Low Epigenetic Variability of the Eurasian Otter *Lutra lutra* (L.) from Europe to Kamchatka[1]

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Abstract—We studied the epigenetic variability of the Eurasian otter *Lutra lutra* from 12 European localities and Kamchatka Peninsula based on 15 nonmetric traits in 692 skulls. The samples from Eastern Germany are close to each other geographically, have small epigenetic distances, and can represent one otter population. Other European samples group with each other and can have a common origin of the European otter populations from one refuge in the post-glacial period. The epigenetic distances for the Kamchatka sample have a similar level of distances between the European samples. This can reflect the low geographical divergence of otter populations within a species area and can be associated with species ecology.

The river otter *Lutra lutra* is a widespread semi-aquatic species of Eurasia and occurs from Ireland in the West to the Kamchatka Peninsula, Sakhalin, Shantar, and Japanese islands in the East (Aristov and Baryshnikov, 2001). A species habitat strongly depends on fish supplies and the river's ecosystem so that otters' area does not have continuous form, especially in the Asian part of the area.

During the twentieth century, the otter populations in Europe declined and became fragmented because of habitat destruction, chemical pollution, and direct persecution (MacDonald and Mason, 1994). In the Asian part of the area, otters were always a thin species because of complicated hydrologic rivers with deep freezing of the water, floods, shoaling, and decreasing fish in the rivers (Vajsfeld, 1977).

Despite the widespread distribution of otters in Eurasia, the geographic variability is low. In all of Europe and Northern Asia, only the subspecies *L. l. lutra* Linnaeus, 1758 is described (Heptner et al., 1967; Wilson and Reeder, 2005). The genetic research of European otters showed the extremely low variability of mitochondrial DNA with a single dominant haplotype that supports the postglacial recolonization of Europe from a single refugium (Ferrando et al., 2004; Honnen et al., 2011). However, analyses for genetic variability using microsatellite loci showed levels of polymorphism and heterozygosity within the range found in

other mammalian species (Dallas and Piertney, 1998; Hajkova et al., 2006). Besides the molecular genetic techniques, classic morphological studies on the skeleton can be used to obtain information about the population's genetic variability (Ansorge, 2001). The evaluation of the "epigenetic distances" between the populations by checking qualitative skull characters is able to complement the question above. Thus, the main goal of our research was to analyse the geographic genetic variability of otters based on the epigenetic traits of the skull.

MATERIAL AND STUDY AREAS

A total of 692 otter skulls from 13 geographic samples were included in the analysis (Figure 1), namely from seven natural regions of eastern Germany (Baltic Coast 27 skulls, Mecklenburg lake and interior land 45 skulls, Mecklenburg-Brandenburg lake and table-land 28 skulls, Oder-Neisse region 25 skulls, Lower Lusatia Brandenburg heath land 36 skulls, Elster region 20 skulls; Upper Lusatia 186 skulls) as well as from Bohemia (64 skulls), Bavaria (60 skulls), Austria (26 skulls), Denmark (36 skulls), Latvia (79 skulls), and Kamchatka (60 skulls).

Kamchatka is one of the regions of Russia where the otter population has always been at a stable, high level because of a good developing lake-rivers system, comparatively mild maritime climate, and low anthropogenic stress (Ilyushkin and Valentsev, 2004). In our

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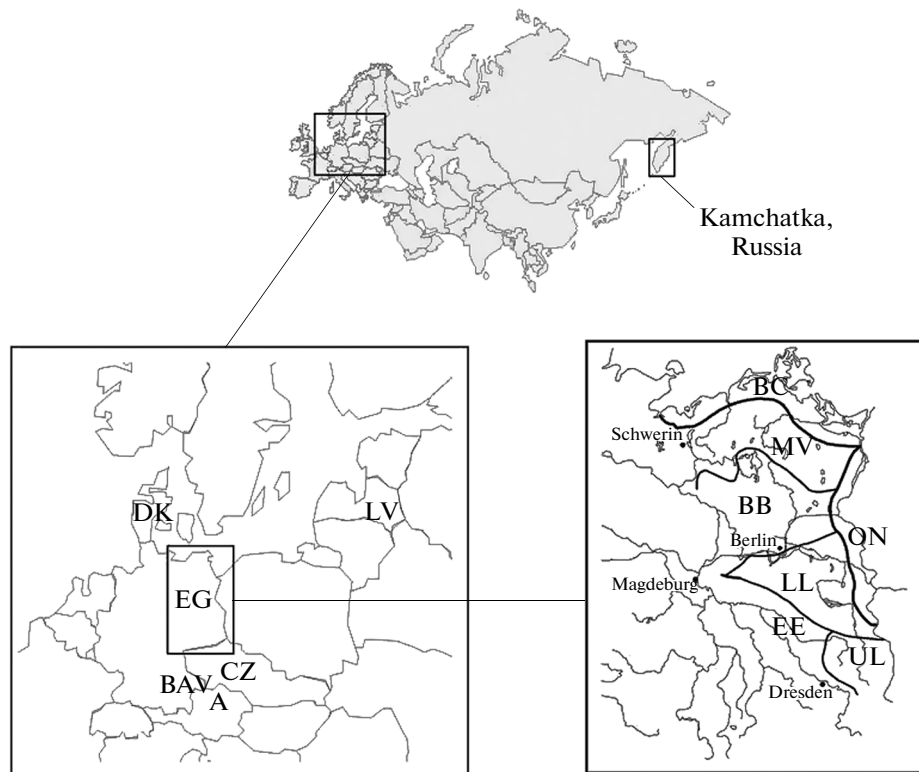
Fig. 1 Geographic locality of otter samples. Kamchatka, Russia − 60 skulls; DK (Denmark) − 36 skulls; LV (Latvia) − 79 skulls; BAV (Bavaria) − 60 skulls; A (Austria) − 26 skulls; CZ (Bogemia) − 64 skulls; EG (East Germany): BC (Baltic Coast) − 27 skulls; MV (Mecklenburg lake and interior land) − 45 skulls; BB (Mecklenburg-Brandenburg lake and tableland) − 28 skulls; ON (Oder-Neisse region) − 25 skulls; LL (Lower Lusatia Brandenburg heath land) − 36 skulls; EE (Elster region) − 20 skulls; UL (Upper Lusatia) − 186 skulls.

research, we used otter skulls trapped by hunters from 1956 to 1989 from the craniological collection of the Pacific Institute of Geography Far Eastern Department Kamchatka Branch, Russian Academy of Sciences.

The otter skulls from *Latvia* were collected from 1985 to 1998 and are kept at Latvian National University. The otter numbers in Latvia decreased in first half of the 20th century when a small increase in population size was noticed between 1945 and 1965 and then a quite rapid decrease number until the 1980s. Around 1990, a stable otter population of approx. 4000 animals was formed again (Ozolins and Pilats, 1995).

The otter samples from *Eastern Germany* are mainly road killed animals collected for the main part since the 1990s, kept in the mammalian collection of the Senckenberg Museum of the Natural History Goerlitz and the Museum of Western Lusatia Kamenz. A general decrease of the otter population size was noticed in the 1930s, but not really extinct. After 1980−1990, there was a remarkable increase in their number and now the otter has become abundant especially in the Upper Lusatian pondland (Teubner et al., 2011; Hertweck, 2012).

Otter samples from *Denmark* are kept in the mammalian collection of the Aarhus University and were collected from 1984 to 1993. Otters were previously distributed all over Denmark, but have severely declined in number during the last four decades. Now, the otter only inhabits the northern regions of Denmark (Pertoldi et al., 2001; Madsen and Prang, 2001).

The otter population in *Czech Republic* rapid increased during the nineties of XX century (Adamek et al., 2003). The Bohemia region is occupied with the most abundant otter population in Czech Republic (Toman, 1992). The sample from Bohemia is of otter skulls collected from the beginning of the 20th century to 1970. The craniological collection is kept in the National History Museum Prague.

The otter sample from *Bavaria* was provided by private hunters from 1995 to 2009 and partly stored in the Senckenberg Museum of Natural History Goerlitz. Otters became nearly extinct in Bavaria during the 1970s, probably earlier (Hodl-Rohn and Becker, 1978). Since the end of the last century, a stable population returned in the mountainous regions along the border of south-eastern Bavaria (Van der Sant and Kraft, 2006).

The *Austrian* population of otter has been expanding since the 1990s (Bodner, 1994; Gutleb, 1994). In our research, we include animals from the mammalian collection of the Museum of Natural History Vienna.

All otter skulls were classified on 15 nonmetric traits (Fig. 2). The characters have been chosen according to the previous studies of otter epigenetic variability (Ansorge and Stubbe, 1995). Bilateral traits were taken from both sides of the skull and registered separately.

Non-metric traits of skull

1 (*Feth*) foramina ethmoidalia completely separated

2 (*Ffr*) foramen frontale present

3 (*Ccd*) canalis condylaris double

4 (*Ccv*) canalis condylaris open ventrally

5 (*laFbt*) lateral accessory foramen bullae tympani present

6 (*maFbt*) medial accessory foramen bullae tympani present

7 (*Fosd*) foramen ovale subdivided

8 (*eFov*) emissary foramen beside the foramen ovale present

9 (P^1) first upper premolar missing

10 (*aFmd*) accessory anterior foramen mandibulare present

11 (*Fcor*) foramen coronoidale present

12 (M_2) last lower molar missing

13 ($aTrP^2$) accessory tooth roots in upper P^2

14 ($aTrP^3$) accessory tooth roots in upper P^3

15 ($aTrP^4$) accessory tooth roots in upper P^4

DATA ANALYSES

We analysed all the non-metric characters for their homogeneity in age and sex. The frequencies of the character expressions of the subsamples were compared using a χ^2-test at a significance level of $p = 0.05$ (Weber, 1980), and sex- or age-dependent characters were excluded from further investigation.

We used two methods for the evaluation of epigenetic divergence between the populations: "Mean Measure of Divergence" (MMD) (Smith, 1972; Sjøvold, 1977; Hartman, 1980) and a standard discriminant analysis (Multrus and Lucyga, 1996).

After eliminating the age- and sex-dependent nonmetric characters, all the remaining traits were used to calculate the MMD by a formula proposed and derived by Sjøvold (1977).

$$\text{MMD} = \frac{1}{r}\sum_{i=1}^{r}[(\Theta_{1i} - \Theta_{2i})^2] - v_i \quad S_{\text{MMD}} = \sqrt{\frac{2\sum_{i=1}^{r} v_i^2}{r^2}},$$
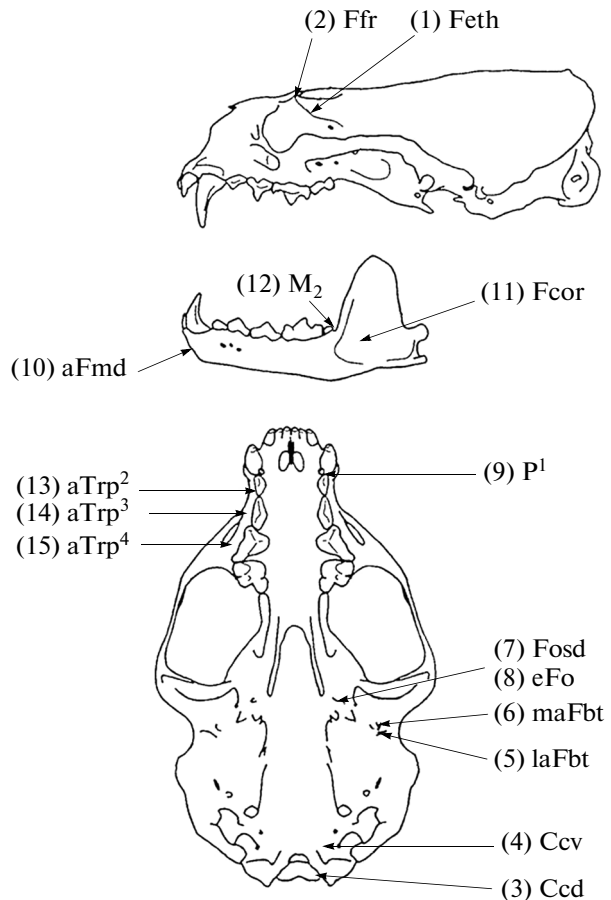

Fig. 2 Position of 15 non-metric characters in the otter skull.

where r = number of traits; n = sample size; p = frequency of traits.

$$\Theta = \arcsin(1 - 2p),$$
$$v_i = 1 / n_1 + 1/n_2.$$

Variance and standard deviation (S_{MMD}) of the MMD indicated the statistical significance at the level of $p = 0.05$ to be MMD > 2S_{MMD}.

We compared all population samples with each other with MMD calculations. Clustering of the MMD matrix was performed by the "unweighted pair group method with average" (UPGMA) because this tree reflects the phenotypic similarities originally developed for constructing taxonomic phenograms. The UPGMA employs a sequential clustering algorithm, in which the tree is built stepwise.

Additionally, we carried out "Standard Discriminant Analyses" ((Multrus and Lucyga, 1996) for evaluating the discriminate power of epigenetic traits and one more method for calculating the distances between groups using Squared Mahalanobis Distances (Lindeman et al., 1980). For the standard discriminant analyses, we selected 532 specimens using only adult animals and skulls with the complete data set.

Table 1. Mean measures of divergence (MMD) between the otter populations based on 11 non-metric skull characters ($n = 692$)

	BC	MV	BB	ON	LL	EE	UL	Den-mark	Latvia	Bavaria	Austria	Bohe-mia
BC												
MV	<0.001											
BB	0.028*	0.018*										
ON	0.028*	0.059*	0.130*									
LL	0.028*	0.005	0.031*	0.027*								
EE	0.031*	0.029*	0.044*	<0.001	<0.001							
UL	0.130*	0.077*	0.173*	0.164*	0.105*	0.150*						
Denmark	0.219*	0.142*	0.106*	0.237*	0.045*	0.045*	0.128*					
Latvia	0.292*	0.254*	0.509*	0.290*	0.276*	0.305*	0.109*	0.295*				
Bavaria	0.391*	0.296*	0.436*	0.473*	0.335*	0.398*	0.124*	0.026*	0.195*			
Austria	0.160*	0.087*	0.193*	0.195*	0.085*	0.164*	<0.001	0.056*	0.025*	<0.001		
Bohemia	0.212*	0.167*	0.167*	0.270*	0.032*	0.085*	0.140*	0.022*	0.235*	0.053*	0.060*	
Kamchatka	0.154*	0.219*	0.311*	0.198*	0.215*	0.205*	0.163*	0.304*	0.147*	0.364*	0.167*	0.264*

Asterisks indicate statistical significance ($p < 0.05$).

For this standard model, the left and right sides of the bilateral traits were pooled and the geographical localities were used as the grouping variable. Because of the absence data about traits 13 aTrP[2], 14 aTrP[3], and 15 aTrP[4] for the Austria, Czech Republic, and Denmark samples, we excluded these traits from standard discriminant analysis.

RESULTS

The analysis of the chosen non-metric characters of homogeneity in age and sex proved age dependence in three characters (1 Feth, 2 Ffr, 6 maFbt) and sex-specific expression in one character (13 aTrP[2]). We excluded these traits from further analysis.

Epigenetic Population Divergence

The pair-wise comparison analyses of the otter samples based on MMD calculation showed varied epigenetic distances from 0.018 to 0.509 (Table 1). Animals from Eastern Germany have a low level of epigenetic divergence and demonstrate the homogeneity of the otter population on this region. We supposed that otters from Kamchatka would widely differ from the European populations but with the epigenetic distances between the Kamchatka sample and European samples not exceeding the divergence within European otter samples.

The resulting cluster tree (Fig. 3) showed three main clusters. All German samples, except Upper Lusatia, combined in one cluster. One more cluster groups otters from Upper Lusatia and European populations. Otters from Latvia and Kamchatka are in a third cluster (Fig. 3).

Supplementary calculations using the Standard Model of Canonic Discriminant Analyses showed similar results (Table 2). The German otter samples do not have significant differences from each other except for the otters from Upper Lusatia. Other European populations and otters from Kamchatka are just about equidistant from each other (Fig. 4). The results of the canonical analysis of the variables showed that 80.3% of the explained data variability was given by the first 3 Canonical Discriminant Functions (CDF). Of these, 42.6% of the explained data variability was from CDF1 (Table 3). All the non-metric characters used in standard discriminant analyses significantly discriminate the samples, except 9P[1] (Table 3).

DISCUSSION

The otter displays very low geographic variability despite been widely distributed throughout Eurasia (Heptner et al., 1967; Aristov and Baryshnikov, 2001). The species exhibits unusually low levels of mtDNA variation, and shows almost no mtDNA geographic structure for European otters (Ferrando et al., 2004; Mucci et al., 2010). Mucci and coauthors (1999) supposed that the observed low mtDNA control region sequence variability could result from a conservative pattern of molecular evolution of the mtDNA in otter. The research of the autosomal microsatellites showed the polymorphism in otter, but the little geographic
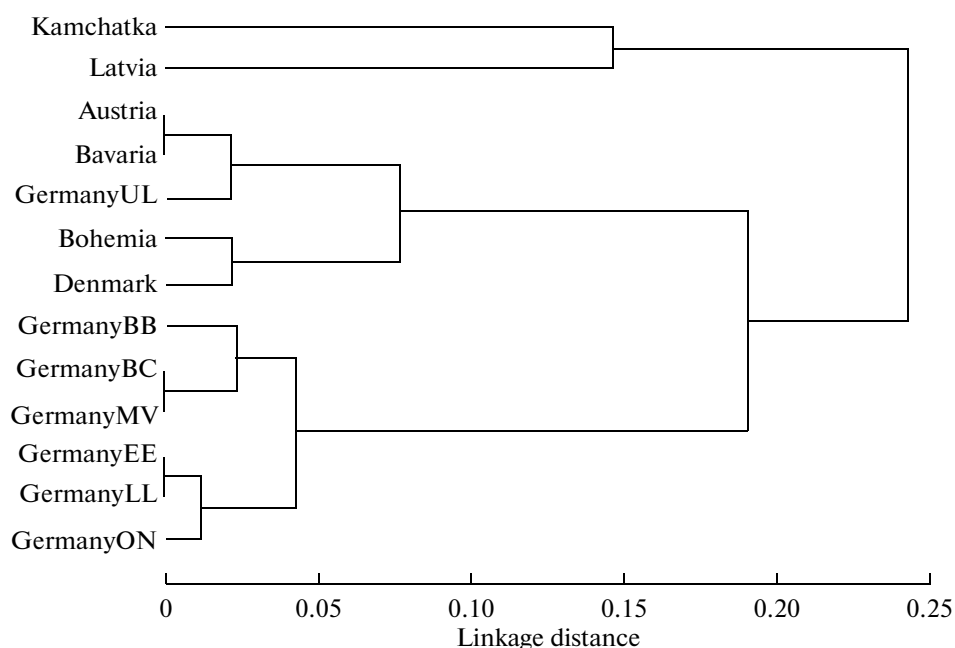
Fig. 3 Unweighted pair-group average (UPGMA) dendrogram of epigenetic distances based on the mean measure of divergence (MMD) derived from 11 non-metric skull characters of the otter samples (*n* = 692).

differentiation was also found at the nuclear level (Dallas et al., 1999; Pertoldi et al., 2001; Randi et al., 2003).

Furthermore, the epigenetic non-metric investigation of genetic variability concerns the more integrative value of the epigenetic level represented by non-metric characters. On the one hand, the development

of the small aberrations of the skull has genetic bases (Gruneberg, 1963; Berry and Searle, 1963). However, different environmental factors may affect the ontological development of organisms (Gruneberg, 1963; Astaurov, 1974; Vasil'ev and Vasil'eva, 2009). This quality makes it a good tool for population research. The obtained epigenetic variability of otter is in agreement with previous research. The samples from East-

Table 2. F-values for distances between groups for the standard discriminant analysis of otter samples based on 9 non-metric skull characters (*n* = 532)

	BC	MV	BB	ON	LL	EE	UL	Den-mark	Latvia	Bavaria	Austria	Bohe-mia
MV	0.31											
BB	1.20	0.70										
ON	1.38	1.59	2.60*									
LL	1.28	1.19	1.21	1.72								
EE	0.91	1.05	1.81	0.57	0.81							
UL	3.00*	4.10*	3.40*	2.52*	2.45*	1.20						
Denmark	4.24*	4.16*	2.36*	3.82*	1.85	1.94*	4.81*					
Latvia	4.17*	6.62*	6.93*	2.00*	3.30*	1.10	5.62*	7.71*				
Bavaria	3.34*	3.66*	2.36*	3.30*	1.87	2.26*	2.98*	0.70	5.03*			
Austria	4.62*	5.27*	4.22*	4.26*	3.62*	3.12*	4.13*	3.36*	5.55*	2.03*		
Bohemia	4.64*	5.09*	2.83*	4.94*	1.18	2.23*	6.94*	1.13	8.52*	1.38	4.13*	
Kamchatka	1.75	3.59*	4.10*	1.73	3.06*	1.27	6.56*	9.04*	4.52*	5.87*	7.28*	10.38*

Asterisks indicate statistical significance (*p* < 0.05).
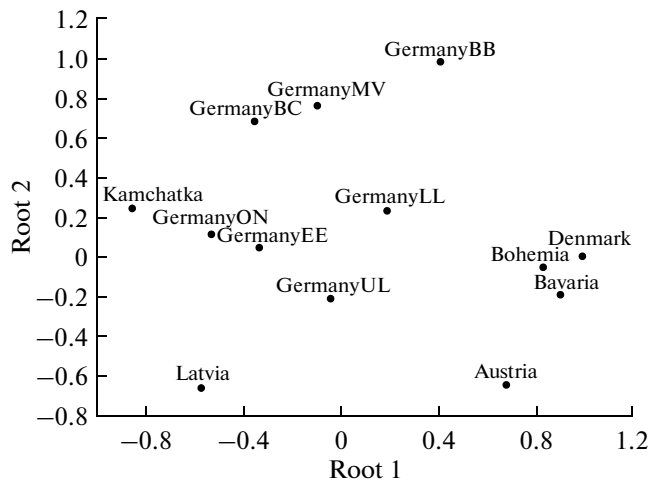
Fig. 4 Means of canonical discriminant functions for the region resulting from standard discriminant analysis of otter samples based on 9 non-metric skull characters ($n = 532$).

ern Germany are close to each other geographically, have small epigenetic distances, and can represent one otter population. Otters from Upper Lusatia with high distances within the German group became extinct in this region at the beginning of the 20th century because of intensive hunting. Thus, the separation of this sample within the German group could be explained by the strong bottleneck 100 years before. Otters from Denmark occupy the western part of the area more but also group with other European samples. This can be the result of a common origin with the European otter populations from one refuge in the post-glacial period.

Surprisingly low epigenetic distances were obtained for otters from Kamchatka. We supposed the easternmost population would vary widely from European otters because of no migration, common origin, and large geographical distances. However, the values of the mean measure of divergence for the Kamchatka

sample have a similar level as the distances between the European samples. This can reflect the low geographical divergence of the otter population within the species area and be associated with species ecology. The otter is a semiaquatic species of mammals and despite the widespread area they prefer specific habitats with a river or another water reservoir where otters can fish during all seasons, especially in wintertime. It should be a river with a special hydrologic regime that does not freeze in wintertime, with a good fish supply and suitable for shelter riverbanks. That is the reason for the net form of the otter area in Asia where winter conditions can be very strong for this species habitat. The otter is a highly adapted semiaquatic mammal species and the specific ecology can be reflected in the low diversity in morphology and the genetics of the species. It is noteworthy that the same low geographic variability is noted for other European mammals with similar habitat requirements − European mink *Mustela lutreola* (Aristov and Baryshnikov, 2001).

Nevertheless, the low epigenetic variability of otter populations is the main reason for the non-geographical dependent epigenetic similarity or distance. The similar results where epigenetic divergences between populations did not correlate with geographic distance were obtained before for the common dormouse *Muscardinus avellanarius* (Ansorge et al., 2012). Obviously this does not reflect the degree of the phylogenetic or microevolutionary relationship.

Table 3. Statistics for standard discriminant analysis of otter samples based on 9 non-metric skull characters ($n = 532$)

Characters	Wilks' Lambda	p-level	Standardized	Coefficients
			1	2
Ccd (3)	0.50	0.026	−0.221	−0.071
Ccv (4)	0.49	0.046	−0.174	0.306
laFbt (5)	0.49	0.069	−0.021	0.158
Fosd (7)	0.51	0.000	0.117	−0.010
eFov (8)	0.61	0.000	0.871	0.367
P^1 (9)	0.49	0.535	−0.020	−0.055
aFmd (10)	0.51	0.002	0.310	−0.196
Fcor (11)	0.56	0.000	−0.244	0.866
M_2 (12)	0.50	0.023	0.036	−0.136
Cumulative dispersion			0.426	0.673

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