Trends of body size evolution in the fossil record of insular Southeast Asia

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ISOLARIO

Island biodiversity and cultural evolution

Naturalis Biodiversity Center

European Union
European Social Fund
OPERATIONAL PROGRAMME
EDUCATION AND LIFELONG LEARNING
investing in knowledge society
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MANAGING AUTHORITY
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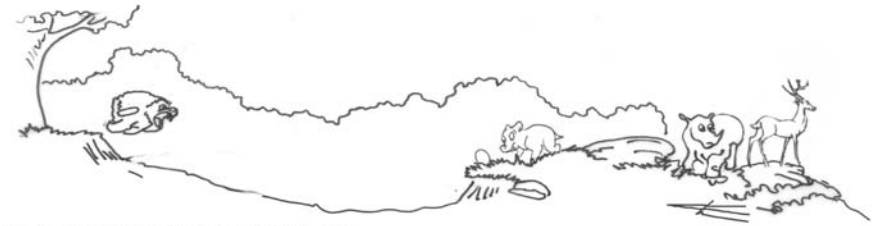
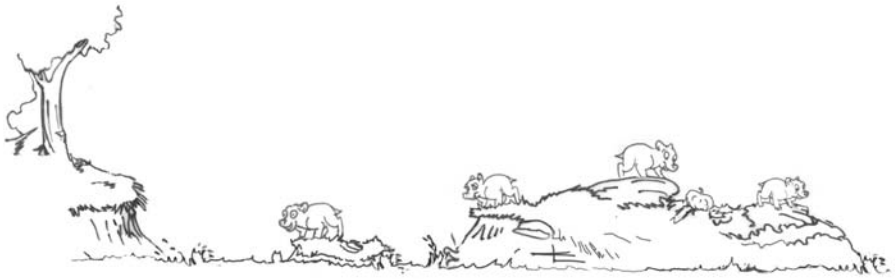
Co-financed by Greece and the European Union

Aim of our project Isolario:
morphological changes in insular endemics
the impact of humans on endemic island species (and vice versa)



I. Peninsula with mainland fauna



II. Isolation and ecological melt-down

III. Colonization of the island

IV. Adaptation to the island environment

V. Sea-level rise and loss of habital

VI .Human occupation and their impact

Study especially episodes IV to VI

Applied to South East Asia

First of all, which fossil, pre-Holocene faunas are known from this area?
Note: fossil faunas are often incomplete (fossilization is a rare process), and taxonomy of fossil species is necessarily less diverse because morphological distinctions based on coat color and pattern, tail tuft, vocalizations, genetic composition etc do not play a role

© *Hoe dieren op eilanden evolueren*; Veen Magazines, 2009


Java

Java, Early Pleistocene

Faunal level: Satir (Bumiayu area)

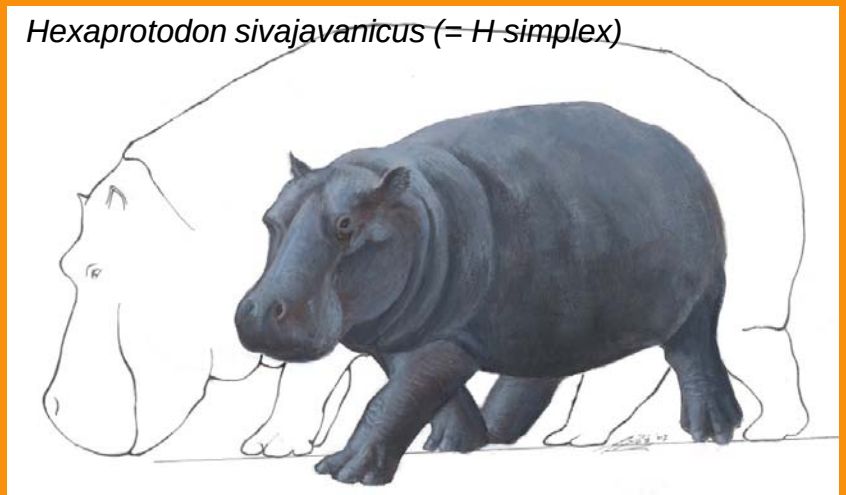
Only endemics (on the species level)

Unbalanced fauna (typical island fauna with hippos, deer and elephants), ‘swampy’ (pollen studies)

Sinomastodon bumiajuensis

3

Hexaprotodon sivajavanicus (= H simplex)



Fossils:

Mastodon (*Sinomastodon bumiajuensis)*
Dwarf hippo (small *Hexaprotodon sivajavanicus*, aka *H. simplex)*
Deer (indet)
Giant tortoise (*Colossochelys*)
? Tree-mouse? (*Chiropodomys*)

?pygmy stegodont? (isolated, scattered findings: Sambungmacan, Cirebon, Carian, Jetis), *Stegodon hypsilophus* of Hooijer 1954
Maybe also *Stegoloxodon indonesicus* from Ci Panggloseran (Bumiayu area)

Java, Middle Pleistocene

Faunal levels: Ci Saat - Trinil HK– Kedung Brubus – Ngandong

Progressively more balanced, marginally impovered ('filtered') faunas (mainland-like), *Homo erectus – Stegodon* faunas, "dry, open woodland"

Endemics on (sub)species level, strongly related to 'Siwaliks' fauna of India

Axis lydekkeri

Duboisia santeng

Elephas hysudrindicus

Bubalus palaeokerabau

Stegodon trigonocephalus

Fossils:

Homo erectus, large and small herbivores (*Bubalus*, *Bibos*, *Axis*, *Muntiacus*, *Tapirus*, *Duboisia*, *Elephas*, *Stegodon*, *Rhinoceros* 2x), large and small carnivores (*Pachycrocuta*, *Panthera* 2x, *Mececyon*, *Lutrogale* 2x), pigs (*Sus* 2x), *Macaca*, rodents (*Hystrix brachyura*, *Maxomys*, five (!) native *Rattus* species), birds (e.g. *Leptoptilos titan*), etcetera.

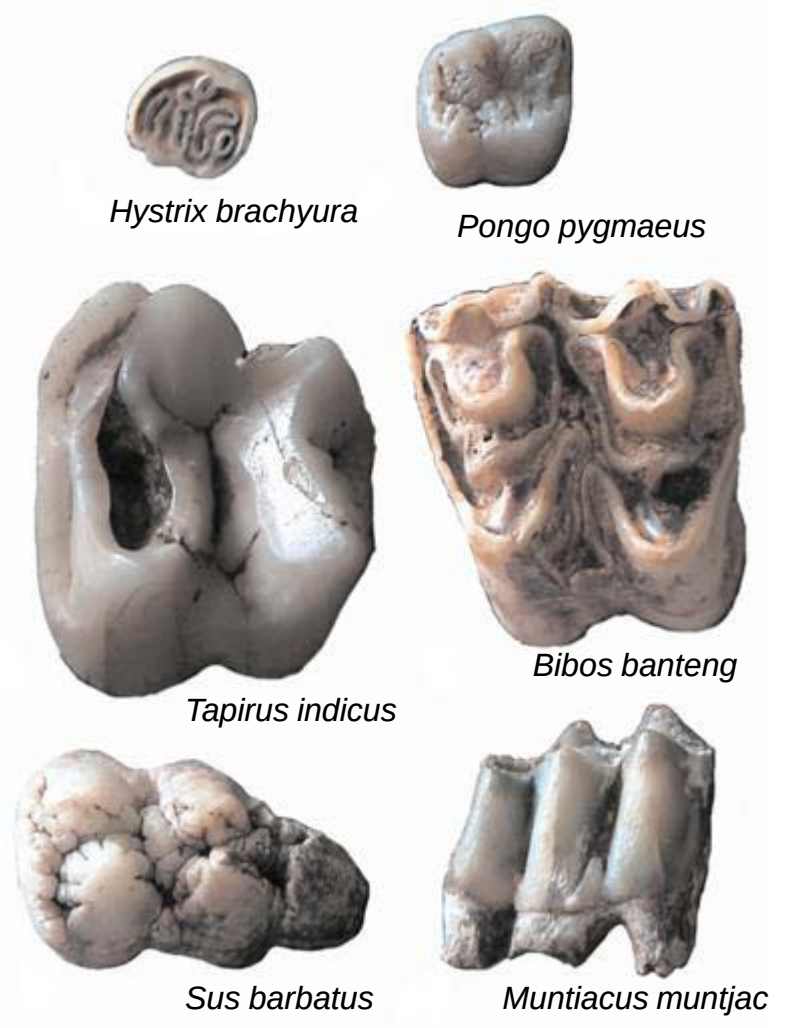
Homo erectus (NBC)

Java, Late Pleistocene

Faunal level: Punung

Balanced mainland fauna ('tropical rainforest'), *Pongo* – *Homo* sapiens fauna

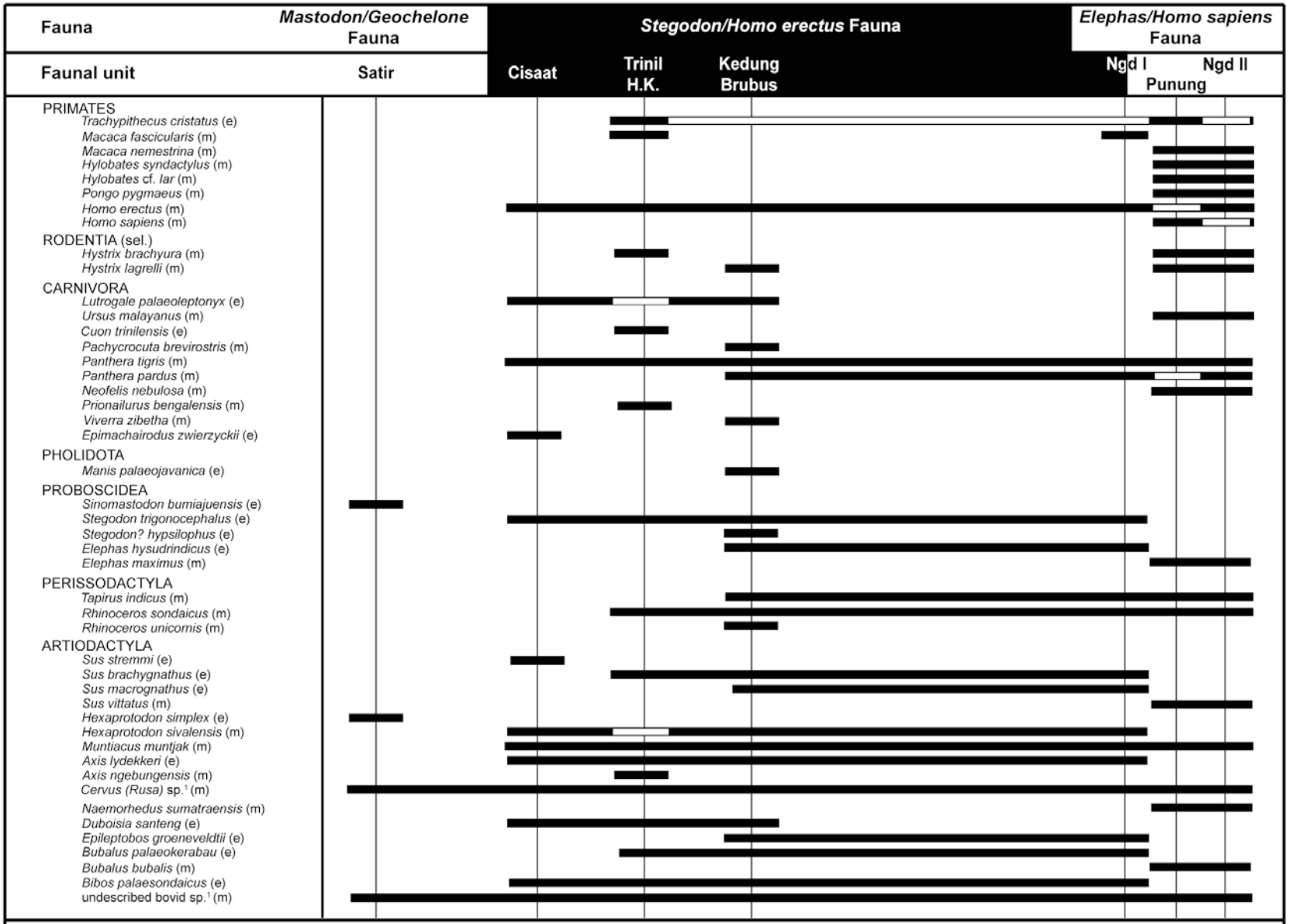
No endemics, same species as (extant) SA mainland, including Sumatra, Sino-Malayan elements; taphonomic peculiarity: only tooth crowns, rest completely eaten by porcupines



Fossils:

Homo sapiens, and further:
Elephas maximus, other primates (*Pongo*, *Hylobates*, *Macaca*, *Trachypithecus*), carnivores (*Panthera tigris sondaica*, *Helarctos malayanus*), ruminants (*Bubalis bubalus*, *Bibos banteng*, *Nemorhaedus sumatraensis*, *Muntiacus muntjac*), tapir (*Tapirus*), pig (*Sus barbatus*), rhinos (*Rhinoceros sondaicus* / *Dicerorhinos sumatrensis*), rodents (*Hystrix*, *Echinosorex*, *Leopoldamys*, *Rattus*), etc
etc……..

Macromammal Stratigraphy



Hertler et al. (in prep.)

Punung

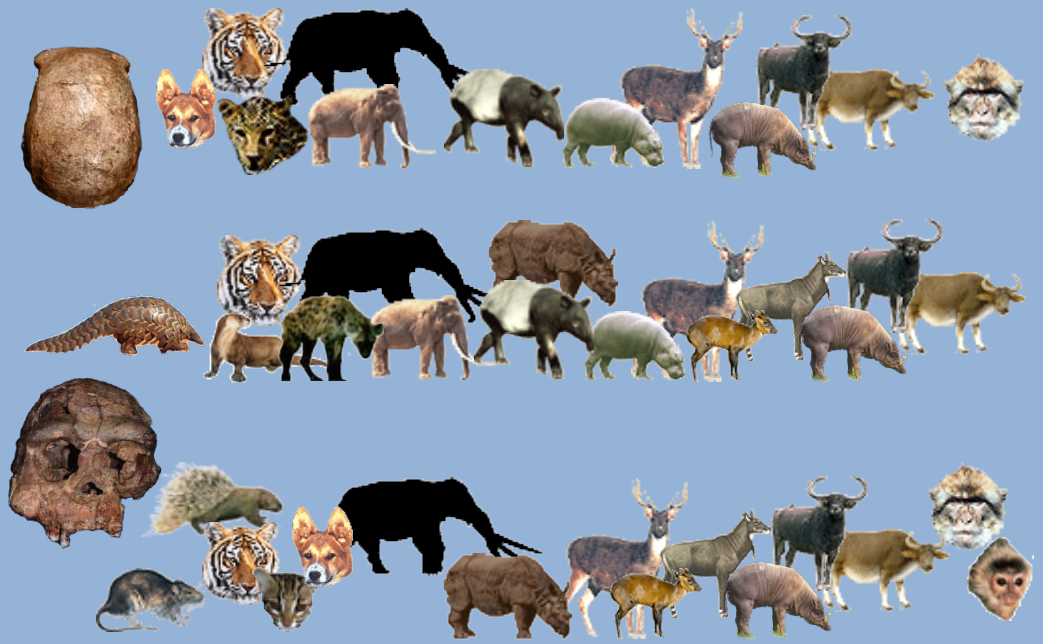
125 ka

Elephas/
Homo sapiens
Fauna

Ngandong

Kedung Brubus

Trinil HK



Stegodon/
Homo erectus
Fauna

Cisaat

1.6 Ma

Satir

1.9 Ma

Mastodon/
Geochelone
Fauna

Flores

Flores, Early Pleistocene

Unbalanced fauna (typical island fauna)

Localities: Tangi Talo (Soa Basin), Ola Bula Member A, Wolo Sege

Endemics on the species level

Stegodon sondaari (Van den Bergh, 1999)

Fossils:

Dwarf stegodont (*Stegodon sondaari*)
Komodo dragon (*Varanus komodoensis*)
Giant tortoise (*Collosochelys azzizi*)

Inferred:
Homo (as indicated by artifacts in situ at Wolo Sege)

Varanus komodoensis (Museum Senckenberg, Frankfurt am Main

Flores, Middle Pleistocene

Unbalanced fauna (typical island fauna)

Localities: Dhozo Dalu, Ola Bula Member B, Mata Menge, Boa Leza

Endemics on the species and genus level

Stegodon florensis florensis (NBC)

<u>New colonisation</u>:

Small stegodont (*Stegodon florensis florensis*)
Humans (*Homo erectus*, inferred from artefacts)
Middle-sized mice (*Hooijeromys nusatenggara*)
Crocodile (perhaps resident)

<u>Resident taxon:</u>
Komodo dragon (*Varanus komodoensis*)

Flores, Late Pleistocene (c 0.1-0.02 Ma)

Locality: Liang Bua

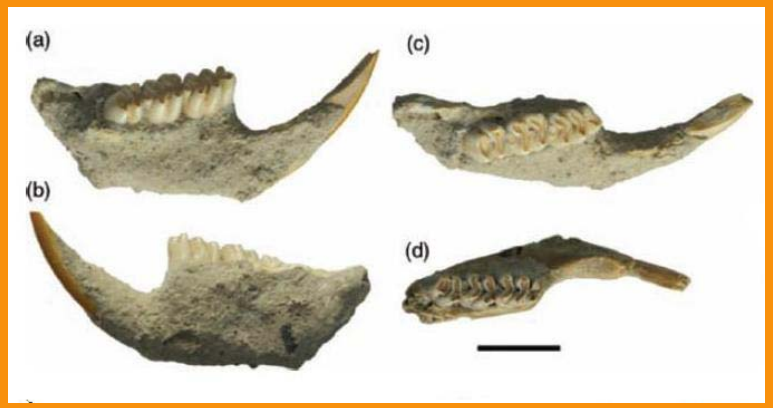
Endemics on the species and genus level

Unbalanced fauna (typical island fauna)

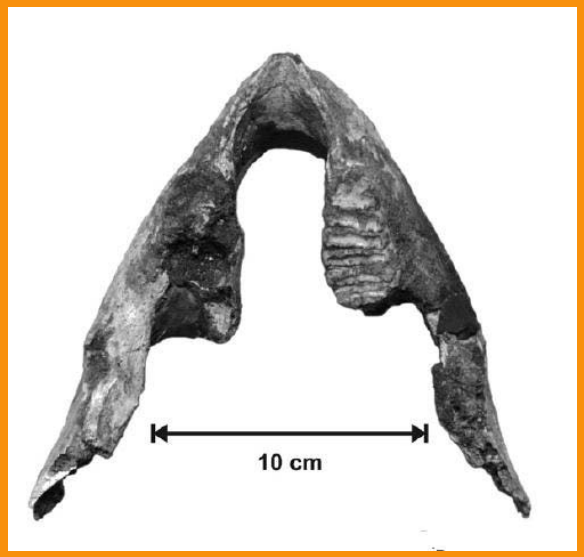
<u>In situ evolution:</u>
Dwarf stegodont (*Stegodon florensis insularis*)
Humans (*Homo floresiensis*)
Giant mice (*Papagomys armandvillei*, *P theodorverhoeveni*) and large mice rats (-> *Paulamys naso*, *Komodomys rintjanus*)
Likely as well: *Spelaeomys florensis*, *Varanus hooijeri*, endemic birds (e.g. *Leptoptilus robustus*) and bats

<u>New colonization:</u>
Small rat (-> *Rattus hainaldi*)

<u>Resident taxon:</u>
Komodo dragon (*Varanus komodoensis*)



Papgomys armandvillei (a,b), *P. theodorverhoeveni*

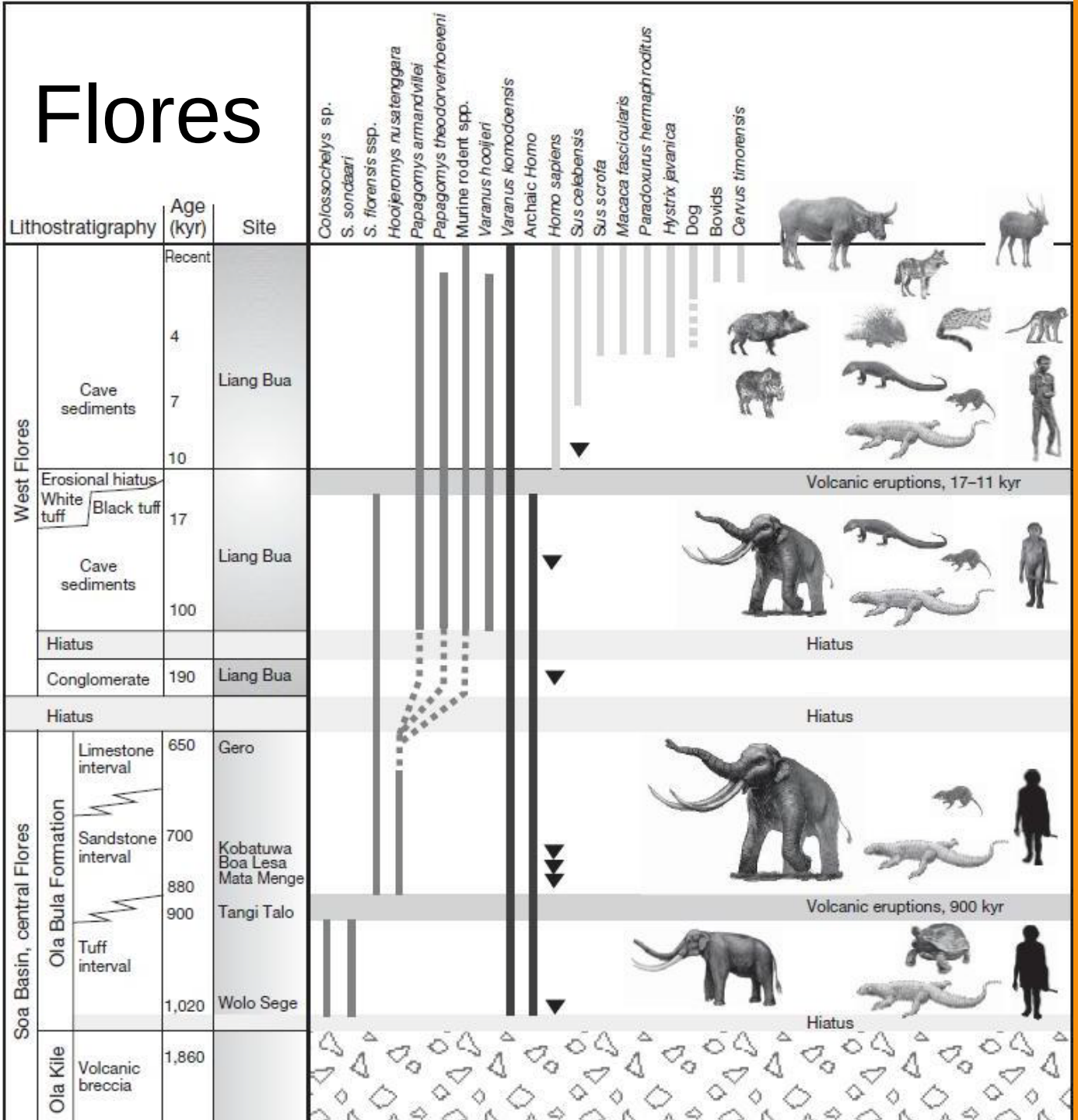


S florensis insularis, Van den Bergh et al., QI 2008

Artefact (Verhoeven collection, NBC)

H floresiensis, cast, photo Paul Storm

Flores



Timor, Pleistocene

Localities: Liang Leluat, Fatak Laen

Endemics on the genus and species level

Unbalanced fauna (typical island fauna)

Coryphomys buehleri (RU Utrecht)

Varanus sp.(vertebra)

Stegodon timorensis (cast)

Fossils:

Dwarf stegodon (*Stegodon timorensis*)
Giant tortoise (*Collosochelys*)
Smalll stegodon (*S timorensis* subsp.D)
Giant monitor (*Varanus* sp.)
Giant rats (*Coryphomys buehleri*, *C. musseri*, 3 more genera under study by Ken Aplin)
Medium- and normal-sized murids (4 genera, under study by Ken Aplin)

Extrapolated:
Shrew (*Crocidura tenuis*)

Philippines

Philippines (Greater Luzon), Pleistocene

Endemics on the genus and species level

Stegodon luzonensis (Museum Manila)

Cervus mariannus

Sus philippinensis

Unbalanced fauna (typical island fauna)

<u>Fossils</u>:

Dwarf proboscideans (*S luzonensis*, *Elephas beyeri*)

Rhinoceros (*Rhinoceros philippinensis*)

Dwarf ruminants (*Bubalus "mindorensis"*, small sambar, could be *Cervus mariannus*)

Pig (*Celebochoerus cagayanensis*)

Celebochoerus cagayanensis (Museum Manila)

<u>Extrapolated</u>:

Rodents (28+ "Old Endemics", 6 "New Endemics")

Shrew (*Crocidura grayi*)

Deer (*Cervus mariannus*)

Pig (*Sus philippinensis*)

Philippines (Greater Negros-Panay), Pleistocene

Endemics on the genus and species level

Unbalanced fauna (typical island fauna)

Cervus sp. (Masbate; Manila Museum)

Rattus everetti (Masbate; Manila Museum)

<u>Fossils</u>:

Dwarf buffalo (*Bubalus cebuensis*)
Dwarf proboscideans (*Elephas* and/or *Stegodon*)
Forest rat (*Rattus everetti*)
Dwarf deer (*Cervus* sp., could be *C alfredi)*

<u>Extrapolated</u>:

Rodents (1 “Old Endemics”, 2 more Rattus)
Shrews (-> *Crocidura mindorus*, *C negrina*, *C panayensis*)
Small deer (*Cervus alfredi*)
Pig (*Sus cebifrons*)
Flying lemur (*Cynocephalus volans*)

Sus cebifrons

Cervus alfredi

Philippines (Greater Mindanao), Pleistocene

Unbalanced fauna (typical island fauna)

Endemics on the genus and species level

Urogale everetti (©Field Museum)

Carlito syrichta

Fossils:
Dwarf proboscideans (*Stegodon mindanensis*)

Extrapolated:
Murids (10 “Old Endemics”, 9 “New Endemics”),
Moonrats (-> *Podogymnura truei*, *P aureospinula*),
Treeshrew (*Urogale everetti*)
Flying lemur (*Cynocephalus volans*)
Pig (*Sus philippinensis*)
Small deer (*Cervus mariannus*)
Shrews (-> *Crocidura beatus*, *C grandis*)
Tarsier (*Tarsius* (or *Carlito*) *syrichta*)
Sciurids (*Sundasciurus philippensis*, *Petinomys crinitus*, *Exilisciurus concinnus*)

Podogymnura truei (©Field Museum)

Sulawesi

Sulawesi, Early Pleistocene

Unbalanced fauna (typical island fauna)

Faunal level: Walanae faunal unit)
Endemics on the genus and species level

<u>Fossil</u>:
Dwarf proboscideans (*Stegodon sompoensis*, *Stegolophodon celebensis*)
Giant pig (*Celebochoerus heekereni*)
Giant tortoise (*Collosochelys*)
Soft-shell tortoise (Trionychidae)
crocodile

Celebochoerus heekereni (© H. Brinkerink)

Stegolophodon celebensis

Sulawesi, Middle and Late Pleistocene

Unbalanced fauna (typical island fauna)

Faunal level: Tanrung and later
Endemics on the genus and species level

Celebochoerus

Sus celebensis

Anoa

Tarsius spp.

Babyroussa

<u>Fossils (Middle Pleistocene, Tanrung FU):</u>
Giant pig (*Celebochoerus*, short-legged form)
Middle-sized stegodon (*Stegodon* sp. B)
Dwarf elephant (*Elephas* sp.)

<u>Fossils (Late Pleistocene; mainly surface findings, same area):</u>
Anoa sp. (-> *Anoa depressicornis* + *A quarlesi*)
Pig (*Sus celebensis*)
+ lithic artefacts

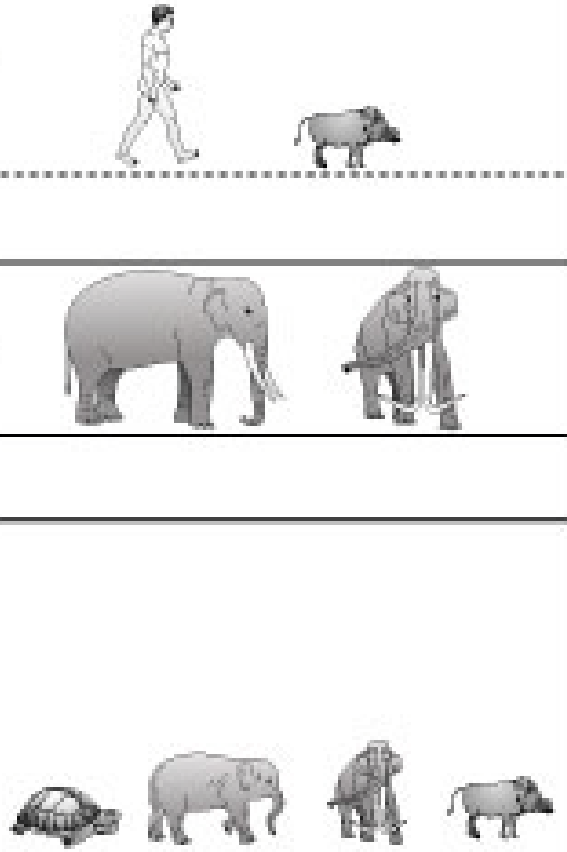
<u>Extrapolated (Late Pleistocene):</u>
Cuscus (-> *Ailurops ursinus*)
Pig (*Babyroussa*, possibly since Oligocene)
Tarsiers (-> *Tarsius* spp.)
Palm civet (-> *Macrogalidia*)
Macaques (-> *Macaca* spp.)
Shrews (*Crocidura* spp., two waves, “Old -” and “New Endemics”)
Squirrels (-> 3 genera, *Rubrisciurus*, *Prosciurillus*, *Hyosciurus*, waves?)
Murids (-> 36 endemic species / genera)

Species

Stratigraphy

Lithostratigraphic Unit	Age	Faunal unit
Cave deposits Toalian sites	Holocene	Subrecent to Recent
Colluvium	Late Pleistocene or Holocene	
Hiatus		
Tanrung Formation	Late or Middle Pleistocene	Tanrung
Hiatus		
Walanae Formation, Beru member, Subunit B	Early Pleistocene	Walanae
Walanae Formation, Beru member, Subunit A	Late Pliocene	
2,5 Ma		
Walanae Formation, Samaoling member	Late Pliocene	

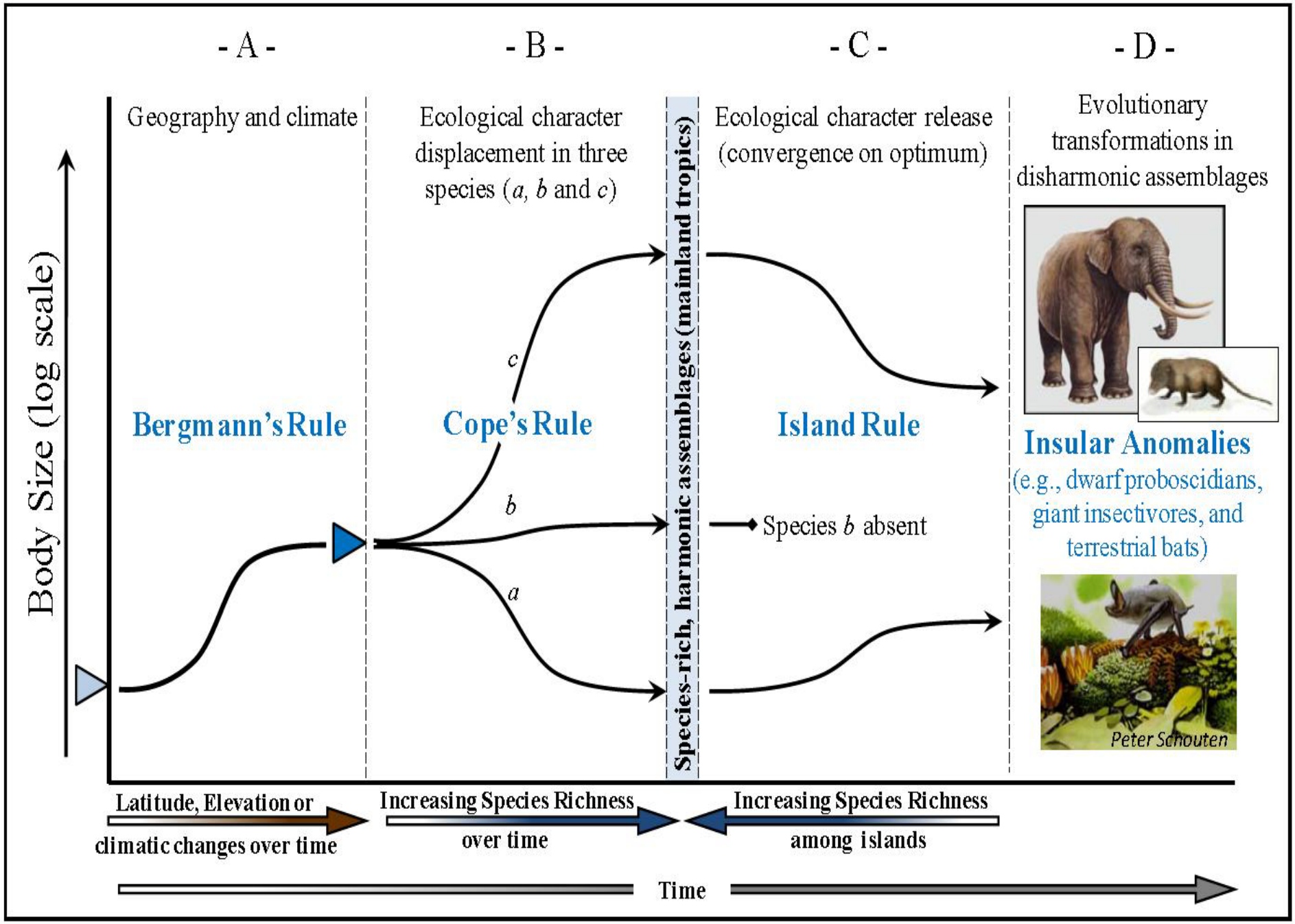
Sulawesi, Pleistocene



Do our observations on the fossil record of Southeast Asian islands fit into the island rule?

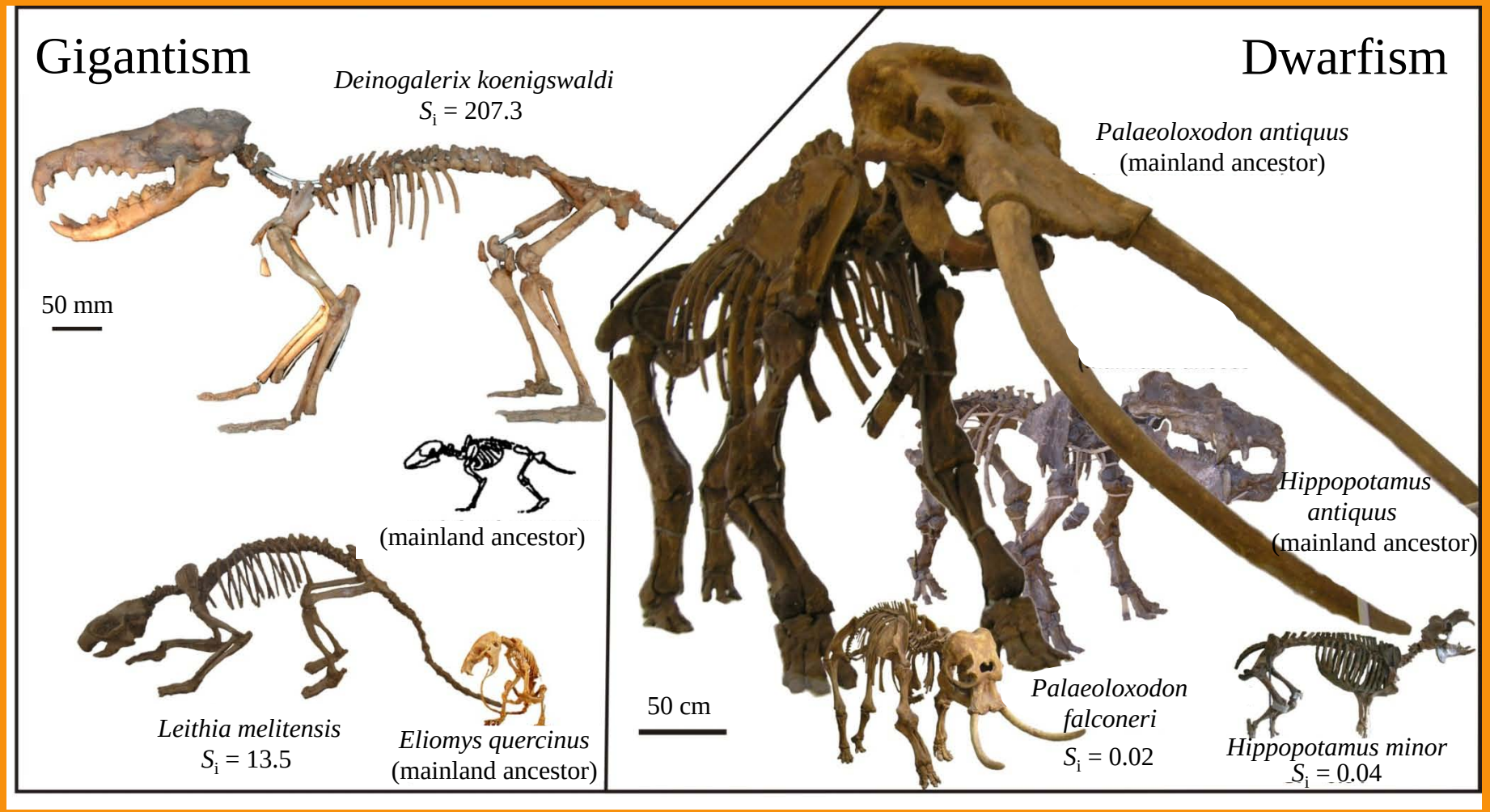
Is there a difference between extant mammals (introduced and native) and the fossil record?

Figure 3. A graphical model of body size evolution over space and time.



The fossil record holds spectacular cases

For insular SA: *Coryphomys buehleri*, *Stegodon sondaari*, *Homo floresiensis*, etc etc



(S_i = mass of insular form divided by that of its ancestral or mainland form

Lomolino et al 2013 Supporting Information and Lyras et al 2010

Body size changes in insular deer and bovids

Duboisia santeng / *Boselaphus tragocamelus* Si =49/180, **Si=0.27**

Bubalus cebuensis / *Bubalus bubalis* Si =157/950, **Si=0.17**

Body size reduction in insular Proboscidea

Stegodon trigonocephalus / *S. ganesa* Si=2773/3680, **Si=0.75**

Stegodon florensis / *S. ganesa* Si=1738/3680, **Si=0.47**

Stegodon sompoensis / *S. ganesa* Si=724/3680, **Si=0.20**

Body size evolution in insular Carnivora

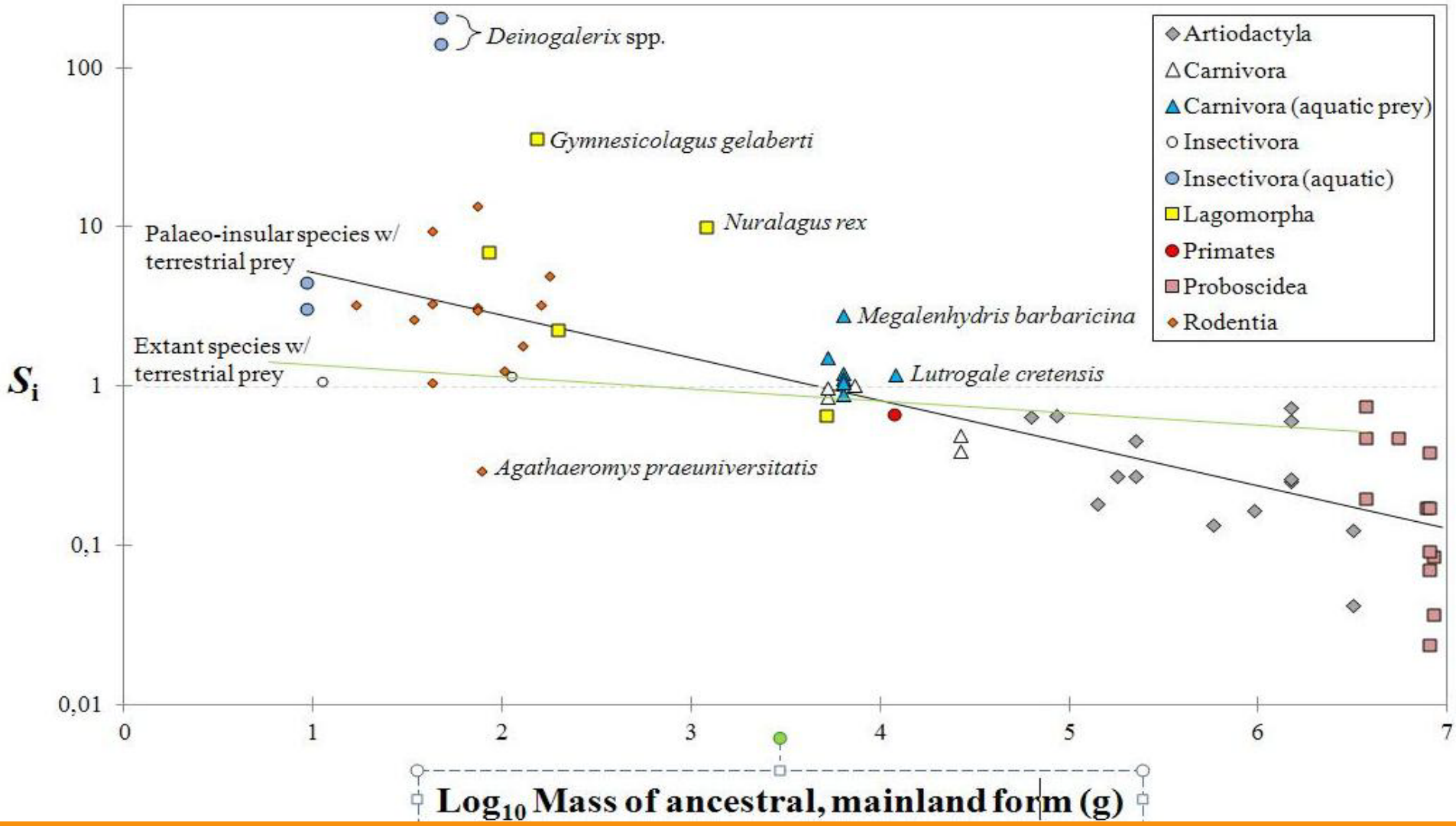
Mececyon merriami / *X. lycaonoides*, Si=10.5/26.6, **Si=0.39**

Body size changes that cannot be estimated

E.g. *Anoa quarlesi*, *A depressicornis*, *Coryphomys buehleri, Homo floresiensis, Celebochoerus* (unknown or unavailable mainland ancestors)

E.g. *Elephas beyeri, Lutrogale palaeoleptonix, L robusta* (unsuitable material for reliable body mass estimations)

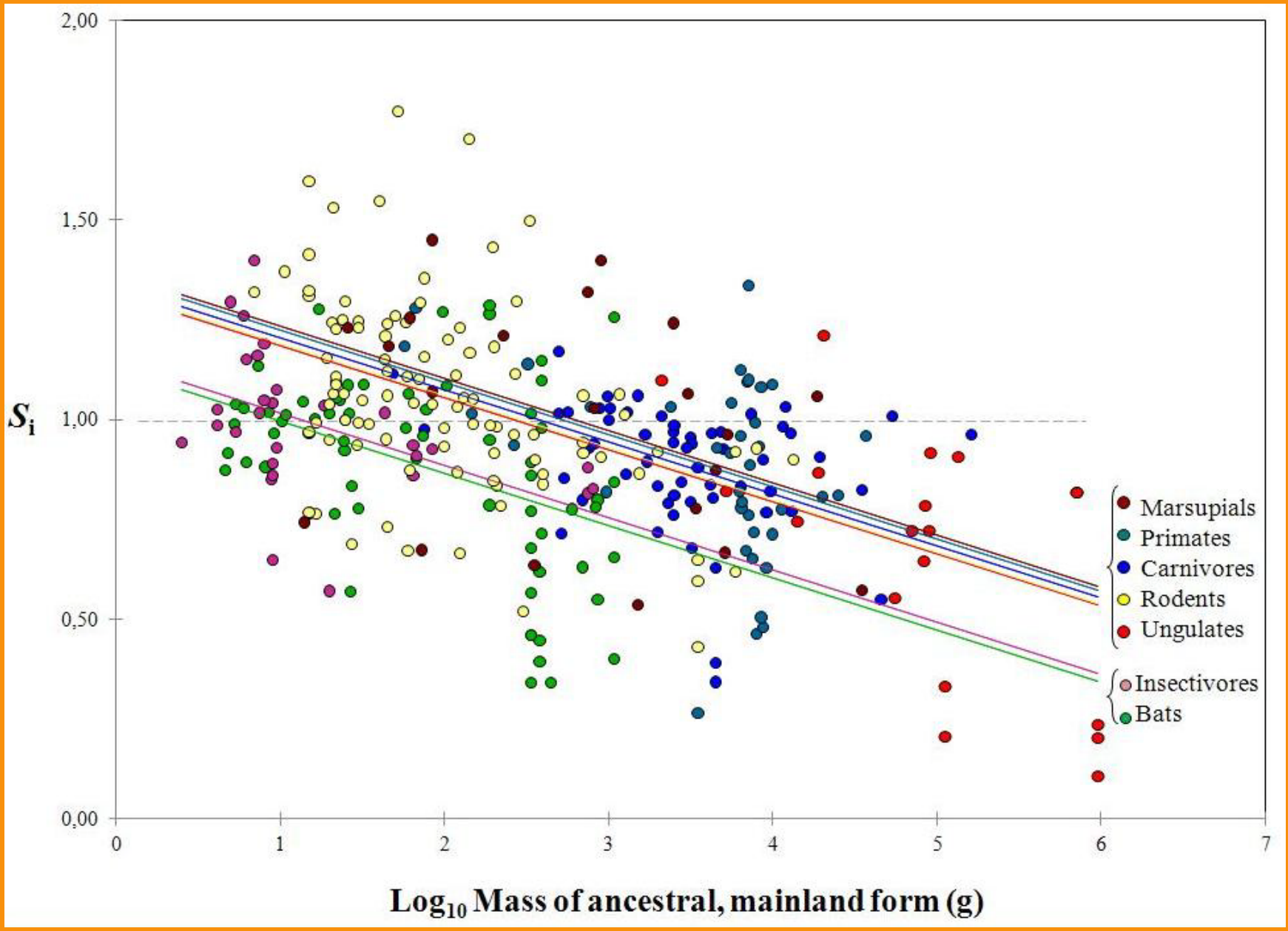
Figure 5 Body size variation among 63 species of palaeo-insular mammals (double le-logarithmic scale) is consistent with the island rule, but the slope of the relationship between insular body size and mass of the ancestral, mainland species is significantly steeper (more negative) for palaeo-insular species (solid, black line) than for extant species of mammals (solid, green line)



Pattern (island rule, or better, island trend) is clear (dwarfism of large animals, gigantism of small animals)

However, testing of extant insular mammals (376 species across 7 orders) shows a considerable scatter !

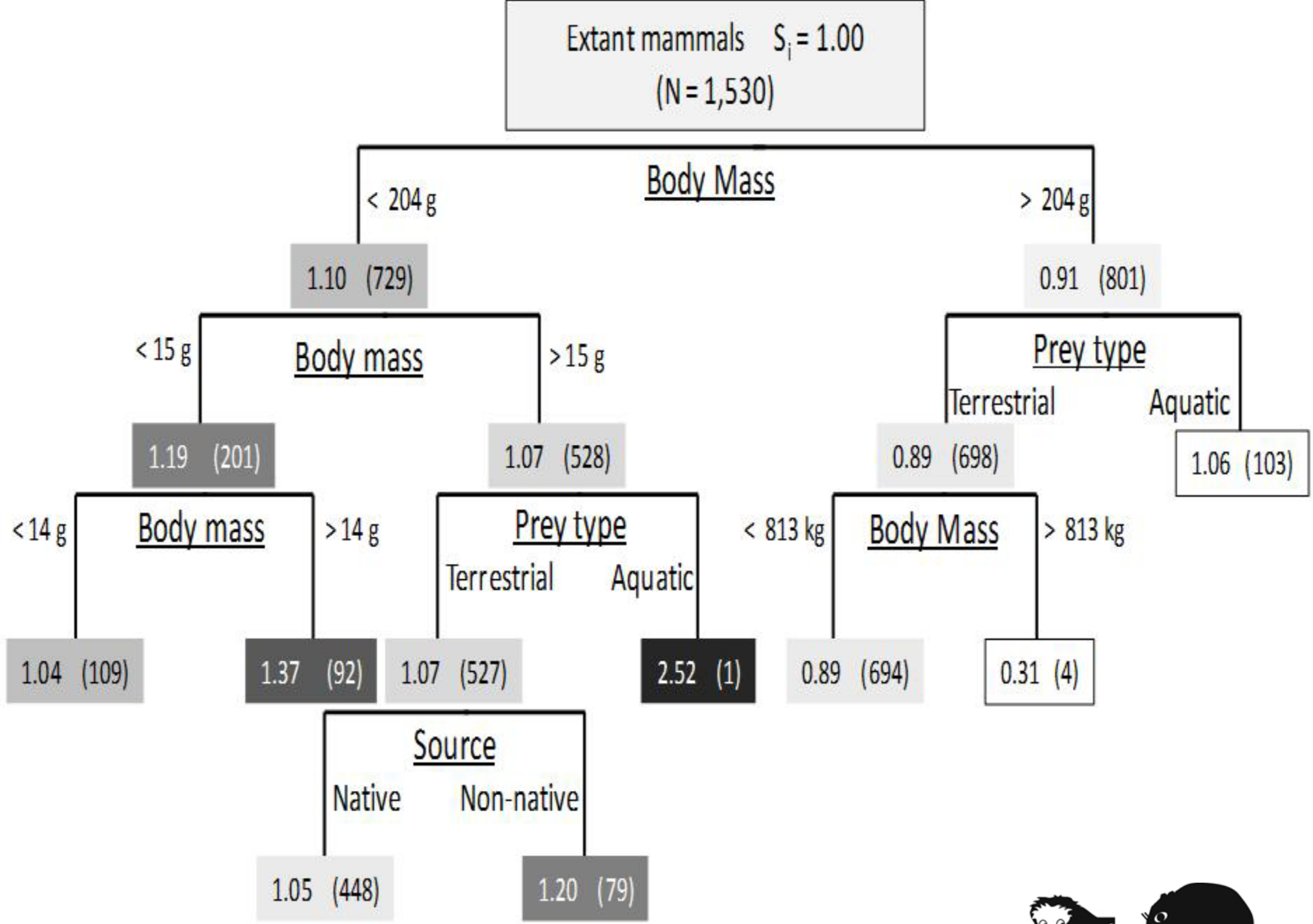
Fig 2 Lomolino et al (2013) Of mice and mammoths: generality and antiquity of the island rule – J of Biogeography



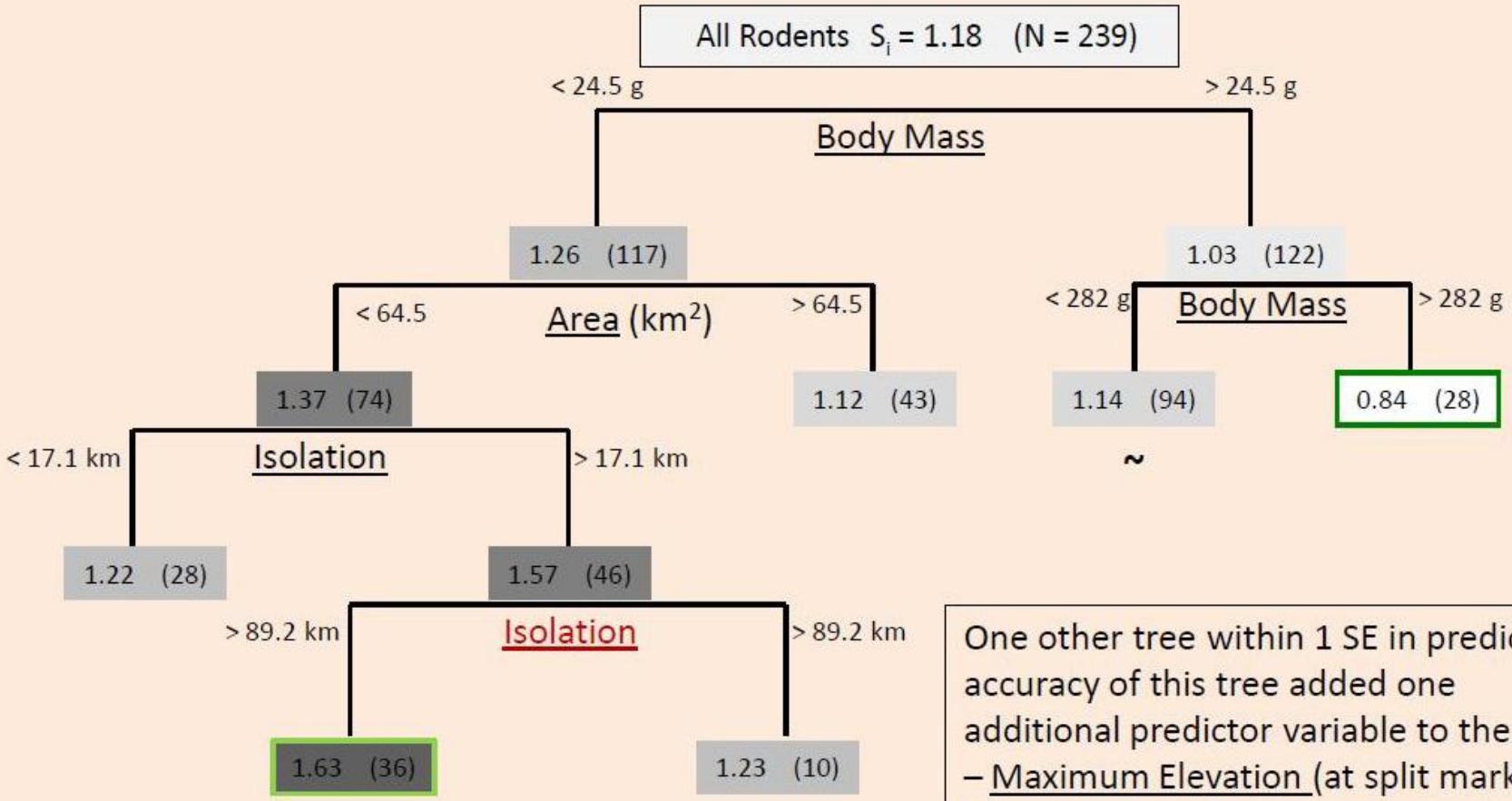
Differences in the island rule pattern among the seven orders of extant mammals with at least 19 species. The intercept of this relationship was significantly lower for bats and for insectivores in comparison to the other orders

Several factors

Time in isolation
Type of resource (mainly terrestrial versus aquatic)
Nature of ecological assemblage (competitors / predators)
Island area (habitat diversity) and isolation (immigrant selection)


Extant mammals S_i = 1.00
(N = 1,530)
Body Mass
< 204 g
> 204 g
1.10 (729)
0.91 (801)
Body mass
< 15 g
>15 g
Prey type
Terrestrial
Aquatic
1.19 (201)
1.07 (528)
0.89 (698)
1.06 (103)
Body mass
< 14 g
>14 g
Prey type
Terrestrial
Aquatic
< 813 kg
Body Mass
> 813 kg
1.04 (109)
1.37 (92)
1.07 (527)
2.52 (1)
0.89 (694)
0.31 (4)
Source
Native
Non-native
1.05 (448)
1.20 (79)

Rodentia: Ecological, Geographic and Climatic Variables (note latitude).

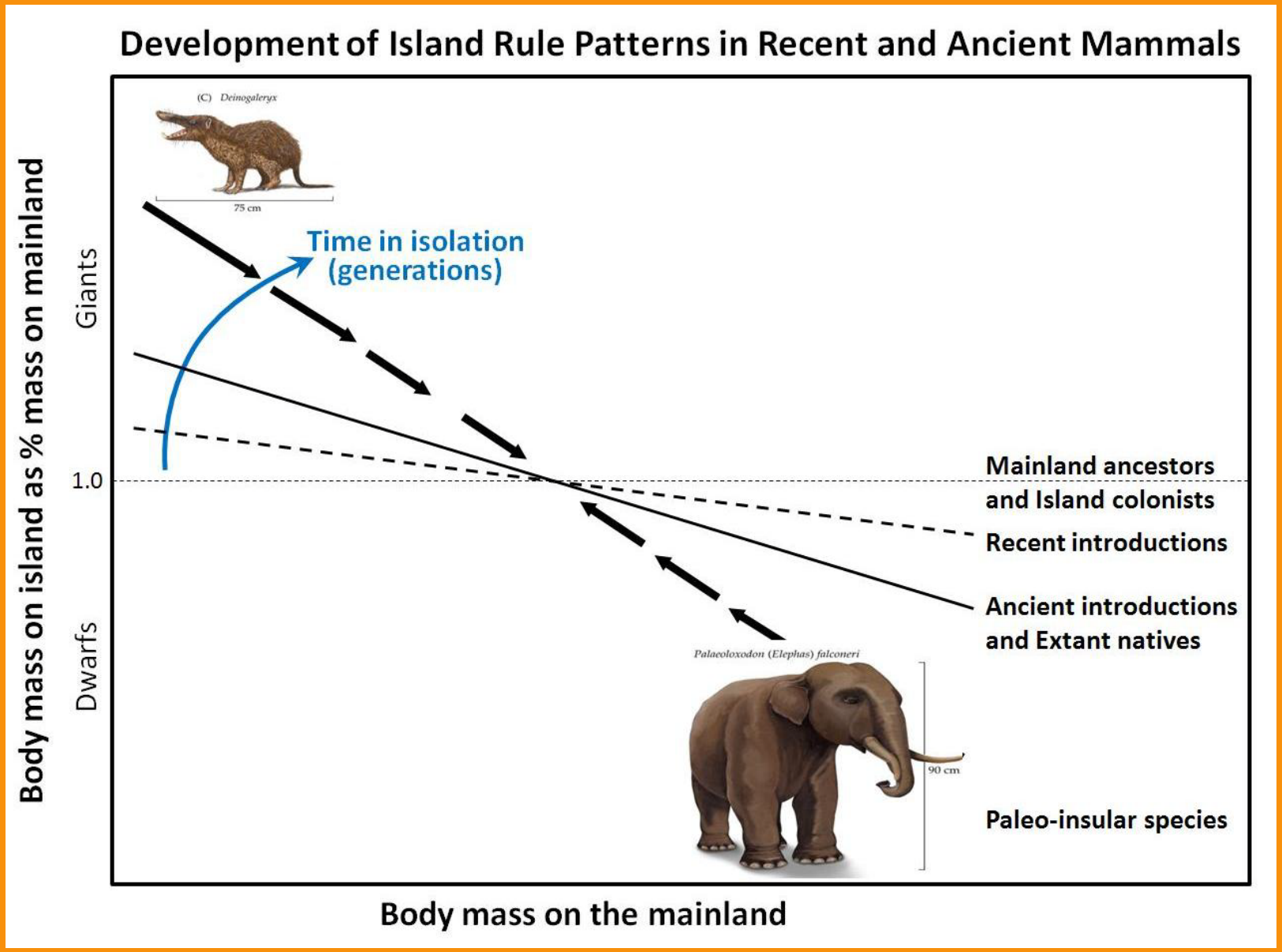


One other tree within 1 SE in prediction accuracy of this tree added one additional predictor variable to the tree – Maximum Elevation (at split marked with ~, = rodents ranging in size from 24.5 to 282 g).

Color code:
Red – counter or partially contrary to predictions (modal patterns)

* Green outlines denote most extreme gigantism or dwarfism.

Fig 1 Lomolino et al (2013) Of mice and mammoths: generality and antiquity of the island rule – J of Biogeogr. (in press)



Because body size evolution of insular mammals should develop with time in isolation, the slope of the line describing the relationship between relative body size of insular mammals (S_i) and mass of mainland or ancestral forms (M) should decrease (become steeper) with age of insular populations (S_i = mass of insular population / M).

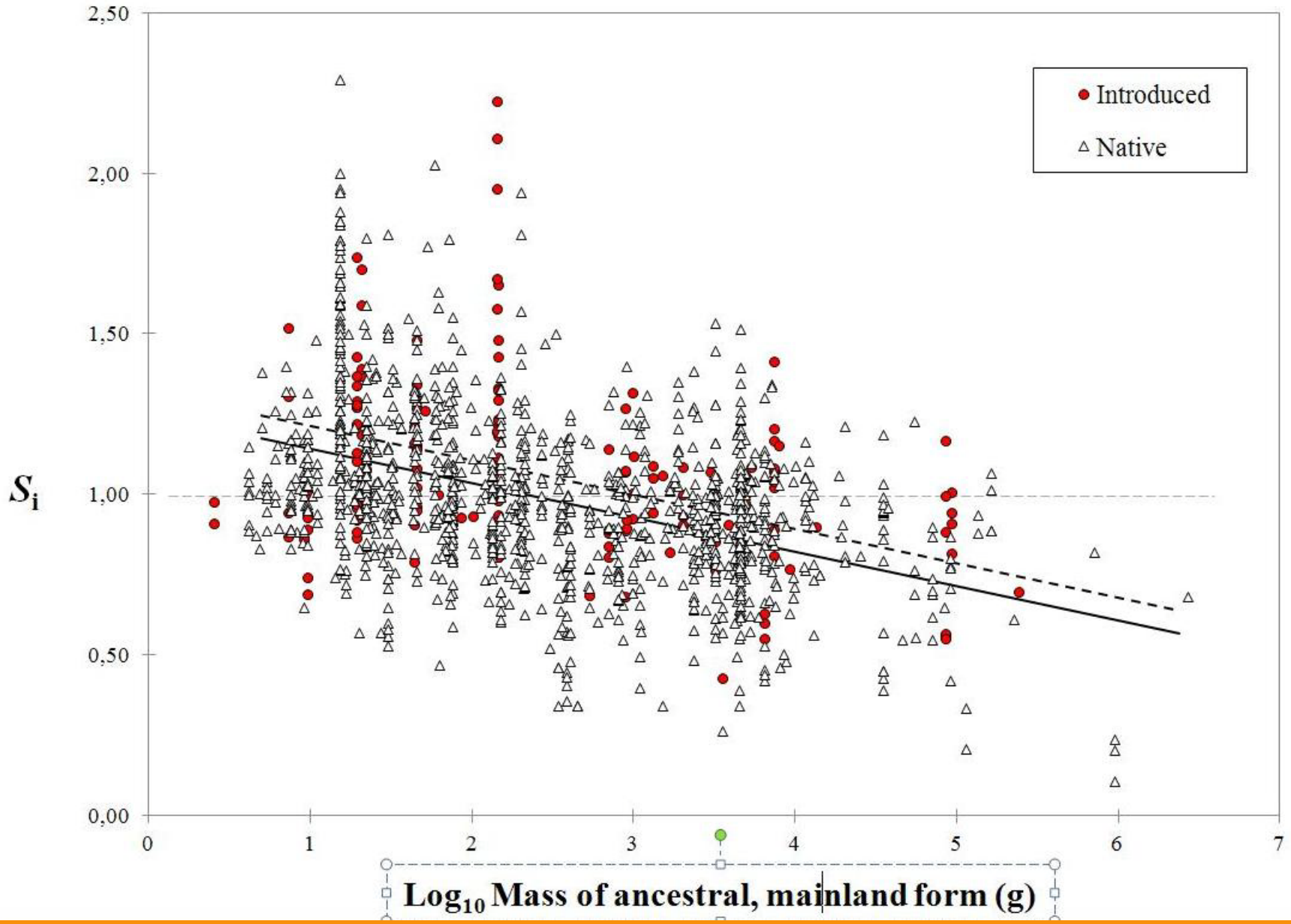

2,50
2,00
1,50
1,00
0,50
0,00
S_i
0
1
2
3
4
5
6
7
Introduced
Native
Log_{10} Mass of ancestral, mainland form (g)

Figure 4 Mammals utilizing aquatic prey tended to exhibit higher insular body sizes (after correcting for mass of ancestral populations), likely reflecting the high subsidy of marine productivity for insular populations. This difference in intercepts of the regression lines was consistent across all extant mammals

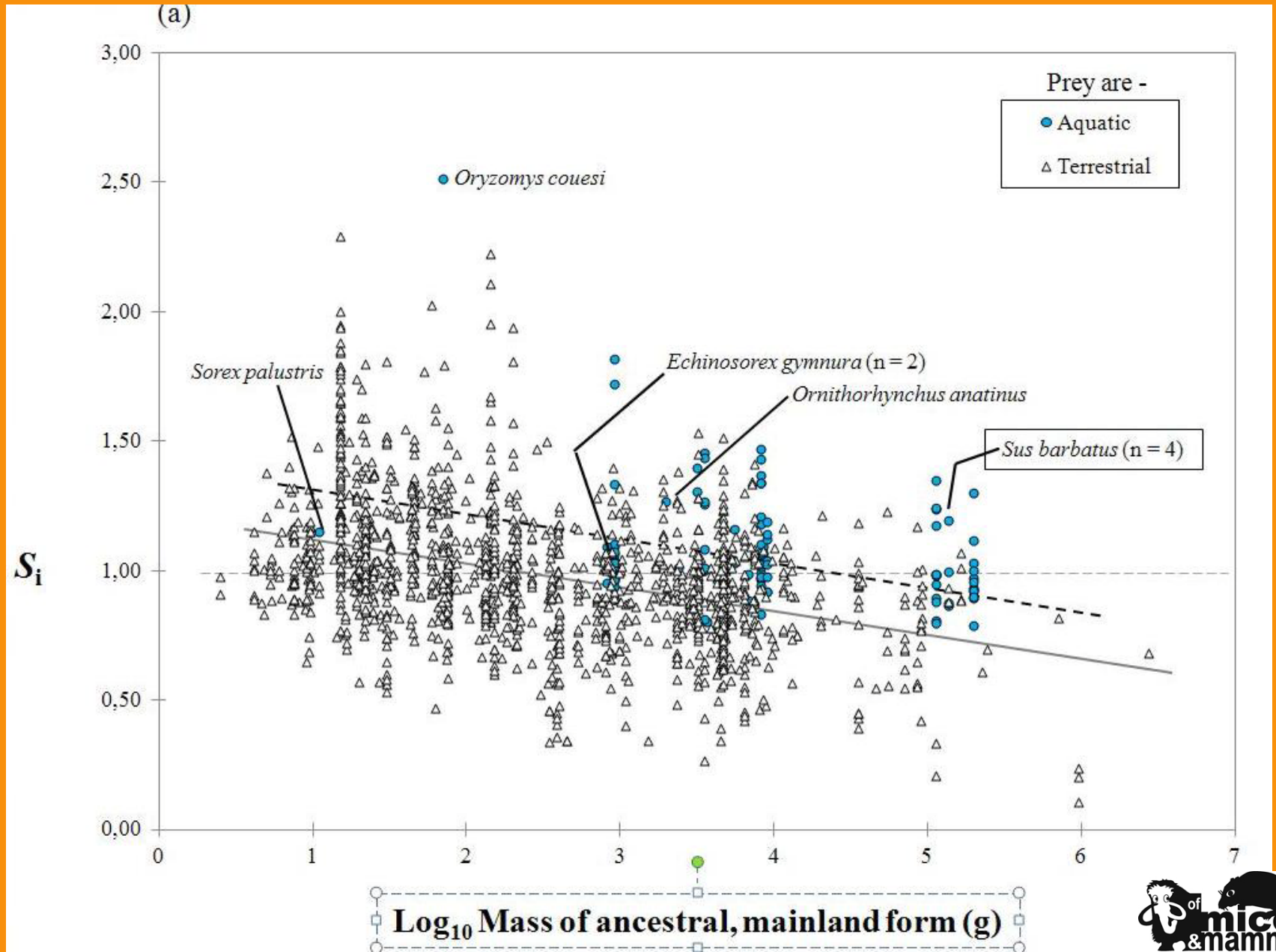
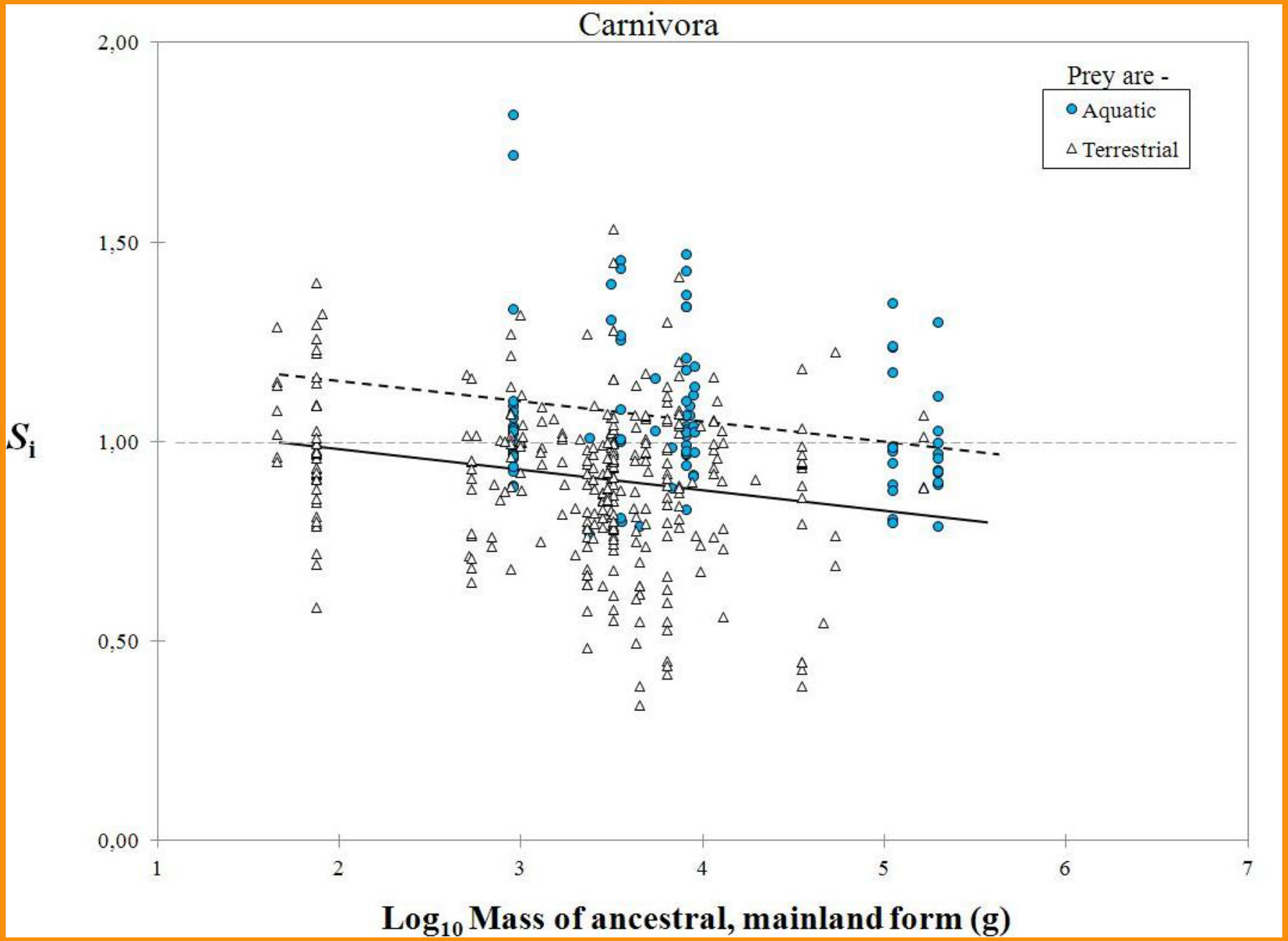
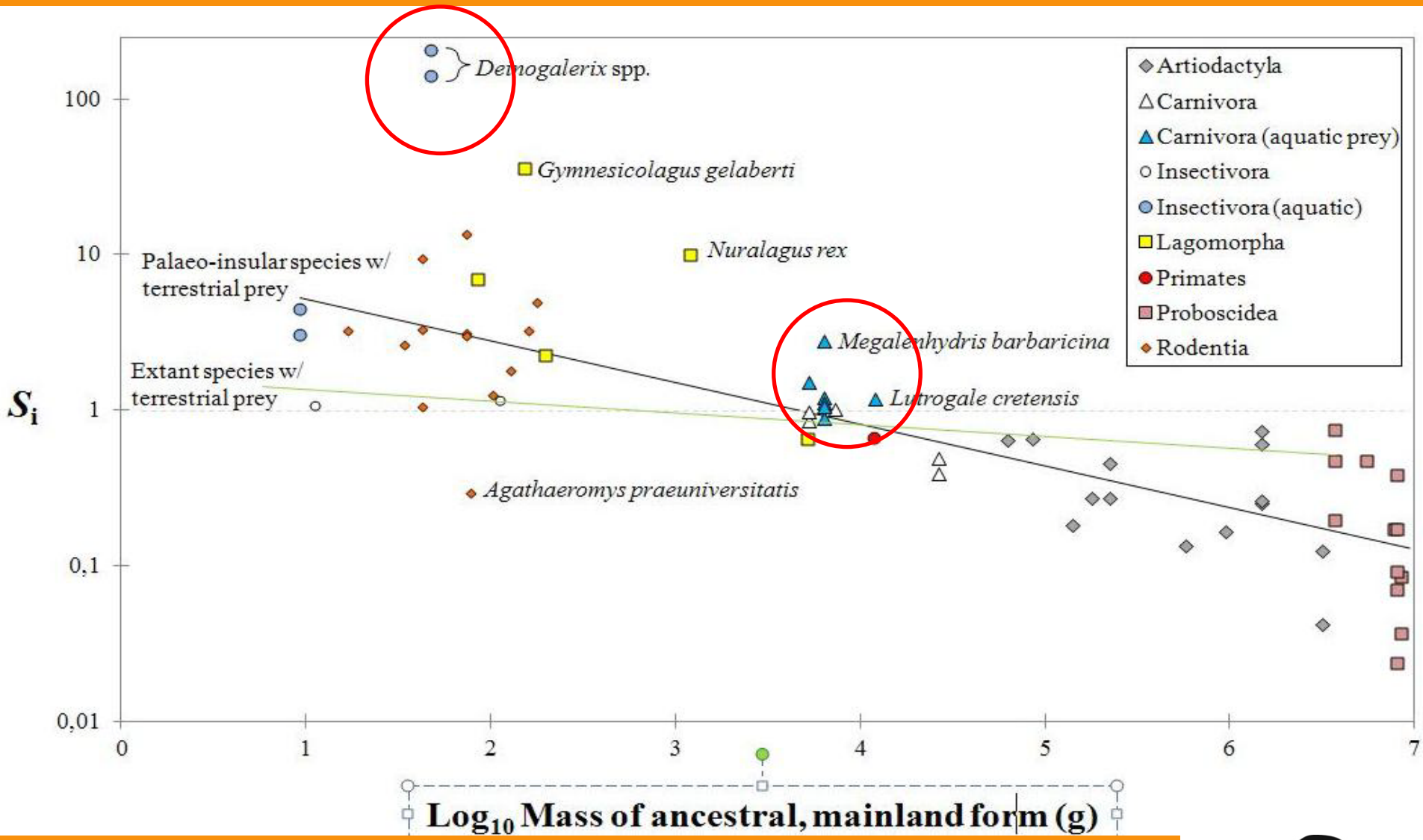


Figure 4b Carnivora considered separately



Consistent with the fossil record



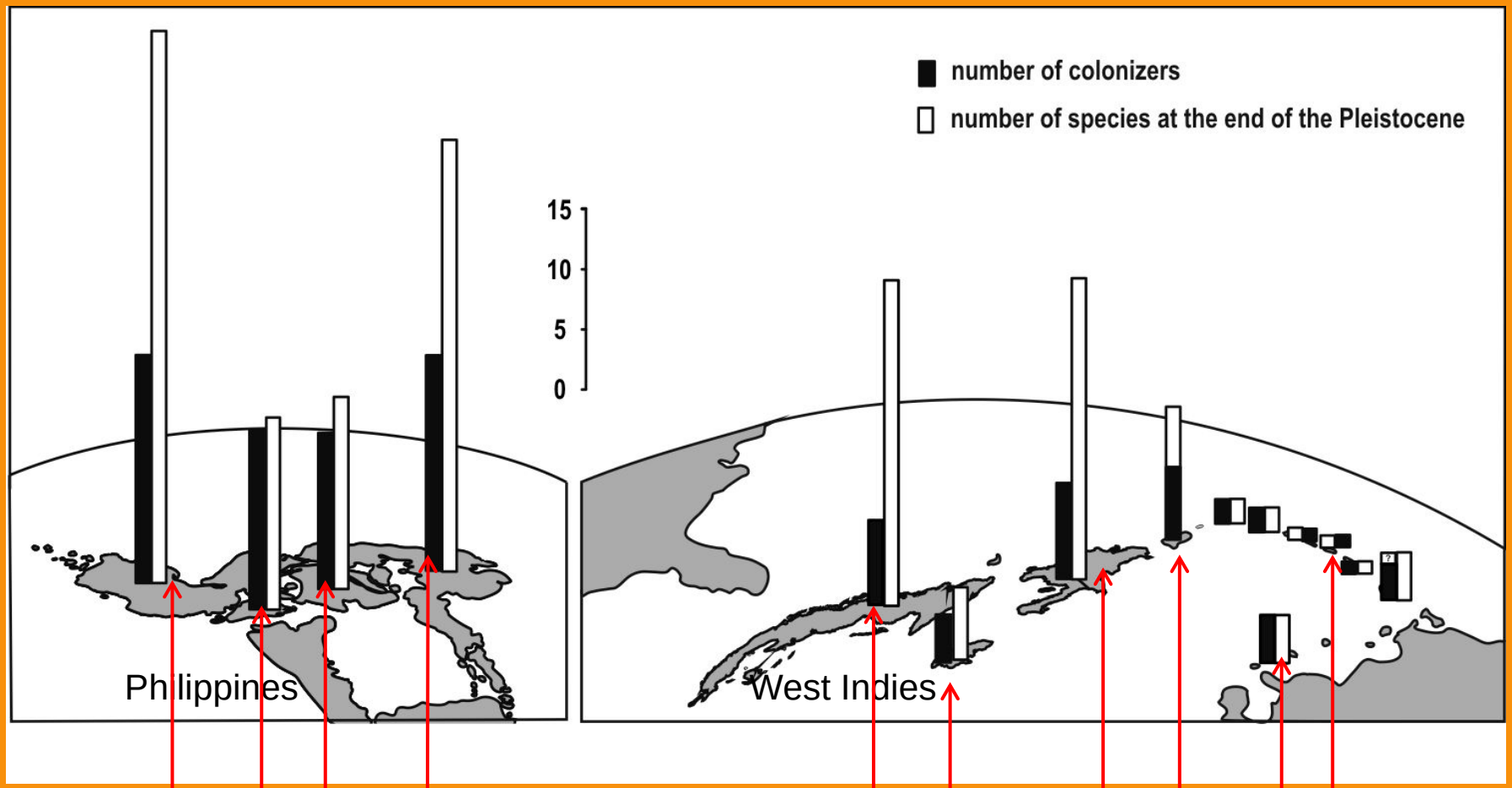
Another phenomenon that may interfer with the body size evolution trend:

speciation (radiation) within one island → (XS), S, M, L (XL) co-occurring !

SA islands: Flores, Philippines, Timor (murids)

A ‘mini’ giant cloud rat
(*Musseromys gulantang*)

Strong relation with island size (~ habitat diversity)



All Extant, Non-Volant Mammals: Summary

- **Gigantism** most prevalent for -
  - Island Rule (*sensu stricto*): Small mammals (< 2.7 kg; < 282 g)
  - Ecological release:
    - On small (64.5 km^2), low and isolated (> 16 km) islands
    - On islands lacking competitors and predators
  - Bergmann's Rule*:
    - In high-temperate latitudes (between 27 and 51 degrees)
    - In regions that are cold and highly seasonally, and/or dry
    - * but, most prevalent in small species, and for insular vs. mainland populations (remember, S_i is standardized by body size of mainland population at about the same latitude)

All Extant, Non-Volant Mammals: Summary

- **dwarfism** most prevalent for -
  - Island Rule (*sensu stricto*): Large mammals (> 2.7 kg)
  - Resource Limitation: species dependent on terrestrial (vs. aquatic) resources, although
    - Contrary to predictions, no evidence for area-per-se resource limitation predicted for large mammals
  - Consistent with predictions, body size evolution in large mammals *not* influenced by isolation, latitude or climate
- Large mammals with aquatic resources (bears) tend toward gigantism on islands lacking their competitors (other bears)

Thank you for your time

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