



Chapter 2

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Chapter 2

Dispersals of Neogene Carnivorans between Asia and North America

QIU ZHANXIANG¹

ABSTRACT

Three major carnivoran dispersal waves of filter-bridge type between Eurasia and North America are recognized in the late Neogene. The first is around 20 Ma, probably from 21 Ma to 19–18 Ma, during which intermittent dispersals might have occurred. The carnivorans migrating from Eurasia to North America included *Cynelos*, *Ysengrinia*, *Amphicyon*, *Cephalogale*, *Phoberocyon*, *Ursavus*, some small-sized mustelids, *Potamotherium*, an ancestral form of *Edaphocyon*, and *Proailurus*. The second wave occurred at about 7–8 Ma. The carnivorans migrating from Eurasia to North America included *Indarctos*, *Agriotherium*, *Simocyon*, *Eomellivora*, *Plesiogulo*, and *Machairodus*. The last wave took place in the early Pliocene ~4 Ma. The Eurasian emigrants recorded in North America are *Ursus*, *Parailurus*, *Lynx* (?), *Felis* (?), *Homotherium*, and *Chasmaporthetes*. At about the same time *Megantereon* and *Pannonictis* migrated from North America to Eurasia.

INTRODUCTION

Carnivorans frequently appear in the zoogeographic literature as a group of highly mobile and widely distributed terrestrial mammals. Nevertheless, the exchange history of carnivorans between Asia and North America during the Neogene has not been systematically untangled at the generic level. The major difficulty herein is the recognition of the same or very closely related genera on distant continents based on incomplete fossil evidence. Generation-long study may be needed to make sure of the identity of such low-level taxa on different continents. An early attempt by Repenning (1967) listed five genera (*Simocyon*, *Indarctos*, *Agriotherium*, *Plionarctos*, and *Lutravus*) as definite and four (*Eomellivora*, *Plesiogulo*, *Lutra*, and *Machairodus*) as questionable migrants from Eurasia to America during the Hemphillian Mammal Age. Among the Blancan carnivorans, Repenning listed seven American genera (*Lynx*, *Trigonictis*, *Canimartes*, *Enhydra*, *En-*

hydriodon, *Ursus*, and *Chasmaporthetes*) as immigrants from Eurasia, although with some degree of uncertainty. Similar endeavors were made by Korotkevitch and Topachevskii (1976) and by B. Kurtén (1986). Tedford et al. (1987) made the major contribution in our understanding of Neogene mammal faunal exchange history, listing 38 North American Neogene carnivorans as exotic to that continent. The majority of these exotic forms was thought to have immigrated from Eurasia. Flynn and Swisher (1995) and Dawson (1999), based mainly on Tedford et al. (1987) data, made further interpretations on the Neogene dispersal events of land mammals between North America and Europe. Flynn and Swisher (1995) listed six major interchange events (their 6–11, see below), with a number of unnamed events of smaller scale for the late Neogene. Regrettably, many of the above inferences were based on evolutionary considerations and phylogenetic interpretation without solid fossil evidence.

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A reliable reconstruction of faunal exchange history needs solid support from both the fossil records and a stable classification. Fortunately, considerable progress has been made in both directions since Tedford et al.'s fundamental contribution. The classification within the Order Carnivora has been extensively studied in recent years. A number of taxonomic revisions of European and North American Neogene carnivorans have appeared (e.g., Hunt, 1996, 1998a, 1998b, 1998c; Werdelin, 1996; Baskin, 1998a, 1998b; Martin, 1998a, b; Ginsburg, 1999). As a result, the classification of the Order Carnivora becomes more refined in recent years, and sometimes more complex, culminating in inserting extra ranks (Infraorder, Parvorder, etc.) by McKenna and Bell (1997). To avoid entangling details of classification of the Order Carnivora, the basic subdivision of the order proposed by the great English anatomist Flower in 1869 (Arctoids, Canoids, and Aeluroids) is used here. On the other hand, the systematic situation in Asia remains little improved. Although a number of carnivoran fossils has been found in early and middle Miocene deposits (Qiu and Qiu, 1995), few of them have been studied so far. Since Beringia was the only route of dispersal between Eurasia and North America during the Neogene, some conclusions can safely be drawn, even with a limited record from Asia, if the evidence from Europe and North America is sufficiently conclusive.

The term "carnivorans" is here used to denote the members of the Order Carnivora in the sense of Van Valen (1969), excluding creodonts and the nonplacental predatory mammals. The term "dispersal" is used here as defined by Brown and Gibson (1983) as the "movement of organisms away from their point of origin". To determine a dispersal event for a certain fossil form, paleontologists should first recognize the disjunct occurrence of the same or immediately ancestral/descendant genera, and then determine the point of origin. The latter is a topic of much discussion. Savage (1958) listed five criteria for determination of origin of fossil mammals. Cain (1944) discussed altogether 13 biological criteria that have been used, as cited by Brown and Gibson (1983). For the

fossil record, the most reliable and decisive among these criteria is *the exclusive occurrence of immediately ancestral form(s) in immediately earlier deposits in one region*.

FOSSIL RECORDS RELATING TO DISPERSALS

ARCTOIDS

AMPHICYONIDS

Following Hunt (1998b), the amphicyonids are here viewed as a separate family of the arctoid carnivorans, comprising four subfamilies: Daphoeninae, Temnocyoninae, Haplocyoninae, and Amphicyoninae. The former two are restricted to North America, the third one is endemic to Eurasia, and the last one is Holarctic in distribution. The amphicyonids originated probably in the Eocene of Eurasia, flourished during the Oligocene and early Miocene in both Eurasia and North America, and became finally extinct at ~8 Ma in Asia (vide infra).

Excluding Paleogene dispersals, three amphicyonine genera may have migrated from Eurasia to North America in the early Miocene: *Cynelos*, *Ysengrinia*, and *Amphicyon*. The earliest record of *Cynelos* is from the Oligocene in Europe: Pech Desse, Quercy, MP28, ~25 Ma (Remy et al., 1987). The earliest *Ysengrinia* is so far very poorly represented in Europe: a mandible with p4-m2 of *Y. tolosanus* from Le Cammas, France (terminal Oligocene), a mandible with p3-m2 of the same species from Flösheim, Germany (MP30, ~24 Ma), and one m2 from Thézels, Aquitan (MP30, de Bonis and Guinot, 1987). The first records of both *Cynelos* and *Ysengrinia* in North America are from the upper Harrison Formation, Nebraska, 19.2 Ma (Hunt, 1998b). So far, no fossils of *Ysengrinia* have been reported from Asia. However, my personal examination of the undescribed carnivoran specimens of the Sihong localities revealed that some of them may belong to *Cynelos* and/or *Ysengrinia*. The Sihong fauna is roughly correlated with the European MN 4, thus is ~18 Ma. The dispersal event of both genera may have occurred from Eurasia to North America at ~20 Ma.

Amphicyon had long been a wastebasket genus until the mid-1960s, when many gen-

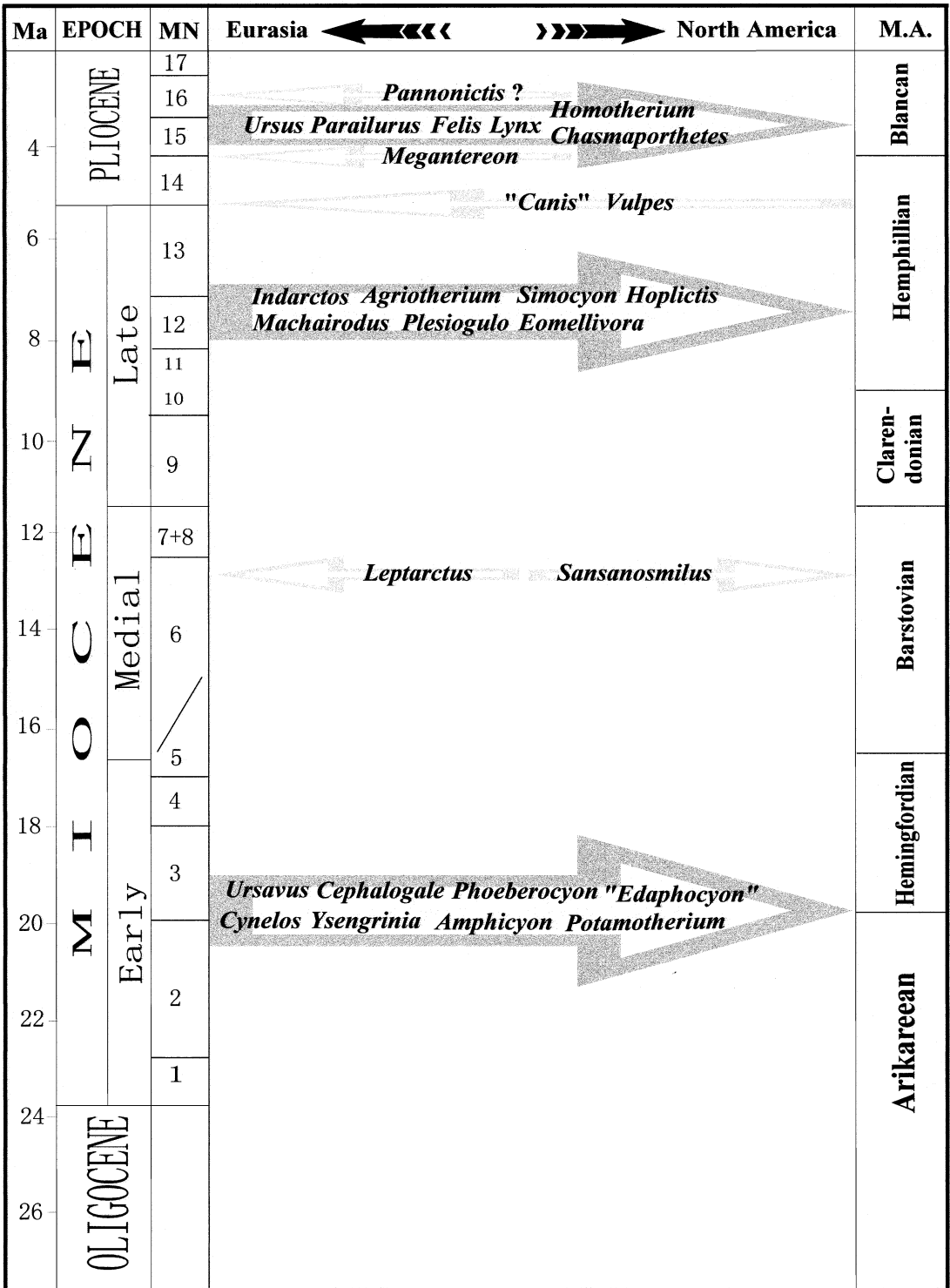


Fig. 2.1. Migration events of Neogene carnivorans between Eurasia and North America.

era were removed from it by Kuss (1965) and Ginsburg (1966). In its restricted sense, *A. astrei* is the earliest species. This species, first reported by Kuss (1962), was based on a mandible with poorly preserved teeth from Garduch (terminal Oligocene, ~24 Ma). According to Hunt (1998b), the first North America *Amphicyon* is represented by undescribed specimens from the Runningwater Formation (early Hemingfordian, 19–18 Ma), Nebraska. They are close to the European *A. giganteus*, the earliest fossils of which were found from Wintershof-West (MN 3, ~20–18 Ma), Germany. In Asia, the earliest *Amphicyon*, *A. confucianus*, is from the Shanwang fauna (comparable to MN 5, ~16 Ma). From Tongxin (comparable to MN 6, ~15 Ma), a form very close to *A. giganteus* is present, but not yet described. The last appearance of the genus may be that from Lufeng (comparable to MN 11, ~8 Ma) and Yuanmo sites that yield *Lufengpithecus*. At any rate, its first dispersal from Eurasia to North America should have occurred at ~20 Ma.

HEMICYONIDS

Three genera are shared in common by Eurasia and North America: *Cephalogale*, *Hemicyon*, and *Agriotherium*. The earliest record of *Cephalogale* in Europe is from the early Oligocene MP22 (Mas de Got, Quercy, France, ~33 Ma), after the “Grande Coupure” according to Remy et al. (1987). The genus is well represented in MP28 (Pech Desse, Quercy, ~25 Ma) and MN 1–2 (Paulhiac, Saint Gerand-le-Puy, 23.8–20 Ma) by numerous species (eight, according to de Bonis, 1973). In North America, there are only a few records of *Cephalogale* (Hunt, 1998a): the late Arikareean (Zia Sand Formation, New Mexico, ~20 Ma; Upper Harrison Formation, Wyoming, 21–20 Ma; Agate Spring Local Fauna, Nebraska, 21–20 Ma) and early Hemingfordian (Marsland Formation, 20–19 Ma; Runningwater Formation, Nebraska, 19–18 Ma). No comparison at the specific level is possible, since none of these North American samples have been described. In Asia, the fossil record of *Cephalogale* is sparse. Tang and Qiu (1979), in a preliminary report, listed two forms of

Cephalogale from the late Eocene Nadu Formation, Guangxi: *Cephalogale* new species and cf. *Cephalogale* sp. Unfortunately, the specimens cannot be located in the IVPP collection. It is uncertain whether they really belong to this genus or not. A definite record of early Oligocene *Cephalogale* is now known from Saint-Jacques, Nei Mongol, China (Wang and Qiu, this volume). Certain *Cephalogale* is known from the early Miocene deposits at Bugti, Pakistan (Forster-Cooper, 1923). Thus the dispersal of *Cephalogale* from Europe to North America should have occurred at ~21 Ma.

Classification of the hemicyonids has become rather complicated. McKenna and Bell (1997) and Ginsburg and Morales (1998) recognized them as a separate family, whereas Hunt (1998a) considered them as a subfamily of the Ursidae. Ginsburg and Morales (1998) further subdivided the Hemicyonidae into two subfamilies: Phoberocyoninae (including *Phoberocyon* and *Plithocyon*) and Hemicyoninae (including *Zaragocyon*, *Hemicyon*, and *Dinocyon*). The earliest occurrence of the hemicyonids in Europe is from MN 2 (22.8–20 Ma) of Spain: *Phoberocyon hispanicus* from Loranca and *Zaragocyon daamsi* from Cetina de Aragon. Deposits from then through MN 9 show that hemicyonids lived continuously in Europe. The earliest hemicyonine so far found from North America is *Phoberocyon johnhenryi* from Thomas Farm local fauna, Florida, 19–18 Ma. Referral of the Thomas Farm species to the genus *Phoberocyon* is confirmed by diagnostic features of the lower dentition: posterior accessory cusps in lower premolars and paraconid in m2. However, it is certainly more derived than *Phoberocyon hispanicus* in being larger and having diastemata between the premolars. All the other American hemicyonids are more advanced in character, and are assigned to *Plithocyon*, known from the Barstovian of California, New Mexico, Nebraska, and Wyoming. All could be assigned to *Plithocyon*. In Asia, the earliest hemicyonid is *Phoberocyon youngi* from Shanwang, Shandong (~16 Ma). It is very close to the North American *Phoberocyon johnhenryi*, as pointed out by Qiu et al. (1985). The latest occurrence in China is from the Tung-Gur Formation, Nei-Mongol

(~13 Ma). This species was first described as *Hemicyon teilhardi*, but according to the morphology of the upper cheek teeth, it should be assigned to *Plithocyon*. The dispersal should thus have occurred from Europe to North America prior to 19 Ma. Whether the North American *Plithocyon* represents another immigration event is hard to say. It is more probable that the American *Plithocyon* might be the descendant of the native *Phoberocyon* and belong to a new genus.

Although very close to *Indarctos* in skull and tooth morphology, *Agriotherium* is here considered a member of the family Hemicyonidae. As pointed out previously (Qiu and Schmidt-Kittler, 1982; Qiu et al., 1991), the presence of a series of hemicyonine characters in *Agriotherium* (unelongated molars, premaxillary fossa, etc.) strongly substantiate its closer affinity with hemicyonines rather than with ursines. *Agriotherium* has its longest history in Asia. The most primitive and earliest form is from a *Hipparion* fauna in Hezheng, Gansu, ~9 Ma (Qiu et al., 1991). All other forms of *Agriotherium* occurred in the Pliocene (5.3 to ~2 Ma) in Eurasia and Africa, leaving a hiatus in the record between 9 and 5.3 Ma. In North America, *Agriotherium* appeared suddenly at the middle Hemphillian and became extinct before the Blancan. Unequivocal *Agriotherium* fossils were found at Coffee Ranch, Texas, and its equivalent Guymon (Optima) Local Fauna, Oklahoma, and Mount Eden Local Fauna, California. The age of the Coffee Ranch Local Fauna is estimated as about 6.6 Ma (Dalquest, 1986). A good sample of *Agriotherium* was recovered from Old Cabin Quarry, Quiburis Formation (late Hemphillian), Arizona. This material remains unstudied. Hunt (1998a) listed 18 localities yielding *Agriotherium* fossils, ranging from California to Florida. The occurrence of *Agriotherium* in North and Central America is thus limited to the later half of the Hemphillian (~7–5 Ma). The most plausible hypothesis is that the American *Agriotherium* emigrated from Eurasia at the beginning of the second half of the Hemphillian Mammal Age (~7 Ma).

URSIDS

Recently the fossil ursids of North America were revised by Hunt (1996, 1998a).

Similar work on a less comprehensive scale was carried out by Ginsburg and Morales (1998) for the European forms. Although slightly different in infrafamilial arrangement, these revisions have proven valuable for defining dispersal events between Eurasia and North America during Neogene time.

Ursavus, the earliest member of the Subfamily Ursinae, was subdivided by Ginsburg and Morales (1998) into *Ursavus* and *Ballusia*. The latter is slightly different from the former in having stronger cingula on the upper molars, higher m1 trigonid, and oval instead of rectangular M2. The first appearance of both genera is MN 3 of Europe (Elm and Wintershof-West in Germany, Savigne-sur-Lathan in France), ~20 Ma. Although not very abundant, fossils of *Ursavus* are frequently found in the middle Miocene of Europe. The latest record in Europe is from the Turolian (Euboa, Greece, 9–8 Ma). Therefore, the distribution of *Ursavus* (and *Ballusia*) in Europe is from MN 3 to MN 11, 20 to 8 Ma.

In North America, a single record of this genus was questionably reported from the early Arikareean (John Day Formation, Oregon), 29 Ma. However, Tedford et al. (1987: 172) unequivocally stated that the Flint Hill local fauna (19 Ma) "has yielded the first North American occurrence of the little bear, *Ursavus*". Hunt also listed the early Hemingfordian Batesland Formation, South Dakota, as producing the earliest *Ursavus*. *Ursavus* became more common during the Barstovian Mammal Age. Hunt listed 10 localities yielding its fossils, mainly in the area west of the Rocky Mountains (Oregon, Nevada, Saskatchewan) with a few from the area east of the Rocky Mountains (Nebraska, Colorado). Taken as a whole, North American *Ursavus* was poorly represented. Little has been studied and published of the five forms (*U. pawniensis*, *U. cf. brevihinus*, *U. cf. primaevus*, and two unnamed species) from 13 localities listed by Hunt (1998a), which limits comparison with the *Ursavus* material of Europe at the specific level.

In East Asia, the only record of this genus is that of Qiu et al. (1986) from Shanwang. It is apparently a quite aberrant form deserving to be classified as a separate genus, as

suggested by Ginsburg and Morales (1998). Its age is early middle Miocene.

The conclusions that can be drawn from the above data seem to be as follows. (1) If the first occurrence of *Ursavus* in the early Arikareean (~29 Ma) in North America is accurate, North America might be the continent where the first *Ursavus* emerged. Then, during the interval from 29 to 20 Ma, it migrated to Europe. The later *Ursavus* of Hemingfordian and Barstovian age may either be direct descendants of this native form or immigrants from Europe. (2) Otherwise, the first appearance of *Ursavus* (and *Ballusia*) is about one m.y. earlier in Europe (20 Ma) than in North America (19 Ma), which, together with its comparatively rich representation in Europe, tends to show that the dispersal might have occurred at the time span between 20 to 19 Ma, and in the direction from Europe to North America.

Except for *Plionarctos* and its possible descendant American endemic tremarctines, the affinities of which are still obscure, there is only one early form of true ursine so far reported from the Pliocene of North America, *Ursus abstrusus*, from the Hagerman and White Bluffs Local Faunas. The Hagerman local fauna has been dated as about 3.75–3.2 Ma (Lundelius et al., 1987) and the White Bluffs slightly older than it, probably not older than 4 Ma. In Europe, the Pliocene true bear, *Ursus*, is rather richly represented (Weze, Baron-Copez, Rouscillion, etc.). The earliest record of *Ursus* is from the Montpellier marine sands (MN 14, 5.3–4.2 Ma). The earliest *Ursus* in Asia is from the top part of the Gaozhuang Formation of the Yushu area (4.5–4.1 Ma). It is likely that *Ursus* migrated from Asia to North America at about 4 Ma.

Indarctos is a separate branch of the subfamily Ursinae. It evidently originated from a form of *Ursavus*. The record of *Indarctos* in Europe is the most complete in comparison with those of Asia and North America. The most primitive species, *I. vireti*, was recorded from Can Llobateres and Can Ponsich, the type section of the Vallesian "stage" in the Vallés-Penedès basin, near Sabadell, Spain. Its age is estimated as ~11 Ma. The next most primitive form in Europe is *I. arctoides*, found in late Vallesian and

early Turolian deposits. From the middle Turolian, the genus is represented by the large *I. atticus*. So far as the Asian fossil record is concerned, the genus is restricted to the Baodean, which is roughly correlative with the European Turolian. There are three species in China. The first is the primitive *I. lagrelii*, intermediate between *I. arctoides* and *I. atticus* in morphology. The second is morphologically inseparable from the European *I. atticus*. The third is new, larger, and more advanced in character. Two other species, *I. salmontanus* and *I. punjabiensis*, are recorded in the Indo-Pakistan subcontinent. Both are from the Dhok Pathan Formation. According to Tedford et al. (1987), the localities containing the first American *Indarctos* are Mulholland Formation, California (7–6 Ma), Cambridge Local Fauna, Ash Hollow Formation, Nebraska (7–6 Ma), Rattlesnake Formation, Oregon (6.6–6.8 Ma for the overlying ash), Smiths Valley Fauna, Nevada (corrected as ~7 Ma, Tedford et al., 1987), Box T Local Fauna, Texas (estimated at 6.5–6 Ma), and Withlacoochee 4A, Florida (7–6 Ma). The earliest appearance of this genus in North America might be the specimen referred to "*Indarctos near oregonensis*", possibly from the very bottom of the Rattlesnake Formation (Merriam et al., 1925). Judging from its size and morphology, it is very close to the European *I. arctoides*. The largest species in North America, and in the World in general, is *I. oregonensis keithi*, described by Schultz and Martin (1975), from Cambridge, Nebraska, and the skull from Florida described by Wolff (1978). There is little doubt that *Indarctos* migrated from Europe to North America at about 7 Ma, as concluded by Tedford et al. (1987).

MUSTELIDS

The mustelids diversified greatly during Neogene time. Recognition of the same taxon from the fossils of different continents is often a difficult task. This renders the reconstruction of the exchange history of the mustelids between the two continents often highly conjectural. Baskin (1998b) postulated 21 immigration events for the North American mustelids. Most of them were inferred from possible ancestry-descendant relationships,

without detailing the occurrences of the same genera on the continents in question.

The first reliable record of migration of the mustelids at the generic level is that of *Potamotherium*. The taxonomic position of this genus is highly controversial. It was traditionally placed in the subfamily Lutrinae. Recently it has been allocated variously: to phocids (Tedford, 1976; de Muizon, 1982), to Oligobuninae (Baskin, 1998b), to a separate subfamily (Ginsburg, 1999), or as a primitive mustelid (McKenna and Bell, 1997). Its first appearance is definitely in Europe, in the late Oligocene, with proliferation since the Aquitanian (~23 Ma). In North America, it is first recorded in the Runningwater Formation (19–18 Ma). Thus, the dispersal event must have occurred prior to 19 Ma.

Of the Mellivorinae and Gulolinae (Ischyriactini according to Baskin, 1998b) three genera are commonly shared by Eurasia and North America. *Hoplictis* has long been considered a subgenus of *Ischyriactis* with hypercarnivorous adaptations of the cheek teeth. It is comparatively well represented in Europe, from MN 3 (20 Ma) to MN 9 (~11 Ma), but only sparsely found in North America. The best specimen is a lower jaw from Ellensburg Formation, Washington (late Clarendonian), originally described as *Beckia grangerensis*. *Hoplictis* sp. was also reported from a few other Clarendonian Mammal Age localities (Love Bone Bed and Juntura Formation). It is certain that *Ischyriactis* originated in Europe, and its migration to North America can only be postulated as prior to 11 Ma. On the other hand, *Plesiogulo* and *Eomellivora* have good records in Eurasia. They are now generally considered to have originated from the *Ischyriactis* group, which is well established in the early and middle Miocene of Europe. Wolsan and Semenov (1996) recently revised *Eomellivora* based on a large sample from a limestone quarry of Turolian age near Gritsev, Ukraine. All the materials published by then, except those from the Siwaliks, were referred to two subspecies of *E. wimani*. The first appearance of this species is from the early Vallesian in Europe (Kalfa and Vallés de Fuentidueña, ~11 Ma). It is well represented in the later half of the Miocene in Eurasia. The first *Plesiogulo* appeared also in Europe, from early Vallesian deposits (Kal-

fa). The genus became rather prosperous in the later half of the Miocene and the Pliocene in Eurasia. In North America, the earliest records of these two genera are from later Hemphillian Mammal Age deposits, but no earlier than 7 Ma.

LEPARCTINES

One of the few carnivorans that migrated from America to Asia during the Neogene is *Leptarctus*. In Eurasia, this genus has so far been found only at Tung-Gur, China (late middle Miocene, ~13 Ma). On the other hand, the leptarctine mustelids are well represented by many forms ranging from early Hemingfordian to late Hemphillian (20–6 Ma) in North America (but see Addendum).

LUTRINES

There are few identical genera of lutrines found in both continents. According to Baskin (1998b), the mandibular fragment with m1 from the Truckee Formation (late Clarendonian) described as *Lutra* sp. may belong to *Limnonyx*, a genus created by Crusafont-Pairo (1950) based on a mandible from the Vallesian type locality, Spain. If this proves true, the migration should have taken place at about 8.8–9.5 Ma (Baskin, 1998b), from Eurasia to North America. *Mionictis* had long been considered a primitive lutrine of Holarctic distribution until Ginsburg and Morales (1996) argued that the European specimens once referred to that genus should be separated from *Mionictis*, and they established two genera for them: *Lartetictis* and *Adroverictis*.

Trigonictis and *Pannonictis* have been considered congeneric by many carnivore students. If this proves true, the generic name *Pannonictis* should be adopted because of its year priority in occurrence. In Europe, it appeared from the Villany (MN 16, ~3.4 Ma), while in North America, the earliest record is from ~4 Ma. Therefore, *Pannonictis* may have had a North American origin and migrated to Eurasia in the time span of 4 to 3.4 Ma. The first *Martes* almost simultaneously occurred in Europe (MN 3) and North America (early Hemingfordian) at about 20 Ma. Since it is a form with mainly plesiomorphic features, its real affinity and the relationship

between the forms of the two continents are still uncertain. *Mustela* similarly appeared late in both continents, at the end of the Pliocene. The origin, time and direction of dispersal of both genera remain unsolved.

PROCYONIDS

The systematic position of the procyonids within the arctoids has been highly controversial. Most systematists currently include them with musteloids in their broader sense. Since the extant procyonids (other than the lesser panda, *Ailurus fulgens*) are restricted to and most of the procyonid fossils are found in the Americas, it has long been thought that the Procyonidae are Nearctic in origin and no essential migration has ever taken place between Eurasia and North America. Baskin (1982) revised North American Neogene procyonids, citing the earliest procyonid record in North America as *Edaphocyon lautus* from the Runningwater Formation, Nebraska (18–19 Ma). In Europe, *Broiliana* from the Wintershof-West (MN 3, 18–20 Ma) is widely accepted as an ancestral form of the procyonids. Similarly, *Amphictis* from Quercy (Oligocene) and Wintershof-West is also considered referable to Procyonidae. Since the procyonids are distinct from all other carnivorans in dental morphology, it seems safe to postulate that the procyonids originated in Europe during Oligocene time and migrated to North America at about 20 Ma.

There is a general agreement in recent years that the extant lesser panda, *Ailurus fulgens*, and rare fossils like *Parailurus* constitute a separate group of procyonids. For quite a long time this group of procyonids was thought to be restricted to Eurasia. Its origin and distributional history remain long enigmatic. Therefore, Tedford and Gustafson's report in 1977 on the discovery of a tooth of *Parailurus* from a Blancan assemblage in Washington was highly unexpected. Just recently, Ginsburg et al. (1997) described an ailurine m2 (*Magerictis imperialensis*) from the locality Estacion Imperial, MN 4–5 (~16–18 Ma), Spain. Based on the highly derived characters of this Spanish form, Ginsburg et al. (1997) postulated that the ailurines originated in Europe and had a

long history there, starting at least from the middle Miocene.

Simocyon has long been referred to the family Canidae. Recently Wang (1997) and Baskin (1998b) transferred it to the family Procyonidae, proposing a sister group relation with the living lesser panda. *Simocyon* has a good record in Europe, from Vallesian to Turolian (11.2–5.3 Ma). In China, only a more advanced species, *S. primigenius*, has been recorded in Baodean age deposits. In North America, a few specimens were reported. A mandible first described by Thorpe (1921) as *Araeocyon marshi* from the Rattlesnake Formation (>6.6–7.5 Ma), Oregon, has been generally considered to belong to *Simocyon*. Its migration from Eurasia to North America should have occurred at ~8 Ma.

CANOIDS

There is no disagreement that North America was the center of origin and radiation of the canids. The earliest record of a true European canid is that of *Canis cipio* from the Turolian deposits (MN 12, 8.2–7.1 Ma) of Spain. It is rather perplexing that no other canid material has since then been found from the Turolian in Europe or equivalent deposits in Asia. On the other hand, various canids, including *Eucyon*, *Nyctereutes*, and *Vulpes*, became richly represented from the Ruscinian (5.3–~3.4 Ma) in Europe and its equivalent in Asia (the early Yushean in China, Calta in Turkey, etc.). According to Tedford et al. (1987), "*Canis*" and *Vulpes* first appeared at the beginning of the Hemphillian mammal age (~9 Ma) in North America. There is no doubt that these two genera migrated from North America to Eurasia. If the finding of the Spanish Turolian *Canis cipio* can be verified in the future, the time of the migration should be fixed at about 8 Ma. Otherwise it should be at about 5 Ma. The distribution of *Nyctereutes*, the raccoon dogs, is restricted to the Palaearctic region. There is little doubt that its ancestor is among the North American canids. This "ancestor" should remain very "*Canis*"-like, lacking major diagnostic *Nyctereutes* characters (the mandible subangular lobe, etc.). Migrating from North America to Eur-

asia at about the same time as “*Canis*” and *Vulpes*, it rapidly evolved into true *Nycter-eutes*.

AELUROIDS

NIMRAVIDS

This group of carnivorans, the first radiation of cat-like mammals, flourished mainly during the Paleogene in both Eurasia and North America. The only Neogene survivors are members of the dirk-toothed Barbour-felines: *Prosansanosmilus-Sansanosmilus* lineage in Eurasia and *Barbourofelis* in North America. The latter is a group of highly specialized dirk-toothed cat-like animals suddenly appearing in the basal Clarendonian (11 Ma). No possible ancestor of this group occurs in North America. So far as is known, the Eurasian middle Miocene *Sansanosmilus* is the only possible candidate for its ancestral form. Its dispersal from Eurasia to North America can thus be placed in the interval of 15 to 11 Ma.

FELIDS

Felids were considerably diversified during the late Cenozoic. Their dispersals between Eurasia and North America must have had occurred many times. The earliest true felids were found in the Oligocene in Europe (*Proailurus*), but are only late early Miocene in North America. According to the latest study by Hunt (1998c), the earliest North American true felids are close to the European *Proailurus*, with more plesiomorphic characters in the auditory area. However, they appeared later than in Europe, in the Hemingfordian (at about 17 Ma). *Pseudaelurus* is known from both Eurasia and North America. In Europe, the earliest occurrence of the genus is in MN 3 (Wintershof-West, etc., 20–18 Ma), while in Asia it is in Sihong (comparable to MN 4, ~18 Ma). In North America, *Pseudaelurus* evolved rather conservatively, resulting mainly in size increase, and became extinct prior to the Blancan Mammal Age (4.2 Ma). However, in Eurasia, especially in Asia, its counterpart evolved into the more specialized *Metailurus*, *Paramachairodus*, and *Dinofelis*, the latter of which lingered into the Pleistocene in both

Asia and Africa. Therefore, the migration of the first felids from Eurasia to North America may have occurred at 18–17 Ma. From then, the two lineages may have evolved separately.

The taxonomy of the extant felids is highly controversial, as are the referral of some Plio-Pleistocene felid fossils and the hypotheses on their relationships. This is particularly true with the North American fossils referred to *Lynx* and *Felis*. Schultz and Martin (1972) referred a felid of Clarendonian age from the Ogallala beds of Colorado directly to the genus *Lynx*: *L. stouti*. It was considered the earliest record of the genus and its progenitor. Martin (1998b) transferred the form to *Pseudaelurus*, following MacFadden and Galiano’s (1981) suggestion. Nevertheless, Martin maintained the North American origin of *Lynx* by including *Felis rexroadensis* in *Lynx*. The earliest record of *L. rexroadensis* is the late Hemphillian (Upper Bone Valley Formation, Florida, 5 Ma). This led Martin to think that the dispersal event of *Lynx* must have been from North America to Eurasia. Hendeby (1974) and Werdelin (1981) thought that Africa could be the continent where *Lynx* originated, based mainly on a mandible referred to *Lynx* aff. *issiodorensis* from Langebaanweg. The materials from both Africa and North America referred to *Lynx* are inadequate. The European *Lynx issiodorensis* is more likely to be referred to *Lynx*. However, it lacks the diagnostic *Lynx* features in its postcranial skeleton (short body but longer hind limb). It is hard to say whether *Lynx issiodorensis* originated from *Felis rexroadensis* or the Langebaanweg *Lynx* aff. *issiodorensis*, based on presently available material. True *Lynx* with the characteristic short body but long hind limb appeared late, and the dispersal event (probably from Eurasia to North America) likely occurred in the late Pleistocene.

Machairodus has a rather continuous record in Europe, from the basal Vallesian through the Turolian. In Asia, *Machairodus* was found only from the Baodean (no earlier than 10 Ma). Morphologically, the genus can be traced back to the genus *Miomachairodus* from the late middle Miocene (Yeni-Eskihisar, Turkey, ~12 Ma). In North America, the earliest record of this genus is from the

Smiths Valley, Nevada (7 Ma; Tedford et al., 1987, fig. 6.2). Therefore, the dispersal event of *Machairodus* from Eurasia to North America should have occurred at the end of the early Hemphillian Mammal Age.

Homotherium (= *Ischyrosmilus* and *Dinobastis*) did not appear until the Blancan Mammal Age. Its earliest appearance in North America cannot be precisely dated. Well-dated material came from the deposits of late Blancan Mammal Age (Cita Canyon, Lisco) and the Pleistocene. Since *Homotherium* species from Yushe (and also from the Siwaliks) are morphologically more primitive than those of North America, it may be safe to say that *Homotherium* appeared first in Eurasia, and then migrated into North America at probably the first half of the Blancan Mammal Age.

The dirk-toothed cat, *Megantereon*, was reported recently by Berta and Galiano (1983) from the latest Hemphillian Mammal Age (Upper Bone Valley Formation, Florida). It is dated as about 4.5 Ma. In Eurasia, the earliest occurrence of this genus has been dated not older than 3.5 Ma (Les Etouaires, France). In Asia, the earliest record of *Megantereon* is probably the undescribed material from Fanchang, Anhui, a Paleolithic site dated as 2.4–2 Ma. If all the above data are correct, the only possible interpretation is the reverse direction of dispersal of the genus *Megantereon*: from North America to Eurasia.

HYAENIDS

Of the hyaenids only the genus *Chasmaporthetes* migrated from Asia to North America early in the Blancan Mammal Age (later than 4.2 Ma). In Asia, the fossil record of this genus is quite long, dating back to ~6 Ma (Yushe) and continuing to about 1.8 Ma (Nihewan).

CONCLUDING REMARKS

Early in 1947, Simpson, one of the greatest pioneer paleozoogeographers among vertebrate paleontologists, pointed out a pronounced endemism of the Clarendonian fauna of North America. This accords nicely with the evidence provided by marine paleontology. Hopkins (1967) made an excellent

summary of the then available data and recognized two major phases of seaway opening in Beringia. The first opening occurred during the late Miocene (10–12 Ma), when a large number of Pacific invertebrates and marine mammals reached the North Atlantic. The reopening of Bering Strait took place in the late Pliocene (3.5–4 Ma), as evidenced by extensive occurrence of the same mollusks on either side of the strait. This would mean that, during the majority of Neogene time other than the two episodes of reopening of the Bering Seaway, Beringia could serve as a land bridge connecting the Eurasian and North American continents.

A considerable step forward was made by Tedford et al. (1987). In using genera exotic to North America to define the beginning of “age” and “subage”, they listed 13 Neogene appearance events for North America. It is not fully clear what “exotic” entails, and do all these immigrants and their first appearances define distinct events? In a comprehensive review of Cenozoic Era dispersal history, Woodburne and Swisher (1995) listed six major Neogene interchange events: (6) beginning of Hemingfordian, 19 Ma, (7) beginning of late Hemingfordian, 17.5 Ma, (8) beginning of Barstovian, 15.9 Ma, (9) beginning of Clarendonian, 11 Ma, (10) beginning of Hemphillian, 9 Ma, and (11) beginning of late Blancan, 2.5 Ma.

From the point of view of carnivorans, it seems that only three major dispersal waves of the filter-bridge type can be recognized. The first is around 20 Ma. The whole duration of the dispersal wave could have lasted 2 or 3 m.y., probably from 21 Ma to 19 or even 18 Ma, during which time, intermittent dispersals might have occurred. The carnivorans that migrated from Eurasia to North America included *Cynelos*, *Ysengrinia*, *Amplicyon*, *Cephalogale*, *Phoberocyon*, *Ursavus*, some small-sized mustelids, *Potamothereium*, an ancestral form of *Edaphocyon*, and *Proailurus*. According to Ginsburg’s compilation (1999), in Europe, the early Miocene contains 37 carnivoran genera, of which at least 8 are recorded from North America. It is noteworthy that these immigrants cover the major carnivoran groups, leaving only the viverrids unrepresented. There is little reason to consider the fossil viverrids radi-

cally different from the living ones ecologically. Their absence in the list of the migrants may indicate that the migration concerned only nontropical elements of the fauna. It is also remarkable that no carnivorans were found to have migrated in the opposite direction, that is, from North America to Eurasia. The only noncarnivoran emigrant from North America to Eurasia during this period of time is *Anchitherium*. Woodburne and Swisher (1995) assigned this exchange event to Simpson's corridor type. Judging from the limited number and the ecological constraints of migrants involved, it is more reasonable to view the above dispersal wave as by filter-bridge.

The next major dispersal wave occurred at about 7–8 Ma, the early part of Hemphillian. The carnivorans migrating from Eurasia to North America included *Indarctos*, *Agriotherium*, *Simocyon*, *Eomellivora*, *Plesiogulo*, and *Machairodus*. As is well known, the carnivorans of the Eurasian *Hipparion* fauna are particularly well represented among fossils and rich in number of taxa, totaling 45 (Ginsburg, 1999). Nevertheless, the number of the emigrants to North America constitutes only a small fraction of the total, only about one-sixth. It is interesting to note that the emigrants are mostly large-sized carnivorans.

The last major dispersal wave is early Blancan, ~4 Ma. The Eurasian emigrants recorded in North America are *Ursus*, *Parailurus*, *Lynx* (?), *Felis* (?), *Homotherium*, and *Chasmaporthetes*. At about the same time, *Megantereon* and *Pannonictis* migrated from North America to Eurasia.

There are two small-scale migration events of carnivorans in the opposite direction, that is, from North America to Eurasia. The dispersal concerns only single taxa. At about 13 Ma, *Leptarctus* migrated from North America to Asia. Probably at the same time, ancestral *Barbourofelis* (a form like *Sansanosmilus*) migrated from Eurasia to North America. At ~5 Ma (or 7 Ma, vide supra), *Canis* and some of its closely related forms might have crossed Beringia. Canids came to Eurasia apparently together with camels.

For noncarnivoran mammals, at least four other dispersal events are well established: the three equid genera emigrated from North America to Eurasia: *Anchitherium* at 20 Ma,

Hipparion at about 11.5 Ma, and *Equus* at 2.5 Ma. *Gomphotherium* spread from Eurasia to North America at 16 Ma.

The above migration scheme (fig. 2.1) grossly accords with that deduced from marine paleontology, if slight adjustment is made. As stated above, the two episodes of opening of the Bering Strait during Neogene time, according to marine paleontology, were in the late Miocene (~12–10 Ma) and the late Pliocene (4–3.5 Ma). Since the migration of *Hipparion* took place at 11.5 Ma, which is extensively verified and in good accordance with sea-level fluctuation data (at the base of TB3), the late Miocene opening of the Bering Strait may have started later than 12 Ma, probably later than the *Hipparion* migration event.

The effects of the migration differ widely from taxon to taxon. Most of the carnivorans did not play important roles after their settlement in the new continent, except two: “*Canis*” and probably the descendants of *Megantereon*. The “*Canis*” species flourished rapidly and diversified after entering Eurasia. It is commonly believed that this group of carnivorans was similar to fossil hyaenas ecologically and probably played an important role in the extinction of the hyaenas in the north part of the Palaearctic region. As stated above, *Smilodon* may be a descendant of *Megantereon* in North America. It became the second dominant group of carnivorans at Rancho La Brea, next to *Canis dirus*. On the other hand, herbivorous emigrants like equids and proboscideans played very important roles in changing faunal composition after having intermingled with native elements.

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Addendum. Just recently a leptarctine skull was found in early Miocene deposits (~19.5 Ma) in the Danghe area, Gansu province, China (Wang et al., in press). This is about the same time as the earliest leptarctine material found in North America. Thus, it is not impossible that the North American leptarctines were immigrants from Eurasia during the first migration wave at about 20 Ma.