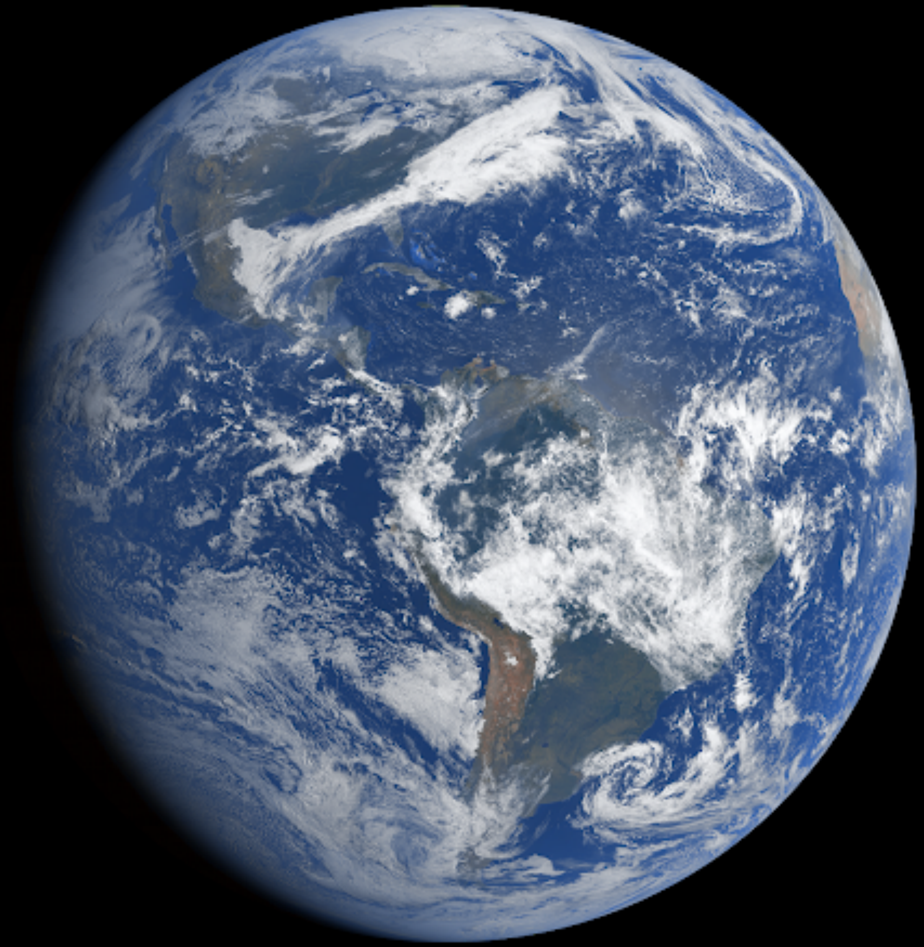
Phylogeography of Arachnids



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Biogeography

Processes responsible for current and past distributions of the biota

Ecological Biogeography – species/intraspecific level
- limiting characteristics of current distribution
- ecological preferences, environmental factors, competition, host distribution….

Historical Biogeography – related taxa, family level
- processes that shaped the distributions into the patterns we observe today
- geological history, climate

…our resulting hypotheses are only as good as our input data and our own biases…

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[particularly in case of Historical Biogeography]

Evolutionary theory + Biogeography - Ch. Darwin (1859), AR Wallace (1869, 1878)

Plate tectonics theory (Continental drift)
formulated 1912 by Wegener not accepted until 1960s

→ **Dispersal** is responsible for today's distribution patters, same geography

X

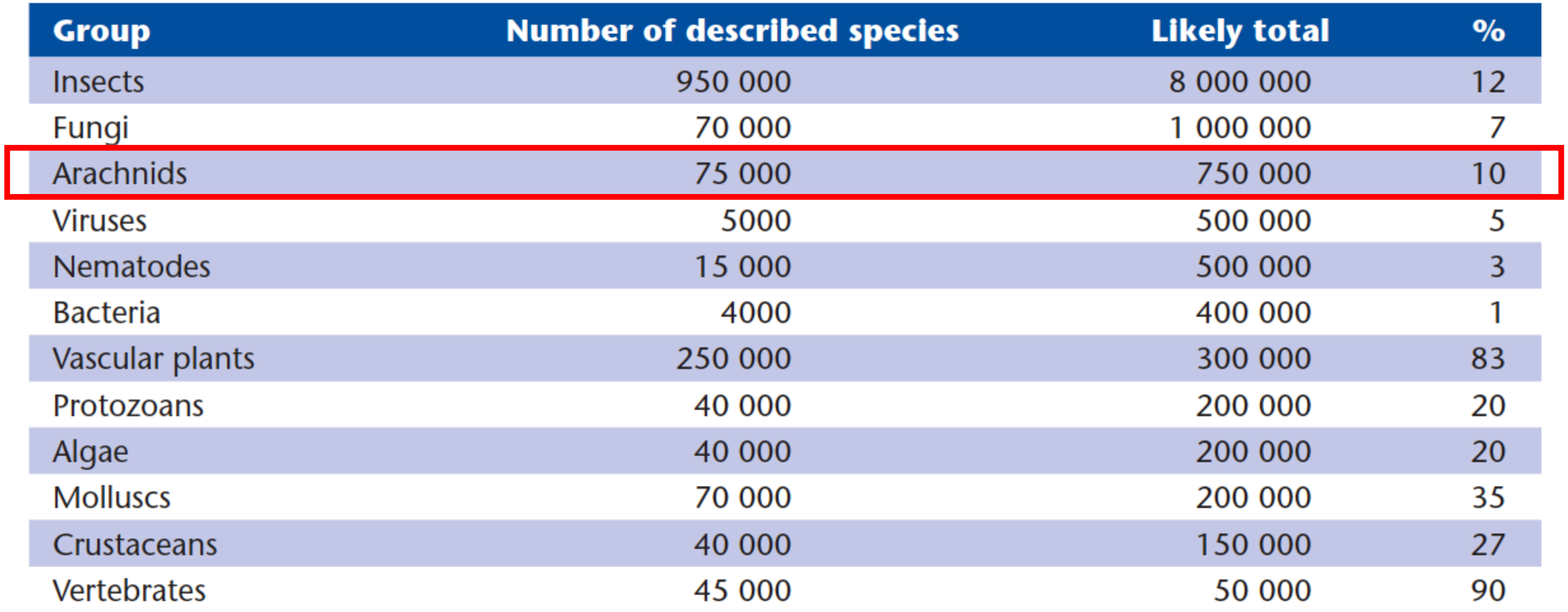
Vicariance – Croizant 1950
The organisms had the same distribution in the past (always!)
- slow steady spread across continuous land, barriers appeared later

What is the contribution of each process?

Fossil record and the lack of thereof
- not very rich in case of Arachnids, extinct lineages - difficult to assign
- modern lineages in amber: Burmese (~100 Ma), Baltic Amber (~44 Ma) Dominican Amber (~30 Ma)
- more resources: https://wsc.nmbe.ch/resources/fossils/Fossils20.5.pdf

…our resulting hypotheses are only as good as our input data and our own biases…
[both Ecological and Historical Biogeography]

Taxonomy/understanding of Biodiversity
- what is a species, how many species there are, how are they related?



Group	Number of described species	Likely total	%
Insects	950 000	8 000 000	12
Fungi	70 000	1 000 000	7
Arachnids	75 000	750 000	10
Viruses	5000	500 000	5
Nematodes	15 000	500 000	3
Bacteria	4000	400 000	1
Vascular plants	250 000	300 000	83
Protozoans	40 000	200 000	20
Algae	40 000	200 000	20
Molluscs	70 000	200 000	35
Crustaceans	40 000	150 000	27
Vertebrates	45 000	50 000	90

Cox *et al* 2010

Resources/Interest and the lack of thereof

Phylogeography

Phylogenetics + Biogeography (Avise 2000)

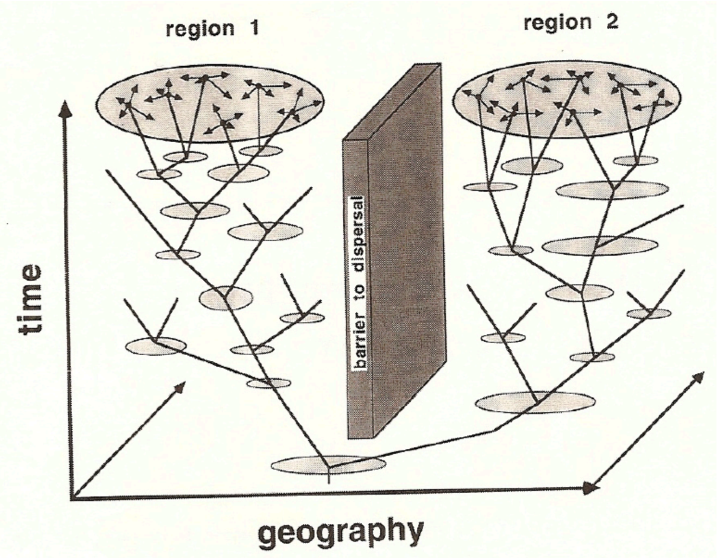
Geographic distribution of genetic lineages (traditionally - closely related)

The question remains:

- Which processes shaped the current and past spatial distributions of these lineages?

Implementation of molecular methods – new perspective

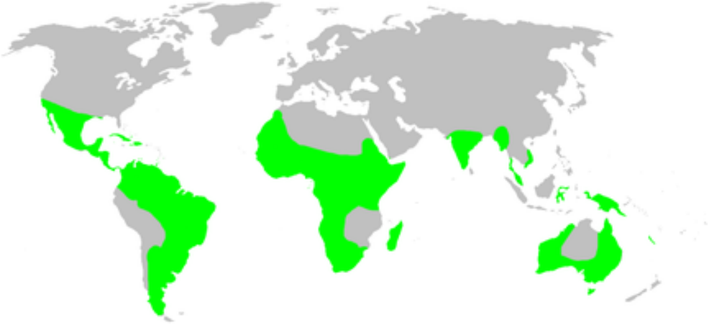
- geographic structure in the populations
    - geographic history, dispersal routes & barriers
    - concordant patterns among different species
    - conservation purposes
- potential existence of cryptic species
    - taxonomy
- molecular dating



Avise 2000

Dispersal? Introduction? Vicariance? Extinction?

Archaeidae



Deinopidae

Salticidae

usually a combination of more than one factor…

Dispersal in Arachnids


Camargo et al 2015

The capability to overcome barriers differs significantly

Key role in colonizing new habitats

- weak population structure in highly mobile groups
- deep population structuring in sedentary groups


Jaeger 2014

Passive dispersal:

Phoresy: pseudoscorpions, mites, *Attacobius attarum*

Rafting – short/long distance dispersal

Accidental introduction: synanthropes in advantage

Airborne/wind: mites

Host mediated - ticks

Active dispersal:

Ballooning: spiders

Walking

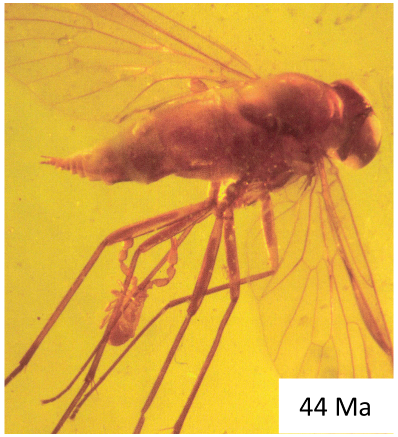
Sailing

Tumbling - *Cebrennus rechenbergi*


Hayashi et al 2015

Phoresy

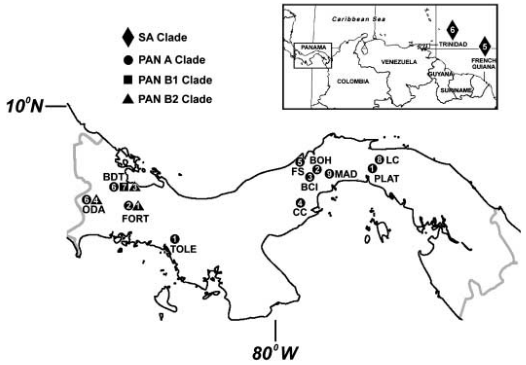
Attaching of non-vagile individual to a different species “carrier”

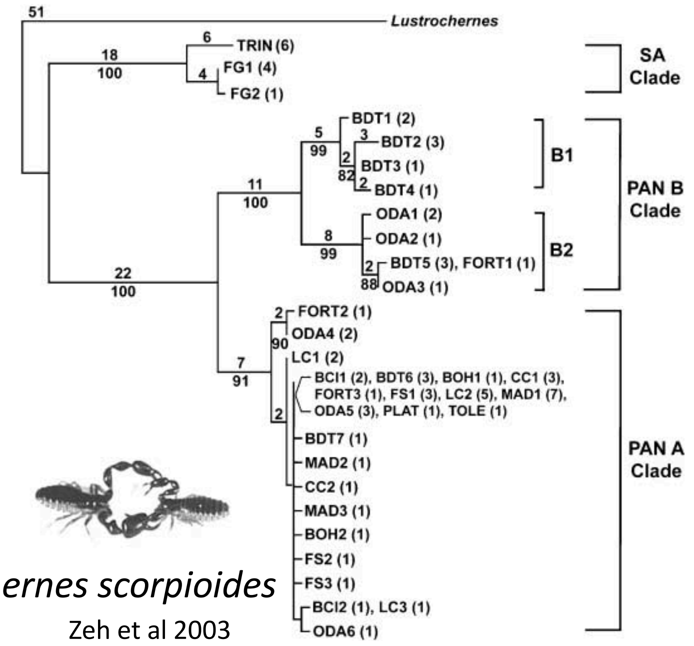


Dunlop & Penney 2012

Colonization of temporary habitats

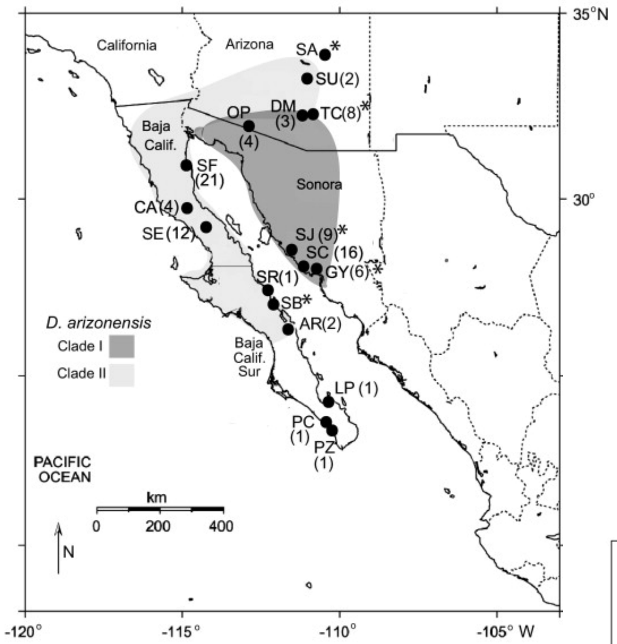
Little information about the genetic structure of phoretic species

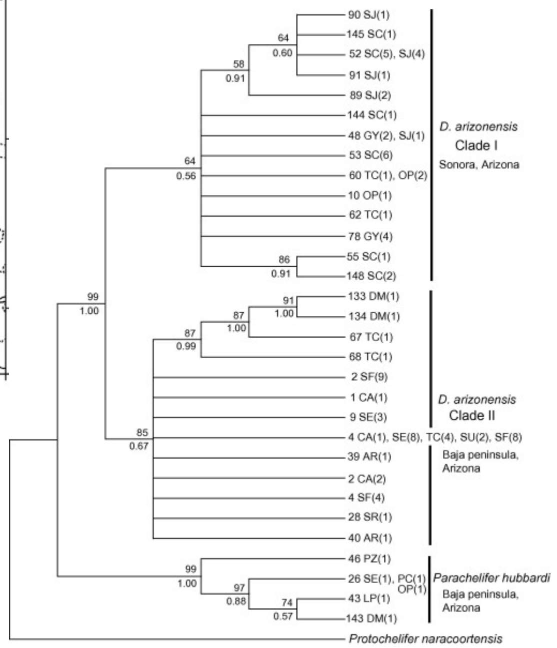




Cordylochernes scorpioides

Zeh et al 2003



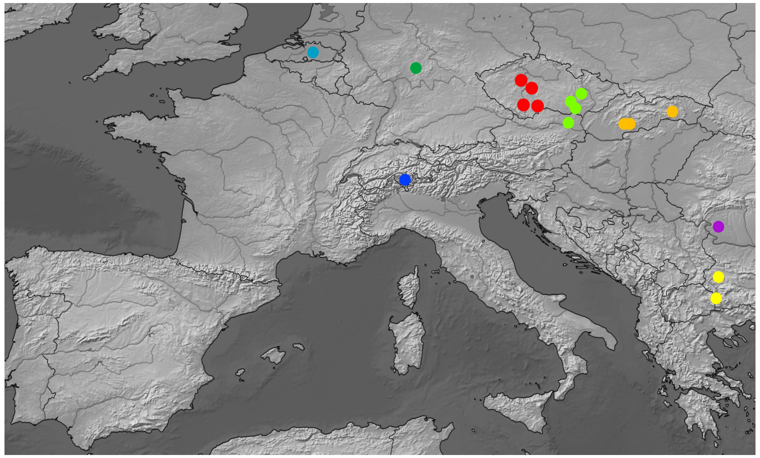


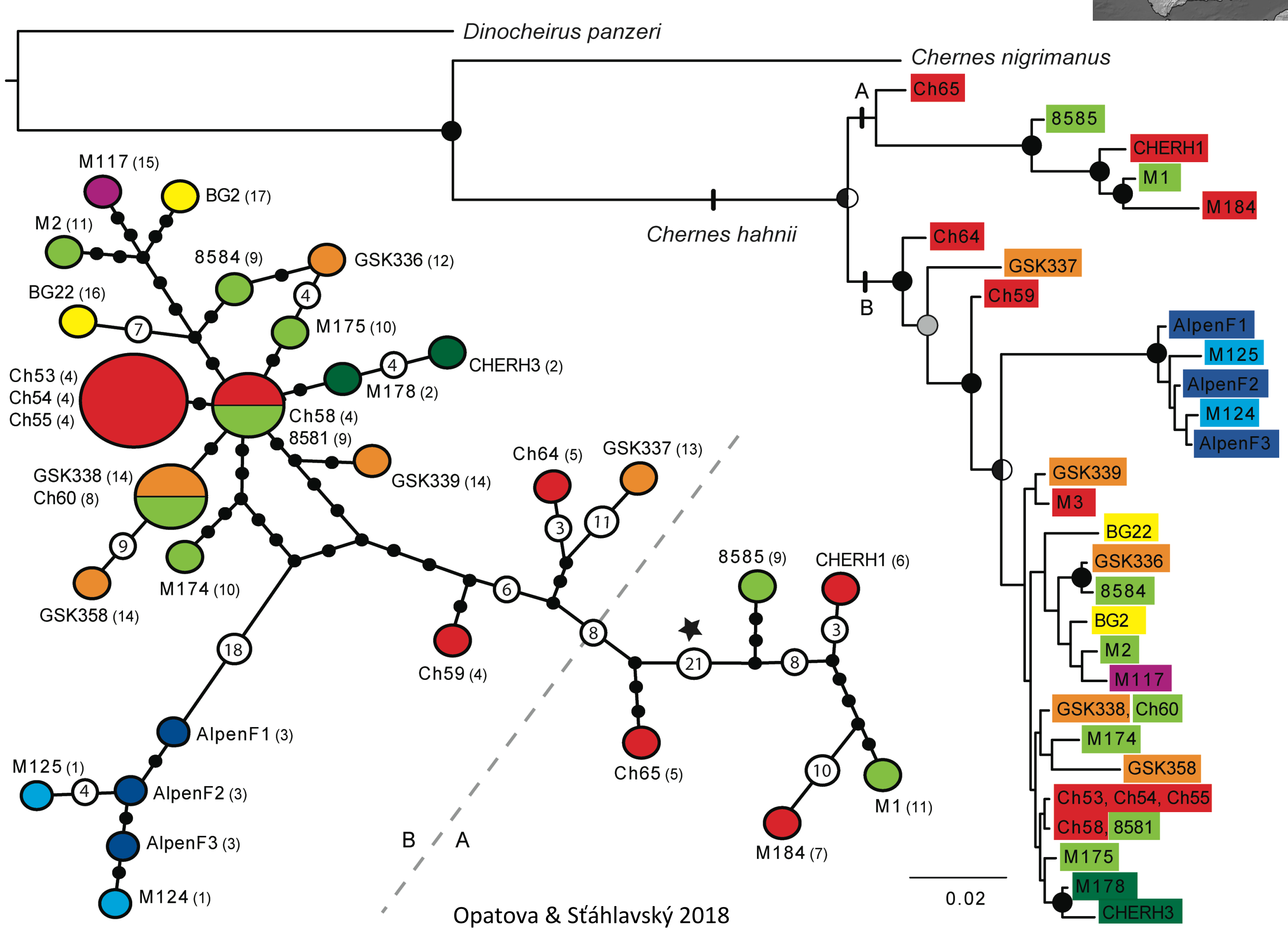
Dinocheirus arizonensis

Pfeiler et al 2009

Chernes hahnii

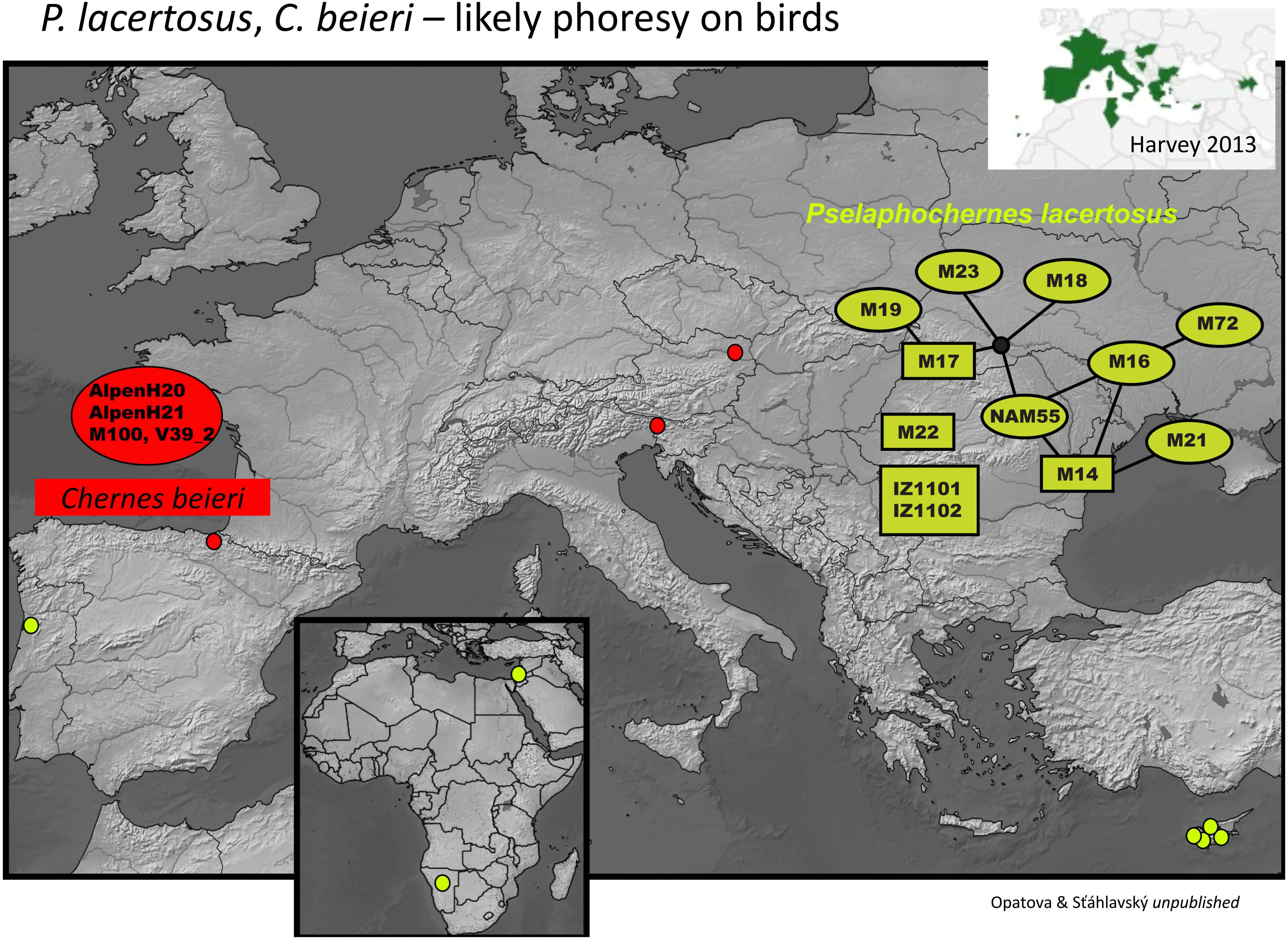
No geographic structure across Central Europe





Opatova & Šťáhlavský 2018

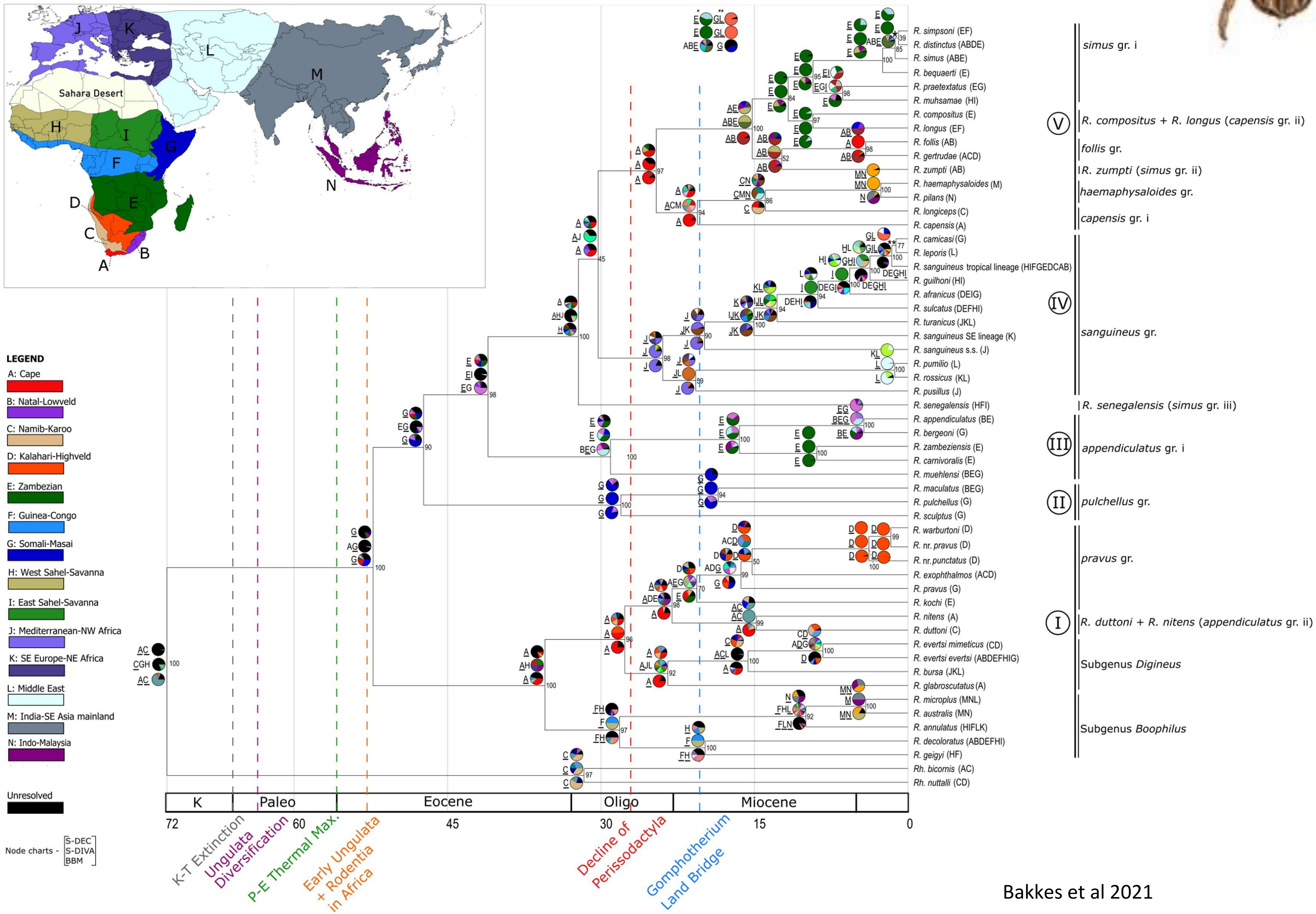
P. lacertosus, C. beieri – likely phoresy on birds



Harvey 2013

Opatova & Šťáhlavský *unpublished*

Host mediated dispersal and radiation - *Rhipicephalus* ticks



Bakkes et al 2021

Host mediated dispersal and radiation - *Rhipicephalus* ticks

Host-enabled dispersal events to new environments

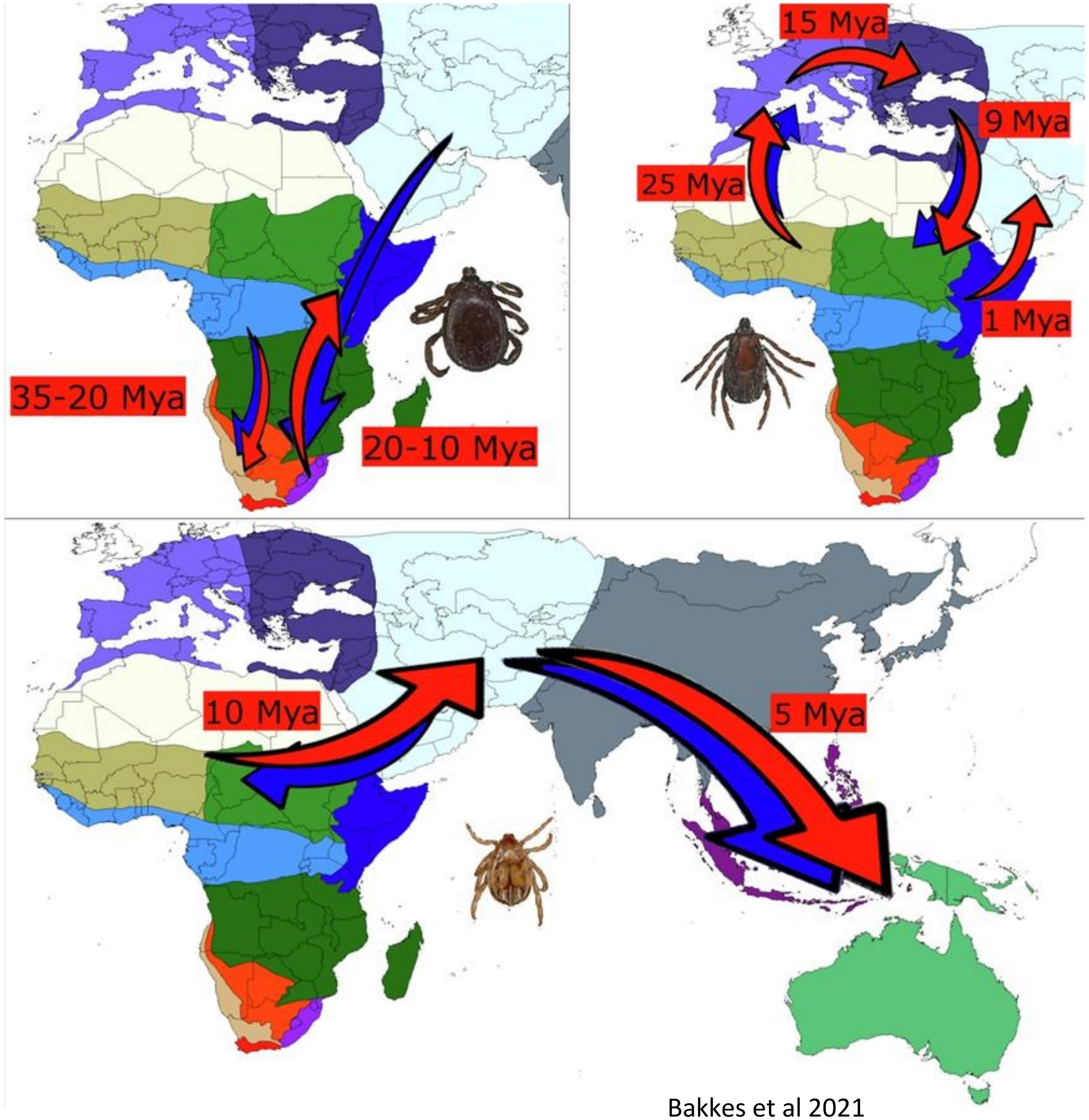
followed by local adaptations

larvae on large and mobile hosts

→ larger ranges, slower rates

larvae on small and less mobile hosts

→ smaller ranges, faster rates



Bakkes et al 2021

Ballooning aerial dispersal

Long/ short distance dispersal

juveniles of large species/ adults of small species

very common in Araneomorphae
- may differ within a family

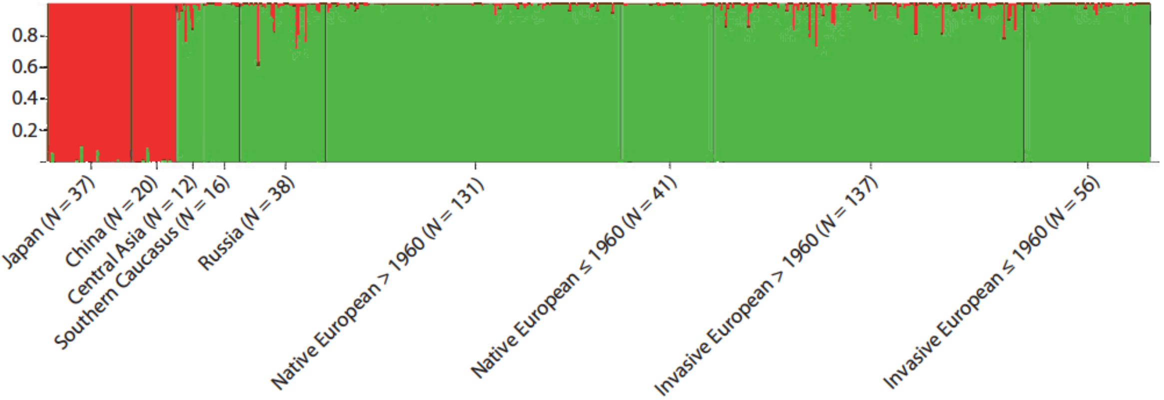
uncommon in Mygalomorphae
- not as effective

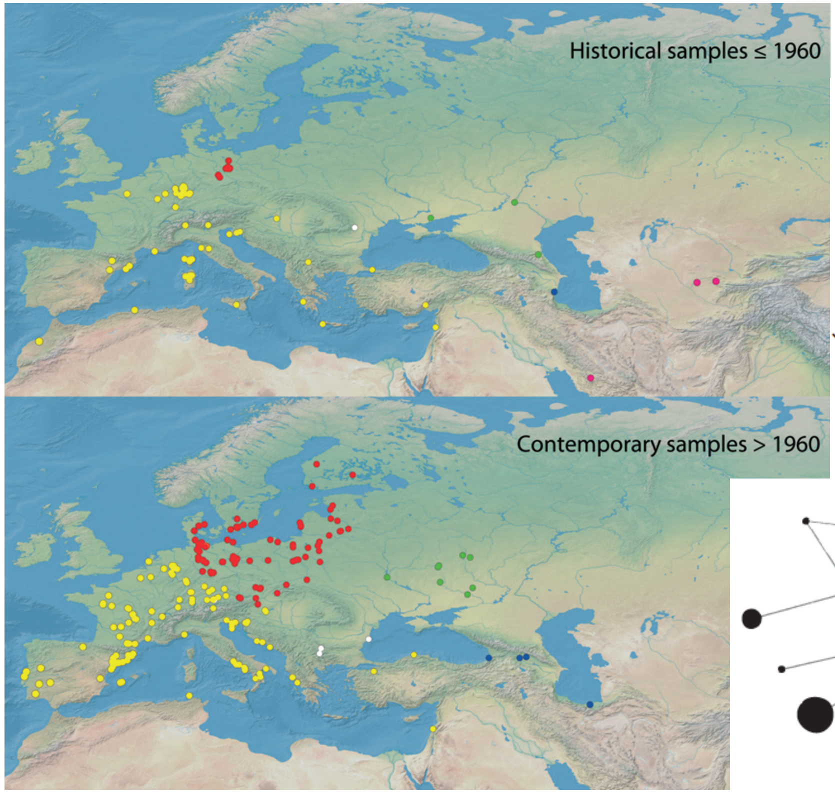
In all cases the ballooning individuals must land in an area with favorable conditions
or be preadapted to novel conditions

Argiope bruennichi – range expansion

Krehenwinkel & Tautz (2013), Mol Ecol
Krehenwinkel et al (2015), Glob Change biol

SNP

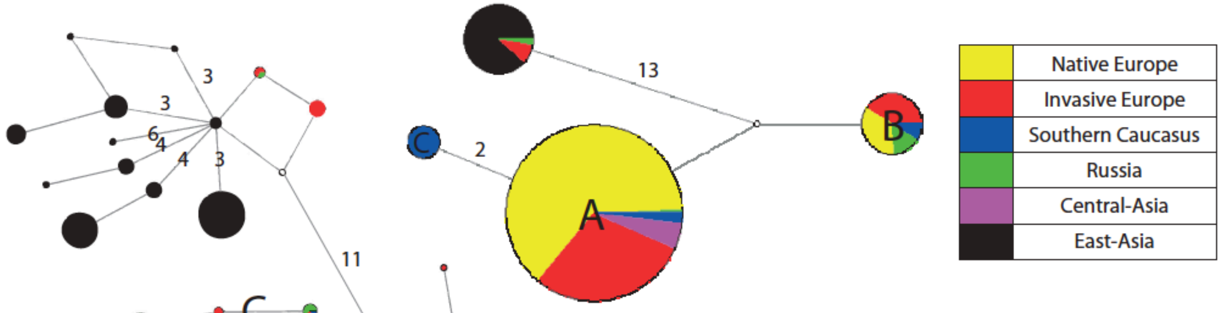


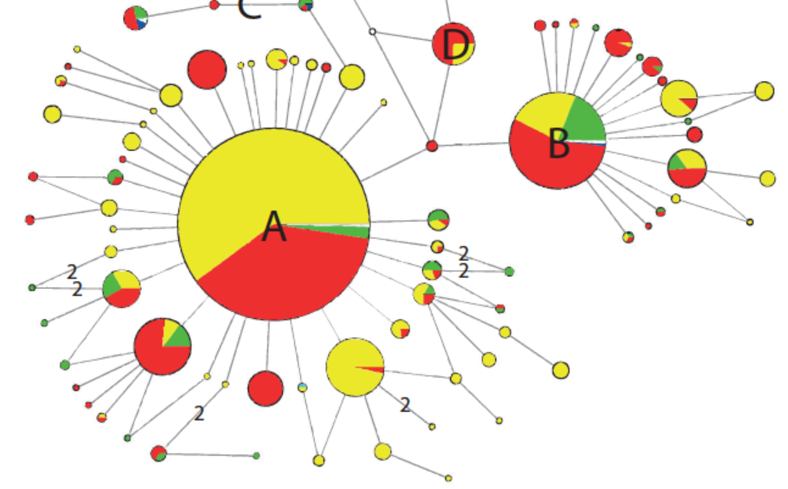


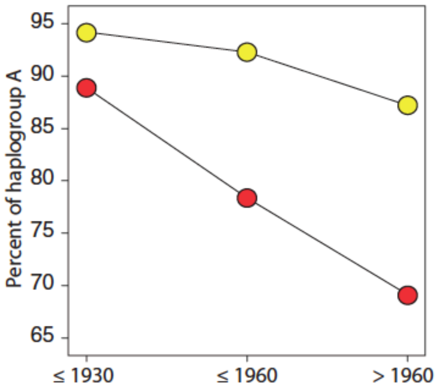
Mt diversity
- higher in invasive populations

Body size
- smaller in invasive populations

Cold tolerance
- differences in gene expression

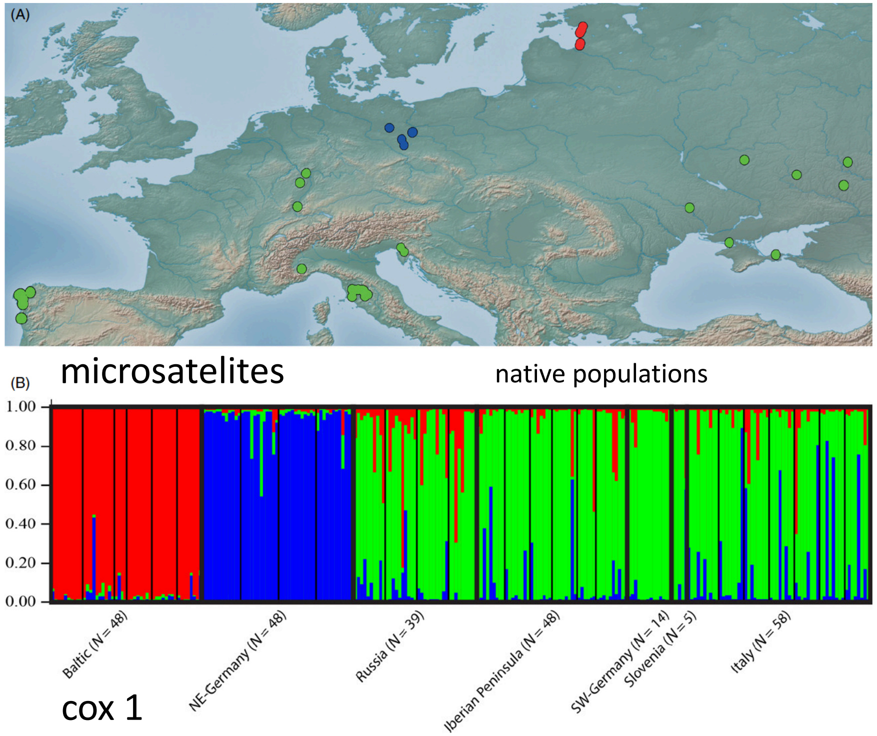






Cheiracanthium punctorium – range expansion

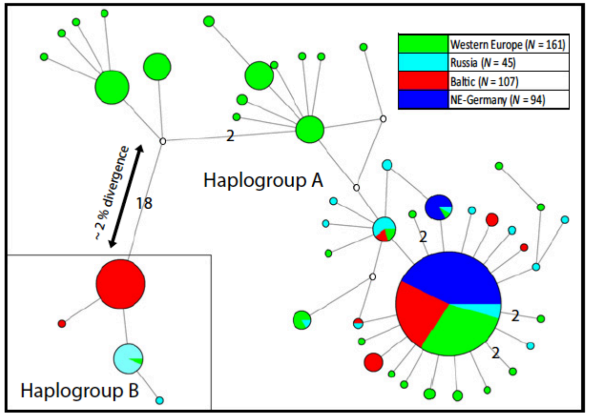
Initial environmental change triggered preadaptation
smaller body size in expanding popuations

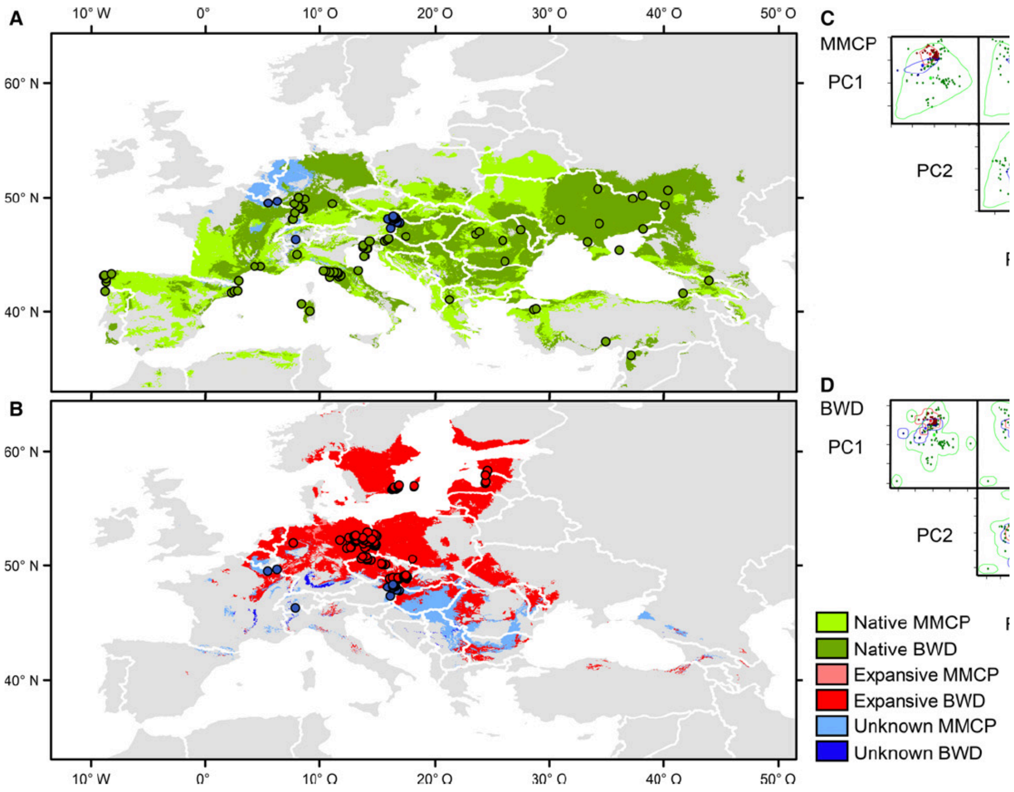


microsatelites

native populations

cox 1

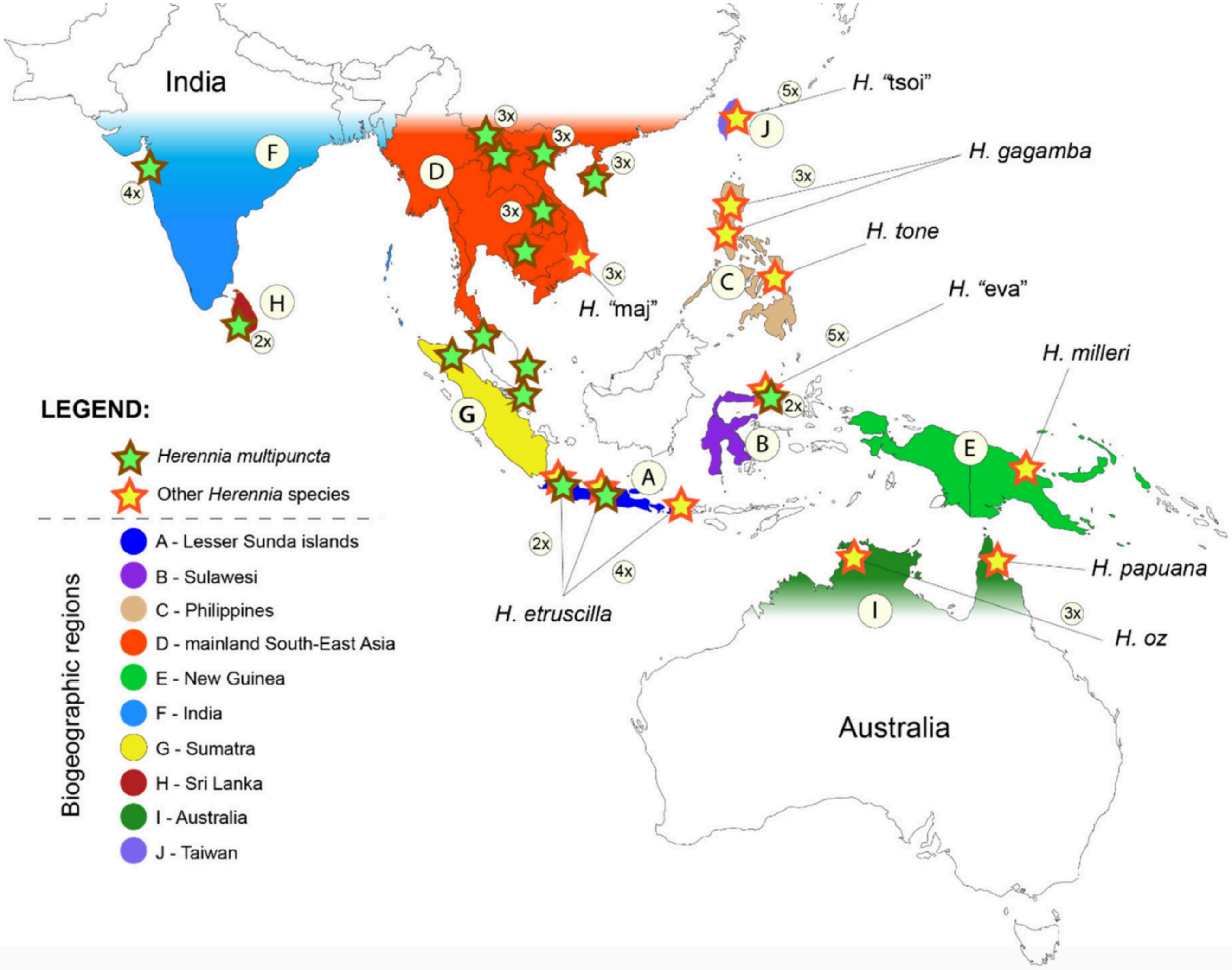




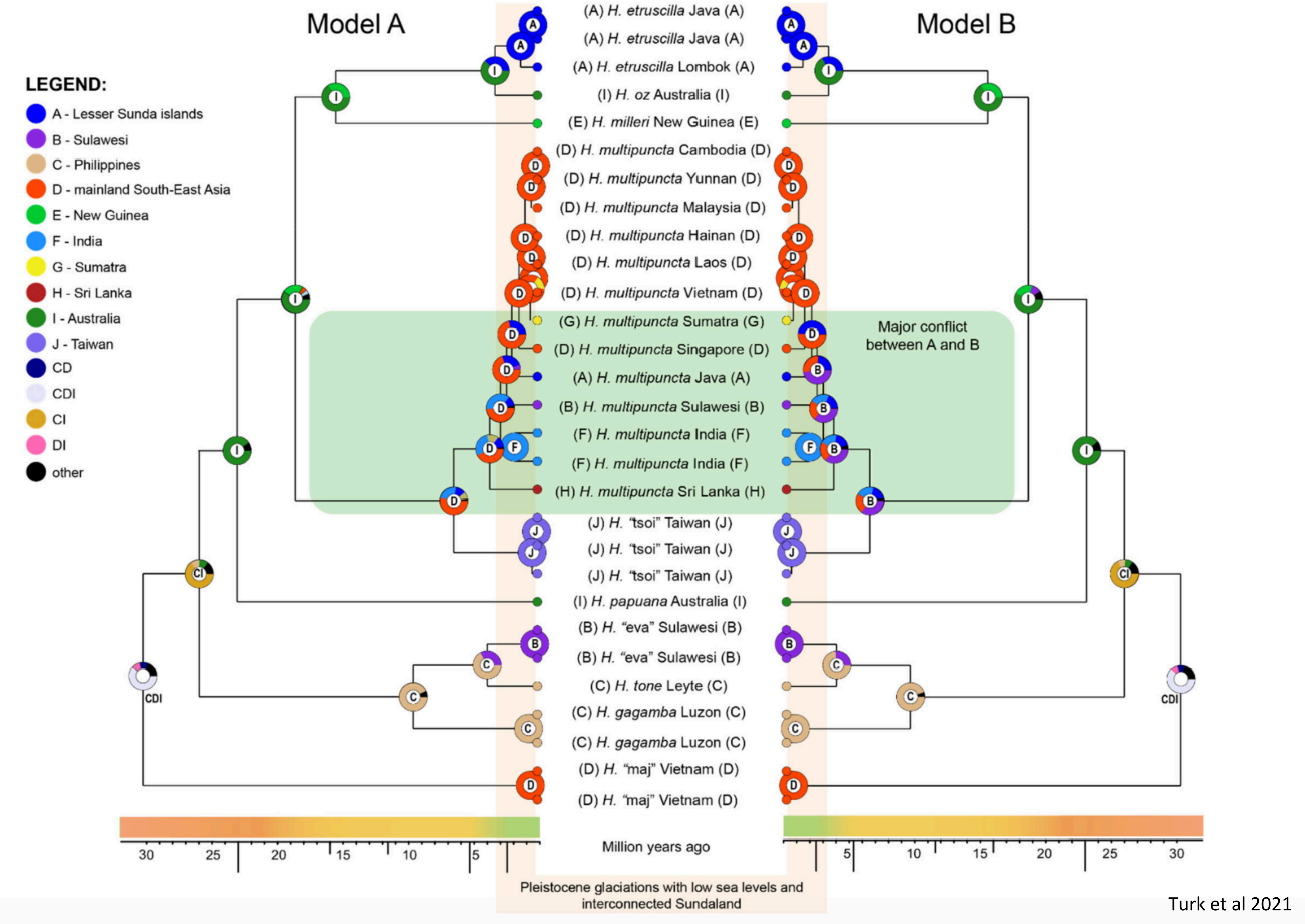
Krehenwinkel et al (2016)

Herennia (Nephilinae) – area expansion or introduction?

Coin spiders presumably do not balloon
Is the Asian distribution range of *H. multipuncta* natural or human-mediated?



Turk et al 2021



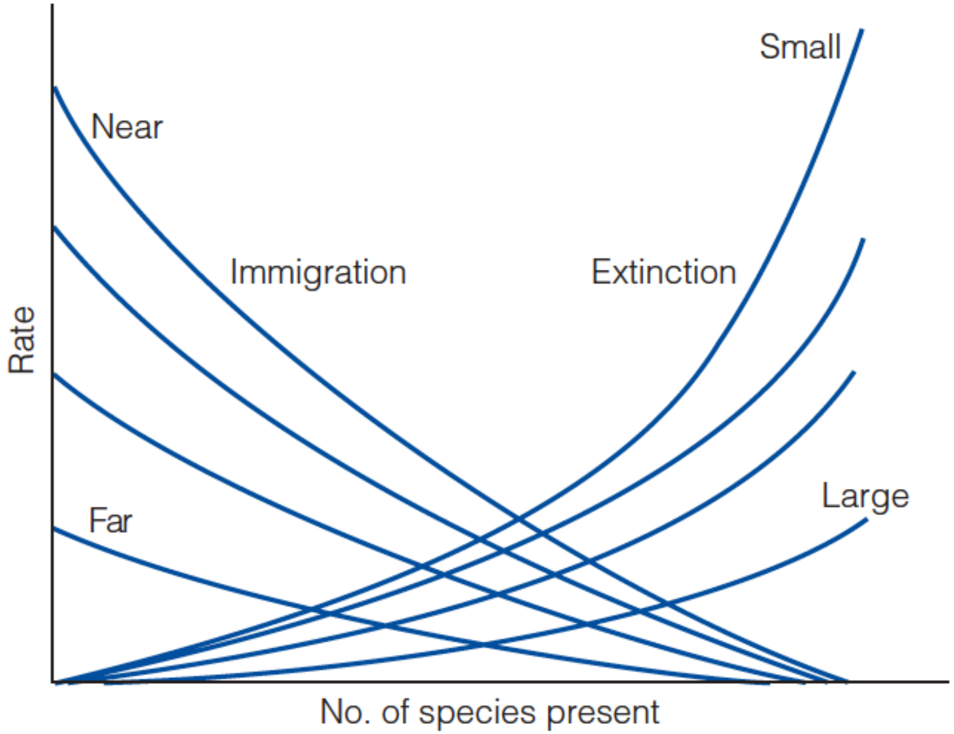
Turk et al 2021

Divergences date back to Pleistocene

Did *Herennia* regained ballooning capability?

Island biogeography dispersal vs. vicariance

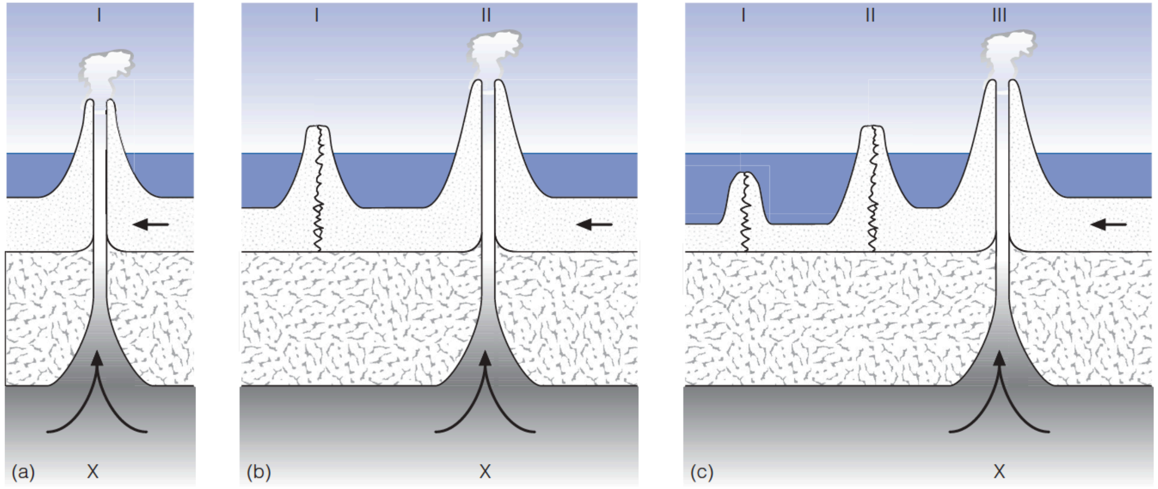
carrying capacity = turnover equilibrium



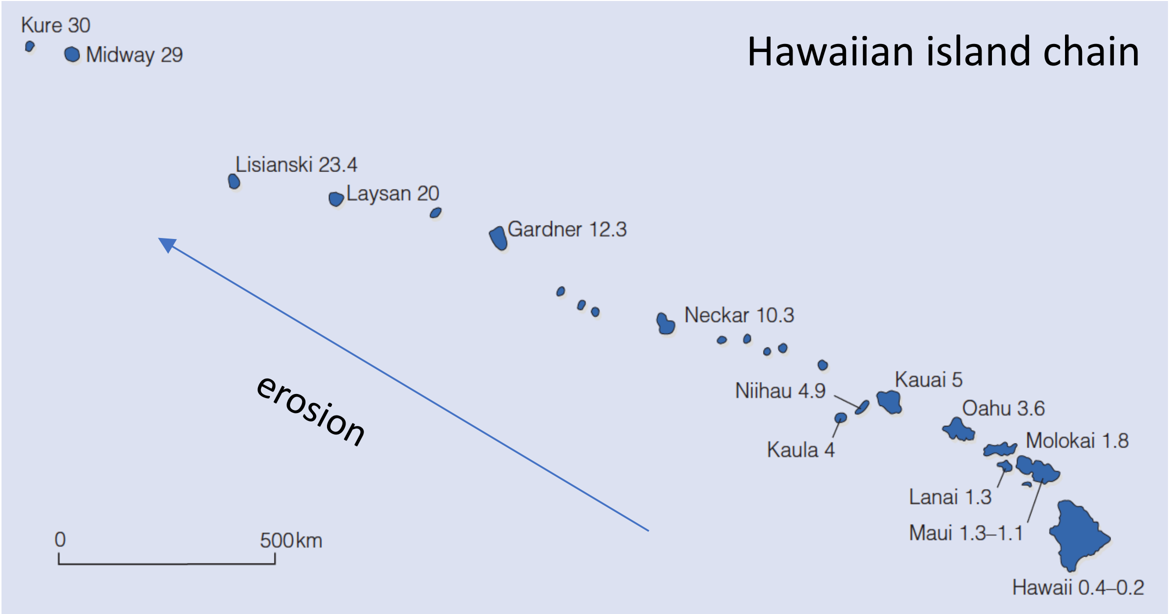
Cox *et al* 2010

Continental islands – split from a larger landmass; vicariance* + dispersal
Oceanic islands – volcanic *de novo* origin; dispersal

Oceanic islands “biodiversity and evolutionary lab”



volcanic hotspot



Hawaiian island chain

erosion

Successive colonization

abundancy of available niches

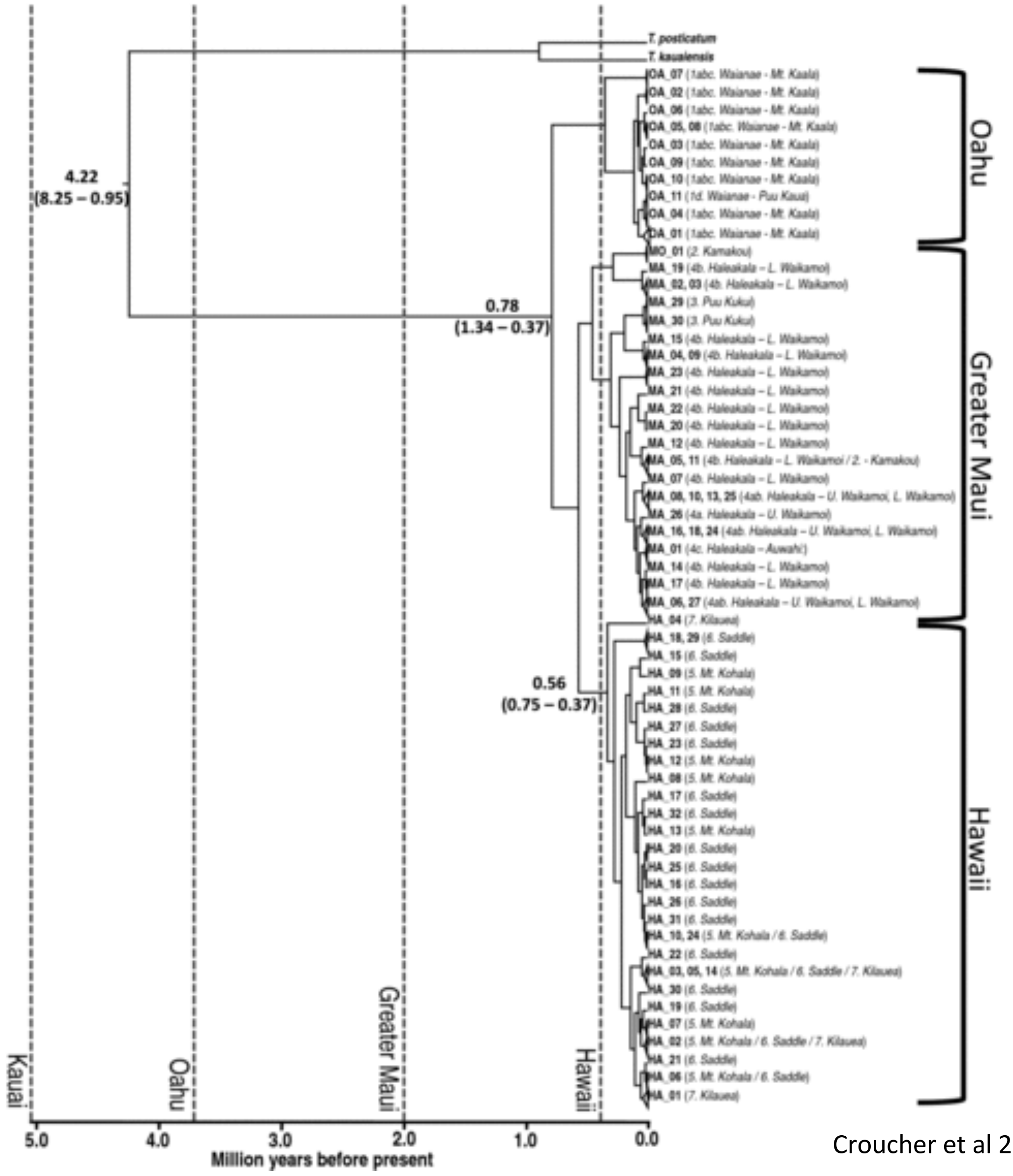
→ adaptive radiation

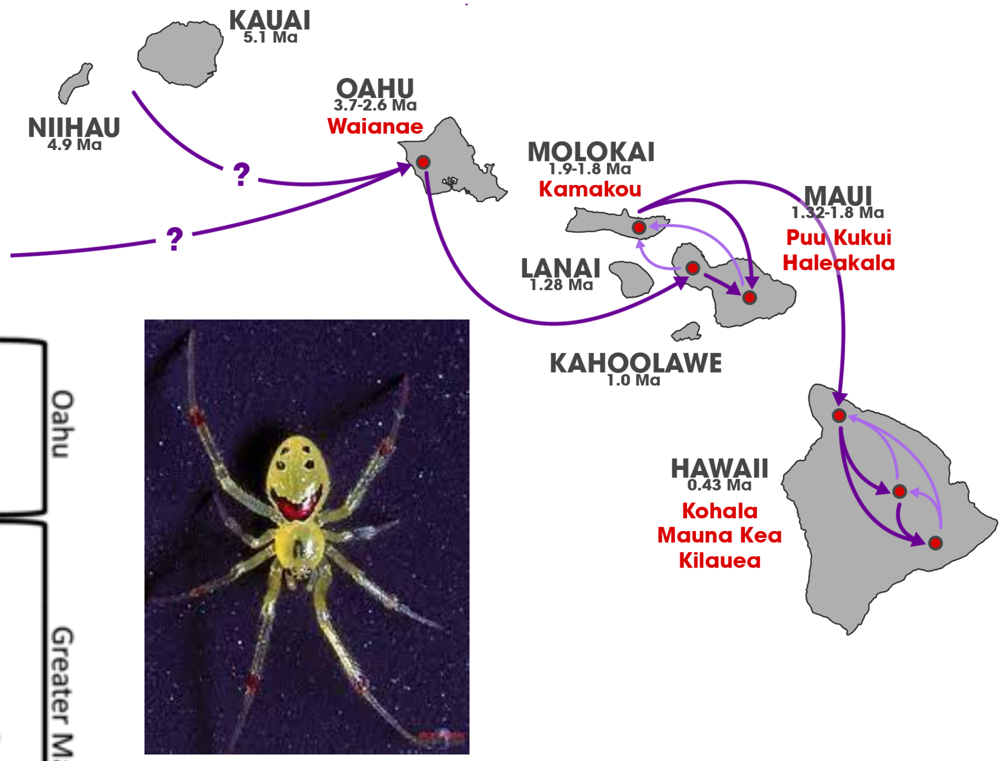
colonization via

- ballooning
- rafting
- anthropogenic introduction

Cox *et al* 2010

Hawaii *Theridion grallator*





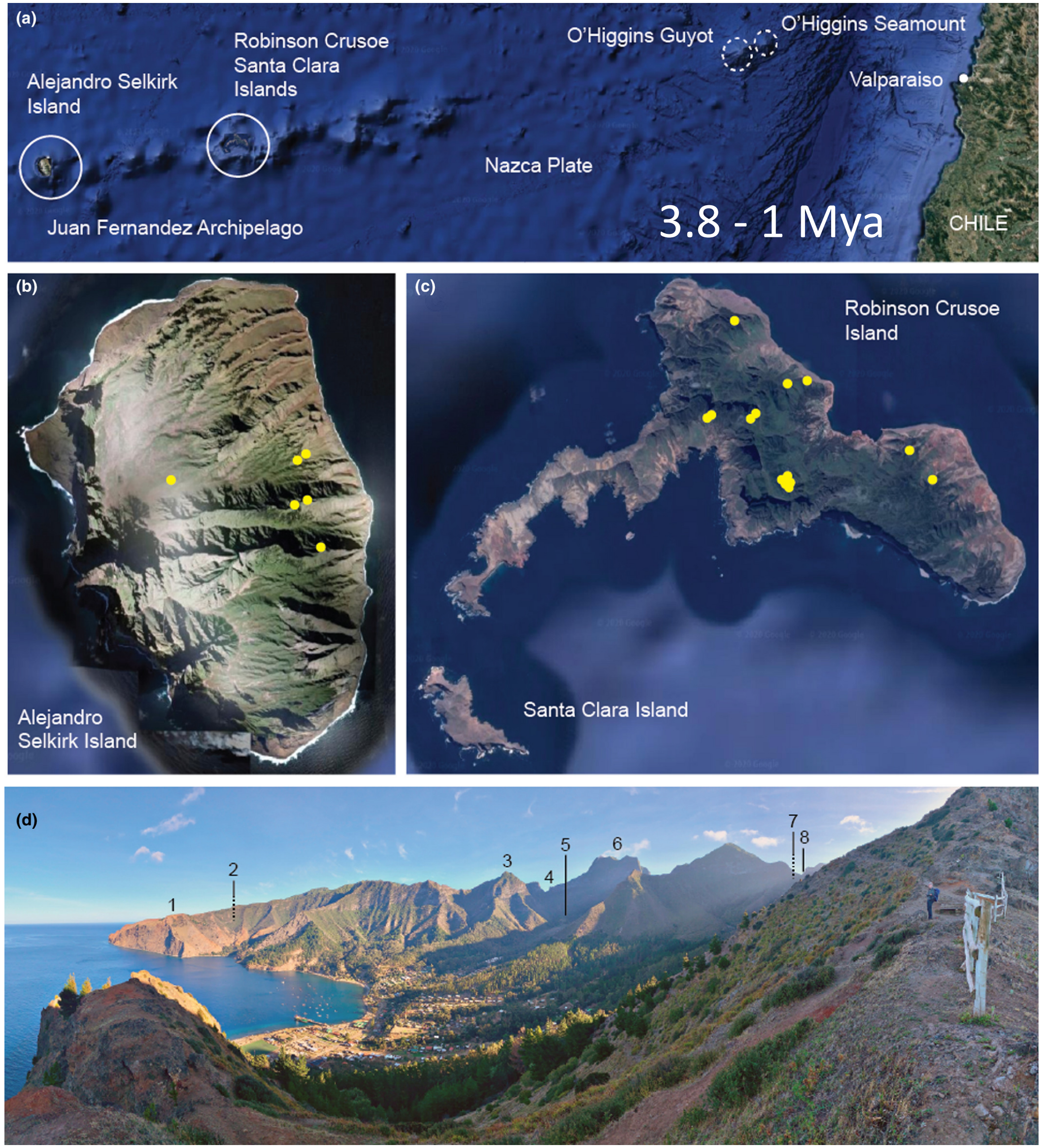
Distinct monophyletic clades
– currently little taxa exchange

Younger island colonized from older ones
– "progression rule"

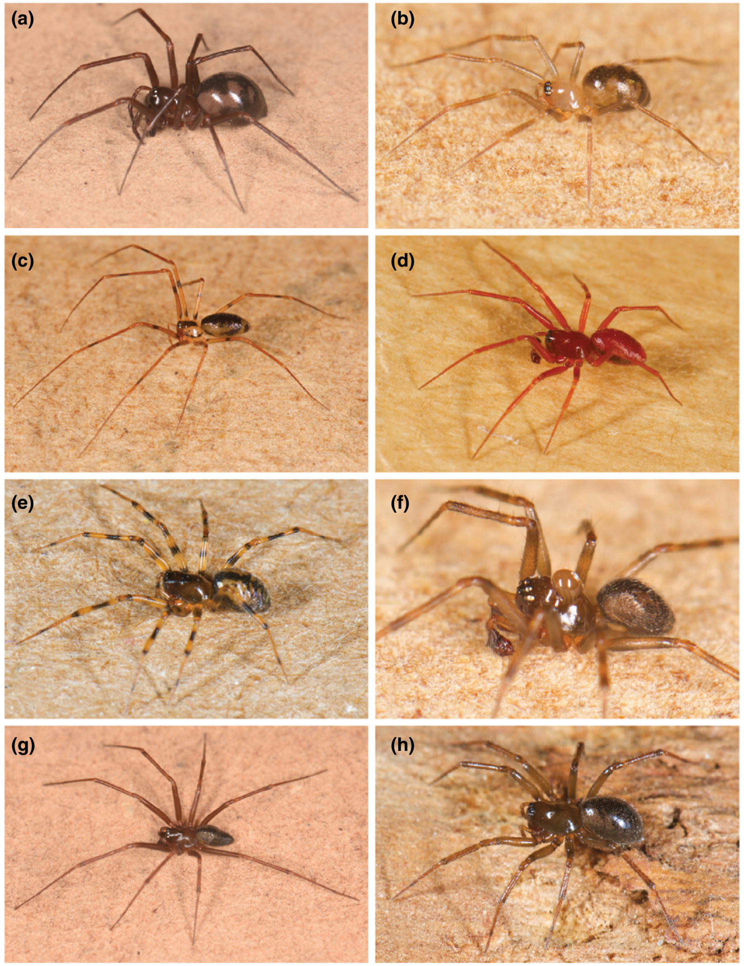
Rapid colonization from Oahu

Croucher et al 2012

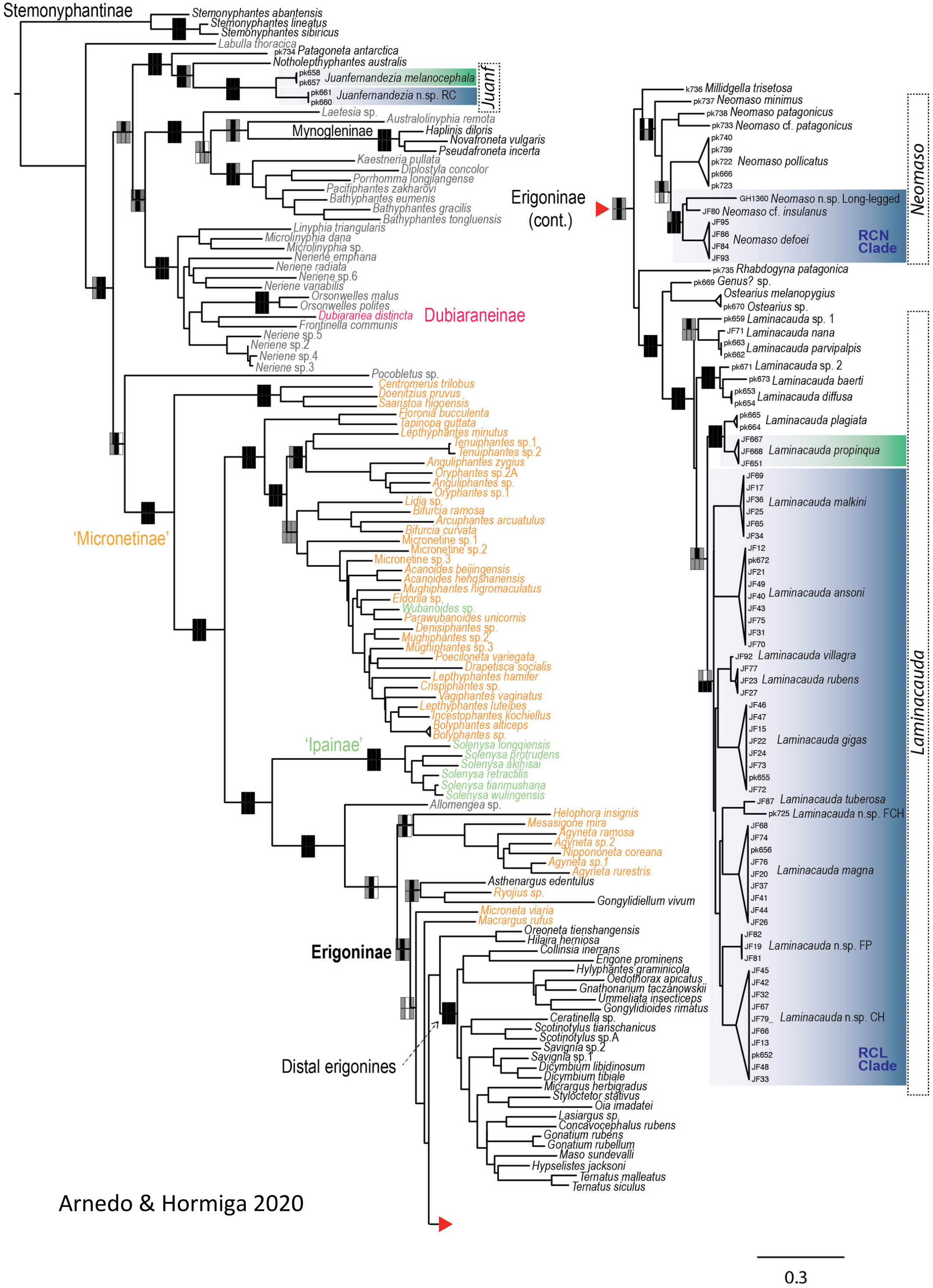
Juan Fernandez *Linyphiidae*



50 native sp. of spiders, ~70 % endemic
40 % Linyphiidae



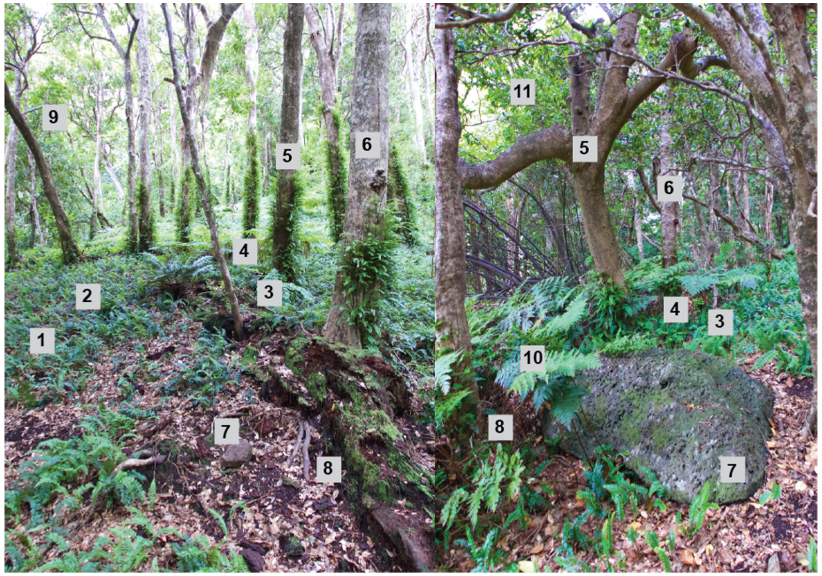
Arnedo & Hormiga 2020



Arnedo & Hormiga 2020

5 independent colonization events (*Laminacauda* 2x)

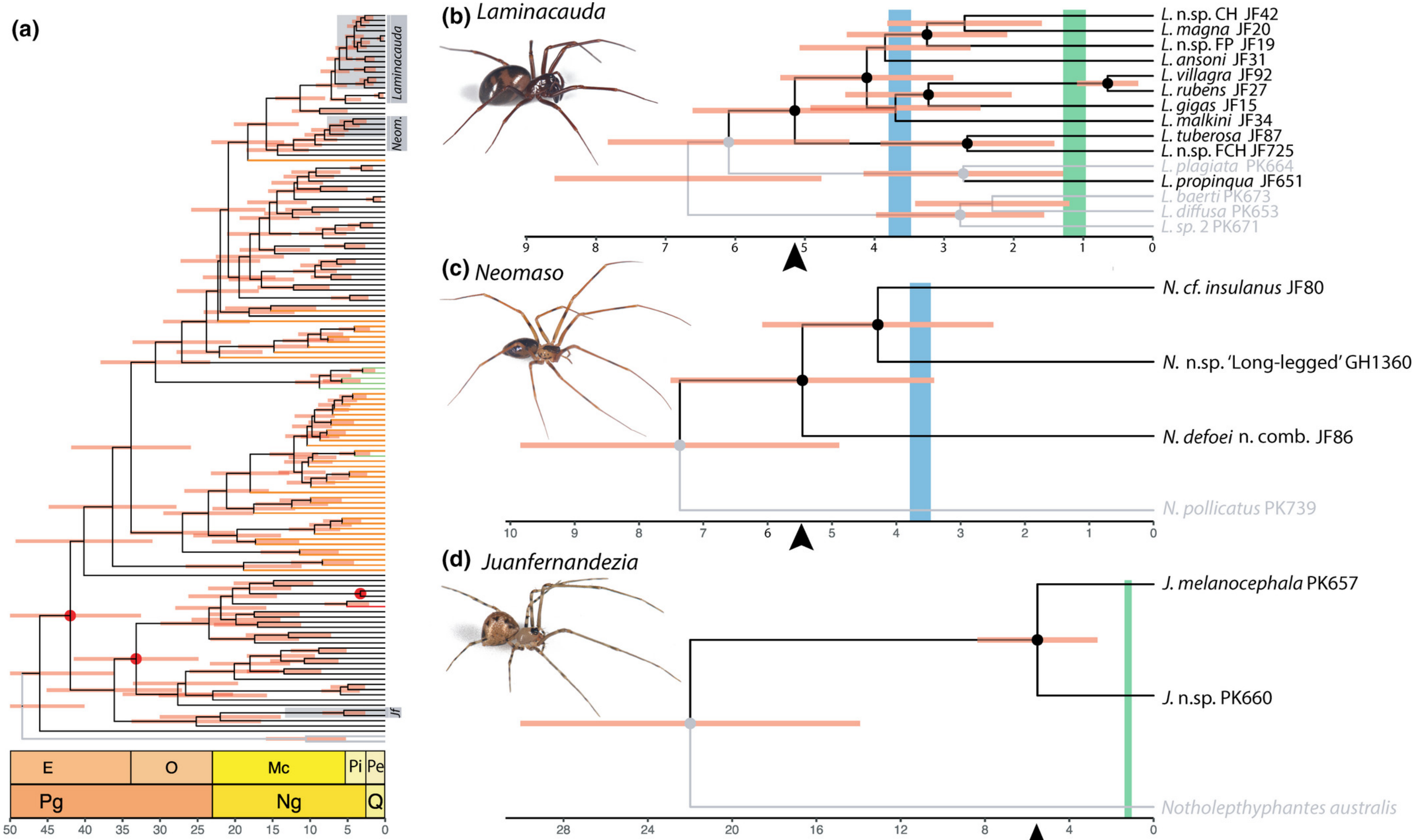
→ adaptive radiation



Laminacauda spp.: 1 = *L.* n. sp. CH; 2 = *L.* n. sp. CO; 3 = *L.* n. sp. FC; 4 = *L.* n. sp. FP; 5 = *L. ansoni* 6 = *L. rubens*; 7 = *L. gigas*; 8 = *L. magna*; 9 = *L. malkini*; 10 = *L. tuberosa*; 11 = *L. villagra*.

- spatial distribution
- foraging strategy

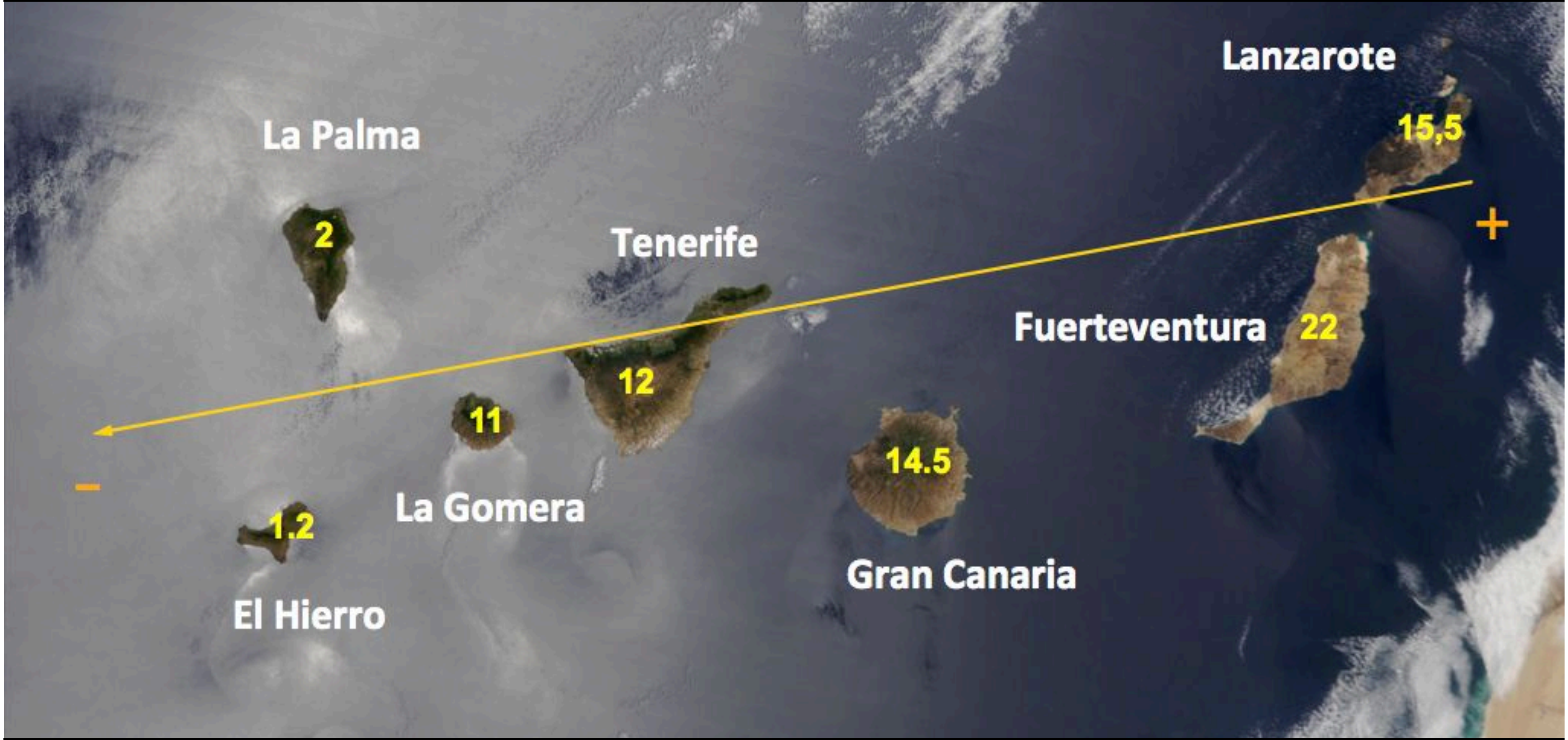
“Old taxa on young islands dilemma”



Arnedo & Hormiga 2020

Fossil and mt rate calibration in agreement

Canary Islands



high levels of endemic organisms

Canary Islands *Dysdera*

oniscophagous

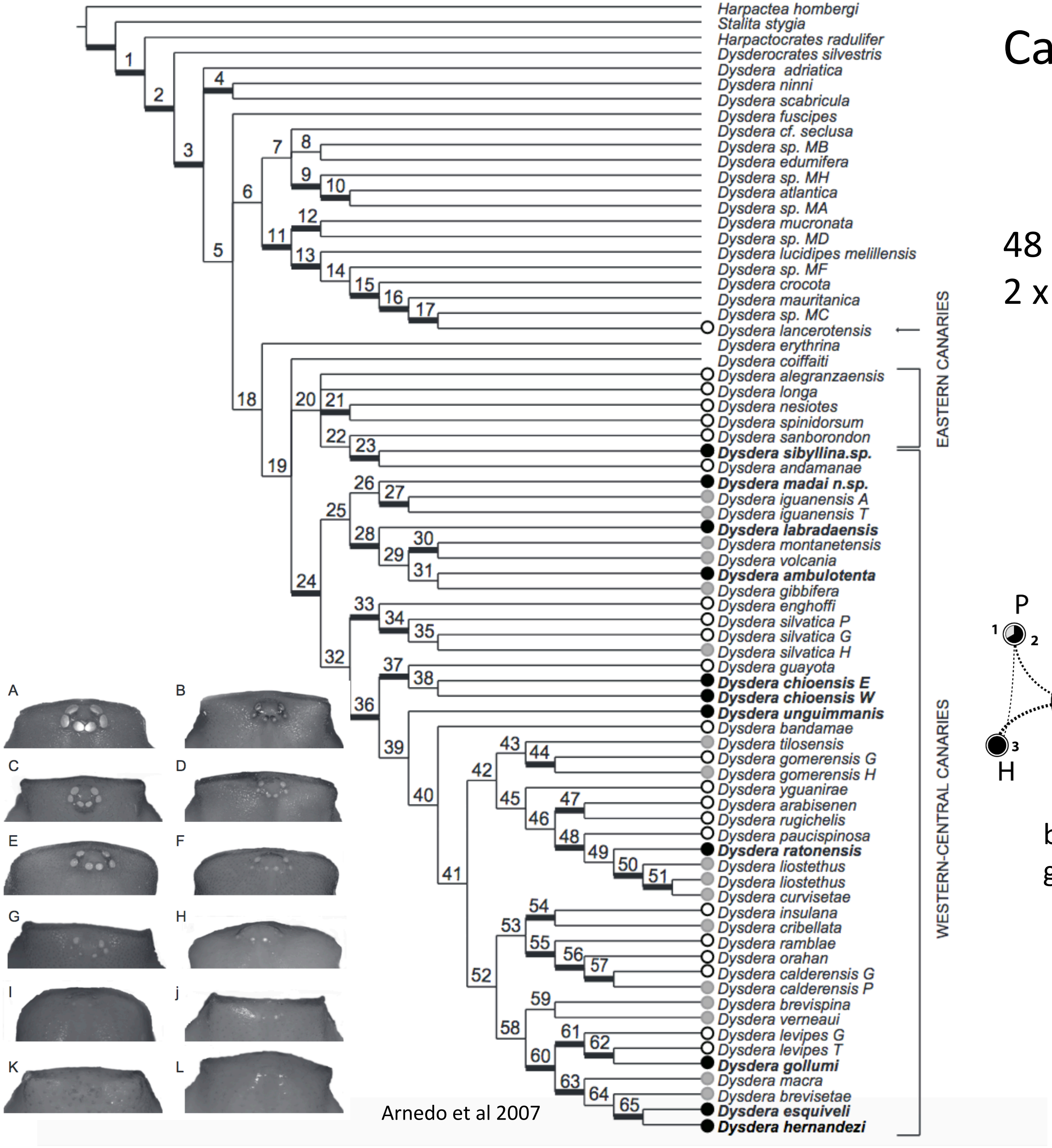
sedentary

dispersal by rafting

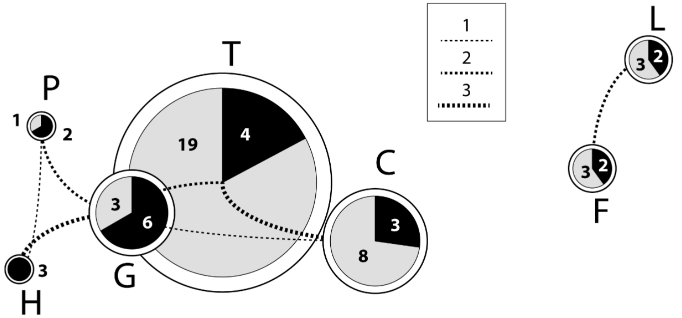
Macías-Hernández et al 2016

Canary Islands *Dysdera*

48 endemic species
2 x colonization, 1 x radiation

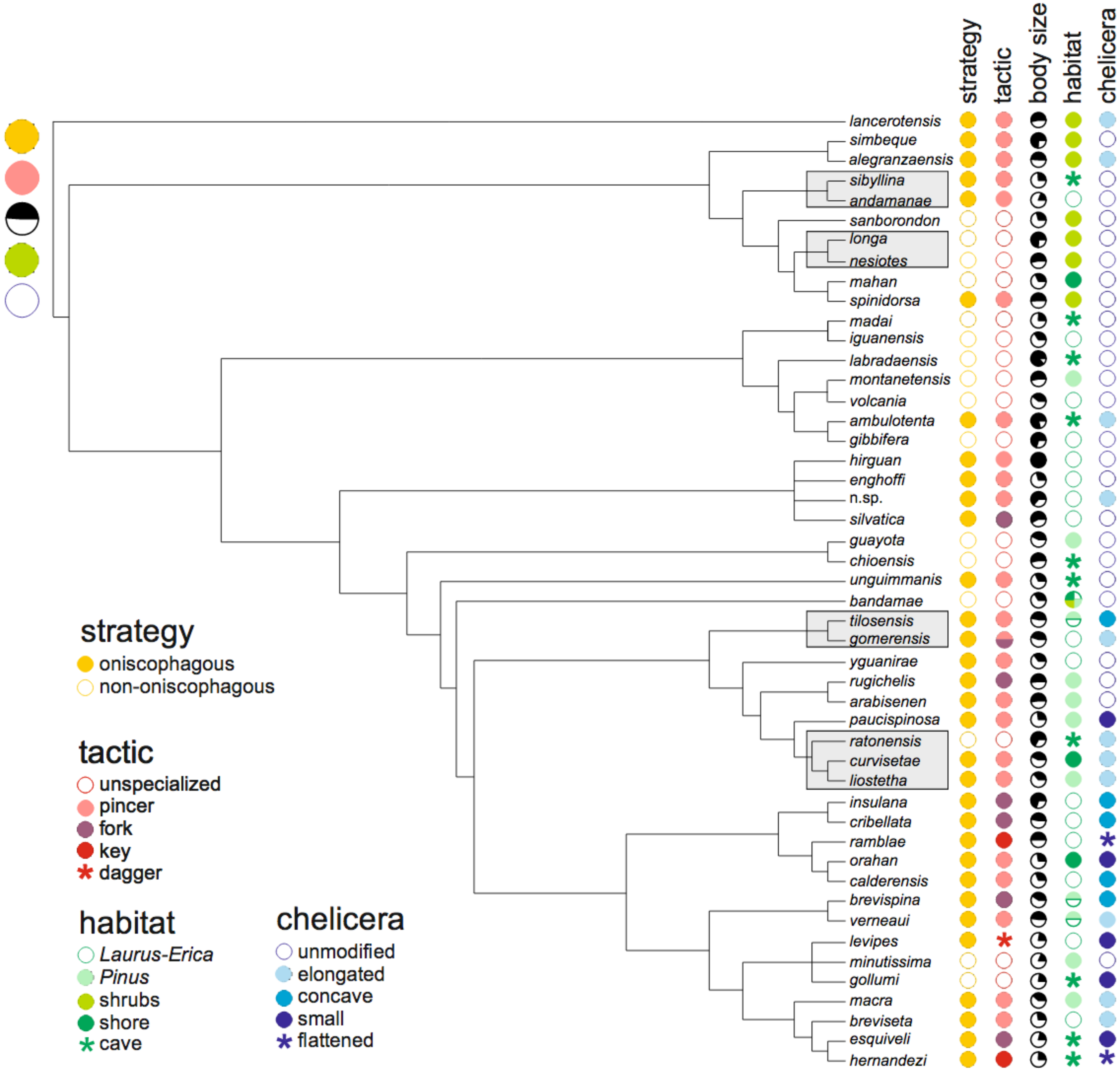


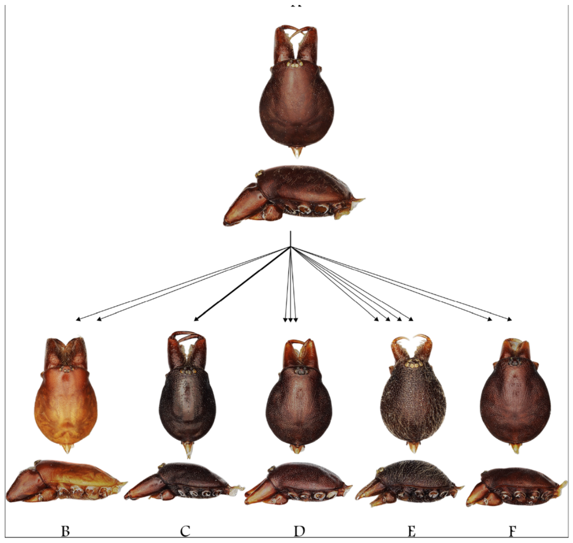
Arnedo et al 2007



black – shared
grey - endemic

Macías-Hernández et al 2016





Co-occurring species

- differences related to prey capture
- different microhabitats

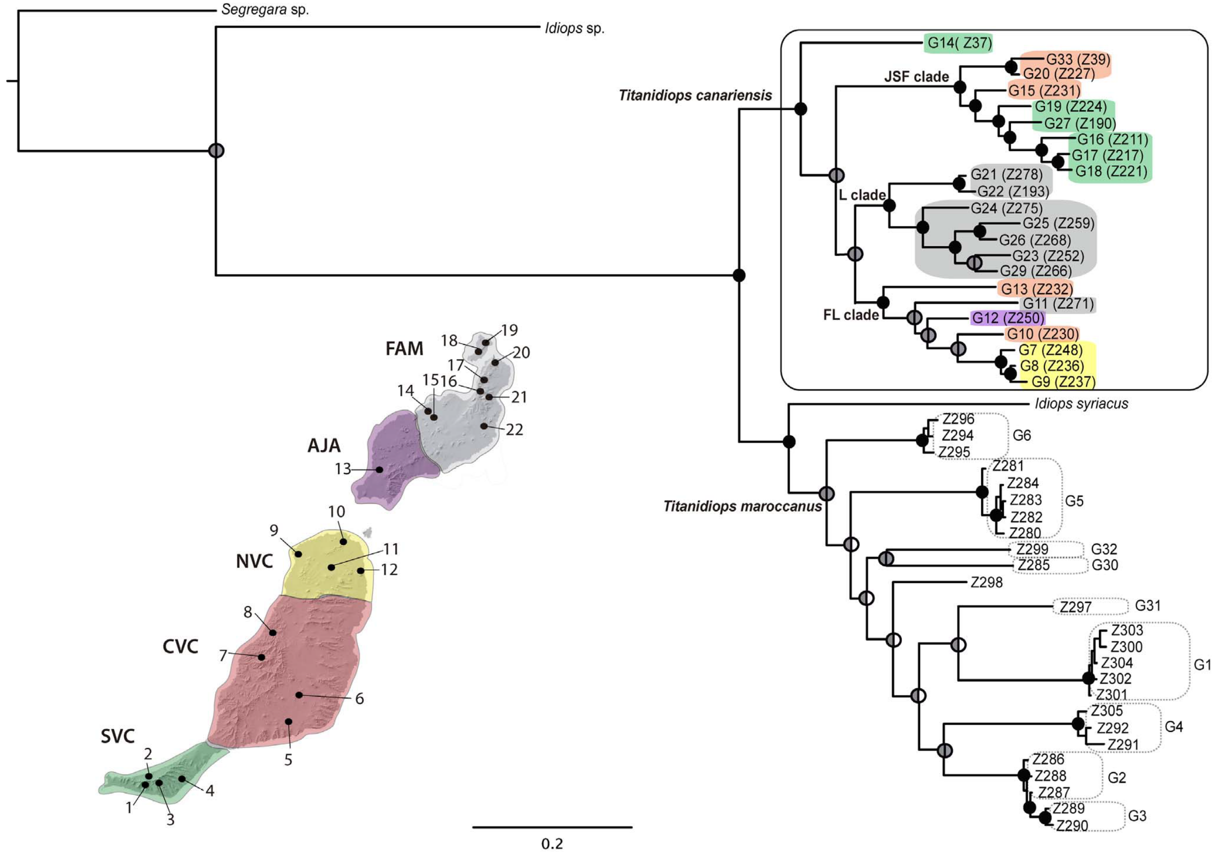
Řezáč et al 2020

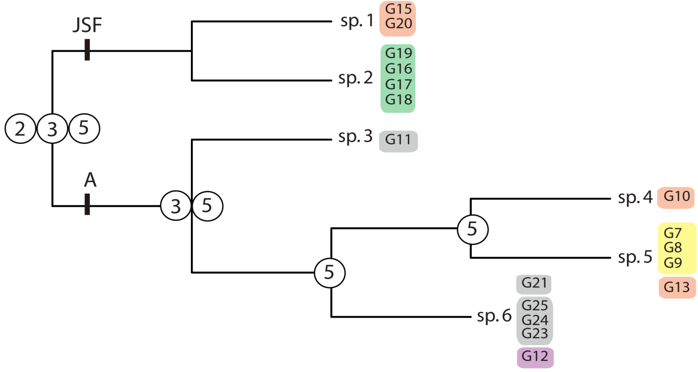
Canary Islands *Titanidiops canariensis*

trapdoor spider

sedentary – colonization via rafting, only 1x 7.5 Ma

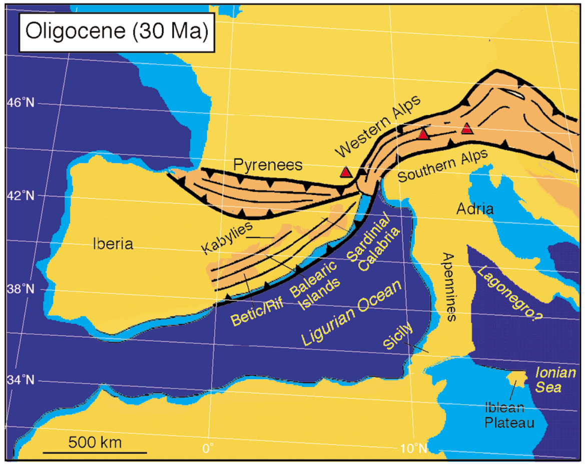
at least 2 cryptic species

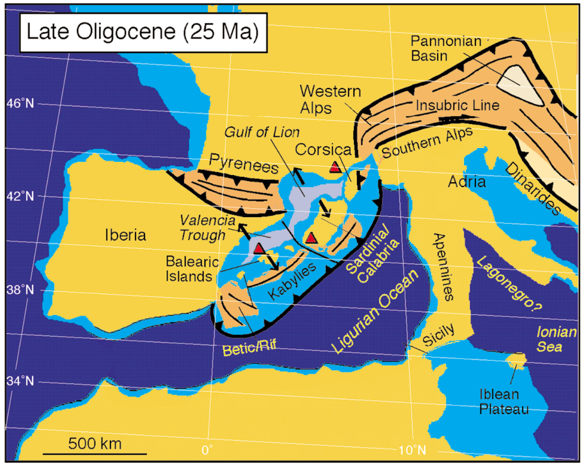


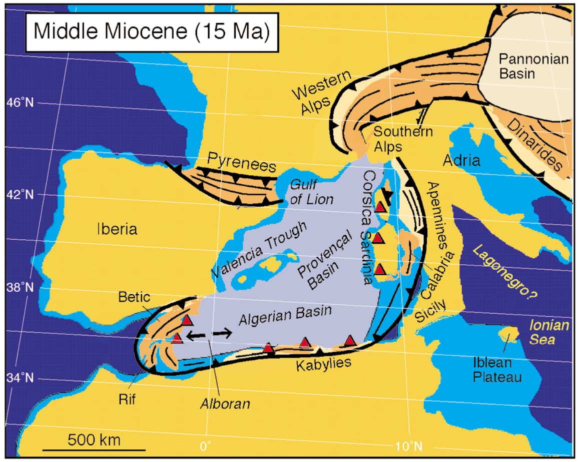


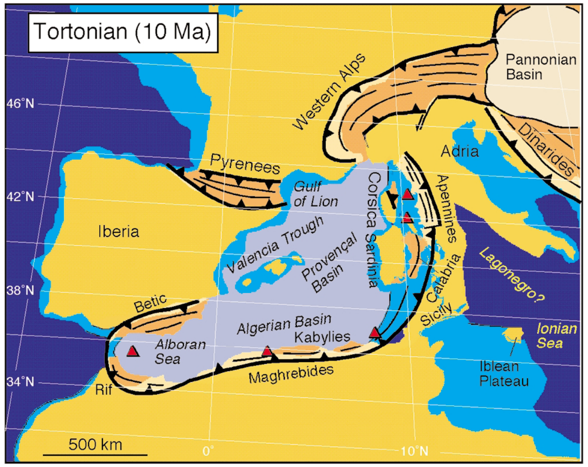
Opatova & Arnedo 2014

Continental Islands – geological history of the Western Mediterranean

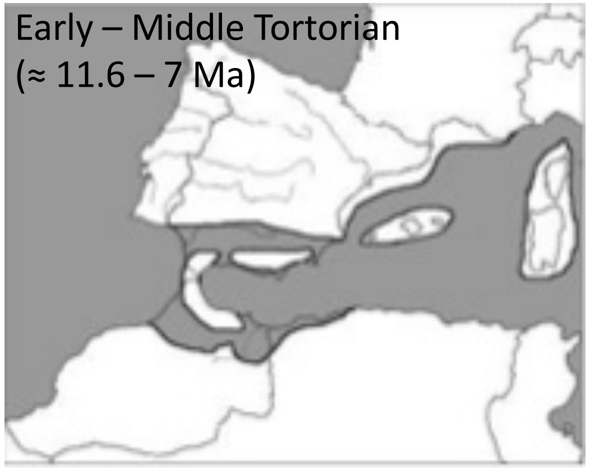






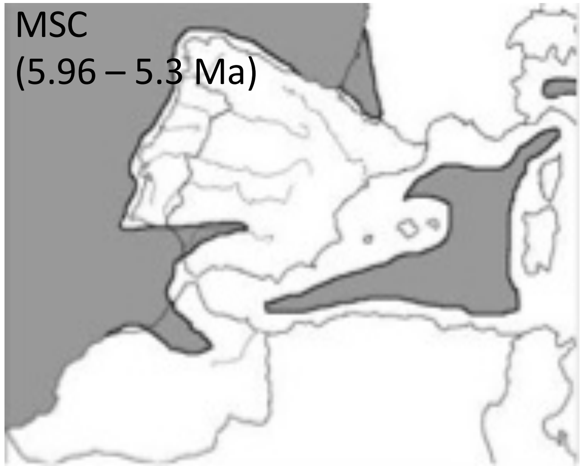


Rosenbaum et al. 2002



Early – Middle Tortonian
(≈ 11.6 – 7 Ma)

Paulo et al. 2008



MSC
(5.96 – 5.3 Ma)

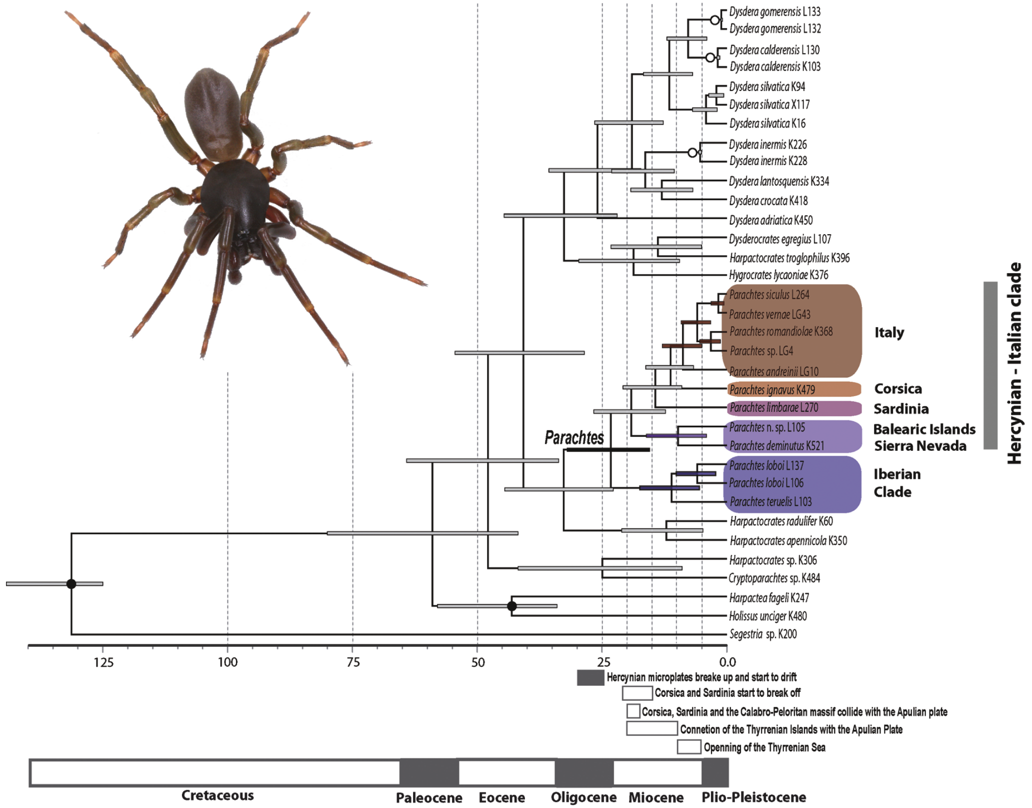
Continental Islands – *Parachtes*

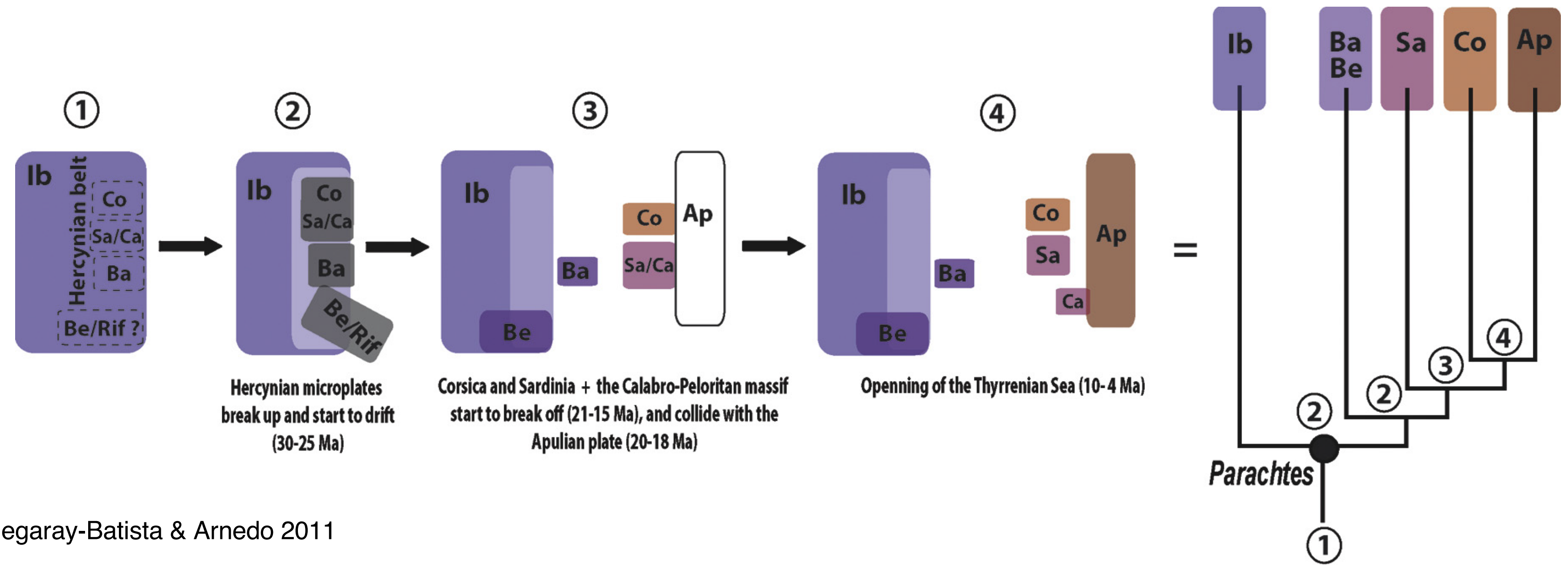
Dysderidae (generalist)

Sedentary

→

Hercynian belt breakup





Hercynian microplates break up and start to drift (30-25 Ma)

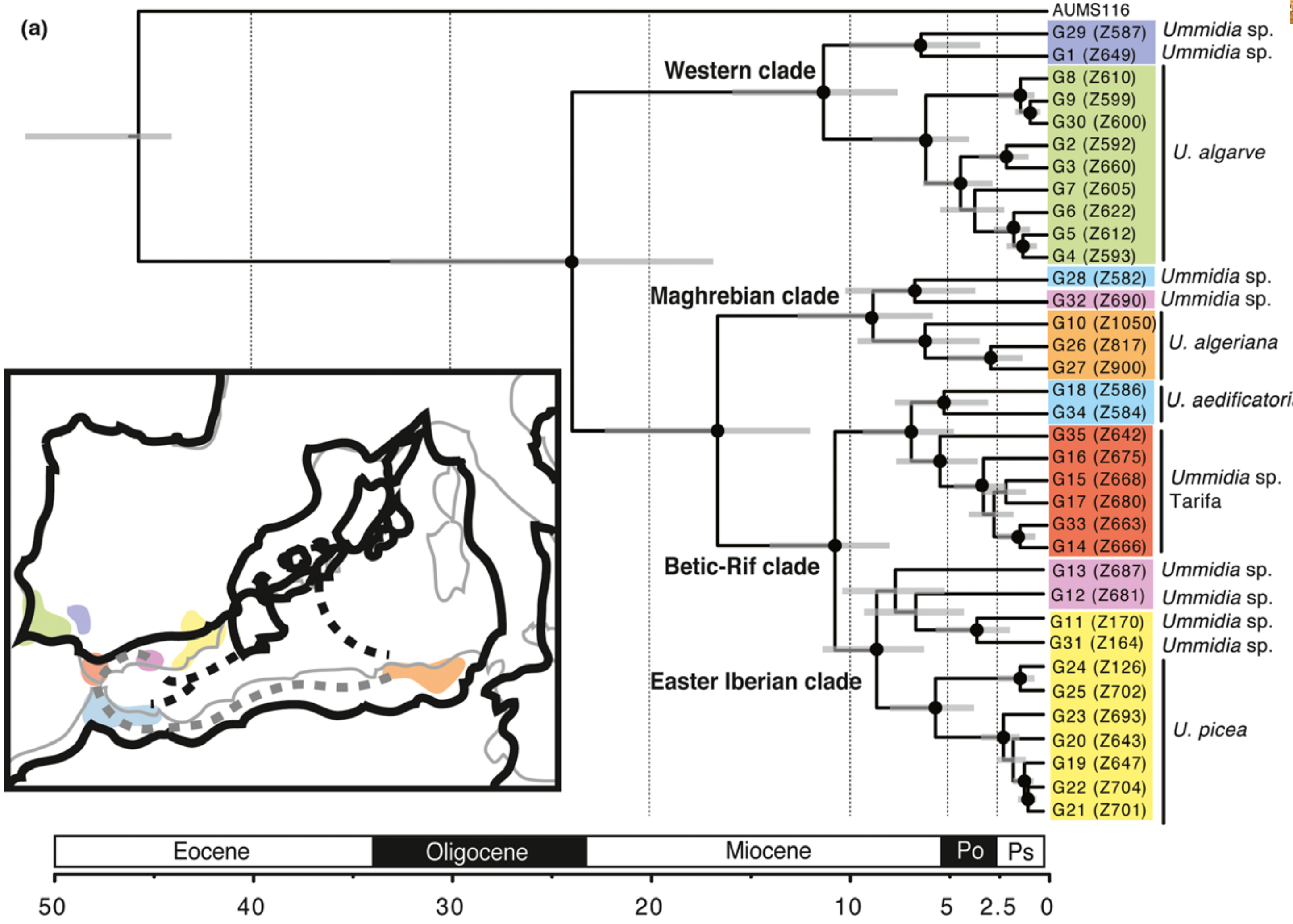
Corsica and Sardinia + the Calabro-Peloritan massif start to break off (21-15 Ma), and collide with the Apulian plate (20-18 Ma)

Openning of the Thyrrenian Sea (10-4 Ma)

Bidegaray-Batista & Arnedo 2011

Continental Islands – *Ummidia*

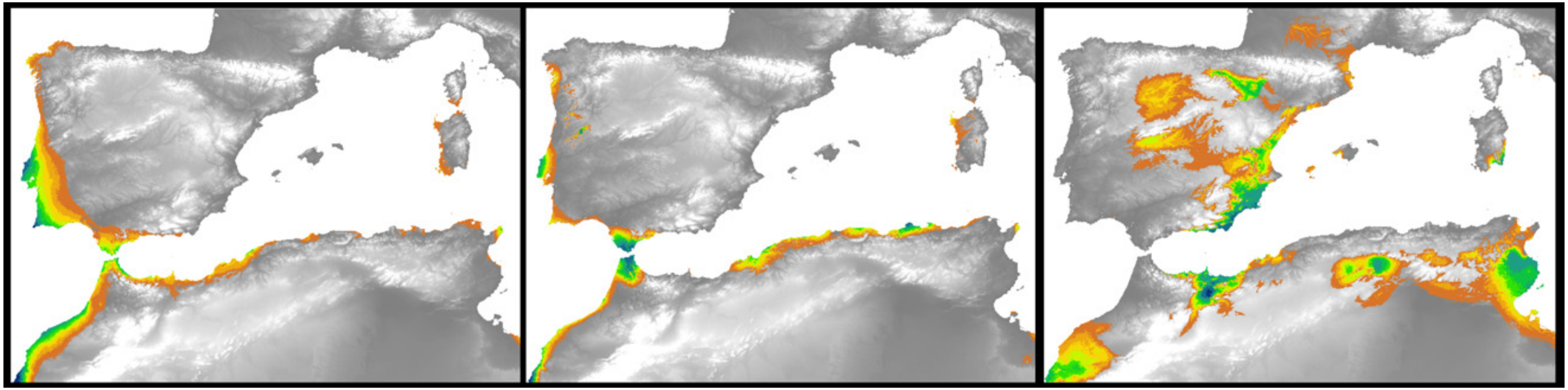
Trapdoor spider with ballooning capability; mostly vicariance

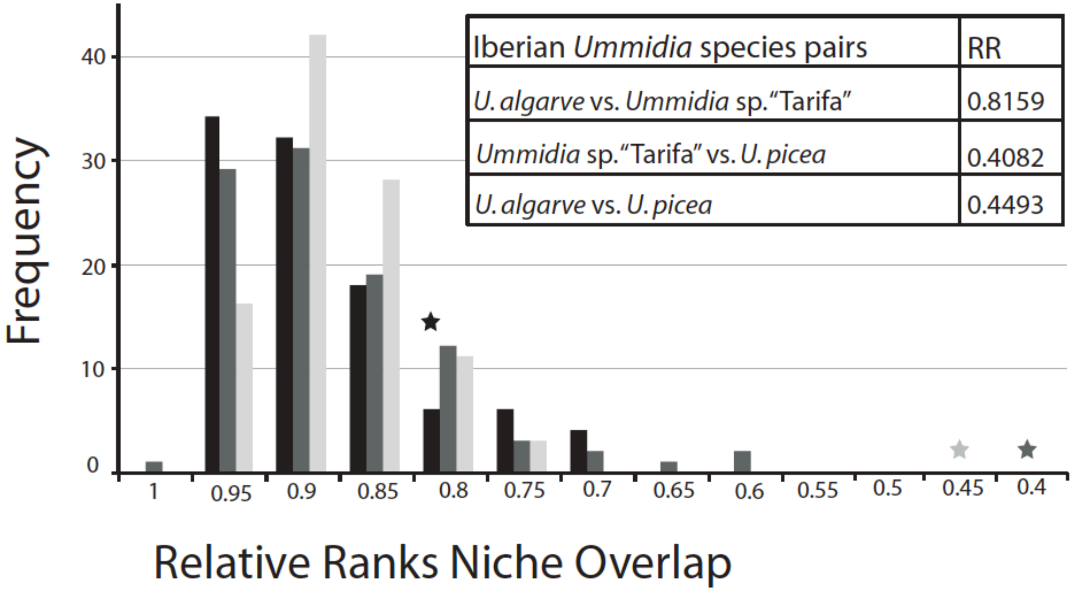


Opatova et al 2016

Distribution modelling – assessing ballooning capabilities

Niche overlap, but no gene flow





Iberian *Ummidia* species pairs	RR
U. algarve vs. *Ummidia* sp. "Tarifa"	0.8159
Ummidia sp. "Tarifa" vs. *U. picea*	0.4082
U. algarve vs. *U. picea*	0.4493

Opatova et al 2016

Pangea formation

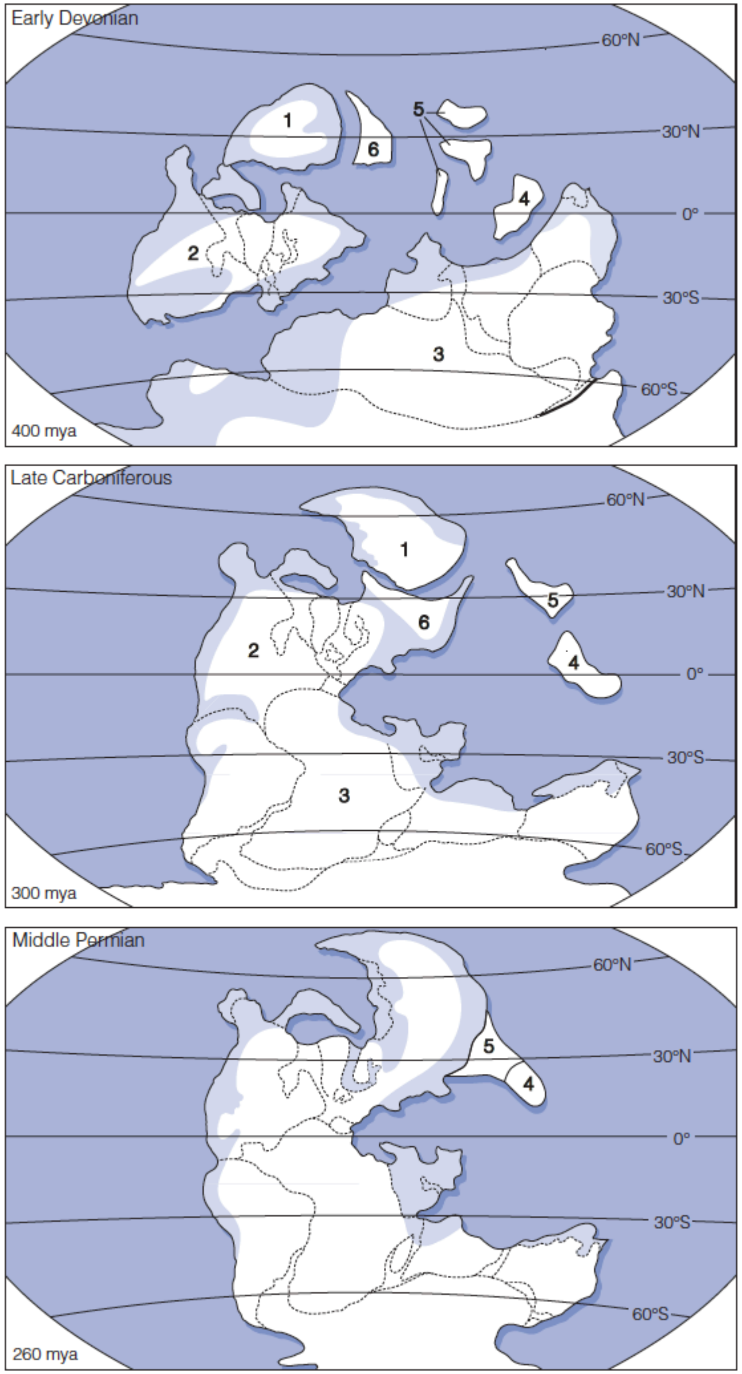
Amalgamation of Gondwana 520 – 510 Ma
- southern hemisphere

Laurentia, Baltica, Siberia – in the north
- formed Laurasia in Paleozoic, ~ 300 Ma

Late Paleozoic – Pangea formation
- lasted ~ 100 Myr

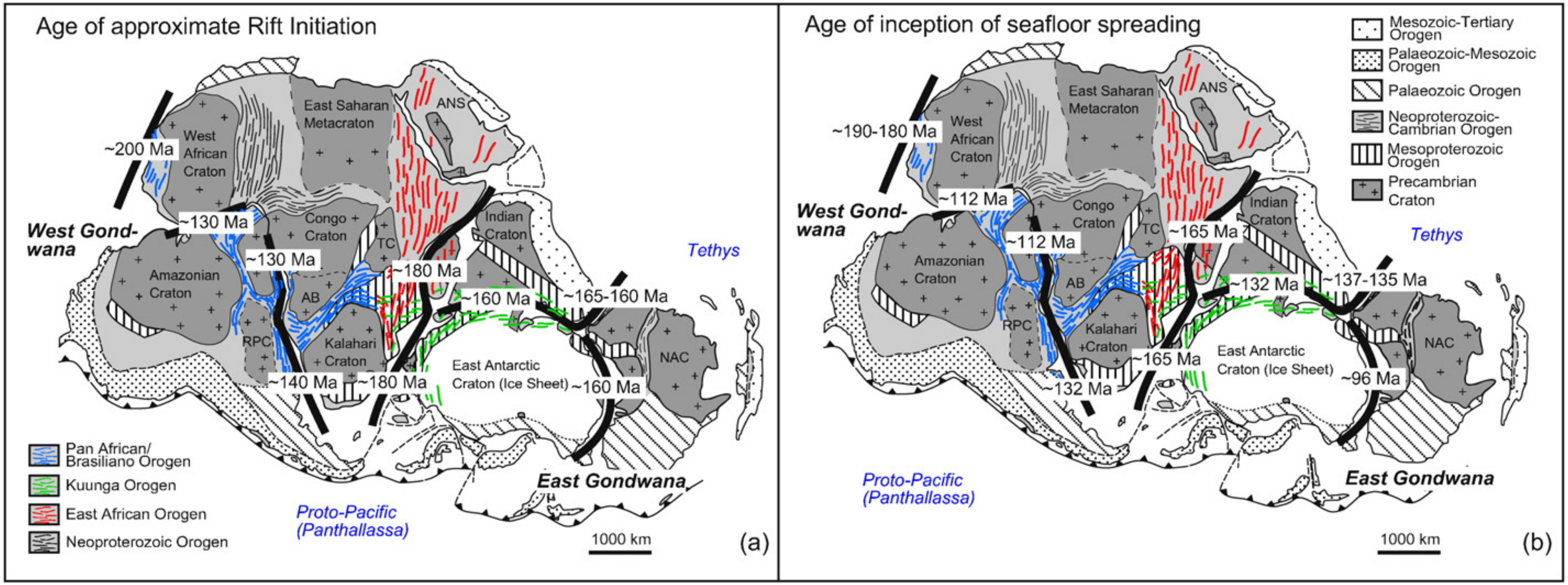
Pangea breakup
- Central Atlantic ridge ~ 200 Ma

Will & Frimmel 2018



Cox *et al* 2010

Gondwana disintegration



Will & Frimmel 2018

breakup from Laurasia
- Central Atlantic ridge ~ 200 Ma

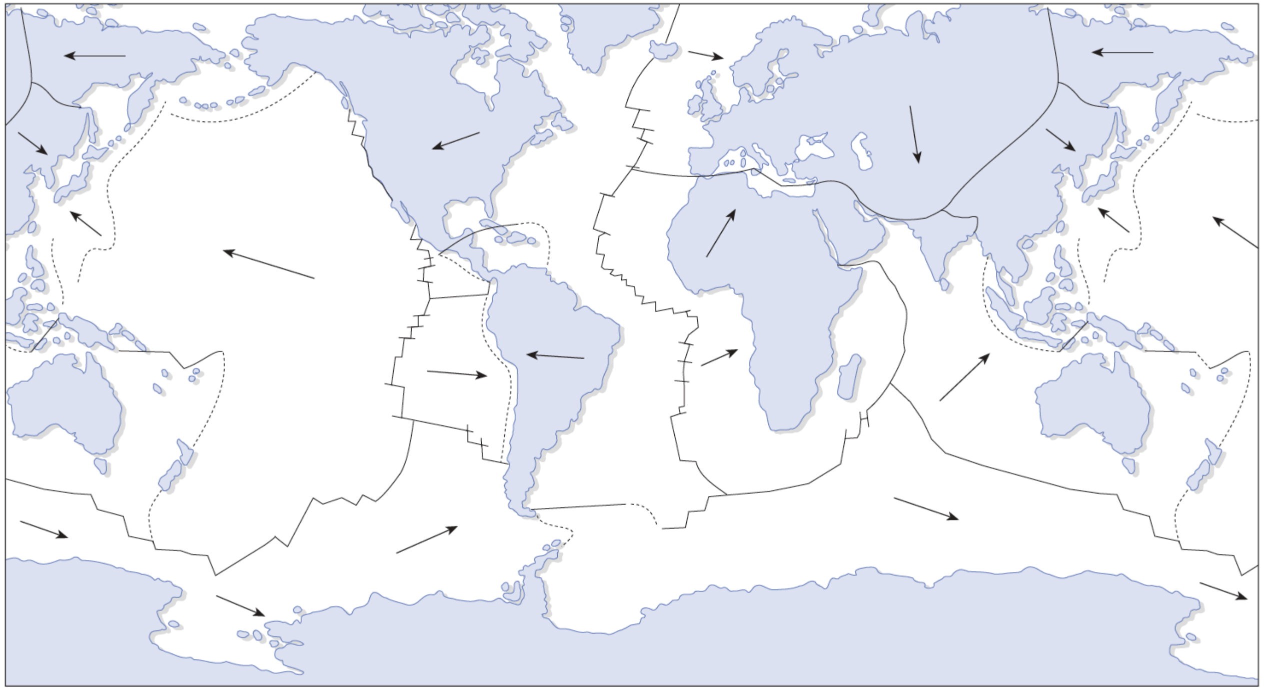
Lower Jurassic ~ 180 Ma East/ West Gondwana breakup
Upper Jurassic ~ 160 Ma India-Madagascar/Antarctica
~ 160 Ma Antarctica/Australia
Lower Cretaceous ~ 140 – 130 Ma S America/Africa
Upper Cretaceous ~ 80 - 90 Ma Madagascar/ India

Laurasia breakup ~ 55 Ma

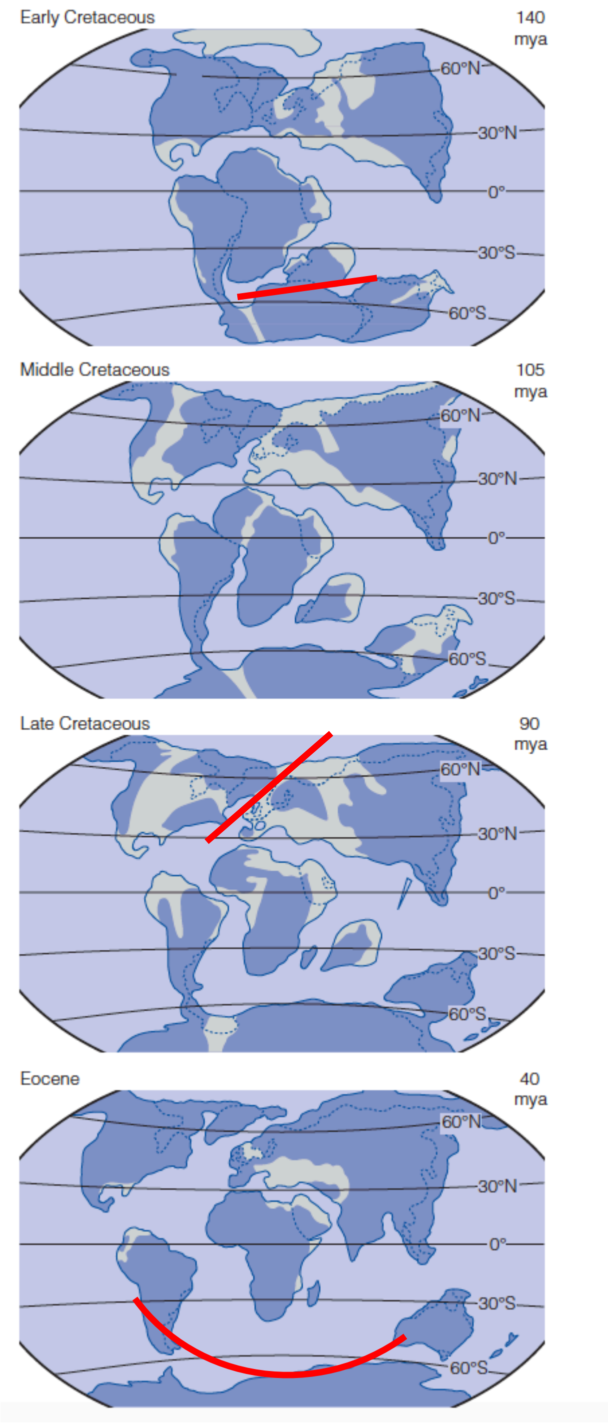
S America – Antarctica – Australia land bridge
up to ~ 30 Ma

timing updated contiguously, controversial topics remain

The movement continues ~ 5 – 10 cm/yr



Cox *et al* 2010



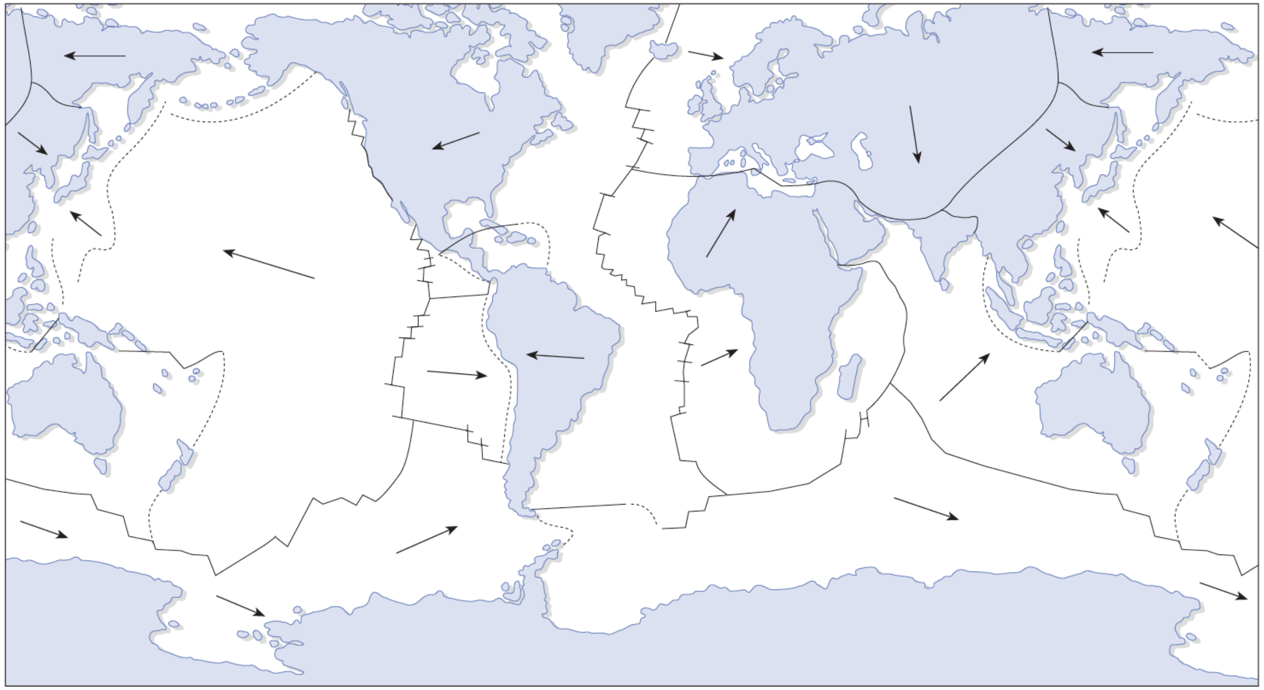
Cox *et al* 2010 Will & Frimmel 2018

Laurasia breakup ~ 55 Ma, land bridge ~ 25 Ma

S America – Antarctica – Australia land bridge
up to ~ 30 Ma

timing updated contiguously, controversial topics remain

The movement continues ~ 5 – 10 cm/yr



Cox *et al* 2010

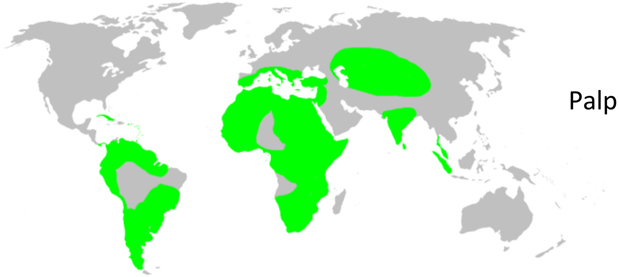
Ms. A. Williams
730 cm/30 yr

Palpimanoidea

continental vicariance?

~ Gondwanan distribution

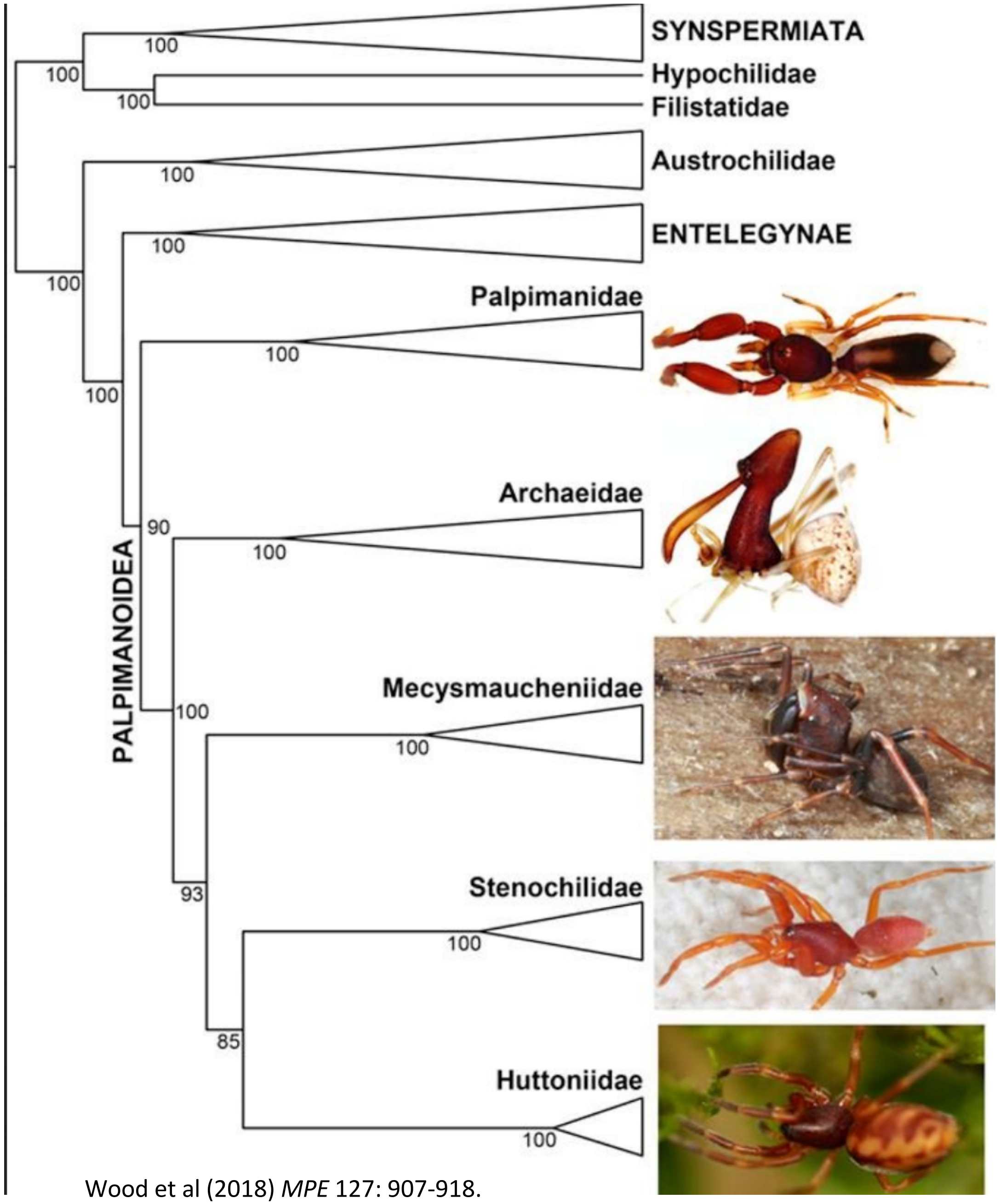
araneophagous: modifications



Palpimanidae

Archaeidae

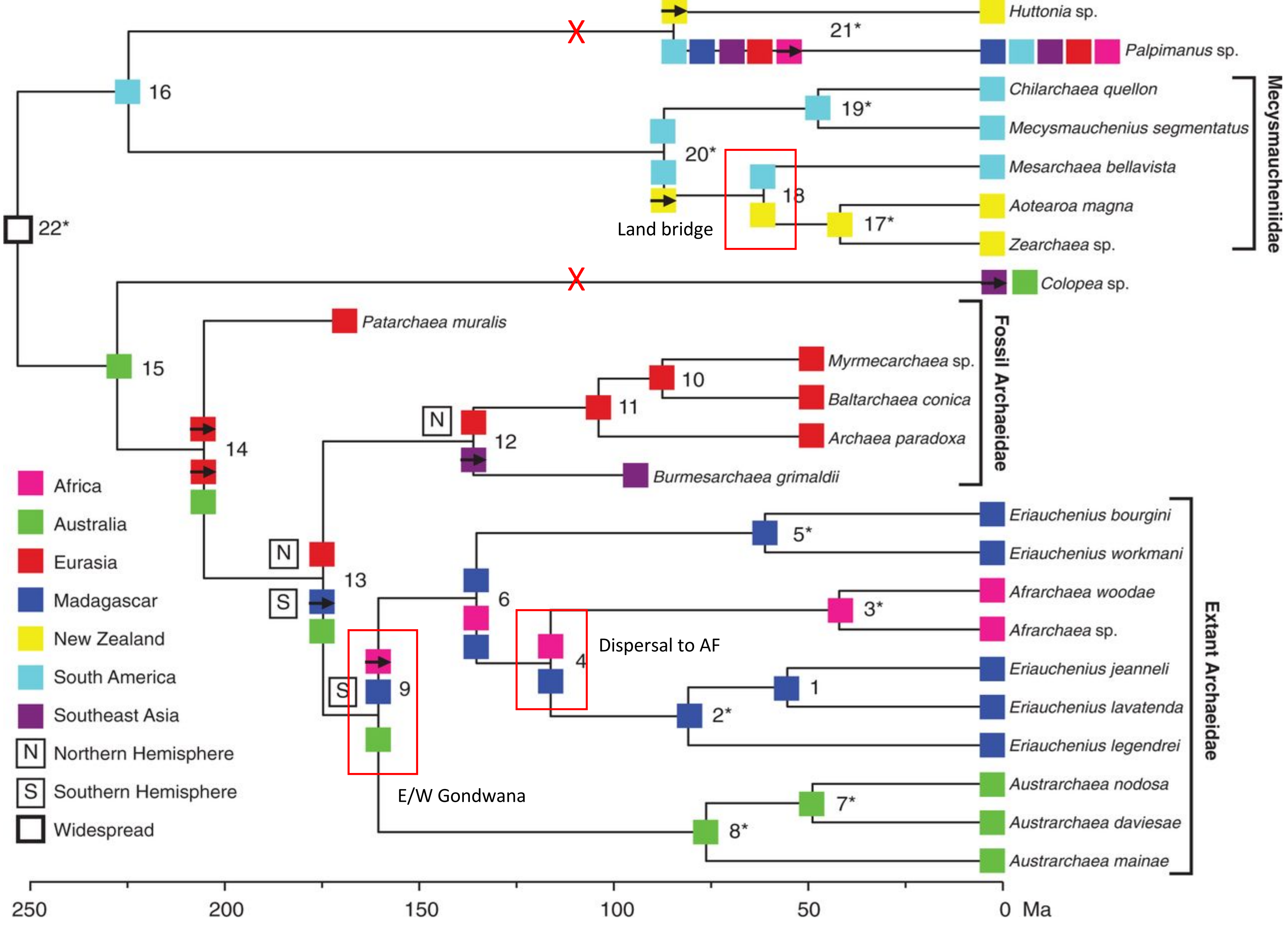
Mecysmaucheniidae



Wood et al (2018) *MPE* 127: 907-918.

Palpimanoidea

continental vicariance?



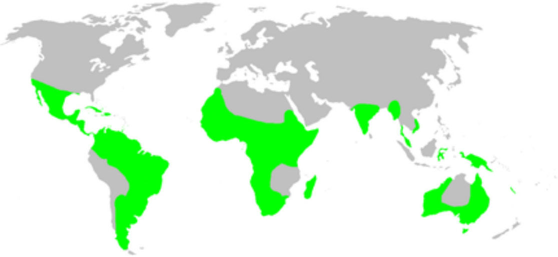
Land bridge

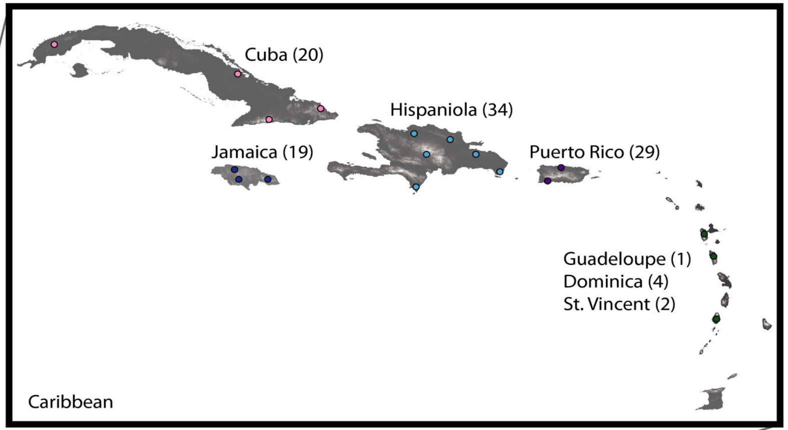
Dispersal to AF

E/W Gondwana

Wood et al (2013) *Syst Biol* 127: 264-284.

Deinopis continental vicariance? GAARlandia land bridge





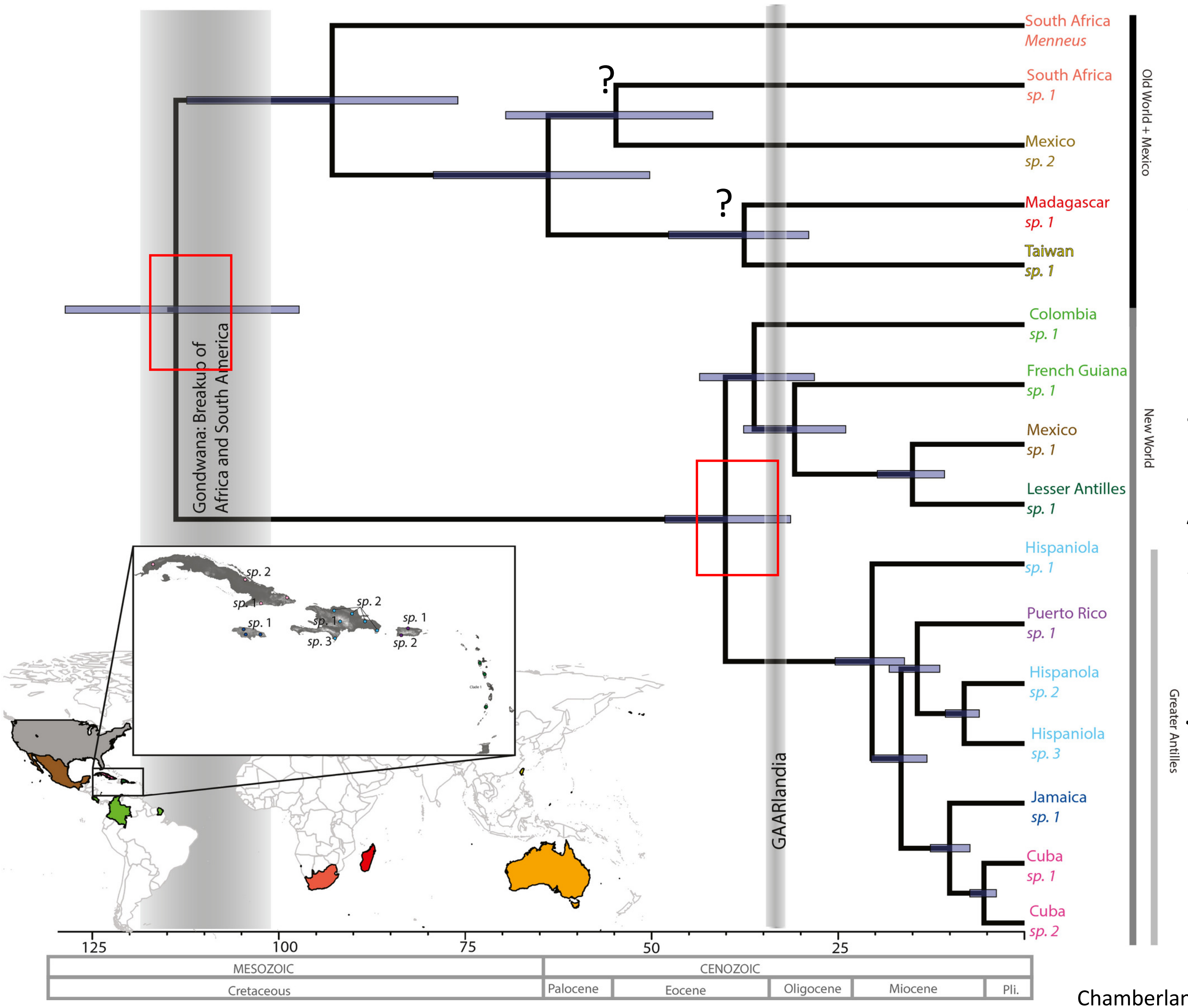
Greater Antilles and Aves Ridge

– land bridge connecting S America with the Greater Antilles

Eocene – Oligocene ~ 35 – 33 Ma

Chamberland et al (2018)

Deinopis continental vicariance? GAARlandia land bridge



Gondwanan origin

? long-distance dispersal

Supports GAARlandia

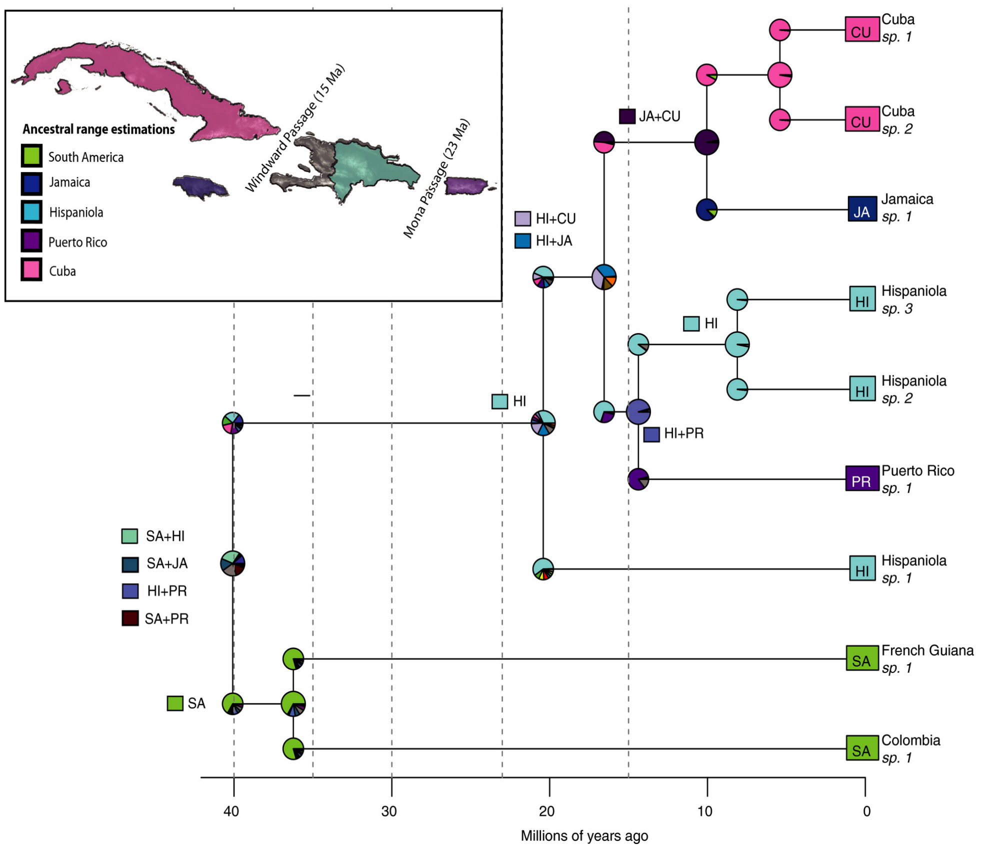
Also in: *Loxosceles, Sicarius Heteroctenus* scorpions

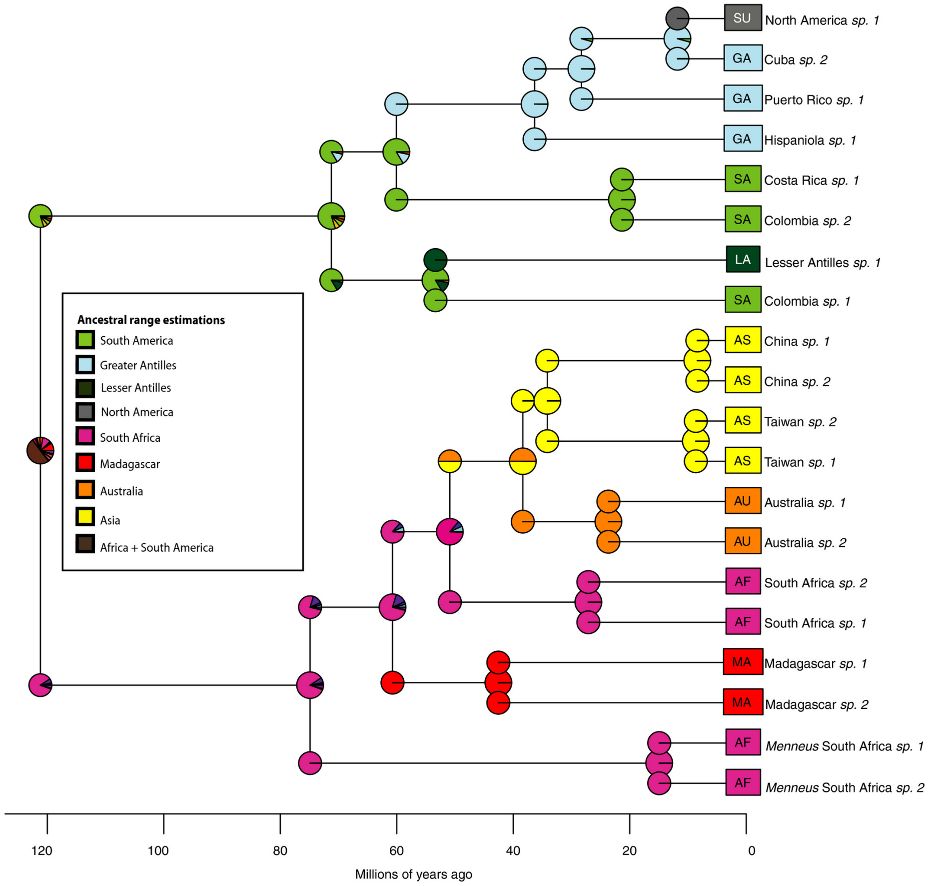
Not in: *Tetragnatha, Selenops*

Binford et al (2008)
Crews & Esposito (2020)
Čandek et al (2021)

Chamberland et al (2018)

Deinopis continental vicariance? GAARlandia land bridge





Chamberland et al (2018)

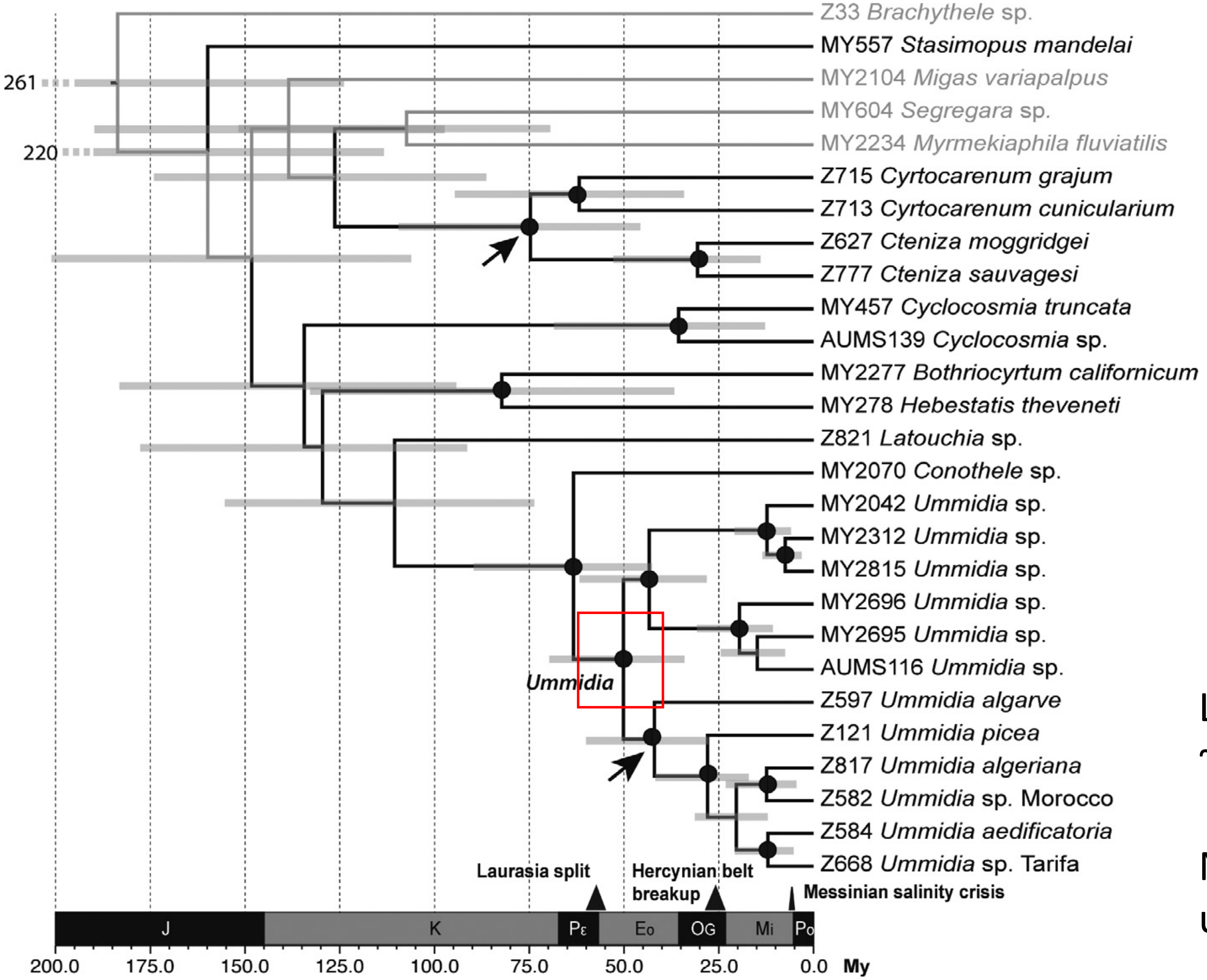
Greater Antilles colonized 1x from S America

→ back colonization

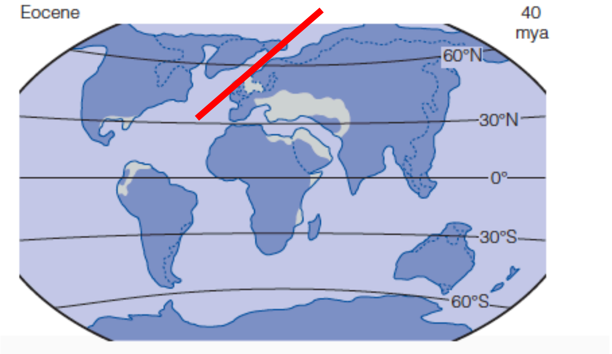
African origin of the Old World taxa

Ummidia continental vicariance?

Halonoproctidae – Laurasia breakup



Opatova et al 2013



Laurasia breakup
~ 55 Ma

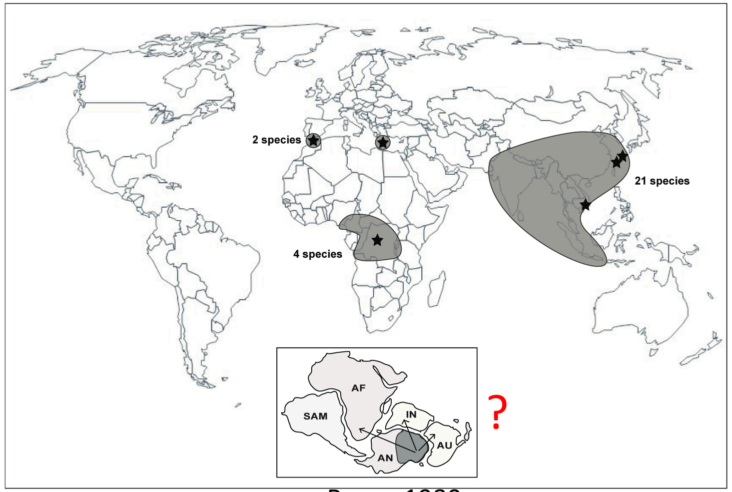
North American land bridge
up to ~ 25 ma

Macrothele continental vicariance?

M. calpeiana
Bern Convention (1987)
EU Habitat Directive (1992)
- Species of community interest, need of strict protection

M. cretica IUCN red list, data deficient category

both considered sedentary



Raven 1980

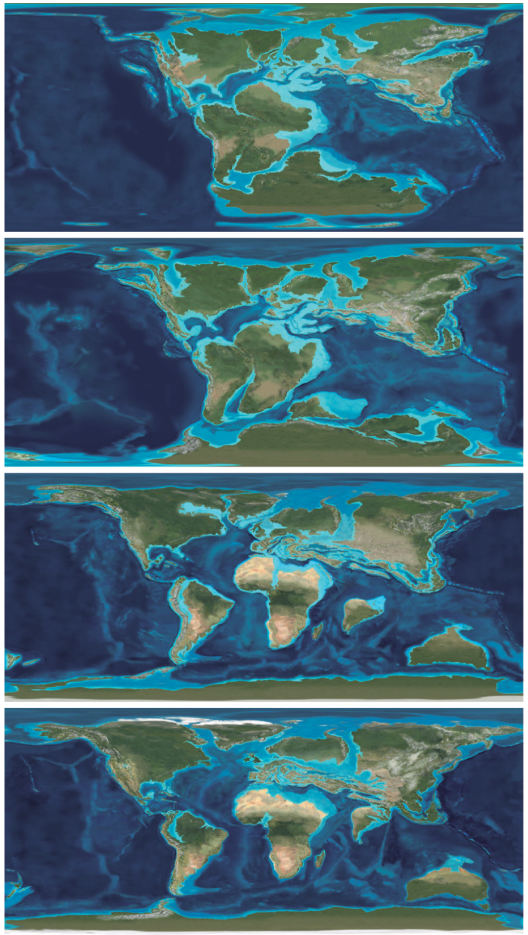
Macrothelidae

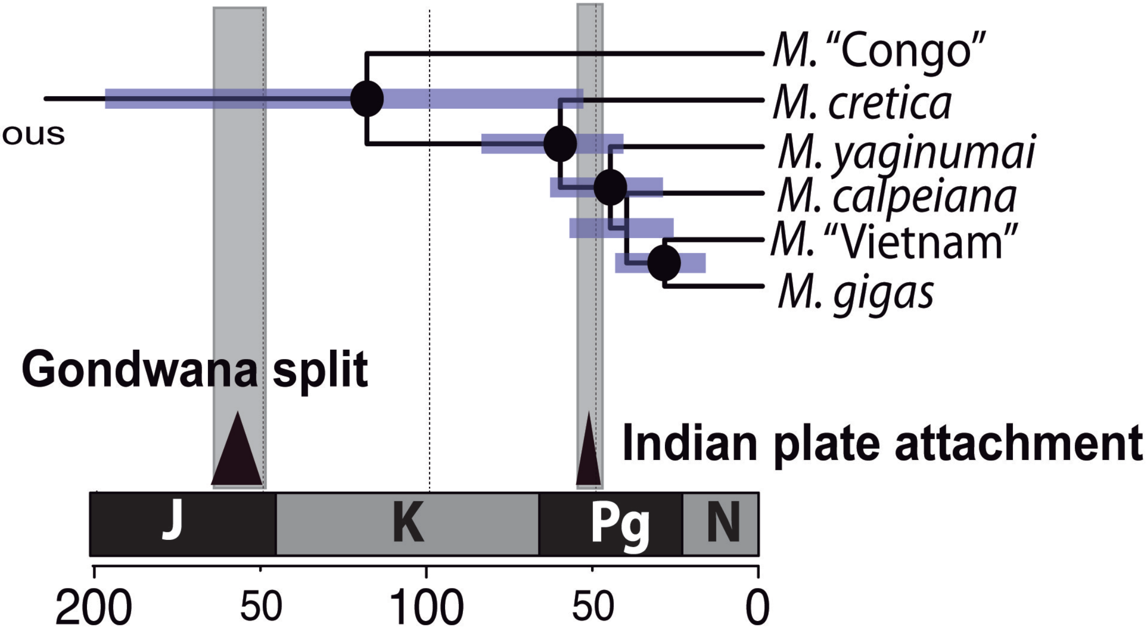
Opatova et al 2014

Macrothele continental vicariance?

Gondwana breakup

European Macrothele are not sister species
2x colonization of the Mediterranean
- Walking

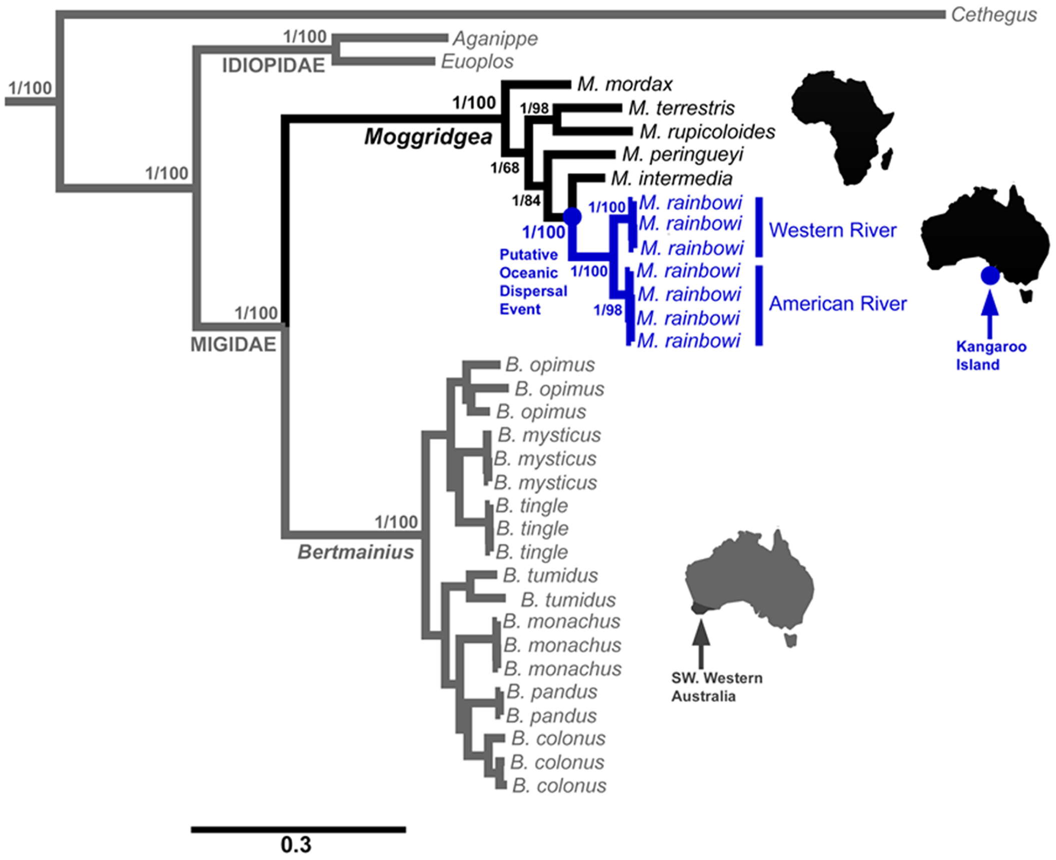




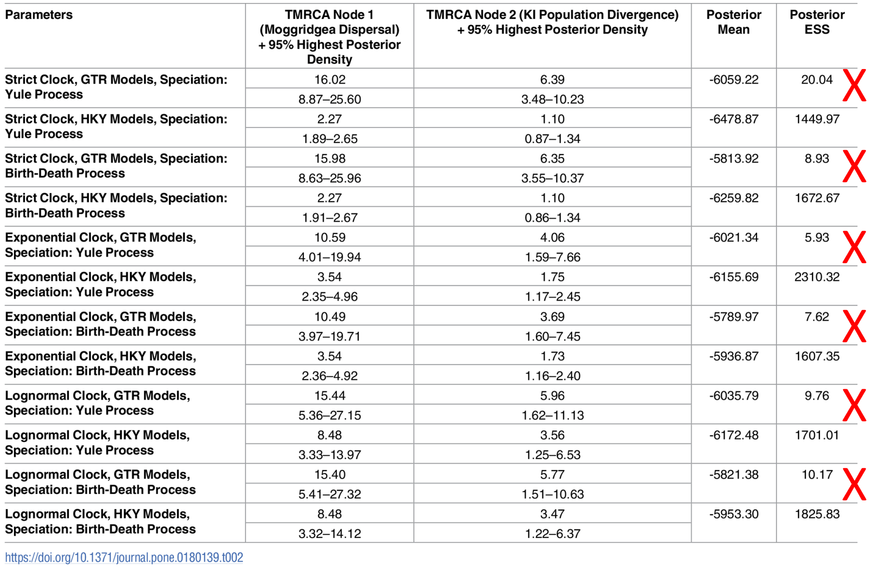
Opatova et al 2014

Moggridgea continental vicariance?

Migidae – Gondwanan distribution



Harrison et al 2017



Parameters	TMRCA Node 1 (Moggridgea Dispersal) + 95% Highest Posterior Density	TMRCA Node 2 (KI Population Divergence) + 95% Highest Posterior Density	Posterior Mean	Posterior ESS
Strict Clock, GTR Models, Speciation: Yule Process	16.02	6.39	-6059.22	20.04 X
	8.87–25.60	3.48–10.23		
Strict Clock, HKY Models, Speciation: Yule Process	2.27	1.10	-6478.87	1449.97
	1.89–2.65	0.87–1.34		
Strict Clock, GTR Models, Speciation: Birth-Death Process	15.98	6.35	-5813.92	8.93 X
	8.63–25.96	3.55–10.37		
Strict Clock, HKY Models, Speciation: Birth-Death Process	2.27	1.10	-6259.82	1672.67
	1.91–2.67	0.86–1.34		
Exponential Clock, GTR Models, Speciation: Yule Process	10.59	4.06	-6021.34	5.93 X
	4.01–19.94	1.59–7.66		
Exponential Clock, HKY Models, Speciation: Yule Process	3.54	1.75	-6155.69	2310.32
	2.35–4.96	1.17–2.45		
Exponential Clock, GTR Models, Speciation: Birth-Death Process	10.49	3.69	-5789.97	7.62 X
	3.97–19.71	1.60–7.45		
Exponential Clock, HKY Models, Speciation: Birth-Death Process	3.54	1.73	-5936.87	1607.35
	2.36–4.92	1.16–2.40		
Lognormal Clock, GTR Models, Speciation: Yule Process	15.44	5.96	-6035.79	9.76 X
	5.36–27.15	1.62–11.13		
Lognormal Clock, HKY Models, Speciation: Yule Process	8.48	3.56	-6172.48	1701.01
	3.33–13.97	1.25–6.53		
Lognormal Clock, GTR Models, Speciation: Birth-Death Process	15.40	5.77	-5821.38	10.17 X
	5.41–27.32	1.51–10.63		
Lognormal Clock, HKY Models, Speciation: Birth-Death Process	8.48	3.47	-5953.30	1825.83
	3.32–14.12	1.22–6.37		

https://doi.org/10.1371/journal.pone.0180139.t002

2.27 – 8.48 Ma

Long distance dispersal – rafting

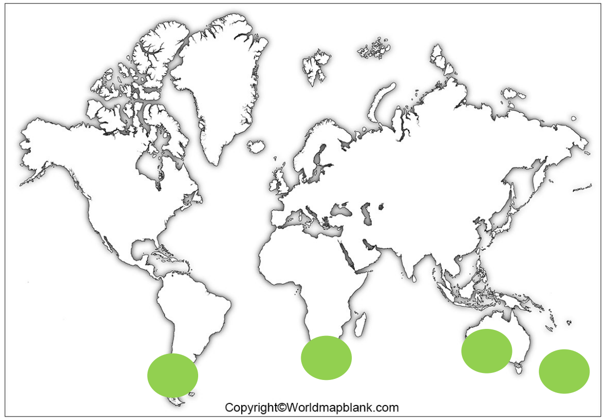
- Also in *Poecilomigas abrahami*

Opatova et al 2020

Amaurobioides continental vicariance?

Anyphaenidae

Around the world in 8 million years - rafting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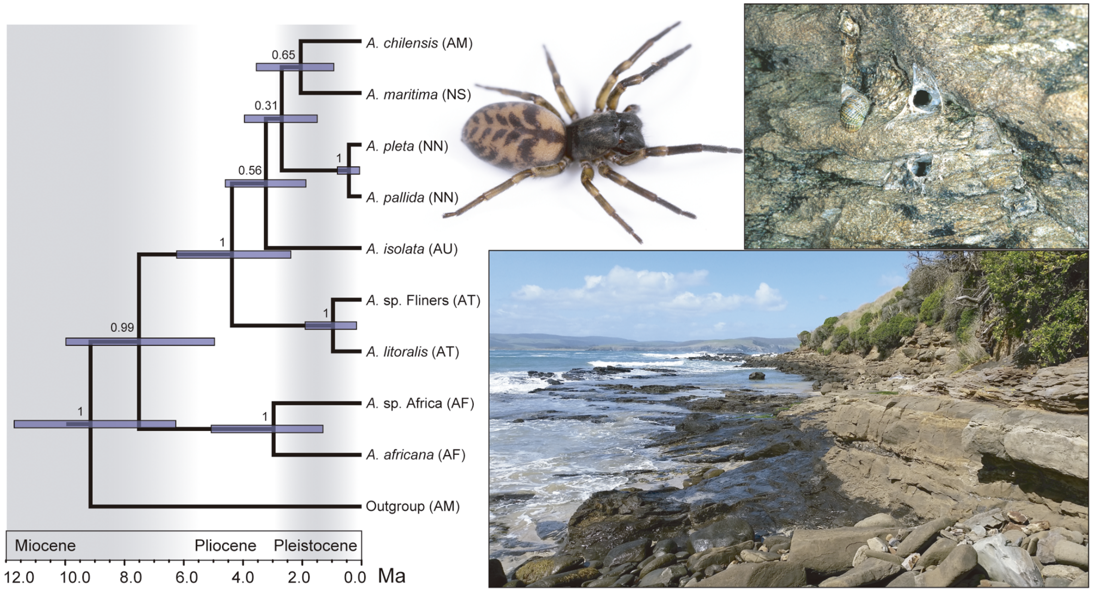
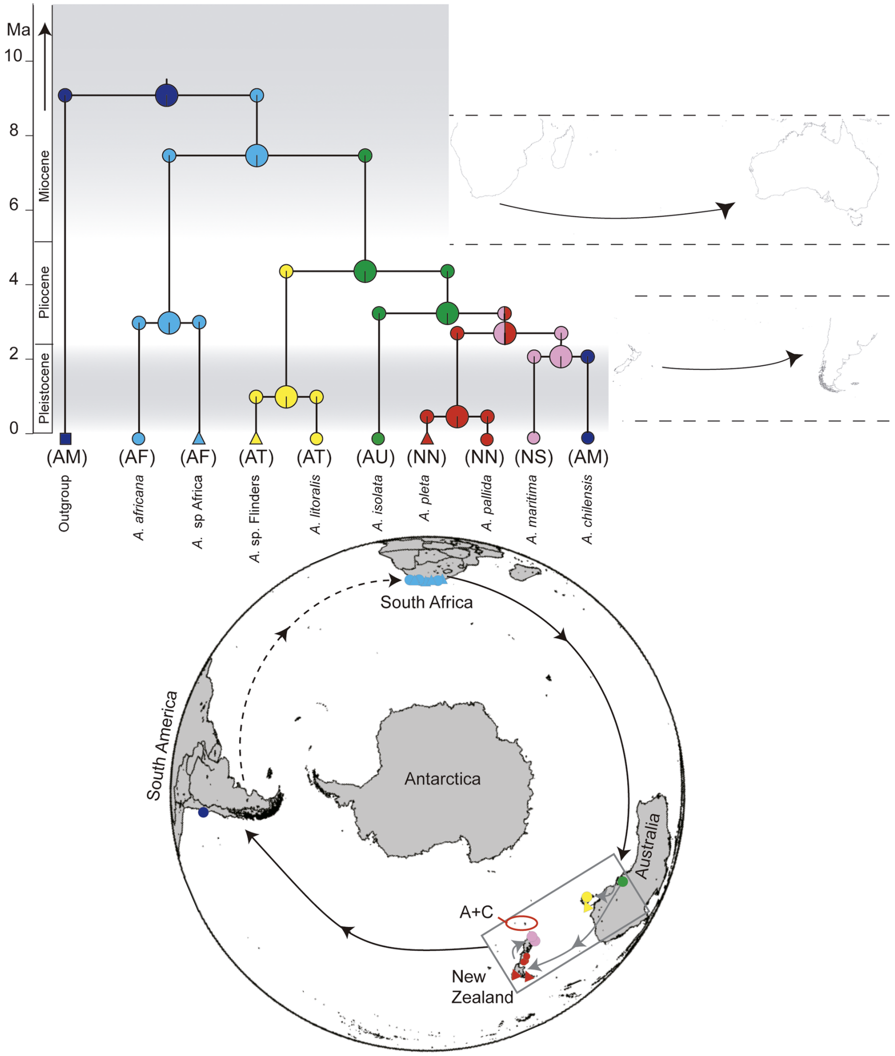


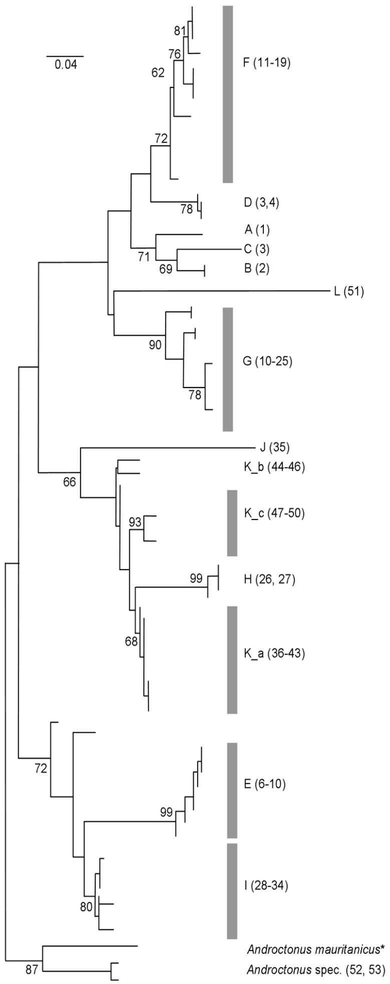


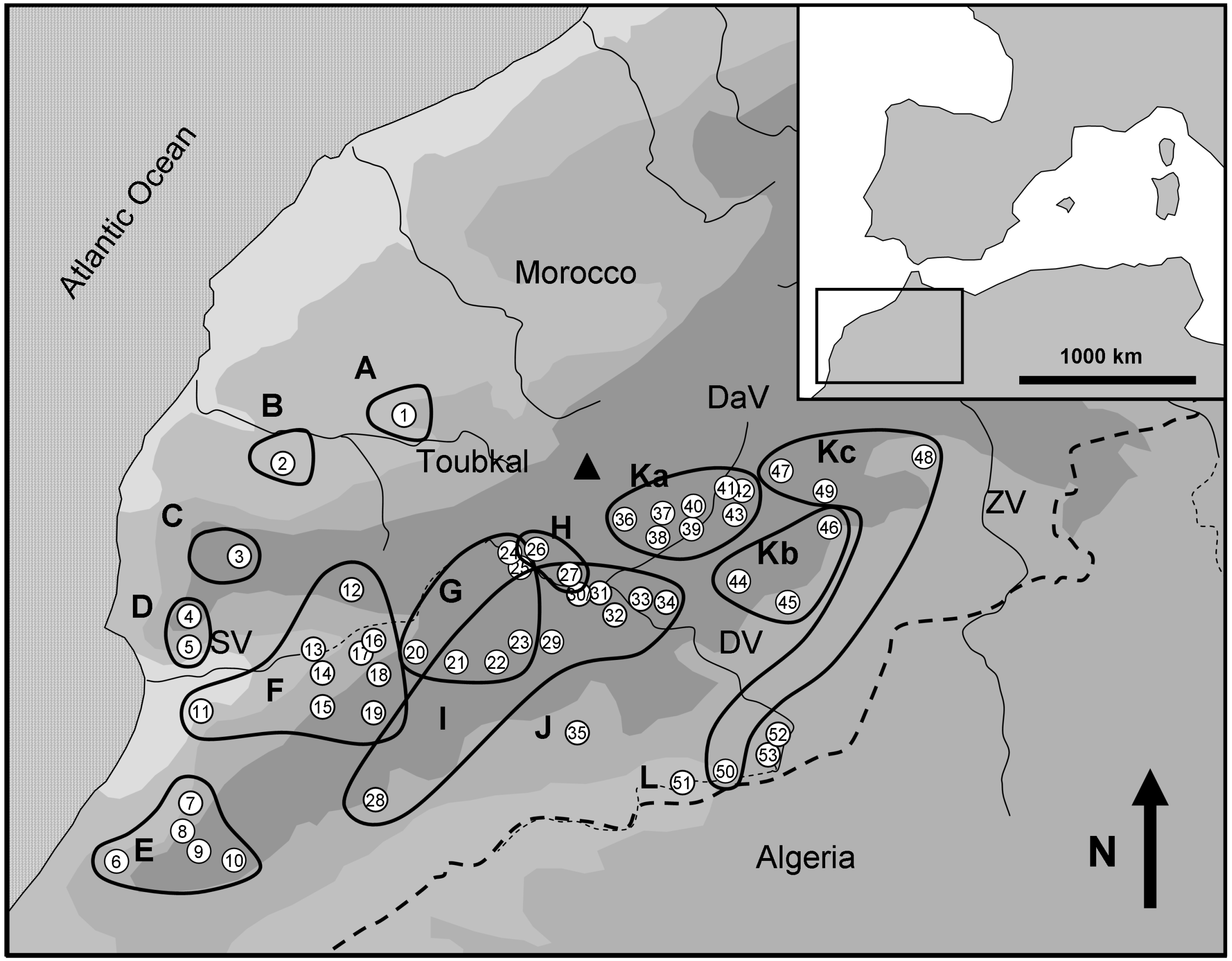
Ceccarelli et al 2016

Buthus scorpions in Atlas Mountains

Mountains – *in situ* radiation, microallopatry

Main clades overlap, subclades parapatric



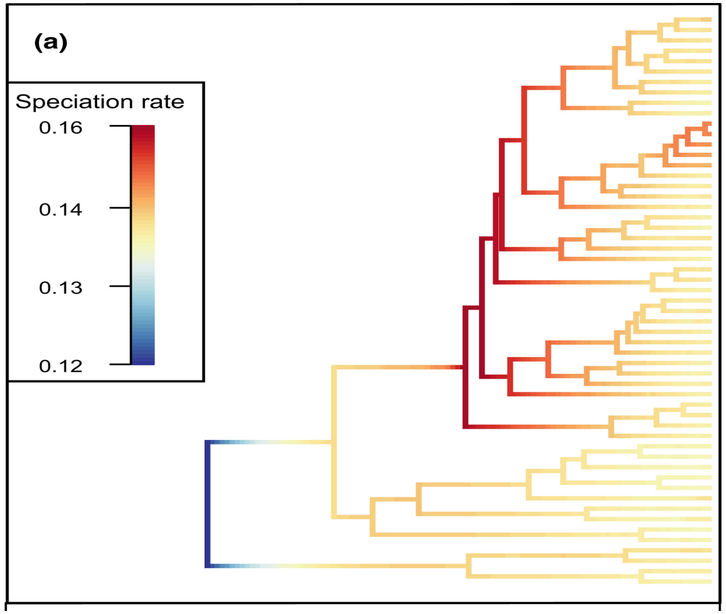


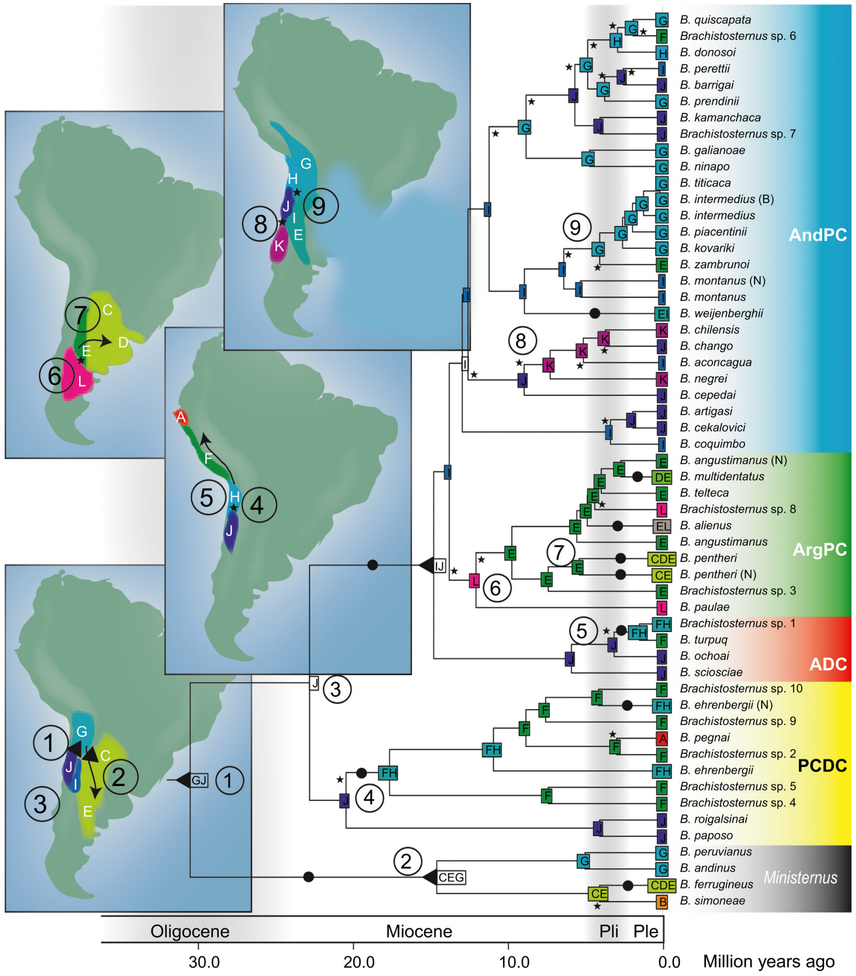
Habel et al 2012

Brachiosternus scorpions in the Andes

Mountains – *in situ* radiation

Coastal habitats stable – source of colonization of adaptive lineages



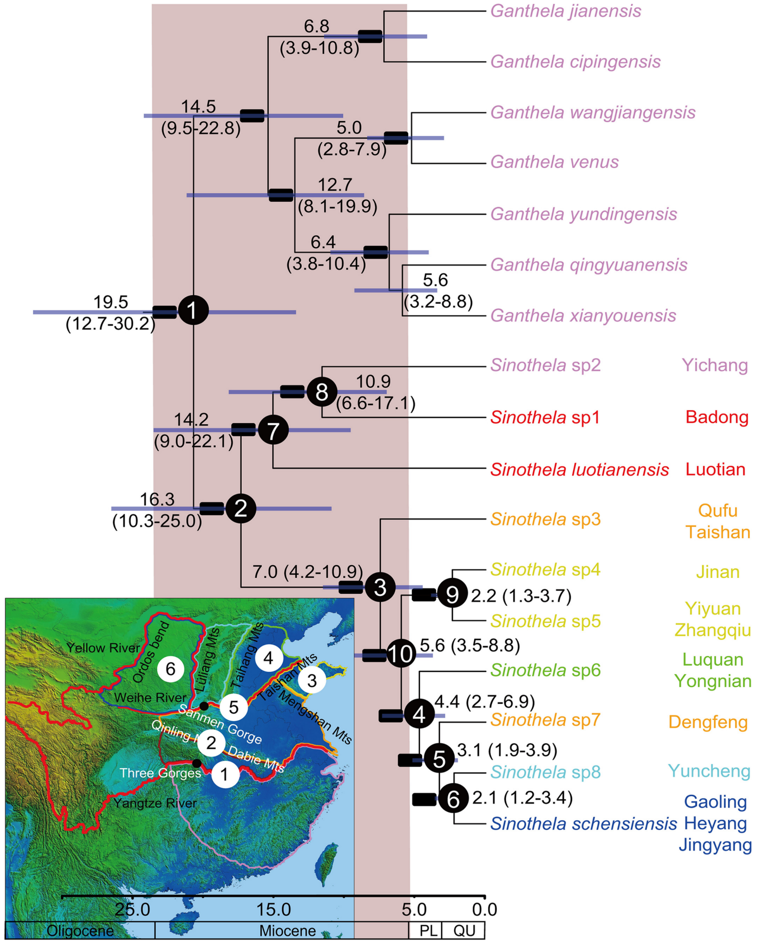


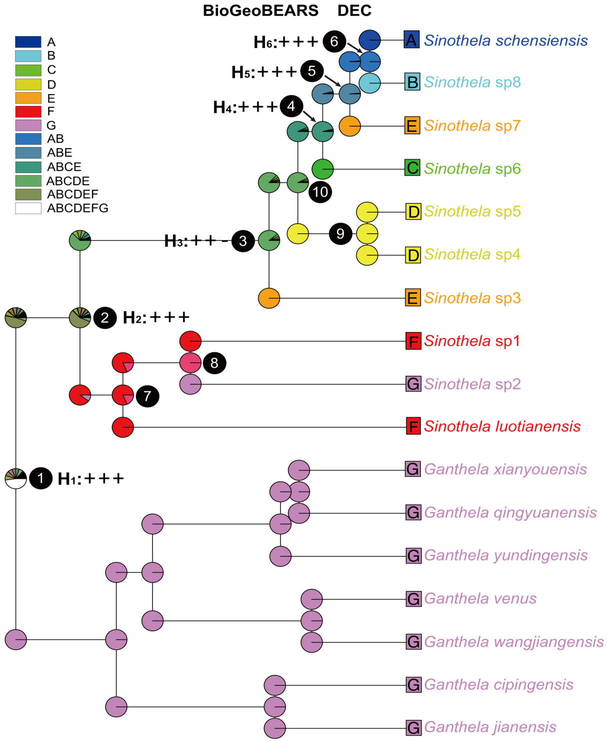
Ceccarelli et al 2016

Primitively segmented spiders SE Asia

Ganthela, *Sinothela*

River formation, mountain uplift





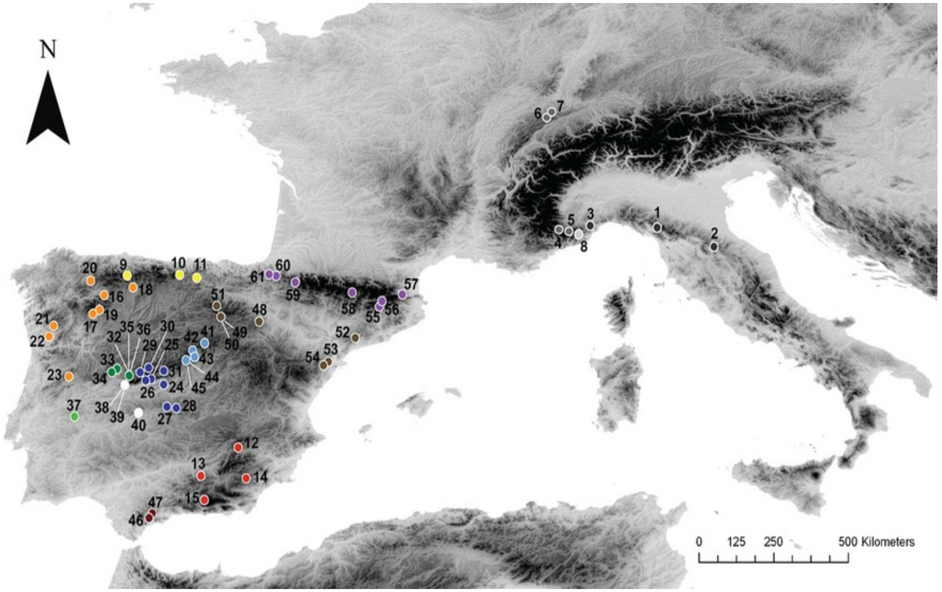
1. Yangtze River formation (23–36.5 Ma)
2. Qinling–Dabie mountains (2.6–23 Ma)
3. Taishan Mts uplift - unsuported
4. Taihang Mts (3.6–5.3 Ma)
5. Yellow River formation (1.8–3.6 Ma)
6. Ordos bend coincide with its origin (1.6 Ma)

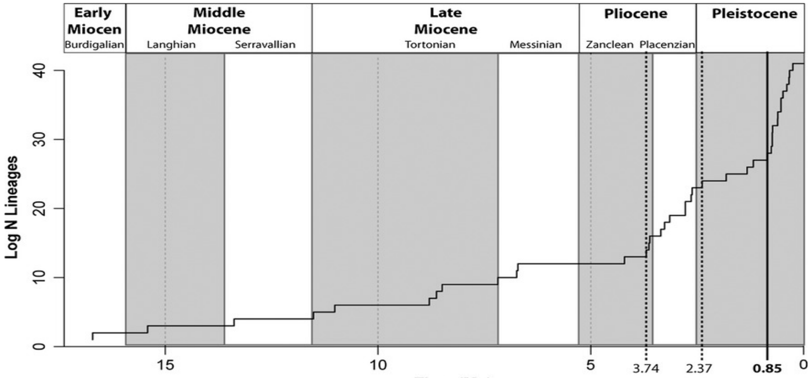
Xu et al 2018

Harpactocrates Climate: Glaciations

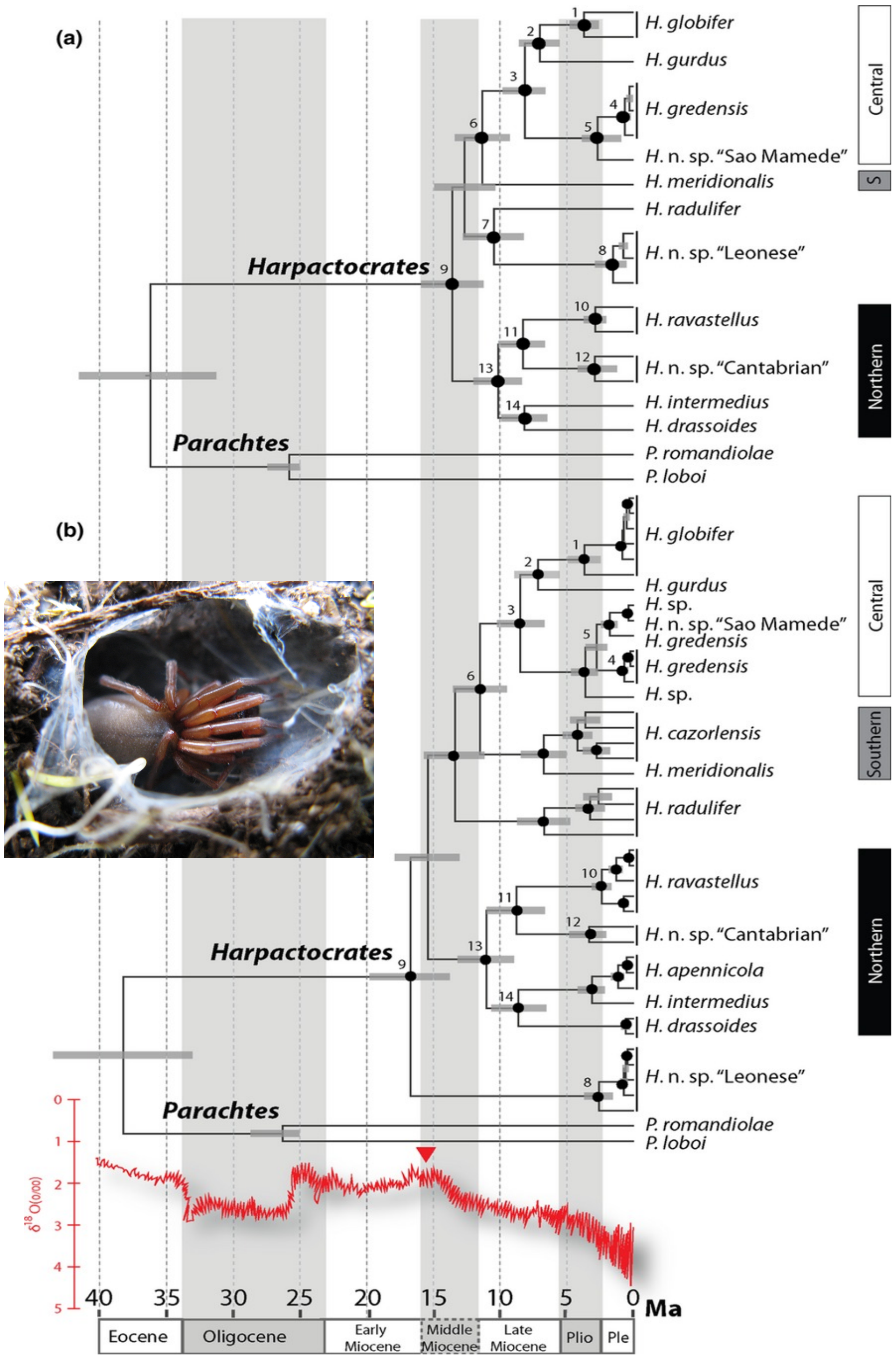
Dysderidae

Ground-dwelling, sedentary
Western Mediterranean



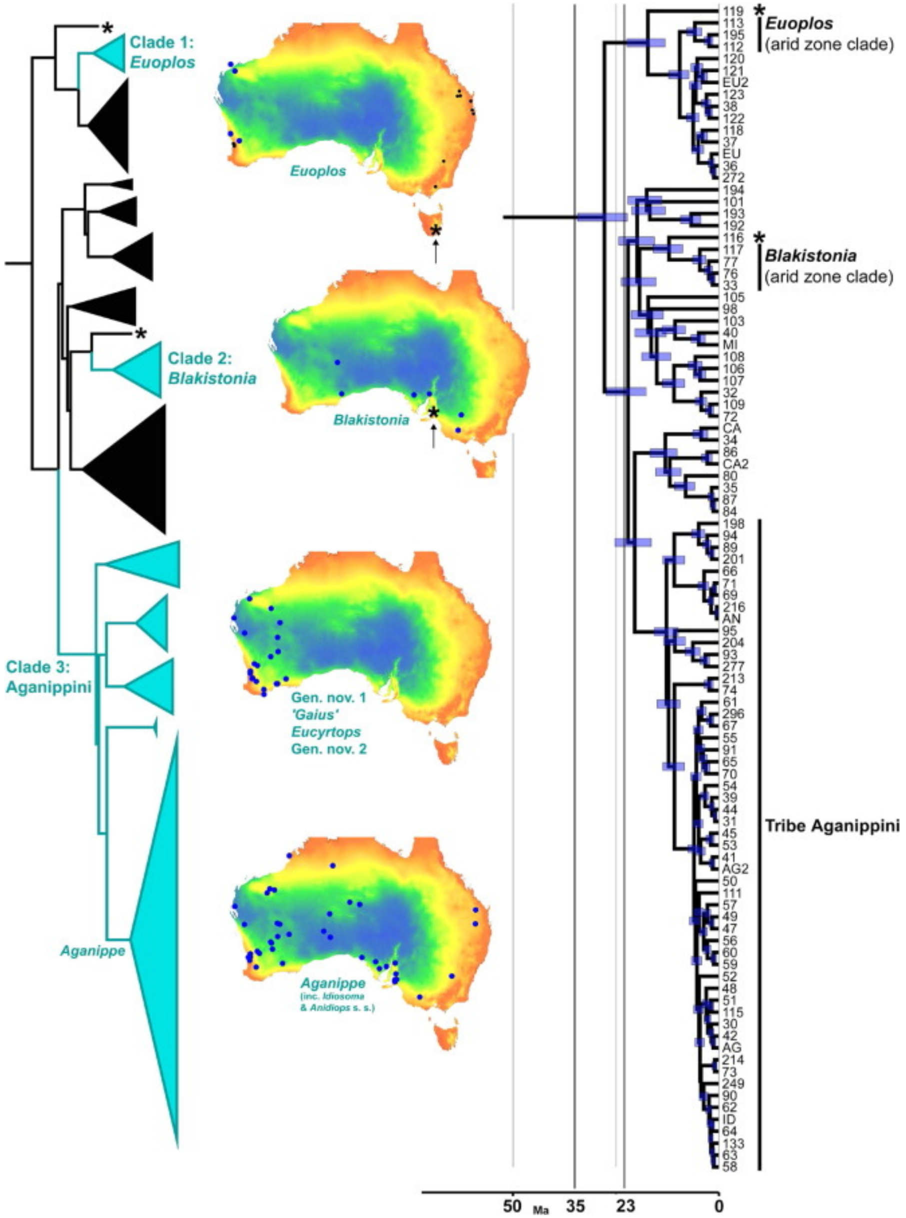


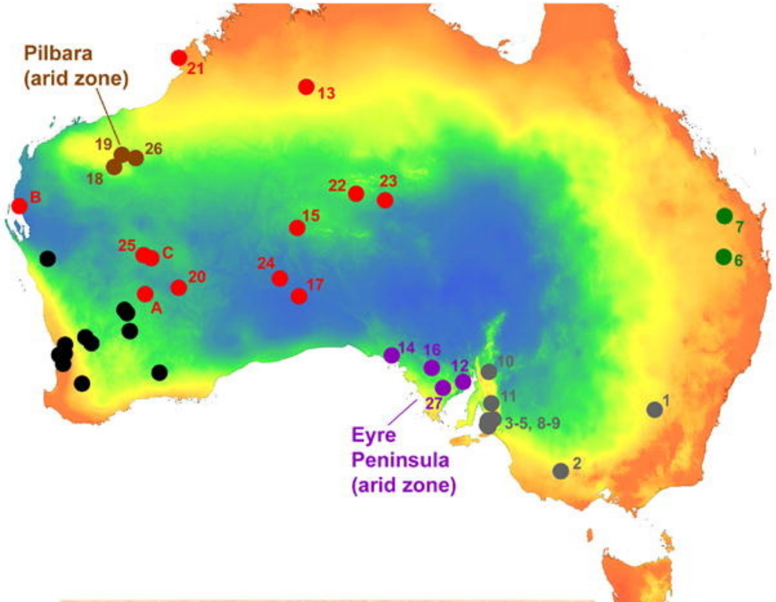
Bidegaray-Batista et al 2014



Idiopidae Climate: Aridification of Australia

Trapdoor spiders





Rix et al 2017

Summary

Amalgamation of Gondwana 520 – 510 Ma
- southern hemisphere

Laurentia, Baltica, Siberia – in the north
- formed Laurasia in Paleozoic, ~ 300 Ma

Late Paleozoic – Pangea formation
- lasted ~ 100 Myr

Pangea breakup
- Central Atlantic ridge ~ 200 Ma

Lower Jurassic ~ 180 Ma E/W Gondwana breakup
Upper Jurassic ~ 160 Ma India-Madagascar/Antarctica
~ 160 Ma Antarctica/Australia
Lower Cretaceous ~ 140 – 130 Ma S America/Africa
Upper Cretaceous ~ 80 - 90 Ma Madagascar/ India
~ 50 Ma India collided with Asia

Laurasia breakup ~55 Ma
N Am land bridge ~ 25 ma

Hercynian belt breakup 30 - 25Ma

Beatic Rif broke of Sardinina + Corsica ~20Ma
→ Sardinia + Corsica collided with Italy,

10 – 5 Ma final separation of Sardinia + It

Messinian Salinity crisis 5.93 – 5.3 Ma

5.3 Ma Opening of Strait of Gibraltar

Last glaciation: 2.58 Ma to 12 000 ya