

# 内蒙古大庙中新世上猿化石地点的 鼠兔科化石<sup>1)</sup>

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**摘要:**鼠兔科虽然是地质历史时期较为繁盛的一个门类,但现在仅有一个属(鼠兔属 *Ochotona*)。*Ochotona* 被认为与 *Bellatona* 有密切的亲缘关系,可能是由后者衍生而来。详细描述了内蒙古大庙上猿化石地点发现的鼠兔科化石,识别出一种古老类型 *Desmatolagus moergenensis* 以及其他三个种 *Bellatona* cf. *B. forsythmajori*, *Bellatonoides eroli*, *Ochotona* cf. *O. lagreli*。归入 *Bellatona*, *Bellatonoides* 和 *Ochotona* 的这三个种的 p3 具有相似的形态,并呈现出连续变化的特征。*Bellatona* 的 p3 具有两个唇侧褶沟,但无舌侧褶沟;*Bellatonoides* 的 p3 具有浅的舌侧前褶沟,但与唇侧前褶沟分开较宽;*Ochotona* 的 p3 则具有深的舌侧前褶沟,与唇侧前褶沟之间仅以很窄的齿质桥连接。M2 从无后突起、较小的后突起至发育的后突起,也呈现出连续变化的特征。中间颊齿则难以区分。因此,推测这三个种之间存在连续的线性演化关系,*Ochotona* 可能直接起源于 *Bellatonoides*。磁性地层学与生物地层学对比结果显示该地点的年代约为 12 Ma,与根据分子钟推测的 *Ochotona* 的分化时间基本一致。

**关键词:**内蒙古,中新世,鼠兔科,鼠兔属,起源

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## MIDDLE MIOCENE OCHOTONIDS (OCHOTONIDAE, LAGOMORPHA) FROM DAMIAO PLIOPITHECID LOCALITY, NEI MONGOL

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**Abstract** Although highly diversified in their early history, only one genus in Ochotonidae, *Ochotona*, survives to the present. *Ochotona* is generally accepted to have originated from the Middle Miocene *Bellatona*. During the 2006–2010 field seasons, we found Miocene localities at Damiao, Siziwang Qi, Nei Mongol, which produced rich materials of ochotonids. Of these localities, DM01 (pliopithecoid locality), dated by the paleomagnetic method and faunal comparison as late Middle Miocene (~12 Ma), yielded rich materials of the *Bellatona*–*Bellatonoides*–*Ochotona* group, and a large-sized relic form assigned to

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*Desmatolagus moergenensis*. The p3 morphology of the *Bellatona*-*Bellatonoides*-*Ochotona* complex conserves a similar tooth outline, but with distinct successive structures. The *Bellatona* form has two labial folds and no lingual fold on p3. The p3 of *Bellatonoides* form has one shallow anterolingual fold that is widely separated from the anterolabial fold. The p3 of *Ochotona* has a deep anterolingual fold that is closely connected with the anterolabial fold by a central bridge. The posterior process on M2 also shows progressive enlargement from *Bellatona* to *Ochotona*. Other cheek teeth of this complex are not distinguishable by either morphology or size. With only teeth found, we tentatively propose successive linear evolutionary relationships of the *Bellatona*-*Bellatonoides*-*Ochotona* complex, and *Ochotona* may have directly originated from *Bellatonoides* during the late Middle Miocene. The geological age of this fossil locality is consistent with the divergence time of *Ochotona* as estimated by molecular dating methods.

**Key words** Nei Mongol, Middle Miocene, Ochotonidae, *Ochotona*, Origin

## 1 Introduction

Pikas are a group of small-sized lagomorphs and are most diversified in Asia (only two species from North America and one from Europe). Asia was generally accepted as the center of origin for Ochotonidae by fossil records. However, the divergence time is still controversial, apparently either Late Eocene or Oligocene in age, with dispute over the family status of *Desmatolagus* (Dawson, 2008; Erbajeva, 1994; Erbajeva et al., 2011). Though diversified in their early history, only one genus in Ochotonidae, *Ochotona*, survives to the present. The origin of *Ochotona* commonly has been accepted as close to *Bellatona* from the Middle Miocene (Dawson, 1961; Qiu, 1996; Erbajeva et al., 2011). In 2003, Sen described a new genus *Bellatonoides* from Sinap Tepe (Vallesian age) which shows its tooth morphology intermediate between that of *Bellatona* and *Ochotona*. He further stated that this new genus should be an Asiatic immigrant. Therefore, late Middle Miocene to early Late Miocene should be a critical time period for the origination of *Ochotona*. Rich materials of *Ochotona* have been found in Chinese Late Miocene to Pliocene deposits. However, most known records of *Ochotona* species are confined to the late Late Miocene (Baodean age) or later (Schlosser, 1924; Qiu, 1987; Ji et al., 1980; Erbajeva et al., 2006; Erbajeva and Zheng, 2005). Records of Bahean and Tunggurian age are rare and not systematically studied until now.

From 2006, we found some new localities from Damiao, Siziwang Qi, Nei Mongol (Inner Mongolia, China). By preliminary faunal comparison, the faunas from different horizons cover the time from Early Miocene to Late Miocene (Zhang et al., 2011). Among these localities, the pliopithecoid locality DM01 (Zhang and Harrison, 2008) yielded rich materials of the *Bellatona*-*Ochotona* group with a large-sized archaic form recognized as ? *Desmatolagus moergenensis*. Systematic study of these materials will improve the understanding of the evolution of Ochotonidae and the origin of *Ochotona*.

## 2 Geological setting

The fossil locality DM01 (N42°00'31.4", E111°34'50") is situated on the east side of the motorway from Wulanhua to Damiao village. The series of exposures investigated extend for about 1 km E-W along a gently sloping gully system. The stratigraphic sequence consists of an approximately 40-m section of fluvial sediments that unconformably overlie the deeply weathered granitic basement. The lower portion of the sequence is dominated by coarse-grained channel-fill deposits, whereas floodplain sands and silts comprise most of the remaining sedimentary succession. The fossils in DM01 are derived from a 1-1.5 m-thick distinct nodule conglomerate that occurs within a fine-grained floodplain sequence. The conglomerate has lateral extent up to 60 m, its cross-sectional shape is tabular and basal surface typically exhibits limited basal ero-

sion. Internally, the conglomerate comprises a series of stacked, clast-supported granule-pebble beds with sandstone alternations. The well-rounded clasts are predominantly composed of reworked calcretic nodules, typically with intense manganese and iron staining. Detailed geological and stratigraphic study of the section can be referred to Kaakinen et al. (in prep). Zhang et al. (2011) gave a primary study of the faunas from this area.

### 3 Materials and method

Fossils found from DM01 are mostly isolated teeth. No skulls or well preserved jaws of ochotonids were discovered by excavation and wet sieving unfortunately. The shortcoming of these materials may lead to uncertainty of taxonomy and limited systematic study, considering the uniformity of tooth morphology of central cheek teeth and individual variation of the anterior and posterior cheek teeth. Because the central cheek teeth of *Bellatona*, *Bellatonoides*, and *Ochotona* are almost indistinguishable, we temporarily use Ochotonidae gen. et sp. indet. for cataloging (IVPP V 18494), and they are not systematically described herein.

Terminology of cheek teeth for Ochotonidae is quite controversial (Erbajeva, 1988; López-Martínez, 1989; Kraatz et al., 2010). Here, we simply describe the tooth morphology, using descriptive and commonly accepted terms to avoid further confusion in not knowing the homology in detail.

Measurements of the teeth are taken under a Zeiss V8 Microscope with an accuracy of 0.01 mm. The photos are taken by Hitachi S3700n Electronic Scanning Microscope. All specimens described in this paper are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

### 4 Systematic paleontology

#### Order Lagomorpha Brandt, 1855

#### Family Ochotonidae Thomas, 1897

#### Genus *Desmatolagus* Matthew & Granger, 1923

#### *Desmatolagus moergenensis* Qiu, 1996

(Fig. 1; Table 1)

**Materials** 2 I2 (IVPP V 18490.1-2), 1 right dp3 (V 18490.3), 1 and half dp4 (V 18490.4-5), 7 left and 3 right p3 (V 18490.6-15), 23 p4/m1 (V 18490.16-38), 3 m2 (V 18490.39-41), 1 DP4 (V 18490.42), 3 P2 (V 18490.43-45), 6 P3 (V 18490.46-51), 8 P4 (V 18490.52-59), 5 M1 (V 18490.60-64), 6 M2 (V 18490.65-70).

**Diagnosis (emended)** Very large sized ochotonid. P2 has two anterior folds, single root. Anterior loph on P3 crosses about two-thirds the width of the tooth, crescentic valley has two symmetrical branches. Upper cheek teeth unilaterally hypsodont and labially curved. Hypostria on P4-M2 crosses about one-third of the occlusal width. The p3 has a subtriangular occlusal surface with only one anterolabial fold crossing about half of the occlusal width. Lower cheek teeth high-crowned and rooted. Lower molar has a posterior cingulum on less worn individuals.

**Measurements** See Table 1.

**Description** I2 is large, moderately curved. The anterior groove divides the labial surface into two parts. The mesial part is narrow and protrudes anteriorly and slowly high up to the mesial side of the tooth, while the distal part is much wider and rounded in shape. The lingual side shows a slightly concave surface.

DP4 is molariform, but smaller than the permanent molars. The occlusal surface is roughly

rectangular, with slightly out-bowed anterior and posterior sides. There are three cusps on the labial side. The central cusp is sharply angled, with the anterior loph laterally extended and connecting with the large labial central cusp, while the posterior loph extends posterolabially, connecting with the posterior labial cusp to enclose a basin-like fold. The hypostria is moderately deep.

**Table 1** Tooth measurements of *Dematolagus moergenensis* from DM01 locality (mm)

|       |            |     |      |      |      |      |      |      |     |     |     |     |      |
|-------|------------|-----|------|------|------|------|------|------|-----|-----|-----|-----|------|
|       | V 18490    | .43 | .44  | .45  |      |      |      |      |     |     |     |     |      |
| P2    | L          | 0.8 | 1.1  | 0.8  |      |      |      |      |     |     |     |     |      |
|       | W          | 1.7 | 2.2  | 1.2  |      |      |      |      |     |     |     |     |      |
|       | V 18490    | .46 | .47  | .48  | .49  | .50  | .51  |      |     |     |     |     |      |
| P3    | L          | 2.5 | 1.8  | 2.4  | 2.6  | 2.4  | 2.0  |      |     |     |     |     |      |
|       | W          | 3.2 | 3.0  |      | 3.5  | 3.5  |      |      |     |     |     |     |      |
|       | V 18490    | .52 | .53  | .54  | .55  | .56  |      |      |     |     |     |     |      |
| P4    | L          | 3.0 | 2.5  | 2.2  | 2.0  | 2.5  |      |      |     |     |     |     |      |
|       | W          | 7.5 | 5.55 | 6.25 | 3.6  | 6.0  |      |      |     |     |     |     |      |
|       | V 18490    | .61 | .62  | .60  | .63  | .64  |      |      |     |     |     |     |      |
| M1    | L          | 2.3 | 2.3  | 2.3  | 2.25 | 2.0  |      |      |     |     |     |     |      |
|       | W          | 4.7 | 3.6  | 4.0  | 4.2  | 3.25 |      |      |     |     |     |     |      |
|       | V 18490    | .65 | .66  | .67  |      |      |      |      |     |     |     |     |      |
| M2    | L          | 2.0 | 2.4  | 2.1  |      |      |      |      |     |     |     |     |      |
|       | W          | 4.0 | 4.3  | 4.25 |      |      |      |      |     |     |     |     |      |
|       | V 18490    | .6  | .7   | .8   | .9   | .10  | .11  | .12  | .13 | .14 | .15 |     |      |
| p3    | L          | 2.3 | 2.2  | 2.1  | 1.5  | 1.5  | 1.45 | 0.9  | 1.5 | 1.7 | 2.2 |     |      |
|       | W          | 2.9 | 2.6  | 2.5  | 1.75 | 1.55 | 1.6  | 1.0  | 2.1 | 1.9 | 2.4 |     |      |
|       | V 18490    | .16 | .18  | .19  | .20  | .21  | .25  | .26  | .28 | .30 | .33 | .36 | .38  |
| p4/ml | L          | 3.5 | 2.8  | 2.25 | 2.25 | 2.0  | 2.5  | 2.15 | 3.3 | 3.5 | 3.0 | 2.7 | 3.25 |
|       | W-trigonid | 3.7 | 2.7  | 2.1  | 2.0  | 2.0  | 2.5  | 2.1  | 3.0 | 3.2 | 2.7 | 2.8 | 2.8  |
|       | W-talonid  | 2.2 | 2.1  | 1.5  | 1.7  | 1.2  | 1.7  | 1.5  | 2.3 | 2.2 | 1.7 | 1.6 | 2.2  |
|       | V 18490    | .39 | .40  | .41  |      |      |      |      |     |     |     |     |      |
| m2    | L          | 2.6 | 1.9  | 2.2  |      |      |      |      |     |     |     |     |      |
|       | W-trigonid | 2.3 | 2.0  | 2.4  |      |      |      |      |     |     |     |     |      |
|       | W-talonid  | 1.9 | 1.6  | 1.5  |      |      |      |      |     |     |     |     |      |

P2 is single rooted, with the shaft slightly curved posteriorly and much shorter than wide, shaping a narrow oval occlusal outline. Two anterior folds separate three cusps. The lingual cusp is the largest, the middle cusp is smaller and protrudes anteriorly, and the labial cusp is the smallest, ridge-like, and antero-posteriorly extended. The lingual fold extends posterolabially and the labial fold antero-posteriorly.

P3 is much larger than P2. The tooth shaft is curved labially. Three roots are visible. The single lingual root is strong on aged individuals; the two labial roots are barely recognizable.

Different from P2, P3 shows strong unilaterally hypsodont. The inner lobe has a slight concave lingual side (namely very shallow hypostria). The anterior ridge of the inner lobe is lower on less worn teeth and extends labially far, crossing two thirds of the occlusal width. The central lobe (central cusp) is the most prominent on the occlusal surface, with two roughly equal length ridges shaping the symmetrical crescentic valley. The inner lobe is round and more isolated.

P4 is the largest upper cheek tooth, with wide rectangular occlusal surface. The shaft is labially curved with one strong lingual root and two small labial roots. The hypostria is shallow and diminishes gradually downward with wear. On the well worn specimens, no hypostria exists and the lingual side has a sharp triangular shape. There are two cusps on the labial side of the tooth. The anterior branch of the crescentic valley extends to the anterior labial cusp.

M1 is similar to P4, but smaller and more oval-shaped with slightly convex anterior and posterior sides. The hypostria is deep and extends to the crescentic valley. On worn individuals, the hypostria is truncated into a shallow lingual groove and an isolated enamel island inside. The posterior labial cusp is slightly lingually located.

M2 has a slightly posteriorly curved shaft and strongly unilaterally hypsodont crown. The lingual root is large, while the labial anterior root is small and the posterior labial root almost unrecognizable. The width of the posterior lobe is narrower than the anterior lobe, due to the lingually shifted and diminished labial posterior cusp and short posterior lingual side. The hypostria is only slightly shorter than on M1. The anterior branch of the crescentic valley extends to the anterolabial cusp and the posterior branch extends backwards to the posterior wall.

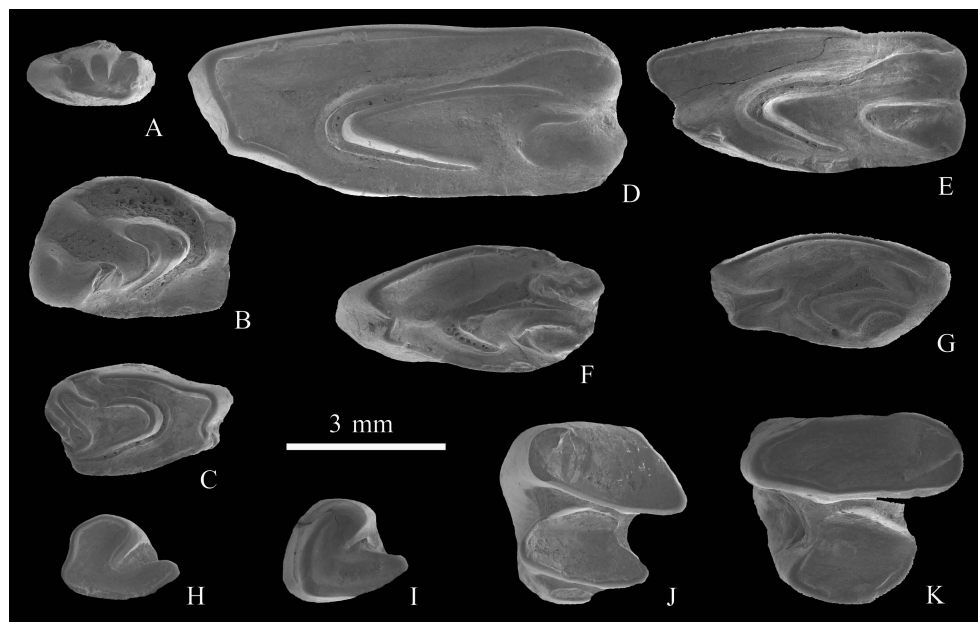


Fig. 1 Cheek teeth in occlusal view of *Desmatolagus moergenensis* from DM01 locality, Nei Mongol A. P2 (IVPP V 18490.43); B-C. P3 (V 18490.46-47); D-E. P4 (V 18490.52-53); F. M1 (V 18490.60); G. M2 (V 18490.65); H-I. p3 (V 18490.13-14); J. m1 (V 18490.38); K. p4 (V 18490.16)

The dp3 has three lobes connected by two central longitudinal bridges. The anterior lobe has a deep and wide groove on the anterolabial side and one very shallow depression on the anterolingual side. The posterior lobe is wider than the middle one. On the anterior wall of the labial side there is an anterior directed protrusion. On the posterior wall of the posterior lobe there exists a small cingulum.

The dp4 has two lobes without enamel connection. The anterior lobe is slightly wider but shorter than the posterior one, which has a posterior cingulum attached.

The p3 has a roughly triangular occlusal surface with only one fold on the antero-labial side. The fold is deep and reaches to about half the width of occlusal surface. On an almost unworn specimen, there is a very shallow groove on the lingual side that soon diminishes with wear. On well worn specimens, the root is strong and fused by two roots. The anterior root below the trigonid is much narrower than the posterior one. The length and width approach a maximum at later wear stage.

The p4 and m1 are very similar in morphology, almost indistinguishable, except that m1 has a slightly curved shaft and possibly a posterior cingulum when unworn. The anterior lobe (trigonid) is short and wide, and the posterior lobe (talonid) is oval-shaped with a shallow depression on its anterolabial side. The length of the anterior lobe is generally shorter than that of the posterior lobe, especially on less worn specimens. There is one fused root that is separated into two on well worn individuals.

The m2 resembles m1, but has a more posteriorly curved shaft. There is also a posterior cingulum on less worn specimens.

**Comparison and discussion** By tooth measurements, the species here described is similar to larger species of *Lepus* in size. However, the separation of two lobes (trigonid and talonid) on the lower p4-m2, non-molariform P3, and the uneven parts of I2 with a sharp elevation on the mesial side are consistent with characters of Ochotonidae. Having roots on cheek teeth, crescentic valley, and shallow hypostria on P4-M2, existence of posterior cingulum on m1-m2, and simplified structure on p3 exclude its relationship with those taxa frequently recorded from the Early and Middle Miocene in China, such as *Sinolagomys*, *Alloptox*, *Bellatona*, and late Neogene ochotonids such as *Ochotona*, *Ochotonoma*, and *Ochotonoides*. The size and tooth morphology of the present form fit very well with *Desmatolagus* ? *moergenensis* Qiu, 1996 discovered from the classical Tunggur fauna. According to Qiu (1996), the species has closer affinity with *Desmatolagus* than *Amphilagus*, and may be referred to a new genus together with ? *Desmatolagus schizopterus* from North America (Dawson, 1965). Given the paucity of materials (no lower premolars and molars), he refrained from naming a new genus and assigned the species in *Desmatolagus* temporarily with question. Hence the correct name should be ? *Desmatolagus moergenensis*.

The type species of *Desmatolagus*, *D. gobiensis* was named by Matthew and Granger (1923) based on specimens from the Hsanda Gol Formation in Mongolia. The most recent study shows that *D. gobiensis* occurred from Biozone A-C from the Valley of Lakes area (Daxner-Höck et al., 2010). However, the early forms *D. vetustus* and *D. ardynense* were recorded in the Late Eocene (Meng and Hu, 2004; Meng et al., 2005). Diagnosis of the genus by Matthew and Granger (1923) was too simple, and only emphasized the reduction of first and last cheek teeth and the same tooth formula as Leporidae. The paucity of well preserved specimens and simple diagnosis led to argument of taxonomy of some species referred to *Desmatolagus* or a new genus (Gureev, 1960; Muizon, 1977; Huang, 1987; Erbaeva and Sen, 1998). A systematic review of *Desmatolagus* is out of the scope of this paper and badly needs better preserved specimens. In general, the species referred to *Desmatolagus* have tooth formula: 2. 0. 3. 3/1. 0. 2. 3, upper cheek teeth unilaterally hypsodont with labial roots, lower cheek teeth high crowned with or without roots, presence of shallow hypostria, and crescentic valley on P4-M2, triangular-shaped occlusal surface of p3 with simple structure. The Damiao specimens here described, although much larger than all published Eocene and Oligocene samples, have tooth morphology close to *Desmatolagus*. Hence we prefer to recognize the existence of *Desmatolagus* during the Middle Miocene and name the Damiao form as *D. moergenensis*.

A few teeth found from the Lower and Upper Miocene localities at Damiao have similar

tooth morphology as the DM01 form (Zhang et al., 2011). Similar form was also found previously from Early to Late Miocene localities in the Aoerban area (Wang et al., 2009). Therefore, *Desmatolagus moergenensis* can be considered as a relic species of the genus which was flourishing during the Late Eocene and Oligocene and survived to the Late Miocene.

### Genus *Bellatona* Dawson, 1961

#### *Bellatona* cf. *B. forsythmajori* Dawson, 1961

(Fig. 2; Table 2)

**Materials** 28 left p3 (IVPP V 18491.1-28), 20 right p3 (V 18491.29-48), 2 P2 (V18491.49-50), 2 M2 (V 18491.51-52).

**Measurements** See Table 2.

**Description** The p3 shaft curves slightly inward. The occlusal surface is basically triangular with a sharp and linguallly shifted anteroconid. The lingual side of the anteroconid varies from a wide and shallow depression on half of the specimens, to no depression on others. On five specimens the anterolabial fold is very shallow without cement filling (Fig. 2A). On the other specimens (42), the anterolabial fold is deeply extended to the central axis of the tooth or even further, and completely filled with cement (Fig. 2B-C). The posterolabial fold is about parallel with the anterolabial fold, slightly less than half the width of the talonid. The lingual side of the talonid, mostly straight longitudinally, has a shallow groove on one specimen.

**Table 2** Statistical data of p3 measurements for *Bellatona* cf. *B. forsythmajori* from DM01 (mm)

|        | N  | Mean | Max  | Min | STDEV |
|--------|----|------|------|-----|-------|
| Length | 32 | 1.41 | 1.65 | 1.1 | 0.133 |
| Width  | 32 | 1.33 | 1.6  | 1.0 | 0.154 |

P2 has a slightly posteriorly curved shaft. The anterior surface is out-bowed and the posterior surface flat or slightly concave. The occlusal surface shows rounded labial and lingual sides. There is an anterior fold filled with cement on one specimen and no fold on the other specimen.

M2 has a slightly narrower posterior lobe. There is no posterior process on one specimen (Fig. 2P) and one slightly protruding process on the other specimen (Fig. 2Q).

**Comparison** Dawson (1961) named the genus and species *Bellatona forsythmajori*, based on specimens from Tairum Nor Basin, Nei Mongol. Later, *Bellatona yanghuensis* was erected by Zhou (1988). Qiu (1996) questioned the validity of *B. yanghuensis* and indicated that the only difference between these two species is the presence or absence of an anterior fold on P2, while waiting for more material to test intraspecific variation. The above described form shows close similarity with *B. forsythmajori* in having an anterolabial fold (either shallow or deep), but differs from *B. yanghuensis*, which has no anterolabial fold on p3. The anterolingual part of the trigonid on p3 from Damiao has a shallow depression on half of the specimens, a feature also recorded from some specimens from Tairum Nor and Moergen II (Qiu, 1996). Of our two P2 specimens, one has no anterior fold and the other has a deep anterior fold. If the assignment of the p3s to *B. forsythmajori* is valid, and the P2s are from the same species, the absence of an anterior fold on P2 may represent individual variation. Of the two M2 specimens from DM01 locality, one has no posterior process, while the other has a slightly protruding process and could be referred to *Bellatona*.

**Genus *Bellatonoides* Sen, 2003**  
***Bellatonoides eroli* Sen, 2003**

(Fig. 2; Table 3)

**Materials** 2 left p3 (IVPP V 18492. 1-2), 4 right p3 (V 18492. 3-6).

**Measurements** See Table 3.

**Description** The tooth size falls in the range observed in *Bellatona*. The tooth shaft and occlusal surface outline are also as in *Bellatona forsythmajori*. The anteroconid is delimited posteriorly by a deep labial fold and a shallow but prominent fold that is not present in specimens referred to *Bellatona*. The anteroconid on the worn specimens is located labially across the mid-line of the tooth. The connection between the labial and lingual anterior fold is wide.

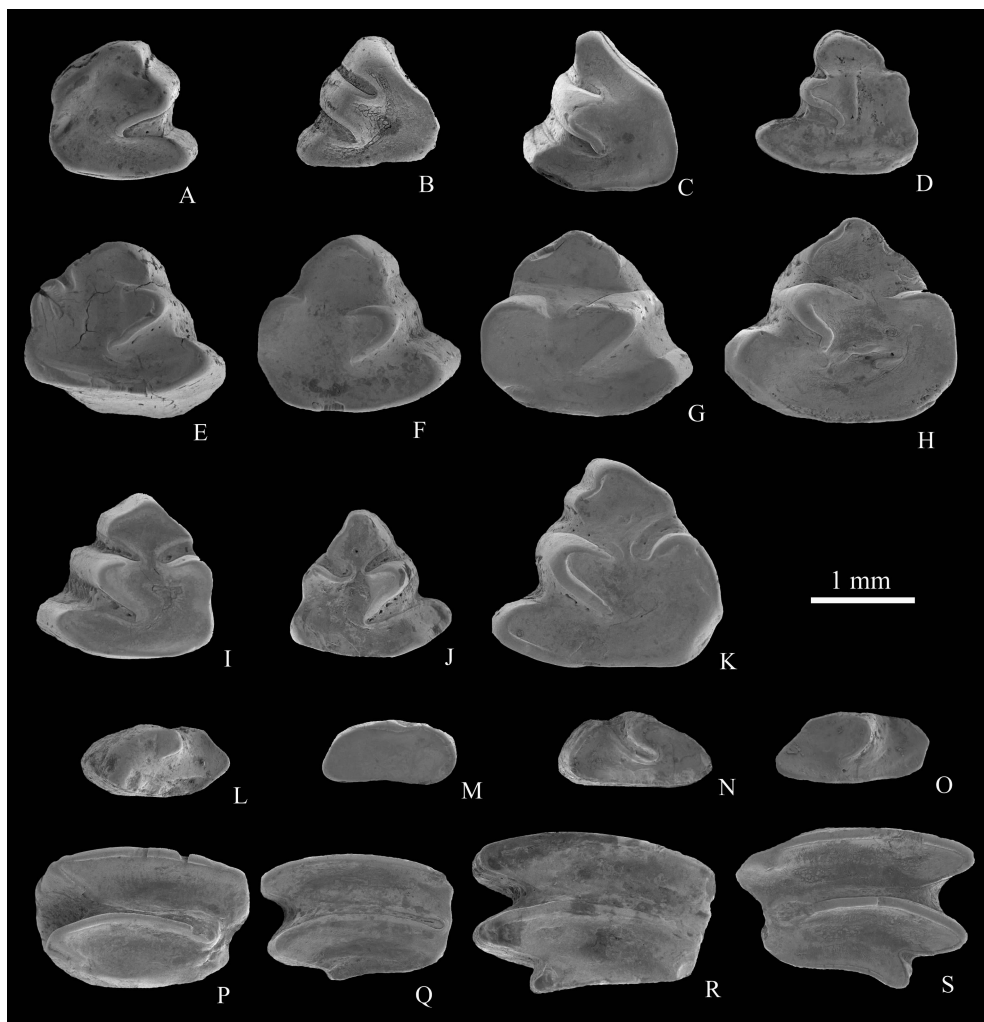


Fig. 2 Selected cheek teeth in occlusal view from DM01 locality, Nei Mongol  
*Bellatona* cf. *B. forsythmajori*: A-C. p3 (V 18491. 29, 1-2), L-M. P2 (V 18491. 49-50), P-Q.  
M2 (V 18491. 51-52); *Bellatonoides eroli*: D-F. p3 (V 18492. 1, 3-4); *Ochotona* cf. *O. lagreli*:  
G-K. p3 (V 18493. 11, 2, 3, 12, 1); Ochotonidae gen. et sp. indet.: N-O. P2 (V 18494. 1-2),  
R-S. M2 (V 18494. 3-4)



**Table 3** Measurements for six p3 of *Bellatonoides eroli* from DM01 locality (mm)

| Specimen | V 18492. 1 | . 2  | . 3  | . 4   | . 5  | . 6   |
|----------|------------|------|------|-------|------|-------|
| Length   | 1. 25      | 1. 3 | 1. 4 | 1. 65 | 1. 4 | 1. 25 |
| Width    | 1. 3       | —    | 1. 5 | 1. 6  | 1. 3 | 1. 1  |

**Comparison and discussion** Among the specimens described as *Bellatona forsythmajori* by Dawson(1961), some of p3s have only a shallow depression on the lingual side of the anteroconid(Dawson, 1961:fig. 6), but no fold. Qiu(1996)included some specimens from Moergen V in *B. forsythmajori* which show a shallow anterolingual fold(Qiu, 1966:fig. 721). This form becomes more abundant in the younger Amuwusu fauna. Sen(2003) named a new genus *Bellatonoides* based on specimens collected from Sinap Tepe Loc. 8A(Vallesian age). This genus is characterized by the labially located and rounded anteroconid that is delimited by a deep labial fold(protoflexid) and a shallow lingual fold(paraflexid). The central bridge is wide. Hence, Qiu et al. (2006) listed the Amuwusu form as *Bellatonoides* sp. However, Fostowicz-Frelik et al. (2010) questioned the validity of *Bellatonoides*, and considered it as *Ochotona*, which quickly dispersed outside China shortly after the last appearance of *Bellatona*. The p3s found from DM01, showing almost identical characters with the type species *Bellatonoides eroli*, seem to confirm the validity of this genus. But M2 on the type species has a strong posterior process similar to that of *Ochotona* species. It is now difficult to recognize which M2s should be assigned to the *Bellatonoides* species.

### Genus *Ochotona* Link, 1795

#### *Ochotona* cf. *O. lagreli* Schlosser, 1924

(Fig. 2; Table 4)

**Materials** 10 left p3(IVPP V 18493. 1-10), 12 right p3(V 18493. 11-22).

**Measurements** See Table 4.

**Table 4** Measurements for p3 of *Ochotona* cf. *O. lagreli* from DM01 locality (mm)

| V 18493 | . 1   | . 2  | . 3   | . 4  | . 5   | . 6  | . 7   | . 8  | . 9   | . 10 | . 11 | . 12 | . 13  | . 14  | . 15 | . 16 | . 17  | . 18  | . 19 | . 20 | . 21  | . 22 |
|---------|-------|------|-------|------|-------|------|-------|------|-------|------|------|------|-------|-------|------|------|-------|-------|------|------|-------|------|
| Length  | 1. 85 | 1. 8 | 1. 4  | 1. 4 | 1. 5  | —    | 1. 75 | 1. 5 | 1. 45 | 1. 4 | 1. 7 | 1. 3 | 1. 4  | —     | 1. 1 | 1. 2 | 1. 45 | 1. 5  | 1. 4 | 1. 5 | 1. 5  | 1. 7 |
| Width   | 2. 0  | 1. 9 | 1. 25 | 1. 3 | 1. 55 | 1. 5 | 1. 55 | 1. 5 | 1. 5  | 1. 1 | 1. 6 | 1. 0 | 1. 15 | 1. 25 | 1. 1 | 1. 1 | 1. 6  | 1. 45 | 1. 5 | 1. 6 | 1. 65 | 1. 4 |

**Description** The p3 shaft is inward curved. The occlusal surface is subtriangular in shape. The anteroconid generally shows a rhombus outline, but is deformed on some specimens. There is a shallow depression on the anterolabial side of the anteroconid on some larger specimens. The anterolabial and anterolingual folds are about equal in depth and closely connected by a narrow bridge. Parallel to the anterolabial fold, the posterolabial fold extends also posterolingually to about half the width of the talonid. The lingual side of the talonid is straight or slightly concave. There is an isolated enamel island in the talonid on one specimen.

**Comparison and discussion** By the tooth size, the Damiao form is larger than *Ochotona minor* recorded from Ertemte(Qiu, 1987). The average size is smaller than *O. lagreli* from Ertemte, but with some overlapping. The tooth morphology is almost indistinguishable with *O. lagreli* and *O. minor*. The occurrence of the central enamel island on the talonid in one specimen from Damiao and one from Ertemte is enigmatic for its homology.

## 5 Evolutionary process of the *Bellatona-Bellatonoides-Ochotona* lineage

### 5.1 Morphological changes

By tooth size, the described specimens respectively assigned to *Bellatona* cf. *B. forsyth-majori*, *Bellatonoides eroli*, and *Ochotona* cf. *O. lagreli* are almost indistinguishable, except that the last species has greater size variation (Fig. 3). The p3s of the three species are all sub-triangular in occlusal outline, and show similar depth of the labial folds. The *Bellatona* form has two labial folds and no lingual fold on p3. The p3 of *Bellatonoides* has one shallow anterolingual fold that is widely separated from the anterolabial fold. The p3 of *Ochotona* form has a deep anterolingual fold that is close to the anterolabial fold. It is highly tenable that the p3 form changes with only deepening of the anterolingual fold from *Bellatona*, via *Bellatonoides* to the *Ochotona* form successively. There are more than 70 specimens of M2 from DM01. The taxonomic assignment is not certain, given the gradual changes of the posterior process, except that *Bellatona* has almost no or only a slightly protruding posterior process. We await better preserved specimens to determine the separation of *Bellatonoides* and *Ochotona*. Hundreds of other cheek teeth found from DM01 locality are difficult to separate by either size or morphology. Hence, we suggest the possible uniformity of these teeth on the three species.

With only isolated teeth found, we tentatively propose successive linear evolutionary relationships of the *Bellatona-Bellatonoides-Ochotona* complex, and *Ochotona* may have originated directly from *Bellatonoides*.

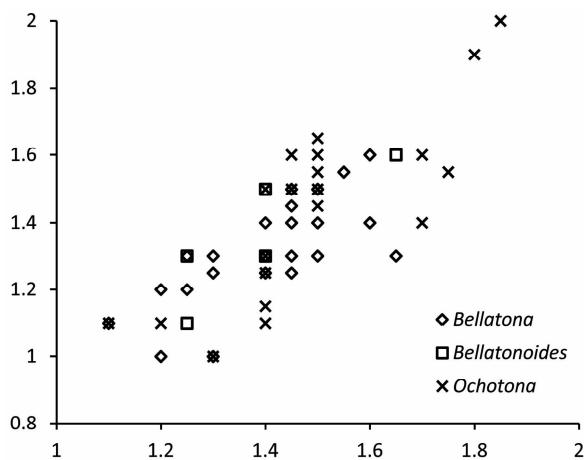


Fig. 3 Scatter plot for p3 size of *Bellatona-Bellatonoides-Ochotona* from DM01 locality, Nei Mongol X-axis: length; Y-axis: width (in mm)

The fragmentary nature of fossils from DM01 and their sedimentary environments may suggest a secondary depositional process and mixture of fossils from different horizons. But the consistency of the faunal composition excludes the possibility for a great mixture of different faunas. Qiu et al. (2006) recognized three subordinated faunas from the traditional Tunggur Formation. The DM01 fauna is very close to the Moergen faun and Tamuqin fauna, and different from the Tairum Nor fauna (Zhang et al., 2011). Therefore, the coexistence of these three closely related ochotonid species may actually reflect a fast speciation process during a relatively short time interval.

### 5.2 Divergence time of *Ochotona*

Preliminary magnetostratigraphic results indicate that the DM01 locality occurs in the chron C5An, about 12-12.4 Ma (Kaakinen et al., in prep). Faunal comparison with the classical Middle Miocene Tunggur faunas, which were paleomagnetically dated in the 11.8-13 Ma range (Wang et al., 2003; Zhang et al., 2011) confirms the dating.

The divergence times inferred from fossil records and molecular dating are not always consistent. For the Leporidae-Ochotonidae split, there are three models, e. g. 31, 37 and 65 Ma models. The 31 Ma scenario was clearly induced by the exclusion of *Desmatolagus* as an

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