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Species identification in pikas *Ochotona* (Lagomorpha: Ochotonidae), on the basis of variation in occlusal surface of the third lower premolar

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SUMMARY. Variation in the occlusal morphology of the third lower premolar tooth is examined in a sample of 369 adult pikas of all recent species. It is shown that, despite a high degree of intraspecific variation, the shape of the p_3 enamel loops reflects the phylogenetic relationships of pika species. While differences between most species pairs require a special multivariate analysis, differences between pika subgenera can be verbalised and recognised visually. For the first time, dental characters have been described that allow a reliable distinction of the members of the subgenus *Alienauroa*.

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KEY WORDS: *Ochotona*, *Alienauroa*, teeth, lower premolar, identification.

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Определение видов пищух *Ochotona* (Lagomorpha: Ochotonidae), на основании изменчивости жевательной поверхности третьего нижнего премоляра

А.А. Лисовский*, Е.В. Оболенская, Д-Я. Ге

РЕЗЮМЕ. На основании выборки из 369 взрослых пищух всех современных видов изучена изменчивость морфологии жевательной поверхности третьего нижнего предкоренного зуба. Показано, что, несмотря на высокую долю внутривидовой изменчивости, форма эмалевых петель p_3 отражает родственные связи пищух. Если нахождение различий между большинством пар видов требует специального многомерного исследования, то различия между подродами пищух могут быть вербализованы и распознаны глазомерно. Впервые описаны дентальные признаки, позволяющие уверенно отличить представителей подрода *Alienauroa*.

КЛЮЧЕВЫЕ СЛОВА: *Ochotona*, *Alienauroa*, зубы, нижний премоляр, определение.

Introduction

Pikas (Lagomorpha, Ochotonidae) are small lagomorphs common in modern Asian and North American communities. Fossil remains of pikas are more widely distributed, including a dense fossil record in Europe (Erbajeva, 1988; Angelone, 2008; Čermák, 2010). The palaeo-diversity of pika species continues to increase, partly due to the lack of knowledge of modern morphological variation.

Identifying pikas is a very actual task, because many species in this genus have similar morphology. In some cases, cranial morphology and skin colour gave taxonomists no clue until recently (Liu et al., 2017). This is the case for the subgenus *Alienauroa* Liu et al., 2017, which had been overlooked for a long time. Furthermore, in some specific cases, an additional character that could help to identify species pairs would be very useful.

Our previous research (Volkova & Lissovsky, 2018; Lissovsky & Kadetova, 2019) has shown that the third

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lower premolar offers the greatest hope for revealing identification features. Despite the fact that this tooth has a large amount of intraspecific variation, it contains a signal for identification, especially considering its size. The previous study was based on only four species. Now we use the complete set of pika species, which allows us to discuss practical issues of modern species identification.

Material and methods

We studied the shape of the enamel loops of the third lower premolars (p_3) in 366 specimens from 34 pika species (Appendix 1). All premolars examined were prismatic in shape (not conical). Several additional specimens (31) not included in the main analysis were juveniles with conical crowns. The specimens were held in the collections of the National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences (IOZCAS), the Zoological Museum of Moscow State University (ZMMU, Moscow) and the Zoological Institute of the Russian Academy of Sciences (ZIN, St Petersburg). We tried to collect a sample of 12 individuals from each species, where possible, consisting of two equal parts representing different subspecies or locations.

We studied two-dimensional projections of p_3 on the left side of the mandible from the occlusal (chewing) surface. Photographs of the tooth surfaces were taken using a Yizhan 4K digital microscope (optical magnification 1:1). The mandibles were fixed with plasticine as follows: the dental row was manually positioned so that the buccal side of the left dentition was perpendicular to the focal plane of the lens. As no positioning error was found in the previous study (Volkova & Lissovsky, 2018), we did not take this factor into account.

We examined the configuration of 23 landmarks on p_3 (Fig. 1). The landmarks were located on the dental images using TPSdig v.2.26 (Rohlf, 2005). Procrustean analysis was performed in MorphoJ 1.08.02 software (Klingenberg, 2011) using the principal axes option for alignment. The dataset was checked using MorphoJ's 'Find outliers' option to find occasional shifts in the position of landmarks. Procrustean coordinates (PrC) were not normalised. Forty six variables (X and Y PrCs for each landmark) characterising the shape of the occlusal surface were used in the analyses. The linear measurements of the teeth were calculated from the raw coordinates and calibrated using the ruler in each photograph.

Evaluating the intersection of specimen clouds is not a trivial task. We used an approach of (Warren et al., 2010; Brown & Carnaval, 2019) modified in (Lissovsky et al., 2024). In the first step, we applied factor analysis to each species pair. The factor analysis aimed to maximise the differences between species (Obolenskaya et al., 2009; Appendix 2). The first two axes (explaining the largest interspecies differences) of the factor analysis were transformed into a rectangular raster with seven columns and five rows, using the number of specimens (points) as raster values. These two rasters were compared with Schoener's D. Thus, if clouds of two species did not overlap on the first two factors, Schoener's D was 0; if they overlapped completely, it was 1.

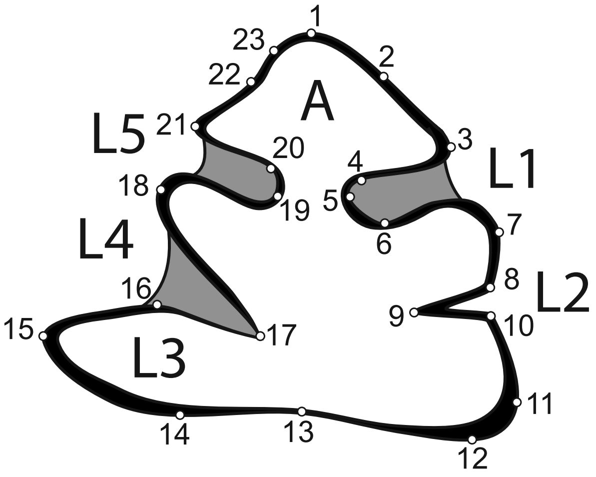


Fig. 1. The chewing surface of a third lower premolar p3 with 23 landmarks used in this study. A — anteroconid; L1 — inward loop corresponding to paraflexid; L2 — lingual inward loop between the middle and posterior p3 segments corresponding to mesoflexid; L3 — labial posterior outward loop; L4 — labial inward loop between the middle and posterior p3 segments; L5 — inward loop corresponding to protoflexid. The thick black line is enamel, grey is cementum, and white is dentin.

The analysis of variance was performed according to previous studies (Volkova & Lissovsky, 2018; Lissovsky & Kadetova, 2019). Only the species factor was used. Sexual dimorphism was not taken into account as previous studies showed its minimal effect. We randomly removed one element from each species group to generate 50 data replicates to assess the range of statistics. This approach was used due to the small sample size.

Cluster analysis was performed on a matrix of Mahalanobis distances between samples of each species/subspecies (where two subspecies samples were available), using the unweighted pair group method with arithmetic mean. The bias induced by the use of samples of different sizes was corrected (Marcus, 1993).

Visualisation of the average landmark configurations and comparison of the two configurations was performed using the original code in R 4.0.2 (Appendix 2). Analysis of variance components and cluster analysis were performed using STATISTICA ver.13.0.

Results

Taking into account the high intraspecific variation found in the previous studies, we first assessed the principle possibility of finding differences between the shapes of enamel loops of different species. By comparing species in pairs, we assessed how much their specimen clouds generally overlapped in multidimensional space. The overlap values (not shown) turned out to be very low: from 0 — no overlap (92.6% of cases) to 0.17 — very little overlap. Nevertheless, the proportion of variance explained by interspecies variation was low, especially within subgenera (Table).

Table. Sum of variance explaining interspecies (Species) and intraspecies (Error) variation. The diapason of each value (in parenthesis) was calculated using subsampling.

	Species	Error
All species	55.9 (54.8–56.5)	44.1 (43.5–45.2)
All species except *Alienauroa*	47.3 (46.3–48.4)	52.7 (51.6–53.7)
Alienauroa	22.5 (12.7–27.1)	77.5 (72.9–87.3)
Conothoa	36.7 (34.6–37.6)	63.3 (62.4–65.4)
Ochotona	28.0 (26.9–28.9)	72.0 (71.1–73.1)
Pika	23.3 (20.7–26.0)	76.7 (74.0–79.3)

In a second step, we tested whether the similarity between the shapes of the enamel loops in different species reflected any genetic affinity. The dendrogram of morphological similarity satisfactorily reflects the structure of the subgenera (Fig. 2). The main outlier is the simplified triangular tooth shape of *O. rufescens*, which is indeed similar to the tooth of *O. pusilla*.

Further, we visualised the average landmark configurations for each species (Fig. 3). The visualisation confirms the result of the cluster analysis, we can evaluate the similarity between species of each subgenus by eye. To understand the differences in tooth size between species, we constructed a box plot of tooth length (distance between landmarks 1 and 12) (Fig. 4A). Variation in some other measurements is shown in Figs. 4B–D and Fig. 5.

Taking into account the result of the previous step, we constructed the average shapes of the representatives of each subgenus together with the directions for each landmark distinguishing each two subgenera (Fig. 6).

We had the opportunity to evaluate the presence of the lingual inward enamel loop between the middle and posterior segments of p_3 (L2, mesoflexid), previously reported as a juvenile character (Lissovsky, 2004), in all pika species. Present in all juvenile specimens examined, this loop generally disappears in adult specimens, with some exceptions. First, the well developed loop is present in all specimens of *Alienauroa* (Figs. 4B, 6). Furthermore, the loop was present in 7 of 12 *O. nubrica* specimens; 1 of 12 *O. alpina*; 2 of 13 *O. cansus*; 1 of 12 *O. dauurica*; 1 of 6 *O. forresti*; 2 of 13 *O. gloveri*; 2 of 13 *O. macrotis*; 1 of 15 *O. mantchurica*; 1 of 12 *O. opaca* and 1 of 12 *O. turuchanensis* (3.6% of all adult and subadult specimens).

Discussion

Our results demonstrate the possibility of identifying pika species on the basis of the shape of the enamel loops of the p_3 tooth. Despite the low proportion of interspecies variance, cluster analysis revealed a very satisfactory subgeneric structure. In addition, the search for gaps between species clouds gave a positive result in the majority of cases. The last result should not be considered very optimistic as a real difference between "shapes of different species", since we searched for interspecies differences between each two species on the

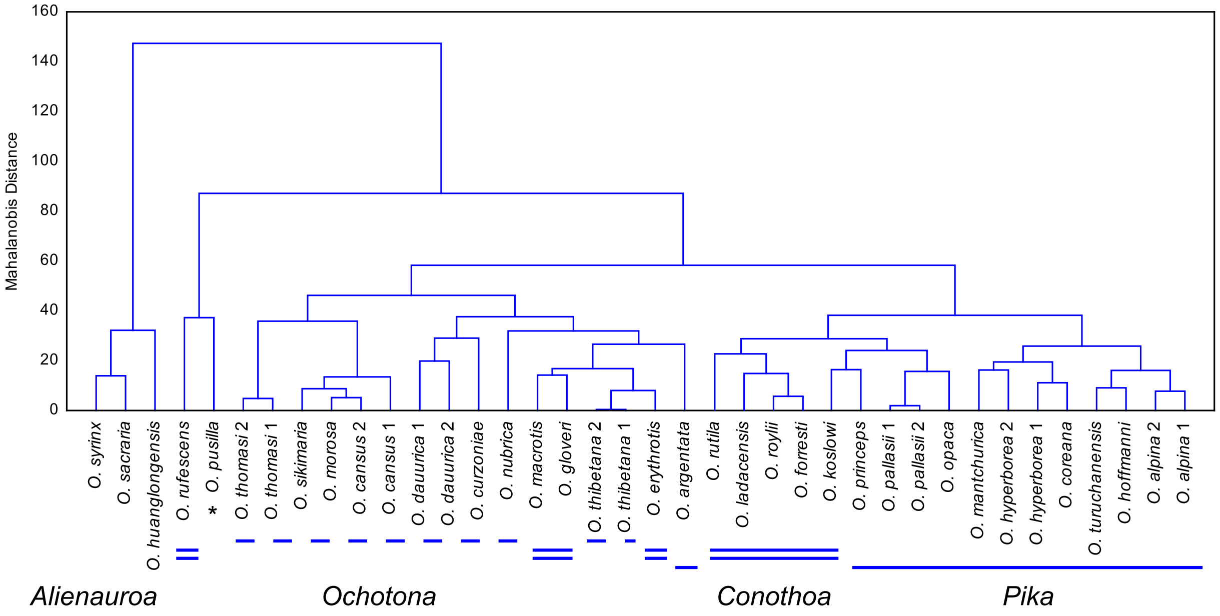
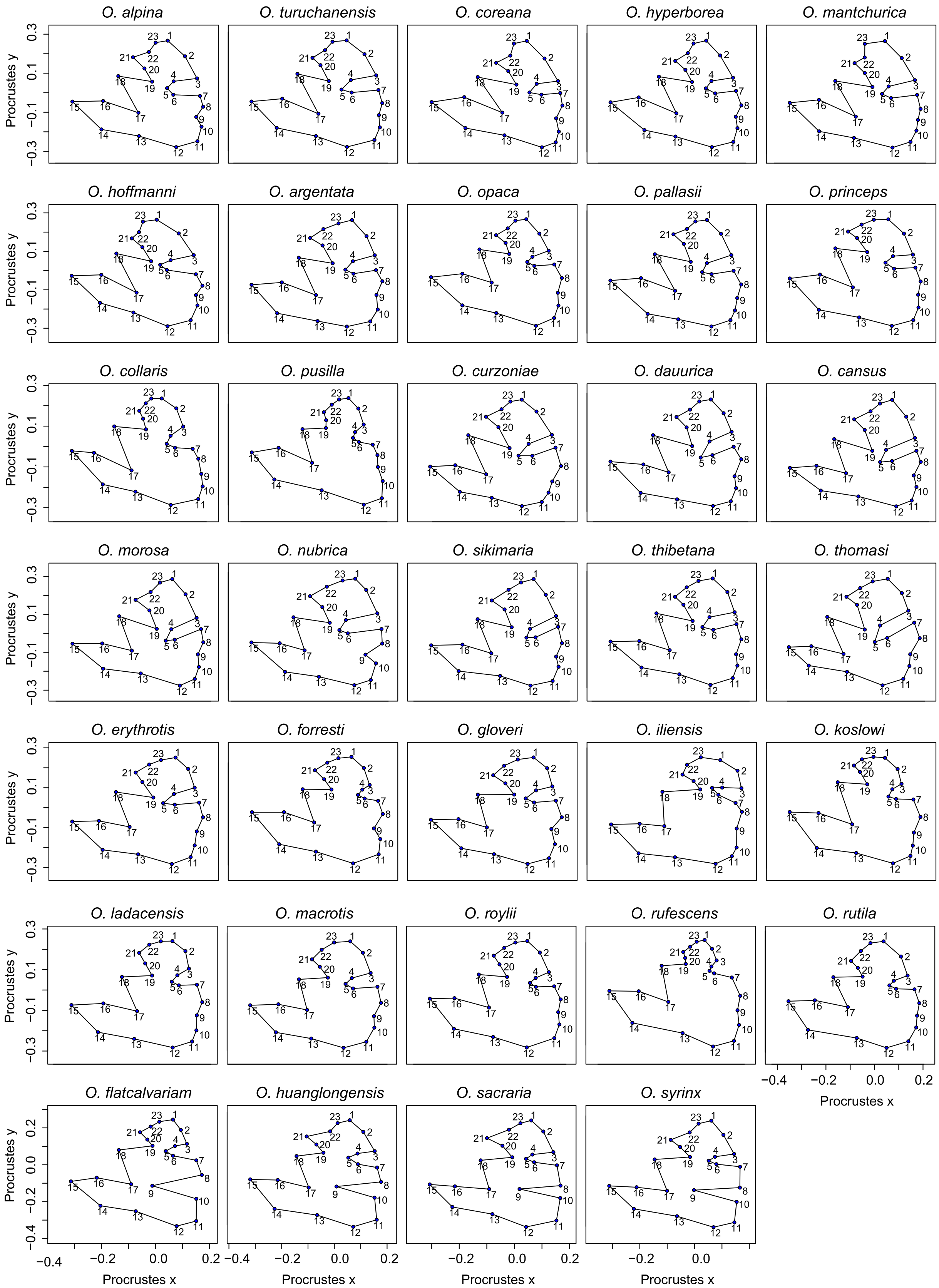


Fig. 2. The dendrogram of morphological similarity of pikas measured on the basis of shapes of third lower premolars p3. The names of the subgenera are listed below the species names. * — subgenus *Lagotona*.



O. alpina *O. turuchanensis* *O. coreana* *O. hyperborea* *O. mantchurica*

O. hoffmanni *O. argentata* *O. opaca* *O. pallasii* *O. princeps*

O. collaris *O. pusilla* *O. curzoniae* *O. dauurica* *O. cansus*

O. morosa *O. nubrica* *O. sikimaria* *O. thibetana* *O. thomasi*

O. erythrotis *O. forresti* *O. gloveri* *O. iliensis* *O. koslowi*

O. ladacensis *O. macrotis* *O. roylii* *O. rufescens* *O. rutila*

O. flatcalvariam *O. huanglongensis* *O. sacraria* *O. syrinx*

Fig. 3. Average landmark configurations in Procrustes space of pikas species.

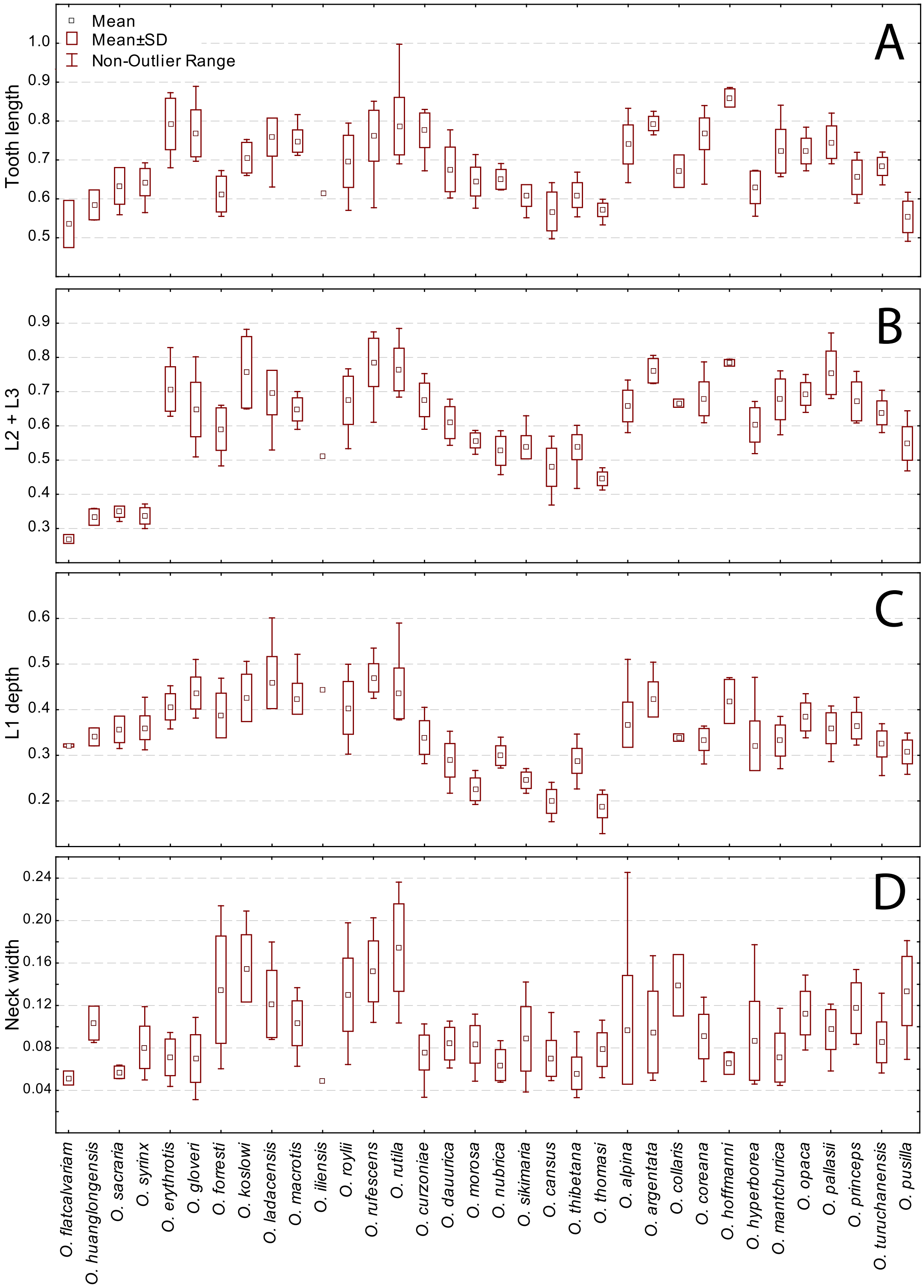


Fig. 4. Linear measurements of third lower premolars in pika species. A — tooth length (landmarks 1–12); B — depth of the L2 and length of the L3 (landmarks 9–15); C — distance between posterior edge of the tooth and the inward loop L1 (landmarks 5–13); D — width of the anteroconid neck (landmarks 5–19).

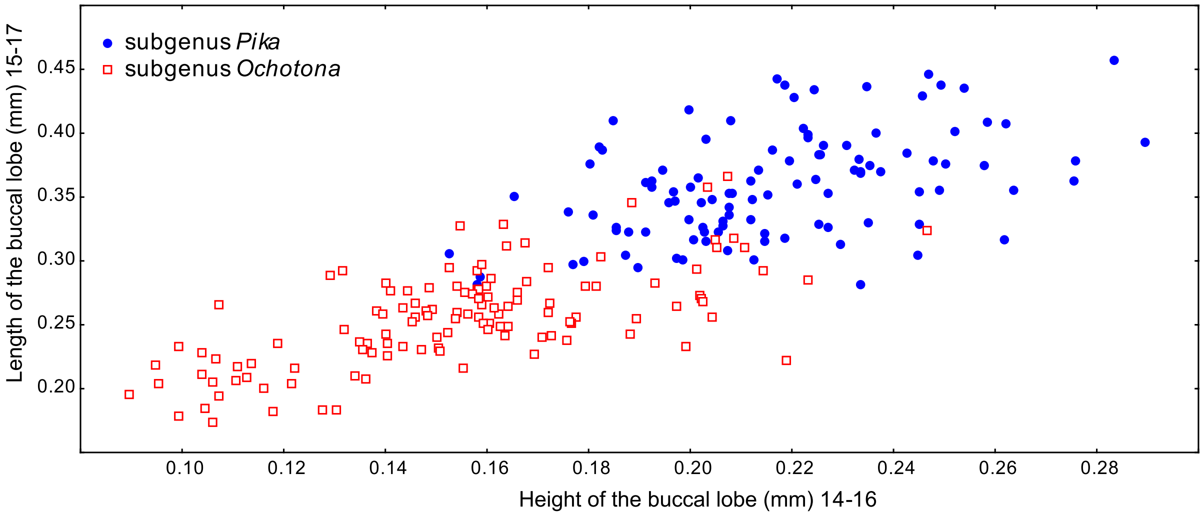


Fig. 5. Shape of the labial outward loop L3 (length vs. height of the loop) of *Ochotona* and *Pika* pikas.

basis of 46 variables. Over-parameterised models may find a difference where it is sometimes absent. However, this means that the variation of different species does not overlap completely. We can suggest that the difference between all pairs of species can be found in a multidimensional study, which can be very useful in a number of study cases. As previously recommended, the addition of tooth size to the analysis can improve the result (Lissovsky, Kadetova, 2019).

Differentiation between subgenera. The result, which is new and interesting, is that in most cases we can distinguish members of different subgenera by the shape of the enamel loops (Fig. 6).

Subgenus *Ochotona* Link, 1795. — Anteroconid relatively large, rhombic. L1 is narrow, usually very deep, pointing downwards: sometimes it comes down close to the posterior edge of the tooth (Fig. 4 C). The “neck” of the anteroconid (landmarks 5–19) is very narrow. Compared to *Pika* and *Lagotona*, L3 is shorter and narrower (Fig. 5). The enamel around the tooth is well developed.

Subgenus *Pika* Lacépède, 1799. — Anteroconid relatively large, rhombic. L1 is broad, usually parallel or at a slight angle to the posterior edge of the tooth. L3 is long and broad. The “neck” of the anteroconid is well developed, not very narrow. The enamel around the tooth is well developed (thick).

Subgenus *Lagotona* Kretzoi, 1941. — The p_3 has a triangular shape. All inward loops are poorly developed. The anteroconid is relatively small and rounded. The only species with a similar p_3 morphology is *O. rufescens*, from the subgenus *Conothoa*, which is, however, much larger. The species of the subgenus can be distinguished from most species by smaller measurements (Fig. 4). The enamel is well developed around the tooth.

Subgenus *Conothoa* Lyon, 1904. — Anteroconid relatively small, rounded. The enamel on the posterior surface of the anteroconid (around the “neck”) is very thin, usually almost invisible. All inward loops are poorly developed. As a result, the “neck” of the anteroconid is wide or almost absent.

Subgenus *Alienauroa*. — Identification of *Alienauroa* pikas has been unclear. Auricle shape characters (Liu et al., 2017) allow identification of live or freshly captured animals. However, they are not applicable to old museum specimens. The skull shape of these pikas has no discrete characters, so this type of identification is only accessible to experienced specialists. This study allows us to identify all *Alienauroa* pikas on the basis of a very deep lingual enamel loop L2 between the middle and posterior p_3 segments (Fig. 4 B). The p_3 of members of this subgenus is characterised by a short and narrow L3. The general appearance of the occlusal surface of the tooth is juvenile.

Expression of mesoflexid. A previous study found mesoflexid (Fig. 1 L2) as a characteristic of the first stage of permanent tooth wear (Lissovsky, 2004). Mesoflexid, which is visible as an L2 loop on the occlusal surface, can be found on the p_3 tooth until the conical part of the new permanent tooth is erased. Both studies (previous and present) found some rare exceptions. This study, using a larger dataset, found that such exceptions represent approximately 3.6% of all adult and subadult specimens. Thus, we can consider the presence of the mesoflexid of p_3 in adult pikas as a rare case. However, we did find the subgenus *Alienauroa*, which has a very well developed mesoflexid in all specimens. The expression of the mesoflexid is notably stronger than even in juvenile specimens of other pikas. The development of the mesoflexid is accompanied by a decrease in the number of outward loops, which is characteristic of juvenile pikas. We can therefore hypothesise that the appearance of such a morphological variant in adult *Alienauroa* was initiated by a paedomorphic process.

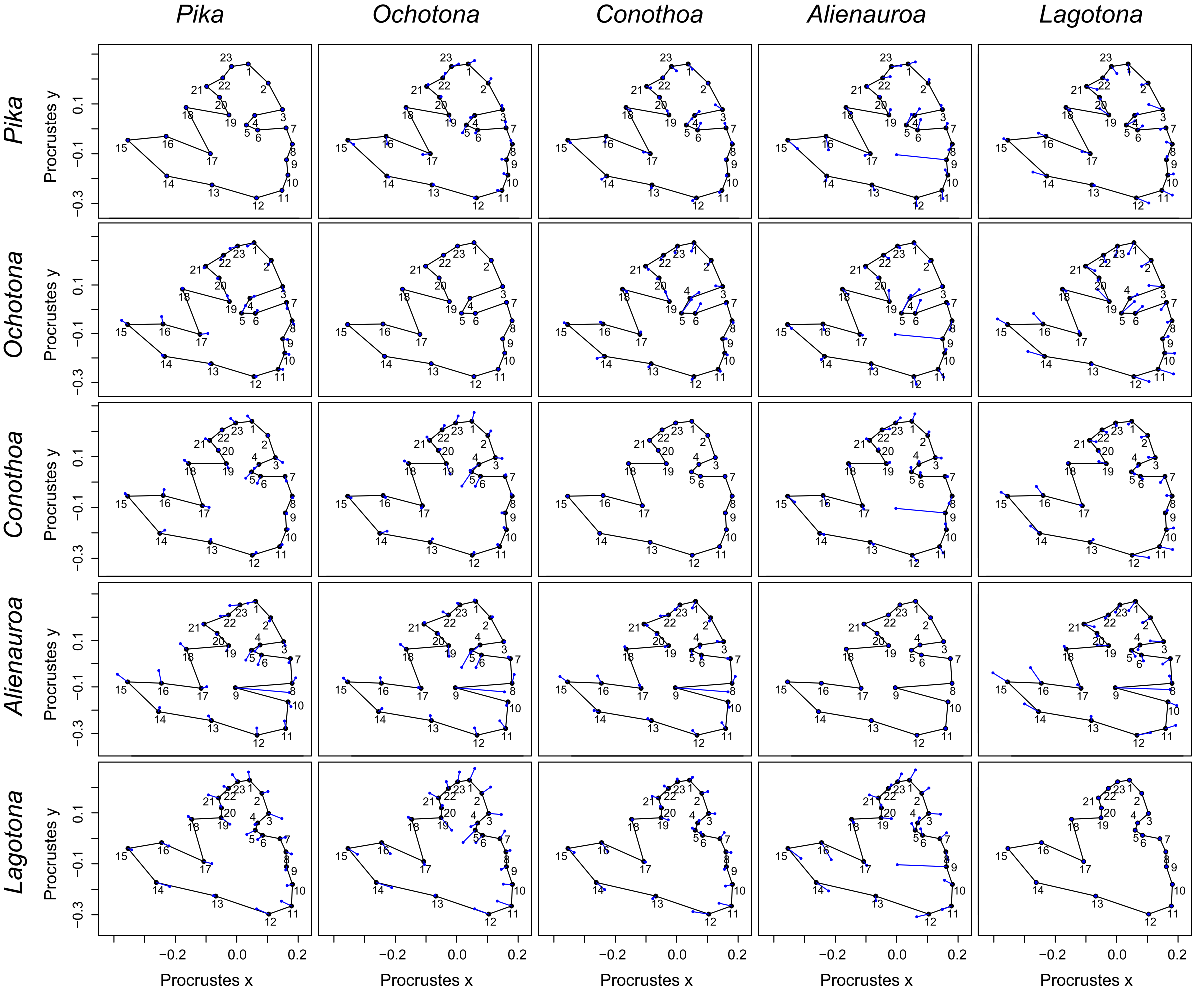


Fig. 6. The comparison of average landmark configurations in Procrustes space of pikas subgenera. The main diagonal contains the very landmark configurations of subgenera. Other cells compare these configurations with other subgenera — lines point to the place of every landmark in the average configuration of the subgenus in each column.

The subgenus *Alienauroa* does not occupy the basal position in the genus (Wang et al., 2020), besides the presence of the mesoflexid is not a common feature in Miocene–Pliocene Ochotonids (Erbajeva, 1988; Erbajeva & Zheng, 2005; Čermák, 2010), so we cannot assume that it is a conservation of some ancestral state of the tooth. It is most likely an apomorphism that appeared and became stabilized only in this group of pikas.

Particular identification issues. Although we cannot provide identification keys for all recent pika species, there are a number of observations we made during the work on this study that may be useful to people working with pika identification. Below we list some of the characteristics that can help with particular problems.

Ochotona rufescens — all specimens examined had a very small anteroconid, inconsistent with other pikas. Although this species is allopatric with other pika species, this feature may be useful in identifying Pleistocene–Holocene specimens.

Ochotona thibetana vs. *O. morosa*, *O. cansus*, *O. thomasi* — many zoologists have difficulty identifying these species, especially of *O. morosa*, which is close to *O. cansus* but larger with a broader skull, more similar to *O. thibetana* (Lissovsky et al., 2019). All four species are parapatric, but the additional character would be useful for identification. The three smaller species (*O. morosa*, *O. cansus*, *O. thomasi*) have a p_3 enamel shape characteristic of the subgenus *Ochotona*. The anteroconid is connected to other segments by a very narrow neck; L1 is very deep — posterior parts of L1 and L5 are clearly on different levels. On the contrary, p_3 of *O. thibetana* is more similar to *Pika*. The depths of L1 and L5 are similar, so their posterior parts are on the same level.

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Appendix 1. List of specimens used in the study

O. alpina
ZMMU S-71634, ZMMU S-71668, ZMMU S-71670, ZMMU S-71674, ZMMU S-71675, ZMMU S-71680, ZMMU S-145817, ZMMU S-145818, ZMMU S-145825, ZMMU S-145841, ZMMU S-145849, ZMMU S-145861

O. argentata
IOZCAS 30887, IOZCAS 30888, IOZCAS 30889, IOZCAS 30890, IOZCAS 30886, ZMMU S-160850, ZMMU S-160851

O. cansus
IOZCAS 16347, IOZCAS 16348, IOZCAS 16367, IOZCAS 16368, IOZCAS 18735, IOZCAS 18756, IOZCAS 18761, IOZCAS 19288, IOZCAS 19294, IOZCAS 19296, IOZCAS 19297, IOZCAS 19300, IOZCAS 19303

O. collaris
ZIN 39391, ZIN 39392

O. coreana
IOZCAS 4720, IOZCAS 4721, IOZCAS 4726, IOZCAS 4729, IOZCAS 4742, IOZCAS 4746, IOZCAS 4759, IOZCAS 4763, IOZCAS 4765, IOZCAS 4771, IOZCAS 4776, IOZCAS 4781, IOZCAS 4785, IOZCAS 24958, IOZCAS 4724, IOZCAS 4766

O. curzoniae
IOZCAS AD18261, IOZCAS AD18263, IOZCAS AD18266, IOZCAS AD18267, IOZCAS BG18233, IOZCAS BG18234, IOZCAS BG18237, IOZCAS BG18246, IOZCAS PL18145, IOZCAS YD18084, ZIN 2710

O. dauurica
IOZCAS 16166, IOZCAS 16175, IOZCAS 16219, IOZCAS 16225, IOZCAS 16228, IOZCAS 16229, IOZCAS 24882, IOZCAS 24884, IOZCAS 24886, IOZCAS 24890, IOZCAS 24891, IOZCAS 24893

O. erythrotis
IOZCAS 16342, IOZCAS 18908, IOZCAS 18910, IOZCAS 25815, IOZCAS 25817, IOZCAS 25819, ZIN 1553, ZIN 1554

O. flatcalvariam
IOZCAS 34432, IOZCAS 34433

O. forresti
IOZCAS 14ZM001, IOZCAS 14ZM002, IOZCAS 35535, IOZCAS 38057, IOZCAS 38058, IOZCAS 27133

O. gloveri
IOZCAS 19277, IOZCAS 19278, IOZCAS 19369, IOZCAS 19370, IOZCAS 19371, IOZCAS 19372, IOZCAS 19373, IOZCAS 40100, IOZCAS 40101, IOZCAS 40102, IOZCAS 40103, IOZCAS 40106, IOZCAS 17724

O. hoffmanni
ZMMU S-145149, ZMMU S-145151, ZMMU S-180456

O. huanglongensis
IOZCAS 40520, IOZCAS 40521, IOZCAS SCH2021542

O. hyperborea
ZMMU S-150556, ZMMU S-150617, ZMMU S-150621, ZMMU S-150622, ZMMU S-150623, ZMMU S-150624, ZMMU S-150649, ZMMU S-150651, ZMMU S-150659, ZMMU S-150661, ZMMU S-150673, ZMMU S-150674

O. iliensis
IOZCAS 28134

O. koslowi
ZIN 2729, ZIN 2730, ZIN 2733, ZIN 2734, ZIN 2735, ZIN 50239

O. ladacensis
IOZCAS 26850, IOZCAS 38150, IOZCAS 38153, IOZCAS 38154, IOZCAS 38156, IOZCAS 38160, IOZCAS 38162, IOZCAS 38174, IOZCAS 38178, IOZCAS 38179, IOZCAS 38181

O. macrotis
IOZCAS 17848, IOZCAS 17849, IOZCAS 22010, IOZCAS 22011, IOZCAS 26845, IOZCAS 38060, IOZCAS 38062, IOZCAS 38194, IOZCAS 38195, ZMMU S-57585, ZMMU S-58825, ZMMU S-58826, ZMMU S-200731

O. mantchurica
IOZCAS 861, IOZCAS 878, IOZCAS 893, IOZCAS 894, IOZCAS 905, IOZCAS 3119, IOZCAS 3166, ZMMU S-178617, ZMMU S-178619

O. morosa
IOZCAS 22783, IOZCAS 22785, IOZCAS 22789, IOZCAS 34440, IOZCAS 34442, IOZCAS 34443, IOZCAS 38099, IOZCAS 38107, IOZCAS 38108, IOZCAS 38109, IOZCAS 38110, IOZCAS 38114, IOZCAS 34427, IOZCAS 34428

O. nubrica
IOZCAS 14BK001, IOZCAS 14BK002, IOZCAS 14BK004, IOZCAS 26793, IOZCAS 26799, IOZCAS 26801, IOZCAS 26804, IOZCAS 26806, IOZCAS 26807, IOZCAS PL18104, IOZCAS PL18122

O. opaca
ZMMU S-144187, ZMMU S-144188, ZMMU S-144189, ZMMU S-144190, ZMMU S-144191, ZMMU S-144194, ZMMU S-144196, ZMMU S-144197, ZMMU S-144198, ZMMU S-148334, ZMMU S-194531, ZMMU S-194532

O. pallasii
IOZCAS 27922, IOZCAS 27923, IOZCAS 27927, IOZCAS 27928, IOZCAS 27930, IOZCAS 27933, ZMMU S-44292, ZMMU S-93840, ZMMU S-93863, ZMMU S-93865, ZMMU S-100565, ZMMU S-183541

O. princeps
ZMMU S-65626, ZIN 16939, ZIN 38938, ZIN 38939, ZIN 39393, ZIN 39394, ZIN 39395, ZIN 40418, ZIN 50323

O. pusilla
IOZCAS 33014, ZMMU S-13306, ZMMU S-14834, ZMMU S-17280, ZMMU S-19375, ZMMU S-42415, ZMMU S-61855, ZMMU S-61856, ZMMU S-61857, ZMMU S-72080, ZMMU S-72081, ZMMU S-72082, ZMMU S-136213

O. roylii
IOZCAS 17846, IOZCAS 25251, IOZCAS 25253, IOZCAS 25254, IOZCAS 26781, IOZCAS 26782, IOZCAS 26784, IOZCAS 26785, IOZCAS 26792, ZIN 50346, ZIN 50347

O. rufescens
ZMMU S-5483, ZMMU S-13344, ZMMU S-15654, ZMMU S-52134, ZMMU S-52136, ZMMU S-52141, ZMMU S-104012, ZMMU S-138894, ZMMU S-138895, ZMMU S-138896, ZMMU S-160794, ZIN 82630, ZIN 82631

O. rutila
ZMMU S-14927, ZMMU S-64872, ZMMU S-64874, ZMMU S-64878, ZMMU S-130142, ZMMU S-130143, ZMMU S-139611, ZMMU S-163699, ZMMU S-181325, ZMMU S-181326, ZIN 23149, ZIN 24382, ZIN 50046, ZIN 50061

O. sacraria
IOZCAS WL15111, IOZCAS WL15170, IOZCAS WL16315, IOZCAS WL140170, IOZCAS WL140184

O. sikimaria
IOZCAS YD18002, IOZCAS YD18011, IOZCAS YD18019, IOZCAS YD18025, IOZCAS YD18032, IOZCAS YD18037, IOZCAS YD18046, IOZCAS YD18048, IOZCAS YD18052, IOZCAS YD18054

O. syrinx
IOZCAS 22787, IOZCAS 22790, IOZCAS 28401, IOZCAS 28402, IOZCAS 28403, IOZCAS 31043, IOZCAS 31046, IOZCAS 31047, IOZCAS 31048, IOZCAS 31049, IOZCAS 31050, IOZCAS 31051, IOZCAS 31053, IOZCAS 31563, IOZCAS 35289, IOZCAS 40905, IOZCAS 26966, IOZCAS 26967

O. thibetana
IOZCAS 17690, IOZCAS 17691, IOZCAS 17699, IOZCAS 17700, IOZCAS 17709, IOZCAS 17715, IOZCAS 17716, IOZCAS 17721, IOZCAS 31626, IOZCAS 31627, IOZCAS 33588, IOZCAS 33590, IOZCAS 33591, IOZCAS 33597, IOZCAS 33600, IOZCAS 33601, IOZCAS 33603, IOZCAS 33607, IOZCAS 34418, IOZCAS 34420, IOZCAS 34421, IOZCAS 34423, IOZCAS 34425, IOZCAS 38059, IOZCAS 38063, IOZCAS 38064, IOZCAS 38281, IOZCAS 38282, IOZCAS 40115, IOZCAS 40116, IOZCAS 40117, IOZCAS 40118, IOZCAS MB240283, IOZCAS MB240303, IOZCAS MB240357, IOZCAS MB240400, IOZCAS MB240410

O. thomasi
IOZCAS 15093, IOZCAS 15097, IOZCAS 15105, IOZCAS 15106, IOZCAS 18733, IOZCAS 18736, IOZCAS 18737, IOZCAS 18745, IOZCAS 18760, IOZCAS 18763, IOZCAS 18764, IOZCAS 25827, IOZCAS 25828, IOZCAS 25837, IOZCAS 25838

O. turuchanensis
ZMMU S-162968, ZMMU S-162969, ZMMU S-162970, ZMMU S-164007, ZMMU S-164016, ZMMU S-164019, ZMMU S-164020, ZMMU S-164022, ZMMU S-164030, ZMMU S-165402, ZMMU S-171384, ZMMU S-175736

Appendix 2. R code of functions, used in the study

Function for factor analysis, maximising intergroup difference. Returns factor matrix

```
rotate.between.groups <- function (X, groups)
#X is a dataset, groups is a vector of grouping variable.
{
 if (is.data.frame(X))
   X <- as.matrix(X)
 else if (!is.matrix(X))
   stop("'X' must be a matrix or a data frame")
 if (!all(is.finite(X)))
   stop("'X' must contain finite values only")
 if (is.na(match('',groups)) == FALSE)
 {
   X1 <- X[-(which(groups == '')),]
 } else {
   X1 <- X
 }
 groups <- factor(groups)
 glev <- levels(groups)
 nlev <- length(glev)
 gsizes <- as.vector(table(groups))
 if (1 %in% gsizes) {
   warning("group with one entry found")
 }
 p <- ncol(X1)
 Gmeans <- matrix(NA, nrow = nlev, ncol = p, dimnames =
list(glev, colnames(X1)))
 for (i in 1:nlev) {
     Gmeans[i, ] <- apply(X1[which(groups == glev[i]), ], 2,
mean)
 }
 B <- cov(Gmeans)
 dimnames(B) <- list(colnames(X1), colnames(X1))
 EV <- eigen(B)
 Factor.res <- as.matrix(X) %*% EV$vectors
 RES <- list()
 RES$eigen.values <- round(EV$values, 6)
 RES$factors <- Factor.res
 return(RES)
}
```

Function returns graphical comparison of a specimen to another specimen or average landmark configuration.

```
shape.distorion <- function(shape.data, sh1, sh2)  # sh2 - 'cen-
troid' or integer
 #shape.data is a dataframe with specimens in rows and coor-
dinates in columns. Sequence: x1, y1, x2, y2...
{
 if(sh2 == 'centroid')
 {
   point.comp <- c(lapply(shape.data, mean))
 } else {
   sh2 <- as.integer(sh2)
   point.comp <- c(shape.data[sh2,])
 }
 x  <- seq(from=1, to=ncol(shape.data), by=2)
 y  <- seq(from=2, to=ncol(shape.data), by=2)
   point.xy <- c(shape.data[sh1,])
   label    <- paste0("Specimen ", sh1, " vs. ", sh2, " (blue)")
 label    <- paste0(row.names(shape.data)[sh1])
  plot(point.xy[x], point.xy[y], xlim=range(point.xy[x])*1.2,
ylim=range(point.xy[y])*1.2,        xlab="Procrustes      x",
ylab="Procrustes y", main=label, pch=16)
   text(point.xy[x],  point.xy[y],  labels=c(1:length(x)),  cex=
0.7, pos=1)
      polygon(point.xy[x],    point.xy[y],    xlim=range(shape.
data[1,x]), ylim=range(shape.data[1,y]))
  points(point.comp[x], point.comp[y], col="blue", cex=0.6,
pch=16)
 for (i in 1:length(x))
  {
         lines(c(point.xy[2*i-1],  point.comp[2*i-1]),  c(point.
xy[2*i], point.comp[2*i]), col="blue")
  }
}
```