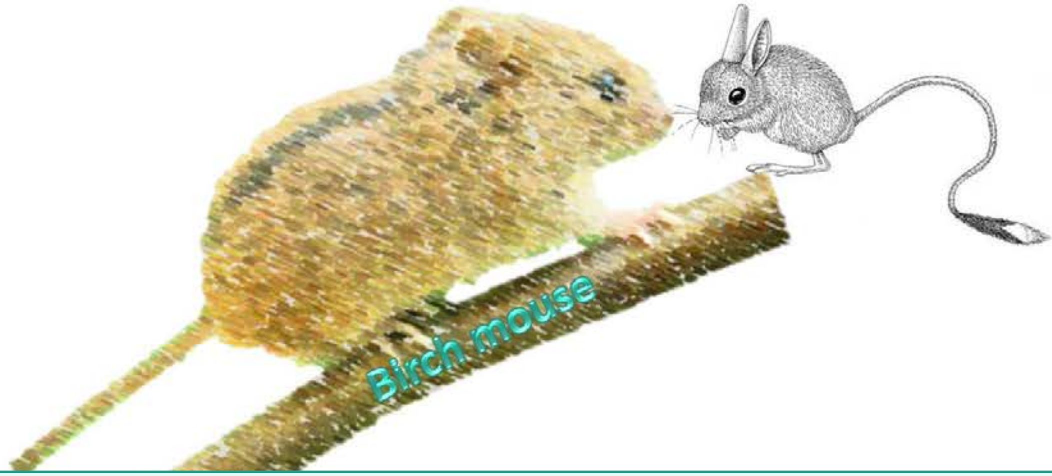


Out-of-Himalaya: The impact of past Asian environmental changes on the evolutionary and biogeographical history of Dipodoidea (Rodentia)

Julie Pisano, Fabien L. Condamine, Vladimir Lebedev, Anna Bannikova,
Jean-Pierre Quéré, Gregory I. Shenbrot, Johan R. Michaux*, Marie Pagès*

Jerboa

Birch mouse

Jerboa

Jumping mouse

Jumping mouse

Original Article submitted in *Journal of Biogeography*

Dipodoidea, a superfamily left out…

Muroidea (≈1,300-1,500 spp.)

Dipodoidea(≈51 spp.)

- Superfamily most closely related to the large and species-rich superfamily Muroidea
- Most studies focus on Muroidea

→ Paid little attention to Dipodoidea

DIPODIDAE
- Cardiocraniinae (7 spp.)
- Euchoreutinae (1 sp.)
- Allactaginae (16 sp.)
- Dipodinae (9 spp.)

→ Jerboas

ZAPODIDAE (5 SPP.)
Syn. Zapodinae → Jumping mice

SMINTHIDAE (13 SPP.)
Syn. Sicistinae → Birch mice

(Holden & Musser, 2005; Lebedev *et al.*, 2012)

Dipodoidea, a superfamily distributed throughout the Holarctic:

- Disjoint distribution patterns (*e.g.* Zapodidae)
- Many species found in different remote arid habitats

Dipodoidea are particularly relevant for testing biogeographic scenarios

BUT

Lack of a suitable phylogenetic framework is still impeding the inference of their biogeographic history

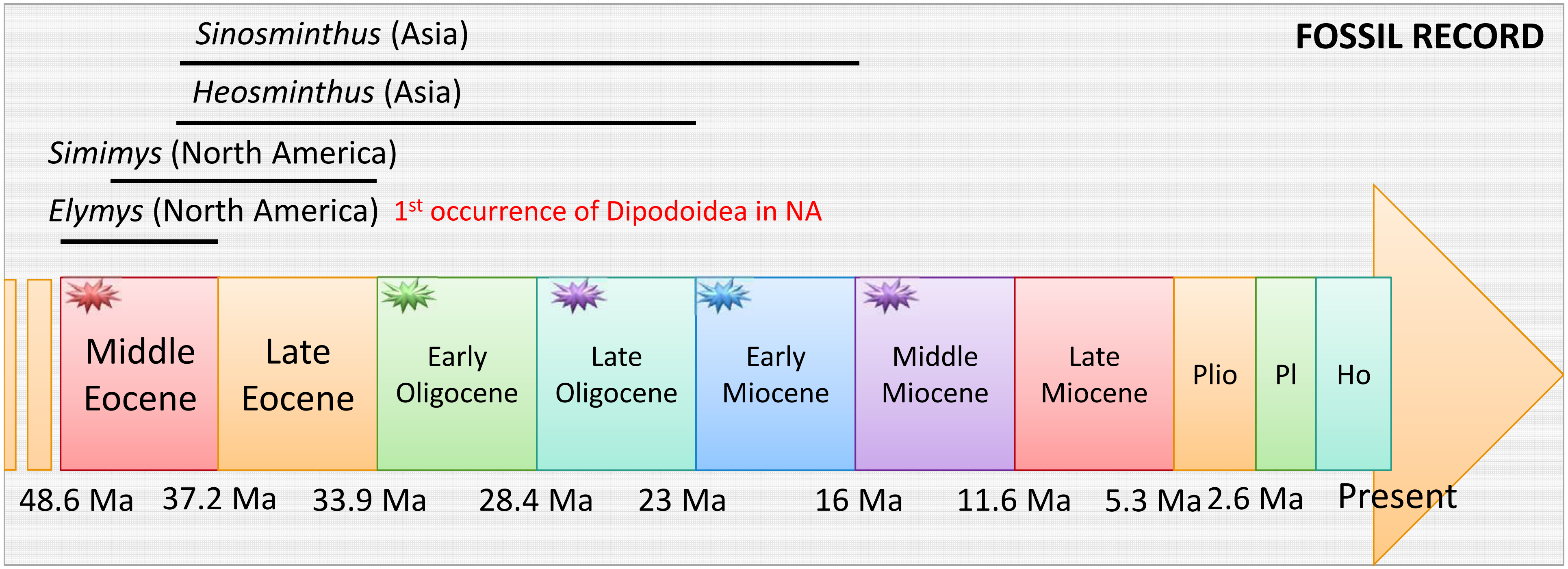
Dipodoidea, investigation of their evolutionary history in progress:

ZHANG *ET AL*. (2012):

- Middle Eocene: Diversification of modern **Dipodoidea** (*i.e.* crown; ≈42.7 Ma)
- Warming period spanning from Late Oligocene through Early Miocene: Diversification of **Sminthidae** (≈16.8 Ma)
- Global cooling following the mid-Miocene climatic optimum: Diversification of **Zapodidae** (≈13.2 Ma) **and Dipodidae** (≈27 Ma)

WU *ET AL*. (2012):

- Early Oligocene: Origin of modern Dipodoidea (*i.e.* crown; ≈32.4 Ma)



Objectives of this study:

Based on the most complete species-level phylogeny (34/51 spp.), we reconstructed the temporal and biogeographic origins of the group with

1. Estimates of divergence times using a Bayesian relaxed molecular clock calibrated with fossils;

2. Inferences of biogeographic and evolutionary history using the dispersal-extinction-cladogenesis model

Let's go…

Follow me…

I will tell you my evolutionary history!

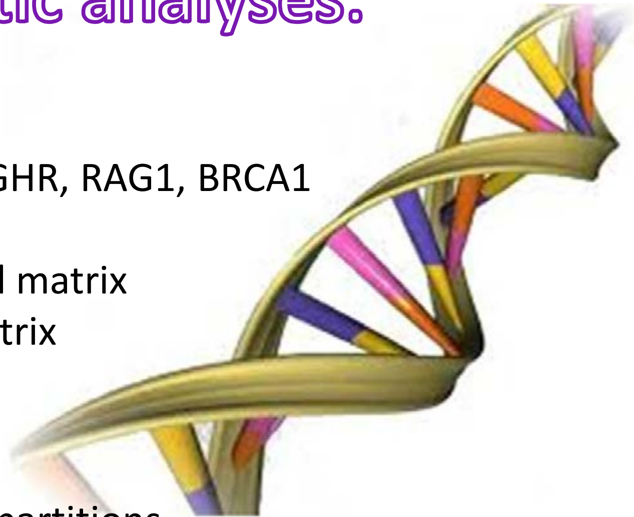
Taxon sampling:

- 34/51 species of Dipodoidea
  - 15/16 genera

  (Single missing genus: *Salpingotulus*)

- 12 outgroup species (Muroidea, Sciuridae, Aplodontiidae)
  - Selected to recovered specific nodes in the phylogeny allowing the use of fossils as calibration points to constrain nodes

Phylogenetic analyses:



- **Molecular datasets:**
  - Markers: Cyt *b*, IRBP, GHR, RAG1, BRCA1
  - Combined matrices:
    - Densely sampled matrix
    - Species-level matrix
- **Partitioning:**
  - ✓ PartitionFinder 1.1.1:
    Appropriate subset partitions
    Appropriate substitution models of sequence evolution
- **Phylogenetic analyses:**

1. PhyML 3.0 & MrBayes 3.2.2: on each gene independently
   - ✓ Congruence between markers
2. raxmlGUI 1.31 and MrBayes 3.2.2:
   - ✓ Analyses on combined datasets
3. **ASSESSMENT OF THE TREE TOPOLOGY:** (solved questions unresovled in Lebedev *et al.* (2012))
   - Bayes factors

   Hypotheses (1st part): The single species of Euchoreutinae with
   a. Allactaginae
   b. Dipodinae

   Hypothesis (2nd part):
   c. Monophyly of Allactaga

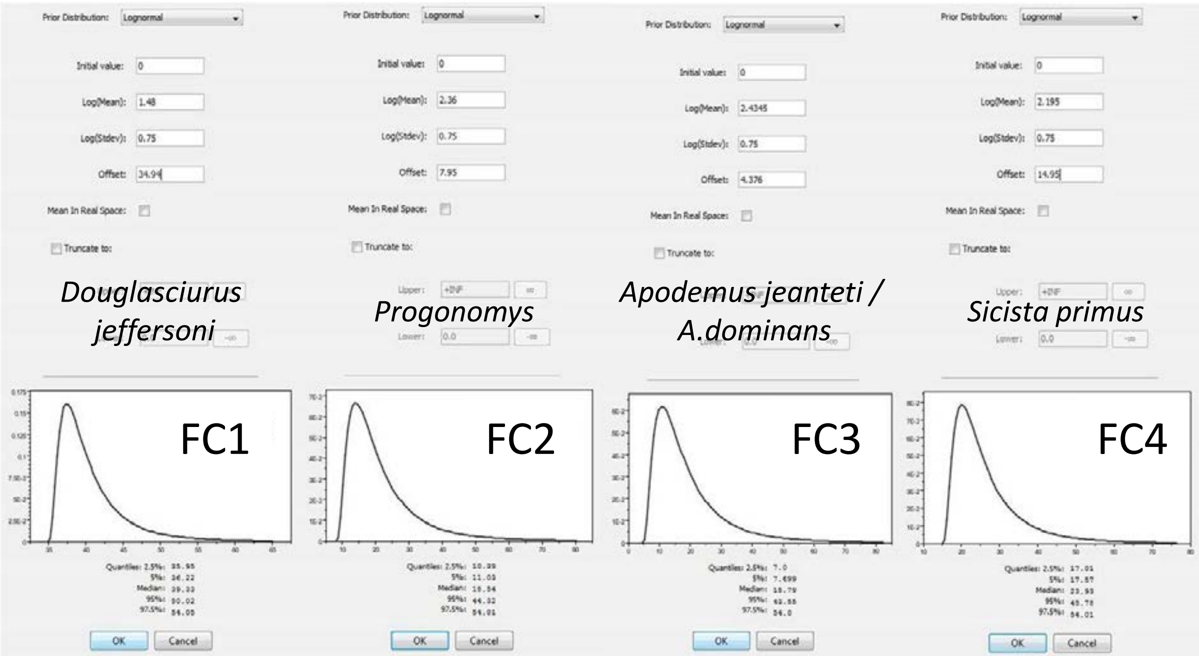
Bayesian divergence time estimations (BEAST 1.8.0)

Molecular divergence dates:

- Bayesian relaxed clock
- *Clock model:* Uncorrelated log-normal relaxed clock
- *Tree model:* Yule / birth-death speciation process

Fossil calibration point parameters:

- Soft bounds:
  - Log-normal distributions :
    - 2.5% quartile = Minimum age of the geological interval where the fossil was found
    - 97.5% quartile = 54 Ma, *i.e.* geological interval where *Erlianomys,* the oldest known fossil of Myodonta, was found



Cross-validation:

- Omission one by one each of the FC in turn to identify putative inconsistencies

In total: 10 dating analyses

Biogeographical analyses (Lagrange-DEC)

Biogeographical model:

Classification proposed in Mammal Species of the World	A Nearctic	B West Palearctic	C Siberia	D Central Asia*	E Altai Mt, Mongolian steppe, Yablonoi Mt	F Persian plateau, Anatolian region and caucasus, iranian plateau	G Himalaya + Tibetan plateau	H Gobi desert, Talkimakan desert	I North Africa + Arabia
Jaculus blanfordi	0	0	0	1	0	1	0	0	0
Jaculus jaculus	0	0	0	0	0	0	0	0	1
Jaculus orientalis	0	0	0	0	0	0	0	0	1

Time Slice 2: 5,3 to 16 Ma (middle Miocene)

	A	B	C	D	E	F	G	H
A	-							
B	0,3	-						
C	0,5	1	-					
D	0,3	0,7	1	-				
E	0,3	0,3	0,7	0,7	-			
F	0	0,5	0,3	0,7	0,3	-		
G	0	0,3	0,3	0,5	0,3	0,5	-	
H	0,1	0,3	0,3	1	1	0,3	0,5	-
I	0	0,5	0,1	0,3	0,1	0,7	0,1	0

Molecular phylogeny of Dipodoidea

As... e tree top...

• ... ct

m...

mo...

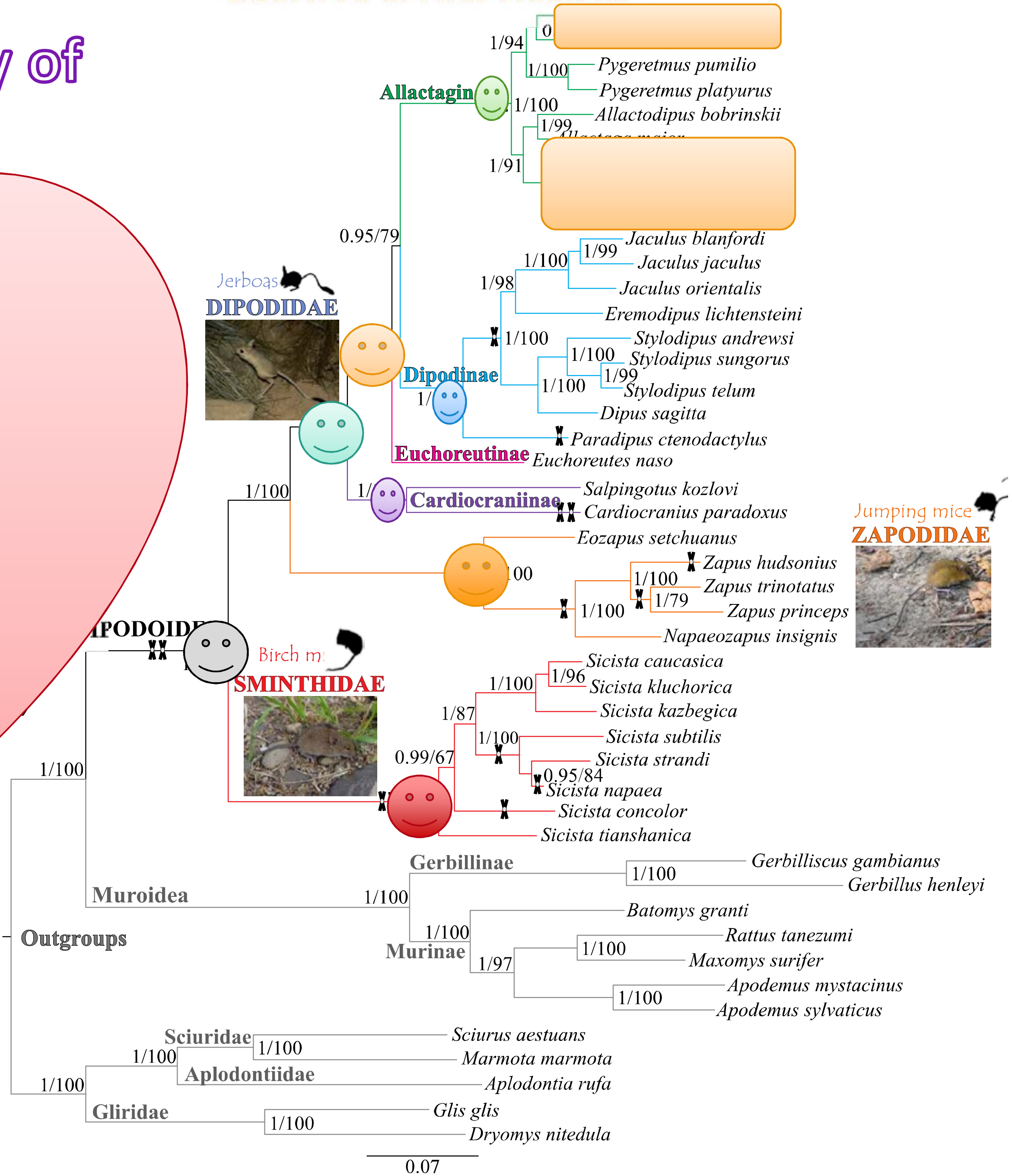
MOST COMPLETE MOLECULAR PHYLOGENY OF DIPODOIDEA TO DATE

- ✓ Congruence with previous studies
- ✓ Answered unresolved questions of Lebedev *et al.* (2012)

- ✓ Th...
- ✓ The ... Dipodid...
- ✓ The **subfa**... ...e, Dipodinae, All...

17 Rare genomic changes:

- Indels of 3 or multiple of 3 nucleotides
  - ✓ Strengthened the obtained topology by confirming several monophylies



Node identification		All FC		No FC1		No FC2		No FC3		No FC4	
		Yule	BD	Yule	BD	Yule	BD	Yule	BD	Yule	BD
1	Crown of Rodentia	64.84 (60-71,72)	64.85 (60.75-71.75)	64.15 (56.18-75.22)	63.97 (56.64-76.01)	64.8 (60.69-71.8)	64.65 (60.65-71.53)	64.4 (60.56-70.79)	64.46 (60.69-71.1)	64.11 (60.46-70.87)	64.18 (60.6-71.37)
3	FC1 – Douglasciurus jeffersoni	37.9 (35.49-42.09)	37.91 (35.51-41.94)	**37.5 (32.84-43.97)**	**37.39 (33.11-44.43)**	37.88 (35.48-41.97)	37.79 (35.46-41.81)	37.65 (35.4-41.38)	37.68 (35.48-41.56)	37.48 (35.34-41.43)	37.52 (35.42-41.72)
9	FC2 – Progonomys (Crown of Murinae)	12.95 (12.12-14.38)	12.95 (12.13-14.33)	12.81 (11.22-15.02)	12.78 (11.31-15.18)	**12.94 (12.12-14.34)**	**12.91 (12.11-14.29)**	12.86 (12.1-14.14)	12.87 (12.12-14.2)	12.8 (12.07-14.15)	12.82 (12.1-14.25)
12	FC3 – Apodemus jeanteti & Apodemus dominans	7.37 (6.9-8.18)	7.37 (6.9-8.16)	7.29 (6.39-8.55)	7.27 (6.44-8.64)	7.36 (6.9-8.16)	7.35 (6.89-8.13)	**7.32 (6.88-8.05)**	**7.33 (6.9-8.08)**	7.29 (6.87-8.05)	7.29 (6.89-8.11)
14	FC4 – Sicista primus (Crown of Sminthidae)	17.9 16.76-19.87)	17.9 (16.77-19.81)	17.71 (15.51-20.76)	17.66 (15.63-20.98)	17.89 (16.75-19.82)	17.85 (16.74-19.75)	17.78 (16.72-19.54)	17.79 (16.75-19.63)	**17.7 (16.69-19.56)**	**17.72 (16.73-19.7)**
6	Split Dipodoidea / Muroidea	58.51 (54.78-64.97)	58.51 (54.82-64.74)	57.89 (50.7-67.88)	57.72 (51.11-68.59)	58.47 (54.76-64.79)	58.34 (54.73-64.55)	58.11 (54.65-63.88)	58.16 (54.77-64.16)	57.85 (54.55-63.95)	57.91 (54.68-64.4)
13	Radiation of Dipodoidea	41.18 (38.55-45.72)	41.18 (38.58-45.56)	40.74 (35.68-47.77)	40.62 (35.97-48.27)	41.15 (38.54-45.6)	41.05 (38.52-45.43)	40.9 (38.46-44.95)	40.93 (38.54-45.15)	40.71 (38.39-45)	40.76 (38.48-45.32)
21	Divergence Zapodidae	34.99 (32.76-38.85)	34.99 (32,78-38.72)	34.62 (30.32-40.59)	34.52 (30.56-41.02)	34.96 (32.75-38.75)	34.89 (32.73-38.6)	34.75 (32.68-38.2)	34.78 (32.75-38.37)	34.6 (32.62-38.24)	34.63 (32.7-38.51)
26	Divergence Cardiocraniinae	27.18 (25.45-30.18)	27.19 (25.47-30.08)	26.89 (16.44-22.01)	26.82 (23.74-31.87)	27.16 (25.44-30.1)	27.1 (25.43-29.99)	27 (25.39-29.68)	27.02 (25.44-29.81)	26.88 (25.35-29.71)	26.91 (25.41-29.92)
28	Divergence Euchoreutinae	22.51 (21.08-25)	22.52 (21.09-24.91)	22.28 (19.51-26.12)	22.21 (19.67-26.39)	22.5 (21.07-24.93)	22.45 (21.06-24.84)	22.36 (21.03-24.58)	22.38 (21.08-24.69)	22.26 (20.99-24.61)	22.29 (21.04-24.78)

Origin and evolutionary history of Dipodoidea

Late Paleocene (≈57.72 Ma): SPLIT BETWEEN DIPODOIDEA AND MUROIDEA

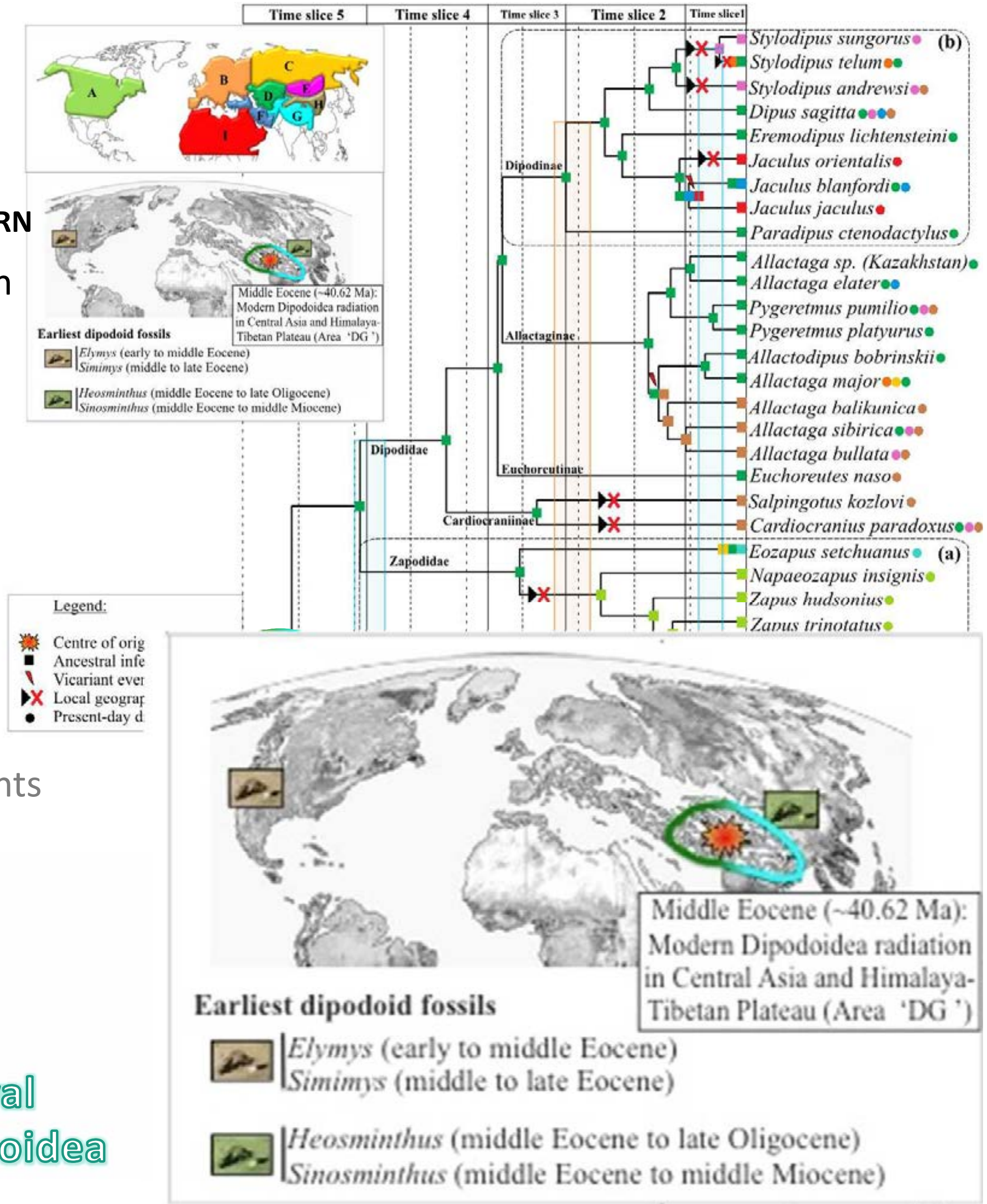
Middle Eocene (≈ 40.62 Ma): RADIATION OF MODERN DIPODOIDEA in Central Asia and Himalaya Tibetan plateau (Area 'DG')

- ✓ Congruent with the fossil record
- ✓ Congruent with environmental changes:

40 Ma: India collided with Asia

Uplift episodes of Himalaya

(Known to have induced vicariant events in many groups; *e.g.* warblers, glyptosternoid fishes)



Likely that this Geological upheaval triggered the diversification of DIpodoidea

Origin and evolutionary history of Dipodoidea

Early Oligocene (≈ 34.52 Ma): Split between Zapodidae and Dipodidae in Central Asia

Global temperature ↓

& Antarctic ice-sheet expanded rapidly

⇩

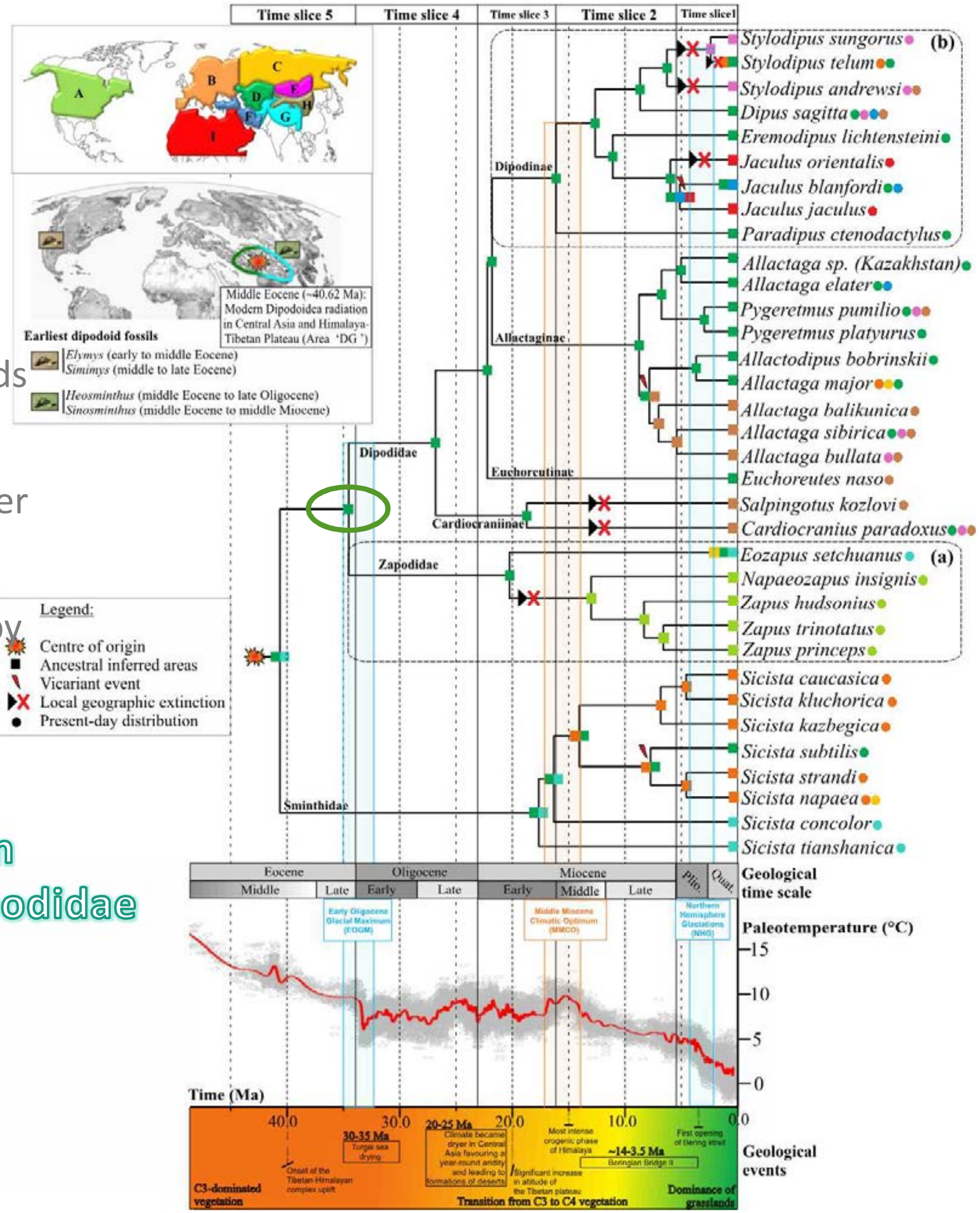
In Palearctic: development of open grasslands

⇩

Great worldwide mammalian faunal turn-over

(*i.e.* the Mongolian remodelling in Asia):

Eocene perissodactyl-dominant faunas replaced by rodent/lagomorph-dominant faunas

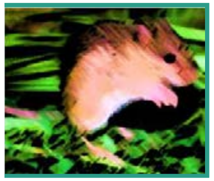


In Central Asia:

Climatic and geological disruption

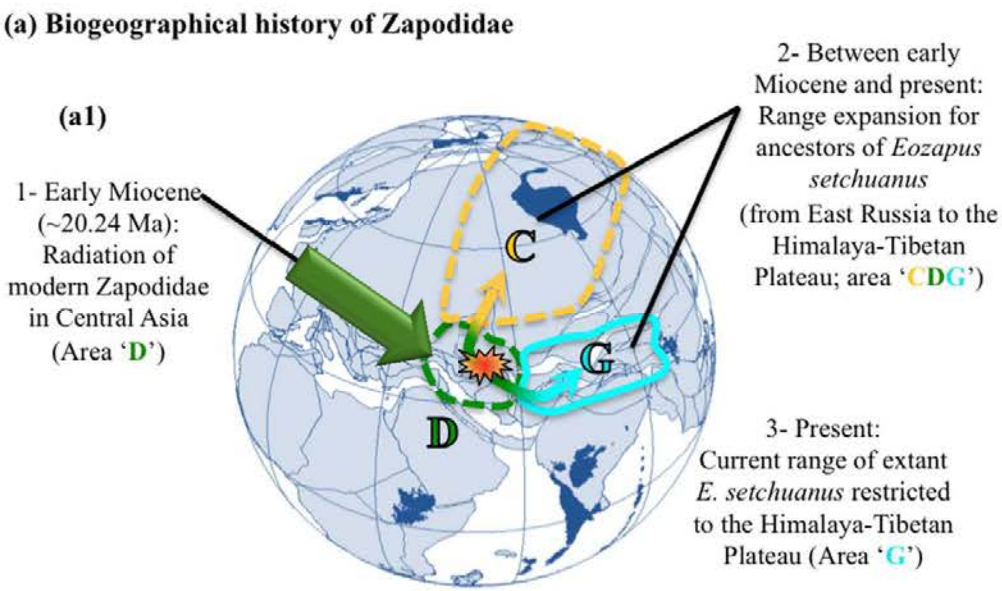
→ likely triggered diversification of Dipodidae

Colonisation of the New World and diversification of the Zapodidae

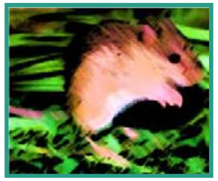


≈20.24 Ma: Radiation of Zapodidea in Central Asia during early Miocene

Altitude of Himalaya-Tibetan plateau ↑ → Aridification of Central Asia → Diversification of Zapodidae likely triggered by these environmental changes

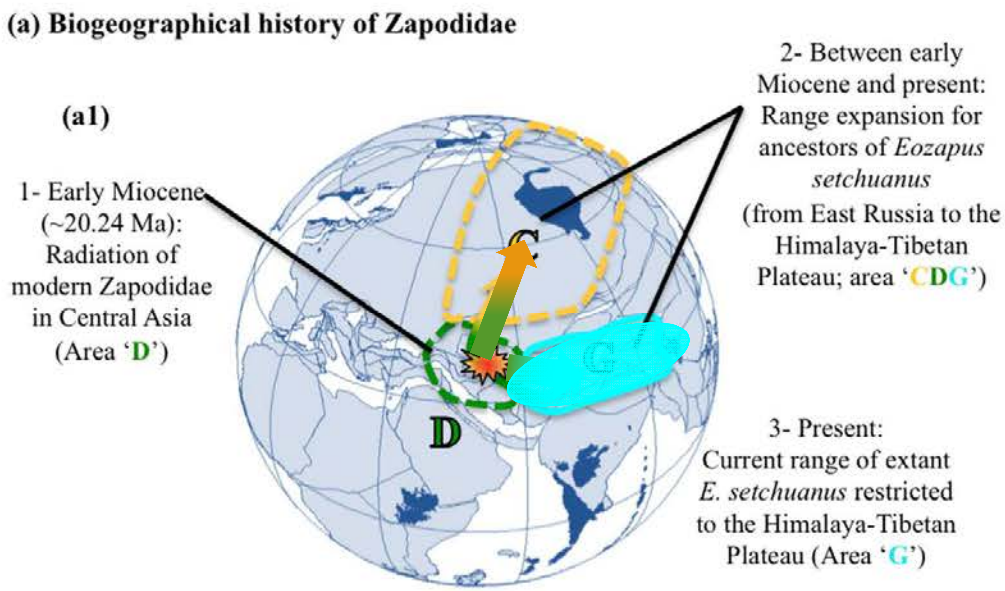


Colonisation of the New World and diversification of the Zapodidae

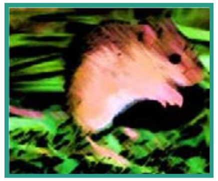


Eozapus setchuanus, the 1st zapodid to diverge

Expansion of the range from East Russia to Himalaya-Tibetan plateau (Area 'CDG') → Present: Restricted to Himalaya-Tibetan plateau (Area 'G')



Colonisation of the New World and diversification of the Zapodidae



Napaeozapus and *Zapus*, the colonists of North America

Between early (≈20.24 Ma) and middle Miocene (≈13.01 Ma): Colonisation of North America

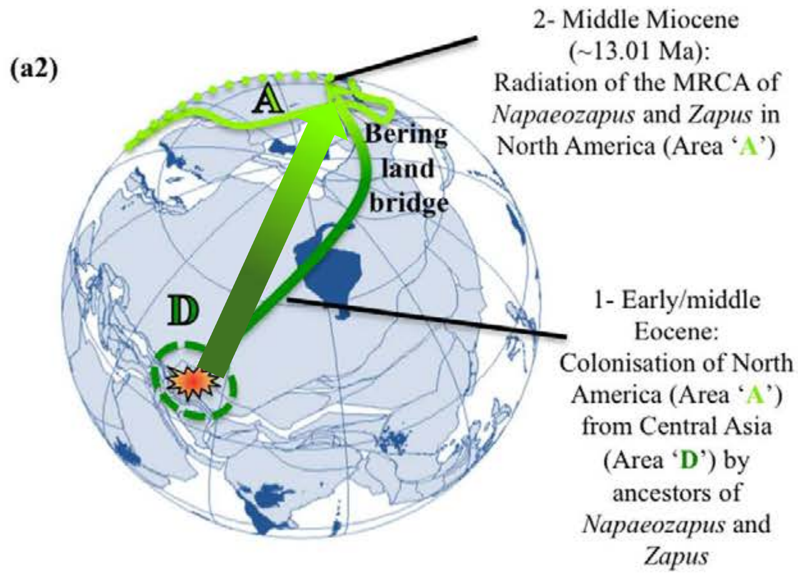
+

Between ≈14 to 3.5 Ma: BLB covered by a continuous boreal coniferous forest belt

=

Suggesting a middle Miocene colonisation of North America

✓ **Congruent with the fossil record**:
Megasminthus, middle Miocene, North America → Oldest known North American fossil of Zapodidae

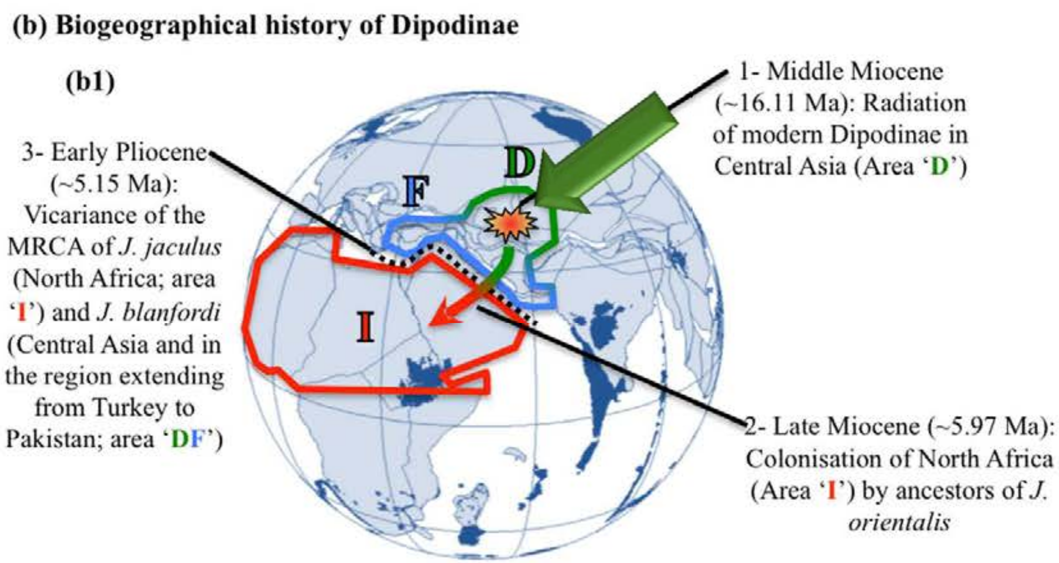


The expansion through Eurasia, the conquest of Africa, and the diversification of Dipodinae

≈16.11 Ma: **Radiation of Dipodinae** in Central Asia at the early-middle Miocene boundary

Most intense orogenic phase of Himalaya + Mid-Miocene climatic optimum: Period of considerable warming = Year-round aridity and formation of deserts and grasslands

Likely to have favour the diversification of Dipodinae

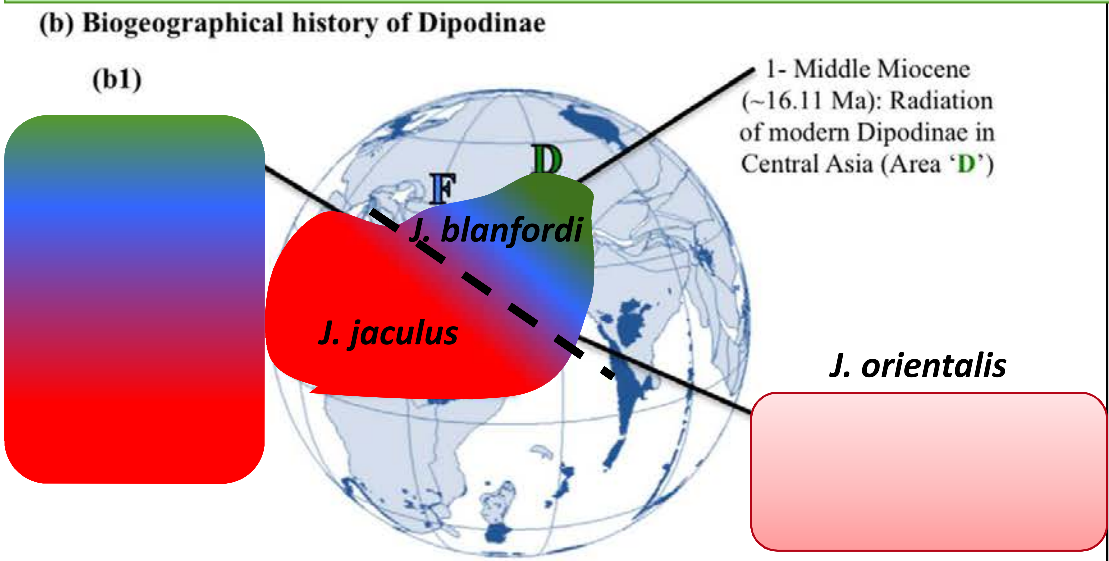


The expansion through Eurasia, the conquest of Africa, and the diversification of Dipodinae

The evolutionary history of *Jaculus* spp.

Between 5.33 and 5.96 Ma, the Messinian Salinity Crisis: Dessication of the Mediterranean sea → Promoted faunal exchanges between Africa and adjacent regions = Late Miocene (≈5.97 Ma): Diversification of *Jaculus* spp. in Central Asia (and colonisation of Africa)

✓ **Congruent with the fossil record**:
e.g. colonisation of Africa by *Mus* around 6.6 – 4 Ma

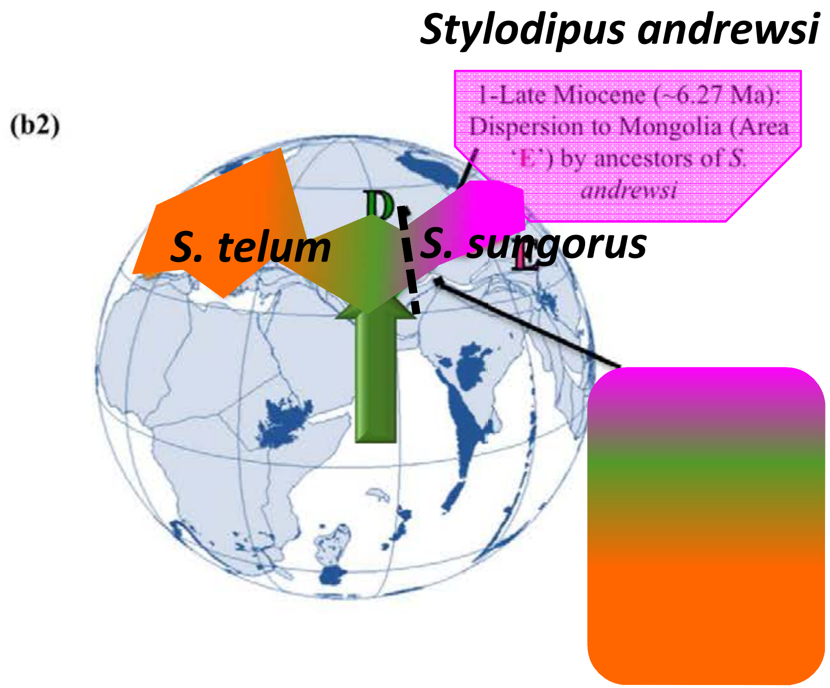


The expansion through Eurasia, the conquest of Africa, and the diversification of Dipodinae

The evolutionary history of *Stylodipus* spp.

Late Miocene (≈8.66 Ma): Diversification of the MRCA of *Stylodipus* and *Dipus* in Central Asia → Coincide with the replacement of woodland-adapted mammals by more-open habitat representatives

Late Miocene: Global cooling promoted grasslands & arid habitats in Europe and Central Asia → Favoured the diversification of these species adapted to open and arid habitats.



Conclusion

- Solved unresolved phylogenetic questions :
  - ✓ Paraphyly of *Allactaga*
  - ✓ Phylogenetic position of Euchoreutinae
- Inference of a sound biogeographical history of the superfamily
  - ✓ Especially thanks to **the exhaustive sampling of Zapodidae and Dipodinae**
    - → Detailed biogeographic scenarios of these two groups
- WHAT MAINLY TRIGGERED THE EVOLUTIONARY HISTORY OF DIPODOIDEA?
  - ✓ **Geological and climatic upheavals of Central Asia**
  - ✓ AND ESPECIALLY **the uplift of the Himalaya-Tibetan plateau**
    - → Induced aridification process
      - → Promoted the development of new habitats (*e.g.* deserts and grasslands)


Thanks for your attention !