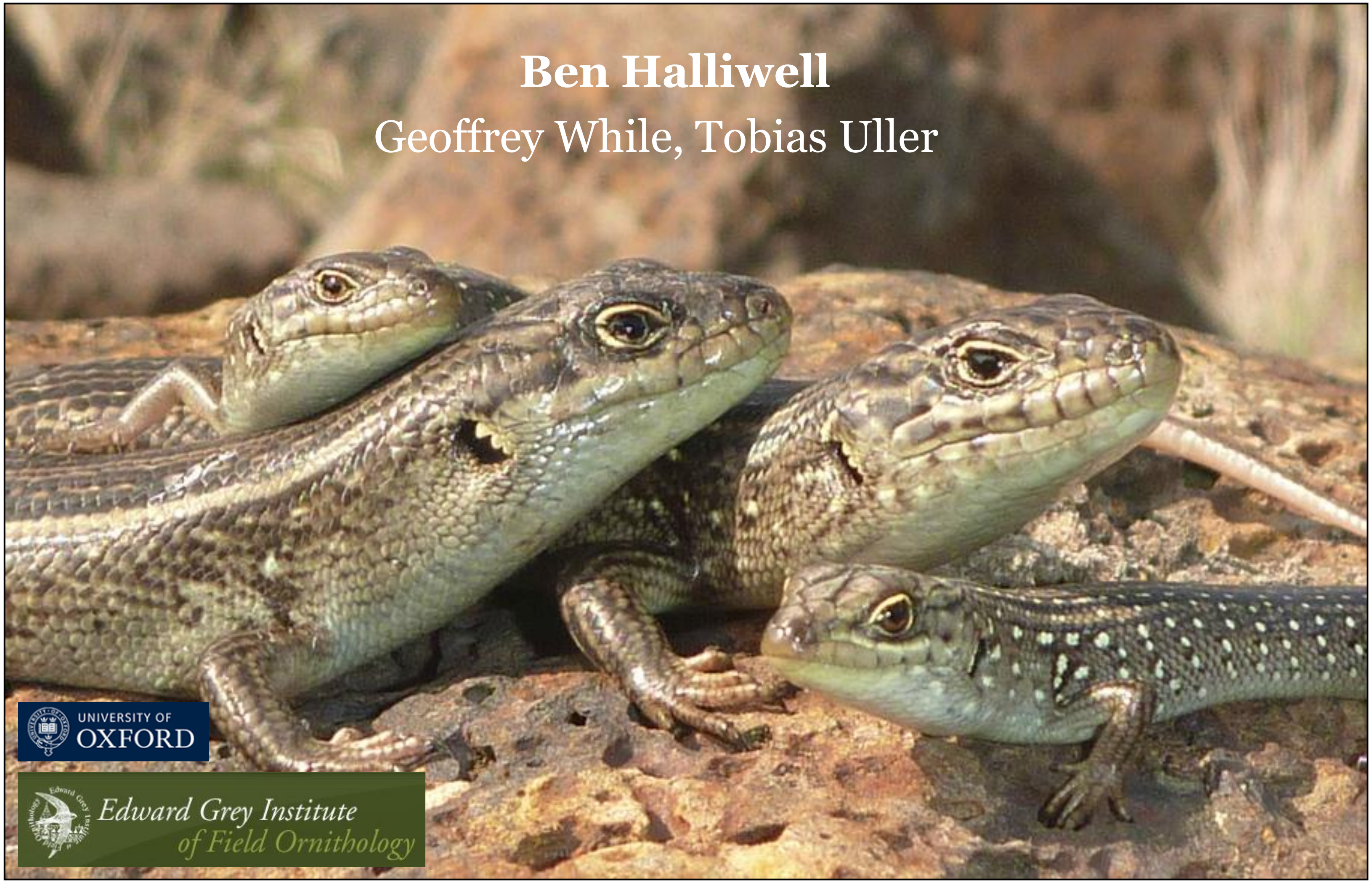
Who Cares? The Evolution of Parental Care in Squamate Reptiles



Ben Halliwell

Geoffrey While, Tobias Uller

UNIVERSITY OF OXFORD

Edward Grey Institute of Field Ornithology

Parental Care

– any instance of parental investment that increases the fitness of offspring

Parental Care

- Majority of research on mammals and birds
- Care is ubiquitous in mammals and birds
- Constrains our ability to:
  - ask questions about the origins of care
  - Understand the role of parental care in the evolution of social complexity.
- Need alternative systems

Parental Care in Reptiles

– Most sophisticated care behaviour found in Crocodilians

– All species provide parental care

– Provisioning of offspring and care after nutritional dependence

Parental Care in Squamates
Lizards and Snakes

- Establishing and maintaining nests, burrows and territories
- Care of fertilised eggs
- Provisioning of offspring before hatching or birth
- Care after hatching or birth
- Care after nutritional dependence

Parental Care in Squamates
Lizards and Snakes

- Establishing and maintaining nests, burrows and territories ✓
- Care of fertilised eggs ✓
- Provisioning of offspring before hatching or birth ✓
- Care after hatching or birth ✓
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Parental Care in Squamates

Lizards and Snakes

- Establishing and maintaining nests, burrows and territories ✓
- Care of fertilised eggs ✓
- Provisioning of offspring before hatching or birth ✓
- Care after hatching or birth ✓
- Care after nutritional dependence

Aims

1. Elucidate the evolutionary pathways (i.e. most common transitions) that have led to current diversity in reptilian care

2. Identify the divergence in key ecological, life-history or phylogenetic characteristics responsible for transitions between modes of care
   – In particular, parent offspring association

3. Understand the evolutionary constraints prohibiting the emergence of more sophisticated modes of care in non-crocodilian reptiles

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Methods

Searched the literature for all reports of parental care behaviour across all squamate reptile species, recording:

1) All forms of parental care

2) Parity mode (oviparity vs. viviparity)

Mapped the data onto a recently published squamate reptile phylogeny (Pyron et al. 2013)

A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes

BMC Evolutionary Biology 2013, **13**:93 doi:10.1186/1471-2148-13-93

Robert Alexander Pyron (rpyron@colubroid.org)
Frank T Burbrink (frank.burbrink@csi.cuny.edu)
John J Wiens (wiensj@email.arizona.edu)

Parental Care in Squamates

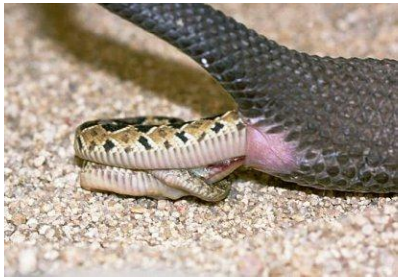
Pre-Hatching/Birth Care

– Nest Construction

- Egg Attendance/Brooding

- Egg/Nest Guarding

- Viviparity



Parental Care in Squamates

Post-Hatching/Birth Care

- Parent Offspring association (POA)

Distribution of Care in the Squamates

Pre Hatch/Birth Care	**1134**
– Viviparity	842 (21%)
– Nesting behaviour	229 (5.8%)
– Brooding/Egg attendance	124 (3%)
– Egg defense	100 (2.5%)
Post Hatch/Birth Care	**79**
– Parent Offspring Association	79 (2%)
No Care Reported/Data Available	**2781**

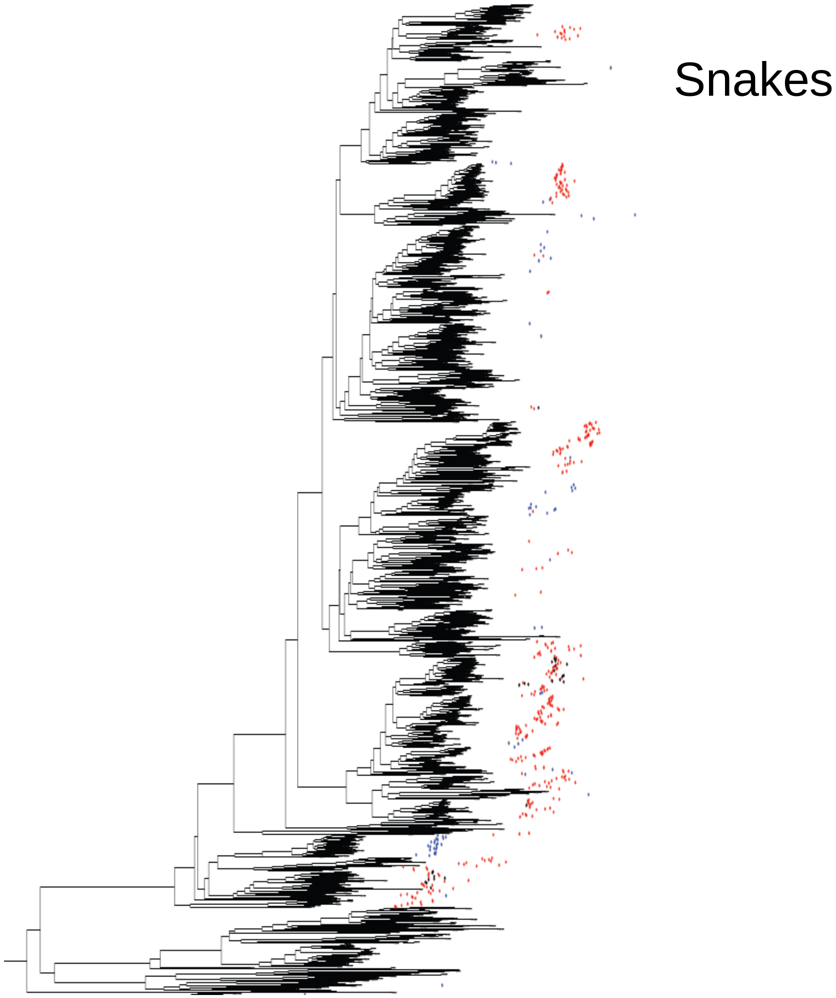
Distribution of Care in the Squamates

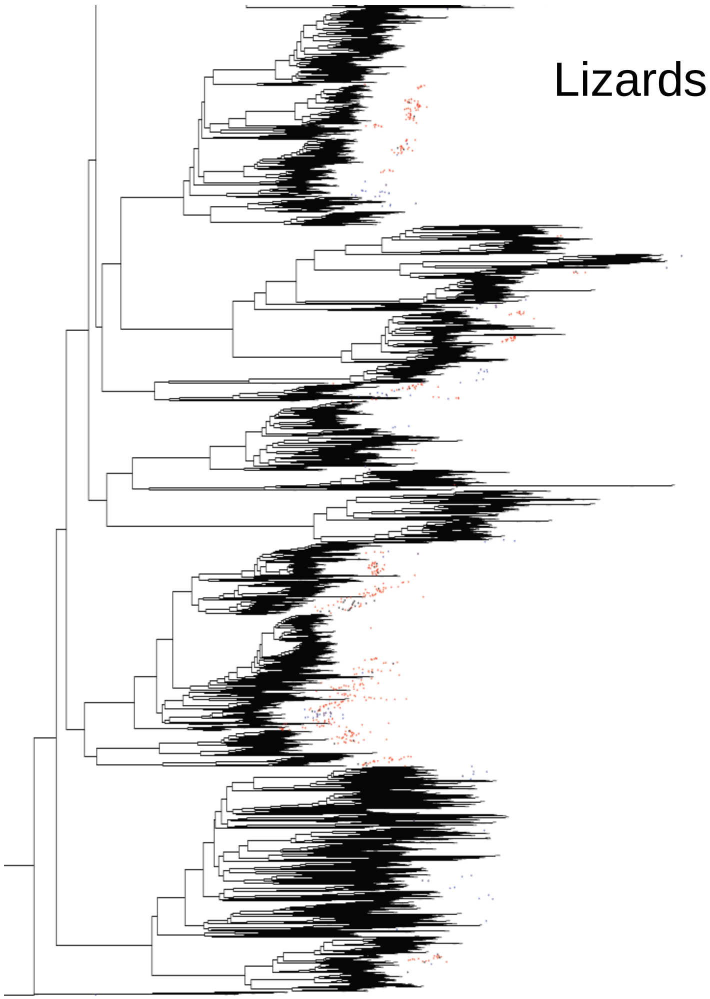
Overall, 28% of squamate species exhibit some form of care
- 43% at the family level

30% of fish families

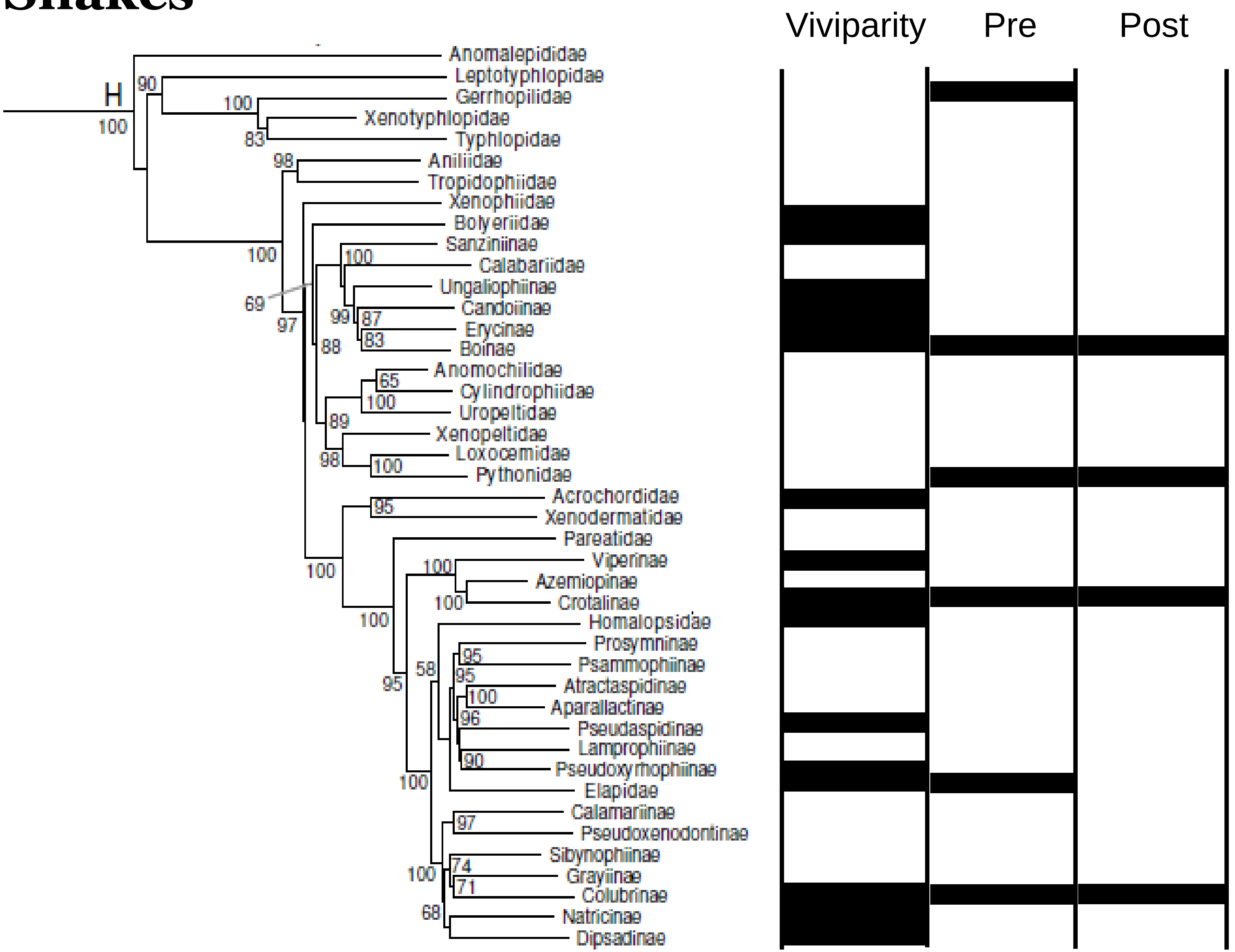
6-15% of anuran species
20% of salamander species

Squamate Tree





Snakes

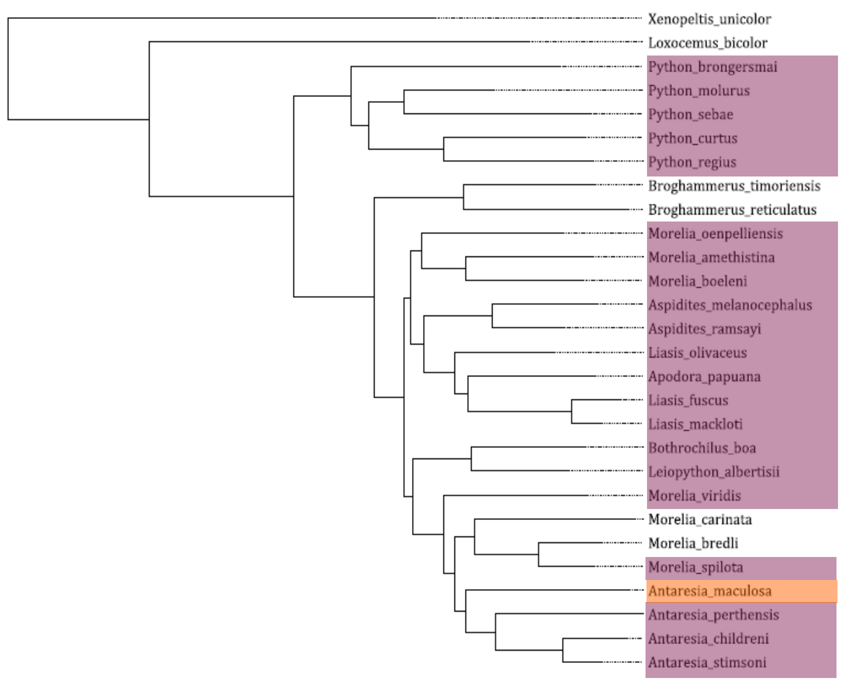


Viviparity
Pre
Post
H
Anomalepididae
Leptotyphlopidae
Gerrhopilidae
Xenotyphlopidae
Typhlopidae
Aniliidae
Tropidophiidae
Xenophiidae
Bolyeriidae
Sanziniinae
Calabariidae
Ungaliophiinae
Candoiinae
Erycinae
Boinae
Anomochilidae
Cylindrophiidae
Uropeltidae
Xenopeltidae
Loxocemidae
Pythonidae
Acrochordidae
Xenodermatidae
Pareatidae
Viperinae
Azemiopinae
Crotalinae
Homalopsidae
Prosymninae
Psammophiinae
Atractaspidinae
Aparallactinae
Pseudaspidinae
Lamprophiinae
Pseudoxyrhophiinae
Elapidae
Calamariinae
Pseudoxenodontinae
Sibynophiinae
Grayiinae
Colubrinae
Natricinae
Dipsadinae

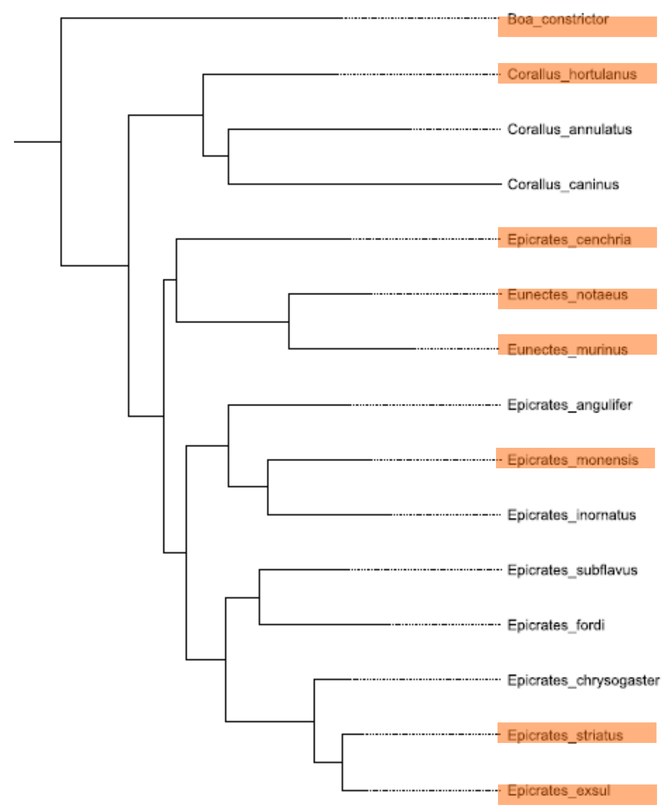
Distribution of Care

Pre   Post

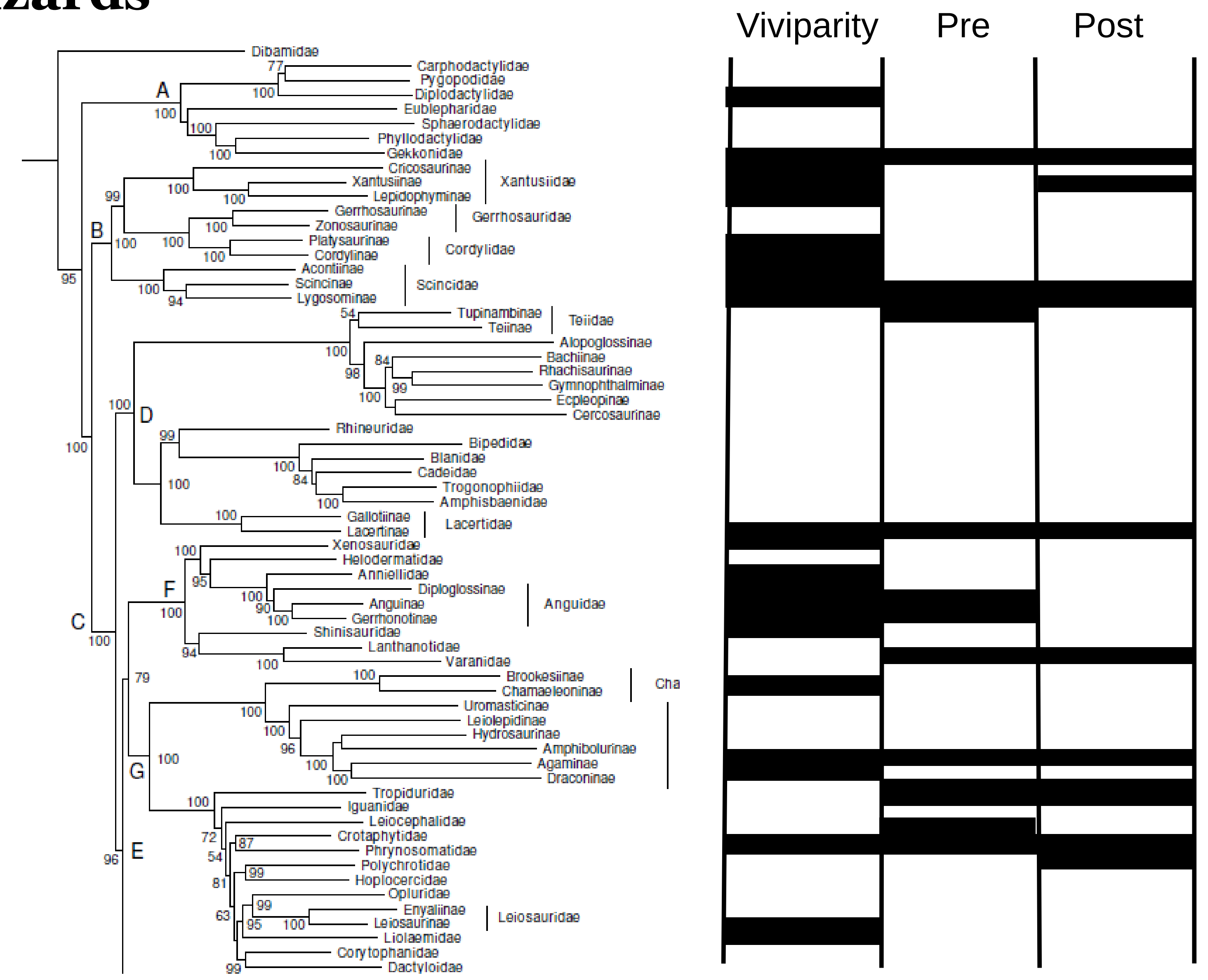
Pythons
(oviparous)



Boas
(viviparous)



Lizards



Viviparity
Pre
Post
Dibamidae
Carphodactylidae
Pygopodidae
Diplodactylidae
Eublepharidae
Sphaerodactylidae
Phyllodactylidae
Gekkonidae
Cricosaurinae
Xantusiinae
Lepidophyminae
Xantusiidae
Gerrhosaurinae
Zonosaurinae
Gerrhosauridae
Platysaurinae
Cordylinae
Cordylidae
Acontiinae
Scincinae
Lygosominae
Scincidae
Tupinambinae
Teiinae
Teiidae
Alopoglossinae
Bachiinae
Rhachisaurinae
Gymnophthalminae
Ecpleopinae
Cercosaurinae
Rhineuridae
Bipedidae
Blanidae
Cadeidae
Trogonophiidae
Amphisbaenidae
Gallotiinae
Lacertinae
Lacertidae
Xenosauridae
Helodermatidae
Anniellidae
Diploglossinae
Anguinae
Gerrhonotinae
Anguidae
Shinisauridae
Lanthanotidae
Varanidae
Brookesiinae
Chamaeleoninae
Cha
Uromasticinae
Leiolepidinae
Hydrosaurinae
Amphibolurinae
Agaminae
Draconinae
Tropiduridae
Iguanidae
Leiocephalidae
Crotaphytidae
Phrynosomatidae
Polychrotidae
Hoplocercidae
Opluridae
Enyaliinae
Leiosaurinae
Leiosauridae
Liolaemidae
Corytophanidae
Dactyloidae
A
B
C
D
E
F
G

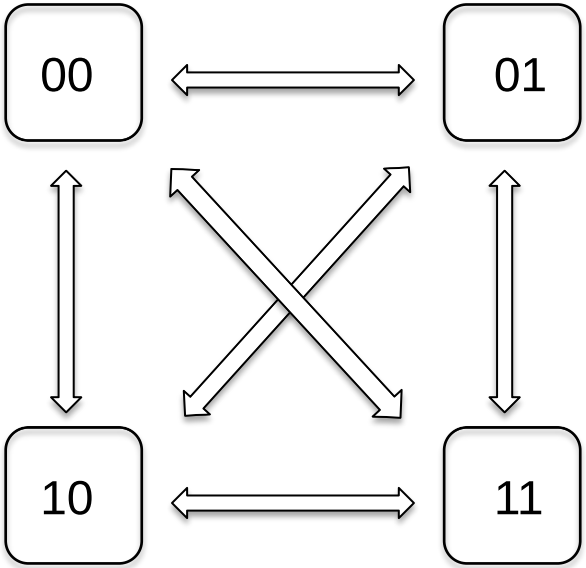
Better do some analyses

– Chi-square shows significance $P < 2.2e-16$

Better do some analyses

- Chi-square shows significance P < 2.2e-16
- Need analytical technique that can separate transitions between states from speciation/radiation once a state has evolved
- MuSSE models
  - Extention of BiSSE

0-	oviparous
1-	viviparous
-0	No POA
-1	POA



Better do some analyses

- Chi-square shows significance   P < 2.2e-16
- Need analytical technique that can separate transitions between states from speciation/radiation once a state has evolved
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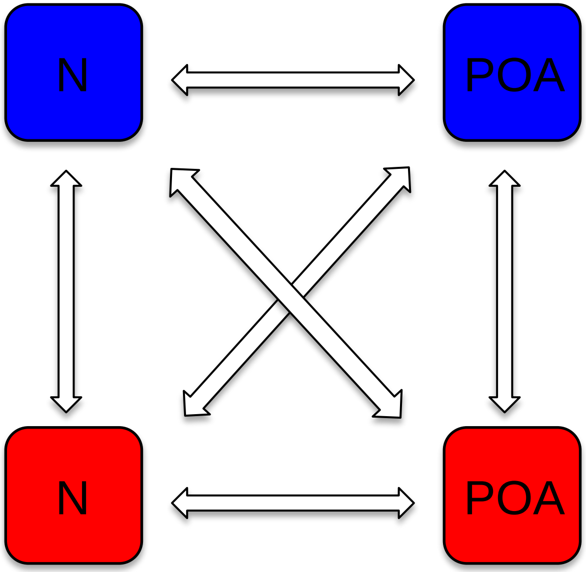
BLUE	oviparous
RED	viviparous
N	No POA
POA	POA



A few snags…

For the 3952 spp. included in the Pyron et al. squamate phylogeny:

- Care data available for only 390 spp. Of those, POA reported in only 79.

Restrict analyses to a monophyletic group with decent amount of data available – Scincidae!

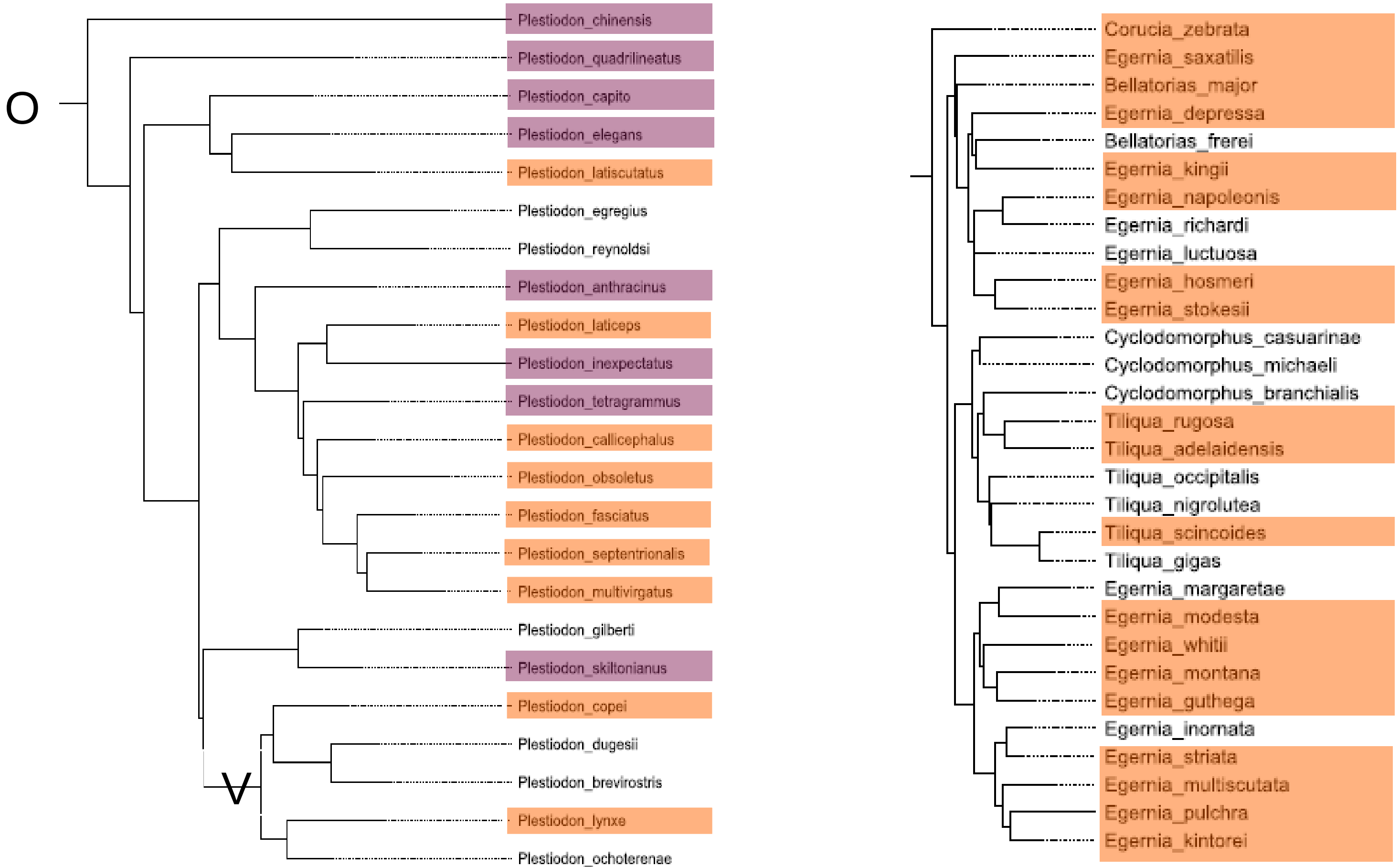
Scincidae

- Monophyletic group
- POA found in 29 spp.

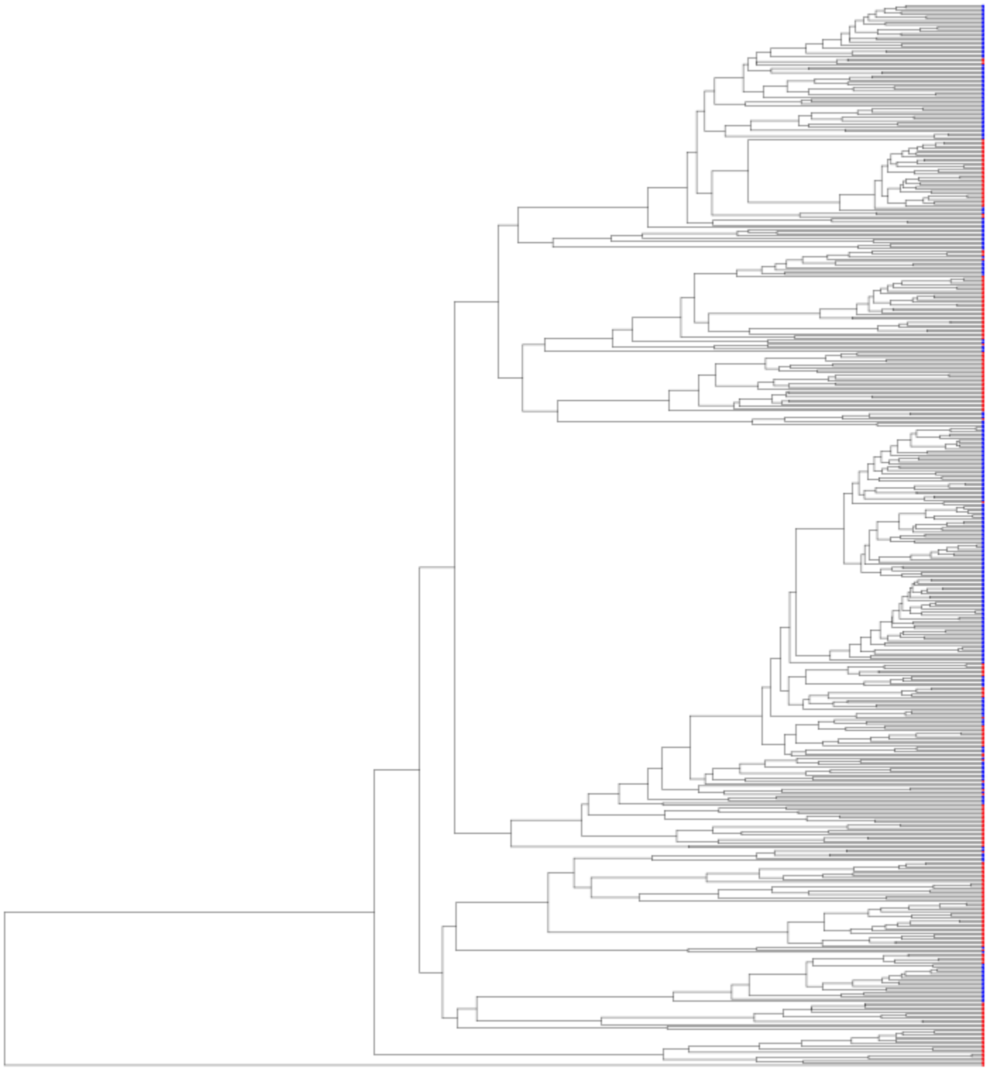
Distribution of Care

Pre | Post

Plestiodon (primarily oviparous) | Egernia (viviprous)



Tree of Scincidae



Approaches

Run Models with:

1. Whole data set (including NA's for care)

2. Reduced data set, including only those species for which care data are available

3. Dummy data sets in which NA's were replaced with randomly assigned care values based on a given probability of care occurring (0.02)

Ran all of these:

1. Constrained and unconstrained speciation and extinction rates

Results

Speciation and Extinction Constrained

	00-01	00-10	00-11	01-00	01-10	01-11	01-00	10-01	10-11	11-00	11-01	11-10
All data	2	4	6	1	7	4	6	5	3	7	7	5
NA's excluded	4	6	7	1	7	4	2	7	3	7	7	5
Rand. datasets	6	3	7	1	7	4	7	7	5	7	7	2

Results

Speciation and Extinction Constrained

	00-01	00-10	00-11	01-00	01-10	01-11	01-00	10-01	10-11	11-00	11-01	11-10
All data	2	4	6	1	7	4	6	5	3	7	7	5
NA's excluded	4	6	7	1	7	4	2	7	3	7	7	5
Rand. datasets	6	3	7	1	7	4	7	7	5	7	7	2

Results

Speciation and Extinction Constrained

	00-01	00-10	00-11	01-00	01-10	01-11	01-00	10-01	10-11	11-00	11-01	11-10
All data	2	4	6	1	7	4	6	5	3	7	7	5
NA's excluded	4	6	7	1	7	4	2	7	3	7	7	5
Rand. datasets	6	3	7	1	7	4	7	7	5	7	7	2

Speciation and Extinction allowed to vary

	00-01	00-10	00-11	01-00	01-10	01-11	01-00	10-01	10-11	11-00	11-01	11-10
All data	3	6	6	6	1	6	5	6	2	4	6	6
NA's excluded	3	4	6	1	6	6	6	6	2	6	5	6
Rand. datasets												

Results

Randomized Data Sets

Speciation and Extinction Constrained

	00-01	00-10	00-11	01-00	01-10	01-11	01-00	10-01	10-11	11-00	11-01	11-10
1	6	3	7	1	7	4	7	7	5	7	7	2
2	6	3	7	1	7	4	7	7	5	7	7	2
3	5	3	7	1	7	4	7	7	5	7	7	2
4	4	6	8	1	1	4	8	8	7	8	8	3
5	6	3	7	1	7	4	7	7	5	7	7	2
6	5	3	7	1	7	4	7	7	6	7	7	2
7	5	3	7	1	7	4	7	7	6	7	7	2
8	4	6	8	1	2	5	8	8	6	8	8	3
9	6	3	7	1	7	4	7	7	5	7	7	2
10	5	3	7	1	7	4	7	7	5	7	7	2
11	5	3	5	1	7	4	7	7	7	7	7	2

Where to from here?

- Conduct more thorough analyses to get at the apparent association between viviparity and POA
  - Extend to whole tree

- Look into multi-trait analysis to see if the current distribution of care modes can be explained by some logical sequence of transitions

e.g. N → B → ED → POA

↳ V → POA

What predicts transitions to parental Care in Squamates?

For care to have evolved from an ancestral state of no care, both ecological and life history traits must favour the transition – these include:

1) Ecological Factors
   - Resource availability
   - Climate (viviparity)

2) Life History Factors
   - Egg size / Investment in offspring
   - Longevity / Age at maturity

3) Association: Care is more likely to evolve when parents regularly encounter their offspring
   - Territoriality
   - Viviparity

Summary

1. Parental care in squamates is more sophisticated than often assumed

2. Care is taxonomically widespread and represents multiple evolutionary transitions

3. These patterns are equivalent to those seen in fish, amphibians and invertebrates – all of which are assumed to have more sophisticated care behaviour compared to reptiles

4. Both life history traits and ecology are likely to be important – specifically, viviparity appears to be an important (but not essential) precursor to parent offspring association

7% of viviparous species in the squamate phylogeny exhibit post-hatching care but only 1% of oviparous

Broader Evolutionary Implications of Parental Care

Family	Species	Parity	General Location
Agamidae	*Phrynocephalus theobaldi*	V	Tibetan plateau
Cordylidae	*Cordylus cataphractus*	V	South Africa
	Cordylus macropholis	V	South Africa
Gekkonidae	*Hoplodactylus duvauceli*	V	New Zealand
Iguanidae	*Leiocephalus schreibersi*	O	Chile
	Liolaemus huacahuasicus	V	Argentina
	Tropidurus flaviceps	O	Ecuador
	Sceloporus jarrovi	V	Mexico
	Sceloporus mucronatus	V	Mexico
Scincidae	*Gnypetoscincus queenslandiae*	V	Australia
	Many *Egernia sp.*	V	Australia
Xantusiidae	*Xantusia vigilis*	V	Southwestern USA
	Xantusia riversiana	V	San Nicolas Is., USA
Xenosauridae	*Xenosaurus newmanorum*	V	Mexico

Questions and Suggestions?