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ARTICLE

When beremendiin shrews disappeared in East Asia, or how we can estimate fossil redeposition

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ABSTRACT

The current paper first time describes a small *Beremendia* from the late Pleistocene deposits in the Koridornaya Cave locality (Russian Far East), which associated with the extinct *Beremendia minor*. The paper is the first attempt to use a comparative analytical method to evaluate a possible case of redeposition of fossil remains of this shrew. In this case, the 'comparative' part of the method corresponds to the 'faunistic approach' of Jelle Reumer, and the 'analytical' part of the method corresponds to his extended 'morphological approach. ' The analytic method uses morphospace size estimation (MSE) based on principal component analysis and estimation of the variance to evaluate redeposition of *Beremendia minor* from the late Pleistocene deposits in the Koridornaya Cave. This result allows us to suggest the significant environmental contribution to the East Asian beremendiin extinction, such as climatic fluctuation, landscape changes and shrew community changes between the late Pliocene and early Pleistocene. We discuss the last remains of East Asian *Beremendia* (*Peisorex*) described from the Chinese early Pleistocene localities (Chiachiashan, Haimao, Renzidong) and the last remains of *Lunanosorex* described from the Chinese late Pliocene localities (Qipanshan Hill and Houxushan Hill). MSE was performed for soricine tribes with the ‘elongated’ condylar process.

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KEYWORDS
Soricidae; *Beremendia*; late Pleistocene; fossil redeposition; morphospace size; East Asia

Introduction

Shrews (Mammalia, Soricidae) have been an important part of mammal fauna since the middle Oligocene to the present (Reumer 1989, 1999; Wolsan and Hutterer 1998; Hutterer 2005). The fossil record gives us material for understanding the development and changes in the taxonomic diversity of shrews in the past, and the modern fauna allows us to find and analyse physiological, environmental and morphological analogies to understand the directions of development of the fossil taxa and the causes of their extinction (see the ‘actualistic approach’ in Reumer 1984, p. 123). One of the important aspects of studying the evolutionary history of the soricids is an analysis of the relationships between paleoclimate fluctuations and the evolution of the Soricidae (Agustí et al. 1999; Reumer 1984, 1989, 1999; Van Dam 2004; Furió et al. 2007, 2010; Mészáros 2014; Rofes et al. 2018; and others). At present, new molecular approaches are also being used for reconstruction of shrew faunal changes in the context of environmental events (Dubey et al. 2007, 2008a, 2008b; Stewart et al. 2010).

Reumer (1984) introduced several new directions to the study of the evolutionary history of Soricidae, such as the ‘actualistic approach’ (searching for analogies between the present and extinct taxa), the ‘morphological approach’ (analysis of the morphological traits), and the ‘faunistic approach’ (analysis of species associations), which were developed in his later works (Reumer 1989, 1999) and by other authors (Storch and Qui 1991; Storch and Zazhigin 1996; Mészáros 1997; Van Dam 2004; Furió et al. 2007, 2010; Flynn and Wu 2017; and others). Reumer (1984, p. 55) analysed the reduction in the size and structure of *Deinsdorfia* (Soricinae) teeth in the evolutionary chain between early Ruscinian *D. janossyi* (slightly reduced M2) and late Ruscinian *D. kordosi* (strongly reduced M2) in the context of the Ruscinian environmental fluctuation (*ibid*., p. 134). In 1989, the author combined known data on the evolutionary history of the soricids and their ecophysiology and palaeoclimatic events and drew conclusions about the impact of climate changes during the Neogene and the Quaternary on speciation, migrations, and the extinctions of shrews (Reumer 1989). Later, Reumer (1999) further developed this conclusion and stated: ‘ … the composition and diversity of soricid faunas can be taken as a measure of ecological adequacy of the environment for shrews’ (Reumer 1999, p. 391). Thus, changes in the shrew species composition ‘can be interpreted in a paleoclimatic sense’ (Reumer 1999, p. 391).

Reumer’s studies described European fossil localities, which were usually significantly richer than Asian localities (at least for North Asian sites) in the number of soricid remains. For instance, 16 early Pliocene to early Pleistocene localities from broad territories in Russia (Siberia), Kazakhstan, and Mongolia contained 56 remains of Beremendiini (Soricinae), whereas Hungarian early Pleistocene Somssich Hill 2 locality contained alone 180 fossils of this group (Botka and Mészáros 2014; Zazhigin and Voyta 2019). This fact slightly limits the use of faunistic and morphologic approaches for the analysis of shrew associations and character traits. However, some North Asian groups such as *Paranourosorex* (Soricinae, Anourosoricini) were described in terms of morphological changes during the late Miocene and early Pliocene (Storch 1995; Storch and Zazhigin 1996); but this group is still undescribed in terms of species associations and does not allow us to consider the issue of the causes of its extinction. We know that *Paranourosorex gigas* Rzebik-Kowalska, 1975 disappeared in the early Pliocene (MN 14) and later (MN 15) appeared (replaced) the beremendiin shrews in Kazakh and Siberian localities (Storch et al. 1998; Zazhigin and Voyta 2019).

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Beremendiini (Soricidae, Soricinae) is an extinct tribe of soricine shrews that existed between the early Pliocene and Middle Pleistocene in the Palearctic. The tribe consists of three valid genera: East Asian *Lunanosorex* Jin and Kawamura, 1996 (late Pliocene in China), South European *Dolinasorex* Rofes and Cuenca-Bescós, 2009 (early Pleistocene in Spain) and broadly distributed *Beremendia* Kormos, 1934. *Beremendia* is the most interesting group due to its broad distribution and its appearance after the extinction of the anourosoricin shrews in both Europe and North Asia (Rzebik-Kowalska 1998; Storch et al. 1998; Botka and Mészáros 2014; Mészáros 2014). Reumer (1984) considered *Beremendia* as an 'opportunist' species with generalist abilities for living in different habitats. However, the reasons for the extinction of *Beremendia* are still unclear. In addition, the period of the final extinction of the genus is also not clear.

Beremendia consists of two broadly distributed valid species, *Beremendia fissidens* (Petényi, 1864) and *Beremendia minor* Rzebik-Kowalska, 1976, and at least two East Asian species, *Beremendia jiangnanensis* Jin et al., 2009 and *Beremendia pohaiensis* (Kowalski and Li, 1963; see Flynn and Wu 2017). It is considered that European and North Asian *Beremendia* representatives became extinct during the early Pleistocene (Rzebik-Kowalska 1998; Storch et al. 1998; Pazonyi et al. 2016; Zazhigin and Voyta 2019). The review of Rzebik-Kowalska (1998, p. 42) also reported middle Pleistocene findings of *B. fissidens* in several European localities. Chinese species occurred between the early Pliocene (*B. jiangnanensis*) and the beginning of the late Pliocene (*B. pliocaenica*) (Flynn and Wu 1994; Jin et al. 2009).

The upper age limit of the genus stratigraphic distribution is important in relation to the most recent first finding of small *Beremendia* from the late Pleistocene Far Eastern Koridornaya Cave locality. This remain was found significantly north of the Chinese sites with *Beremendia* species, the Mazegou locality (early/late Pliocene; *B. pliocaenica*) and the Renzidong locality (early Pleistocene; *B. jiangnanensis*), and the far eastern Mongolian Bural-Obo 1C locality (early Pleistocene) with known remains of *Beremendia minor* (Figure 1). The main question about the Far Eastern finding relates to whether there was survival of *Beremendia* until the late Pleistocene or whether there was redeposition of material from Neogene and early Pleistocene deposits. Despite redeposited remains of *Beremendia* having been recovered from several Russian localities (Kartashovo, Kizikha, Sibiryachikha Cave localities; see Zazhigin and Voyta 2019) we cannot unambiguously recognise redeposition in the Koridornaya Cave locality. The main reason for this is a description of several remains (Tiunov et al. 2016; Borodin et al. 2018; Kosintsev et al. 2020) from other late Pleistocene deposits of the Russian Far East, which usually correspond to an earlier time period. In the current paper, we suggest applying Reumer's approaches to detecting redeposition or proving a regional survival of *Beremendia* until the latest Pleistocene. The solution to this particular question in the current paper is relevant in the context of the fossil record incompleteness and does not apply to the regional Far Eastern fauna only. In addition, possible late Pleistocene survivors should be explored carefully in the East Asian localities due to the higher taxonomic diversity of beremendiin shrews there than in other parts of Asia and Europe.

To investigate the probability of the survival of *Beremendia* until the late Pleistocene, we tested two questions. First, how do the shrew species associations from the Koridornaya Cave locality correspond to the associations from Chinese localities with known *Beremendia* species (Reumer's faunistic approach)? Second, can we use the morphological characters and in what form as redeposition markers (Reumer's morphological approach)? We proceeded from the following logical assumptions:

(1) Late Pleistocene environments are radically different than late Miocene, Pliocene, and early Pleistocene environments

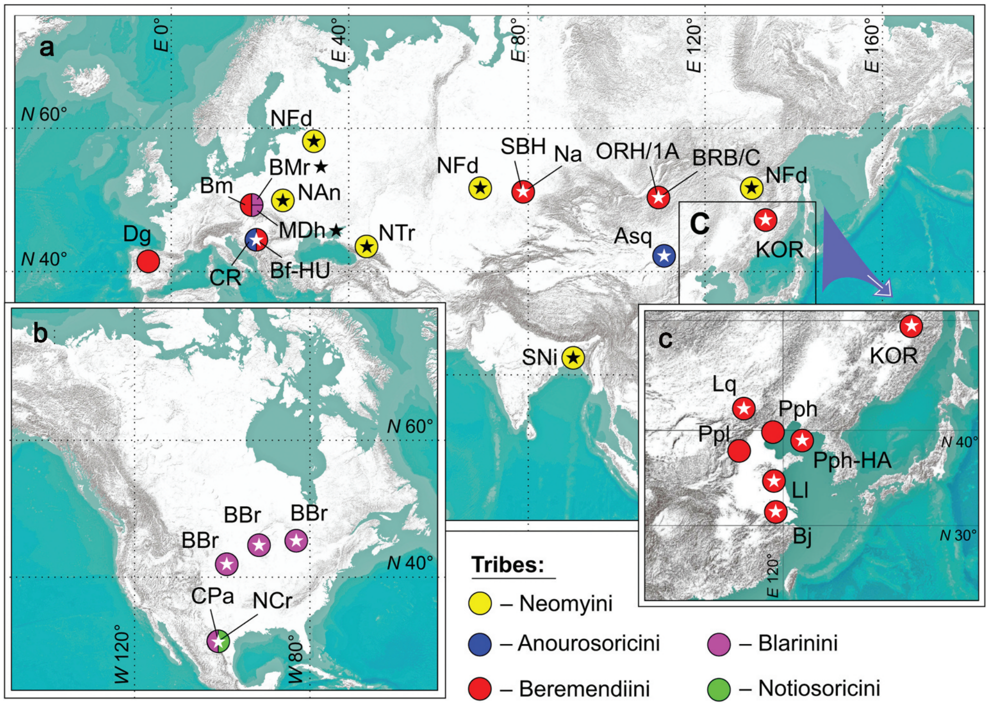


Figure 1. Map of the Eurasia (A) and North America (B) showing the locations of shrew samples of five tribes; tribe representatives are coloured. (C) Detail of East Asia. Star mark samples used in mandibular shape analysis and MSE. Map data from resource ESRI (http://www.esri.com/) using SASPlanet software (v.160707.9476). Sample abbreviation see in Table 1.

anywhere in Eurasia (Suc 1984; Agustí and Antón 2002; Jiménez-Moreno and Suc 2007; Popescu et al. 2010; Jiménez-Moreno et al. 2015; and so on). A similar environment change situation was observed in East Asia as a result of the Tibetan Plateau uplift (Zhisheng et al. 2001; Lu et al. 2020; and so on).

(2) If beremendiins survived into the late Pleistocene then they would inhabit very different environments than they occupied elsewhere.

(3) If *Beremendia* from Koridornaya Cave is really from the late Pleistocene, we would expect it to have evolved specialisations not found in other beremendiins, which would increase the morphological disparity of the tribe considerably.

The idea that environmental changes cause turnover in biota underlies modern insights into faunal compositions, changes and extinctions (Simpson 1953). Van Valen (1973), based on the 'adaptive zone' statement (Van Valen 1971) and the application of a 'survivorship curve' approach (Simpson 1944), formulated the 'Law of Extinction.' Since then, survivorship analysis has become widely used to compare patterns of evolution among invertebrate higher taxa with an estimation of the 'turnover rate' and 'extinction rate' (Stanley 1973; Van Valen 1973; Levinton 1974; Foote 1988). Foote (1991), (Foote 1992) moved from the analysis of the survivorship, i.e. analysis of the evolution among different taxonomic and ecologic groups, to the analysis of morphological diversity in these groups, which led to the formulation of the idea of morphospace assessment. Foote (1991, p. 482) saw an increase in the 'morphological discontinuity' between groups of Palaeozoic marine invertebrates and proposed two possible explanations: the influence of stochastic processes or 'radiation into a new adaptive zone.' Subsequent authors extended the morphospace concept to the detection of the morphological selectivity of extinction (Foote 1992, 1999; Eble 2000, 2002). For instance, Eble (2000) detected a morphological selectivity of extinction of some Mesozoic atelostomate echinoid (Echinoidea, Atelostomata) groups during a period of known environmental crises (e.g. the end-Cretaceous mass extinction), which means changes in the morphological disparity values (morphospace size). Eble's approach to the disparity estimation uses principal component analysis (PCA) and allows for the detection of the disparity values of each group as well as their particular character contributions (Eble 2000). It should be noted that Wills et al. (1994) were the first to revised Foote's approach and use variance and PCA to assess a morphospace and used the term 'disparity.'

The morphospace concept gives a methodological basis and an approach to its estimation (through estimation of the variance) for comparisons of taxa above the species level. Is it possible to use this concept/approach to assess possible morphological changes within taxa of mammals? Here, we come across the concept of the 'width of ecological niche' (Simpson 1953) and the use of morphological disparity for estimation of interspecies competition in recent faunas (Davies et al. 2007; Meloro 2011; Abramov and Puzachenko 2012; Werdelin and Wesley-Hunt 2014; Abramov et al. 2016). The methodological basis of the morphospace concept (applied to high-level taxa comparisons) and the width of the ecological niche concept (applied to interspecies comparisons) corresponds to adaptive zones in the usages of Simpson (1953) and Van Valen (1971), (1973). In general, the terms of this basis correspond to the following thesis: the occupation of a new adaptive zone entails an increase in the morphological disparity or, in other words, an increase of the morphospace size. This concept is similar to Reumer's view on the significance of environment changes for Soricidae evolution: his 'faunistic' approach is based on the taxa composition comparisons, and the 'morphological' approach can be supplemented by estimation of the variance in the sense of Foote (1992) and Eble (2000). This common methodology and careful approach can be applied to assess fossil redeposition.

Material and methods

Modern and ancient samples

A total of 32 hemimandibles of 11 genera and five soricine tribes were studied: two genera of Anourosoricini, two genera of Beremendiini, four genera of Blarinini, two genera of Neomyini and one genus of Notiosoricini (Table 1; Figure 1). The target group of morphometric analysis is Beremendiini; other groups selected as bearing 'elongated' condylar process.

The new finding of *Beremendia* (KOR) is represented by the right fragment of the hemimandible with p4–m3 and almost the whole mandibular ramus (the angular process is broken off) (Figure 2). The bone and teeth are slightly rounded. Specimen FSC RJARV-KorC-01 is held as part of the fossil collection at the Federal Scientific Centre of the East Asia Terrestrial Biodiversity Far Eastern Branch of the Russian Academy of Sciences (Vladivostok, Russia).

Geometric morphometrics

Mandibular shape was described using a configuration of five true landmarks (types I and II *sensu* Bookstein 1991), together with 45 semi-landmarks (Figure 3). Semi-landmarks were prepared using the tpsDig2 ver. 2.31 software (Rohlf 2007) with the assistance of the 'Draw background curves' tool and the subsequent procedure of 'aligning of the curve' by length ('Resample curve' tool). Given that some of the hemimandible fossils (i.e. the specimen from the Far East and comparable materials) were damaged, we used bones with preserved coronoid and condylar processes and the portion of the dentary from the anterior margin of the m2 anterior alveolus to the back. The appropriate baselines enabled us to combine the landmark and semi-landmark digitising processes (Figure 3). The material investigated in the shape analysis study comprised 32 specimens of 17 species and four soricine tribes (see below). The special link- and slider-files were prepared with the tpsUtil ver. 1.28 software (Rohlf 2004). The Procrustes superimposition procedure and principal component analyses (PCA; 'relative warp analyses') were calculated with the tpsRelw ver. 1.35 software (Rohlf 2003). PCA was based on the 'Procrustes coordinates' (the Cartesian coordinates of each landmark after the Procrustes superimposition procedure; see Rohlf and Slice 1990).

Image acquisition and measurements

Pictures of hemimandibles and teeth were taken with a digital camera (Canon EOS 60D; Olympus DP74) combined with a stereomicroscope (LOMO Micromed MSP-1; Olympus SZX16). The measurements were taken according to the method of Zazhigin and Voyta (2019). All measurements are given in mm. High-resolution images were acquired using an scanning electron microscope (Zeiss ESEM Quanta 250), with the surfaces covered by platinum sputter-coating (technical support by 'Taxon' Research Resource Centre (http://www.ckp-rf.ru/ckp/3038/) of the Zoological Institute, Russian Academy of Sciences (Saint Petersburg, Russia), and a field emission electron microscope

Table 1. Modern and fossil samples of shrews. Biom, filled for recent taxa (source: https://www.iucnredlist.org/); Locality/Age, filled for fossil taxa; ^{t}, type specimen; N, number of hemimandibles included in the morphometric analysis.

Species	Country	Biom	Locality/Age	Code	N	Number
Anourosoricini						
Anourosorex squamipes	China	Forest (E. and S-E. Asia)	Recent	Asq	1	ZIN 38946
Crusafontina kormosi	Hungary		Polgárdi 4, late Miocene	CR	1	no. abs. (image from Mészáros 2014: Figure 2B)
Beremendiini						
Beremendia fissidens	Hungary		Beremend 5, late Pliocene	Bf-HU	1	ZIN 104895/hu-02
Beremendia fissidens	Mongolia		Orkhon 1A, late Pliocene	ORH/1A	1	GIN 959/1243
Beremendia fissidens	Russia		Sibiryachikha Cave, redeposited	SBH	1	ZIN 104893/01
^{t}*Beremendia jiangnanensis*	China		Renzidong, early Pleistocene	Bj	1	IVPP V 13961.21 (image from Jin et al. 2009: Figure 2)
Beremendia minor	Mongolia		Bural-Obo 1C, early Pleistocene	BRB/C	1	GIN 959/1242
Beremendia minor	Russia		Koridornaya Cave, redeposited	KOR	1	FSC RJARV-KorC-01
^{t}*Lunanosorex lee*	China		Qipanshan Hill, late Pliocene,	Ll	1	IVPP V 14973.1 (image from Jin et al. 2007: Figure 2)
^{t}*Lunanosorex qiui*	China		Bilike, early Pliocene	Lq	1	IVPP V 11890.8 (image from Qiu and Storch 2000: pl. 3, figure 8)
^{t}*Nectogalinia altaica (= B. fissidens)*	Russia		Razdol'e, early Pleistocene	Na	1	GIN 664/201
Peisorex pochainensis (= B. fissidens)	China		Haimao, early Pleistocene	Pph_HA	1	DH8951 (image from Jin and Kawamura 1996a: figure, p. 6)
Blarinini						
Blarinoides mariae	Poland		Węże 1, early Pliocene	BMr	1	ZIN 104901/BM-10
Blarina brevicauda	USA	Forest, Shrubland, Wetlands (inland) (N. America)	Recent	BBr	10	ZIN 40073, 57486, 65805–810, 67639, 90551
Cryptotis parvus	USA	Forest, Shrubland, Grassland, Wetlands (inland), Rocky areas (N. America)	Recent	CPa	1	ZIN 71059
Mafia dehneli	Poland		Podlesice, early Pliocene	MDh	1	ZIN 104907
Neomyini						
Neomys anomalus	Russia	Wetlands (inland) (Europe)	Recent	NAn	1	ZIN 67644
Neomys fodiens	Russia	Forest, Grassland, Wetlands (inland), Marine Intertidal, Marine Coastal (Europe, N. Asia)	Recent	NFd	3	ZIN 11883, 21693, 34050
Neomys teres	Russia	Forest, Wetlands (inland) (W. Asia)	Recent	NTr	1	ZIN 72288
Soriculus nigrescens		Forest, Shrubland, Rocky areas (S-E. Asia)	Recent	SNi	1	ZIN 99109
Notiosoricini						
Notiosorex crawfordi	USA	Forest, Shrubland, Grassland, Desert (N. America)	Recent	NCr	1	ZIN 09529
				Total:	**32**	

(Zeiss SIGMA 300 VP), with the surfaces covered by chromium sputter-coating (A.V. Zhirmunsky National Scientific Centre of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences).

Morphospace size comparisons

In this study, the morphological disparity of a particular group was calculated as the sum of the univariate variances in the sense of Eble (2000, p. 60); in other words, these are the variances or eigenvalues of the PC axes (or in some cases the variances of the scores of the taxa on those axes). The principal component analysis was based on the correlation matrix of the mandibular shape used for the morphospace description (Wills et al. 1994; Eble 2000, 2002). The number of ordered components was selected using the 'broken-stick model' with 1000 bootstrap replicates (Jackson 1993). The components (i.e. univariate variables) located above the 'broken-stick' were used for the disparity estimation. We used this method in the description of the Ethiopian white-toothed shrews (Lavrenchenko et al. 2016). The total variance (TV) was calculated as a sum of the selected univariate variables; the morphospace size of a particular group (tribe) was calculated as the sum of the intragroup variance (IGV). The variance of each taxon/specimen was calculated using the 'PCA Score' values on the selected univariate variables in the 'Univariate statistics' block of the PAST with 500 bootstrap replicates under the 'adjusted percentile method' (regarding the need to use the bootstrap approach, see Foote 1992; Eble 2000; Navarro et al. 2004). All analyses were performed with the PAST ver. 2.04 software (Hammer et al. 2001).

Geological setting for Beremendia from Russian Far East

The limestone Koridornaya Cave locality is situated in the south-eastern spurs of the Lesser Khingan Ridge, the southern part of the Pompeevskii Ridge and the right bank of the Stolbukha River (approximately N 48°00′, E 130°59′; Jewish Autonomous Oblast, Far East, Russia; see Figure 1) (Yushmanov et al. 2009). The fieldwork was carried out during 2017 and 2018. Sediments were

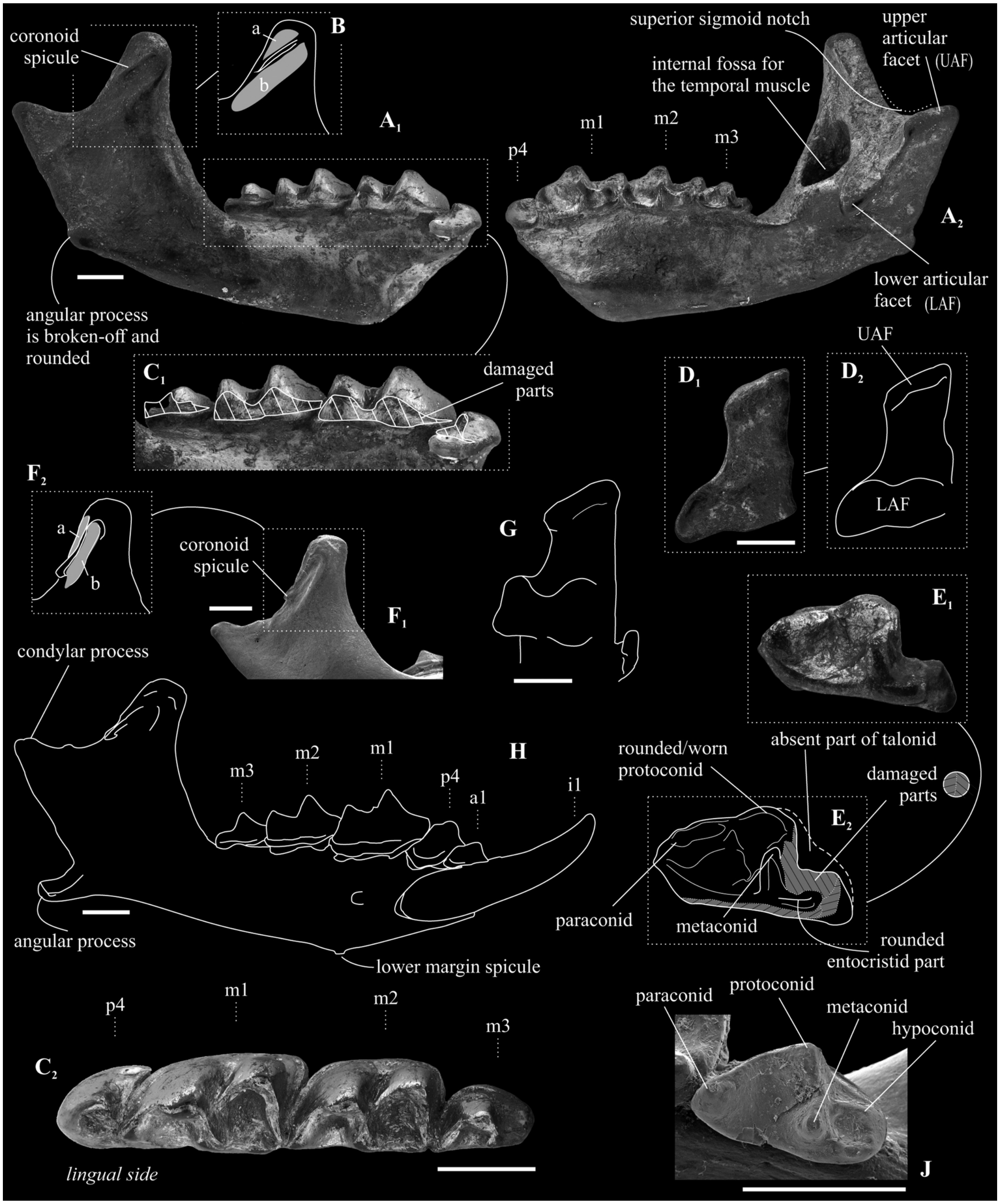


Figure 2. Hemimandibles of *Beremendia minor* Rzebik-Kowalska, 1976 from Koridornaya Cave (FSC RJARV-KorC-01; A–E) and from Mongolian Bural-Obo 1C locality, (GIN 959/1242; F–H, J). (A) Fragment of right hemimandible in lateral (A_1) and medial (A_2) views. (B) Diagrammatic image of the right coronoid process tip with posterior (a) and anterior (b) portion of the external fossa for the temporal muscle in lateral view. (C) Right lower tooth-row (cut images) in buccal (C_1) and occlusal (C_2) views. D. Right condylar process (cut image) in an articular view (D_1, photo image; D_2, diagrammatic image). (E) Third lower right molar (cut image) in subocclusal view (E_1, photo image; E_2, diagrammatic image). (F) Right mandibular ramus (cut mage) with posterior (a) and anterior (b) portion of the external fossa for the temporal muscle in lateral view (F_1, photo image; F_2, diagrammatic image). (G) Diagrammatic image of right condylar process in an articular view. (H) Diagrammatic image of the whole right hemimandible in lateral view. (J) Third lower right molar (cut image) in occlusal view. Scale bars 1 mm.

selected during excavation with a conditional horizon of 10 cm. The sediment samples taken in the field were screen-washed with 1.0 mm mesh for microvertebrates.

The small *Beremendia* remains (fragment of the right hemimandible with p4–m3) was found in loose deposits of the horizontal cave section 15 metres from an entrance 60–70 cm deep. A roe

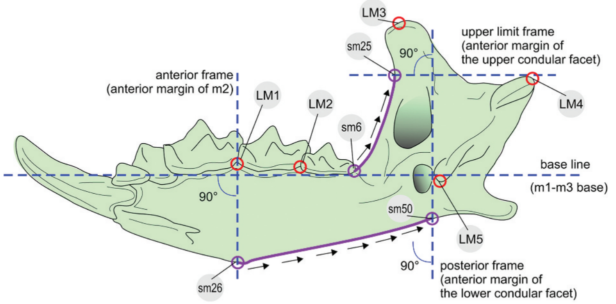


Figure 3. Diagrammatic image of the reference frames (dotted lines), five 'true' landmarks (LM1–5; red rings) and 45 semi-landmarks (sm6–25, sm26–50; violet rings) position on the medial side of *Beremendia minor* Rzebik-Kowalska, 1976 right hemimandible (GIN 959/1242). Violet lines display position of semi-landmarks, arrows display the landmarks shifting direction 'one-by-one.'

deer metacarpal bone from the layers underlying the *Beremendia* remains (depth is approximately 110–120 cm) was 14 C-dated by the AMS method to ca. 49,435 yr BP. AMS analyses of the roe deer metacarpal bone (IGANAMS-7598) were performed using equipment from the Research Resource Centre of the Laboratory of Radiocarbon Dating and Electronic Microscopy of the Institute of Geography, Russian Academy of Sciences (Moscow, Russia), and the Centre for Applied Isotope Studies of the University of Georgia (CAIS; Georgia, USA).

The following mammals are represented in the cave deposits between the upper and lower layers (from depths of 10 to 120 cm): *Sciurus vulgaris, Tamias sibiricus, Myospalax psilurus, Rattus norvegicus, Craseomys rufocanus, Myopus schisticolor* and several species of *Alexandromys* (Rodentia); in addition, *Canis lupus, Vulpes vulpes, Ursus arctos, Martes zibellina, Mustela* spp. (Carnivora); *Sus scrofa, Moschus moschiferus, Capreolus pygargus, Alces alces, Cervus elaphus* (Artiodactyla) are present. These species live around the cave presently except the muroid *M. psilurus* with a more southern modern geographic range (Tiunov and Vinokurova 2019). The species list is still being clarified.

Shrew associations from the cave deposits were determined and are represented by nine species (ranging in taxonomic position and abundance): *Sorex caecutiens* Laxmann, 1785 (species is dominant in all layers), *S. isodon* Turov, 1924, *S. daphaenodon* Thomas, 1907, *S. roboratus* Hollister, 1913, *S. minutissimus* Zimmermann, 1780, *S. tundrensis* Merriam, 1900 (Soricinae: Soricini); very rare *Neomys fodiens* (Pennant, 1771) (Soricinae: Neomyini); *Crocidura lasiura* Dobson, 1890 (subdominant species in all layers), and *C. shantungensis* Miller, 1901 (Crocidurinae). These shrew species presently inhabit the area around the cave, except for *C. shantungensis*, which is currently distributed more southward.

According to the mammalian species association and the degree of preservation of fossil remains, all the layers above a depth of 120 cm are considered Holocene and late Pleistocene with lower limit later than 130,000 yr BP.

Results

Species determination of Beremendia from Russian Far East

The material is represented by a single fragment of the right hemimandible with p4–m3, the whole coronoid and condylar processes; the angular process is broken off (FSC RJARV-KorC-01). The hemimandible belonged to small beremendiin shrew. The teeth are damaged, so small crown elements such as entoconids and entostylids are difficult to distinguish. The metaconids of m1–m3 are significantly damaged. The dentary is dark-brown colour. The enamel of the buccal side of the teeth was probably exposed to chemical leaching and mechanical rounding (Figure 2C); tooth pigment is weakly visible. Despite the specimen condition, we can determine the main proportion and qualitative characteristics of this *Beremendia* member. The fourth lower premolar (p4) is soricine-like in shape with a strong anterior shift of the high protoconid and developed shallow posterolingual basin and a high posterocristid buccal arm; the end of the posterocristid and the posterobuccal angle of the crown are slightly damaged. The lower molars are graded in size, which is typical for *Beremendia*: the first molar is the largest, the second is slightly smaller, and the third is much smaller. The lower third molar (m3) includes a developed trigonid and a smaller talonid; the talonid elements are fully damaged (Figure 2E). The mandibular body is robust and high. The ventral margin of the hemimandible gradually tapers from the anterior broken edge to the posterior end, which is also typical for *Beremendia* (Figure 2A cf. 2H). The mandibular ramus is moderately long and large; its anterior margin is tilted posteriorly and bends in the upper part so that the tip of the coronoid process is strongly tilted towards the anterior. The coronoid process includes a developed coronoid spicule and two well-delineated external fossae for the temporal muscle (Figure 2B). The condylar process is large with a broad interarticular area; the upper articular facet is short and slightly tilted; the lower facet is longer than the upper facet (Figure 2D).

The species determination of the shrew from Koridornaya Cave deposits is based on the general proportions of the hemimandible in comparison with the extremely well-preserved specimen from Mongolian Bural-Obo 1C locality. These proportions are following: the relative position and tilting of the coronoid and condylar processes in the lateral view, i.e. the outline of the superior sigmoid notch (Figure 2A); the expressed tapering of the dentary with the lower margin bend below the hypoconid of m1. These character sets are similar to the described *B. minor* specimen from Bural-Obo; slight differences (KOR specimen with more concaved the sigmoid notch than shows the specimen from Bural-Obo) within the range of species variability as well as the more expressed differences in the coronoid spicule length and shape (KOR specimen has the shorter spicule than specimen from Bural-Obo) and differences in the condylar lower facet shape (Figure 2D vs. 2G). Other characters such as a presence of the lower margin spicule (Figure 2H) and the mental foramen position are unknown for the KOR specimen due to the dentary damaging. The most reliable characters for species determination are linear measurements (Table 2). The KOR specimen slightly smaller in the length of m1 (2.23 vs. 2.44 mm), the length of m3 (1.21 vs. 1.33 mm) than *B. minor* from European Somssich Hill 2 locality and more similar in size to *B. minor* from Mongolian Bural Obo 1C locality (Table 2). The KOR specimen differs from the *B. fissidens* and *B. jiangnanensis* in the significantly smaller size (e.g. L(m1) is 2.23 mm in the KOR specimen vs. 2.85 mm in *B. fissidens* and 3.01 mm in *B. jiangnanensis*; Table 2). The KOR specimen differs from small *L. qiui* in having narrower m1 and m2 (see TRW and TAW characters), higher dentary (seen on the level of the m1/m2 junction) and narrower tip of the coronoid process (Table 2; Figure 2A–2C; cf. plate 3 in Qiu and Storch 2000).

The fossil remains of *B. minor* from Koridornaya Cave are the most north-easterly discovery. To date, the East Asian *Beremendia* species from south of Koridornaya Cave are found in numerous Chinese Pliocene and early Pleistocene sites: Chiachiashan site (= Jiajiashan; near Tangshan prefecture-level city, Hebei Province, China) fossiliferous sediments attributed to the early Pleistocene (Storch et al. 1998, p. 106); Haimao site (near Haimao village,

Table 2. Dental and bone measurements (mm) of *Beremendia* from European and Asian localities. Measurements are presented as the mean, range and the number of specimens in parentheses; [1], Somssich Hill 2 locality (Hungary, early Pleistocene; Botka and Mészáros 2014); [2], Bural-Obo 1C locality (Mongolia, early Pleistocene; Zazhigin and Voyta 2019); [3], Renzidong locality (China, early Pleistocene; Jin et al. 2009); [4], Mazegou locality (China, late Pliocene; Flynn and Wu 2017); [5], Bilike locality (China, early Pliocene; Qiu and Storch 2000); [KOR], Koridornaya Cave locality (FSC RJARV-KorC-01; Russia, late Pleistocene); HC, height of condylar process; L, length of tooth; LLF, lower condylar facet length; LUF, upper condylar facet length; MRH, mandibular ramus height; TAW, talonid width; TRW, trigonid width; W, width of tooth.

Measurements	*B. minor* [KOR]	*B. fissidens* [1]	*B. minor* [1]	*B. minor* [2]	*B. jiangnanensis* [3]	*B. pliocaenica* [4]	*L. qiui* [5]
L(p4)	1.17 (1)			1.27 (1)	1.88/1.41–2.08 (8)		
L(m1)	2.23 (1)	2.85/2.67–3.00 (20)	2.44/2.33–2.60 (3)	1.99, 2.37 (2)	3.01/2.43–3.38 (28)	2.71 (1)	2.31/2.12–2.49 (10)
TRW(m1)	1.10 (1)			1.08, 1.24 (2)		1.46 (1)	1.51/1.40–1.60 (10)
TAW(m1)	1.25 (1)	1.61/1.47–1.73 (20)	1.31/1.13–1.40 (3)	1.14, 1.31 (2)		1.57 (1)	1.55/1.32–1.68 (10)
L(m2)	1.87 (1)	2.30/1.93–2.47 (24)	1.90/1.80–2.07 (6)	1.71, 2.06 (2)	2.53/2.20–2.89 (32)	2.27 (1)	2.02/1.88–2.12 (10)
TRW(m2)	1.08 (1)			0.92, 1.14 (2)		1.54 (1)	1.44/1.32–1.52 (10)
TAW(m2)	1.10 (1)	1.44/1.33–1.63 (24)	1.16/1.07–1.33 (6)	0.96, 1.23 (2)		1.33 (1)	1.42/1.32–1.52 (10)
L(m3)	1.21 (1)	1.62/1.50–1.73 (14)	1.33 (2)	1.31, 1.57 (2)	1.89/1.70–2.08 (17)	1.65 (1)	1.46/1.28–1.56 (10)
W(m3)	0.79 (1)	0.95/0.83–1.13 (14)	0.84/0.80–0.87 (2)	0.73, 0.88 (2)	1.08/1.00–1.25 (17)	0.99 (1)	0.98/0.88–1.04 (10)
MRH	5.32 (1)			4.88 (1)	7.09/6.04–7.92 (17)		
HC	3.13 (1)			2.76 (1)			
LLF	2.09 (1)			2.03 (1)			
LUF	1.34 (1)			1.34 (1)	1.88/1.30–2.08 (18)		

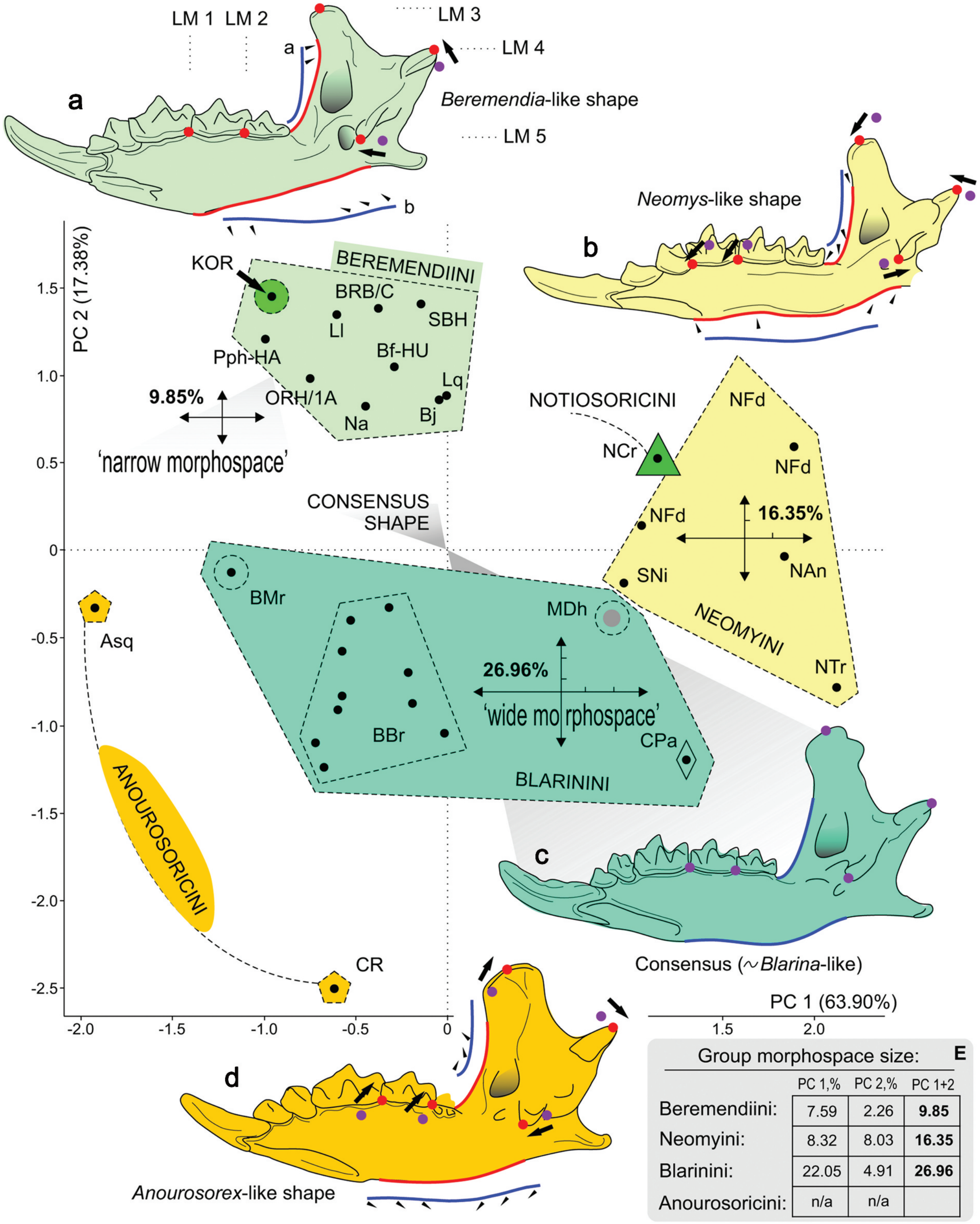
Ganjingzi District, Dalian city, Liaoning Province, China; see Jin et al. 1999) fossiliferous sediments attributed to the early Pleistocene (Jin and Kawamura 1996a, p. 100); Renzidong site (near Suncun town, Fanchang County, Anhui Province, China) fossiliferous sediments attributed to the early Pleistocene (Jin et al. 2009); Mazegou site (near Yushe town, Yushe County, Shanxi Province, China) fossiliferous sediments attributed to the late Pliocene (dated 3.3 Ma in Flynn and Wu 2017); Qipanshan Hill (near Xingtunzhi town, Yinan County, Shandong Province, China) fossiliferous sediments attributed to the late Pliocene (Jin and Kawamura 1996b, p. 479); Houxushan Hill site (Queshan County, Henan Province, China) fossiliferous sediments attributed to the late Pliocene (Jin et al. 2007, p. 85); Bilike site (Huade County, Inner Mongolia, China) fossiliferous sediments attributed to the early Pliocene, Yushean, zone MN 14 (Qiu and Storch 2000, p. 173). The nearest *B. minor* remains are found west of the cave in the Mongolian early Pleistocene Bural-Obo 1C locality situated in Selenge Aimag (Zazhigin and Voyta 2019; Figure 1).

Mandibular shape and morphospace size estimation

The first purpose of the mandibular shape analysis is to estimate the shape differences between known beremendiin shrews and the ‘late Pleistocene’ survivor from the Far East because we suspect that hemimandible proportions changed during the middle and late Pleistocene; i.e. the belated *Beremendia* should not be like Neogene and early Pleistocene beremendiins. An example of these differences is the morphological changes in proportions and qualitative characters during the existence of the shrew group within the local region (East Asia), which we can see in the genus *Anourosorex* (Soricinae, Anourosoricini). The late Miocene *Anourosorex oblongus* Storch and Qiu, 1991 from the Chinese Shihuiba locality differs from the Recent *A. squamipes* in tooth proportions and several qualitative characters (Storch and Qui 1991), which accumulated/developed during group evolution under particular regional conditions (climatic fluctuation, landscape changes, shrew community changes, *etc.*).

Our results reveal the closely related positioning of *B. minor* (KOR) among species of the tribe (Figure 4). A previous study (Zazhigin and Voyta 2019) of mandibular shape variability revealed fewer differences within the Beremendiini (*Beremendia* vs. *Peisorex* vs. *Lunanosorex*) than within the Blarinini (*Blarina* vs. *Blarinoides* vs. *Mafia* vs. *Cryptotis*). In this study, we confirm this ‘narrow’ variability compared to Neomyini (*Neomys* vs. *Soriculus*) and Anourosoricini (*Crusafontina* vs. *Anourosorex*). In general, beremendiin taxa display (i) sharp narrowing of the dentary posteriorly and (ii) anterior shifting of the rough condylar process (Figure 4A). These main tendencies slightly vary between genera and species within the tribe but are not very broad (this inference needs confirmation from more European material). *Blarina* displays a mandibular shape (Figure 4C) that within the current analysis is mostly close to the consensus configuration, although the taxa of the Blarinini widely diverge along the PC 1 and 2. *Mafia* and *Cryptotis* show a trend towards the Neomyini mandibular outline (along the PC 1); these taxa display a shorter condylar length and slenderer and longer dentary than *Blarina* and *Blarinoides*. The shortened and ‘vertical condylus’ of Neomyini (partly with *Mafia, Cryptotis* and *Notiosorex*) corresponds to the *Sorex*-like morphotype and in fact corresponds to the plesiomorphic state of the condylar process in Crocidosoricinae Reumer, 1987. Anourosoricin shrews have the shortest and most massive dentary and longest condylar process.

The second purpose of the mandibular shape analysis is to estimate the inter-group relations in the hemimandible shape in the context of supposedly inevitable hemimandible proportion changes in the belated *Beremendia* and the expected shift of the shape to another ‘adaptive zone,’ or more precisely, to increase the morphological disparity of the particular group of ‘long-condylus’ shrews. The Anourosoricini tribe is represented by two taxa (Figure 4D) and is not used for analysis, but their extremely specialised genera, *Amblycoptus* Kormos, 1926 and *Kordosia* Meszaros, 1997, with missing M3/m3, suggest the broadest morphospace. In the current study, Blarinini has the broadest morphospace, which is 26.96% IGV (22.05% along PC 1 with a range of 4.73–37.03%; 4.91% along PC 2 with a range of 2.47–7.98%; n = 13) within the TV of the 1st and 2nd PCs (TV of PC 1 and 2 is 81.28%); i.e. this tribe shows a high value of morphological disparity due to the wide habitat divergence of its representatives. The intermediate morphospace size revealed in Neomyini is 16.35% IGV (8.32% along PC 1 with range 7.78–12.13%; 8.03% along PC 2 with range 2.39–14.47%; n = 6). Beremendiini has the



Group morphospace size:

	PC 1,%	PC 2,%	PC 1+2
Beremendiini:	7.59	2.26	**9.85**
Neomyini:	8.32	8.03	**16.35**
Blarinini:	22.05	4.91	**26.96**
Anourosoricini:	n/a	n/a	

Figure 4. Results of mandibular shape analysis for the samples of Beremendiini, Anourosoricini, Neomyini and Blarinini tribes: principal component plot for extant and extinct shrews (first vs. second axes). (A) Diagrammatic image of *Beremendia minor* Rzebik-Kowalska, 1976 (GIN 959/1242) hemimandible in medial view to present the average *Beremendia*-like shape. (B) Diagrammatic image of *Neomys fodiens* (Pennant, 1771) (ZIN 11883) hemimandible in medial view to present the average *Neomys*-like shape. (C) Diagrammatic image of *Blarina brevicauda* (Say, 1823) (ZIN 40073) hemimandible in medial view to present the consensus shape (similar to *Blarina*-like shape). (D) Diagrammatic image of *Anourosorex squamipes* Milne-Edwards, 1872 (ZIN 38946) hemimandible to present the average *Anourosorex*-like shape. (E) The morphospace size calculated based on the univariate variance of PC 1–2 for each tribe separately. *Beremendia minor* from Koridornaya Cave (FSC RJARV-KorC-01) is marked by light-green colour (KOR). Short black arrows indicate landmark shifting vectors; black triangles represent semi-landmark shifting vectors; violet points and blue solid lines show consensus configurations; red points and red lines mark outline shifting relative consensus. Numbers 1–5 are landmarks (see Figure 3). Abbreviations for samples see in Table 1.

smallest morphospace size, which is 9.85% (7.59% along PC 1 with a range of 4.25–11.36%; 2.26% along PC 2 with a range of 1.23–3.60%; n = 10; Figure 4E).

Discussion

General remarks

Our investigation of new original material from the Far Eastern Koridornaya Cave locality expands the geographic range of the extinct *Beremendia minor*. At present, we know that the species was broadly distributed from Central Europe to the Far East (middle part of the Amur River Basin). This species is poorly represented in the fossil record everywhere.

The hemimandibles of small mammals and shrews are also the most common remains in fossil deposits after isolated teeth, but the beremendiin hemimandible presents the least taxonomically informative remains (see Zazhigin and Voyta 2019). The single hemimandible from the Koridornaya Cave locality has rounded and damaged teeth that make species determination based on qualitative dental characters difficult. First, we can associate this specimen with *Beremendia* based on the condylar process characters (*Beremendia* differs from *Lunanosorex* in the shorter upper facet and relatively shallow medial notch of the interarticular area; see Jin et al. 2007, figs. 2, p. 3) and on the coronoid process characters (*Beremendia* differs from *Lunanosorex* in the narrower and relatively smooth tip of the process). Second, we can associate this specimen with *Beremendia minor* based on the hemimandible proportions (the relative position and tilting of the coronoid and condylar processes in the lateral view, the expressed tapering of the dentary with the lower margin bend below the hypoconid of m1 in comparison to *B. minor* from Mongolian Bural Obo 1C site), measurements (Table 2) and mandibular outline analysis (Figure 4).

Redeposition issue

The new finding of *Beremendia* in the Russian Far East is in itself an important event for the palaeogeography of the group. However, the greatest interest in this case is focused on the age of the enclosing deposits. *B. minor* disappeared in Europe in the late Pliocene and in Asia in the early Pleistocene (Rzebik-Kowalska 1998; Botka and Mészáros 2014; Zazhigin and Voyta 2019). All materials from later Pleistocene deposits have been asserted to be 'redeposited,' e.g. *B. fissidens* from the Sibiryachikha Cave locality (Altay, late Pleistocene enclosing deposits; ZIN 104893/01–02; see Zazhigin and Voyta 2019).

Far Eastern cave late Pleistocene and Holocene deposits that were investigated in the last decades included several findings of small mammals that usually come from late Pliocene or early–middle Pleistocene deposits, such as *Mimomys* (Rodentia: Arvicolinae) representatives, namely, *Mimomys chandolensis* Tiunov et al., 2016 from Medvezhyi Klyk Cave locality (Tiunov et al. 2016) and *Mimomys* sp. from the Tetyukhinskaya Cave locality (Borodin et al. 2018). These authors concluded that 'species of *Mimomys* managed to exist here much longer, than anywhere else, owing to some specific environmental conditions (i.e. local refugium – LV) in the South-Eastern part of the mammoth fauna geographic range' (Tiunov et al. 2016, p. 209); however, they did not exclude redeposition events (Borodin et al. 2018, p. 15).

If we suppose late Pleistocene survival of *Beremendia* representatives, there is a wide temporal gap between known early Pleistocene (Jin and Kawamura 1996a) and hypothetical late Pleistocene Asian findings. In contrast, Jin et al. (1999) and Flynn and Wu (2017) described faunal changes between the late Pliocene and early Pleistocene epochs in North and East China. Flynn and Wu (2017) described the multi-layered formation and deposits from the Yushe Basin that clearly show the presence of fundamental alterations in shrew (and other) communities between the late Pliocene and early Pleistocene. These authors suggested that 'declining insectivoran diversity corresponds with a hypothetical decline in mean annual temperature.' Jin et al. (1999, p. 16) described a similar decline in shrew diversity in the Pliocene/Pleistocene of North China; the late Pliocene fauna consisted of *Sorex* spp., *Paenelimnoecus* sp. and *Beremendia* (Mazegou and Daodi Faunas); the early early Pleistocene fauna consisted of *Sorex* only (Danangou Fauna); the late early Pleistocene fauna consisted of *Sorex bor* and *S. minutus* and added *Crocidura*. The authors supposed *Beremendia* inhabited North China during this period but not later in the middle Pleistocene (Zhoukoudian 1 locality). These conclusions based on the analysis of shrew associations and their changes exclude the possibility of late Pleistocene survival of *Beremendia* in the Far Eastern habitats. Otherwise the shrew community from Koridornaya Cave includes only modern species of *Sorex, Neomys* and *Crocidura*; the layer with *B. minor* (60–70 cm) contained: *S. daphaenodon* (two remains), *S. minutissimus* (single remain), *S. caecutiens* (five remains), *S. tundrensis* (single remain), *S. isodon* (five remains), *C. lasiura* (single remain). The analysis of shrew specimens from this layer reveals the colouration and surface condition differences between damaged specimens including *B. minor* specimen and other specimens of *Sorex, Crocidura* (rounded and chemical leached surface and dark-brown/black colour) and well-preserved specimens without visible damages of a surface and slightly coloured (sandy and beige) or uncoloured.

On the other hand, we have the recent Asian genus *Anourosorex*, which is known in China from the late Miocene Shihuiba locality (Storch and Qui 1991) as *A. oblongus*. Miocene *Anourosorex* coexisted with *Heterosorex wongi, Blarinella* sp. and *Sorex* sp. Recent *A. squamipes* (*s. lato*) coexists with *Chodsigoa* sp., *Soriculus* sp. (Alexei Abramov, personal communication) and *Suncus murinus* (Kawada et al. 2014). As we can see, species communities vary. However, we can suppose the existence of lower-latitude refugia (Hewitt 2000) suitable for *Anourosorex* persistence (e.g. see He et al. 2015), which are less likely at higher latitudes due to the Pleistocene huge climatic fluctuations.

However, these suggestions about 'redeposition' or 'survival' are only possibilities because the fossil records are not complete. The question of the sampling effect always remains. In this case, we attempt to apply the morphometric approach based on the suggestion of inevitable morphological changes as a result of adaptations to the broad climatic and ecological fluctuations during the middle and late Pleistocene. These changes would broaden the morphospace size that we can estimate using mandibular shapes with PCA (Figure 4). The largest size of the Blarinini morphospace reflects the morphological divergence by the mandibular outline between analysed genera with broad ecological divergences of the included species (Table 1). The Neomyini morphospace also reflects the divergence between different species of *Neomys*: broad-ranged *N. fodiens* vs. narrow-ranged *N. teres*. However, the morphospace of Beremendiini shows a slightly diverging shape compared to Blarinini and Neomyini. *B. minor* from Koridornaya Cave is located within the morphospace of typical beremendiin. This result confirms the assumption of redeposition of *B. minor* remains from earlier unknown deposits and allows us to precisely suggest the significant environmental contribution to the East Asian beremendiin extinction, such as climatic fluctuation, landscape changes and shrew community changes between the late Pliocene and early Pleistocene sense of Jin et al. (1999) and Flynn and Wu (2017). In summary, the last remains of East Asian *Beremendia* (*Peisorex*) described from the Chinese early Pleistocene localities: Chiachiashan (*P. pohaiensis*; Storch et al. 1998), Haimao (*P. pohaiensis*; Jin and Kawamura 1996a) and Renzidong (*B. jiangnanensis*; Jin et al. 2009); the last remains of *Lunanosorex* described from the Chinese late Pliocene localities: Qipanshan Hill (*L. lii*; Jin and Kawamura 1996b) and Houxushan Hill (*L. lii*; Jin et al. 2007).

Conclusion

The new finding of *Beremendia* in the Russian Far East is an important event for the palaeogeography of the group that expands the geographic range of the extinct *B. minor*. The important question regarding the presence of *B. minor* in the late Pleistocene deposits in the Koridornaya Cave locality is whether it indicates ‘late Pleistocene survival’ or ‘redeposition of earlier remains in later deposits.’ The current paper suggests using two of Reumer’s approaches (1984) with some additions to resolve this question: (i) species association comparisons when we estimate ‘typical’ shrew associations for the particular taxon in question and (ii) the morphospace size when we search for an ‘exit to another niche’ connected with hypothesised morphological changes as a result of adaptations. The species associations from Koridornaya Cave consist of modern species of shrew (*Sorex, Neomys* and *Crocidura*) that are significantly different from the fossil associations in the Chinese late Pliocene and early Pleistocene localities where *Beremendia* was present. Jin et al. (1999) and Flynn and Wu (2017) directly point to significant changes in shrew associations that were associated with climate changes between the late Pliocene and early Pleistocene epochs in North and East China. This conclusion is consistent with Reumer’s view on a role of environmental factors in soricid evolution.

We have expanded Reumer’s ‘morphological’ approach using an assessment of morphospace size estimation (MSE) based on the PCA method and estimation of the variance to reveal redeposition of *Beremendia*. The morphospace (disparity value) in a similar sense was previously developed in the works of Foote (1992), Wills et al. (1994) and Eble (2000), (Eble 2002) for the investigation of Palaeozoic and Mesozoic invertebrates and in the works of mammalogists (Davies et al. 2007; Meloro 2011; Abramov and Puzachenko 2012; Werdelin and Wesley-Hunt 2014; Abramov et al. 2016) for the investigation of interspecies differences in the width of ecological niches.

Our results prove redeposition of *B. minor* from earlier sediments to later strata of Koridornaya Cave. The shrew specimens surface condition and colouration do not allow unambiguously determine the redeposition due to the different set of these characters in the layer with *B. minor*: from the undamaged specimens with the natural colouration of bones and teeth to damaged and coloured specimens. However, due to the large size and robust bone, the remain of *B. minor* perhaps more resistant to mechanical and chemical impacts than other shrews remain. In summary, the KOR specimen condition also indicates redeposition. Previously in the introduction part, we suspect: if this occurrence is really from the late Pleistocene, we would expect it to have evolved specialisations not found in other beremendiins, which would increase the morphospace size of the group considerably. The morphospace size assessment allows us to conclude that even with the new find of *B. minor* from the Far East, beremendiins have a very ‘narrow morphospace’ compared to other relevant shrew groups, Blarinini and Neomyini. Therefore, it seems more likely that this is actually an early Pleistocene fossil that has been redeposited rather than a true survivor.

In addition, the MSE approach, in our opinion, has additional development prospects for estimating the rate of morphological changes in late Pleistocene and Holocene small mammal groups. This method can be an important tool for studying the effects of species habitat fluctuations on local extinction events (extinction of local populations). He et al. (2015), based on the molecular (CYT B, ND2) and GIS-modelling (MAXENT) data sets, showed the population structure changes in *A. squamipes* (s. lato) during the late Pleistocene and Holocene of Southwest China. They revealed ‘two phylogenetic clades and significantly higher genetic diversity’ of *A. squamipes* as a result of the influence of the Last Interglacial Maximum with a high degree of seasonality (He et al. 2015, p. 23). Other authors revealed morphometric differences among several geographic populations of *A. squamipes* (Motokawa and Lin 2002) and cytogenetic changes in species karyotypes (Motokawa et al. 2004; Kawada et al. 2014), which were most likely determined by population structure fluctuations as revealed by He et al. (2015). These results in the focus of the MSE approach show that relatively short-term (within the late Pleistocene) changes in the population structure of the species can rapidly develop into morphological differences. Thus, there is less doubt that Far Eastern *Beremendia* could have survived into the middle Pleistocene without any particular morphological changes. However, additional studies on late Pleistocene/Holocene materials (e.g. mole shrews) with an assessment of molecular changes vs. the size of the morphospace are required.

Our work is the first attempt to use the comparative analytical method to determine the possible redeposition of fossil remains. In this case, the ‘comparative’ part of the method corresponds to the faunistic approach of Reumer (1984), and the ‘analytical’ part of the method corresponds to his extended morphological approach. However, one important result from Eble (2000) requires attention. The author revealed the partitioning of disparity into different morphological systems (in the original text, ‘plastral’ and ‘nonplastral’ components of echinoids), which reflected different degrees of their developmental entrenchment and functionality. In this context, our result needs to be checked in the future, since the hemimandible of beremendiins with the smallest morphospace size can be an inert structure (like to some of Eble’s structures), and then the disparity in this group should be evaluated by other morphological systems (e.g. teeth). In addition, our results on *Beremendia* redeposition cannot be unambiguously transferred to other possible mammalian finds from East Asia.

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Authors' contributions

LV: a general conception, design, analysis and interpretation of the data and results; drafting the article and preparing of all graphic materials; geometric morphometric analysis; corresponding author.

VO, MT and MV: excavation of *Beremendia* remains (FSC RJARV-KorC-01) from Koridornaya Cave locality (Russian Far East); revising the manuscript text and images; discussion on the *Beremendia* redeposition possibility; approval of the final version.

VO: preliminary preparation of fossil remains of *Beremendia* (FSC RJARV-KorC -01); species determination and taphonomic description of the material on other shrews specimens from Koridornaya Cave (9 species of *Sorex, Neomys* and *Crocidura*; n = 717); SEM-imaging, shrew measurements; revising the manuscript text and images.

Disclosure statement

No potential conflict of interest was reported by the authors.

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