AN ANOMALOUS TOOTH OF A CAVE BEAR (*URSUS KANIVETZ* VERESHCHAGIN, 1973) FROM POBEDA CAVE IN THE SOUTHERN URALS

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Abstract: An isolated tooth, of morphology unusual for cave bears, is described from Late Pleistocene deposits (MIS 3) of Pobeda Cave (54.1000° N, 56.5100° E) in the Urals. Analysis of ancient DNA showed that it belongs to the Ural cave bear *Ursus kanivetz*, which was widespread in the Pleistocene in the Urals. The fossil find was identified as an anomalous upper canine tooth, which got its unusual appearance due to a deviation from normal development under the influence of some unknown internal or external causes.

Key words: *Ursus kanivetz*, cave bears, Late Pleistocene, teeth, abnormal development, ancient-DNA analysis

Introduction

Pathological changes caused by various diseases are not uncommon in the bones and teeth of cave bears from European localities (Esper 1774, Wagner 1970, Bachmayer et al. 1975, Capasso 1998, Withalm 2004, Stuller et al. 2011, Nowakowski and Stefaniak 2015), but they are found much less often in cave bears from the Urals (Kosintsev and Vorob'ev 2001) and from the Caucasus (Baryshnikov 2020). Anomalies related to deviations of normal development of teeth are even less common. Their causes are usually not known precisely, but studying them may be important for understanding the evolution and biology of cave bears and other extinct taxa.

The purpose of this work was to describe an anomalous fossil tooth from Pobeda Cave in the Southern Urals. The tooth is quite unusual, and initially, there was uncertainty regarding its systematic interpretation. Nonetheless, an analysis of ancient DNA revealed that it belonged to the cave bears (*Ursus* (*Spelaearctos*)).

Location, material, and methods

The isolated anomalous tooth was found in Pobeda (Kinderlinskaya) Cave, in the Gafuriysky District of Bash-kortostan (Russia; 54.1000° N, 56.5100° E). The cave is of karst origin. It has a length of 16,395 m and a complex structure. Remains of Late Pleistocene and Holocene vertebrates were found only in the first hall of the cave. The loose deposits in the hall are mostly composed of light loam with a large amount of limestone rubble, up to 0.7 m thick. Bone remains lie in loose deposits, from the surface to a depth of 0.4 m. In total, >15,000 bone remains of mammals have been collected here (Sataev 1994, Vorob'ev and Plasteeva 2006). Among them, remains of the Late Pleistocene age are predominant.

Associated fauna

Species composition of the Late Pleistocene mammalian complex from Pobeda Cave includes *Lepus timidus* Linnaeus, 1758, *Marmota bobak* (Müller, 1776), *Canis lupus* Linnaeus, 1758, *Cuon alpinus* (Pallas, 1811), *Vulpes vulpes* (Linnaeus, 1758), *Vulpes lagopus* (Linnaeus, 1758), *Ursus arctos* Linnaeus, 1758, *Martes zibellina* (Linnaeus, 1758), *Mustela eversmanii* Lesson, 1827, *Gulo gulo* (Linnaeus, 1758), *Panthera spelaea* (Goldfuss, 1810), *Crocuta spelaea* (Goldfuss, 1823), *Rangifer tarandus* (Linnaeus, 1758).

Chronology

Two AMS radiocarbon dates (not calibrated) were determined from bones of a Ural cave bear 60,600 ± 3,600 BP (OxA-19678), 47,600 ± 900 BP (OxA-19679) (Kosintsev et al. 2016), and another one from the tooth being described 39,843 ± 279 BP (NSKA-1355, UGAMS-23138; not calibrated). For a cave lion bone, an AMS date was available >39800 (OxA-10845) (Stuart and Lister 2011). Judging by the fauna composition and the obtained dates, the deposits containing bone remains of large mammals were dated to the mid-Late Pleistocene, and can be attributed to the third marine isotope stage (MIS 3). The age of the fauna and calibrated dates are discussed in more detail in other publications (Kosintsev and Bachura 2013, Danukalova et al. 2020).

Taphonomic notes

This cave's fauna includes ~14,000 remains of cave bears. Almost all bones are intact. Signs of gnawing by predators are very few. No traces of human activity were found. All parts of the skeleton are present. They come from animals of various age groups: newborns, young, subadults, and adults. This set of skeletal elements shows that entire corpses of cave bears of all ages got buried in the cave, consistently with their nonviolent death, for example, during hibernation.

Ancient DNA analysis

This analysis was performed to determine taxonomic affiliation of the tooth. Genetic analyses were completed at the Australian Centre for Ancient DNA (ACAD) at the University of Adelaide. Ancient-DNA assays: A section of tooth root was irradiated with UV light for 15 min, then had the surface layer abraded using a Dremel tool with a carborundum cutting disc, before being reduced to powder using a BioPulverizer (BioSpec). 100 mg of powder was subjected to a DNA extraction protocol optimised for recovery of short DNA fragments (Dabney et al. 2013). Briefly, this protocol comprised decalcification in 1 mL 0.5 M EDTA for 1 hour at 37 °C under constant rotation, after which the EDTA was removed and replaced with 980 μL of fresh 0.5 M EDTA and 20 μL of Proteinase K (20 mg/mL). The reaction was then incubated overnight under constant rotation at 55 °C, after which the digestion buffer was mixed with 13 mL of a modified PB buffer (12.6 mL PB buffer [Qiagen], 6.5 μL Tween-20, and 390 μL of 3M sodium acetate) and bound to silicon dioxide particles, which were then washed with 80 % ethanol. Bound DNA was eluted in 150 μL of TE buffer.

The extracted DNA was enzymatically repaired and blunt-ended, and had custom adapters ligated following the protocol of Meyer and Kircher (2010), but with the addition of the partial uracil-DNA-glycosylase treatment described by Rohland et al. (2015). Adapter sequences featured unique 7mer barcodes, to allow identification and exclusion of any downstream contamination (P5: AGTAGAC; P7: GACCGCT). The resulting library was subjected to a short round of PCR to increase the total quantity of DNA, using primers complementary to the adapter sequences. The template was split into eight separate PCRs to minimise PCR

bias and maintain library complexity. Each individual PCR (25 μL) contained 3 μL of undiluted library, 1× Platinum Taq DNA Polymerase High Fidelity buffer (ThermoFisher Scientific), 2 mM MgSO4 (ThermoFisher Scientific), 0.25 mM of each dNTP (ThermoFisher Scientific), 0.4 μM of each primer (IS7 & IS8), and 0.2 U of Platinum Taq DNA Polymerase High Fidelity (ThermoFisher Scientific), in laboratory grade water. Cycling conditions were as follows: 94 °C for 6 min; 12 cycles of 94 °C for 30 s, 60 °C for 30 s, 68 °C for 40 s; and 68 °C for 10 min. PCR products were pooled and purified using AMPure magnetic beads (Agencourt). Following Mitchell et al. (2016), we used commercially synthesised biotinylated 80-mer RNA baits (MYcroarray, MI, USA) to enrich the library for placental mammal mitochondrial DNA. The enriched library was sequenced on an Illumina NextSeq 500, using 2×75 bp paired-end chemistry.

We used "sabre" (http://github.com/najoshi/sabre) to identify raw sequencing reads based on the unique barcode combination assigned to the library. Using AdapterRemoval v2.1.2 (Schubert et al. 2016), we trimmed residual adapters and low-quality bases (<Phred20 –minquality 4); merged overlapping paired-end reads (minimum overlap = 11 nt); and discarded merged reads <30 bp (–minlength 30). Using BWA v0.7.8 (Li and Durbin 2009; aln -t 8 -l 1024 -n 0.04 -o 2), we mapped the remaining merged reads to ten alternative mitochondrial references. Reads with a mapping quality Phred score >30 were selected and retained using the SAMtools v1.4 (Li et al. 2009) view command (-q 30), and duplicate reads were discarded using "FilterUniqueSAMCons.py" (Kircher 2012). We then counted the reads that mapped to each reference to identify the closest match: 4030 reads mapped to *Ursus rossicus* Borissiak, 1930 (MW491933), 4028 reads mapped to *Ursus kanivetz* (MW491932), 4009 reads mapped to *Ursus ingressus* Radeber et al., 2004 (KX641331), 3959 reads mapped to *Ursus spelaeus* Rosenmüller, 1794 (KX641308), 3497 reads mapped to *Ursus praekudarensis* (Baryshnikov, 1998) (MW491935), 3340 reads mapped to *Ursus kudarensis* Baryshnikov, 1985 (MW491934), 2870 reads mapped to *Ursus arctos* (OK512965), 2374 reads mapped to *Ursus eremus* Radeber et al., 2004 (KX641335), 225 reads mapped to *Panthera spelaea* (OK513004), and 163 reads mapped to *Homotherium latidens* (Owen, 1846) (MF871702). On the basis of these results, the specimen appears to correspond to a taxon belonging to the Eurasian cave bear species complex.

To test the relationships of our specimen to recognised cave bear taxa in a phylogenetic framework, we first used Geneious Prime v2020.2.4 to make a 75 % majority consensus sequence based on the 4030 reads mapping to *Ursus rossicus* (MW491933), calling nucleotides for sites only with a minimum depth-of-coverage of 3× (mean read depth 15.4×). We then aligned this consensus sequence with the other *Ursus* sequences listed above using the MUSCLE algorithm (Edgar 2004), as implemented in Geneious. Finally, we inferred a maximum likelihood phylogeny based on 15,449 bp of the mitochondrial genome using IQ-TREE v1.6.11 (Nguyen et al. 2015), with the best-fitting substitution model (TN93+G) selected using ModelFinder (according to the Bayesian Information Criterion) as implemented in

IQ-TREE (Kalyaanamoorthy et al. 2017) and 1000 ultrafast bootstrap replicates to assess topological support (Hoang et al. 2017).

Studied and comparative specimens

The tooth (No. 467/3153) is stored in the Museum of the Institute of Plant and Animal Ecology (the Ural Branch of the Russian Academy of Sciences, Yekaterinburg, Russia). For comparison, 56 upper canines (C1), 65 lower canines (c1), and 122 upper third incisors (I3) of Ural cave bears from the same cave were employed. The morphological structures of the tooth are described according to S. Hillson (2005: fig. 1.26). The orientation of the tooth is described according to Hillson (2005: figs 1.2, 1.26).

Results

Morphological characterisation

The tooth is rod-shaped, whole; the crown is without additional tubercles. It is similar to the third upper incisor or a canine of a large carnivorous mammal. The pulp cavity is closed, and the apical foramen at the root tip is less than 1 mm in diameter, indicating that the find belongs to a set of permanent teeth. In size and structure, it also differs substantially from deciduous teeth of cave bears.

The tooth is slightly curved in the antero-posterior direction and has no curvature in the bucco-lingual plane (Text-fig. 1). The root is very long, more than two times longer than the crown. In the neck cross-section, it is oval-rectangular, almost square. The mesial groove on the distal side of the root is well-pronounced and runs from the crown to the root tip.

The crown is fang-shaped, with a sharp apex. It is flattened in the bucco-lingual direction, and when viewed from above the occlusal surface, has a suboval outline. The lingual side of the crown is concave in the antero-posterior section and slightly convex in the lingual-buccal section. The buccal side is slightly convex in the antero-posterior and bucco-lingual sections. The buccal wall of the crown is smooth, without a cingulum or ridges. The mesial and distal ridges are well pronounced. The cutting edges are not sharp. The mesial tubercle is small, and the distal bulge is not pronounced. The lingual cingulum is not complete, it is interrupted in the middle, though it is clear-cut in the mesial and distal parts. The shape of the crown base is not even. On the buccal side, the edge of the crown is almost straight and rises somewhat above the root. In the area where the mesial groove adjoins the crown, the cingulum forms a well-defined acute angle pointed at the crown apex.

The enamel is slightly wrinkled. At the top of the tooth, there is a small wear facet with an area of less than 1 mm², on which the enamel had been worn down to dentin. There are no other signs of wear, and there are no contact areas for adjacent teeth. Tooth sizes (mm): largest length: 72.4; largest height crown (buccal side): 27.6; minimum height crown (from mesial tubercle to top crown): 16.6; greatest antero-posterior length crown: 14.5; bucco-lingual breadth crown: 13.3; root length from the distal bulge to the apical tip: 57.2; antero-posterior length and bucco-lingual width at the thickest part of the root: 13.7 and 13.0.
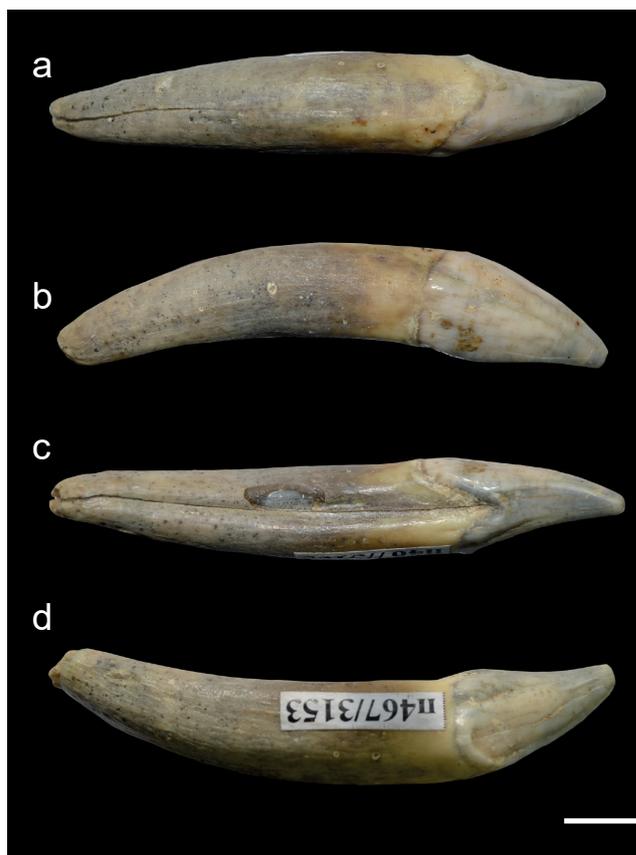
Text-fig. 1. The anomalous tooth, probably C sup. dex., of a Ural cave bear *U. kanivetz* from Pobeda Cave. a: mesial view, b: buccal view, c: distal view, d: lingual view. Scale bar = 1 cm.

Comparison

Interpretation of the tooth was difficult. Its structure has signs of both a canine and of the third upper incisor (I3). Canine teeth of Ural cave bears are high. The upper and lower canines differ well in the degree of curvature of the tooth and in shapes of the crown and root. The upper canine (C1) is curved in the antero-posterior plane almost exclusively. The lower canine (c1) is curved in two planes: antero-posterior and bucco-lingual. The crown of the upper canine in the bucco-lingual section is almost symmetrical and oval. The crown of the lower canine is asymmetrically oval in the bucco-lingual section. The root of the upper canine has an almost symmetrical oval shape in axial section, and is weakly flattened on the buccal side. The lower canine has an asymmetrically oval shape in axial section, and is noticeably flattened on the buccal side. Crown surfaces of the upper and lower canines are without any concave structures. On roots of both canines, the mesial groove is not pronounced. The distal ridge and mesial ridge are present. The cutting edges are not sharp. The distal bulge and mesial tubercle are not pronounced. There are no contact areas for adjacent teeth.

The upper third incisor (I3) in bears is relatively short. The crown and root are subtriangular in cross-section. The buccal side of the crown has convex sagittal and axial profiles. The lingual side has a concave sagittal profile and a slightly convex axial profile. On the crown, the distal bulge is absent; the mesial tubercle is well defined, and there are a distal ridge and a mesial ridge. From the mesial tubercle, along the posterior edge of the basis of the crown, there is
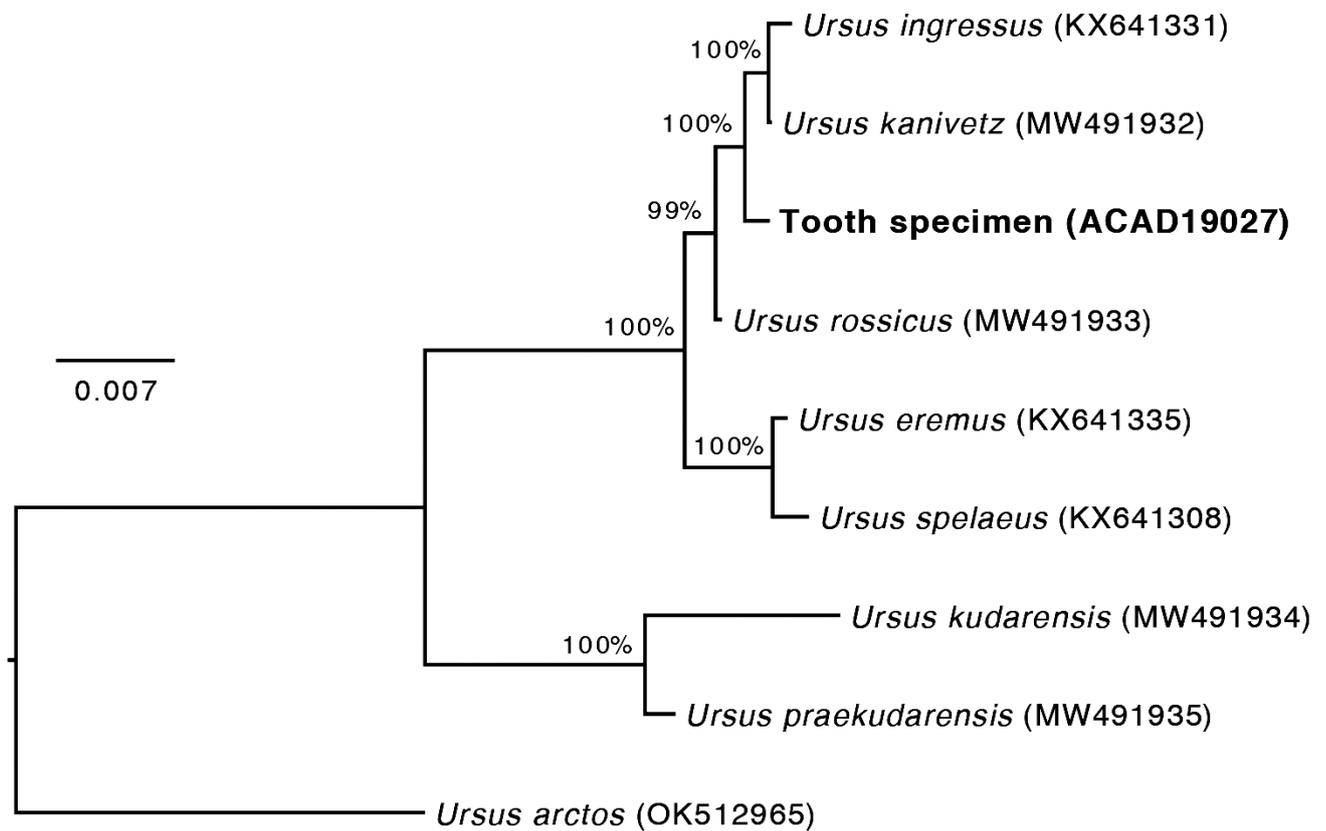
Text-fig. 2. Phylogenetic position of anomalous tooth of *U. kanivetz* from Pobeda Cave based on ancient mtDNA.

a distinct ridge-shaped cingulum. In the region of the mesial tubercle, there is a contact area for adjacent incisor I2. The mesial groove on the root is not clear-cut.

The tooth under study is similar in some ways to the upper canine, and in other ways, to the third upper incisor (Tab. 1). It resembles the upper canine because of the long

Table 1. Measurements (mm) and morphology characteristics of C1 and I3 teeth of *U. kanivetz* and the anomalous tooth No. 467/3153 from Pobeda Cave.

Characteristics	Anomalous tooth	*Ursus kanivetz*	
	No. 467/3153	C1 (n = 46)	I3 (n = 92)
Length	72.4	80.5–109.5	45.6–57.2
Crown: greatest length	14.5	20.1–24.9	15.3–21.2
Crown: breadth	13.3	14.5–19.4	12.7–19.8
Root: maximum length	13.7	21.1–28.8	14.1–15.3
Root: maximum breadth	13.0	13.6–21.1	11.1–14.6
Crown: axial section	suboval	oval	subtriangular
Root: axial section	oval-rectangular	oval	subtriangular
Lingual side crown, antero-posterior section	concave	slightly convex	concave
Lingual side of crown, bucco-lingual section	slightly convex	slightly convex	slightly convex
Buccal side of crown, antero-posterior direction	slightly convex	slightly convex	slightly convex
Buccal side of crown, bucco-lingual section	slightly convex	slightly convex	slightly convex
Crown: mesial ridge	pronounced	pronounced	pronounced
Crown: mesial tubercle	not pronounced	not pronounced	well-pronounced
Crown: distal ridge	pronounced	pronounced	pronounced
Crown: distal bulge	not pronounced	not pronounced	not pronounced
Crown: contact area for adjacent tooth	absent	absent	present
Crown: buccal cingulum	absent	absent	absent
Crown: lingual cingulum	present	absent	present
Root: mesial groove	present	absent	present

root weakly curved only in the antero-posterior plane, the absence of the mesial tubercle and of the "collar," and the nearly oval axial cross-section of the crown and root. It is similar to tooth I3 by the presence of the mesial groove and a concave sagittal contour of the lingual side of the crown.

Results of the ancient-DNA analysis

Our maximum likelihood phylogeny is very highly supported (bootstrap support ≥99 % at all nodes) and recapitulates the cave bear mitochondrial topology inferred by Barlow et al. (2021). Our specimen belongs to the monophyletic mitochondrial clade comprising *U. ingressus*, *U. kanivetz* and *U. rossicus* (from Kizel Cave, the Urals) (Text-fig. 2). However, the exact taxonomic identity of our specimen within that clade is equivocal – it appears to be sister lineage to a clade comprising the *U. ingressus* and *U. kanivetz* matrilines. Undoubtedly, the tooth belonged to a cave bear. All cave bear remains from Pobeda Cave belong to *U. kanivetz*. The same species lived throughout the Urals in the Late Pleistocene (Gimranov and Kosintsev 2022), which differed in morphology from other cave bears (Baryshnikov 2007, Baryshnikov and Puzachenko 2011, Baryshnikov et al. 2018). Therefore, the described tooth probably belongs to *U. kanivetz*. Maximum likelihood phylogeny of *Ursus* mitochondrial lineages were inferred using IQ-TREE. Values associated with branches represent ultrafast bootstrap support. Scale is in number of substitutions per site.

Discussion

Our study shows that this anomalous tooth is not a dental pathology or teratology, but a tooth formed normally during ontogenesis. Normally, cave bears do not have such a tooth; therefore, this is a deviation from the norm that we call an anomaly. The fossil specimen is fang-shaped and is most similar in size and morphology to an upper canine (Text-fig. 1, Tab. 1). Shapes of the root and crown indicate that the tooth was located in the right upper jaw. Theoretically, it could be a supplementary tooth and located next to a normal canine or between a canine and the third incisor. Nevertheless, the fossil tooth contains no contact areas for other teeth. Consequently, it could be situated either at the site of the canine or on the diastema, as a homolog of one of anterior premolars P1–3 of the brown bear (*Ursus arctos*). The latter is unlikely. The latter interpretation is anatomically unlikely because the tooth is large, and its root had to come into contact with a root of a normal canine, thereby creating a mark on our tooth's root, but this mark is absent. Thus, the tooth was most likely located in the place of a normal canine. The positioning and shape of the occlusal surface are similar to those on upper canines of cave bears.

The tooth belonged to an adult animal. Weak wear suggests that the tooth was not actively involved in the grinding of food. The positioning and shape of the occlusal surface indicate that it functioned similarly to upper canines of bears. The size of the tooth corresponds to an animal of a hyena size, to a small bear, or a large cat. Collections of I3 teeth (more than 600 specimens) and C1 teeth (more than 400 specimens) of cave bears were examined in the Museum of the Institute of Plant and Animal Ecology (the Ural Branch

of the Russian Academy of Sciences, Yekaterinburg), at the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), and at the Paleontological Institute of the Russian Academy of Sciences (Moscow). We failed to find any analogues to our tooth in these collections. It has no analogues in descriptions of thousands of teeth of cave bears (*Ursus spelaeus* sensu lato) from European locations. We also could not find analogues among teeth of other modern and fossil carnivores stored in these collections or published in the literature.

Conclusion

The analysed isolated tooth of the Ural cave bear (*U. kanivetz*) has an unusual morphology. Its structure combines features of the upper third incisor (I3) and of the upper canine (C1). In size, shape, and function, this tooth is more like a canine. It was probably located at the site of the upper right canine. In its appearance, this is a "normal" tooth, without signs of pathology or teratology. Its anomalous structure formed during ontogenesis owing to an alteration of morphogenetic processes, and these data suggest that the alteration was mostly due to genetic factors.

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