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New Late Cenozoic Ochotonids from China

by

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Summary

Cranial material of fossil Ochotonidae is relatively uncommon and serves to differentiate extinct species of the genus *Ochotona*. *Ochotona* includes the living pikas, which are diverse, and the fossil record shows equal diversity. We present three new pika species based on late Cenozoic fossil specimens present in museum collections of the American Museum of Natural History (New York). In addition to dental features and size, the specimens are distinguished by features of the palate, cranial height, interorbital constriction, and the brain case. Two of these new taxa are Late Miocene in age, and one is Late Pliocene. All are from Shanxi Province. As evident today, fossil *Ochotona* species may reflect local biogeography and many possibly had relatively restricted distribution.

Key words: *Ochotona*, Miocene, Pliocene, China, Lagomorpha.

Zusammenfassung

Cranialmaterial von fossilen Ochotoniden sind relativ selten, dienen aber zur Unterscheidung der ausgestorbenen Arten der Gattung *Ochotona*. *Ochotona* inkludiert die sehr diversen, heutigen Pikas und der Fossilbefund belegt eine ähnliche Diversität. Wir präsentieren in der vorliegenden Arbeit drei neue Pika-Arten, basierend auf känozoischen Fossilmaterial aus dem American Museum of Natural History (New York). Außer an Zahnmerkmalen und der Größe, konnten Unterschiede am Palatinum, in der cranialen Höhe, der interorbitalen Einschnürung und der Gehirnkapsel festgestellt werden. Zwei dieser neuen Taxa stammen aus dem Obermiozän und eine aus dem Oberpliozän. Alle sind aus der Shanxi Province. Wie man heute weiß, spiegeln fossile *Ochotona*-Arten eine lokale Biogeographie wieder und viele hatten wahrscheinlich eine relativ eingeschränkte Verbreitung.

1. Introduction

The Order Lagomorpha includes small mammals assigned to two families, the familiar Leporidae (rabbits and hares) and the Ochotonidae, the pikas of northern continents. Erbajeva (1988) has made the case that the recently extinct genus *Prolagus* requires separate familial rank, but this is not universally accepted.

Ochotonidae are typically Holarctic in distribution, but dispersed into Africa in the mid-Tertiary. They are represented by the single living genus *Ochotona*. Most species of *Ochotona*, including the pika of North America, inhabit rocky slopes in mountainous terrain. However, the genus is surprisingly diverse, including nearly thirty species across Eurasia (Hoffman & Smith, 2005), ranging from mountainous to steppic to low-elevation desert terrain. Paralleling this diversity, Erbajeva (1988) documented at least 20 species of *Ochotona* in the late Cenozoic fossil record, principally of northern Asia, and Erbajeva & Zheng (2005) add four more Late Miocene and Pliocene species. Not surprisingly, there is some indication that the preferred habitat of these fossil species was not solely high elevation, but apparently some occupied niches in mesic and lower elevation environments, as in the late Neogene Yushe Basin, of Shanxi Province, China.

Late Miocene and Pliocene ochotonids representing the living genus *Ochotona* and the extinct, derived *Ochotonoides* are rather well known from China as well as

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northern Asia (Schlosser, 1924; Boule & Teilhard de Chardin, 1928; Teilhard de Chardin & Piveteau, 1930; Teilhard de Chardin & Young, 1931; Ji et al., 1980; Zheng, 1982; Zheng & Li, 1982; Agadjanian & Erbajeva, 1983; Qiu, 1987; Qiu & Storch, 2000; Erbajeva & Zheng, 2005). However, the diversity of fossil *Ochotona* from China is probably underestimated for lack of good cranial material. It is now apparent that the Chinese fossil record demonstrates greater diversity among pikas than previously recognized.

Among the Frick Collection of the American Museum of Natural History (AMNH) are fossils from the late Neogene of Shanxi Province, China. Some are from Yushe Basin, but a larger proportion are from localities in northwestern Shanxi, near Baode, and eastern Shanxi, 100 km to the north of the Yushe Basin, from the Shouyang area, which is east of the provincial capital Taiyuan. The Frick material includes cranial remains of ochotonids, which form the basis of the present analysis and represent species newly described herein.

2. Material and methods

The material described in this paper is conserved at the American Museum of Natural History (AMNH), New York. Originally as part of the Frick Collection, the fossils were found in the 1930s by Kan Chuanpo ("Buckshot" of the earlier Central Asiatic Expeditions of the AMNH) and by Liu Hsi Kou. Childs Frick had engaged these skilled collectors to acquire material representative of the later Cenozoic of China, especially of Shanxi Province. It appears that Liu concentrated on the area in northern Shanxi, which had become famous for yielding the classic Baode faunas; Buckshot focused on central to southeastern Shanxi. The specimens came to be housed in the Frick Wing at the AMNH, and were studied by several investigators since 1980. No comprehensive review of this material, however, has been conducted up to now. Restudy of the fossils carried out in 2000 under the auspices of the AMNH visiting scholar study program, has revealed new taxa, the description of which is given below.

The fossils described here are isolated skulls with mandibles from the vast portion of China also known as the Loess Plateau. In short, and all too simplistically, the valleys of Shanxi underwent aggradation with accumulation of late Tertiary sediments, often bearing fossils – the so-called Red Clay Hipparion faunas. The later phase of aggradation was dominated by loess deposition. The "loess" is quite thick in some areas and includes some fluvial sediments and fossils. Older museum collections often fail to distinguish whether fossils came from stratified fluvio-lacustrine deposits or loess.

Circumstances of preservation and collection have disassociated the ochotonid specimens from any postcrania or additional individuals that might originally have been present in adjacent matrix. They stand alone as representatives of their respective taxa. Possibly the crania were buried after ingestion by a carnivore or raptor, but it seems likely that this would have caused greater destruction. It is also possible that the crania were preserved in burrows, but one would expect more complete material in this case. Clues could be found by relocating the actual fossil sites. Future fieldwork would also allow testing stratigraphic provenance by duplicating the finds.

The terminology used here to describe dental structures follows López Martínez (1989), but with emendation from Erbajeva (1988). Capital and lower-case letters, P/p (premolars) and M/m (molars) refer to upper and lower cheek teeth, respectively. All cheek tooth measurements are given with respect to the occlusal surface, from external borders of the enamel, and they are given in millimeters as maximum length (L) and width (W) of each tooth.

3. Systematic paleontology

Class Mammalia

Ordo Lagomorpha Brandt, 1855

Familia Ochotonidae Thomas, 1897

Subfamilia Ochotoninae Thomas, 1897

Type Genus: *Ochotona* Link, 1795

Included Genera: *Marcuinomys* Groizet, 1839, *Lagopsis* Schlosser, 1884, *Proochotona* Chomenko, 1914, *Ochotonoides* Teilhard de Chardin & Young, 1931, *Paludotona* Dawson, 1959, *Alloptox* Dawson, 1961, *Pliolagomys* Erbajeva, 1983, *Albertona* López Martínez, 1986, *Ochotonoma* Sen, 1998.

Geological Age Range: Early Miocene to Recent.

Geographical Distribution: Holarctic: Europe, Asia, and North America.

Genus *Ochotona* Link, 1795

***Ochotona tedfordi* nov. sp.**

Figs. 1A-B, 2A-D; Tables 1, 2

Diagnosis: Moderately large-size *Ochotona* with deep skull and short palate. P2 short and wide with deep anterointernal flexid and shallow anteroexternal depression. P3 is almost triangular in shape, with a short anteroloph. The rhomboid type of anteroconid (angular anterior apex) on p3 is nearly separated from the large posteroconid; the posteroconid is as long as it is wide, and has a deep hypoflexid.

Holotype: Damaged mandible and skull with complete face and dentition; basicranium, occiput and much of the temporal regions are missing. Catalogued as AMNH F: AM 141395 (originally field number 26-B185).

Locality: Chang Chia Chuang, China, collected in 1933 by Kan Chuanpo. Associated fauna (*Promephitis*, cf. *Dinocrocuta*, *Ictitherium*, *Chleuastochoerus stehlini*, *Gazella gaudryi*, *Stegodon* sp.) are elements of the late Miocene Mahui Fm. assemblages of Yushe Basin, late Baodean mammal age.

Figure 1: *Ochotona tedfordi* nov. sp. Skull AMNH F:AM 141395 (A – dorsal view, B – ventral view).

Geological age: Late Miocene.
Etymology: after the eminent investigator of Chinese faunas Prof. Richard H. Tedford
Description: The skull is deep dorsoventrally and convex at the frontal-parietal suture. Rostrum is short and relatively robust. The anterior one third of the nasal bones is wide; posteriorly the lateral borders of the nasals are almost parallel, and span 2/3 the width of the rostrum, before narrowing toward their ends (Fig. 1A, Table 1). The frontal bone is rather long, relatively wide and with a shallow depression along its length. Infra-orbital foramen is of triangular shape. Orbits are large, longer than wide. Judging from the preserved part of the jugal bone, the zygomatic arch was wide and moderately robust. Anterior processus zygomaticus is unexpanded but well developed. Incisive and palatal foramina are widely confluent, and they extend to the posterior margin of P3. Palate is relatively short, and anteriorly the upper tooth rows are set close to the palatal foramina; tooth rows gradually diverge posteriorly (Fig. 1B). Posterior palatal vacuity extends to the level of the anterior part of M1.
The upper incisor is twice as wide as its antero-posterior dimension. The prominent groove is well medial to the midline. The second upper incisor is quite small relative to size of the skull and to other species of *Ochotona*.
The lower jaw is deep and robust, with a long, almost straight ascending ramus. The anterior face of the ascending ramus is relatively wide with two well-developed tubercles, one distinctly crest-like at the mid-height of the ramus, and the second below the first, behind and slightly above the dentition. The dorsal surface of the condyle is triangular in shape, wide anteriorly and narrowing behind. The lower incisor extends to below the anterior part of m1. Its cross section is oval in shape, being wider dorsally. Enamel is restricted to the lateral and lateroventral sides. Both lingual and lateral surfaces of the mandible are flat. Along the base of lower jaw, a shallow groove extends as long as the length of the tooth row. The mental foramen is below p3-p4, lateral to the root of the incisor.

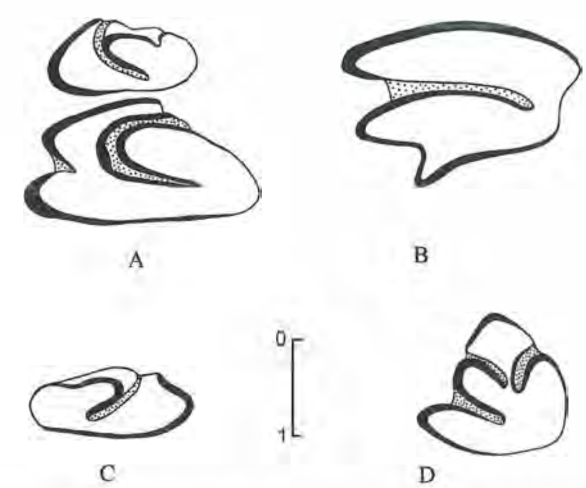

Figure 2: *Ochotona tedfordi* nov. sp. dentition of AMNH F:AM 141395: A. left P2-P3, H. left M2, C. right P2, D. left p3

P2 is oval in shape (Fig. 2A, C). A deep flexus filled with cement is situated at one-third of the tooth width from the lingual side, and externally there is a shallow depression without cement.
P3 (Fig. 2A) has an anteroloph that crosses nearly half of the tooth width. The U-shaped paraflexus filled with thin cement begins and ends at the level of one quarter of the tooth width. The hypostria is short and filled with a thin layer of cement. The anterior border is much narrower than the posterior border of the tooth. The enamel band is thicker on the anterior and lingual sides of the tooth.
P4 and M1 are typical for *Ochotona*, with a deep, straight hypostria filled with cement. On M2 (Fig. 2B) the anteroloph is slightly wider than the posteroloph; the latter has a sharp, well-developed posterolingual process. The hypostria is deep and filled with thin cement.
p3 (Fig. 2D, Table 2) has a relatively large, rhombus shape anteroconid with almost equal sides and angled anterior margin. The anteroconid is almost completely separated from posteroconid. The prominent posteroconid is as wide as long. Paraflexid and protoflexid are nearly the same depth and filled with cement. The protoflexid is directed toward the posterointernal angle, and the paraflexid is oriented almost straight backward. The deep hypoflexid, filled with cement, crosses half the tooth.
Comparisons: *Ochotona tedfordi* nov. sp. differs from other ochotonids described here in its smaller size and its p3 anteroconid being nearly separated from the posteroconid. It is closer to *Ochotona lagreli* in lower tooth structure, and the dimensions of p3 appear to fall within the range of variation for samples of the latter taxon from Ertemte and Harr Obo (QIU, 1987). However, the new species may

have somewhat smaller mean size, because most dental dimensions for *O. tedfordi* fall below the average for *O. lagreli*. There is a slightly shorter P2 and posteroconid of p3 in *O. lagreli*. Differences in p3 of *O. lagreli* include a deeper hypoflexid (posteroexternal re-entrant), and a rounded posterointernal wall, not the flat or even indented border of many *O. lagreli*.

Ochotona tedfordi nov. sp. differs from *Ochotona guizhongensis* from Guizhong County in Tibet (Ji et al., 1980) by its smaller size and by its shorter P2 (length P2 is 0.75 in contrast to 1.14 in *O. guizhongensis*). The structure of P2 differs as well, with the anterior flexus in the pika from Tibet being very short.

This species resembles extant *Ochotona curzoniae* and *O. dauurica* in the structure of p3: rhomboid anteroconid, deep paraflexid directed backward, and deep hypoflexid, and these are compared in Table 2. However, the extinct species differs significantly in larger size of the teeth and the longer posteroconid of p3. In contrast, *Ochotona curzoniae* and *O. dauurica* have a short posteroconid on p3, with significantly greater width than length.

Ochotona chowmincheni nov. sp.

Figs. 3, 4; 5A-C, E-F; Tables 1, 2

Diagnosis: Moderately large-size *Ochotona*. Skull is flat with extremely wide interorbital region, nasals extraordinarily broad posteriorly. Wide anteroconid of p3 with two shallow anterior flexids.

Holotype: Incomplete, damaged skull without basicranium and occiput, left processus zygomaticus broken; dentition is complete; well-preserved left and right jaws, both bearing p3-m3. Catalogued as AMNH F:AM 141394, originally L5 on 1933 listing.

Locality: Liu Wang Kou, China collected 1931 by Liu Hsi Kou in the Baode area, perhaps equivalent to Loc. 31 of Zdansky (1923; see north part of map, originally Tafel V). Associated fauna (Kurten, 1952) are elements of the Late Miocene Baodean age mammal assemblages. Some Baode sites are apparently early Pliocene in age, but no evidence of Pliocene fauna is apparent at Loc. 31.

Geological age: Late Miocene.

Etymology: Species name after outstanding paleontologist Prof. Chow Minchen, who founded the modern era of vertebrate paleontology in China.

Description: Skull is relatively long and narrow, with moderately robust rostrum. The nasal bones span nearly the entire rostrum and their external borders are almost parallel as they extend posteriorly. The nasals become slightly narrower as they end abruptly (Fig. 3, Table 1). Frontals are long and wide, contributing to the broad interorbital region. They are flat anteriorly; slightly dorsally convex posteriorly. Parietals display weak convexity toward the midline. The infra-orbital foramen, of triangular shape and long, extends forward along half the length of the rostrum. Orbits are relatively small, and longer than wide. Jugals are wide and moderately robust. Anterior processus zygomaticus is reduced and the posterior one

Measurements (mm)	*Ochotonoides complicidens* AMNH F:AM 116228	*Ochotona gudrunae* n.sp. AMNH F:AM 141396	*Ochotona chowmincheni* n.sp. AMNH F:AM 141394	*Ochotona tedfordi* n.sp. AMNH F:AM 141395
1. Length of skull	59.83	50.9	52	—
2. Length of nasals	—	15.32	17.98	17.09
3. Anterior width of nasals	—	6.4	8.24	5.96
4. Posterior width of nasals	—	3.82	7.3	4.04
5. Width of jugals	—	30.63	24.76	—
6. Interorbital width	8.5	5.05	7.98	5.69
7. Diastema	13	14.17	13.8	12.7
8. Palatal length	—	3.68	2.19	3.28
9. Width between P4	—	9.88	8.5	9.22
10. Alveolar length P2-M2	11.5	12	10	10.6
11. Alveolar length P2-M1	8.5	9	7.3	8
12. Alveolar length P3-M1	6.5	7	5.8	6
13. Crown length P2-M2	10.2	10.7	9.1	8.7
14. Crown length P3-M2	8.7	9.6	8	7.8
15. Crown length P3-M1	6	6.8	5.6	5.5
16. Crown length P3-P4	3.8	4	3.6	3.4
17. Length P2	1.1	0.9	1	0.75
18. Width P2	2	1.6	2.05	1.9
19. Length P3	1.7	1.7	1.55	1.5
20. Width P3	3.4	3.4	3.4	3
21. Length M2	2.2	2.4	2	2
23. Width M2	3	3.4	3.25	2.6

Table 1: Measurements of upper teeth and skull of new species of *Ochotona*, in comparison with *Ochotonoides complicidens*. For dentitions, measurements for left and right sides are averaged; in some cases only one side of the tooth row was available.

is relatively long and thin. Incisive and palatal foramina, in wide confluence, are pear-shaped, and extend almost to the posterior border of P4. The palate is very short (Fig. 4), and the broad posterior vacuity extends forward to opposite the anterior portion of M1.

The body of the lower jaw is deep and robust, with a long ascending ramus, nearly vertical, unlike the sloping ramus of living species. The anterior face of the ramus is robust, wide relative to most *Ochotona*, and with a well-developed tubercle at mid-height. Below this tubercle there is another distinct, smaller tubercle. The antero-posterior dimension of the ascending ramus is 5 mm, and the posterior edge is quite thin bone. The dorsal surface of the condyle of the ascending ramus is triangular in shape, wide anteriorly, and sharply narrower backward. The diastema is short. The lower incisor extends backward to the anterior portion of m1, and forms a small but distinct tubercle on the lingual part of the mandible. Along the ventral border of the lower jaw, slightly above the base of the mandible, extends a shallow groove that is as long as the tooth row. Mental foramina are located below p3 and m2. The height and thickness of the mandible below p4 is much greater than that below m3.

The first upper incisor is not oval, but asymmetrically longer medially than laterally. A moderately deep groove without cement continues along the whole length of anterior surface of the incisor. The second upper incisor is oval in cross section. The cross section of the lower incisor is triangular in shape, with medial and dorsal sides at nearly a right angle. The hypotenuse is gently rounded; enamel is restricted to this side. All upper and lower teeth, in general, are of typical ochotonid structure (Fig. 5A-B). Both upper and lower tooth rows are long (Tables 1, 2).

P2 (Fig. 5A, F) is oval in shape, with a deep anterior flexus directed toward the posterolabial angle and filled with cement. The internal side of the tooth is much longer than the external side. It bears a distinct vertical depression without cement in contrast to the external margin, which is rounded in shape. The enamel thickness is great on the antero-internal surfaces of the tooth; it is thin or absent elsewhere.

P3 (Fig. 5A) is trapezoidal in shape due to its anterior border being significantly narrower than the posterior border. The relatively short anteroloph covers two thirds of the tooth width. A rather long paraflexus begins at the level of one fourth of the tooth width, extends inward, and turns postero-externallly to reach a point at one-third of the tooth width from the labial side. The anterior border of P3 is somewhat prominent. Its protocone and hypocone are almost of the same size. The short hypostria includes a thin layer of cement. The enamel band is thick on the anterior and internal sides of the tooth, and thin or lacking on the posterior and external margins.

P4-M1 are of almost the same shape in occlusal view. The hypostria in these teeth (and of M2) is deep, almost

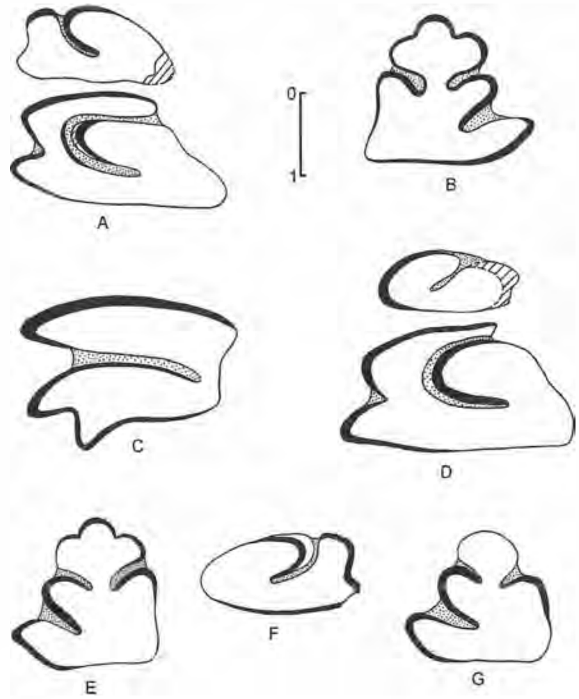

Figure 5: Selected dentition of *Ochotona chowmincheni* nov. sp., (A, B, C, E, F) and *O. gudrunae*, nov. sp. (D, G). AMNH F: AM 141394: A. left P2-P3, B. right p3, C. left M2, E. left p3, F. right P2. AMNH F:AM 141396 *Ochotona gudrunae* nov. sp.: D. right P2 and left P3, G. left p3.

Figure 3: *Ochotona chowmincheni* nov. sp. Skull AMNH F: AM 141394 (dorsal view).

Figure 4: *Ochotona chowmincheni* nov. sp. Skull AMNH F: AM 141394 (ventral view).

reaching the labial border of the tooth, and is filled with thin cement.
On M2 (Fig. 5C) the anteroloph and posteroloph are almost of the same width. The posterolingual process from the posteroloph is relatively large and forms a distinct angle with the posteroloph.
The first lower premolar (p3) (Fig. 5B, E, Table 2) has a relatively large anteroconid that is wider than long. Two anterior shallow grooves without cement extend downwards to the bottom of the tooth. These grooves accentuate prominent lateral and medial lobes of the broad anteroconid. The anterior border of the tooth is smooth and rounded. The anteroconid and posteroconid of p3 are widely connected. The short posteroconid is wide, and the same length on both internal and external sides. The paraflexid and protoflexid are of the same depth, and the hypoflexid is only slightly deeper; all are filled with thin cement. This tooth is large compared to p3 of other species of *Ochotona*.
Comparisons: *Ochotona chowmincheni* nov. sp. differs from all known extinct and extant ochotonids by its very wide nasal and frontal bones (Fig. 3) and by the peculiar p3 structure with broad, three-lobed anteroconid. Some single ochotonid specimens from Gousinyi Perelet in northern Kazakhstan and several specimens of *Ochotona lagreli* from Ertemte 2 and Harr Obo 2 have similar p3 morphology, i.e., having two shallow anterior grooves (Qiu, 1987, p. 391, text figs. 94-96). However, the latter species has a p3 that is significantly smaller. *Ochotonoides complicidens* from Nihowan (Teilhard de Chardin & Piveteau, 1930:125, fig. 41A and B) has a similar premolar morphology, but it differs from *Ochotona chowmincheni* nov. sp. by its completely separated anteroconid and posteroconid in its p3, and by having the broad anteroconid of the latter tooth with prominent external and internal lobes.

***Ochotona gudrunae* nov. sp.**
Figs. 5D, G; 6A-B; Tables 1, 2

Diagnosis: Large size *Ochotona*, larger than any living species and other fossils described here, with robust lower jaw and teeth; p3 with small, rounded anteroconid lacking enamel, wide confluence of anteroconid and posteroconid; inter-orbital region of skull narrow, incisive and palatal foramina are open and widely confluent.
Holotype: Incomplete skull, preserved in hard sediment, with nasals damaged anteriorly, and crowns of P2-M2. Fragments of the left and right lower jaws with p3-m3 belong to this skull. Catalogued as AMNH F:AM 141396; original field number B-765.
Locality: Tsao Chuang, 12 km south of Shou Yang, China, collected in 1936 by Kan Chuanpo and Liu Te Shun. The bone is dark and embedded in hard matrix, not derived from loess. Associated faunal elements (*Pachycrocuta perrieri*, *Nyctereutes sinensis*, *Eucyon*, *Ursus*, *Lynx shansius*, *Archidiskodon*) and preservation indicate provenance from Late Pliocene stratified deposits equivalent to Nihewan, and to the Haiyan Formation of Yushe Basin.
Geological age: Late Pliocene, Nihewanian.
Etymology: Species name in honor of paleontologist and mentor Gudrun Daxner-Höck, in recognition especially of her explorations in Mongolia and advancement of small

Measurement (mm)	*Ochotonoides complicidens* AMNH F:AM 116228	*Ochotona tedfordi* n.sp.	*Ochotona chowmincheni* n.sp.	*Ochotona gudrunae* n.sp.	*Ochotona lagreli* (Ertemte) n	mean	*Ochotona curzoniae* n	mean	*Ochotona dauurica* n	mean
1. Alveolar length p3-m3	12.6	10	10.8	12		9.8		8.3		8.14
2. Alveolar length p4-m3	9.6	8	8.2	9.5		—		—		—
3. Crown length p3-m3	11.3	8.8	9.9	10		—		7.3		7.19
4. Crown length p3-m2	10.4	7.9	8.9	9.1		—		6.58		6.44
5. Crown length p3-m1	7.6	5.3	6.7	6.5		6.7		4.82		4.73
6. Crown length p3-p4	5	3.7	4.5	4		—		3.11		3
7. Crown length p4-m3	9	7	7.4	8.5		—		5.81		5.77
8. Crown length p4-m2	7.9	6.1	6.4	7.4		—		5.07		5
9. Length p3	2.45	1.6	2.1	1.75	77	1.80	24	1.50	31	1.47
10. Length anteroconid p3	1.35	0.85	1.1	0.7	75	0.81	24	0.77	31	0.76
11. Length posteroconid p3	1.3	1.1	1.2	1.15	75	1.21	24	0.92	31	0.88
12. Width anteroconid p3	1.3	0.8	1.2	1	72	0.84	24	0.80	31	0.74
13. Width posteroconid p3	2.1	1.7	1.95	2.25	75	1.79	24	1.45	31	1.47
14. Antero-posteroconid connection	—	0.03	0.2	0.2		—		—		—
15. Diastema	—	7.4	7.7	9		—		4.87		5.09
16. Mandible height below p4	8.7	7.1	8.6	7.8		9.2		5.35		5.44
17. Mandible height below m3	7.8	6.7	8	7.7		—		5.09		5.12
18. Mandible thickness at p4	4.26	4.1	4.6	5.5		4.7		3.57		3.4
19. Mandible thickness at m3	4.1	3.7	3.7	4.1		—		2.86		2.82

Table 2: Measurements of lower jaws and teeth of new ochotonids compared to *Ochotona lagreli*, *O. curzoniae*, and *O. dauurica*, and to *Ochotonoides complicidens*.

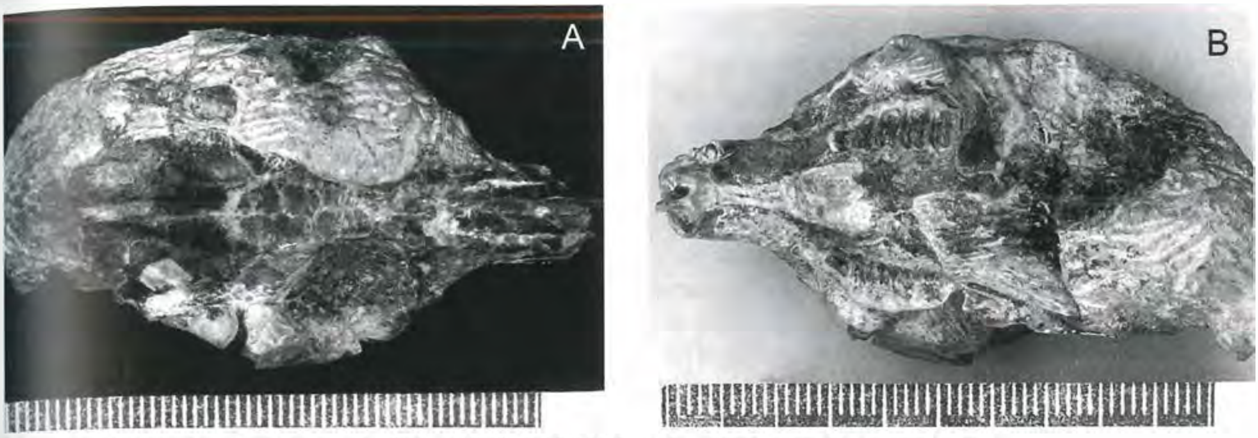

Figure 6: *Ochotona gudrunae* nov. sp. Skull AMNH F:AM 141396 (A – dorsal view, B – ventral view).

mammal paleontology in Asia.

Description: Skull of large size with rather prominent frontals (Fig. 6A; Table 1). Rostrum is relatively short (it does not appear to be collapsed). Nasal bones narrow in their mid-part, narrower anteriorly, and joining frontals. Infra-orbital foramen is large and of triangular shape. Orbits are longer than wide and oval in shape. Interorbital region is narrow with a shallow depression along the midline. Parietals are rather flat. Jugals are wide and rather robust, but the anterior processus zygomaticus is not robust. Confluent incisive-palatal foramina make a pear-shaped opening. The palate is long and wide (Fig. 6B). All cheek teeth are moderately robust and wider than long.

Upper incisors with prominent ochotonid groove demarcating a larger medial and smaller lateral portion. Simple second upper incisor with D-shaped cross section.

The right P2, partially preserved (Fig. 5D), is oval in shape, with a deep but narrow anterior flexus directed posteroexternally and filled with cement, enamel is thick externally.

Left P3 (Fig. 5D) is trapezoidal in shape, its anterior border rather prominent and narrower than its posterior one. The hypostria is short and filled with thin cement. The thin anteroloph is broken and its length may not have exceeded half the tooth width. The U-shaped paraflexus is comparatively short, covering one-third of the tooth width, and is filled with thin cement. The enamel band is thick on the anterior and lingual sides of the tooth and paraflexus. The protocone is considerably wider and longer than the hypocone.

The hypostria of P4-M2 is deep and filled with cement. The anterior portion of M2 is wider than the posterior one, which has a well-developed posterolingual process.

The horizontal ramus of the mandible is robust and deep, being of the same height below p4 and m3. The lower incisor extends posteriorly along the ventral border to the level of m1, and forms on both the medial and lateral sides of the ramus a distinct tubercle at the root end, below p4. The external surface of the mandible body is flat. The lower incisor is oval in cross section, its greatest dimension being in a parasagittal plane, narrower ventrally; enamel restricted ventrolaterally. The diastema is relatively long (Table 2).

All the lower teeth are represented in the specimens, and p3 is relatively large (Fig 5G, Table 2). The occlusal surface is triangular with rounded borders. The anteroconid is rounded in shape, slightly wider than long. The posteroconid is wider than long, and confluent with the anteroconid (Fig. 5G). The paraflexid and protoflexid are narrow and of the same depth, and filled with cement. The hypoflexid is deeper, but not crossing half the tooth, and is wide and filled with cement. The enamel band is thick on the anterior and external side of the posteroconid, but thin to absent on its posterior border. Enamel is completely lacking on the anteroconid.

p4 is a little narrower than m1 and m2; its trigonid is narrower than its talonid, while m1 and m2 have trigonid and talonid of the same width.

Comparisons: *Ochotona gudrunae* sp. nov. differs from all extant species of the genus *Ochotona* by its large size. However, in some morphological characters such as convexity of skull, narrow inter-orbital region, and outline of the occlusal surface of p3, this species resembles extant *Ochotona ladacensis* and *Ochotona koslowi*. However, it differs from the latter species by slightly larger size of skull and teeth as well by the wide confluence of incisive and palatal foramina. The comparison of *Ochotona gudrunae* sp. nov. with all large sized extinct taxa shows that it differs from the Late Miocene *Ochotona lagreli* by its robust teeth and by the structure of its p3, with the rounded anteroconid having wide confluence with the posteroconid. *O. gudrunae* differs from Transbaikalian and Mongolian large sized pikas *Ochotona tologoica*, *O. gromovi*, *O. zazhigini*, as well from *O. whartoni* from Alaska by its robust and larger dentition, and by its broadly confluent anteroconid and posteroconid on p3; in contrast, the latter species have rhomboid anteroconids nearly isolated from posteroconids on p3.

4. Discussion and conclusions

Previously in China, Late Neogene specimens of *Ochotona* were usually ascribed to the species *O. lagreli* or *O. minor*. *Ochotona lagreli* is a large pika common on the loess plateau in deposits of Late Miocene and Early Pliocene age. *O. lagreli* may range into the later Pliocene if a fragmentary pika from a locality in Yushe Basin, Shanxi

Province, dating to the early Gauss magnetic chron (ca. 3.4 Ma), is correctly identified (ongoing research of Wu Wenyu, personal communication.).

O. minor was recognized by Bohlin (1942) as a member of a small body-size Pliocene lineage. Qiu (1987) measured the alveolar length of the lower tooth row in a specimen of *O. minor* from Ertemte as 6.6 mm. Qiu (1985) noted that diminutive *Ochotona* persisted into the Late Pliocene to Early Pleistocene of the Nihewan area, Hebei. He named *Ochotona nihewanica*, one specimen of which has a lower tooth row length (p3-m3) of 6.7 mm (Qiu, 1985). These species are considerably smaller than any of the pikas named in this study.

While *O. minor* and *O. nihewanica* are markedly smaller than the new pikas named here, *O. lagreli* is close in size to *O. chowmincheni* and *O. tedfordi*. As discussed above, the lower premolar (p3) of *O. chowmincheni* is distinctive: although a few examples of *O. lagreli* have a similarly grooved anteroconid, the anteroconid of *O. chowmincheni* is connected by a broad area of dentine to the posteroconid, unlike *O. lagreli* and *O. tedfordi*. The anteroconid shape for many *O. lagreli* is rhomboid as in *O. tedfordi*. Differences in the latter include a deeper hypoflexid and a rounded posterointernal wall, not the flat or even indented border of many *O. lagreli*.

Ochotona gudrunae is larger than any of these species. The holotype is latest Pliocene or possibly earliest Pleistocene in age, certainly younger than *O. lagreli*, which did not survive into the Nihewanian mammal age (Plio/Pleistocene) of China. *O. gudrunae* displays derived cranial and dental conditions: constricted interorbital region, rounded anteroconid on p3 with enamel reduced anteriorly.

Qiu (1987) illustrated the range of variation observed in the dentition of a large sample of the ochotonid species *O. lagreli*. We have recorded characteristics for the single specimens of each of our new species and have attempted to highlight important, diagnostic features. While appreciating that we cannot typify the range of variation likely to be encountered in each new species, we conclude that all of these pikas are distinct.

The described ochotonid taxa are new for the fossil record in China, and consistent with the hypothesis that the Late Miocene and Pliocene species diversity of the genus *Ochotona* was considerable in China as it is today. They also tend to support the related idea that many of the fossil ochotonids were relatively local in distribution. In addition to previously known *Ochotona*, the genus was represented in Shanxi by two new Late Miocene species, *Ochotona chowmincheni* and *O. tedfordi*, but these were from different basins, over 200 km apart. The Late Pliocene *O. gudrunae* was distinctive, a rather large species for the Plio/Pleistocene.

We are beginning to see that some fossil *Ochotona* species had a limited distribution as many do today. They may reflect local variation of the mammalian fauna according to habitat (the northwestern area being more continental) much as other elements of the fauna appear to indicate this (Kurten, 1952). In addition, some species may have been confined in distribution to individual basin or mountain complexes, rather than broadly across the Loess Plateau.

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6. References

Agadjanian, A.K. & Erbajeva, M.A., 1983. Late Cenozoic rodents and lagomorphs of the USSR. — Nauka, **1983**: 1–189, Moscow [in Russian].

Bohlin, B., 1942. A revision of the fossil Lagomorpha in the Palaeontological Museum, Upsala. — Geological Institute Upsala Bulletin, **30** (**6**):117–154, Upsala.

Boule, M. & Teilhard de Chardin, P., 1928. Le Paléolithique de la Chine (Paléontologie). — Archives de l'Institut de Paléontologie Humaine, Mémoires, **4**:95, Paris.

Erbajeva, M.A., 1988. Cenozoic pikas (taxonomy, systematics, phylogeny). — Nauka, **1988**:1–224, Moscow [in Russian].

Erbajeva, M.A., & Zheng, S., 2005. New data on Late Miocene-Pleistocene ochotonids (Ochotonidae, Lagomorpha) from North China. — Acta Zoologica Cracoviensia, **48A** (**1-2**):93–117, Krakow.

Hoffmann, R.S. & Smith, A.T., 2005. Order Lagomorpha. — [in:] Wilson, D.E. & Reeder, D.M. (eds.). Mammal Species of the World, **1**:185-211 (The Johns Hopkins University Press) Baltimore.

Ji, H., Hsu, C. & Huang, W., 1980. The *Hipparion* fauna from Guizhong Basin, Xizang. — Paleontology of Tibet, **1**:18–32, Beijing.

Kurtén, B., 1952. The Chinese *Hipparion* fauna. — Commentationes Biologicae, **13** (**4**):1–82, Helsinki.

López Martínez, N., 1989. Revision sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. — Memorias Museo Paleontoloxico, Universidad Zaragoza, (**3**) **3**:1–343, Zaragoza.

Qiu, Z., 1985. A New ochotonid from Nihewan Bed of

Yuxian, Hebei. — Vertebrata PalAsiatica, **23**:276–286, Beijing.

QIU, Z., 1987. The Neogene mammalian faunas of Ertemte and Harr Obo in Inner Mongolia (Nei Mongol), China. – 6. Hares and pikas – Lagomorpha: Leporidae and Ochotonidae. — Senckenbergiana Lethaea, **67**:375–399, Frankfurt am Main.

QIU, Z. & STORCH, G., 2000. The early Pliocene Micromammalian Fauna of Bilike, Inner Mongolia, China (Mammalia: Lipotyphla, Chiroptera, Rodentia, Lagomorpha). — Senckenbergiana Lethaea, **80**:173–229, Frankfurt am Main.

SCHLOSSER, M., 1924. Tertiary vertebrates from Mongolia. — Palaeontologia Sinica, (C), **1**:1–119, Beijing.

TEILHARD DE CHARDIN, P. & PIVETEAU, J., 1930. Les Mammifères fossiles de Nihowan (Chine). — Annales de Paléontologie, **19**:121–125, Paris.

TEILHARD DE CHARDIN, P. & YOUNG, C.C., 1931. Fossil mammals from the late Cenozoic of Nothern China. — Palaeontologia Sinica, (C), **9** (**1**):1–88, Beijing.

ZDANSKY, O., 1923. Fundorte der Hipparion-Fauna um Pao-Te-Hsien in NW-Shansi. — Bulletin of the Geological Survey, China, **5**:69–82, Peking.

ZHENG, S., 1982. Middle Pliocene micromammals from the Tianzhu Loc. 80007 (Gansu Province). — Vertebrata PalAsiatica, **20**:138–145, Beijing.

ZHENG, S. & LI, Y., 1982. Some Pliocene lagomorphs and rodents from Loc. 1 of Songshan, Tianzu Xian, Gansu Province. — Vertebrata PalAsiatica, **20**:35–44, Beijing.