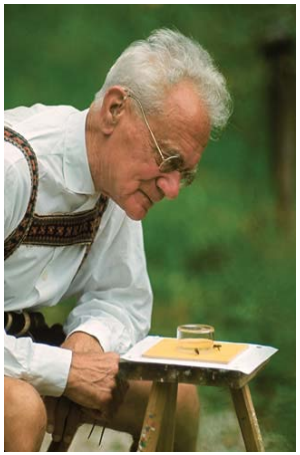
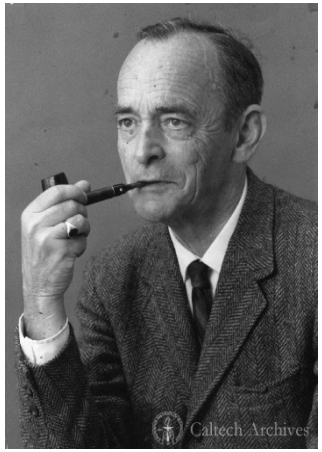
In Search of the Devonian Toolkit:
Reconstructing behavioral modules of ancestral organisms

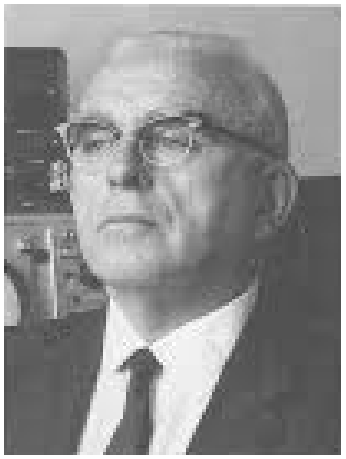
Niko Tinbergen (1907-1988) Konrad Lorenz (1903-1989)



Karl von Frish (1886-1982)



Cornelius Wiersma (1904-1987)

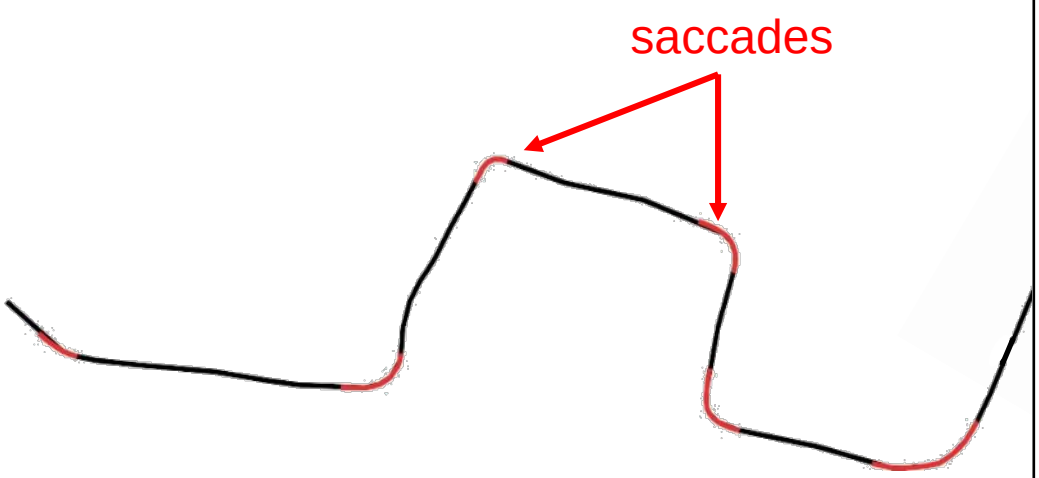


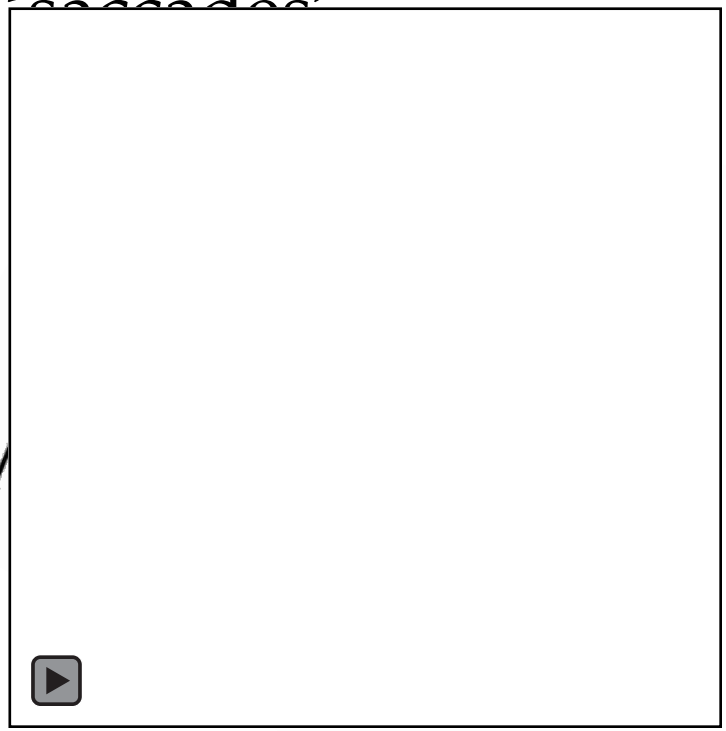
Kenneth Roeder (1908-1979)

Dickinson (2014). Death Valley, *Drosophila*, and the Devonian Toolkit.

Florian Muijres

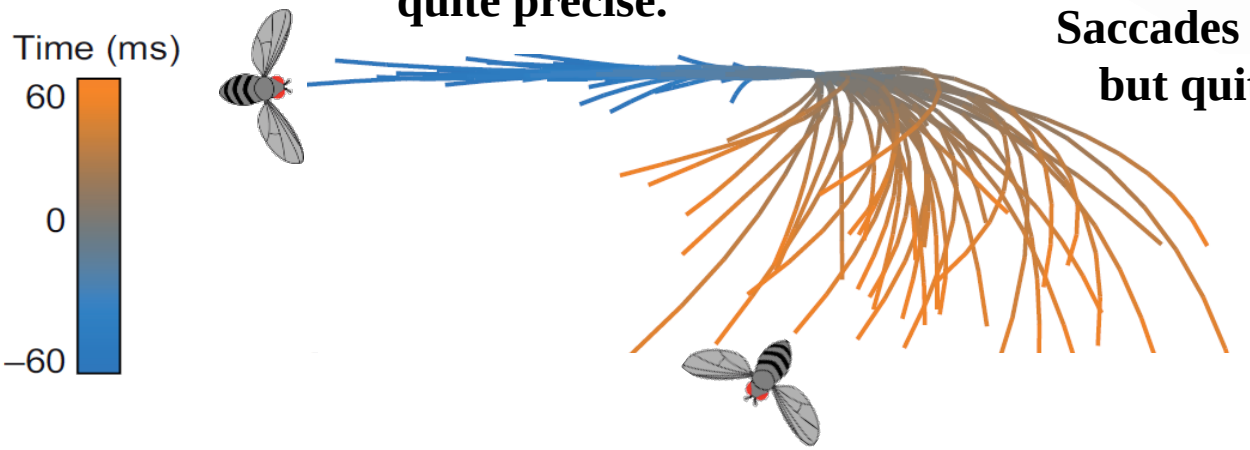
Fly flight consists of straight sequences interrupted by rapid turns called 'saccades'





Straight flight is quite precise.

Saccades are very fast, but quite variable.



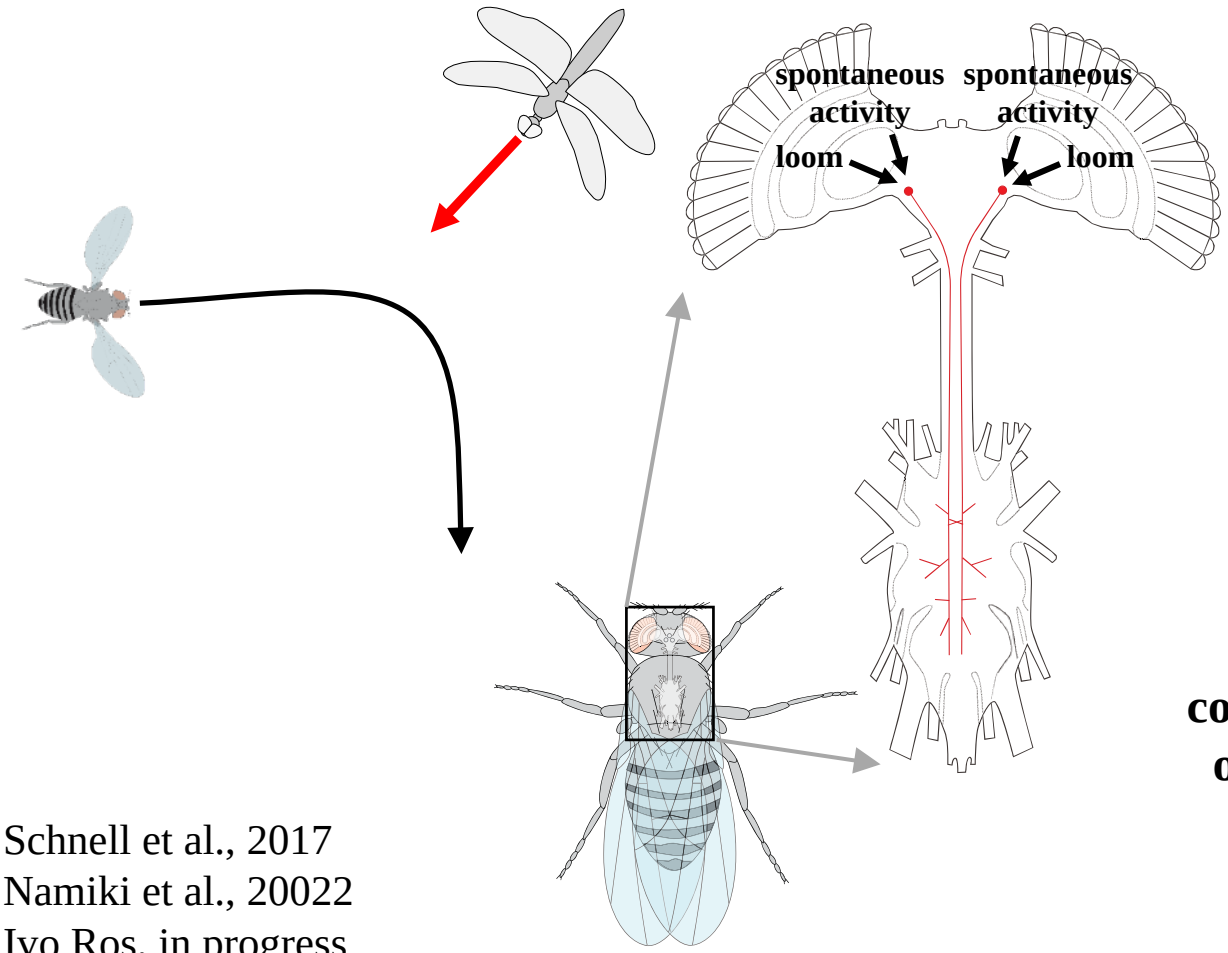
Muijres, et al., 2014, 2015

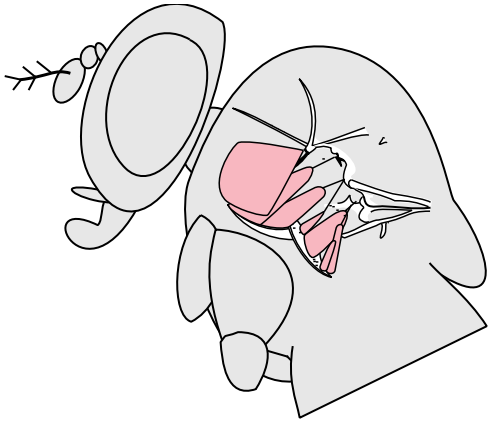
Rapid Maneuver System

Behavior
Rapid maneuver

Brain
1 pair of command neurons

Wing control
Large, sporadically-active muscles.



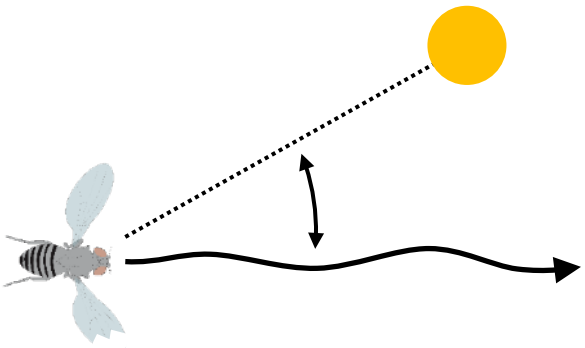


Rapid turns are controlled by a small set of command neurons.

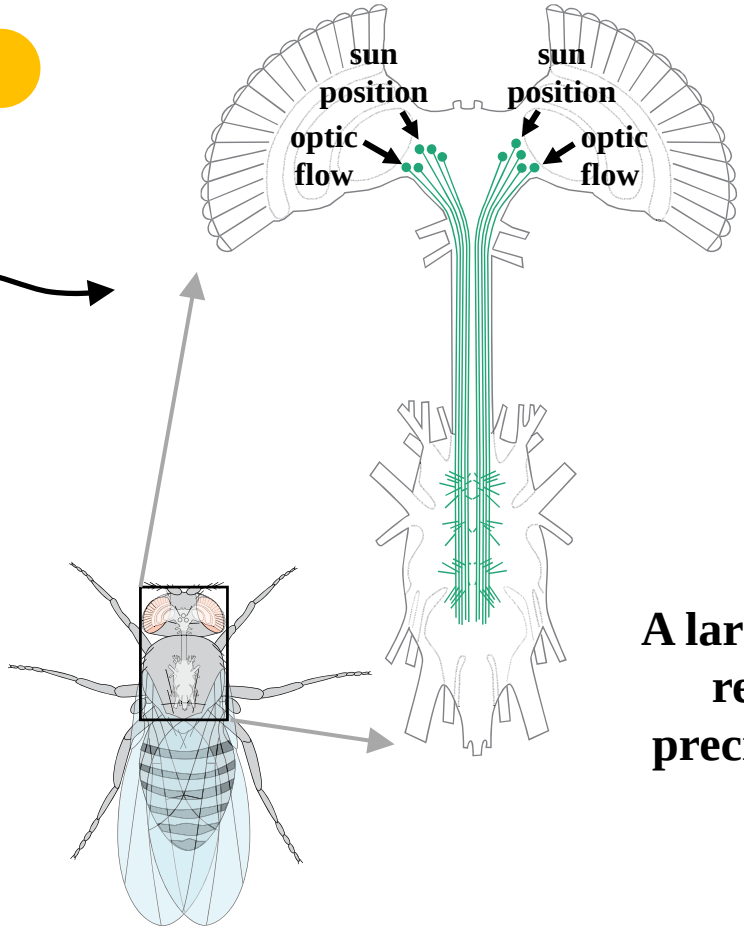
Schnell et al., 2017
Namiki et al., 20022
Ivo Ros, in progress
Emily Palmer, in progress

Straight Flight System

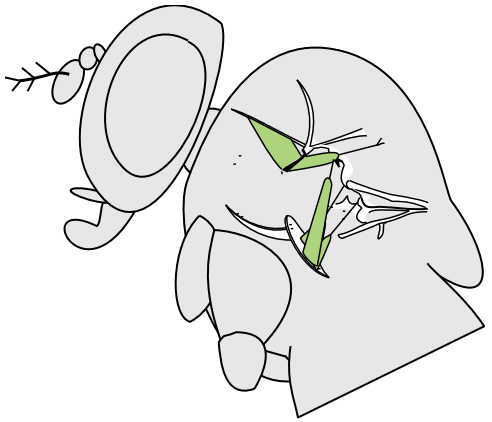
Behavior
Straight flight



Brain
>24 pairs of neurons using a population code



Wing control
Small, continuously-active muscles.

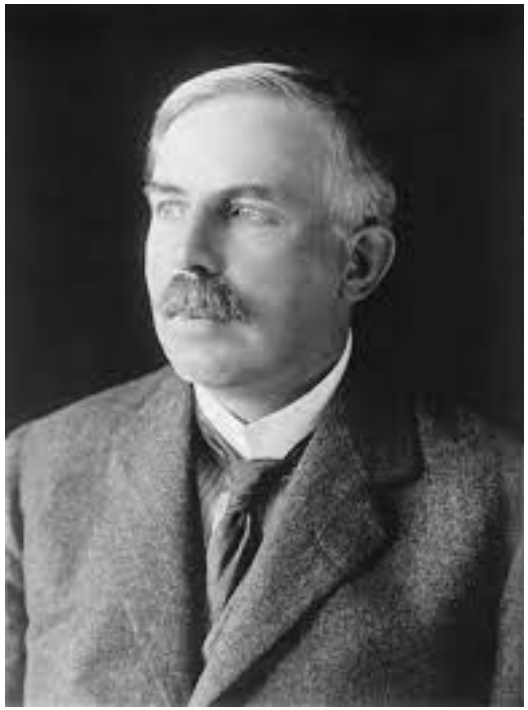


A larger number of neurons is required to provide the precision and dynamic range for straight fight.

Schnell et al., 2017
Namiki et al., 20022
Ivo Ros, in progress
Emily Palmer, in progress

Both these guys can't be right.

"All science is either physics or stamp collecting."



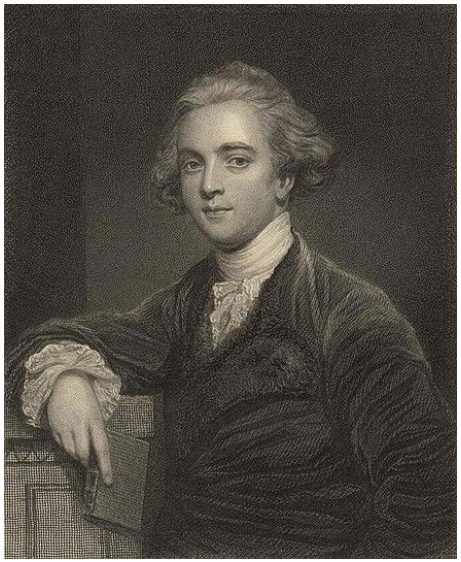
Ernest Rutherford
(1871-1937)

"Nothing in Biology makes sense except in the light of evolution."

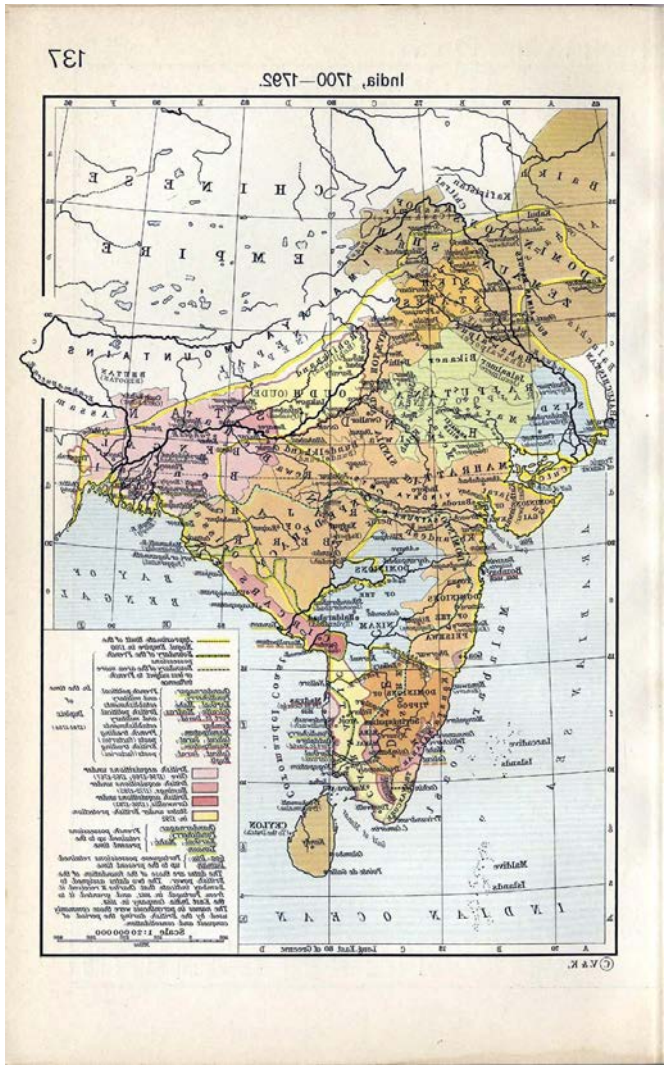
Theodosius Dobzhansky
(1900-1975)

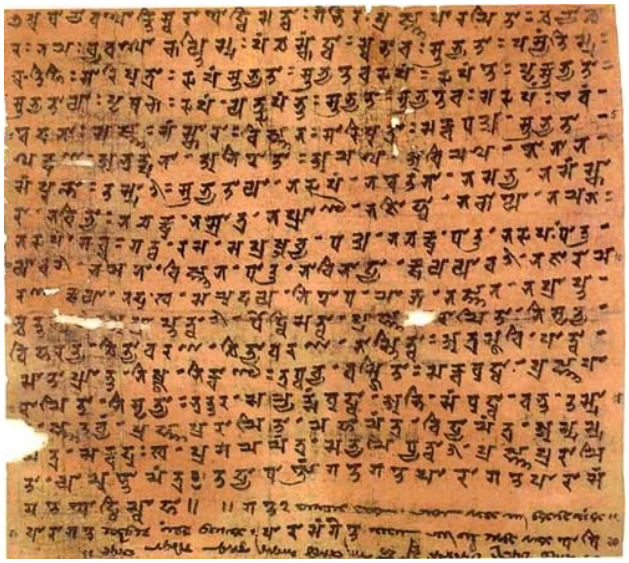
I am sorry mother, but I cannot hunt horses with you today. My legs are tired and I promised grandmother I would help her weave three wool blankets from father's sheep.

The Story of PIE
(Proto Indo-European)



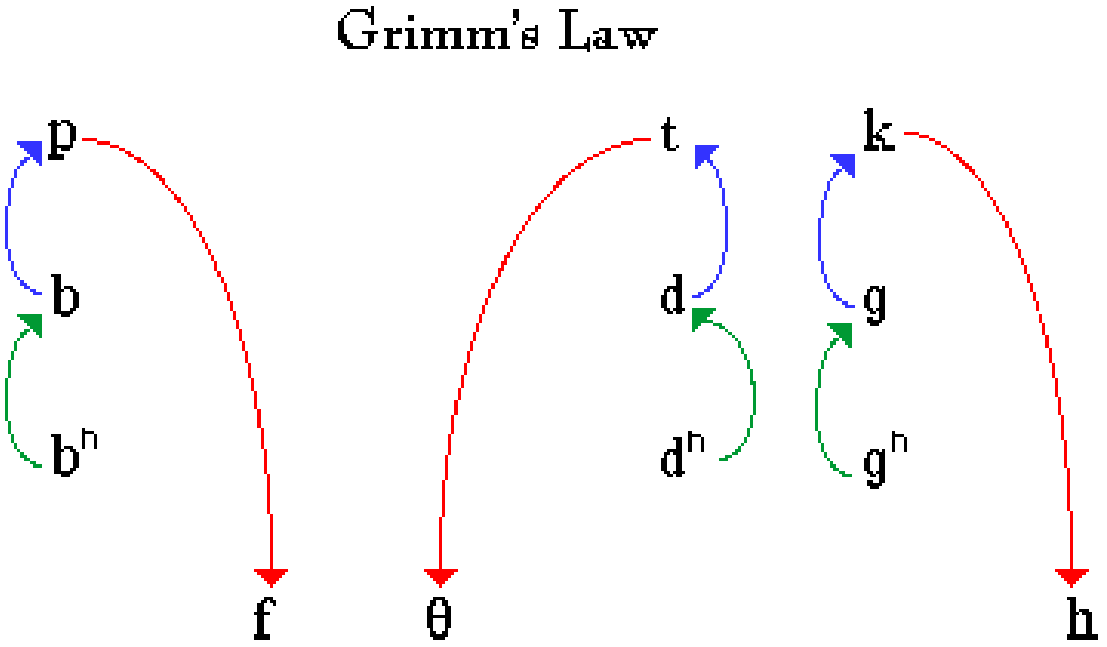
Sir William Jones
1746-1794



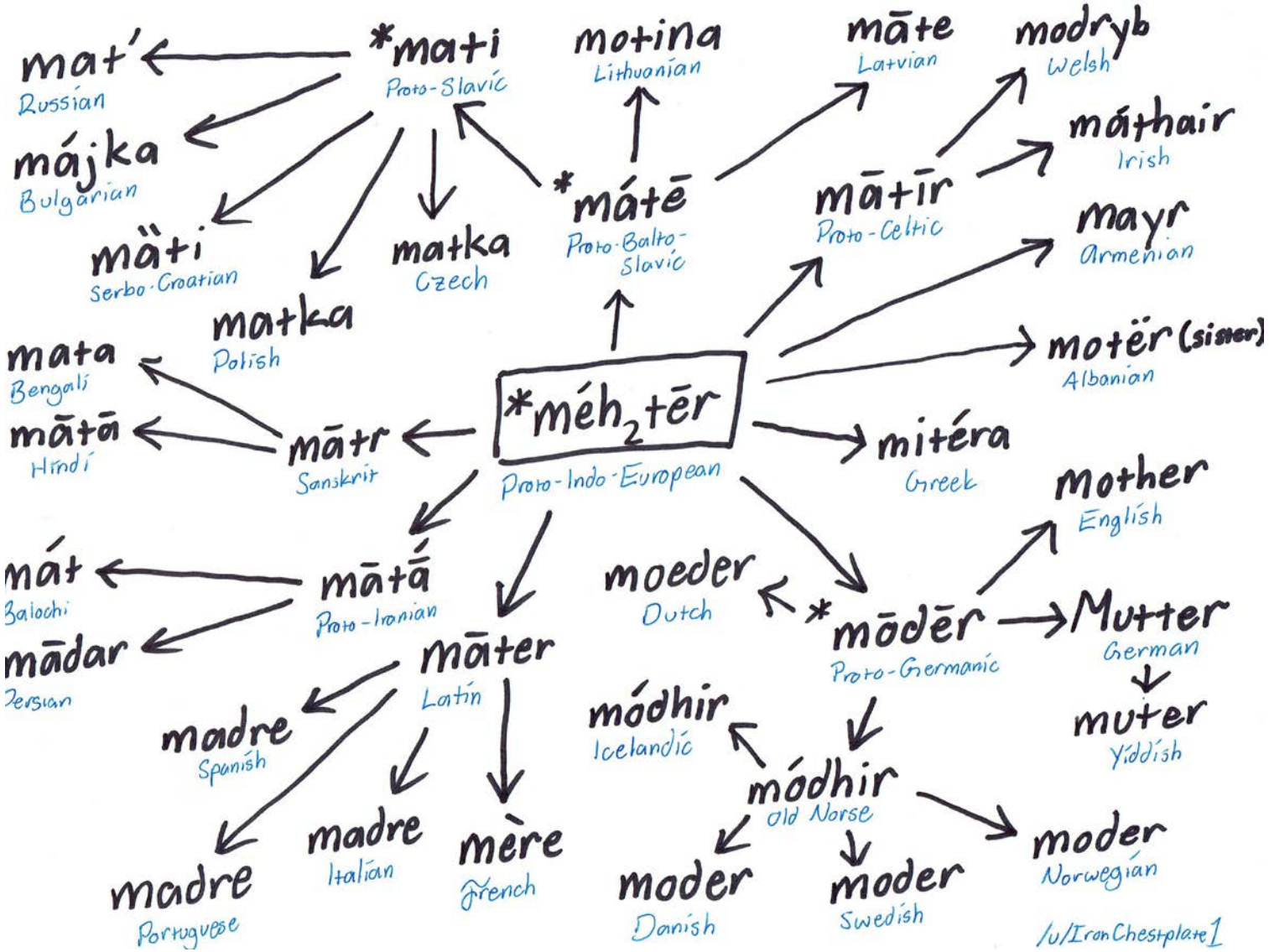


The story is Grimm.

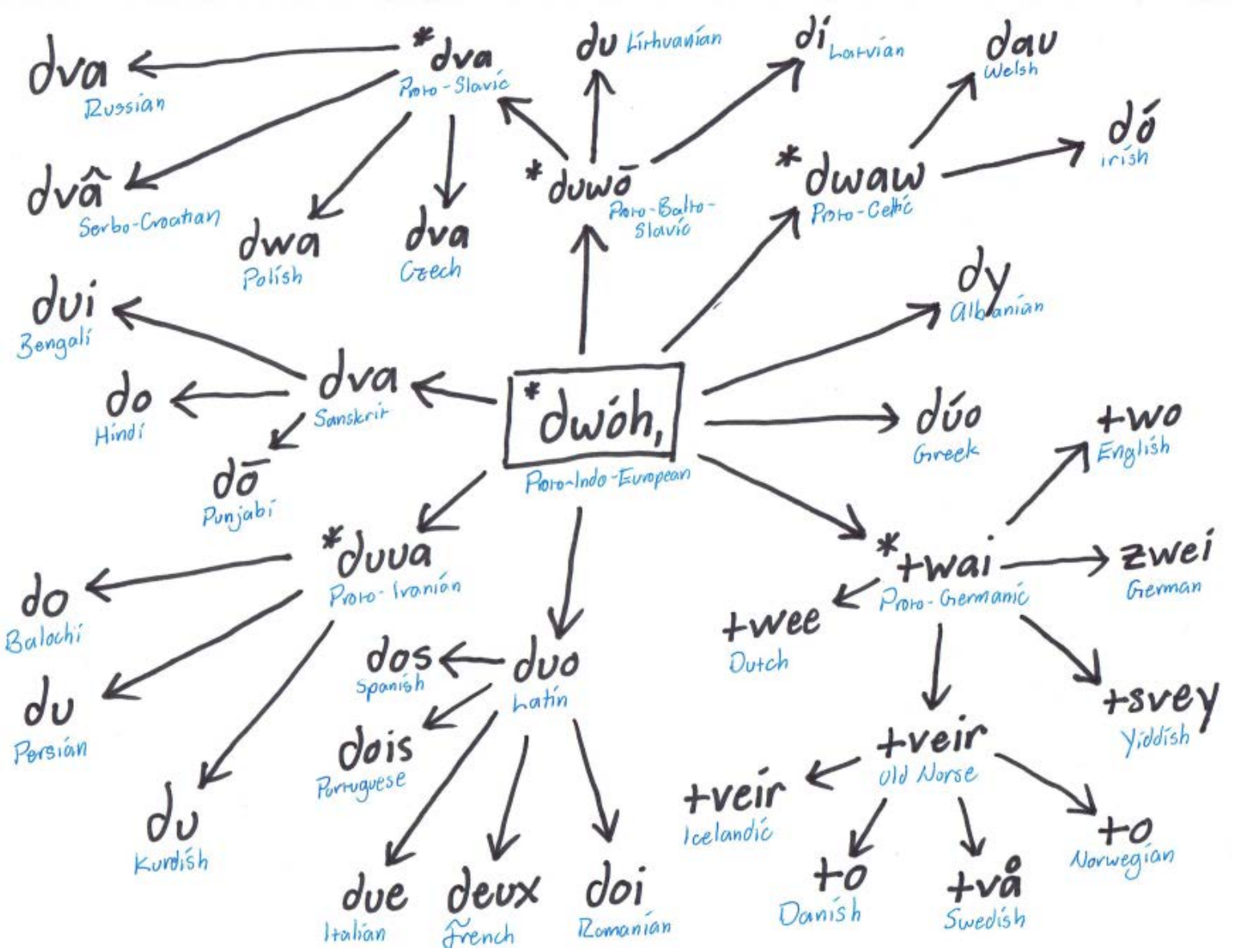
Jacob Grimm (1785–1863)
Wilhelm Grimm (1786–1859)



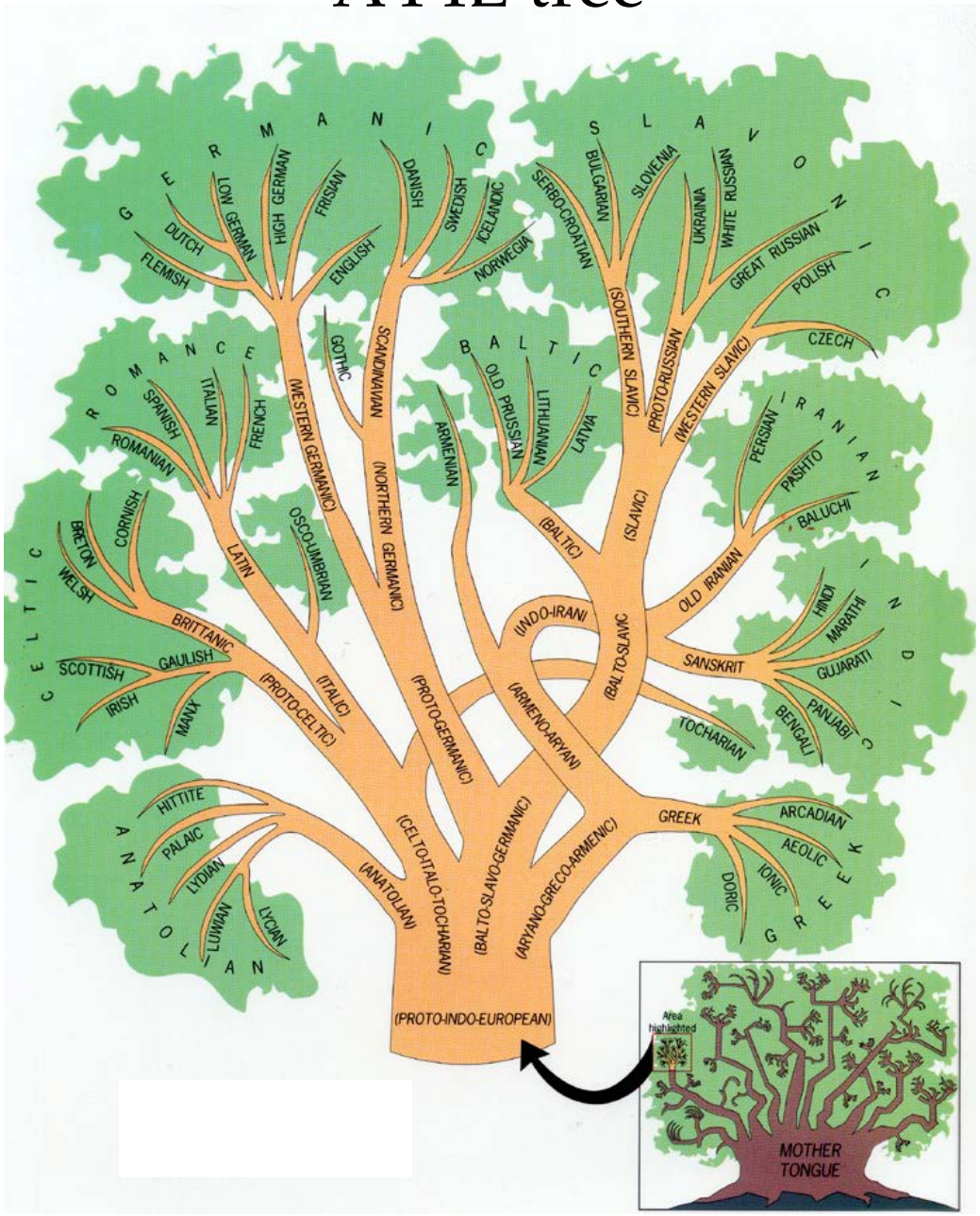
We all have a mother.



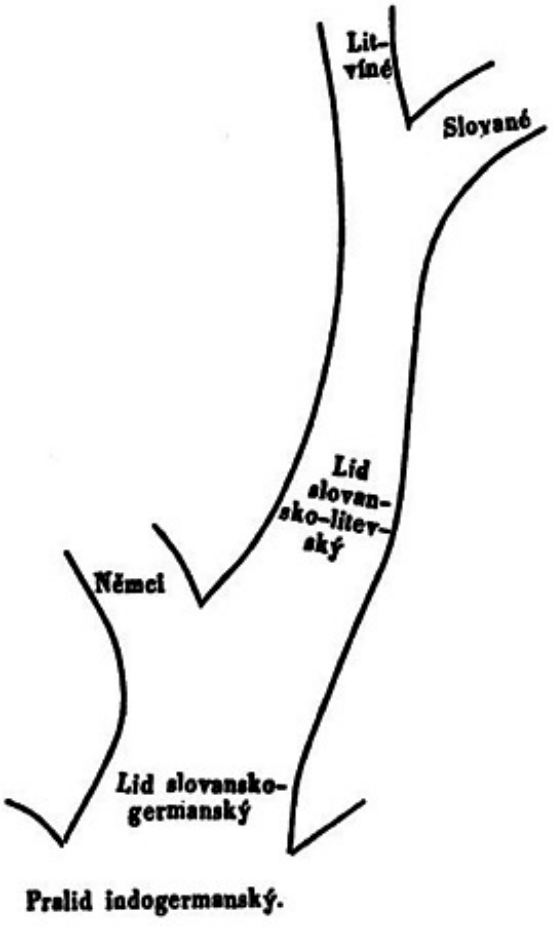
Counting to two



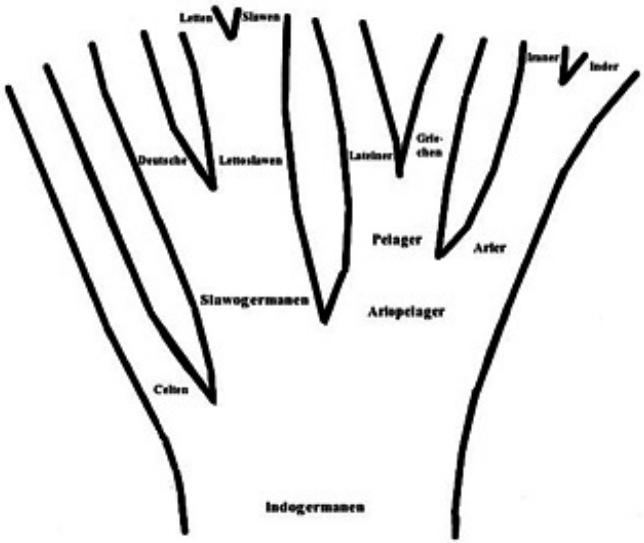
A PIE tree


GERMANIC
DUTCH
FLEMISH
LOW GERMAN
HIGH GERMAN
FRISIAN
ENGLISH
DANISH
SWEDISH
ICELANDIC
NORWEGIA
SLAVONIC
SERBOCROATIAN
BULGARIAN
SLOVENIA
UKRAINIA
WHITE RUSSIAN
GREAT RUSSIAN
POLISH
CZECH
ROMANCE
SPANISH
ITALIAN
FRENCH
ROMANIAN
GOTHIC
SCANDINAVIAN
(WESTERN GERMANIC)
(NORTHERN GERMANIC)
BALTIC
OLD PRUSSIAN
LITHUANIAN
LATVIA
(SOUTHERN SLAVIC)
(PROTO-RUSSIAN)
(WESTERN SLAVIC)
IRANIAN
PERSIAN
PASHTO
BALUCHI
ARMENIAN
(BALTIC)
(SLAVIC)
CELTIC
BRETON
CORNISH
WELSH
BRITTANIC
SCOTTISH
GAULISH
IRISH
MANX
LATIN
OSCO-UMBRIAN
(ITALIC)
(PROTO-CELTIC)
(INDO-IRANI
(BALTO-SLAVIC)
OLD IRANIAN
INDIC
HINDI
MARATHI
SANSKRIT
GUJARATI
PANJABI
BENGALI
TOCHARIAN
(PROTO-GERMANIC)
(ARMENO-ARYAN)
GREEK
ARCADIAN
AEOLIC
IONIC
DORIC
ANATOLIAN
HITTITE
PALAIC
LYDIAN
LUWIAN
LYCIAN
(CELTO-ITALO-TOCHARIAN)
(BALTO-SLAVO-GERMANIC)
(ARYANO-GRECO-ARMENIC)
(PROTO-INDO-EUROPEAN)
Area highlighted
MOTHER TONGUE

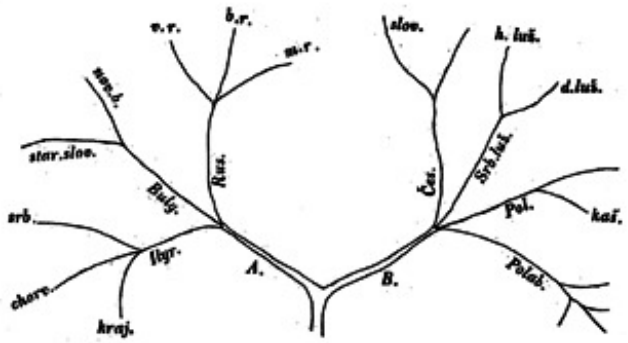
Early PIE trees



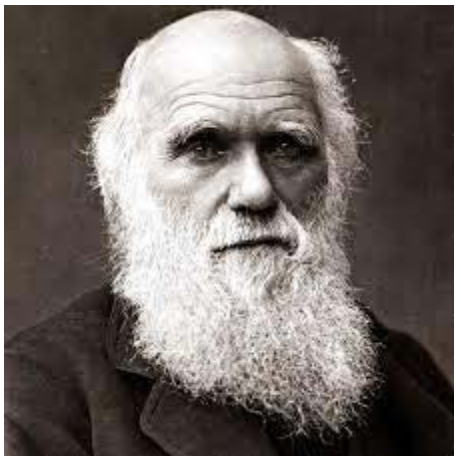
A) August Schleicher, 1853

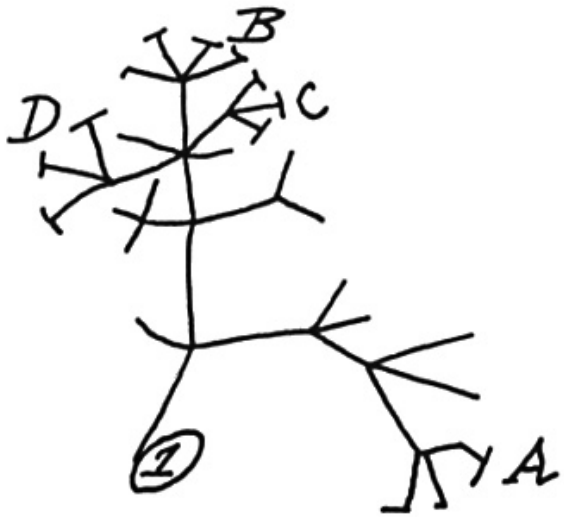


B) August Schleicher 1853



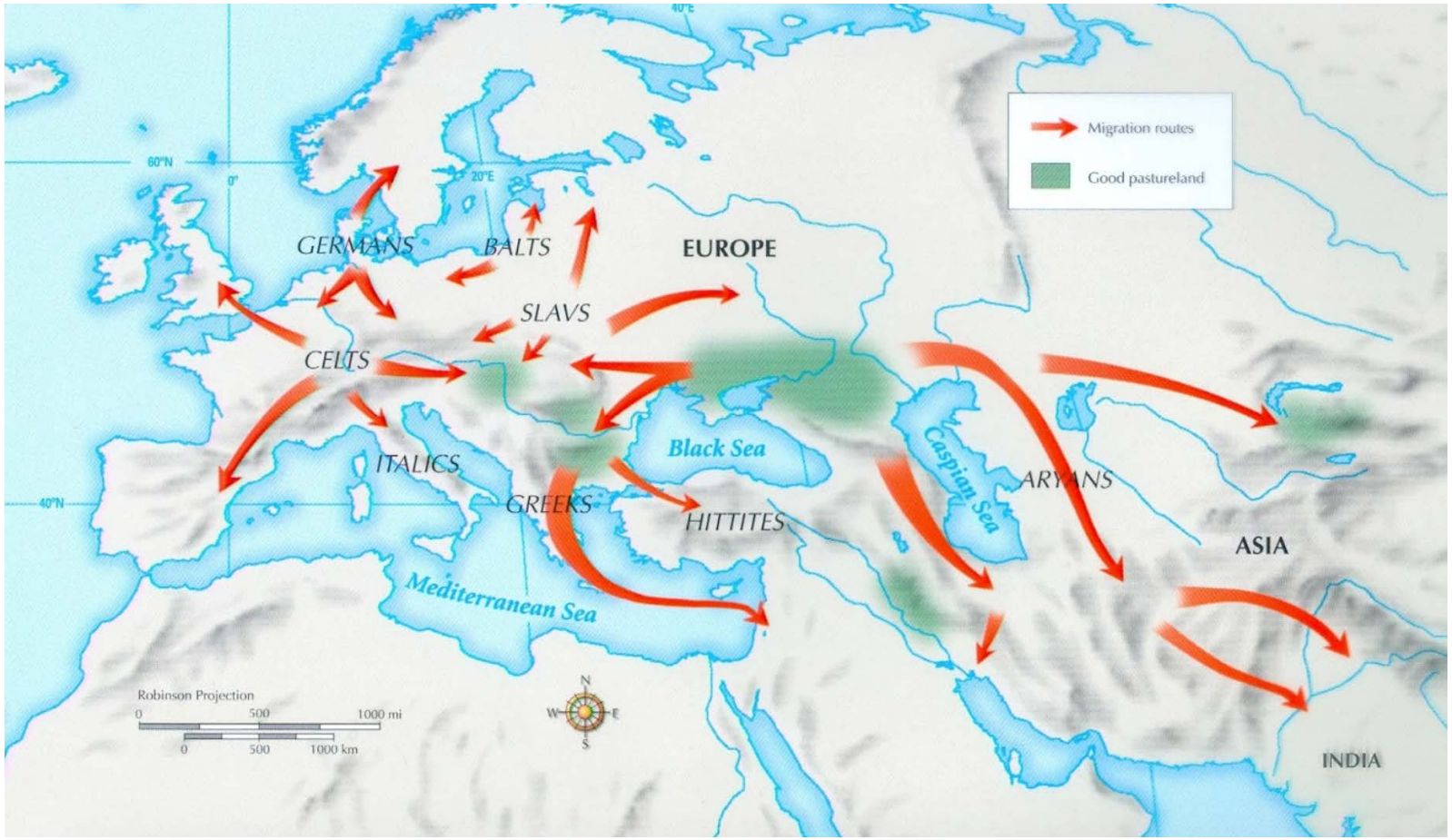
C) František Ladislav Čelakovský 1853



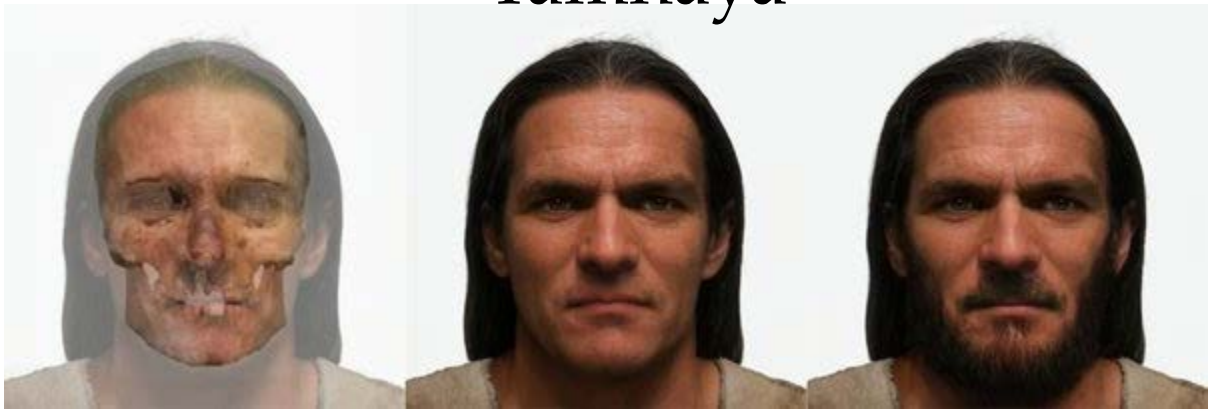


Darwin, 1837
notebook sketch

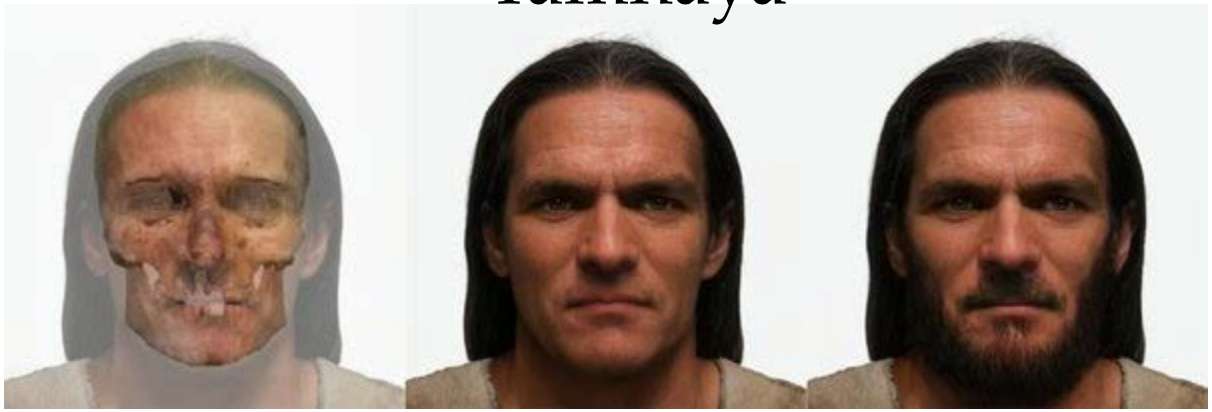
Proto Indo-European migrations

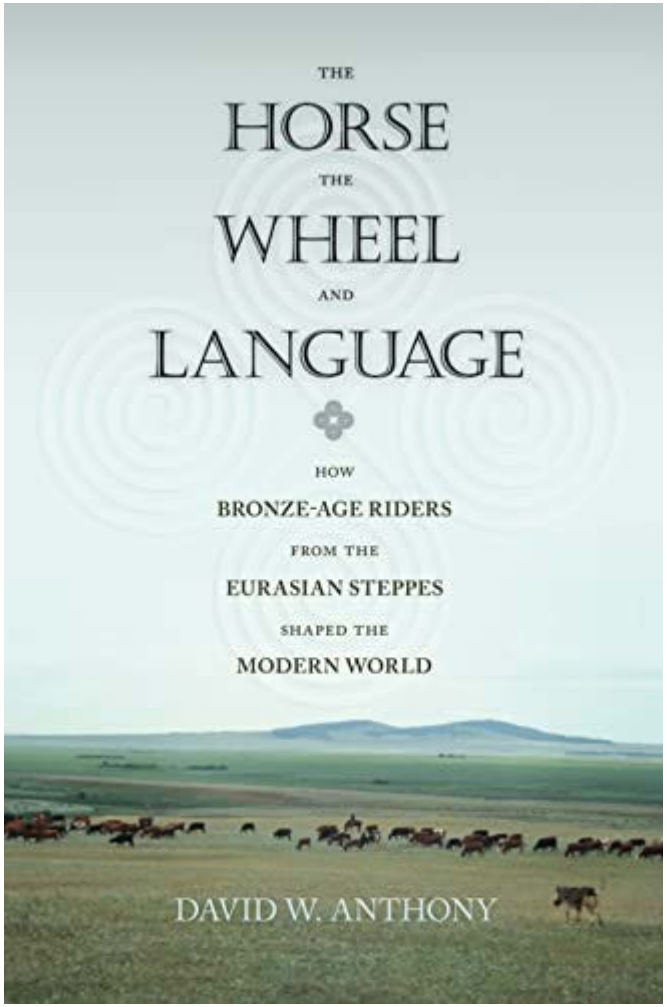


Yamnaya



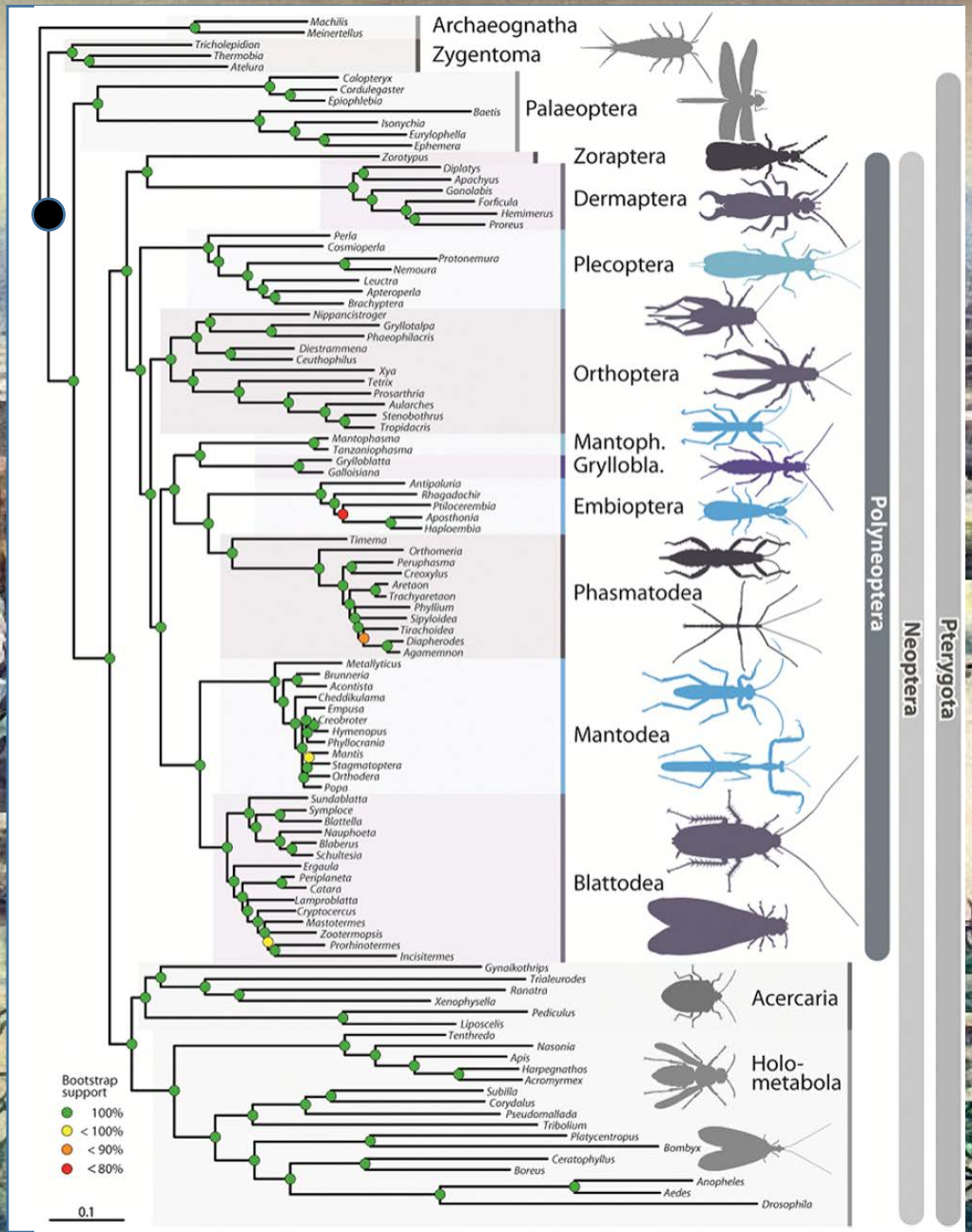
Yamnaya

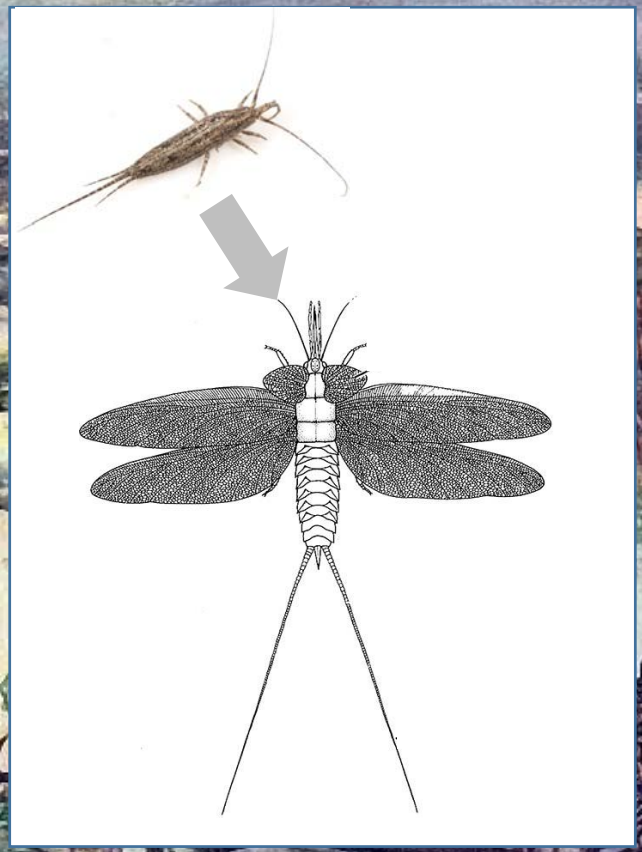



THE
HORSE
THE
WHEEL
AND
LANGUAGE
HOW
BRONZE-AGE RIDERS
FROM THE
EURASIAN STEPPES
SHAPED THE
MODERN WORLD
DAVID W. ANTHONY


Kevin Stroud
History of
English Podcast

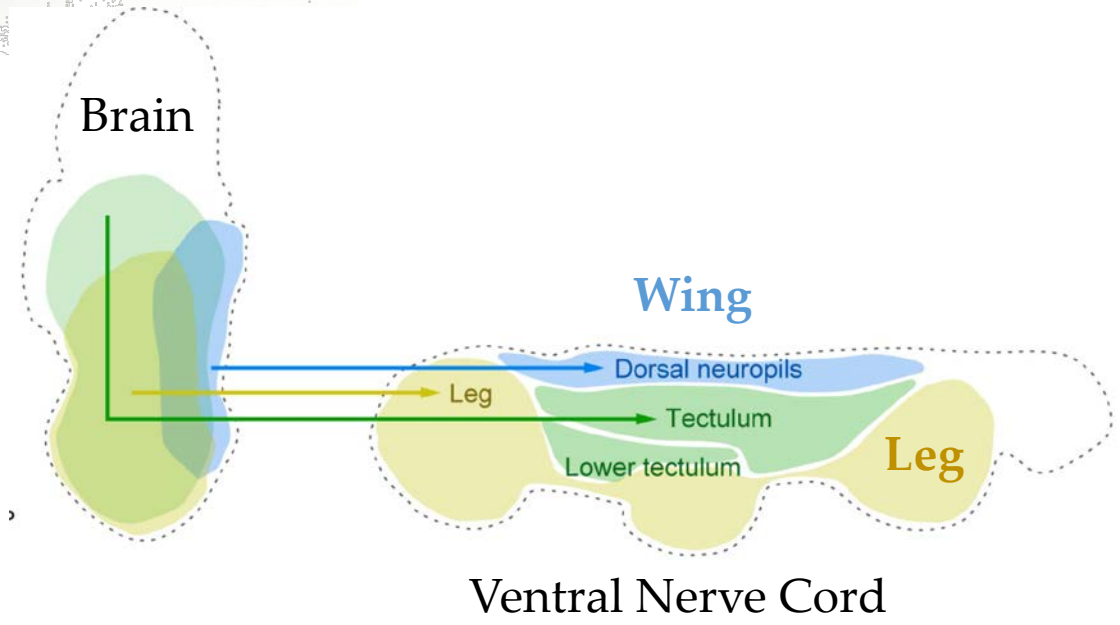
Devonian Landscape ~420-360 mya



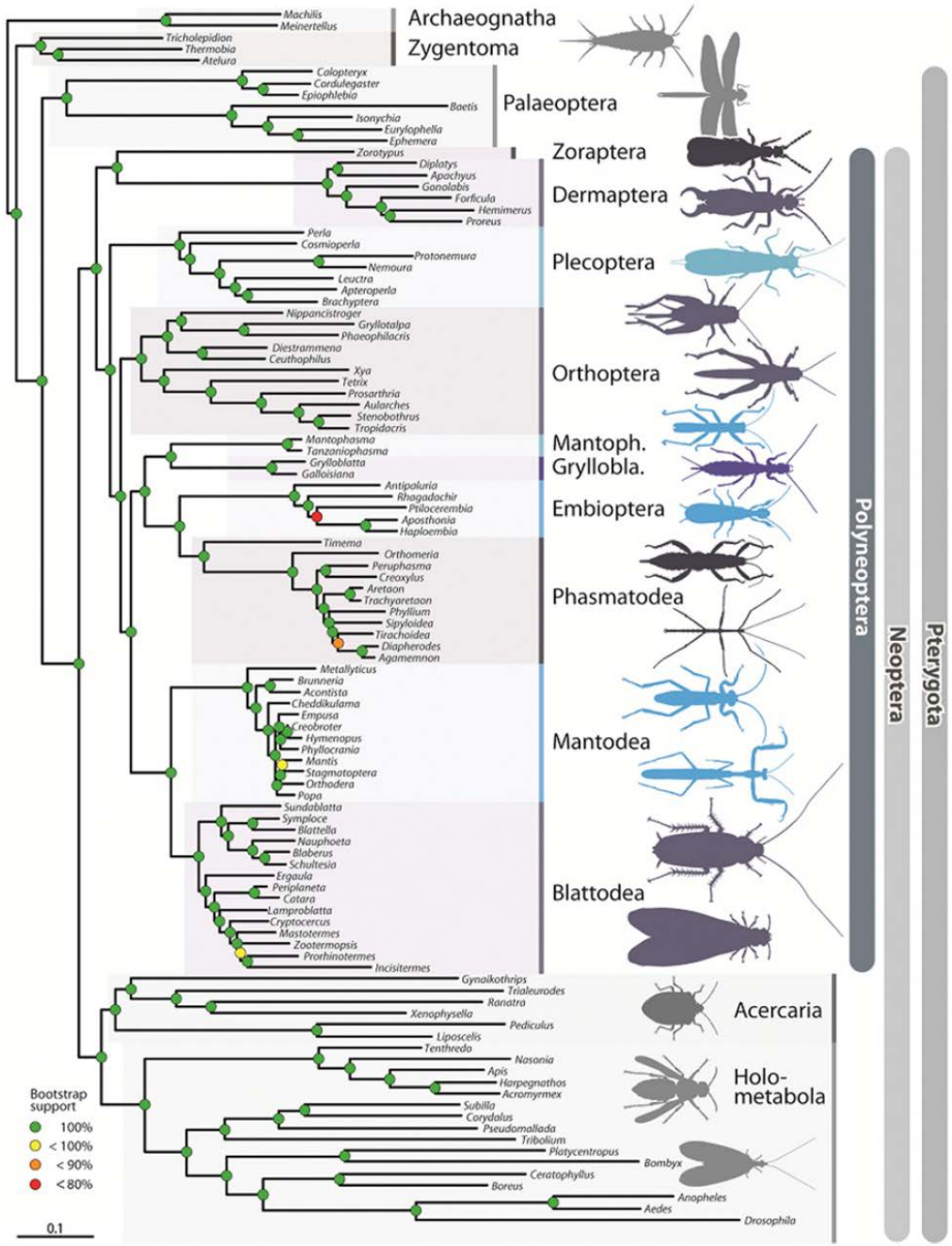


Active flight evolved four times...

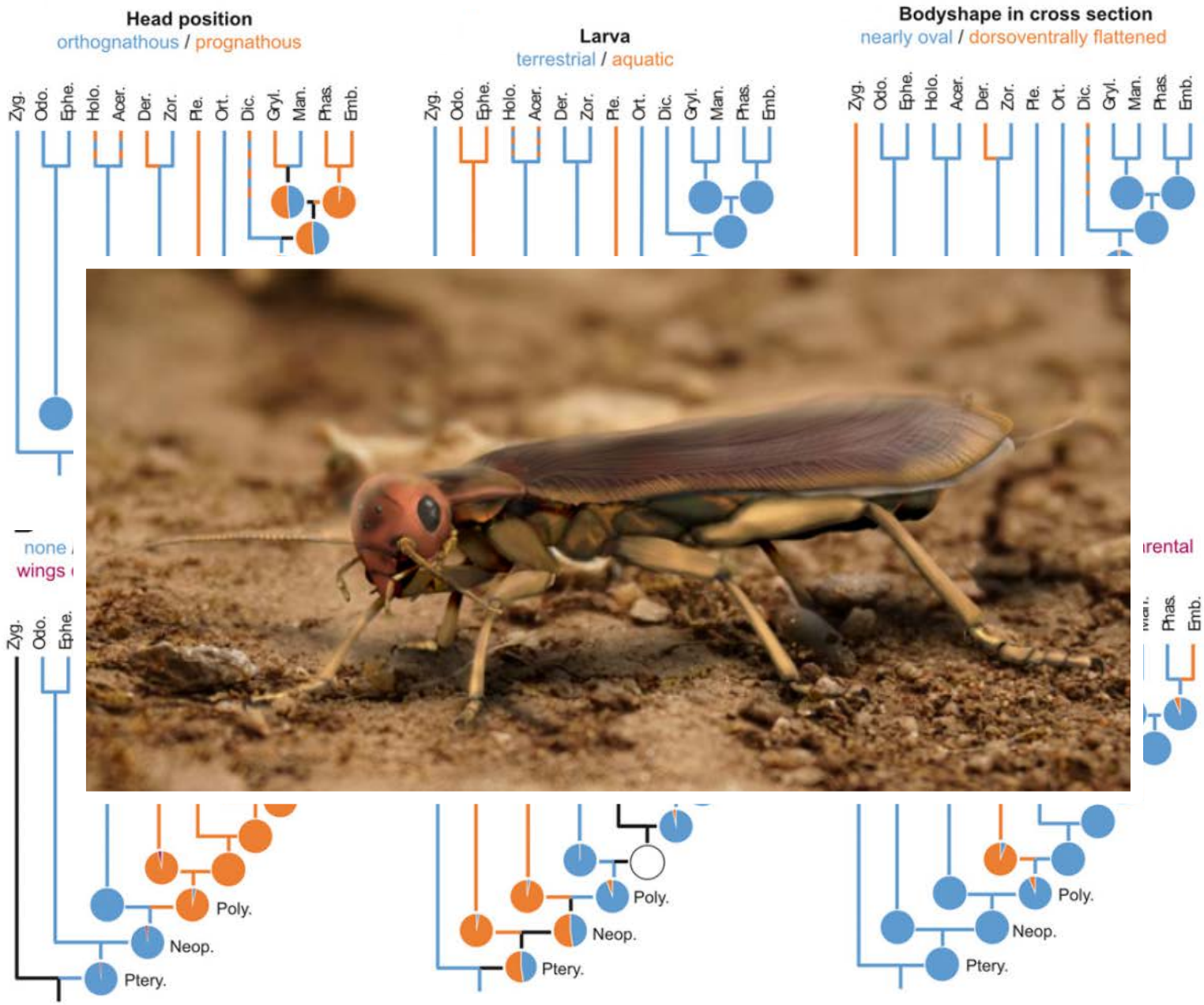
…but only insects don't fly wing legs.



Namiki et al., 2018



Wiplfer et al., 2019



Wiplfer et al., 2019

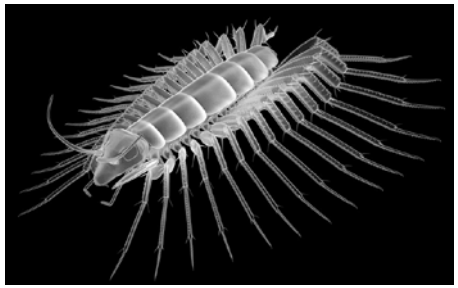
MIND THE GAP

The Paleozoic Timeline

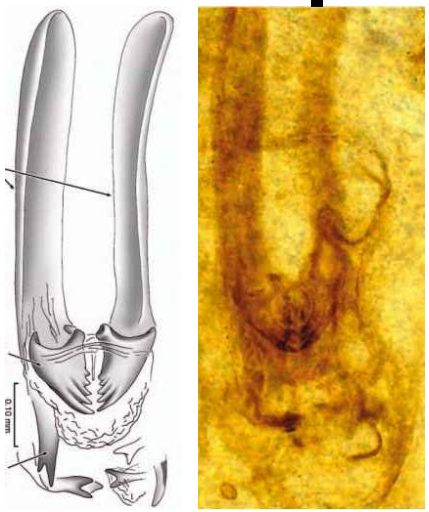
541 MYA — 252 MYA

Paleozoic Era					
Cambrian Period	Ordovician Period	Silurian Period	Devonian Period	Carboniferous Period	Permian Period

~100 million years



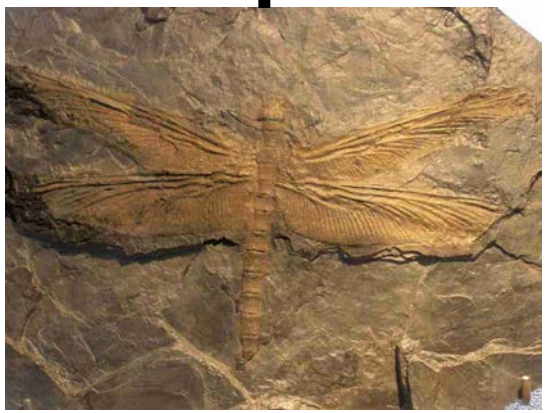
Haug & Haug, 2017



Rhyniognatha

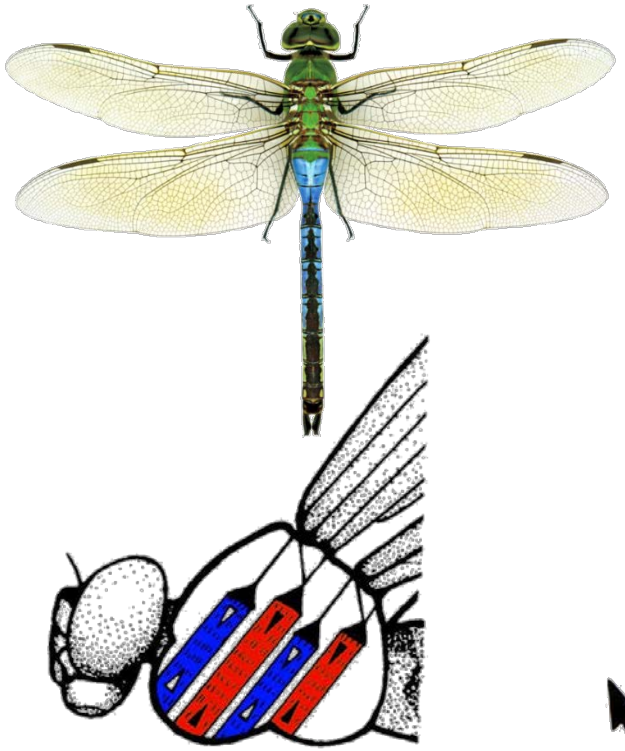
Grimalidi & Engel, 2004

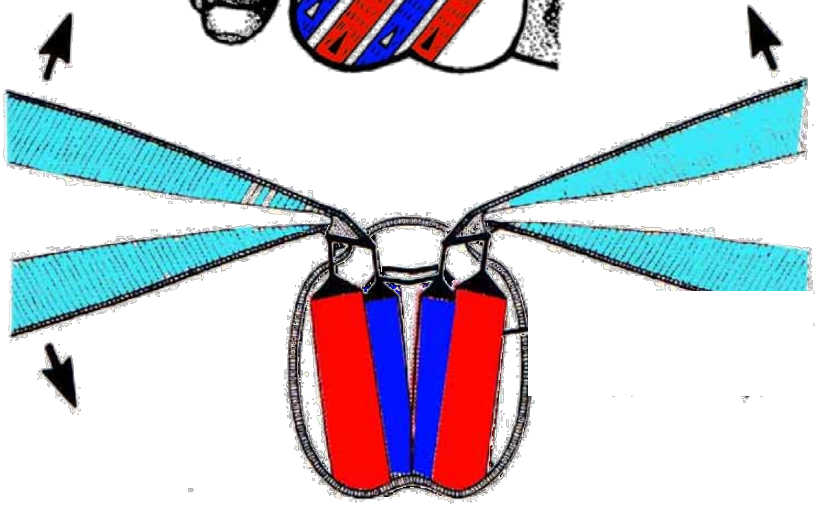
Late Devonian mass extinction



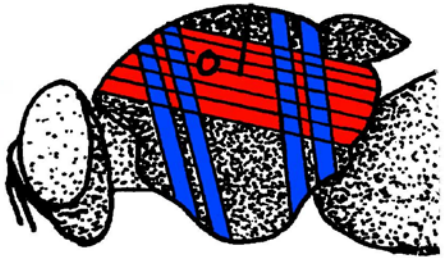
Meganeura

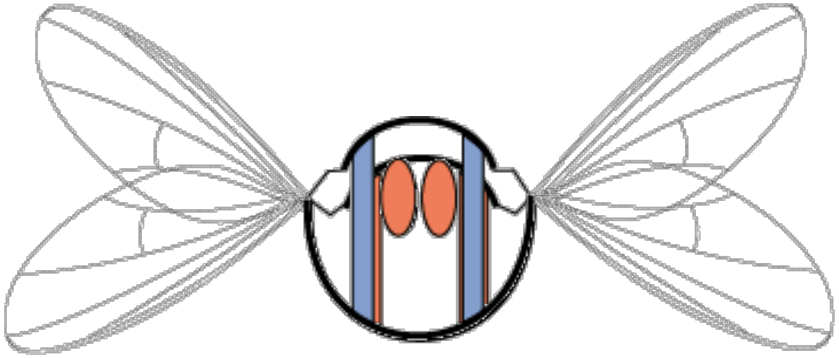
Paleopteran insect



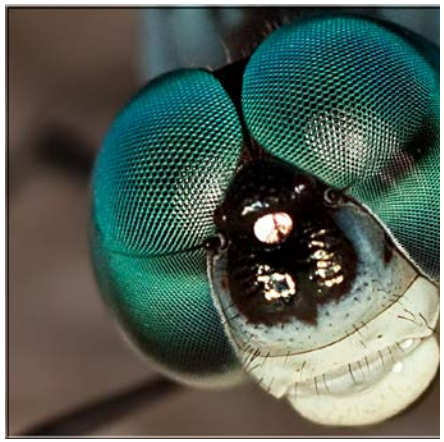


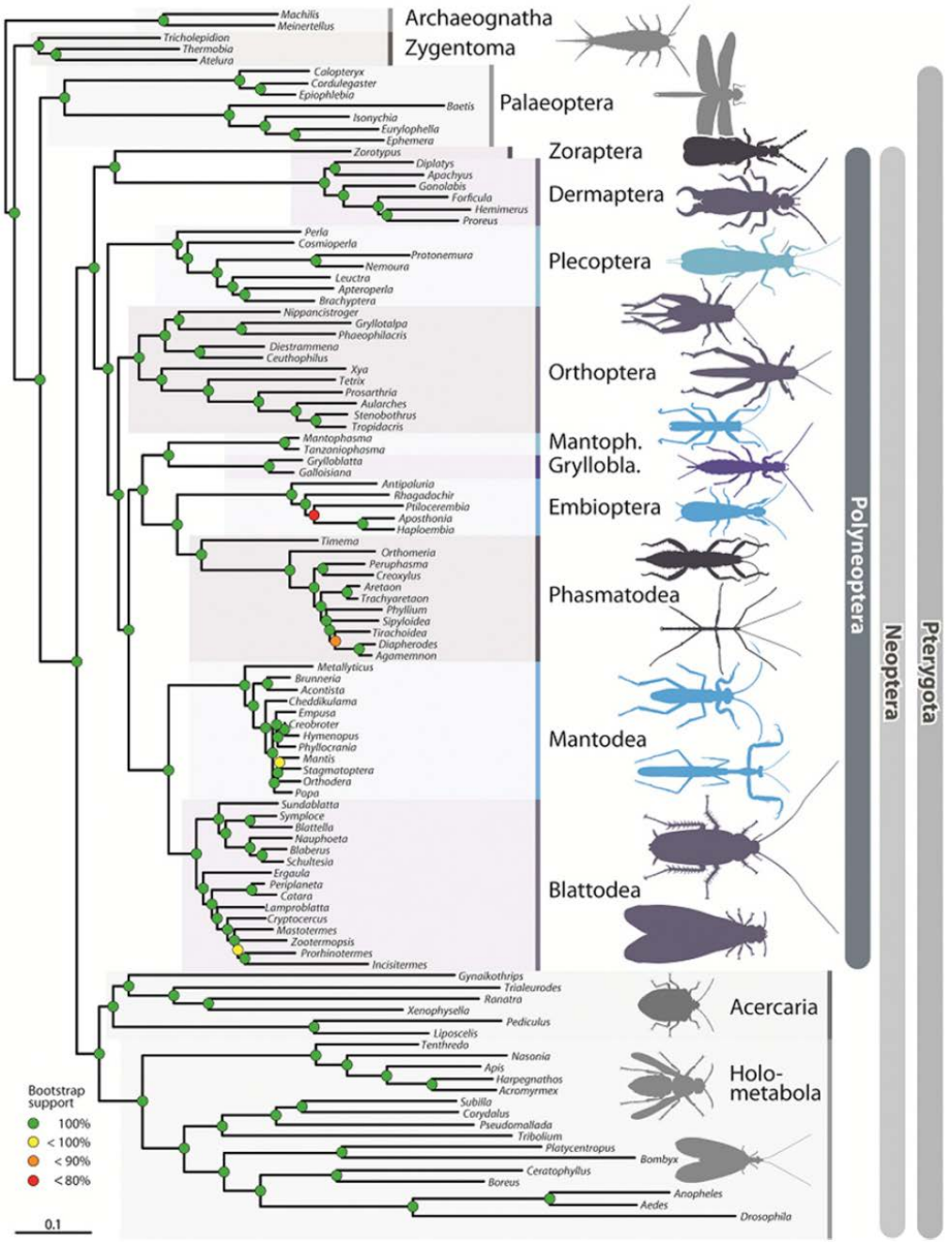
Neopteran insect





Specializations of dragonflies:
can't smell
can't walk
can't fold wings
high acuity eyes
etc.



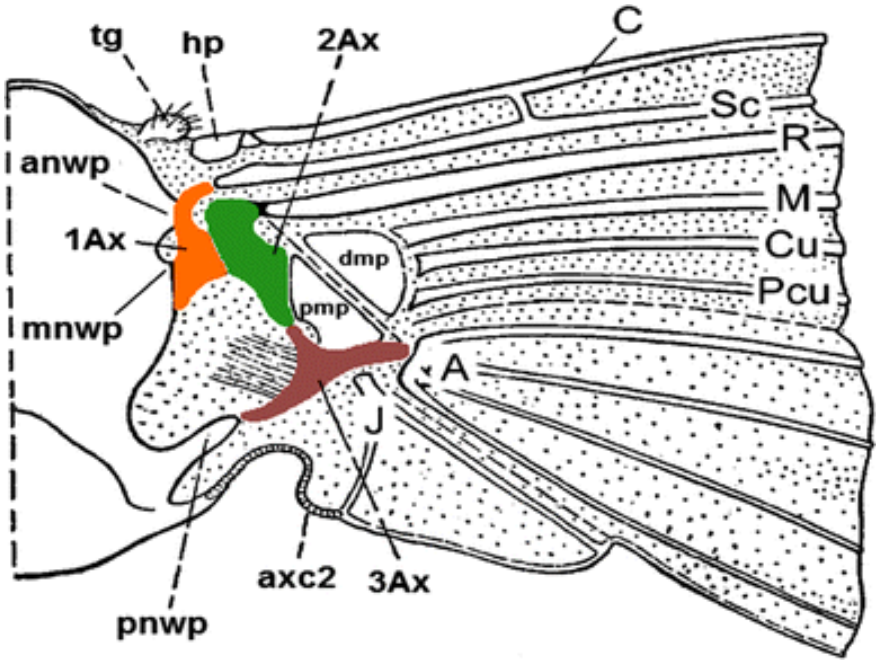


Wipfler, 2019)

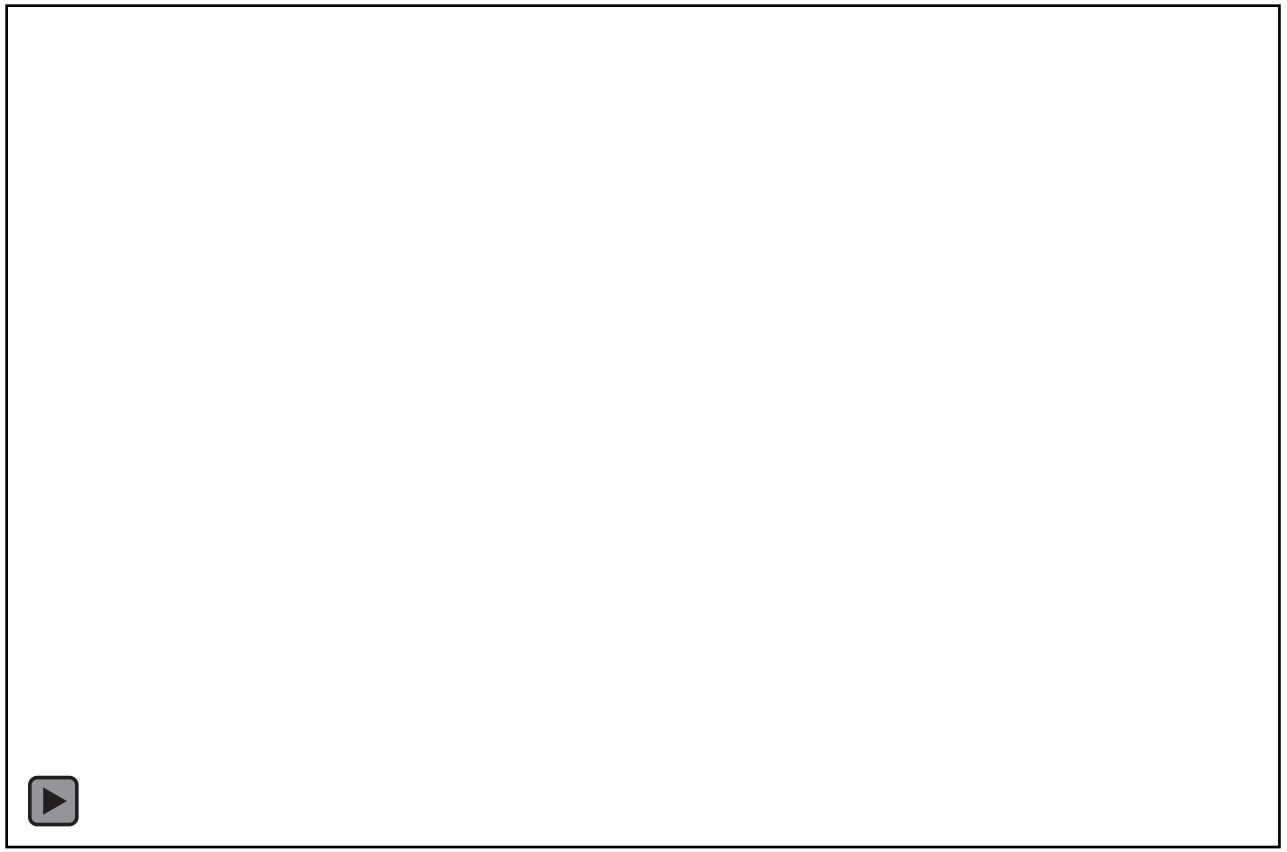
Neopteran insect

Paleopteran insect

Snodgrass model of ancestral wing 1934



The hinge mechanically programs wing motion

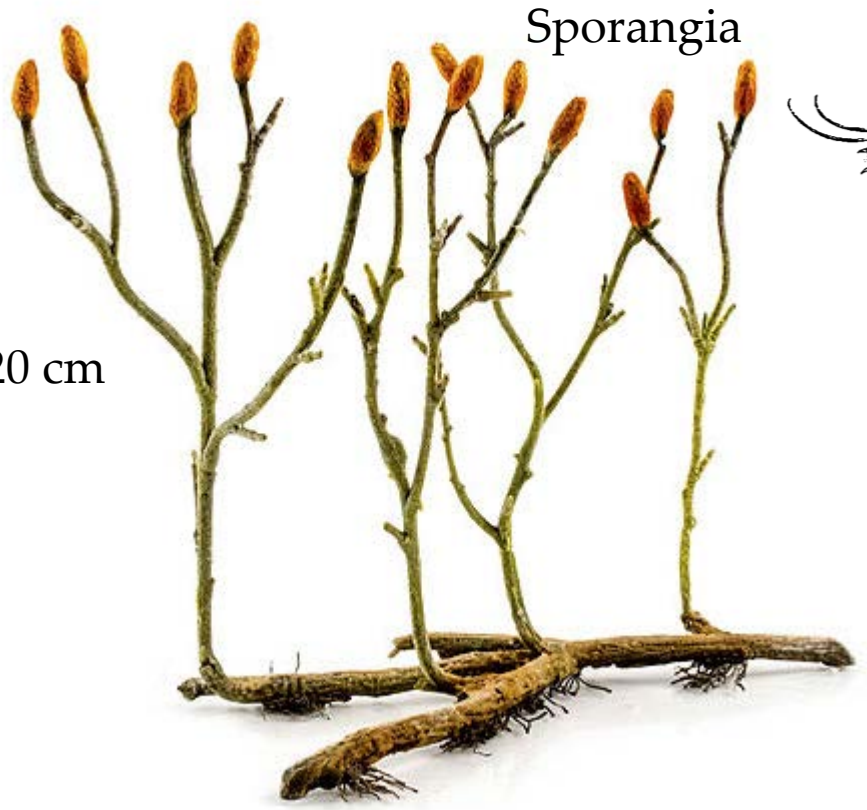


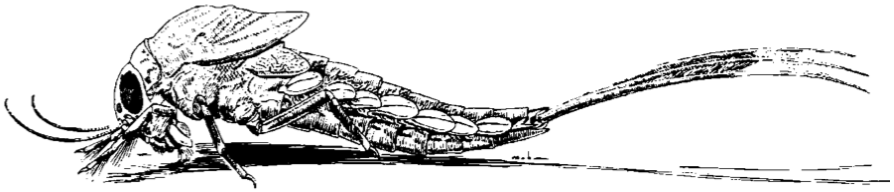
Early Devonian shit

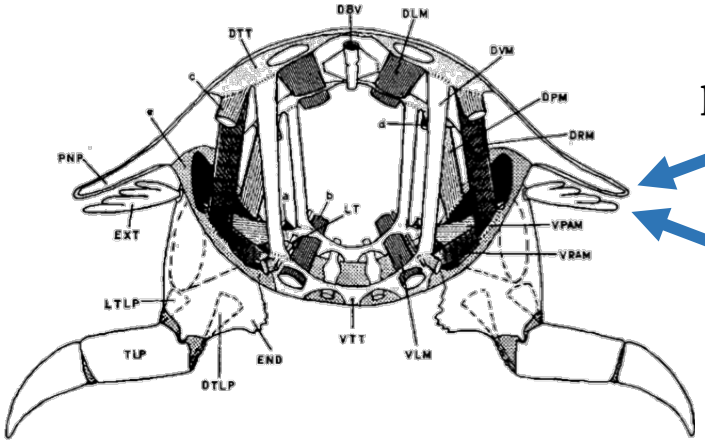
Rhynia

Sporangia

20 cm

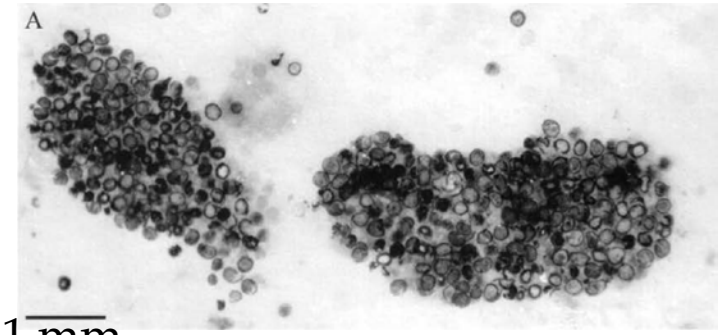






paranotal lobe

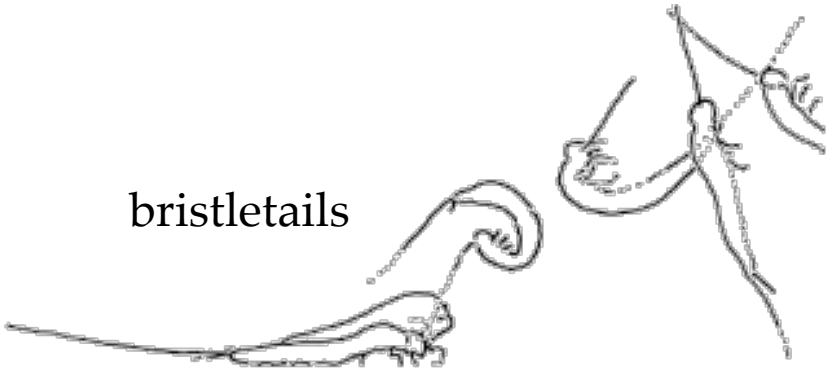
leg ~~excite~~



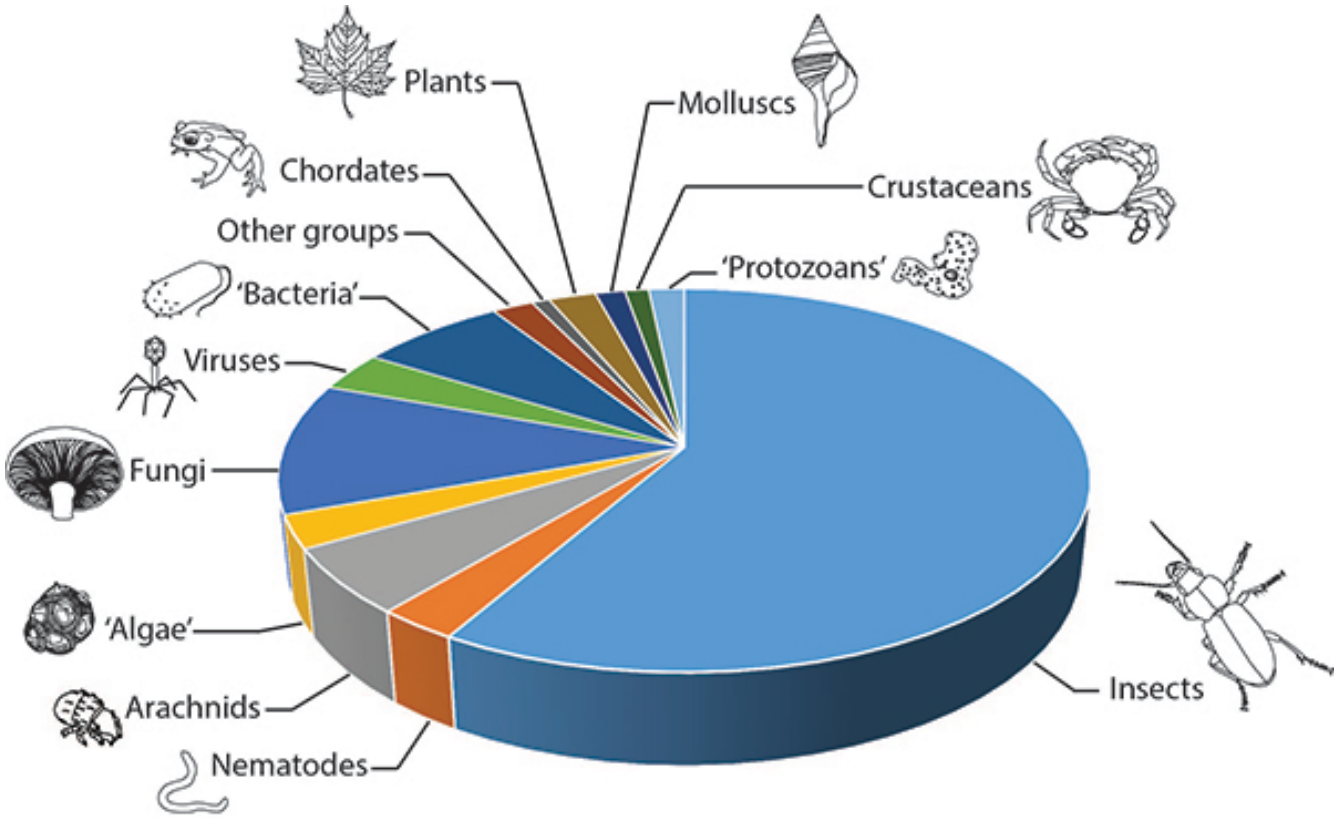
1 mm

Edwards et al., 1993

bristletails



Hassenfuss, 2002

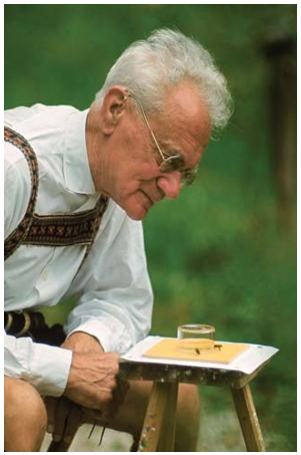

Plants
Molluscs
Chordates
Crustaceans
Other groups
'Protozoans'
'Bacteria'
Viruses
Fungi
'Algae'
Arachnids
Nematodes
Insects

Forward to the Past

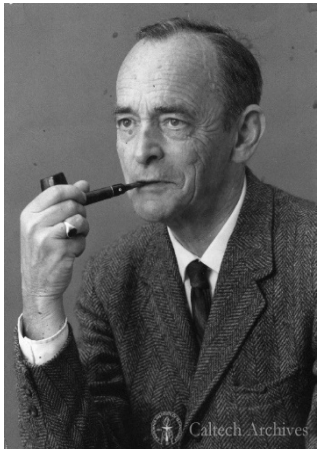
Toward a New Synthesis of Ethology

Niko Tinbergen (1907-1988)

Konrad Lorenz (1903-1989)

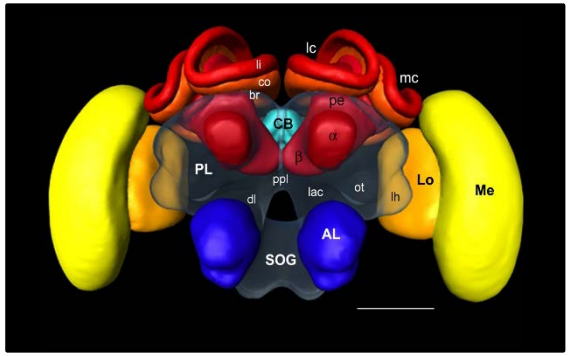


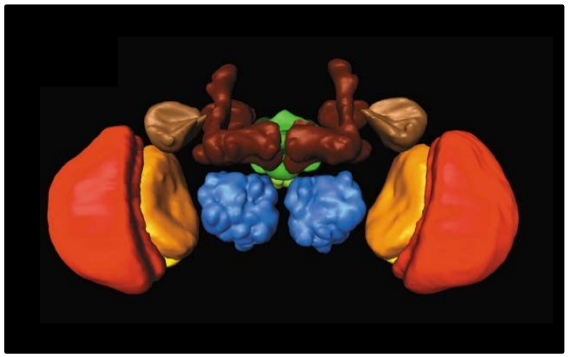
Karl von Frish (1886-1982)



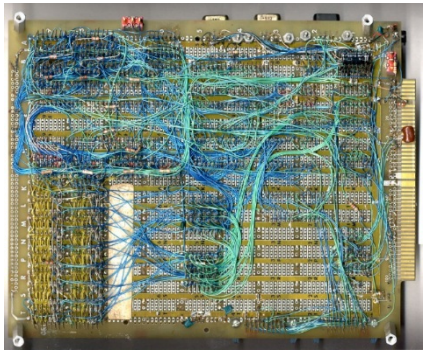
Cornelius Wiersma (1904-1987)

Nervous systems are anatomically similar.





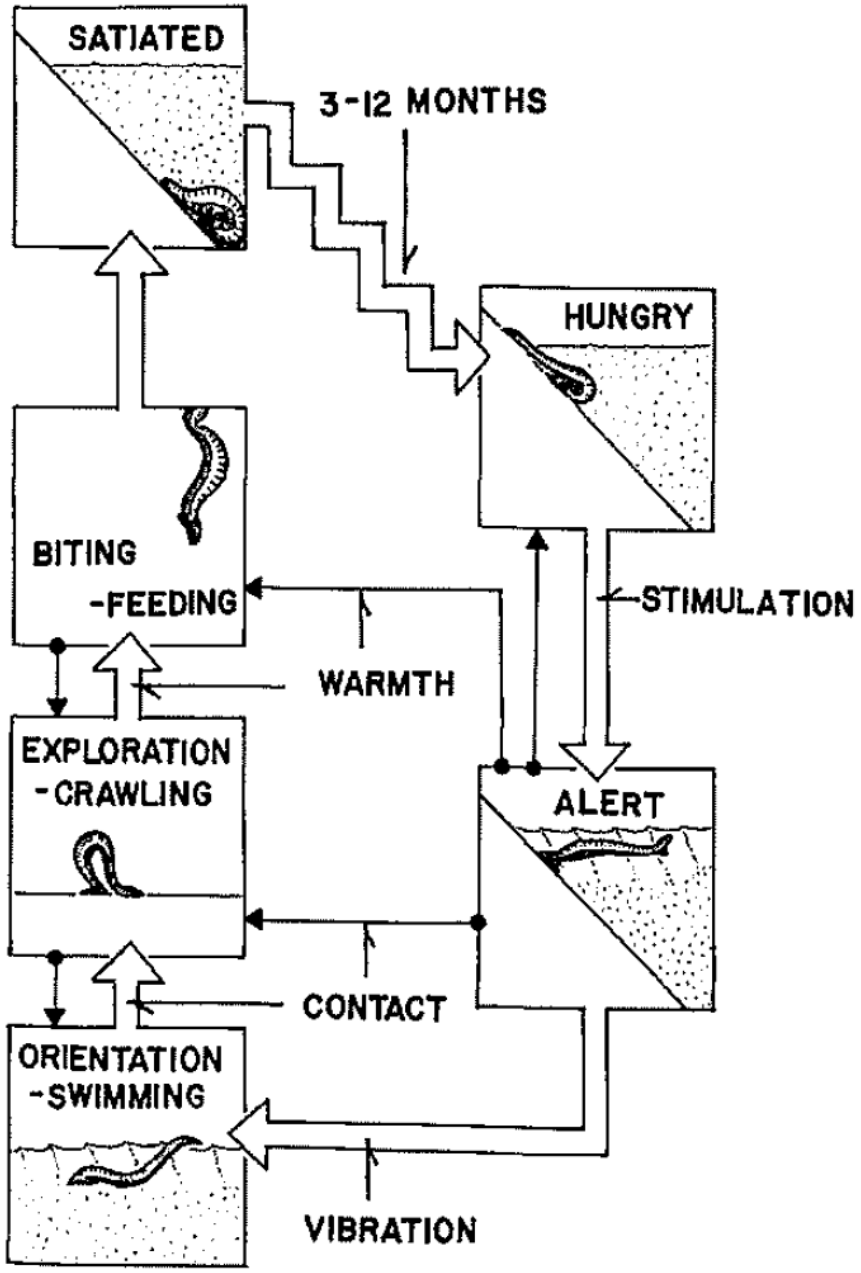
vs.



Feeding behavior of the medicinal leech, *Hirudo medicinalis* L.

Michael H. Dickinson and Charles M. Lent
J. Comp. Physiol. 1984

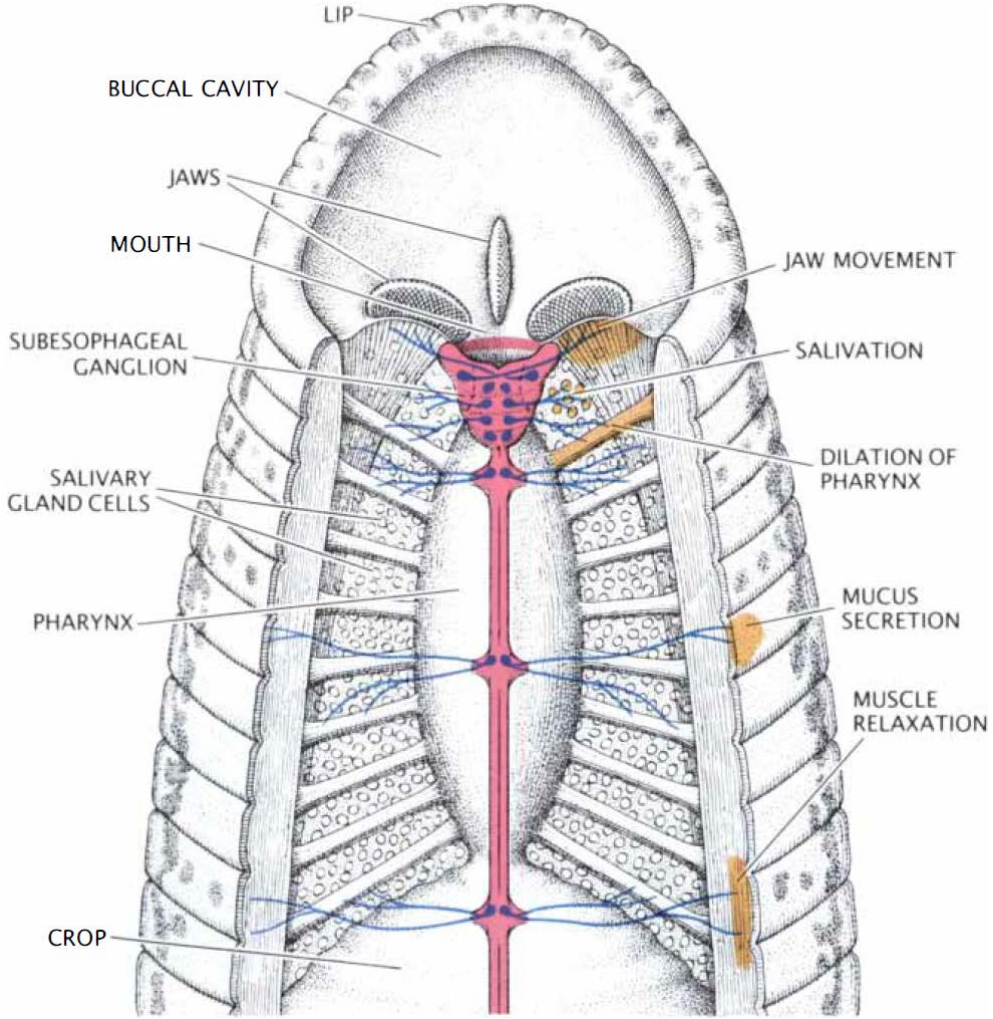
- Behaviors consists of complex, flexible sequences of modules or states.
- Transition probability between states is influenced by sensory experience, internal state, memory, etc.



Serotonin integrates the feeding behavior of the medicinal leech

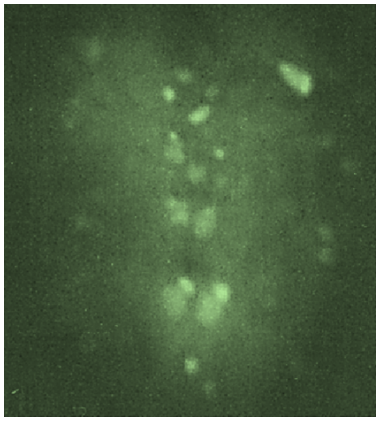
Charles M. Lent and Michael Dickinson

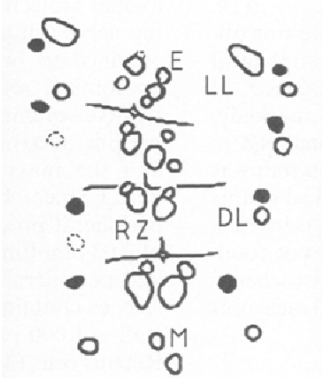
J. Comp. Physiol. 1984



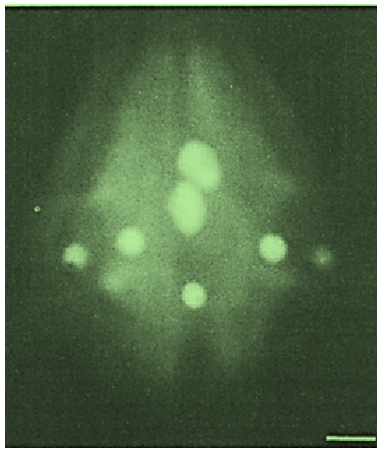
serotonin neurons

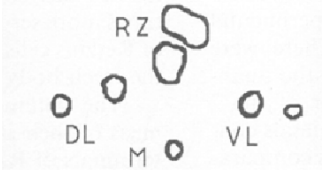
brain





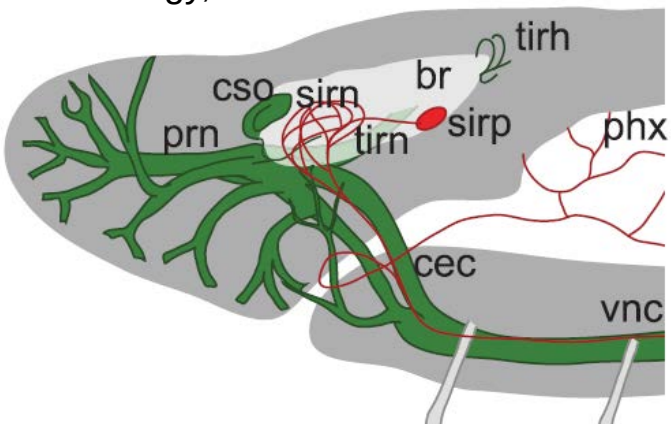
segmental ganglion





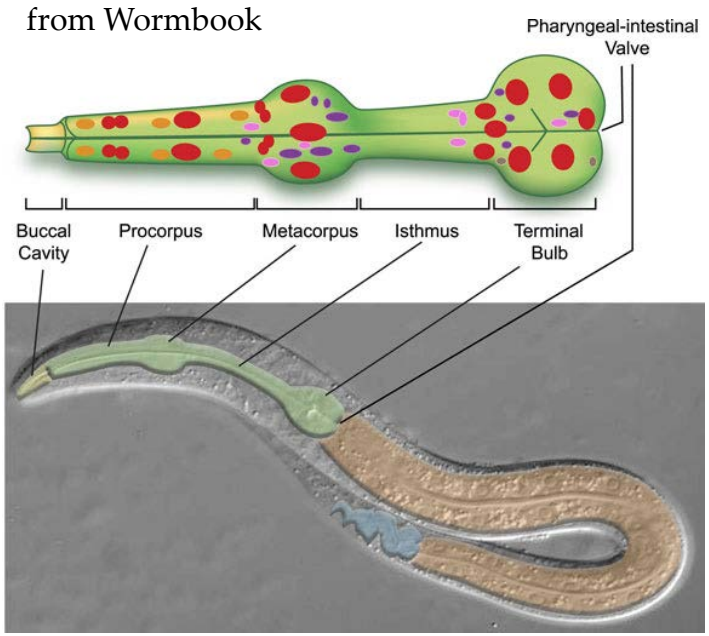
Fine taxonomic sampling of nervous systems within Naididae (Annelida: Clitellata) reveals evolutionary lability and revised homologies of annelid neural components

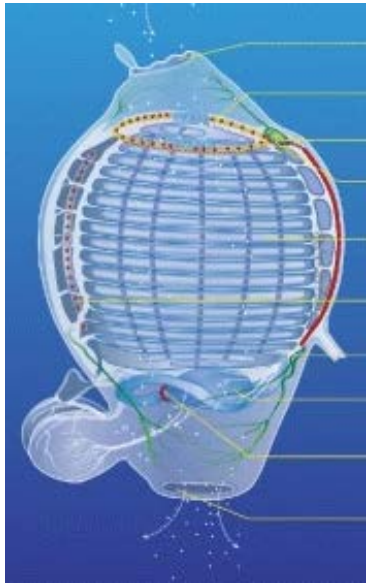
Zattara and Bely
Frontiers-in-Zoology, 2015



Serotonin activates overall feeding by activating two separates neural pathways in *Caenorhabditis elegans*

Song and Avery
J. Neurosci. 2012





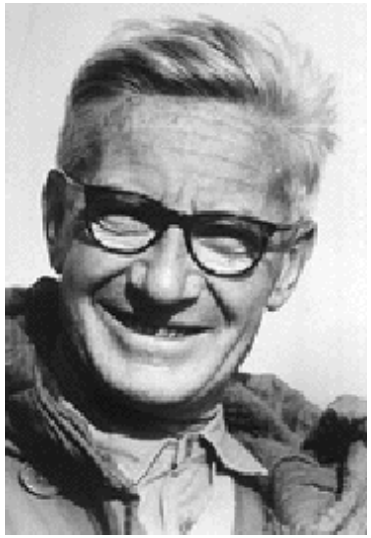
Comparative localization of serotonin-like immunoreactive cells in Thaliacea informs tunicate phylogeny

Valero-Gracia et al.,
Frontiers in Zoology, 2016

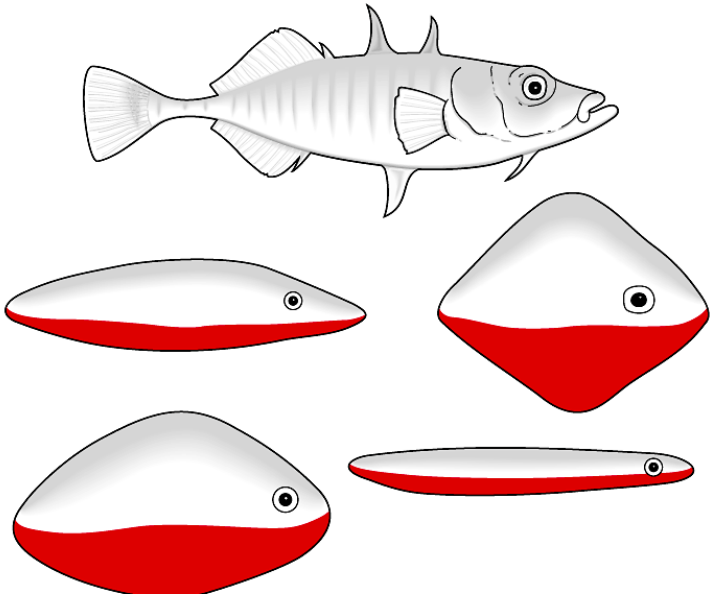
Behavioral modules and the circuits that underlie them may represent deep homologies…

…but similarities might also emerge via convergent evolution using similar molecular & cellular components.

Evidence for behavioral modules



Niko Tinbergen



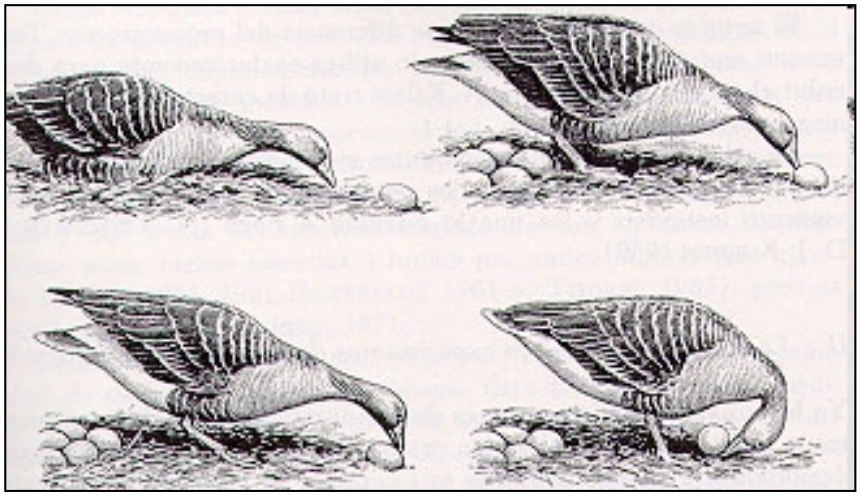
sign stimulus
(releaser)

↓

fixed action
pattern

Evidence for behavioral modules

Konrad Lorenz



Evidence for behavioral modules

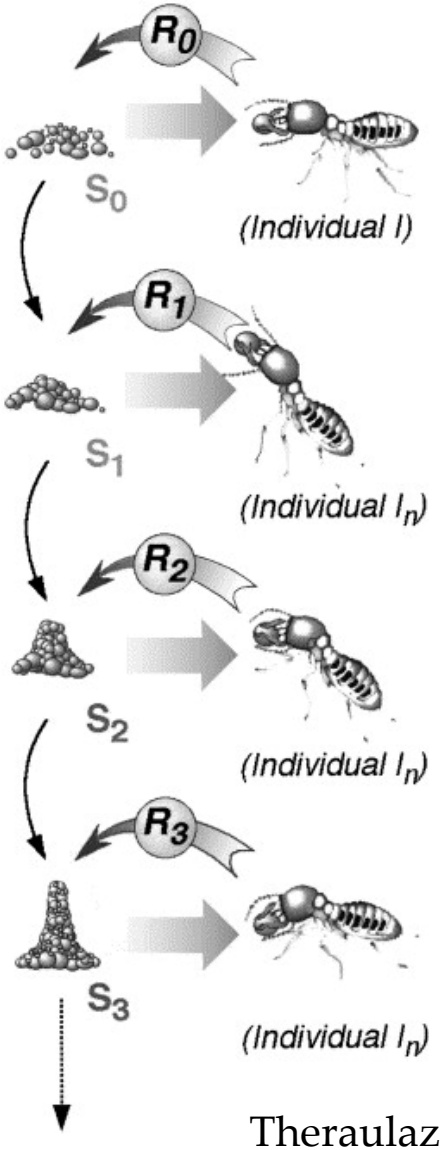
Paul Lemmons

Evidence for behavioral modules

Pierre-Paul Grassé

Stigmergy

"An agent's actions leave signs in the environment, signs that it and other agents sense and trigger subsequent actions."

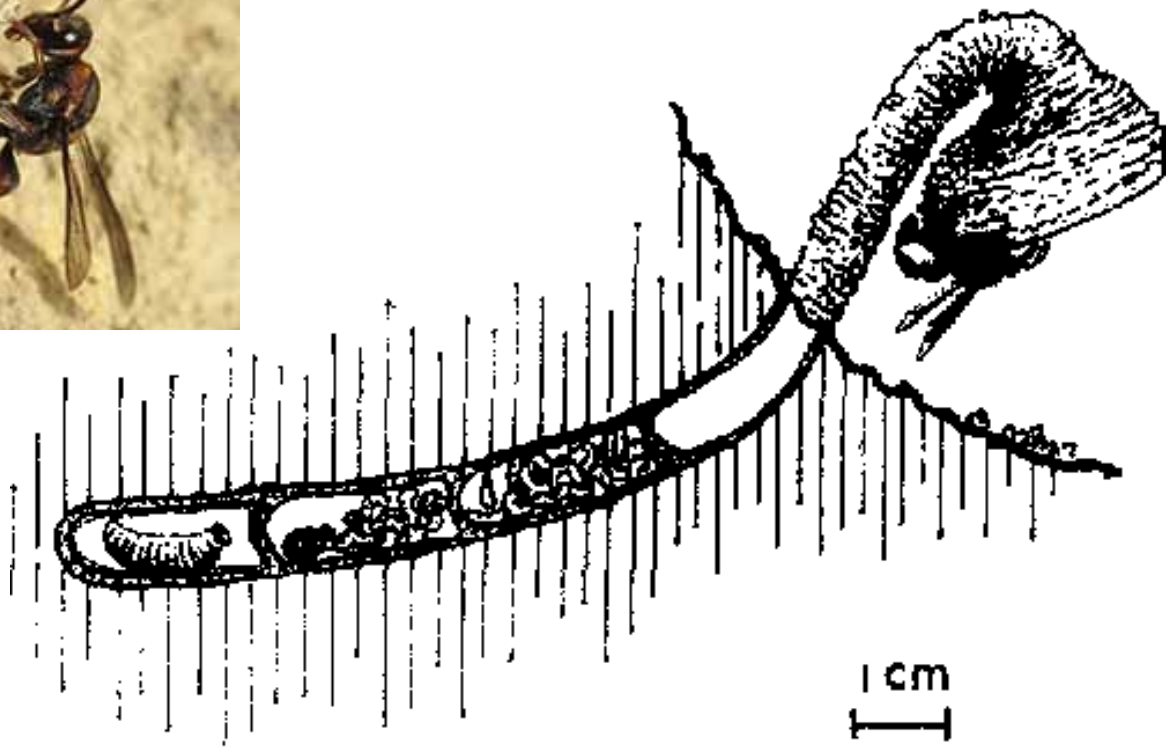


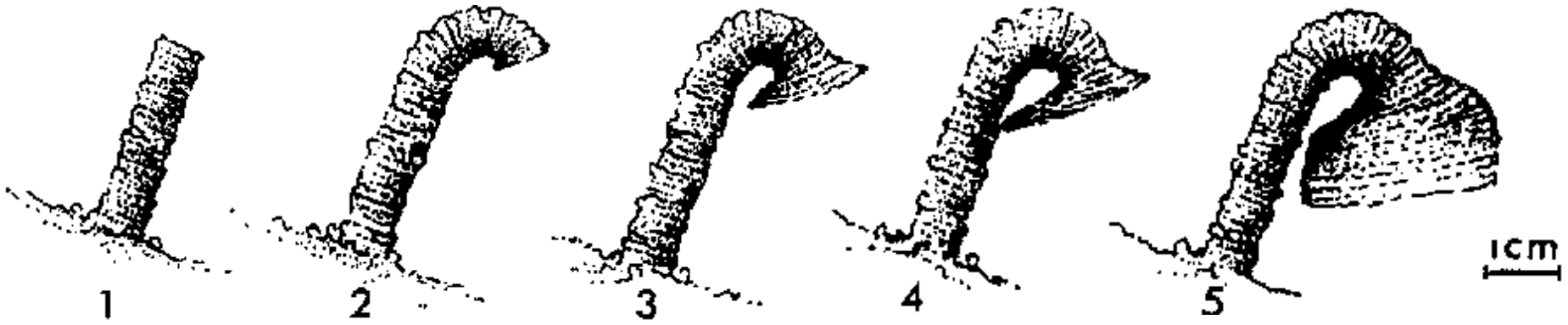
Theraulaz & Bonabeau, 1999

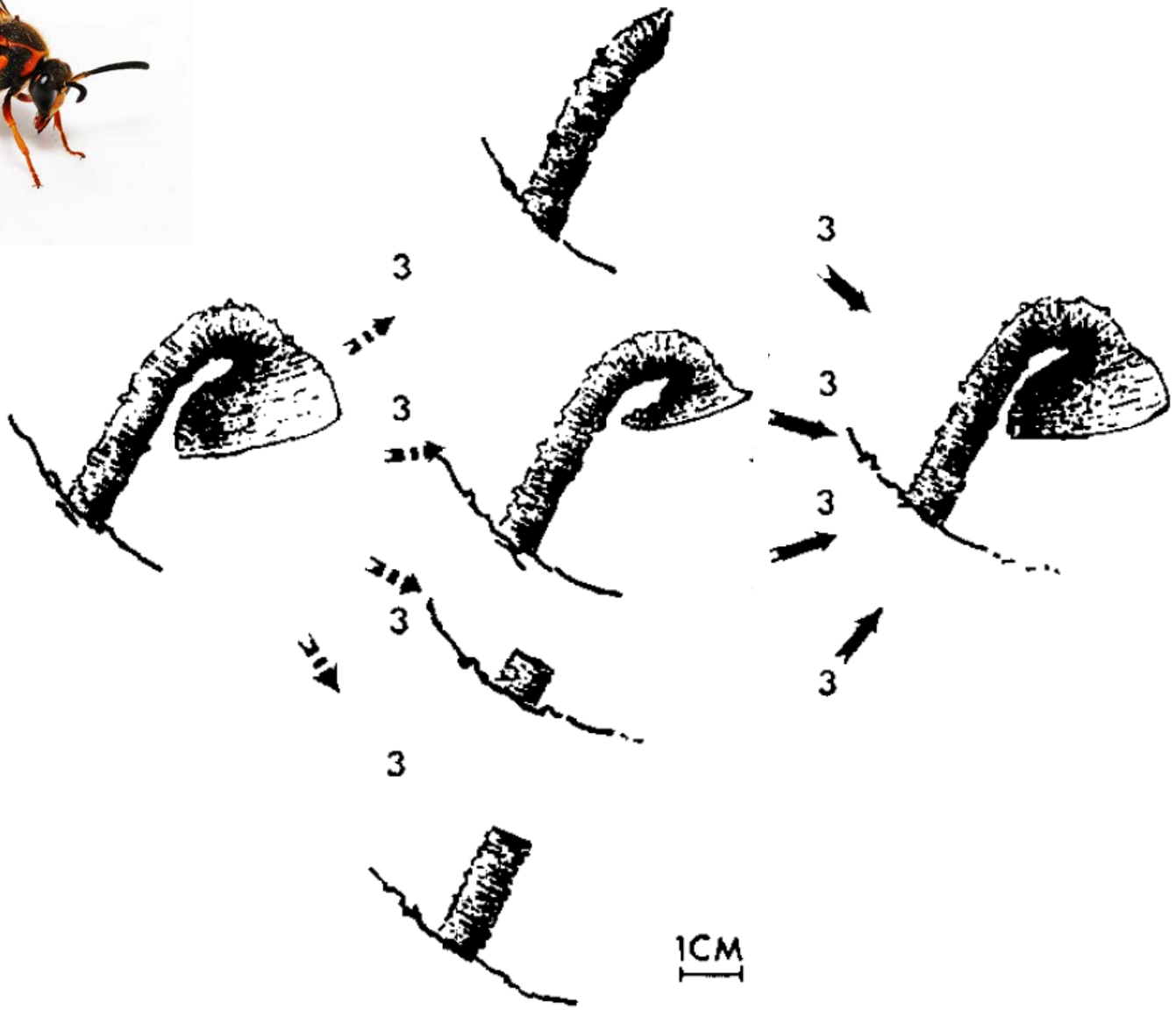
Anim. Behav., 1978, **26**, 232–240

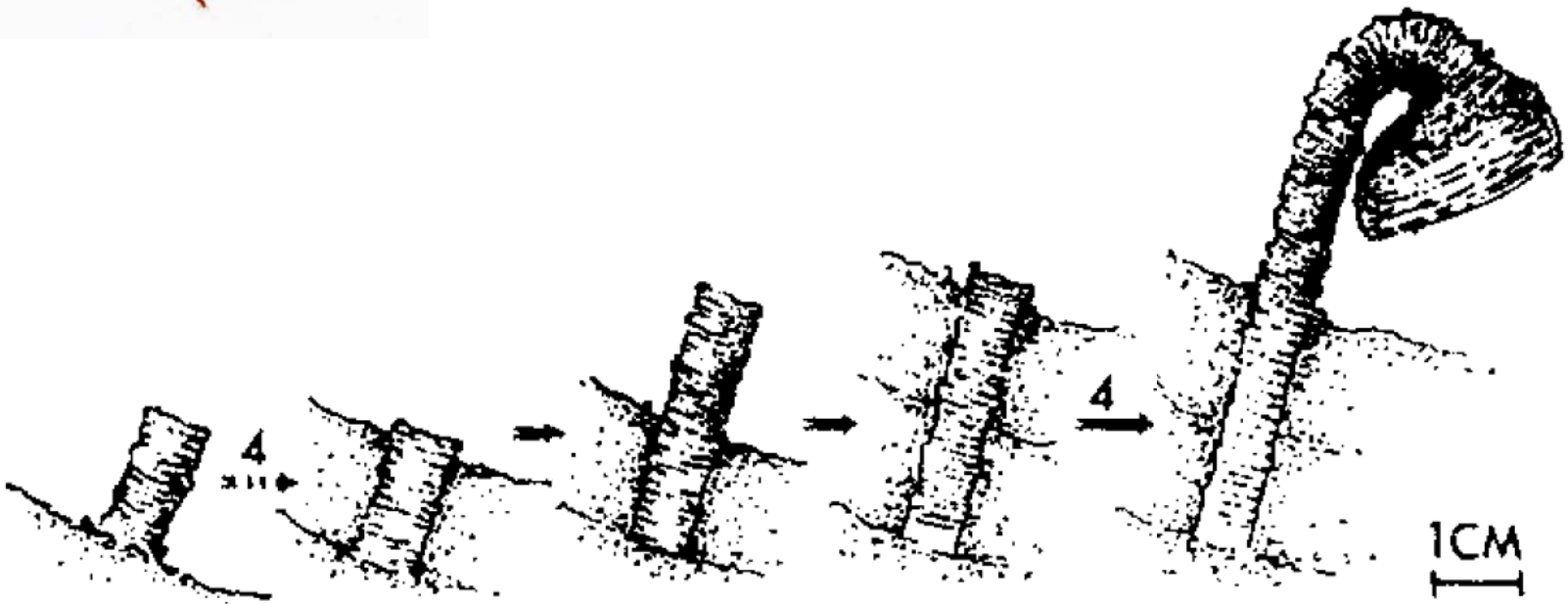
AN INVESTIGATION OF THE MECHANISMS UNDERLYING NEST CONSTRUCTION IN THE MUD WASP *PARALASTOR* SP. (HYMENOPTERA: EUMENIDAE)

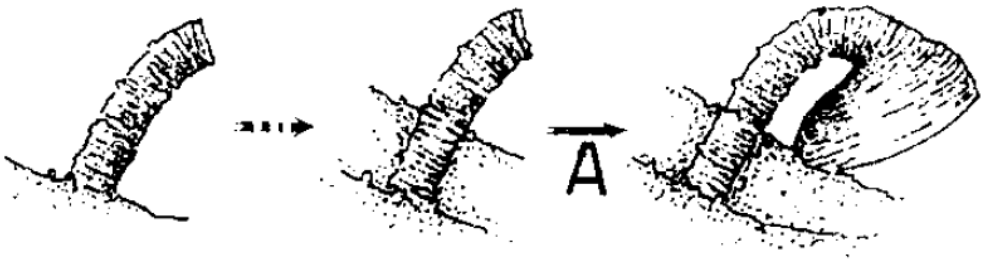
BY ANDREW P. SMITH*
Zoology Department, University of Sydney




1
2
3
4
5
1cm


3
3
3
3
3
3
3
3
1CM


4
4
1CM



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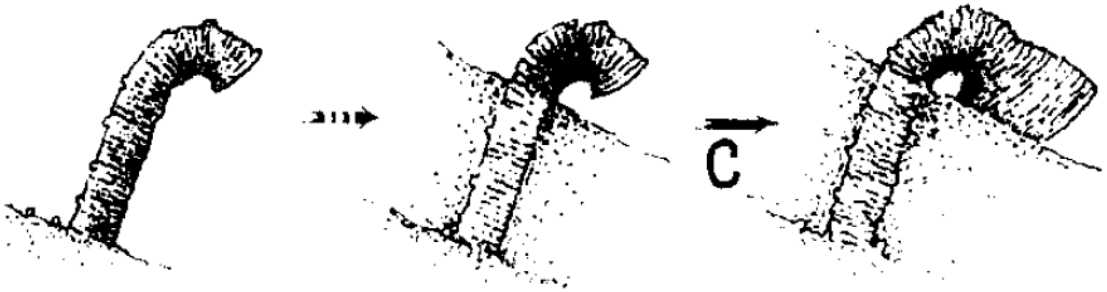
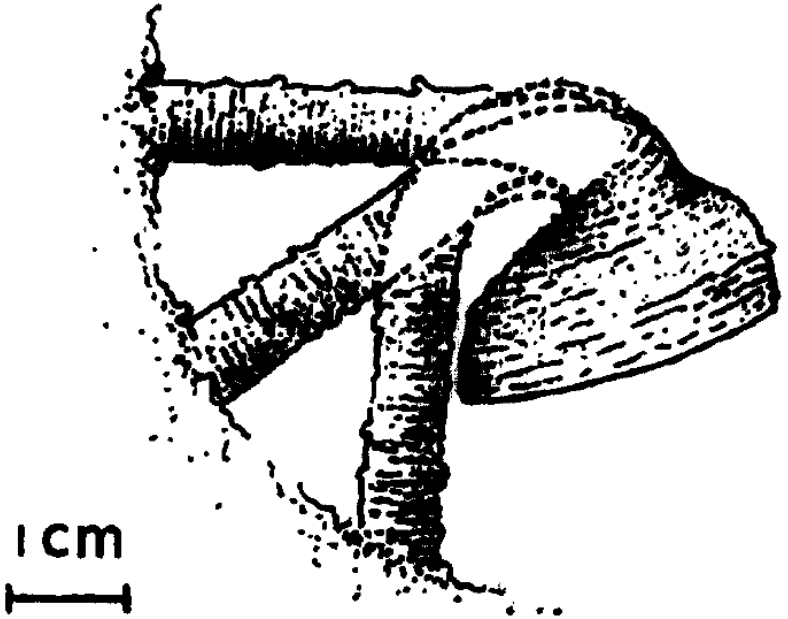
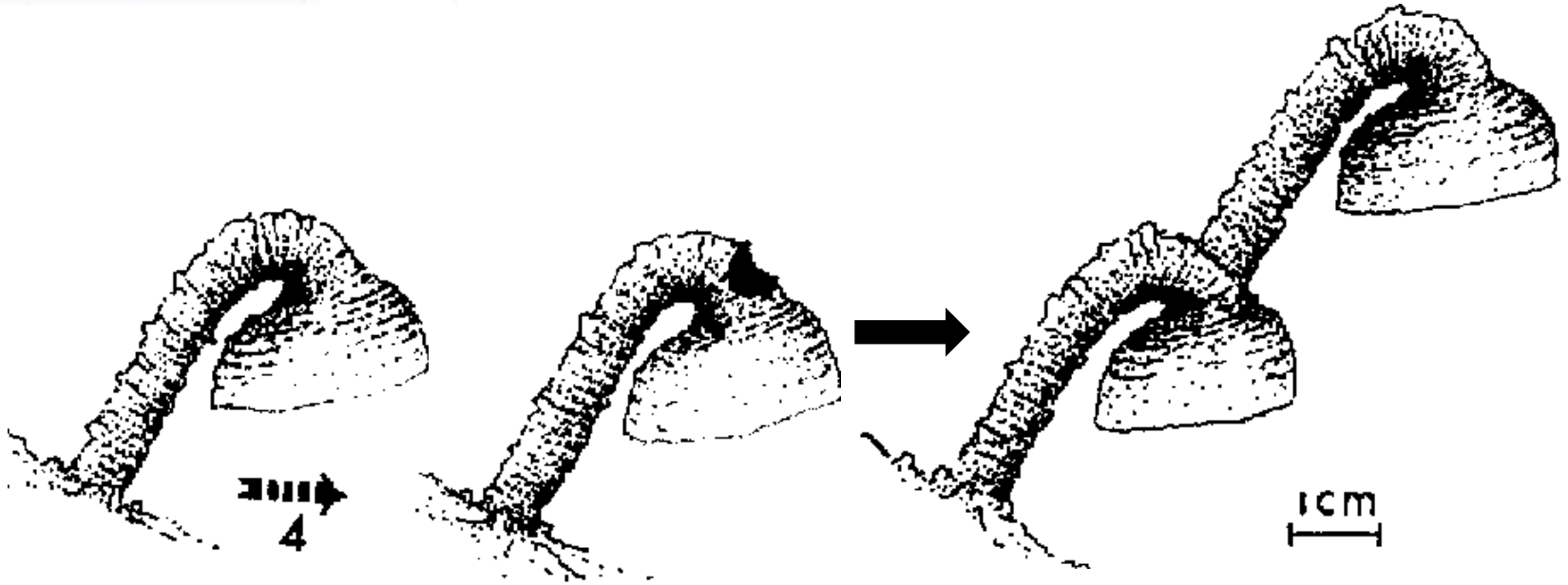



1 cm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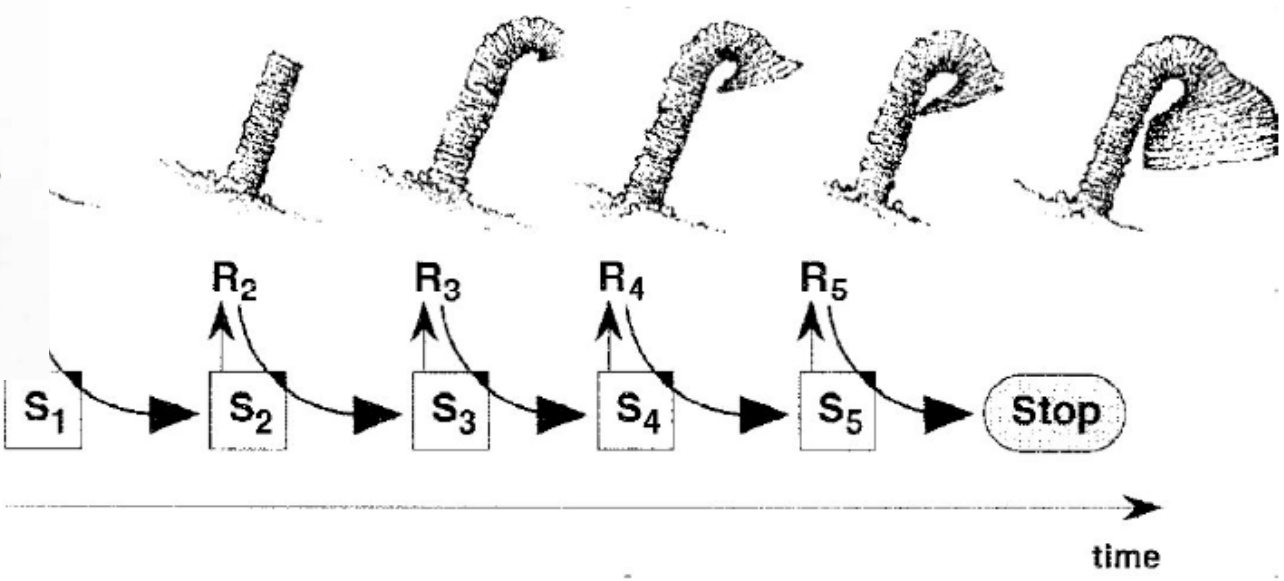
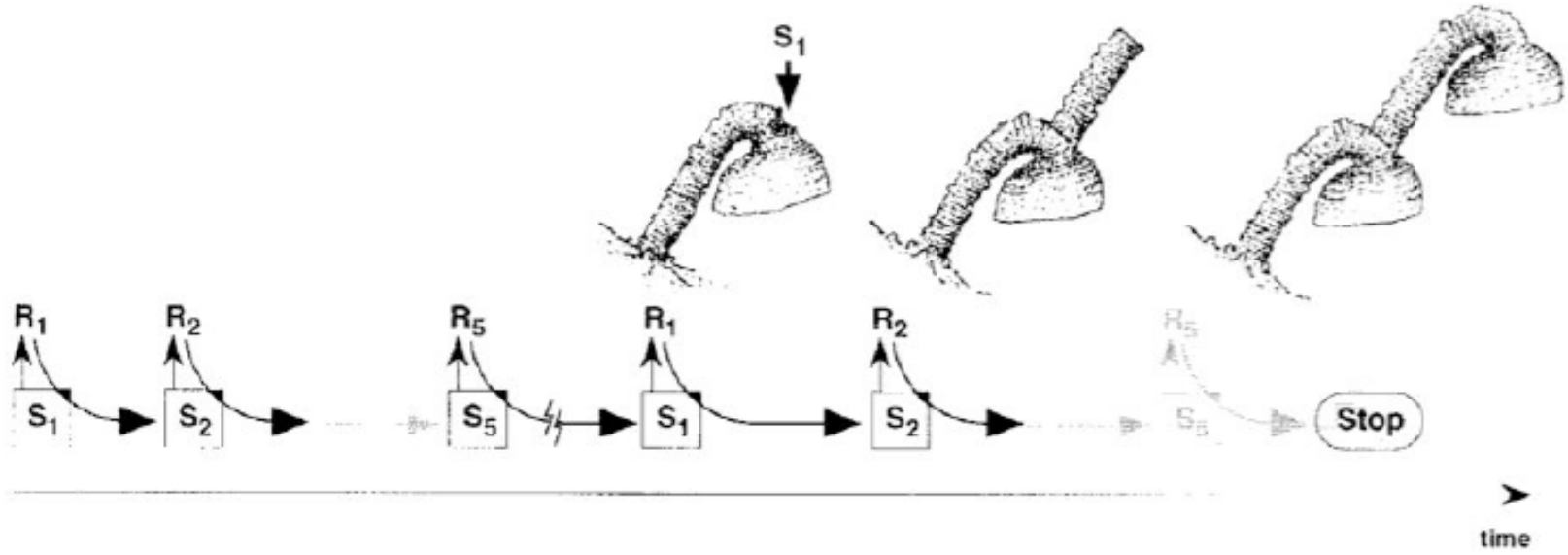
1cm

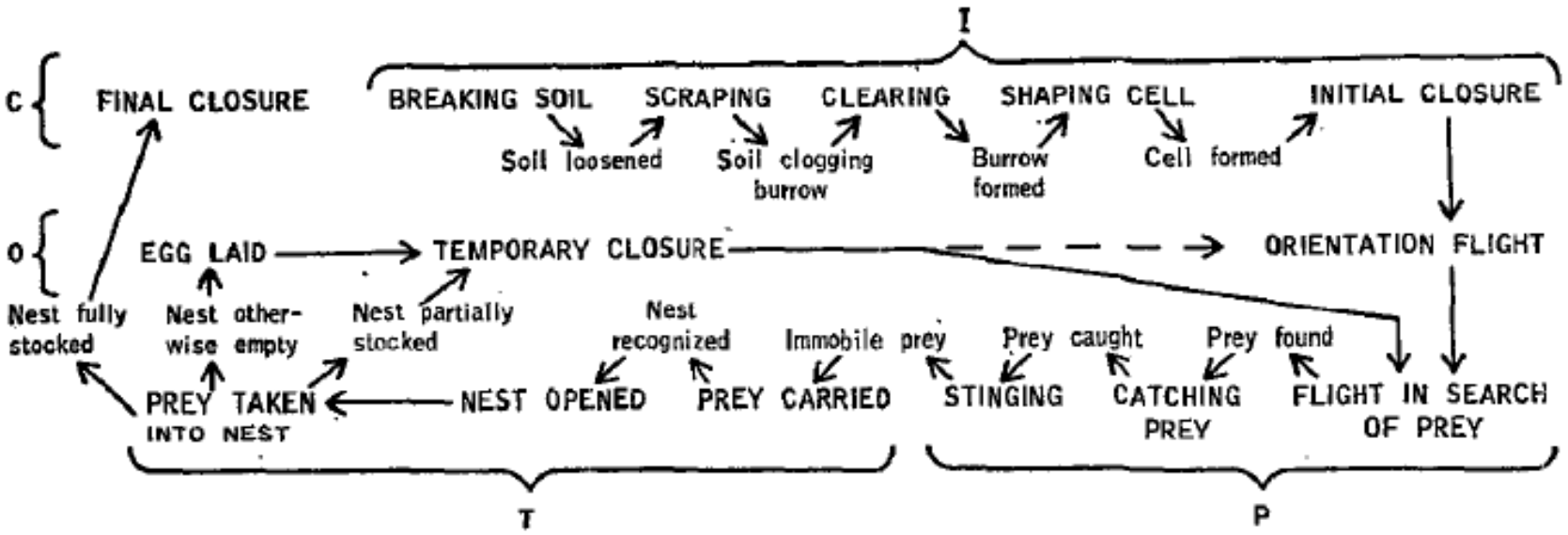




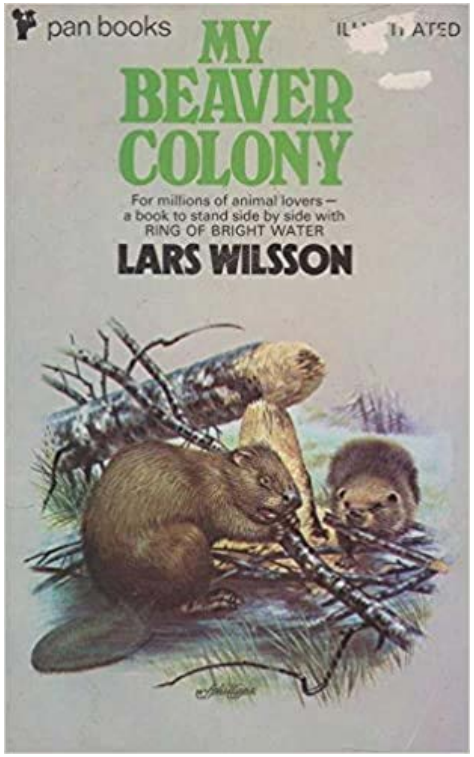
Theraulaz &
Bonabeau, 1999

Behavior patterns are to be understood not only in terms of their function and causation but also in terms of their evolutionary history.

Howard R. Evans, 1966



Evans, *Annual Review of Entomology*, 1966

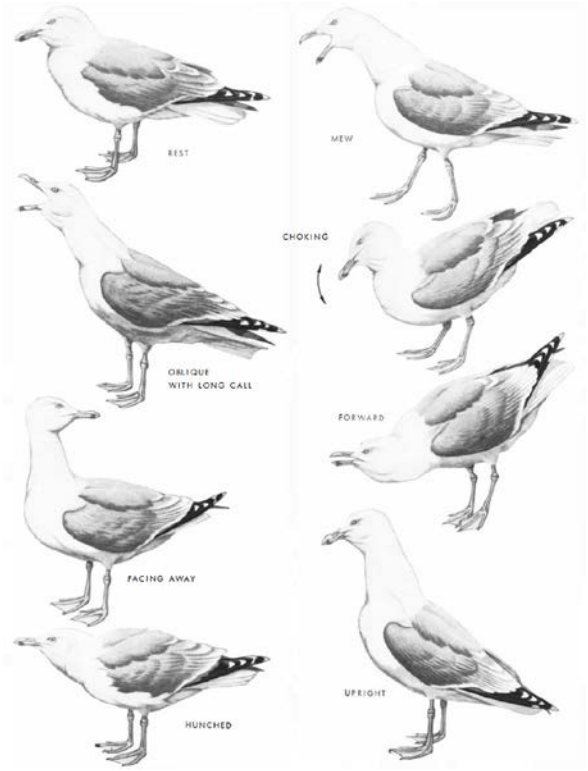


Nadine Halston

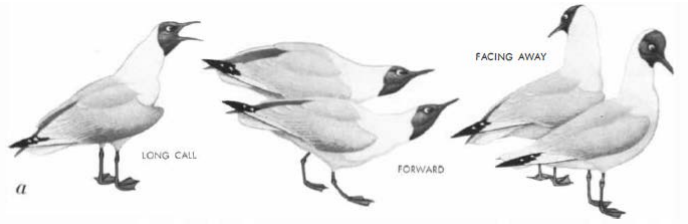
The Evolution of Behavior in Gulls

Gulls communicate with one another by means of calls, postures and movements. Differences in the signaling behavior of various species reflect the influence of environment on gull evolution

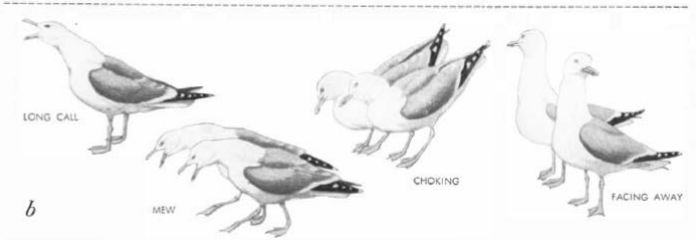
Principle display postures



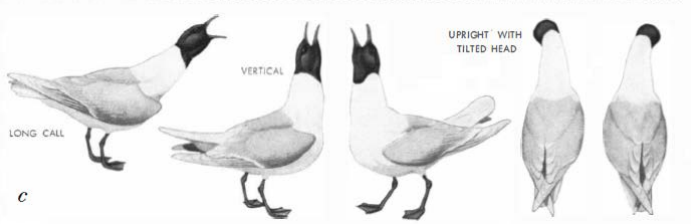
Black-headed gull



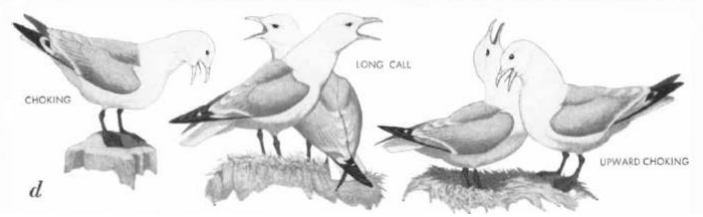
Herring gull



Little gull



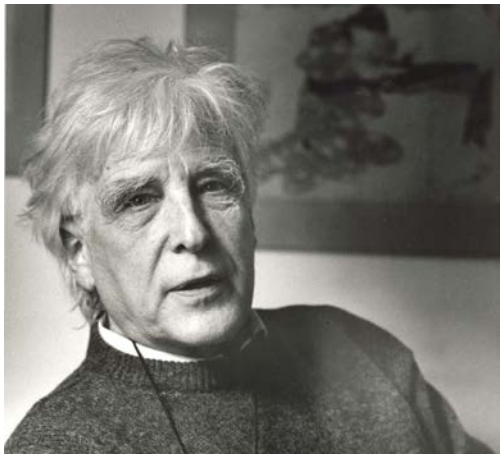
Kittiwake

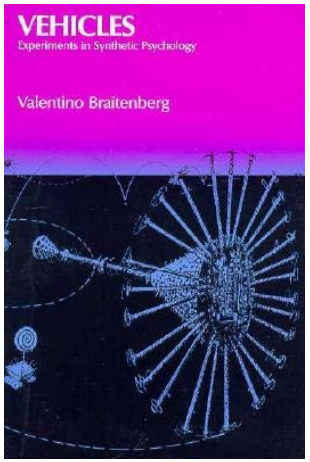


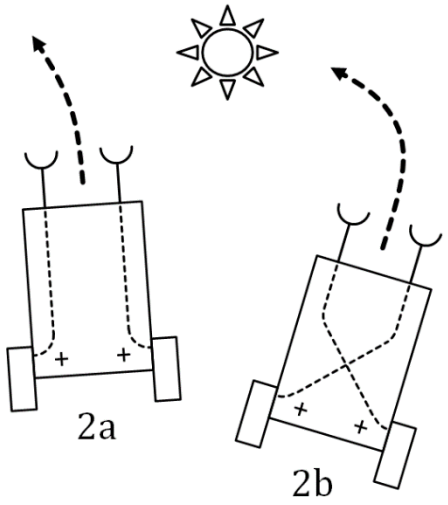
Tinbergen, *Scientific American*, 1960

Some perspectives in engineering

Braitenberg Vehicles

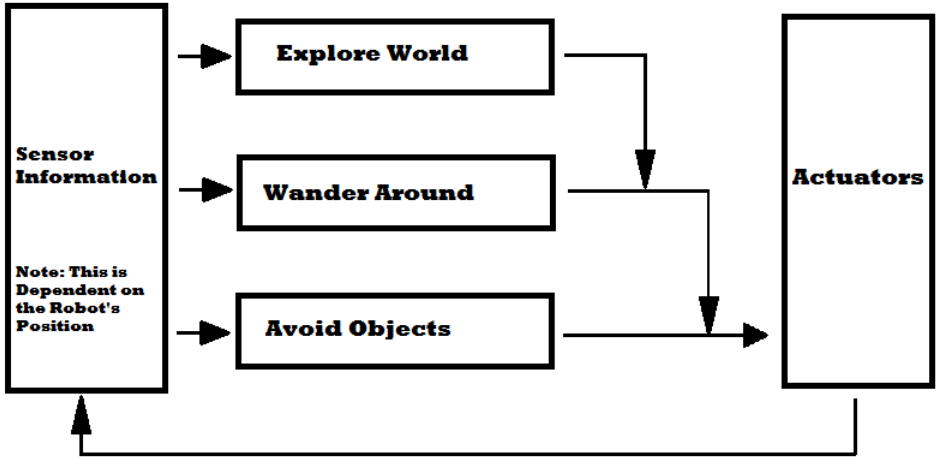


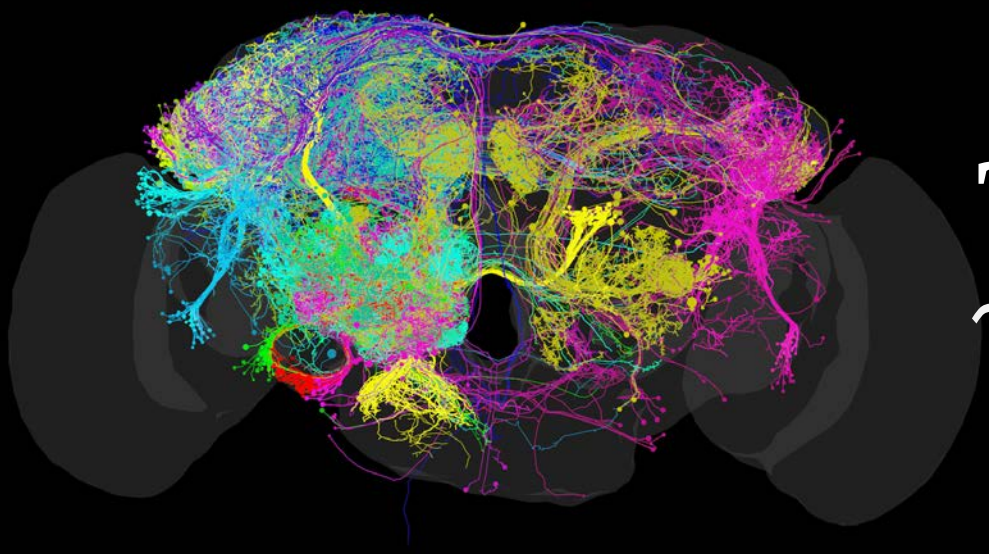




Subsumption Architecture

Rodney Brooks





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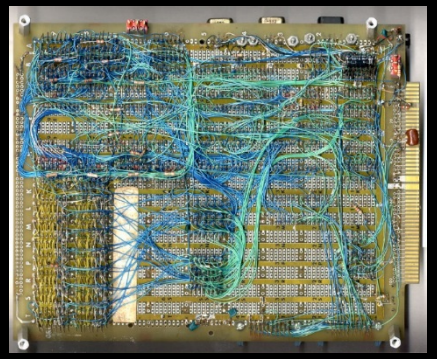
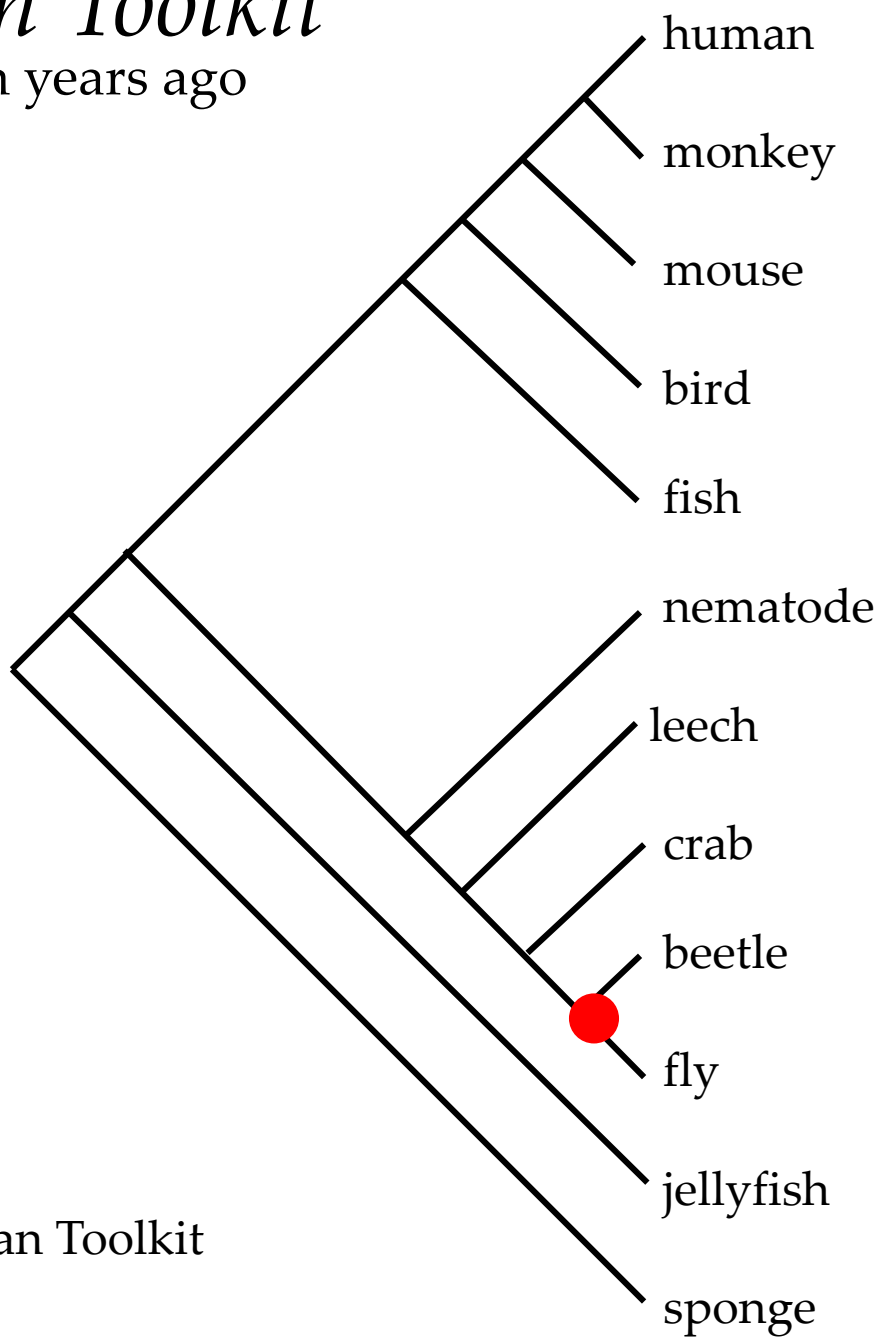


Drosophila connectome, JRC

Devonian Toolkit

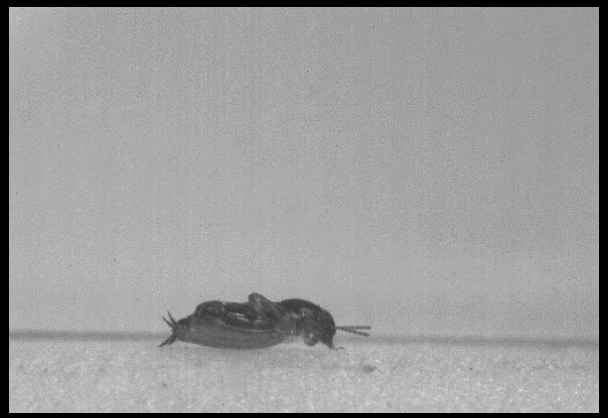
400 million years ago

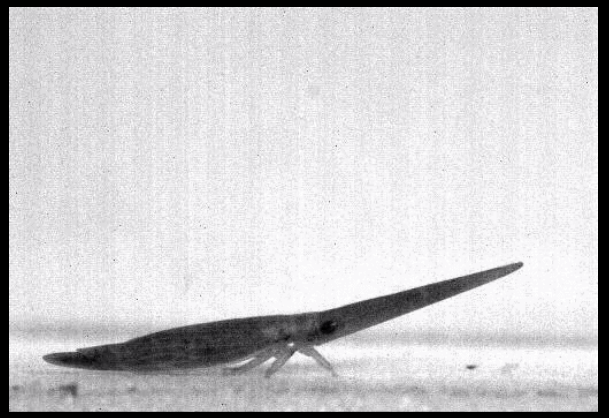
Wipfler et al., 2019

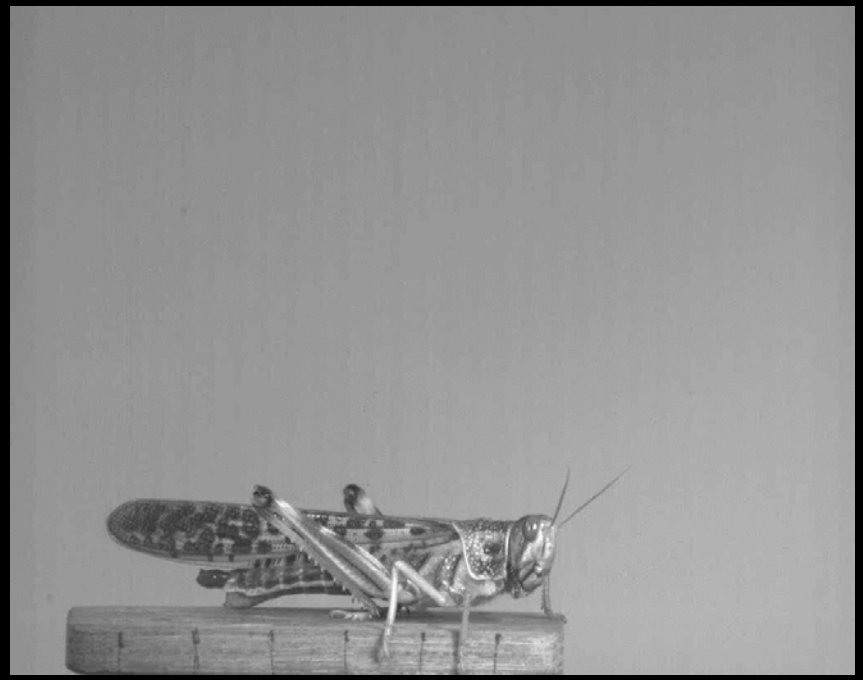


Death Valley, *Drosophila*, and the Devonian Toolkit
Annual Review of Entomology, 2014

Escape behavior

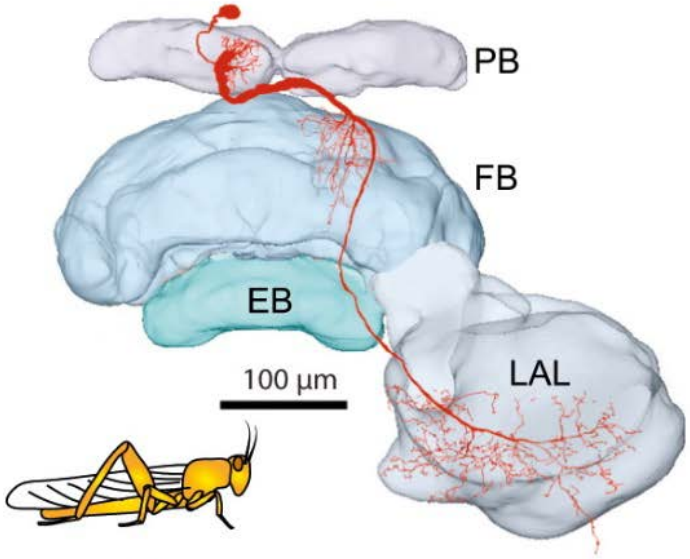


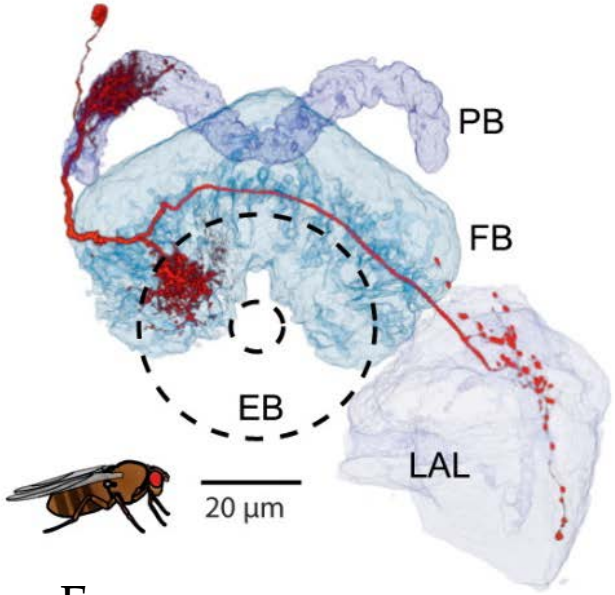




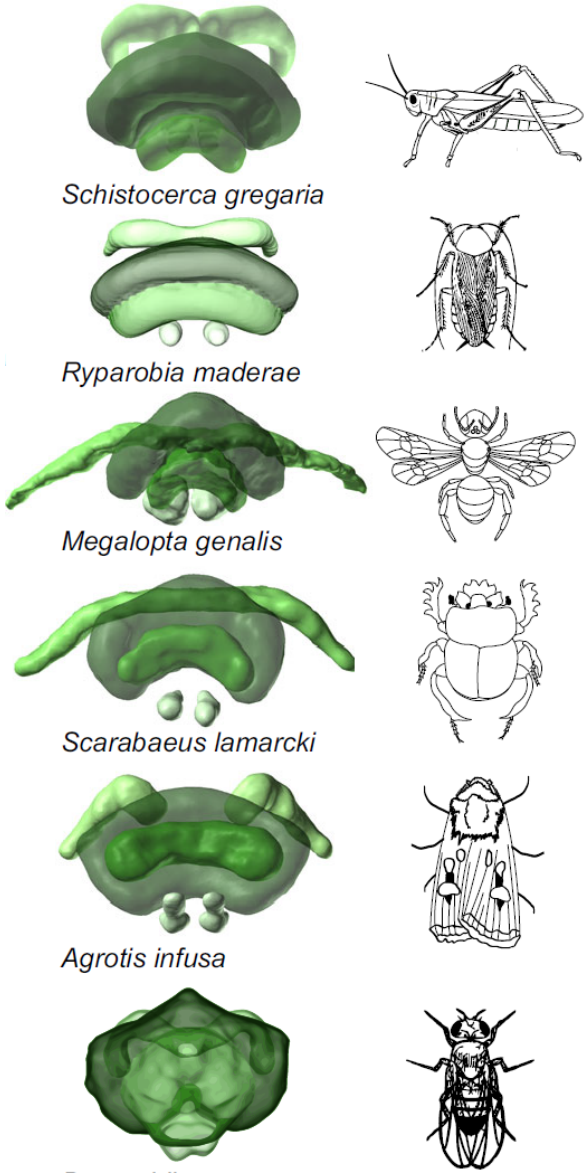
Malcolm Burrows, Gwyneth Card

Homology within Central Complex





Turner-Evans
& Jayaraman



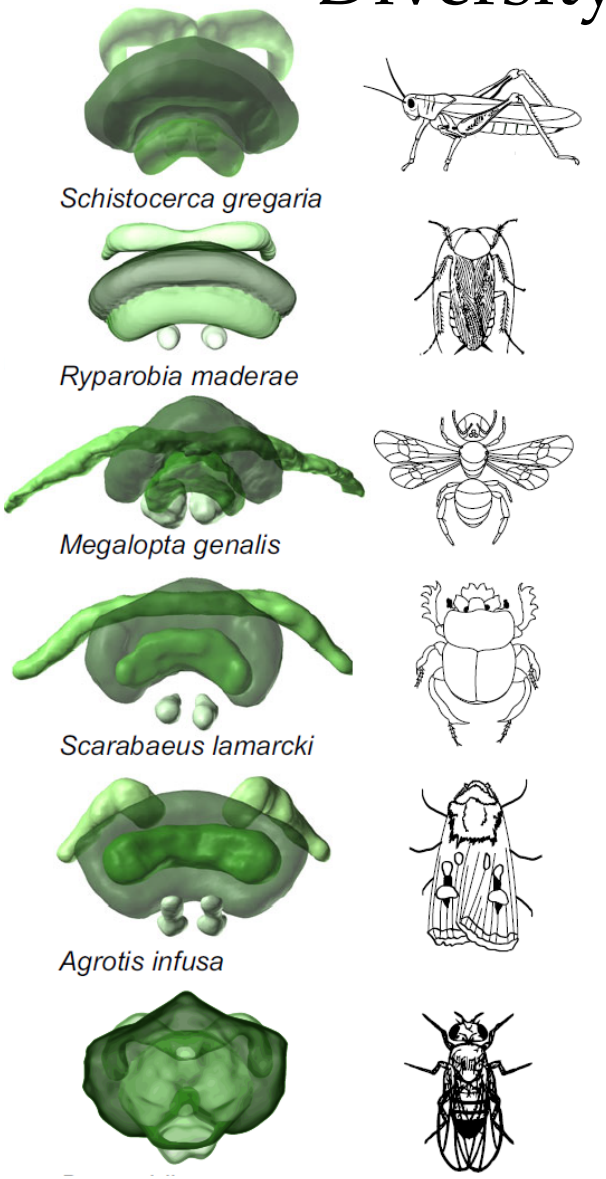
Honkanen, et al., 2019

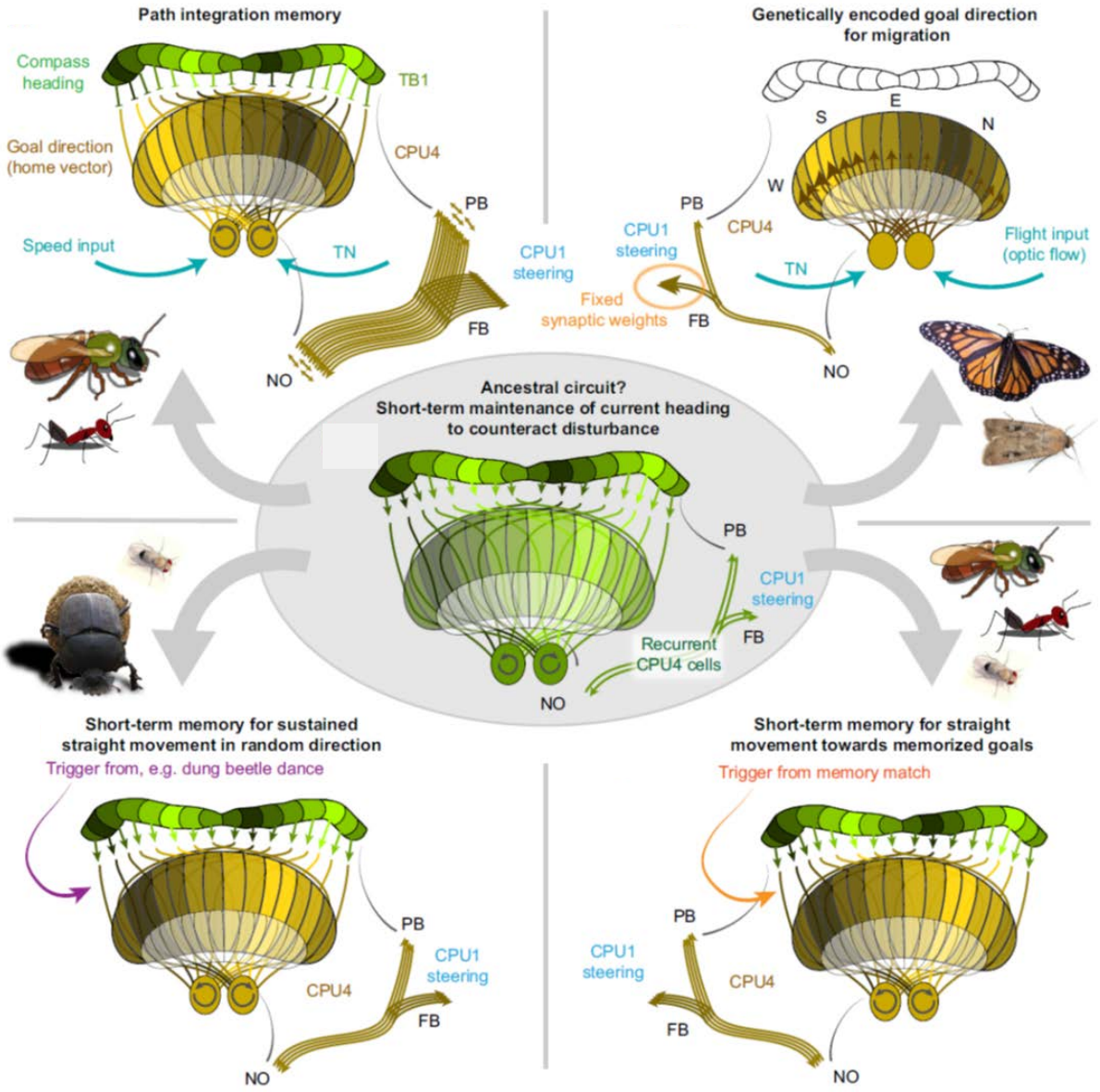
Marie Dacke and Basil el Jundi

Marie Dacke and Basil el Jundi

Marie Dacke and Basil el Jundi

Diversity of Central Complex function





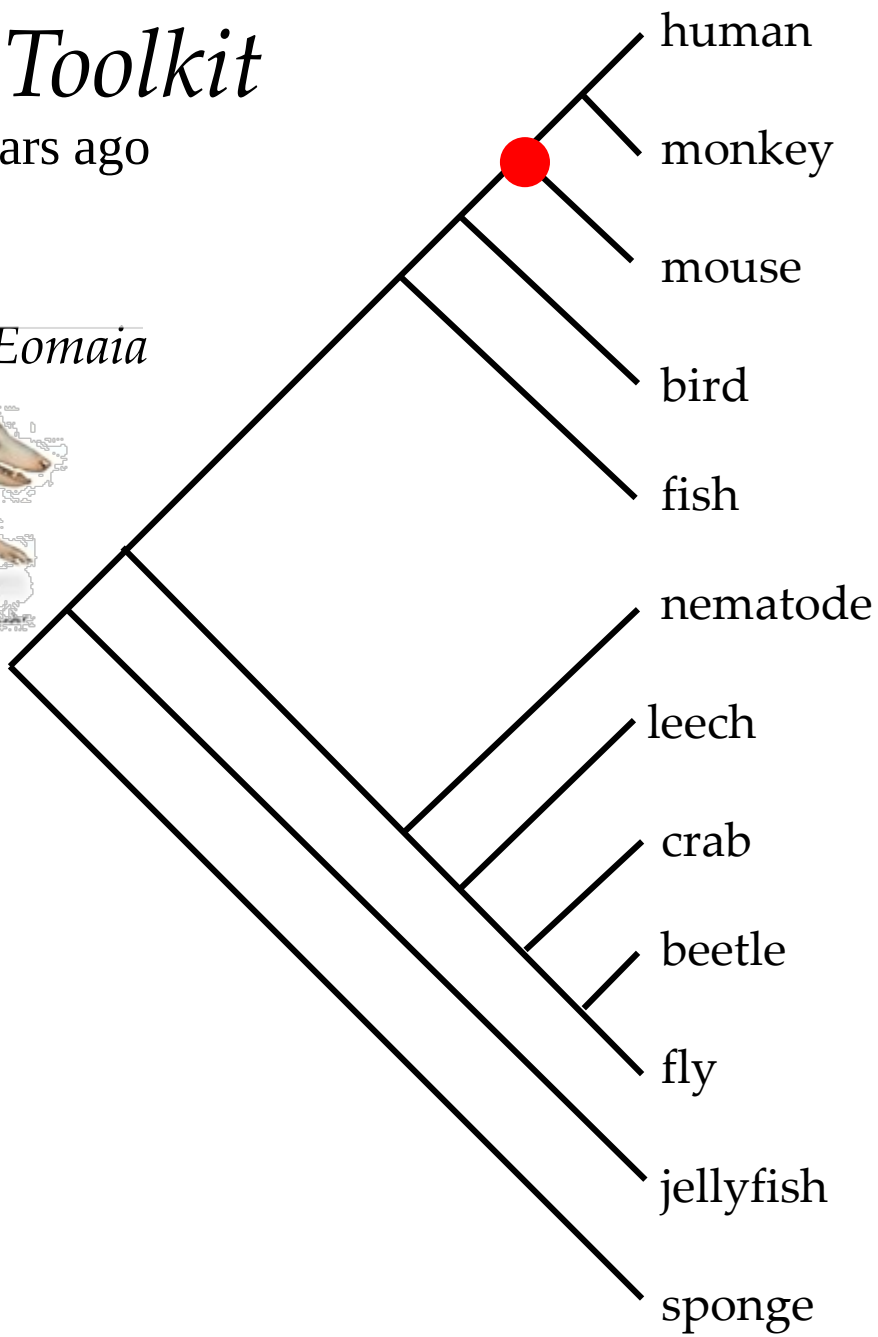
Honkanen, et al., 2019

Cretaceous Toolkit

125 million years ago

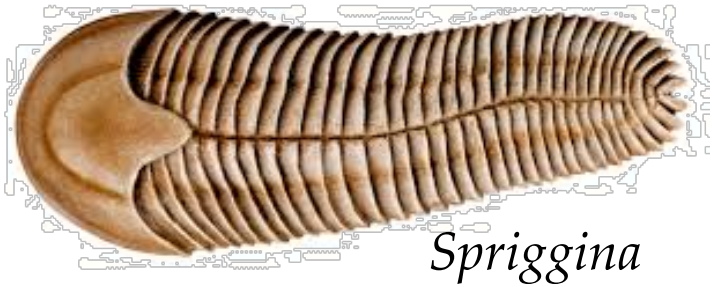
Eomaia

O'Leary et al., 2013

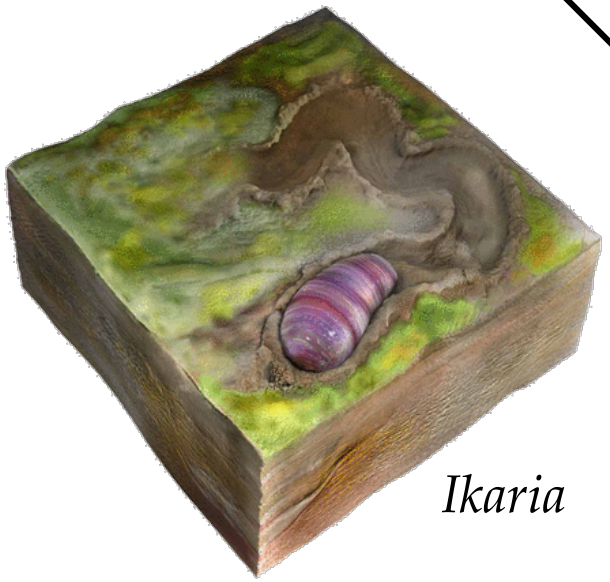


Ediacaran Toolkit

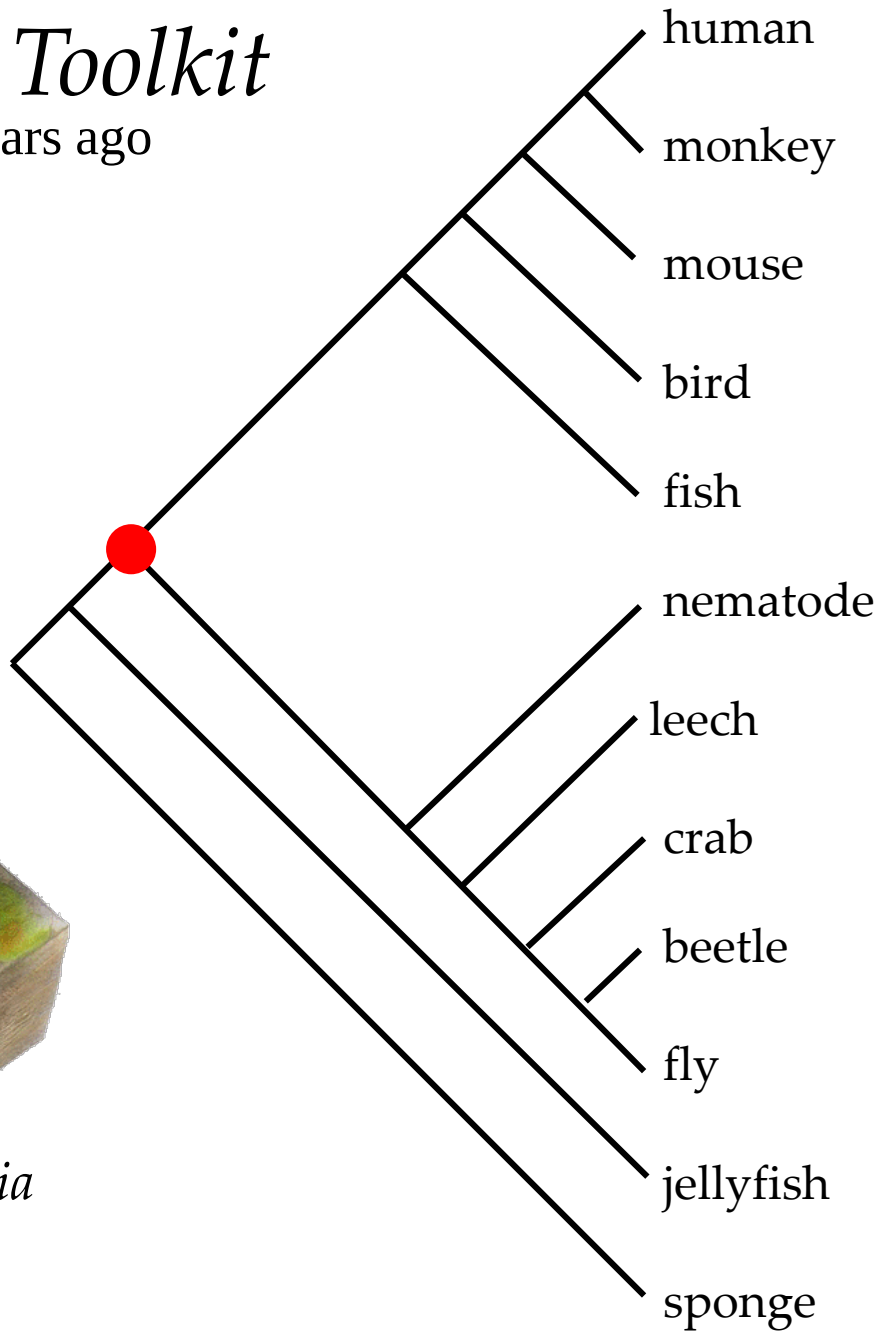
600 million years ago



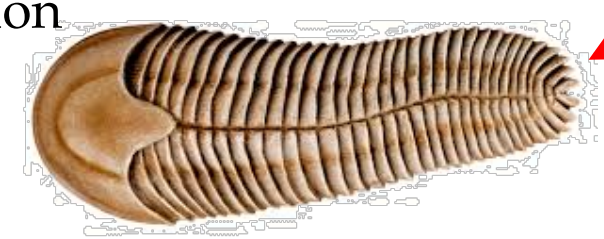
Spriggina



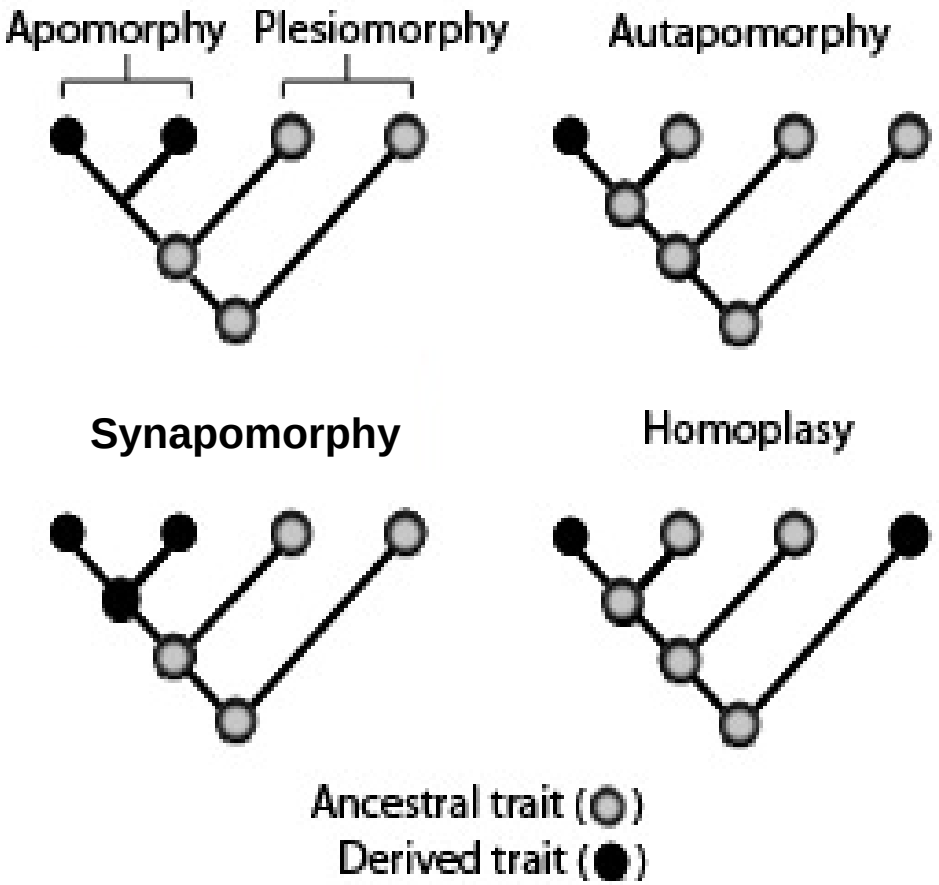
Ikaria



Locomotion
Foraging
Water/salt regulation
Face recognition
Sleep
Aggression
Spatial memory
Optomotor response
Odor discrimination
Navigation
Fear

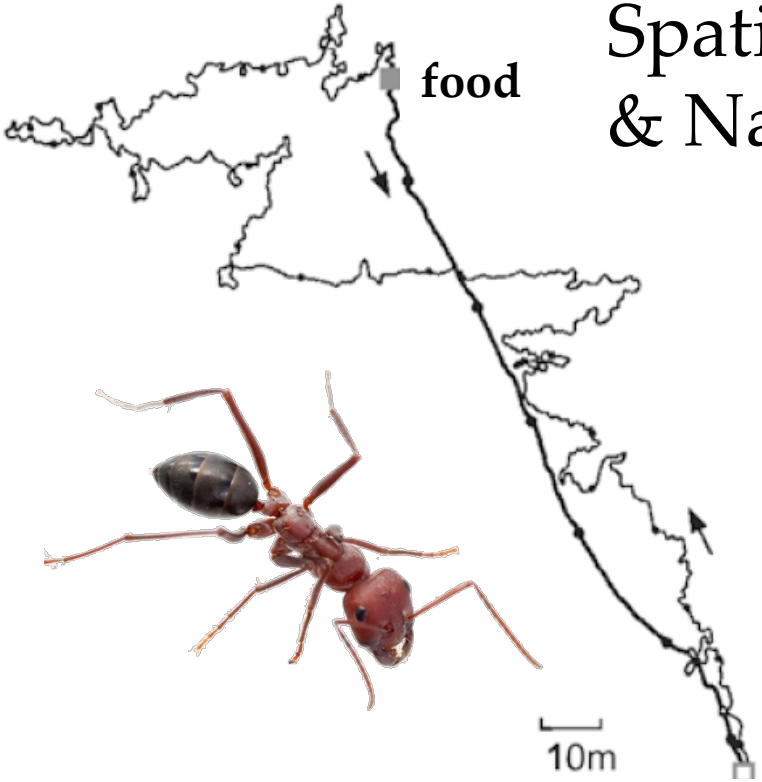


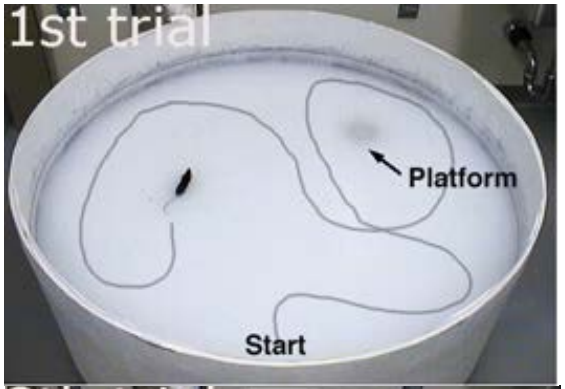
Cladistics are important.

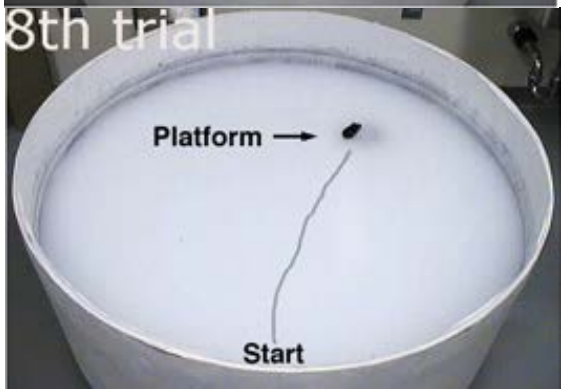


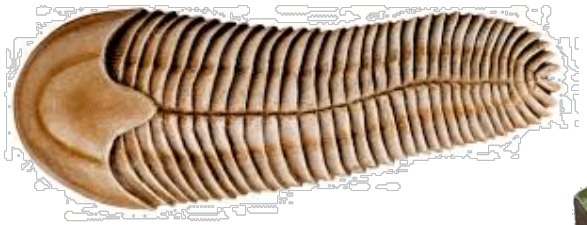
Wikipedi, after Willi Hennig

Spatial Memory & Navigation









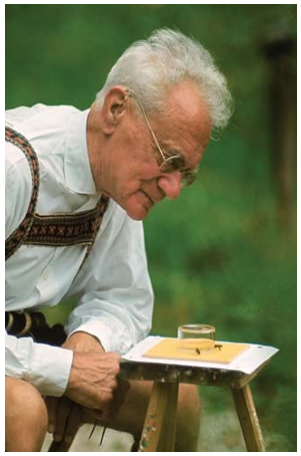
Spriggina

Ikaria

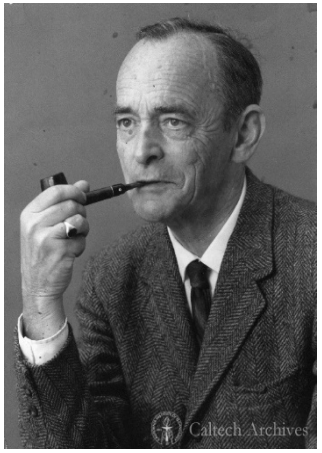
The Ethologists got many things right.

Niko Tinbergen (1907-1988)

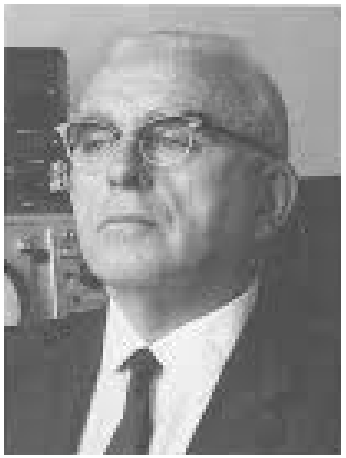
Konrad Lorenz (1903-1989)



Karl von Frish (1886-1982)



Cornelius Wiersma (1904-1987)

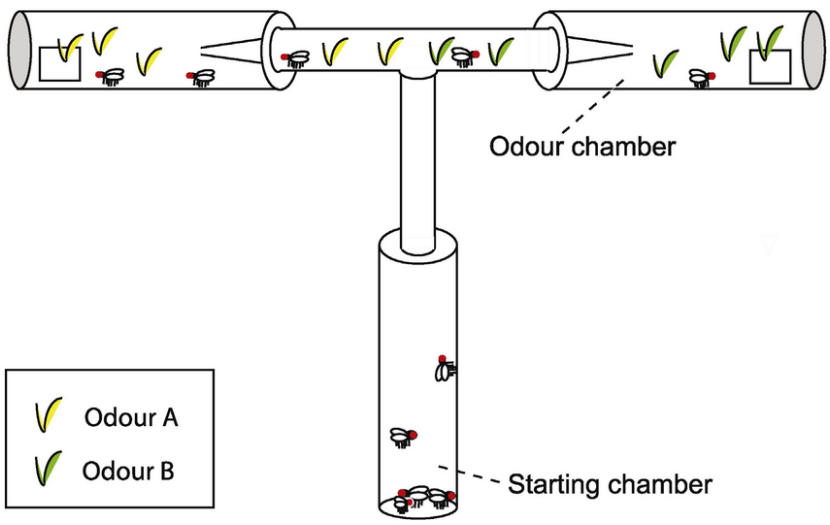


Kenneth Roeder (1908-1979)

Behavior is highly modular, and this modularity is reflected in both the underlying neural circuitry and evolutionary history.

Behavior is best understood within the context of the animal's natural history and ecology and with reference to its evolutionary past.

Trends in Systems Neuroscience



Behavior is something that we teach animals to do under constrained laboratory conditions so we can learn about the brain.

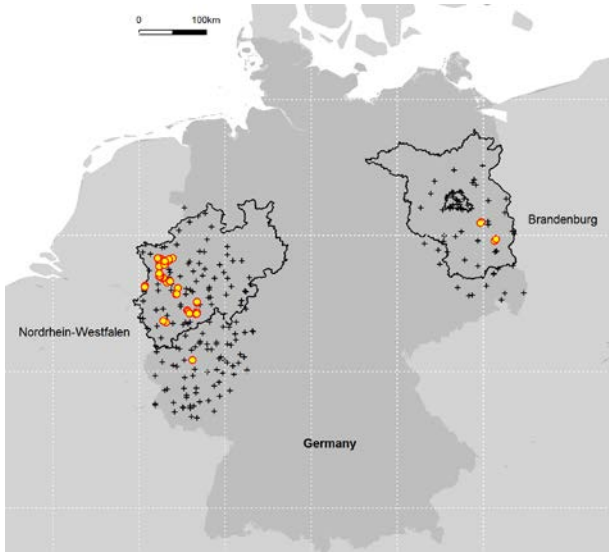
Innate behaviors are simple and often not worth studying.

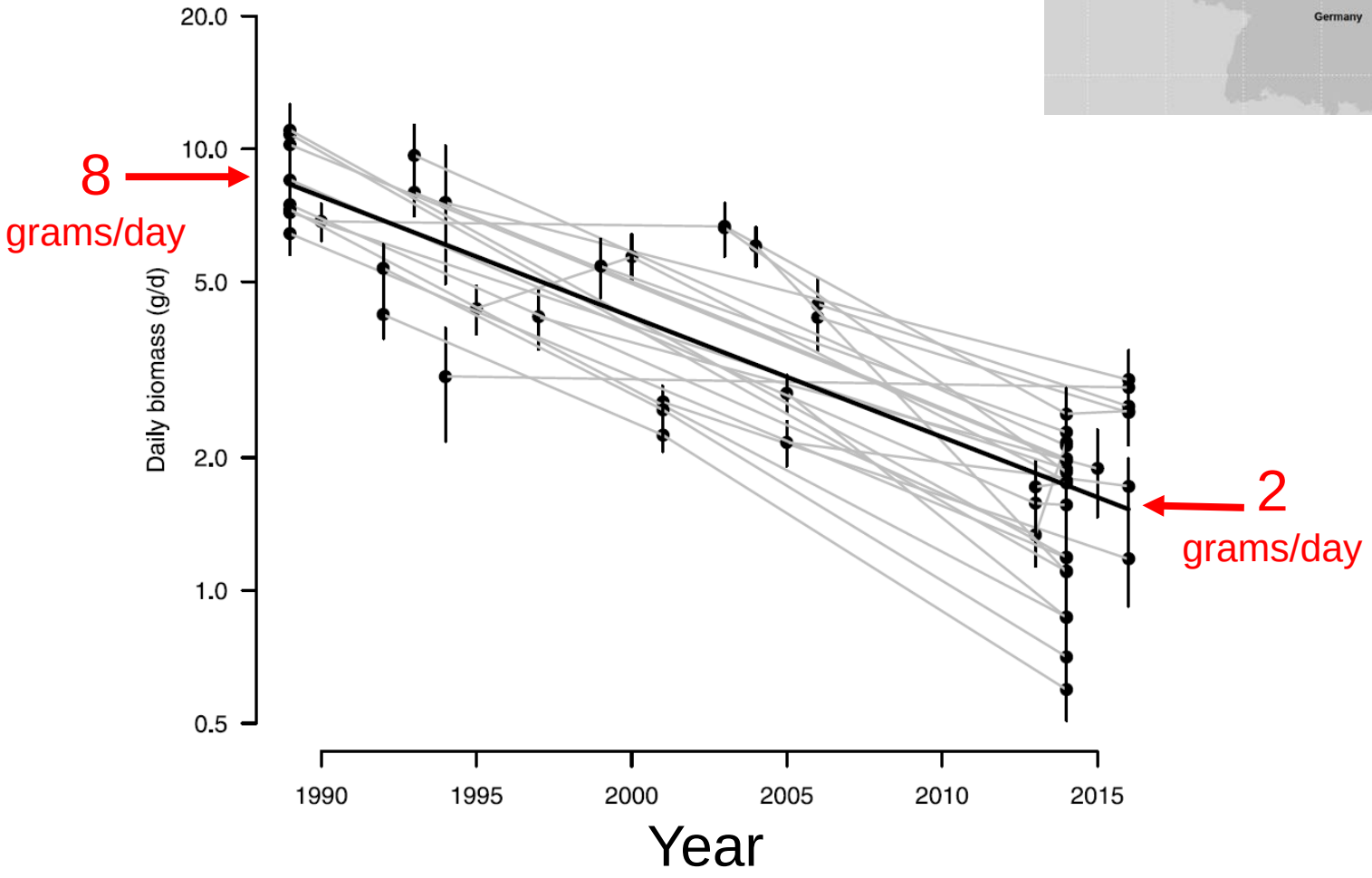
Driven by the need to generalize behaviors from humans to model organisms, we deemphasize – or worse – deliberately obscure the proper evolutionary context.

RESEARCH ARTICLE

More than 75 percent decline over 27 years in total flying insect biomass in protected areas

Caspar A. Hallmann[1]*, Martin Sorg[2], Eelke Jongejans[1], Henk Siepel[1], Nick Hofland[1], Heinz Schwan[2], Werner Stenmans[2], Andreas Müller[2], Hubert Sumser[2], Thomas Hörren[2], Dave Goulson[3], Hans de Kroon[1]





Science, September 19, 2019

Decline of the North American avifauna

Kenneth V. Rosenberg[1,2]*, Adriaan M. Dokter[1], Peter J. Blancher[3], John R. Sauer[4], Adam C. Smith[5], Paul A. Smith[3], Jessica C. Stanton[6], Arvind Panjabi[7], Laura Helft[1], Michael Parr[2], Peter P. Marra[8]†

An Ecological 'Crisis' as 2.9 Billion Birds Vanish

Steep Losses Even for Abundant Species, a Study Shows

By CARL ZIMMER

The skies are emptying out.

The number of birds in the United States and Canada has fallen by 29 percent since 1970, scientists reported on Thursday. There are 2.9 billion fewer birds taking wing now than there were 50 years ago.

The analysis, published in the journal Science, is the most exhaustive and ambitious attempt yet to learn what is happening to avian populations. The results have shocked researchers and conservation organizations.

In a statement on Thursday, David Yarnold, president and chief executive of the National Audubon Society, called the findings "a full-blown crisis."

Experts have long known that some bird species have become vulnerable to extinction. But the new study, based on a broad survey of more than 500 species, reveals steep losses even among such traditionally abundant birds as robins and sparrows.

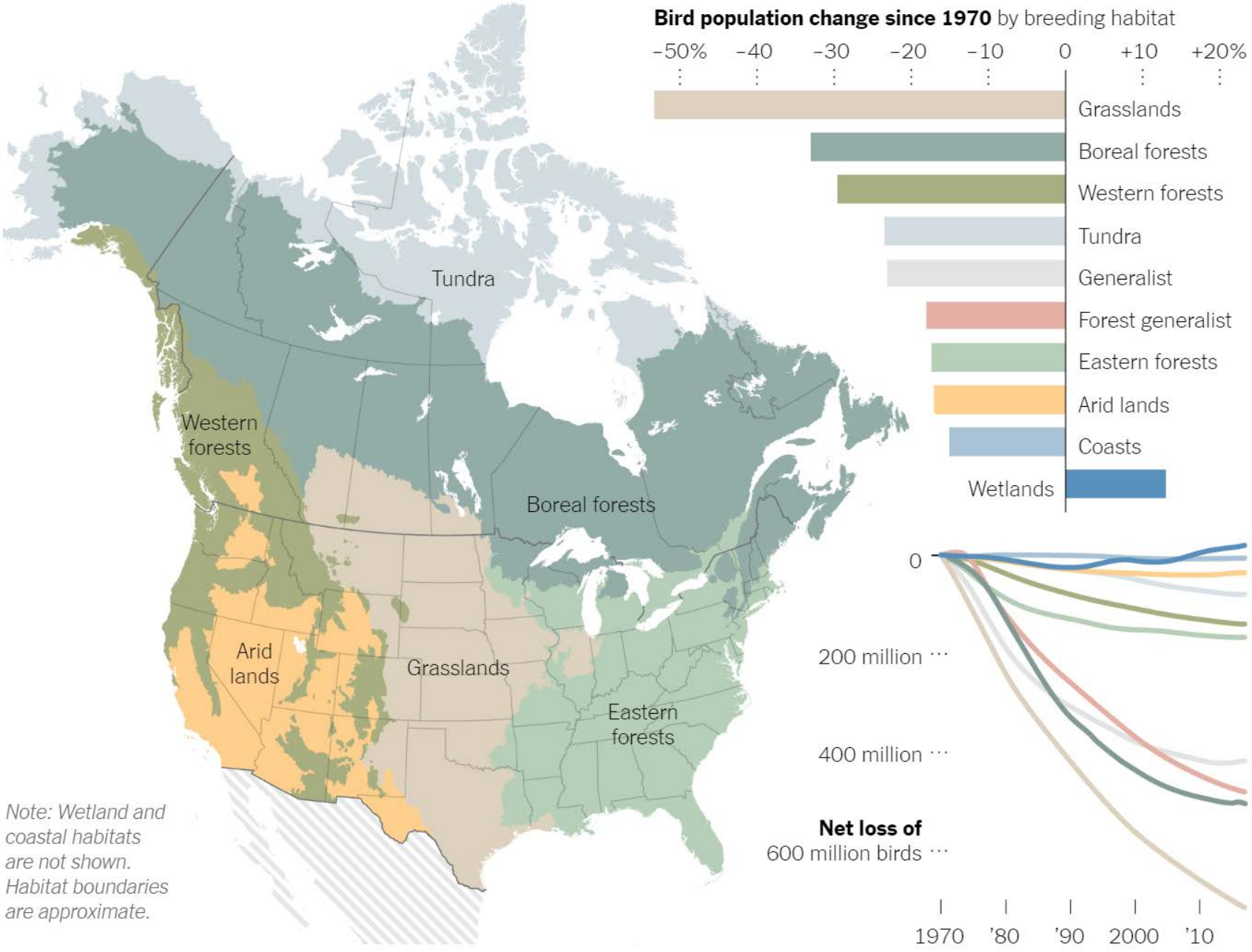
There are likely many causes, the most important of which include habitat loss and wider use of pesticides. "Silent Spring," Rachel Carson's prophetic book in 1962 about the harms caused by pesticides, takes its title from the unnatural quiet settling on a world that has lost its birds:

"On the mornings that had once throbbed with the dawn chorus of robins, catbirds, doves, jays, wrens, and scores of other bird voices, there was now no sound."

Kevin Gaston, a conservation biologist at the University of Exeter, said that new findings signal something larger at work: "This is the loss of nature."

Common bird species are vital to ecosystems, controlling pests, pollinating flowers, spreading

Continued on Page A22



By The New York Times | Source: Science