonids from the La Fage and Baume de Gigny localities belong to *Ochotona pusilla*. This material allows us to describe their morphology. Closer examination of these extinct small pikas from France and comparison with all known specimens of *Ochotona pusilla* has shown that the small ochotonids from the La Fage and Gigny localities differ from all taxa of the "*pusilla*" group in size and in mandible and tooth morphology (Figs 3; 4A-H, Q; Tables 2; 3).

MORPHOLOGICAL DESCRIPTION

The studied specimens are housed in the collections of the University of Burgundy, UMR CNRS BIOGEOSCIENCES 5561. The mandibles are small and robust at p4, while the diastema is short (Table 3). The lower incisor extends posteriorly along the ventral border of the mandible approximately in a line below p4 with well-developed tubercles on both the lingual and labial sides of the mandibular ramus at the root end of the incisor. A rather deep groove beginning under the inner tubercle extends posteriorly along the ventral border of the mandible approximately to the end of the row of teeth on the lingual side of the mandible (Fig. 3B-D). Almost all of the teeth (upper – P2, P3, P4, M1, M2 – and lower – p3, p4, m1, m2, m3) are preserved in the specimens.

The first lower premolar (p3) of *Ochotona pusilla occidentalis* n. ssp. is triangular, consisting of two conids with a wide confluence. The anteroconid of p3 is comparatively large with a rounded and blunt anterior part in adult individuals and with

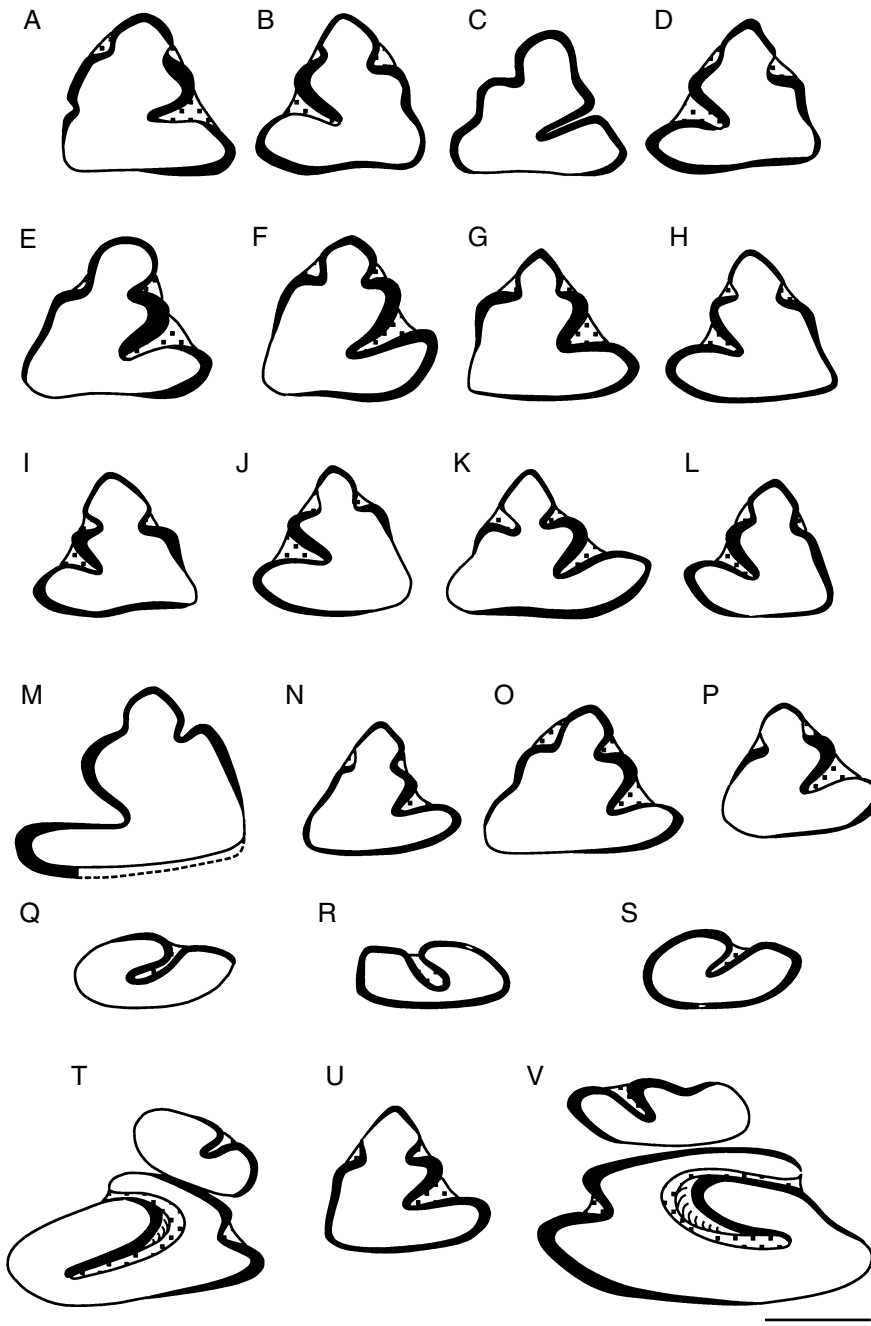

FIG. 4. — Tooth structure of *Ochotona pusilla*; **A**-**H**, p3 of *Ochotona pusilla occidentalis* n. ssp.; **A**, holotype, p3 dex (F-3414); **B**, p3 sin (F-3444); **C**, p3 sin (F-3444), bottom side view; **D**, p3 sin (F-4862); **E**, p3 dex (F-1244); **F**, p3 dex (F-1244a) from La Fage; **G**, p3 dex (G-61000); **H**, p3 sin (G-61001) from Gigny; **I**, p3 sin of *O. pusilla* ssp. from loc. Orgnac 3; **J**, p3 sin of *O. pusilla* ssp. from loc. Yar; **K**, p3 dex of *O. pusilla* ssp. from loc. Malta; **L**, p3 sin of *O. pusilla* ssp. from loc. Piliszantö; **M**, p3 sin of *O. pusilla* ssp. from loc. Emirkaya; **N**, p3 dex of *O. pusilla pusilla*; **O**, p3 dex of *O. pusilla angustifrons*; **P**, p3 dex of *O. pusilla* ssp. from loc. la Baume; **Q**, P2 dex of *O. pusilla pusilla*; **R**, P2 sin of *O. pusilla spelaea*; **S**, P2 dex of *O. pusilla* ssp. from loc. Piliszantö; **T**, P2-P3 dex of *O. pusilla pusilla*; **U**, p3 dex of *O. pusilla spelaea*; **V**, P2-P3 sin of *O. pusilla angustifrons.* Scale bar: 1 mm.

TABLE 2. — Measurements of maxilla and teeth of *Ochotona pusilla* Pallas, 1768.

Feature measured	*O. p. occidentalis* n. sp. (La Fage)			*O. p. spelea* (Kent's Hole, UK)			*O. pusilla* (Recent)		
	n	x	lim	n	x	lim	n	x	lim
Alveolar length P2-M2	7	7.4	7.0-8.0	9	7.6	7.2-8.0	20	7.8	7.5-8.6
Alveolar length P2-M1	9	5.7	5.3-6.2	15	5.7	5.4-6.0	20	6.1	5.8-7.0
Coronar length P3-M1	5	4.3	4.2-4.5	5	4.3	4.0-4.6	20	4.5	4.3-4.8
Coronar length P3-P4	6	2.8	2.6-3.5	5	2.7	2.5-2.9	20	2.7	2.5-2.9
P2: length	2	0.5	0.5	2	0.6	0.6	20	0.6	0.5-0.7
Width	2	1.02	1.0-1.05	2	1.22	1.2-1.25	20	1.3	1.1-1.5
P3: length	5	1.08	1.0-1.2	6	1.08	1.0-1.15	20	1.1	1.0-1.25
Width	5	2.2	2.0-2.5	6	2.3	2.1-2.5	20	2.16	1.8-2.5
M2: length	1	1.5		4	1.46	1.4-1.5	20	1.4	1.2-1.5
Width	1	2.1		4	2.15	1.9-2.3	20	2.2	1.9-2.4

TABLE 3. — Measurements of mandibles and teeth of *Ochotona pusilla* Pallas, 1768.

Feature measured	*O. p. occidentalis* n. sp. (La Fage)			*O. p. spelea* (Kent's Hole, UK)			*O. pusilla* (Recent)		
	n	x	lim	n	x	lim	n	x	lim
Alveolar length p3-m3	24	7.3	7.2-7.8	37	7.8	7.4-8.6	22	7.8	7.2-8.2
Coronar length p3-m3	3	6.65	6.5-6.8	7	6.8	6.4-7.0	22	6.6	6.1-7.2
Coronar length p4-m3	9	5.4	5.2-5.5	20	5.7	5.4-6.2	22	5.5	5.0-6.1
p3: total length	10	1.07	1.0-1.14	12	1.05	1.0-1.1	22	1.06	1.0-1.2
Anteroconid length	10	0.38	0.3-0.5	12	0.37	0.35-0.45	22	0.4	0.3-0.5
Anteroconid width	10	0.4	0.3-0.45	12	0.4	0.35-0.45	22	0.4	0.35-0.6
Posteroconid length	10	0.7	0.6-0.8	12	0.7	0.65-0.8	22	0.67	0.6-0.75
Posteroconid width	10	1.15	1.0-1.2	12	1.15	1.0-1.25	22	1.35	1.1-1.5
Conids confluence distance	10	0.26	0.2-0.3	12	0.3	0.25-0.35	22	0.22	0.15-0.3
Diastema	15	4.4	4.0-4.7	33	4.4	3.8-5.0	22	4.8	4.1-5.4
Mandible height at p3	20	4.2	3.8-4.5	30	4.5	4.0-5.2	22	4.6	4.1-5.7
Mandible height at m2	22	4.7	4.3-5.2	32	5.0	4.6-5.5	22	5.0	4.4-5.7
Mandible width at p4	18	3.8	3.3-4.2	31	3.6	3.2-3.8	22	3.5	2.8-3.8
Mandible width at m2	19	2.8	2.6-3.8	31	2.8	2.5-3.2	22	2.7	2.5-3.1

a rather sharp one in young individuals. Its length and width are almost equal (Table 3). The posteroconid of p3 is about two thirds narrower anteriorly than posteriorly because its lingual side is greatly extended intero-posteriorly (Fig. 4A-H). p3 has two persistant external folds and one internal fold filled with cement. The depth of the antero-external and antero-internal folds varies greatly. The lower molariform teeth are similar in shape to those of other *Ochotona*. The largest of the lower teeth is m1 and the smallest is p4. The talonid of the p4 is wider than the trigonid. The talonids of m1 and m2 are almost as wide or slightly narrower than the trigonid. m3 consists of a single narrow column (Fig. 5B).

The upper teeth, except for P2, do not differ morphologically from the corresponding teeth of all *Ochotona pusilla* taxa. The single-lobed P2 (Fig. 4Q) is oval with a narrow and rather deep, cement-filled anterior fold directed postero-externally. The anterior side of its inner part is flat and its external part is oval. The trapezoidal P3 is flattened, with its anterior part much narrower than the posterior one. Its deep, cement-filled, antero-labial fold begins at a point at one quarter of the tooth width and finishes at approximately

the same level. The hypostria is short and filled with thin cement. P4, M1 and M2 have deep, cement-filled hypostriae. M2 has a posteriorly directed process as in all *Ochotona* species (Fig. 5A).

COMPARISONS

Ochotona pusilla occidentalis n. ssp. differs from all of the taxa of Eurasian *Ochotona pusilla*, particularly from *Ochotona pusilla spelea* Owen, 1846 (Kent's Hole, UK), in that it is either smaller or larger and has different tooth proportions and mandible structures. It differs from extant species and from extinct taxa from the Ukraine (Loc. Novgorod-Severskyi), from Crimea (Loc. Alimovskyi naves and Adji Koba) and from Transcaucasus (Barakaevo Cave, Azyh) in both its small size and its much shorter diastema (Gromov 1961; Rekovets 1985; Erbajeva 1988). The taxon from France is slightly smaller than the forms from the Urals (Medvezhia Cave, Yarsino and Alabuga localities), from Moldavia (Loc. Brinzeny) (Kuzmina 1965; Maleeva & Federyagina 1984; Lozan 1970; Smirnov *et al.* 1986) and from Germany (Obere Franken). However it is as large or slightly larger than the Siberian pika from the Yar locality on the Biryusa River (eastern Siberia), which also has small and low mandibles. *Ochotona pusilla occidentalis* n. ssp. differs from both extant subspecies in having more robust, shorter and mandibles (Figs 3; 6) as well as in its tooth morphology. *Ochotona pusilla pusilla* (Pallas, 1769) possesses a small and narrow P2 and a triangular P3 (Fig. 4T). *Ochotona pusilla angustifrons* Argyropulo (1932) is characterized by a wide P2 and the flattened shape of P3 (Fig. 4V). The pika from France has a wider P2 (Fig. 4Q) than the P2 of *Ochotona pusilla pusilla* and one that is much narrower than the corresponding tooth of *O. p. angustifrons. Ochotona pusilla occidentalis* n. ssp. is characterized by wider confluences between the anteroconid and posteroconid of p3 than in extant species. *Ochotona* from the Gigny and La Fage localities differs from all extinct Eurasian subspecies in its anteroconid shape and by the highly variable depth of the antero-internal and antero-external folds of this tooth. While the extinct pika from the Orgnac-3 locality (France) housed in the Muséum d'Histoire naturelle of Lyon resembles *Ochotona pusilla occidentalis* n. ssp. in p3 morphology and in mandible structure, it differs from the latter in its narrower confluence between antero- and posteroconid and its wider p3 (Fig. 4I).

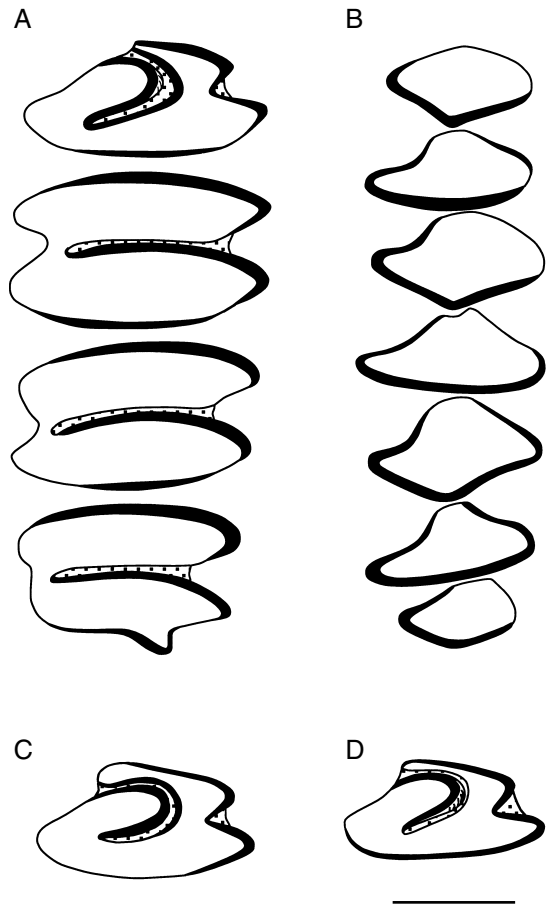

FIG. 5. — *Ochotona pusilla occidentalis* n. ssp.; **A**, P3-M2 dex (G-61024) from Gigny; **B**, p4-m3 sin (G-61017) from Gigny; **C**, P3 dex (F-4862) from La Fage; **D**, *O. pusilla* ssp., P3 dex from loc. Piliszanto. Scale bar: 1 mm.

HISTORY OF STEPPE PIKA

It is known that the history of *Ochotona pusilla* unfolded in western Siberia at least until the end of the late Pliocene – onset of the Pleistocene

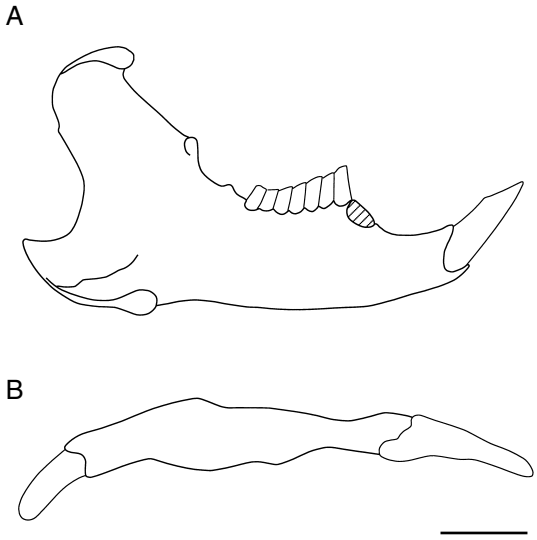

FIG. 6. — *Ochotona pusilla pusilla* (Pallas, 1769), dex mandible with p3-m3; **A**, labial view; **B**, occlusal surface. Scale bar: 5 mm.

(Erbajeva 1988, 1994). Accordingly its ancestors may have evolved in Asia. The first pika belonging to *Ochotona pusilla* appeared in Asia at the end of late Pliocene-beginning of the Pleistocene. It was represented by a primitive subspecies *Ochotona pusilla aktogaiensis* Savinov, 1981 found at the Aktogai locality in Kazakhstan with an associated *Allophaiomys* fauna (Kozhamkulova *et al*. 1981). This fauna suggests a relatively mild climate. The pika similar to this taxon found in western Siberia at the Kizikha locality is of the same geological age. Probably *Ochotona* sp. from the Emirkaya locality (Turkey) associated with *Hypolagus* sp. can be considered as one of the early *Ochotona pusilla* too (Montuire *et al.* 1994). During the middle and late Pleistocene successive glacial and interglacial stages resulted in periodical changes in the palaeoenvironment. With colder and drier climates, steppe became widespread in Eurasia. At that time, vast areas of Eurasia were covered by the characteristic steppe-tundra ecosystem also known as "mammoth steppe". Throughout Pleistocene times, Asia was extensively connected with Europe with no major barriers such as ice-sheets. This evidence makes it clear that Asian steppe faunas such as ochotonids, jerboas and lagurids migrated extensively to Europe. At that time *Ochotona pusilla* radiated widely and diversified considerably. The vast plains of Europe and Asia from southern England and France in the West, from the Negev and Turkey in SW Asia to eastern Siberia in the East were inhabited by *Ochotona pusilla* (Fig. 7). New fossil finds of this species in three Prebaikalian localities (Malta, Yar and Razdolinskaya) allow us to extend its range further East than was known previously when it was thought that the Yenisey River marked the eastern boundary of the distribution area of steppe pika. A number of middle and late Pleistocene subspecies and forms have been recognized within the species *Ochotona pusilla* (Erbajeva 1988). During postglacial time until the Holocene, the more moderate climate was associated with the reestablishment of forest and grassland. This restricted the range of *Ochotona pusilla*. Holocene fossil remains are known from the Crimea, Hungary and even in historical times there are considerable data on the occurrence of *Ochotona pusilla* in SE Europe and the southern Urals. Towards recent times *Ochotona pusilla* seems to have been gradually restricted to its current range in Eurasia. The total recent area includes steppes from the Middle Volga East through North Kazakhstan and the southwestern slopes of the Altai mountains to the border of China (Fig. 7).

CONCLUSION

The 200 Pleistocene sites in France have yielded highly varied ochotonid remains which are described here for the first time. The early Plesitocene ochotonids differ significantly from contemporary forms found in Eurasia. They are described as the new species *Ochotona valerotae* n. sp. from the Les Valerots *Allophaiomys* site (Nuits-Saint-Georges, France) (Laplana *et al.* 2000). The more recent middle and late Pleistocene forms are part of a morphological variey of small *Ochotona pusilla* described under the subspecies name *occidentalis.*

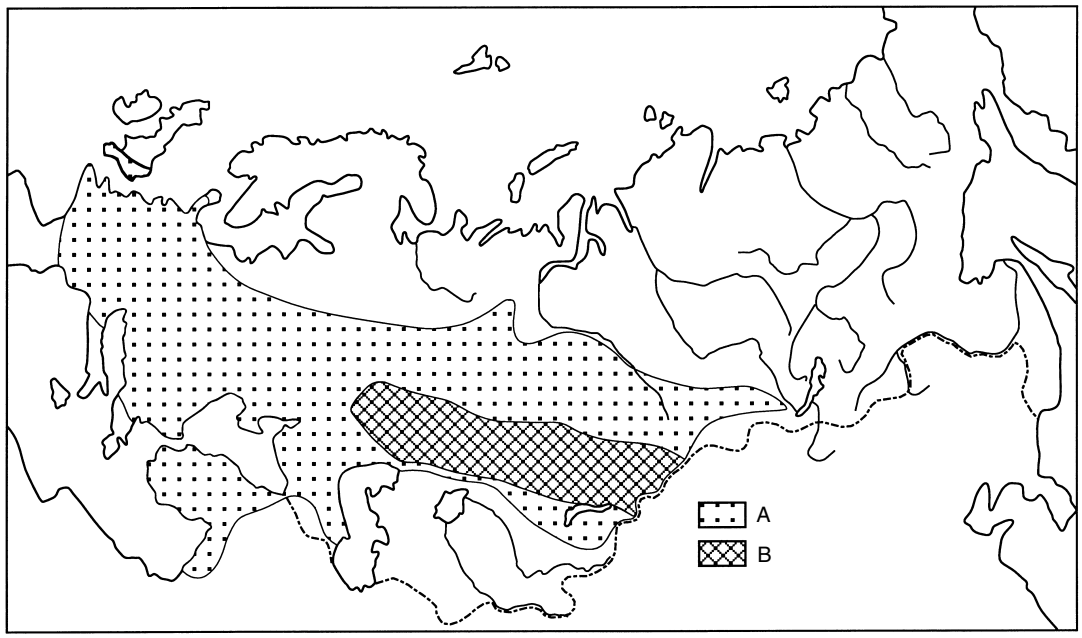

FIG. 7. — Distribution area of *Ochotona pusilla* Pallas, 1768; **A**, during Pleistocene times; **B**, present-day.

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