

Lousy Phylogenies:

Phthiraptera systematics and the antiquity of lice

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Lice (Phthiraptera): biology

i. Diversity

- 4,384 spp “chewing lice” (3,508 bird & 402 mammal spp)
- 543 spp sucking lice (812 spp mammal)

ii. Physical characteristics

- wingless, dorsoventrally flattened, 0.3-11mm, 3 nymphal instars
- feed on feathers, fur & skin debris (“chewing lice”) or blood
- adaptations against host grooming

iii. Distribution

- mirror host distribution worldwide in virtually every habitat
- absent on Chiroptera, Cetacea, Microbiotheria, Monotremata, Notoryctemorphia, Pholidota & Sirenia.

iv. Cophylogeny, cospeciation & coevolution

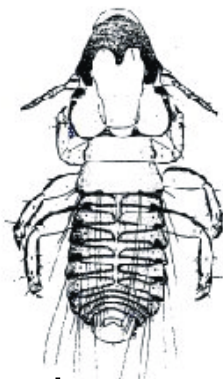
Lice (Phthiraptera): taxonomy

Chewing Lice “Mallophaga”

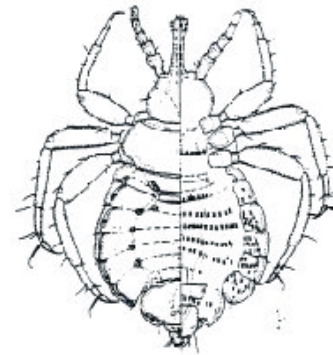
Sucking Lice (Anoplura)



Amblycera



Ischnocera



Rhynchophthirina



Anoplura

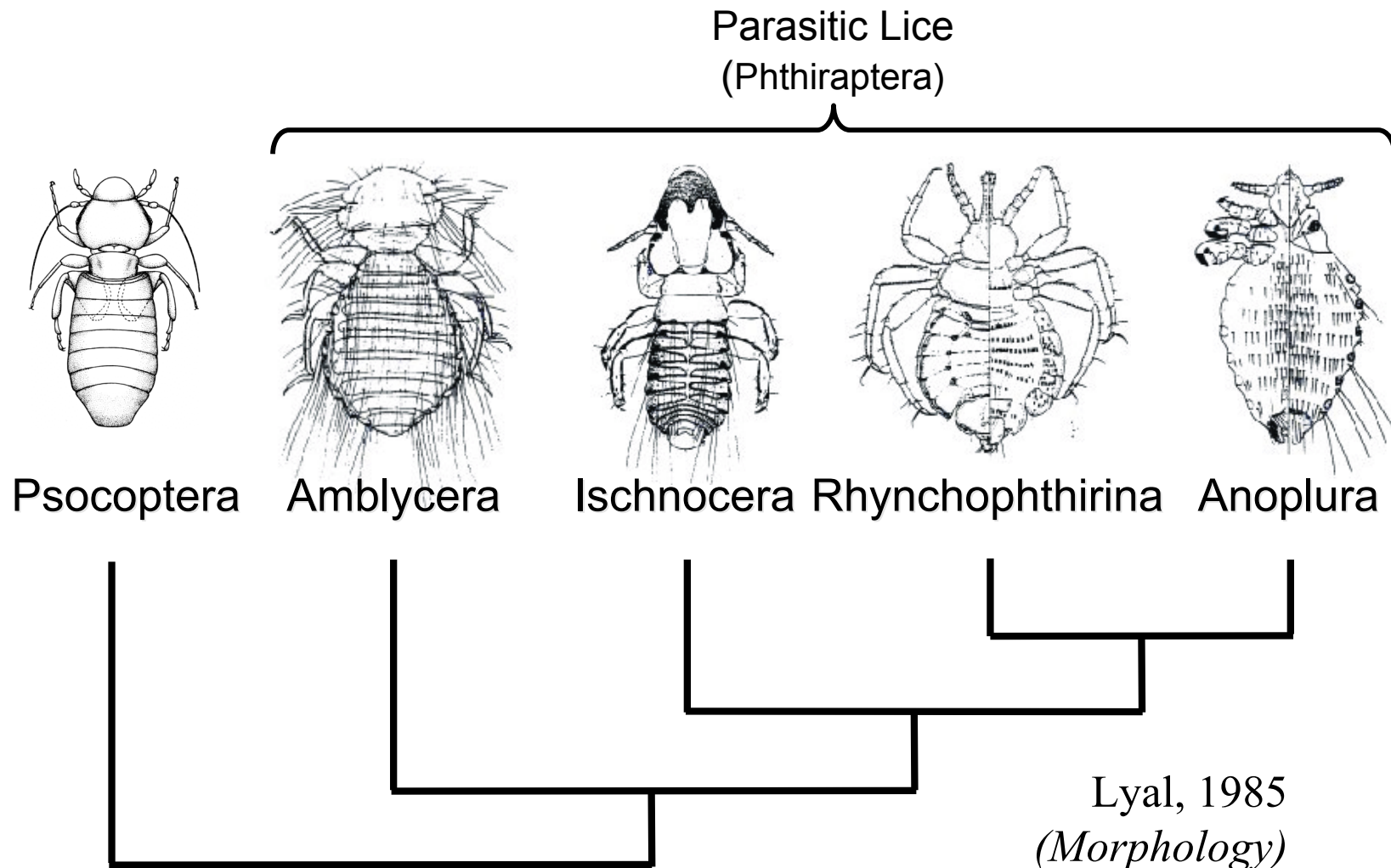
- 1,350 spp in 6 families
- Most “primitive” suborder
- More vagile, less host specific
- Widespread on birds
- 2 fam. South American mammals & marsupials
- 1 fam. on Australasian marsupials

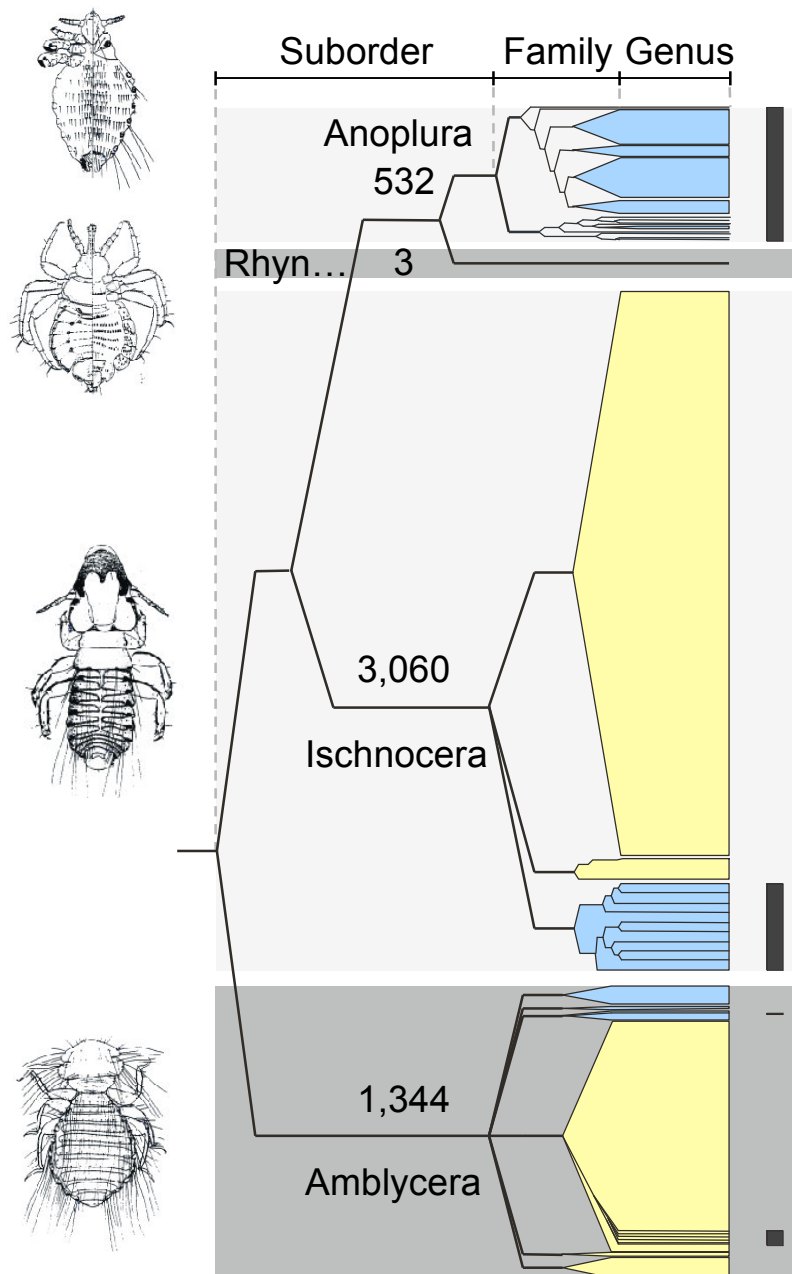
- 3,060 spp., # families ?
- Widespread, ~90% spp. on birds
- Avian groups poorly known
- Highly host specific
- Niche restricted
- Mammal infesting species of veterinary significance

- Just 3 species
- On unrelated hosts
- Acquired via shared use of watering holes?
- Tiny mandibles present at end of a long rostrum pierce hosts thick skin

- 550 spp. in 16 families
- Absent from birds
- Well studied
- Greatest medical & veterinary significance
- Vectors of several important diseases
- Low prevalence on healthy hosts

Lice (Phthiraptera): phylogeny

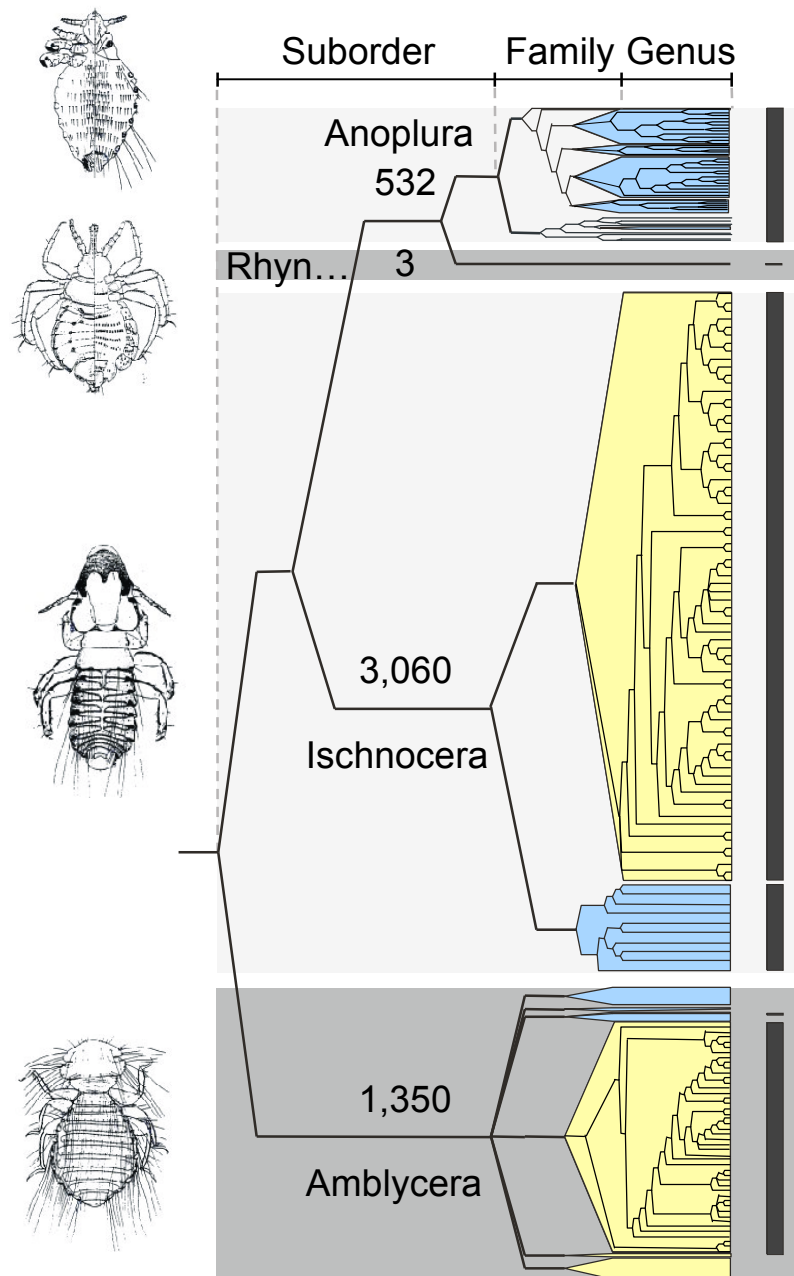




Phthiraptera:

Phylogenetic
resolution, 1996

 *Birds*
 *Mammals*

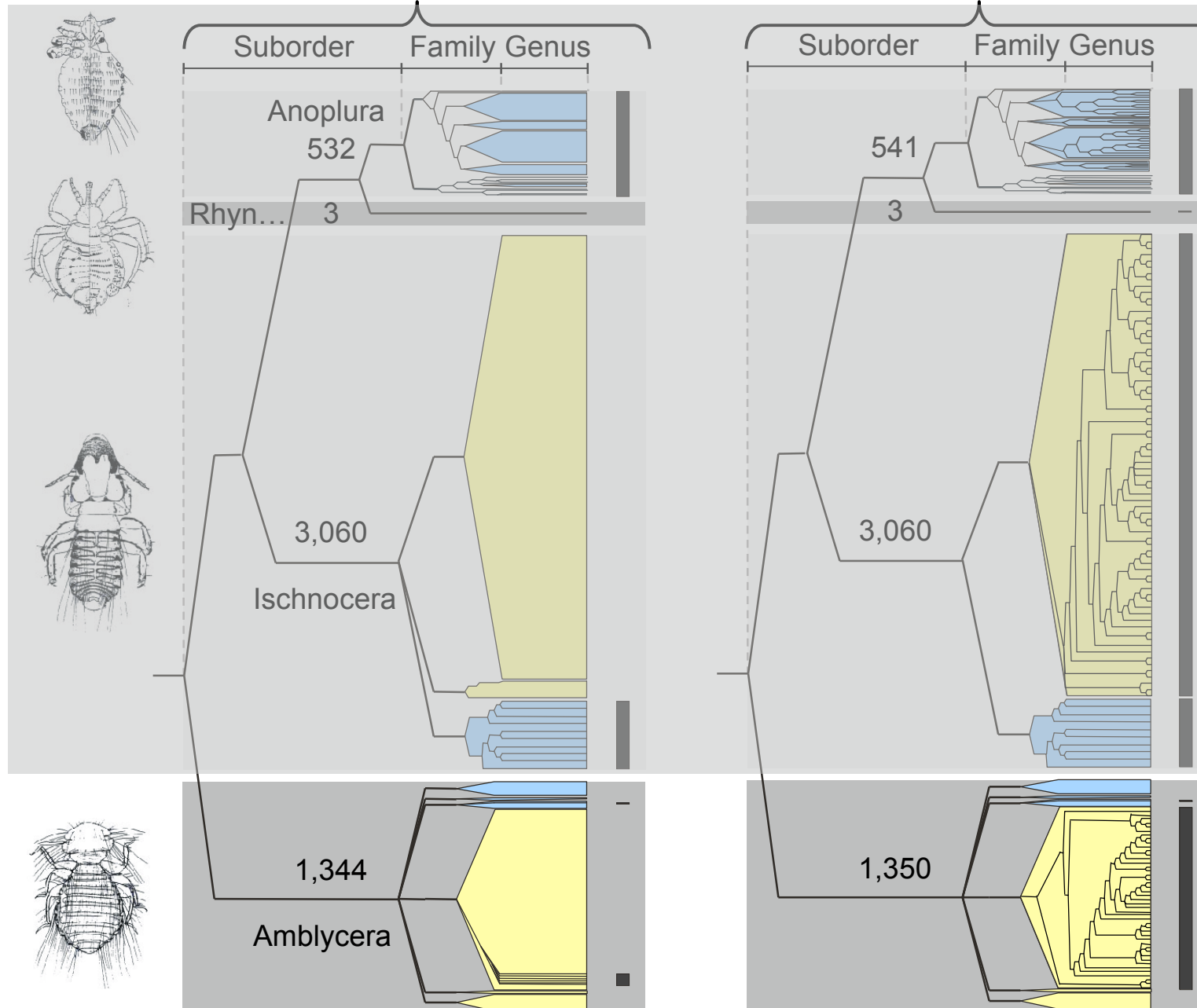


Phthiraptera:

Phylogenetic
resolution, 2003

1996

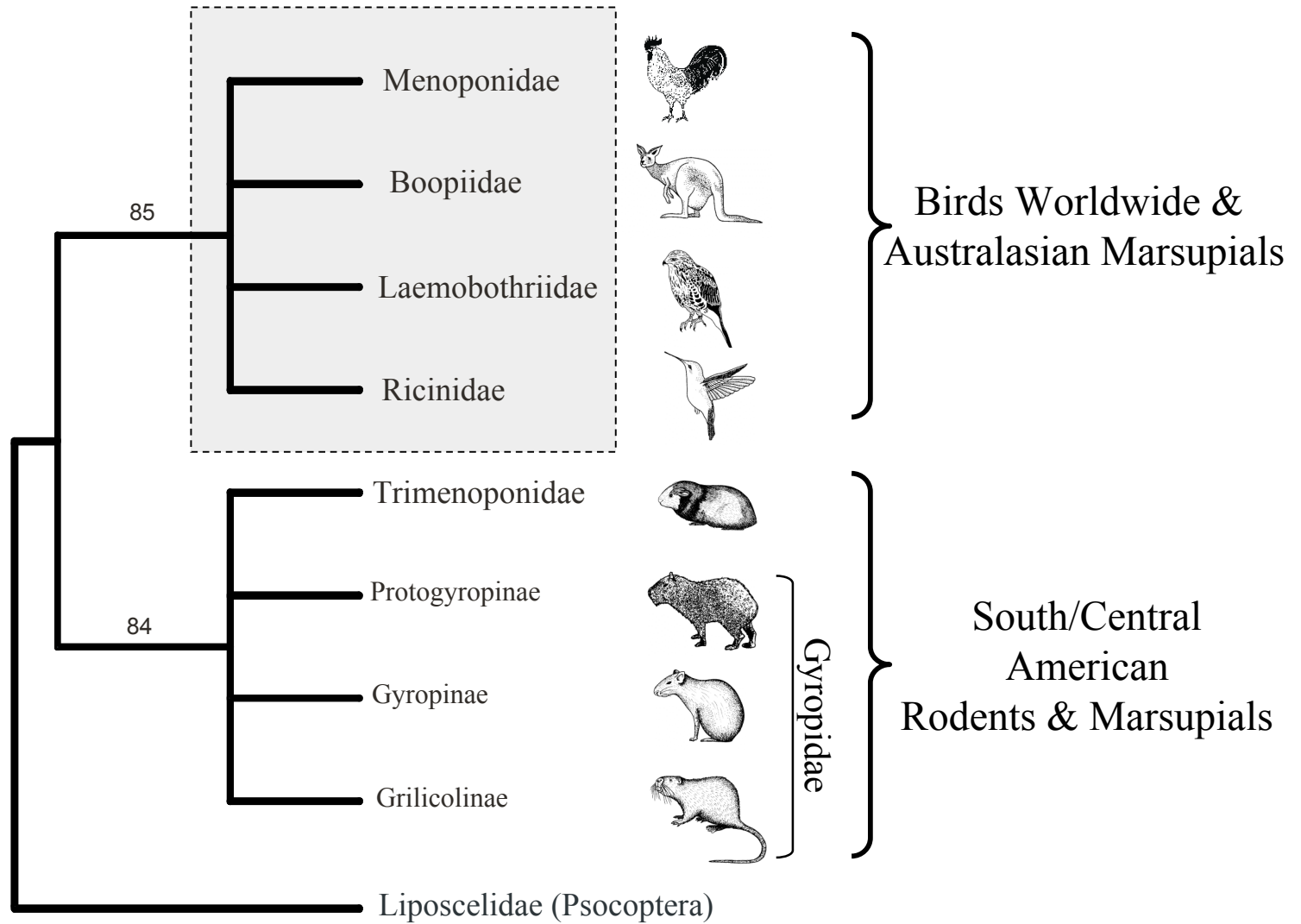
2003



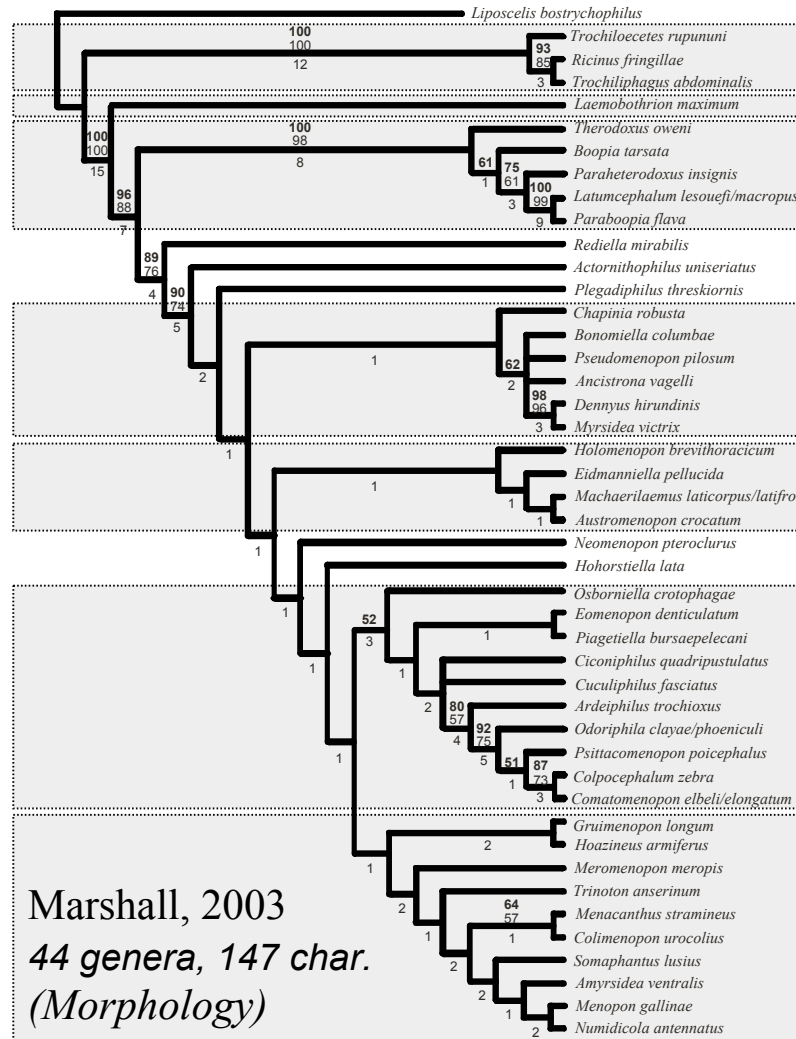
Amblyceran Families



Analysed by
Marshall, 2003
from Clay, 1970
(*Morphology*)



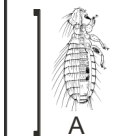
Avian Amblycera



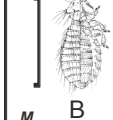
Ricinidae
- Hummingbirds



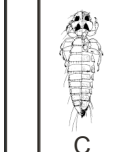
Boopidae
- Australasian marsupials



Dennyus-complex
- Birds worldwide



Austromenopon-complex
- Aquatic birds



Colpocephalum-complex
- Birds worldwide



Menacanthus/Menopon-cpx.
- Birds worldwide

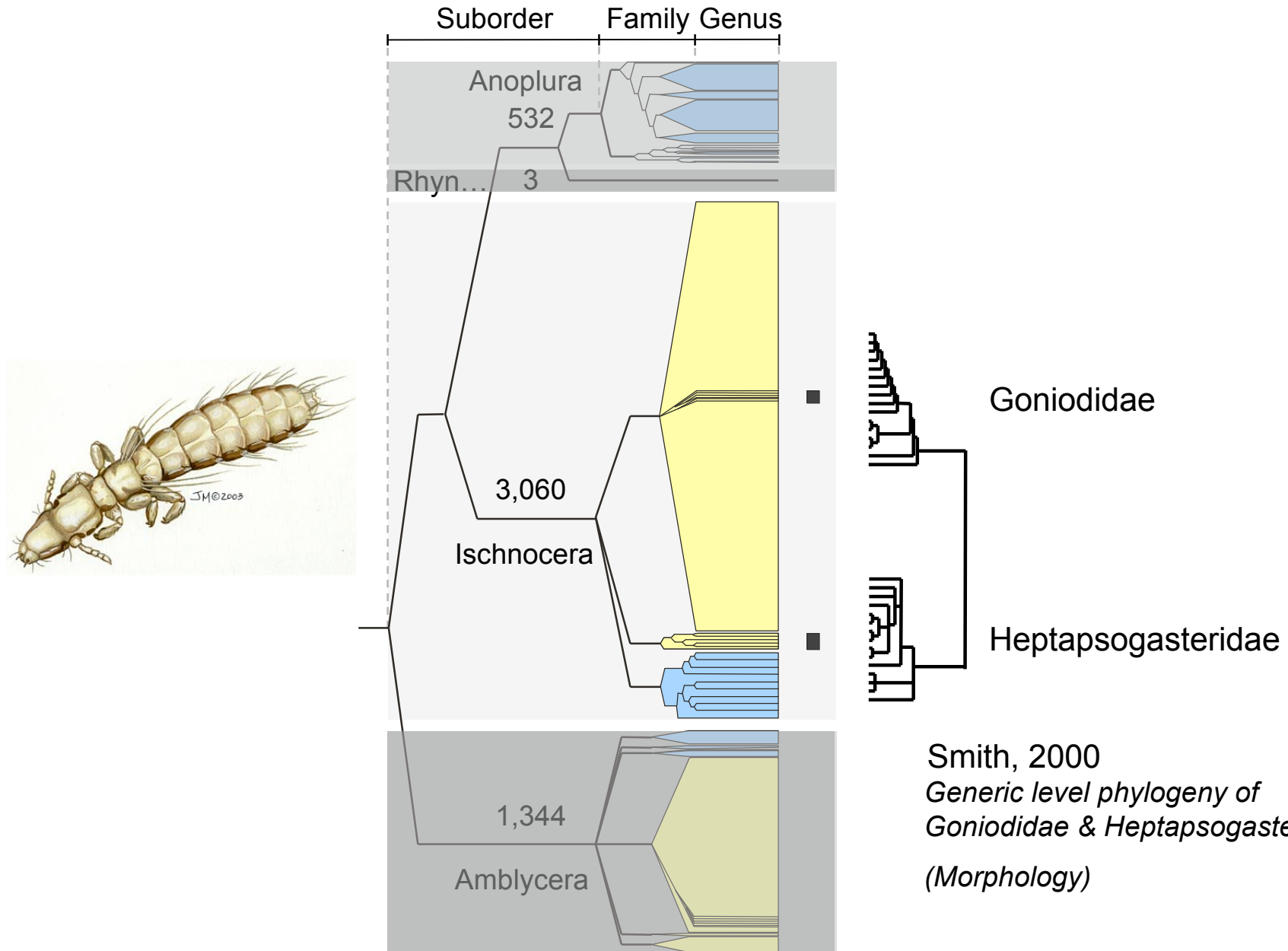
Laemobothriidae
- Falconiforms

First Fossil Louse (Amblycera: Menoponidae)

- Collected Eckfeld maar near Eifel, Germany
- Middle Eocene (Middle Lutetian, 44.3 ± 0.4 Ma)
- First fossil louse
- Completes ordinal representation of fossil insects?
- Excellent preservation
- Phylogenetic affinities with modern feather lice
- Parasite of Anseriformes or Charadriiformes
- Crown group position
- Points to a long coevolutionary history with birds
- Suggests lice are very old
- Useful molecular calibration point

Wappler, Smith &
Dalglish , In prep.

Ischnoceran Families



Smith, 2000
*Generic level phylogeny of
 Goniodidae & Heptapsogasteridae
 (Morphology)*

Avian Ischnoceran Phylogeny

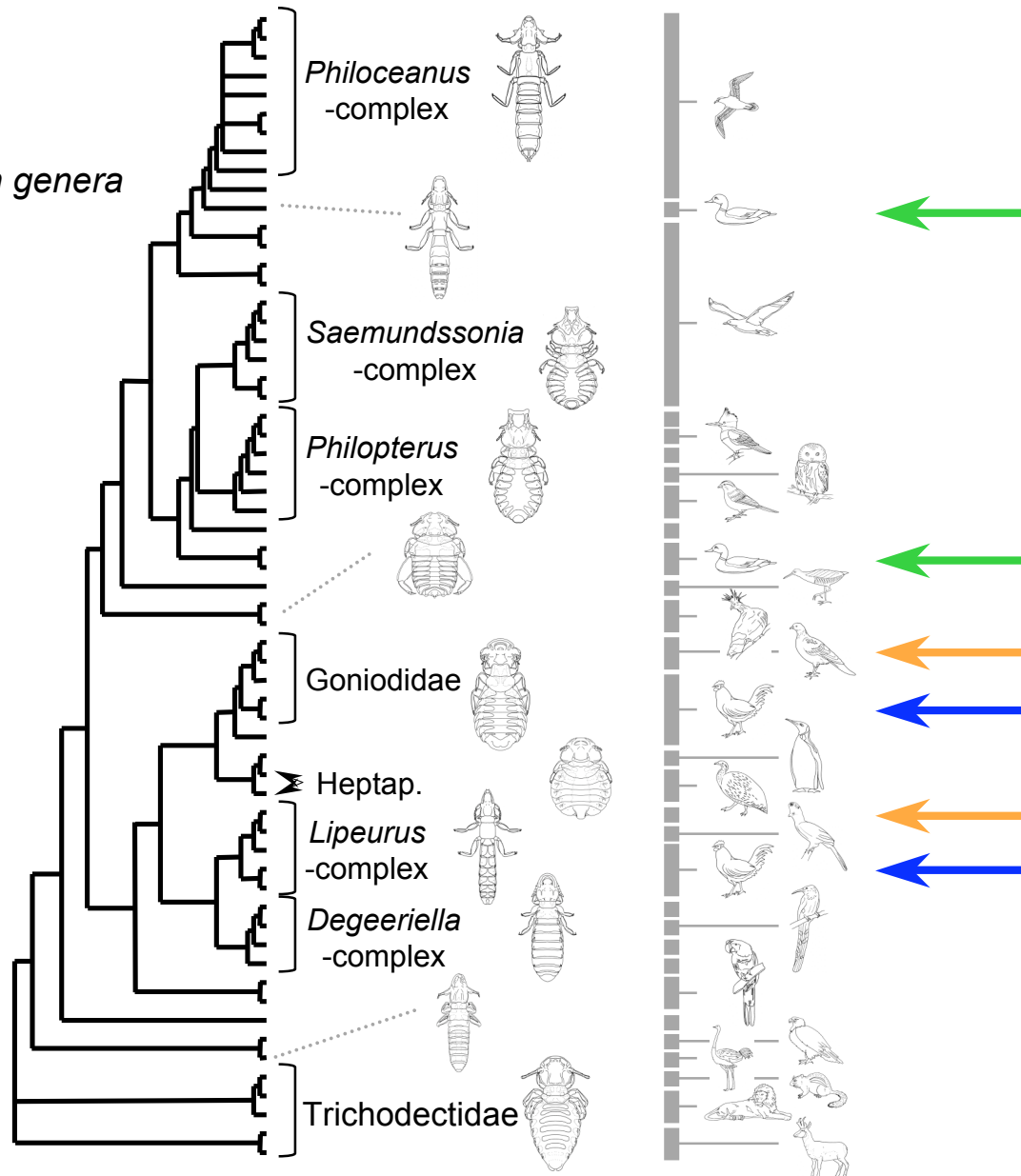
Smith, 2001

Generic level phylogeny

Approx. 1/3rd of all ischnoceran genera

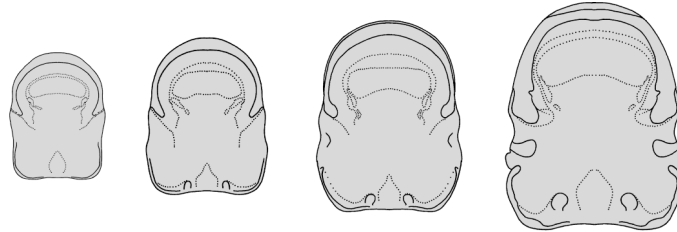
51 genera, 138 characters
(Morphology)

Multiple clades of lice
on the same host

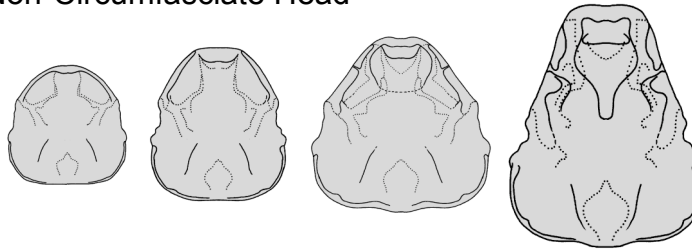


Characters Defining Major Ischnoceran Clades

A. Circumfasciate Head



B. Non-Circumfasciate Head



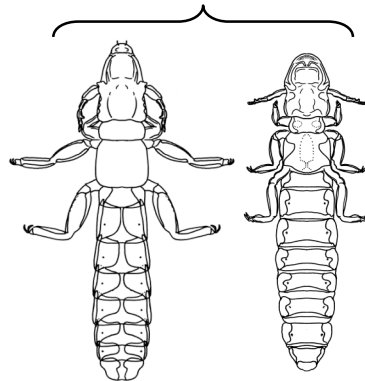
N I

N II

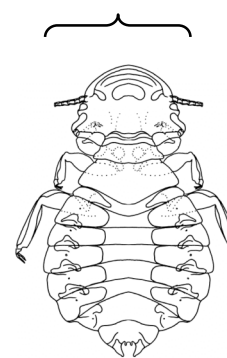
N III

Adult

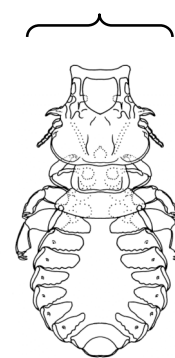
C. Wing Lice



D. Body Lice



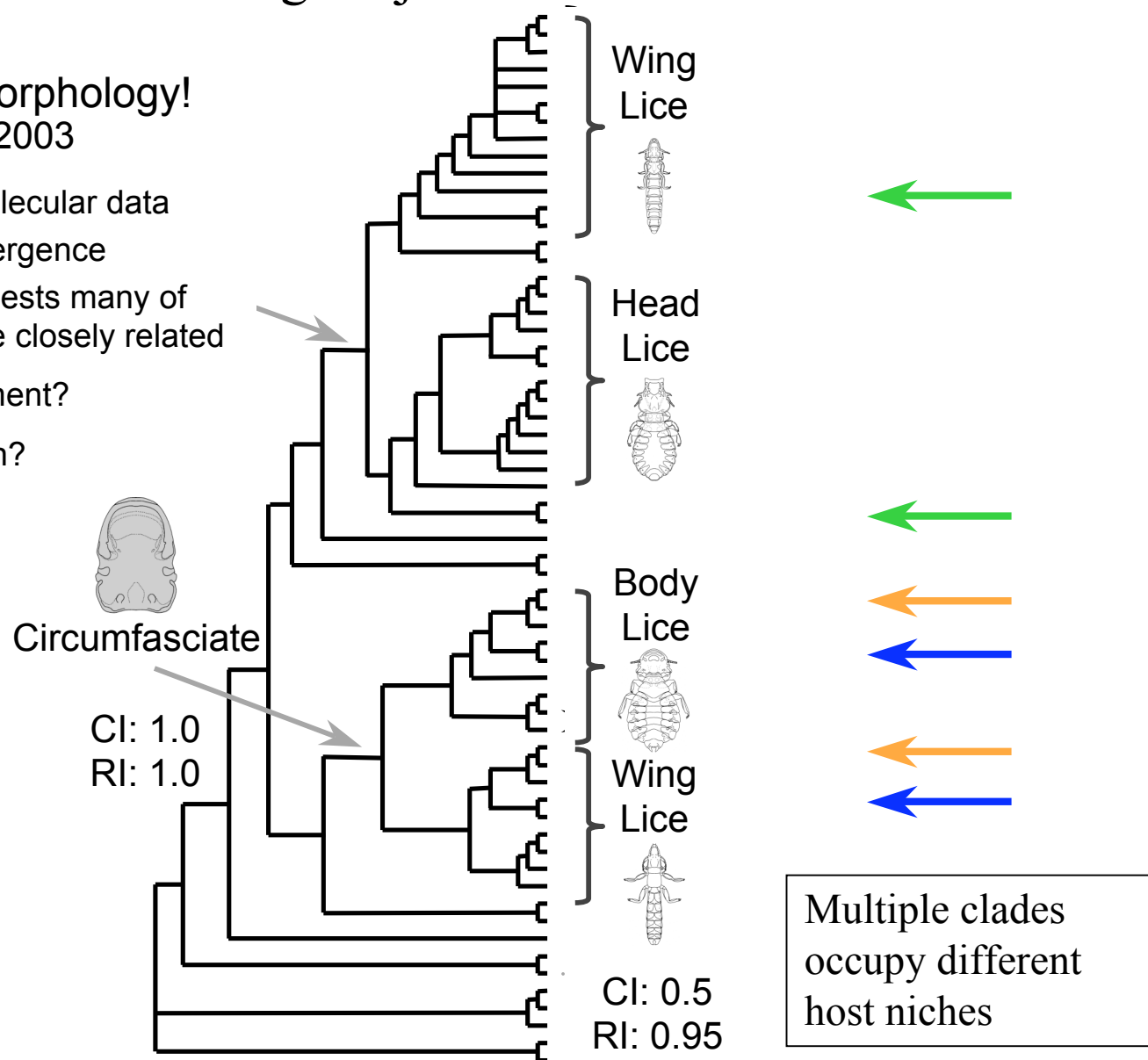
E. Head Lice



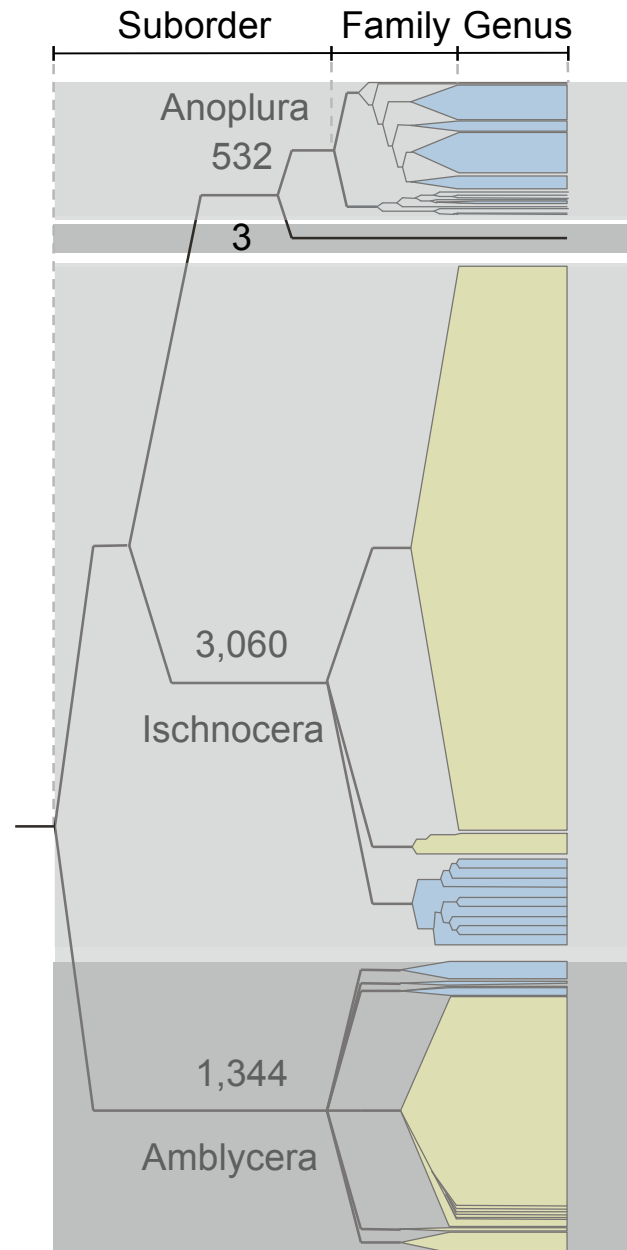
Characters Defining Major Ischnoceran Clades

Problems with Morphology! Smith et al, 2003

- Incongruent with molecular data
- Morphological convergence
- Molecular data suggests many of these pairs are more closely related
- Character displacement?
- Sympatric speciation?



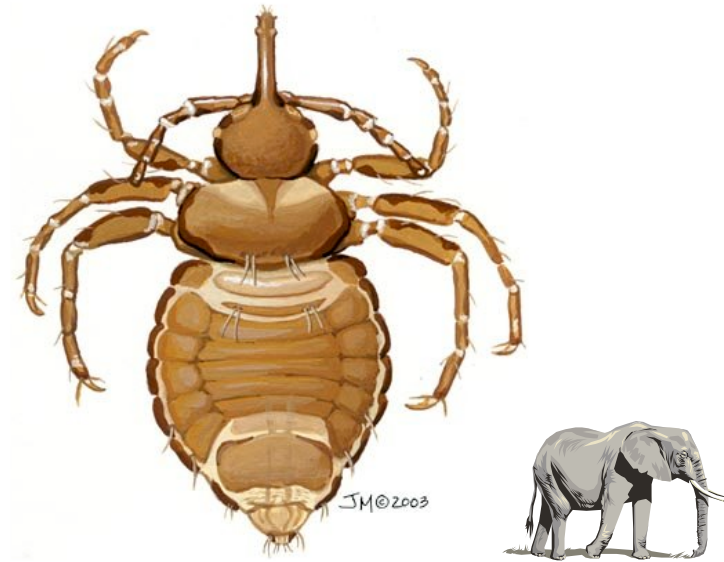
Rhynchophthirina: Haematomyzidae



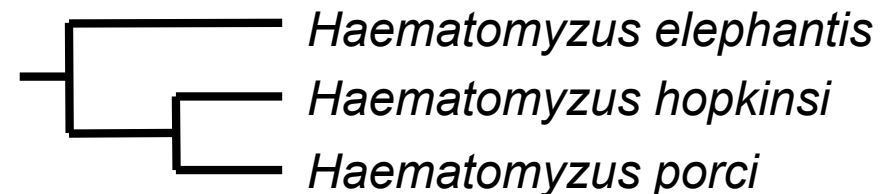
⇒ Rhynchophthirina

Rhynchophthirina: Haematomyzidae

- Just 3 species in 1 family
- Present on elephants, wart hog & bush pig (perhaps also mammoths?)
- Monophyly & sister placement with Anoplura well supported
- Chewing lice (have outwardly opposing mandibles)
- Pool blood feeders (telmophages) cf vessel feeding Anoplura
- Spread via shared use of watering holes?
- Possible cryptic species? (morphologically identical species on African & Asian elephants)
- Specimens hard to come by!

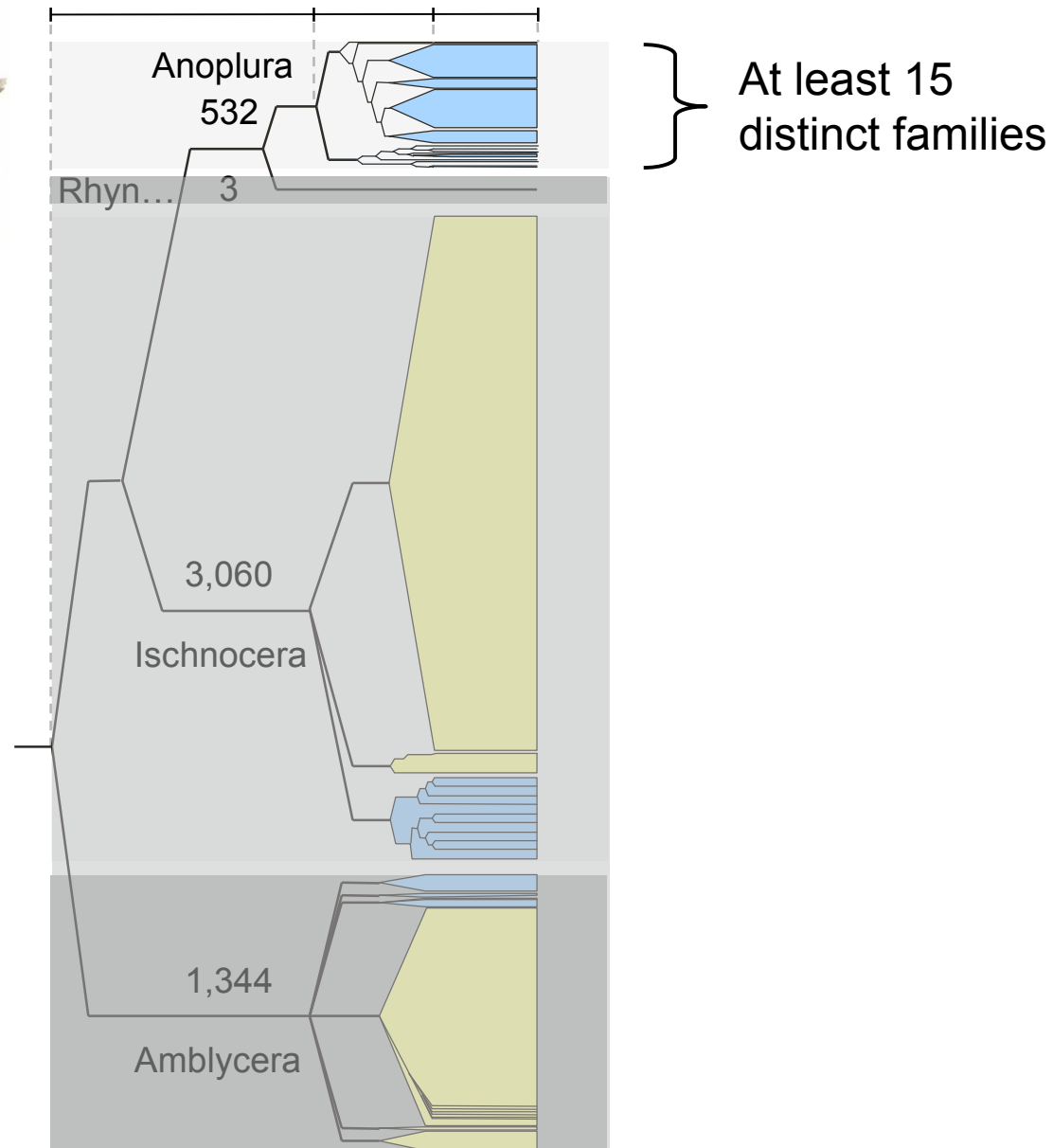


Haematomyzus elephantis
ex Asian / African elephant



Part of Smith, in prep.
51 genera, 76 species
184 characters
(Morphology)

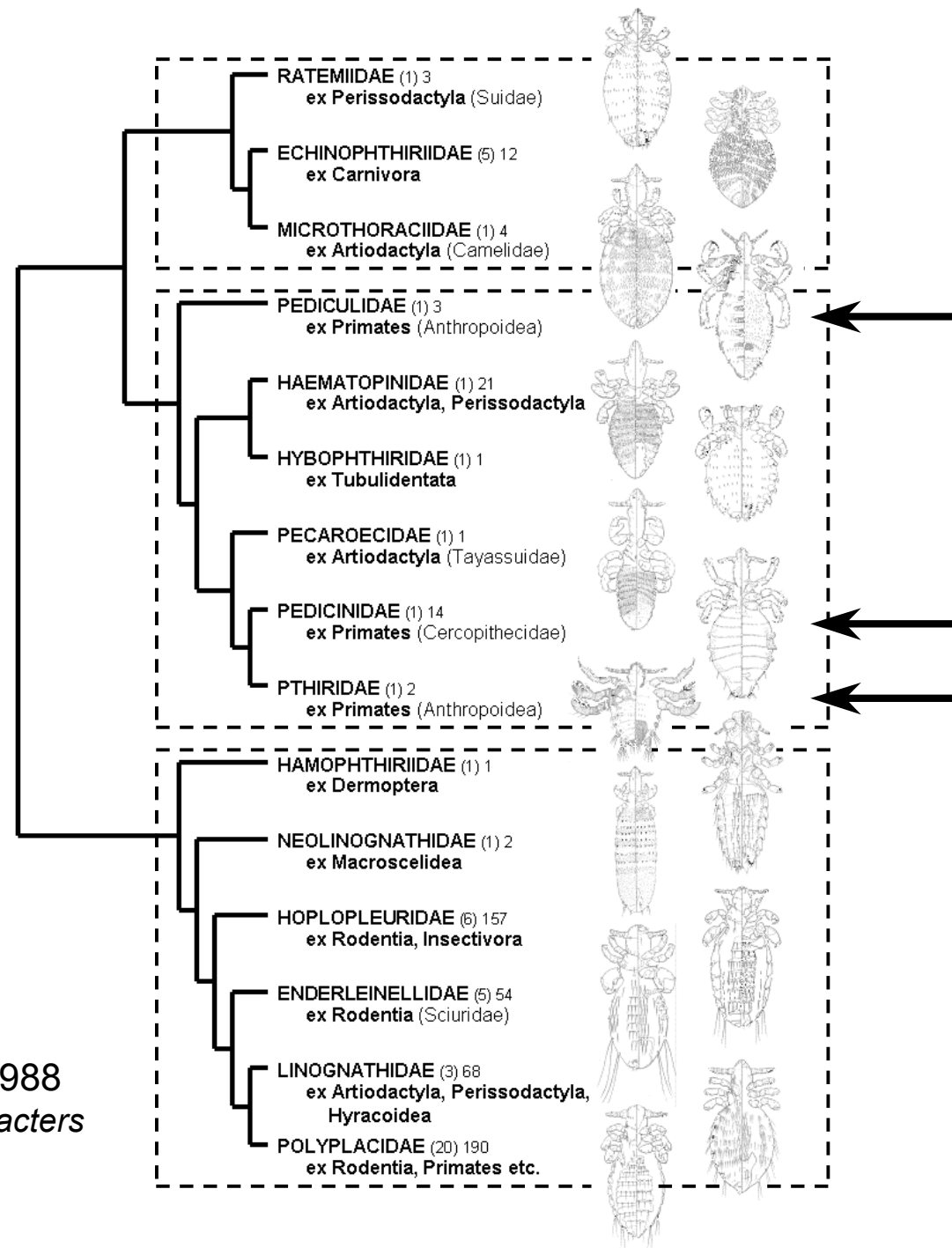
Anopluran Families



Anoplura: familial phylogeny

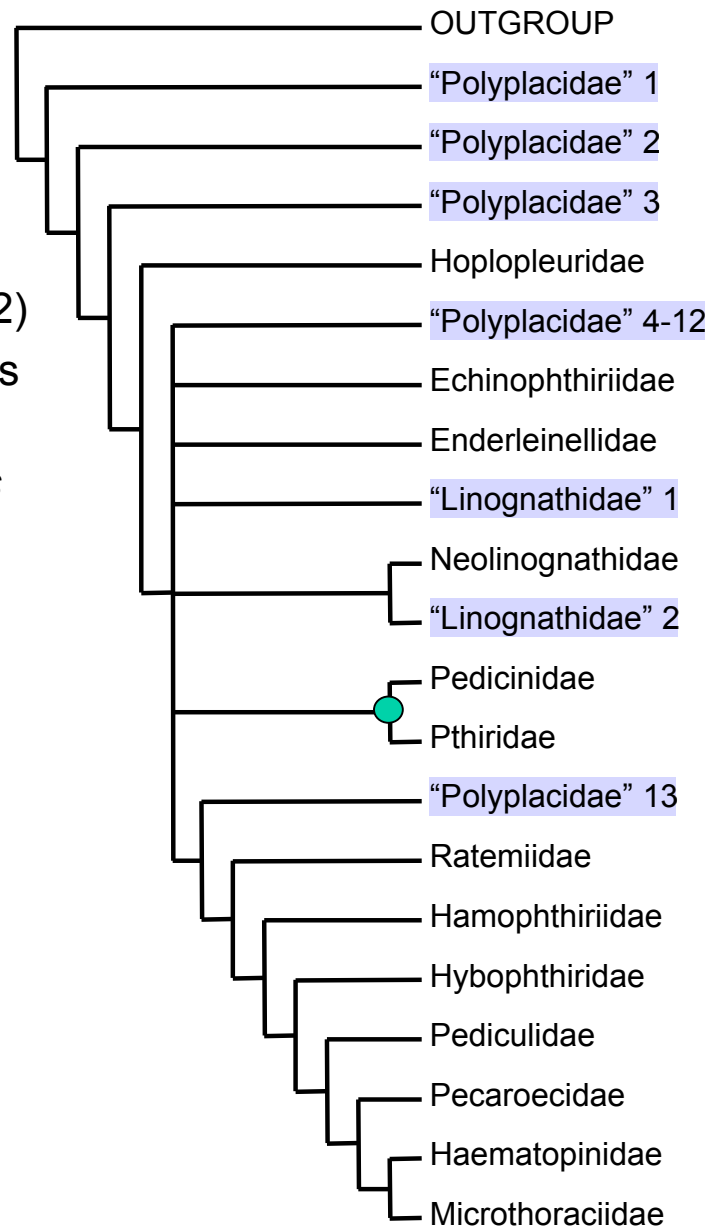
- 541 spp. in 15 families
- Patchily distributed across mammals
- Monophyly of all 15 families supported
- 3 basal clades
- Many lice of host groups (including Primates) paraphyletic

Based on Kim, 1988
47 genera, 39 characters
(Morphology)



Kim's dataset re-analysed:

- Length=219 (CI=0.26, RI=0.62)
- Paraphyly of 2 of the 5 families that were not monogenic
- *Just 1 node agrees with Kim's original tree!*
- *Only 3 other nodes are compatible with Kim's tree*

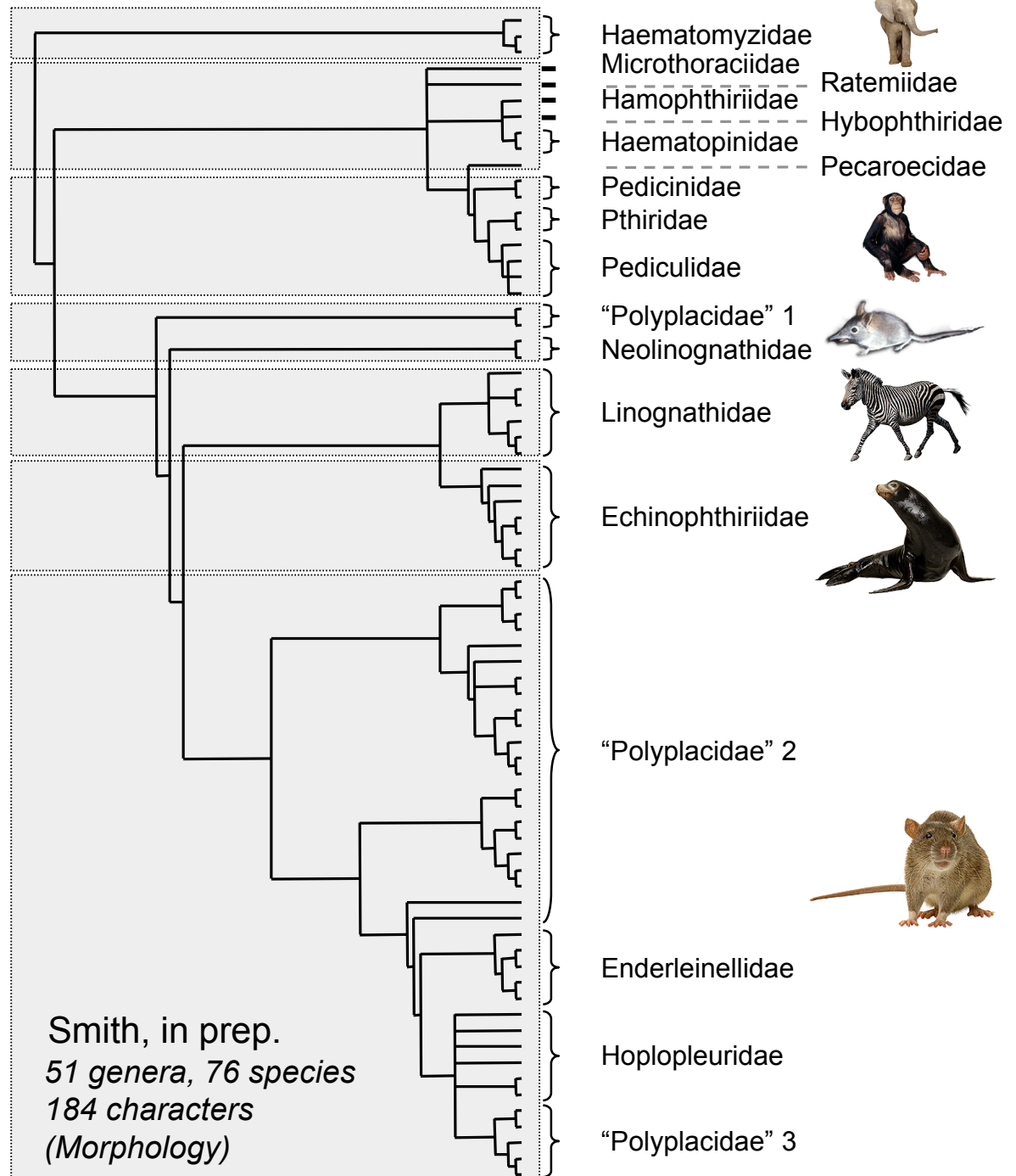


Kim, 1988 reanalysed
Strict Consensus

Anoplura: phylogeny



- Why are rodents so lousy?
- Why are other mammals relatively louse free cf. birds
- Good evidence for cophylogeny in some clades
- *Comparative studies underway using these trees*



Louse Molecular Studies

Mitochondrial

- COI (400-1500bp)
- 12S rRNA (450bp)
- Cyt. B (450bp)
- ND4 (500bp)

- *Easy to amplify*
- *Limited phylogenetic utility outside families*
- *Often restricted to use within closely related genera*

Nuclear

- EF1- α (350-450bp)
- 18S rRNA (1500+bp)
- Wingless, PEPCK, DDC

- *Hard to amplify*
- *Multiple copies*
- *RNA alignment issues*
- *Utility varies between genes & taxa*

Need New Genes!

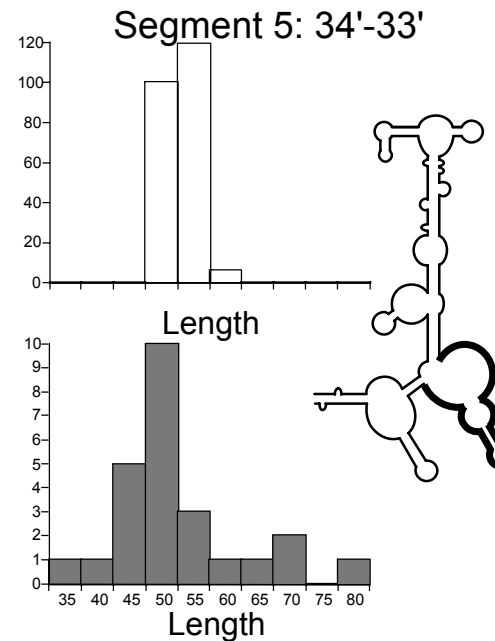
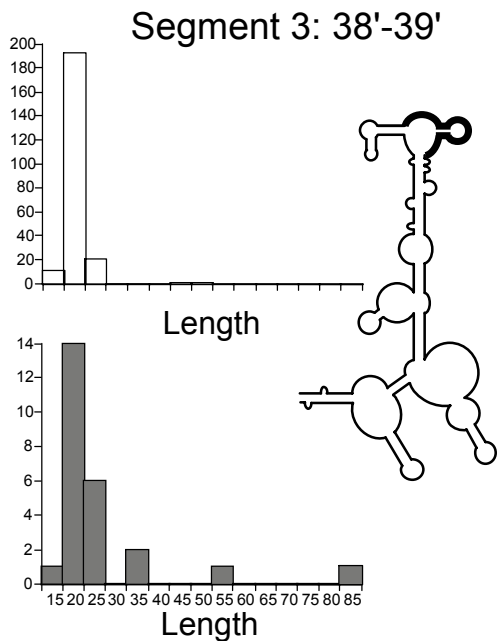
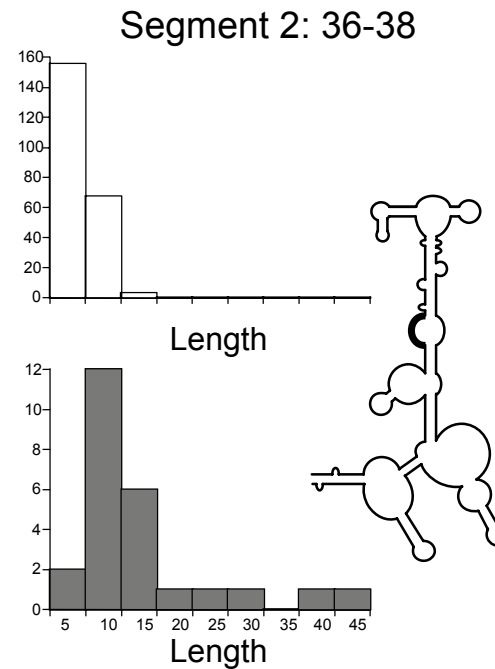
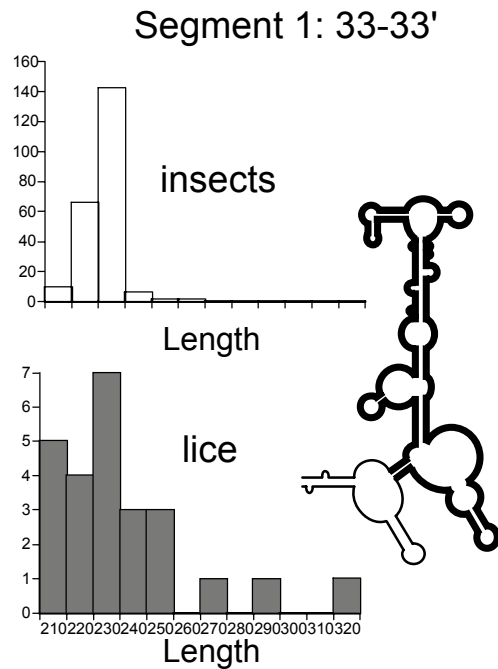
Relative Substitution Rate

(Mit. COI vs nuc. EF1- α)

Data Set		Sites	Rate Parameter		Ratio (COI:EF1 α)
			COI	EF1- α	
Lice	Physconelloidinae	all sites	1	0.018	55.6
		pos. 1	1	0.013	76.9
		pos. 2	0.12	0.016	7.5
		pos. 3	129.9	0.41	316.8
	<i>Columbicola</i>	all sites	1	0.016	61.5
		pos. 1	1	0.039	25.6
		pos. 2	0.15	0.017	8.8
		pos. 3	169.78	0.8	212.2
	aphids	all sites	1	0.25	4.1
		pos. 1	1	0.20	5.0
		pos. 2	0.0001	0.0001	1.0
		pos. 3	44.79	2.49	18.0

mit. 12S rRNA
Page et al, 2002



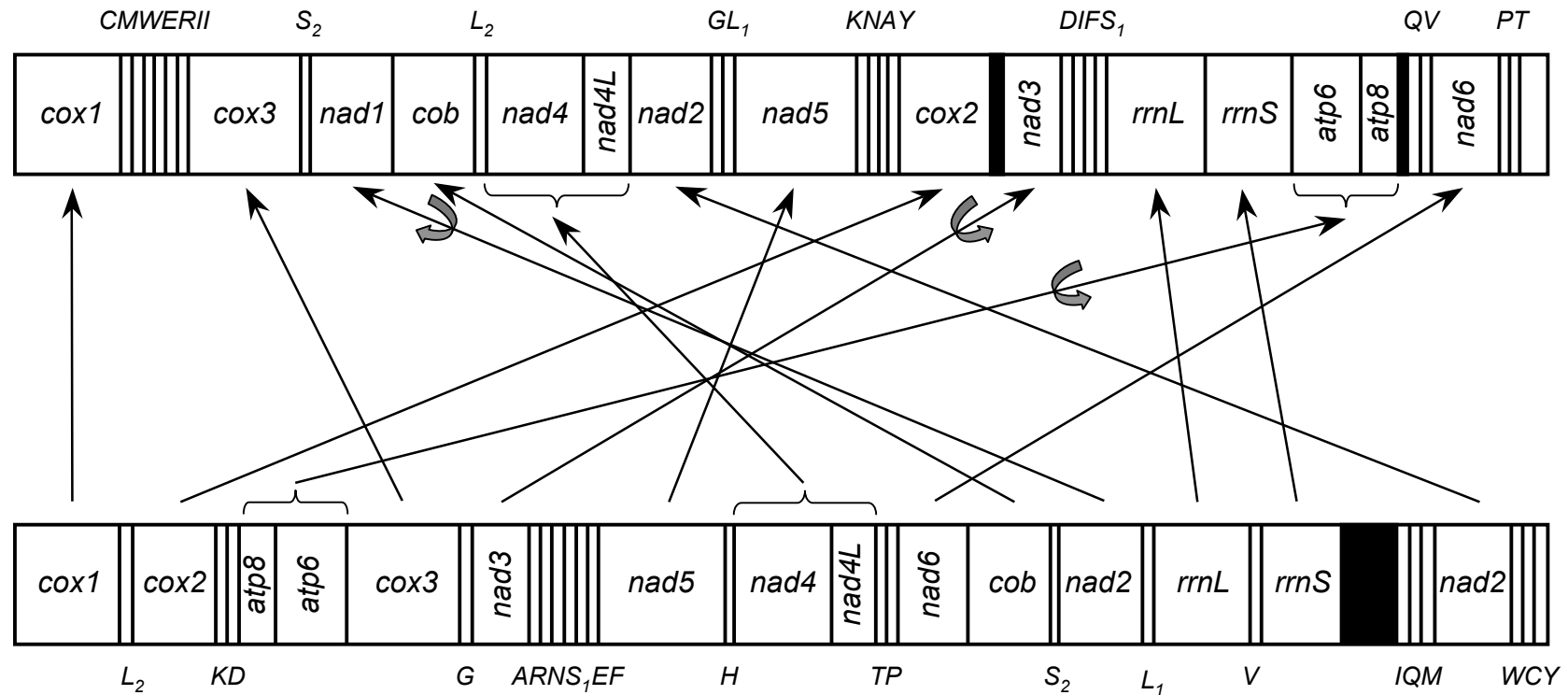


12S Length Variation

Insects vs.
Lice
Page et al, 2002

Louse Mitochondrial Genome

Gene arrangement of *Heterodoxus macropus* (Amblycera)



Inferred gene arrangement of ancestral insect

Adapted from Shao, Campbell & Barker, 2001

Louse Molecular Studies

Mitochondrial

- COI (400-1500bp)
- 12S rRNA (450bp)
- Cyt. B (450bp)
- ND4 (500bp)

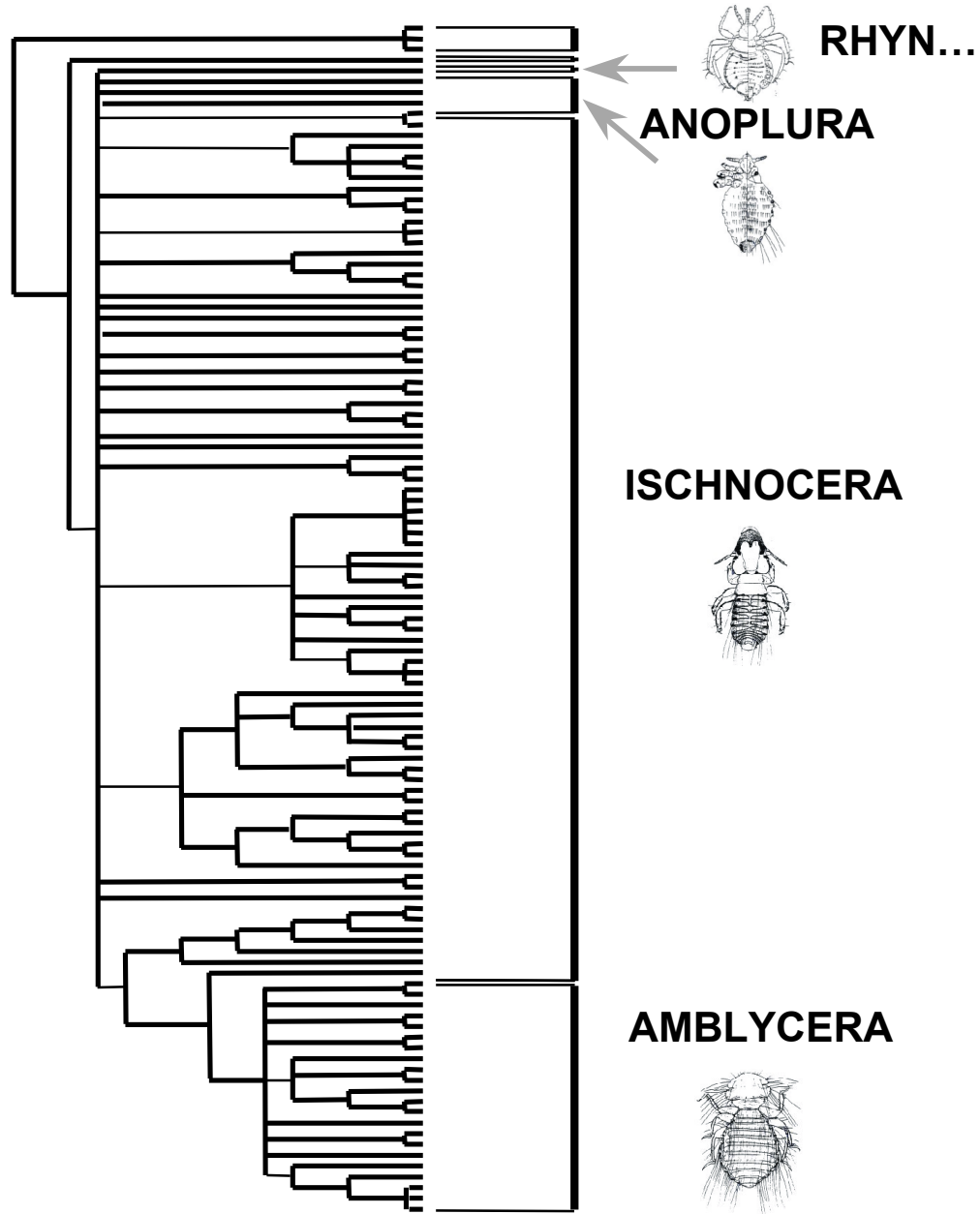
- *Easy to amplify*
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Nuclear

- EF1- α (350-450bp)
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- *Hard to amplify*
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Need New Genes!



Louse Nuclear Genes

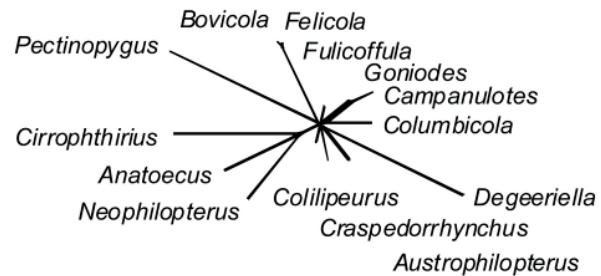
What Not to do!

- *350 bp single copy EF1- α*
- *Limited phylogenetic utility above families*

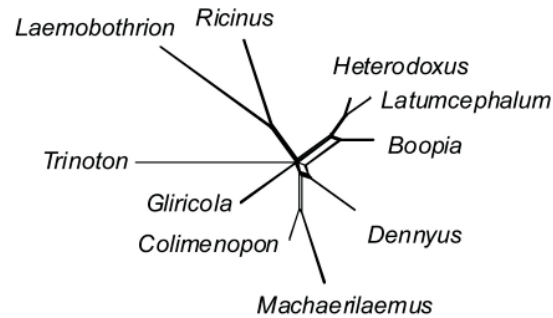
Cruickshank et al, 2001

Phylogenetic Utility 18S rRNA

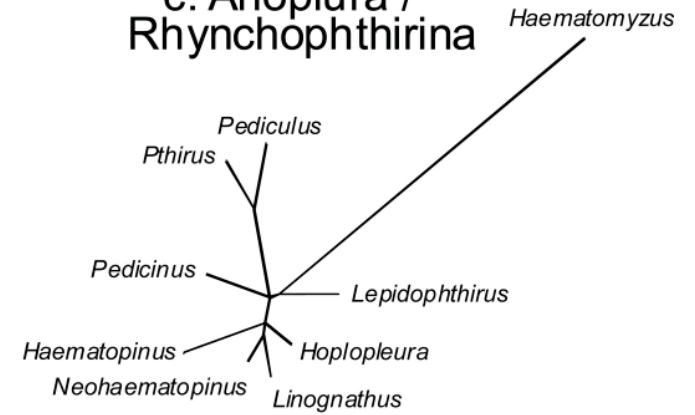
a. Ischnocera



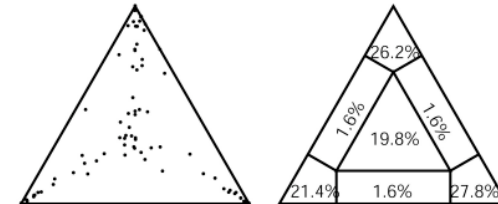
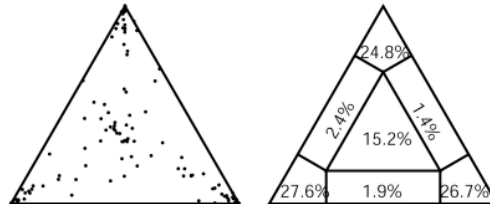
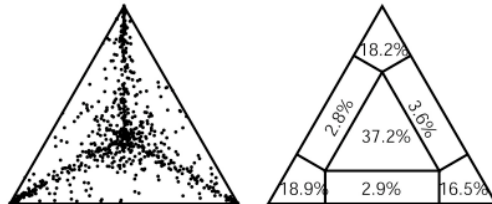
b. Amblycera



c. Anoplura / Rhynchophthirina



0.01



Smith et al, 2003

Conclusions...

- Much recent progress on basal phthirapteran phylogeny
- Monophyly of suborders well supported
- Complex pattern of host-louse relationships
- Distinctive molecular evolution in lice
- Incongruence between molecules & morphology

Ongoing Questions...

- *To what extent do lice cospeciate with their hosts?*
- *Why are some hosts more lousy than others?*
- *How old are the major louse clades?*
- *Are Phthiraptera truly paraphyletic?*

Acknowledgements

Collaboration

Stephen Barker

Dale Clayton

Tom Ford

Kevin Johnson

Rod Page

Isabel Marshall

David Reed

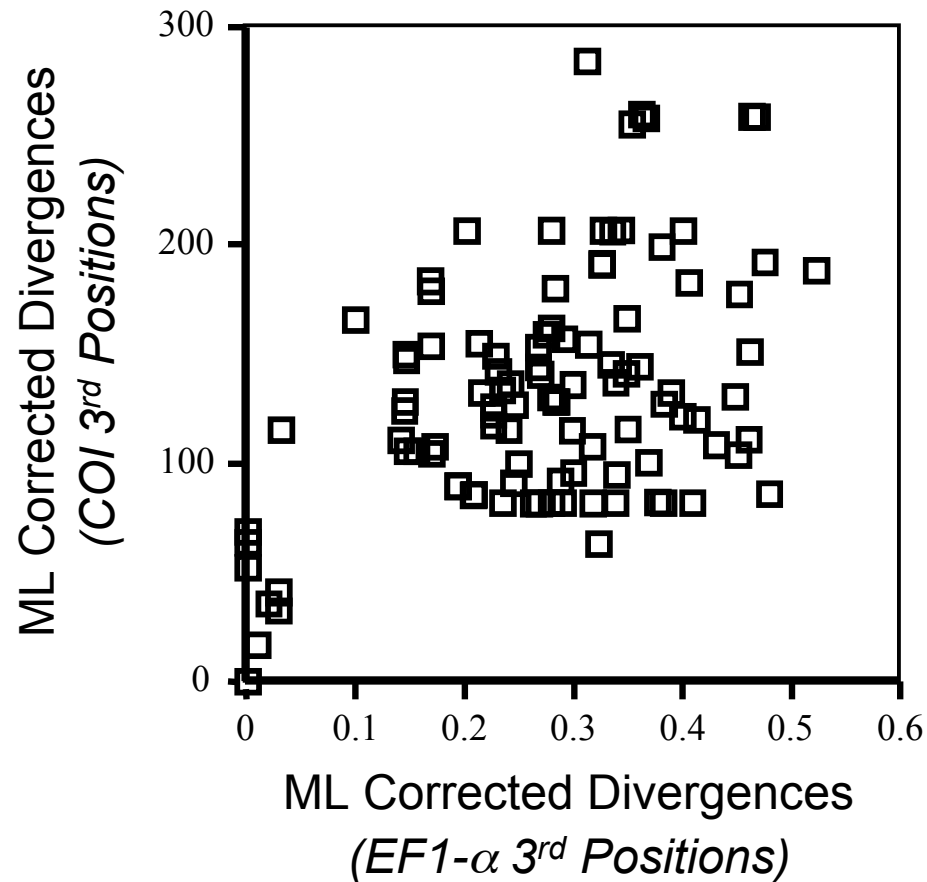
Funding

Wellcome Trust, UK

Natural Environment Research Council, UK



Pairwise ML Corrected Distances for 3rd Sites (*Nuclear EF1- α against Mit. COI*)



Slope
approximates
relative rate

Around 1000:1 !!!

Johnson et al, 2003

18S – not a panacea for basal louse Phylogeny!

