

• 研究简报 •

青海湖地区狗獾分类地位和狗獾属进化历史探讨

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摘要: 本研究选择线粒体细胞色素*b* (cytochrome *b*, Cyt *b*)和控制区(control region, CR)片段作为分子标记, 探讨了青海湖地区狗獾(*Meles* sp.)的系统发育地位和狗獾属分歧时间。研究结果支持目前将狗獾属分为4个种的结论。Cyt *b*和CR片段序列拼接后总长1,652 bp, 23条序列共定义了21个单倍型。研究结果表明欧亚大陆狗獾分为东西两个支系, 每个支系进一步分为两个种: 东部支系包括亚洲狗獾(*M. leucurus*)和日本狗獾(*M. anakuma*); 西部支系包括欧洲狗獾(*M. meles*)和西南亚狗獾(*M. canescens*)。贝叶斯树和单倍型网络关系图都支持青海湖地区狗獾属于亚洲狗獾。分歧时间的估算结果与古生物学证据相符, 东部支系和西部支系在2.24 Ma左右产生分歧, 西南亚狗獾在1.27 Ma左右从欧洲狗獾分出, 而日本狗獾和亚洲狗獾的分化时间为0.99 Ma左右。

关键词: 狗獾; 青海湖地区; 细胞色素*b*; 控制区; 系统发育关系

The taxonomic status of badgers in the Qinghai Lake area and evolutionary history of *Meles*

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Abstract: To investigate the phylogenetic status of badgers (*Meles* sp.) in the Qinghai Lake area and to estimate the divergence time within Eurasian badgers, the cytochrome *b* gene and the partial control region (CR) of mitochondrial DNA were examined as genetic markers. Our results indicated that *Meles* is divided into four species. Twenty one haplotypes were identified in 23 combined sequences (1,652 bp) of Cyt *b* and CR sequences. Results showed that Eurasian badgers were clearly divided into two major lineages: one of Western lineage, composed of badgers from Europe and Southwest Asia, and the other of Eastern lineage, composed of badgers from North and East Asia (including Japan). Furthermore, the Bayesian tree and the haplotype network indicated that the badgers in the Qinghai Lake area are Asian badgers (*M. leucurus*). The estimated divergence time was consistent with palaeontological evidence. The first split between the Western lineage and Eastern lineage occurred approximately 2.24 Ma. After the separation, the Southwest Asia clade split from Europe approximately 1.27 Ma and the Japan clade split from continental Asia approximately 0.99 Ma.

Key words: badger; *Meles*; Qinghai Lake area; cytochrome *b*; control region; phylogenetic relationship

狗獾属(*Meles*)隶属于食肉目鼬科, 是鼬科动物中分布最广的类群, 现生的狗獾广泛分布于古北界的森林和草原(图1), 北至斯堪的纳维亚和西伯利亚, 南至伊朗、巴勒斯坦和中国南部, 东达日本岛,

西界延伸到伊比利亚半岛(Wozencraft, 2005)。狗獾起源于上新世亚洲的温带森林, 在晚上新世至早更新世向西扩散到欧洲(Neal & Cheeseman, 1996), 在中更新世地层中发现的狗獾化石的形态与现生狗

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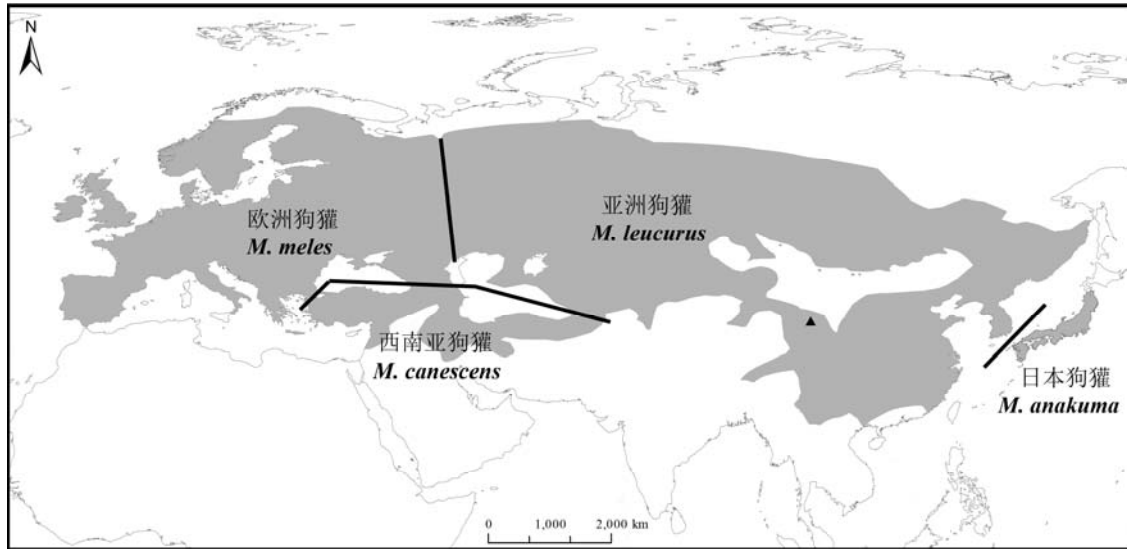


图1 欧亚大陆狗獾分布示意图。灰色区域表示狗獾分布范围, 黑色粗线表示各种群的分界线, 黑色三角符号为采样点。
Fig. 1 Geographic distribution of Eurasian badger. The grey area shows the range of Eurasian badger, the black lines represent geographic boundaries of each phylogenetic group and the black triangle indicates our sampling locality.

獾十分接近(Kurten, 1968; Petter, 1971)。

由于不同地区狗獾形态差异大, 狗獾的分类一直是科学家们争论的话题, 早期研究认为现生狗獾属仅有1个物种*M. meles* (Corbet, 1978; Wozencraft, 1993; Nowak & Paradiso, 1999)。Baryshnikov和Potapova (1990)基于牙齿形态的差异, 将狗獾分为两个种, 其中欧洲及西南亚地区的狗獾为*M. meles*, 而将俄罗斯、中亚和日本的狗獾定为*M. anakuma*。Lynch (1994)依据头骨的大小和形态差异, 认为只有日本分布的狗獾为*M. anakuma*, 而其余种群都归为*M. meles*。尔后, Abramov等(Abramov, 2001, 2002; Abramov & Puzachenko, 2005, 2006)根据阴茎骨和头骨形态的不同将狗獾分为欧洲狗獾(*M. meles*)、亚洲狗獾(*M. leucurus*)和日本狗獾(*M. anakuma*), 并认为三者之间的差异达到了种的差异水平。近年来, Abramov和Puzachenko (2013)将欧亚大陆狗獾分为东部和西部两个支系, 而每个支系又各分为两个不同的进化支。Marmi等(2006)基于线粒体DNA控制区序列的分析也将欧亚大陆的狗獾分成了4个支系: 即欧洲狗獾、西南亚狗獾、东亚和北亚狗獾以及日本狗獾。基于核基因(Del Cerro et al, 2010)和SRY基因(Tashima et al, 2011a, b)的分析亦证实了上述结论。Del Cerro等(2010)以及Abramov和Puzachenko (2013)提出将西南亚地区分布的狗獾列为独立的种: 高加索狗獾(*M. canescens* Blanford, 1875)。但上述系统发

育研究均不包括中国的狗獾样本。

历史上, 狗獾在中国境内广泛分布, 除台湾和海南省外, 中国其余省份均有分布记录(高耀亭, 1987)。但近几十年来由于栖息地破坏和乱捕滥猎, 狗獾数量锐减, 在部分地区已濒临灭绝(谢志刚, 2011; 徐循等, 2012)。尽管狗獾广泛分布于中国, 但国内对狗獾的研究不多, 且大多集中在食性(叶晓堤等, 2000; Li et al, 2013)和行为(杨会涛等, 2010; 李峰和蒋志刚, 2014)。针对狗獾属的系统进化研究中, 关于中国狗獾的报道只有: Zhou等(2015)测定了1例黑龙江地区狗獾的线粒体基因组并加入鼬科系统发育分析, Koh等(2014)将GenBank数据库中中国狗獾的3条Cyt *b*序列加入亚洲狗獾系统发育分析中。

青海湖地区是已知的狗獾分布区的海拔上限, 为确定青海湖地区狗獾的分类地位, 本研究采集了狗獾样本, 选择线粒体细胞色素*b* (Cyt *b*)和控制区(control region, CR)序列作为分子标记, 并从GenBank数据库中下载其他地区狗獾的序列信息, 对青海湖地区狗獾的系统发育地位进行探讨, 并结合分歧时间估算来讨论狗獾属的进化历史。

1 材料与方法

1.1.1 样本采集

本实验从青海湖湖东地区采集了6只狗獾的组织样本, 所有样本均用无水乙醇浸泡保存。

1.1.2 总DNA提取、目的片段扩增

取采集的组织样本,按照TIANamp Genomic DNA Kit (天根生化科技有限公司)说明书提取总DNA。

本研究对细胞色素*b* (Cyt *b*)及控制区(CR)序列片段进行扩增。扩增Cyt *b*采用Kurose等(2000)设计的引物Cb-M1 (5'-CTCACATGGAATCTAACCATGAC-3')和Cb-MR1 (5'-TCTTCCTTGAGTCTTAGGGAG-3');扩增CR采用Marmi等(2006)设计的引物MelCR1 (5'-AGCACCCAAAGCTGATATTCT-3')和MelCR6 (5'-CCATTGACTGAATTGCACCT-3')。

PCR反应总体积为50 μ L,其中DNA模板5–10 μ L, dNTP 1 μ L (20 mmol/L), 10 \times PCR loading buffer 5 μ L, 正反向引物各2.5 μ L (20 mmol/L), Taq DNA聚合酶1–2 U, 灭菌ddH₂O 28–33 μ L。PCR反应条件为: 95 $^{\circ}$ C预变性5 min; 95 $^{\circ}$ C变性45 s, 52 $^{\circ}$ C退火30 s, 72 $^{\circ}$ C延伸45 s, 共35个循环; 72 $^{\circ}$ C延伸7 min, 4 $^{\circ}$ C终

止反应。

1.1.3 测序和拼接

PCR产物送北京诺赛基因组研究中心进行测序,测序引物与扩增引物相同。序列拼接使用DNASTAR中的SeqMan软件(DNASTAR, Inc.)进行,测序结果在NCBI数据库中进行比对,确定采集样本为狗獾后,使用ClustalX 1.8 (Thompson et al, 2002)进行序列比对。从GenBank数据库中下载17个样本的Cyt *b*和CR序列(表1),由于线粒体基因为连锁遗传,为增加系统发育树的准确度,将Cyt *b*和CR序列在SequenceMatrix (Vaidya et al, 2011)中进行拼接。

1.2 数据分析

1.2.1 遗传多样性

使用DnaSP v5.0 (Librado & Rozas, 2009)进行遗传多样性检测,计算单倍型数目和核苷酸多样性。基于Kimura's two-parameter (K2P)模型使用

表1 本研究中的线粒体DNA序列信息

Table 1 The mitochondrial DNA sequences information in this study

单倍型 Haplotype	样本代码 Sample code	样本编号 Sample no.	采样点 Sampling locality	序列号 Accession no.	
				Cyt <i>b</i>	Control region
H1	QH1	B1	中国青海 Qinghai, China	KU361236	KU361238
H2	QH2	B2	中国青海 Qinghai, China	KU361237	KU361239
H2	QH3	B3	中国青海 Qinghai, China	KU361237	KU361239
H3	QH4	B4	中国青海 Qinghai, China	–	KU361239
H4	QH5	B5	中国青海 Qinghai, China	–	KU361240
H4	QH6	B6	中国青海 Qinghai, China	–	KU361240
H5	China	–	中国黑龙江 Heilongjiang, China	KU052604	KU052604
H6	Sweden	–	瑞典 Sweden	AM711900	AM711900
H7	Mongolia	45Mo	蒙古 Mongolia	HQ711950	AJ563694
H8	Greece	80Cr	希腊克里特岛 Crete Island, Greece	HQ711947	GU247573
H9	Israel1	49Is	以色列 Israel	HQ711946	AJ563686
H10	Israel2	48Is	以色列 Israel	HQ711945	AJ563685
H11	Spain	35Sp	西班牙 Spain	HQ711943	AJ563676
H12	Russia1	ZIS33	俄罗斯外贝加尔地区 Transbaikalia, Russia	AB049807	AB538995
H13	Russia2	ZIS36	俄罗斯列宁格勒州 Leningrad Province, Russia	AB049808	AB538997
H14	Russia3	ZIS35	俄罗斯列宁格勒州 Leningrad Province, Russia	AB049809	AB538998
H15	Japan1	K1	日本九州大分县 Oita, Kyushu, Japan	AB049806	AB538971
H16	Japan2	K6	日本九州大分县 Oita, Kyushu, Japan	AB049800	AB538971
H17	Japan3	K7	日本九州大分县 Oita, Kyushu, Japan	AB049802	AB538971
H18	Japan4	K8	日本九州福冈县 Fukuoka, Kyushu, Japan	AB049799	AB538971
H19	Japan5	YMG1	日本本州山口县 Yamaguchi, Honshu, Japan	AB049795	AB538983
H20	Japan6	MR1	日本九州岩手县 Iwate, Kyushu, Japan	AB049791	AB538977
H21	Japan7	KPM-NF1002945	日本本州神奈川县 Kanagawa, Honshu, Japan	AB291075	AB291075
	<i>Arctonyx collaris</i>	YP6001		HM106329	HM106329

MEGA 6.0软件(Tamura et al, 2013)计算种内和种间遗传差异。

1.2.2 系统发育分析

以猪獾 (*Arctonyx collaris*) 作为外群, 在 MrBayes v3.2 (Ronquist & Huelsenbeck, 2003)中构建系统发育树。最佳碱基替换模型在 Modeltest v3.7 软件(Posada & Crandall, 1998)中进行计算, 选择赤池信息量准则(Akaike Information Criterion)下的最佳模型为HKY+I+G模型, 程序运行1,000万代, 每隔1,000代取样1次, 舍弃(burn in)前25%的结果。采用 Network 4.6 (Bandelt et al, 1999) 中的 Median-joining法构建单倍型网络图。

1.2.3 分歧时间估算

采用BEAST v1.8软件(Drummond & Rambaut, 2007; Drummond et al, 2012)估算狗獾属分歧时间, 模型设置与贝叶斯分析一致, 分子钟选择 strict clock, 碱基替换速率参照伶鼬(*Mustela nivalis*)和白鼬(*M. erminea*)的CR碱基替换速率1.92%/(Ma · site)

(Marmi et al, 2006), 采用Song等(2009)中的方法, 计算出联合片段的替换速率为2.02%/(Ma · site), 程序运行1,000万代, 每1,000代取样1次。在TRACER 1.6中检验有效性, ESS大于200则结果可信。结果采用TreeAnnotator程序进行总结, 并舍弃前10%的运行结果。

2 结果

通过PCR扩增获得青海湖地区狗獾的3个Cyt *b* 全序列和6个CR序列片段, 并从GenBank数据库中下载17个样本的Cyt *b*和CR片段, 共计23个样本。拼接后线粒体基因全长1,652 bp, 其中Cyt *b*序列为1,140 bp, CR序列为512 bp, 包括1,373个保守位点 (conserved sites)、275个可变位点(variable sites)、175个简约信息位点(parsim-informative sites), 核苷酸多样性为0.026 ± 0.003, 共定义21个单倍型。

基于线粒体基因构建的贝叶斯系统发育树(图2)分东部和西部两个大的支系, 其中东部支系又包

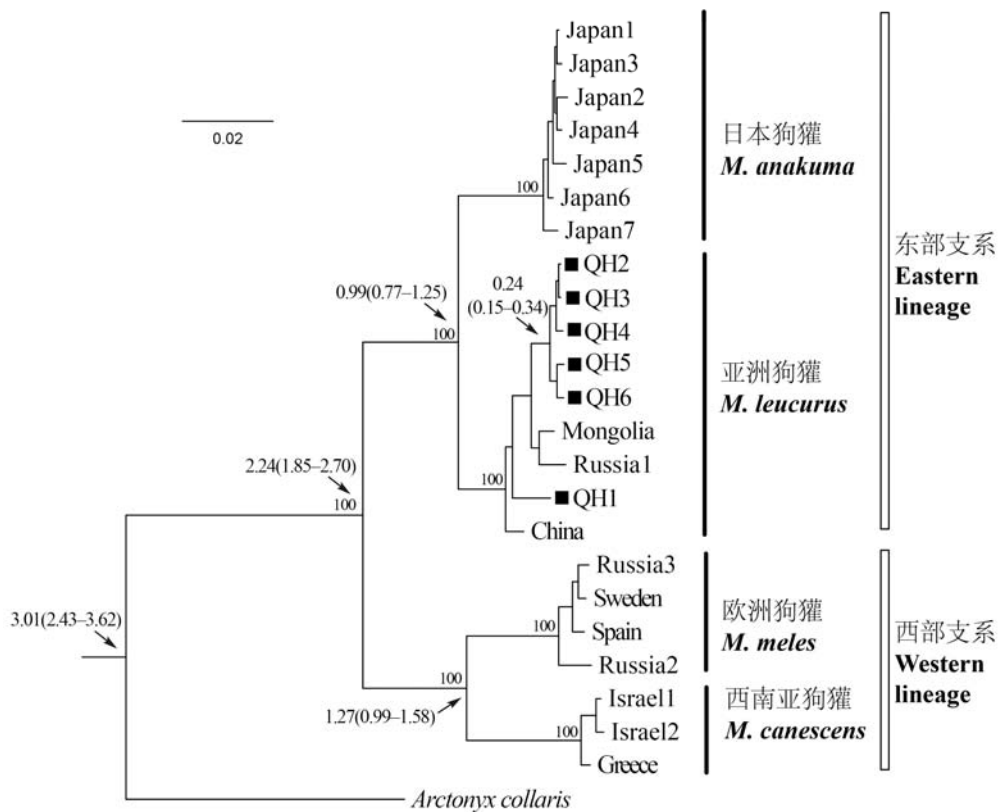


图2 根据线粒体DNA构建的贝叶斯系统发育树。样本代码见表1, 其中QH1-6为青海湖地区狗獾, 枝上数字为主要分支的贝叶斯后验概率和分歧时间(95%置信区间)。

Fig. 2 Phylogenetic tree of mitochondrial DNA obtained from Bayesian analysis. The sample codes correspond with those in Table 1, in which QH1-6 represent badgers of Qinghai Lake area. The numbers on the branch indicate Bayesian posterior probability and estimated divergence time (with 95% HPD).

表2 欧亚狗獾不同类群间遗传距离

Table 2 Genetic distances among different Eurasian badger groups

	西南亚狗獾 <i>M. canescens</i>	欧洲狗獾 <i>M. meles</i>	日本狗獾 <i>M. anakuma</i>	亚洲狗獾 <i>M. leucurus</i>
欧洲狗獾 <i>M. meles</i>	0.034 ± 0.007			
日本狗獾 <i>M. anakuma</i>	0.042 ± 0.009	0.043 ± 0.008		
亚洲狗獾 <i>M. leucurus</i>	0.040 ± 0.008	0.041 ± 0.008	0.021 ± 0.005	
青海湖地区狗獾 Badger in the Qinghai Lake area	0.038 ± 0.008	0.041 ± 0.008	0.020 ± 0.006	0.017 ± 0.004

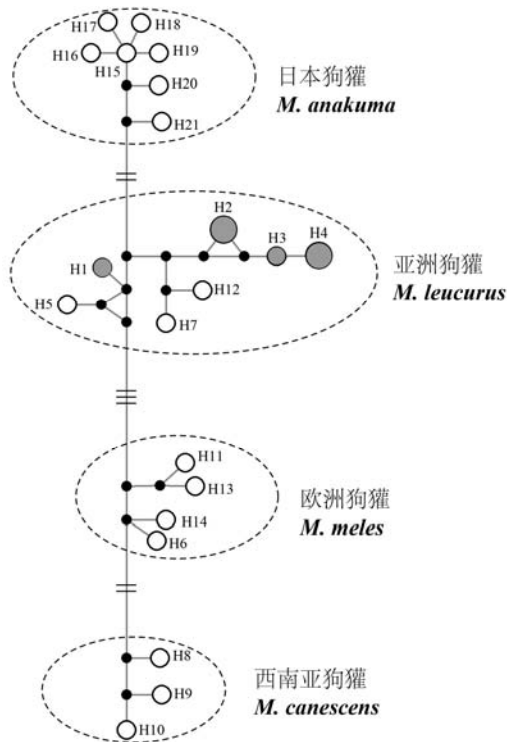


图3 欧亚狗獾线粒体基因21个单倍型的网络关系图。单倍型H1-4为青海湖地区狗獾(灰色), 各单倍型信息见表1, 黑色圆点表示缺失单倍型, 圆点大小与单倍型频率成正比。对应的4个分支用虚线圈出。

Fig. 3 The network based on 21 haplotypes of Eurasian badgers mitochondrial DNA. H1-4 represent Qinghai badgers (in grey). All haplotypes are displayed in Table 1. The black circles represent missing haplotypes. The sizes of the white circles in the network represent the frequencies of each haplotype. Four badger's groups are circled by dotted line.

括亚洲狗獾和日本狗獾两个分支, 而西部支系则包括欧洲狗獾和西南亚狗獾两个分支, 每个分支的后验概率均达到100%。单倍型网络图(图3)的结构和系统发育树基本一致, 即欧亚大陆狗獾分为4个相对独立的进化支系, 分别对应欧洲狗獾、亚洲狗獾、西南亚狗獾和日本狗獾。系统发育树和单倍型网络关系图中, 青海湖地区狗獾样本与亚洲狗獾聚到

一起。

计算类群间遗传距离时, 我们将青海湖地区的狗獾作为一个单独的类群处理(表2), 结果显示青海湖地区狗獾与亚洲狗獾的遗传距离最近, 为0.017, 与日本狗獾的遗传距离次之, 而与欧洲狗獾和西南亚狗獾的遗传距离均较远, 说明青海湖地区狗獾应该归属于亚洲狗獾。

分歧时间的估算结果在图2的进化树节点处显示, 狗獾和猪獾在3.01 Ma (95%置信区间: 2.43-3.62 Ma)发生分歧, 而东部支系和西部支系的分歧时间是2.24 Ma (95%置信区间: 1.85-2.70 Ma)。欧洲狗獾与西南亚狗獾的分化时间在1.27 Ma (95%置信区间: 0.99-1.58 Ma), 亚洲狗獾和日本狗獾的分化时间在0.99 Ma (95%置信区间: 0.77-1.25 Ma)。青海湖地区狗獾QH2-6的分化时间显示为0.24 Ma (95%置信区间: 0.15-0.34 Ma)。

3 讨论

在系统发育树和单倍型网络关系图中, 青海湖地区的狗獾样本都与亚洲狗獾聚在一起, 并且两者间的遗传距离最近, 说明青海湖地区的狗獾属于亚洲狗獾, 通过分子遗传学方法确定了青海湖地区狗獾的分类地位。此外, 在数据分析中, 我们发现青海湖地区的QH1与其他几个样本具有较大的遗传差异, 在系统进化树中并不聚在一起, 从单倍型网络关系图中可以更清晰地看出QH1与其他单倍型相距较远, 提示青海湖地区狗獾可能起源于多个最近祖先, 或者是由多次扩散而来, 也可能是与其他地区种群有基因交流。

古生物学研究表明狗獾可能起源于上新世时期中国的*Melodon* (Viret, 1950), 在晚上新世至最早新世向西扩散至欧洲(Neal & Cheeseman, 1996)。本文对狗獾属分歧时间的估算结果与狗獾的起源和进化历史基本一致。基于线粒体DNA序列的分析表

明, 狗獾和猪獾在3.01 Ma (2.43–3.62 Ma)发生分歧, 这与Koepfli等(2008)和Marmi等(2004)的估算结果基本一致。狗獾的化石种在上新世末期就广泛分布于古北界(Madurell-Malapeira et al, 2011), 化石证据表明欧洲狗獾和亚洲狗獾的共同祖先在1.8 Ma前已发生分歧, 这与本文估算的东西部支系的分歧时间(2.24 Ma)接近。西南亚狗獾和日本狗獾均受地理隔离影响而分别与欧洲狗獾、亚洲狗獾发生分歧(Marmi et al, 2006), 分化时间分别为1.27 Ma (0.99–1.58 Ma)和0.99 Ma (0.77–1.25 Ma), 西南亚狗獾受到黑海、里海及高加索山脉的阻隔, 而日本狗獾和亚洲狗獾被日本海峡分隔开来。谱系地理研究认为欧洲狗獾具有较明显的遗传结构, 推测与末次冰期狗獾由伊比利亚和欧洲东南部避难所向北扩散有关(Frantz et al, 2014)。但日本狗獾可能受到末次冰期后种群扩张的影响, 各种群间并没有明显的分化(Marmi et al, 2006; Tashima et al, 2011a), 本研究在青海湖地区采集的6个样本没有形成单独的分支, 由于本研究样本有限, 无法对青海湖地区狗獾的系统分化做出更多解释, 未来需基于更多的中国狗獾样本对其种群遗传结构进行深入分析。

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参考文献

- Abramov AV (2001) Notes on the taxonomy of the Siberian badgers (Mustelidae: *Meles*). Proceedings of the Zoological Institute, Russian Academy of Sciences, 288, 221–233.
- Abramov AV (2002) Variation of the baculum structure of the Palearctic badger (Carnivora, Mustelidae, *Meles*). Russian Journal of Theriology, 1, 57–60.
- Abramov AV, Puzachenko AY (2005) Sexual dimorphism of craniological characters in Eurasian badgers, *Meles* spp. (Carnivora, Mustelidae). Zoologischer Anzeiger, 244, 11–29.
- Abramov AV, Puzachenko AY (2006) Geographical variability of skull and taxonomy of Eurasian badgers (Mustelidae, *Meles*). Zoologicheskii Zhurnal, 85, 641–655. (in Russian with English abstract)
- Abramov AV, Puzachenko AY (2013) The taxonomic status of badgers (Mammalia, Mustelidae) from Southwest Asia based on cranial morphometrics, with the redescription of *Meles canescens*. Zootaxa, 3681(1), 044–058.
- Bandelt HJ, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution, 16, 37–48.
- Baryshnikov GF, Potapova OR (1990) Variability of the dental system in badgers (*Meles*, Carnivora) of the USSR fauna. Zoologicheskii Zhurnal, 69, 84–97. (in Russian with English abstract)
- Corbet GB (1978) The Mammals of the Palearctic Region: A Taxonomic Review. Cornell University Press, London and Ithaca.
- Del Cerro I, Marmi J, Ferrando A, Chashchin P, Taberlet P, Bosch M (2010) Nuclear and mitochondrial phylogenies provide evidence for four species of Eurasian badgers (Carnivora). Zoologica Scripta, 39, 415–425.
- Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology, 7, 214.
- Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular Biology and Evolution, 29, 1969–1973.
- Frantz AC, McDevitt AD, Pope LC, Kochan J, Davison J, Clements CF, Elmeros M, Molina-Vacas G, Ruiz-Gonzalez A, Balestrieri A, Berge KVD, Breyne P, Do Linh San E, Gren E, Suchentrunk F, Schley L, Kowalczyk R, Kostka BI, Cirovic D, Sprem N, Colyn M, Ghirardi M, Racheva V, Braun C, Oliveira R, Lanszki J, Stubbe A, Stubbe M, Stier N, Burke T (2014) Revisiting the phylogeography and demography of European badgers (*Meles meles*) based on broad sampling, multiple markers and simulations. Heredity, 113, 443–453.
- Gao YT (1987) Fauna Sinica, Mammalia: Vol. 8, Carnivora, pp. 214–223. Science Press, Beijing. (in Chinese) [高耀亭 (1987) 中国动物志·兽纲: 第八卷, 食肉目, 214–223页. 科学出版社, 北京.]
- Koepfli KP, Deere KA, Slater GJ, Begg C, Begg K, Grassman L, Lucherini M, Veron G, Wayne RK (2008) Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. BMC Biology, 6, 1–22.
- Koh HS, Kryukov A, Oh JG, Bayarkhagva D, Yang BG, Ahn NH, Bazarsad D (2014) Two sympatric phylogroups of the Asian badger *Meles leucurus* (Carnivora: Mammalia) identified by mitochondrial DNA cytochrome *b* gene sequences. Russian Journal of Theriology, 13, 1–8.
- Kurose N, Abramov AV, Masuda R (2000) Intrageneric diversity of the cytochrome *b* gene and phylogeny of Eurasian species of the genus *Mustela* (Mustelidae, Carnivora). Zoological Science, 17, 673–679.
- Kurten B (1968) The Pleistocene Mammals of Europe. Weidenfeld & Nicolsan, London.
- Li F, Jiang ZG (2014) Is nocturnal rhythm of Asian badger (*Meles leucurus*) caused by human activity? A case study in the eastern area of Qinghai Lake. Biodiversity Science, 22, 758–763. (in Chinese with English abstract) [李峰, 蒋志刚 (2014) 狗獾夜间活动节律是受人类活动影响而形成的吗? 基于青海湖地区的研究实例. 生物多样性, 22,

- 758–763.]
- Li F, Luo ZH, Li CL, Li CW, Jiang ZG (2013) Biogeographical patterns of the diet of Palearctic badger: Is badger an earthworm specialist predator? *Chinese Science Bulletin*, 58, 2255–2261.
- Librado P, Rozas J (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25, 1451–1452.
- Lynch JM (1994) Morphometric variation in the badger (*Meles meles*): clinal variation in cranial size and shape across Eurasia. *Small Carnivore Conservation*, 10, 6–7.
- Madurell-Malapeira J, Alba DM, Marmi J, Aurell J, Moyà-Solà S (2011) The taxonomic status of European Plio-Pleistocene badgers. *Journal of Vertebrate Paleontology*, 31, 885–894.
- Marmi J, López-Giráldez F, MacDonald DW, Calafell E, Zholnerovskaya E, Domingo-Roura X (2006) Mitochondrial DNA reveals a strong phylogeographic structure in the badger across Eurasia. *Molecular Ecology*, 15, 1007–1020.
- Marmi J, López-Giráldez JF, Domingo-Roura X (2004) Phylogeny, evolutionary history and taxonomy of the Mustelidae based on sequences of the cytochrome *b* gene and a complex repetitive flanking region. *Zoologica Scripta*, 33, 481–499.
- Neal E, Cheeseman C (1996) *Badgers*. T & AD Poyser Ltd., London.
- Nowak RM, Paradiso JL (1999) *Walker's Mammals of the World*. Cambridge University Press, London.
- Petter G (1971) Origine, phylogénie et systématique des blaireaux. *Mammalia*, 35, 567–597. (in French)
- Posada D, Crandall KA (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- Song G, Qu Y, Yin Z, Li S, Liu N, Lei F (2009) Phylogeography of the *Alcippe morrisonia* (Aves: Timaliidae): long population history beyond late Pleistocene glaciations. *BMC Evolutionary Biology*, 9, 143.
- Tamura K, Stecher G, Peterson D, Filipowski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
- Tashima S, Kaneko Y, Anezaki T, Baba M, Yachimori S, Abramov AV, Saveljev AP, Masuda R (2011a) Phylogeographic sympatry and isolation of the Eurasian badgers (*Meles*, Mustelidae, Carnivora): implications for an alternative analysis using maternally as well as paternally inherited genes. *Zoological Science*, 28, 293–303.
- Tashima S, Kaneko Y, Anezaki T, Baba M, Yachimori S, Abramov AV, Saveljev AP, Masuda R (2011b) Identification and molecular variations of CAN-SINEs from the ZFY gene final intron of the Eurasian badgers (genus *Meles*). *Mammal Study*, 36, 41–48.
- Thompson JD, Gibson T, Higgins DG (2002) Multiple sequence alignment using ClustalW and ClustalX. *Current Protocols in Bioinformatics*, Chapter 2 (Unit 2.3), doi: 10.1002/0471250953.bi0203s00.
- Vaidya G, Lohman DJ, Meier R (2011) SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics*, 27, 171–180.
- Viret J (1950) *Meles thoralis* n. sp. du loess villafranchien de Saint-Vallier (Drôme). *Eclogae Geologicae Helvetiae*, 43, 274–287. (in French with English abstract)
- Wozencraft WC (1993) Order Carnivora. In: *Mammal Species of the World: A Taxonomic and Geographic Reference*, 2nd edn. (eds Wilson DE, Reeder DM), pp. 279–348. Smithsonian Institution Press, Washington, DC.
- Wozencraft WC (2005) Order Carnivora. In: *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd edn. (eds Wilson DE, Reeder DM), pp. 532–628. Johns Hopkins University Press, Baltimore.
- Xie ZG (2011) *Studies on the Population Ecology of Badger (Meles meles) in Shanghai*. PhD dissertation, East China Normal University, Shanghai. (in Chinese with English abstract) [谢志刚 (2011) 上海地区狗獾生态学研究. 博士学位论文, 华东师范大学, 上海.]
- Xu X, Xie ZG, Cui YY, Chu KL, Jiang WZ, Pei EL, Xu HF (2012) Activity patterns of reintroduced badgers in seminatural area. *Chinese Journal of Zoology*, 47(3), 49–52. (in Chinese with English abstract) [徐循, 谢志刚, 崔勇勇, 褚可龙, 蒋文忠, 裴恩乐, 徐宏发 (2012) 重引入狗獾秋冬季行为的初步研究. *动物学杂志*, 47(3), 49–52.]
- Yang HT, Liu ZS, Xu K, Song CL, Wu MF, Sun JH (2010) Autumn habitat selection of Eurasian badgers (*Meles meles amurensis*): a case of Fangzheng Forestry Bureau, Heilongjiang Province, China. *Acta Ecologica Sinica*, 30, 1875–1881. (in Chinese with English abstract) [杨会涛, 刘振生, 徐坤, 宋丛亮, 吴木芬, 孙景海 (2010) 狗獾秋季对生境的选择——以黑龙江省方正林业局为例. *生态学报*, 30, 1875–1881.]
- Ye XD, Ma Y, Wang RH, Dong AY (2000) Review of the diet of Eurasian badgers. *Chinese Journal of Zoology*, 35(2), 43–50. (in Chinese) [叶晓堤, 马勇, 王润海, 董安渝 (2000) 欧亚大陆狗獾食性的研究概述. *动物学杂志*, 35(2), 43–50.]
- Zhou WW, Yu L, Tan BY, Liu YT, Zhang L, Hua Y (2015) Phylogenetic relationship of Asian badger *Meles leucurus amurensis* revealed by complete mitochondrial genome. *Mitochondrial DNA*, published online, doi: 10.3109/19401736.2015.1127365.

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