Towards a Periodic Table of Lizard Niches

Eric R. Pianka
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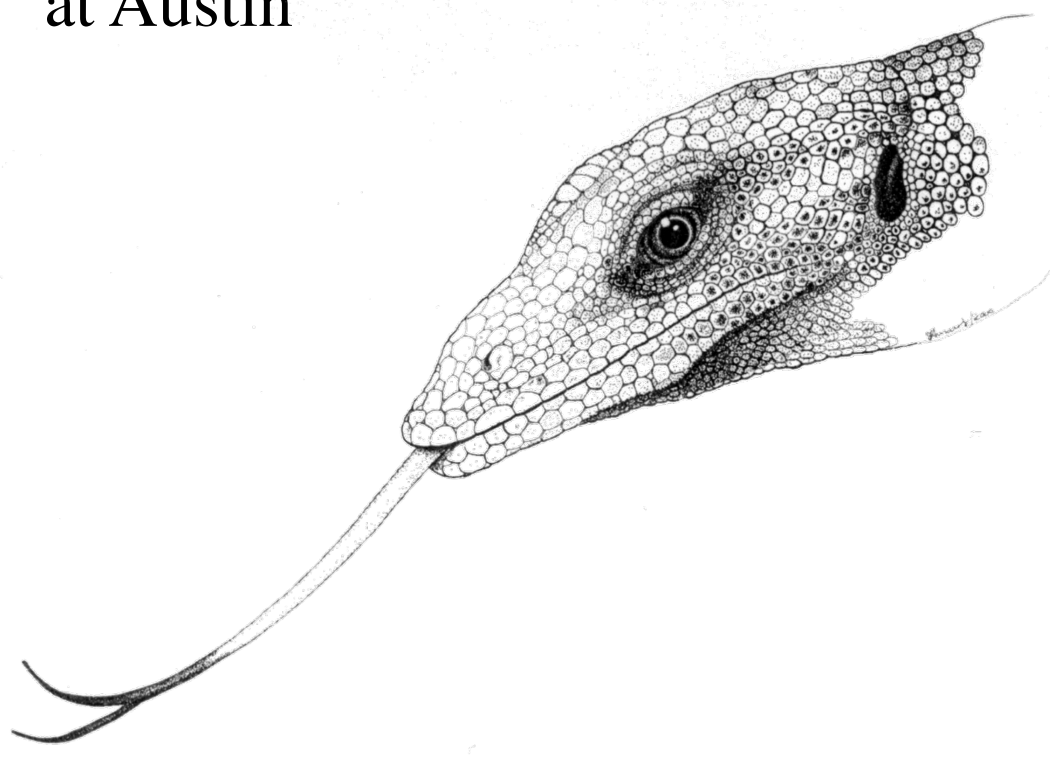
University of Texas
at Austin



Robert H. MacArthur
1930-1972

"I predict there will be erected a two- or three-way classification of organisms and their geometrical and temporal environments, this classification consuming most of the creative energy of ecologists. The future principles of the ecology of coexistence will then be of the form for organisms of type A, in environments of structure B, such and such relationships will hold." R. H. MacArthur "Coexistence of species" in Behnke (1972) "Challenging Biological Problems" AIBS, Oxford U. Press.

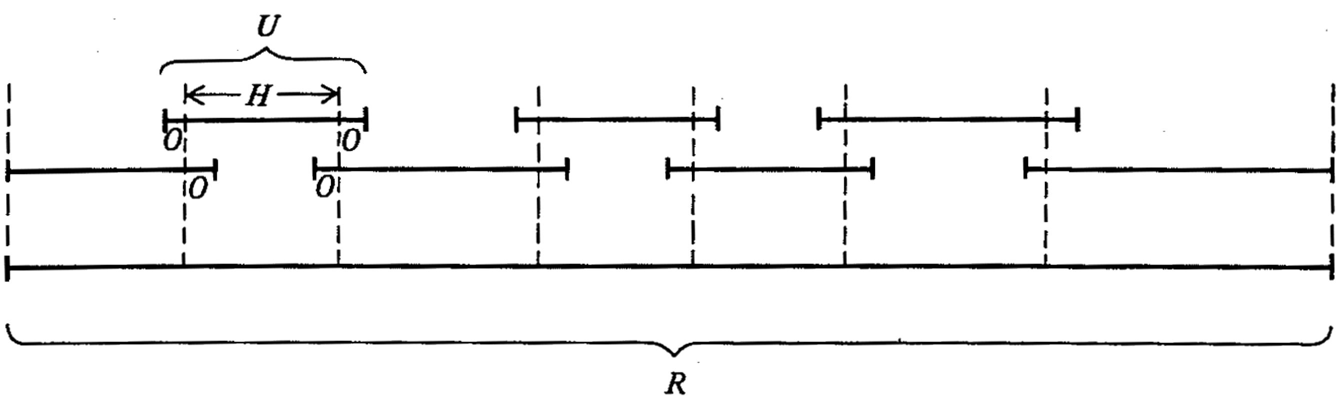
Robert H. MacArthur

Geographical Ecology

Range of Available Resources

Average Niche Breadth

Niche Overlap



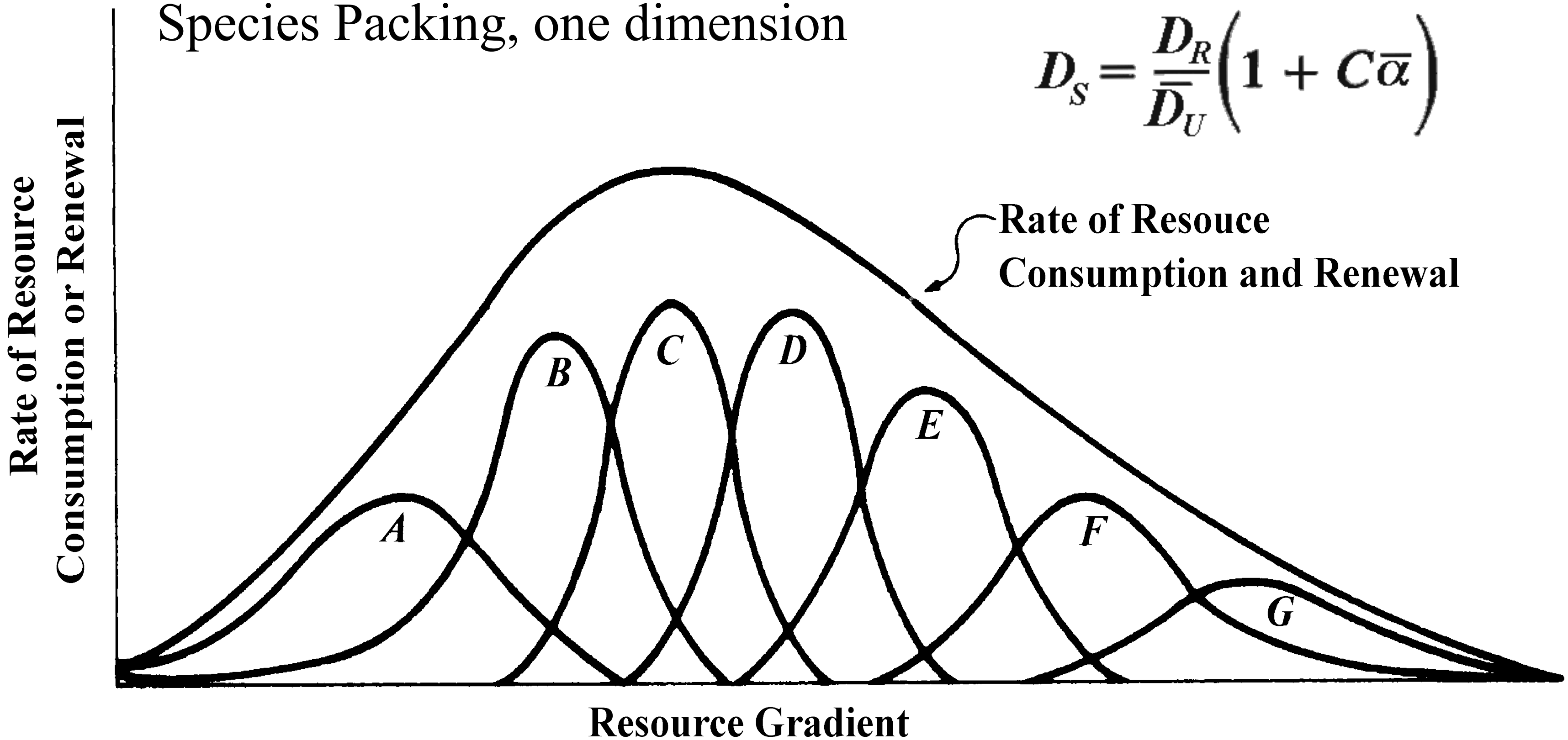
$$N = \frac{R}{\overline{U}}\left(1 + C\,\frac{\overline{O}}{\overline{H}}\right)$$

$$D_S = \frac{D_R}{\overline{D}_U}\left(1 + C\overline{\alpha}\right)$$

MacArthur, R. H. 1970. Species packing and competitive equilibrium for many species. Theoret. Population Biol. 1: 1-11.

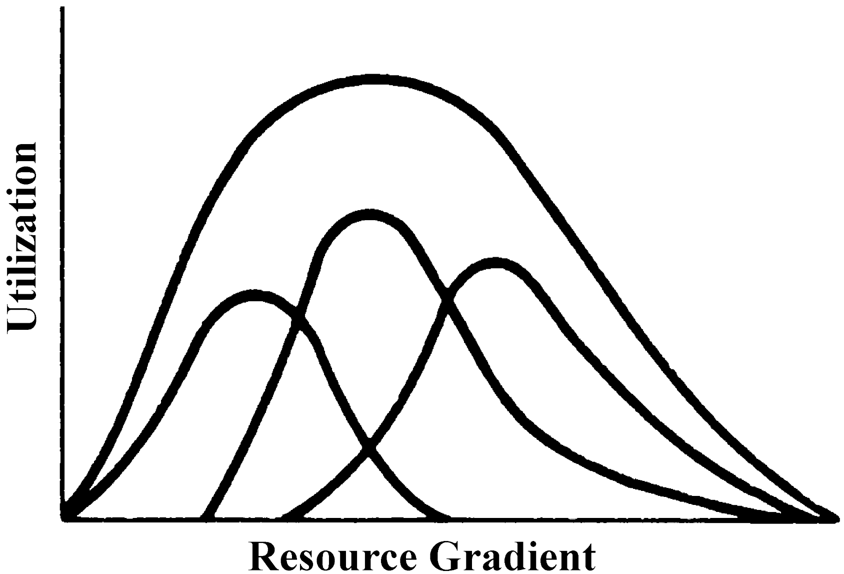
Species Packing, one dimension

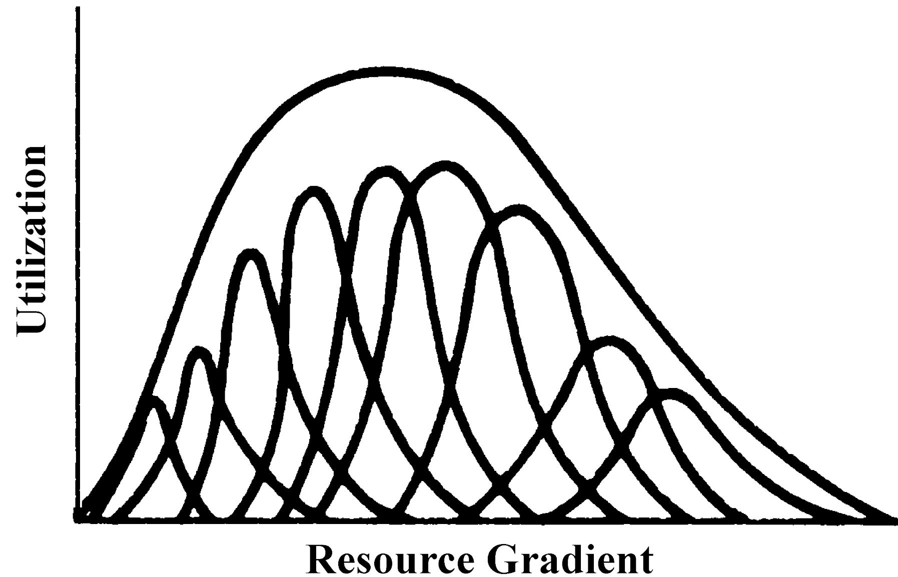
$$D_S = \frac{D_R}{\overline{D}_U}\left(1 + C\overline{\alpha}\right)$$



Resource Utilization Functions = RUFs

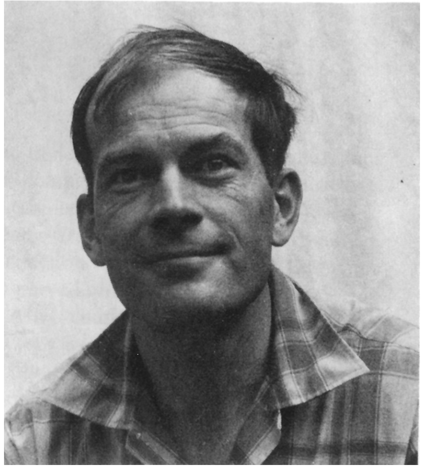
Species Packing , one dimension, two neighbors in niche space





Three generalized abundant species with broad niche breadths

Nine specialized less abundant species with with narrow niche breadths



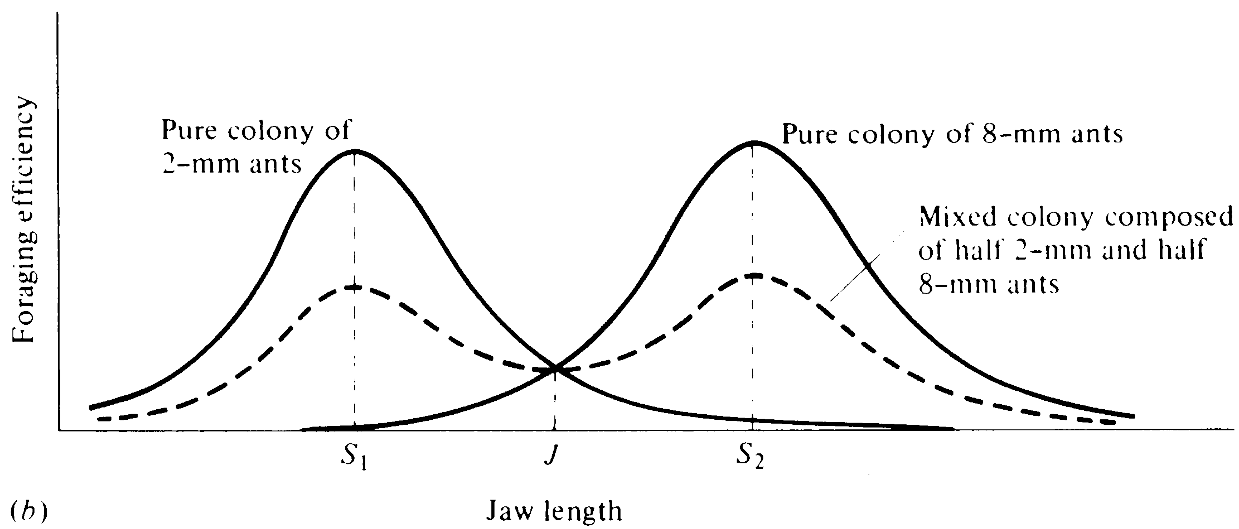
Robert H. MacArthur

Niche Breadth

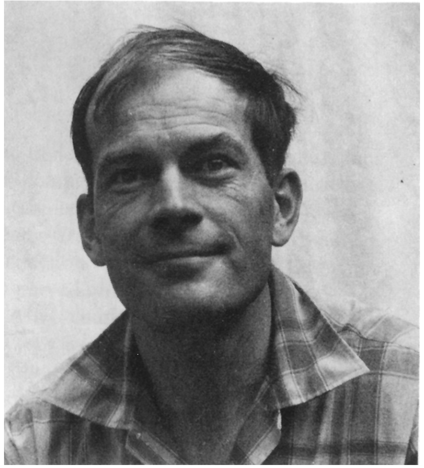
Jack of all trades is a master of none

MacArthur & Levin's Theory of Limiting Similarity

Richard Levins



Specialists are favored when resources are very different



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Niche Breadth
Jack of all trades is a master of none

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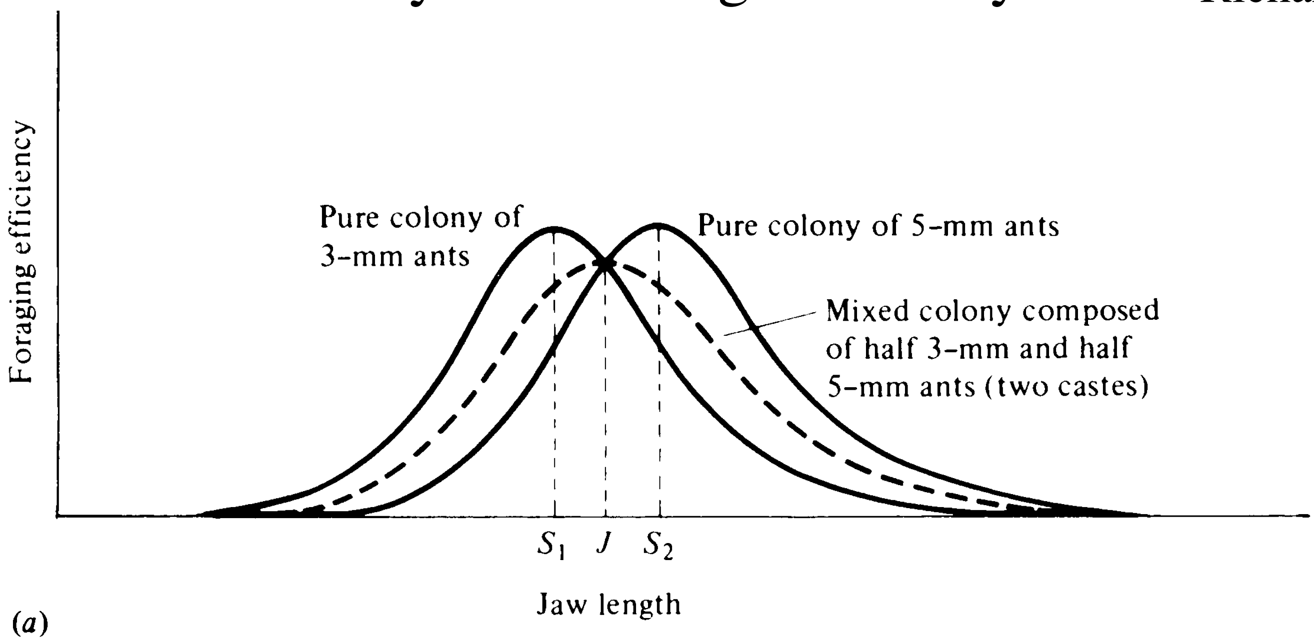
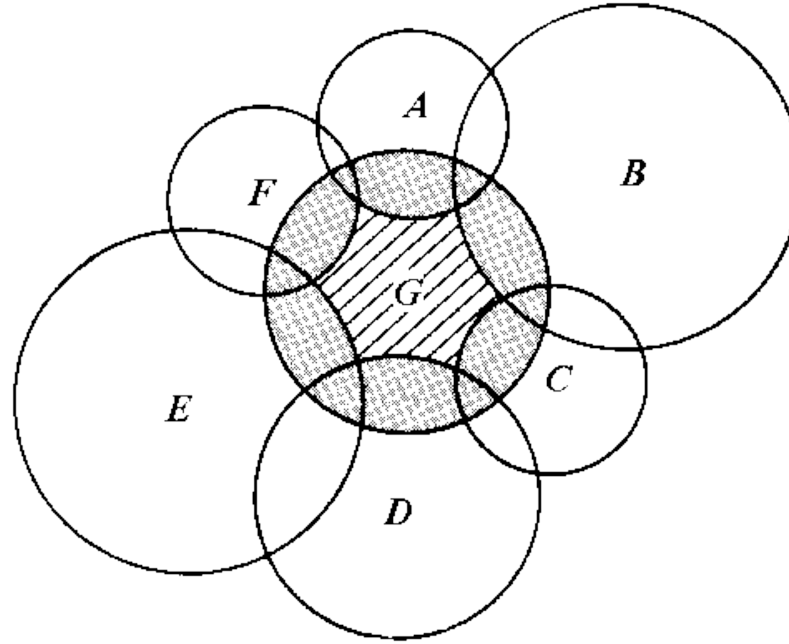
MacArthur & Levin's Theory of Limiting Similarity



Generalists are favored when resources are more similar

Niche Dimensionality



1 D = ~ 2 Neighbors

2 D = ~ 6 Neighbors

3 D = ~12-16 Neighbors

4 D = ~ 18-24 Neighbors?

Diffuse Competition

$dN_i/dt = r_i N_i(K_i - N_i - \Sigma\alpha_{ij} N_j)$

$dN_i/dt = 0$ when $N_i = K_i - \Sigma\alpha_{ij} N_j$

Periodic Table of Niches

Trophic Niches

r–K Selection continuum	Primary Producers	Herbivores	Carnivores
r	Annual plants	Caterpillars Aphids Maggots Bees Flies Adult butterflies	Mantids Dragonflies
	Shrubs	Lemmings Squirrels Fruit bats	Weasels Flycatchers Insectivorous bats
K	Perennial plants (especially trees)	Deer Antelope Bison Parrots	Cougars Wolves Falcons Eagles

From Pianka "Evolutionary Ecology"
(1974, 1978, 1983, 1988, 1993, 2000)

The many dimensions of a lizard's ecological niche

E. R. Pianka

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Introduction

The ecological niche is defined as the sum total of the adaptations of an organismic unit, or as all of the various ways in which a given organismic unit conforms to its particular environment (Pianka, 1974). The niche concept has gradually become inextricably linked to the phenomenon of interspecific competition, and, in the U.S. it is increasingly becoming identified with patterns of resource utilization (Pianka 1981). Niche relationships among competing species are frequently visualized and modeled with bell-shaped resource utilization curves along a continuous resource gradient, such as prey size or height above ground. Emphasis on resource use is operationally tractable.

1993. Chapter 9 (pp. 121-154) in E. D. Valakos, W. Bohme, V. Perez-Mellado, and P. Maragou (eds.) *Lacertids of the Mediterranean Basin*. Hellenic Zoological Society. University of Athens, Greece.

Five Major Niche Dimensions

(Analyze each separately, then combine)

Habitat and anatomical surrogates

Life History – Clutch Size, reproductive effort (relative clutch mass RCM), expenditure per progeny, early vs. delayed reproduction, clutch frequency, viviparity

Trophic – Foraging Mode + major prey categories

Metabolism – Slope, intercept, mean air & body temperature

Defense – Armor (osteoderms), Crypsis, Color change, Autotomy, Tail Colors, Mimicry, Saltation, Thanatosis, Spines, Mucous, Bite, Flee, Threat, Venom

Pianka, E R. 1993. Chapter 9 (pp. 121-154) in E. D. Valakos, W. Bohme, V. Perez-Mellado, and P. Maragou (eds.) *Lacertids of the Mediterranean Basin*. Hellenic Zoological Society. University of Athens, Greece.

Many Dimensions of the Lizard Niche

1. Spatial Niche

   Habitat

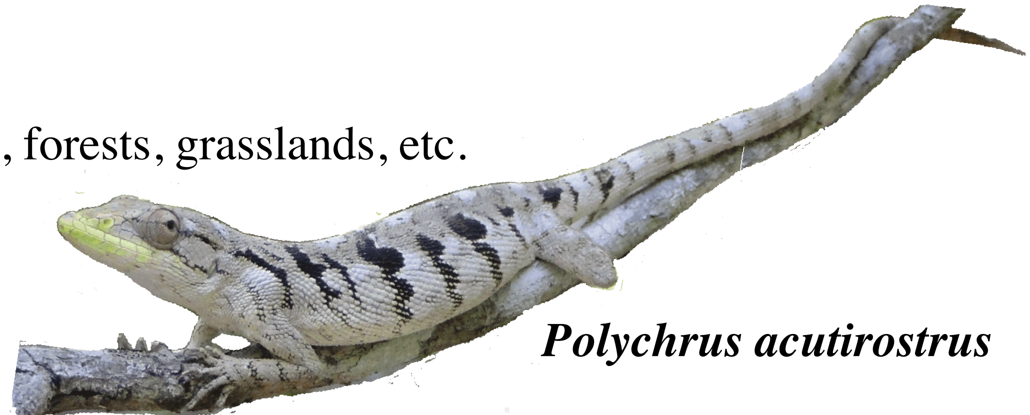
   - deserts, shrubby habitats, forests, grasslands, etc.
   - sandridges
   - sandplains
   - rocky outcrops

   Microhabitat

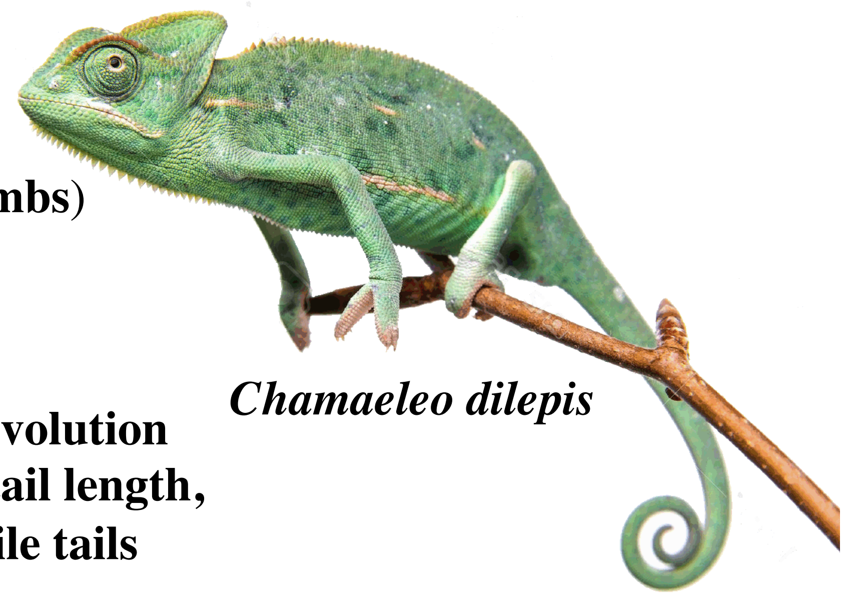
   - arboreal —> terrestrial
   - open versus vegetation
   - fossoriality (subterranean, **reduced limbs**)
   - aquatic
   - diurnal, nocturnal retreats

   Anatomical Correlates -- Convergent Evolution

   size, head proportions, leg lengths, tail length, toe lamellae, shovel snouts, prehensile tails

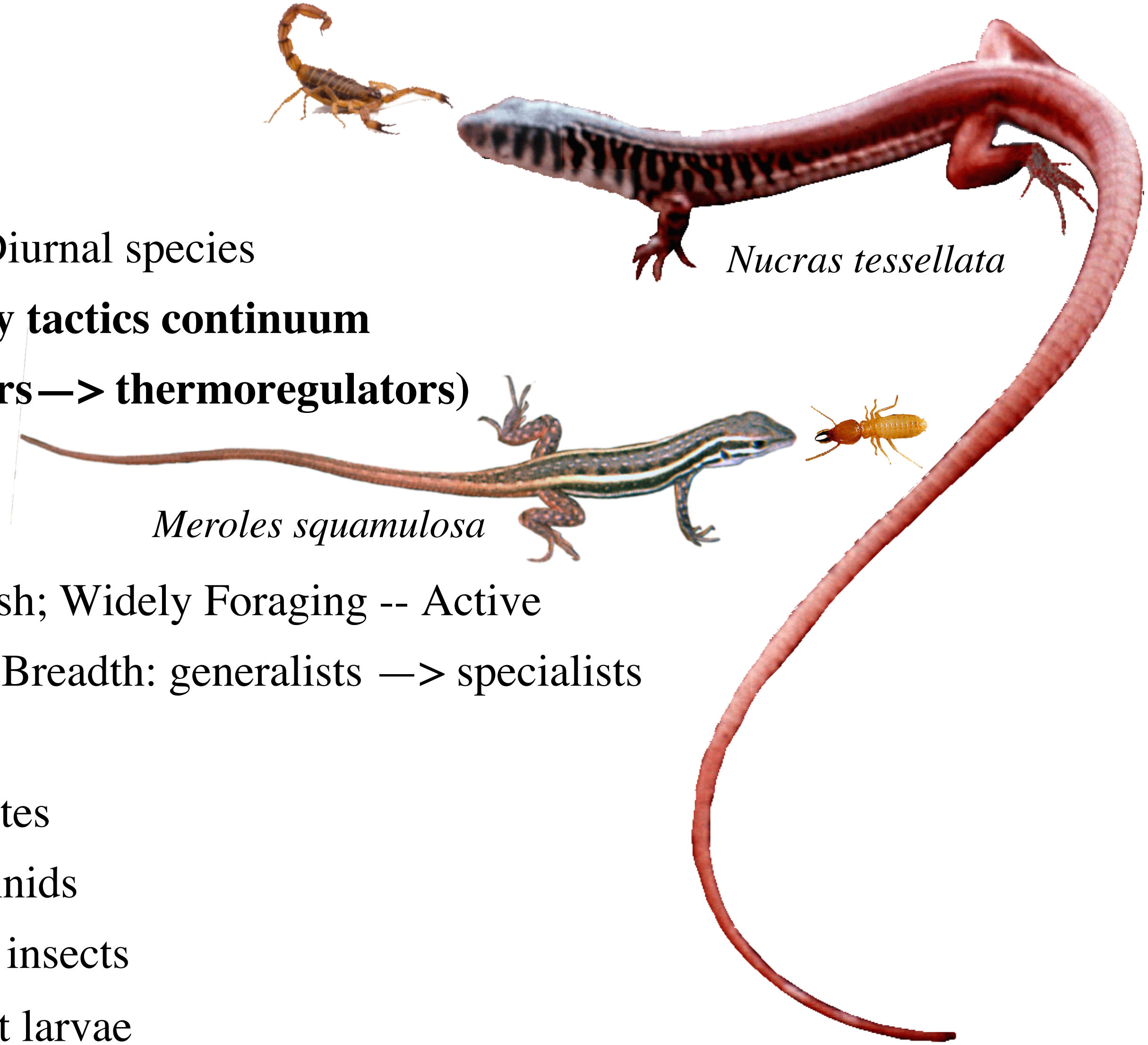


Polychrus acutirostrus



Chamaeleo dilepis

Many Dimensions of the Lizard Niche (continued)



Nucras tessellata

2. Temporal Niche

Time of Activity

Nocturnal versus Diurnal species

Thermoregulatory tactics continuum

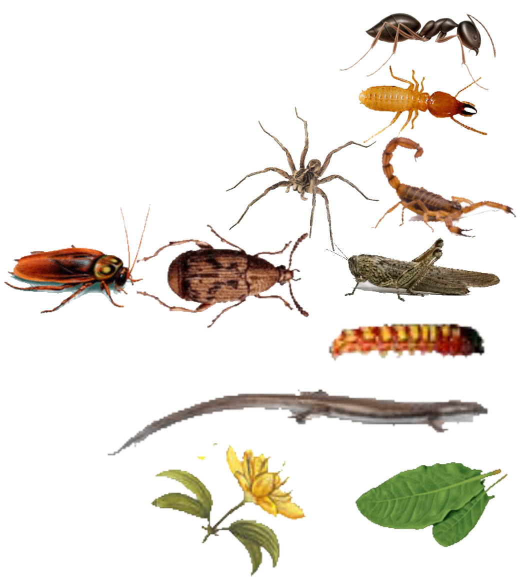
(thermoconformers —> thermoregulators)

Meroles squamulosa

3. Trophic Niche

Sit&Wait -- Ambush; Widely Foraging -- Active

Dietary Niche Breadth: generalists —> specialists



ants

termites

arachnids

large insects

insect larvae

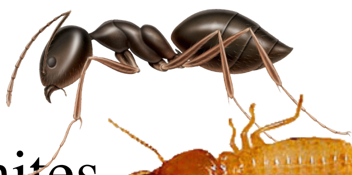
vertebrates

some plant foods

Trophic Dimension: Foraging Mode and Diet

Foraging mode included as a component of the trophic niche dimension, scoring iguanians as sit-and-wait ambush predators, geckos and herbivores plus a few other taxa as intermediate, and anguimorphs as widely foraging active predators.
Foraging mode strongly affects diet (Vitt and Pianka 2005).

1) ants
2) termites
3) arachnids
4) large insects (beetles, bugs, roaches, and orthopterans)
5) insect larvae, pupae, and eggs
6) vertebrates
7) plants












Many Dimensions of the Lizard Niche (continued)

3. Trophic Niche (continued)

Anatomical Correlates -- head length x prey size, hinged teeth

Mode of Foraging

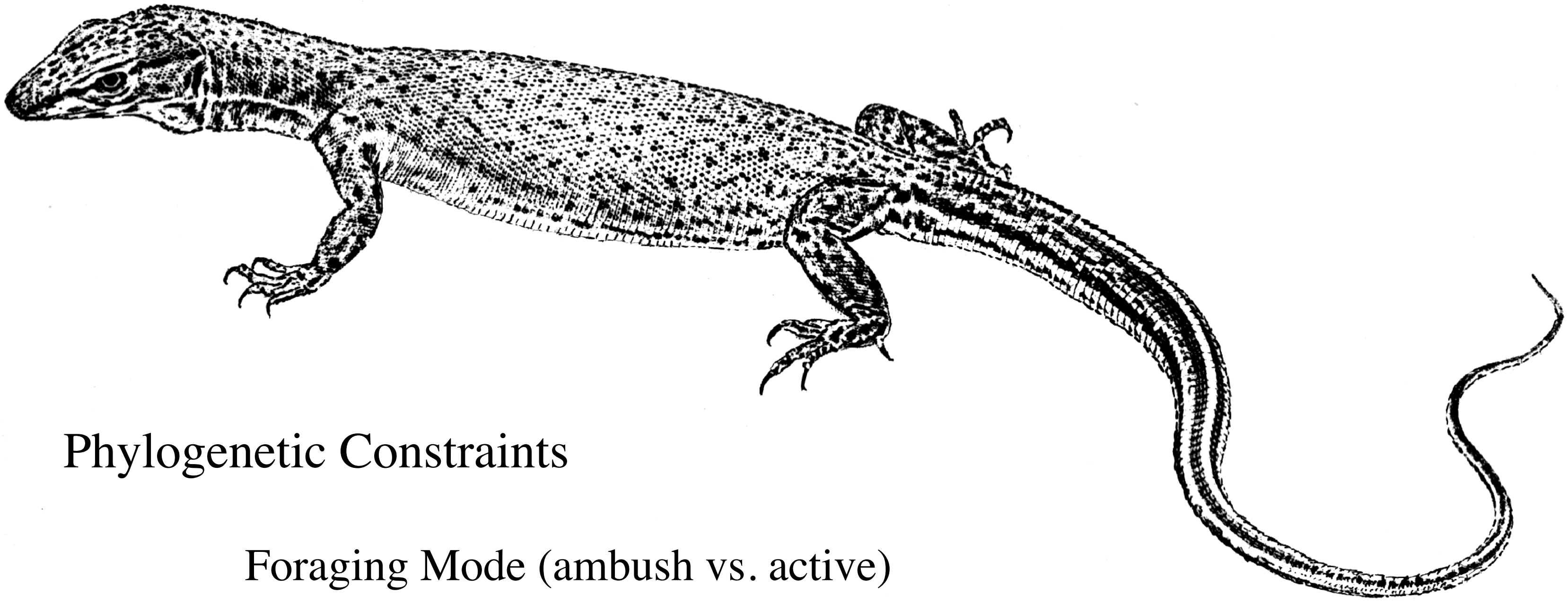
ambush hunters, sit-and-wait predators
active, widely-foraging predators
search vs. pursuit, energetic costs & profits, etc.

4. Reproductive Tactics

clutch size, reproductive effort (relative clutch mass RCM), expenditure per progeny, early vs. delayed reproduction, clutch frequency, viviparity

5. Predator Escape Tactics

Armor (osteoderms), crypsis (camoflague), color change, autotomy, tail colors, mimicry, saltation, thanatosis, spines, mucous, speed (**leg length**), wariness, agility, **body shape**, **tail length** bite, flee, threat, venom



Phylogenetic Constraints

Foraging Mode (ambush vs. active)
(lingual vs. jaw prehension, diet)

Escape Tactics (camouflage vs. wariness)

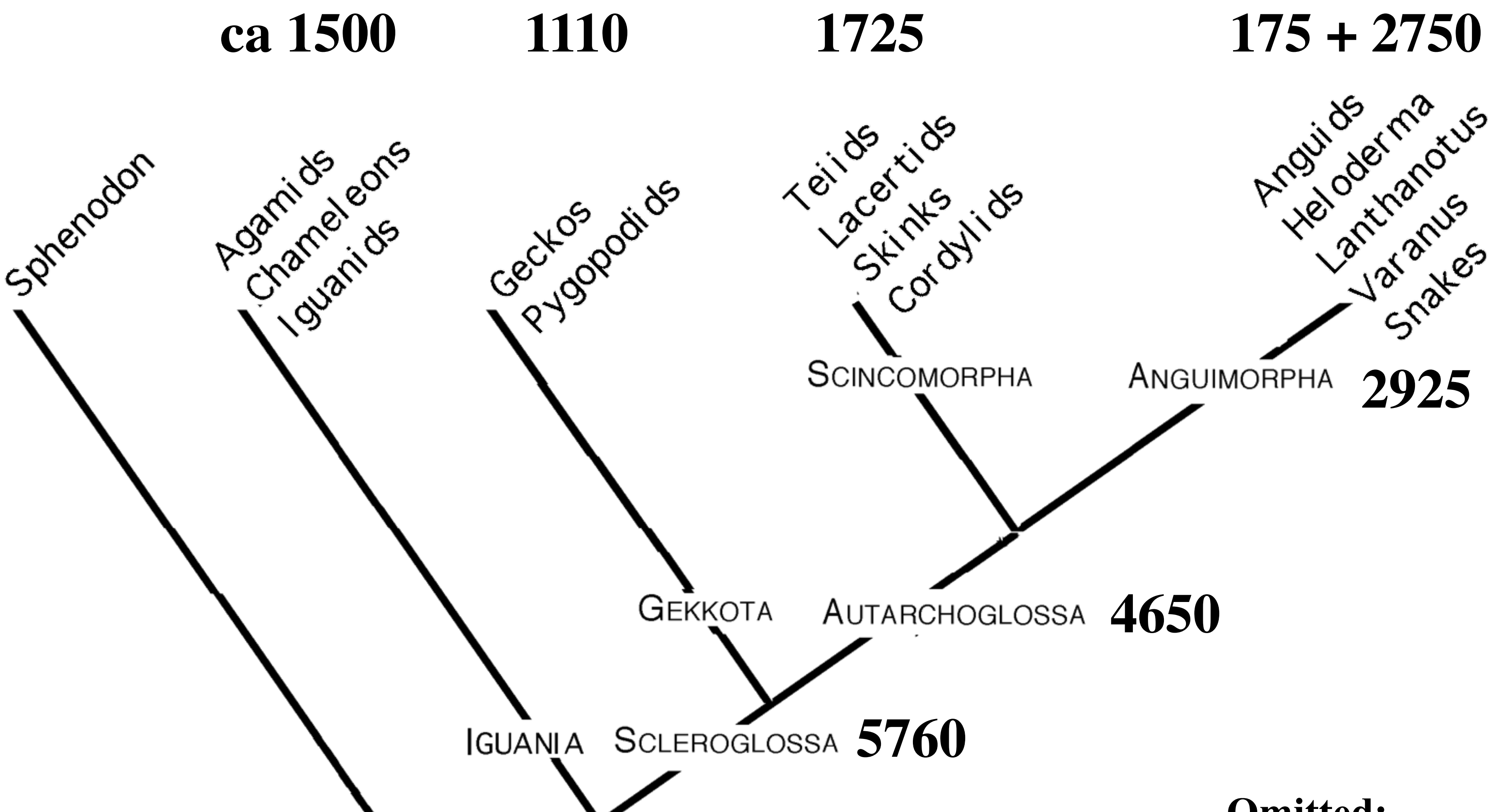
Diurnal vs. Nocturnal (most geckos)

Arboreality (long tails, toe lamellae, sharp claws)

Fossoriality (reduced limbs, never in iguanians)

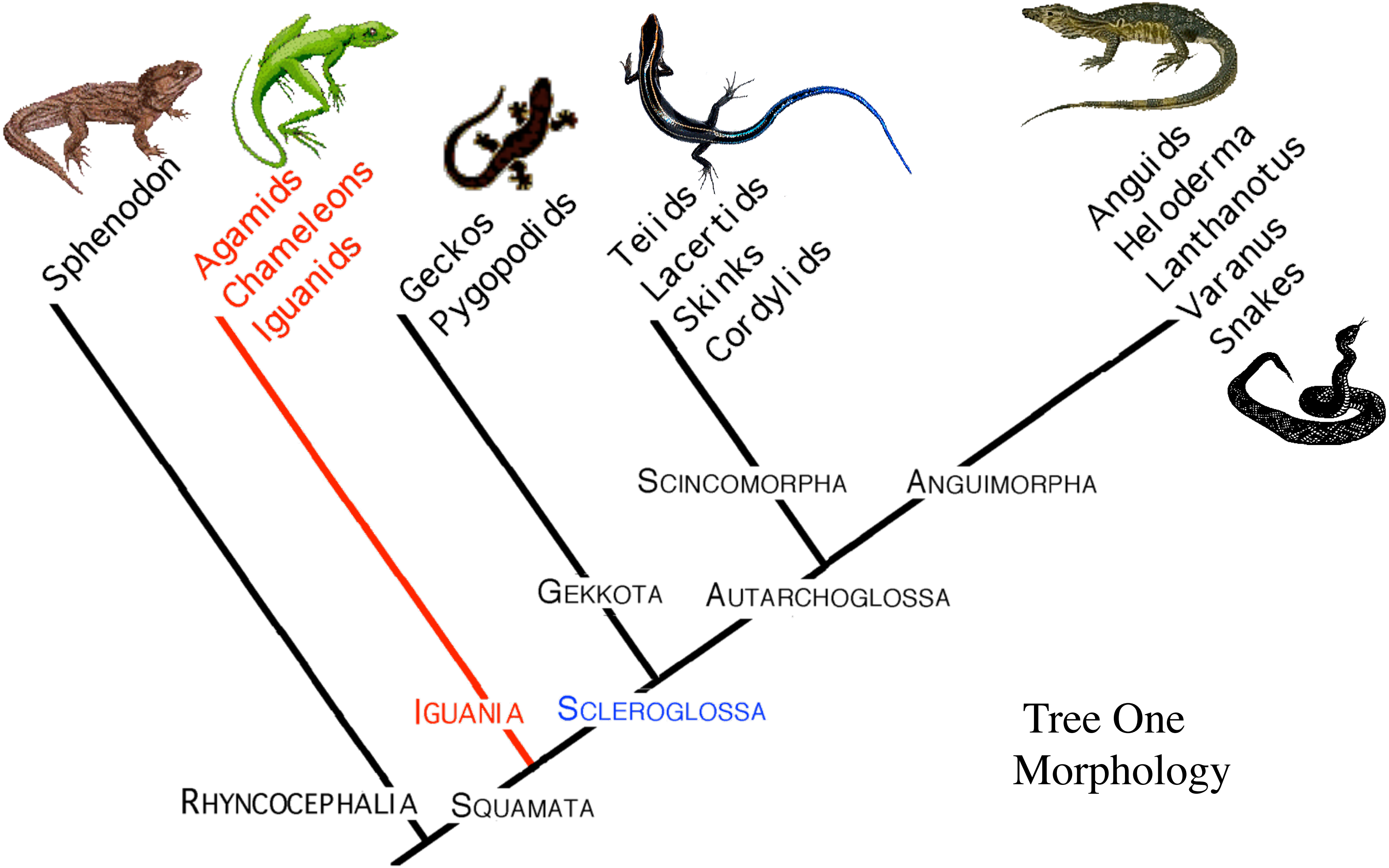
Clutch/Litter Size (fixed in geckos and anoles)

Egg laying vs. Live bearing

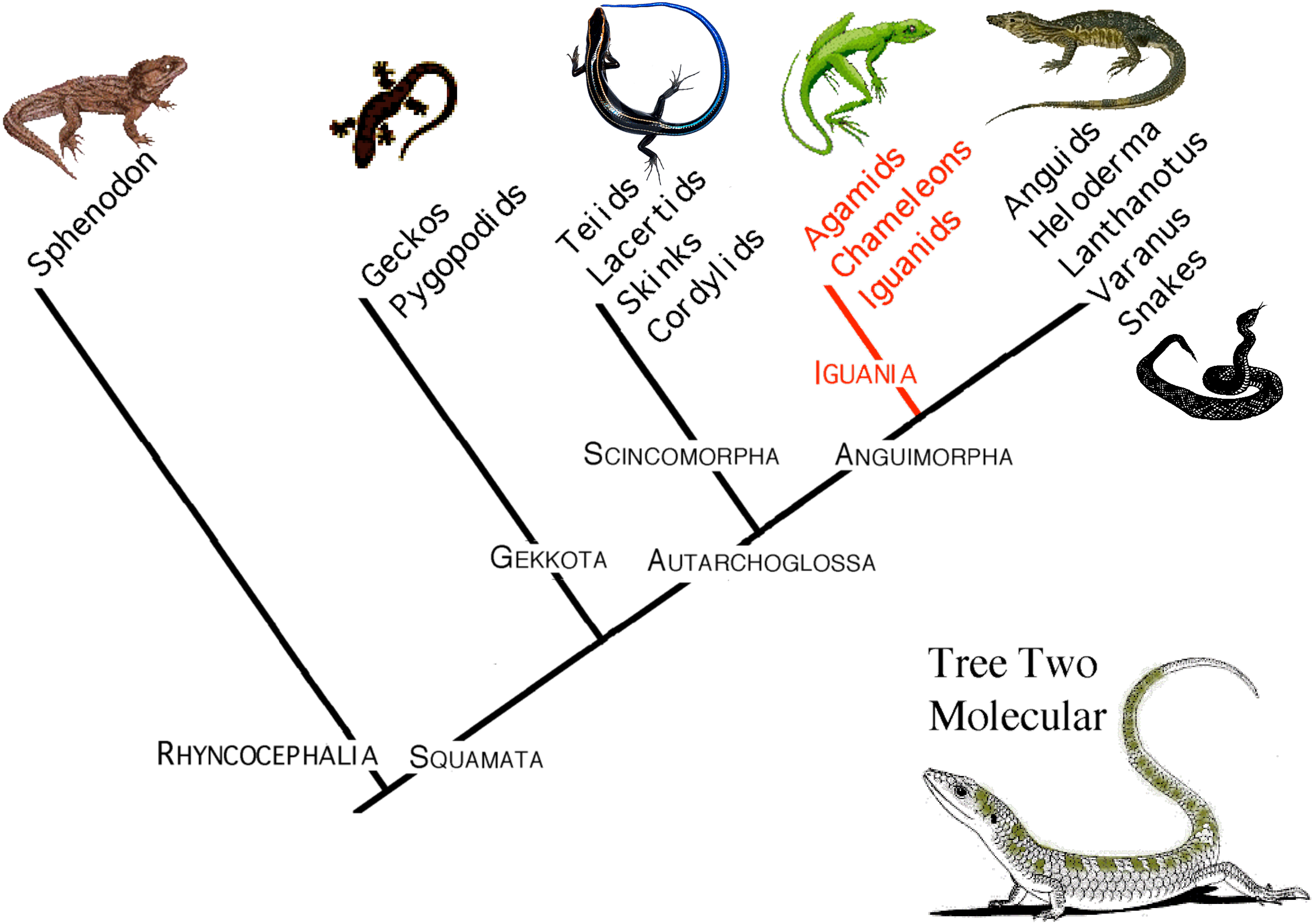


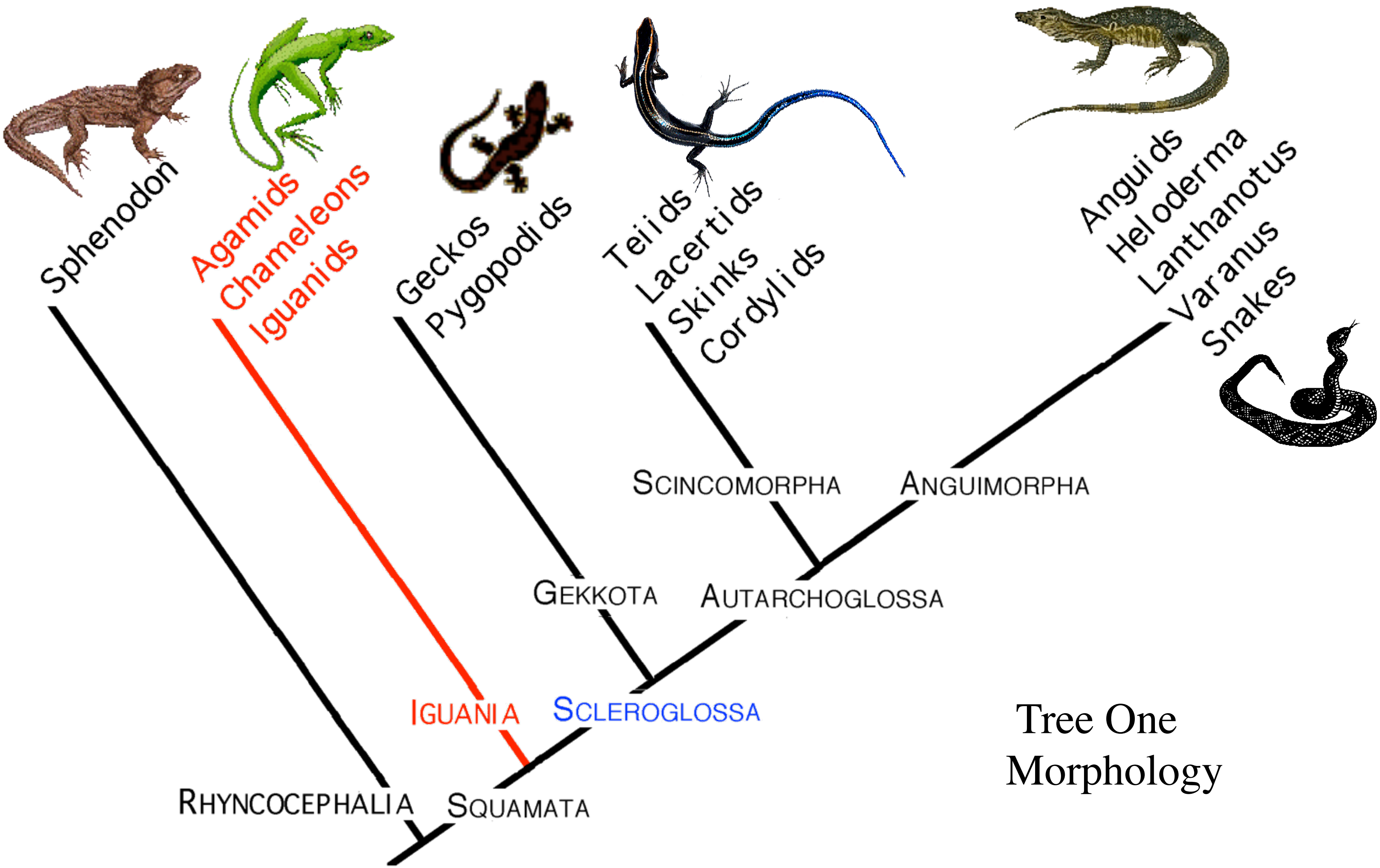
Potamites ecpleopus

Omitted:
Amphisbaenians
Dibamids
Gymnophthalmids
Xantusiids
Xenosaurids



Tree One
Morphology


Sphenodon
Geckos
Pygopodids
Teiids
Lacertids
Skinks
Cordylids
Agamids
Chameleons
Iguanids
Anguids
Heloderma
Lanthanotus
Varanus
Snakes
IGUANIA
SCINCOMORPHA
ANGUIMORPHA
GEKKOTA
AUTARCHOGLOSSA
RHYNCOCEPHALIA
SQUAMATA
Tree Two
Molecular



Tree One
Morphology

Natural Dichotomies

Ambush vs. Active Foraging

Diurnal vs. Nocturnal

Terrestrial vs. Arboreal

Egg Laying vs. Live Bearing

Gerrhonotus infernalis **Daniel Mesquita**

Crocodilurus amazonicus **Davi Pantoja**

Platysaurus broadleyi **Martin Whiting**

	Sit-and-Wait	Widely-Foraging
Nocturnal	Terrestrial Geckos / Arboreal Geckos	Some Australian Skinks
Diurnal	Most Iguanian Lizards / Arboreal Iguanian Lizards	Autarchoglossan Lizards / Arboreal Autarchoglossans




	Sit-and-Wait	Widely-Foraging
Nocturnal	Terrestrial Geckos Arboreal Geckos	Some Australian Skinks **Empty Niche**
Diurnal	Most Iguanian Lizards Arboreal Iguanian Lizards	Autarchoglossan Lizards Arboreal Autarchoglossans





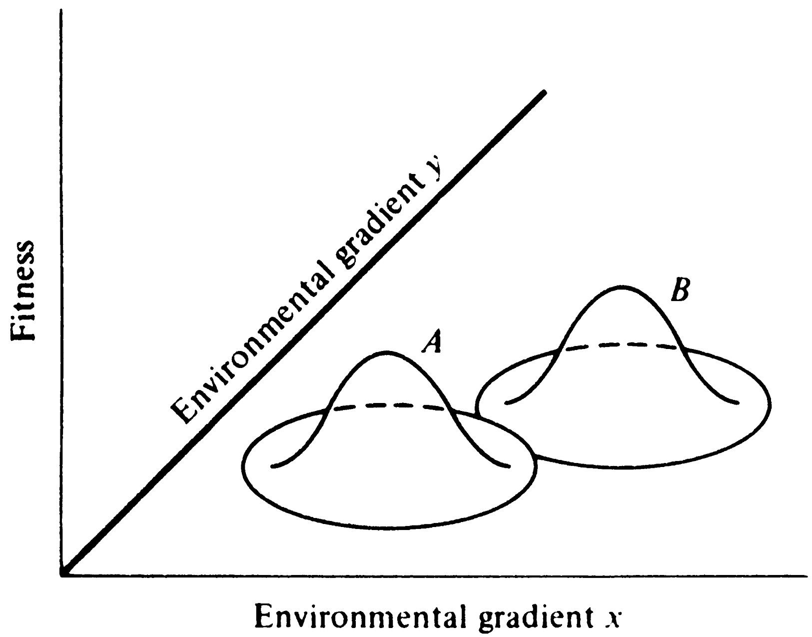
G. E. Hutchinson

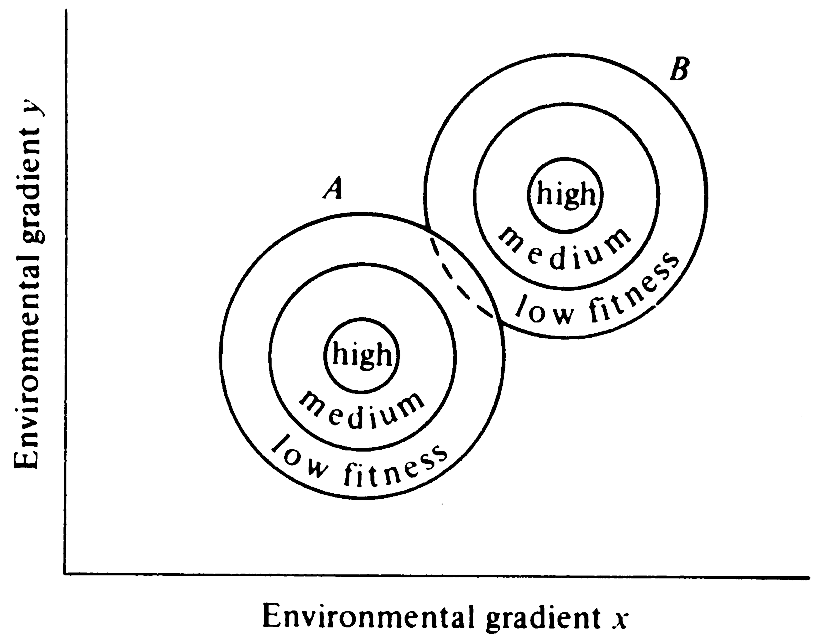
n-Dimensional Hypervolume

Fitness density

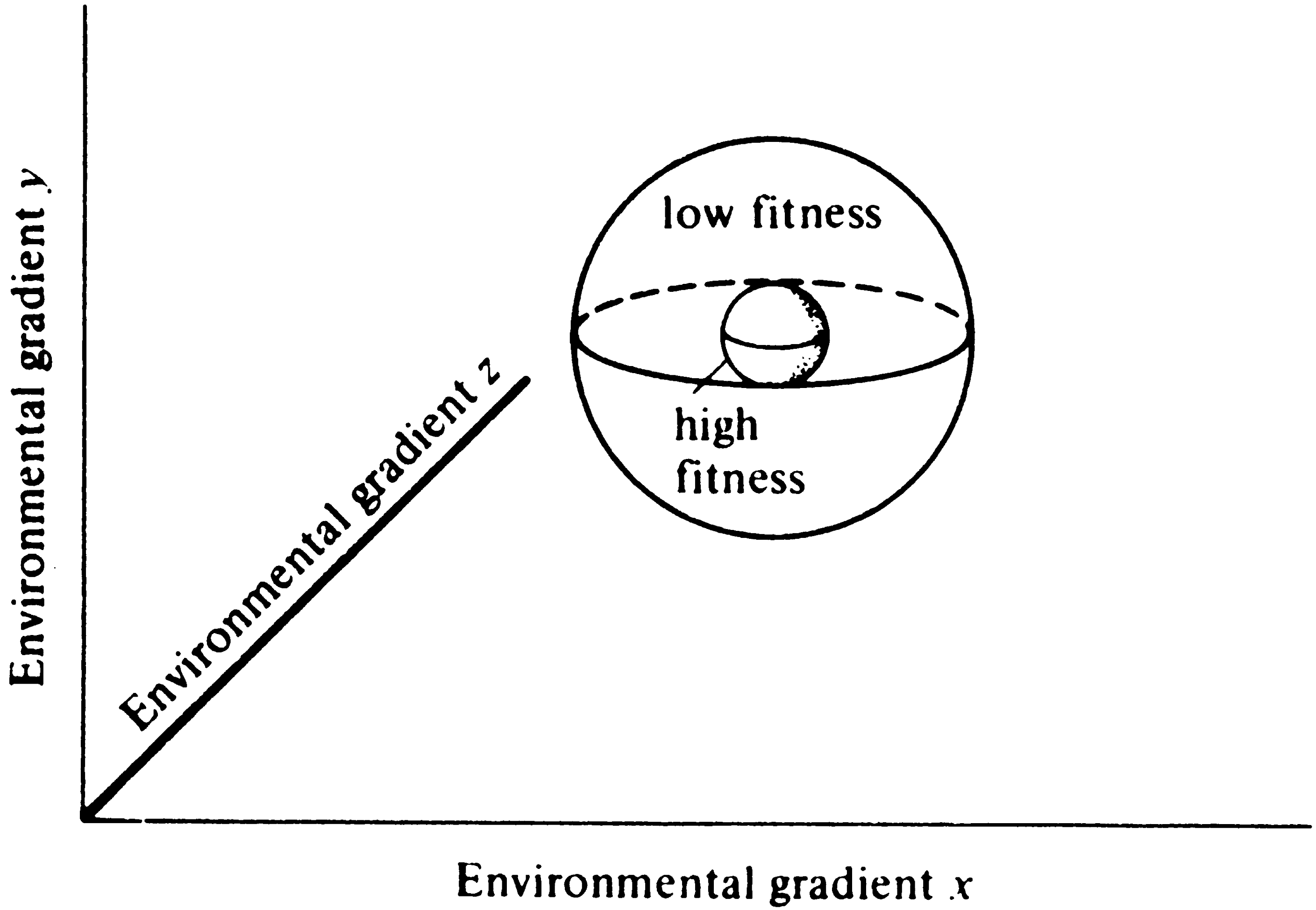
Fundamental versus Realized Niches

Reducing Dimensionality (Set Theory)

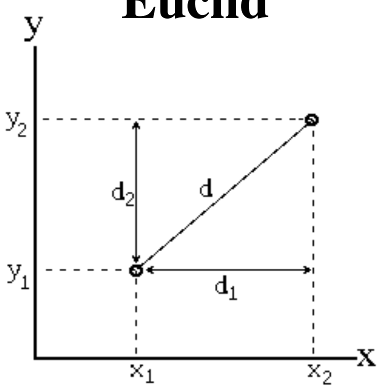


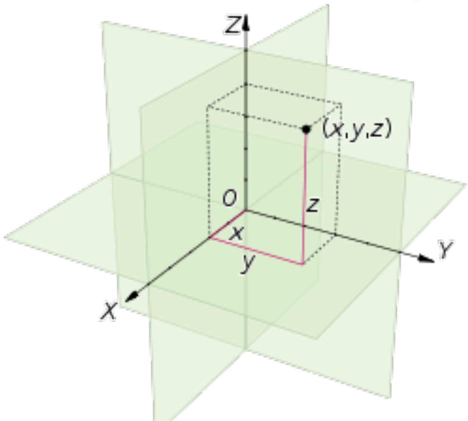


4-Dimensional Plot



Euclid





One Dimension:

Distance between two points along a line: simply subtract smaller value from larger one

$x_2 - x_1 = d$

Two Dimensions:

Score position of each point on the first and second dimensions. Subtract smaller from larger on both dimensions. $d_1 = x_2 - x_1$

$d_2 = y_2 - y_1$

Square these differences, sum them and take the square root. This is the distance between the points in 2D: sqrt $(d_1^2 + d_2^2) = d$

Three Dimensions —> n-dimensions: follow this same protocol summing over all dimensions $i = 1, n$: sqrt $\Sigma d_i^2 = d$

Euclidean distance between two species in *n*-space

***n*-dimensional hypervolume**

$$d_{jk} = \text{sqrt}\left[\sum_{i=1}^{n} (p_{ij} - p_{ik})^2\right]$$

Euclid

where j and k represent species j and species k

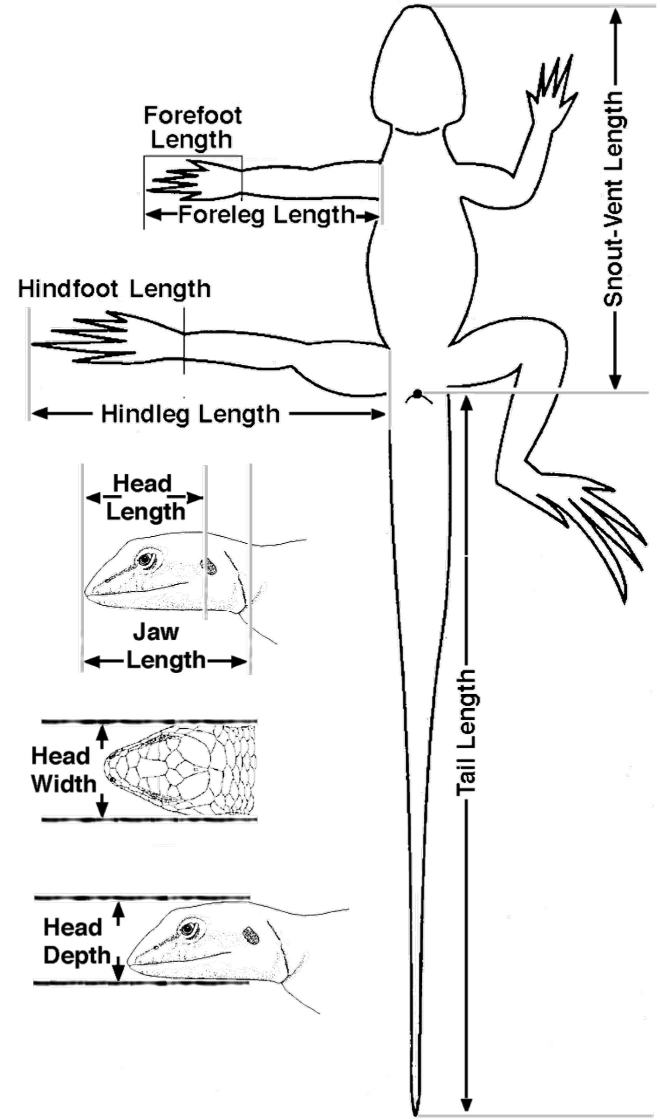
the p_{ij} and p_{ik}' s represent the proportional utilization or electivities of resource state i used by species j and species k, respectively and the summation is from $i = 1$ to n.

[n is the number of resource dimensions]

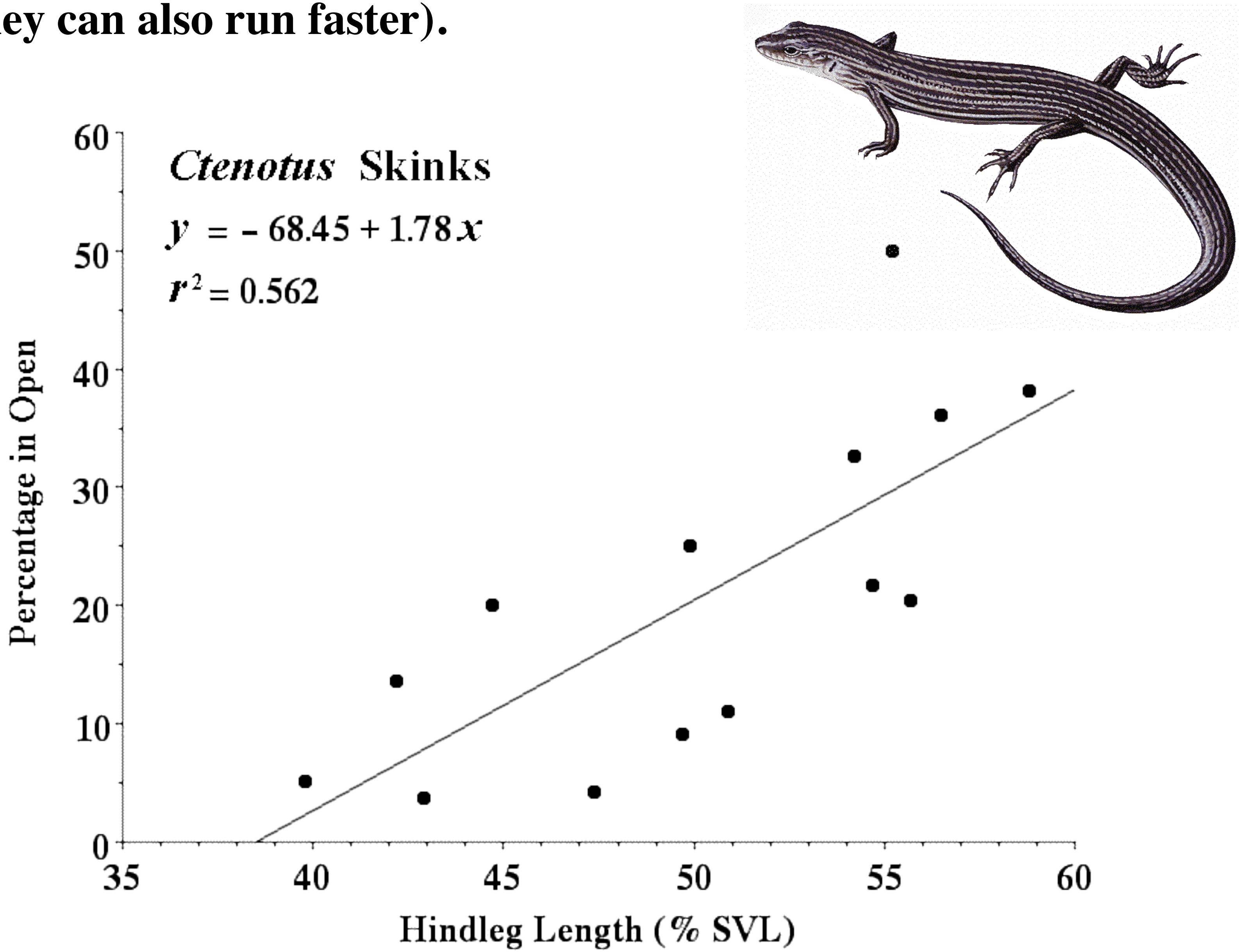
Anatomical Correlates of Ecology (Surrogates)

Ten Morphometrics

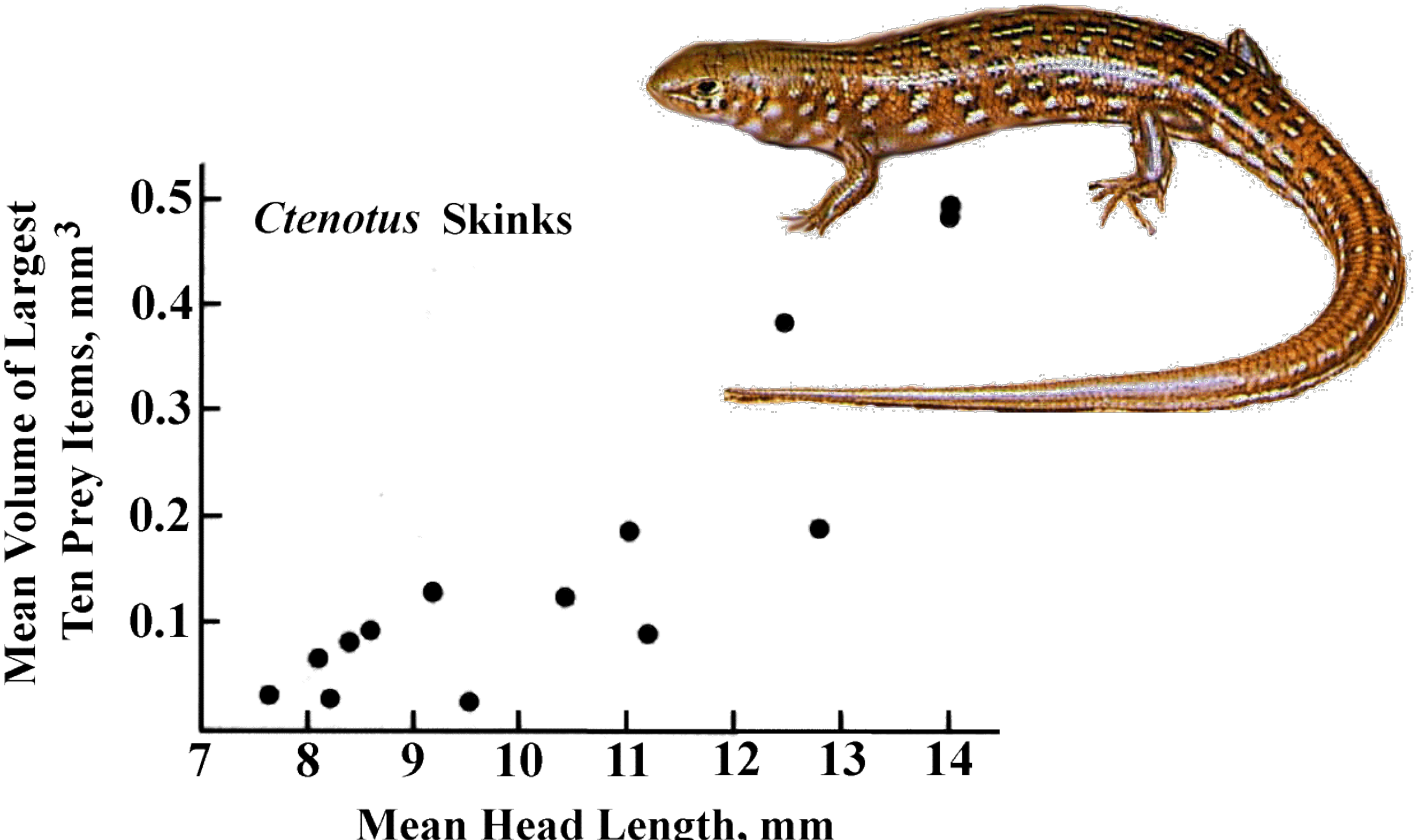
- Snout-vent length
- Tail length
- Head length
- Head width
- Head depth
- Jaw length
- Forefoot length
- Foreleg length
- Hindfoot length
- Hindleg length



Lizards with longer hindlegs spend more time in the open away from cover (they can also run faster).



Lizards with bigger heads consume larger prey items.



Multivariate techniques (principal components, ordination)

Principal Components Analysis

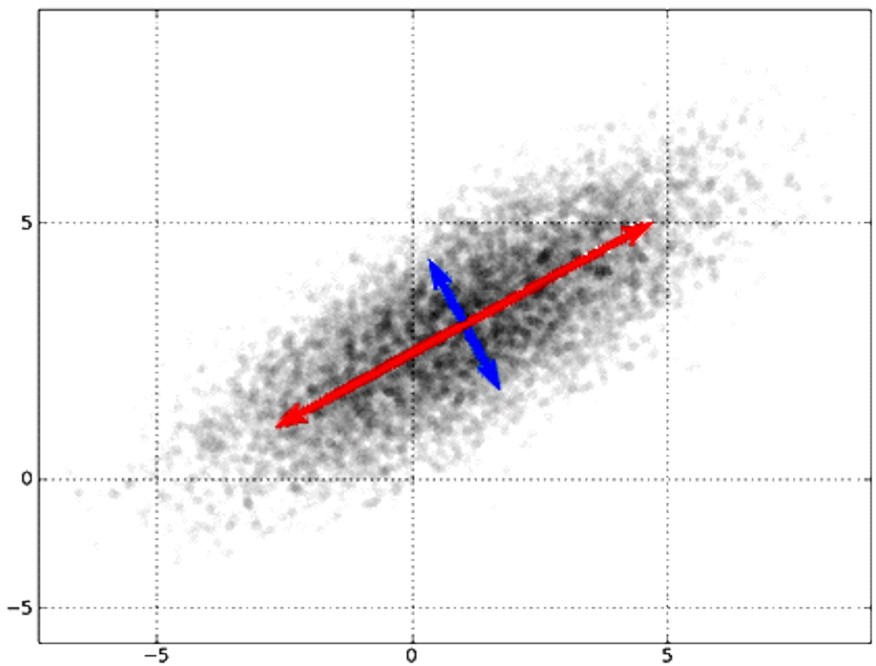
Reduces dimensionality (correlated data)

Changes coordinate system (data positions unchanged)

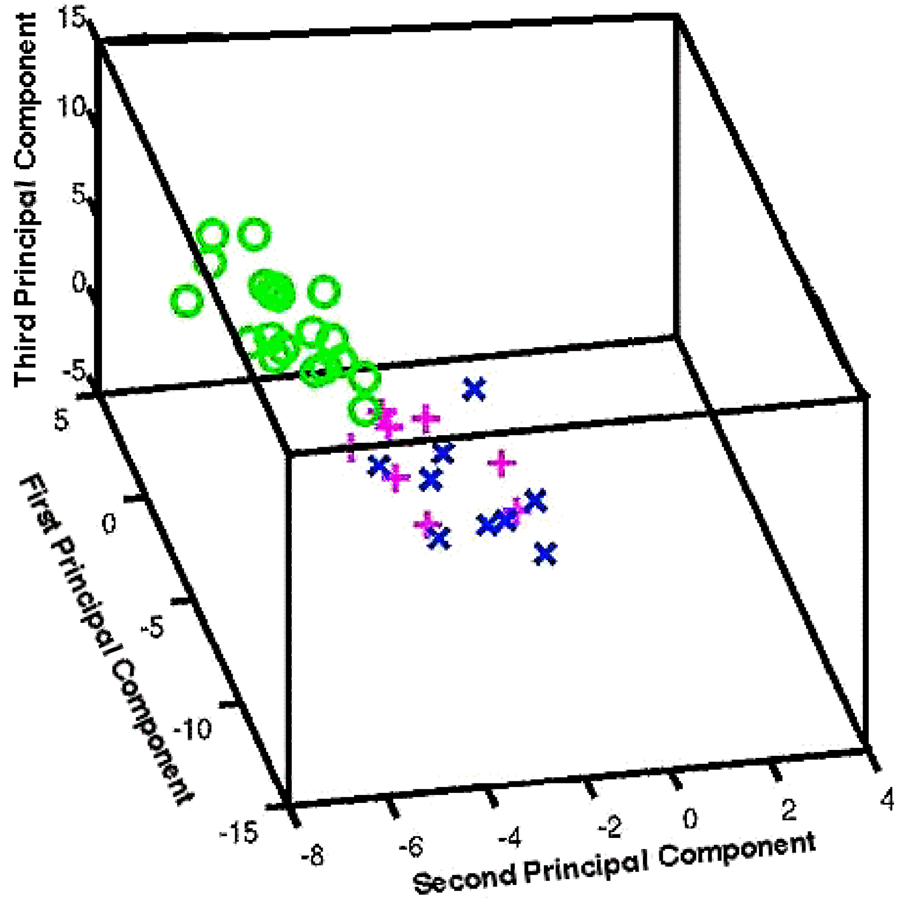
Transform data: Log transformation

Correlation Matrix

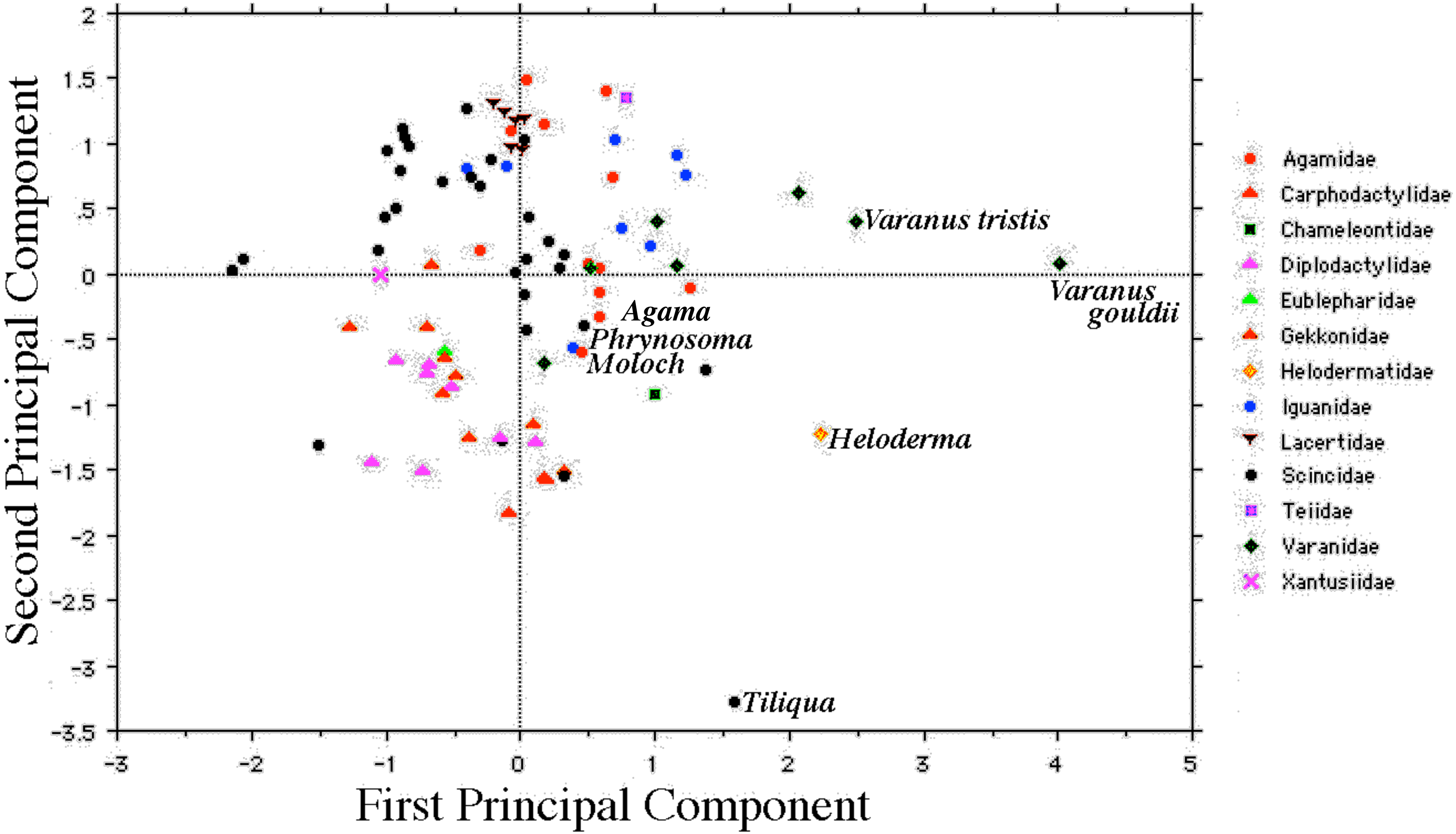
	log SVL	log Tail L.	log Head L.	log Head W.	log Head D.	log Jaw L.	log FFL	log FLL	log HFL	log HLL
log SVL	1.000	.678	.937	.871	.898	.953	.747	.803	.658	.780
log Tail L.	.678	1.000	.658	.516	.598	.690	.712	.604	.834	.756
log Head L.	.937	.658	1.000	.938	.928	.985	.837	.900	.718	.853
log Head W.	.871	.516	.938	1.000	.970	.936	.809	.892	.665	.820
log Head D.	.898	.598	.928	.970	1.000	.935	.824	.880	.706	.829
log Jaw L.	.953	.690	.985	.936	.935	1.000	.835	.889	.725	.849
log FFL	.747	.712	.837	.809	.824	.835	1.000	.954	.895	.919
log FLL	.803	.604	.900	.892	.880	.889	.954	1.000	.808	.922
log HFL	.658	.834	.718	.665	.706	.725	.895	.808	1.000	.944
log HLL	.780	.756	.853	.820	.829	.849	.919	.922	.944	1.000



First Principal Component
Second Principal Component



First Two Principal Components capture 92.4% of variance in anatomy



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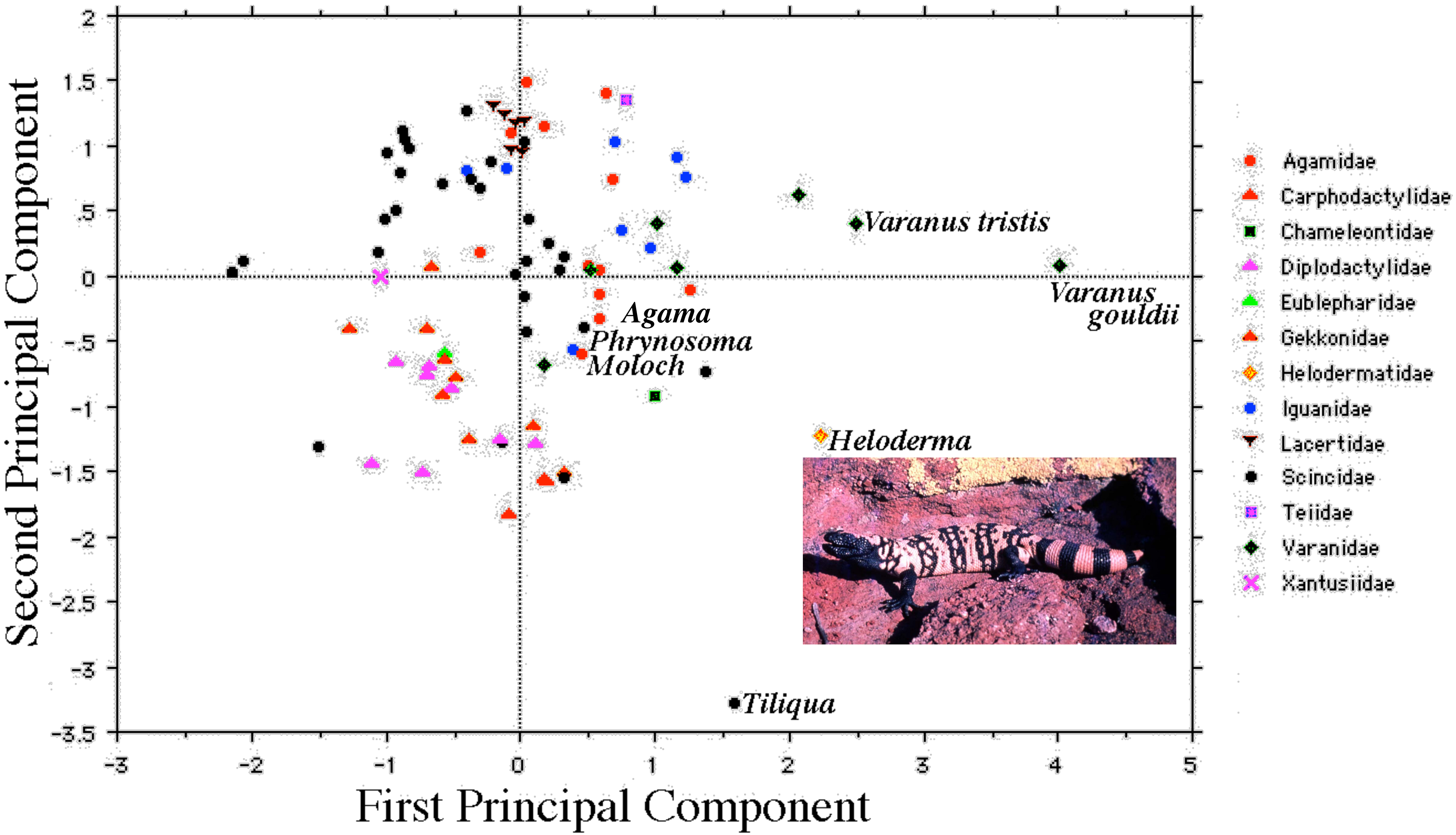

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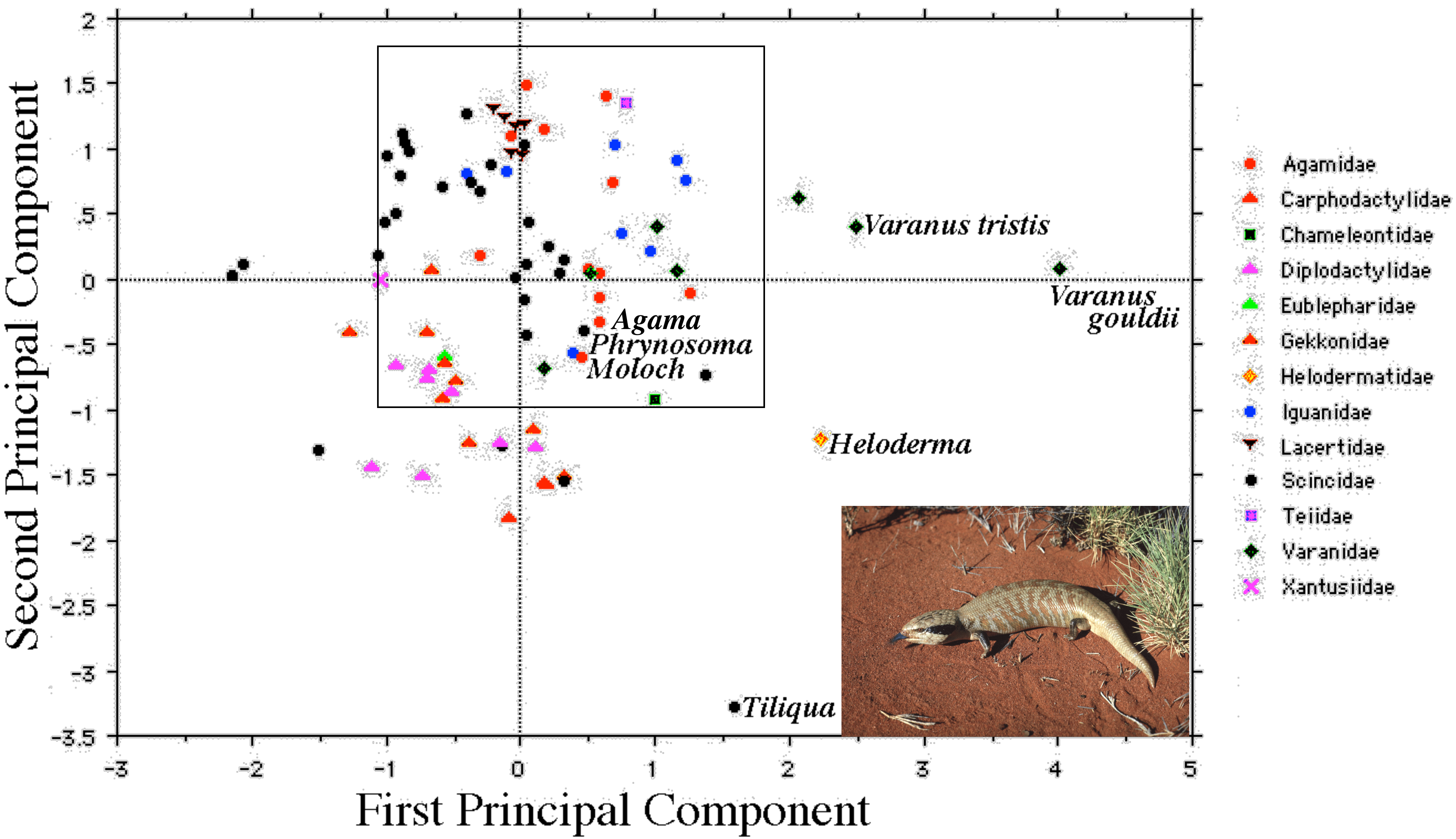
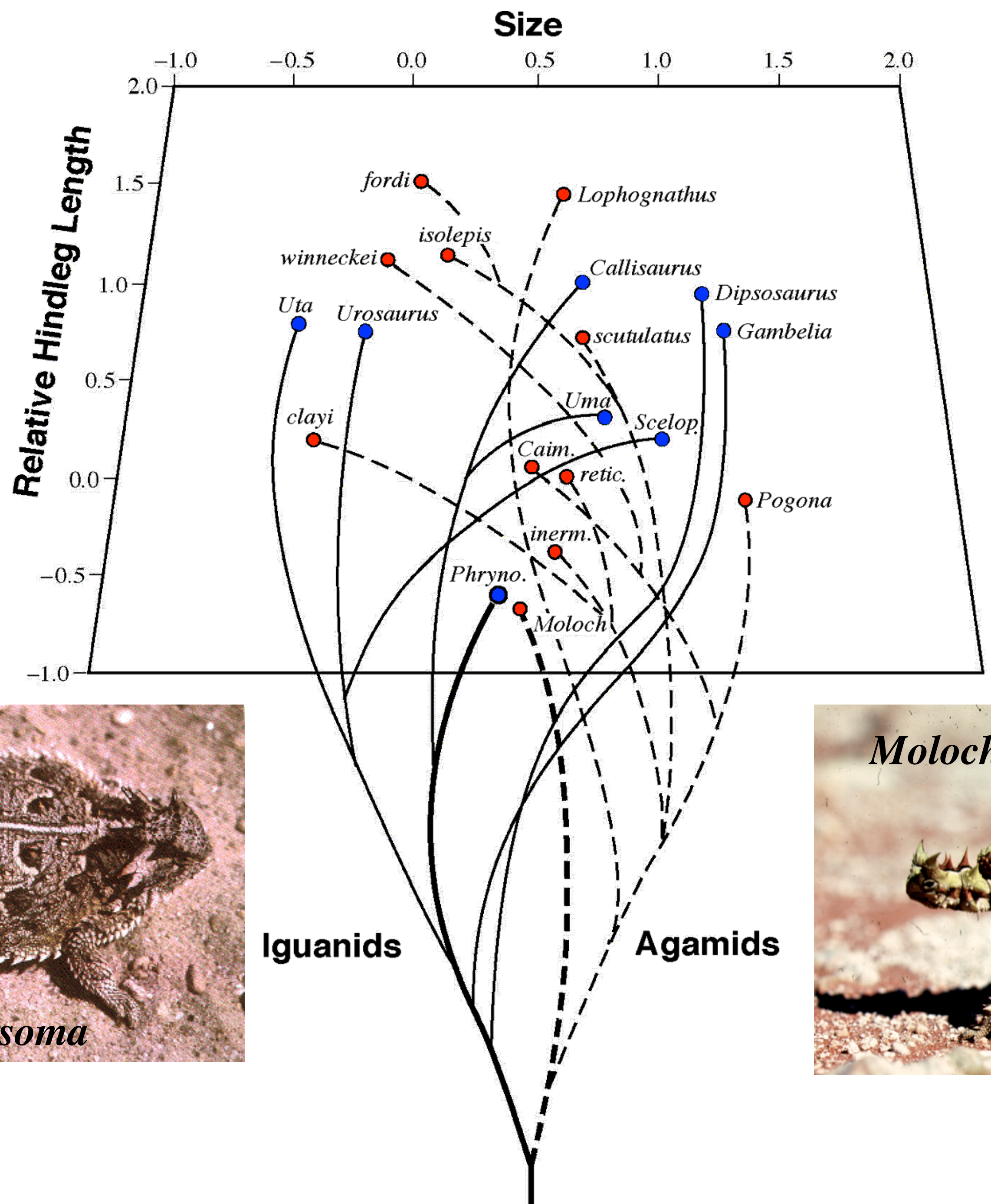
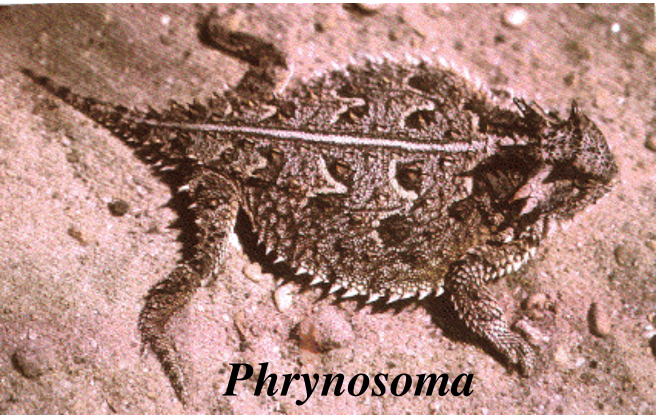
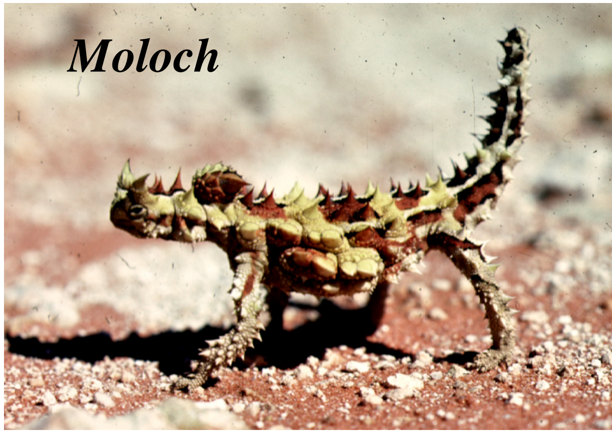



Size
−1.0
−0.5
0.0
0.5
1.0
1.5
2.0
Relative Hindleg Length
2.0
1.5
1.0
0.5
0.0
−0.5
−1.0
fordi
Lophognathus
isolepis
winneckei
Callisaurus
Dipsosaurus
Uta
Urosaurus
scutulatus
Gambelia
Uma
clayi
Scelop.
Caim.
retic.
Pogona
inerm.
Phryno.
Moloch
Iguanids
Agamids


Phrynosoma


Moloch

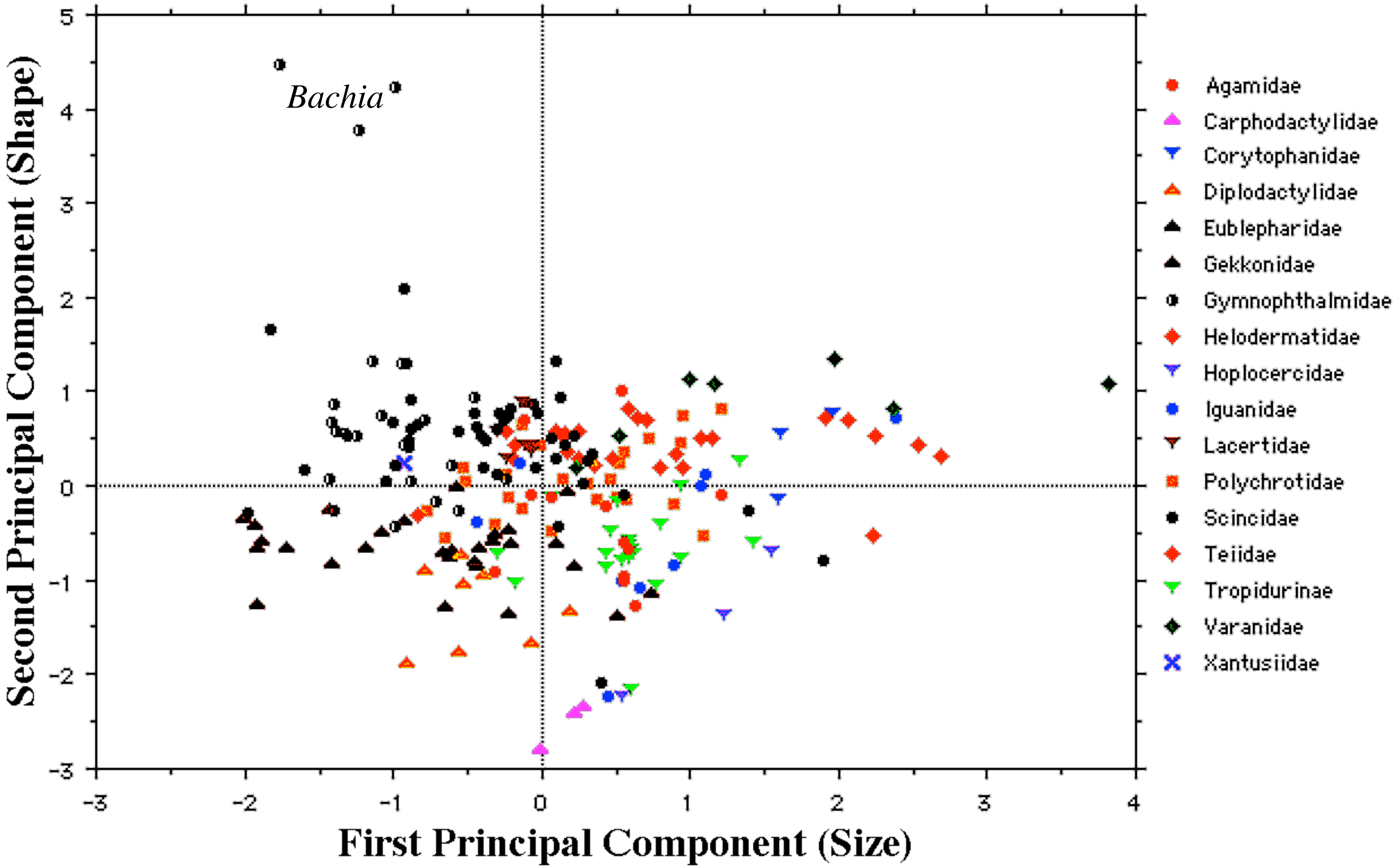
Eight Anatomical Variates, 239 species

Laurie Vitt

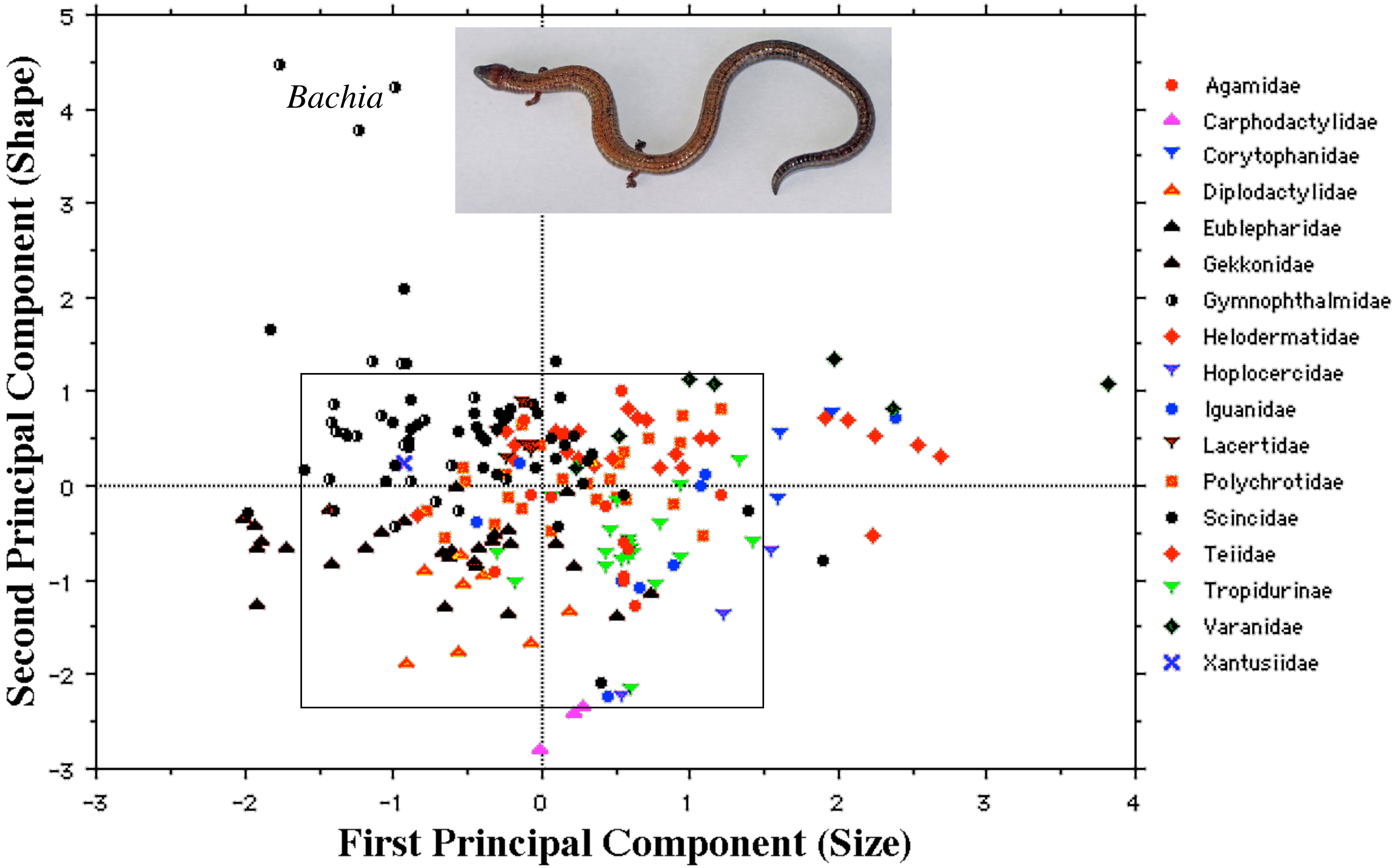
Snout-vent length
Tail length
Head length
Head width
Head depth
Body Weight (cube root)
Foreleg length
Hindleg length

Guarino Colli

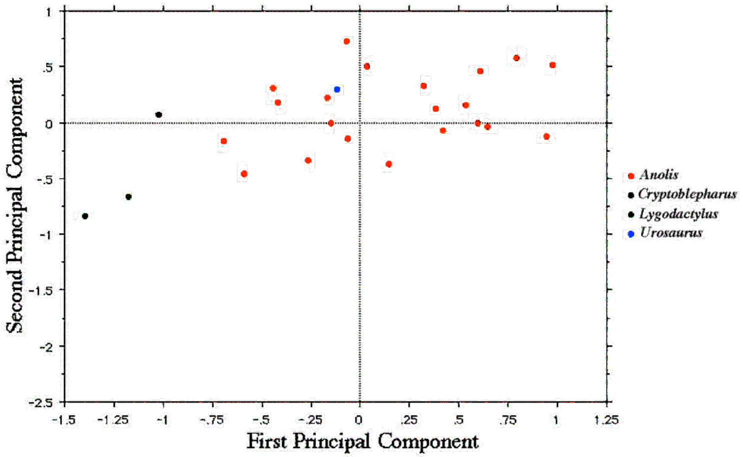
First Two Principal Components reduce variance by 93.5%



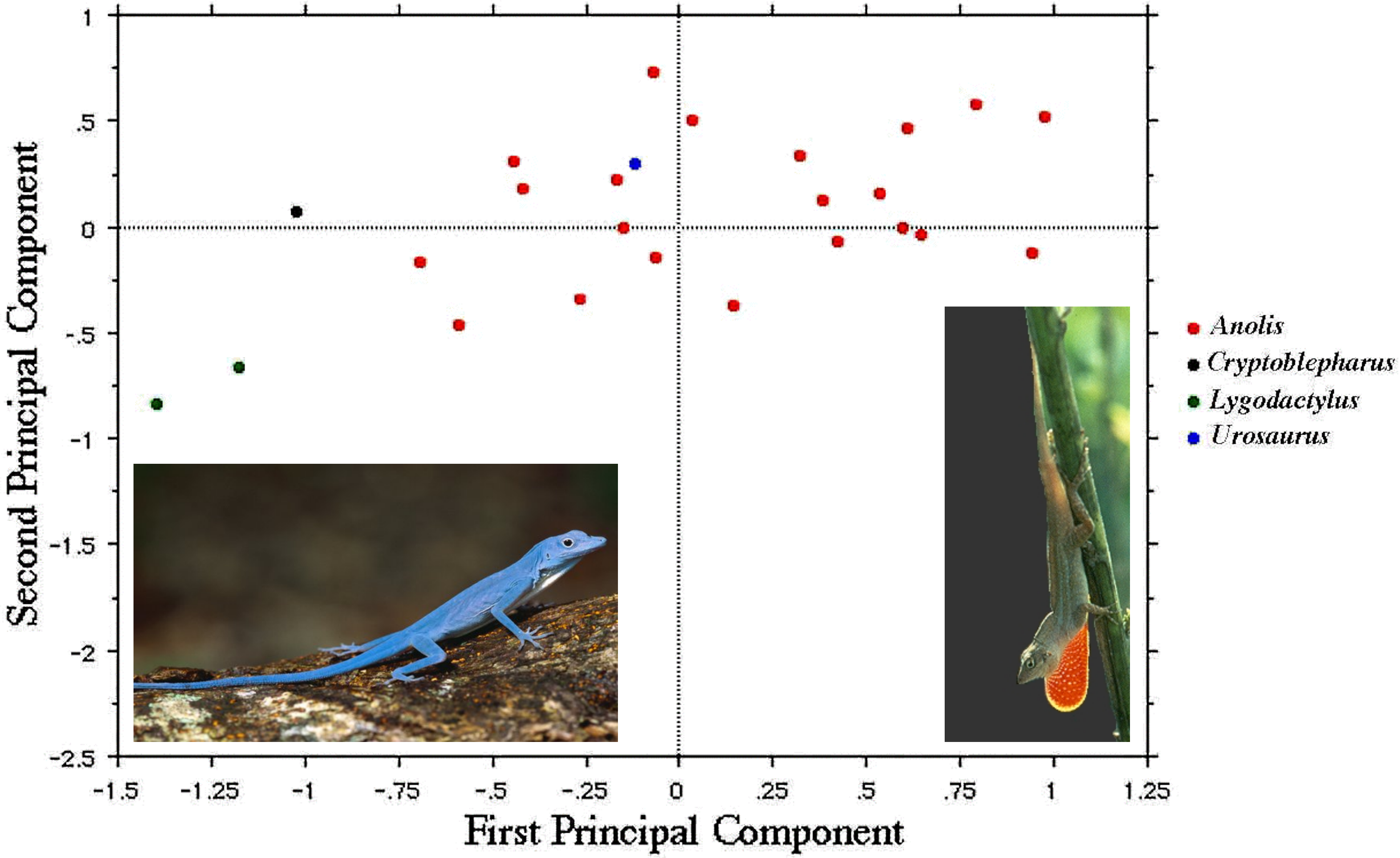
First Two Principal Components reduce variance by 93.5%



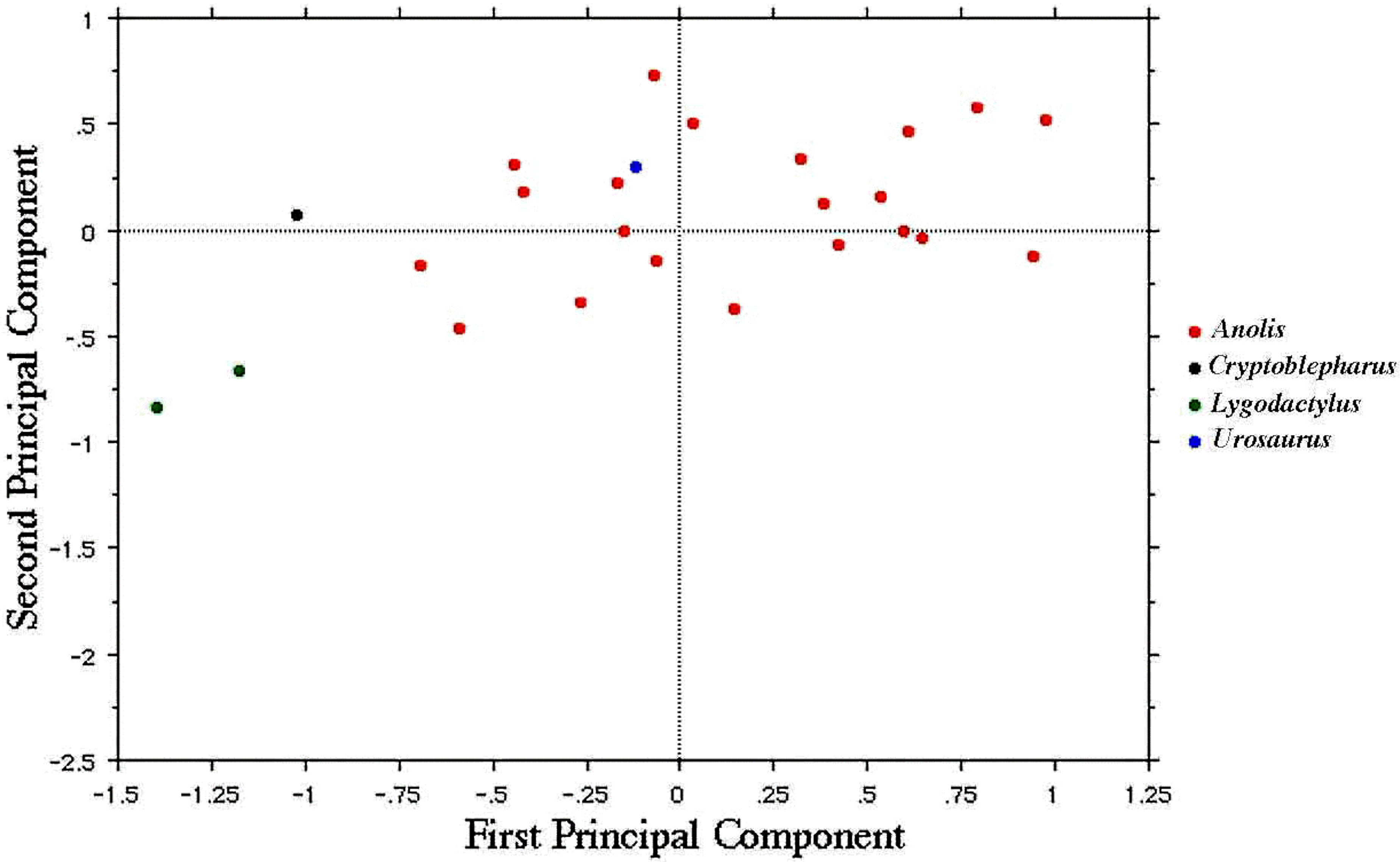
Anolis Morphology



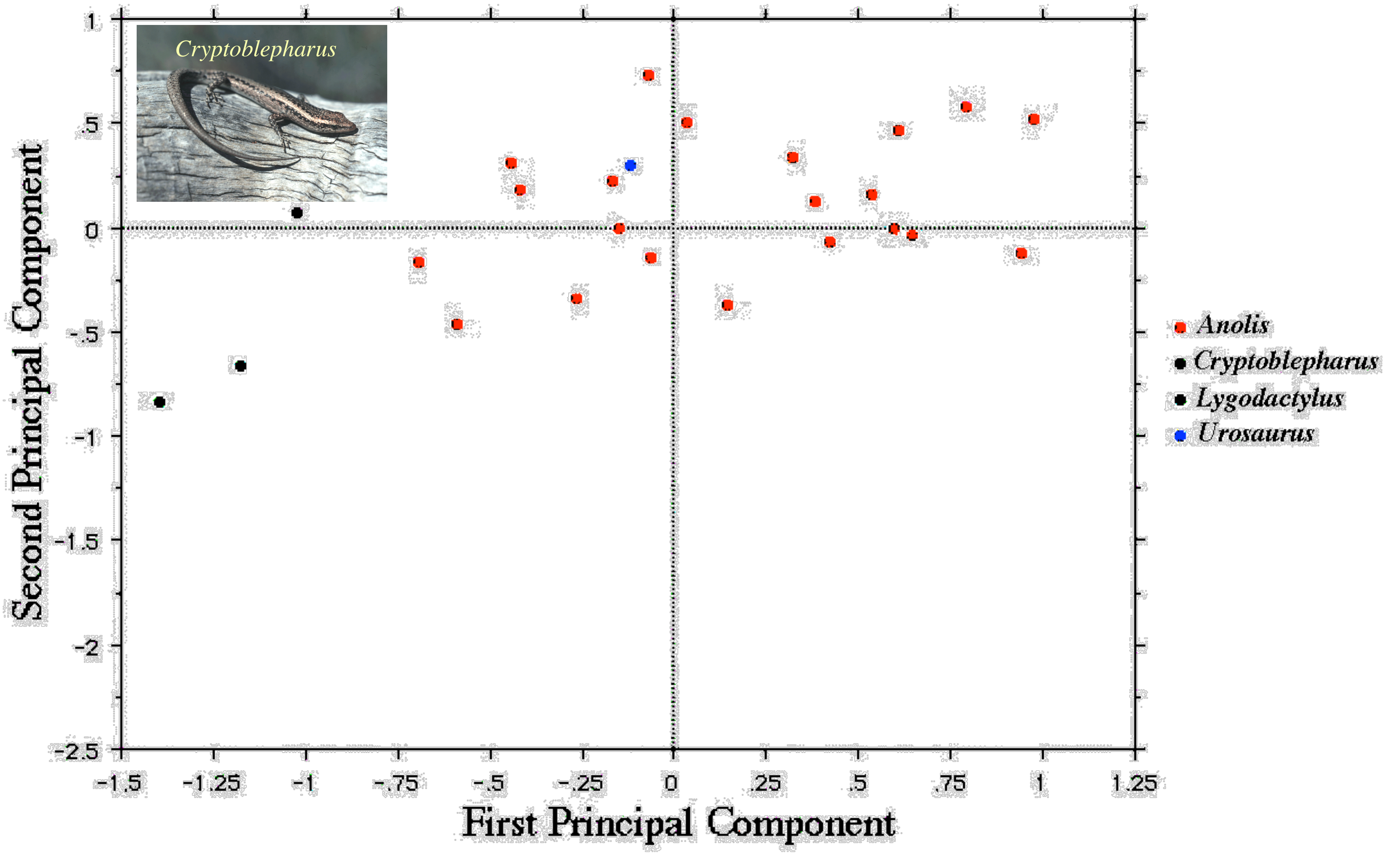
Anolis Morphology



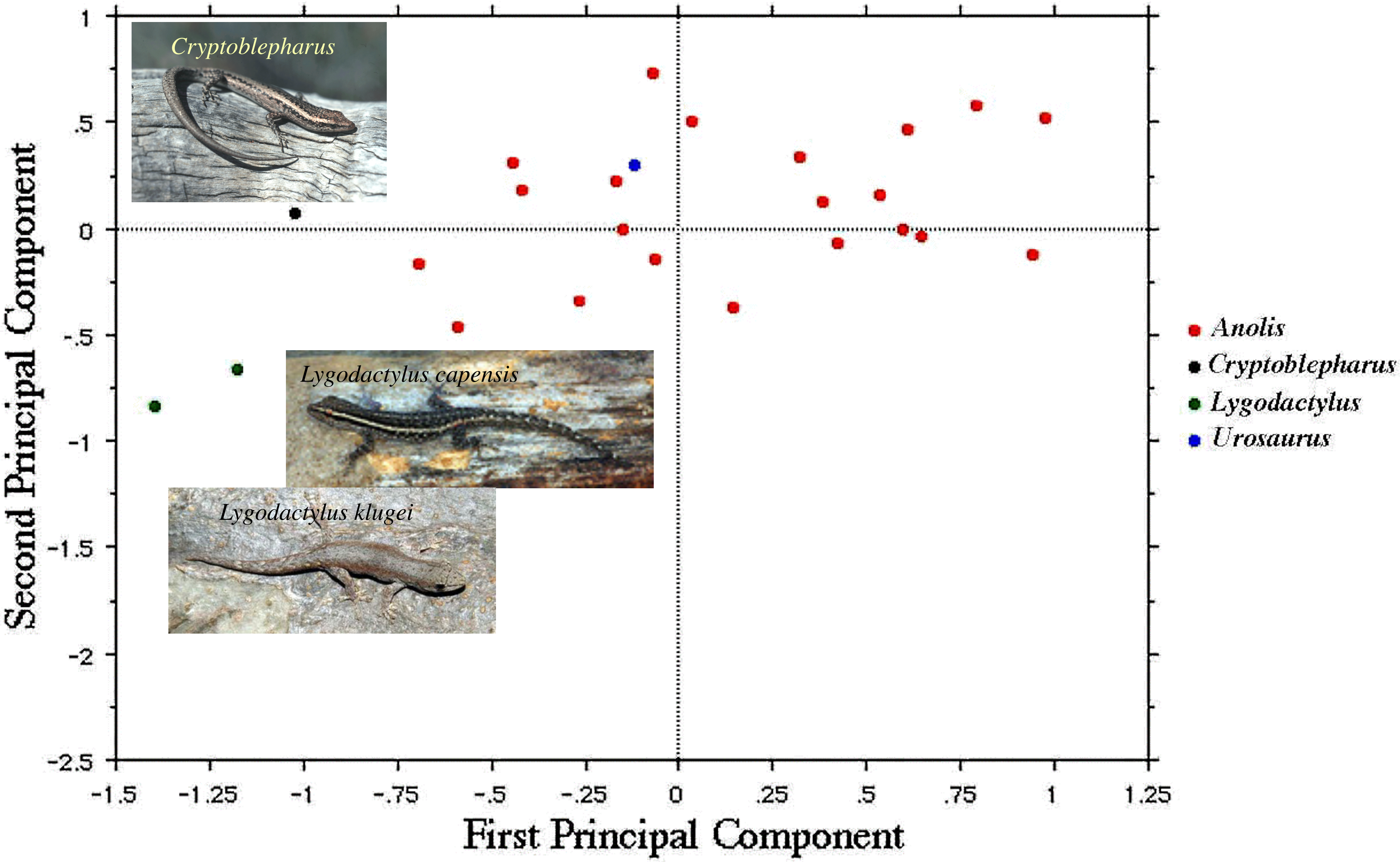
Anolis Morphology



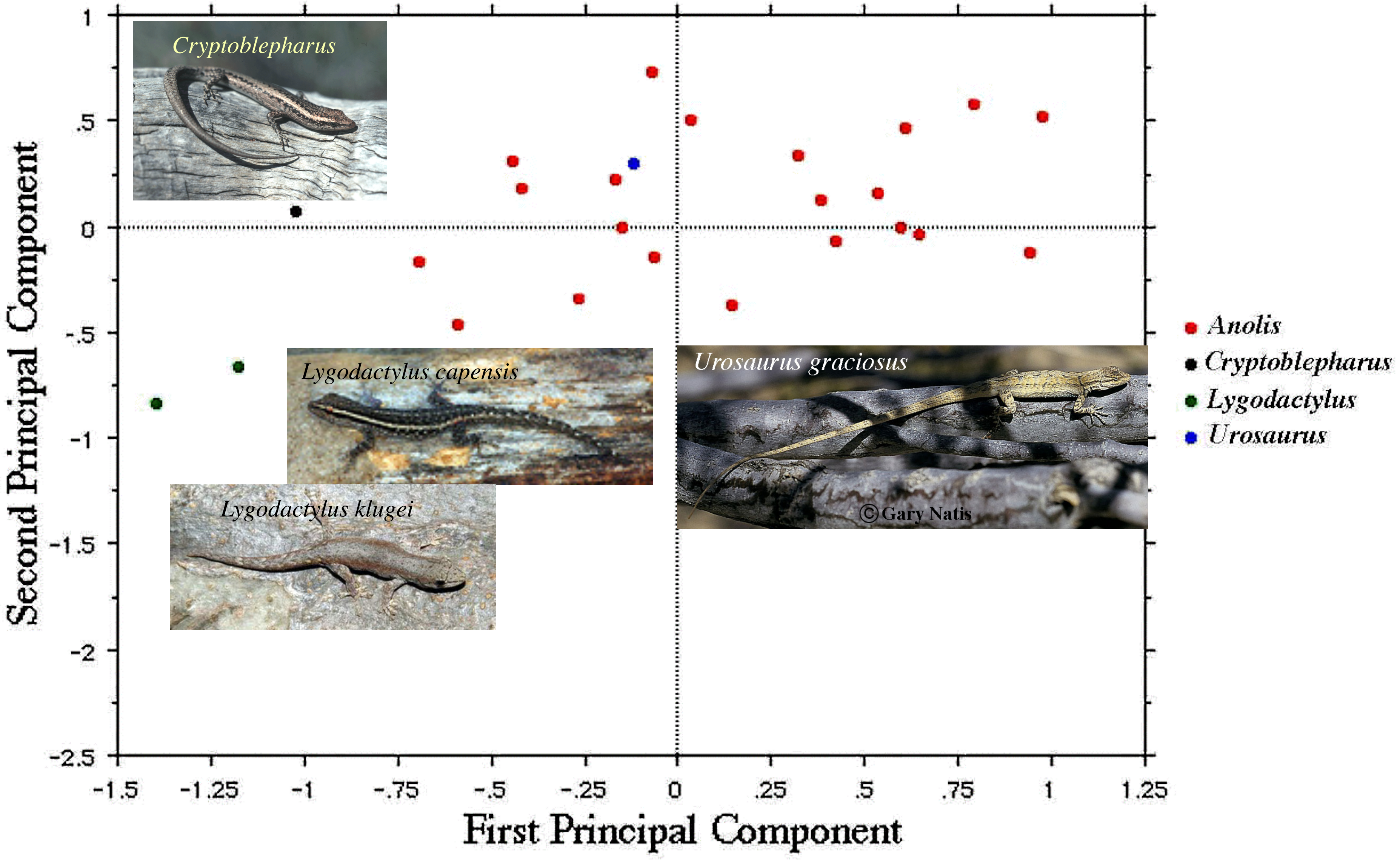
Anolis Morphology

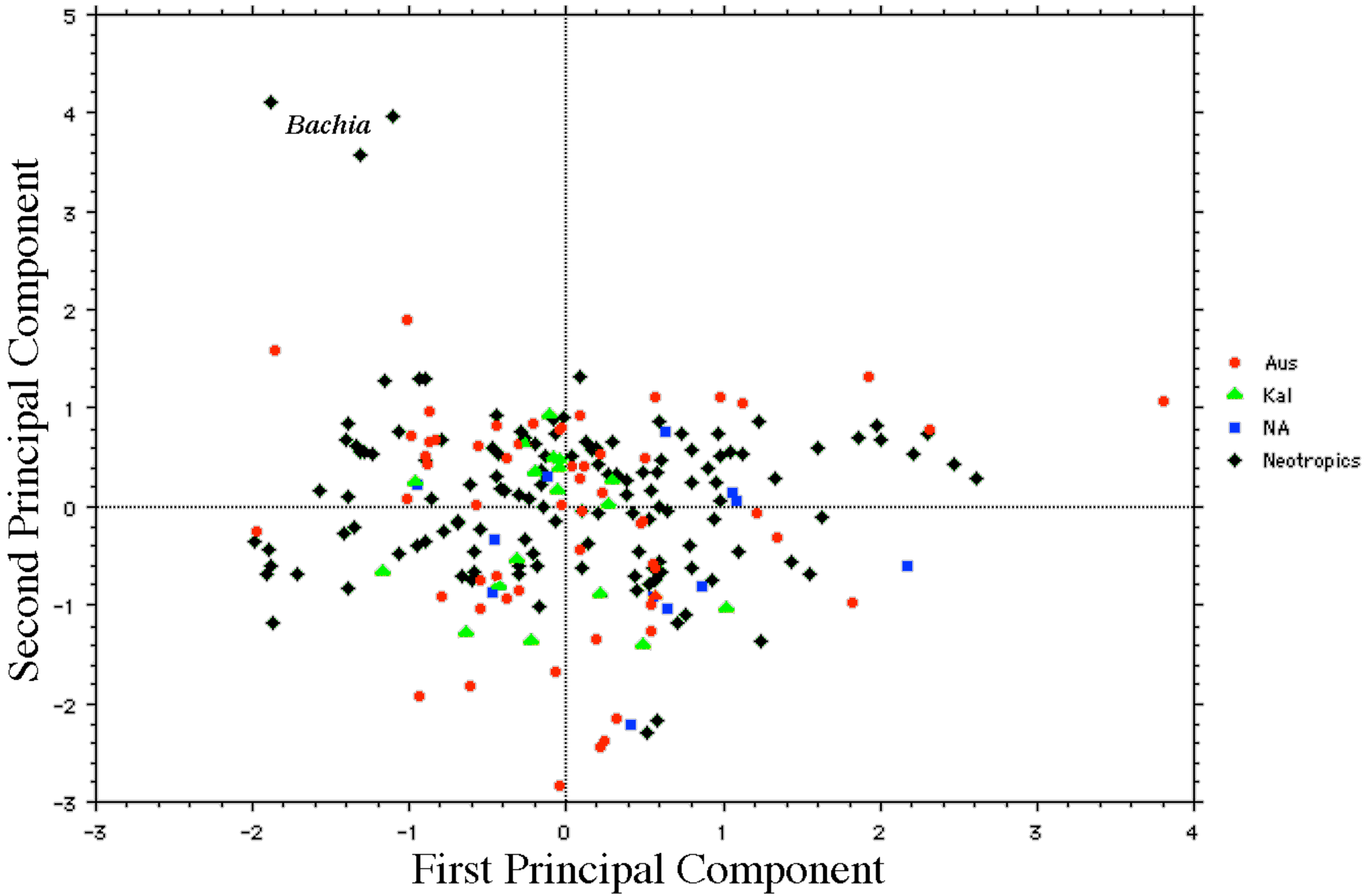


Anolis Morphology



Anolis Morphology




Bachia
Second Principal Component
First Principal Component
5
4
3
2
1
0
−1
−2
−3
−3
−2
−1
0
1
2
3
4
Aus
Kal
NA
Neotropics

Lizard niche dimensions appear to evolve in concert; recent evidence indicates synchronous transitions in life history and trophic traits. Some lizard clades reveal great dietary or life history diversification, whereas others do not. Families with phylogenetic structure for life history traits are nearly the same as those having phylogenetic structure with respect to diet. These observations hint as to how to construct a periodic table of niches. If dietary and life history dimensions covary, much of the variation in lizard ecology might be captured within a space of relatively low dimensionality.

The Biology of Lacertid lizards. Evolutionary and Ecological Perspectives (2004). Pérez-Mellado, V., Riera, N. and Perera, A. (eds.). Institut Menorquí d'Estudis. Recerca, 8: 139-157.

HISTORICAL PATTERNS IN LIZARD ECOLOGY: WHAT TEIIDS CAN TELL US ABOUT LACERTIDS

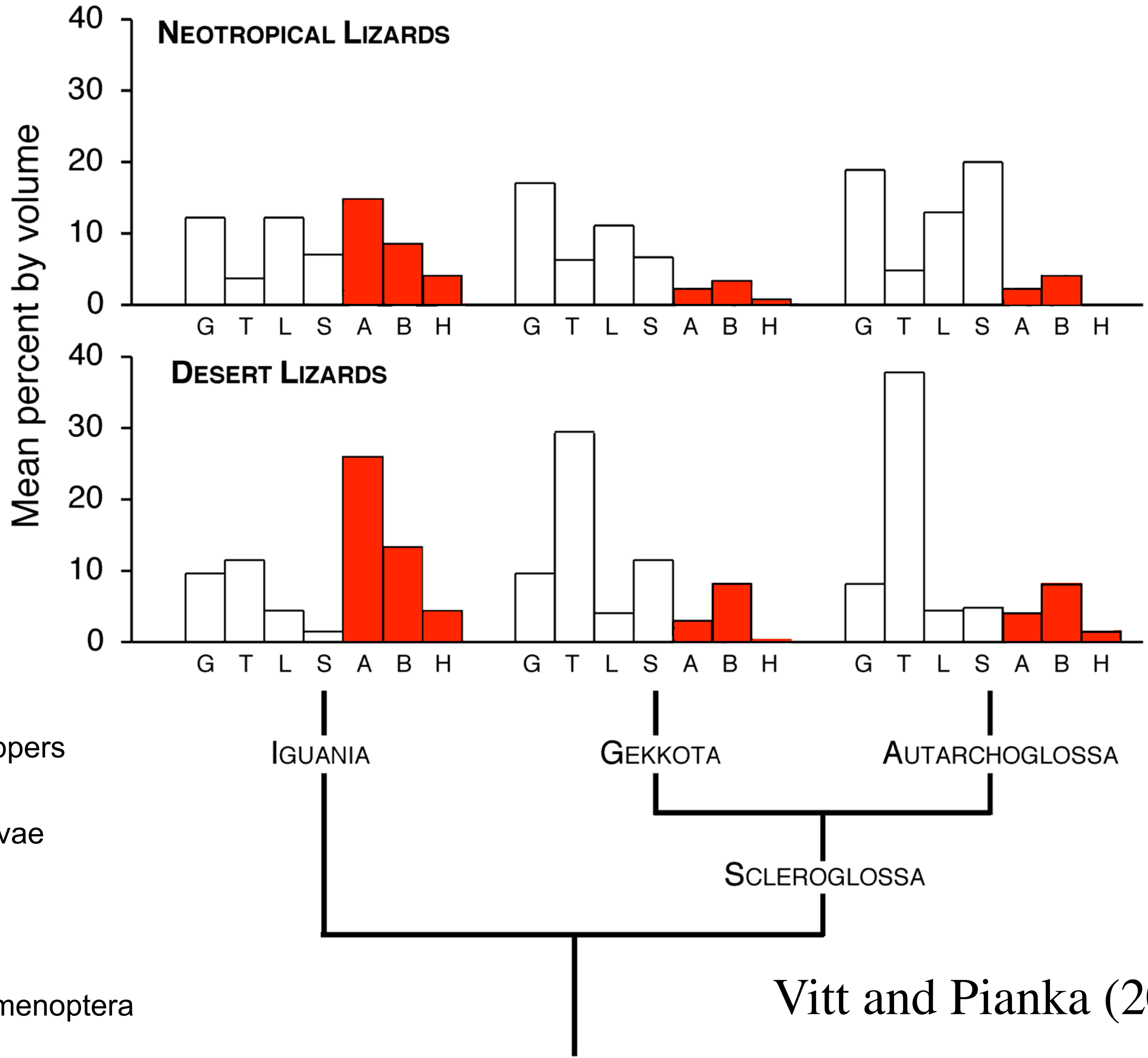
VITT, L. J.[1] & PIANKA, E. R.[2]

Abstract: Lacertid, teiid, and gymnophthalmid lizards share much of their evolutionary history. We explore ecological traits of these lizards in an attempt to identify similarities that may have a historical origin as well as differences that may reflect the effects of differing ecological settings on the portion of their histories that is independent. Within Teioidea, major divergence in body size occurred producing Gymnophthalmidae (small size) and Teiidae (larger size). Small body size in gymnophthalmids affected their ecology differently than larger body size did in teiids, particularly in respect to thermal ecology. that future comparisons can be more meaningful.

Keywords: Lacertidae, lizard diets, lizard ecology, historical ecology, phylogeny, Teiidae.

Resumen: Patrones históricos en la ecología de lagartos: Qué nos enseñan los teidos acerca de los lacértidos. -Lacertidae, Teiidae y Gymnophthalmidae comparten gran parte de su historia evolutiva. Exploramos los rasgos ecológicos de estos lagartos en un intento para identificar las similitudes que pudieran tener un origen histórico, así como las diferencias que puedan reflejar

Types of Prey Eaten by Lizards



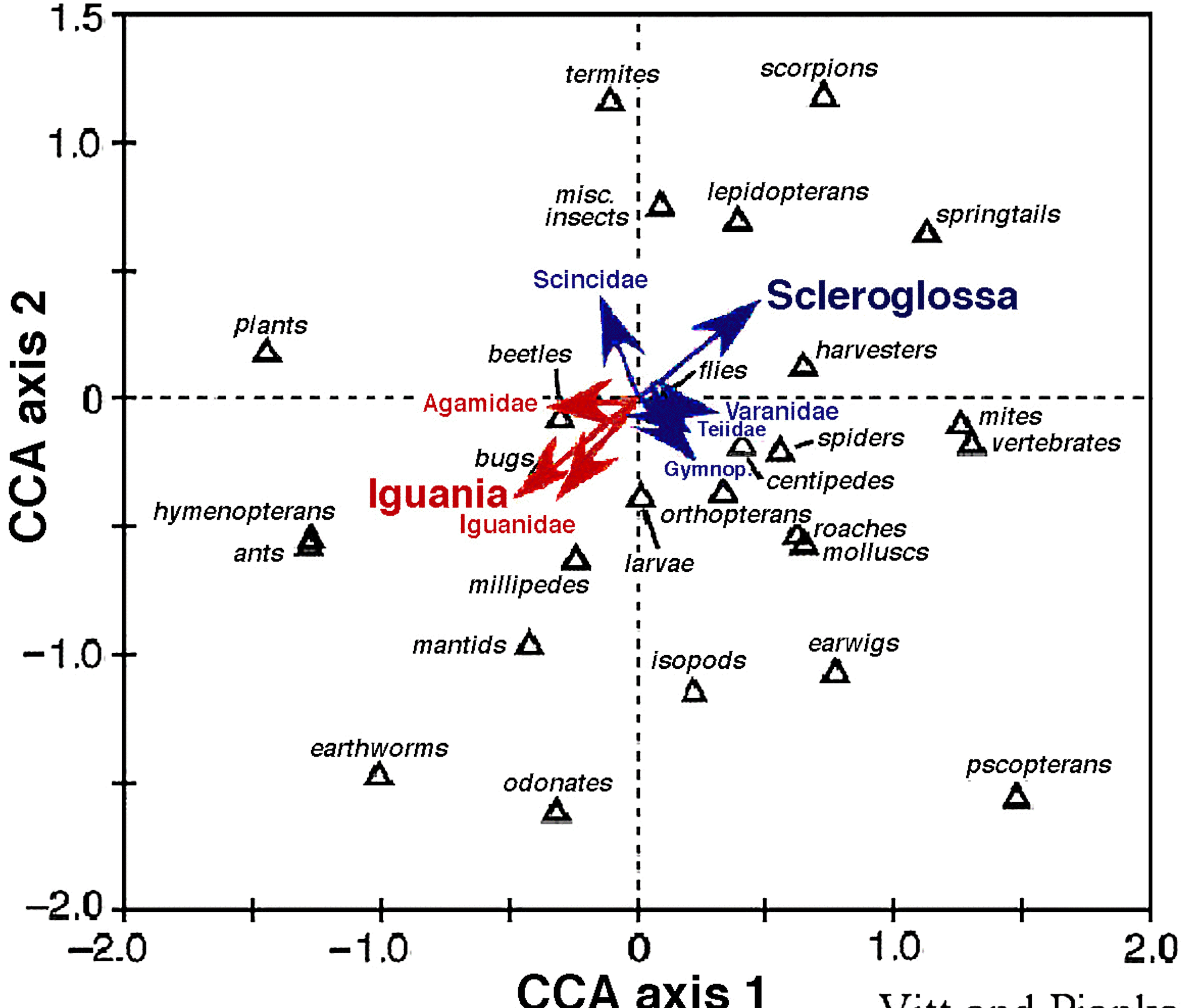
G = grasshoppers
T = termites
L = insect larvae
S = spiders
A = ants
B = beetles
H = other hymenoptera

Vitt and Pianka (2003)

Diets for 184 lizard species summarized based on 27 prey categories:

- ants
- beetles
- bugs (hemiptera+homoptera)
- centipedes
- earthworms
- earwigs
- flies
- grasshoppers/crickets
- hymenopterans (non-ant)
- isopods
- larvae/eggs/pupae
- lepidopterans
- mantids/phasmids
- millipedes
- misc. insects
- mites
- mollusks
- odonates
- harvesters
- plants
- psocopterans
- roaches
- scorpions
- spiders
- springtails
- termites
- vertebrates

Vitt and Pianka (2005)



Vitt and Pianka (2005)

VOL. 51, NO. 3 September, 1976

THE QUARTERLY REVIEW of BIOLOGY

COSTS AND BENEFITS OF LIZARD THERMOREGULATION

By RAYMOND B. HUEY[1,3] and MONTGOMERY SLATKIN[2]

[1]*Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138;*
[2]*Department of Biophysics and Theoretical Biology, University of Chicago, Chicago, Illinois 60637*

Microhabitats

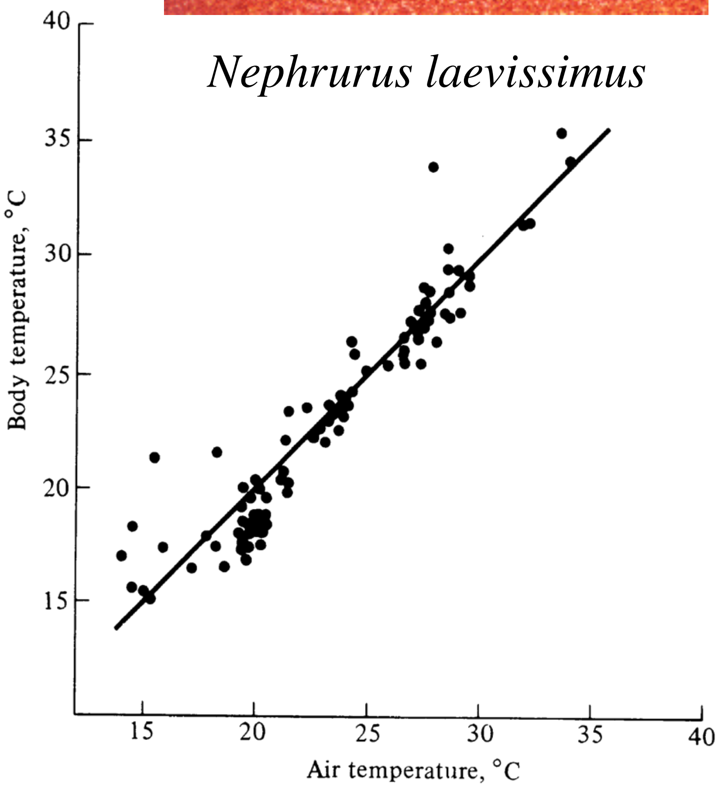
Similarly, desert lizards position themselves perpendicular to the sun's rays in early morning, when environmental temperatures are low, but during the high temperatures of midday, these same lizards reduce their heat load by climbing up off the ground into cooler air, facing directly into the sun, thereby reducing heat gained.

Passive thermoconformer

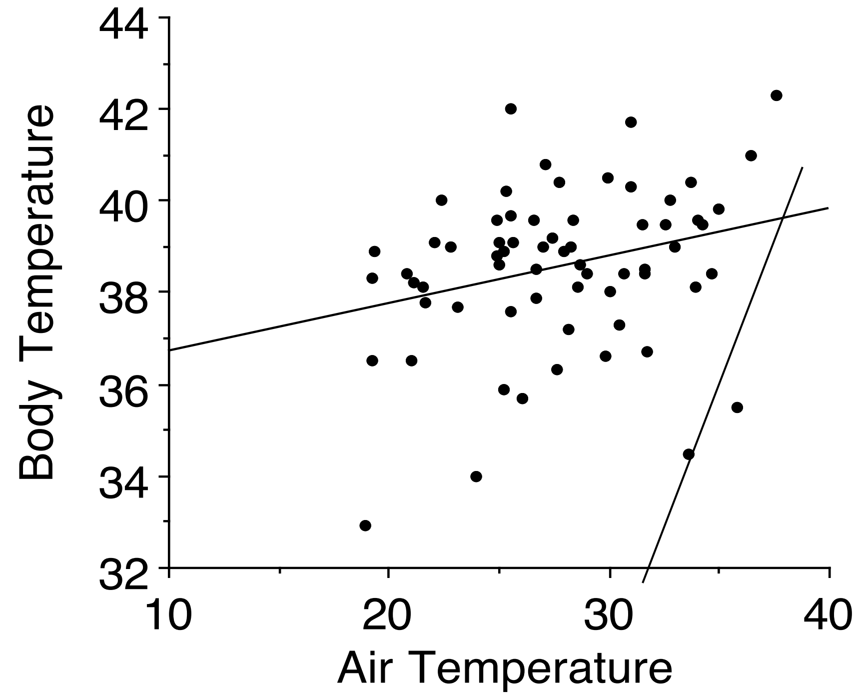
Active Thermoregulator

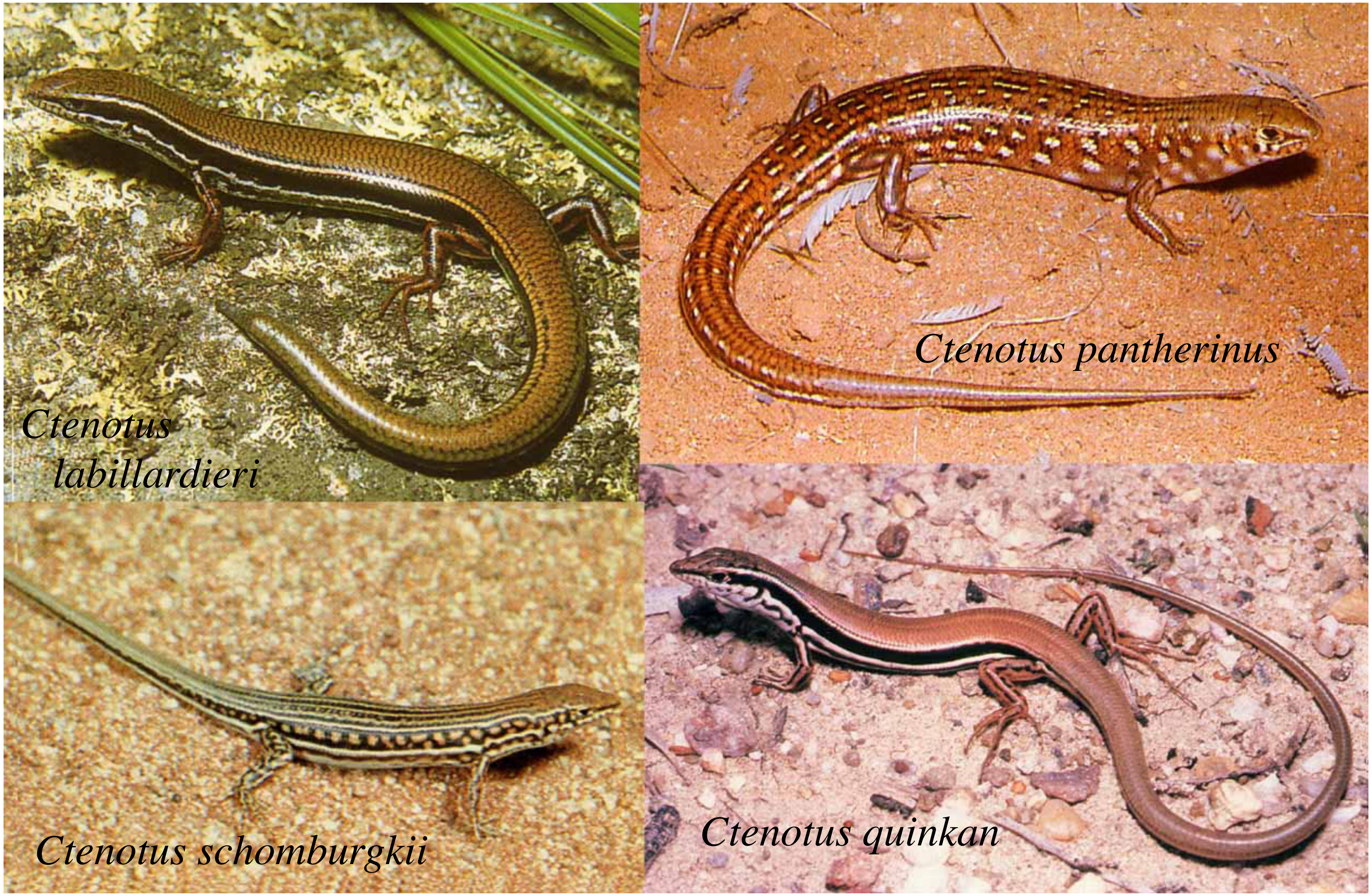
Slope of Regression (one to zero)

Nephrurus laevissimus

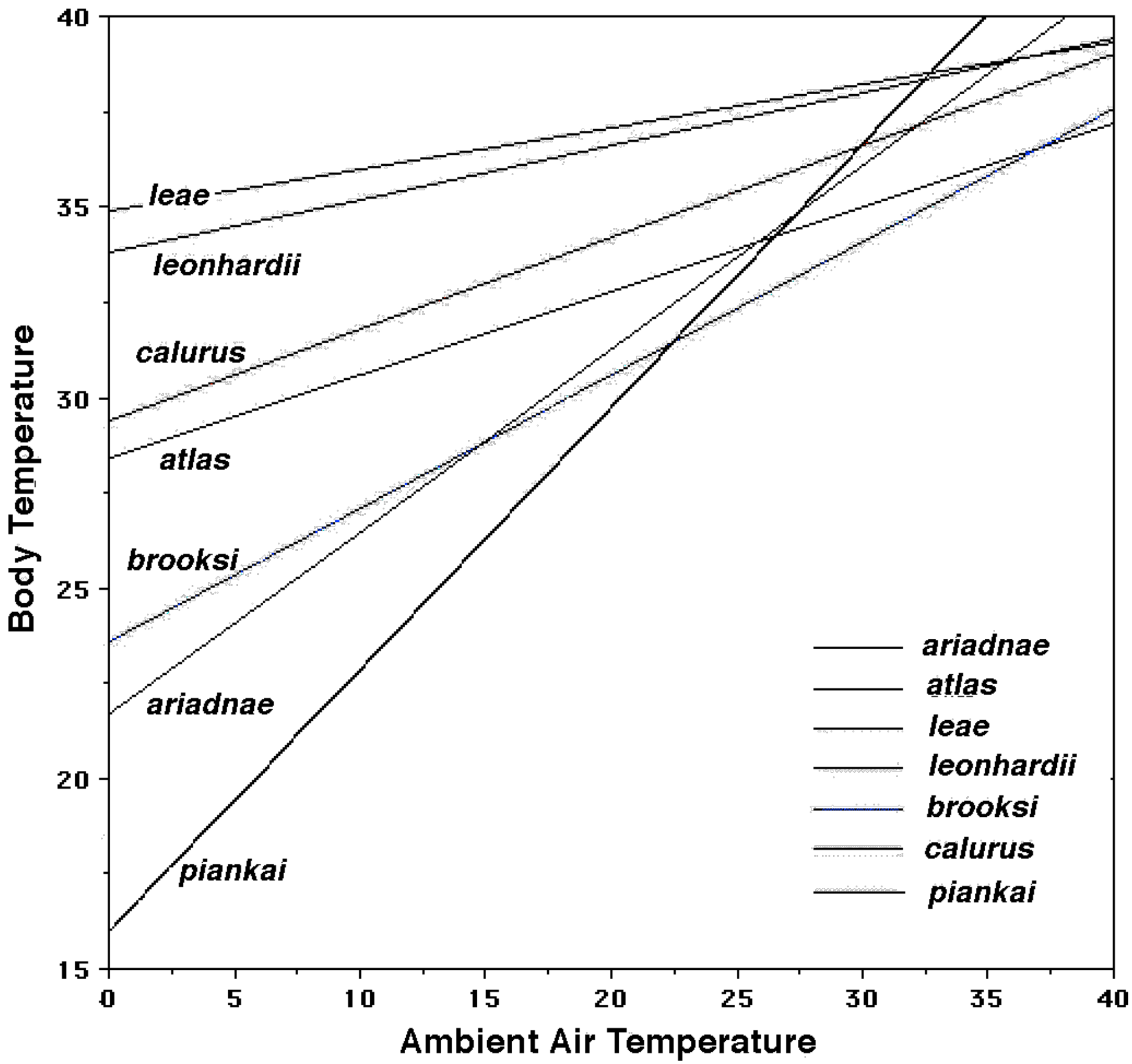


Ctenophorus isolepis





Australian comb-eared skinks, genus *Ctenotus*



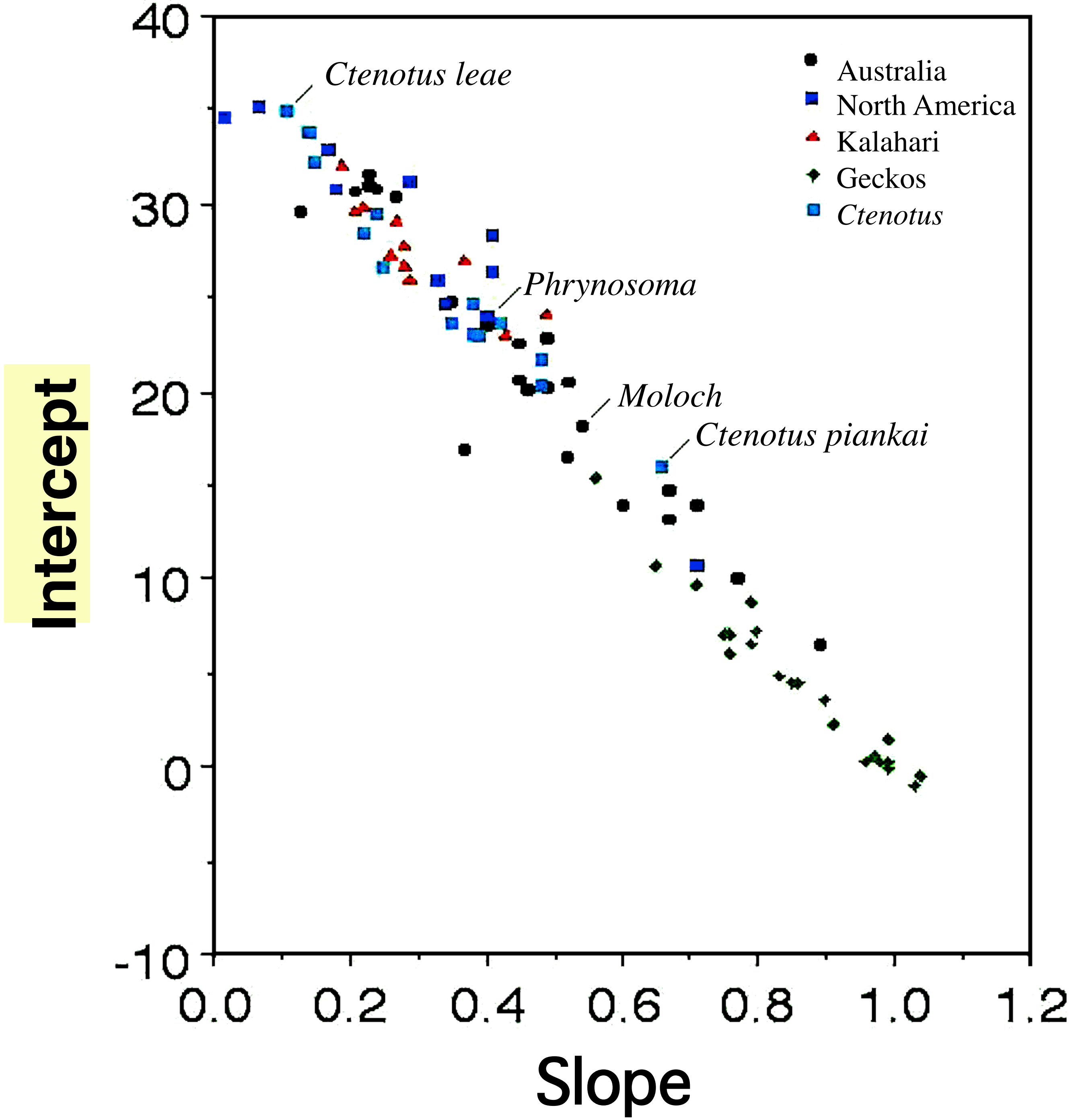
Ctenotus leae

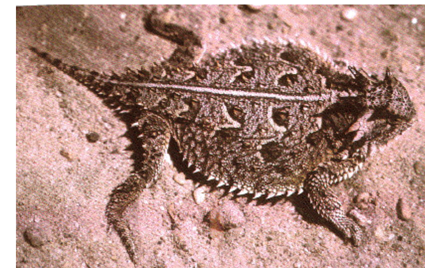
Ctenotus piankai

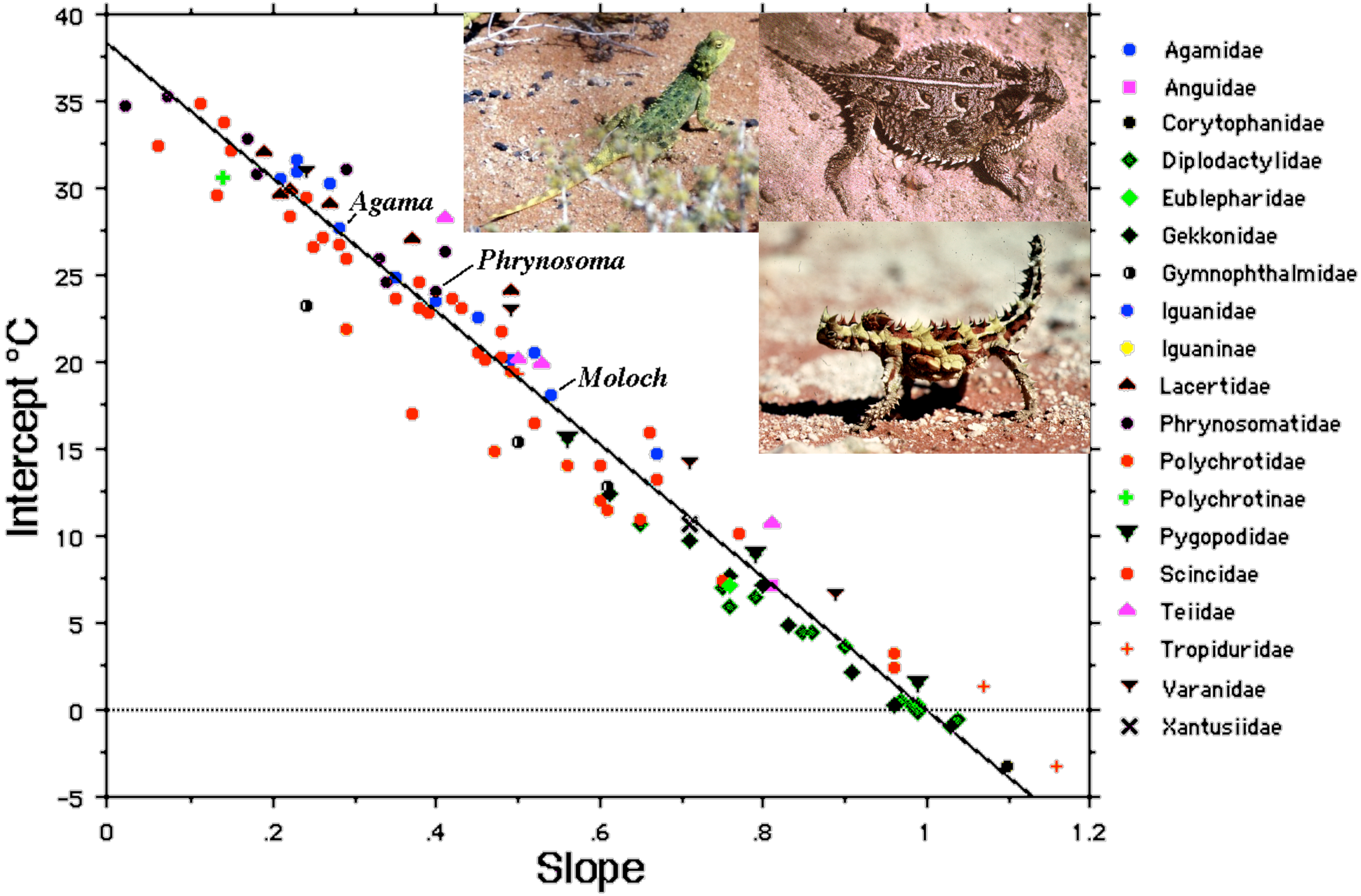
Slope of regression of active T_b on T_a is a surrogate measure for microhabitat and time of activity. A useful single number that informs us about a lizard’s ecology

Challenge: Reducing dimensionality

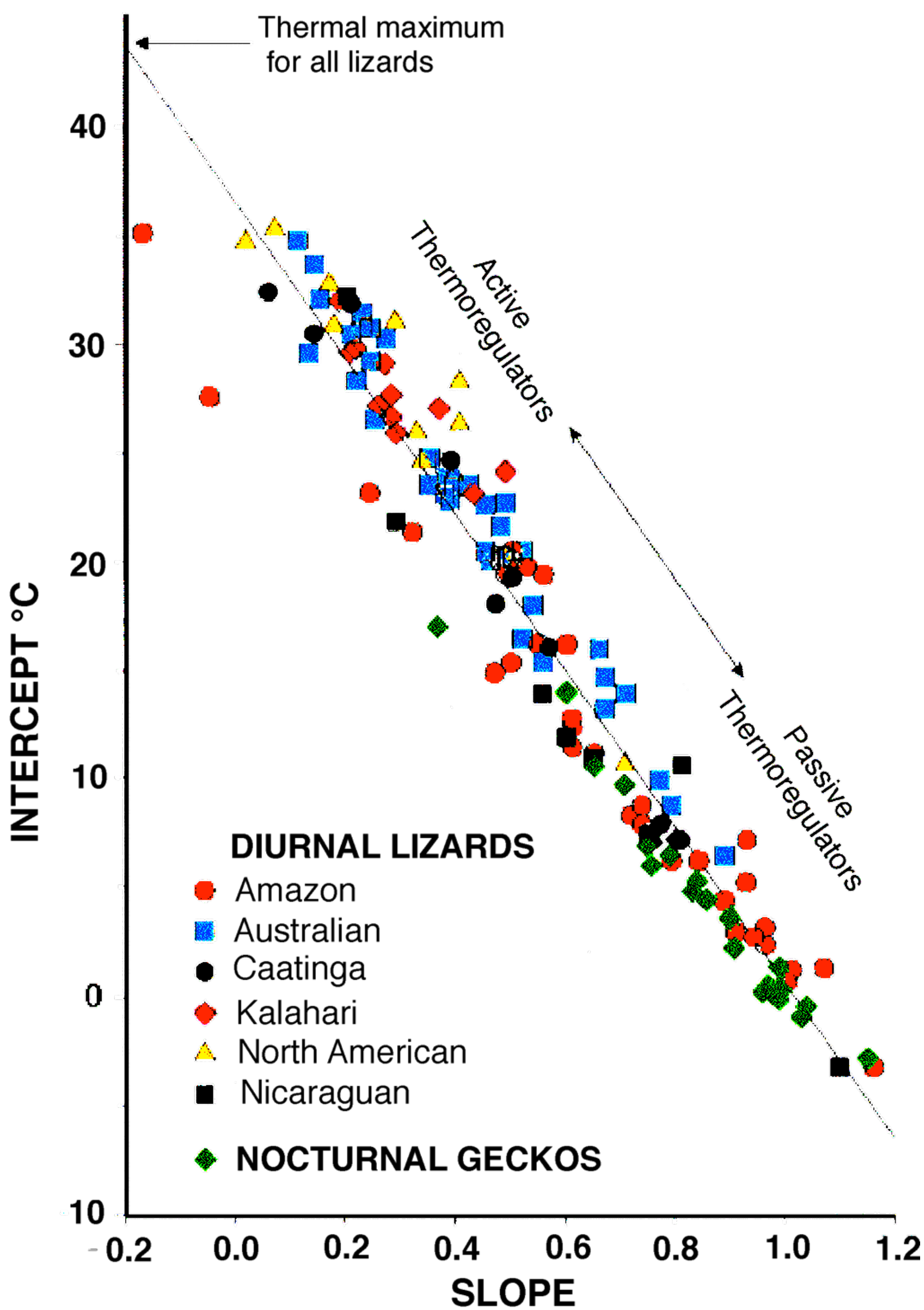
Plot a line as a point in the coordinates of slope vs. intercept


Intercept
Slope
40
30
20
10
0
-10
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Australia
North America
Kalahari
Geckos
Ctenotus
Ctenotus leae
Phrynosoma
Moloch
Ctenotus piankai

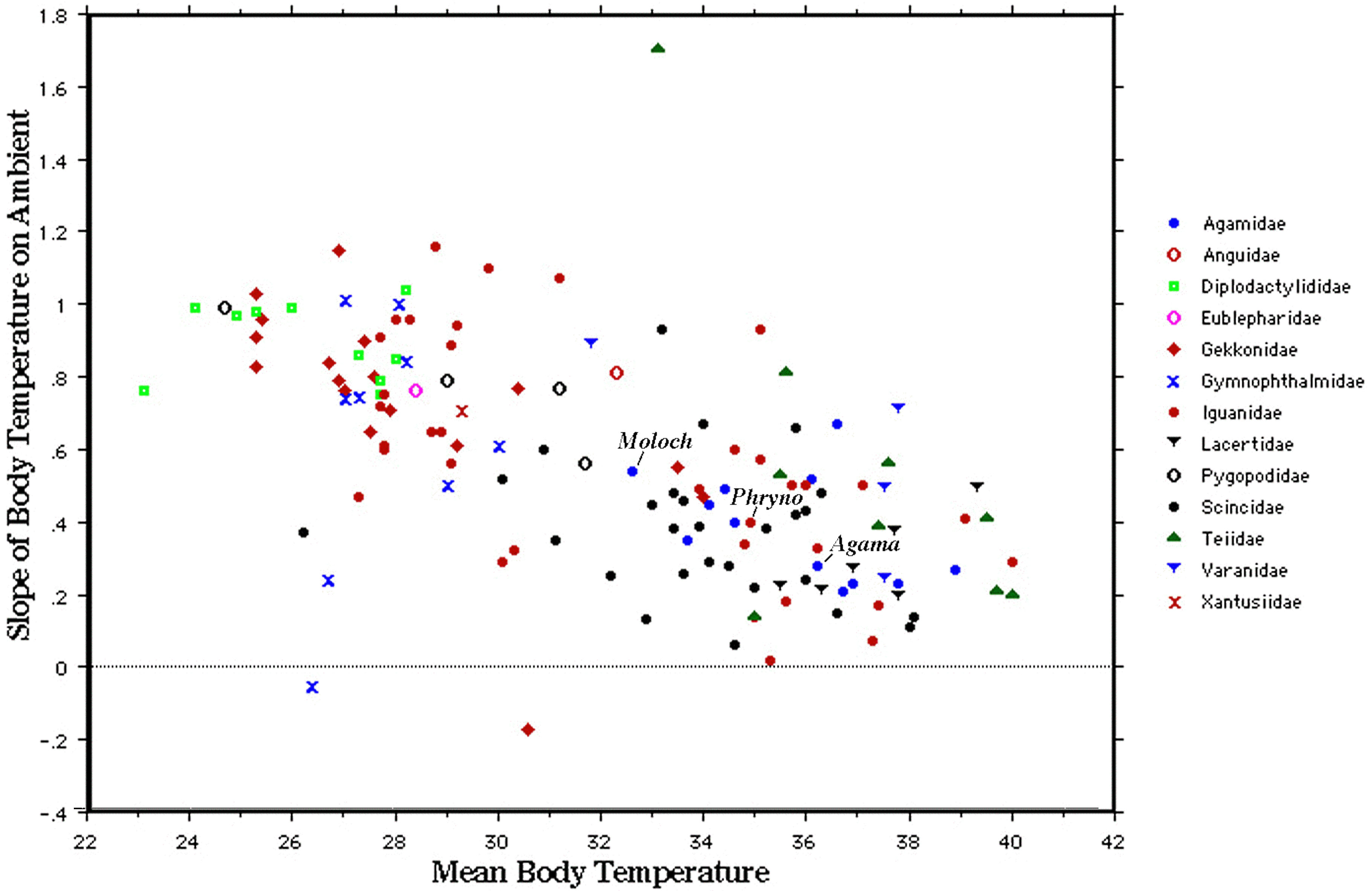




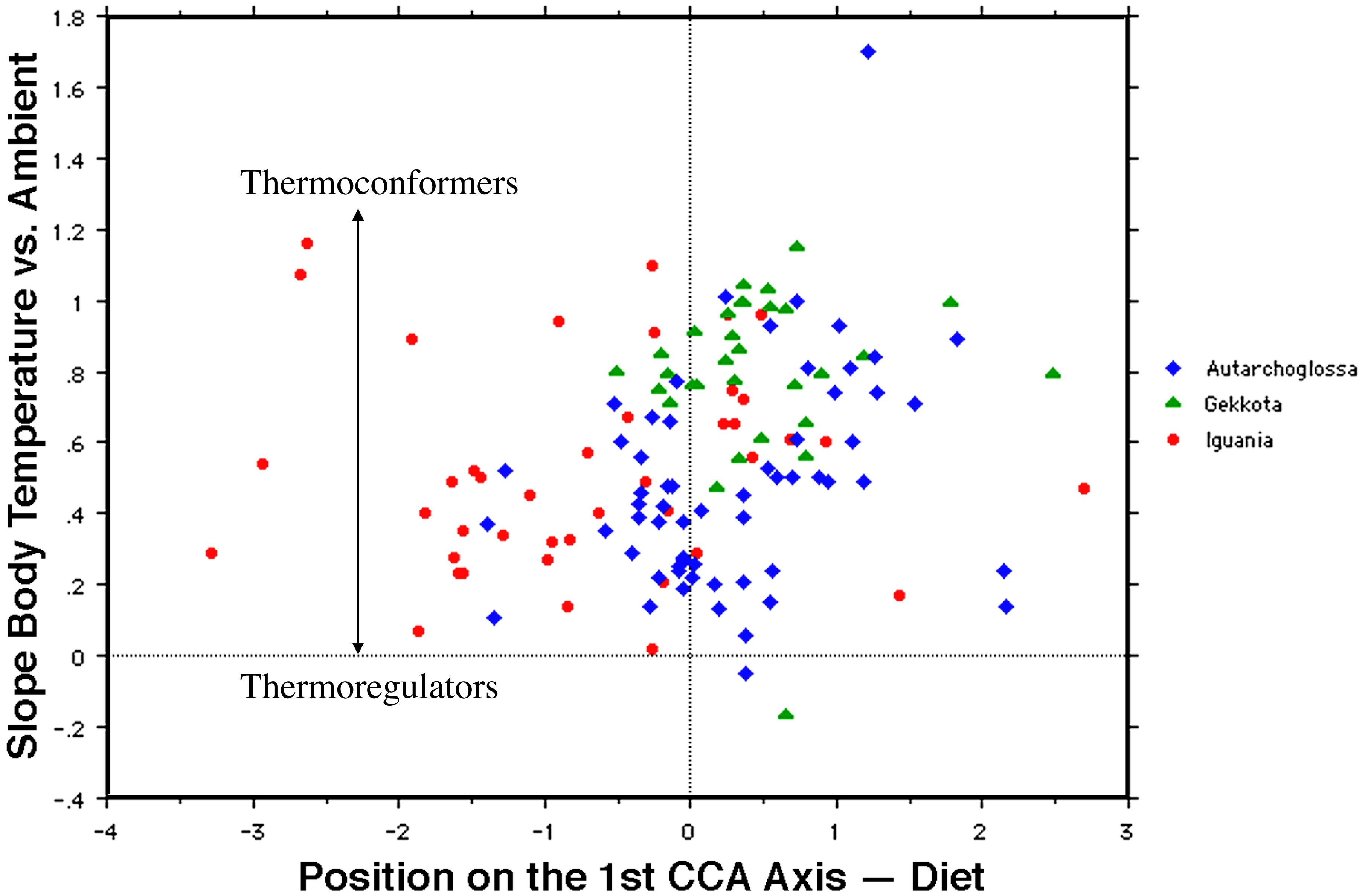
Intercept °C
Slope
40
35
30
25
20
15
10
5
0
-5
0
.2
.4
.6
.8
1
1.2
Agama
Phrynosoma
Moloch
Agamidae
Anguidae
Corytophanidae
Diplodactylidae
Eublepharidae
Gekkonidae
Gymnophthalmidae
Iguanidae
Iguaninae
Lacertidae
Phrynosomatidae
Polychrotidae
Polychrotinae
Pygopodidae
Scincidae
Teiidae
Tropiduridae
Varanidae
Xantusiidae



Thermal maximum
for all lizards
Active
Thermoregulators
Passive
Thermoregulators
INTERCEPT °C
40
30
20
10
0
10
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
SLOPE
DIURNAL LIZARDS
Amazon
Australian
Caatinga
Kalahari
North American
Nicaraguan
NOCTURNAL GECKOS



Slope of Body Temperature on Ambient
Mean Body Temperature
1.8
1.6
1.4
1.2
1
.8
.6
.4
.2
0
-.2
-.4
22
24
26
28
30
32
34
36
38
40
42
Moloch
Phryno
Agama
Agamidae
Anguidae
Diplodactylididae
Eublepharidae
Gekkonidae
Gymnophthalmidae
Iguanidae
Lacertidae
Pygopodidae
Scincidae
Teiidae
Varanidae
Xantusiidae



Thermoconformers
Thermoregulators
Slope Body Temperature vs. Ambient
Position on the 1st CCA Axis — Diet
1.8
1.6
1.4
1.2
1
.8
.6
.4
.2
0
-.2
-.4
-4
-3
-2
-1
0
1
2
3
Autarchoglossa
Gekkota
Iguania

Today I have outlined many of the dimensions required to construct a periodic table of lizard niches. Though I have been unable to achieve this goal, I hold high hopes that lizard niches can eventually be classified in a space of moderately low dimensionality using axes such as the thermoregulator-thermoconformer continuum and a discriminant function axis linking mode of foraging to body size and reproductive tactics.

Unfortunately, only 13 of the 82 species used to generate the first axis and included among the 91 species used to generate the second axis. More data on lizard niches need to be gathered before such an analysis will come to fruition.