

ANNALS of CARNEGIE MUSEUM

CARNEGIE MUSEUM OF NATURAL HISTORY

4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 48

30 NOVEMBER 1979

ARTICLE 24

EASTERN NORTH AMERICAN PLEISTOCENE *OCHOTONA* (LAGOMORPHA: MAMMALIA)

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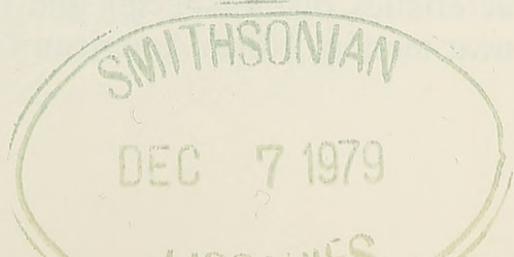
ABSTRACT

Fossil remains of *Ochotona* sp. from four Appalachian cave deposits in Maryland, West Virginia, and Virginia are compared with Recent North American *O. princeps* and *O. collaris*. They appear to be slightly smaller but the fossil material is insufficient for subgeneric allocation. *O. spanglei* from the late Pliocene of Oregon is discussed and its type description emended.

INTRODUCTION

The Holarctic genus *Ochotona* comprises a closely related group of perhaps 12 Palaearctic (Ellerman and Morrison-Scott, 1951) and two (Hall and Kelson, 1959) Nearctic species. They are morphologically conservative, differing among themselves in details of proportion, size, and pelage. The dental pattern varies little throughout the known Pliocene to Recent History of the genus. Despite their basic anatomical similarities some species of *Ochotona*, depending upon the degree of local geographic isolation, break up into races described primarily on the basis of pelage coloration. *Ochotona princeps* from the central Rocky Mountain Cordillera has 36 currently recognized subspecies (Hall and Kelson, 1959) reflecting the strong isolating role of post-Pleistocene, low-latitude montane refugia. The northern North American *O. collaris* or *O. p. collaris* (see Youngman, 1975) reported from Alaska, Yukon, Northwest Territories, and northwestern British Columbia, in a boreal region where post-Pleistocene limiting factors are

Submitted for publication 22 May 1979.



less intense than in lower latitudes, does not exhibit this polymorphic pattern.

All North American and most Palaearctic species are largely confined to rocky skree, usually at higher altitudes, a circumstance reflecting perhaps more upon the distribution of skree than upon the physiological limits of pikas. In Alaska, *O. collaris* occurs in dry alpine tundra, or dry microhabitats within high boggy tundra meadows above 2,000 ft (Guthrie, 1973). *Ochotona pusilla*, occurring on the Russian Steppes from approximately latitude 45°N to 55°N, often is found “. . . in dense thickets, wheatfields, wild cherry brush, among weeds, along fences in the village” (Ognev, 1940:88).

The Ochotonidae, once the most varied and successful lagomorphs, first appeared in the fossil record in the Oligocene of Asia. They subsequently spread to Europe, Africa, and North America. The genus *Ochotona*, possibly of Asian origin, appeared in the Pliocene of Europe, Asia, and North America. *Ochotona* is the only pika known from mid-latitude North America from late Pliocene (Hemphillian) times to the present (Dawson, 1967). There is a gap in the known North American *Ochotona* record of perhaps three million years, from *O. spanglei* from the Hemphillian McKay Reservoir local fauna of Oregon, to *Ochotona* sp. from the mid-Pleistocene (Irvingtonian) of the mid-Appalachians of eastern North America. All other North American records south of the sub-Arctic are from Rancholabrean to Recent times in western North America.

A fossil “ochotonid” was described by E. D. Cope (1871:93–94, fig. 20) from Port Kennedy Cave, Montgomery County, Pennsylvania, under the name *Praotherium palatinum*, later *Lagomys palatinus* (Cope, 1899:209–210). The interpretation of this specimen, AMNH 8574, a partial palate with four molariform teeth on each side, has always been controversial. Cope himself was uneasy about its taxonomic affinities. Dice (1923) examined the specimen and stated that it was not *Ochotona*. It is definitely a young leporid (M. Dawson, personal communication). Cope states that *Lepus sylvaticus* Bach. (= *Sylvilagus* sp.) was common in the Port Kennedy deposit.

In order to assess the taxonomic affinities of the Appalachian material, the holotype and only known specimen of *O. spanglei* was examined, a partial left jaw with P₃-M₂ (M₃ mentioned in the diagnosis has apparently been lost). The original diagnosis reads, “A pike [sic] about the size of the living North American species. The character of the P₄-M₃ is similar, but there is a rounded external lobe on P₃. Posterior and anterior faces of this tooth are straight.” (Shotwell, 1956:726–727). The diagnosis does not adequately describe the characteristics of the species and is here emended. The specimen is not near modern North American *Ochotona* in size, but is smaller than *O.*

Table 1.—Dental measurements, in mm, various *Ochotona*, Recent and fossil.

Taxon	Locality	Age	$\bar{x}$ Mean	OR	SD	CV	N
Alveolar length, P ₃ -M ₃							
<i>O. princeps</i>	western North America	Recent	8.5	7.7-9.7	.51	5.99	50
<i>O. collaris</i>	Alaska	Recent	8.2	7.8-8.5	-	-	4
<i>Ochotona</i> sp.	Cumberland Cave, Maryland	Irvingtonian	8.1	7.8-8.4	.26	3.19	13
<i>Ochotona</i> sp.	Rapp's Cave, West Virginia	Pleistocene	8.3	-	-	-	1
<i>O. spanglei</i> **	Oregon	Hemphillian	7.3 est.	-	-	-	1
Alveolar length, P ₃ -M ₂							
<i>O. whartoni</i> **	Cape Deceit, Alaska	Early Pleistocene	9.7	-	-	-	1
Alveolar length, P ² -M ²							
<i>O. princeps</i>	western North America	Recent	8.3	7.1-9.5	.20	2.4	43
<i>O. collaris</i>	Alaska	Recent	8.0	7.8-8.4	-	-	4
<i>Ochotona</i> sp.	Cumberland Cave, Maryland	Irvingtonian	-	8.0-8.2	-	-	2
<i>O. pusilla</i>	Great Doward Cave, England	Pleistocene	7.5	-	-	-	1

* Holotype, University of Oregon, UOMNH F-4083. Other measurements include P₃-M₂ = 6.5 mm; P₃ length = 1.36 mm, width = 1.36 mm; P₄ length = 1.36 mm, anterior width = 1.36 mm, posterior width = 1.55 mm; M₁ length = 1.65, anterior width = 1.55 mm, posterior width = 1.65 mm; M₂ length = 1.65 mm, anterior width = 1.65 mm, posterior width = 1.45 mm. Depth of jaw below M₁ = 4.46 mm.

** From Guthrie and Matthews, 1971.

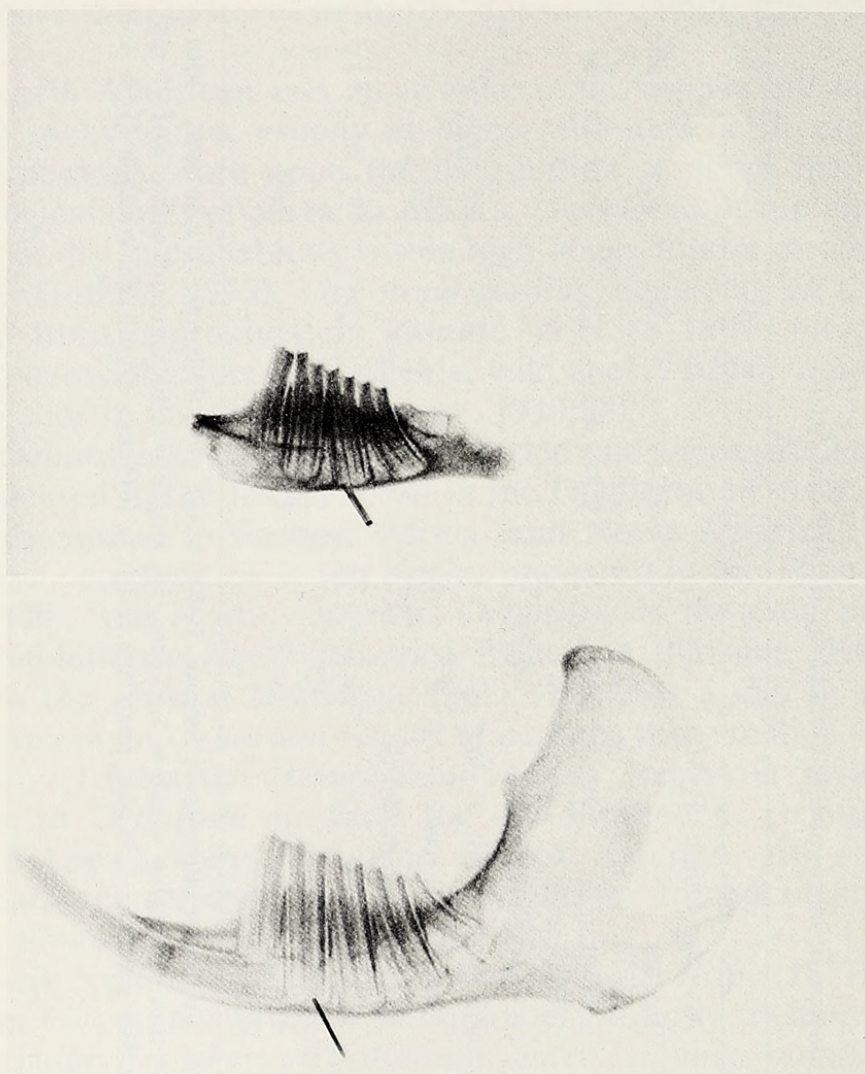


Fig. 1.—X-rays, lingual aspect, anterior to left. Line indicates posterior limits of lower incisor. Top: *Ochotona spanglei*, University of Oregon F-4083. Late Pliocene (Hemphillian), P_3 - M_2 and root of incisor. Bottom: *Ochotona princeps*. Recent, CM 20198, full dentition.

princeps in all dimensions (see Table 1). The details of the occlusal pattern of P_3 , as stated by Shotwell, do not serve to distinguish it from other species of *Ochotona*. *Ochotona spanglei* does differ markedly from all modern *Ochotona* in the position of the posterior end of the lower incisor. The incisor extends back in the jaw to a position under the mid-point of M_1 . This can be seen in the X-ray (Fig. 1) and is apparent externally by a swelling on the lingual aspect of the jaw. In modern *Ochotona* the origin of the incisor has migrated forward to a position under the P_4/M_1 junction. This forward migration is a continuation of a trend noted in older, more primitive ochotonids where the incisor is even more posterior than in *O. spanglei* and is apparently a device to accommodate increasing hypsodonty of the cheek teeth (M. Dawson, personal communication). Therefore, although the orig-

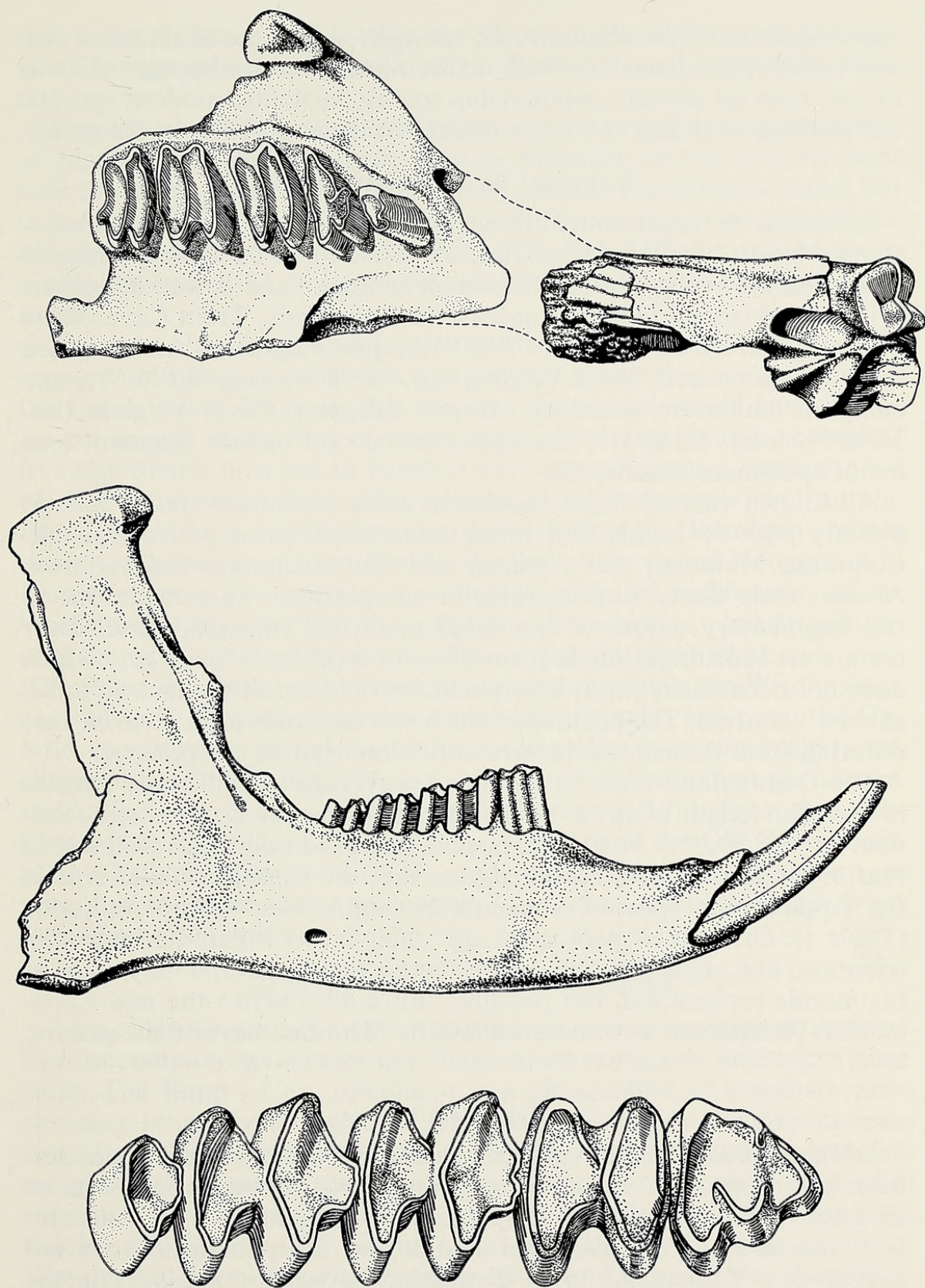


Fig. 2.—*Ochotona* sp. Cumberland Cave, Maryland. Anterior to right. Top: right maxilla with P²-M², USNM 12379; premaxillary fragment with partial right incisor, USNM uncatalogued, ventral views. Center: partial right mandible, USNM 12380, labial view. Bottom: right lower dentition with P₃-M₃, USNM 12380, occlusal view (from Dawson, 1967:301, Figs. 4-5).

inal diagnosis was inadequate, *O. spanglei*, by virtue of its small size and incisor placement, is a well marked and primitive species of *Ochotona*, with no obvious relationship to any particular modern species, but nothing to disbar it from a direct ancestral position in the genus.

EASTERN NORTH AMERICA

Ochotona sp. is presently known from four mid-Appalachian sites—Cumberland Cave, Maryland (lat. 39°41'N, long. 78°47'W), where it was common, represented by complete upper and lower dentitions (Fig. 2) and isolated teeth of at least 13 individuals; Trout Cave, West Virginia (lat. 38°36'N, long. 79°22'W), jaw fragments and isolated teeth; Rapp's Cave, West Virginia (lat. 37°58'N, long. 80°23'W), one complete immature mandible; Jasper Saltpeter Cave, Virginia (lat. 36°46'N, long. 82°48'W), one upper molar and incisor fragment (see list of specimens examined).

All known eastern fossil specimens were examined and compared directly with 56 crania and lower jaws of *O. princeps* from Utah, Colorado, Montana, and Alberta, and four *Ochotona collaris* from Alaska. Only dental and mandibular comparisons were made due to the fragmentary nature of the fossil material. The upper and lower teeth were indistinguishable from those of modern *O. princeps*, which does not necessarily imply conspecificity because of the lack of intra-generic variation. The position of the lower incisor is as in *O. princeps*, differing from the more primitive condition seen in *O. spanglei*.

The Cumberland Cave fossil material averages significantly smaller in alveolar length of lower tooth row than Recent *O. princeps* (Student's $t = 2.59$, $P = <.01-.02$) but the observed range falls well within that of modern adult *O. princeps*, so that the slightly smaller size of the Appalachian specimens cannot be appreciated except in series (Table 1). Given their geological age, their (now) isolated eastern distribution, and slight size difference, better fossil material may warrant taxonomic recognition, but pending future discoveries the mid-Appalachian Pleistocene *Ochotona* cannot be identified beyond the generic level.

DISCUSSION

Did the present North American species of *Ochotona* evolve *in situ* from an *O. spanglei* stock, or represent a post-Pliocene invasion, or invasions, of more progressive species of *Ochotona* from the Palaearctic? The present distributional hiatus and morphological (but not karyotypic, Youngman, 1975) distinction between *O. collaris* to the north and *O. princeps* to the south in the Rocky Mountain Cordillera suggests that more than one stock is represented, that the southern *O. princeps* population antedates at least the Wisconsinan glaciation, and

that several glacial refugia may have been involved from which post-glacial range adjustments took place, Beringian and western periglacial.

There is no pre-Wisconsinan Pleistocene record of *Ochotona*, south of Alaska, from the American West or Midwest. In the western montane areas this may be due to a lack of suitable preservation sites, but in the numerous Great Plains Pleistocene faunas *Ochotona* is conspicuously absent (Hibbard et al., 1965). The Great Plains served as an ecological barrier to *Ochotona* throughout the Pleistocene, as it does today.

The most plausible immigration route into the Appalachians for *Ochotona* would have been from a northwesterly direction, circumventing the Great Plains. To make this traverse the animal would have had to spread across areas free of rocky talus, implying greater ecological freedom than it now has in North America, perhaps as a consequence of less competition from other similar sized herbivores such as the many terrestrial sciurids present at lower latitudes. Dawson (personal communication) points out that the decline of the varied Neogene ochotonids in post-Miocene times coincides with the proliferation of arvicolids, and suggests that the voles may have been an important limiting factor in ochotonid fortunes. The recent Ontario find of *Ochotona* (Churcher and Dods, 1979) from an undated, possibly pre-Wisconsinan cave breccia, may lie along this route. Surprisingly, however, the Ontario specimen, a partial femur from Kelso Cave, in the Niagara escarpment, 45°30'N, 79°55'W, is from a large animal about the size of the extinct *O. whartoni* Guthrie and Matthews, 1971, from the early Pleistocene Cape Deceit local fauna, Alaska, and the Old Crow Basin of the Yukon (Harington, 1978), and, on the basis of size alone, is unrelated to the smaller Appalachian *Ochotona* sp. of Maryland, West Virginia, and Virginia.

ECOLOGY OF EASTERN *OCHOTONA*

Two of the four known mid-Appalachian sites containing *Ochotona* have accompanying species that make some ecological inferences possible. The Rapp's Cave specimen is a chance find of unknown provenience by a private collector. The Jasper Saltpeter Cave specimens were in sediments disturbed by Civil War mining activities and the meager accompanying small mammal fauna is both chronologically suspect and noncommittal. However, Cumberland Cave, Maryland (Gidley and Gazin, 1938; Guilday and Handley, 1967; Holman, 1977; Van der Meulen, 1978; Zakrzewski, 1975), and Trout Cave, West Virginia (Guilday, 1971; Zakrzewski, 1975), have extensive accompanying faunas. On the evidence primarily of arvicolid dental morphology, the Cumberland Cave local fauna has been allocated to the Irvingtonian,

ca. 700,000 years BP, slightly older than the late Kansan Cudahy fauna (Van der Meulen, 1978). *Ochotona* is not present in any of the numerous Wisconsinan to early Holocene cave faunas from the Appalachians (Guilday et al., 1977, 1978) and was apparently gone from eastern North America by Rancholabrean times.

Present with *Ochotona* at Cumberland and Trout caves were several vertebrates of western affinities; a thomomine pocket gopher *Thomomys potomacensis* and an ictidomyine ground squirrel *Spermophilus* cf. *tridecemlineatus*; and at Cumberland Cave a coyote *Canis priscolatrans* and a badger *Taxidea marylandica*. An extensive amphibian and reptile fauna of at least 30 species including one of mid-western affinities, the fox snake, *Elaphe vulpina*, has been reported from Cumberland Cave (Holman, 1977). Cumberland Cave also produced a variety of large browsers and grazers, a horse *Equus*, a tapir *Tapirus*, two peccaries *Platygonus* and *Mylohyus*, an ovibovid *Euceratherium*, two cervids *Odocoileus*, *Cervus*, a ground sloth *Megalonyx*, and the mastodon *Mammut*. Two arboreal sciurids, *Tamiasciurus* and *Glaucomys*, and a woodland zapodid, *Napaeozapus*, were present. Voles of boreal affinities were present at both Trout and Cumberland caves—*Phenacomys*, *Clethrionomys*, *Synaptomys* (*Mictomys*). However, these boreal rodents were a rare element in the numerically large vole sample from each site, which consisted primarily of *Microtus*, *Pedomys* and *Pitymys*. A wolverine *Gulo* was present at Cumberland Cave.

This partial listing of species from these two eastern *Ochotona*-bearing sites, Cumberland Cave and Trout Cave, suggests a more varied fauna than the closed, largely oak-dominated forests of the central Appalachians were capable of supporting in Holocene times, indicating a greater variety in the ecological landscape. Such faunas could best have been accommodated by a cool-temperate environment, relatively drier than it is today. The presence of so many extinct species makes it impossible to suggest a modern analog, but the broad analogy of a varied grassland/deciduous-coniferous forest situation superimposed upon the regional Ridge and Valley topography (Hunt, 1974) seems most appropriate.

This environmental interpretation is not consistent with the usual concept of what *Ochotona* "likes" based upon modern habitats of North American pikas, implying either that the Eastern North American Irvingtonian form was indeed a separate species with its own set of environmental requirements, and/or that *Ochotona* today is closely confined to its rocky niche by interspecific pressures, and not by evolutionary specialization—that it lives where it does because of competitive factors rather than physiological or anatomical strictures.

ACKNOWLEDGMENTS

I thank Harold W. Hamilton and Allen D. McCrady, whose field efforts resulted in the recovery of most of the Appalachian specimens here discussed; Hugh H. Genoways and Susan McLaren, Section of Mammals, Carnegie Museum of Natural History, for the loan of Recent *O. princeps* specimens, Don E. Wilson, National Museum of Natural History, for specimens of *O. collaris*, and Eric Gustafson, University of Oregon, for the loan of the holotype specimen of *O. spanglei*. X-ray by Allen D. McCrady. I also thank Alice M. Guilday and Elizabeth Hill for secretarial assistance, Mary R. Dawson for sharing her ochotonid expertise, and C. S. Churcher, Royal Ontario Museum, for a preprint of his paper on the Niagara Escarpment ochotonid.

SPECIMENS EXAMINED

Recent.—*Ochotona collaris*, Alaska: USNM 148590, 157225, 157227, 512900. *O. princeps*, Utah: CM Recent Mammal no. 9469–9471, 9473, 9475, 9477–9484, 12021–12024, 14719–14720, 14726–14733, 16020, 16022–16024, 16026–16028, 16030, 16032, 20200–20201, 20203–20204, 20607–20608; Colorado: 20193–20198; Montana: 22143–22144, 22146, 22374; Alberta: 22906–22908, 22912.

Pleistocene.—*O. pusilla*, Great Doward Cave, England, CM 12666. *Ochotona* sp., Jasper Saltpeter Cave, Virginia, CM 30264; Rapp's Cave, West Virginia, CM 24290; Trout Cave, West Virginia, CM 12722, 12793, 12818, 12837, 12864, 12879; Cumberland Cave, Maryland, USNM 7689, 7768–7770, 12378–12379, 12381, CM 20242–20243, 20247, 20249–20250, 20477, 20479–20480.

Pliocene.—*O. spanglei*, McKay Reservoir, Oregon, UOMNH F-4083.

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