Geographic Variation

Geographic variation may be
* molecular only or expressed in phenotype
* neutral or adaptive
* run gamut from trivial to dramatic
* clinal or discrete

Cougar: *Puma concolor*

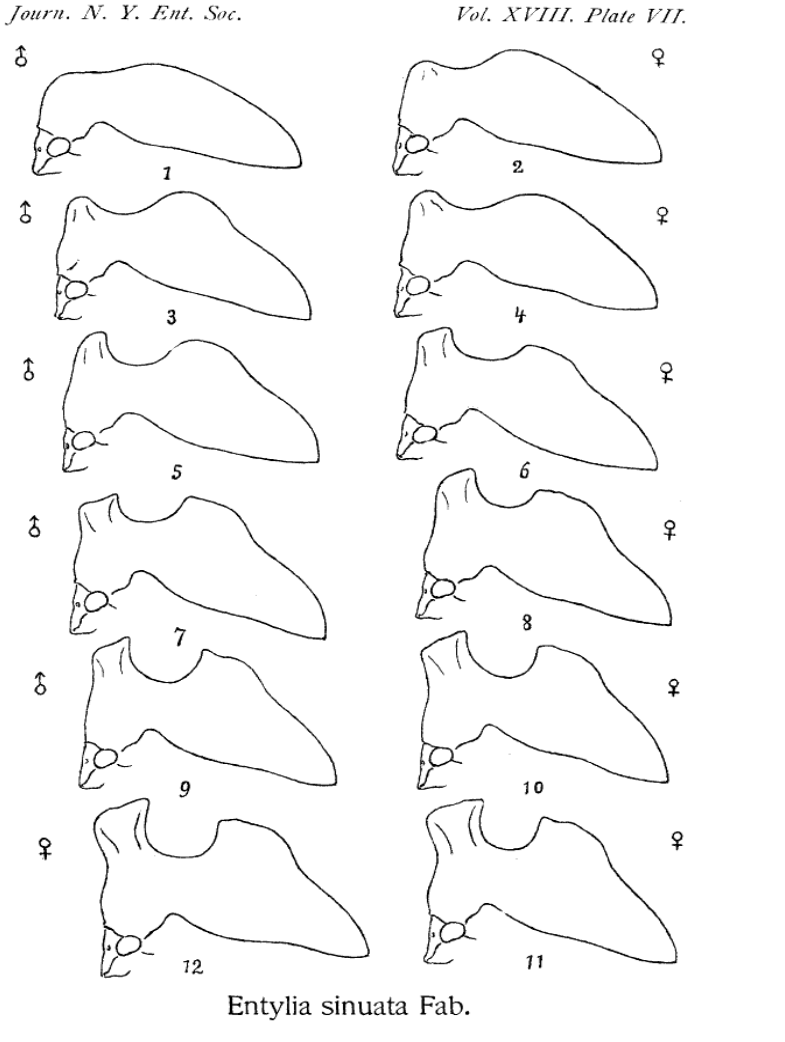
Known aliases: mountain lion, panther, puma

Puma concolor Linnaeus 1771

Once thought to be 15 different subspecies, molecular evidence suggests 6 subspecies (Culver et al. 2000):

- *P. c. couguar* - North America
- *P. c. costaricensis* - Central America
- *P. c. capricornensis* - eastern South America
- *P. c. concolor* - northern South America
- *P. c. cabrerae* - central South America
- *P. c. puma* - southern South America

mtDNA haplotypes specified by SNPs

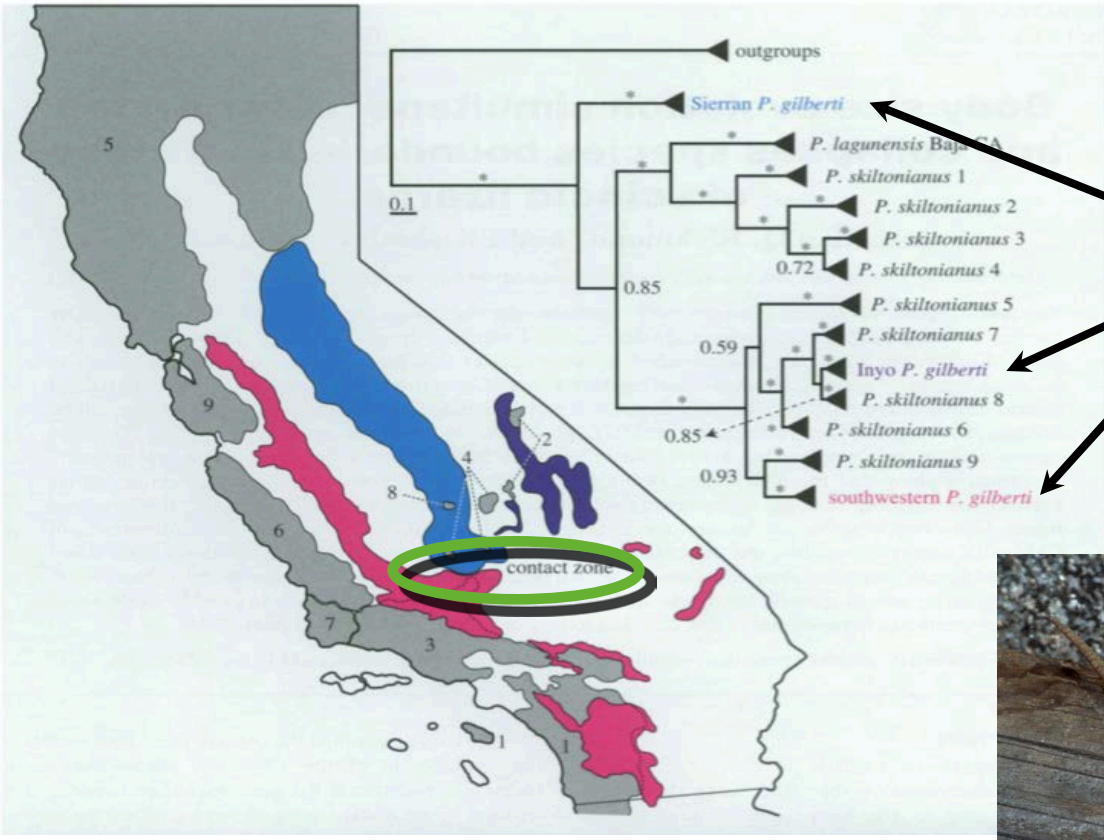


Matausch, 1910

Other names and synonyms:
E. sinuata, bactriana, emarginata, decisa, accisa, indecisa, reducta, torva, impedita, inequalis, mira, concava, vittata, oedipus, moesta, fuscodorsa…
(Goding, 1929)

Gilbert's Skink
Plestiodon gilberti

Red headed peramorphic form arises 3 times



Adult *P. gilberti*

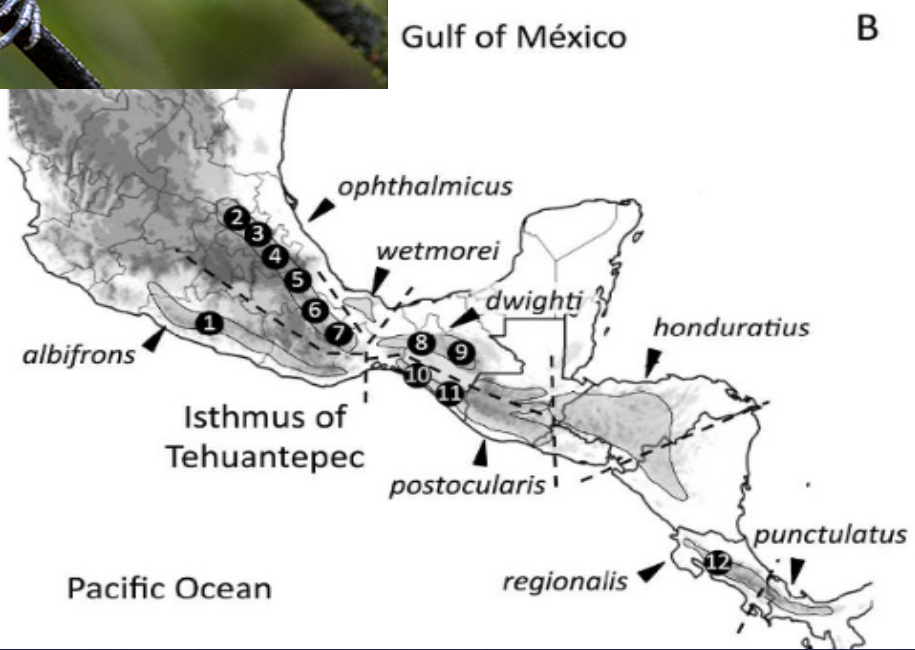
Juvenile southwestern *P. gilberti*

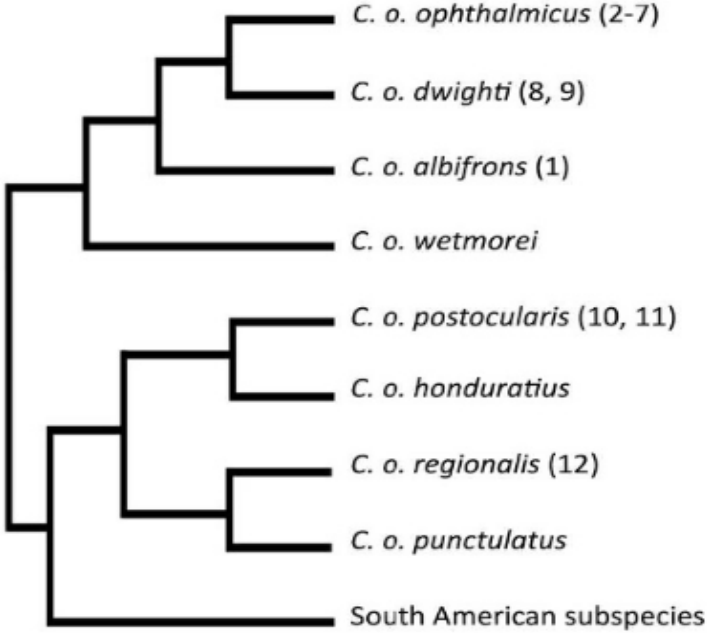
Juvenile Sierran *P. gilberti*

Juvenile *P. gilberti* collected from contact zone

Vocal Geographic Variation in Mesoamerican Common Bush Tanagers (*Chlorospingus ophthalmicus*)

Sosa-Lopez et al. 2013





- 27 disjunct populations restricted to cloud forest patches from Mexico to Argentina
- Study of fine structural characteristics of songs of 5 subspecies
- 2 found to be distinct, 3 others similar

There are 4 subspecies of Moose in North America:

Alces americanus gigas is black-brown with brighter back and pale brown legs. Face and nose of the cow are redish-brown, while the bull has a black nose.

Alces americanus andersoni is brownish-black and medium sized.

Alces americanus shirasi is medium-sized with relatively wide nose-openings. The back is colored more pale/grayish compared to the other American sub-species.

Alces americanus americanus is Mahogany-brown in color and the smallest North American subspecies.

The primary factors limiting the geographic distribution of moose are food and cover in the northern regions and climate in the southern regions

Alces americanus gigas

Alces americanus andersoni

Alces americanus shirasi

Alces americanus americanus

GEOGRAPHIC SUBSPECIFIC VARIATION

Subspecies concept

- Darwin showed that there was no essential difference between species and ‘‘varieties’’; species were simply varieties which had diverged more, and which could coexist without intermediates being common.

- However, with his term ‘‘varieties’’ Darwin did not clearly distinguish between polymorphic variants within populations and the identifiable geographic populations normally today considered as geographic ‘‘races’’ or ‘‘subspecies.’’

- To Darwin the distinction was unimportant, because polymorphic variants, clinal variation, geographic races or subspecies, and ‘‘good’’ species formed a continuum. Darwin demonstrated that this continuum was excellent evidence for an evolutionary origin of the taxa we call species.

- Geographic replacement forms, subspecies and semispecies, would be incipient species,

Geographic variation

- **Darwin showed that there was no essential difference between species and ‘‘varieties’’; species were simply varieties which had diverged more, and which could coexist without intermediates being common.**

- **In progress allopatric speciation may be a good example of the subspecific variation due to geographical migration/separation.**

- ***Lagothrix lugens* (Primates: Atelidae) demonstrate that geographical variation (allopatric speciation) may lead to the rise of different morphotypes, variants or subspecies.**

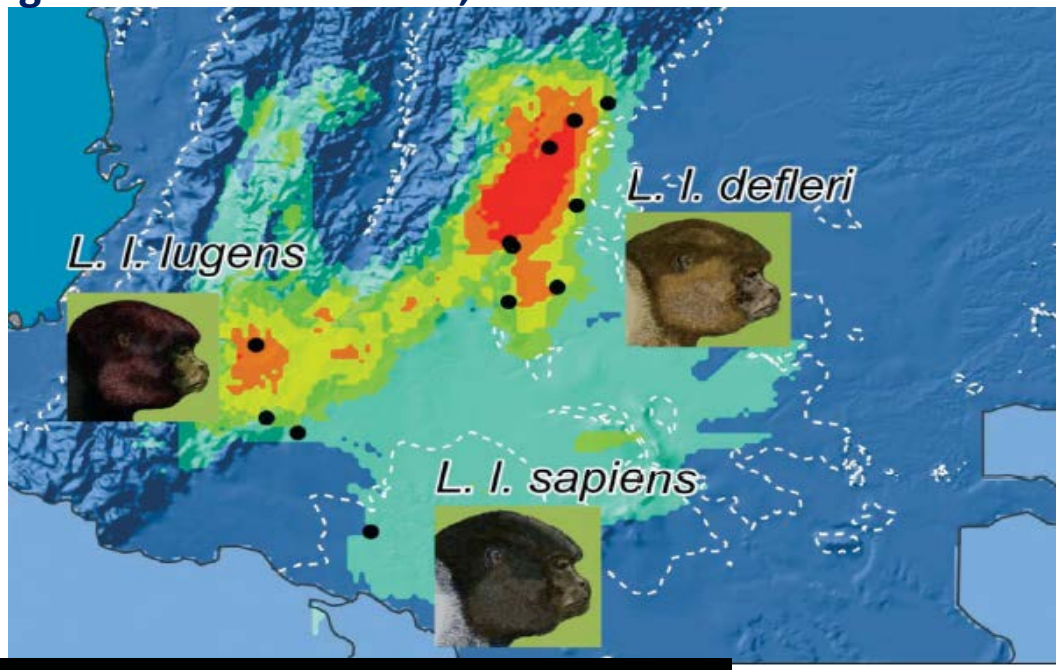
Bibliography:

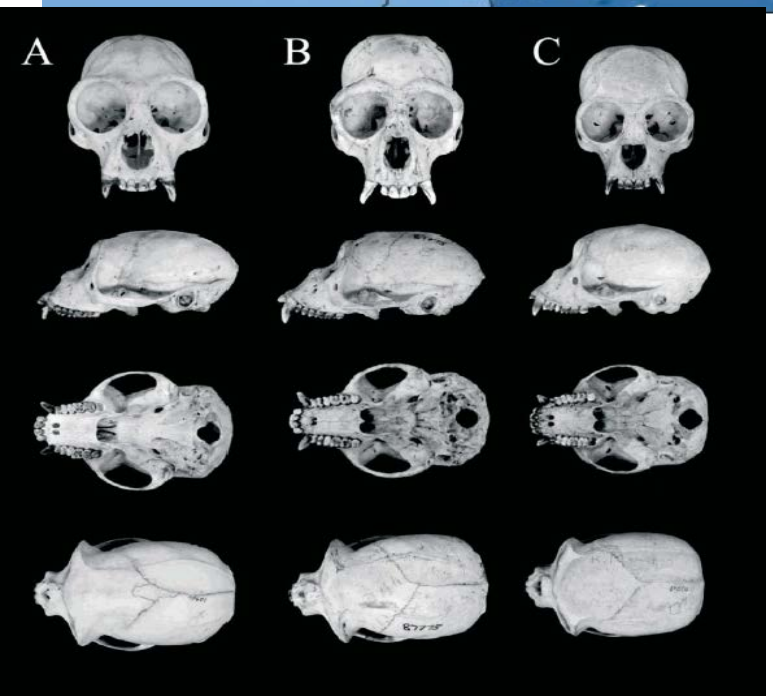
Gregorin R. 2006. Taxonomia e variacao geografica das especies do genero Alouatta Lacepede (Primates, Atelidae) no Brasil. Rev. Bras. Zool. 21(3): 64-144.

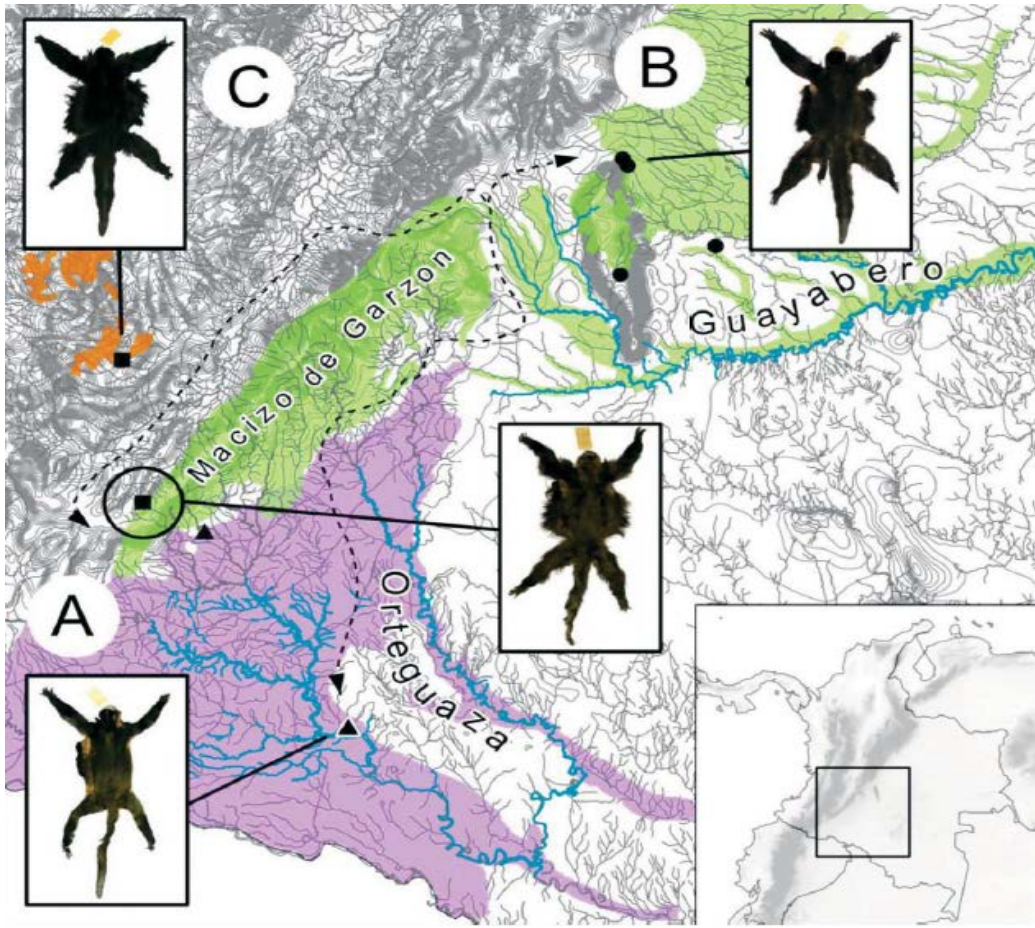
Mantilla-Meluk, H. 2013. Subspecific Variation: An Alternative Biogeographic Hypothesis Explaining Variation in Coat Color and Cranial Morphology in Lagothrix lugens (Primates: Atelidae). : Primate Conservation, 26(1):33-48.

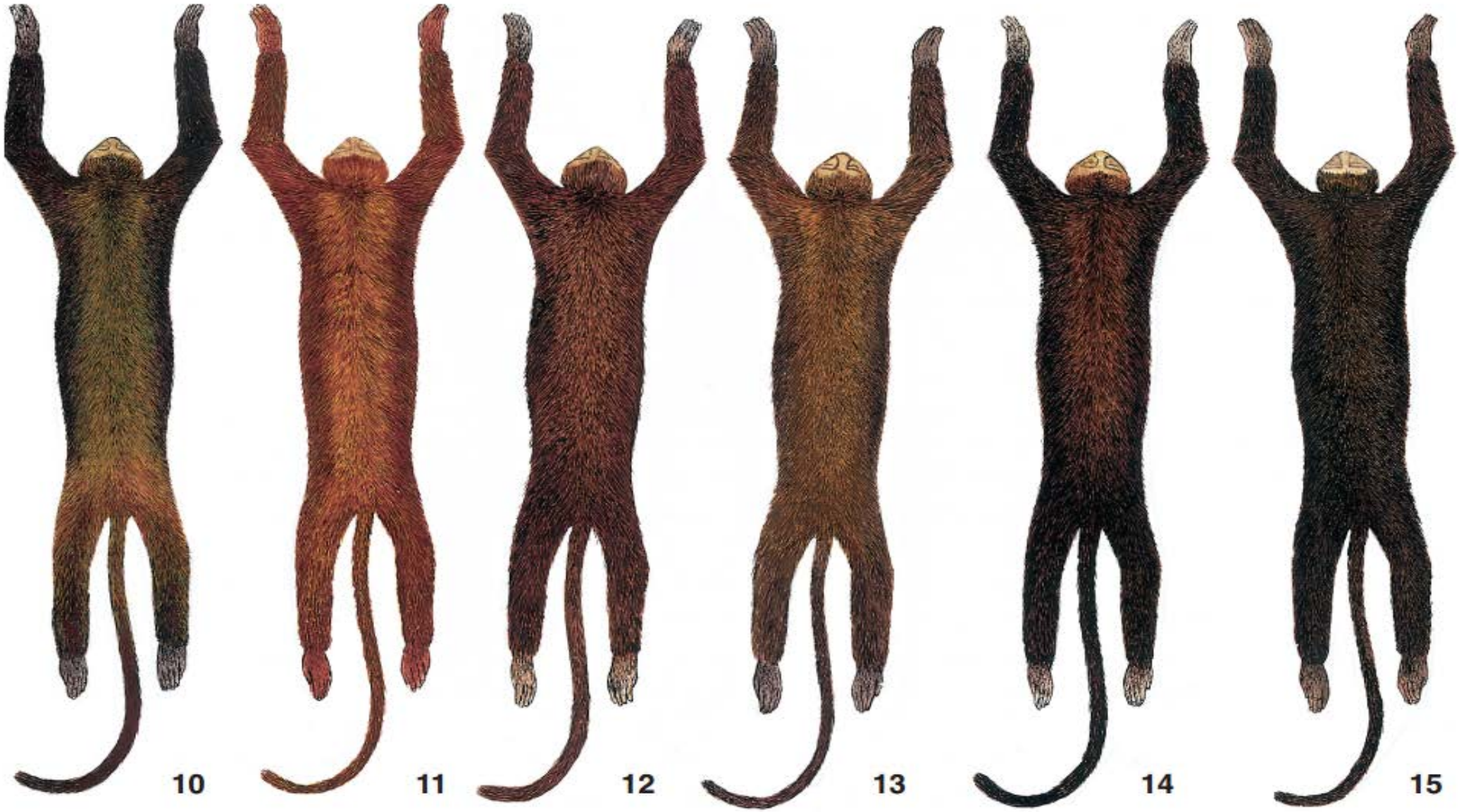
Mallet, J. 2001. Subspecies, semispecies, superspecies. - pp. 523-526, in: Levin, S. A.: Encyclopedia of biodiversity. Volume 5. R-Z. -- pp. i-xxxi [= 1-31], 1-1103. Amsterdam. (Elsevier).

Figures: Mantilla-Meluk, H. 2013.









Gregorin 2006

Haida Gwaii and BC Black bears

Ursus americanus carlottae Osgood, 1901
This island restricted subspecies has distinctly different morphology and feeding habbits. Believed to have come from a refugium (Wisconsin).

http://shaggygod.proboards.com/index.cgi?board=americanus&action=display&thread=623

What is a subspecies?

* Mayr & Ashlock (1991): An aggregate of local populations of a species inhabiting a *geographic subdivision* of the range of the species and differing taxonomically from other populations of the species.

* Historically subspecies were anything: races, color forms, aberrations, natios, etc.
  - interpretation varied among workers
  - botanists and zoologists had different ideas

* Standardized by Karl Jordan and Sir Walter Rothschild (in zoology)

Subspecies

* The codes give workers/taxonomists a rather wide margin
* Definition from Zoological Code of Nomenclature (1985)
  "...taxon...characteristic of a particular geographic area, or environmental or ecological context, or host species, or ecological horizon and did not expressly give it infrasubspecific rank by using, for example, aberration, ab., morph..."

Latest Zoological Code (1999/2000) does not define subspecies

Subspecies: Historical View

* Received early naming (recognition) because these forms thought to be evolutionarily important
* It wasn't until about 1950, i.e., during The Modern Synthesis that many biologists got their first inkling of how much variation might be out there in nature
* Prior to 1960 (and even 1970) many evol. biol. felt that most variation was maintained by natural selection
  - electrophoresis didn’t come to biology until 1966 … first clues as to magnitude of neutral variation
  - early workers felt much variation was selected/adaptive

Subspecies: Historical View

* It was logical then, to assume that geographic variants represented locally adapted entities
  - that variation had been selected for
  - subspecies were recognized by as a few as 1 or 2 characters

* Mayr (1942) and others accorded evolutionary importance to subspecies
  - often treated subspecies as “incipient species”
  - subspecies thought to represent evolutionary units held together by gene flow
* Many systematists named them: common in botany, ornithology, malacology, mammalogy, entomology, etc.

Subspecies frequently based on one or few obvious characters

Plate 28

RAT SNAKES (*Elaphe*)

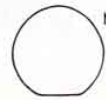
(See also Plate 32)

All have weakly keeled scales and divided anal plates.

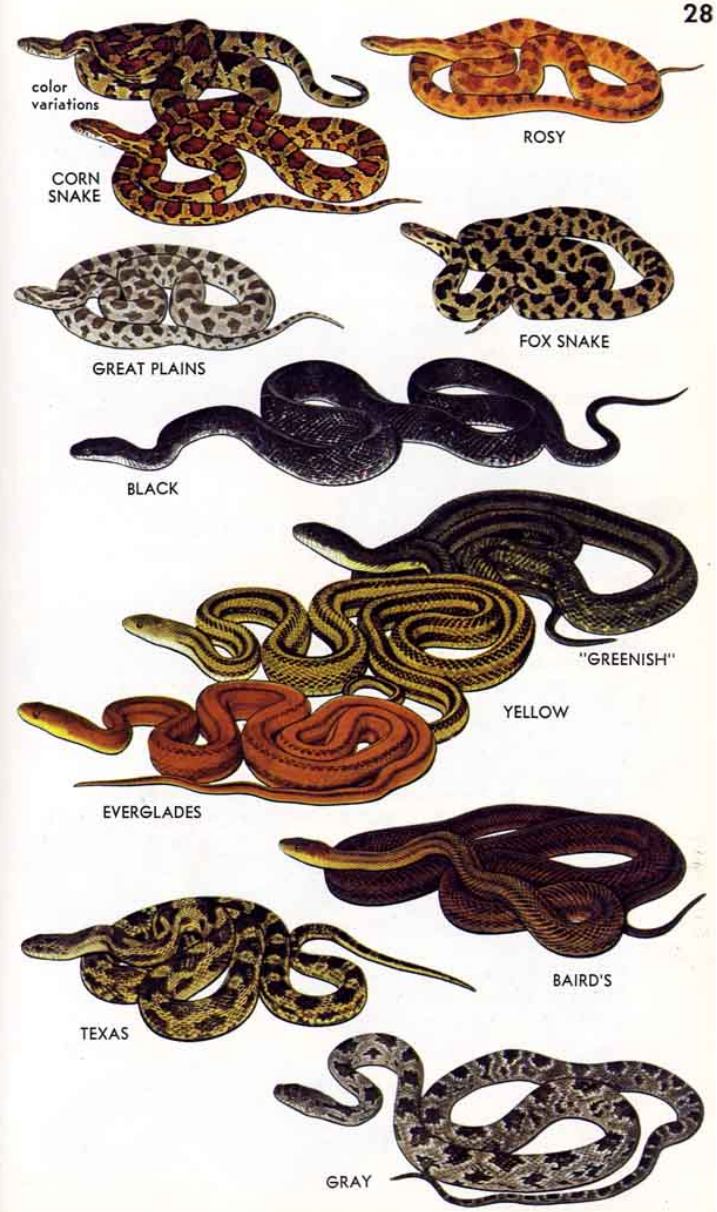
	Map	Text
CORN SNAKE, *E. guttata guttata* Reddish blotches with black borders on a ground of gray, tan, yellow, or orange.	150	190
ROSY RAT SNAKE, *E. guttata rosacea* Like Corn Snake but with black greatly reduced or absent.	150	191
GREAT PLAINS RAT SNAKE, *E. guttata emoryi* Brown blotches on a gray ground; neck lines unite to form a spearpoint on head (Fig. 44, p. 191).	150	191
FOX SNAKE, *E. vulpina* (ssp.) Dark brown blotches on a yellowish ground; no spearpoint on head (Fig. 44, p. 191).	148	192
BLACK RAT SNAKE, *E. obsoleta obsoleta* Uniform black or with faint traces of spotted pattern; throat light. *Young:* Patterned like Gray Rat Snake (below).	149	193
"GREENISH RAT SNAKE" (Intergrade: *obsoleta* × *quadrivittata*) 4 dark stripes on a ground of dark olive-gray.		194
YELLOW RAT SNAKE, *E. obsoleta quadrivittata* 4 dark stripes on a ground of yellow to olive.	149	194
EVERGLADES RAT SNAKE, *E. obsoleta rossalleni* (ssp.) 4 dark stripes on a ground of orange.	149	195
BAIRD'S RAT SNAKE, *E. obsoleta bairdi* 4 poorly defined dark stripes on a dark ground.	149	196
TEXAS RAT SNAKE, *E. obsoleta lindheimeri* Brownish- or bluish-black blotches on a ground color of yellow or gray.	149	196
GRAY RAT SNAKE, *E. obsoleta spiloides* (ssp.) Grayish in general appearance, but coloration variable (see text).	149	195

Fig. 58. CROSS SECTIONS OF SNAKES

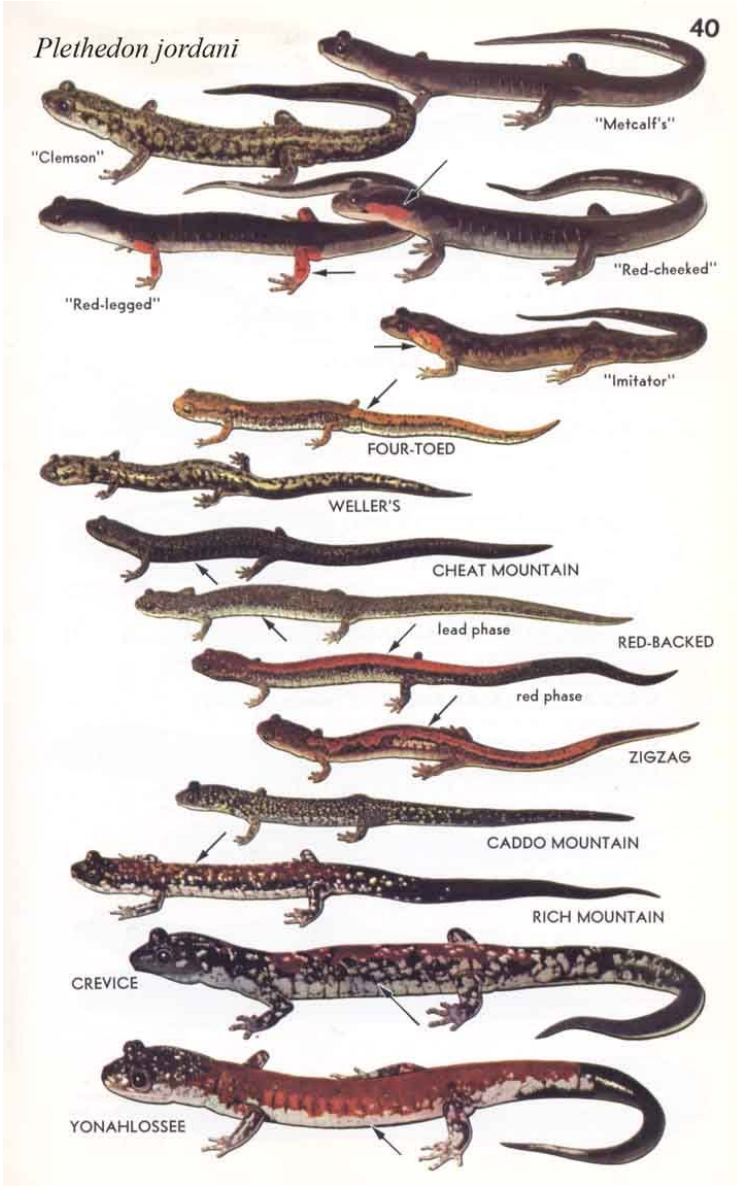
RAT SNAKES Like a loaf of bread



MOST OTHER SNAKES Body more rounded



Problems with Subspecies: Discordance among characters



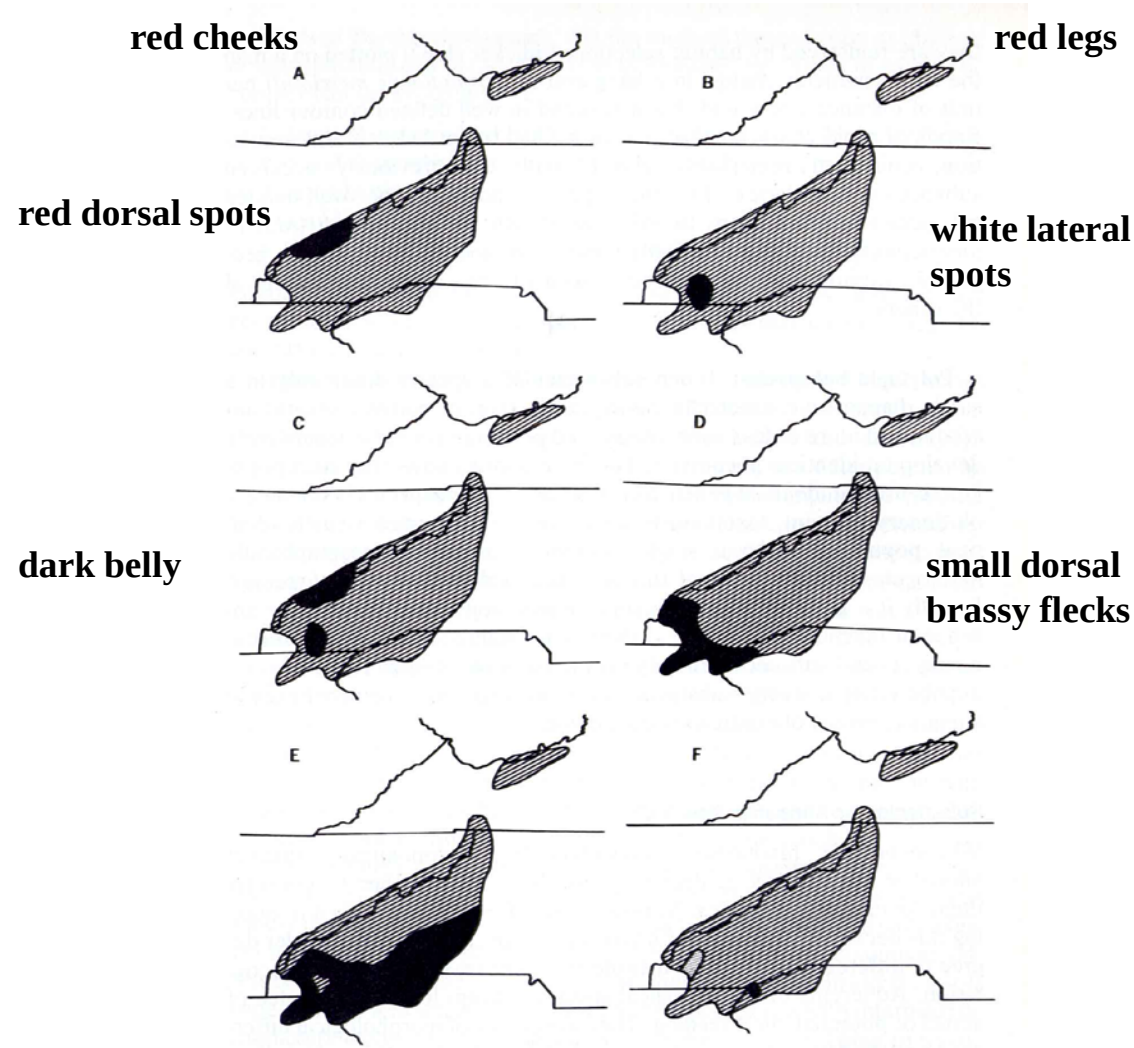


FIGURE 5-6
Discordant geographic variation in the salamander *Plethodon jordani*. Darkened areas represent regions where more than 95 percent have (A) red cheeks, (B) red legs, (C) dorsal red spots in newly hatched young, (D) lateral white spots, (E) a dark belly, (F) small dorsal brassy flecks. An area with small dorsal white spots is indicated by stippling in (F). (*From Highton 1962.*)

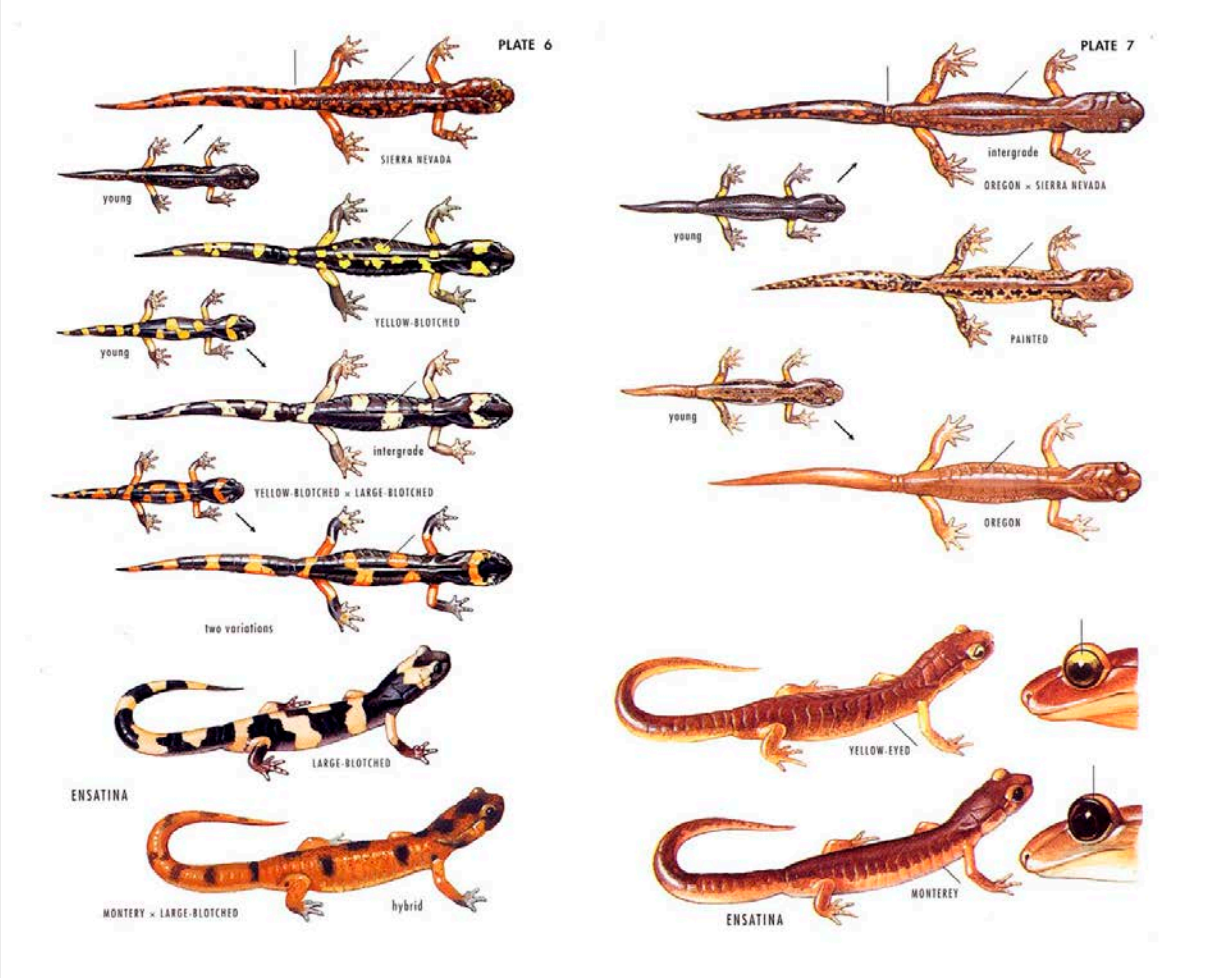
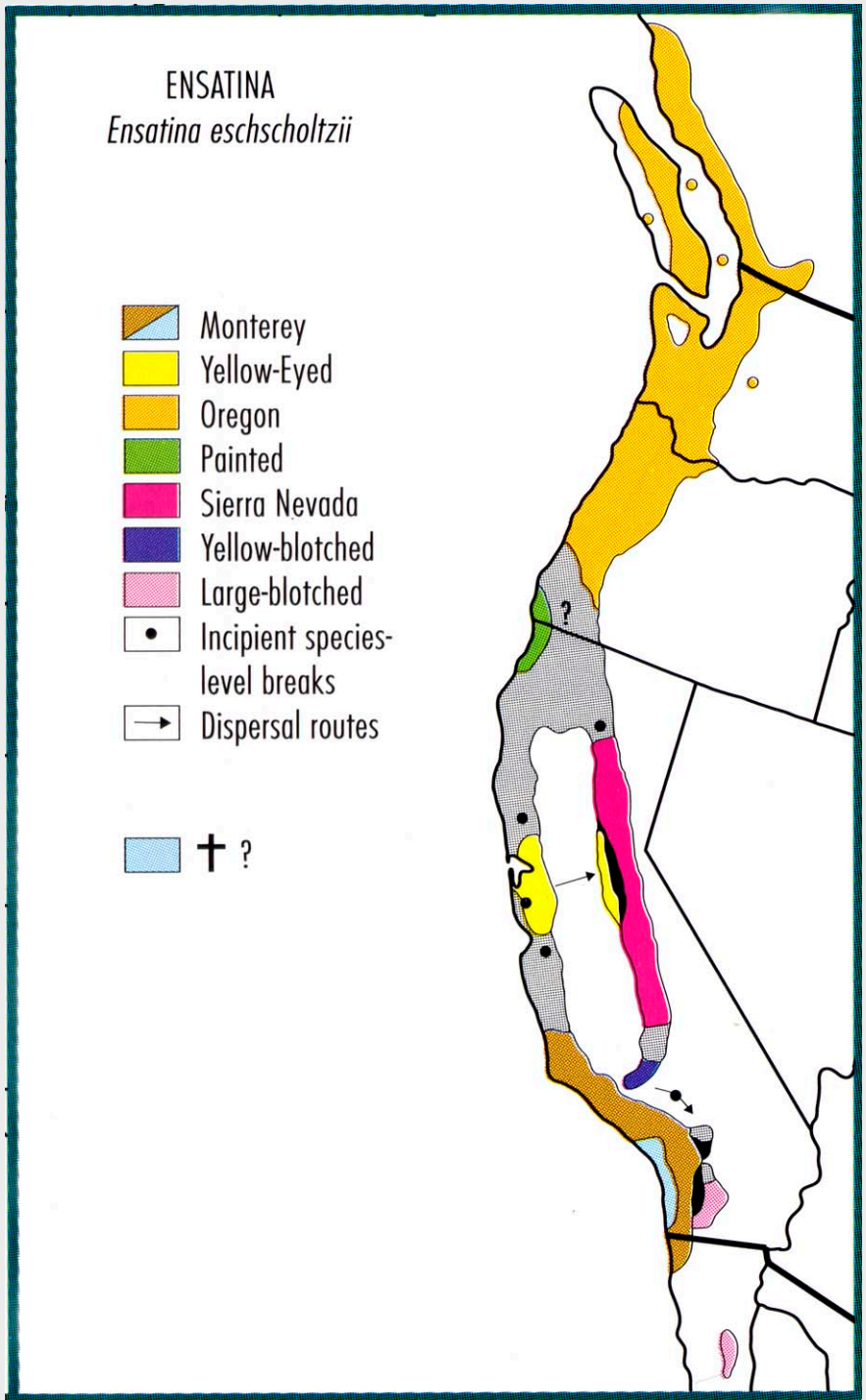
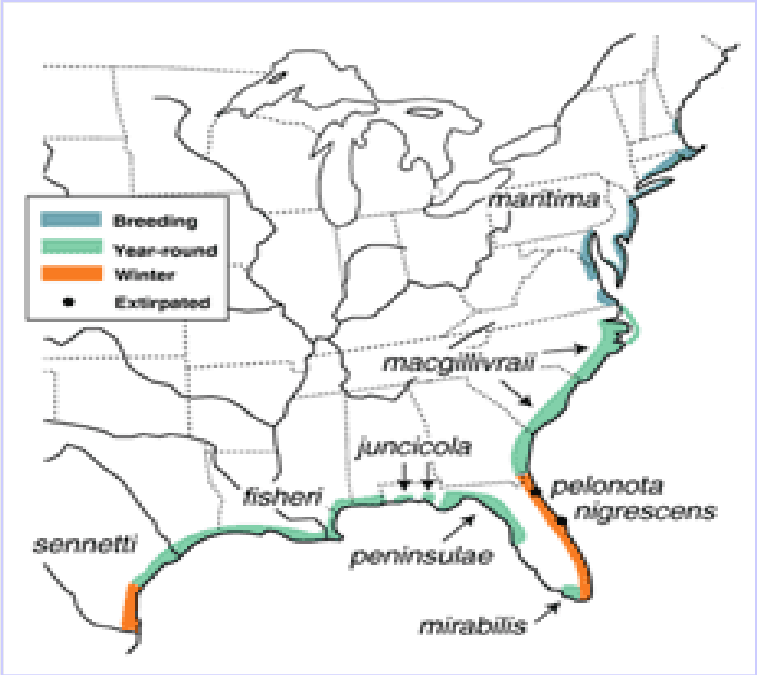


PLATE 6
SIERRA NEVADA
young
YELLOW-BLOTCHED
young
intergrade
YELLOW-BLOTCHED × LARGE-BLOTCHED
two variations
LARGE-BLOTCHED
ENSATINA
MONTERY × LARGE-BLOTCHED
hybrid
PLATE 7
intergrade
OREGON × SIERRA NEVADA
young
PAINTED
young
OREGON
YELLOW-EYED
MONTEREY
ENSATINA


ENSATINA
Ensatina eschscholtzii
Monterey
Yellow-Eyed
Oregon
Painted
Sierra Nevada
Yellow-blotched
Large-blotched
Incipient species-level breaks
Dispersal routes
†?
?

Problems with Subspecies: Arbitrariness in delimitation

* naming (automatically) lends credibility
* some subspecies based on a single discrete character
* existing (taxonomic) delimitation may even be *evolutionarily misleading* if naming leads to obfuscation of real evolutionary units
  - Example: Dusky Seaside Sparrow: "a morphologically unique form of seaside sparrow was selected for conservation, but mtDNA data suggested a different discontinuity among seaside sparrows…



Avise and Nelson (1989) claim conservation efforts directed at the Dusky Seaside Sparrow were misguided. The major evolutionary disjunction was between Atlantic and Gulf coasts

Dusky Seaside Sparrow

Subspecies: Polytopy :

* same phenotype occurring in more than one (isolated) populations/(region)
* usually based on one or two prominent features (with simple underlying genetics)
  Example: green color forms/populations in tiger beetles
  Example: cave phenotypes and paedomorphic races in salamanders
* often an underlying ecological or evolutionary explanation
  Example: coastal populations of plants grow lower to ground (because of salt and wind) sometimes have

Subspecies: Microgeographic Races :

* differentiation at very local levels
* common in plants...because they are sessile organisms
* extreme examples in some terrestrial snail genera: *Cepaea*, *Patula*, *Achatinella*, & *Helix*
  - marked turnover in phenotype over short stretches
* vertebrate example: ground-inhibiting rodents, e.g., pocket gophers in the genus *Thomomys*

Thomomys pocket gophers

Smithsonian
National Museum of Natural History

MSW Scientific Names

Query Home Help

Parent Synonyms

Thomomys bottae

- `Author.....` : (Eydoux and Gervais, 1836).
- `Citation.....` : Mag. Zool., Paris, 6:23.
- `Common Name...` : Botta's Pocket Gopher
- `Original Name.` : *Oryctomys* (*Saccophorus*) *bottae* Eydoux and Gervais.
- `Distribution..` :SW and W USA, north to Oregon, east to Colorado, and south to Sinaloa and Nuevo Leon (Mexico).
- `Type Locality.` :USA, coast of California (restricted to vicinity of Monterey, Monterey Co., by Baird, 1857ref).
- `Comments......` : Subgenus *Megascapheus*. The taxonomic history of this, and related species has been contentious. Hall and Kelson (1959ref) included *bottae* within *umbrinus* but considered *baileyi* and *townsendii* as separate species, but ...[more]...

Distribution Map for *Thomomys bottae*:

Search USNM Collections for *Thomomys bottae*

SI-WDB 1.4 Send comments to dennis@smithson.si.edu

MSW Synonym List for *Thomomys bottae*

Synonym	*Valid Name*
abbotti	*(bottae)*
absonus	*(bottae)*
abstrusus	*(bottae)*
acrirostratus	*(bottae)*
actuosus	*(bottae)*
adderrans	*(bottae)*
affinis	*(bottae)*
agricolaris	*(bottae)*
albatus	*(bottae)*
albicaudatus	*(bottae)*
alexandrae	*(bottae)*
alienus	*(bottae)*
alpinus	*(bottae)*
alticolus	*(bottae)*
altivallis	*(bottae)*
amargosae	*(bottae)*
analogus	*(bottae)*
angularis	*(bottae)*
angustidens	*(bottae)*
anitae	*(bottae)*
apache	*(bottae)*
aphrastus	*(bottae)*
ardicola	*(bottae)*
argusensis	*(bottae)*
aureiventris	*(bottae)*
aureus	*(bottae)*
awahnee	*(bottae)*
baileyi	*(bottae)*
basilicae	*(bottae)*
birdseyei	*(bottae)*
bonnevillei	*(bottae)*
boregoensis	*(bottae)*
boreorarius	*(bottae)*
borjasensis	*(bottae)*
brazierhowelli	*(bottae)*
brevidens	*(bottae)*
cabezonae	*(bottae)*
cactophilus	*(bottae)*
camargensis	*(bottae)*
camoae	*(bottae)*
caneloensis	*(bottae)*
canus	*(bottae)*
carri	*(bottae)*
catalinae	*(bottae)*
catavinensis	*(bottae)*
cedrinus	*(bottae)*
centralis	*(bottae)*
cervinus	*(bottae)*
chiricahuae	*(bottae)*
chrysonotus	*(bottae)*
NEXT 50	
cinereus	*(bottae)*
collinus	*(bottae)*
collis	*(bottae)*
comobabiensis	*(bottae)*
concisor	*(bottae)*
confinalis	*(bottae)*
connectens	*(bottae)*
contractus	*(bottae)*
convergens	*(bottae)*
convexus	*(bottae)*
crassus	*(bottae)*
cultellus	*(bottae)*
cunicularis	*(bottae)*
curtatus	*(bottae)*
depauperatus	*(bottae)*
depressus	*(bottae)*
desertorum	*(bottae)*
desitus	*(bottae)*
detumidus	*(bottae)*
diaboli	*(bottae)*
dissimilis	*(bottae)*
divergens	*(bottae)*
estanciae	*(bottae)*
extenuatus	*(bottae)*
flavidus	*(bottae)*
fulvus	*(bottae)*
fumosus	*(bottae)*
grahamensis	*(bottae)*
growlerensis	*(bottae)*
guadalupensis	*(bottae)*
harquahalae	*(bottae)*
homorus	*(bottae)*
howelli	*(bottae)*
hualpaiensis	*(bottae)*
hueyi	*(bottae)*
humilis	*(bottae)*
imitabilis	*(bottae)*
incomptus	*(bottae)*
infrapallidus	*(bottae)*
ingens	*(bottae)*
internatus	*(bottae)*
jacinteus	*(bottae)*
jojobae	*(bottae)*
juarezensis	*(bottae)*
lachuguilla	*(bottae)*
lacrymalis	*(bottae)*
laticeps	*(bottae)*
latirostris	*(bottae)*
latus	*(bottae)*
lenis	*(bottae)*
NEXT 50	
leucodon	*(bottae)*
levidensis	*(bottae)*
limitaris	*(bottae)*
limpiae	*(bottae)*
litoris	*(bottae)*
lorenzi	*(bottae)*
lucidus	*(bottae)*
lucrificus	*(bottae)*
magdalenae	*(bottae)*

Problems with Subspecies: Rapid "Subspeciation"

* Some introduced taxa seem already to have subspeciated

  Example: House Sparrow

  - recognizable entities after only 100 years
  - light morphs in American Southwest, some of the lightest in Death Valley—(Gloger's Rule)
  - darker morphs in Pacific Northwest, especially Vancouver Island
  - body size correlated with Bergmann's Rule (for warm-blooded vertebrates) (larger body size in higher latitudes)
  - differentiation in as few as 50 generations

Subspecies: Nomenclatural Treatment :

* Nomenclaturally the subspecies is the rank between the **species** and **infrasubspecific forms:**
* In both botany and zoology handled as a trinomen
  Strix occidentalis caurina (Merriam 1898)
* In Zoology treated as a *species group name*: which means subspecific and specific names compete at the same level in nomenclatural matters of priority and synonymy
* In botany: the subspecies rank occupies a separate rank: i.e., names do not compete for synonymy and priority
  - varieties accorded same taxonomic status as subspecies

Nomenclature Treatment of Subspecies

* In botany subspecific names treated as one of the infraspecific ranks
* thus subspecies can be essentially equivalent to variety (varietas)
* subspecies if differentiated is of higher rank than variety, subvariety, form, or subform, i.e., there can be varieties, subvarieties. etc., within a subspecies, but many authors don’t use “subspecies” and use varieties in the way that zoologists do as a trinom.

Nomenclature Treatment of Subspecies

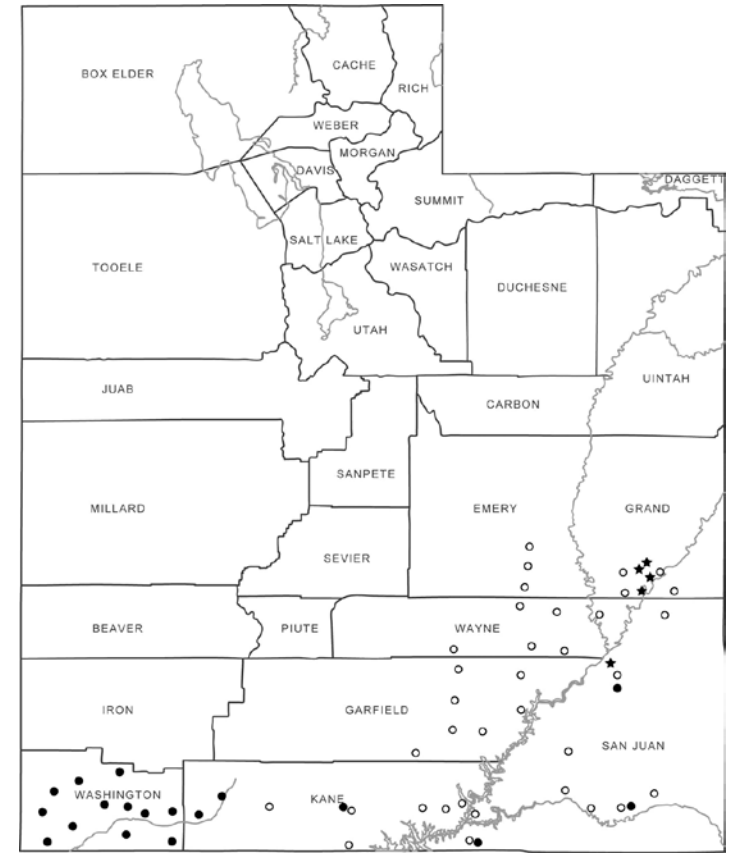
In different editions of the zoological code subspecies can be treated differently, e.g.,

- infrasubspecific names that were not specifically designated as infrasubspecific automatically are regarded as validly published subspecies before 1961
- but not for name published after 1961 when subspecific and infrasubspecific names had to be explicitly identified as to what rank they were intended to apply

Nomenclature Treatment of Subspecies

* most present-day systematists are reluctant to name subspecies accept in well-worked taxa/examples
  - happy to just use species name with locality as recommended by Brown and Wilson (1953)
* groups with amateurs, e.g., butterflies, tiger beetles, snails, typically have many subspecific names
* One advantage of recognition (if you are pretty certain you have a good or incipient species (for example an unusual host is implicated): if your subspecies is ever elevated to a species your name (and authorship) carries with the taxon (in perpetuity)

FIGS. 1–6. *Catocala benjamini* adults. (1) *Catocala benjamini ute* holotype male, Arches Natl. Park, Grand Co., UT. (2) *Catocala benjamini ute* female, SR 313, Grand Co., UT. (3) *Catocala benjamini ute* male venter, Arches Natl. Park, Grand Co., UT. (4) *Catocala benjamini benjamini* male, Hualapai Mtn. Rd., Mohave Co., AZ. (5) *Catocala benjamini benjamini* female, near Payson, Mohave Co., AZ. (6) *Catocala benjamini benjamini* male venter, near Payson, Mohave Co., AZ.



Known distribution of *Catocala benjamini ute* (stars), *Quercus turbinella* (solid circles), and *Quercus x pauciloba* [*Q. gambelli x turbinella*] (open circles). Map reproduced from on-line version of Albee et al. (1988): http://earth.gis.usu.edu/plants/index.html (accessed January 2009).

Nomenclature Treatment of Subspecies

* another reason people name subspecies is to draw attention to a cohesive segregate, e.g., for legislative protection

“Good” Subspecies	“Bad” Subspecies
isolated geographically	contiguous geographically
variation discrete	variation clinal
monotopic	polytopic
variation concordant	variation discordant

Recommendations

1. Consider biogeographic history of the area and species that are under study then
2. Sample thoroughly within and between populations
3. Employ multiple characters, avoid according much weight to one or a few characters, esp. those under obvious selection
4. Employ (selectively neutral) molecular characters where possible

Bottom line: focus on identifying meaningful **evolutionarily significant units**