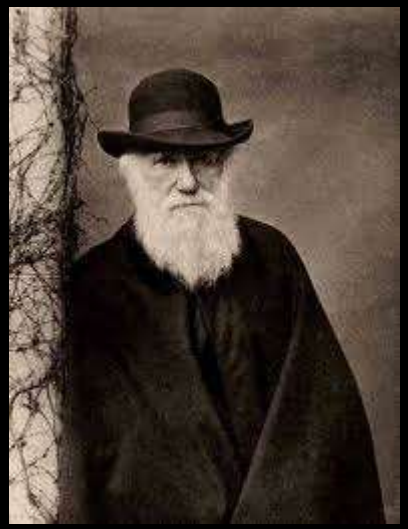
CURRENT ISSUES IN CORAL MOLECULAR SYSTEMATICS AND UNDERSTANDING SPECIES BOUNDARIES

Zac H. Forsman

To be considered for listing under the Endangered Species Act, a group of organisms must constitute a "species." –BRT review report



What is a species?

"No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species."

- Charles Darwin 1859

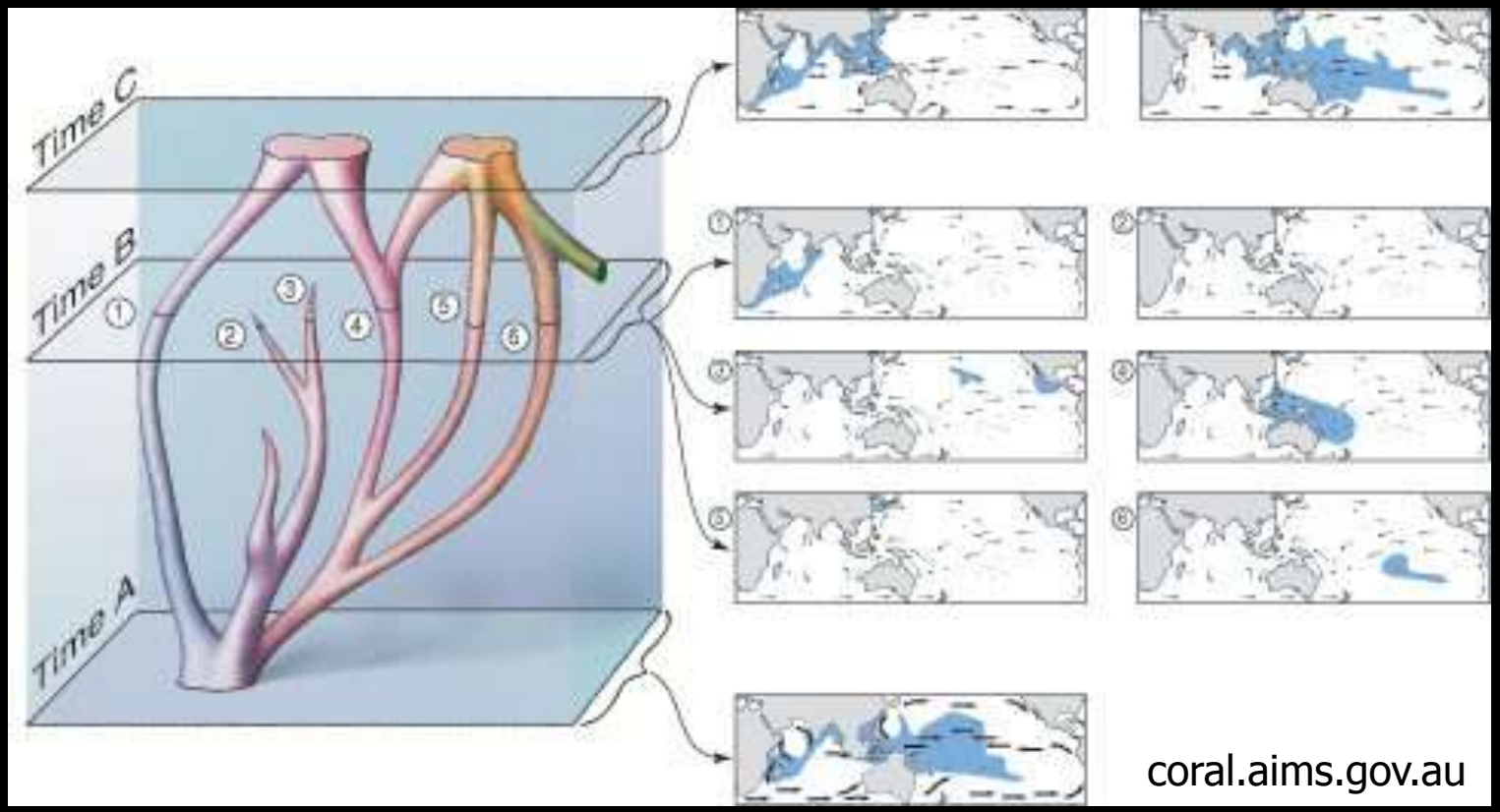
"the term species includes any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." -ESA

Biological species concept (Mayr)

Prevailing view: morphospecies

Reticulate evolution by sea surface vicariance (Veron)

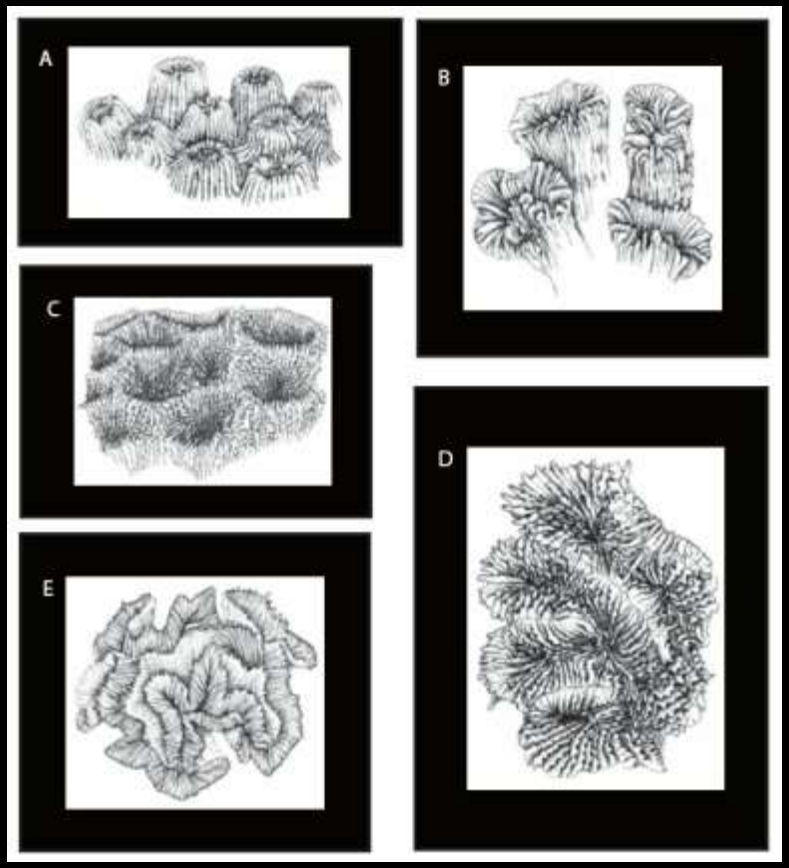
Endangered?
Endemic?
Range?
Speciation?



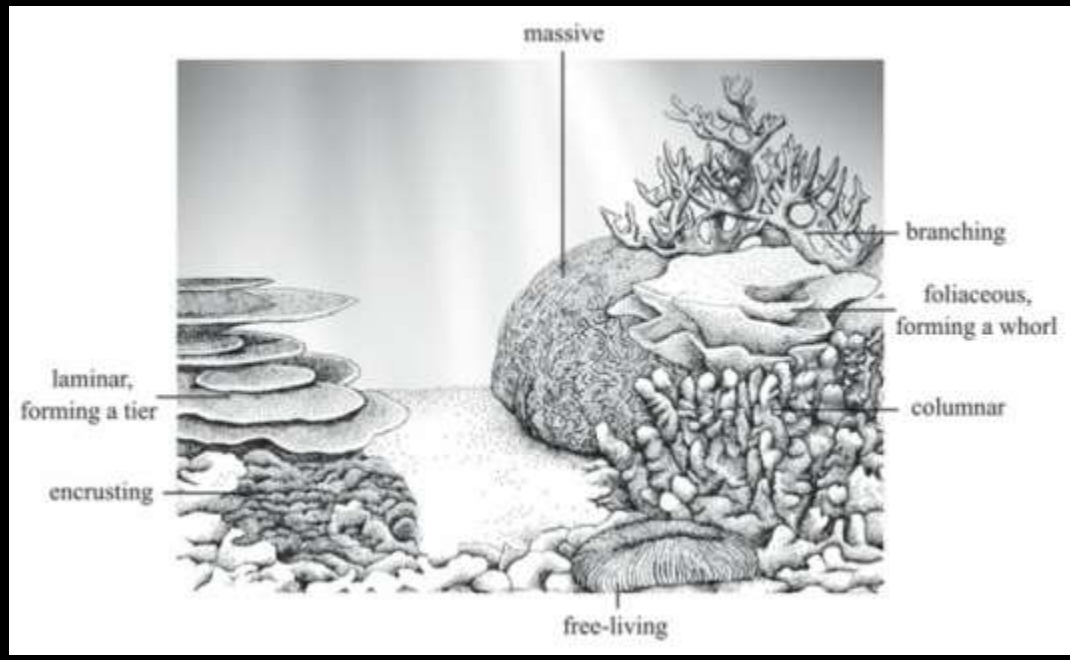
coral.aims.gov.au

Morphological taxonomy

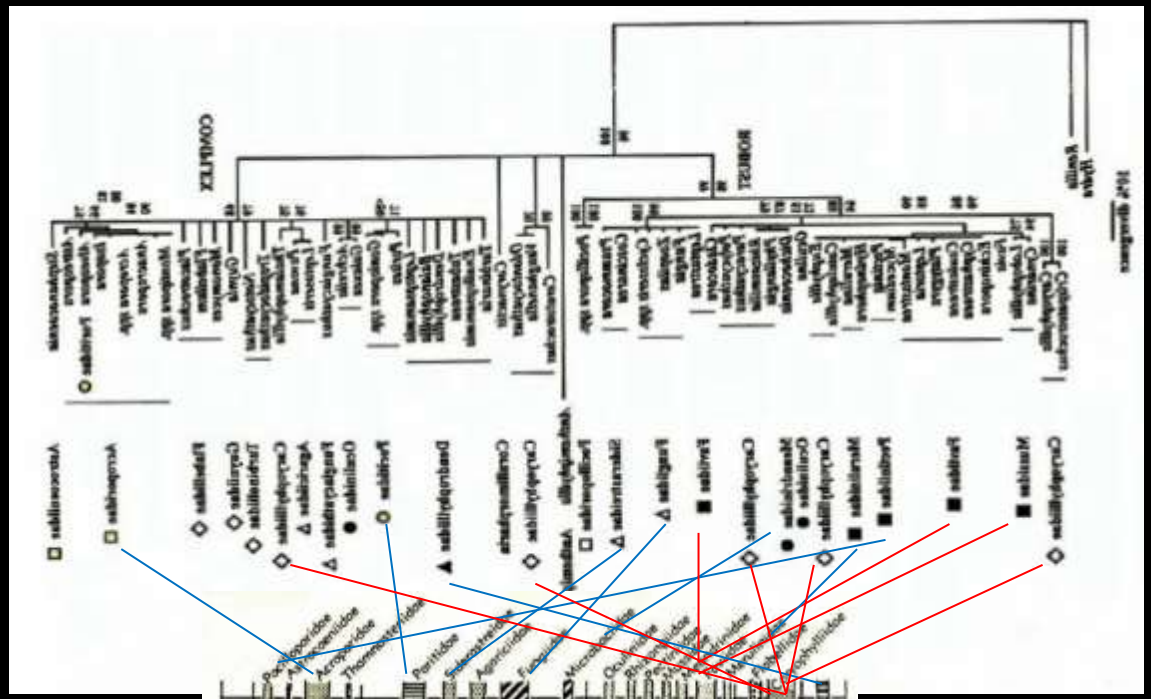
Corallite-level morhphology



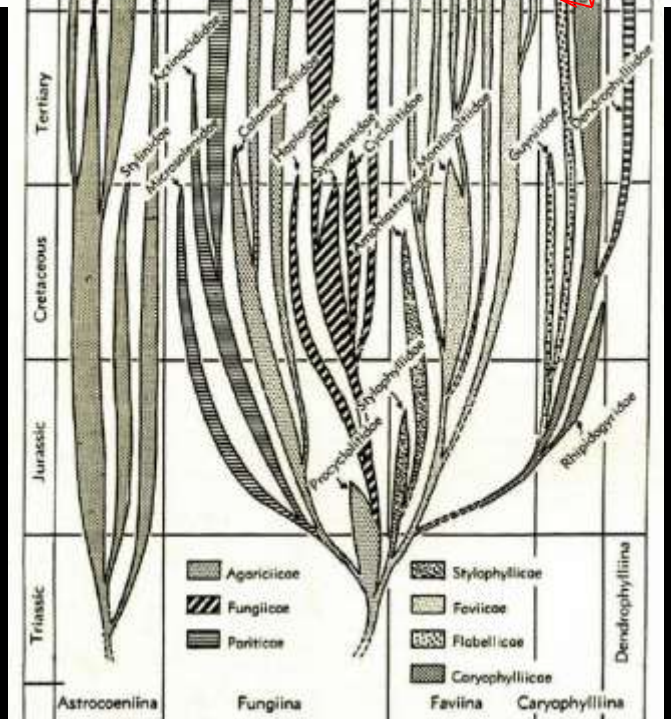
Colony-level morphology



Veron 1986



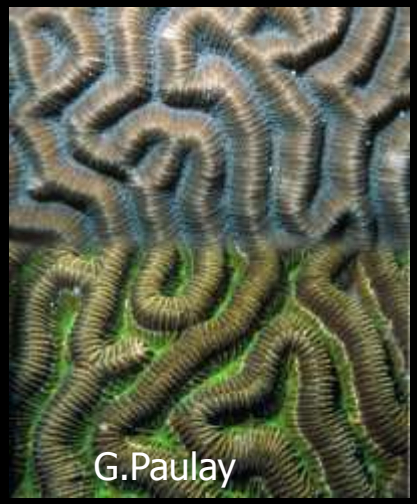
Romano and Palumbi 1996
Romano and Cairns 2000



Wells 1956

- Cryptic diversity
- Polyphyletic groups

- Fukami et al. 2004
  - Extraordinary example of convergence
  - “Bigmessidae”



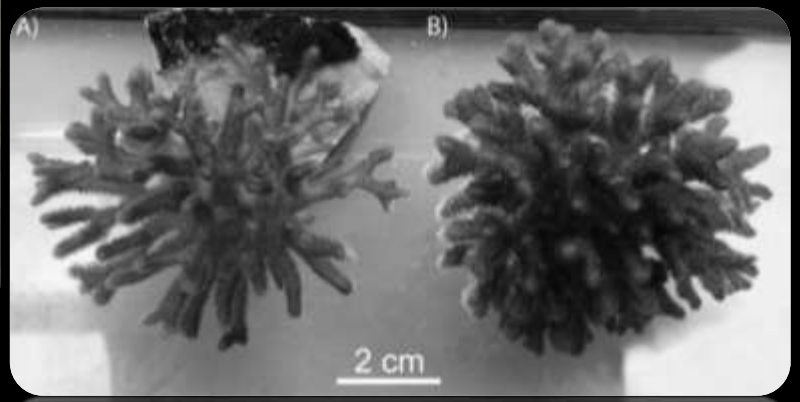
- Huang et al. 2009
  - Confirmed Fukami et al. 2004, literature survey; pervasive polyphyly – why? –probably selection

- Budd et al. 2010
  - Closer examination of micro-morphology

Species-level studies challenges & limitations

Hybridization, polymorphism, plasticity?

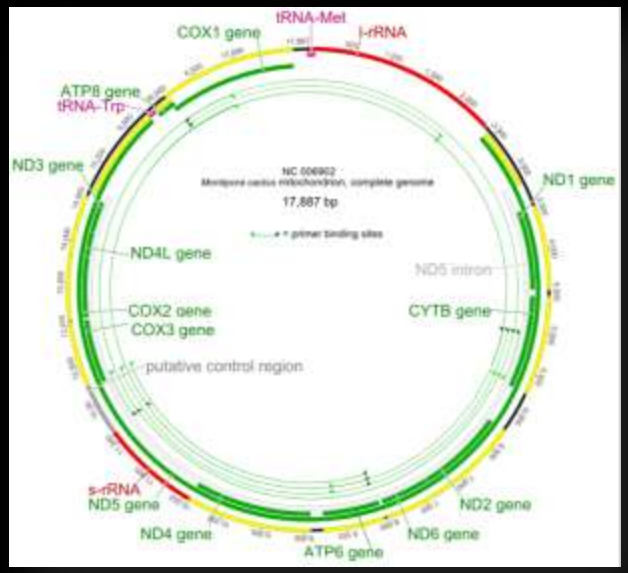
- Light
- Water motion
- Sedimentation
- Intraspecific
- Intraclonal
- Gravity



Todd 2008, Biol. Rev.

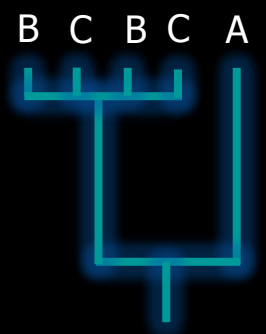
Species-level studies challenges & limitations

mtDNA



Conserved markers

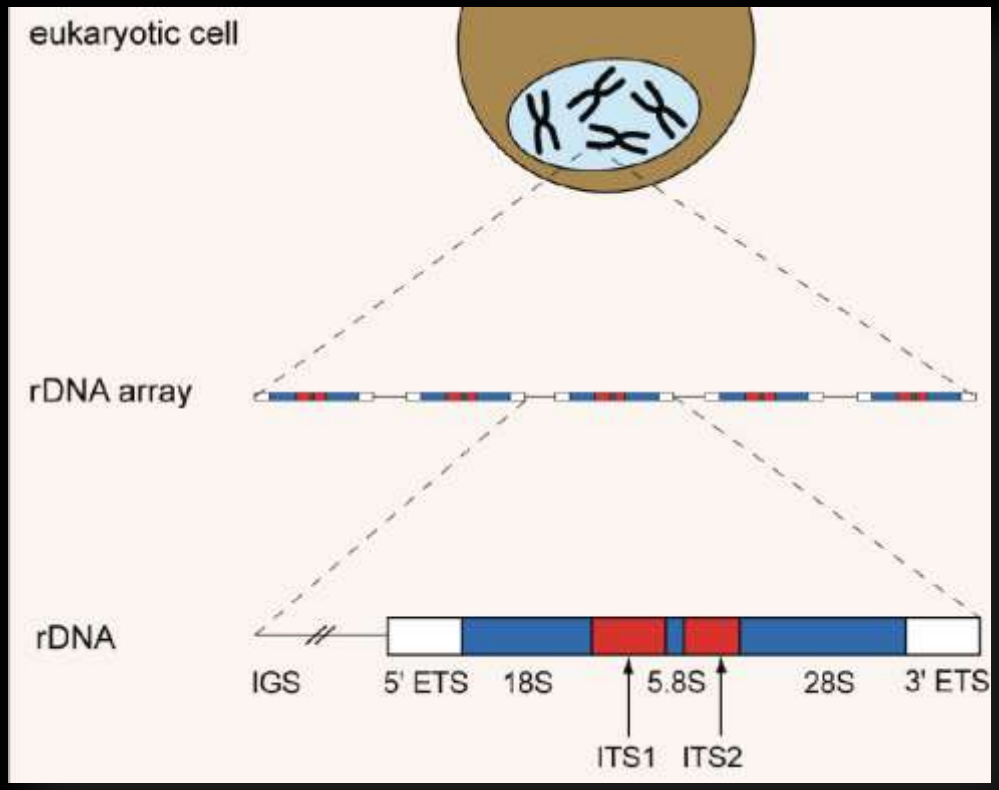
Homoplasy, Poor resolution

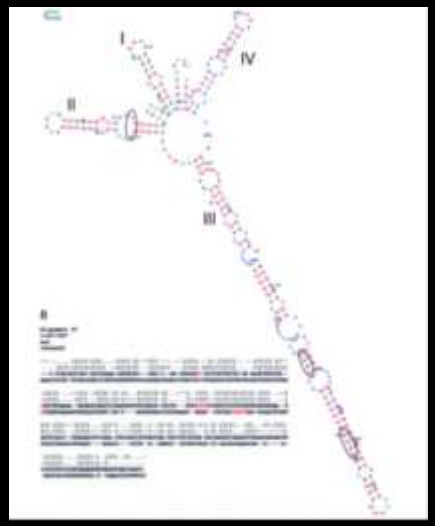


Stat M, Baker A, Correa A, **Forsman ZH**, Huggett M, Pochon X, Skillings D, Starger C., van Oppen M, Gates RD (in press) Advances in Marine Biology.

Species-level studies challenges & limitations

Internal Transcribed Spacer (ITS Region)

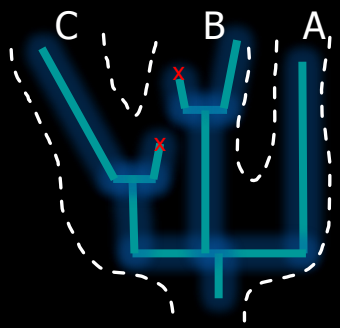




Shultz et al 2005

Paralogy?

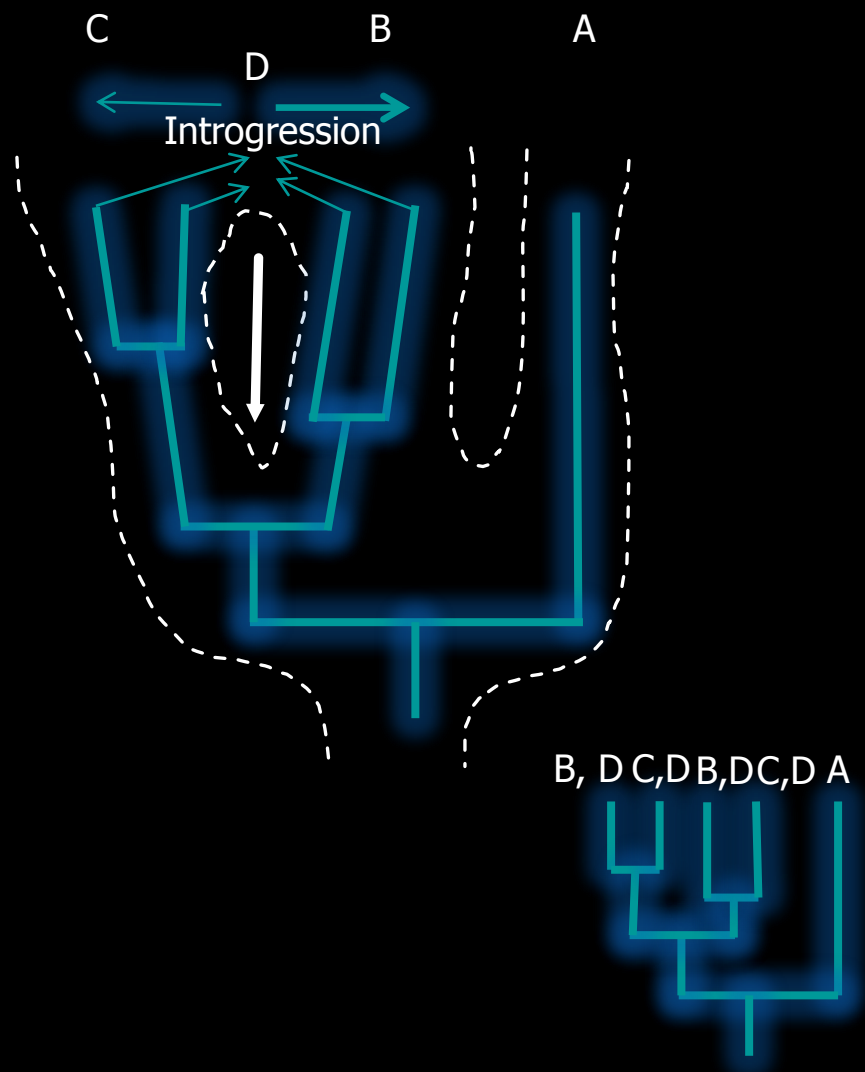
Gene duplication, loss



<u>Complex evolution:</u> Homogenized by recombination?

Stat M, Baker A, Correa A, **Forsman ZH**, Huggett M, Pochon X, Skillings D, Starger C., van Oppen M, Gates RD (in press) Advances in Marine Biology.

Hybridization

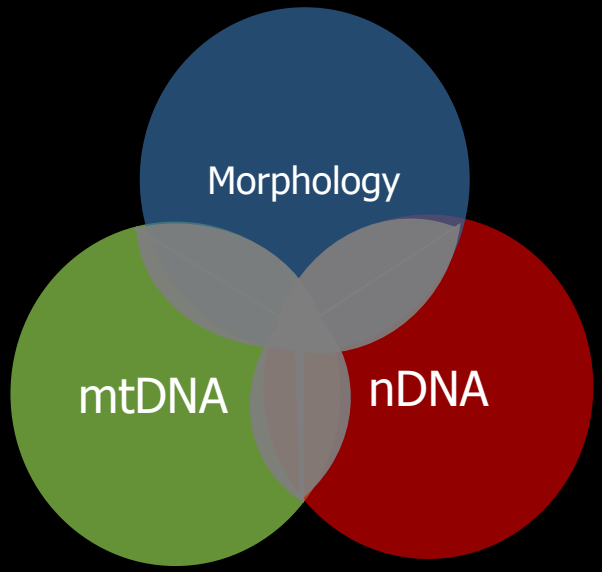


Incomplete lineage sorting

Modified from Funk & Omland (2003) An. Rev. Ecol. Evol. Sys. 34(1)

Species-level limitations

Polymorphism & Plasticity



Conserved markers

Paralogy

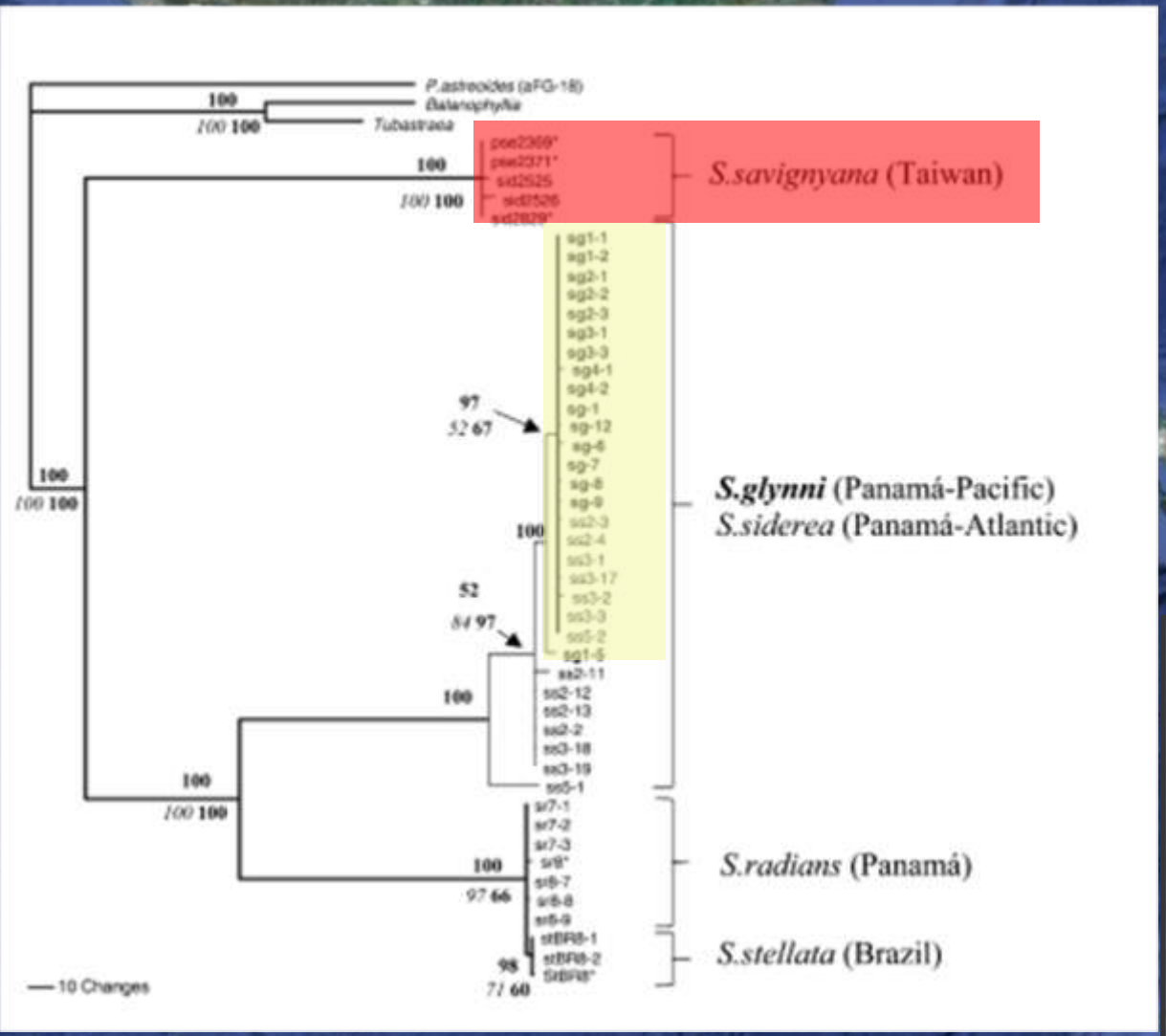
Example studies:

Siderastrea

endangered species?

- Only 5 colonies
- Only 5 species in the genus
- Genus does not occur in EP
- 3 hypotheses:
  1. Long distance dispersal from indo-pacific
  2. Allopatric fragmentation from rise of Isthmus of Panama
  3. Transport through canal

Forsman et al 2005 *Coral Reefs*



3 hypotheses:

1. Long distance dispersal from indo-pacific
2. Allopatric fragmentation from rise of Isthmus of Panama
3. Transport through canal

Forsman et al 2005 *Coral Reefs*

Species status of *Siderastrea glynni*?
Dilemma:
Reproductively isolated
Separate evolutionary trajectory

Forsman et al 2010 PLoS One

Montipora

Petitioned species:

M. dilatata ,*M. flabellata, M. patula*

M. dilatata (NOAA SOC) Endangered coral, hybrid, or ecomorph?

5 Mitochondrial genes

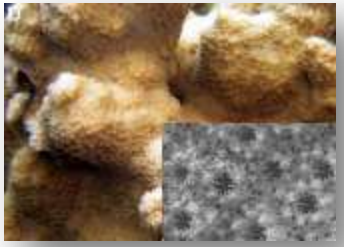
- Control Region
- COI
- CytB
- 16S
- ATP6

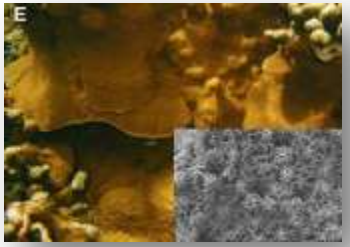
} 3,200bp~1.6bp/10^6 y

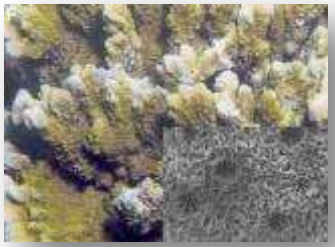
2 Nuclear genes

- atpsB intron
- ITS

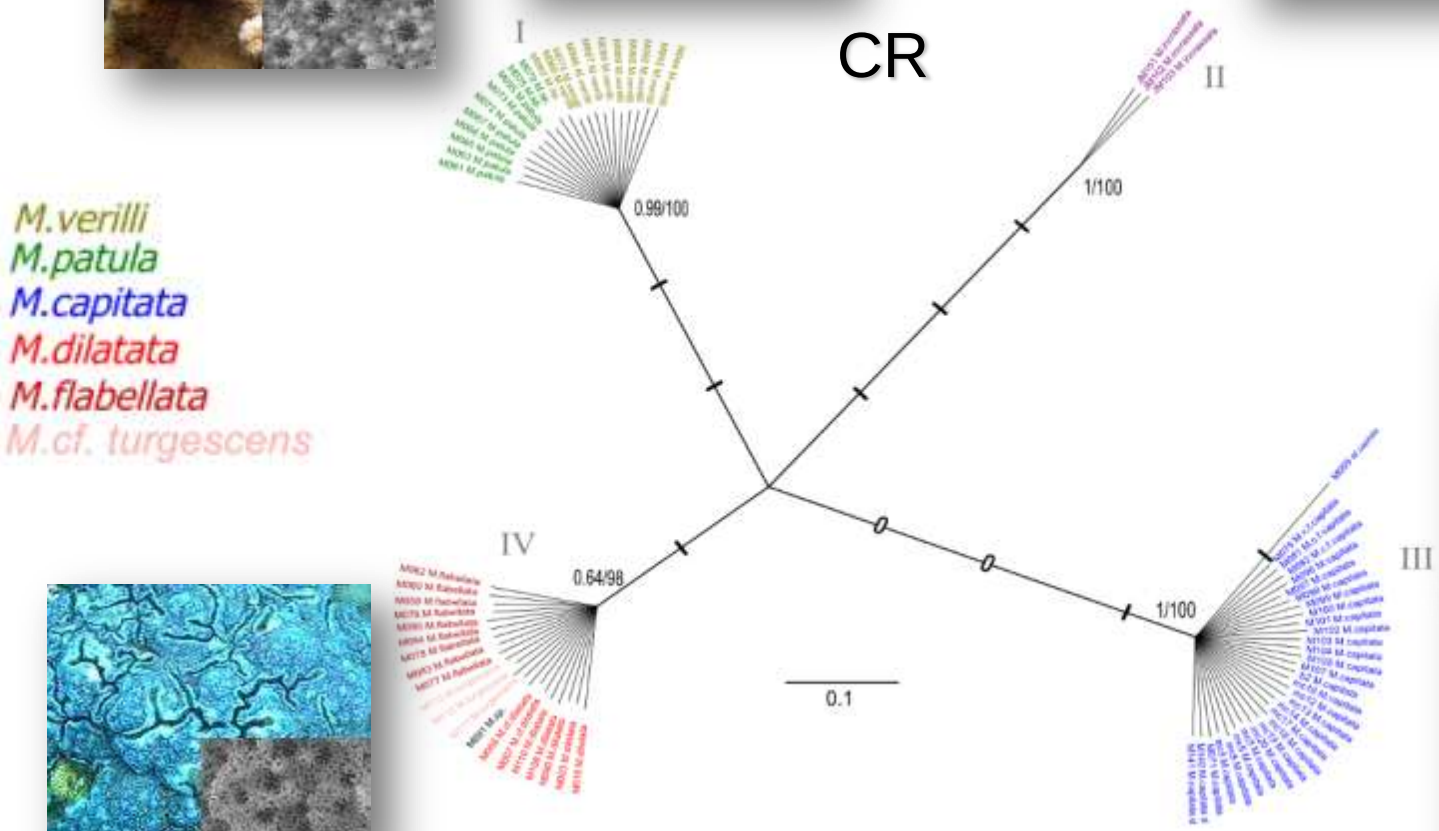
Forsman et al 2010 PLoS One

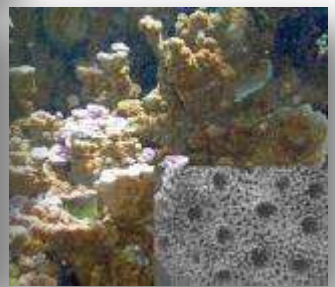


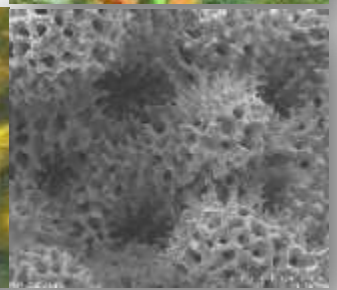




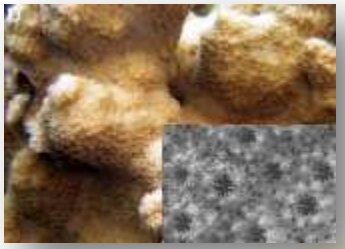
CR

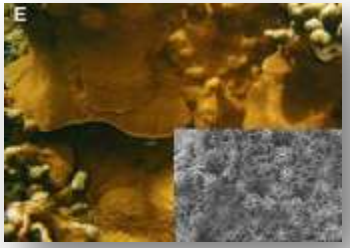


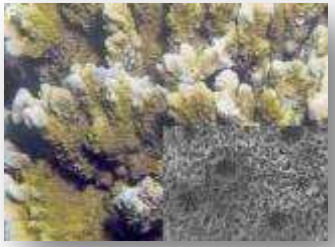




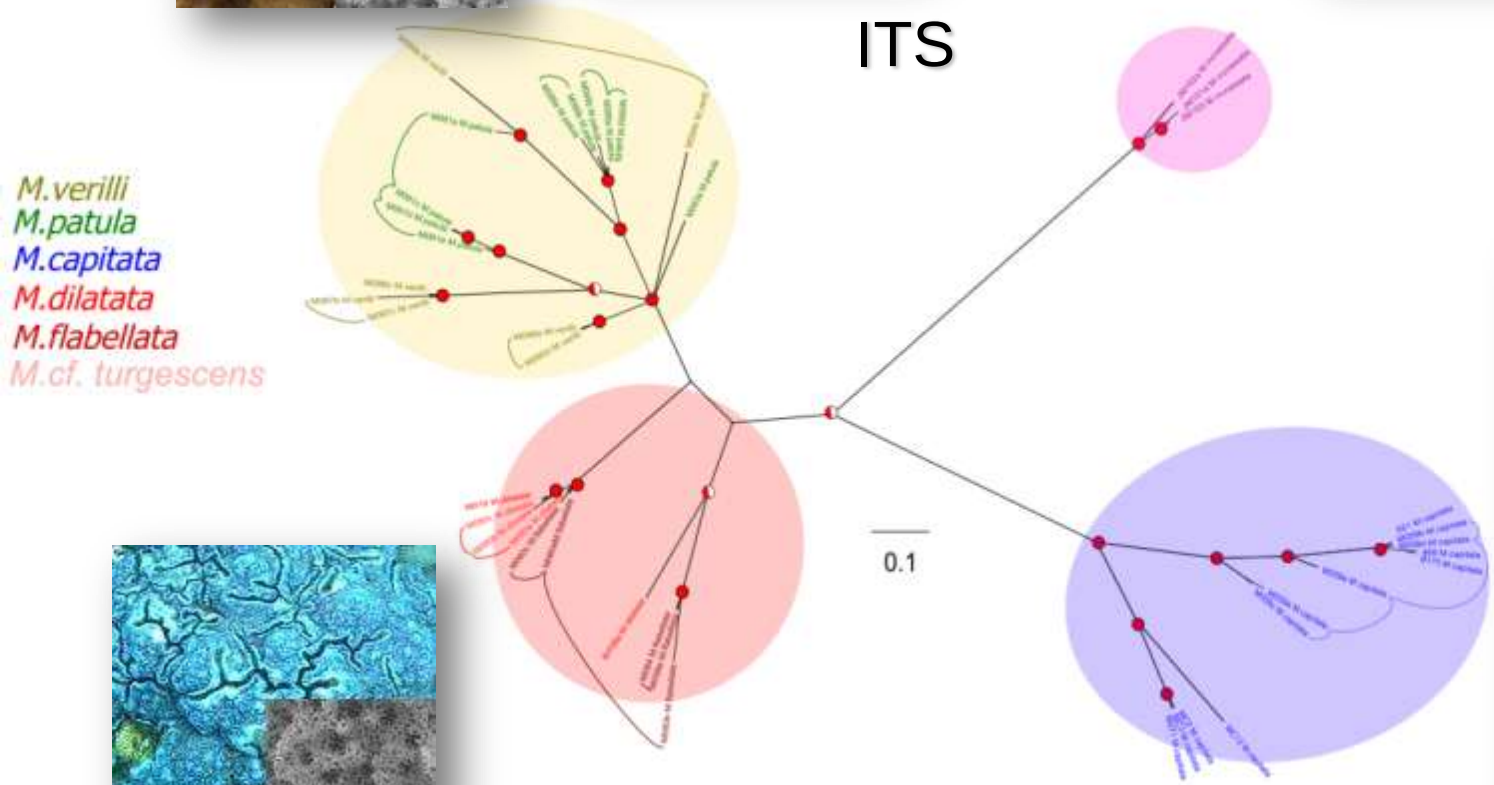
Forsman et al 2010 PLoS One

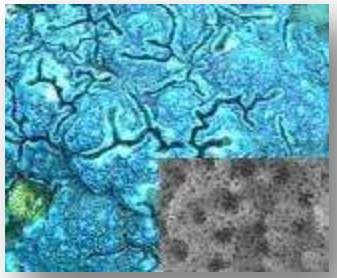


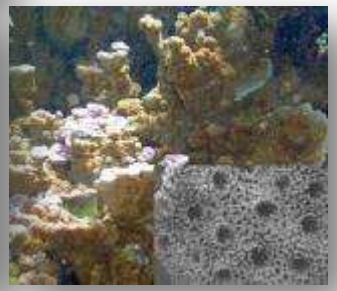


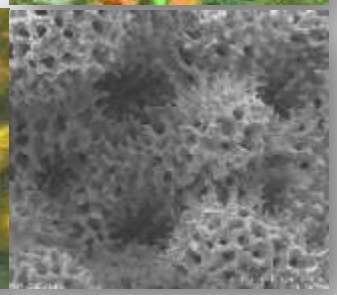


ITS









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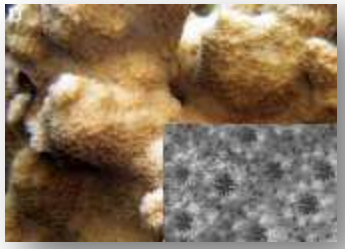
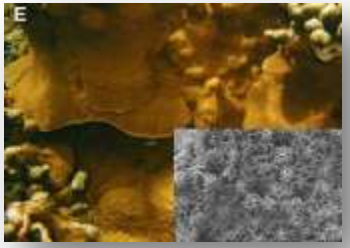
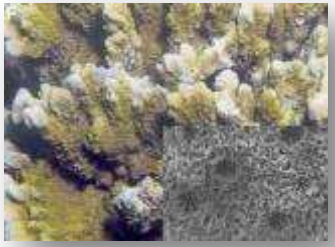
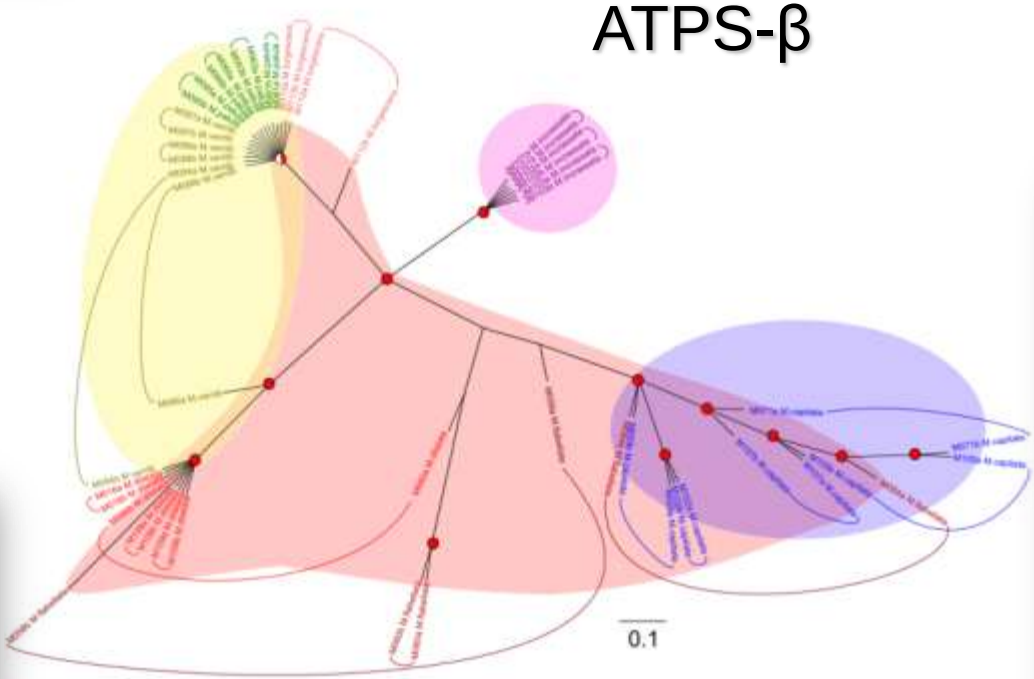


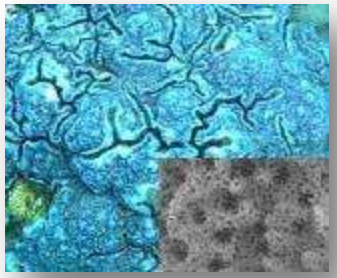


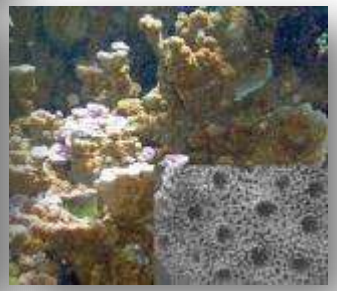


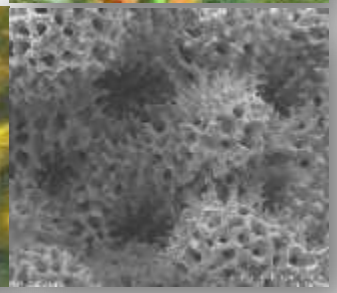
ATPS-β

M.verilli
M.patula
M.capitata
M.dilatata
M.flabellata
M.cf. turgescens









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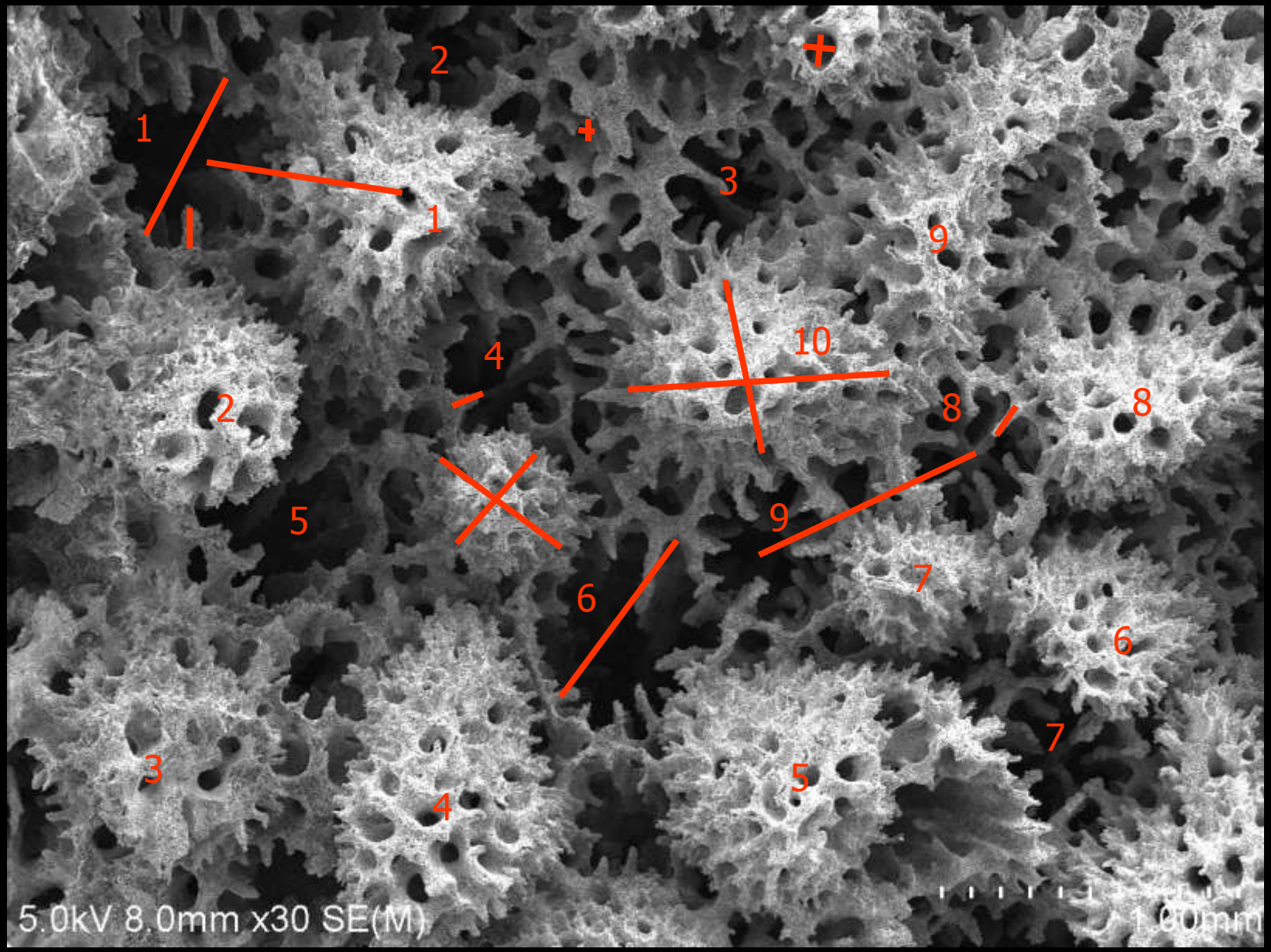

NC
MXD A
MXD B
Dist
SL 1
SL 2
SL 3

NTP
BC
LBmx
LBmn
SBmx
SBmn
LPmx
LPmn
SPmx
SPmn

MXDvSL
LBp
SBp
LPp
SPp

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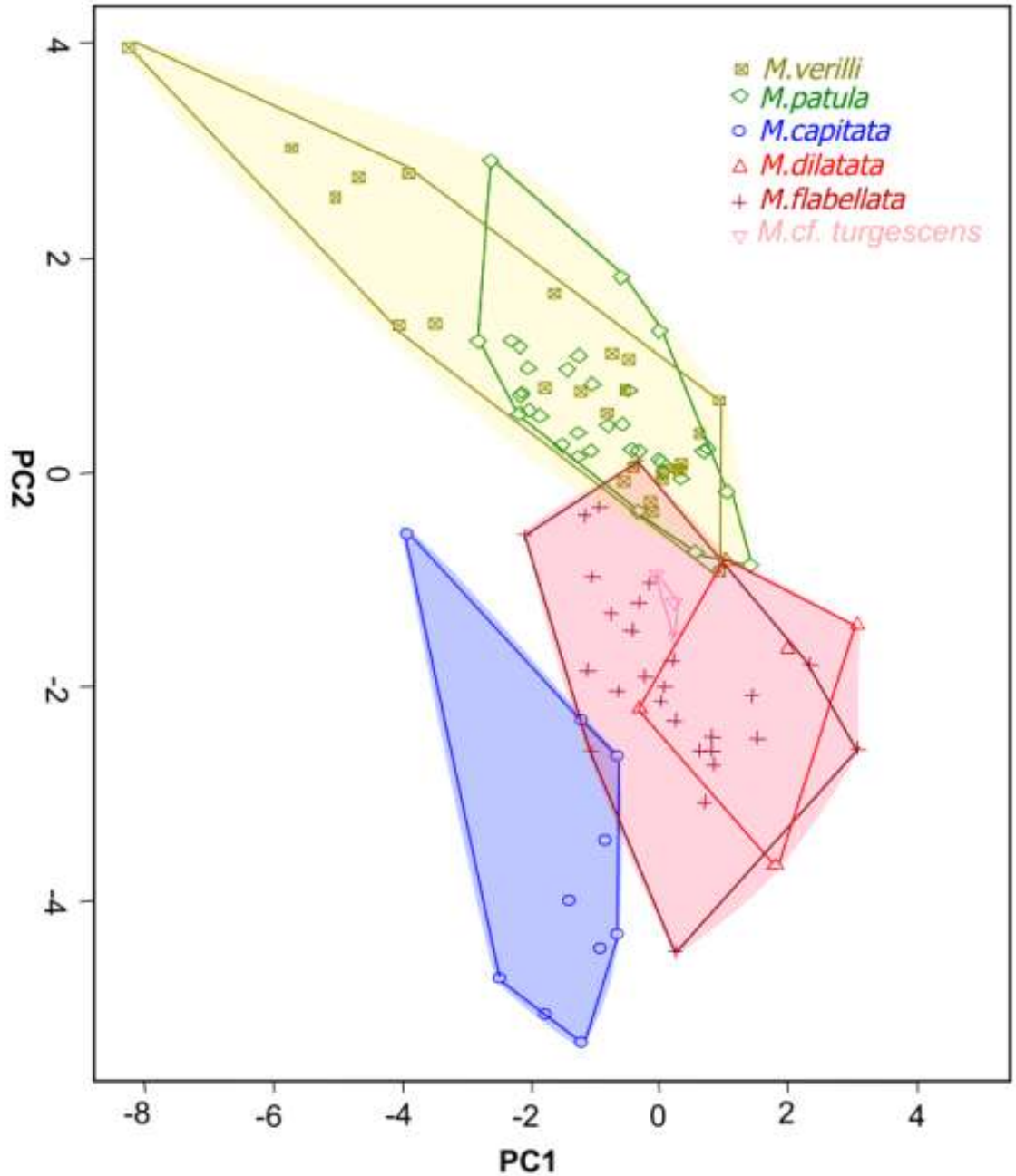
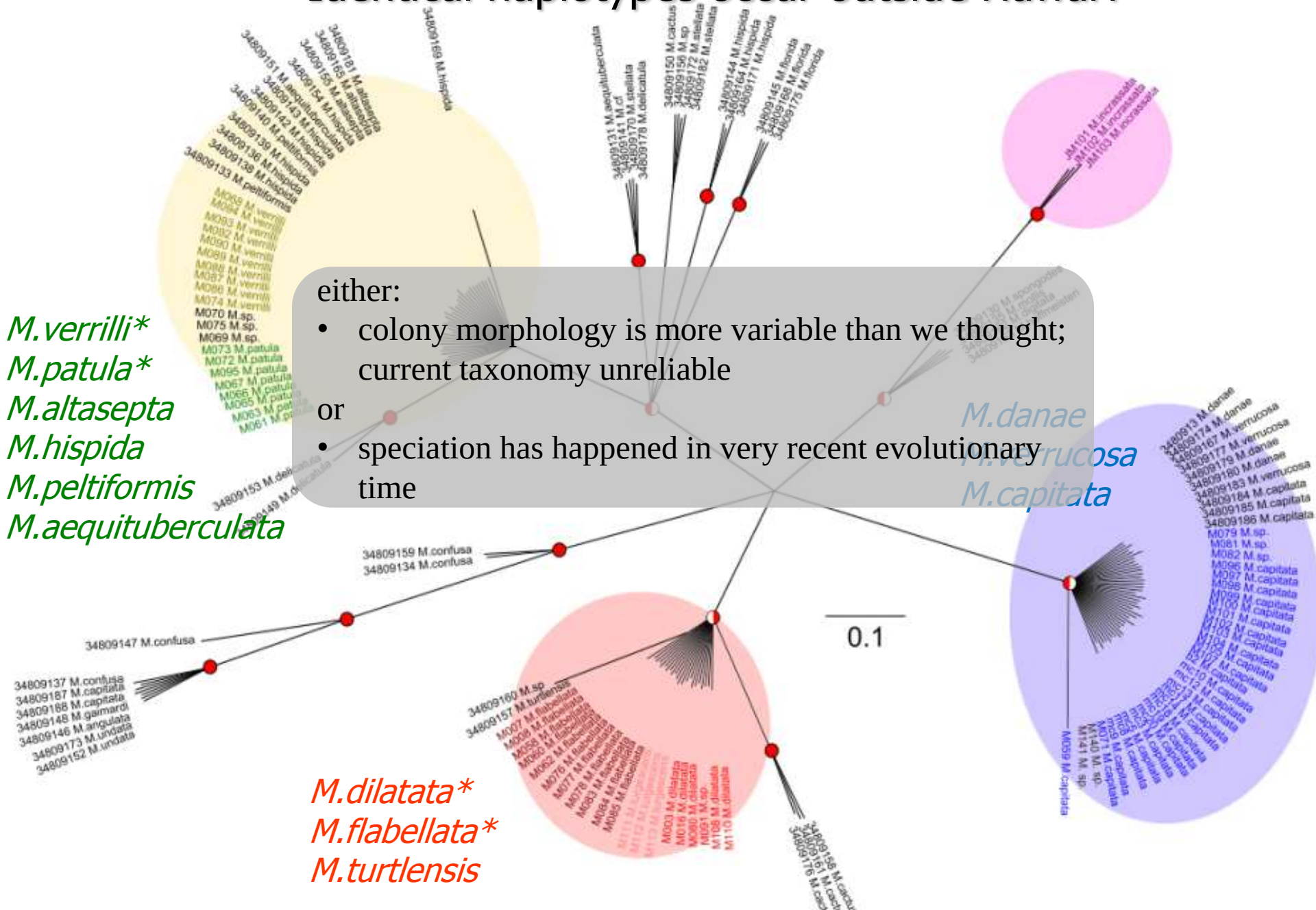


Type II MANOVA
(Wilks test statistic)

Species p = ns
Genetic group $p < 0.0001$

Forsman et al 2010 PLoS One

Identical haplotypes occur outside Hawai'i

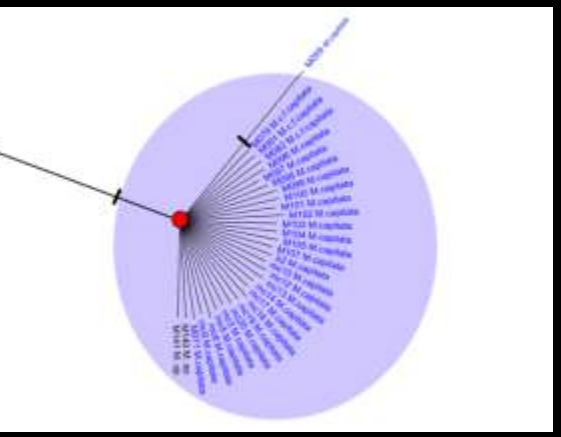


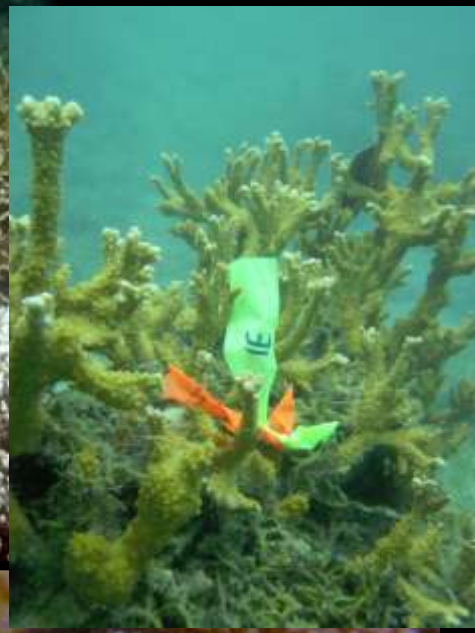
either:

- colony morphology is more variable than we thought; current taxonomy unreliable

or

- speciation has happened in very recent evolutionary time





S.Coles

10/01/2009

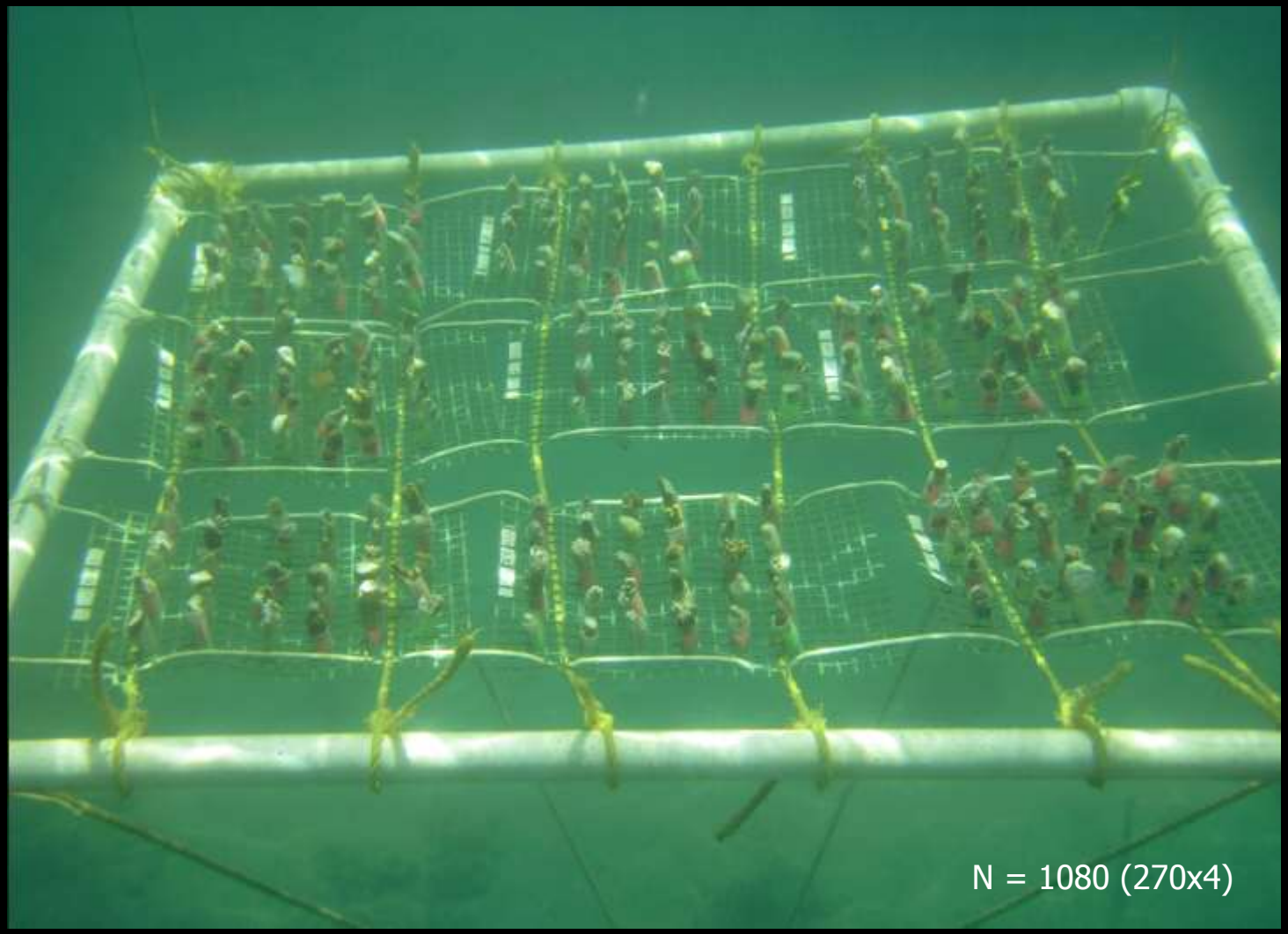
11/04/2009

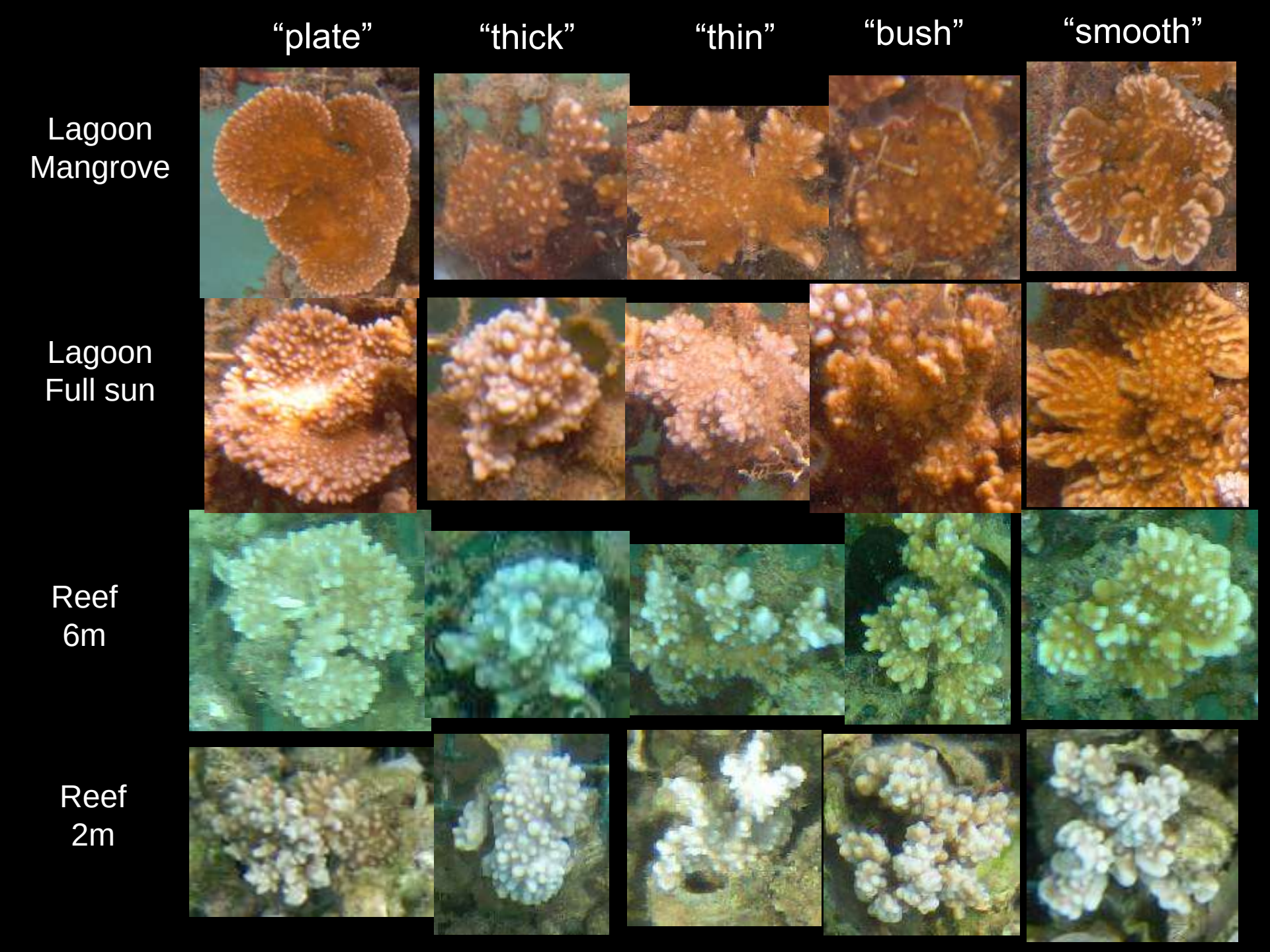
11/17/2009

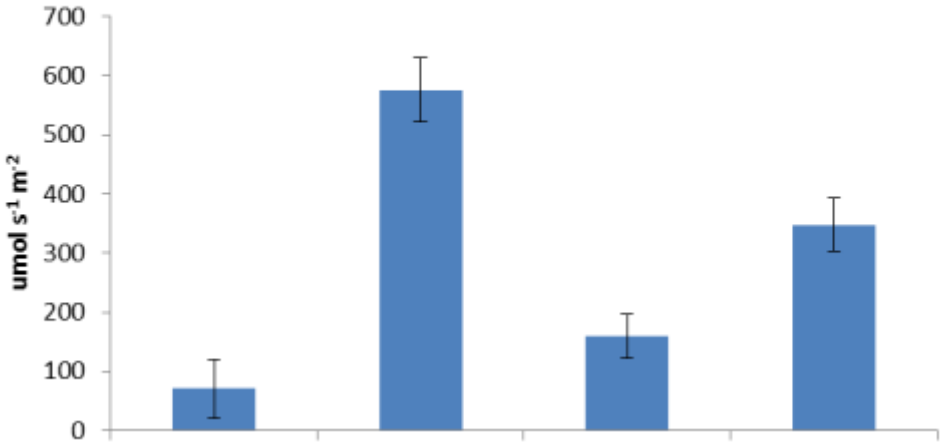
G x E reciprocal transplant experiment

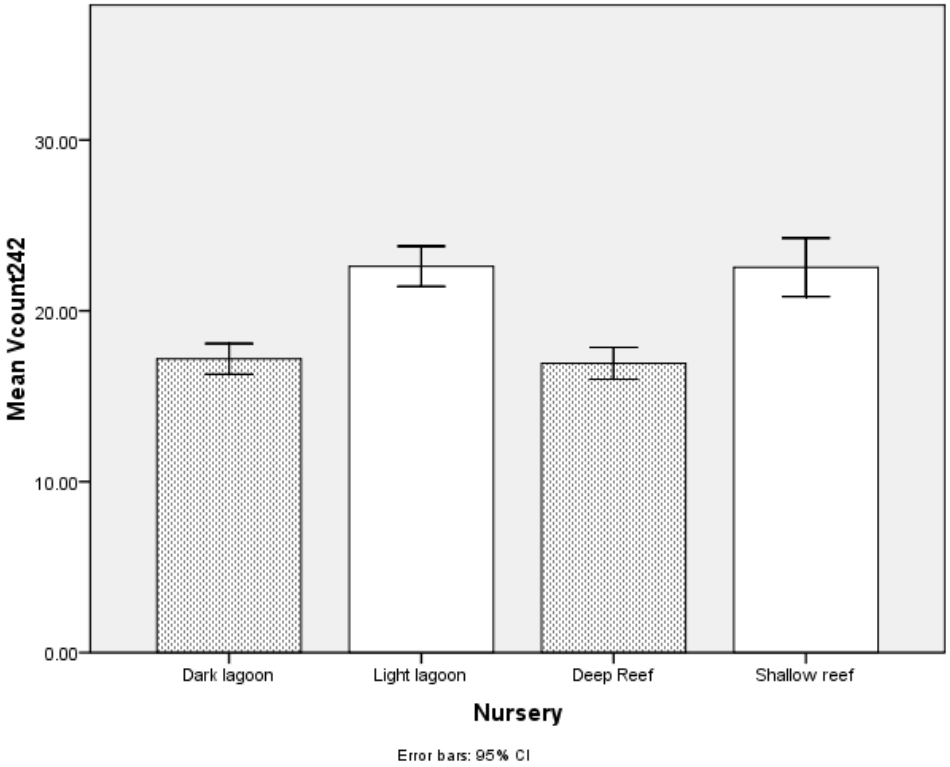
Lagoon | Reef

Shaded mangroves | Full sun | 2m | 6m




“plate”
“thick”
“thin”
“bush”
“smooth”
Lagoon Mangrove
Lagoon Full sun
Reef 6m
Reef 2m


light
700
600
500
400
300
200
100
0
umol s-1 m-2


30.00
20.00
10.00
0.00
Mean Vcount242
Dark lagoon
Light lagoon
Deep Reef
Shallow reef
Nursery
Error bars: 95% CI

M. dilatata dilemma:

If ecomorph then:
M. flabellata transplant experiments

If recent species then:
reproductive studies

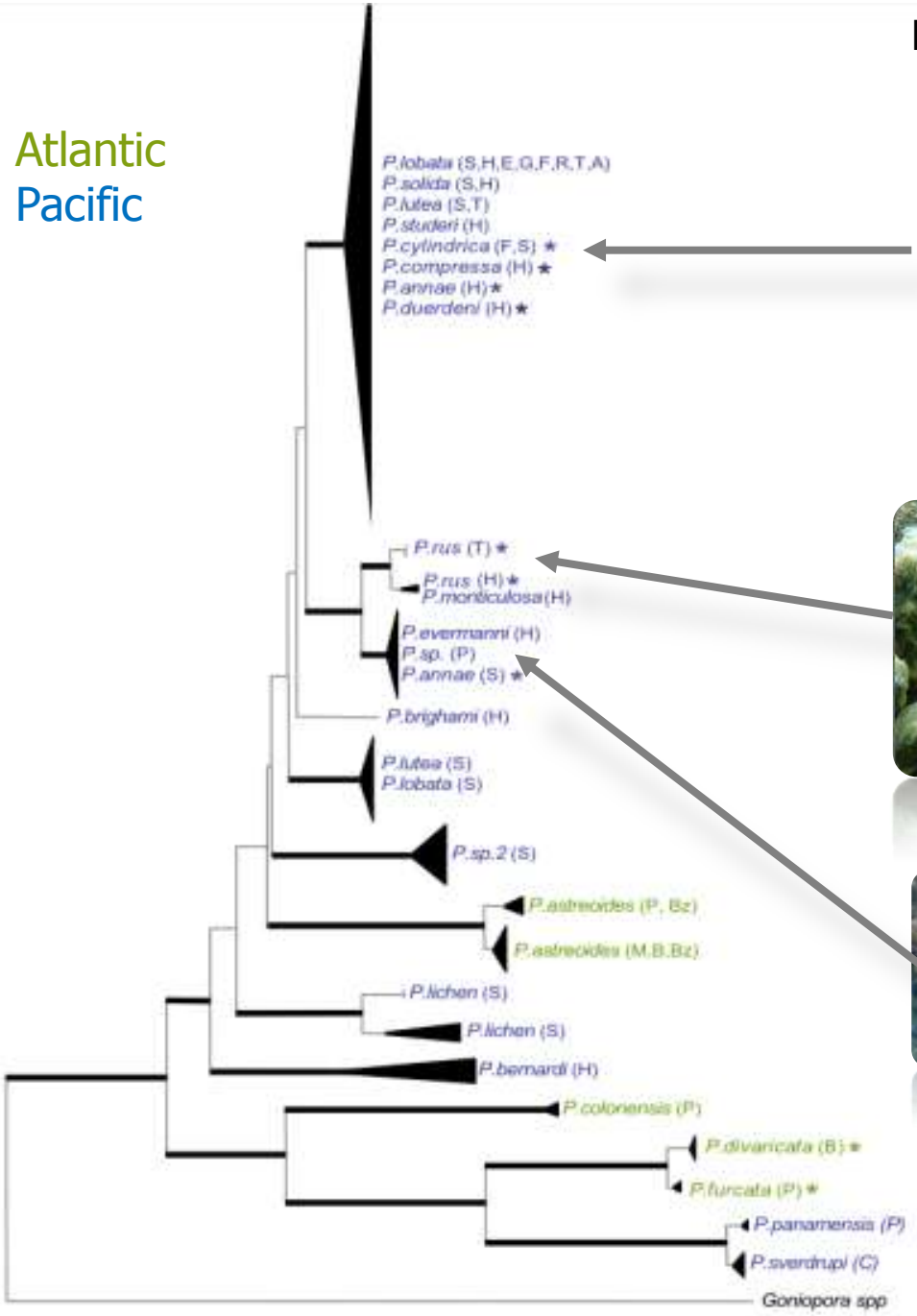
Need range-wide genetic/ morphological surveys

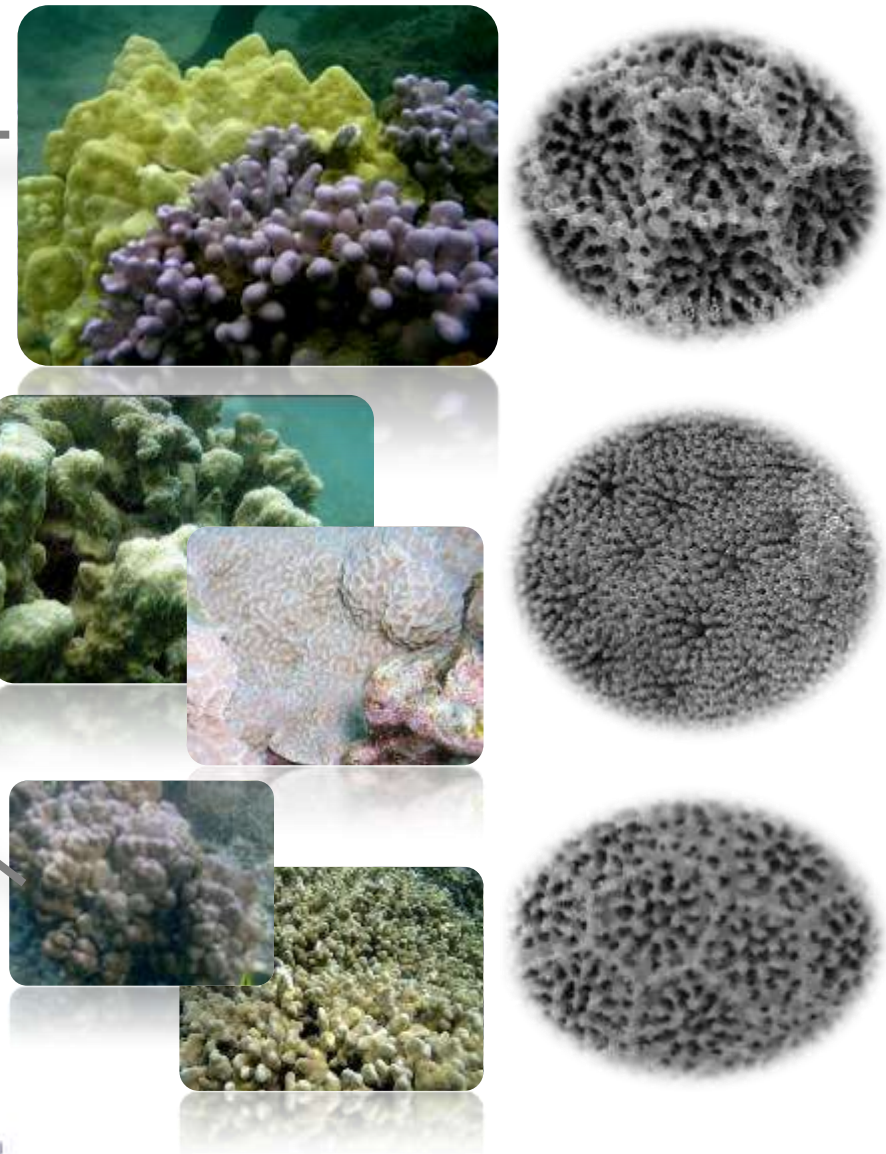
Porites pukoensis

C. Hunter & D. Potts
last to see living colony
~ 1996?

Morphologically different / genetically similar

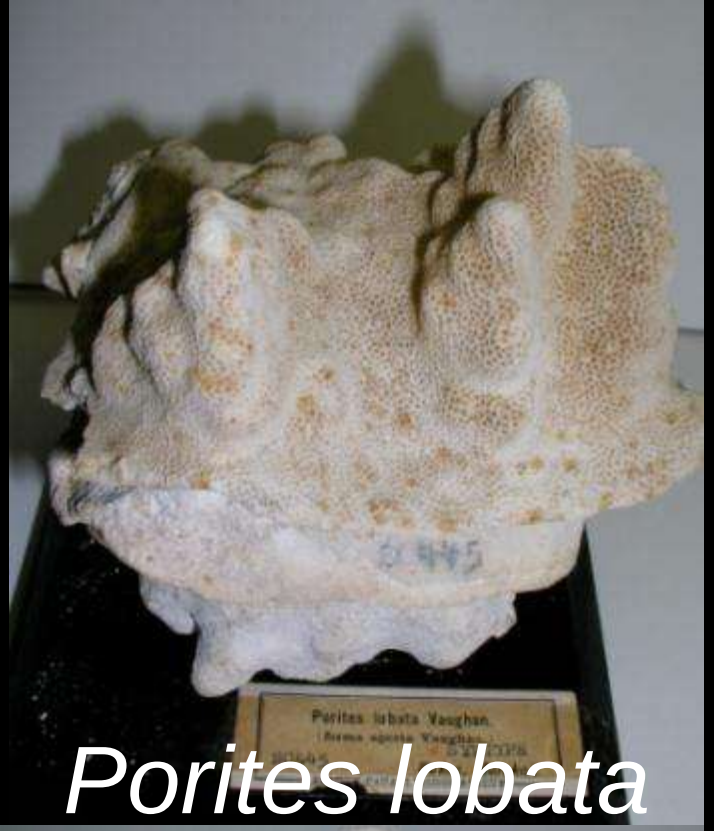
Atlantic
Pacific





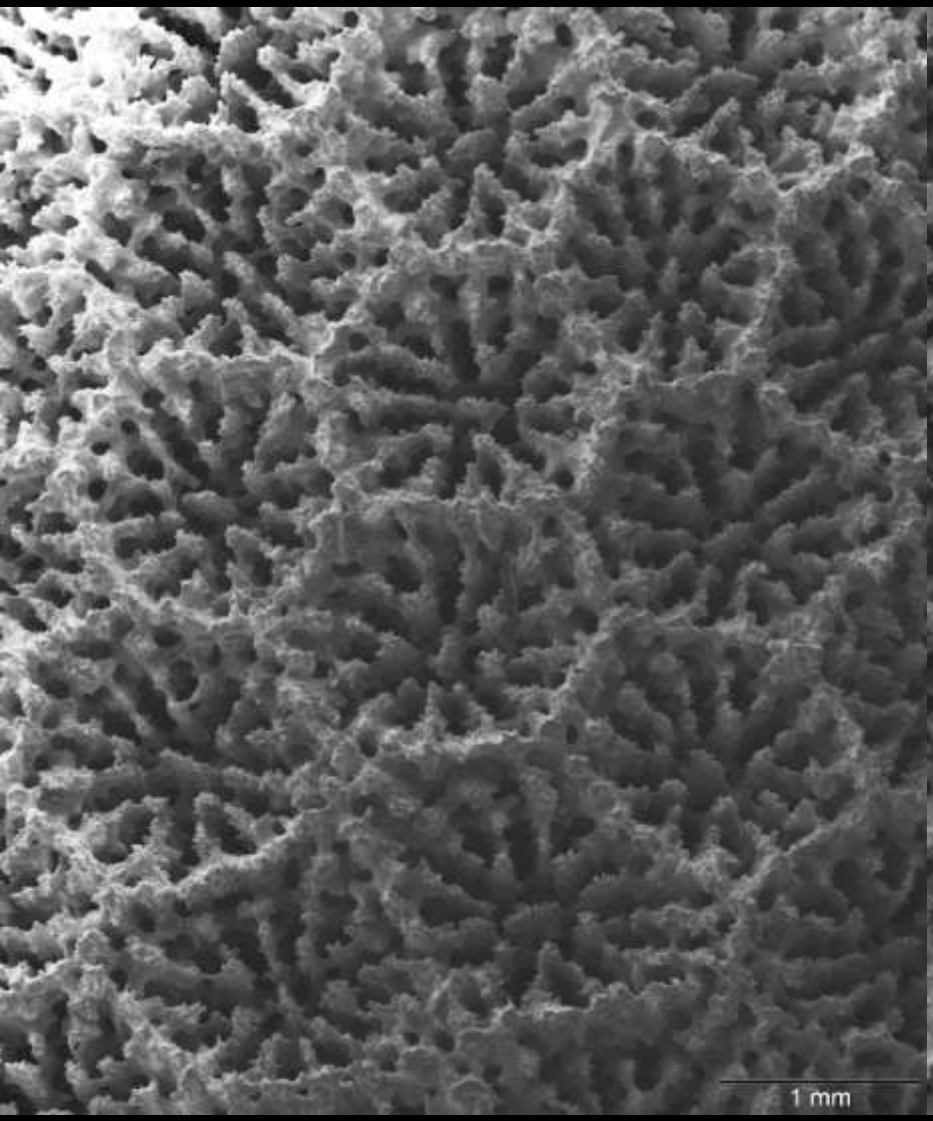
Forsman et al 2009 *BMC Evol Biol*

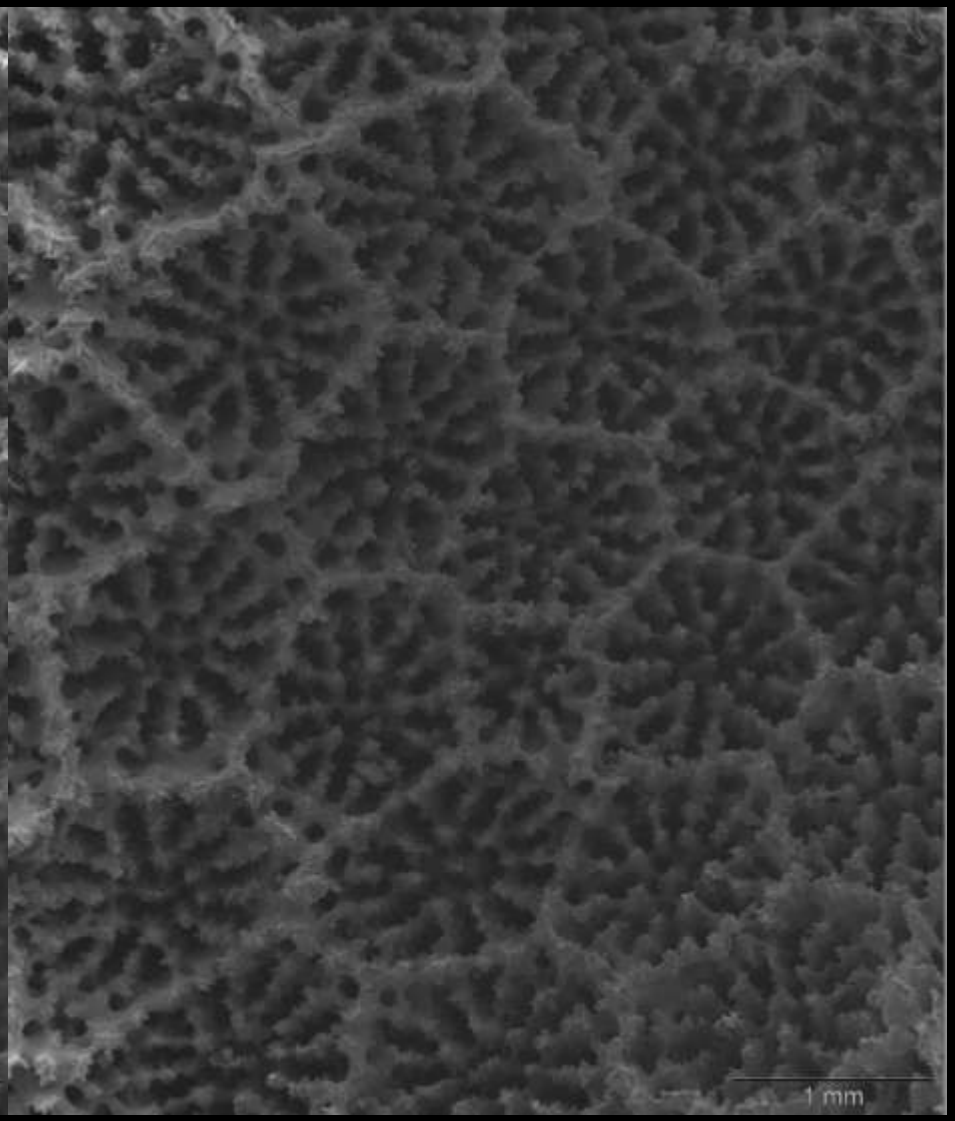
Porites pukoensis



Porites lobata

Porites lobata



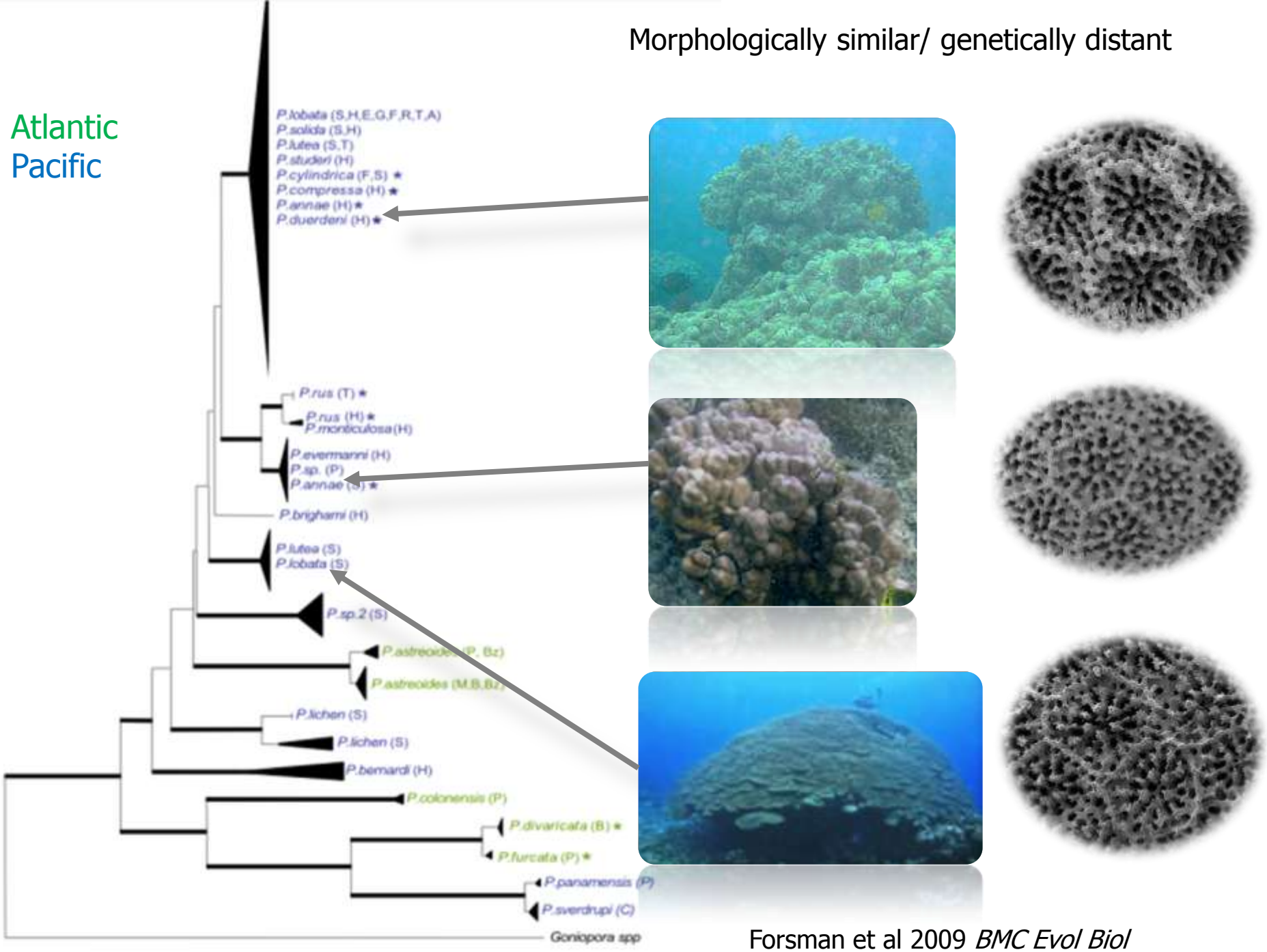


Porites pukoensis

Porites lobata

Morphologically similar/ genetically distant

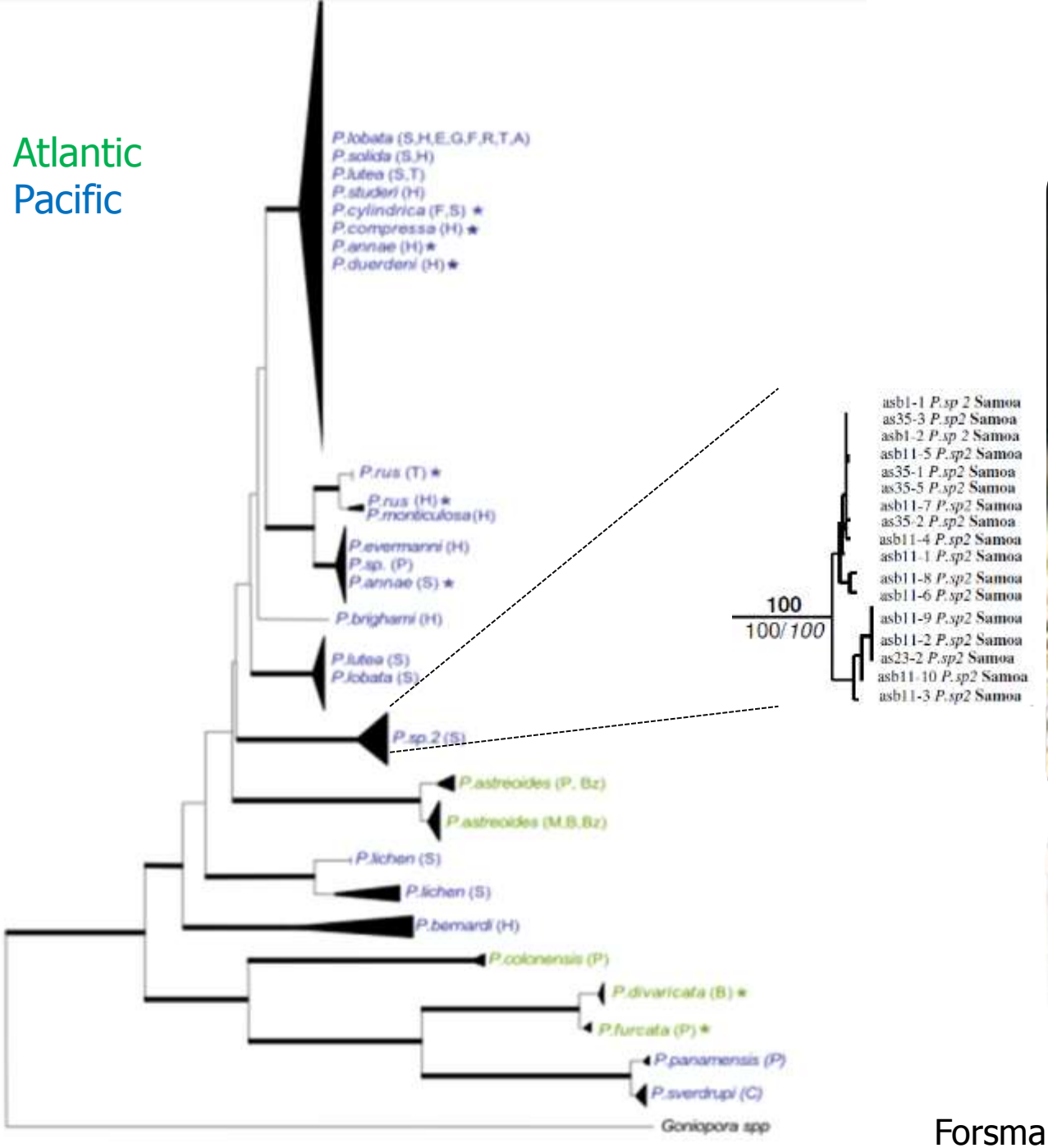
Atlantic
Pacific



Forsman et al 2009 *BMC Evol Biol*

Cryptic taxa

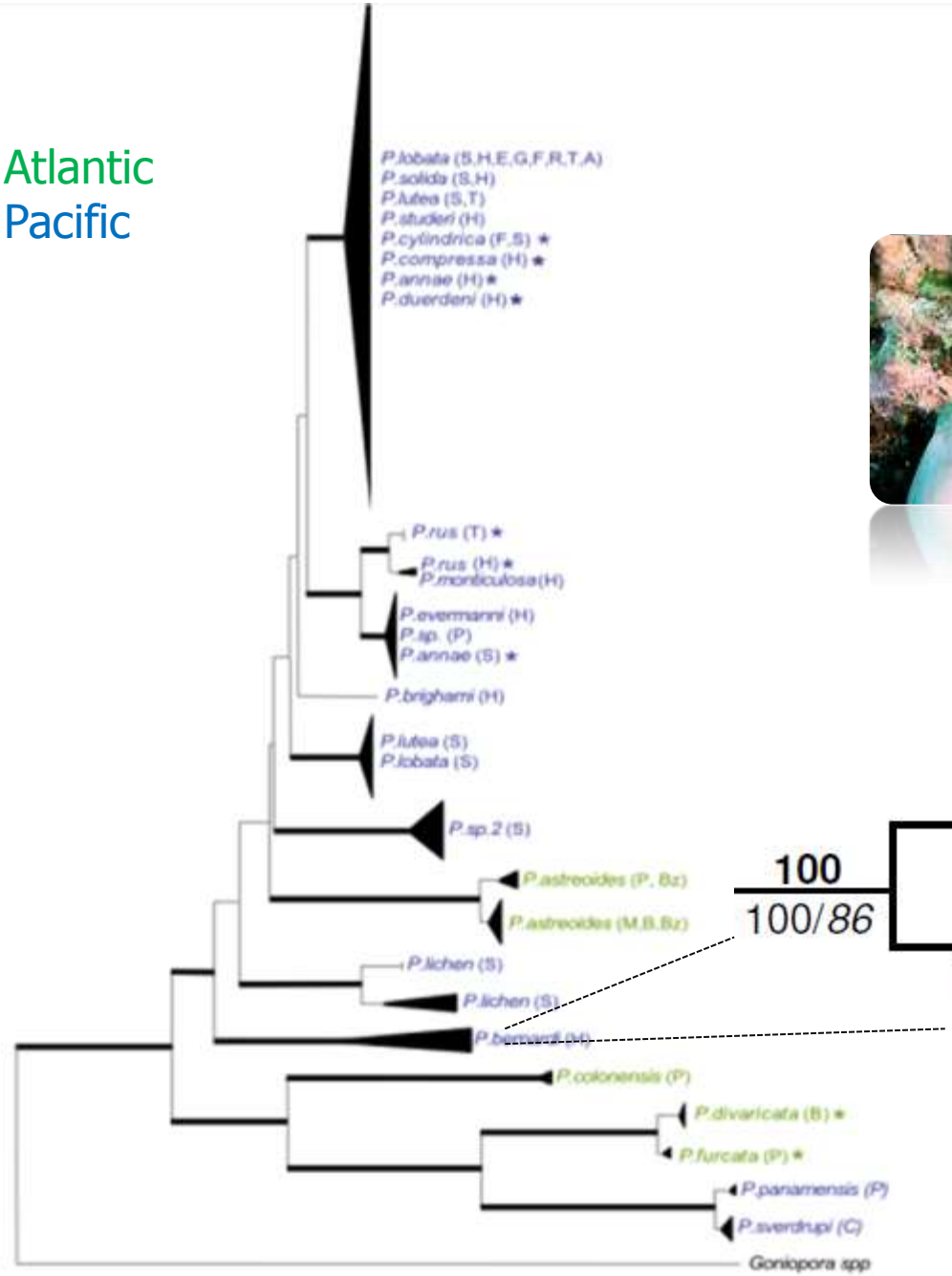
Atlantic
Pacific



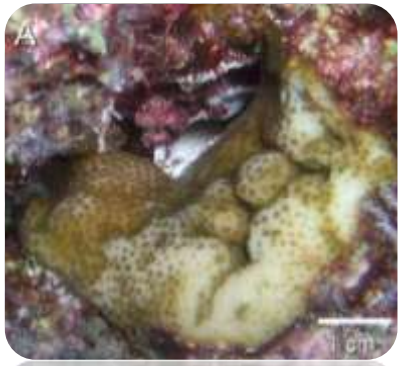
Porites randalli

Forsman & Birkeland 2009 *Zootaxa*

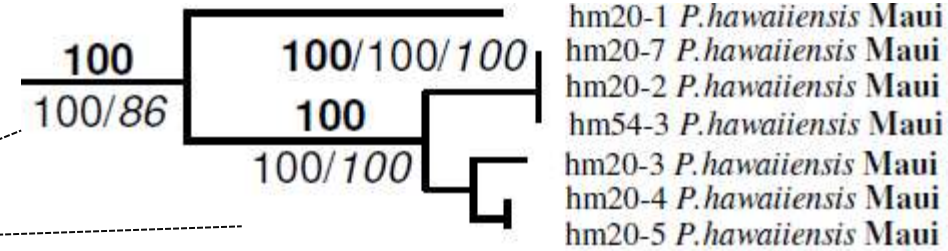
Atlantic
Pacific



Cryptic taxa



Porites hawaiiensis



Forsman et al 2010 *Zootaxa*

Porites dilemma:

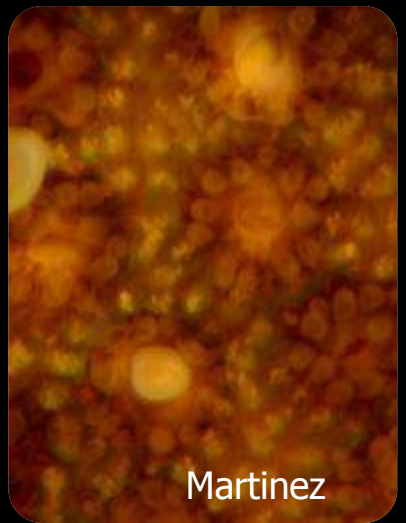
Porites pukoensis

need to find living colony

Porites randalli

Forsman & Birkeland 2009 *Zootaxa*

need to range-wide surveys



Martinez JA, Anson J, Macduff S, **Forsman ZH**, Richmond RH (in prep)

Pocillopora elegans

http://www.marinelifephotography.com

Pocillopora danae

Photograph: Neville Coleman

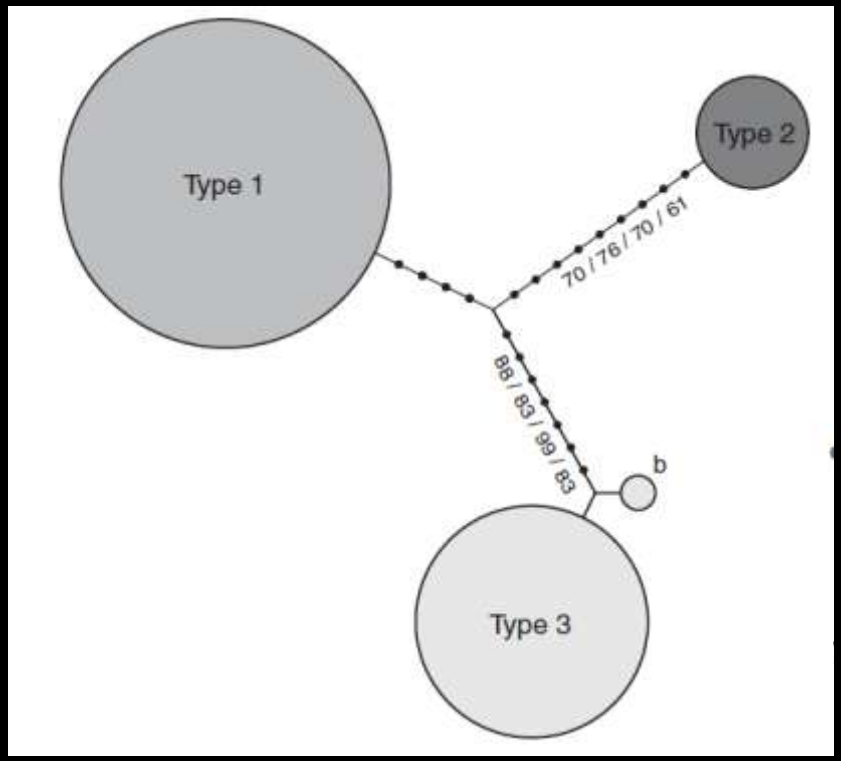
Photograph: Doug Fenner

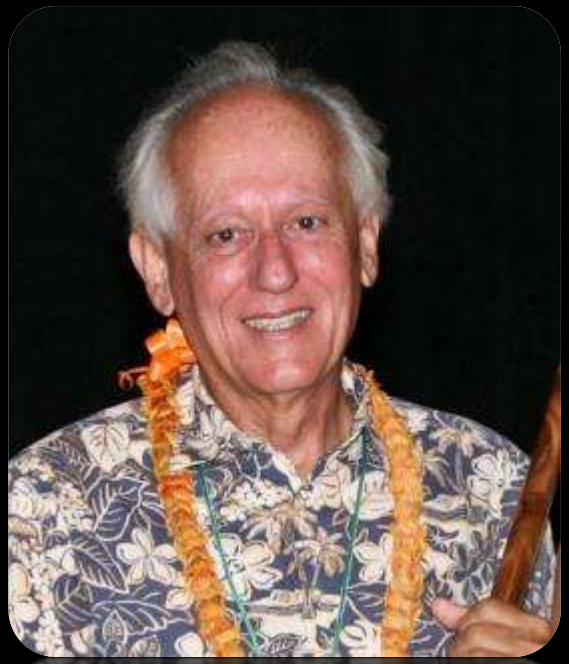
http://sdmas.com/corals

Pocillopora

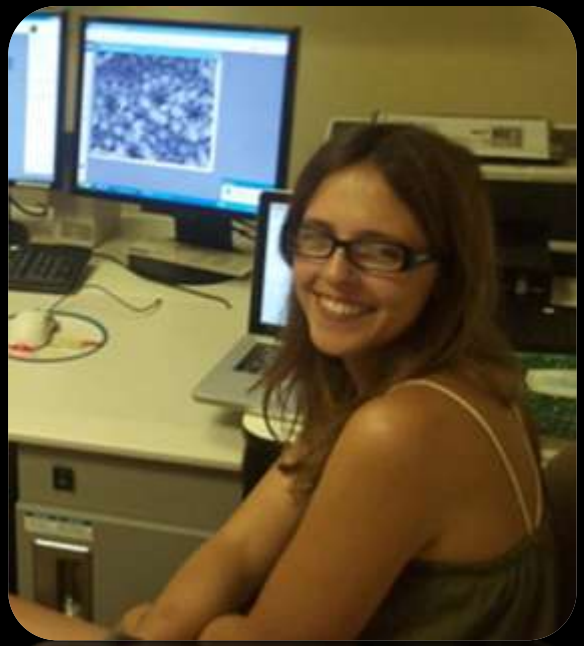
Pinzon & LaJeunesse (2010) Molecular Ecology 20, 311-325 -14 *P. elegans*

mtDNA	3
DDGE ITS2	3
mSAT	3
Zooxanthellae	3



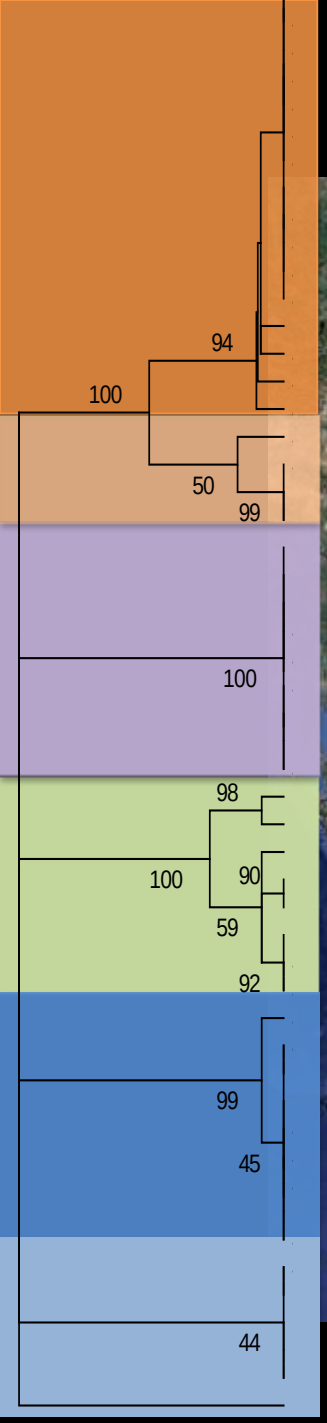


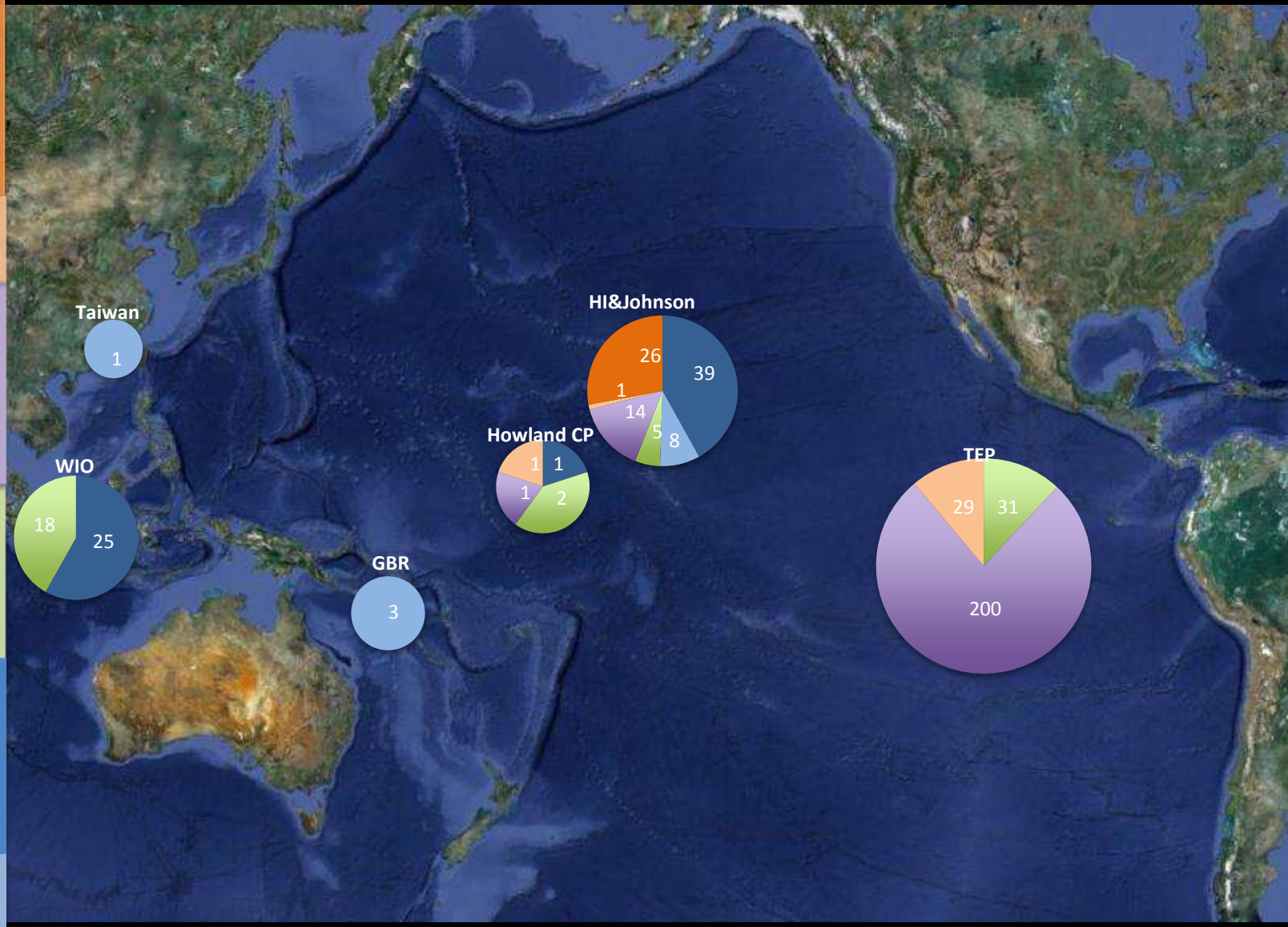
James Maragos USFWS



Patricia Marti-Puig
MS thesis (August 2011)
Ghent University, Belgium

113 seq + GenBank ORF





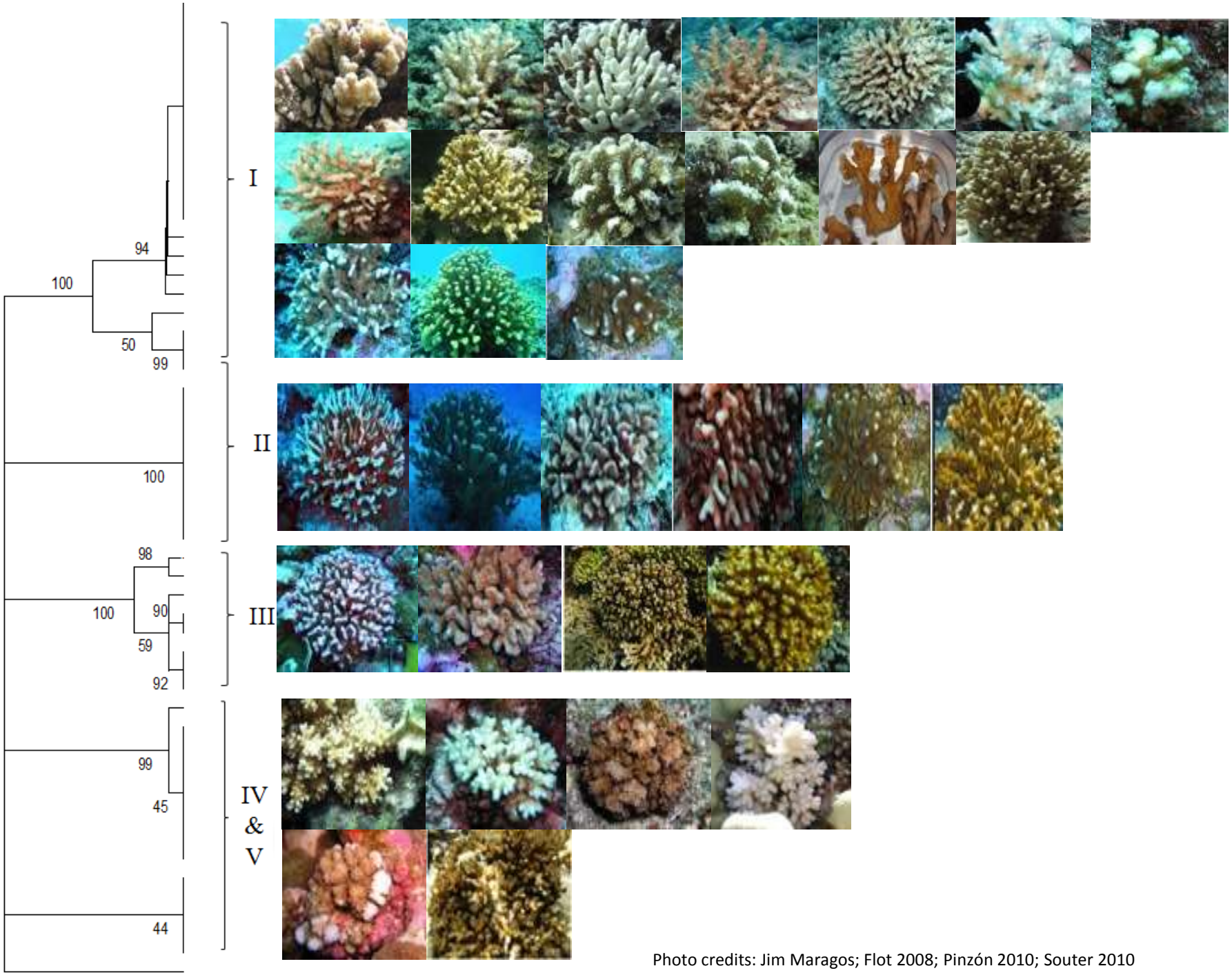
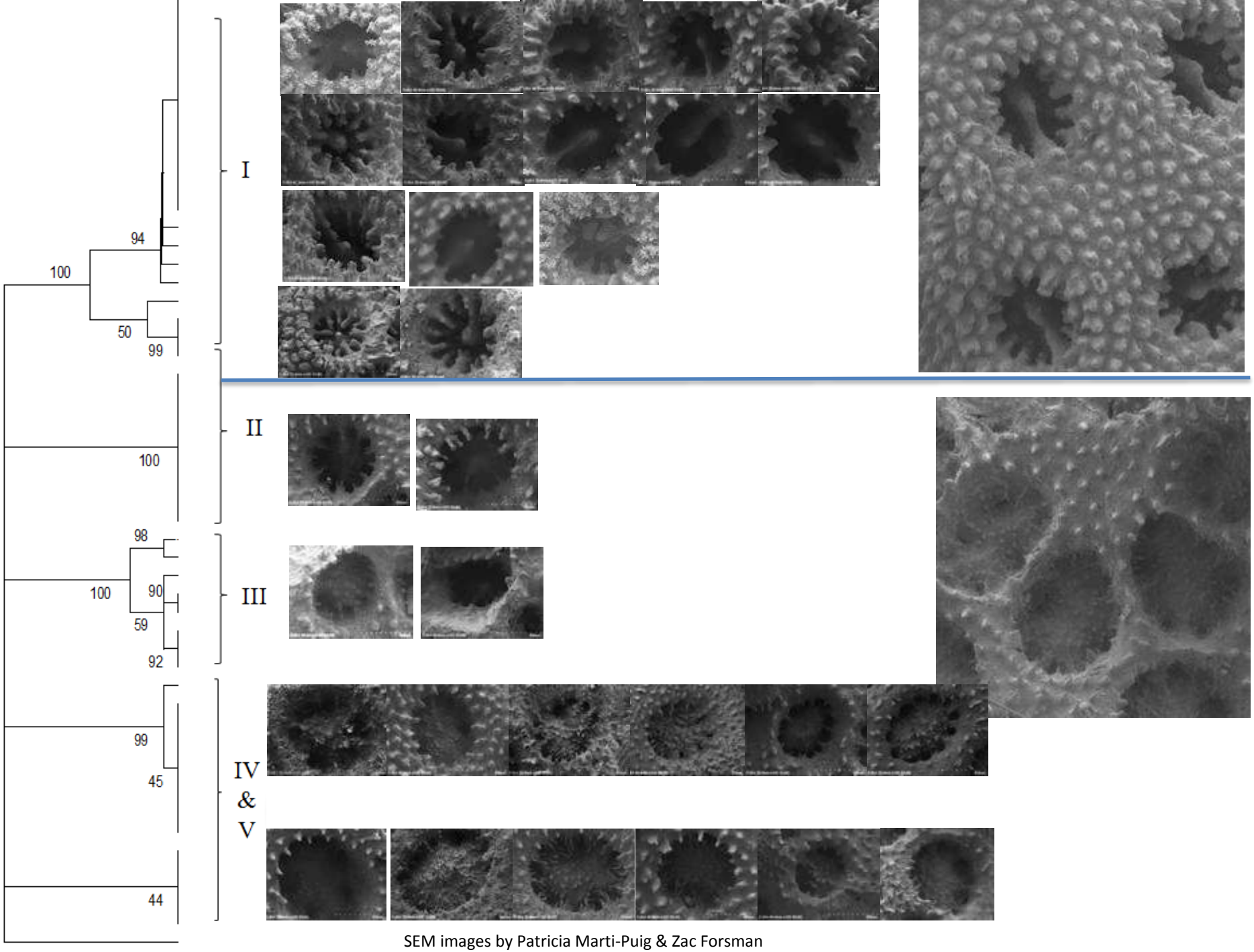
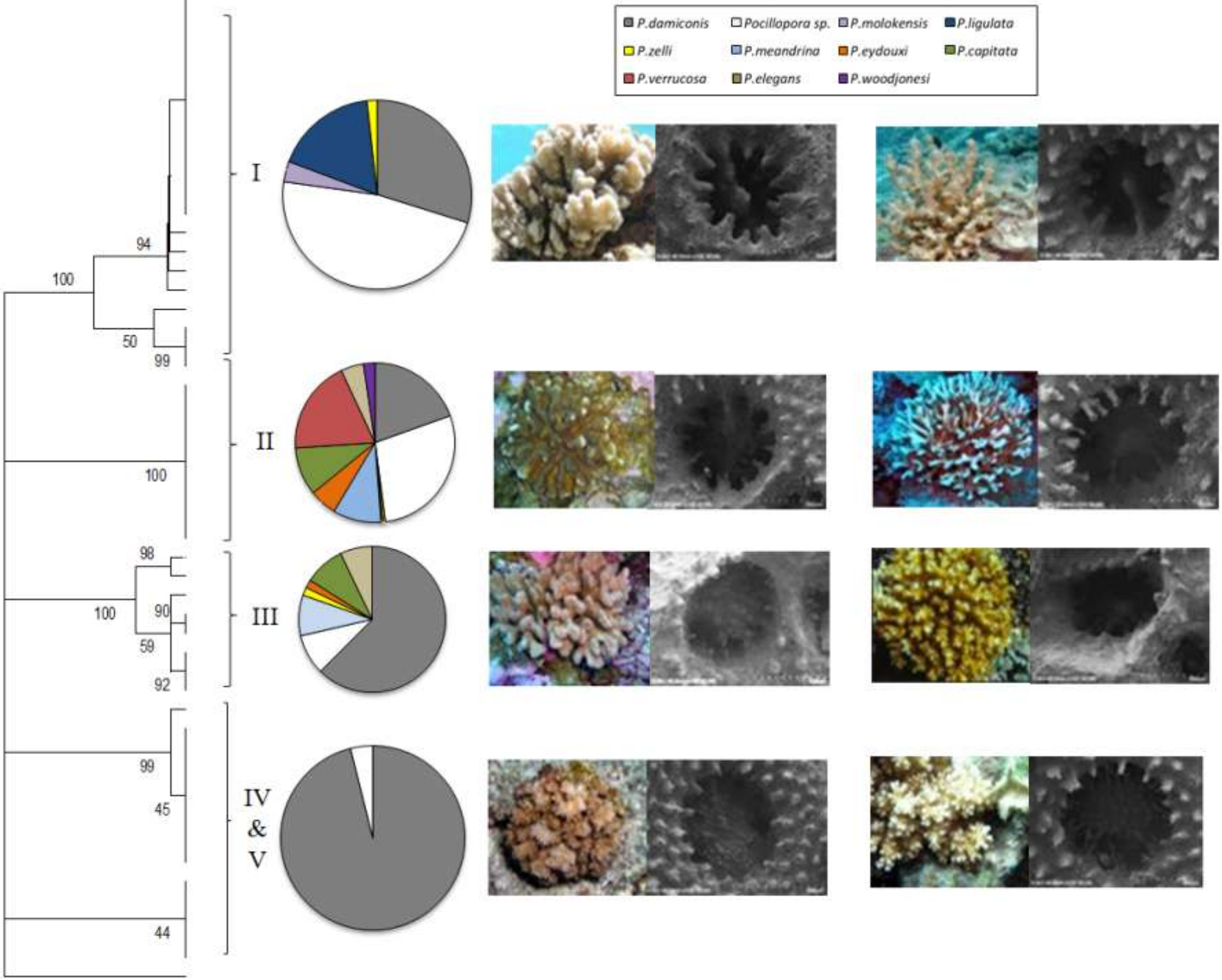


Photo credits: Jim Maragos; Flot 2008; Pinzón 2010; Souter 2010

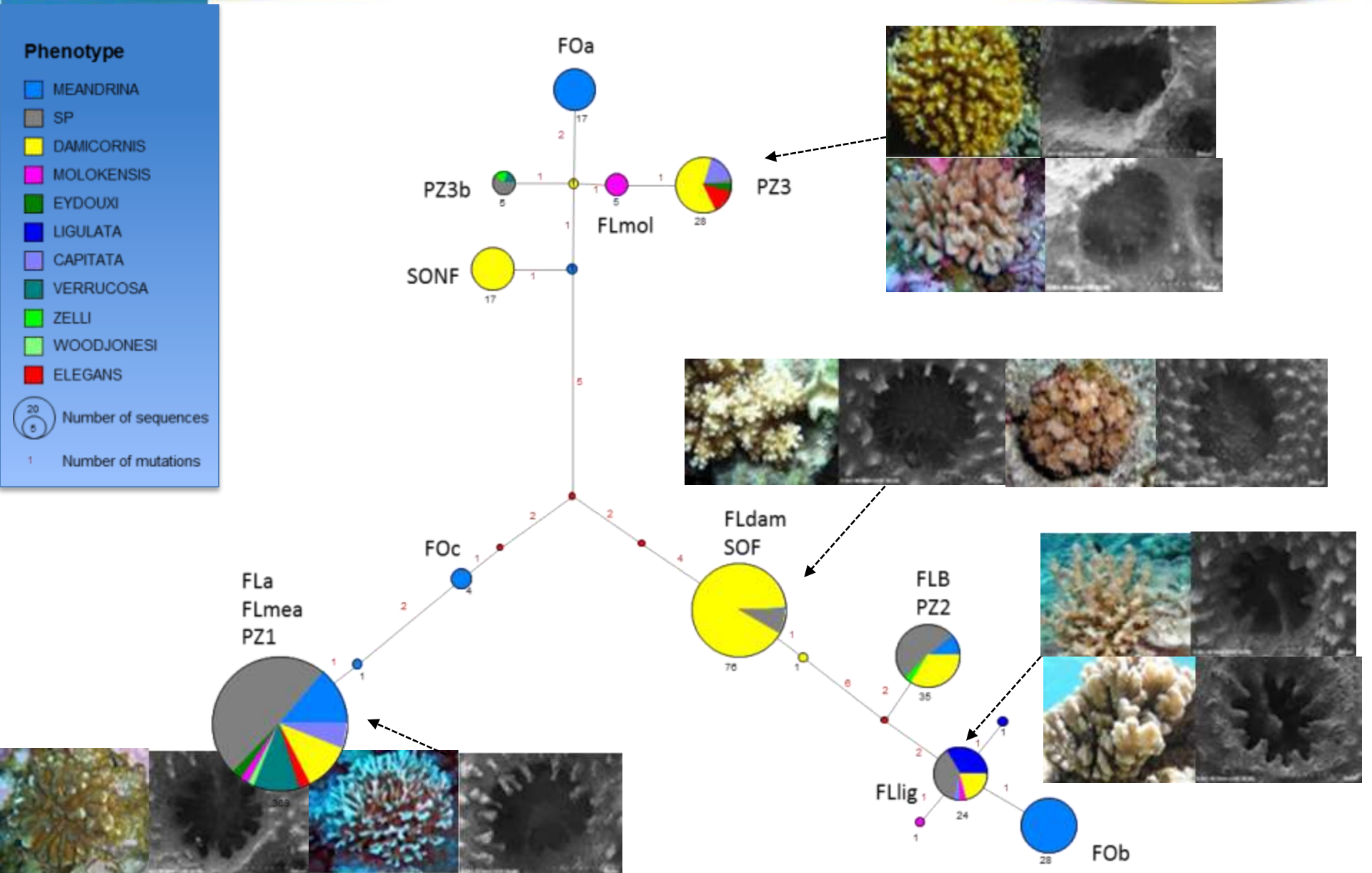


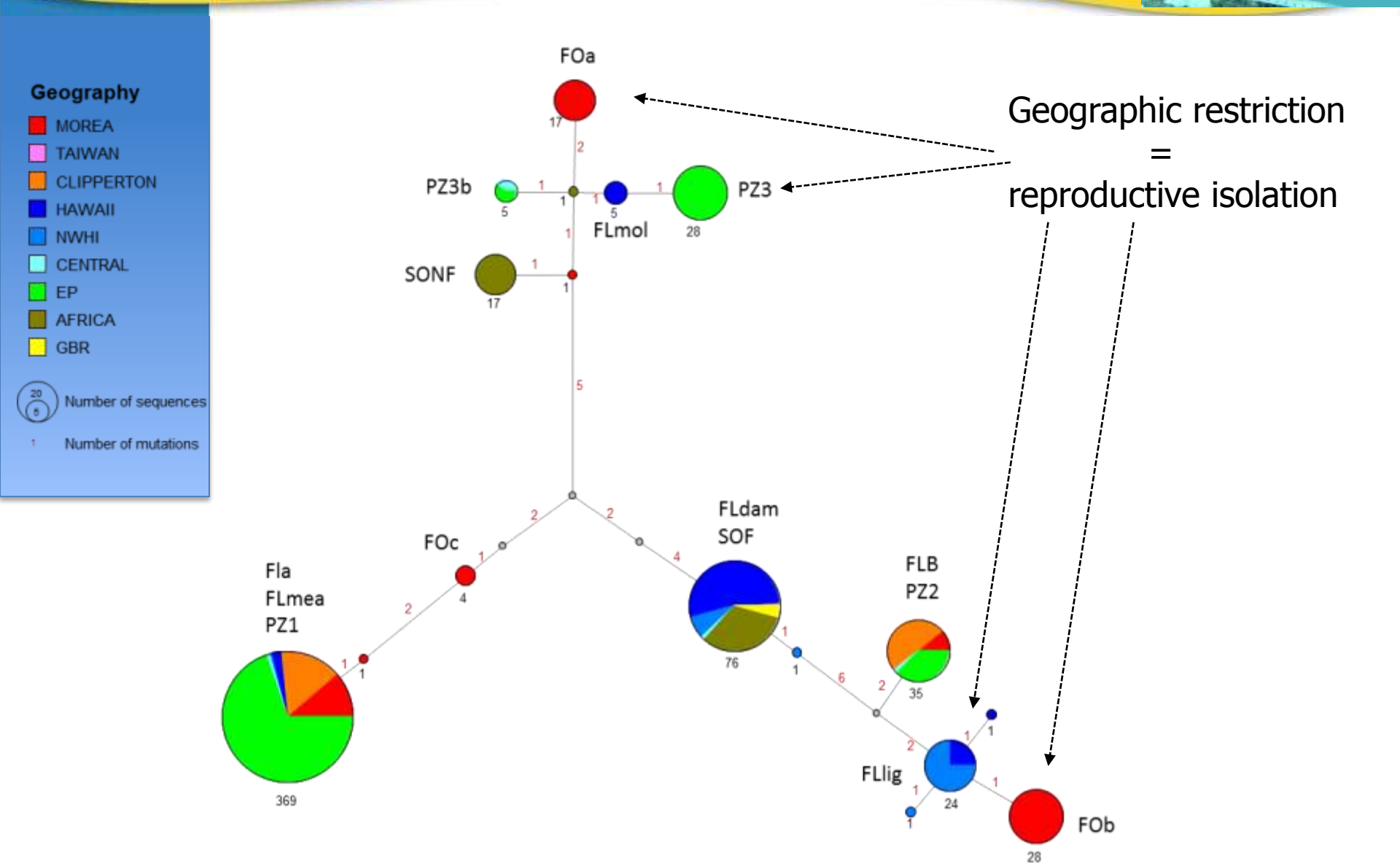
SEM images by Patricia Marti-Puig & Zac Forsman


P.damiconis
Pocillopora sp.
P.malokensis
P.ligulata
P.zelli
P.meandrina
P.eydouxi
P.capitata
P.verrucosa
P.elegans
P.woodjonesi
I
II
III
IV & V
94
100
50
99
100
98
100
90
59
92
99
45
44

Moorea Coral Reef LTER

Member of the NSF Long Term Ecological Research Network





Geographic restriction
=
reproductive isolation

How do we solve *Pocillopora* dilemma?

- Genus needs revision;
  - Voucher images
  - Increased geographic sampling
  - Standardized quantative morphological measurements

Leptoseris

L. yabei

L. incrustans

Pavona

P. venosa

P. cactus

P. bipartia

P. diffuens

P. decussata

Pavona/Leptoseris

Luck et al. (in prep)

- *Leptoseris/Pavona* polyphyletic
- Cryptic diversity in *Leptoseris* by depth

Pochon et al. (in prep)

- Cryptic diversity in Leptoseris and Symbiodinium by depth
- *Leptoseris/Pavona* polyphyletic

Conclusions

- Colony-level morphology more variable than thought

  Why so variable?

  1) phenotypic variation (population level)
  2) incipient speciation (sympatry)

- Surprises:

  What was thought to be rare might not be

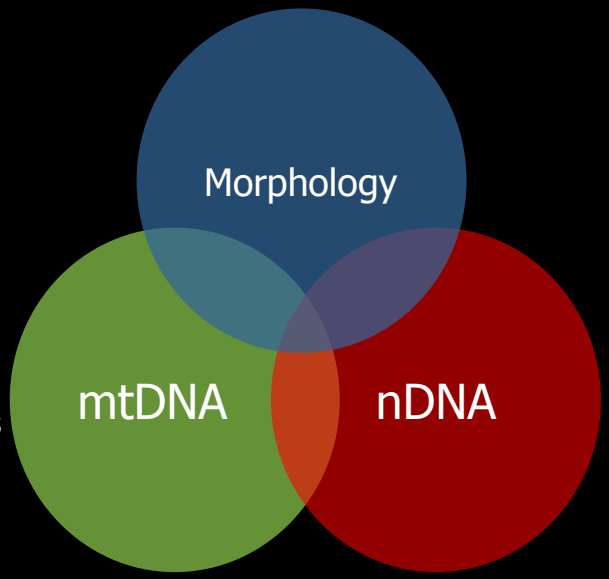
  What seems to be common may hide rare cryptic species

The biodiversity map needs improvement!

Fra Mauro map of the world c.a. 1450

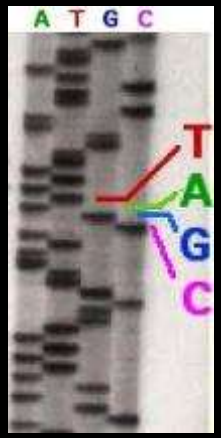
limitations are rapidly disappearing

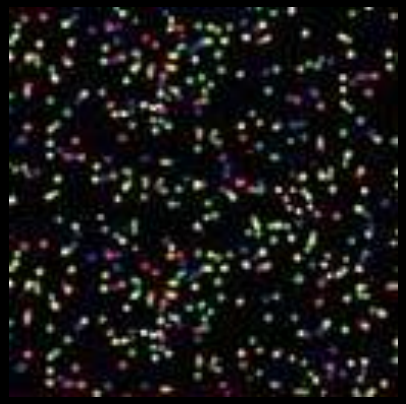
plasticity
polymorphism



Poor resolution
Homoplasy, conserved markers

Paralogy
Gene duplication, loss





Mahalo!

- **HCRI – Hawaii Coral Reef Initiative**
- **NOAA – National Marine Fisheries (NMFS) Species of Concern (SOC)**
- **NOAA – Papahānaumokuākea Marine National Monument (PMNM)**
- **NOAA – National Marine Sanctuaries**
- **National Science Foundation: Experimental Program to Stimulate Competitive Research (NSF EPSCoR)**

- Rob Toonen
- Brian Bowen
- Cindy Hunter
- Sterling Keeley
- Jim Maragos
- Ruth Gates
- Chris Farrar
- Paul Jokiel
- Ku'ulei Rodgers
- Fenny Cox
- Steve Coles
- Bob Richmond
- Doug Fenner
- Michael Stat
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- Dan Barshis
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- Tina (Weatherby) Carvalho

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- Greg Concepcion
- Roxanne Haverkort
- Kim Conklin
- Michelle Gaither
- Joey DeBattista

Mahalo!

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Dan Luck (committee HPU)

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Pauleeno Blagot
Nikita Aidachi
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Noelle Victoria (WCC-paces)
Kekainani Lucero (WCC-paces)
Anuhea Lym (WCC-paces)
Jaslynne Chang (WCC-paces)

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Lauren Ho
Molly Jean Martin
Carrie Pederson
Megan Deagle

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Yasuhiro Fujiwara (UH animal science)
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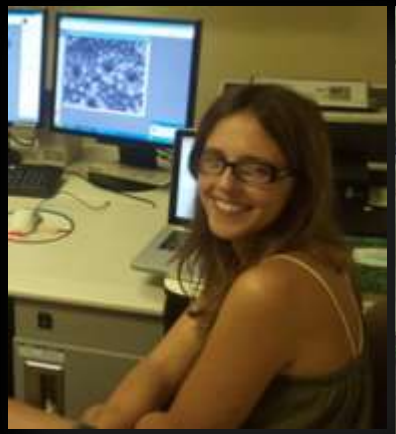
Pakki Reath (funded technician)
Kelsey Fees (UH workstudy)
Yuka Irei (visiting scholar)
Nadiera Sukhraj (funded R.A.)
Olga Olberu (funded R.A.)



QUESTIONS?

zac@hawaii.edu

Pocillopora other studies

Flot et al. (2008) Comptes rendus biologies 331(3) 239-47 (Hawaiii)

mtDNA	5	(similar to morph)
ITS	2	
calmodulin	1	
EF1-a	0	
ATPsB	0	

Incomplete lineage sorting

Combosch et al (2008) Molecular Ecology 17, 1304-1312
EP

ITS	2	+ intermediate

hybridization

Variable colony morphology

Souter (2010) Mar. Biol. 157:875-885
IP cryptic species