Diversification of the livebearing Mexican Goodeidae:
Pattern and process in macroevolution

Shane A. Webb, Ph.D.
Department of Biology
NORTH GEORGIA
COLLEGE & STATE UNIVERSITY

Acknowledgments

Mike Ritchie, Jeff Graves & Anne Magurran
University of St. Andrews, Scotland

Diarmaid O'Foighil and LMS, UMMZ

Constantino Macias G. & Edgar Avila L., UNAM

ALA, Jim Langhammer,
Juan Migual Artigas A., John Lyons

Department of Biology and
School of Science & Health Professions, NGCSU

Talk coverage

Ritchie, M., R.M. Hamill, J.A. Graves, A.E. Magurran, **S.A. Webb**, and C. Macias-Garcia. 2007. Sex and differentiation; Population genetic divergence and sexual dimorphism in Mexican goodeid fish. J. Evol. Bio. 20(5): 2048-2055.

Ritchie, M.G., **Webb, S.A.**, Graves, J.A., Magurran, A.E. and Macías Garcia, C. 2005. Patterns of speciation in Mexican Goodeid fish: Sexual conflict or adaptive radiation? J. Evol. Bio. 18(4): 922-929.

Webb, S.A., J.A. Graves, C. Macias-Garcia, A.E. Magurran, D. Ó Foighil, & M.G. Ritchie. 2004. Molecular phylogeny of the live-bearing Goodeidae (Cyprinodontiformes). Mol. Phyl. Evol. 30: 527-544.

Patterns

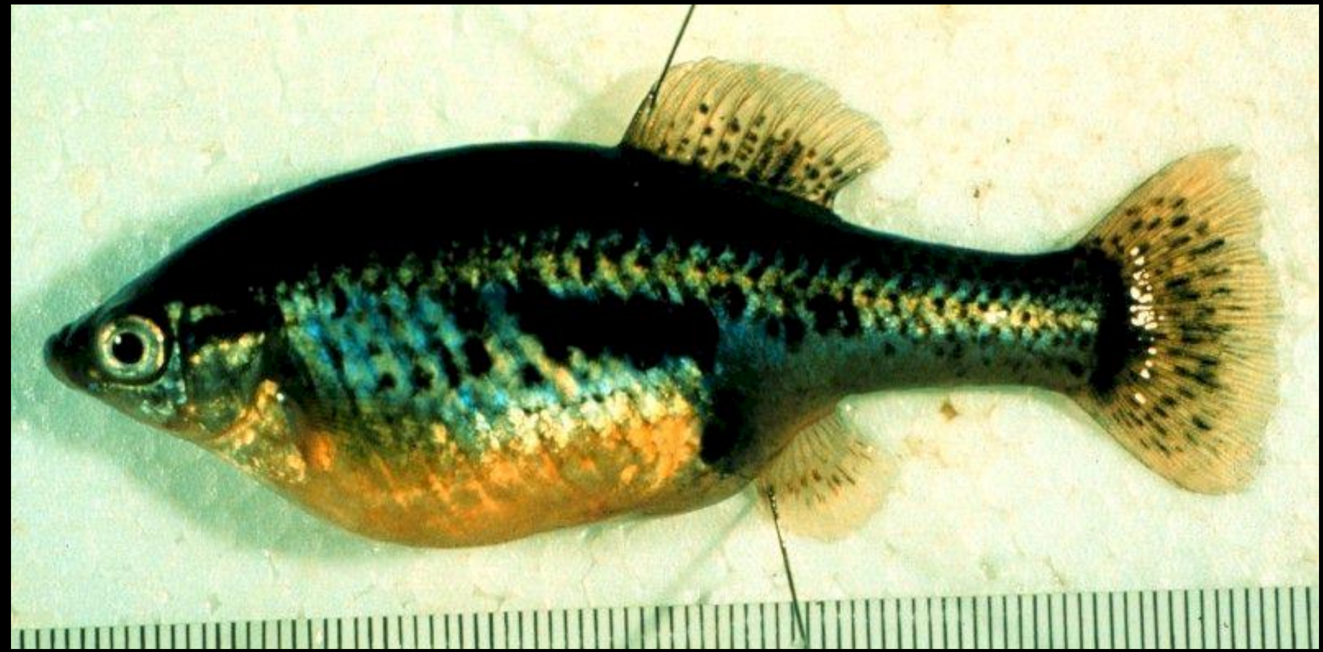
- Why are there many species in some places? *Are there special places?*

- The U.S. has 10-35 fish species per drainage system along the active margin, but these are members of ~12 different fish groups.

- In Mexico the Goodeidae contains ~40 species

Process

Or are there special processes?



Sexual selection

- Described by Darwin (Origin and Descent)
  - Male-male competition (intrasexual) → weapons
  - Female mate choice (intersexual) → ornaments

- Positive feedback (Fisher)
- Handicap principle (Hamilton et al.)
- Good genes / “bright” male (Hamilton & Zuk)
- Sensory exploitation (Ryan)
- *Etc.*

Objectives

I. Build a molecular phylogeny of the Goodeidae (historical biology based on inference) and compare results with previous work

II. Determine patterns of diversification within this natural group

III. Try to infer the processes important in diversification of this group

Introduction to the Goodeidae

- Composition and some natural history
- Sexual selection and diversification

Methods

- Datasets and phylogenetic analyses
- Calculation of the goodeid molecular clock
- Quantifying sexual dimorphism

Results and Discussion

- Phylogeny
- Patterns of divergence and the role of geologic events in diversification
- A role for sexual selection?

INTRODUCTION

Diversity and natural history

Sexual selection and diversification


Empetrichthyinae
Goodeinae
Profundulus

Empetrichthyinae

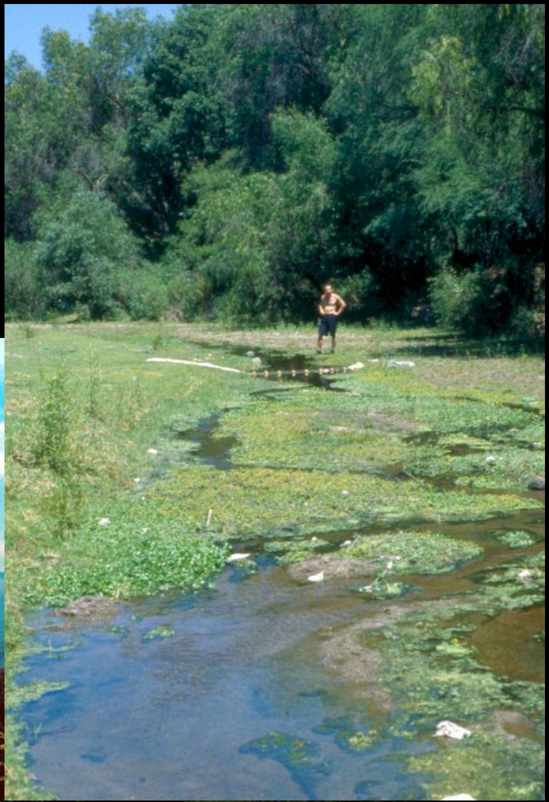
Crenichthys baileyi

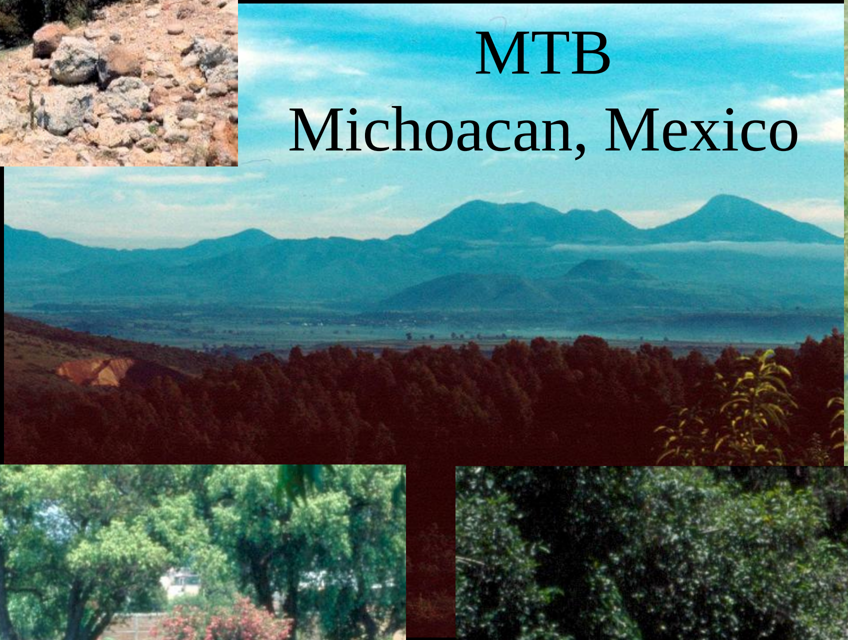
Image courtesy of Dr. Paul Loiselle

Empetrichthys latos

Pahrump Valley, NV, USA
Photo by J. Deacon

Goodeinae





Hubbsina turneri (male)

Image courtesy of ALA

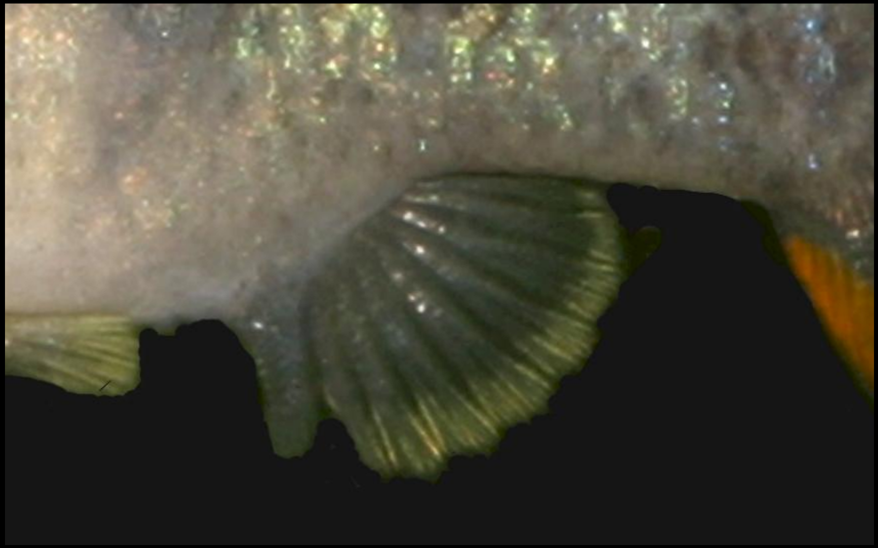
Characodon lateralis (male)

Image courtesy of C. Grimes

Ilyodon furcidens (male)

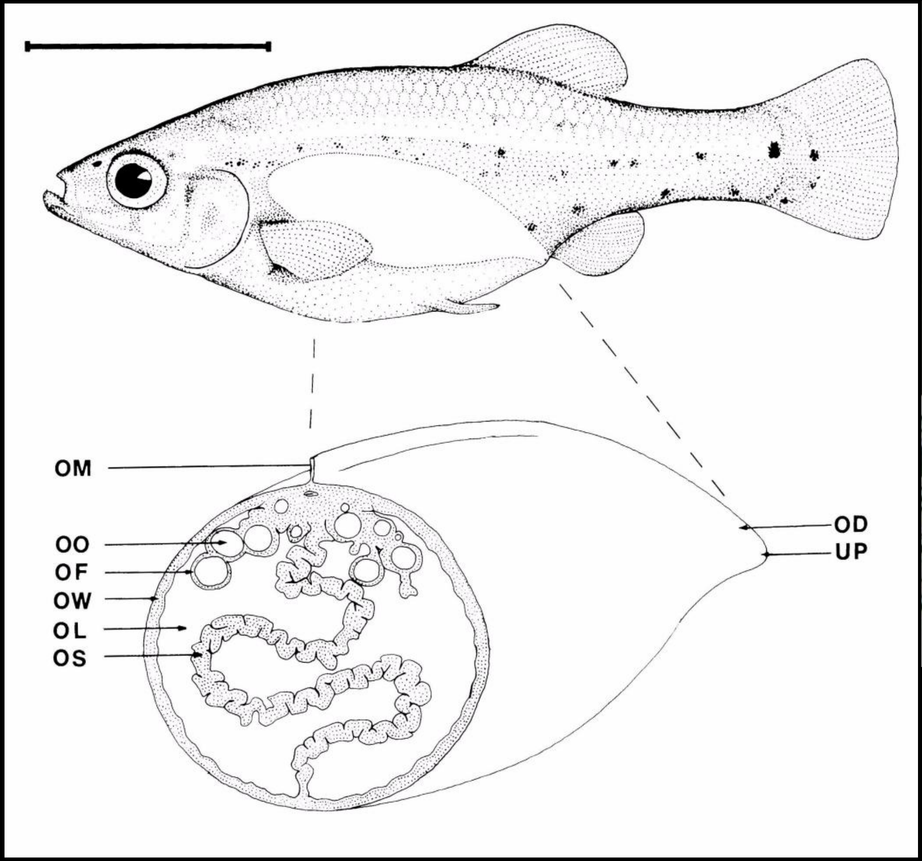
Skiffia lermae (male)

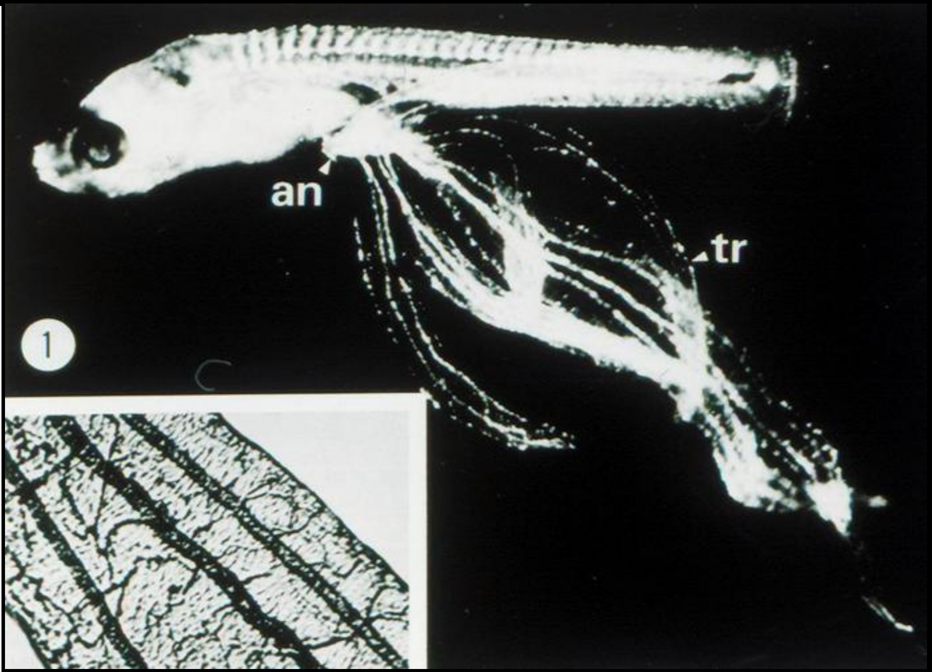
viviparity



Girardinichthys viviparus (female)

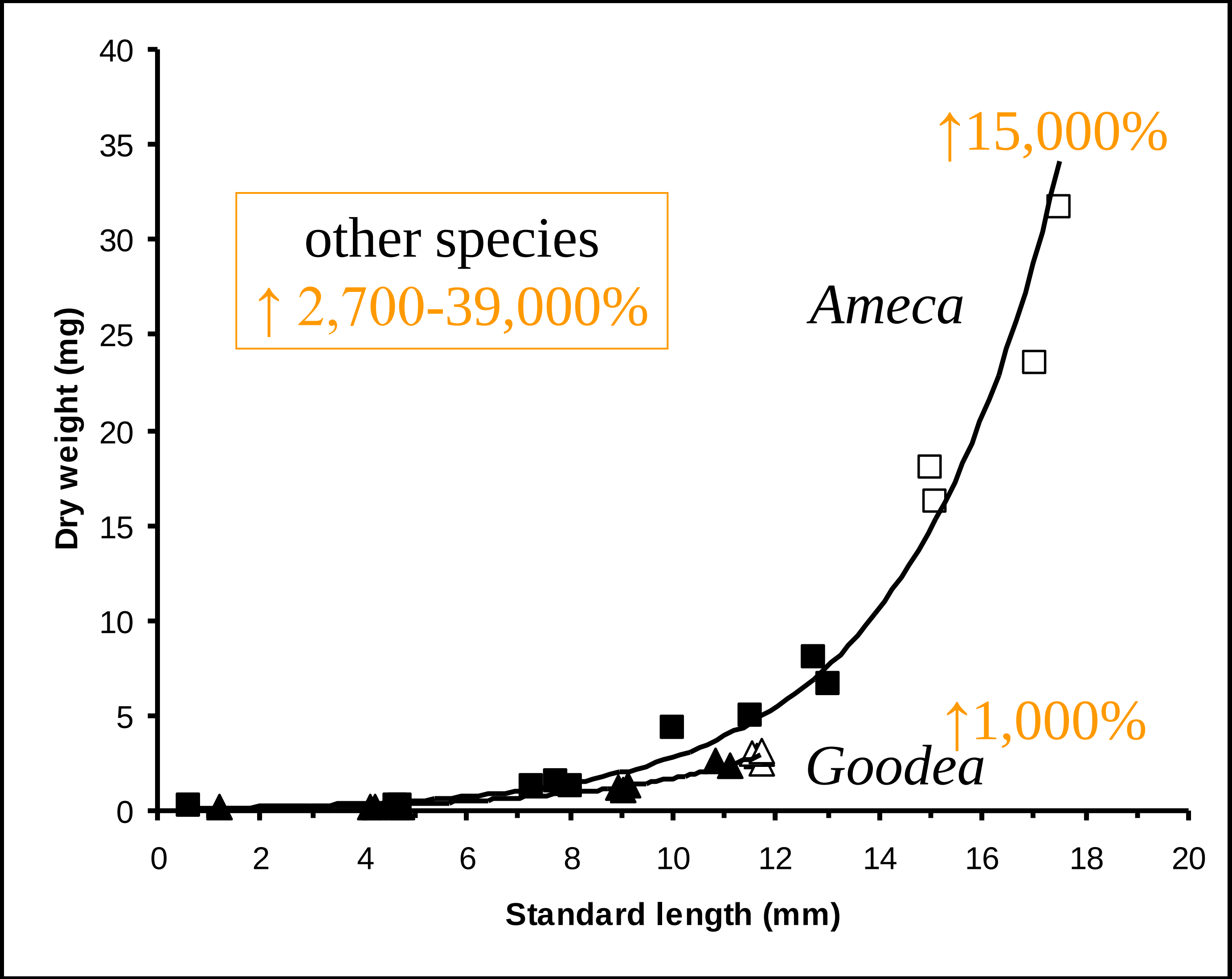
matrotrophy





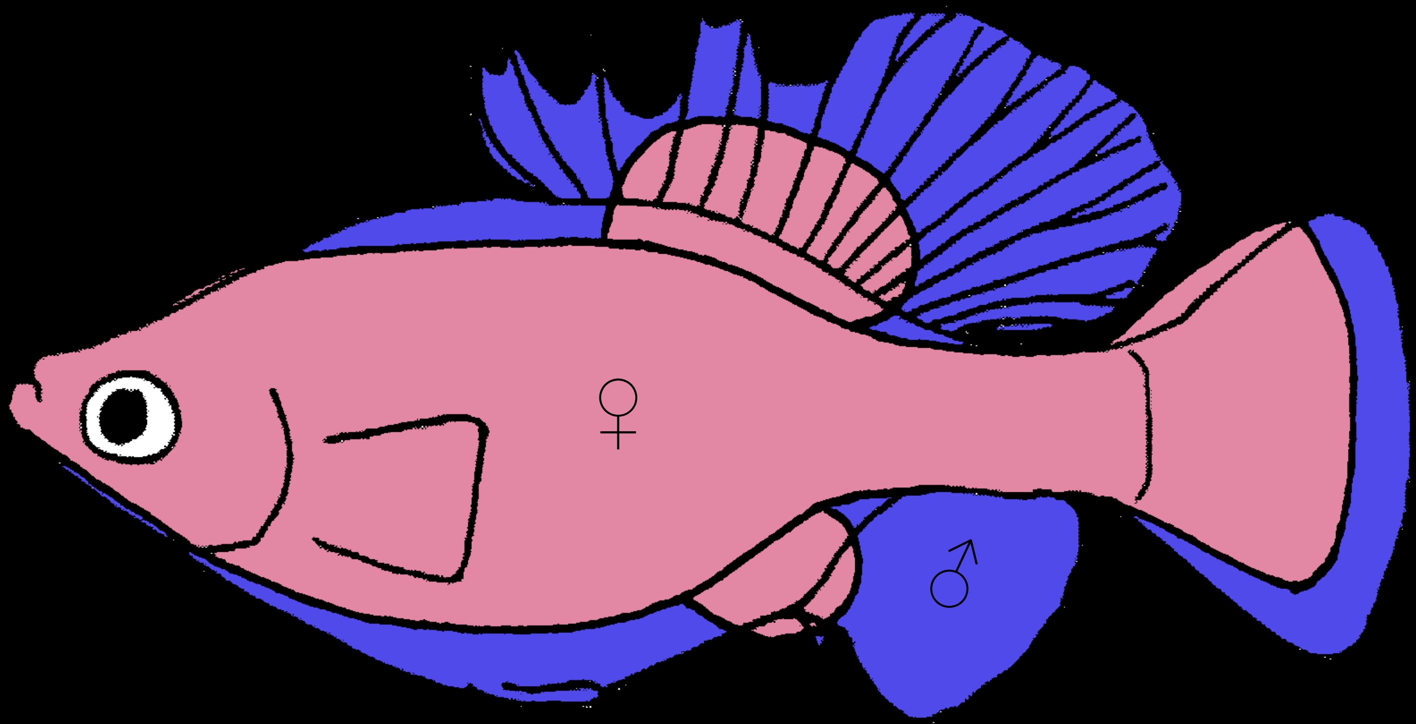
Lombardi & Wourms 1985

matrotrophy (embryogenesis)



Lombardi & Wourms 1988

sexual dimorphism



Skiffia multipunctata
Presa de Orandino, Michoacan

costly ornaments
predation by *Thamnophis*

prediction

Degree of sexual dimorphism should correlate with diversity

Arnqvist et al. 2000; Gavrilets et al. 2001; Martin & Hosken 2003

i.e. Sexually dimorphic groups should be more speciose (possess higher speciation rates)

H_O : Species richness is independent of sexual dimorphism.

If no correlation, what is the pattern of speciation in the group?

Is most speciation allopatric?

Not necessarily exclusive of sexual selection.

What is the rate of speciation?

Is speciation clocklike (i.e. relatively constant through time)?

METHODS

dataset 1

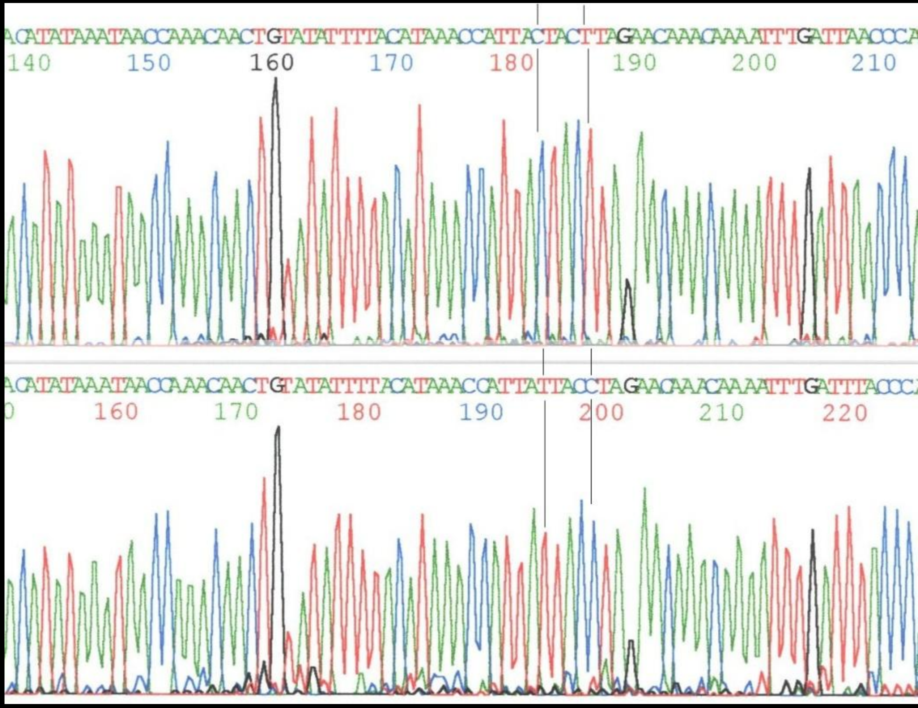
mtDNA sequence data

- Uniparentally inherited (maternal)
- Evolves rapidly (doesn't recombine)
- Protein coding and non-coding regions
- Circular dsDNA molecule (~16kb)

- COI (627 bp) and Control region (~400 bp) of 37 taxa

DNA protocol

- DNA extraction from tissues
- PCR → Amplification of desired loci
- Fragment isolation
- Sequencing reactions
- Autosequencing
- Proofreading 2 strands



aligned sequence data (mtCOI)

```
Allodhub    TATTTAGTATTTGGTGCCTGAGCCGGCATAGTTGGTACCGCCCTAA
Allodzon    .................T..........................G.
Alloorob    ...................................C........T.
Allotcat    ..........................T...........T.......
Allotdug    ...................................C..T...T...
Amspl       ..........................T........C..........
Ataentow    .................T..............G.....T.......
Chapenc     ..........................T........C..........
Charaud     .......................T..T...................
Charlat     .......................T..T........C..........
Girmult     ......C.......................................
Girviv      ..........C...................................
Gooatr      ...................................C..........
Hubtur      ..........................T...............T...
Ilyfur      ..............................................
Skifbil     .................T.................C..........
Skiffran    ....................G..............C..........
Skifmult    ....................G..............C..........
Xenocapt    ..........................T........C..........
Xenres      ...C......................T.................GT
Xenvar      ..........................T........C..........
Zoogquit    ..........................T.....G.............
            123..3..3..3..3..3..3..3..3..3..3..3..3..3..3.
```

phylogenetic analyses

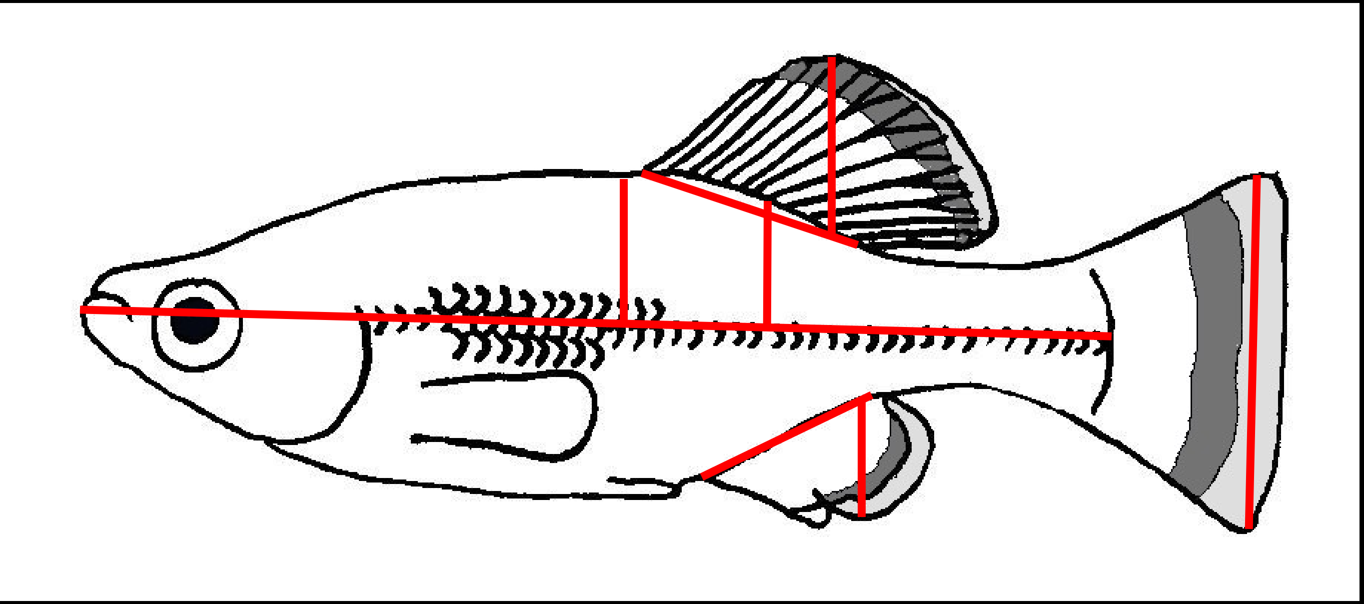
- Outgroup – close relatives outside group
  - *Profundulus labialis*
- Ingroup – 36 species of goodeines

- Parsimony analysis (PAUP 4)
  - Heuristic searches
  - 20 random stepwise addition replicates

dataset 2

sexual dimorphism

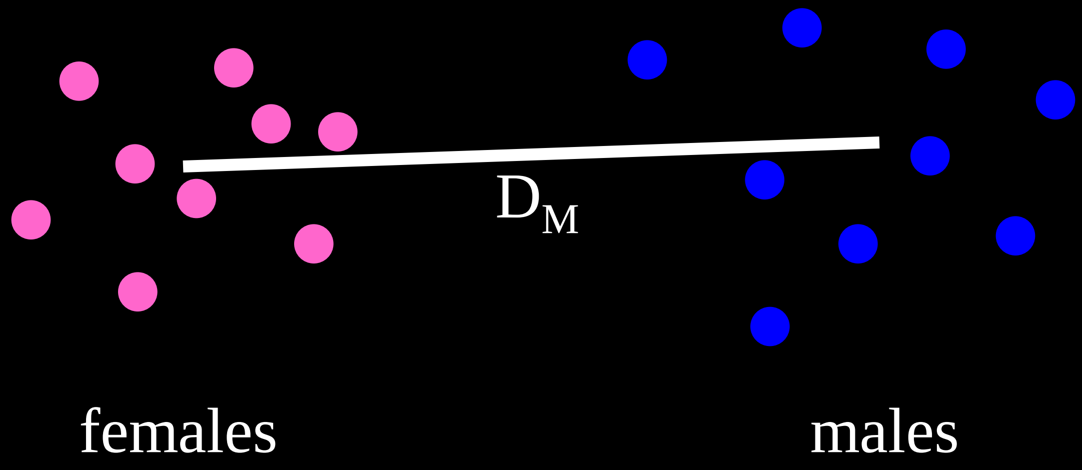
- Standard length
- Mid body depth
- Body depth at midpoint of dorsal fin
- Dorsal, caudal, and anal-fin heights
- D-, C- & A-fin areas
- D- & A-fin bases



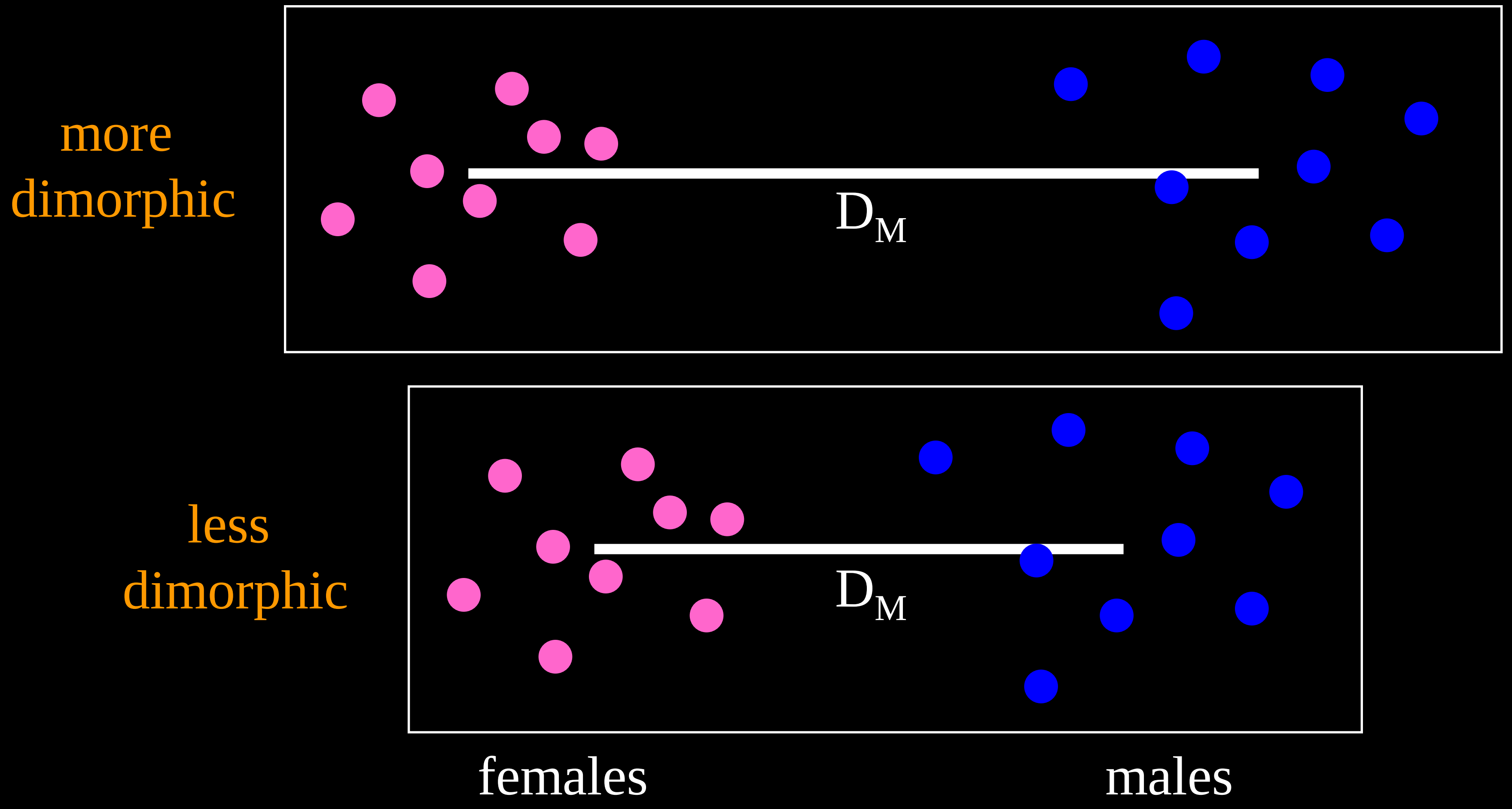
Caveat: No measurement of color or behavior in our analyses

Mahalanobis distance

- Multivariate
- Discriminant function analysis



quantifying dimorphism



dataset 3

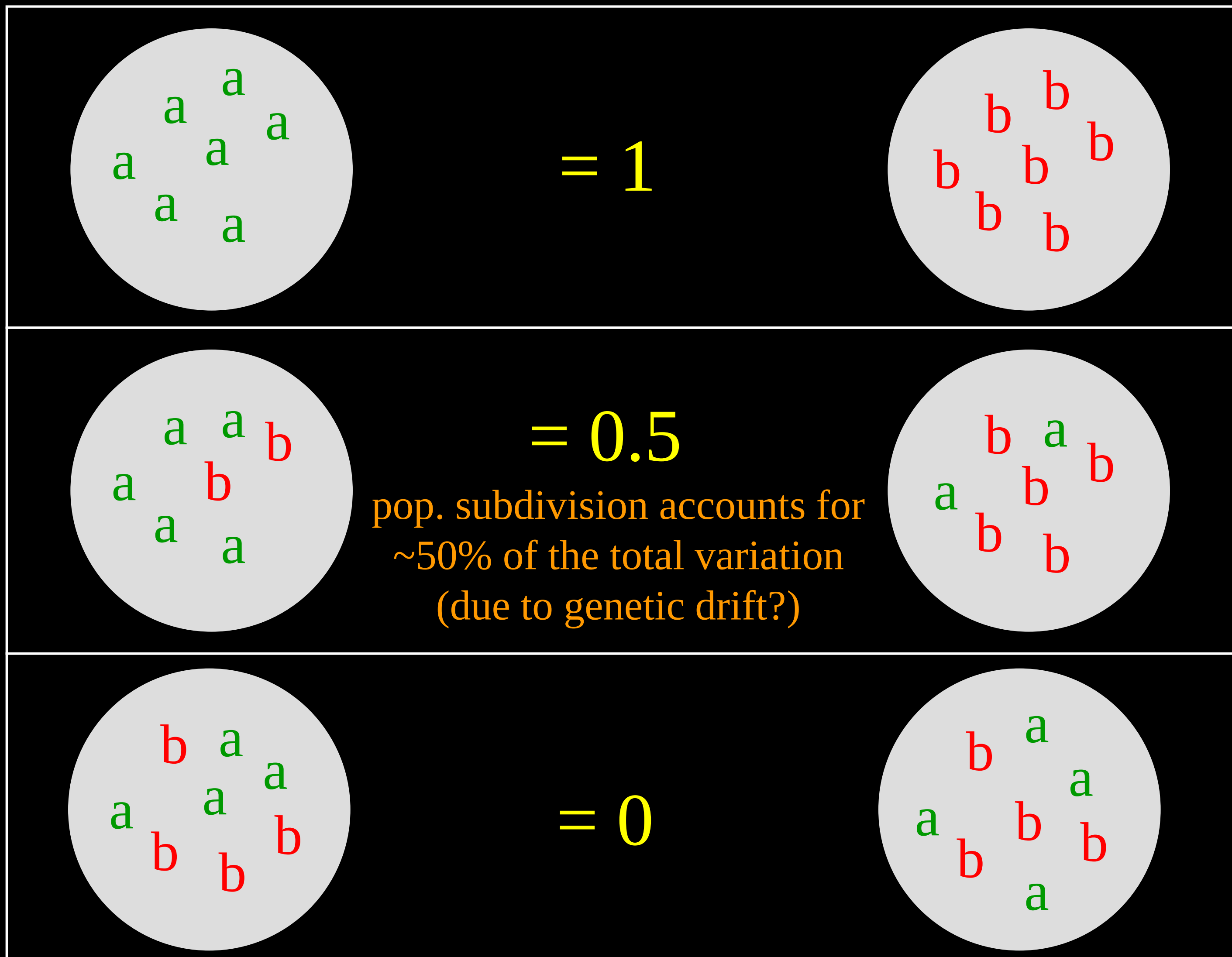
microsatellite data

- 5-7 neutral loci were employed for each of four species that vary in sexual dimorphism
  - (*X. melanosoma, C. lateralis, Z. quitzeoensis, G. atripinnis*)
- Genotypes were determined for 30 individuals (15males / 15females) of each species from four populations
- F_{ST} was calculated and adjusted for geographic distances among populations

Loci from Boto & Doadrio 2003 and Hamill et al. 2007

F_{ST}

population 1 population 2



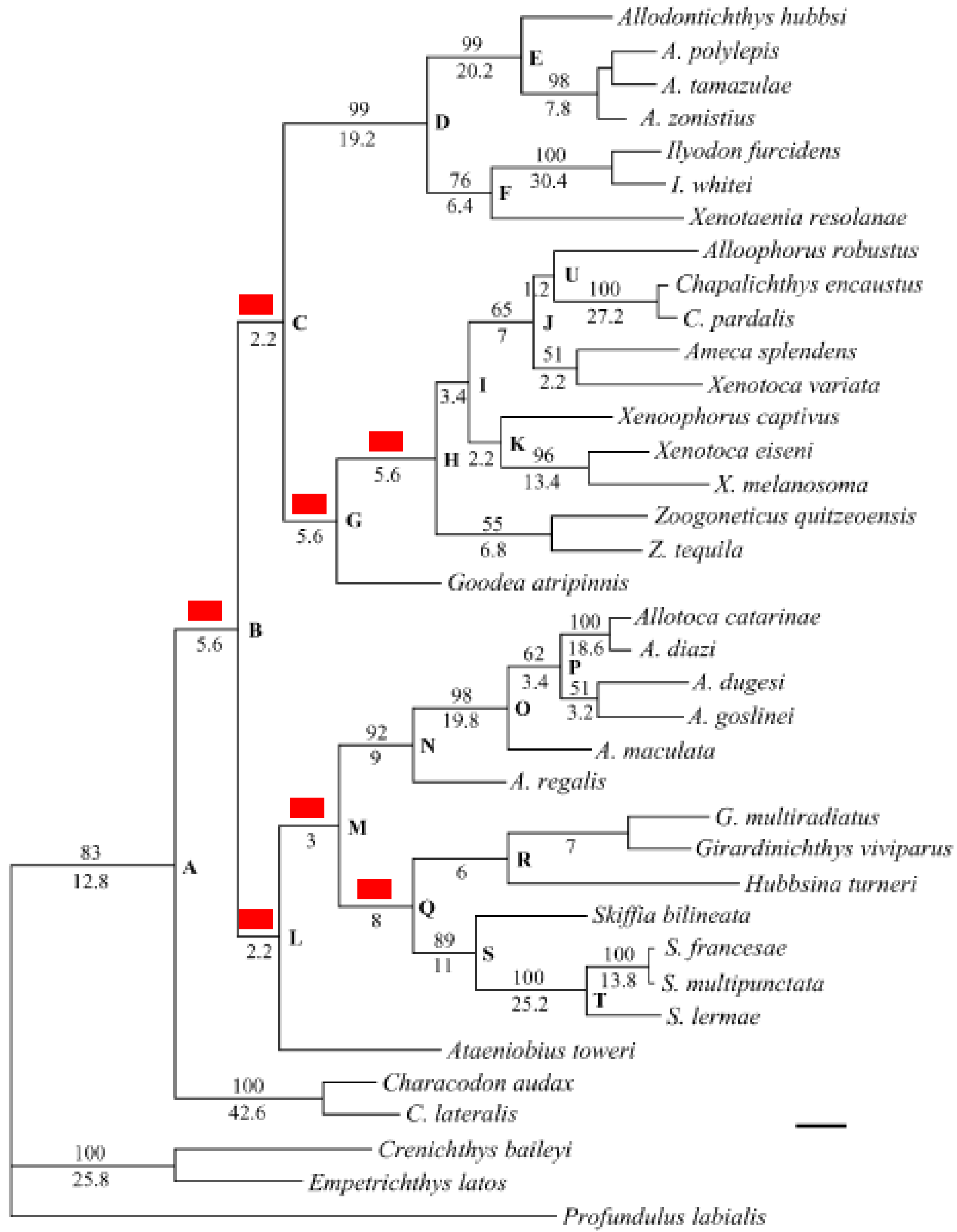
RESULTS
&
DISCUSSION

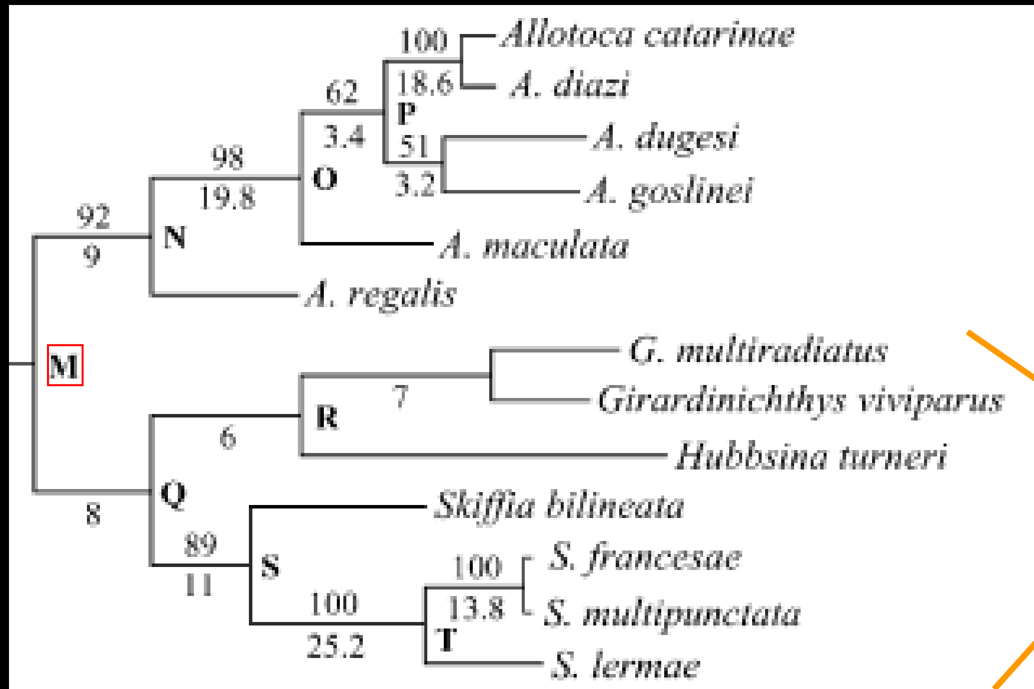
molecular phylogeny

(mtCOI + CR)

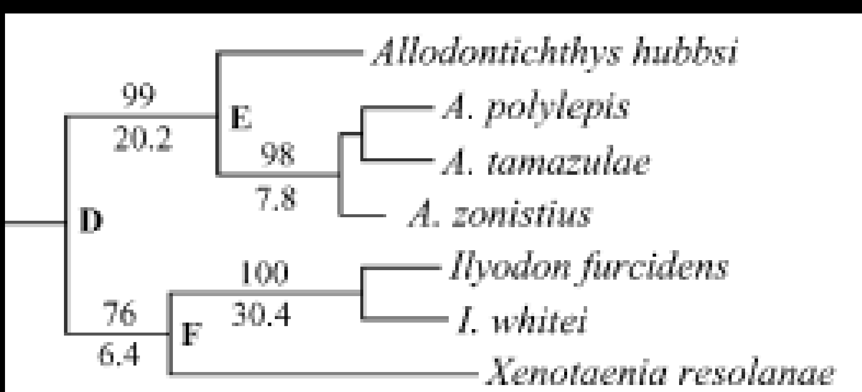
dataset 1

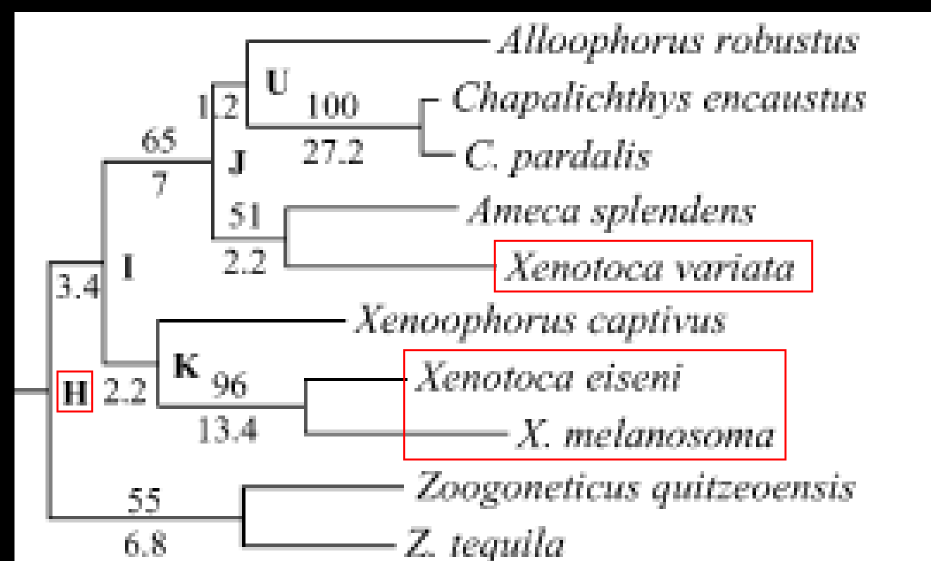
Webb et al. 2004



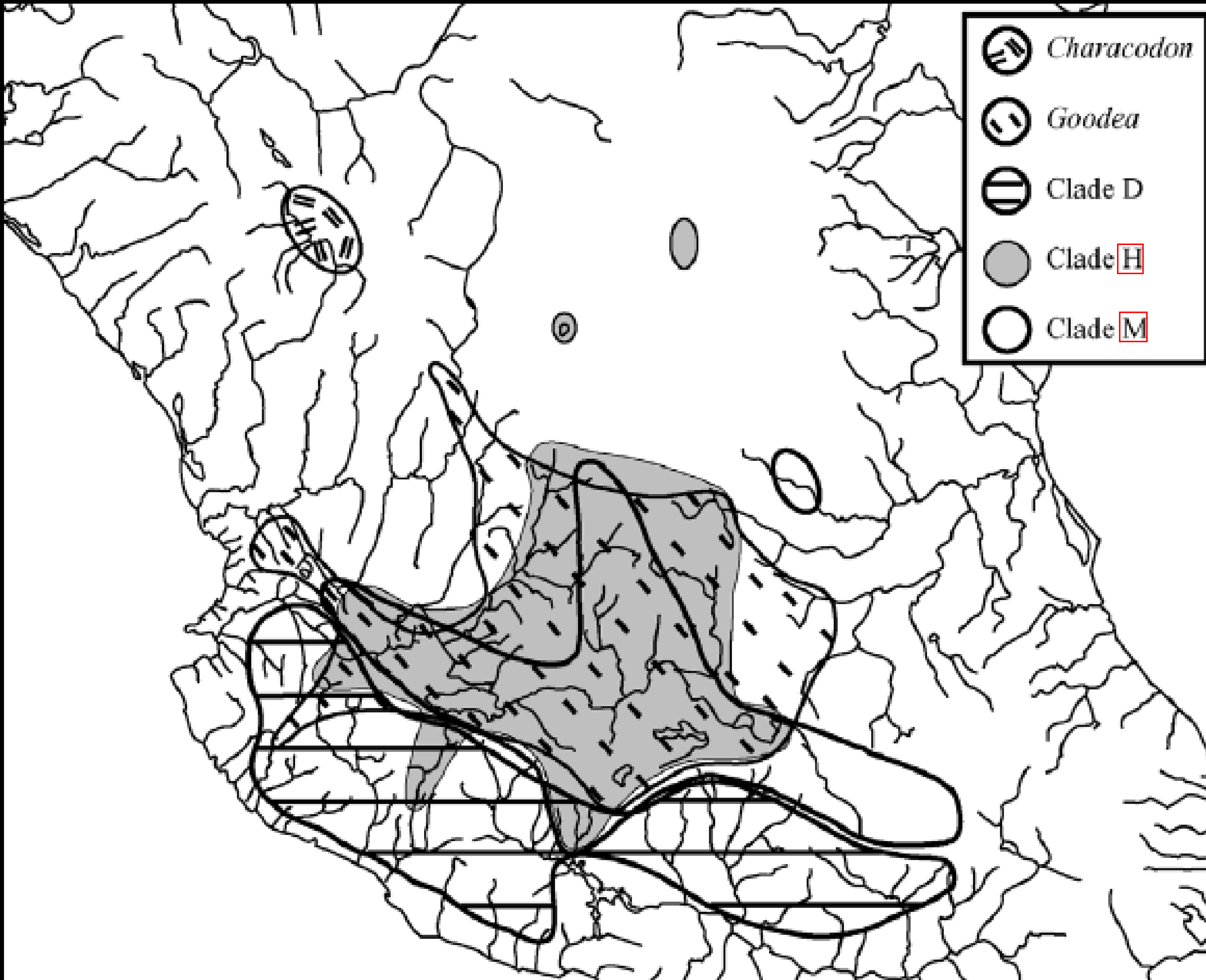


extreme fin dimorphism



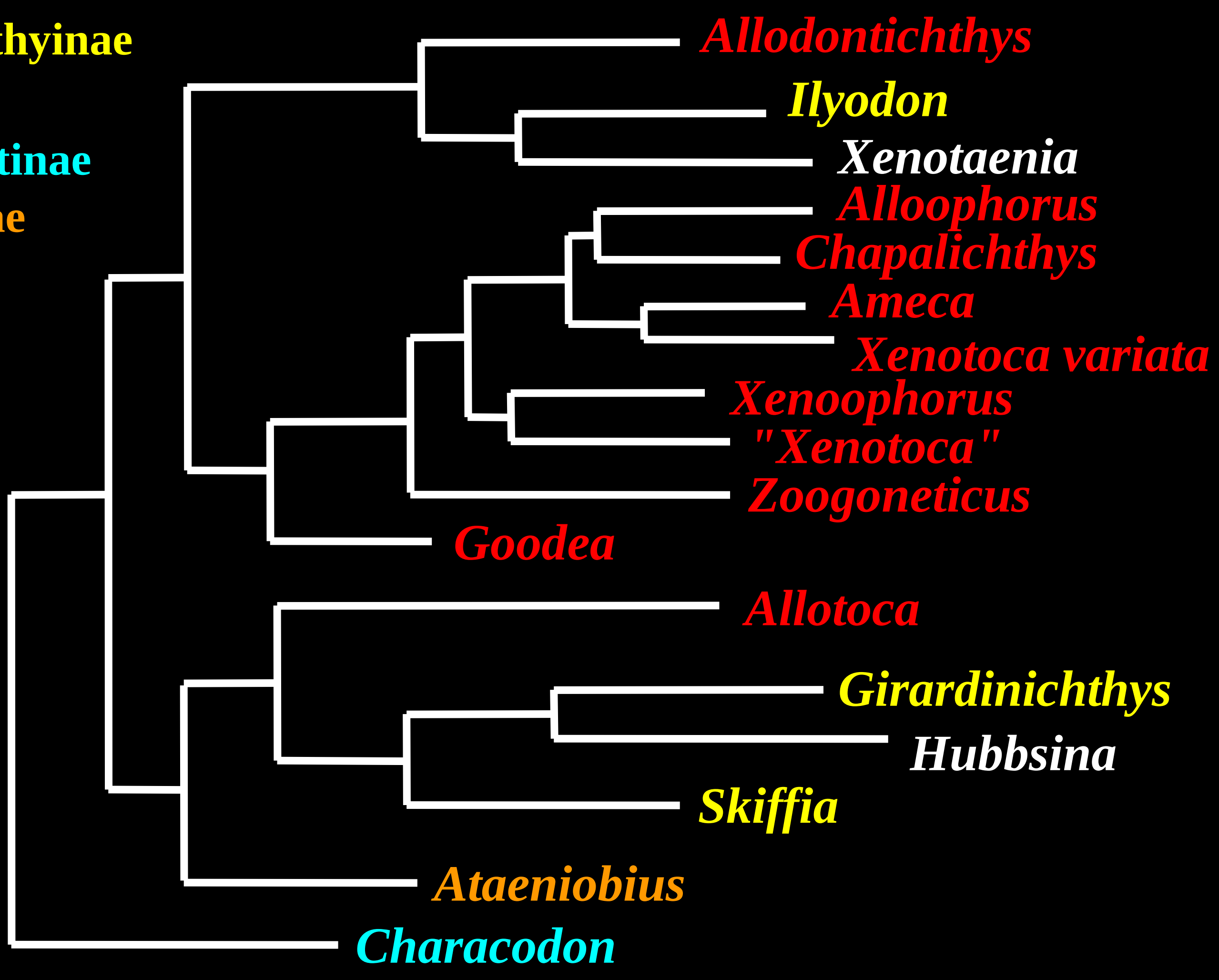


riverine clade

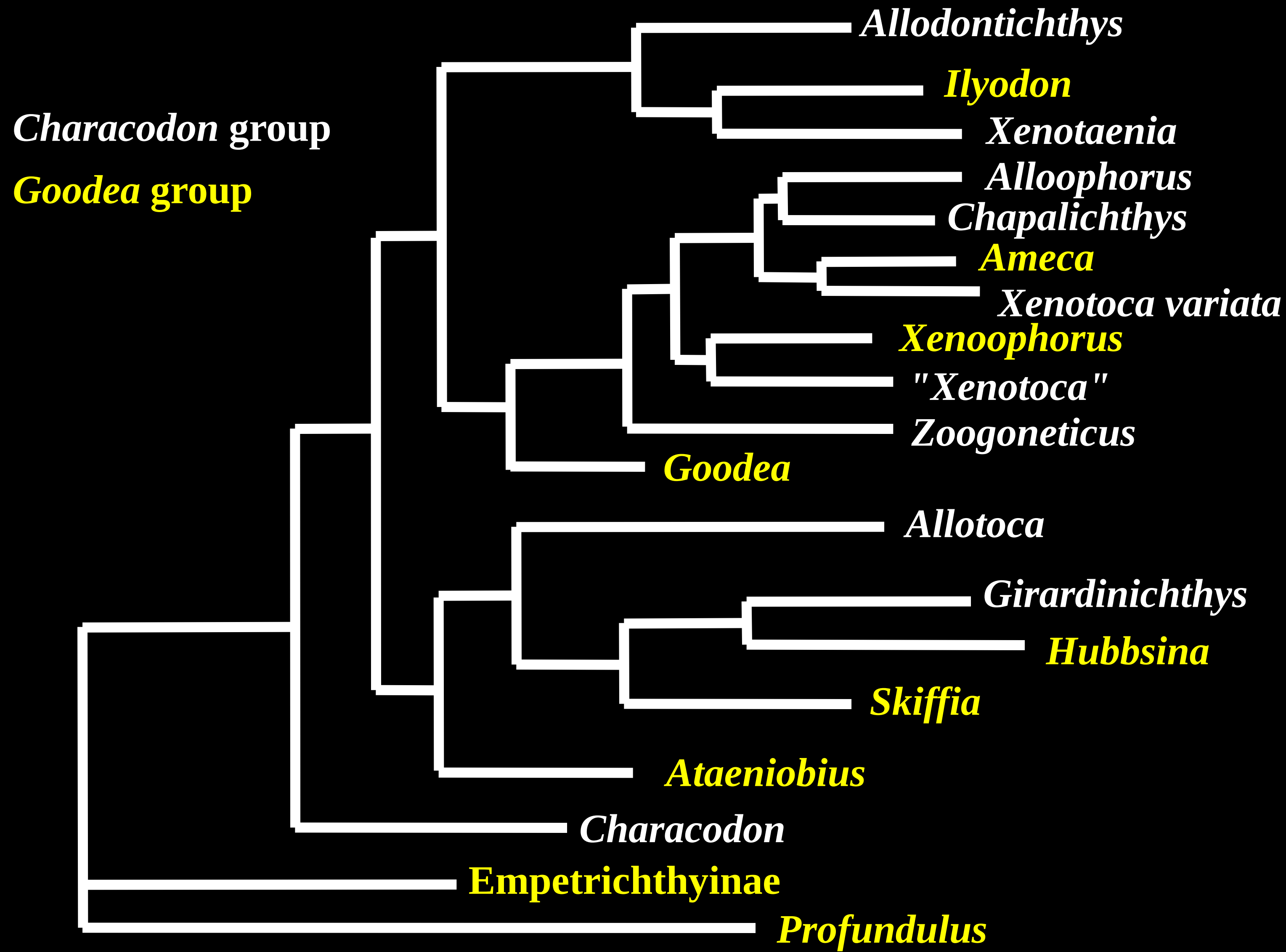

Characodon
Goodea
Clade D
Clade H
Clade M

hypothesis of Hubbs and Turner 1939

Girardinichthyinae
Goodeinae
Characodontinae
Ataeniobiinae
undescribed

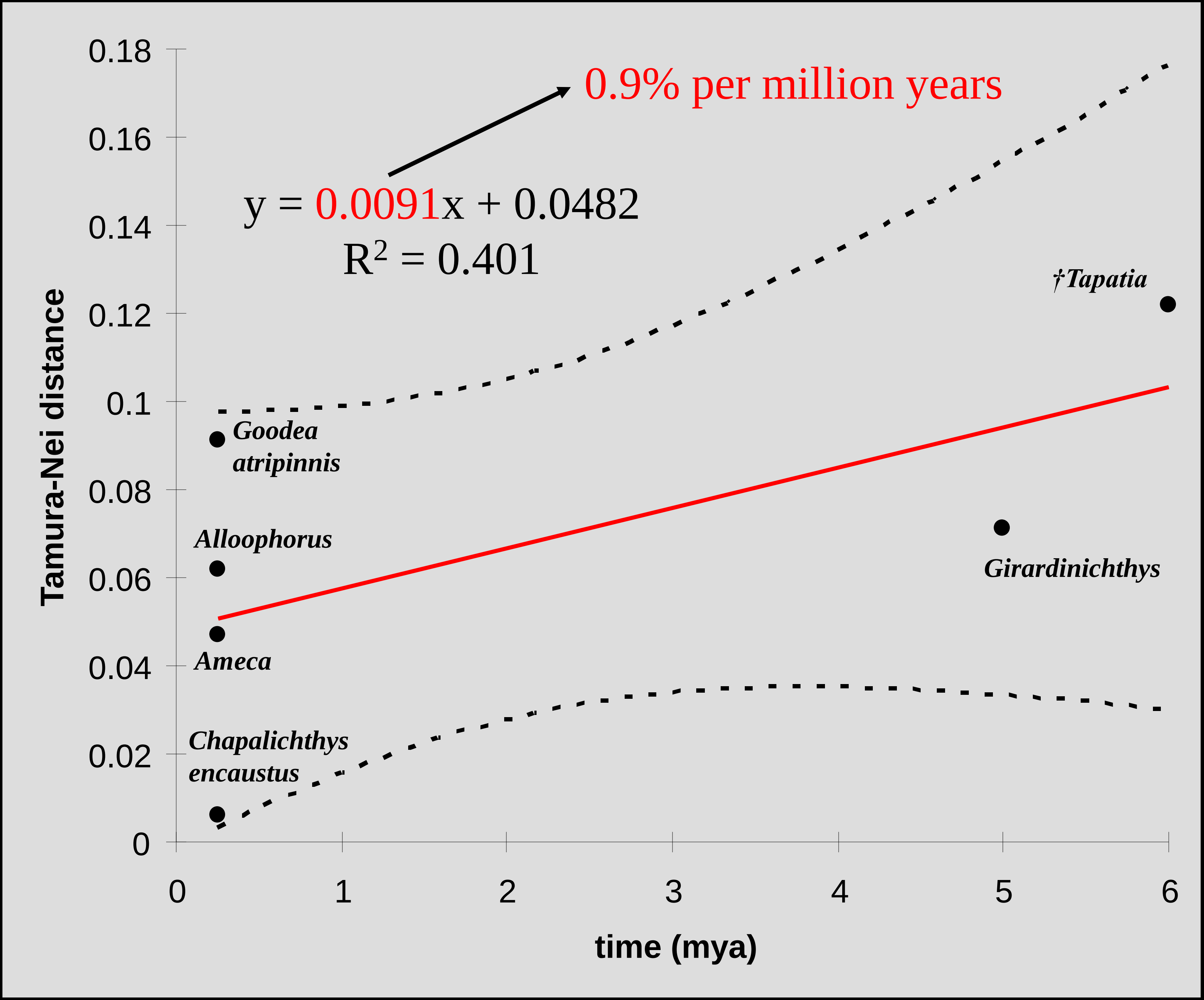


hypothesis of Smith 1980



goodeine molecular clock (mtCOI)

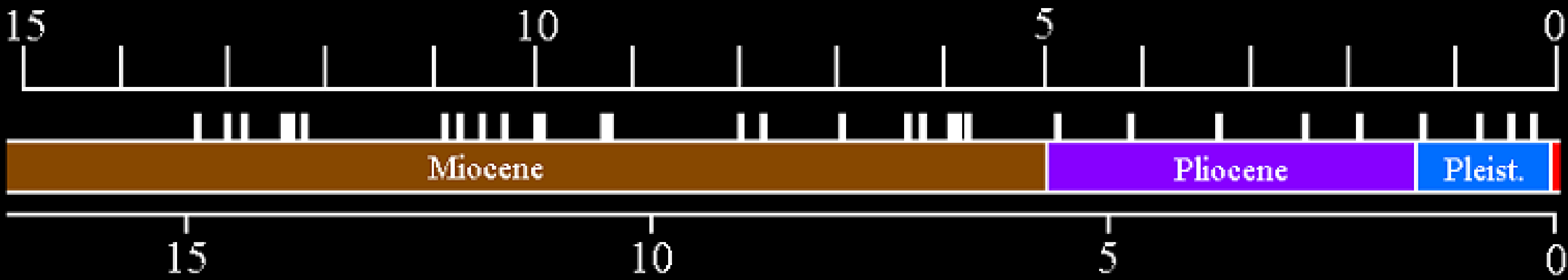
- Calibrated with fossil and geological data:
  - *Alloophorus*, *Ameca*, *Chapalichthys encaustus*, *Goodea atripinnis* fossils are mid-late Pleistocene (250 kya; Smith et al. 1975)
  - Allopatric speciation of *Girardinichthys* (Sierra Madre de las Cruces ~5 Mya; Barbour 1973)
  - †*Tapatia occidentalis* (sister group of girardinichthyins) fossils dated as late Miocene (~6 Mya; Smith 1980, Smith & Miller 1986)
- Corrected divergence (%) ÷ time of event
- Denominator is an underestimate with fossils, but shouldn't affect overall relationship (slope)



0.9% per million years
y = 0.0091x + 0.0482
R2 = 0.401
†Tapatia
Goodea atripinnis
Alloophorus
Ameca
Girardinichthys
Chapalichthys encaustus
Tamura-Nei distance
time (mya)
0
0.02
0.04
0.06
0.08
0.1
0.12
0.14
0.16
0.18
0
1
2
3
4
5
6

chronology of speciation events

Tamura-Nei sequence divergence (%)



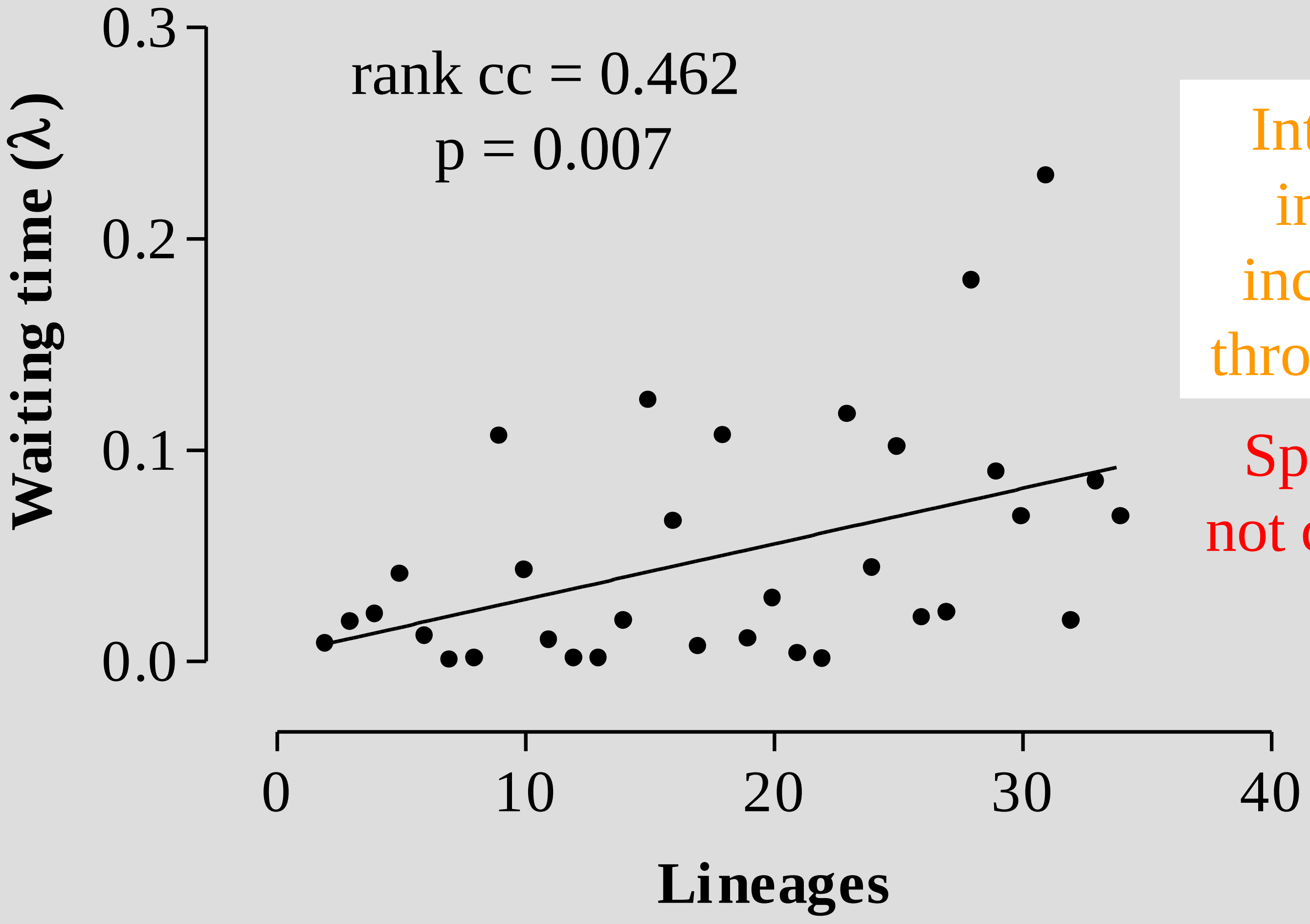
Time (Mya)

you are here

from Webb et al. 2004

dataset 1

time to speciation



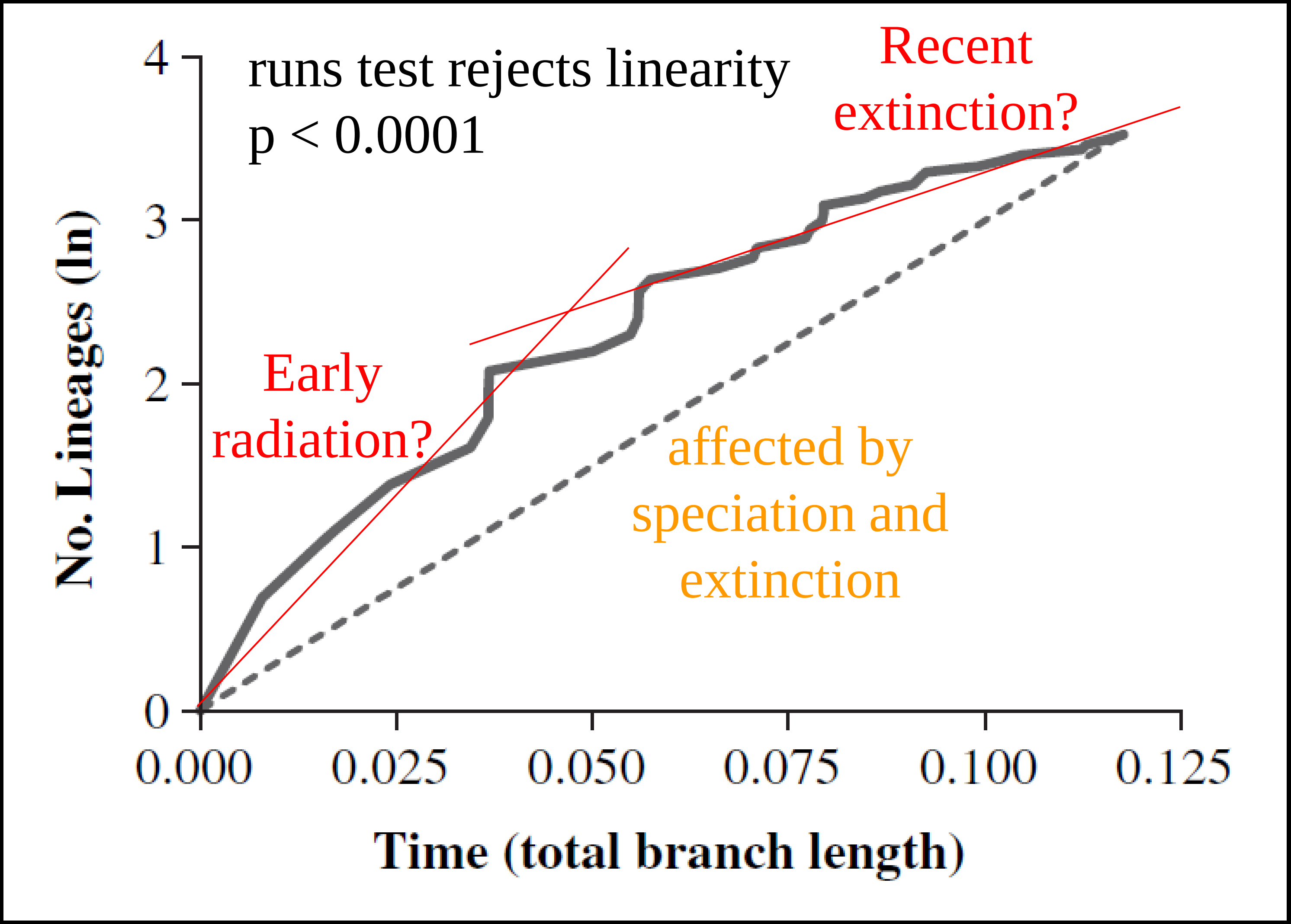
Internode interval increasing through time

Speciation not clocklike.

from Ritchie et al. 2005

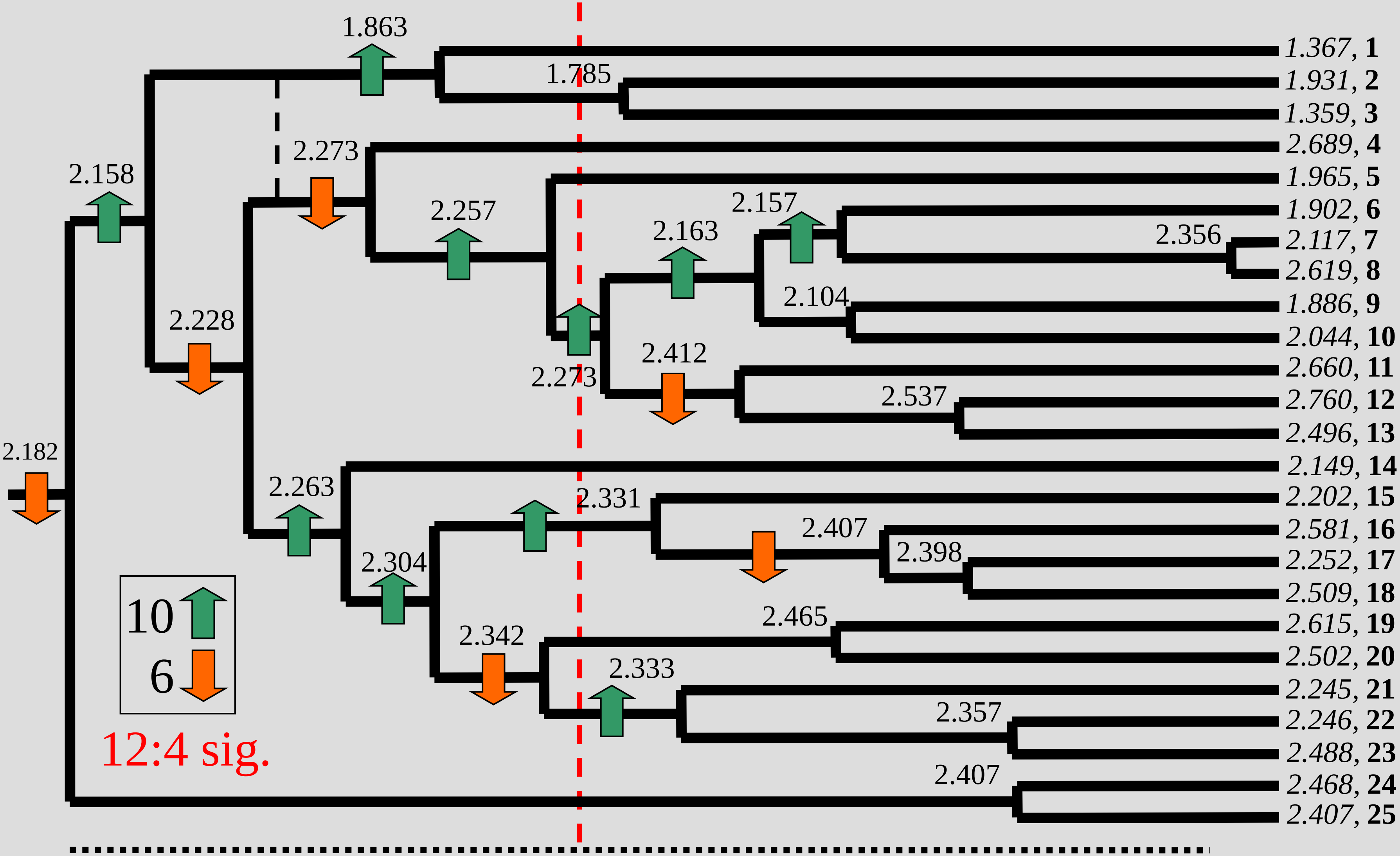
lineages through time plot

dataset 1



from Ritchie et al. 2005

sexual dimorphism and speciation



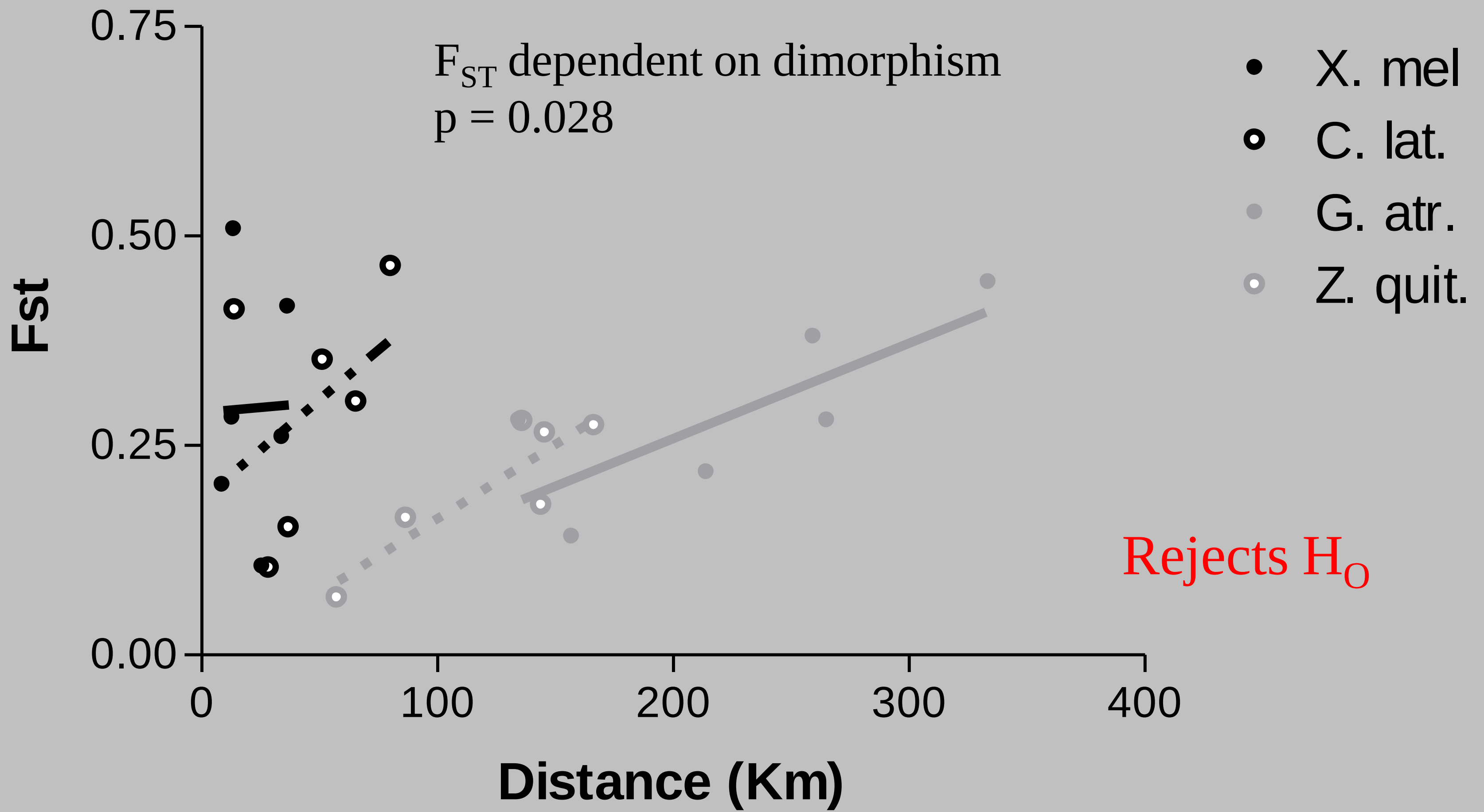
$p = 0.14$

from Ritchie et al. 2005

Does not reject H_O

dataset 3

F_{ST} vs. geographic distance



Rejects H_O

from Ritchie et al. 2007

Conclusions

- The goodeid "clock" suggests the group is ~16.8 Myrs old, the Goodeinae is 14.9 Myrs old, and that approximately 3/4 of goodeine divergence events occurred during the Miocene (i.e. older).

- All goodeine genera but *Xenotoca* are monophyletic. Findings of previous authors not supported.

- The biogeographical history of the Goodeinae is difficult to reconstruct. There has been significant range change in older groups.

Conclusions

- Comparative analysis failed to find a relationship between sexual dimorphism and rate of speciation, but intraspecific variation suggests a role for sexual selection in genetic differentiation.
- Speciation rate appears to decline over time (are goodeines an adaptive radiation?).
- *Role of vicariance (atherinopsids and cyprinids), other extrinsic factors?*


Agave tequilana

Sequential linear regression model

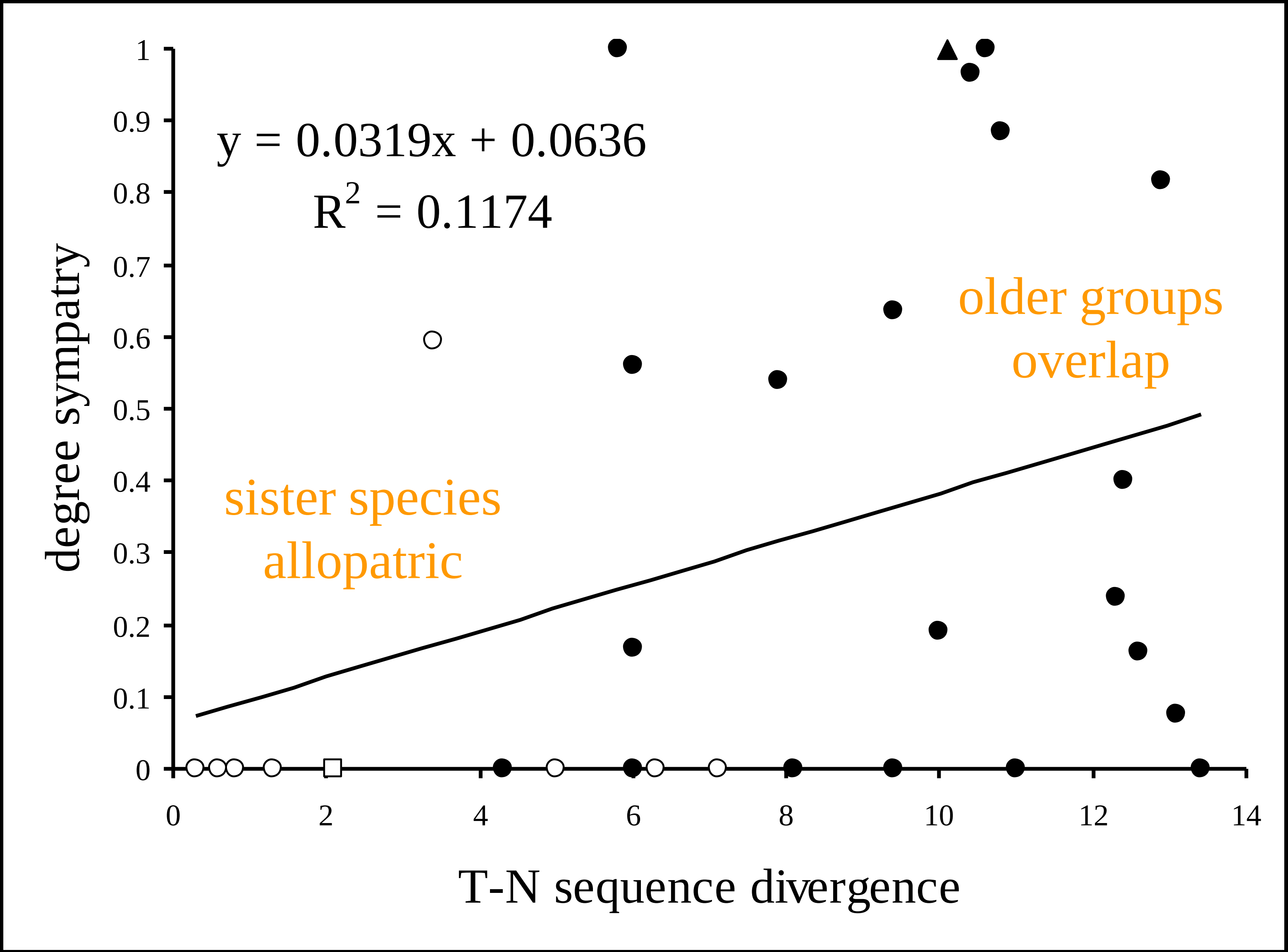
- Distance as a covariate
- Mono- vs. dimorphism as a factor (dimorphism)
- Species nested within dimorphism

- F_{st} dependent on dimorphism ($F_{1,18} = 5.7$; $p=0.028$)

- ANCOVA → least squares mean F_{st} for dimorphic species = 0.25; mono- = 0.16

vicariance plot

dataset 1



Method of Barraclough et al. 1998