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Comparative skull morphology of two pika species (*Ochotona princeps* and *O. hyperborea*): implications for differences in feeding habits

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ABSTRACT. To examine the hypothesis that cranium and mandible morphology influence different feeding habits in pikas, we compared two samples: *Ochotona princeps* from California and Nevada, USA and *O. hyperborea* from Hokkaido, Japan. These pika species show similar ecological traits, are allopatrically distributed in Northern Hemisphere, and inhabit rocky hillsides on mountain. Of all measurements, 55% showed no significant differences, indicating the two samples had similarly sized and shaped skulls. Measurements with significant differences were related to origins and terminations of chewing muscles. Morphological differences between these two samples may result from differences in feeding habits.

KEY WORDS: American pika, northern pika, chewing muscles, cranium, mandible

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Сравнительная морфология черепа двух видов пищух (*Ochotona princeps* and *O. hyperborea*): различия в пищевой специализации

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РЕЗЮМЕ: Для проверки влияния пищевой специализации на морфологию черепа и нижней челюсти было проведено сравнение двух выборок пищух: *Ochotona princeps* из Калифорнии и Невады, США и *O. hyperborea* с о-ва Хоккайдо, Япония. Эти виды пищух сходны по экологии и аллопатрически распространены в Северном Полушарии, населяя каменистые склоны гор. По 55% промеров не обнаружено различий между видами, что свидетельствует о сходных размерах и морфологии черепа обоих видов. Промеры, показывающие наибольшие различая, связаны с местами крепления жевательных мышц. Эти морфологические различия могут свидетельствовать о разной пищевой специализации исследованных видов.

КЛЮЧЕВЫЕ СЛОВА: американская пищуха, северная пищуха, жевательные мышцы, череп, нижняя челюсть.

Introduction

There is a direct correlation between feeding characteristics and skull morphology in mammals (e.g., Feldhamer *et al*., 2004). This correlation is among genera, families, and orders, as well as within species and among closely related species. For instance, the differences in skull morphology among populations of raccoon dog *Nyctereutes procyonoides* may result from the differences in their carnivorous diets (Kauhala *et al*., 1998). There is a correlation between feeding type and mandibular corpus height in populations of sika deer *Cervus nippon* (Ozaki *et al*., 2006). Examination of skull morphology helps to explain environmental adaptation of feeding habits in mammals.

To examine how skull shape changed with feeding habits, we compared with skull measurements of two pika species: the American pika *Ochotona princeps* and the northern pika *O. hyperborea*. In the Northern Hemisphere, 31 *Ochotona* species are identified (Wilson & Reeder, 2005). Of them, we selected two allopatric species (*O. princeps* and *O. hyperborea*) based on distribution, external characteristics, and habitat.

Ochotona princeps occurs in the western part of North America. *Ochotona hyperborea* is widely distributed in northern part of Eurasia, Sakhalin Island of Russia, and Hokkaido Island of Japan (Abe *et al*., 2005; Wilson & Reeder, 2005). The external characteristics

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of *Ochotona princeps* are very similar to those of *O. hyperborea* (Smith & Weston, 1990). In fact, these two species, and other two species (*O. alpina* and *O. collaris*), have been treated as a single species (*O. alpina*) (Argiropulo, 1948; Gureev, 1964; Corbet, 1978). In addition, both species inhabit rocky banks in mountain areas, showing similar ecological traits (e.g., Smith *et al.*, 1990).

These two species, however, are not closely related to each other (Niu *et al.*, 2004; Lissovsky *et al.*, 2007). The similar morphological and ecological characteristics between them may indicate adaptive convergence for a specific habitat. Although both species commonly inhabit rocky banks, the vegetation spectrum in *O. hyperborea* habitat is so huge and various that is covers not only *O. princeps*'s spectrum, but some additional species also. The spectrum of *O. hyperborea* in Hokkaido Island, however, is different from that of *O. princeps*. Any significant differences in skull measurements, such as mandible height, are likely to result from differences in feeding behavior, as a resulted from differences in vegetation.

Of all *Ochotona* species, the food habits of these two species are well studied: *O. princeps* mainly uses grasses, forbs, and cushion plants (Huntly *et al.*, 1986) and lichens (Conner, 1983), and *O. hyperborea* also feeds grasses and forbs (Inukai, 1931; Sakagami *et al.*, 1956; Haga, 1960). The food resources of two pika species, however, evidently differ in species of plants. These differences in food may affect the shape of cranium and mandible associated with chewing muscles. For instance, jaw muscles of pika species that successfully eat more indigestible resources may be more powerfully developed, and this may affect the shape of mandible because jaw muscles attach directly the mandible. Although it is difficult to morphologically compare different species because each species may have geographic variations (Lissovsky, 2003), we preliminary discuss how differences in skull and mandible morphology influenced food habits in these two pika species by using the respective local sample.

Materials and methods

We examined 31 skulls of *Ochotona princeps* and 18 skulls of *O. hyperborea* (Appendices 1 and 2). To avoid the influences of geographic variation on morphological characteristics, we used each local sample in this study: sample of *O. princeps* was from California and Nevada, USA and that of *O. hyperborea* was from Hokkaido, Japan. These specimens are deposited in the University of California Museum of Vertebrate Zoology, Berkeley; the Museum of Botanic Garden of Hokkaido University, Sapporo; the National Science Museum, Tokyo; the Mt. Apoidake Visitor Center, Samani; the Higashi Taisetsu Museum of Natural History, Nukabira; and the Laboratory of Wildlife Ecology, Obihiro University of Agriculture and Veterinary Medicine, Obihiro. We considered all specimens adults because of the degree of closure of cranial structures and the presence of a sagittal crest. Measurements of skulls of American pikas older than one year indicate no size differences between sexes (Weston, 1981; Smith & Weston, 1990). Therefore, we combined the sexes for this examination.

We followed the definitions of Abe (1991) and Otsuka *et al.* (1980) for the 19 cranial and mandible measurements included in this study (Fig. 1): greatest length (GL), nasal length (NL), condylobasal length (CBL), basilar length (BL), palatal length (PL), upper diastema length (UD), length of upper tooth row (LUT), mastoid breadth (MB), zygomatic breadth (ZB), interorbital breadth constriction (IBC), rostrum breadth (RB), distance between first upper premolars (PMD1), breadth across upper tooth rows (BTM), distance between first upper molars (MD1), minimum length of auditory bulla (LAB1), maximum length of auditory bulla (LAB2), mandible height (MH), length of mandible (LM), and length of lower tooth row (LLT). For more detailed morphological information, we added 17 measurements: length from postnarial anterior margin to basilar bone (PABB), length of basilar bone (BB), distance between temporal foveae (TF), length between temporal fossa and zygomaticotemporal process (TFZP), distance between processes of upper part of zygomatic arch (PZA), breadth of frontal bone (FB), distance between unique processes (UP) of anterior part of zygomatic bone (PAZB), minimum length between lateral margins of maxillae (LMM), breadth across occipital condyles (BOC), maximum length of aditus orbitae (LAO), maximum length across auditory bullae (LAAB), height of cranium (HC), distance between UP and lateral margin of zygomatic bone (UPZB), breadth of condyloid process (BCP), breadth of angle of the mandible (BAM), length from angular process to incisive alveolus (APIA), and lower diastema (LD). All of measurements were taken to the nearest 0.01 using mm by digital calipers.

To estimate differences in skull size between two local samples, we compared each variable with a Student's *t*-test. Principal component analysis (PCA) and stepwise discriminate analysis clarified variation between two samples for cranial and mandible measure-

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(BB), distance between temporal fossae (TF), length between temporal fossa and zygomaticotemporal process (TFZP), distance between processes of upper part of zygomatic arch (PZA), breadth of frontal bone (FB), distance between unique processes (UP) of anterior part of zygomatic bone (PAZB), minimum length between lateral margins of maxillae (LMM), breadth across the occipital condyles (BOC), maximum length of aditus orbitae (LAO), maximum length across auditory bullae (LAAB), height of cranium (HC), distance between UP and lateral margin of zygomatic bone (UPZB), breadth of condyloid process (BCP), breadth of angle of the mandible (BAM), length from angular process to incisive alveolus (APIA), and lower diastema (LD). Figure was adapted from Abe (2000).

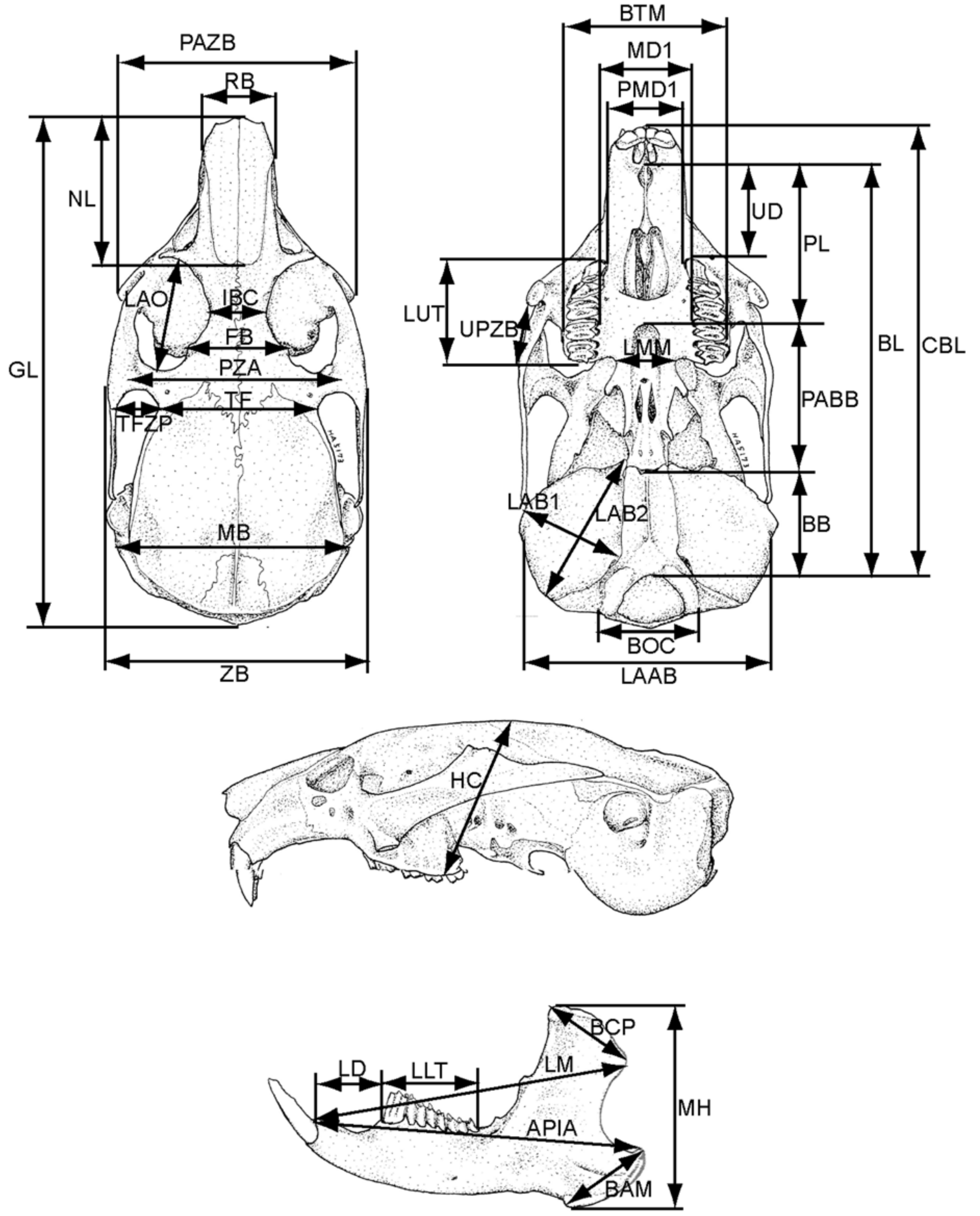

Figure 1. Skull measurements in *Ochotona princeps* and *O. hyperborea*. Greatest length (GL), nasal length (NL), condylobasal length (CBL), basilar length (BL), palatal length (PL), upper diastema (UD), length of upper tooth row (LUT), mastoid breadth (MB), zygomatic breadth (ZB), interorbital breadth constriction (IBC), rostrum breadth (RB), distance between first upper premolars (PMD1), breadth across upper tooth rows (BTM), distance between first upper molars (MD1), minimum length of auditory bulla (LAB1), maximum length of auditory bulla (LAB2), mandible height (MH), length of mandible (LM), and length of lower tooth row (LLT). In addition to these measurements, to resolve more highly the morphological information, we used 17 measurements: length from postnarial anterior margin to basilar bone (PABB), length of basilar bone

Table 1. The skull measurements (mm) of *Ochotona princeps* and *O. hyperborea* (n: number of specimens, mean, and SD: standard deviation) and results of t-test (*P*). Abbreviations corresponded to those in Fig. 1. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, and ns: $P > 0.05$.

Variable	*O. princeps*			*O. hyperborea*			*p*
	n	mean	SD	n	mean	SD	
GL	27	40.83	0.91	17	41.45	1.26	ns
NL	31	12.28	0.52	17	12.42	0.59	ns
CBL	25	34.59	1.10	14	35.75	0.83	**
BL	25	31.87	0.99	14	32.92	0.79	**
PL	29	13.19	0.54	17	13.10	0.45	ns
PABB	27	10.15	0.45	14	11.02	0.26	***
BB	25	7.90	0.40	14	8.04	0.35	ns
UD	31	7.70	0.39	18	7.71	0.26	ns
LUT	31	8.05	0.34	18	7.98	0.31	ns
MB	26	17.86	0.79	17	17.60	0.60	ns
TF	26	13.57	0.32	17	12.93	0.42	***
TFZP	30	3.42	0.22	17	3.56	0.16	*
ZB	25	20.53	0.52	17	20.80	0.44	ns
PZA	26	15.90	0.43	18	15.05	0.36	***
FB	28	9.11	0.37	18	7.79	0.58	***
IBC	30	5.15	0.38	18	4.57	0.34	***
RB	31	5.48	0.27	18	5.52	0.31	ns
PMD1	29	5.73	0.26	17	6.06	0.24	***
PAZB	25	18.84	0.60	16	19.16	0.55	ns
BTM	28	7.16	0.37	17	7.33	0.25	ns
MD1	28	12.02	0.41	18	12.15	0.29	ns
LMM	27	4.86	0.18	17	4.71	0.23	**
LAAB	22	19.82	0.50	14	19.75	0.54	ns
BOC	27	7.57	0.31	15	7.58	0.25	ns
LAO	31	9.27	0.30	18	9.31	0.24	ns
LAB1	27	7.78	0.45	15	7.62	0.32	ns
LAB2	27	12.48	0.53	15	12.70	0.35	ns
HC	30	12.35	0.41	17	12.01	0.73	*
UPZB	30	6.23	0.57	18	7.54	1.04	***
BCP	27	6.42	0.35	16	7.01	0.32	***
BAM	28	7.74	0.59	16	7.74	0.55	ns
LM	27	26.28	0.88	15	26.87	0.62	*
APIA	27	25.98	0.92	17	27.31	1.28	**
MH	28	15.85	0.53	15	16.87	0.50	***
LLT	31	7.80	0.26	17	7.76	0.26	ns
LD	31	5.74	0.27	17	5.79	0.41	ns

ments. All statistical analyses were performed with the JMP IN (SAS Institute Inc., 2004).

Results

Six skull measurements (TF, FB, PZA, LMM, IBC, and HC) were significantly larger for *O. princeps* than for *O. hyperborea* (Student's *t*-test, $P < 0.05$: Tab. 1). In contrast, ten skull measurements (CBL, BL, PABB, TFZP, MD1, UPZB, BCP, LM, APIA, and MH) were significantly smaller for *O. princeps* than for *O. hyperborea* (Student's *t*-test, $P < 0.05$: Tab. 1).

In a PCA using all cranial and mandible measurements, the 1st and 2nd principal component axes explained 40.3% and 16.7% of the total variation, respectively (Tab. 2). These two principle components adequately separated the two local species (Fig. 2). On the 1st principle component, variables GL, CBL, BL, ZB, LAAB, LAB2, BAM, LM, APIA, and MH were somehow heavily loaded. On the 2nd principle component, variables TF, PZA, FB, and IBC were heavily positive and variables PABB and UPZB were heavily negative (Tab. 2).

A stepwise discriminant analysis selected eight variables in this order: FB, PMD1, LAB1, BCD, BAM, LAAB, LLT, BTM, APIA, and PZA. These variables correctly classified 100% of the skulls by species (Fig. 3).

Discussion

The 20 measurements (55% of all measurements) showed no significant differences between the two samples ($P > 0.05$) for measurements comparison. Especially, as there were no significant differences in some major values to represent essential external trait of skulls such as greatest length (GL), zygomatic breadth

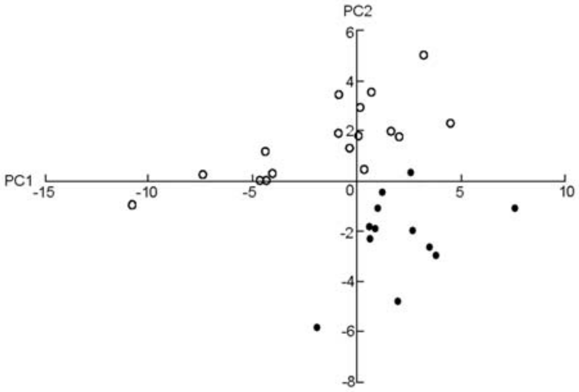

Figure 2. First (PC1) and second (PC2) principle components of principle component analysis of skull measurements of *Ochotona princeps* (solid circles) and *O. hyperborea* (open circles).

Table 2. First principal component (PC1) and second principal component (PC2) of skull comparing skull measurements of *Ochotona princeps* and *O. hyperborean*. Abbreviations corresponded to those in Fig. 1.

Variable	PC1	PC2
GL	0.2392	0.0325
NL	0.1218	0.1340
CBL	0.2484	-0.0551
BL	0.2469	-0.0526
PL	0.1688	0.1637
PABB	0.1567	-0.2575
BB	0.1592	0.0069
UD	0.1467	0.1613
LUT	0.1684	0.1036
MB	0.1613	0.1824
TF	-0.0304	0.3397
TFZP	0.1534	-0.0791
ZB	0.2265	0.0725
PZA	-0.0191	0.3509
FB	-0.1101	0.3432
IBC	-0.0086	0.3349
RB	0.1684	0.0435
PMD1	0.1652	-0.0892
PAZB	0.1978	0.0375
BTM	0.1762	0.0740
MD1	0.1839	0.0442
LMM	0.0841	0.2483
LAAB	0.2110	0.1323
BOC	0.0581	-0.1032
LAO	0.1360	-0.0387
LAB1	0.2113	0.0520
LAB2	0.0765	0.1954
HC	0.0098	0.2345
UPZB	0.1485	-0.2599
BCP	0.1968	-0.1502
BAM	0.2007	0.0616
LM	0.2290	-0.0052
APIA	0.2146	-0.0720
MH	0.2333	-0.1358
LLT	0.1202	0.0520
LD	0.1031	0.0771
Eigenvalue	14.5129	6.0279
Proportion	40.3136	16.7440
Cumulative	40.3136	57.0577

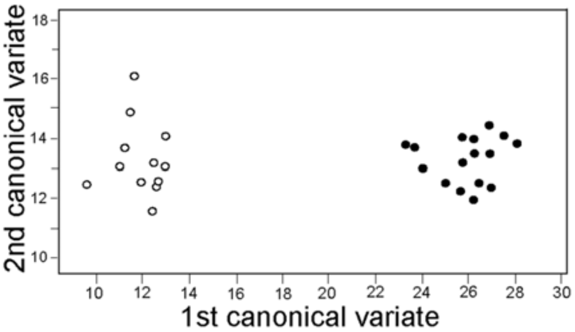

Figure 3. Stepwise discriminant analysis of 36 cranial and mandible measurements of *Ochotona princeps* (solid circles) and *O. hyperborea* (open circles).

(ZB), and mastoid breadth (MB), two samples could have similar skull in both size and shape.

Principle component analysis and discriminant analysis of skulls, however, showed clear separation in the two samples (Figs 2 and 3). *Ochotona princeps* has larger TF, FB, PZA, IBC, LMM, and HC. Of them, TF, FB, PZA, and IBC were also loaded heavily positively in principle component analysis as a second principle component. The FB was first selected in discriminant analysis. Larger TF, FB, PZA, and IBC mean that the upper part of cranium of *O. princeps* could be wider than that of *O. hyperborea*.

In contrast, *O. hyperborea* has larger CBL, BL, PABB, TFZP, MD1, UPZB, BCP, LM, APIA, and MH. The APIA and BAM were selected in discriminant analysis. The PABB was heavily negatively loaded in principle component analysis as a second principle component. The larger CBL, BL, and PABB explain that under part of cranium of *O. hyperborea* could be longer than those of *O. princeps*, in spite of no significant differences in GL. Moreover, the larger BCP, LM, APIA, and MH mean that *O. hyperborea* could have larger mandible.

The TF of *O. hyperborea* was significantly shorter than that of *O. princeps*. This measurement may reflect differences in chewing behavior between the two samples. The temporal muscle originates from the temporal fovea and terminates at the condyloid process of mandible (e.g., Kato, 1979; Popesko *et al*., 1992). If the TF is narrower, the temporal muscle may have more increased beside temporal bone. Narrowing of PZA and FB may be helpful in increasing temporal muscle. The IBC is also closely associated to the origin of the temporal muscle. This muscle may have increased on the narrower postorbital constriction of *O. hyperborea*. The longer CBL, BL, and PABB in *O. hyperborea* may indicate that some bones in the cranium, especially the sphenoid bone, are longer. The external pterygoid muscle (necessary for mastication) originates from pterygoid process of sphenoid bone, and terminates at condyloid process of mandible (Kato, 1979). Moreover, the internal pterygoid muscle originates from pterygoid process of sphenoid bone, palatine bone, and pterygoid bone, and terminates at pterygoid of mandible (Kato, 1979). As sphenoid bone lengthens, these pterygoid muscles can increase in size. Moreover, the larger mandible of *O. hyperborea* could be result of development of the masseter muscle. This muscle widely attaches with the mandible (Kato, 1979).

Although both pikas are herbivorous, *O. hyperborea* from Hokkaido may have more developed chewing muscles than *O. princeps* from California and Nevada. By adapting its feeding behavior to utilize the environment (vegetation), *O. hyperborea* from Hokkaido may have developed larger temporal muscle and evolved narrower IBC and TF, longer CBL, BL, and PABB, and larger mandible.

We suggest that differences in skull characteristics were related to feeding behavior. This should be tested for different *Ochotona* species with different feeding behaviors. Since we compared local sample of *O. princeps* to that of *O. hyperborea* (Appendices 1 and 2), intra-specific differences should be examined using different populations living in different environments. Moreover, to clarify the relationship in *Ochotona* between muscle development and skull shape and size, chewing muscles should be anatomically examined.

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References

Abe H. 1991. [Measurement and specimen preparation] // Kusano T., Mori H., Ishibashi N. & Y. Fujimaki Y. (eds.). Laboratory and Field Experiments for Applied Zoology. Tokyo: Zenkoku Noson Kyoiku Cooperative. P.10–17 [in Japanese].

Abe H. 2000. Illustrated Skulls of Japanese Mammals. Sapporo: Hokkaido University Press. 279 p. [in Japanese].

Abe H., Ishii N., Ito T., Kaneko Y., Maeda K., Miura S. & Yoneda M. 2005. A Guide to the Mammals of Japan. Kanagawa: Tokai University Press. 206 p.

Aho K., Huntly N., Moen J. & Oksanen T. 1998. Pikas (*Ochotona princeps*: Lagomorpha) as allogeneic engineers in an alpine ecosystem // Oecologia. Vol.114. P.405–409.

Argiropulo A.I. 1948. A review of recent species of the family Lagomyidae Lilljeb., 1886 (Lagomorpha, Mammalia) // Trudy Zoologicheskogo Instituta AN SSSR. Vol.7. P.124–128 [in Russian].

Conner D.A. 1983. Seasonal changes in activity patterns and the adaptive value of haying in pikas (*Ochotona princeps*) // Canadian Journal of Zoology. Vol.61. P.411–416.

Corbet G.B. 1978. The Mammals of the Palearctic Region: A Taxonomic Review. British Museum (Natural History). New York: Cornel University Press. 314 p.

Dearing M.D. 1996. Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps* // Oecologia. Vol.108. P.467–468.

Feldhamer G.A., Drickamer L.C., Vessey S.H. & Merritt J.F. 2004. Mammalogy: Adaptation, Diversity, and Ecology, Second Edition. New York: McGraw-Hill. 550 p.

Gureev A.A. 1964. Fauna of the USSR. Mammals. Vol.3. Part 10, Lagomorpha. Moskva: Nauka. 275 p. [In Russian].

Haga R. 1960. Observations on the ecology of the Japanese pika // Journal of Mammalogy. Vol.41. P.200–212.

Huntly N.J., Smith A.T. & Ivins B.L. 1986. Foraging behavior of the pika (*Ochotona princeps*), with comparison of grazing versus haying // Journal of Mammalogy. Vol.67. P.139–148.

Inukai T. 1931. A food-hoard of *Ochotona* from Taisetsuzan, the central mountains of Hokkaido // Transactions of Sapporo Natural History Society. Vol.11. P.210–214.

Kato Y. 1979. [The Illustrated Comparative Anatomy of Domestic Animals] Tokyo: Youkendo. 661 p. [in Japanese].

Kauhala K., Viranta S., Kishimoto M., Helle E. & Obara I. 1998. Skull and tooth morphology of Finnish and Japanese raccoon dogs // Annales Zoologici Fennici Vol.35. P.1–16.

Lissovsky A.A. 2003. Geographic variation of skull characters in pikas (*Ochotona* Lagomorpha) of the *alpina-hyperborea* group // Acta Theriologica. Vol. 48. P.11–24.

Lissovsky A.A., Ivanova N.V. & Borisenko A.V. 2007. Molecular phylogenetics and taxonomy of the subgenus *Pika* (*Ochotona*, Lagomorpha) // Journal of Mammalogy. Vol.88. P.1195–1204.

Niu Y., Wei F., Li M., Liu X. & Feng Z. 2004. Phylogeny of pikas (Lagomorpha, *Ochotona*) inferred from mitochondrial cytochrome *b* sequences // Folia Zoologica. Vol.52. P.141–155.

Otsuka J., Toyomitsu Y. & Nishinakagawa H. 1980. Linear measurements of the bones of *Lepus brachyurus brachyurus* Temminck, *Pentalagus furnessi* Stone and *Oryctolagus cuniculus* Linnaeus (JW-NIBS) // Experimental Animal. Vol.29. P.441–455.

Ozaki M., Suwa G., Kaji K., Ohba T., Hosoi E., Koizumi T. & Takatsuki S. 2006. Correlation between feeding type and mandibular morphology in the sika deer // Journal of Zoology. Vol.272. P.244–257.

Popesko P., Rajtová V. & Horák J. 1992. A Colour Atlas of the Anatomy of Small Laboratory Animals 2: Rat, Mouse, Golden Hamster. London: Wolfe Publishing Ltd. 253 p.

Sakagami S., Mori H. & Kikuchi H. 1956. Miscellaneous observations on a pika, *Ochotona* sp. inhabiting near the lake Shikaribetsu, Taisetsuzan National Park, Hokkaido // Japanese Journal of Applied Zoology. Vol.21. P.1–9.

SAS Institute Inc. 2004. JMP Start Statistics. Third Edition. Cary: SAS Institute Inc.

Smith A.T., Formozov N.A., Hoffmann R.S., Changlin Z. & Erbajeva M.A. 1990. The Pikas // Chapman J.A. & Flux J.E.C. (eds.). Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan. Oxford: IUCN. P.14–60.

Smith A.T. & Weston M.L. 1990. *Ochotona hyperborea* // Mammalian Species. No.352. P.1–8.

Weston M.L. 1981. The *Ochotona alpina* complex: a statistical re-evaluation // K. Myers K. & MacInnes C.D. (eds.). Proceedings of the World Lagomorph Conference. Ontario: Guelph University Press. P.73–89.

Wilson D.E. & Reeder D.M. 2005. Mammal Species of the World: a Taxonomic and Geographic Reference. 3rd ed. Baltimore: The Johns Hopkins University Press. 2142 p.

Appendix 1. Thirty-one specimens of *Ochotona princeps* examined in the present study. All specimens were used through the loan system of Museum of Vertebrate Zoology, University of California.

Identitiy number	Sex	Collecting locality	Identitiy number	Sex	Collecting locality
MVZ Mamm105609	male	Mono Co., California	MVZ Mamm105629	male	Mono Co., California
MVZ Mamm105610	male	Mono Co., California	MVZ Mamm105630	male	Mono Co., California
MVZ Mamm105611	male	Mono Co., California	MVZ Mamm105631	male	Mono Co., California
MVZ Mamm105612	female	Mono Co., California	MVZ Mamm105632	male	Mono Co., California
MVZ Mamm105613	male	Mono Co., California	MVZ Mamm105635	female	Mono Co., California
MVZ Mamm105614	male	Mono Co., California	MVZ Mamm105637	male	Mono Co., California
MVZ Mamm105615	male	Mono Co., California	MVZ Mamm105662	female	Mono Co., California
MVZ Mamm105616	female	Mono Co., California	MVZ Mamm105663	male	Mono Co., California
MVZ Mamm105617	male	Mono Co., California	MVZ Mamm105664	male	Mono Co., California
MVZ Mamm105618	male	Mono Co., California	MVZ Mamm107330	female	Mineral Co., Nevada
MVZ Mamm105619	female	Mono Co., California	MVZ Mamm107332	female	Mineral Co., Nevada
MVZ Mamm105620	male	Mono Co., California	MVZ Mamm107334	female	Mineral Co., Nevada
MVZ Mamm105621	male	Mono Co., California	MVZ Mamm107335	female	Mineral Co., Nevada
MVZ Mamm105622	female	Mono Co., California	MVZ Mamm135058	female	Mono Co., California
MVZ Mamm105626	female	Mono Co., California	MVZ Mamm135064	female	Mono Co., California
MVZ Mamm105628	female	Mono Co., California			

Appendix 2. Eighteen specimens of *Ochotona hyperborea* examined in the present study.

Institute	Identitiy number	Sex	Collecting locality
National Science Museum	M8524	female	Hokkaido, Japan
	M8738	unknown	Hokkaido, Japan
Hokkaido University	24676	unknown	Hokkaido, Japan
	24677	unknown	Hokkaido, Japan
	24679	unknown	Hokkaido, Japan
	42944	unknown	Hokkaido, Japan
	43373	unknown	Hokkaido, Japan
	50298	unknown	Hokkaido, Japan
	54845	unknown	Hokkaido, Japan
	55173	unknown	Hokkaido, Japan
Obihiro University of Agriculture and Veterinary Medicine	1	female	Hokkaido, Japan
	2	male	Hokkaido, Japan
	3	female	Hokkaido, Japan
	4	female	Hokkaido, Japan
	6	male	Hokkaido, Japan
	7	female	Hokkaido, Japan
Higashi Taisetsu Museum of Natural History	Higashi 01	unknown	Hokkaido, Japan
Apoi Mountain Visitor Center	Apoi 01	unknown	Hokkaido, Japan