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Origin and early dispersal of the squirrels and their relatives

The first appearances of squirrels and aplodontids in both Europe and North America point to an unknown origin in between both continents. More recent analyses of the tectonic history of the North Atlantic and Arctic ocean basins are consistent with the hypothesis, that an exchange between both sides of the Atlantic has been possible at least until the early Oligocene, the time of origin of both groups. The long lasting isolation of Northern Europe from both the southern parts of the continent and Asia gives enough room for the assumption of a separate evolutionary centre.

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INTRODUCTION

Squirrels (Sciuridae Gray, 1821) are a holarctic rodent group, appearing first in Europe as immigrants of the Grande Coupure at the beginning of the Lower Oligocene together with the probably related Aplodontidae Trouessart, 1897. In North America however, there appear related genera, partly with a protrogomorphous skull, partly with a superficial masseter halfway from the protrogomorphous to the sciuromorphous or even a myomorphous structure. All possible ancestors of squirrels or aplodontids in any Eocene fauna are too far from these groups to establish a near relationship. Emry & Korth (1996) suggest "some *Reithroparamys* like ischyromyid" as an early ancestor of both families. But most of the shared dental characters could also be suspected to be mere parallelisms within the vast group of Ischyromyidae.

As our knowledge of Eocene mammal faunas is restricted to some well known areas, it is not astonishing to find immigrants without a known origin. To get an idea in which of the empty spots on our paleobiogeographic map we should look for the origin of squirrels and aplodontids, we have first to analyse the relationships of both families to one another and with more or less similar isolated genera.

THE DATA

Characters and clades

To get an idea of the interrelationship of the various genera that have been assigned to the sciurid-aplodontid group I undertook several attempts of a character analysis, using the following taxa:

As outgroup some rather primitive paramyines: *Paramys delicatus* Leidy, 1873; *Paramys copei* Loomis, 1907; and *Leptotomus leptodus* (Cope, 1873).

As species of probable but unknown relation to squirrels or aplodontids: *Ailuravus macrurus* Weitzel, 1949 (*A. picteti*

as a later member of the same lineage could be omitted); *Mytonomys robustus* (PETERSON, 1919); *Paracitellus cingulatus* HEISSIG, 1979; *P. marmoreus* HEISSIG, 1979; *P. eminens* DEHM, 1950; *Cedromus wilsoni* KORTH & EMRY, 1991; and *Douglassia jeffersoni* (DOUGLASS, 1901).

As representatives of early aplodontids including Prosciurinae and Allomyinae:
Spurimus scotti BLACK, 1971; *Prosciurus relictus* (COPE, 1873); *Campestrallomys dawsonae* (MACDONALD, 1963); *Campestrallomys annectens* KORTH, 1989; *Campestrallomys siouxensis* KORTH, 1989; *Ephemeromys hospes* WANG & HEISSIG, 1984; and *Plesispermophilus angustidens* FILHOL, 1882, as a primitive Allomyinae.

As earliest representatives of true squirrels:
Palaeosciurus goti VIANEY-LIAUD, 1974; *Oligopetes radialis* HEISSIG, 1979; and *Oligopetes lophulus* HEISSIG, 1979.

These 20 species have been analysed according to 27 dental characters with different cladistic methods. The results yielded, if any, very similar pictures. Generally there is an outgroup comprising *Leptotomus leptodus*, *Paramys copei* and *Spurimus scotti*. So this last species cannot be comprised within the Aplodontidae and this family therefore arrives in North America not before the beginning of the Oligocene. The arrangement of these three species is varying according to the weighting of different characters.

There are three main clades of rather constant composition. One comprises the three species of true squirrels, sometimes with *Cedromus wilsoni* as a sistergroup at the base, a result obtained also by Korth & Emry (1991: 993) on the basis of skull characters. The second one comprises the early Aplodontidae, including *Campestrallomys annectens* in a rather basal position. The third one comprises the group of unclear affinities, in most solutions including *Paramys delicatus*, but excepting *Mytonomys robustus* and

Douglassia jeffersoni. These two species are grouped nearly together in all obtained trees, sometimes forming a separate clade, sometimes forming a sistergroup of the true squirrels. The last species is clearly set off from all true squirrels by the separate entoconid with a long labial spur (entolophid). So it may belong to some ancestral stock, separated by a protrogomorphous masseter and this plesiomorphic tooth detail. The squirrel-like skull and skeleton demonstrated by Emry & Thorington (1982) may be due to convergence.

The clade of the species of undefined affinities may form a sistergroup of one of the two other main clades, but these never can be grouped with one another. In the pure pattern cladistic cladogram this group is attached to the aplodontid clade and the squirrels are isolated, without the sistergroup of *Cedromus wilsoni*. If the characters are weighted in three levels and the form of the protoconule, the anterior connection of the mesostyle and the reduction of the labial crest of the entoconid are considered to be irreversible, this clade of doubtful species appears as the sistergroup of the squirrel clade. In this case the pair of *Mytonomys* and *Douglassia* is excluded from the relationship of squirrels.

With all these manipulations it was impossible to rearrange the tree into two main clades, the intermediate forms being sorted in both of them. This result has consequences for the formation of a biogeographical hypothesis. The results of the analysis can not be summarized in one or more cladograms, first because of the subjectivity of the character selection, second because of the unknown degree of character variability in most involved species. Even characters traditionally used are highly variable in some species. On the other hand the interior configuration of the three main clades is rather stable against manipulations, so that there may be some reason to accept them as real units. So the idea of any closer relationship between squirrels and aplodontids depends on the subjective high value of the elongation of the protocone at the cost of the hypocone.

The paleobiogeographical distribution pattern

There is only one species in the Eocene of Europe which shows undoubted affinities to one of the three main clades: *Ailuravus macrurus* from Messel. *Mytonomys* from North America, which was considered by Wood (1976) and Korth (1984) to be a member of the Ailuravinae, never shows a grouping together with this species but is always near the protrogomorphous but otherwise squirrel-like *Douglassia jeffersoni*. On the other hand *Ailuravus macrurus* is by far too big to be ancestral to any of the Oligocene species.

The bulk of the Aplodontidae and Sciuridae appear without doubt at or near the base of the Oligocene on both continents. The sciurids are restricted to Europe in this first time, but members of both subfamilies, Sciurinae and Petauristinae occur probably at the same time with the Grand Coupure. Members of the other clades appear on both sides of the Atlantic. As there is still some uncertainty where the Eocene-Oligocene boundary has to be placed within the Chadronian of North America, the results remain a little doubtful. There is no comparable immigration event as in Europe. The undoubted Aplodontidae appear in Europe with the subfamilies Prosciurinae (*Ephemeromys*) and Allomyinae (*Plesispermophilus* and *Sciurodon*) whereas in America the Prosciurinae appear first (*Prosciurus vetustus* MATTHEW, 1903; *Oligospermophilus douglassi* [KORTH, 1981]). The Allomyinae, however, and most of the Prosciurinae, including possibly also *Campestrallomys annectens*, are not known earlier than the middle or late Oligocene.

Members of the third clade are also known from both sides of the Atlantic, but here too the earlier appearances seem to be on the European side. Not only the early offshoot *Ailuravus macrurus* with its descendants points to this direction, but also the presence of two species of *Paracitellus* in the early Oligocene of Europe, whereas the species *Campestrallomys dawsonae* and *C. siouxensis*, which show up always within this clade and not with *Campestrallomys annectens*, appear not earlier than in the middle or late Oligocene.

The paleogeographic situation of possible land bridges

According to the rapidly decreasing faunal similarity of North America and Europe from the base of Middle Eocene onwards, the opening of the Atlantic was assumed by paleontologists to begin at that date (e.g. Simpson 1947, Kurtén 1966, McKenna 1972, Springhorn 1984). More recent tectonic investigations have revealed, however, that the earliest spreading zone extended west of Greenland before the spreading activity was restricted to the eastern branch of the Atlantic around 36 Ma BP (Eldholm 1990). The final separation of the Barents shelf from the northern edge of Greenland must therefore have occurred some time later, probably during the Oligocene (Fig. 1). This assumption is corroborated by the transpressive folding of Eocene strata on Spitsbergen (Geyssant & Lepvrier 1982), indication of a direct neighbourhood of Greenland during most of the Eocene.

On the other hand, there was a broad nearly continuous epicontinental seaway along the Polish lowlands from the Middle Eocene till the lower Oligocene, separating the Baltic shield from the islands of Central and Western Europe. There is less evidence of intermittent marine barriers in the Barents sea and east of Greenland. According to the reconstruction of Eldholm (1990) the possibility of an Iceland-Bridge existed also probably for shorter times (Fig. 2).

The large migrations at the beginning of the Oligocene have always been considered a result of emerging land bridges, mainly across the Turgai straits east of the Ural mountains. Whereas this epicontinental seaway was apparently one of the most stable faunal boundaries during the Paleogene we know little about the exact time of emersion
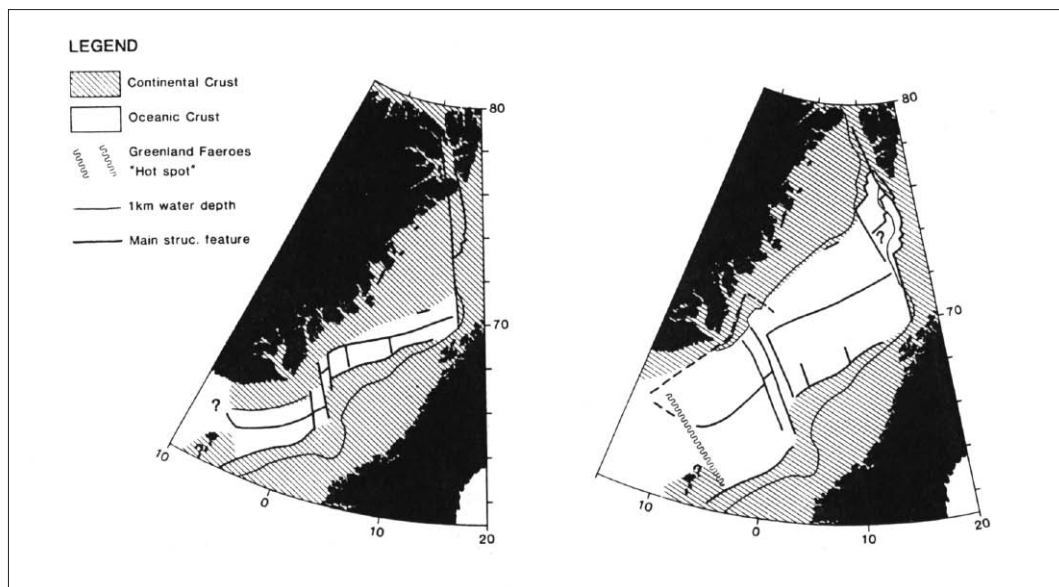
Figure 1 The relative position of Greenland and Spitsbergen in the Lower Eocene (left) and around the Eocene-Oligocene transition (right) (from Eldholm 1990).

of Beringia. There is evidence of isolated marine faunas of the Arctic and the Pacific oceans since the Paleogene (Hopkins 1967: 452) and several expanding Eocene species apparently crossed the bridge in both directions. There is no distinct immigration wave in America at or near the Eocene-Oligocene boundary (Prothero & Heaton 1996). After Marincovich & Gladenko (1999: 150) the late Miocene marine faunal exchange across Beringia shows the first interruption of a land bridge that was stable since the middle Cretaceous. There must have been other reasons why a rather big number of mammalian groups did not succeed in crossing this region.

DISCUSSION

Possible regions of squirrel origin
Actually we do not know any ancestral form of aplodontids or squirrels prior to the Early Oligocene. We have to look for their origin in one of the blank spaces in the north of Europe and America, because it is there where the regression at the end of the Eocene

opened the pathways for migration. We have to exclude the wide region of northern Siberia because Ischyromyidae never have been involved in a greater amount in one of the trans Bering migrations and are only a very restricted component of Asian faunas.

As the first Eocene faunas from the northernmost parts of America did not reveal any possible sciurid ancestors we have to concentrate on the two only punctually united landmasses between America and Western Europe, Greenland and the Baltic shield. The sudden appearance of members of all three clades at the very base of the Oligocene in Europe in contrast with the partly earlier, partly somewhat later appearance of relatives of only two of them in America (the true squirrels appear as late as the Early Miocene) points to a Baltic origin of the squirrels and probably also of the Aplodontidae. This view is consistent with the appearance of *Ailuravus* in the Middle Eocene of Europe as a first offshoot of these unknown northern ancestors (if *Meldimys* MICHAUX,1968 from the Early Eocene appears to belong to the same clade there is no need to assume a special migra-
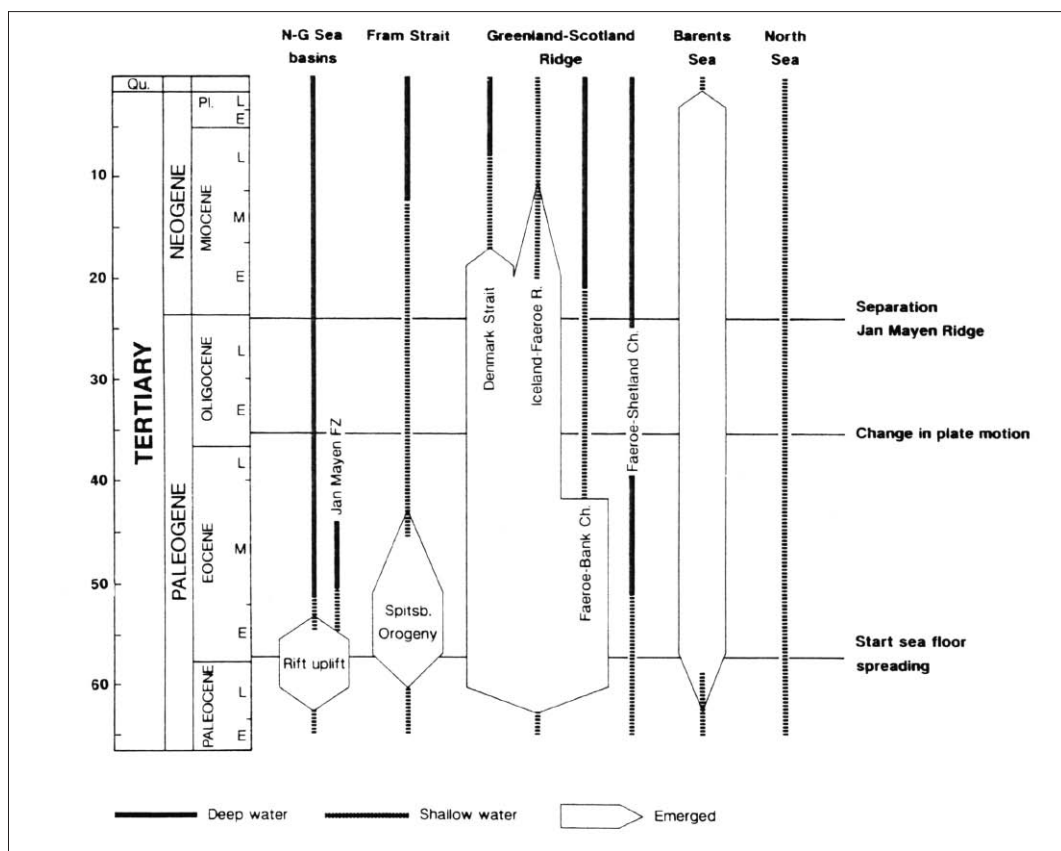
Figure 2 Water depth and emersions, tectonic and volcanic events in different parts of the North Atlantic. The Greenland-Scotland Ridge is the region of a possible Iceland Bridge. The Faroe-Bank Channel and the Faroe-Shetland Channel together form for most of the time a narrow marine interruption of a possible land bridge. (from Eldholm 1990, time scale used: Berggren *et al.* 1985).

tion).

The early immigration of Prosciurinae in North America may indicate an earlier immigration of their ancestors to Greenland before the regression opened their way to America. The more important immigrations to America during the Orellan may indicate the time of a last regression in the Barents sea, opening for a last time the way directly from the Baltic land to North America. This seems more probable than the assumption of a migration across northern Asia over the Bering land bridge. This way was probably followed by the Miocene squirrels entering America. It can not be definitively excluded for the Oligocene migrations.

Other faunal elements supporting the hypothesis

During the Paleogene there are several groups of mammals with sudden appearances on one or both sides of the Atlantic which can not be traced back to Asian origins. One group consists of the dominant big artiodactyls of the Late Eocene and Early Oligocene, the Oreodonta OSBORN, 1910 of America and the Anoplotheriidae BONAPARTE, 1850 of Europe (Heissig 1993). Both appear in several immigration waves. Their relationship can only be established by some rather general characters: the selenodont molars with smooth enamel surface and the short astragalus with a very special socket for the *malleo-*

lus tibiae. The European Dacrytheriidae DEPERET, 1917 are probably near the common ancestors, but their autopodial structure is totally unknown. The greater structural difference of the cheek teeth, especially in the later genera, indicates an early and strict separation of the American and the European groups. Both show more immigration events than the rodents. Larger mammals may cross unfavourable regions more easily than small ones.

The Chadronian immigration of *Epoicotherium* SIMPSON, 1927 in North America and probably at the same time of the related *Molaetherium heissigi* STORCH & RUMMEL, 1999 in Europe points in the same way to a common ancestry but also to a certain time of separate differentiation before the migration to the south.

The case of beavers is more questionable. It is still doubtful, if the beavers of the Oligocene can be traced back to Eocene Eutypomyidae MILLER & GIDLEY, 1918. Even the content of this family is under discussion. *Agnotocastor* STIRTON, 1935, the undoubted member of Castoridae (subfamily Agnotocastorinae KORTH & EMRY, 1997) comes as an immigrant roughly simultaneous to Asia and North America (the Chadronian is here considered to be partly of Late Eocene, partly of Early Oligocene age). In Europe, however, the genus *Steneofiber* GEOFFROY, 1833 (a member of the subfamily Castorinae) appears at the same time. These relationships are too complex to support any biogeographical hypothesis.

The Grande Coupure in Europe

Up to now the question is open, whether the immigration wave at the beginning of the Oligocene was contemporaneous or diachronous in the different parts of Central and Western Europe (Sigé & Vianey-Liaud, 1979). There is, however, no difference of the evolutionary level of the most frequent immigrants as, e.g., the Cricetidae or the ruminants. The time difference in the environmental change in the regions of southern

Germany and southern France may partly be due to regional differentiation, partly biased by local or taphonomic conditions of the compared faunas and is therefore no useful tool for correlation. The strong endemism of the indigenous faunal elements contrasts with the Europe-wide distribution of immigrant taxa. It shows that Europe, even after the regression, was divided into faunal provinces.

It may be possible to add to the hypothesis of a proper evolutionary centre in northern Europe as a source of several immigrants of the Grande Coupure, the idea that several other groups have been present in this region already before they immigrated to Europe, even if they have a known origin in either America or Asia. Only the few groups already found in the Eocene of southeast Europe such as the Cricetidae or the Anthracotheriidae have to be excluded from this possibility. Nevertheless, most of the contemporaneous immigrations have been caused by the emerging Polish lowlands rather than by the regression in the Turgai straits.

Climatic influence?

Are the changes of the Eocene/Oligocene boundary induced only by the changing paleogeographic situation, or perhaps also by a strong climatic deterioration during the Late Eocene? Probably the shifting of floral elements from north to south enhanced the migration in the same direction of animals adapted to this more boreal flora. This may be one of the reasons why squirrels and aplodontids did not migrate together with the anoplotheres during the Upper Eocene and why there was no anoplothere immigration at the Grande Coupure, when possibly this group had already died out in the cooler climate of northern Europe.

One of the necessary adaptations of squirrels was probably sciuromorphy, a strengthening of the superficial masseter which enabled a higher pressure on the incisors. As in beavers, where it serves to cut wood particles, it enabled the squirrels to cut the hard wooden cover of nuts. Thus, they had this

food available during the winter, when fruit production ceased and leaf production was restricted to the evergreen elements of the vegetation. The aplodontid adaptation, however, was the strengthening and sharpening of the cutting edges of the cheek teeth together with a transverse shearing motion of the jaws. In a more seasonal vegetation, they could shift to a folivorous diet during times when fruits were not available.

CONCLUSION

Several Paleogene mammal groups with a probably northern European evolutionary centre and the possible presence of several other participants of the Oligocene migration wave in this region may encourage paleontologists in all countries on the Baltic shield up to the western slopes of the Ural mountains to look for continental or even coastal sediments of middle to late Eocene age as possible sources for remains of the mammal fauna of this blank space in the history of European mammal faunas.

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