



Dispersing or Contracting: A Perspective on the Evolutionary History and Population Conservation of Musk Deer

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Abstract: Musk deer, as a small hornless group, are of great significance in the phylogenetic evolution of ruminants. Clarification of their evolutionary history has the potential to contribute to an understanding of the total phylogeny of both cervids and bovids. In this paper, based on a comprehensive review of the literature, an integrated rearrangement of moschid fossils is proposed. Our review has produced the following results on the evolution and conservation of moschids: (1) the family Moschidae probably appeared abruptly at a around 30±5Ma, and evolved in parallel with Cervidae and Bovidae; (2) compared with Tragulidae and other Pecora, the Moschidae have acquired a number of progressive traits in common with Cervidae and Bovidae while maintaining certain primitive features, while in their own evolutionary history, they developed a suite of derived features to meet with new environmental circumstances while retaining the most important primitive traits; (3) the origin, divergence, diversification, dispersal and ultimate disappearance of moschids in Europe and North America are essentially closely related with the fluctuation of the global climate and local environmental changes; (4) an overall picture of the evolutionary history of *Moschus* is given; (5) multiple causes are responsible for the global downturn and near-extinction of all musk deer species and populations in recent decades, but it is due mainly to the international background of musk smuggling and domestic anthropocentric factors, particularly overpoaching using Gansitao. All in all, Early moschids underwent over 20Ma of "boom and bust" history from the late Oligocene to the end of Miocene in Europe and North America, and only the Eastern part of Asia sheltered the recent representatives during the Quaternary glacial cycles, but there is still a very long way to go before we can reconstruct the family's phylogenetic history in full, and the conservation of today's musk deer populations is currently the most urgent mission.

Keywords: Evolution, Fossil, Moschidae, *Moschus*, Cervidae, Bovidae, Ruminants

1. Introduction

As a group of primitively hornless ruminants, moschids are of considerable significance in exploring the phylogenetic connections and relationships of Ruminantia. The question of the affinities, and content, of the Moschidae, with which many mid-Tertiary Eurasian and North American hornless pecorans have been associated, is still debated (Dawson *et al.* 2007). On the other hand, populations of the living moschids (now reduced to a single genus, *Moschus*) have been in decline and increasing danger of extinction for some decades, and given

rise to extensive concern (Sheng 1987,1992,1996, Sheng & Ohtaishi 1993, Green 1986,1987,1989, Liu & Sheng 2000a, Liu *et al.*2000b, Yang *et al.*2003, Zhou *et al.* 2004, Khan *et al.* 2006, Liu & Sheng 2008, Rao *et al.* 2010, Joshi 2011, Aryal & Subedi 2011, Liu & Groves 2014).

In the present paper, we have made an integrative review on the evolution and conservation of moschids, and proposed some open questions about the dispersion and contraction of musk deer for further study, as well as do our best to promote international cooperative conservation practices for the precious natural resources.

2. Methods

For decades, we have focused on the biology of ruminants, including the taxonomy, phylogeny and conservation of musk deer. We have consulted relevant literature on the evolutionary history, biogeography, molecular analysis and conservation biology of Moschidae, Cervidae, Bovidae and other ruminant groups are at our hand, including recent online contributions. We have examined some relevant specimens, mainly of living musk deer but also of some fossils ascribed to Moschidae (also see Groves *et al.* 1995, Sheng & Liu 2007, Liu & Groves 2014).

3. Results and Discussion

3.1. Classification and Distribution of Moschid Fossils

Different opinions exist as to precisely which fossils belong to the Moschidae (Stirton 1944, Flerov 1952, Webb & Taylor 1980, Janis & Scott 1987, Scott & Janis 1987). Recently, Prothero (2007) assigned those fossils found in Europe (including *Dremotherium*, *Pomelomeryx*, *Hispanomeryx*, *Bedomeryx*, *Friburgomeryx*, *Oriomeryx*, *Hydropotopsis*), plus the Blastomerycinae in North America and Moschinae in Eurasia, to Moschidae, while Vislobokova and Lavrov (2009) suggested that Moschidae should be divided into two subfamilies: Moschinae and Hispanomerycinae. Based on this literature, and on our own research, we here propose an integrative rearrangement of moschid fossils as in Fig. 1.

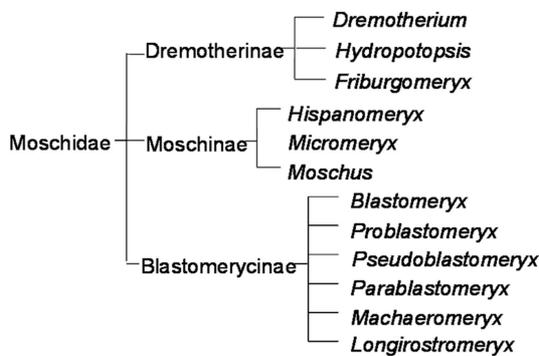


Fig. 1. The fossils of moschids.

Dremotheriinae, relatively smaller than recent *Moschus*,

were primitive moschids living in Eurasia from late Oligocene to early Miocene. They had no cranial appendages, but selenodont-brachyodont teeth with a Palaeomeryx fold in the molars, and poorly molarized premolars; they had well-developed upper canines in males, and either one or two lacrimal orifices inside the orbit. Their long basioccipital and high occipital regions were adapted to browsing high vegetation (Janis & Scott 1987, Prothero 2007). The subfamily Dremotheriinae includes the genera *Dremotherium*, *Friburgomeryx* and *Hydropotopsis*. For differences among these genera, see Prothero (2007).

Blastomerycinae, spreading to North America during the early Miocene, constitute an endemic peculiar radiation of moschids that have been poorly understood until recently (Prothero 2007). The distinguishing features of *Blastomeryx* from *Dremotherium* and *Moschus*, and those of genera within Blastomerycinae (*Problastomeryx*, *Pseudoblastomeryx*, *Parablastomeryx*, *Machaeromeryx*, *Longirostromeryx*, *Blastomeryx*), have been discussed by Webb & Taylor (1980) and Prothero (2007), respectively.

Moschinae, the only subfamily still retaining recent species (*Moschus* spp.), have many cranial, dental and limb characters distinguishing them from Hypertragulidae, Tragulidae, Leptomerycidae, Gelocidae and other primitive hornless ruminants, but share many features with *Dremotherium* and *Blastomeryx* (Webb & Taylor 1980), which is why they are attributed to a single family Moschidae. It was not until recently that *Micromeryx* was attributed to the Moschidae based on detailed morphological comparison, and the new data on its molarization pattern in premolars also confirm its close relationships with *Moschus* (Vislobokova and Lavrov 2009). Moreover, its dental morphology also resembles *Hispanomeryx*, which was firmly assigned to the Moschidae by Sánchez & Morales 2006; see also Vislobokova 2007, Vislobokova & Lavrov 2009). *Hispanomeryx* shows a relatively high degree of molarization of P4, and the absence of metaconid-protoconid fusion distinguishes it from *Micromeryx* and *Moschus* (Vislobokova & Lavrov 2009). We consider that subfamily Moschinae, containing *Micromeryx*, *Hispanomeryx* and *Moschus*, represents a well-developed evolutionary clade, first known in the Middle Miocene and culminating in recent musk deer (Table 1).

Table 1. The fossil Moschinae of Eurasia.

Names of Species	Localities (No.)	Epochs (Ma)	Source
<i>Micromeryx florensianus</i>	La Grive, France	M. Miocene	1
	Sansan, France	M. Turolian (7-8)	1
<i>Micromeryx styriacus</i>	Goriach, Austria	MN5 (around 15)	2
<i>Micromeryx mirus</i>	Dorn-Dürkheim, Germany	E. Turolian (8-9)	2
	Kohfidisch, Austria	L. Miocene	2
<i>Micromeryx</i> sp.	Sihong, Jiangsu, China (1)	Miocene (>16)	3
	Tongxin, Ningxia, China (2)	M. Miocene (16)	3
	Ertian, Inner Mongolia, China (3)	Miocene (11.5)	3
<i>Hispanomeryx duriensis</i>	Vallesian, Spain	L. Miocene	4
<i>Hispanomeryx</i> sp.	Spain; Asia Minor	M.-L. Miocene	5

Names of Species	Localities (No.)	Epochs (Ma)	Source
<i>Moschus granaeevus</i>	Lake Baikal, Russia (4)	L. Miocene (7.5)	5
	Taralyk-Cher, Tuva, Russia (5)	L. Miocene (7.5)	5
	Huade, Inner Mongolia, China (6)	Pliocene (5-7)	3
<i>Moschus moschiferus</i>	Fangshan, Beijing, China (7)	L. Pleistocene	6
<i>M.m.</i> var. <i>pekinensis</i>	Fangshan, Beijing, China (8)	E. Pleistocene	7
		M. Pleistocene	8
<i>M.m.</i> <i>plicodon</i>	Wangxuan, Sichuan, China (9)	M. Pleistocene	8
<i>Moshchus</i> sp	Lufeng, Yunnan China (10)	L. Miocene (8)	3
	Yushe, Shanxi, China (11)	Pliocene (5.2-3.4)	3
	Southern Qinglin, Shaanxi, China (12)	M. Pleistocene	9
	Nielamu, Tibet, China (13)	M. Pleistocene	10
	Yushu, Jilin, China (14)	L. Pleistocene	11
	Lantian, Shaanxi, China (15)	L. Pleistocene	12

Notes: E=Early, M=Middle, L=Late; The numbers in brackets indicate the approximate ages of epochs. Source: 1=Vislobokova (2007); 2=Prothero (2007); 3=Qiu & Qiu (1995); 4=Morales *et al.* (1981); 5=Vislobokova & Lavrov (2009); 6=Tong *et al.* (2008); 7=Pei (1932); 8=IPP (1979); 9=Chen *et al.* (1981); 10=Zhang (1978); 11=Xue (1959); 12=Ji (1974)

3.2. Origin and Phylogenetic Position of Moschidae

Although traditionally considered as a genus or a subfamily of Cervidae (Flower 1875, Allen 1940, Simpson 1945, Viret 1961, Gao 1963, Romer 1966), the status of moschids as a separate family (Gray 1821, Stirton 1944) has increasingly been elucidated by the combination of paleontological, morphological, ecological and ethological analysis, and especially with modern molecular data (Webb & Taylor 1980, Scott & Janis 1987, Groves & Grubb 1987, Groves *et al.* 1995, Su *et al.* 1999, Cap *et al.* 2002, Li *et al.* 2003, Hassanin & Douzery 2003, Kuznetsova *et al.* 2005, Fernández *et al.* 2005, Sheng & Liu 2007, Guha *et al.* 2007, Groves & Grubb 2011). Lately, a new debate over the phylogenetic status of Moschidae has arisen: which are the sister group of Moschidae, bovids or cervids? Different phylogenetic trees have produced different results (Su *et al.* 1999, Cap *et al.* 2002, Hassanin & Douzery 2003, Fernández *et al.* 2005, Kuznetsova *et al.* 2005, Guha *et al.* 2007).

Extant *Moschus*, with cervid-type metatarsus (closed gully) and bovid-type lacrimal orifices (singular), shows a mixture of bovid and cervid characteristics (Flower 1875, Leinders & Heintz 1980). It has the original elongated one-lacrimal-orifice-inside-the-orbit configuration similar to the Tragulidae, which is generally accepted as the common ancestral state of both bovids and cervids, but at the medial border of the orifice in *Moschus* there is a small protuberance, which gives the impression that the single orifice is either the result of fusion of two separated orifices or that it corresponds to an early stage of transformation from one into two, the latter being the normal configuration in cervids (Leinders & Heintz 1980). Do these hint that the phylogenetic position of moschids, morphologically at least, is as plesiomorphic sister group to cervids? – Indeed, some behavioural characters of musk deer have a surprising similarity to Alces (Cap *et al.* 2002).

Fernández *et al.* (2005) suggested that Moschidae originated together with other four extant pecoran families in the early Oligocene between 32.0-28.1 Ma; this date has been

put by other authors at somewhat earlier than the Oligocene/Miocene transition, at 26.1-26.2 Ma by Hassanin and Douzery (2003) and at 26.03 Ma by Liu (2003). Guha *et al.* (2007) suggested that Bovidae+Moschidae split from the Cervidae during the early Oligocene around 32.5±5.5Ma, in the period within which grassland had begun appearing (Janis *et al.* 2004). There is also a possibility that Moschidae appeared almost simultaneously, and evolved in parallel, with Cervidae and Bovidae.

As early as 1875, Flower remarked presciently: “*Moschus* appears to be an animal belonging to the stock, of which it is a low and little-specialized form, not having the characteristic peculiarities of either the Bovidae, the Giraffidae, or the Cervidae, being probably descended from the stock before either of those forms was well established, and having undergone comparatively little modification, though on the whole its affinities are nearest to the last-named group (Cervidae)”. We here (Table 2) make a rough comparison of some characters among the three families, showing how close today’s views are to those of Flower, even though he eventually placed musk deer within Cervidae merely as a genus rather than regarding it as a separate family. Moreover, Eisenberg (1987) reminded us that artiodactyl adaptive radiation commenced in the Eocene and that the earliest forms were adapted to browsing niches in forests, and that the “proto-ungulate” as a browser became more cursorial in its locomotor adaptation.

3.3. Some Primitive and Derived Characters of Moschids

Compared with other Pecora, the family Moschidae has acquired a number of progressive traits while maintaining certain primitive features, especially in the skull structure and extremity morphology (Table 3). Some of these characteristics appear adaptive to tearing off lichens and cutting the soft parts of plants, and others relate to their leaping movement pattern (Flerov 1952, Sheng & Liu 2007). The living genus *Moschus* also, as noted earlier, possesses a number of autapomorphies with the fossil Blastomerycinae, and both share with horned

pecorans a number of derived features that make them more advanced than the gelocids; other features which distinguish moschids from horned ruminants are, however, plesiomorphic,

including the retention of a subarcuate fossa on the endocranial side of the petrosal and the retention of a median branch of the carotid artery (Scott & Janis 1987).

Table 2. Comparison of some characters of three families.

Character	Cervidae	Moschidae	Bovidae
frontal appendages	antlers (most deer)	—	horns
upper canines in male	developed (few deer)	saber-like	entirely lost
no. of lacrymal orifices (LO)	two	one	one
position of LO	rim of orbit	inside orbit	inside orbit
metatarsal gully	closed	closed	open
outer metacarpals	fairly developed (some deer)	fairly developed	disappear
outer toes	sometimes rudimentary	well-developed	rudimentary
preputial glands	—	+	—
autorbitual glands	+	—	—
interdigital glands	+	+(front feet)	+
caudal gland	+(some deer)	+	—
gall-bladder	—	+	+
Cowper's glands	— (usually)	—	+
psalterium	—	+	—
brain	well-developed	less	well-developed
spots in juvenile	nearly universal	+	—
habitat	forest area (most deer)	forest area	grassland (most bovids)
feeding habit	browsing	snibbling	grazing

Notes:+Existence; — Inexistence; Data mainly summarized from the literature (Flower 1875, Pocock 1910, Leinders & Heintz 1980)

Interestingly, musk deer not only have some characteristics in common with Jarman's (1974) bovid Category A, small bodied antelopes which live as solitary individuals in forest environments and browse selectively shoots, buds, young leaves and other more nutritious items, but their hornless skulls and lack of sexual dimorphism in size, with a weight of generally less than 15 kilograms, accords with Janis's finding

that horns first appeared when body size increased to about 18 kilograms, at which size living ruminants are able to digest a more fibrous diet. At the same time, musk deer have a much wider range of possible diets and ecological options and territorial behavior, traits attributed to Category B by Jarman (1974).

Table 3. Some primitive and derived/retained characters of moschids.

Character	Primitive	Derived/retained
Morphological		
Body size	Small or medium	larger
Cranial appendages	absent	absent
Basicranium	straight	straight
Saberlike canines in male	well-developed	well-developed
Lacrima foramen	mostly singular	mostly singular
Dentition	selenodont-brachydont	hypodont
Palaeomeryx fold	present or poorly developed	absent or very weak
Musk deer fold	none	formed
Premolar	unreduced	reduced
P ₄	poorly molarized	well molarized
Vascular groove of metapodial	half-open or weakly closed	closed
Ecological-ethological		
Climate	milder and humid	various climates
Habitat	forest-steppe or drier woodland	forest-dependent
Diet	less specialized, more diverse	very diverse
Locomotion	saltatory	saltatory-cursorial

Notes: Based on various sources (Prothero 2007, Vislobokova & Lavrov 2009, Groves & Grubb 1987)

As noted above, moschids have inherited from a tragulid-like ancestor the inside-orbit configuration of a single lacrimal orifice, through which the lacrimal ducts connect the orbits with the nasal cavity for the draining of surplus lacrimal

fluid from the eyes to the nostrils. This may be beneficial for humidifying and warming the inspired air, and so be adaptive to dry and cold climatic environmental conditions through their evolutionary history. Conversely, the

two-lacrimal-on-the-rim configuration of cervids should be adaptive to humid and warm climatic zones, and pre-adapt to the marking behavior of antorbital glands. And the long muzzle of the Alpine musk deer is also an adaptation for breathing cold air in the high mountains (Gao 1985).

3.4. Radiation, Dispersing and Extinction of Early Moschids

It is evident that moschids arose first in Eurasia (see above), the original center possibly being in the northern part of the Alps. Retaining primitive features and conservative lifestyle, moschids did not undergo the same extensive radiation as did Cervidae and Bovidae, in which five main episodes of cladogenesis coinciding with climate events have been proposed by Fernández & Vrba (2005). Such as it is, the divergence, diversification, dispersal and ultimately the disappearance of moschids in Europe and North America are essentially closely related with fluctuations of the global climate and local environmental changes.

As noted above, moschids possibly appeared much earlier along with other early Pecora, but the oldest fossil recognized by most paleontologists is *Dremotherium*, which lived in Eurasia from the late Oligocene to early Miocene. This was succeeded by two small-sized early Miocene genera, *Pomelomeryx*, characterised by a rabbit-like body type, and *Fribergomeryx*, with selenodont-brachydont teeth. Most moschids vanished before the middle Miocene except for the tiny long-legged *Micromeryx*, which lasted until MN11 (about 8-9Ma ago), after which moschids disappeared from Europe and survived only in Asia (Prothero 2007) (Table1). Spain was the centre of high specific diversity during the Middle and Upper Miocene with an ancestor-descendant series of *Micromeryx* spp. and the endemic *Hispanomeryx*, but here too the family became totally extinct 8 Ma ago (Sánchez & Morales 2006).

Blastomerycinae, widespread and diverse in North America, flourished through almost the whole of the Miocene from an early radiation to ultimate extinction; the true cause of their final extinction is unclear. A possible interpretation is that at the start of the Miocene (about 28Ma ago), small and hornless ruminants underwent adaptive radiation in the global subtropical woodland that predominated at that time, but by the end of the epoch (about 5Ma ago) many varieties of large, horned types had emerged in response to the progressively more open savanna habitat, and that a change in global climate and vegetation had influenced the diets, body sizes, and reproductive behaviors of the ruminant lineages (Janis, 1986), certainly including moschids. However, a diminutive deer-like form {lately described by Dawson and Harington (2007) as a new genus and species of artiodactyl of uncertain familial relationships} similar to the living musk deer was unearthed in a peat deposit on Ellesmere Island (78°33'N, 82°22'W), Nunavut, Canada, with an Early Pliocene (4-5Ma) arctic mammalian fauna, which is similar to the Early Pliocene deposits of the Yushe Basin, northeastern China, at 37°N latitude and 1,000m elevation, where the fossil of *Moschus primaevus* Teilhard was found (Tedford & Harington 2003).

3.5. Origin and Dispersal of the Genus *Moschus* and Its Species

Dwelling in forests, moschids are strongly territorial and stenobiotic-habitat species with a more structured phylogeographic pattern than highly mobile migrating inhabitants of open landscapes like *Saiga tatarica*, and thus their genetic differences from different parts of the range are quite obvious (Kholodova 2009). Moreover, the times of diversification of the ancestral lineages and dispersal routes can be inferred based on molecular data obtained.

The study of polymorphism in the hypervariable sites of the mtDNA control region strongly suggests Eastern Siberia as the source area for the musk deer dispersal to the Far East and Sakhalin Island (Kholodova & Prikhod'ko 2006). And Su *et al.* (1999) suggest that the historical dispersion of musk deer might be north to south in China, based on the phylogenetic study of complete cytochrome b gene in *Moschus* using museum samples.

Additionally, almost all studies on the morphological, ethological and molecular phylogeny of recent moschids have concluded that *Moschus moschiferus* is probably the sister-taxon to all other species, or branched off the earliest from a common ancestor of moschids (Groves *et al.* 1995, Su *et al.* 1999, Li *et al.* 2003, Liu 2003, Fernández & Vrba 2005, Sheng & Liu 2007).

Within the genus *Moschus*, various evolutionary scenarios on inter-and-intraspecies relationships have been provided by different authors. Su *et al.* (1999) calculated that *M. moschiferus* first at about 0.7Ma ago separated from other species, which then bifurcated forming the *M. berezovskii* lineage and the lineage clustering together *M. fuscus*, *M. chrysogaster* and *M. leucogaster* around 0.37Ma, with quite low cytochrome b gene sequence divergences among them, while the most recent speciation events were inferred to happen at only 0.14Ma. Liu (2003) showed that a specimen ascribed to *M. fuscus* had an identical 12SrRNA gene sequence to *M. chrysogaster*. Li *et al.* (1999) defined the musk deer from Dabie, Anhui Province of China as a distinct species mainly based on the divergence of partial mtDNA cytochrome b sequences, while two other analyses gave completely different results, finding that the 12SrRNA gene sequence divergence between the Dabie musk deer and *M. berezovskii* fall within the level that was normally intraspecies (Sheng & Liu 2007, Liu XD pers.com.2012). Xia *et al.* (2004) suggested that the populations of *M. sifanicus* from Tibet, Sichuan and Gansu shared a common ancestor 1 Ma ago, and that the Gansu population diverged from that of Sichuan at 0.8 Ma ago, and that from Xizang (Tibet) separated from the Gansu and the Sichuan populations 0.34-0.57 and 0.9-1.0 Ma ago, respectively, based on 352bp of mitochondrial cytochrome b gene sequencing analysis. Most recently, Joshi (2011) has concluded that there are, in the Lower Mustang region of Nepal, multiple separate species of musk deer, which includes the "Kulu form" mentioned by Groves *et al.* (1995).

By means of an integrative analysis of palaeoclimate, palaeobiology, molecular phylogeny and eco-biology data of

moschids, we propose for discussion an open picture about the evolutionary history of the Genus *Moschus* (Fig. 2).

Moschus plausibly originated from the northern part of East Asia (see above); the original center might be just in the Mongolia Plateau and the neighboring forested mountains during the warmer period of the Late Miocene (around 8-9 Ma). Just as Flerov (1952) pointed out long ago, musk deer either arose in more southerly latitudes or, if in the north, then during a warmer epoch. *Moschus* might derived from *Micromeryx*, which only remained and survived in small numbers in faunas ranging in age from middle to late Miocene

(about 15-8Ma ago) in Europe and from the middle Miocene of Asia, after the extinction of most European moschids (Prothero 2007). The dental system of the *Micromeryx-Moschus* lineage showed a gradual transformation, which proceeded from more forest-steppe habitats (*Micromeryx*) to more wooded and mountain biotopes (*Moschus*), where epiphytic lichens and mosses became the major forage, so that the range covered nearly all woodland mountain areas of eastern Eurasia (Vislobokova & Lavrov 2009).

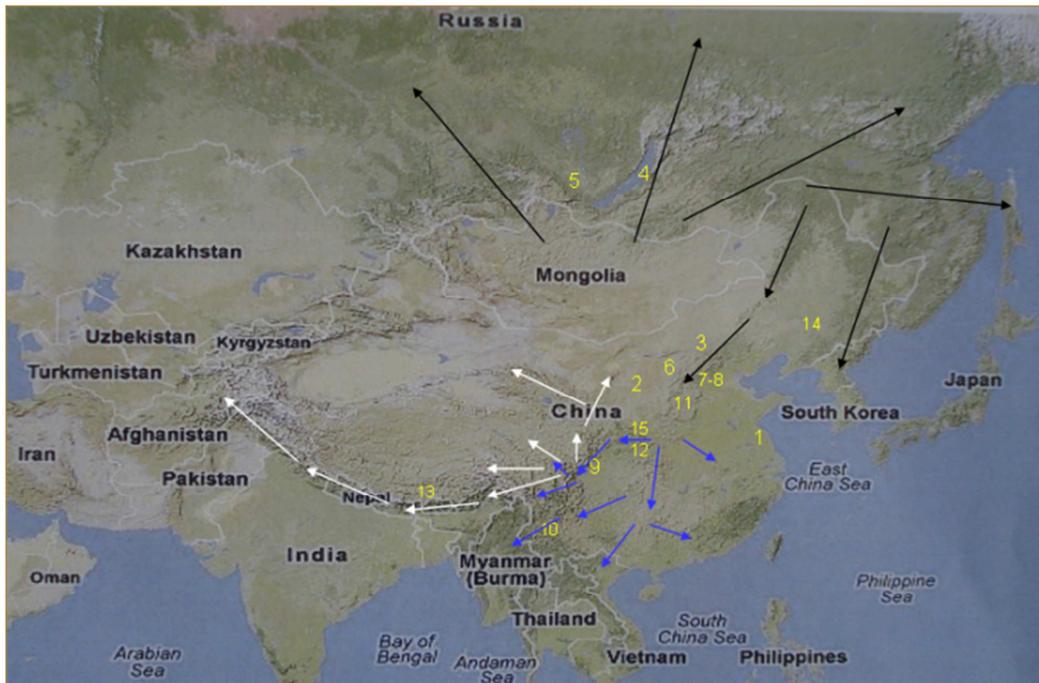


Fig. 2. Fossil distribution of the genus *Moschus* and the dispersal routes of the species.

Notes: The locality numbers correspond to those in Table 1; Dark, blue and white arrow line for *M. moschiferus*, *M. berezovskii* and *M. chrysogaster*, respectively.

The earliest fossil species ascribed to the genus *Moschus*, *M. primaevus* Teilhard, 1926 from the Middle Miocene of China, has been attributed by Vislobokova and Lavrov (2009) to *Lagomeryx* (Cervidae: Muntiacini). The most primitive species of the genus is *M. granaevus* Schlosser, 1924, which lived in the woodland of the Mongolia Plateau and surrounding mountains at around 5-9Ma. Vislobokova & Lavrov (2009) have provided a detailed description of this species, from abundant new material. *M. moschiferus* might have branched off from one population of *M. granaevus* in the Early Pliocene (before 5Ma), and then became widespread to the northern part of East Asia in the Late Pliocene and the whole Quaternary.

The Earth's climate became cooler through the Tertiary with frequent oscillations that increased in amplitude and led to the series of major ice ages of the Quaternary (since 2.4Ma ago), which caused the extinction, dispersion and modern pattern of distribution of the species (Hewitt 2000). These climate oscillations were expressed differently in various

parts of the globe, and especially during the last ice age northern Russia was not so affected by ice as compared with more highly glaciated neighbouring regions (Hewitt 1996). Thus it is likely that *M. moschiferus* migrated along the forest zone along the margin of the Arctic Ocean during the interglacial, and arrived in Sakhalin Island during one of the glacial periods through a transient land bridge. Eastern China, not covered by any continental ice sheet, served as a refugium for the survival of temperate and tropical/subtropical faunas during their retreat southward during one or more cold stages (Zhang 2004). By the Middle Pleistocene, *Moschus*, as like some other palaeartic mammals, had penetrated south of the Qingling mountain range (Chen *et al.* 1981), which form an important physical geographical division between northern and southern faunas in Eastern China, along with the uplift of the Qinghai-Tibetan Plateau since the middle Quaternary (Zhang 2002).

Actually, there had already existed subtropical-tropical evergreen forests and humid-hot climate south of the Qingling

during the early Tertiary (Chen *et al.* 1981), but to the north, temperate forests and grassland and dry climatic environments began to form in the early Pleistocene as the strength of the increased. Under such peculiar conditions, there appeared a new species, *M. berezovskii*, separated from the ancestral *M. moschiferus*-like form around the early/middle Pleistocene boundary (around 1.8Ma ago), or perhaps earlier--late Pliocene/early Pleistocene (3.3-1.8Ma ago).

Subsequently, *M. berezovskii* dispersed southward along both the eastern and western margins of the Sichuan Basin. The eastern route started from the Qingling-Dabashan mountains of southern Shaanxi, via the Wuling mountains along the provincial borders of Hubei, Hunan, Guizhou and Chongqing, towards the Nanling mountains along the provincial borders of Hunan, Guangxi, Guangdong and Jiangxi, then through Guangxi Province to the northern subtropical rainforest of Vietnam, and through the Yunnan-Guizhou Plateau to the northern forests of Burma. The western dispersal route was from the western Qingling-Dabashan, along the forests of southern Gansu and western Sichuan, through the Hengduan mountain system, and established of south-north migration for animals, to the southeastern edge of Tibetan Plateau. On the way, it not only dispersed into the eastern forests of Qinghai-Tibetan Plateau, but its body size also gradually became smaller to the south, corresponding to Allen's rule, resulting in the subspecies recognized by Wang *et al.* (1993).

The musk deer of the Dabie Mountain of Anhui Province retained some plesiomorphic features like *M. moschiferus*, speciated in isolation around 1.8Ma ago.

M. chrysogaster, the distinctive species to alpine areas, might have originated in the mountains of western Sichuan. Fossils of *M. m. plicodon* were found in Wangxuan, Sichuan, from middle Pleistocene, and those of *Moschus* sp. indet. from the same epoch were excavated in Nielamu, southern Tibet, within the range of recent *M. chrysogaster*. These allows us to infer that *M. chrysogaster* might have already appeared by the early/middle Pleistocene boundary (about 1.8Ma ago). Subsequently, the species spread in an arc-shaped direction along the Qinghai-Tibetan Plateau, from western Sichuan via southern Gansu west to the Qiliang mountains, then north to Helan mountain bordering Inner Mongolia and Nixia Hui Autonomous Region (Liu & Sheng 2000c), as well as via the Hengduan mountain system and southeastern Tibet west to the forests and alpine areas of the Himalaya mountains, where they have diversified to *leucogaster*, *cupreus*, Kulu form, Pepper-and-Salt form, Zhuangmu/Khumjung form and no doubt others, possibly since the beginning of the middle Pleistocene (around 0.8Ma ago) depending on the unique geological and climatic conditions caused by the uplift of the Plateau (Li *et al.* 2001, 2004).

3.6. Population Downturn and Extinction of Extant Moschids

As implied above, the living musk deer, *Moschus*, are extensively distributed in the hilly and mountainous forests of the eastern part of Asia, from the forest areas neighboring

the Arctic Circle, through China, to the subtropical rainforest of North Vietnam and Burma, and westward to the conifer and oak forests of Afghanistan. The first specimen of musk deer to reach Europe, as suggested by Allen (1930), was perhaps the one brought back by the Venetian traveler, Marco Polo, who mentioned musk deer as abundant in the Altai and northern China, especially about Si-fan. Allen (1940) noted again that musk deer were plentiful in the forested mountainous areas in Shansi, North China, while Flerov (1952) specifically noted that musk deer were numerous and widespread in many provinces of China at that time. The gross population size of musk deer in China has been estimated at between 2.5-3.0M individuals based on the musk harvest records of the whole country during the 1950s to the early 1960s, and the Chinese musk deer resource was at that time not fully used (Sheng & Liu 2007).

Unfortunately, since the mid-1960s, particularly the late-1970s, the population density and size of musk deer in China have dropped dramatically, the major cause being poaching with Gansitao, a circular tool made of steel or iron wires (Fig. 3), which is indiscriminate, killing individuals of any age or sex (nearly 1:1). This kind of easy-to-make-and-use trap is extremely destructive to musk deer populations (Liu *et al.* 2000b, Sheng & Liu 2007, Liu & Sheng 2008), because a network of Gansitao is not only easily set for a low cost in forest, but effective in the long-term at catching musk deer as well.



Fig. 3. A Gansitao set in the shrub as a trap for catching and strangling musk deer.

Such as it is, investigations by Liu (1997) showed that there existed relative higher population densities of musk deer in Xinglong Mountain and Shoulu Nature Reserve, Gansu Province, than elsewhere in China in the mid-1990s (Liu *et al.* 2001, 2002a), and that Alpine musk deer have stronger ecological adaptability than other species, and may even benefit to a certain extent from the reduction of the forest area and to some extent from the fragmentation and isolation of the habitat (Liu & Sheng 2002b). Nevertheless, in April of 2008, a further rough survey over the two reserves by Liu *et al.* (unpublished data) indicated that there were only around 10%-30% of the population densities of the previous decade as

a result of a lack of enthusiasm for conservation by the authorities.

Conservation success basically benefits from strict management, which particularly depends on the sense of responsibility and working ability of the heads of the reserves. More importantly, however, the economic cost and benefit relationship of wildlife conservation should be adjusted by modifying the relative Wildlife Conservation Law to stimulate positive activities in the reserves by their staff (Liu 1997, Liu & Sheng 2008).

The threatened status of the Himalayan musk deer first received international recognition in 1974, due to continuous overuse and habitat deterioration for over a century, and the populations in Afghanistan, Pakistan, Northern India, Kashmir and Nepal were very sparse; those in Sikkim and Bhutan were believed to be the least severely depleted (Green 1986, 1987). Although currently, in North Myanmar, Rao *et al.* (2010) still recorded the presence of musk deer by cameras deployed for 1199 trap nights, they were absent from all hunting records as confirmed by hunters, who evidently recognized musk deer as the most commercially valuable and highly preferred species as before. And at present, the musk deer populations in the Mustang district of Nepal, notwithstanding conservation efforts, face considerable threat from livestock, climate change and forest fires despite the Government listing it as a protected species as in other range countries; combined measures of regular patrolling, awareness campaigns, management of livestock, with international cooperation and working together to control the poaching of musk deer and the smuggling of musk pods, need to be taken (Joshi 2011).

All in all, multiple causes are responsible for the global downturn and threatened extinction of musk deer species and populations, but mainly there are both the international background of musk smuggling and the domestic anthropocentric factors, particularly rampant poaching (Green 1986, 1987, Yang *et al.* 2003, Zhou *et al.* 2004, Khan *et al.* 2006, Sheng & Liu 2007, Liu & Sheng 2008, Aryal & Subedi 2011).

3.7. To Create an Open Path for Relict Musk Deer Populations Toward the Future

Early moschids underwent over 20 Ma of boom and decline history from the late Oligocene to the end of Miocene in Europe and North America. The eastern part of Asia sheltered the recent moschids during the Quaternary over a roughly 0.1 Ma cycle of glaciations interrupted by relatively short warm interglacials such as we enjoy at present (Hewitt 1996). Li *et al.* (2004) pointed out that only in a few mountains such as the Taibaishan of Shaanxi and the Changbaishan of Jilin in the east China, can distinct Quaternary glacial landform and deposits be seen, and that in the mountainous regions of west China, there have been 3-5 identified glaciations dated to the late and middle Pleistocene, but there is no positive evidence to show an ice sheet covering the whole Tibetan Plateau. Thus China and neighboring nations possess the peculiar geological

history and extremely diversified natural conditions, suitable to have served as the evolutionary center of the genus *Moschus*. Unfortunately, there is really not enough time for musk deer to survive the present Gangsitao-overpoaching, although they can successfully escape from shooting and other traditional hunting traps or snares. Nonetheless as pointed out by Barrette (1987), musk deer, together with other small solitary forest ruminants, exhibit a great plasticity and a great capacity to adapt to numerous habitat types over a wide range, so hope remains.

Where are, however, the new refuges for musk deer? They are in fact in the hands of the Gangsitao-poacher! Combating this evil is the common responsibility of the whole of society, as well as the rangers, administrators and anti-musk-smugglers. In addition to taking certain initiative measures to benefit conservation efforts, education of the public about nature conservation, and of course severe punishments for poaching, should be further strengthened; meanwhile the techniques such as inventing a musk detector and training musk-detection dogs, to fight against Gangsitao poaching and musk smuggling, need to be improved (Liu & Sheng 2008).

If not so, the vestigial small isolated populations would disappear forever, and our future generations would neither enjoy musk deer and the musk.

And more perplexing questions remain. Which species should the fossil moschids be from the late Miocene (8Ma ago) of Lufeng, Yunnan Province, China (Table 1), and why did they come here so early? Are there possibly any correlations between the recent *Moschus chrysogaster* living in Qinghai-Tibetan Plateau and the fossil moschid *Longirostromeryx* from North America, both of which possess an elongated rostrum? What are we to make of striking suggestions that the southern species might actually be more primitive (Flerov 1952), and that *M. leucogaster* might be considered as the most ancient existing musk deer form (Sokolov & Prikhod'ko 1998)? Combining the new data with the early suggestion by Stirton (1944) that *Moschus* fits somewhere into the Cervioidea+Bovioidea complex, is it possible that Moschidae could result from hybridisation between bovid and cervid forms in their early evolutionary history? Absolutely too many problems remain for future researchers, and currently the most urgent mission for our generations is to ensure that the relict moschids survive the hands of the poachers, otherwise nothing for the future.

4. Conclusion

There is yet a very long way to go for reconstruction of the moschids' phylogenetic history, which depends on new palaeontological discovery and the proceedings of modern biology on living musk deer. In the meantime, we can still attempt to work out the basic outline of moschid evolution based on the limited data at hand.

Possibly almost simultaneously at a period about 30±5Ma, Moschidae appeared abruptly in Eurasia, and evolved in parallel with Cervidae and Bovidae, plausibly from an original center might be in the northern part of the Alps mountain

range. The divergence, diversification, dispersal and ultimate disappearance of moschids in Europe and North America are closely related with the fluctuation of the global climate and local environmental changes, leaving the eastern part of Asia as the refugium during the Quaternary glaciations, related to the peculiar geological history and extremely diversified natural conditions in the region.

Although the recent moschids (*Moschus*) have strong eco-adaptability and evidently dispersed comparatively recently through Chinese territory and neighboring areas, they are facing an extremely serious survival crisis caused by overpoaching by the Gansitao network and by habitat destruction since the 1960s-1970s. Only when more positive effective measures for conservation can be taken both nationally and internationally, will musk deer set hoof on their own path to the future, to the benefit of human beings.

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