

"Behavioral Characters Perform Well as Indicators of Phylogeny"

Caracteres Comportamentais Representam
Excelentes Indicadores de Filogenia

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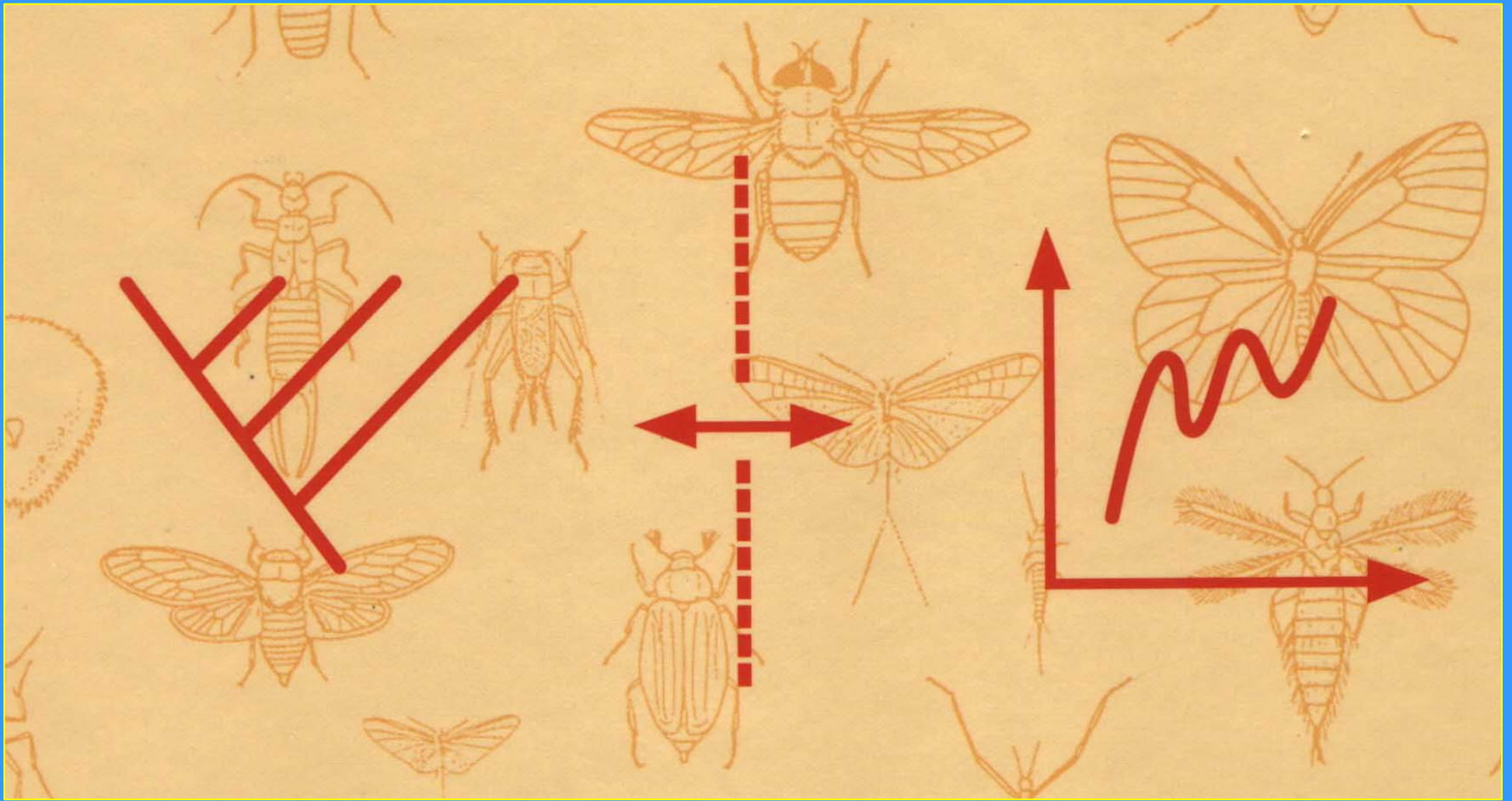
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São Paulo

2010



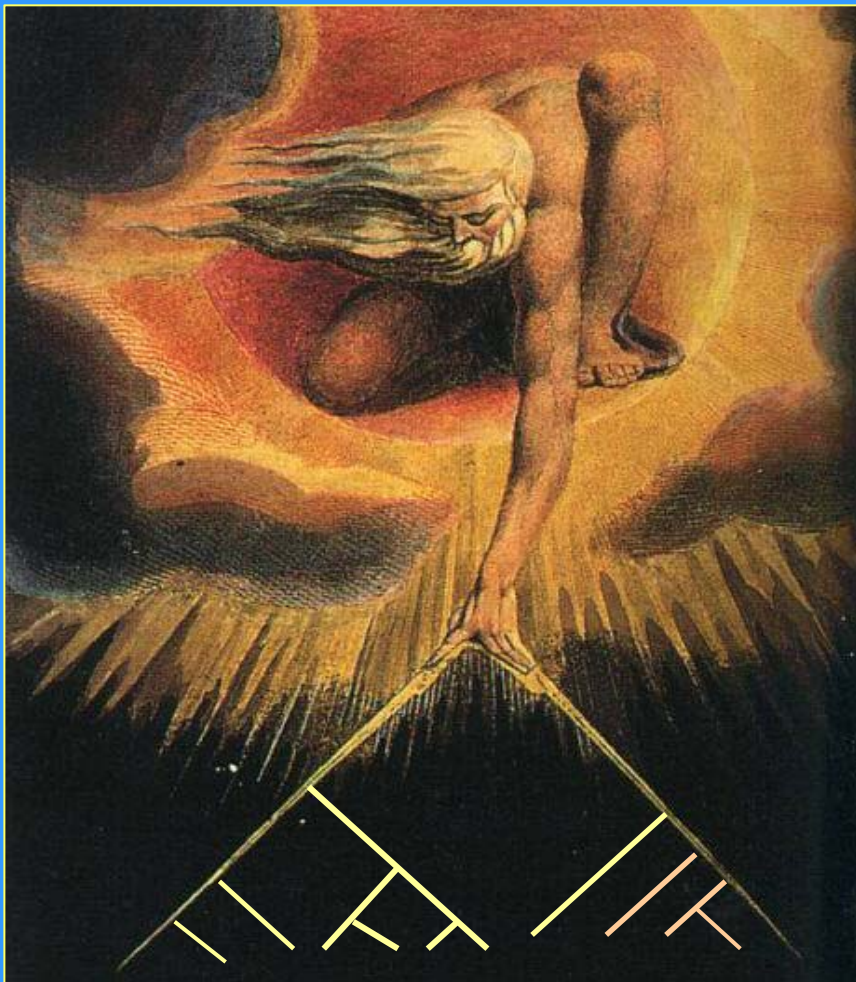
Evolutionary biology advances by studies of both pattern and process.

Pattern studies tend to be phylogenetic, process studies tend to be based on model species.

The point of this talk is that modern tools of phylogenetics permit new levels of study of behavior, and new perspectives on behavioral evolution.

This is NOT a rejection of statistical hypothesis testing, or ontogenetic perspectives, or "the comparative method," or use of models, or any of the alternative epistemologies of science. We need all these tools.

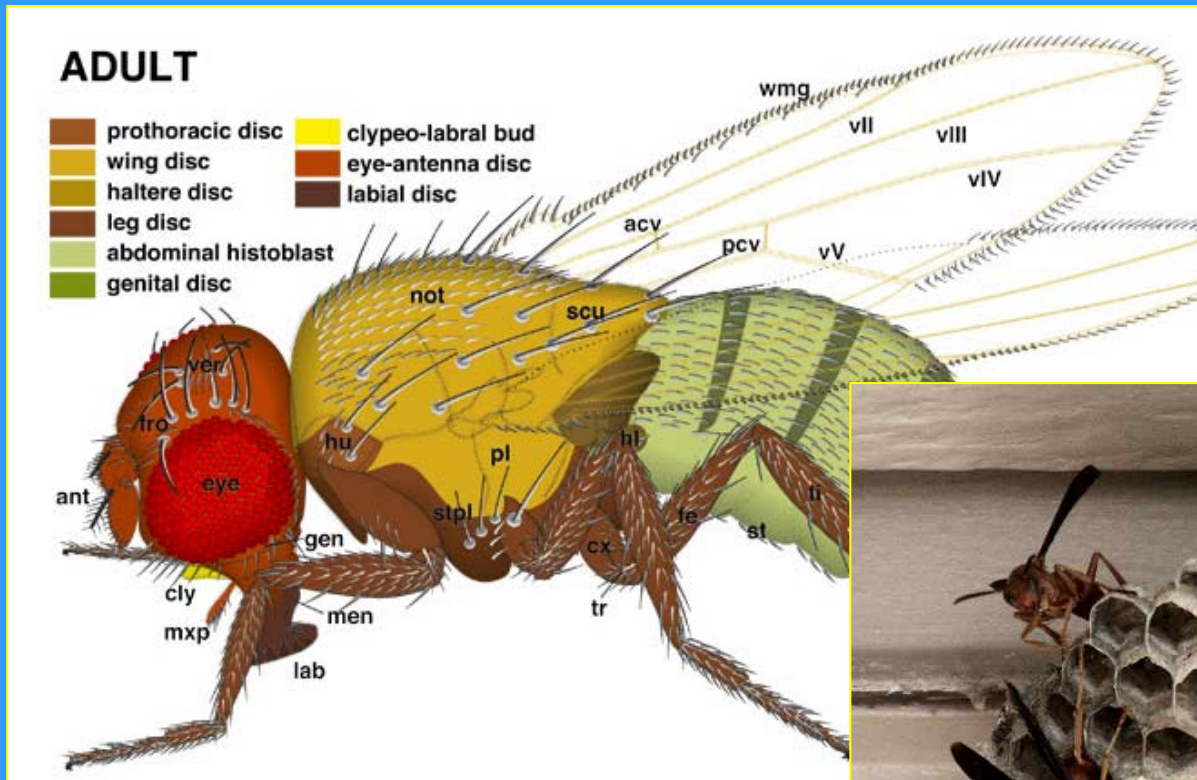




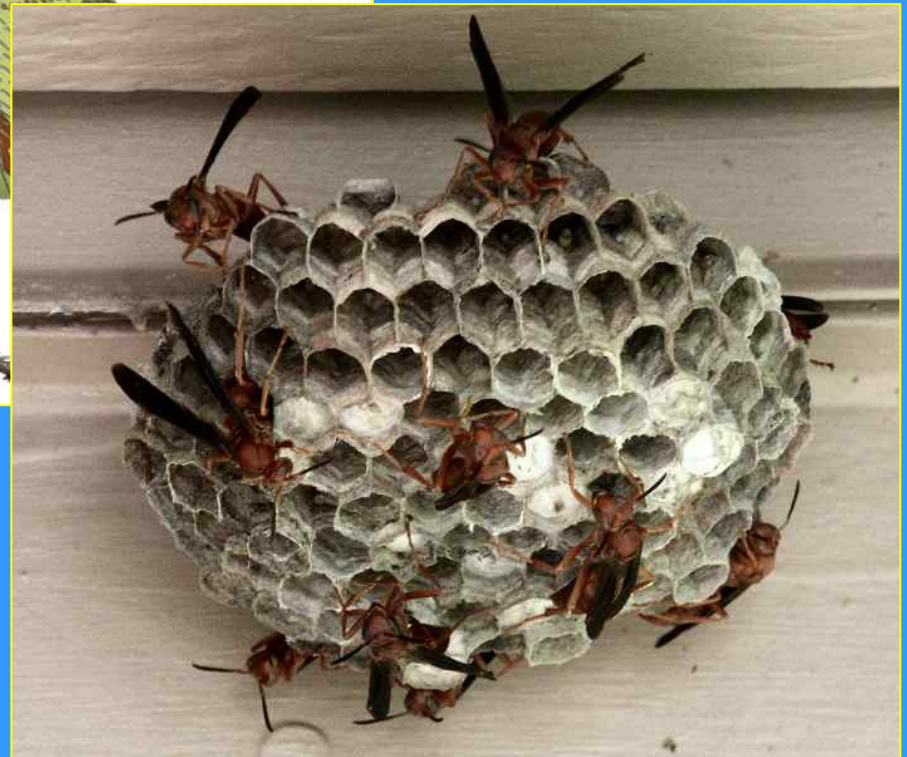
1. Limits of model systems.
2. Classical ethology, and performance of behavioral data in evolutionary studies
3. Conflict with status quo definitions in behavioral ecology.
4. Comparison with DNA

Much of what we know about “evolution” is based on model organisms.

Genetics:
Drosophila



Evolution of social
behavior: *Polistes*





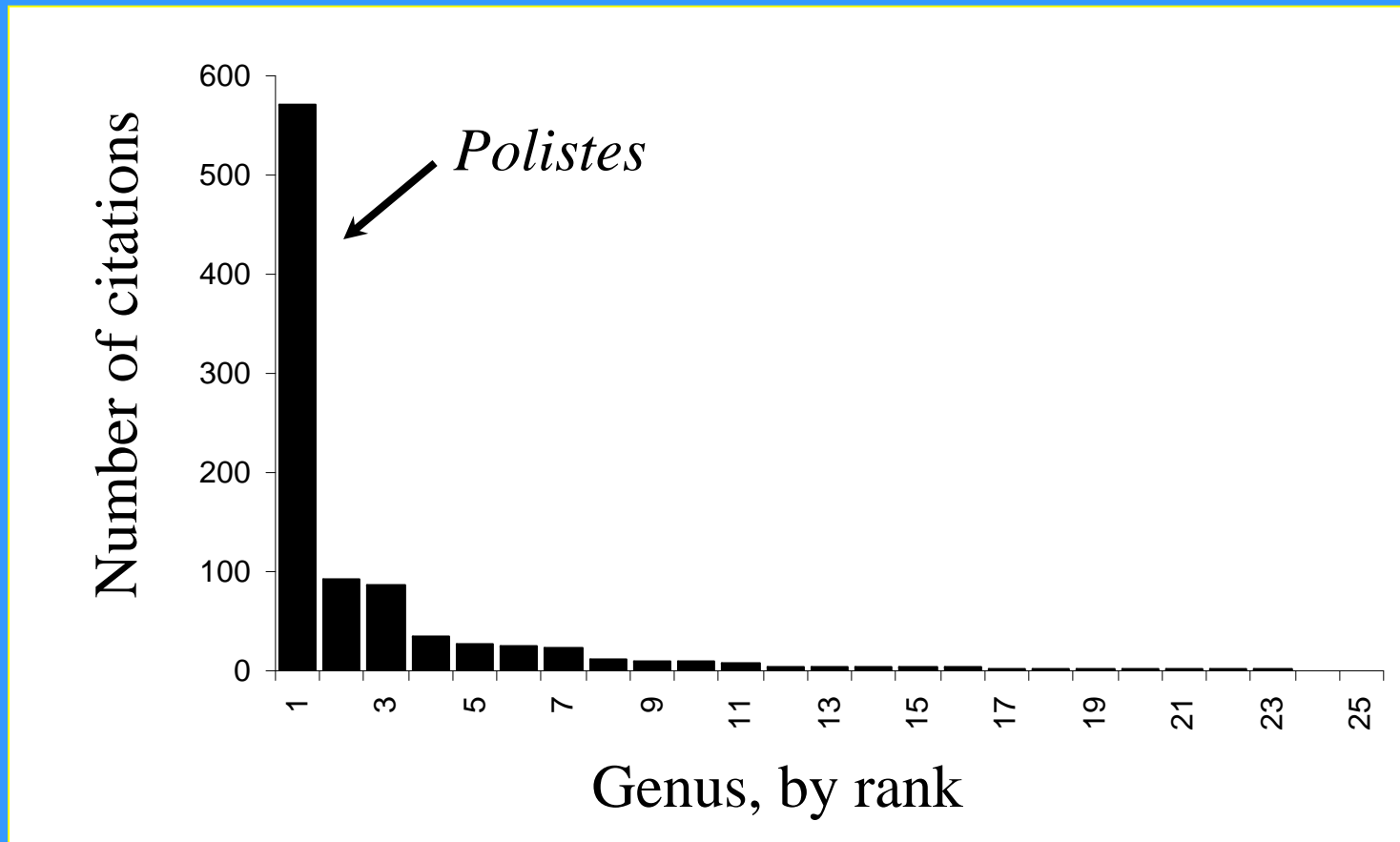
UNESP - SÃO JOSÉ DO RIO PRETO

Asteloeca ujelhyi

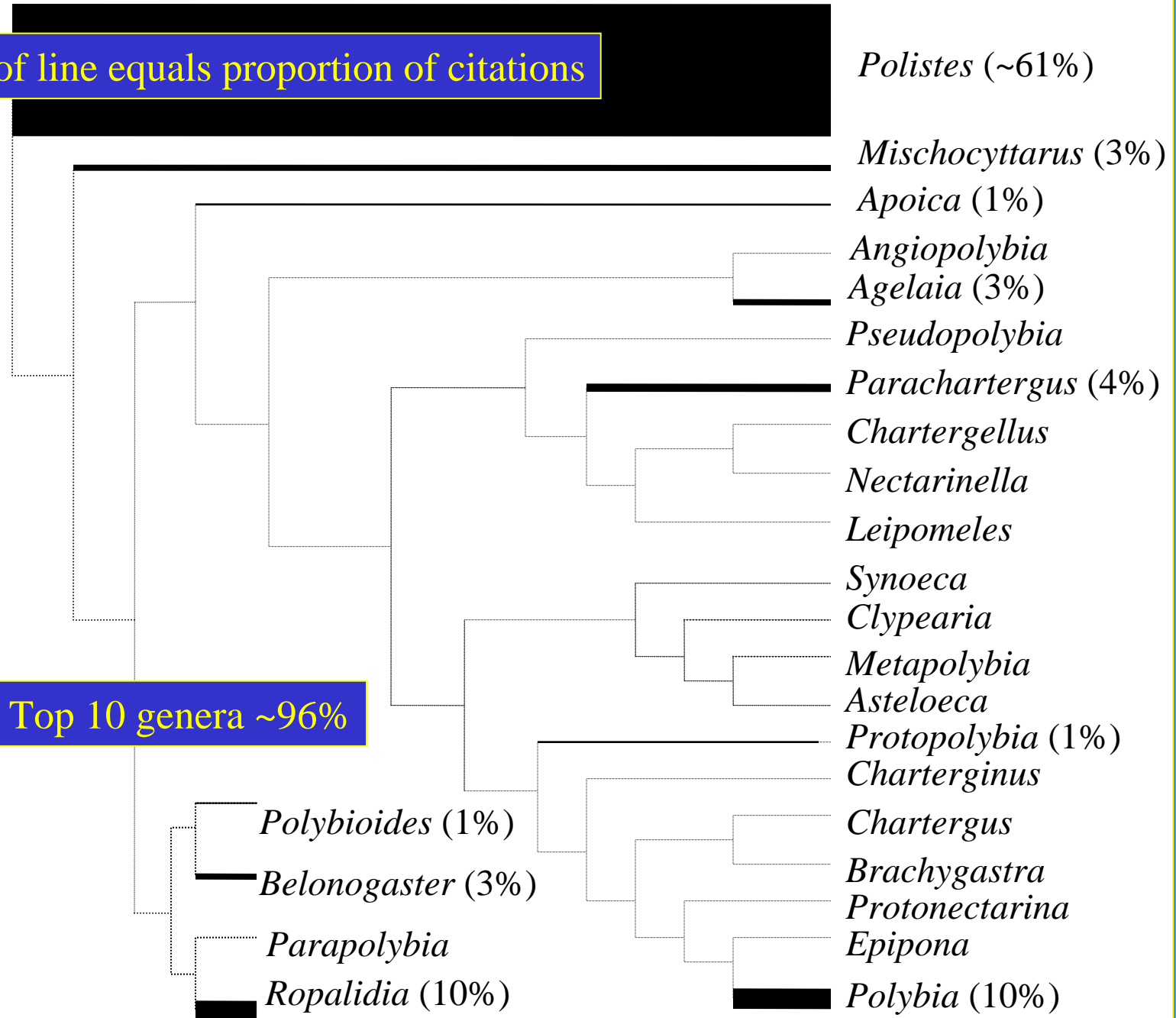
Nova Mutum, MT

But what do models teach us?

SCI Citations from 1980-2004 for 25 genera of polistine wasps, genus name in title, abstract or key words (925 papers total)

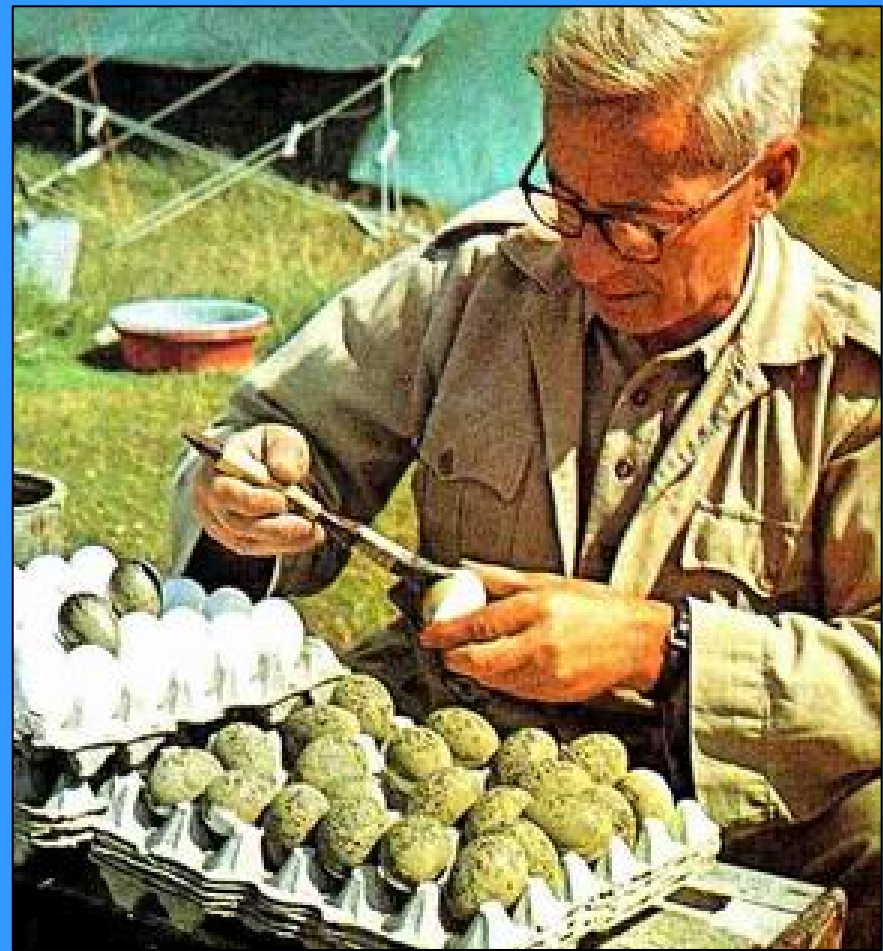


Width of line equals proportion of citations



Top 10 genera ~96%

Tinbergen's four categories of questions regarding behavior



Function: selective context, adaptation

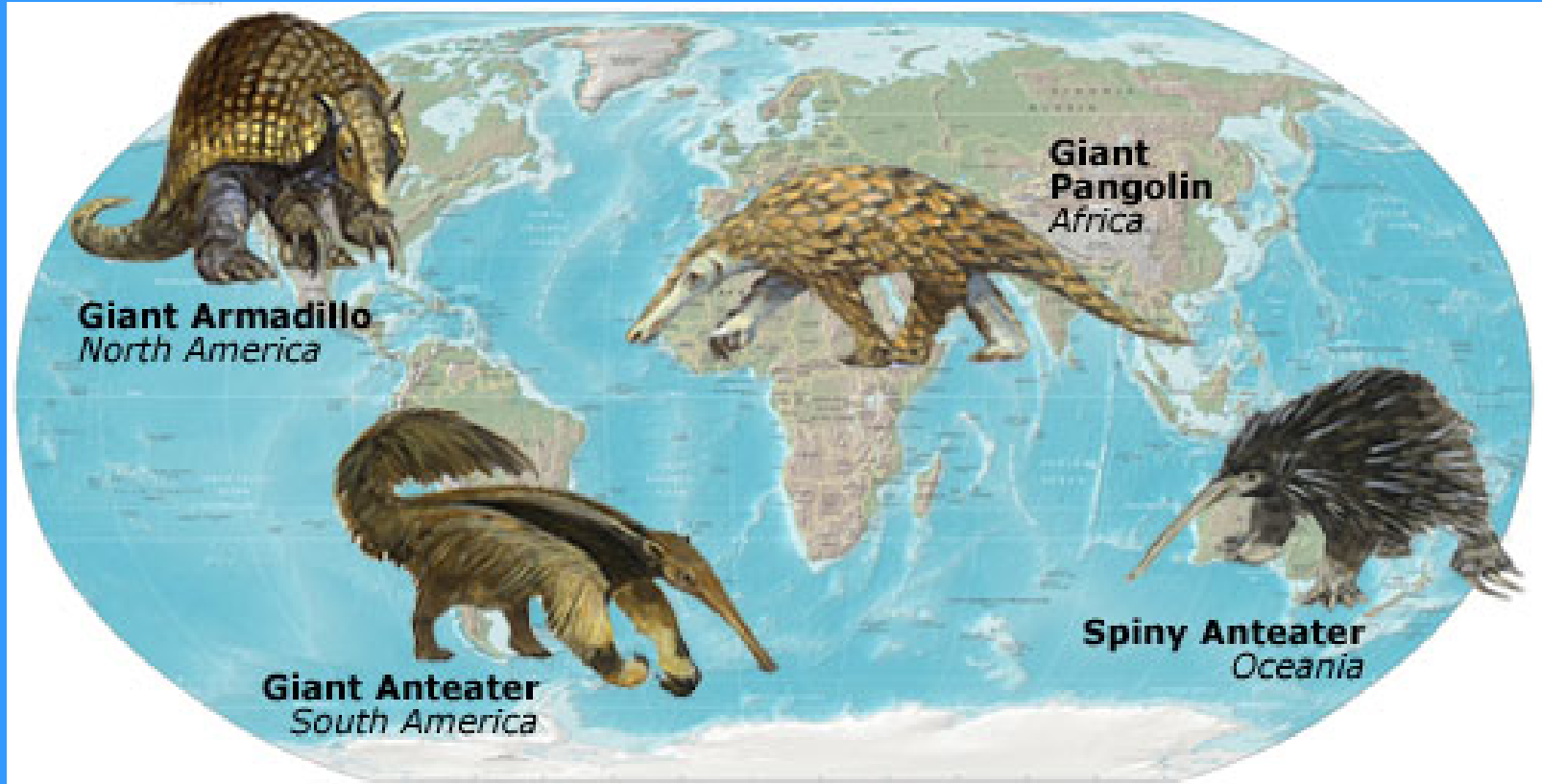
Phylogeny: origin and history (*models not appropriate*)

Proximate mechanisms: physiology, motivation, perception

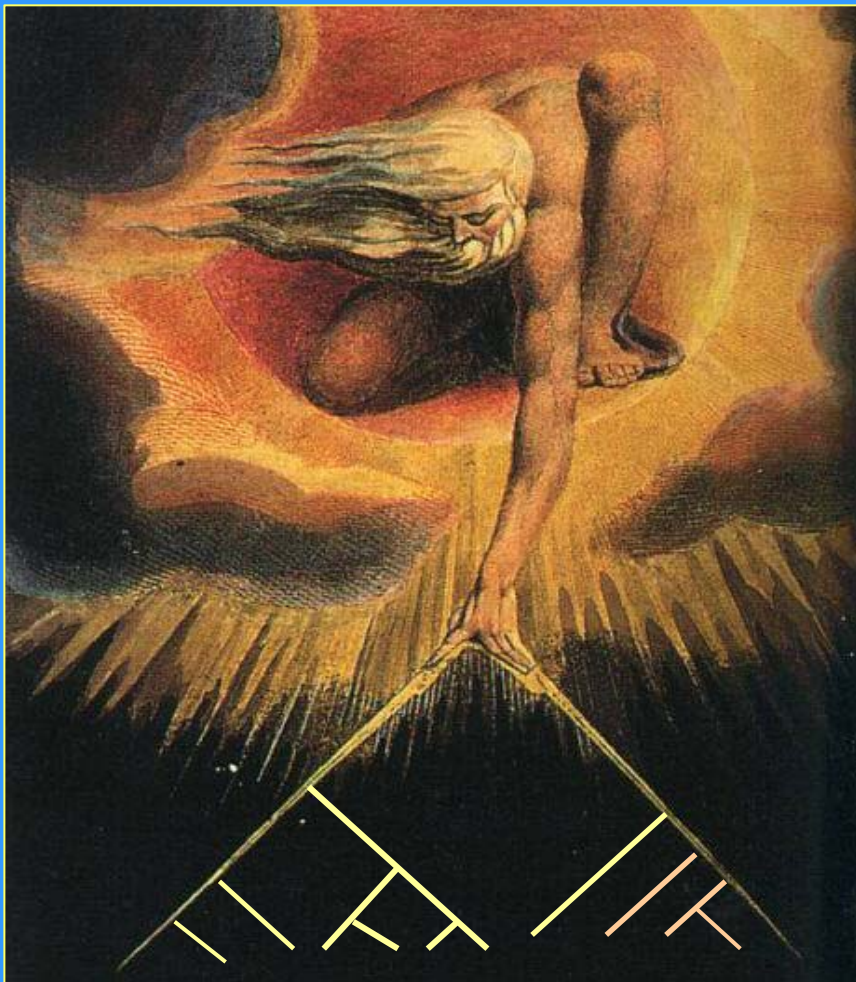
Ontogeny: development, gene-environment interaction

Convergence

Widely feared as a problem in inferring evolutionary history, but is it really a difficulty in actual studies of evolution?



Phylogenetic perspectives are *exactly* what we need to discover common heritage and convergence.



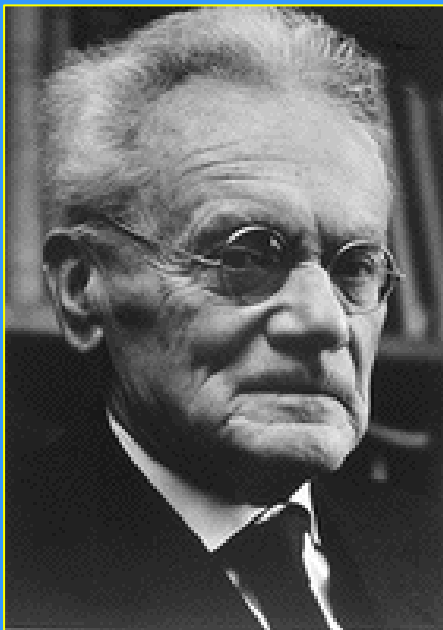
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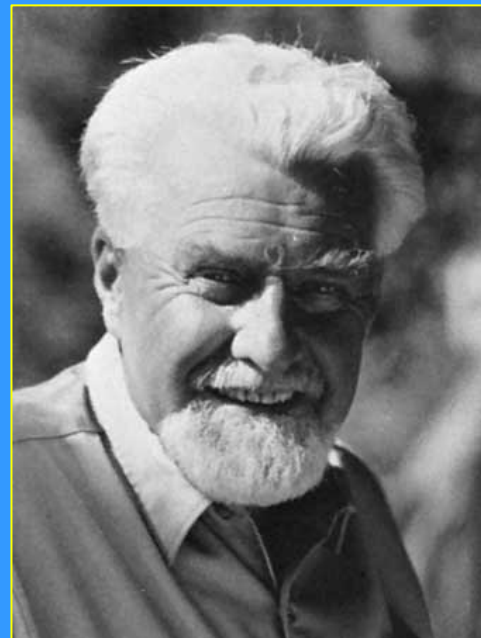
Ethology was explicitly evolutionary

Oskar Heinroth. 1910. Beitrage zur Biologie, namentlich Ethologie un Psychologie der Anatiden.

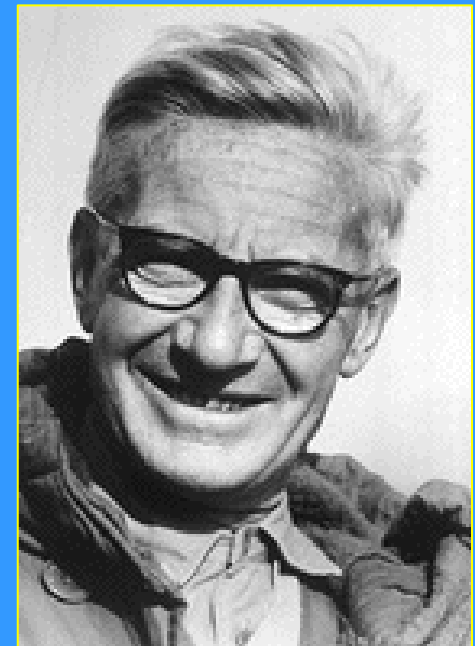
1973 Nobel Prize in Medicine awarded to three ethologists



Karl von Frisch



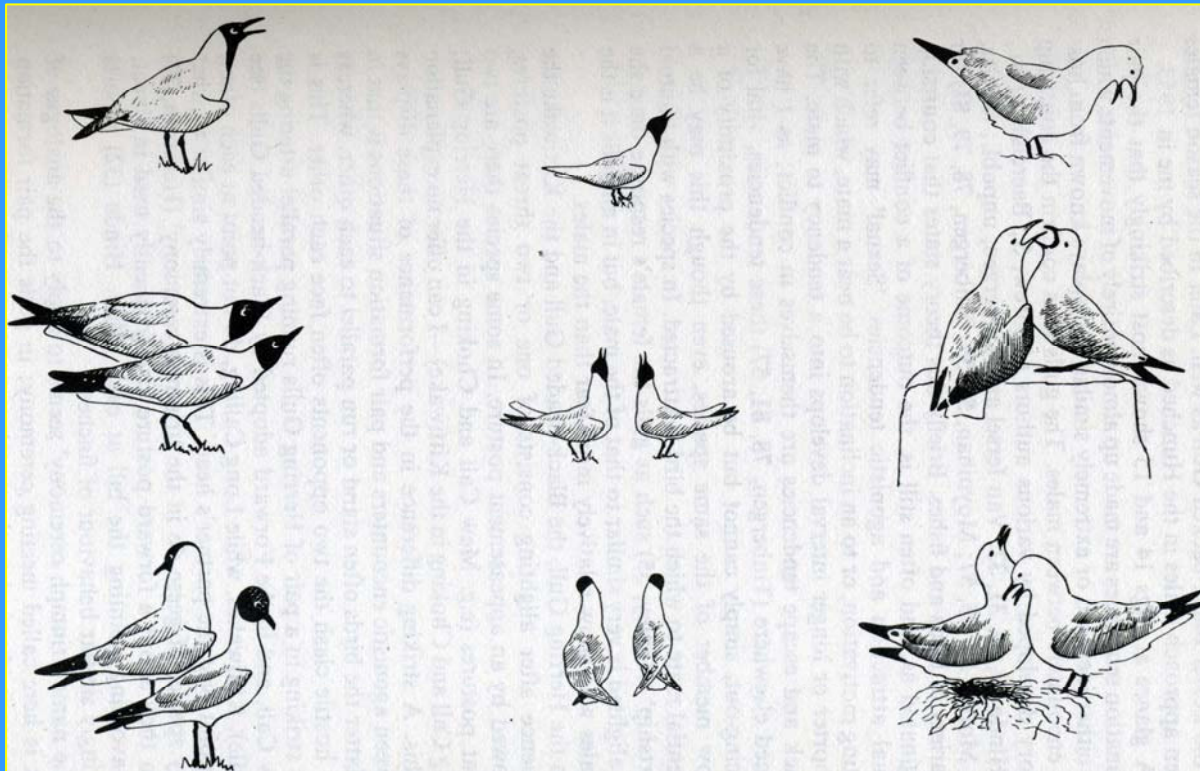
Konrad Lorenz



Niko Tinbergen

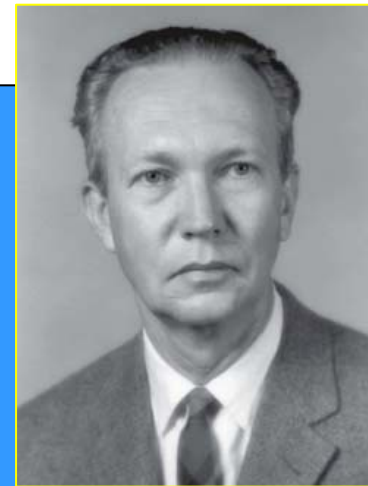
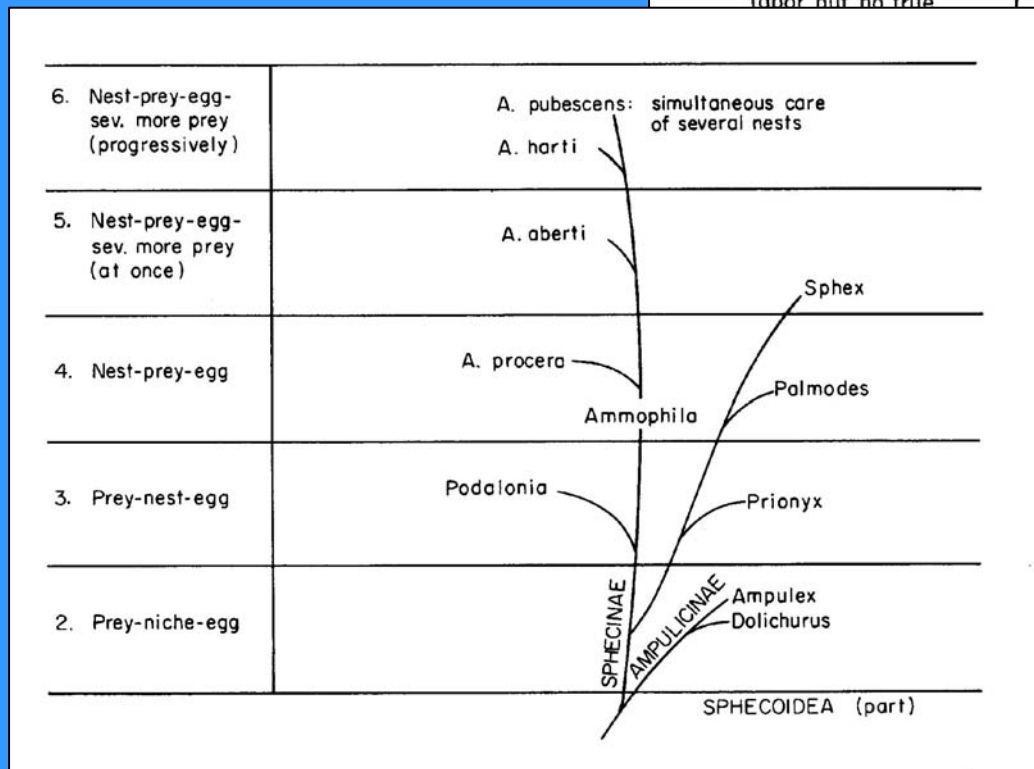
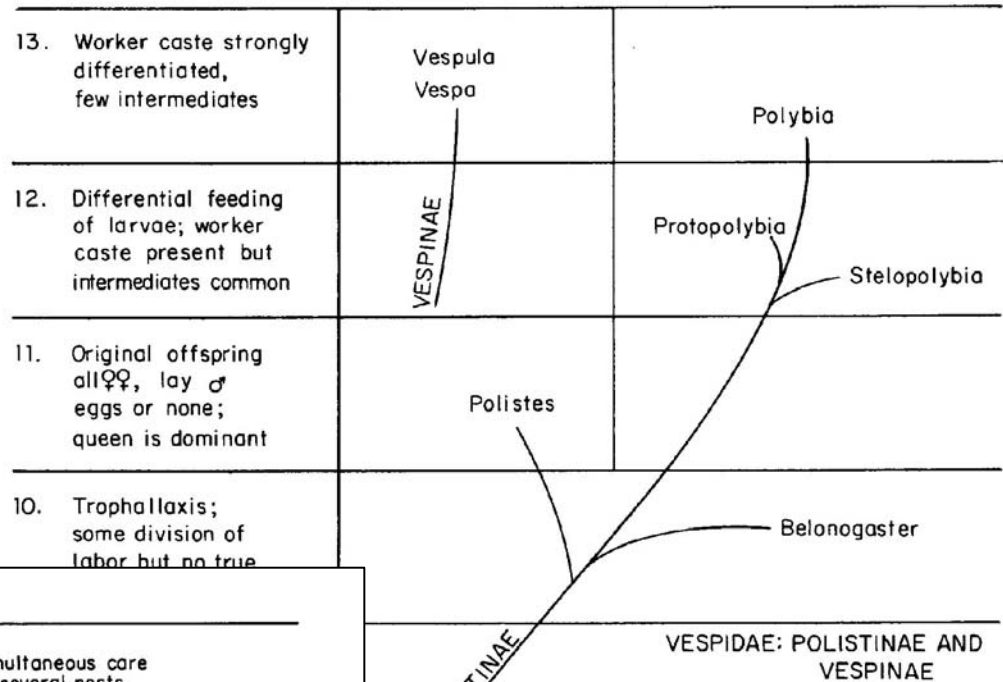
- Homologia: similaridade em forma devido a uma origem única, presente em um **único** ancestral comum.
- Homoplasia: similaridade em forma não devido a uma única origem. Eventos evolutivos distintos.

Behavioral homology can be proposed using Remane's classical criteria of position (in a sequence) special quality (function) or connection by intermediates (developmentally, or other species.)

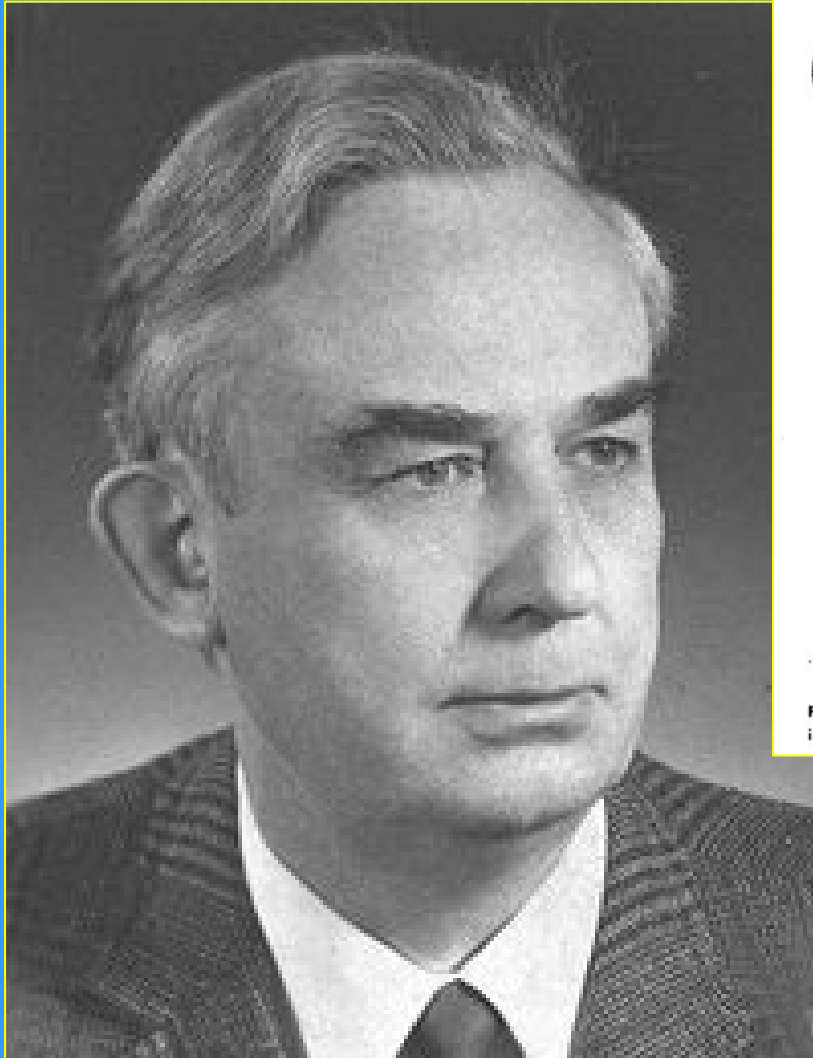


From Tinbergen

Evolution of nesting behavior in wasps, as *scala naturae* (from Evans 1958, as drawn in Wilson 1971)



Howard Evans



Willi Hennig

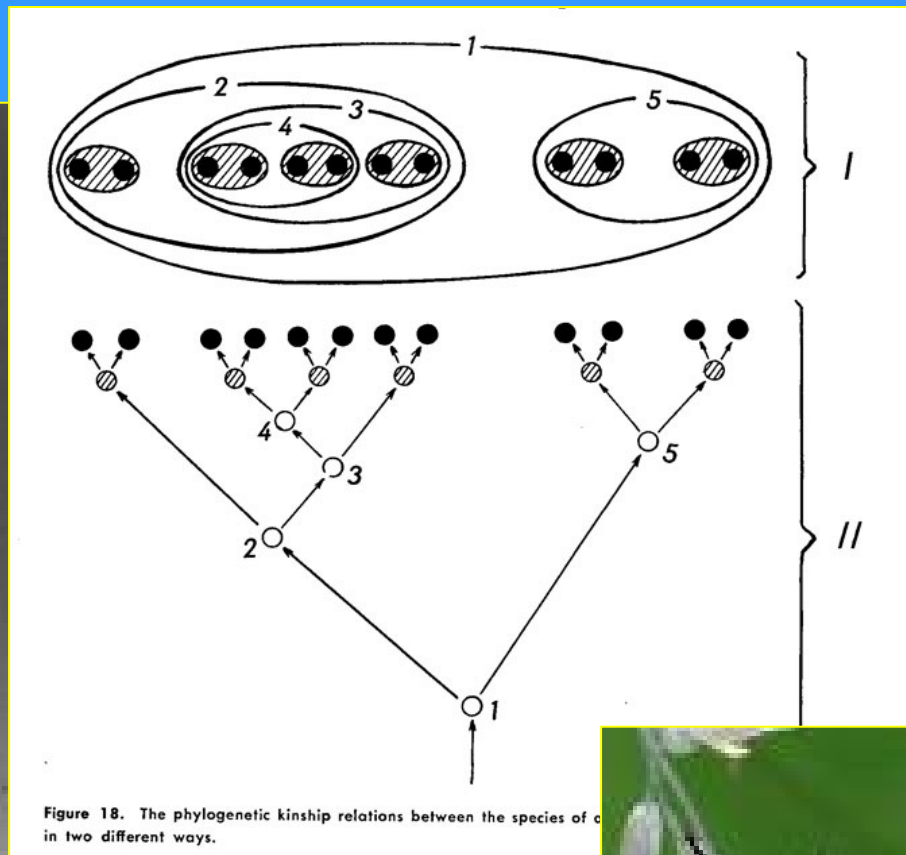


Figure 18. The phylogenetic kinship relations between the species of Odonata in two different ways.

Congruence with other data.

Synapomorphy



Table 1 Criteria of behavioral homology used in several studies, in chronological order, beginning 1951.

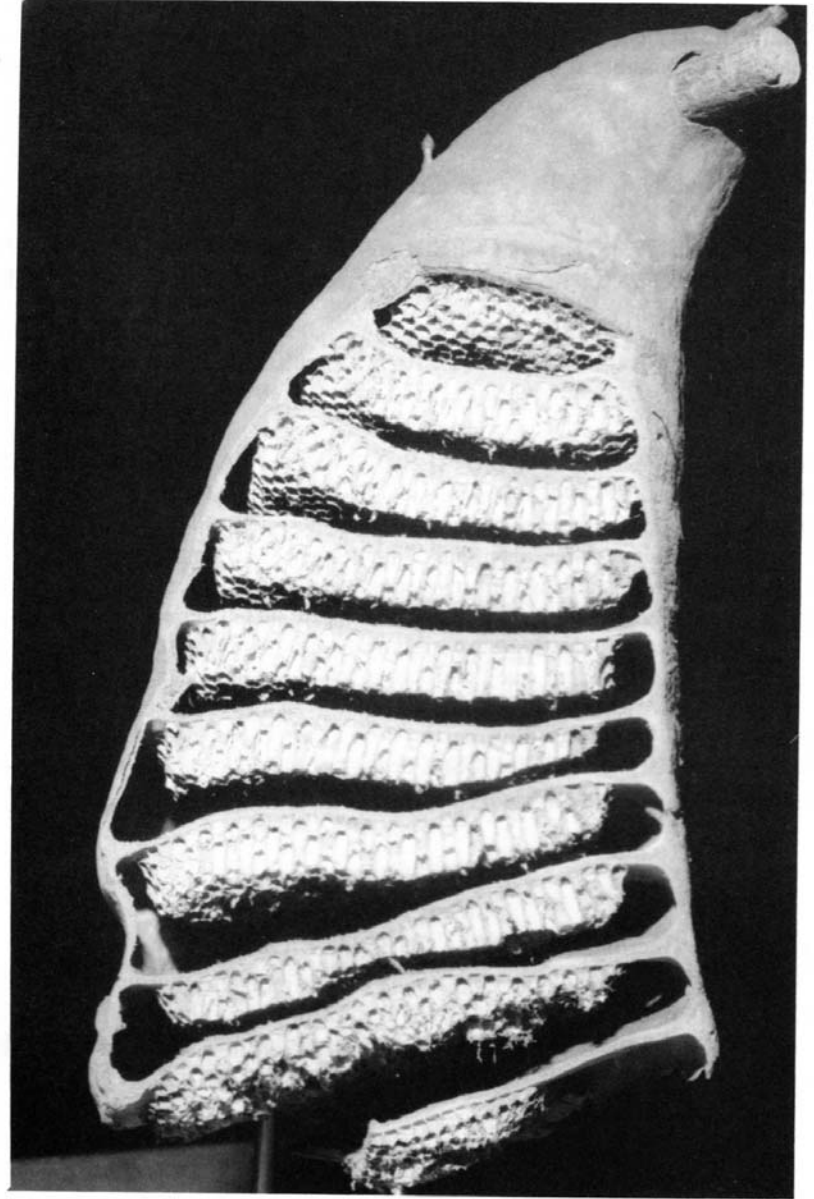
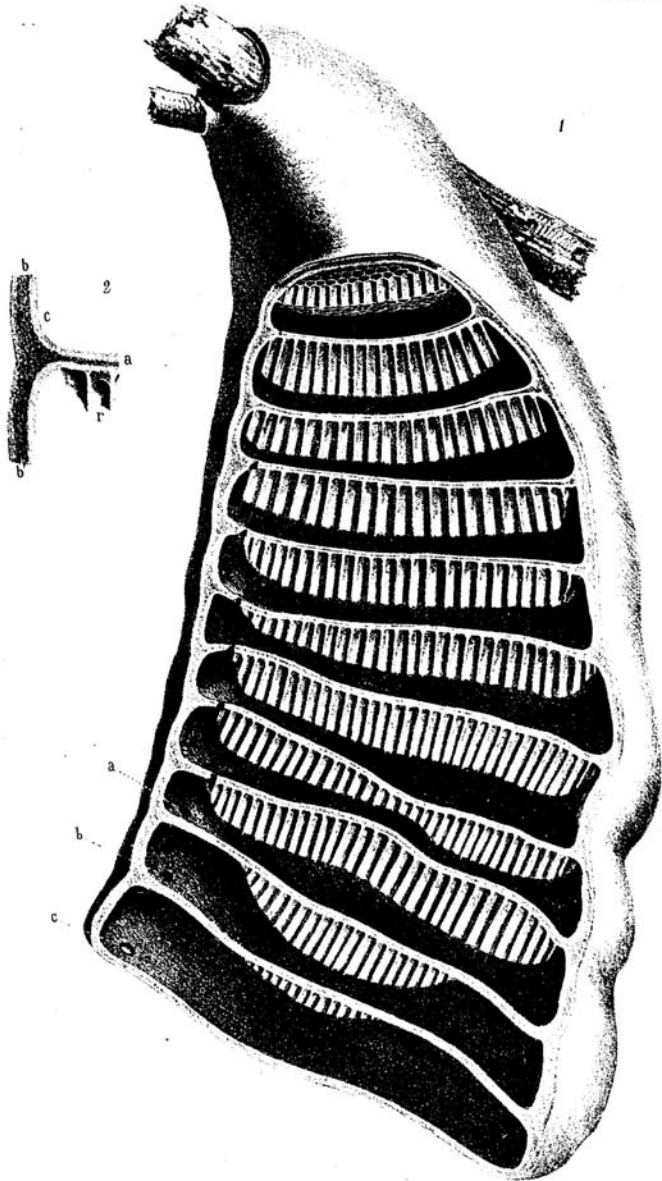
Taxa	Traits used	Homology criteria ^a	Author
Diverse birds	Locomotion, ritual motions	Remane	Daanje (23)
4 genera of Balloon flies	Courtship	Connection by intermediates	Kessel (50)
General discussion		Morphology, motivation, Remane	Baerends (3)
Many cricket species	Songs	Special quality	Alexander (1)
Red jungle fowl	Entire repertoire	Ontogeny, special quality	Kruijt (53) ¹
22 families of caddisflies	Architecture, weaving	Special quality, ontogeny	Ross (85)
45 families of insects	Grooming	Morphology, special quality	Jander (49)
General discussion		Morphology, Remane	Atz (2)
General discussion		Morphology	Hodos (45)
12 subfamilies of Balloon flies	Courtship	Congruence with other data	Chvála (14)
4 genera of finches	Songs	Motivation, Remane	Mundinger (75)
7 subfamilies of spiders	Architecture, weaving	Special quality, morphology	Eberhard (28)
7 genera of sunfish	Feeding	Congruence with other data	Lauder (54)
5 genera of yellow-jackets	Architecture, social traits	Congruence with other data	Carpenter (11a)
7 species of fruit flies	Courtship	Congruence with other data	Grimaldi (39)
6 genera of social wasps	Architecture, social traits	Congruence with other data	Carpenter (12a)
7 genera of sticklebacks	Courtship	Congruence with other data	McLennan et al (67)
13 species of sandpipers	Songs	Special quality	Miller et al (72)
16 families of caddisflies	Architecture	Special quality	Wiggins & Wichard (111)
19 genera of spiders	Architecture, weaving	Congruence with other data	Coddington (18)
21 species of manakins	Courtship	Congruence with other data	Prum (83)
24 families of caddisflies	Architecture	Congruence with other data	Weaver (102)
29 genera of paper-wasps	Architecture	Ontogeny, congruence with other data	Wenzel (105, 106)

^a Remane's criteria (placement, special quality, connection by intermediates) are listed separately unless an author used more than one, in which case only "Remane" is listed. In many cases there was no explicit statement of criteria used.

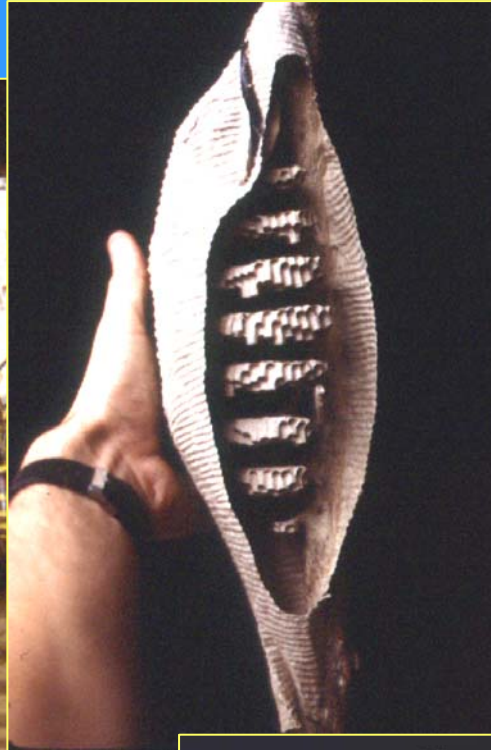
From Wenzel, 1992

23 authors across many animal groups, from species to families used the same criteria to homologize behavior as morphologists use.

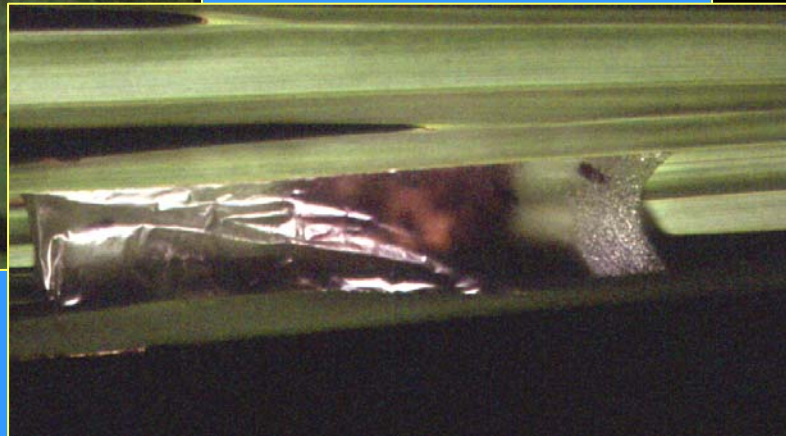
Courtship and nest architecture dominate among the "useful" behaviors. Grooming is also useful (and often less problematic for homology.)



na tatua, n° 763. Ce nid, décrit par Cuvier (1797), a été figuré par Saussure (1853-1858) un
tard. Il est toujours bien conservé.

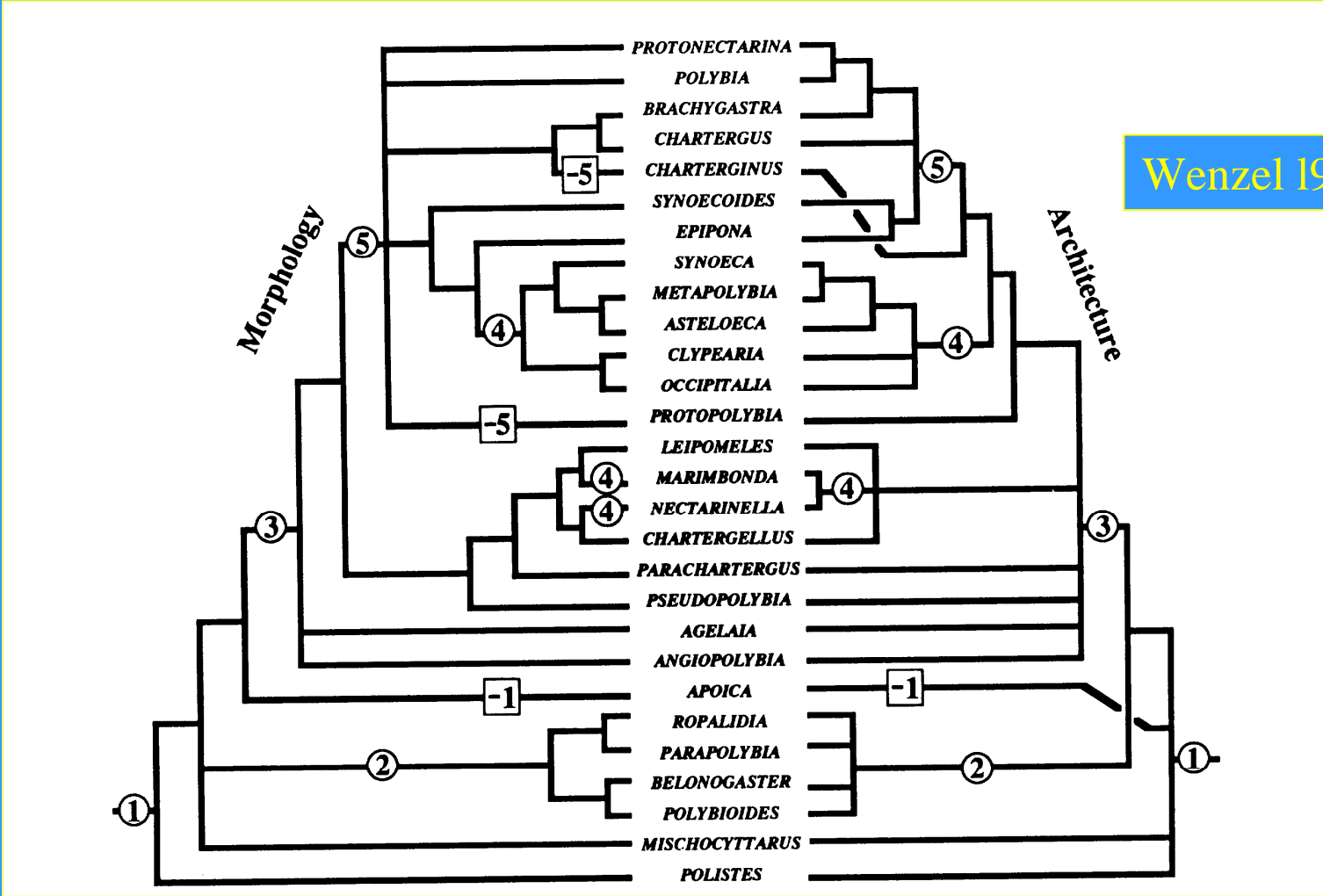


Combs can be simple, with an envelope around them, or built upon the envelope. They can be built gradually or in sudden bursts of effort.



Cryptic nests can be colored, countershaded, invisible, lined, or even built to resemble the structure of the leaf.

Wenzel 1993



Cladogram of building behaviors matches cladogram of morphology fairly well. Behavioral data is more stable than morphology (higher CI), including if behavior is simply plotted on morphology tree.

TABLE 1. Systematic data sets used for comparison of character CIs within data sets. See text for description. RANK is the taxonomic rank of the terminal taxa among which relationships were investigated. MCHAR and BCHAR are the number of morphological and behavioral characters, respectively. MCI and BCI are the CIs for morphological and behavioral characters, respectively. The references include those from which the morphological and behavioral characters being analyzed were taken as well as any others that provided information used to construct trees.

Set	Taxon	RANK	#TAXA	MCHAR	BCHAR	MCI	BCI	REF.
1	Polistine wasps	genera	28	34	18	0.60	0.62	1
2	Eumenine wasps	genera	25	25	1	0.86	1.00	2
3	Vespine wasps	spp/gen	7	17	8	0.88	0.71	3, 4
4	Vespid wasps	subfam	6	20	8	0.78	0.96	5-7
5	<i>Apis</i> bees	species	6	9	3	0.94	0.83	8
6	Meloid beetles	genera	9	21	2	0.87	1.00	9
7	Arachnids	orders	11	63	1	0.71	1.00	10
8	Shrimps	orders	5	3	1	0.83	1.00	11
9	Gasterosteiform fishes	genera	6	18	17	0.86	0.96	12, 13
10	No. Amer. Hylid frogs	species	13	9	4	0.94	0.66	14-18
11	Pipid frogs	spp/gen	7	52	2	0.88	0.75	19, 20
12	<i>Triturus</i> newts	species	9	2	11	0.52	0.81	21-26
13	Seaducks	spp/gen	10	12	2	0.83	0.75	27-29
14	Alcid birds	species	23	31	2	0.82	0.70	30
15	Pelecaniform birds	families	13	26	5	0.92	1.00	31
16	Ochthoeca flycatchers	genera	5	5	2	0.90	1.00	32
17	Tody-tyrant flycatchers	genera	9	8	2	1.00	0.75	33
18	<i>Myiobius</i> flycatchers	genera	5	8	2	0.85	1.00	34
19	Empidonax flycatchers	genera	7	6	3	1.00	0.83	32
20	Manakin birds	species	19	36	29	0.90	0.84	35, 36
21	Squamate reptiles	families	19	61	3	0.68	0.67	37-39
22	Sand lizards	species	10	36	2	0.87	0.67	40

References: 1. Carpenter and Wenzel, unpubl. data; 2. Carpenter and Cumming, 1985; 3. Carpenter, 1987; 4. Carpenter, 1989a; 5. Carpenter, 1982; 6. Carpenter, 1988; 7. Carpenter, 1989b; 8. Alexander, 1991; 9. Pinto, 1984; 10. Schultz, 1990; 11. Schram, 1986; 12. McLennan et al., 1982; 13. McLennan et al., 1982; 14. Cannatella and Arnold and Burton, 1978; 15. Cannatella and Burton, 1978; 16. Cannatella and Burton, 1978; 17. Cannatella and Burton, 1978; 18. Cannatella and Burton, 1978; 19. Cannatella and Burton, 1978; 20. Cannatella and Burton, 1978; 21. Cannatella and Burton, 1978; 22. Cannatella and Burton, 1978; 23. Cannatella and Burton, 1978; 24. Cannatella and Burton, 1978; 25. Cannatella and Burton, 1978; 26. Cannatella and Burton, 1978; 27. Cannatella and Burton, 1978; 28. Cannatella and Burton, 1978; 29. Cannatella and Burton, 1978; 30. Strauch, 1985; 31. Cracraft, 1985; 32. Cracraft, 1985; 33. Cracraft, 1985; 34. Cracraft, 1985; 35. Cracraft, 1985; 36. Cracraft, 1985; 37. Estes et al., 1988; 38. Presch, 1988; 39. Presch, 1988; 40. Presch, 1988.

CI morph = 0.84

CI behav = 0.84

De Querioz and Wimberger, 1993

Ethological data sets are often of the highest quality

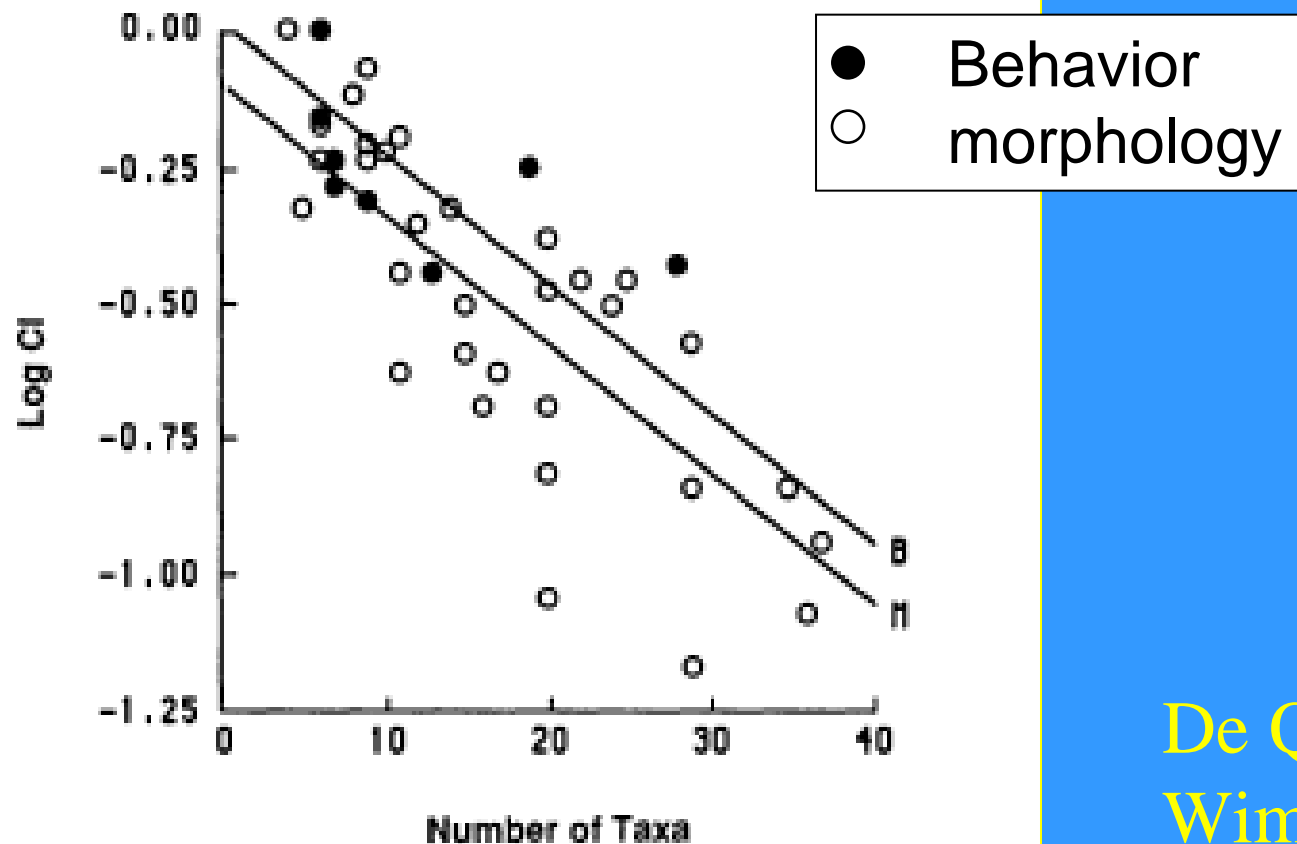


FIG. 2. Overall log CIs for entire data sets plotted against number of taxa. Open circles are for morphological data sets, closed circles are for behavioral data

De Queiroz &
Wimberger, 1993

Ethological data sets are often of the highest quality

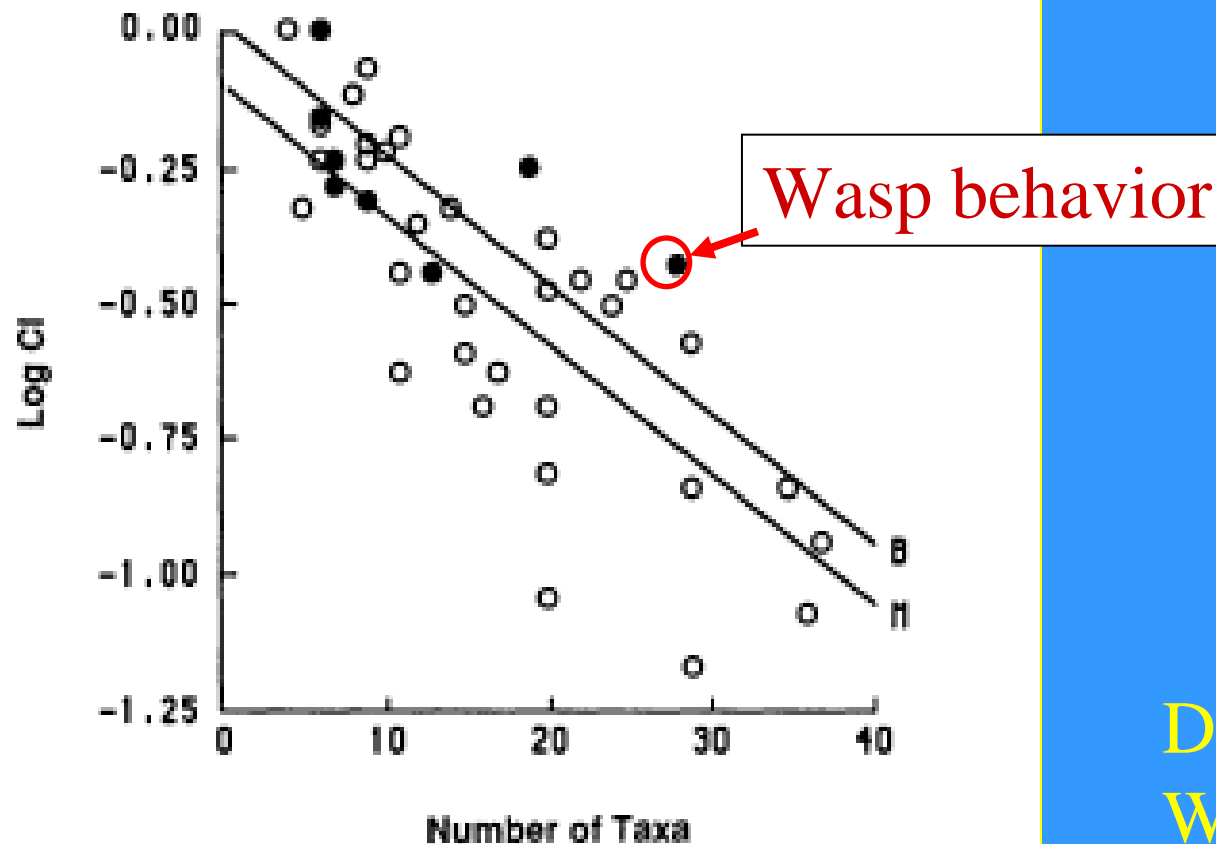


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De Queiroz &
Wimberger, 1993

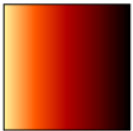
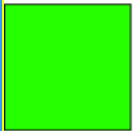
Evolution of phase change in locusts, Hojun Song.



Isolated / Sedentary

Background color

Black pattern

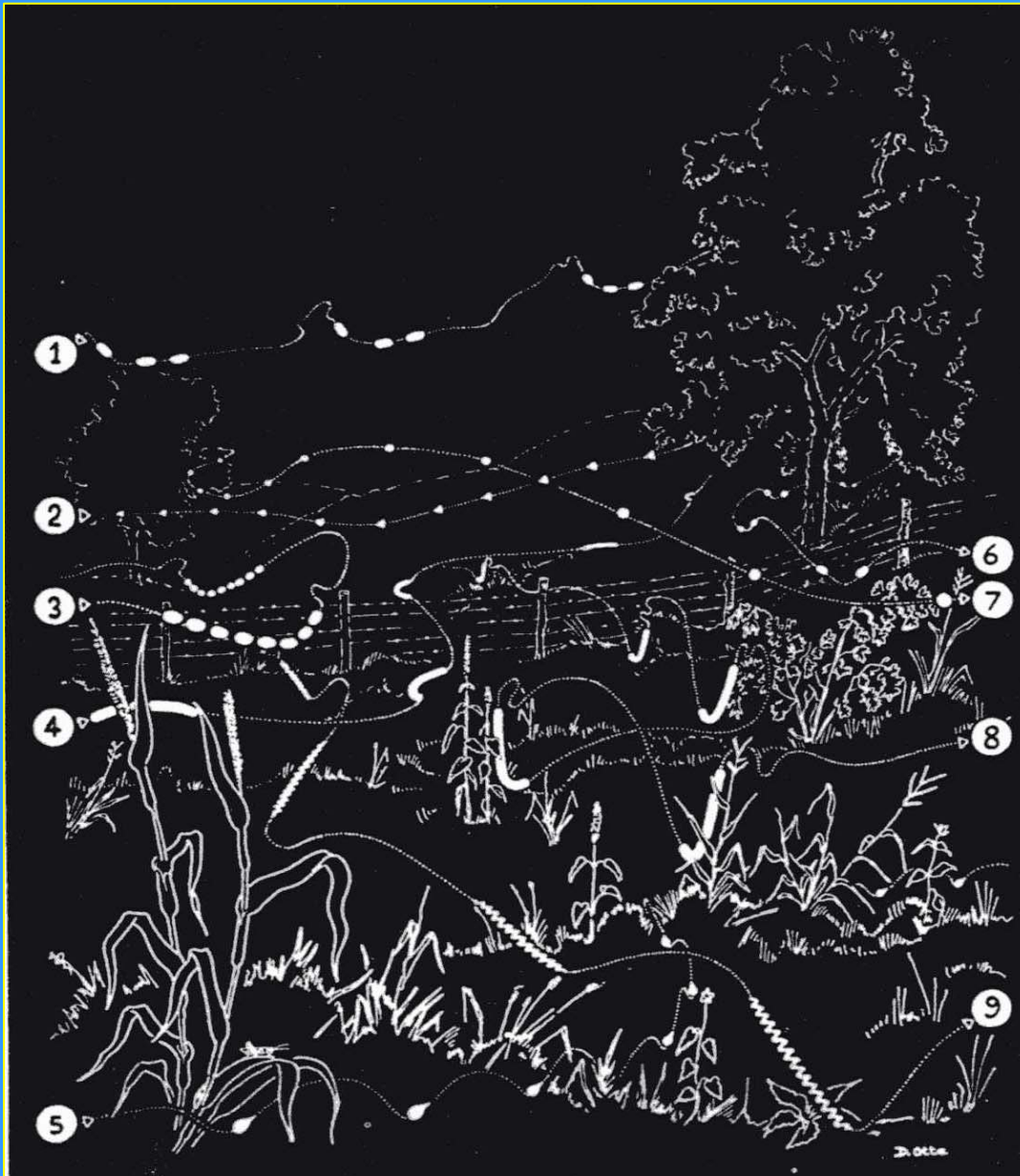


Schistocerca piceifrons

Evolution of host plant choice in leaf-mining moths, Sibyl Bucheli.

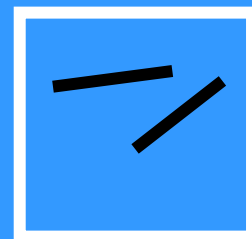
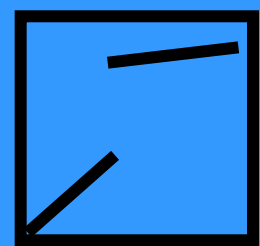
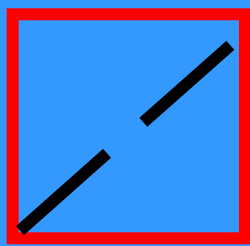
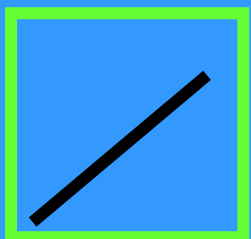
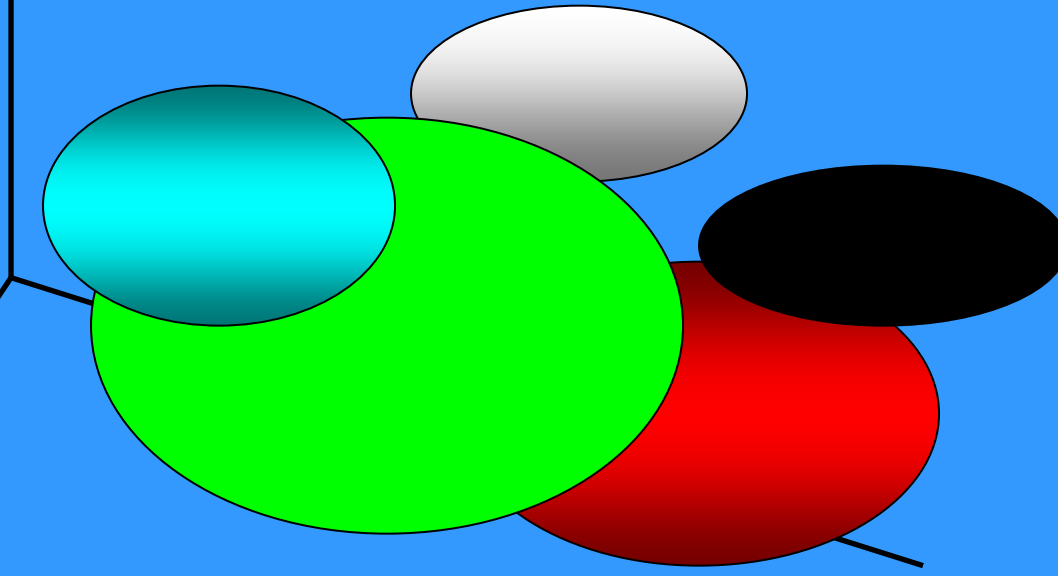
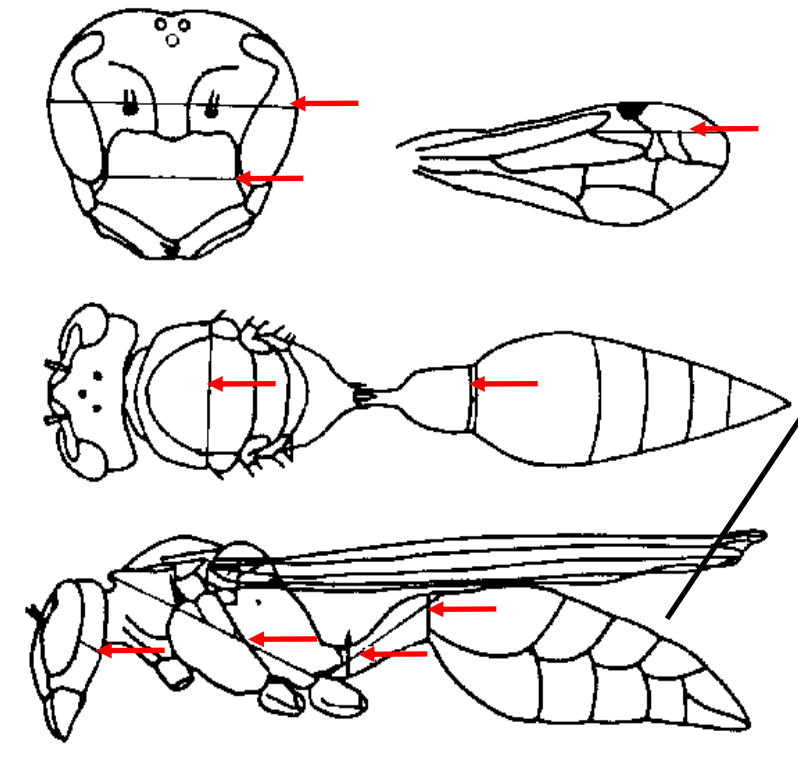


Evolution of photic sexual signals in fireflies, Marc Branham



Coleoptera:
Lampyridae

Caste determination in wasps



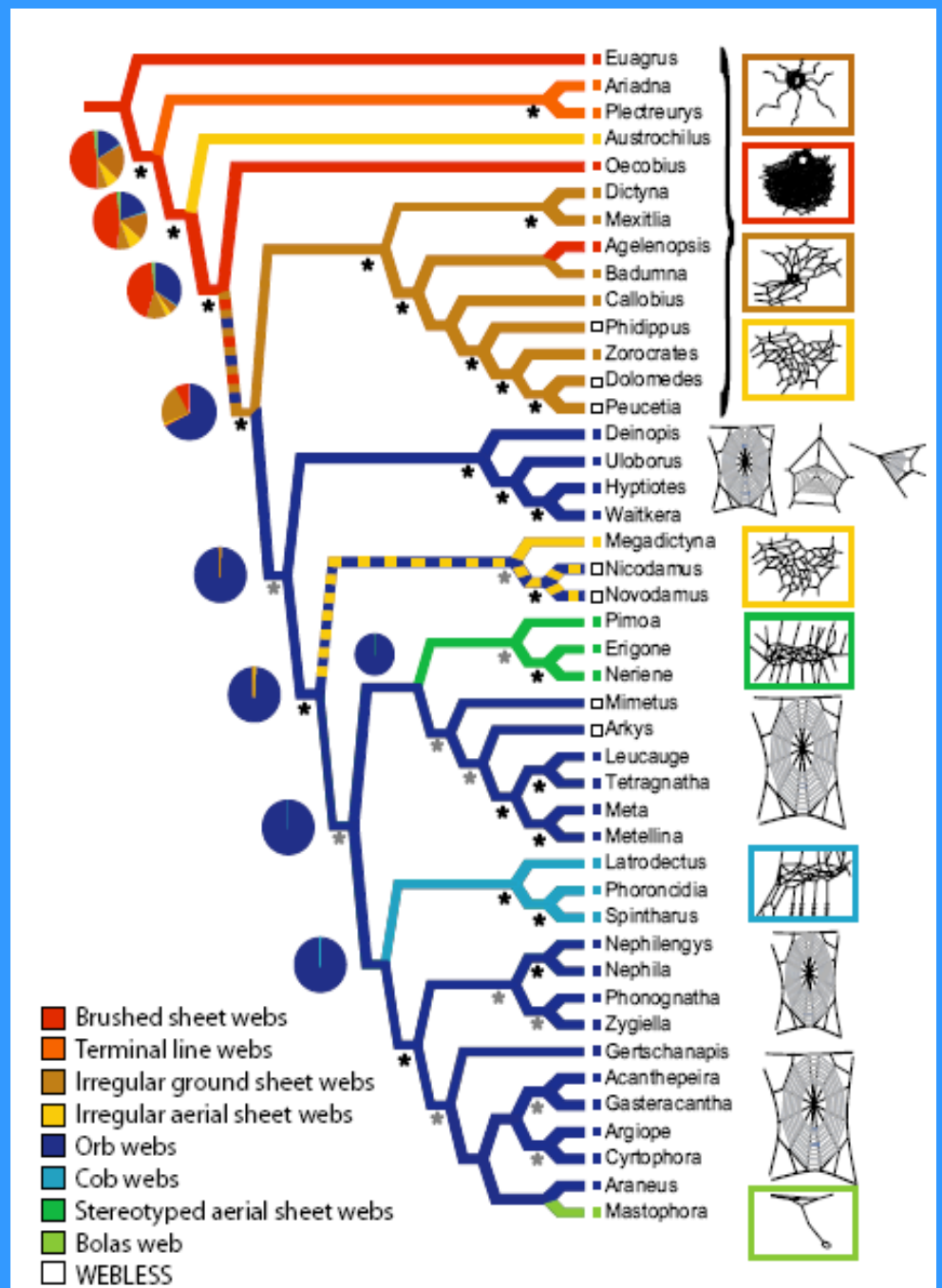
Fernando Noll

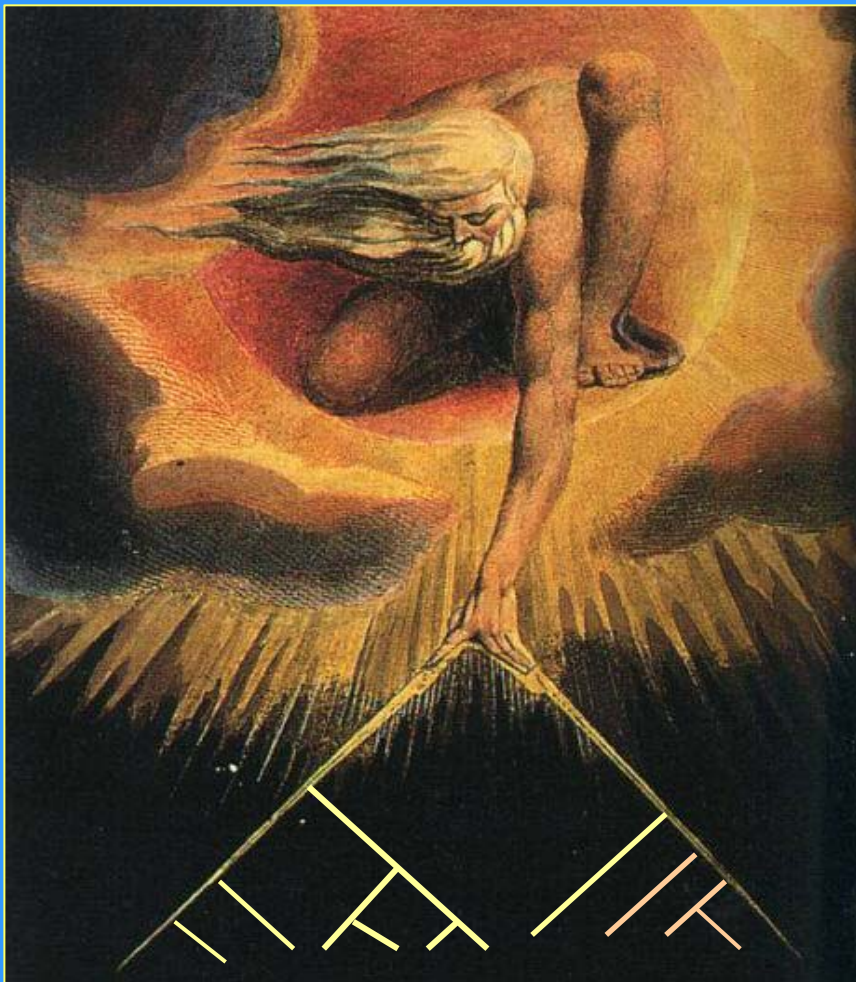
Blackledge et al, 2009.
PNAS 106: 5229-5234



Orb web design in spiders
appears to constrain
evolution

Ecological diversification
follows loss of the orb web
design in separate lineages,
repeatedly.





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Evolutionary studies of adaptation tend toward circular or teleological weakness

“Vertebrates evolved lungs to breathe air”

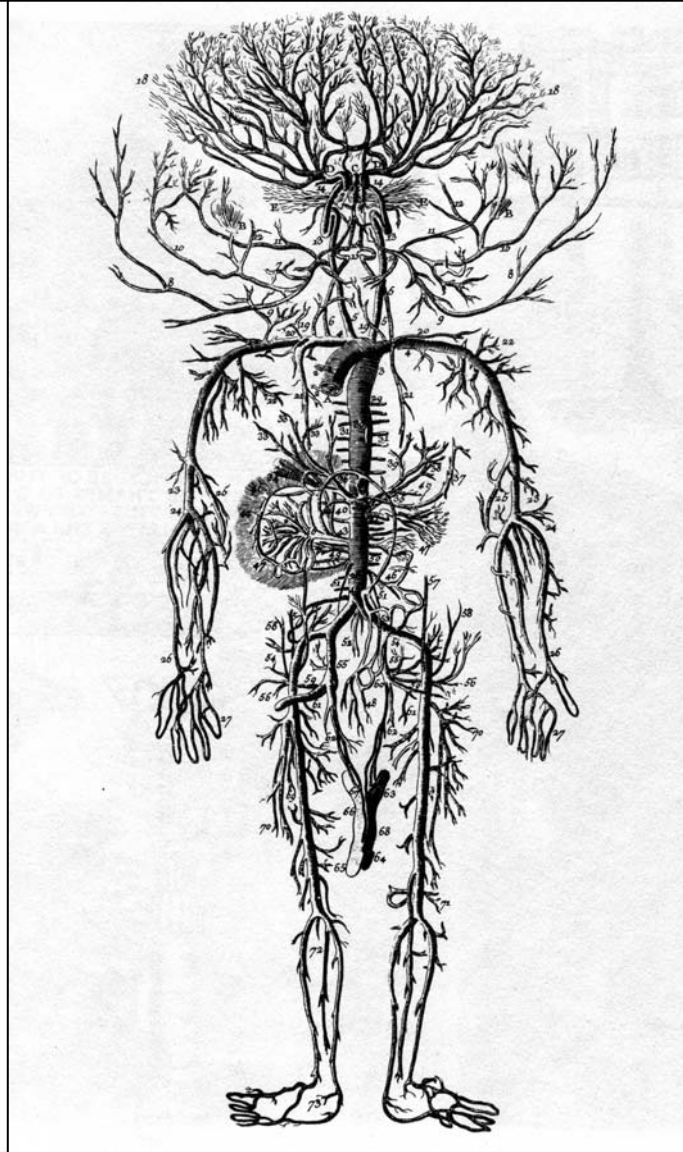
Origin of “adaptive” characters must precede selection that shapes them into their present function

Ethologists study a monophyletic group, a clade, and look for behavioral characters that are informative. This works well in defining descent with modification.

What about studies that focus on the behavioral or ecological characteristics first, and then search different taxa for meaningful evolutionary patterns?



A Gentleman



Studies of “descent with modification” would seem to enforce need to reconstruct history (“descent”) as much as possible.

However, students of behavior and ecology tend to define characters of interest outside of historical context.

“Herbivore”



- Homologia: similaridade em forma devido a uma origem única, presente em um **único** ancestral comum.
- Homoplasia: similaridade em forma não devido a uma única origem. Eventos evolutivos distintos.

Philosophy (but don't take it too far)

“Intensional” definition. The sum of attributes of a thing to which a given term is applied. Can apply to individuals natural groups and historical lineages.

Amnion of the egg defines all animals that are Amniota.

“Extensional” definition. Groups formed by pointing to members. Can be used for groups that do not have a unique set of attributes . No necessary relationship to history. Ecological definitions often take this form.

Turtles, snakes, lizards, and dinosaurs are reptiles.

Ecological principles (laws) tend to take a form such as
“Aquatic animals are streamlined”

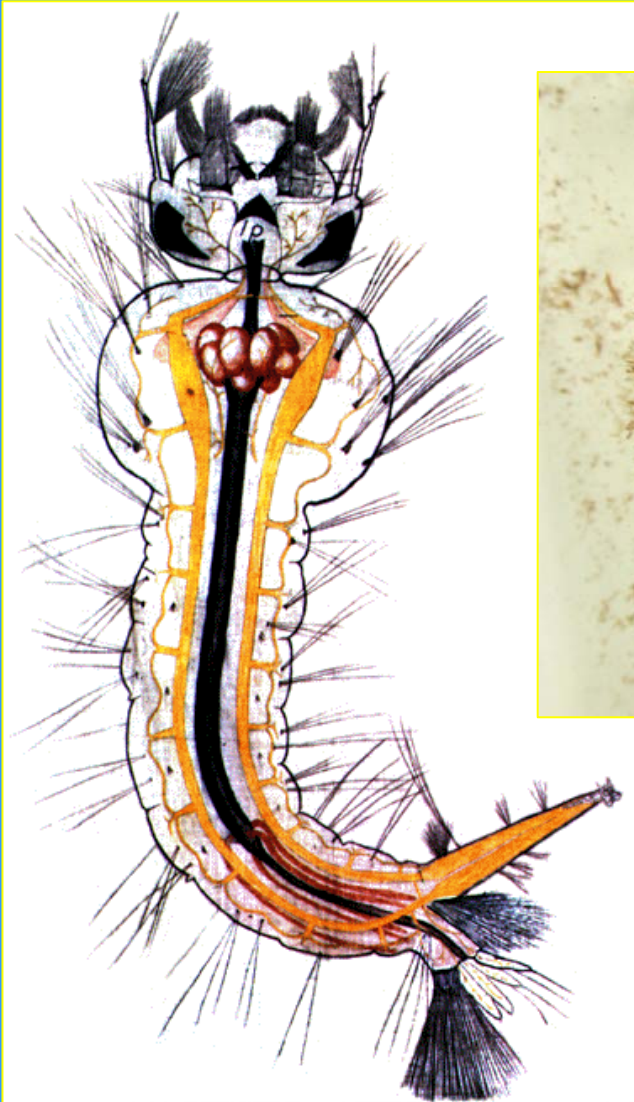
This looks like an intensional definition...



Carlyn Iverson



...but, then, someone points to aquatic animals that are *not* streamlined, and asks if these violate the principle...



...and the law is revised to say “If an aquatic animal is large, *then* it is streamlined.”



And someone points out large aquatic animals that are not streamlined....



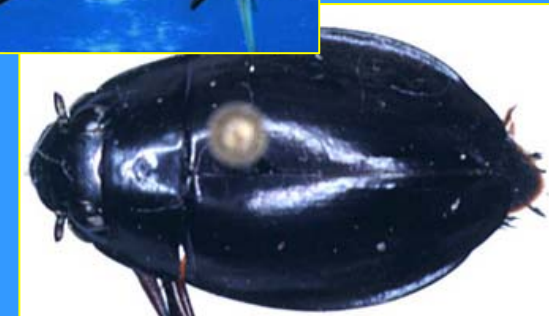
...and the principle is revised again to say “*If an aquatic animal is large and fast moving, then it is streamlined.*”



Eventually, we are happy with the principle in its revised form. It is become an extensional definition, where we are really just pointing to the members.

We narrow the first part to exclude counter examples, and keep the second part broad and non-specific, as inclusive as possible. Then we say it is a general law.

O objetivo principal em ecologia é encontrar um padrão que *não* se relacione com a história. “Animais aquáticos são todos elípticos.” Utilizamos muitos exemplos distintos e não de uma único evento evolutivo. Desse modo, não causa surpresa que a sistemática filogenética não seja útil.



Mas, similaridades gerais não causam problemas nos estudos detalhados.

“... ecologists define their characters of interest very broadly in order to *maximize the probability of homoplasy*.”

--Proctor, 1996, (emphasis in original),
in Sanderson and Hufford (eds), *Homoplasy*

“**parental behavior**” (Gittleman 1981)

“**lekking**” (Höglund 1989)

“**gregariousness**” (Sillén-Tullberg 1988)

“**mating frequency**” (Ridley 1989)

“**assortative mating**” (Crespi 1989)

“**cooperative breeding**” (Edwards and Naeem 1993)

“**polygamy**” (Wiklund and Forsberg 1991).



Behavioral characters often are used in a typological form, concealing useful detail, or combining things that are alike in only one way

- **Sexual dimorphism: absent (0); present (1)**
- **Sociality: none (0); primitive (1); highly eusocial (2)**
- **Parental care: absent (0); present (1)**

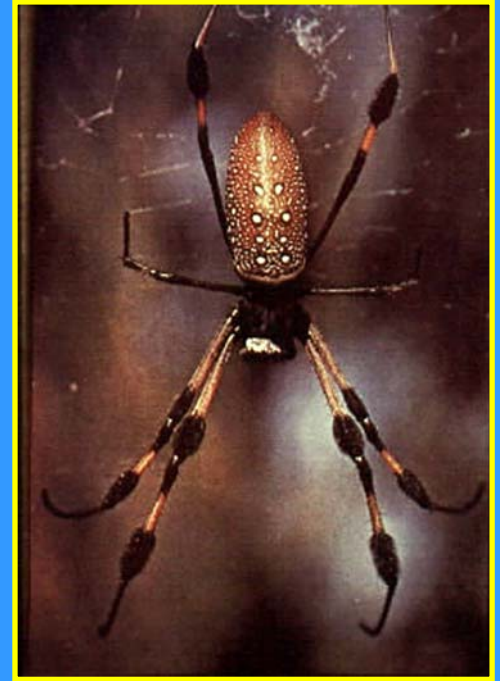
Vollrath showed frequent evolution of “Dimorphism” in araneids.

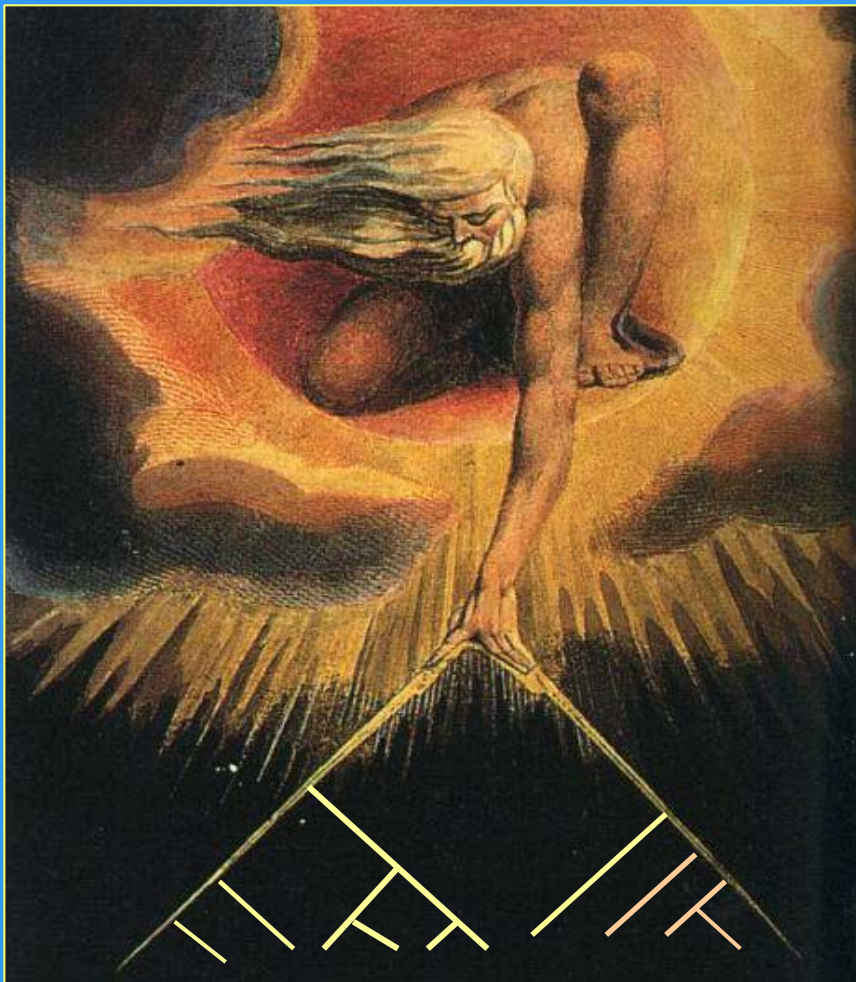
--Hormiga et al. show that the situation complex, with “dimorphism” appearing and disappearing in various ways, and not inferring any single process.

Imagine different selective pressures:

1. females get larger for fecundity
2. males get smaller (and numerous) for finding females better
3. males get smaller (mature earlier) to avoid steep mortality curves
4. males get larger to compete for mates better

These are different processes. Dimorphism is not a single characteristic, so it is no surprise to find multiple origins





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Mouse genome compared to the human genome



Mammal !

Mouse genome compared to the human genome



Mammal !

(amniote)

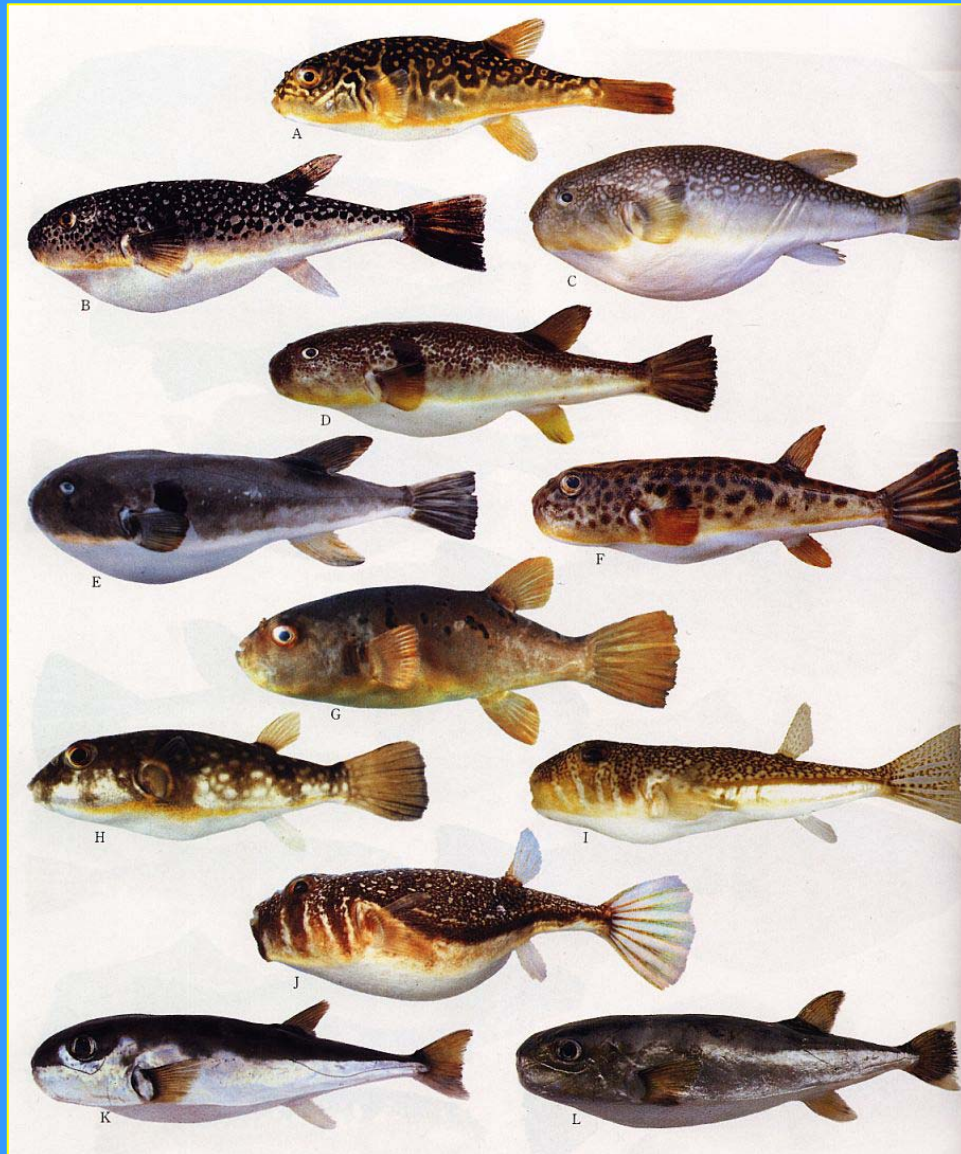
(tetrapod)

(vertebrate)

(deuterostome)

(eukaryote)

Explaining phenotypes is the goal



Variation in phenotypes is where we find the information we want to study. Model-based genome-level data will not be useful to us any time soon.

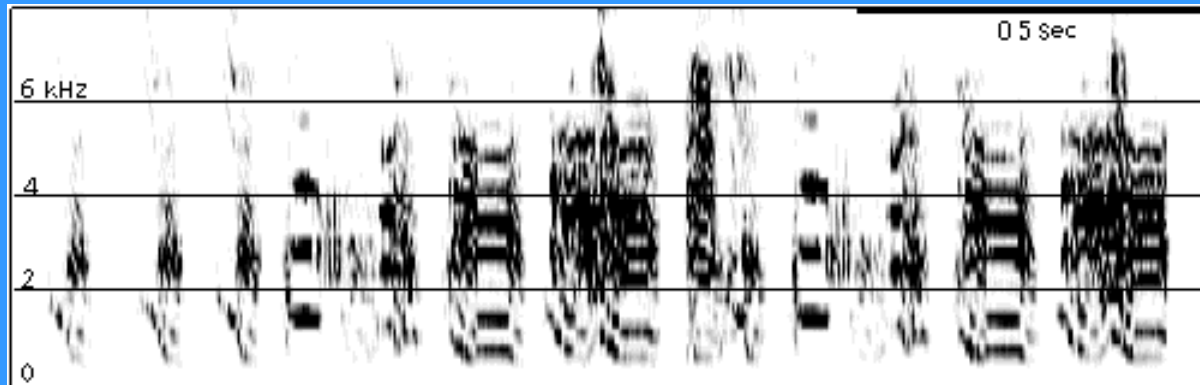
Analysis of DNA is widely thought to be the most desirable method for tracing evolutionary history. But, by what *justification* do we prefer DNA to other data?



Low quality of DNA : Standard warnings about difficulties of DNA data:

- Random evolution will lead to two species sharing the same nucleotide by chance (rather than by ancestry) about 25% of the time
- Rapid evolution saturates some base positions (usually the third position of the codon) with enough noise that those positions must be eliminated entirely from the study
- Regions of sequences that have many insertion and deletion events cannot be aligned reliably to make statements of homology
- Greatly varied rates of evolution between species leads to data that cannot be accepted in raw form because they will lead to incorrect answers
- Models of genetic evolution must be chosen carefully or the true phylogeny will not be reconstructed from sequence data
- Genes may evolve by different mechanisms and cannot be used simultaneously in one study
- Genes may actually have different histories and would never give a single coherent answer
- Ancient polymorphisms can lead to modern lineages whose phylogenetic history is not reflected by the DNA data.

Intraspecific transmission: Learning, and song.



Many bird songs are more conservative than allozyme variation



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DNA evidence shows vocalizations to be a better indicator of taxonomic limits than plumage patterns in *Zimmerius* tyrant-flycatchers

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clear DNA in the



Migration patterns



Propensity to migrate is inherited, but not path itself (like secondary structure). Migration patterns are learned, and may be older than the present populations. Change in behavior comes first, genetic differentiation comes later.

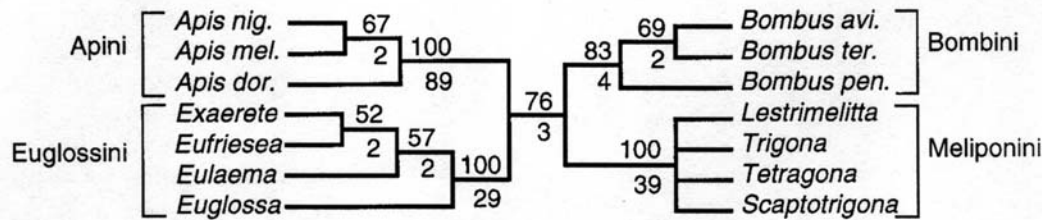


Maternal care in tree hopper insects. Syst. Biol. June 2004

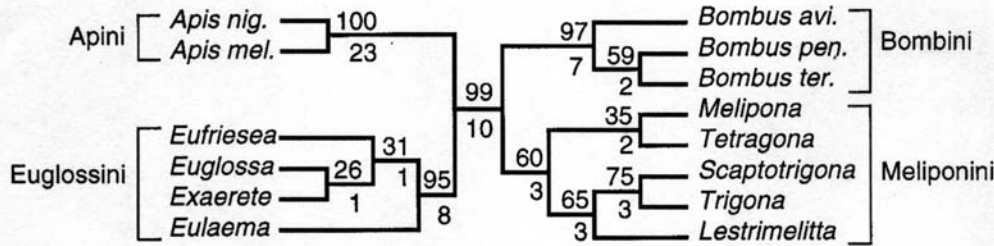
Abstract

The treehopper subfamily Membracinae (Insecta: Hemiptera: Membracidae) comprises the majority of genera and species diversity in the New World tropics. These treehoppers exhibit a wide range of social behaviors, making them an excellent group for studying patterns of social evolution in insects. However, to date the tribal and generic relationships have remained unclear. We reconstructed the phylogeny of the Membracinae using a combined mitochondrial (COI, COII, tRNA-Leu, and 12S) and nuclear (Wg) gene data set. A total of 2608 aligned nucleotide sites were obtained for 112 species, representing 25 of 38 currently recognized genera and all four tribes. A strict consensus of five equally parsimonious trees recovered the subfamily and three of its four tribes. The majority rule consensus tree derived from the Bayesian analyses based on the GTR+I+G and mixed-models recovered many clades shared with the parsimony trees and is identical to the single best tree inferred from maximum likelihood analysis, aside from the rearrangement of one node. A comparison of mitochondrial and nuclear genes indicated that Wg provided higher consistency index (CI), data decisiveness (DD), partitioned Bremer support (PBS) than any of the mitochondrial genes analyzed. The combined mitochondrial and nuclear DNA provide strong support for the monophyly of the subfamily and three of its four tribes (Aconophorini, Hoplophorionini, and Hypsoprorini). Membracini is paraphyletic with respect to Hoplophorionini and contains two lineages, the Membracini *sensu strictu* and the newly resurrected tribe Bolbonotini. Our analyses show that there is a strong phylogenetic component to the evolution of maternal care. **Given the widespread occurrence of maternal care within the subfamily, this trait is estimated to have ≤ 3 origins, two reversals, and one loss. Our results suggest that the evolution of maternal care in insects may not be as evolutionarily labile as previously thought.**

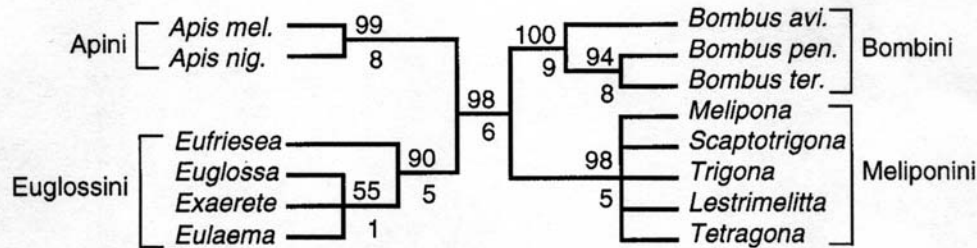
Opsin



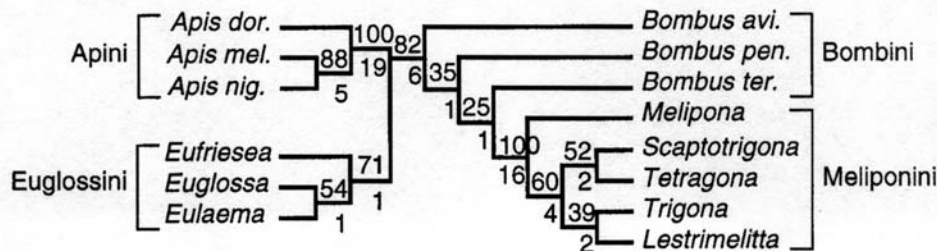
Cytochrome b



28S



16S



Cameron's study of "social behavior" in bees

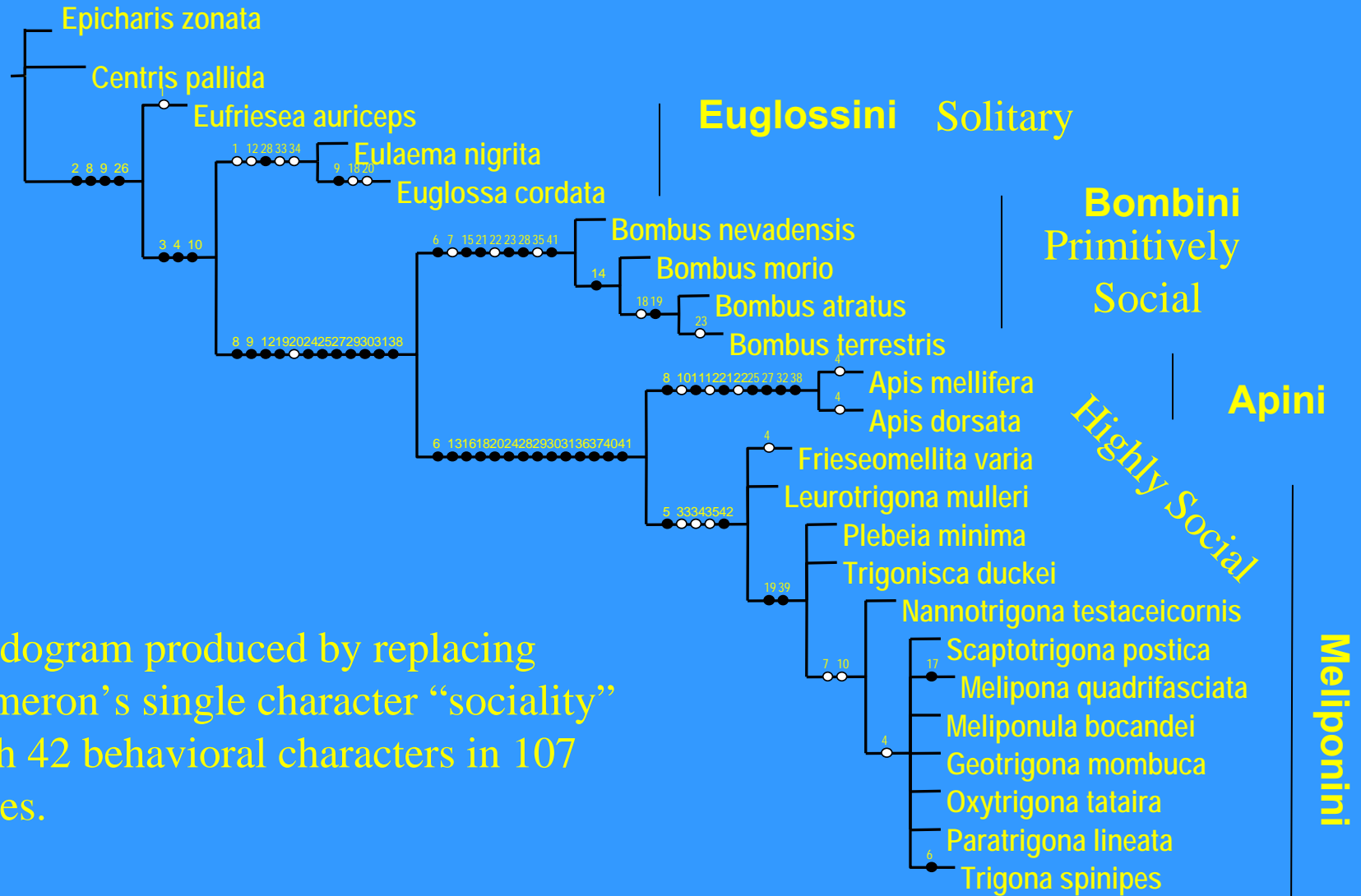
Three mitochondrial genes, and one nuclear gene, 13 species.

Cameron says it is important that none of her trees look like the classical tree derived by Michener in 1944 from morphology.

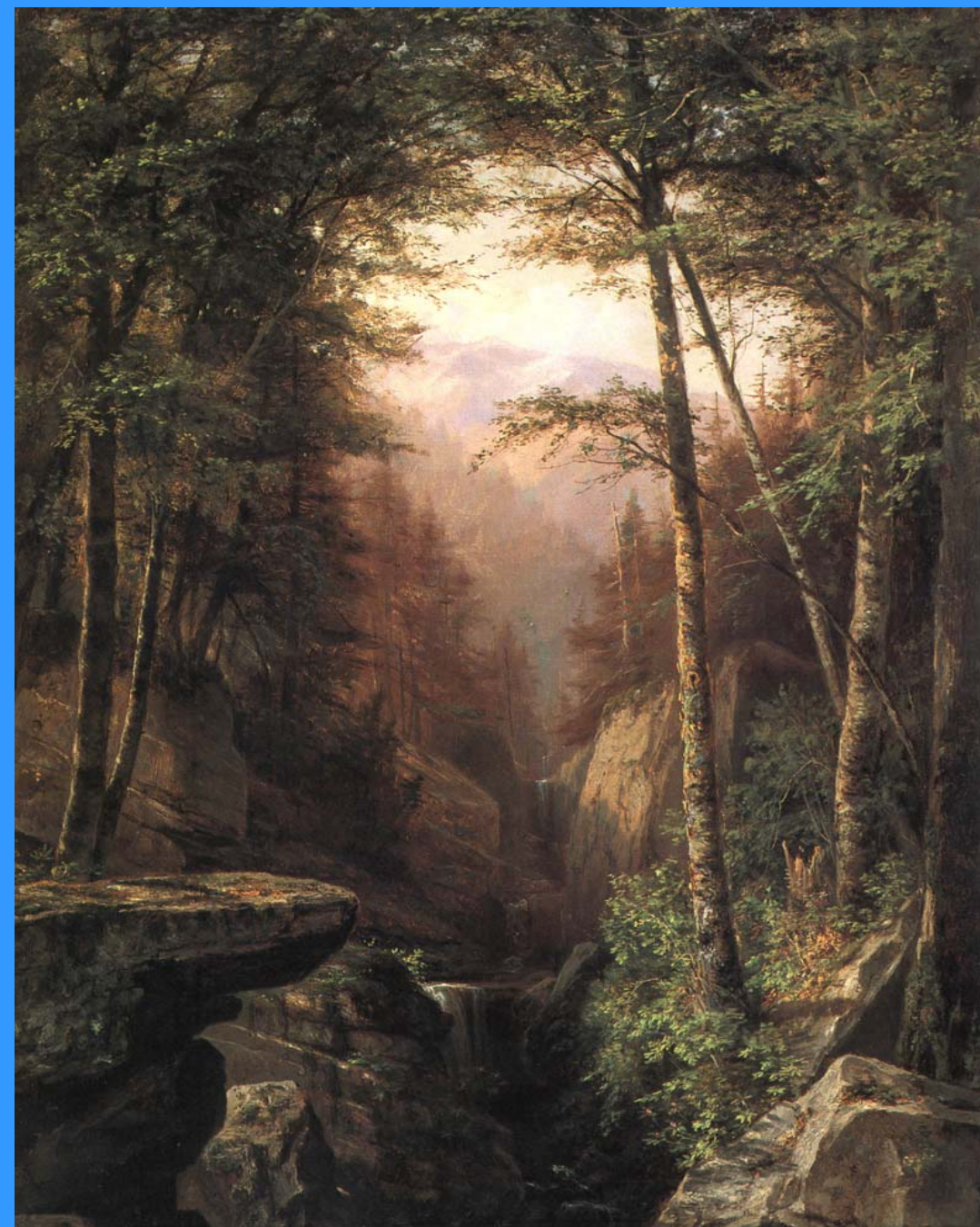
But, what about the behaviors?

- **Sociality:**
- **none (0);**
- **primitive (1);**
- **highly eusocial (2)**

Behavioral phylogeny of corbiculate bees (Noll, 2002)



Cladogram produced by replacing Cameron's single character "sociality" with 42 behavioral characters in 107 states.

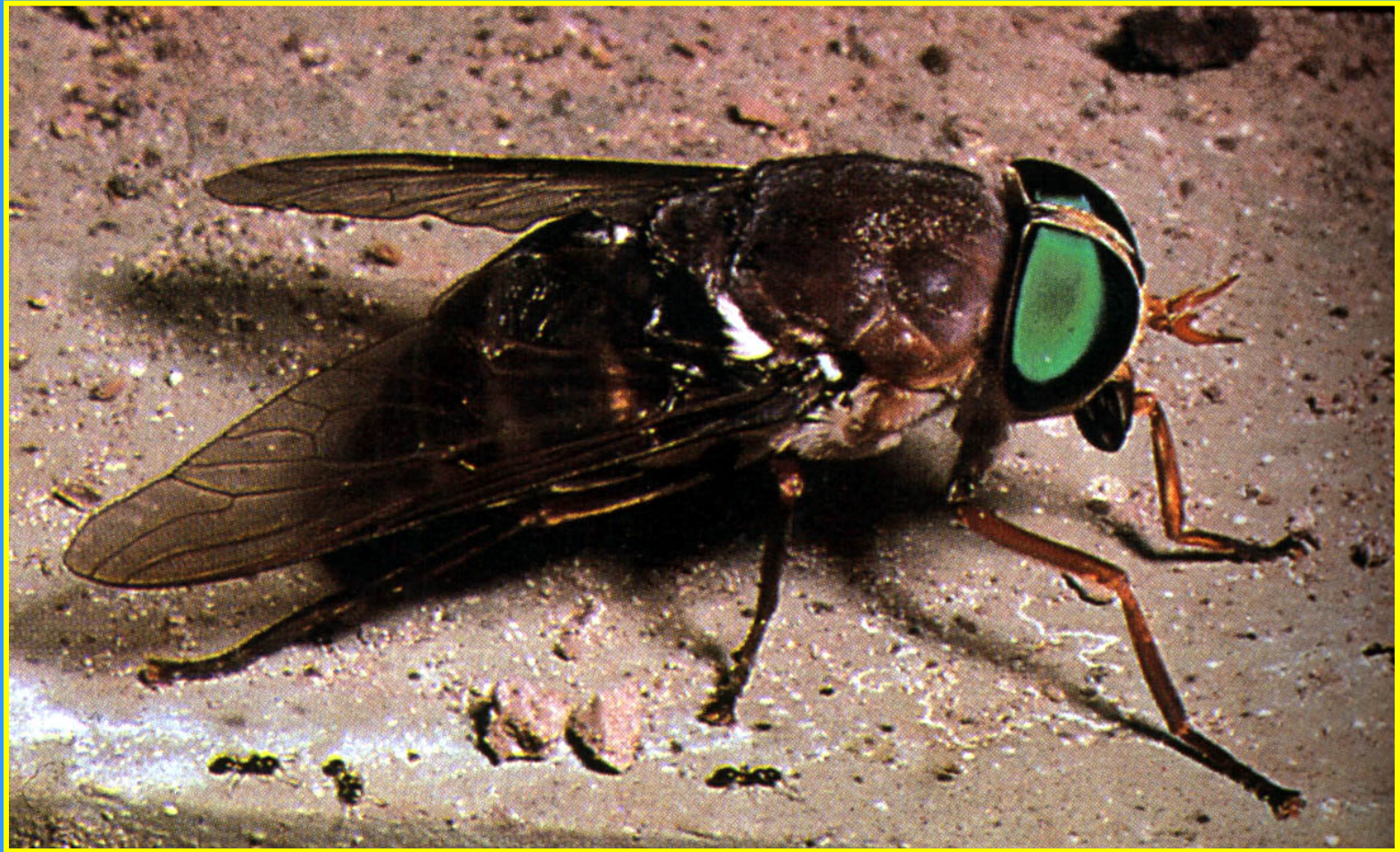


Phylogenetic studies provide tools that work outside the limits of model systems.

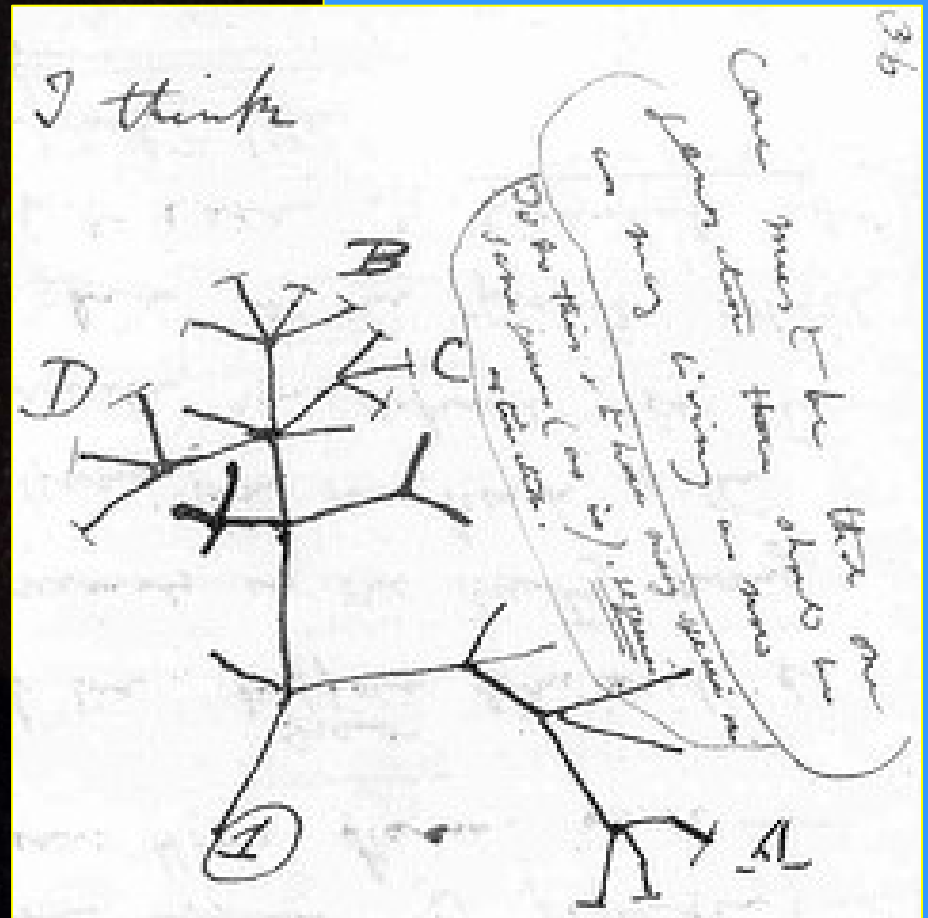
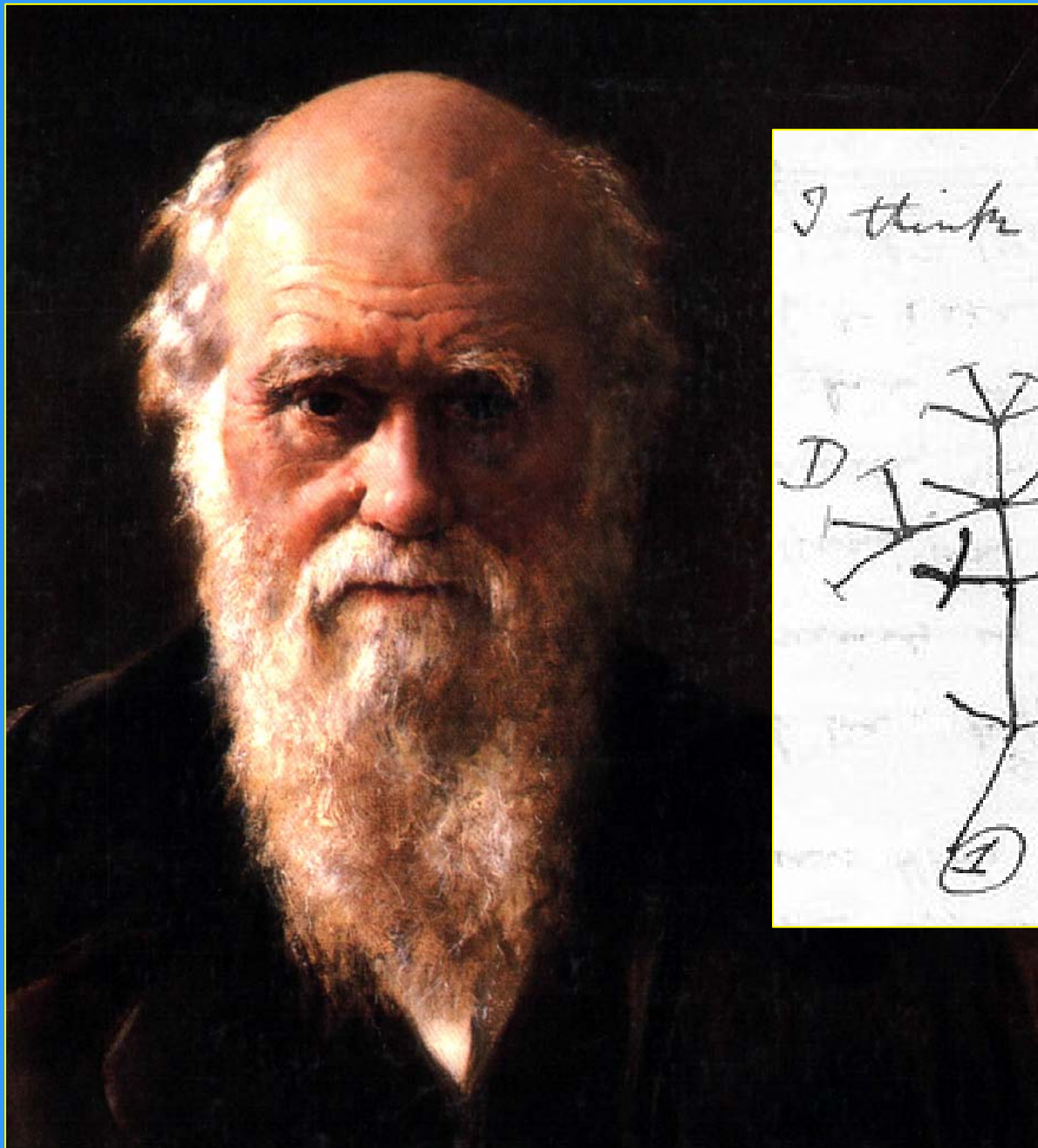
Classical ethology provides a foundation that performs well in modern cladistic paradigm.

Much of the difficulty of interpreting behavioral or ecological data in a phylogenetic context is due to extensional definitions used in ecology, not to the facts of biology.

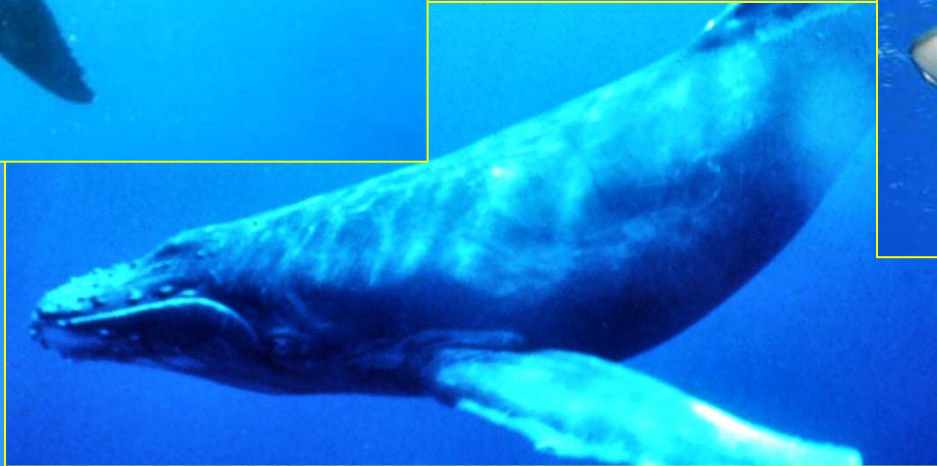
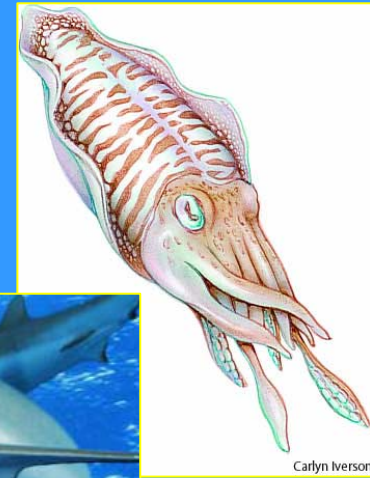
Behavioral data are rich and perform as well as DNA or better in studies of phylogenetic ancestry.



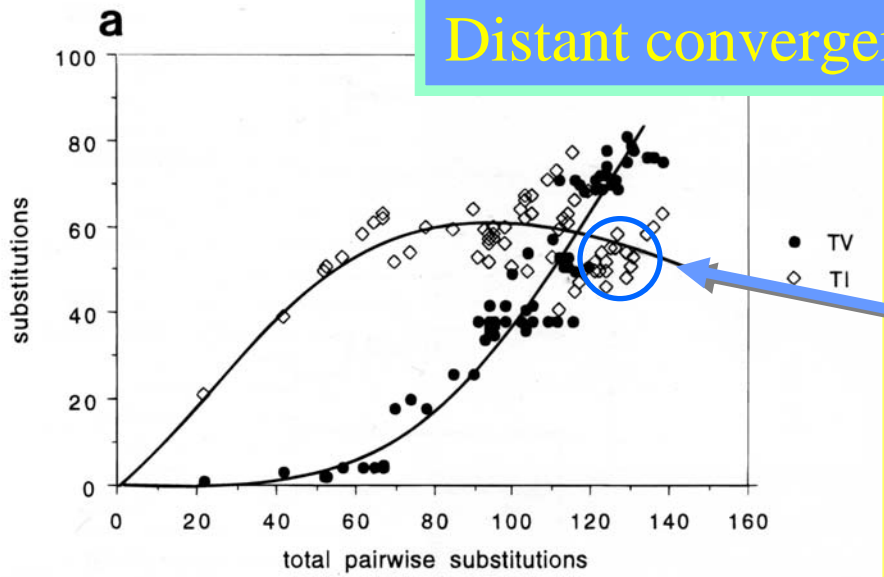
Phylogenetics without reference to phenotype is pointless. We study how things are related as a way to understand phenotypes.



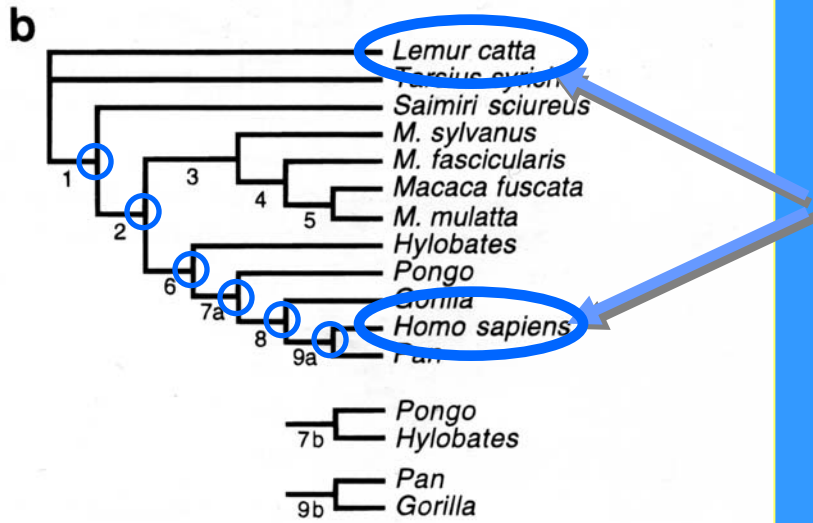
The entire point is to find a pattern that does *not* relate to history, so that we have many distant examples. Researchers aim to find a pattern that is not explained by a unique evolutionary event. Then, it can be no surprise that phylogenetics may not be helpful.



Distant convergence is not necessarily a problem !



Saturation rates are pairwise, but pairwise “similarity” of taxa is not necessarily a problem.



Chance convergence of *Lemur* and *Homo* will have to be very high before all of the internal nodes of the tree are compromised.

FIG. 5. The primate data set of Hayasaka *et al.* (1988) yielded a typical saturation curve for third-position transitions relative to transversions versus total divergence (a). Numbers at nodes (b) cor-