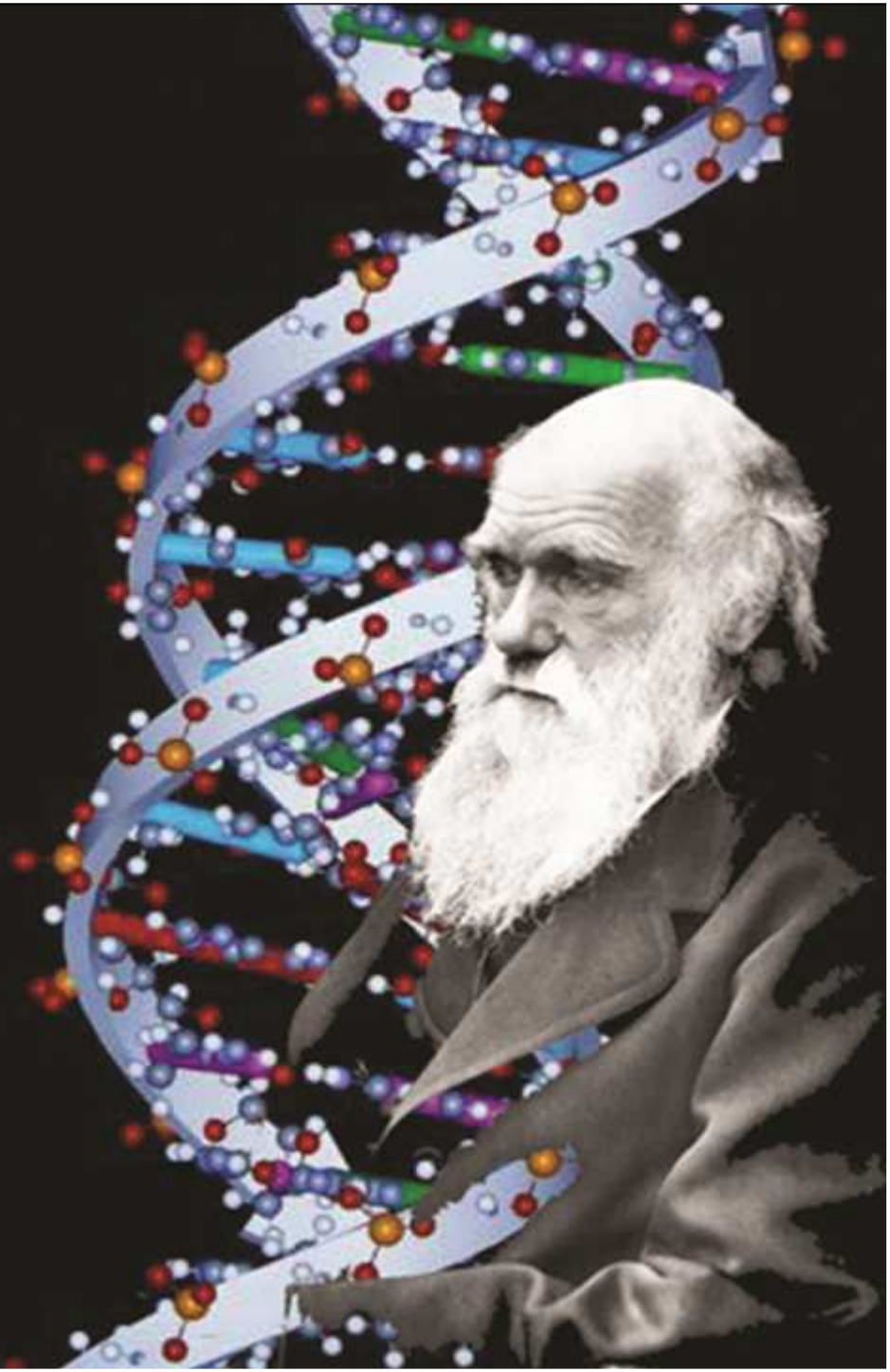
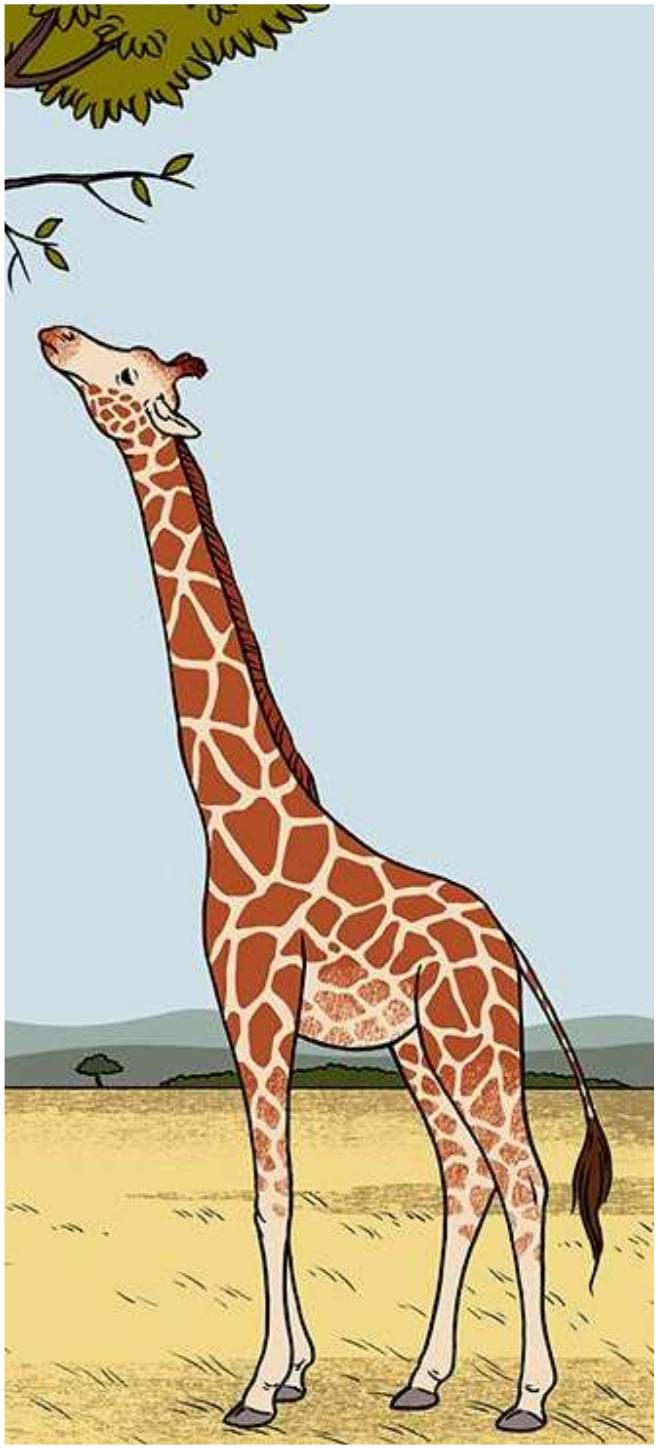
Evo-devo



Maurijn van der Zee
Assistant Professor
Evolutionary Developmental Biology

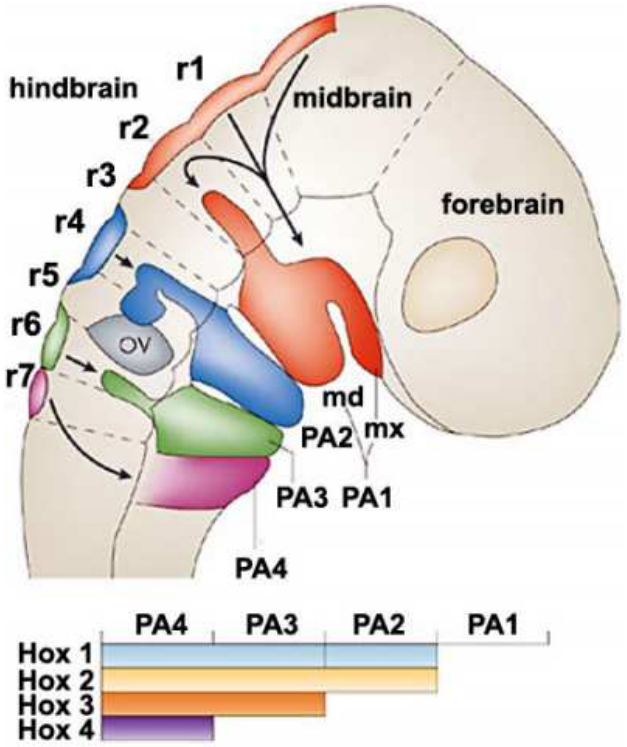
Universiteit Leiden



Evo-devo

Evolutionary developmental biology

…probeert de genetische en ontwikkelingsbiologische basis van evolutionaire veranderingen te achterhalen



Evolution and development

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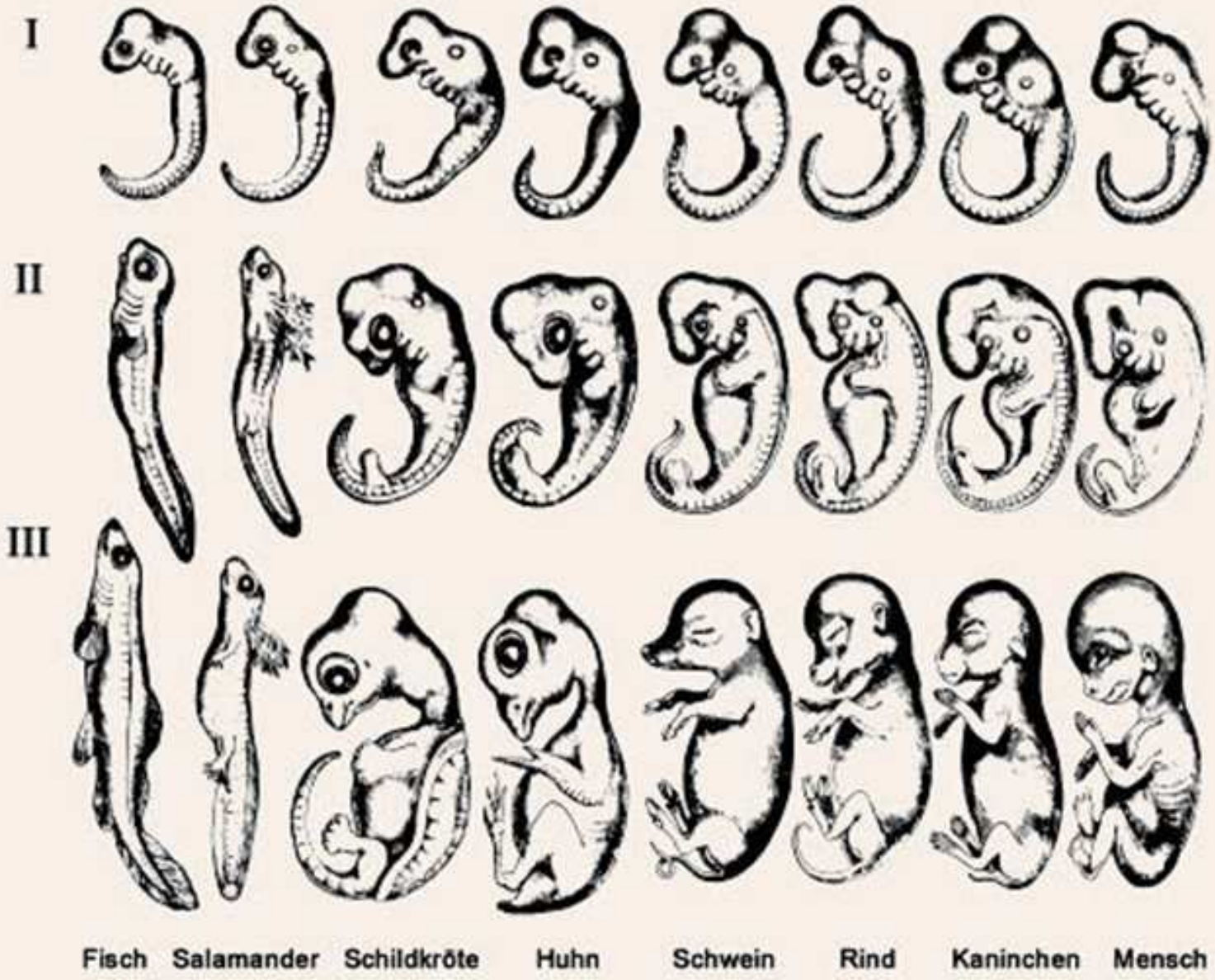
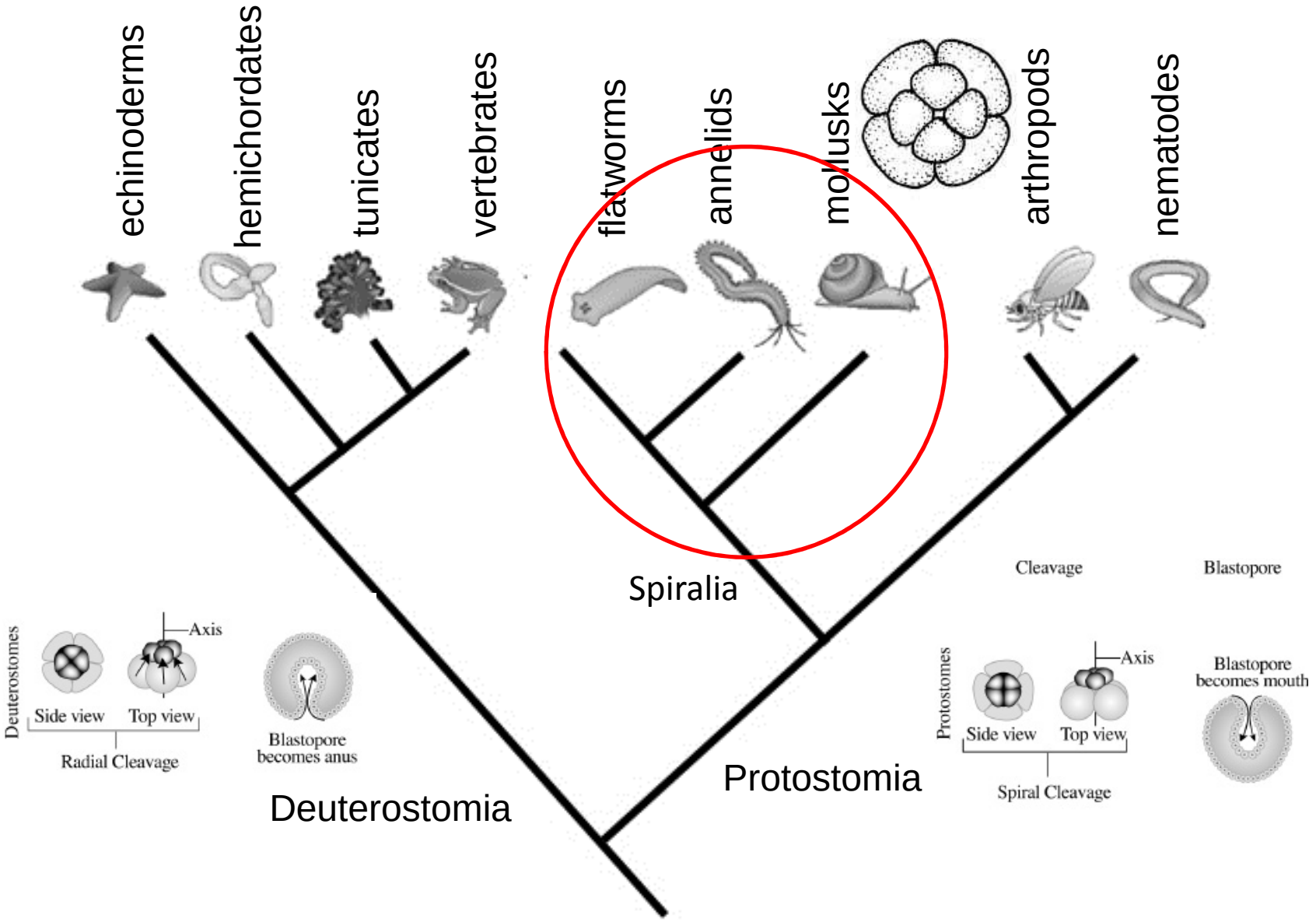
5. Embryonale ontwikkeling kan de evolutie in bepaalde richtingen sturen.

Ernst Haeckel: 1834-1919: **De ontogenie herhaalt de fylogenie**



Bilateralia



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The search for homologous genes is quite futile except in very close relatives.

Ernst Mayr, 1963

Evolution and development

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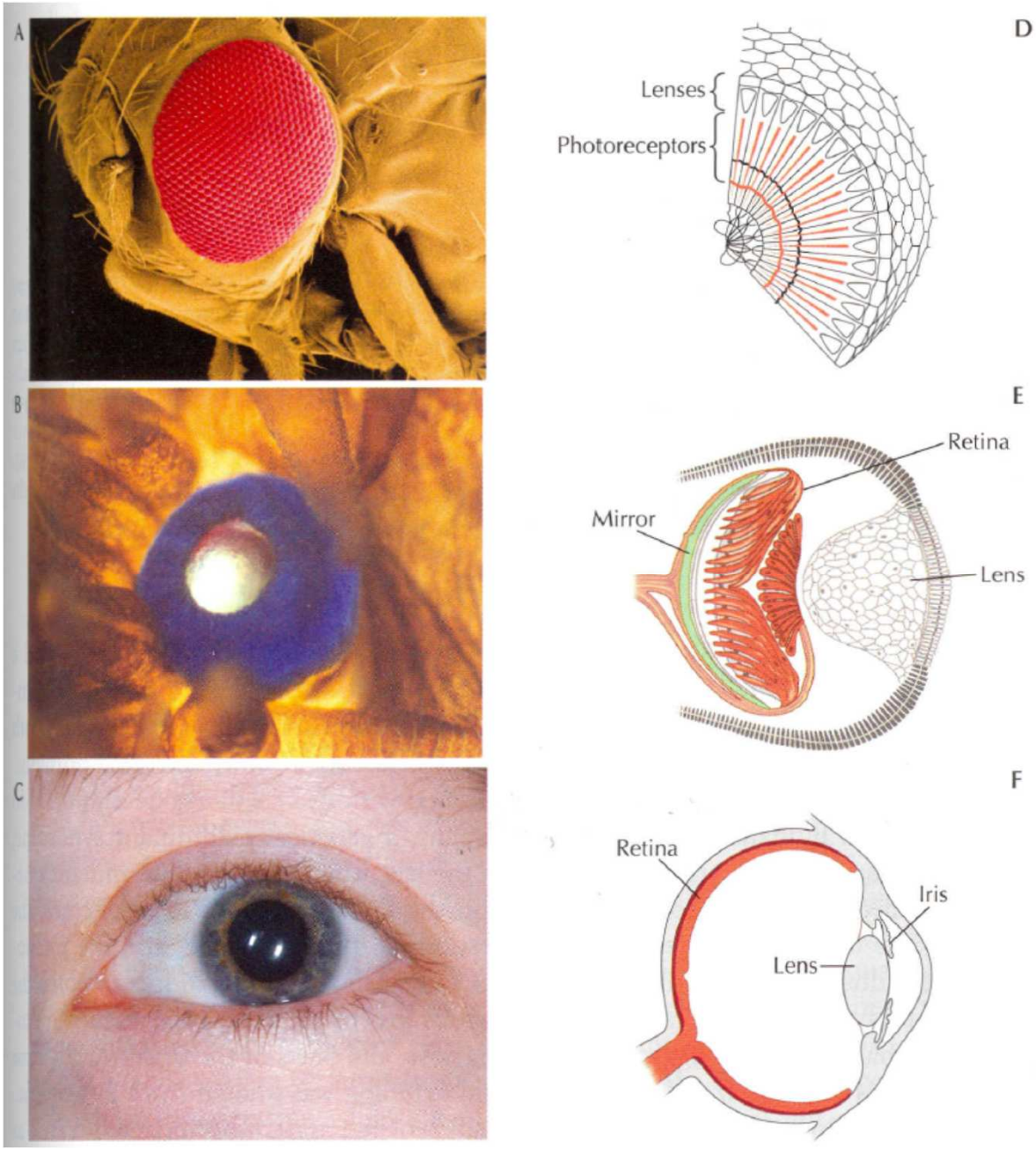
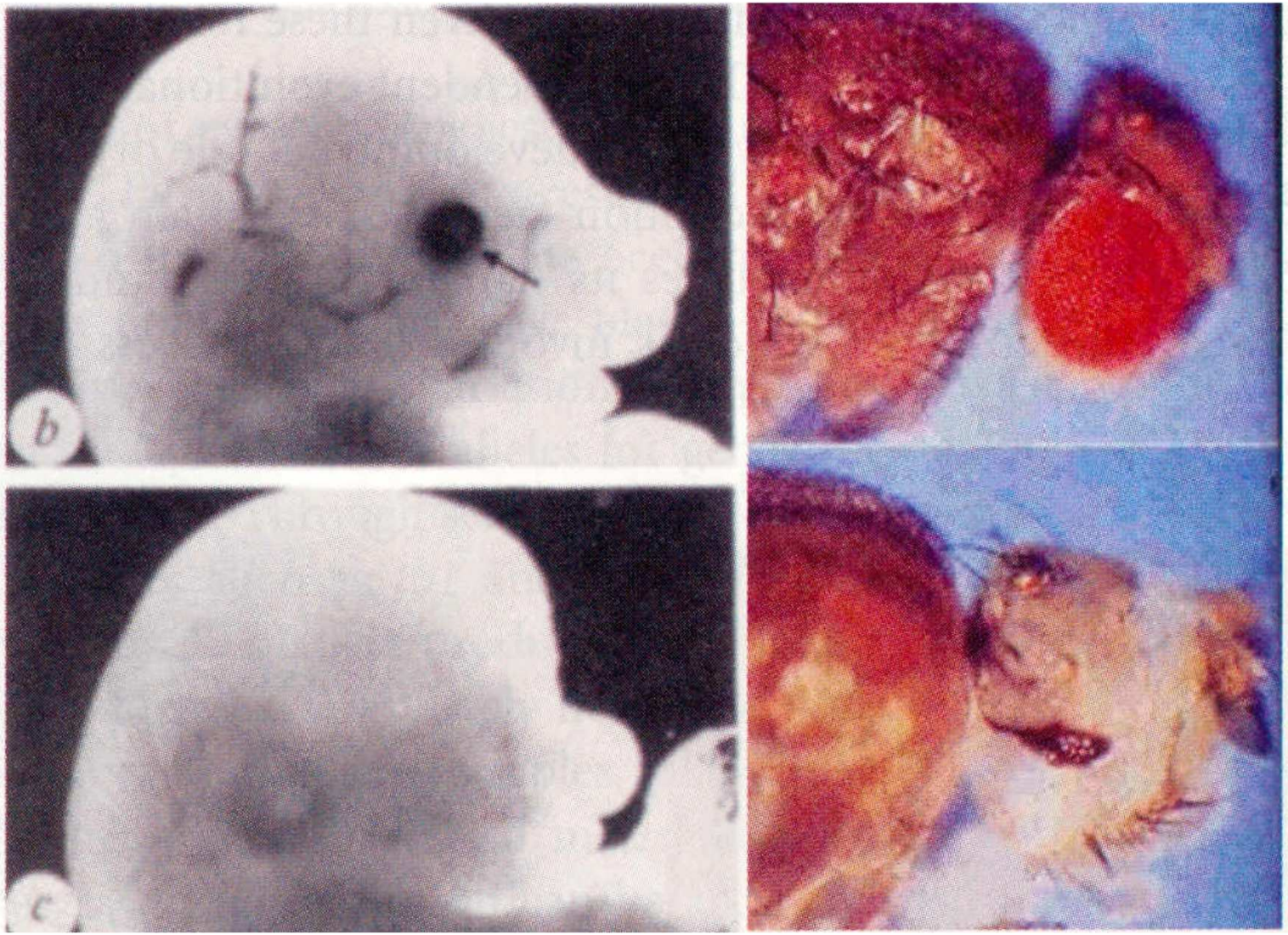
Ogen in Arthropoden, Mollusken and gewervelden zijn niet homoloog…



…maar staan allemaal onder controle van Pax6



Pax6 mutants in mice and flies

Ectopische expressie van Pax6 leidt tot ectopische ogen

Distalless expressie in protostomen and deuterostomen

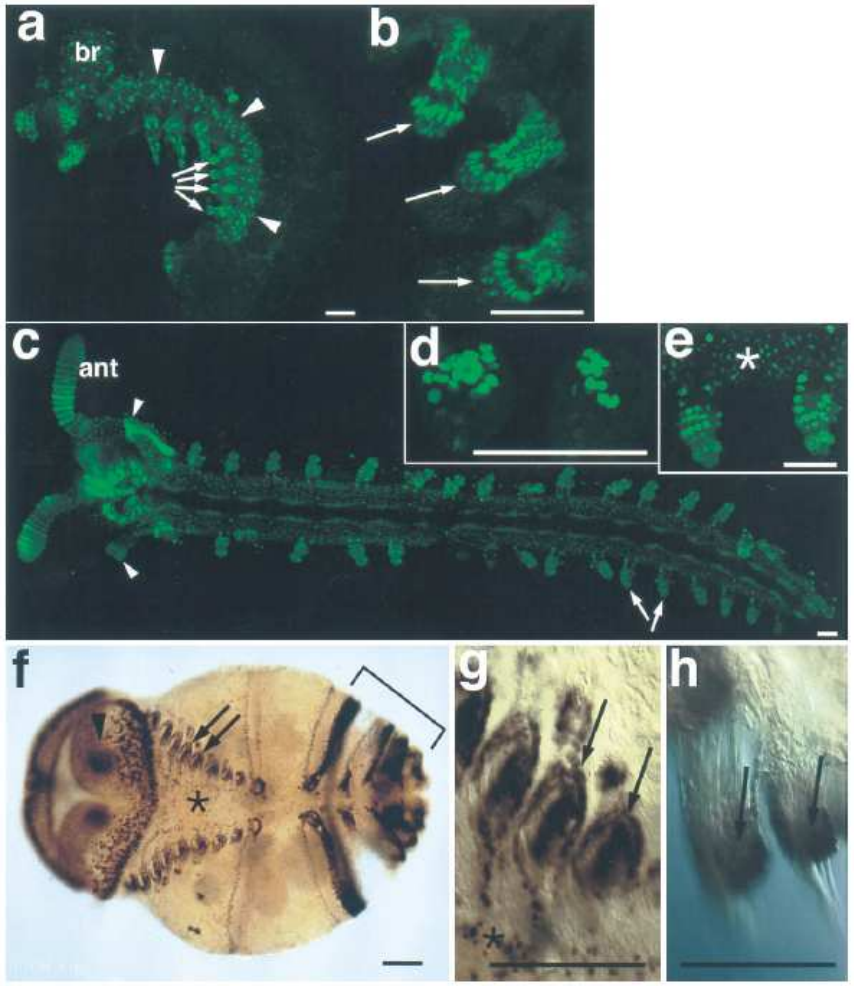


FIG. 1. Dll expression in representative protostomes. (*a*) Lateral view of a late stage *Precis coenia* butterfly embryo stained with the Dll antibody. Arrows (→) point to the distal tips of the left abdominal prolegs. Dll expression is detected in central nervous system in the brain (br) and in the ventral nerve cord (►). (*b*) Higher magnification image of abdominal prolegs (→) from an embryo similar to that shown in *a*. (*c*) Ventral view of a late stage *Peripatopsis capensis* onychophoran embryo stained with the Dll antibody. The antennae (ant), oral papilla (►) and lobopods express Dll. The lobopods shown in higher magnification in *e* are indicated with →. (*d*) Right halves of two segments from a young *P. capensis* embryo stained with the Dll antibody. Dll expression is detected in the ectoderm of the presumptive lobopods prior to the formation of visible buds. (*e*) Higher magnification view of the lobopods indicated in *d*. (•) The neurogenic ectoderm, which also expresses Dll. (*f*) Polychaete annelid *Chaetopterus variopedatus*, ventral view of larva just prior to metamorphosis. Dll expressing cells are visible in parapodial rudiments (→), antennae (out of focus on opposite dorsal surface, (►), prospective feeding organs (n), and in the neurogenic ectoderm (•). (*g*) *C.variopedatus*, same specimen at a higher magnification, showing Dll reactive ectodermal nuclei in prospective distal cells of the anterior parapodia (→) and in the neurogenic region (•). (*h*) Later stage *C. variopedatus* larva showing staining in distal portions of two anterior parapodia (→). Anterior is to the left in all panels. (Bars = 0.1 mm.)

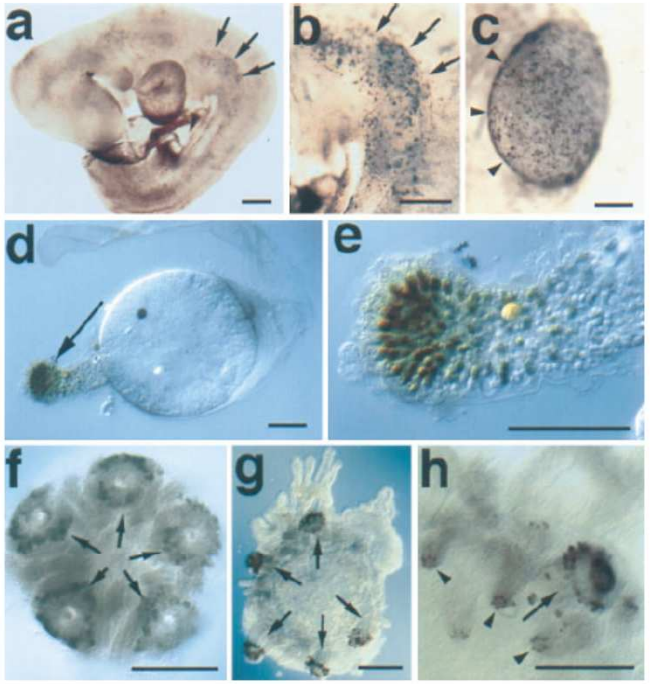


FIG. 2. Dll expression in representative deuterostomes. (*a*) Nine-day mouse embryo stained with the Dll antibody. Arrows (→) point to medial border of cells expressing one or more *Dlx* genes in the presumptive forelimb. Dlx expression can be detected in developing mouse limbs as the bud forms from the flank, and somewhat earlier than previously reported for mice or other vertebrates (6–11). (*b*) Higher magnification view of the forelimb indicated in *A*. (*c*) Dorsal view of the forelimb of a 10-day mouse embryo stained with the Dll antibody. (►) The position of the apical ectodermal ridge. (*d*) Three-day *Molgula occidentalis* ascidian larva from which an ampulla is extending. Cells at the distal tip of the ampulla express Dll (→). (*e*) Higher magnification view of the ampulla shown in *d*. (*f* and *g*) Metamorphosing *Strongylocentrotus droebachiensis* sea urchin larvae stained with Dll antibody. Cells at the distal tip of the tube feet (→) express Dll prior to (*f*) and during (*g*) extension from the body wall. (*h*) Higher magnification view of a tube foot (→) and spines (►) from an *S. droebachiensis* larva similar to that shown in *g*. Cells at the distal tip of the developing spines, as well as the tube feet express Dll. (Bars = 0.1 mm.)

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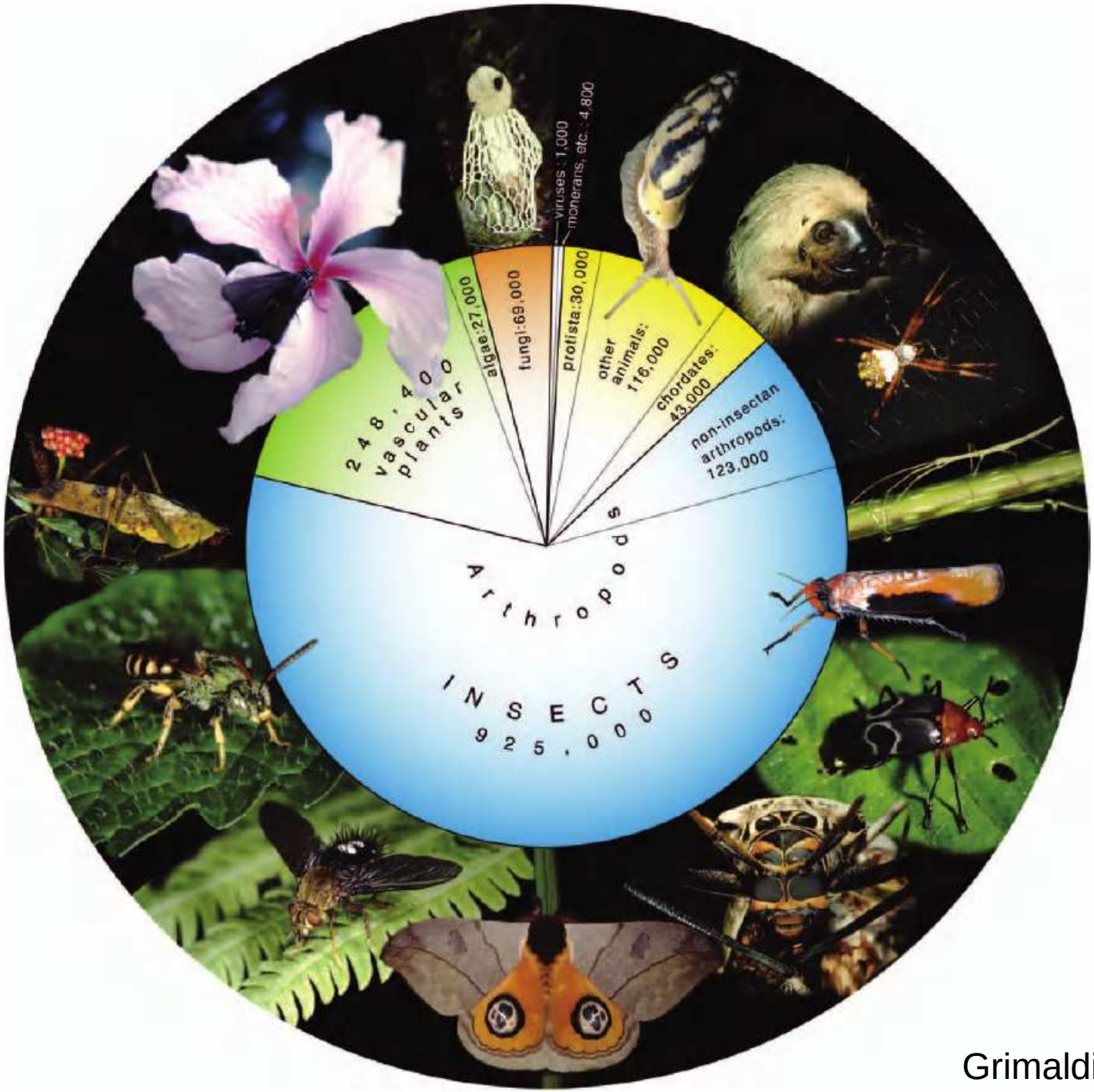
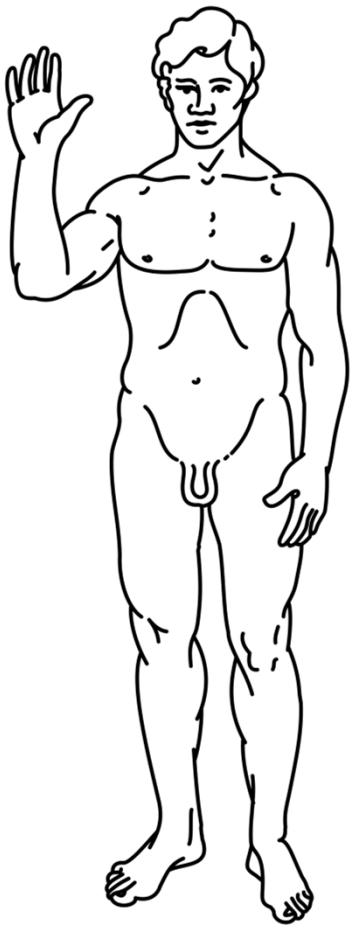
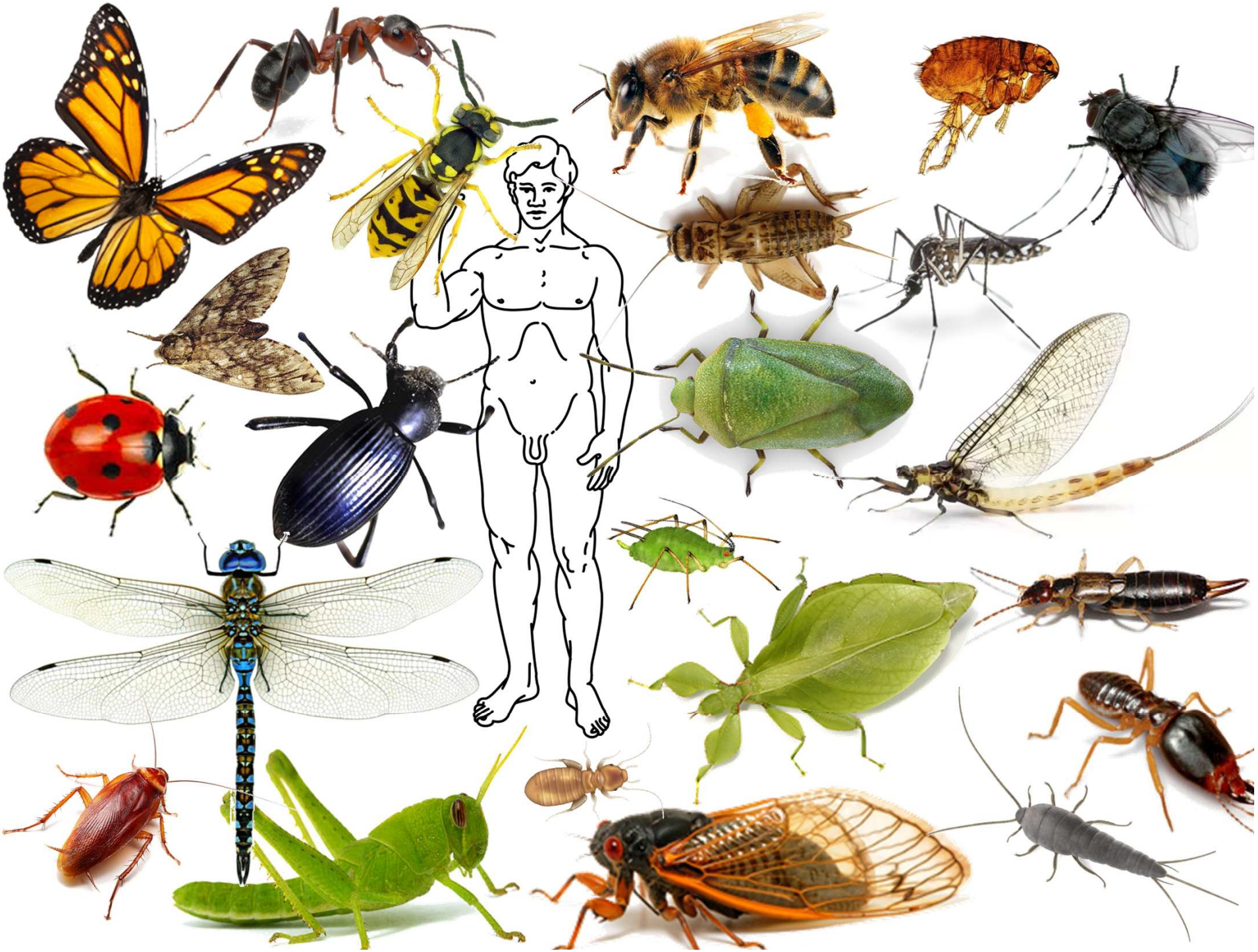
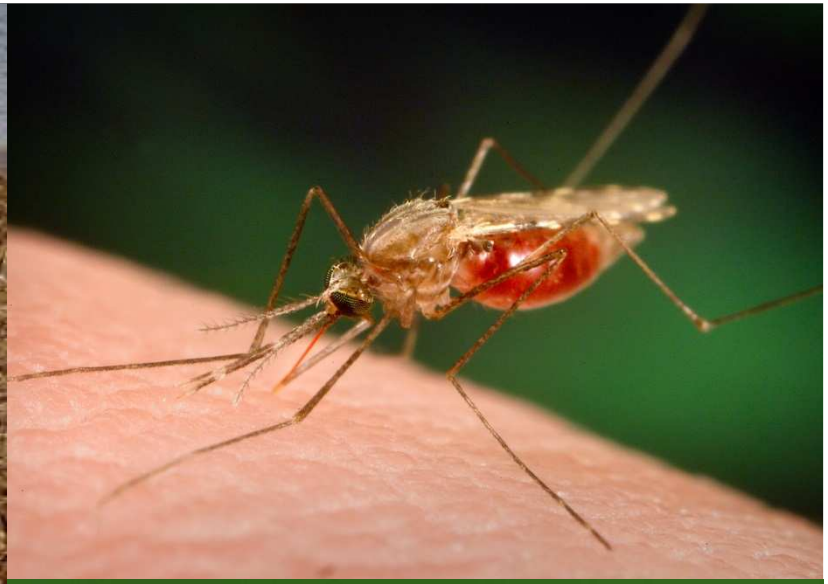
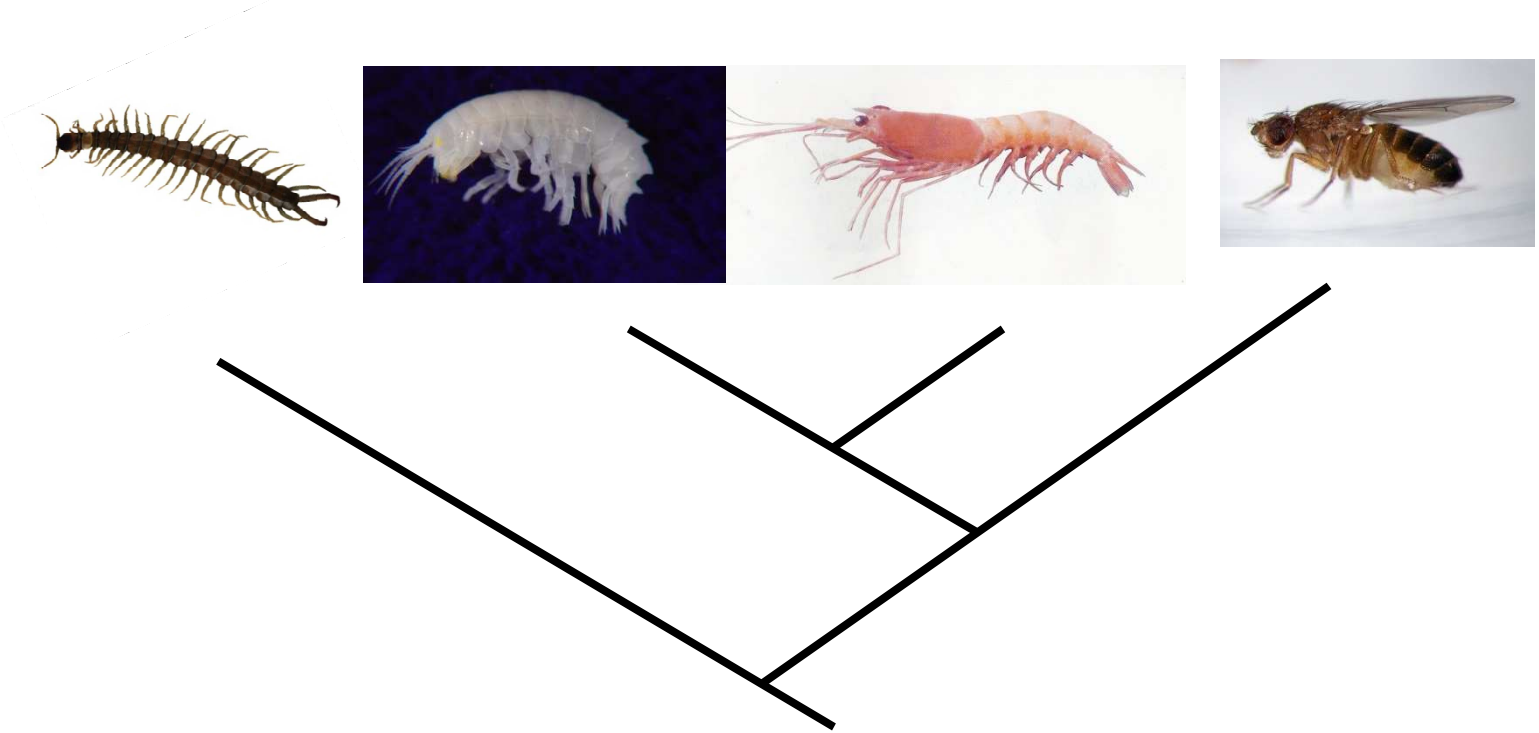


Grimaldi & Engel 2005

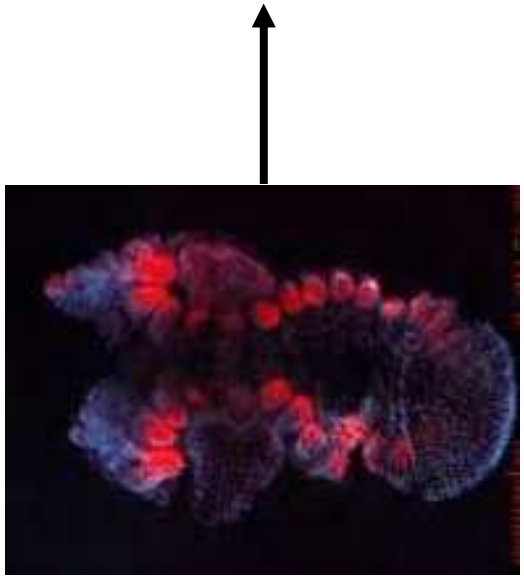


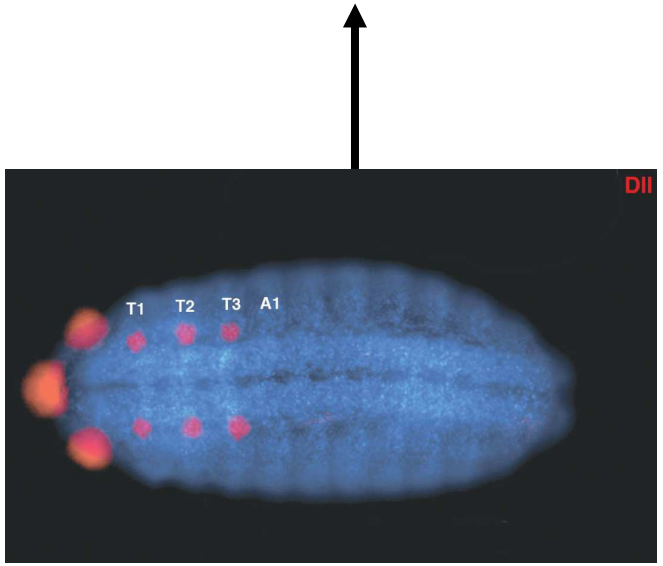


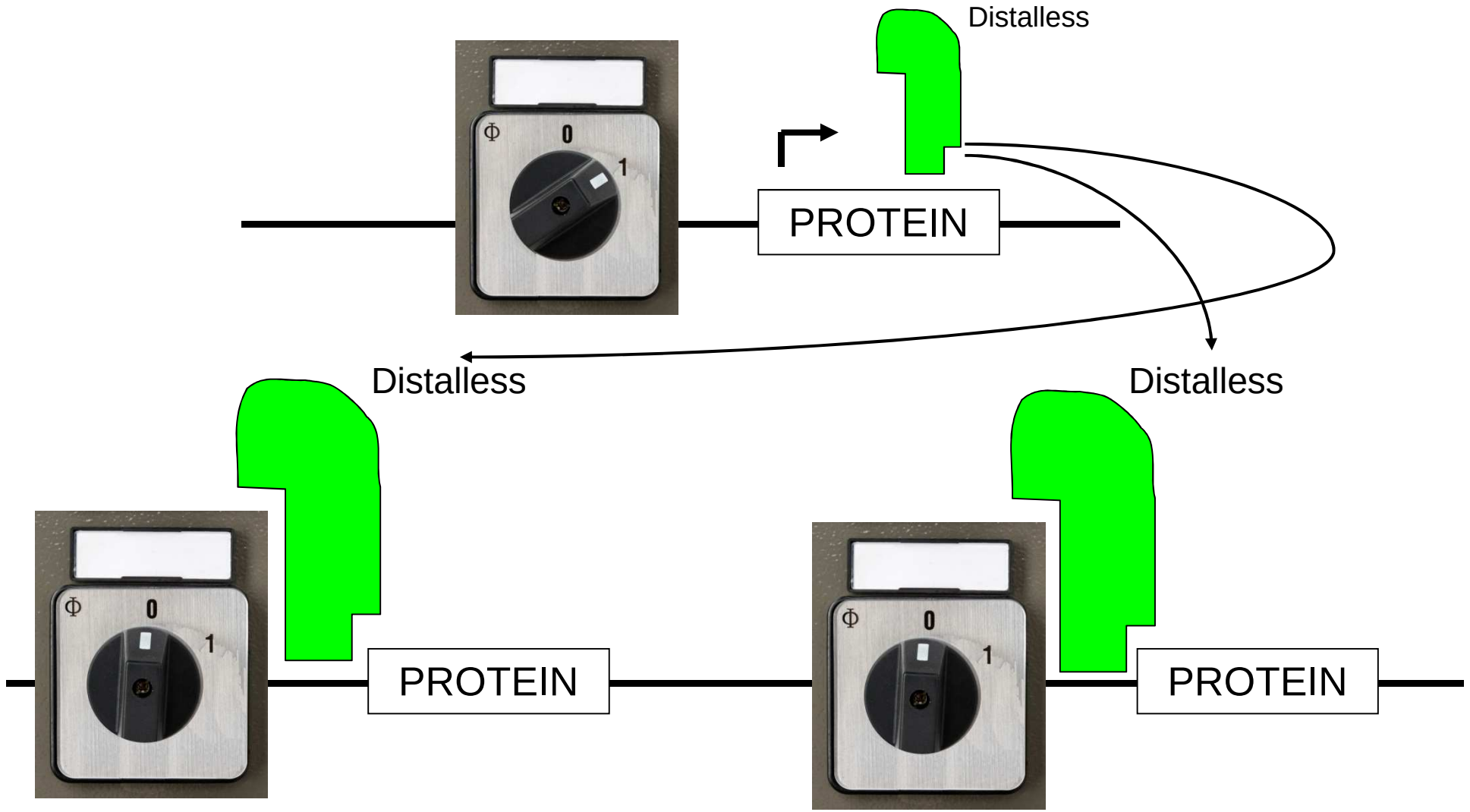




Distalless-expressie



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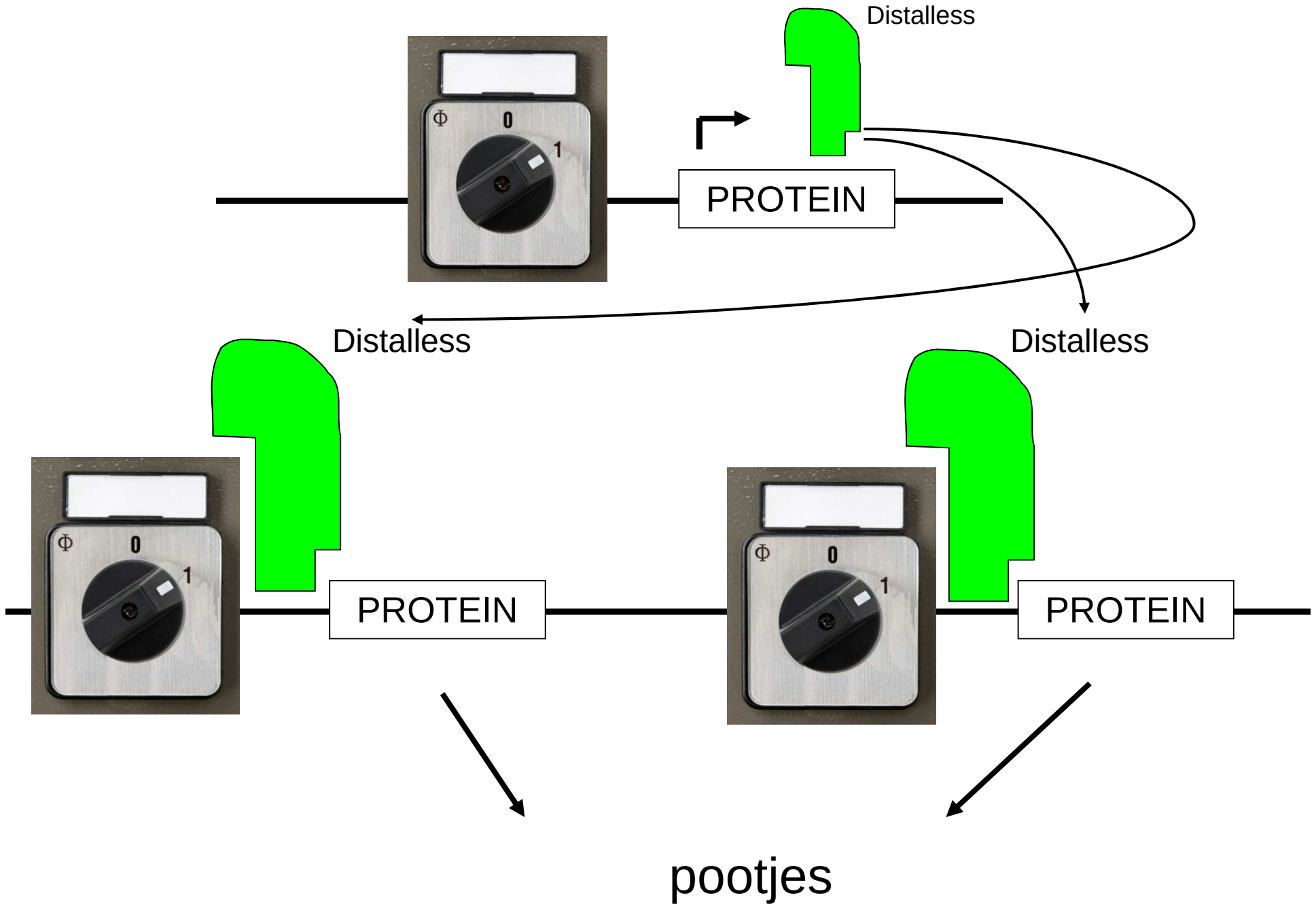
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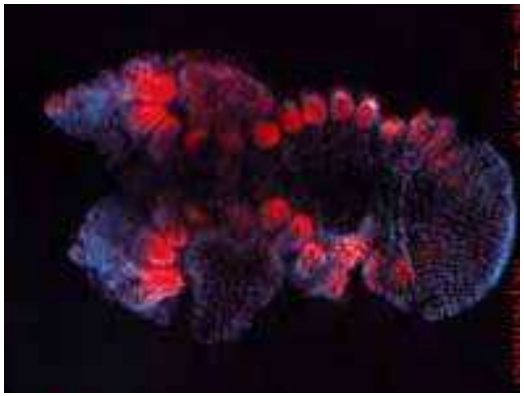

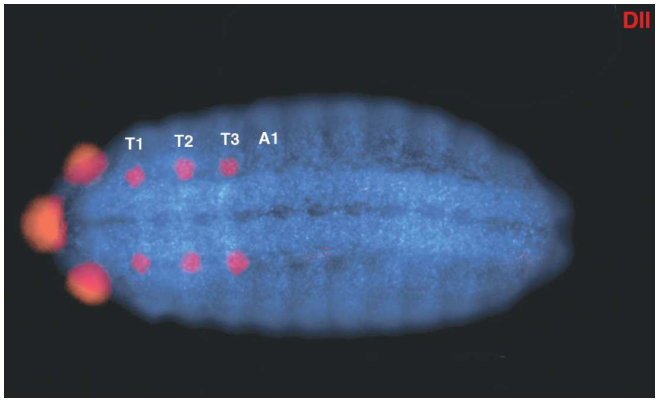
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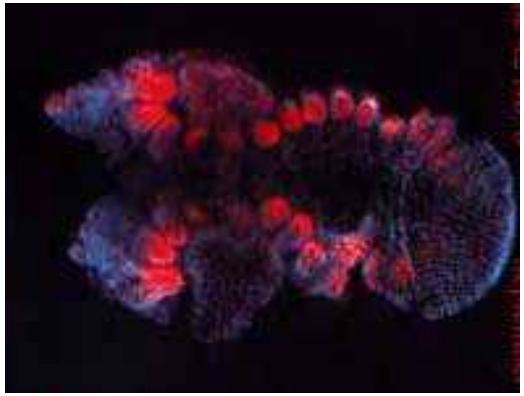
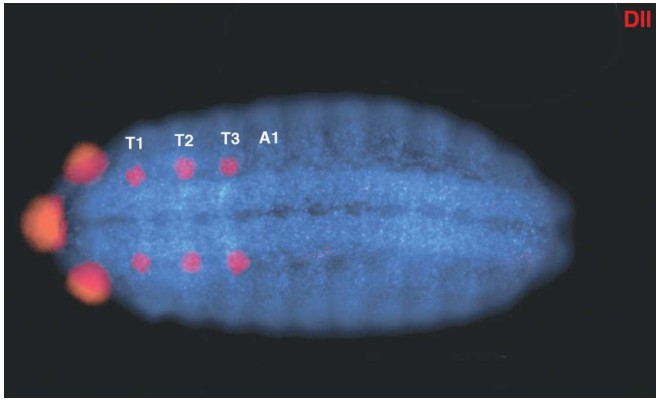
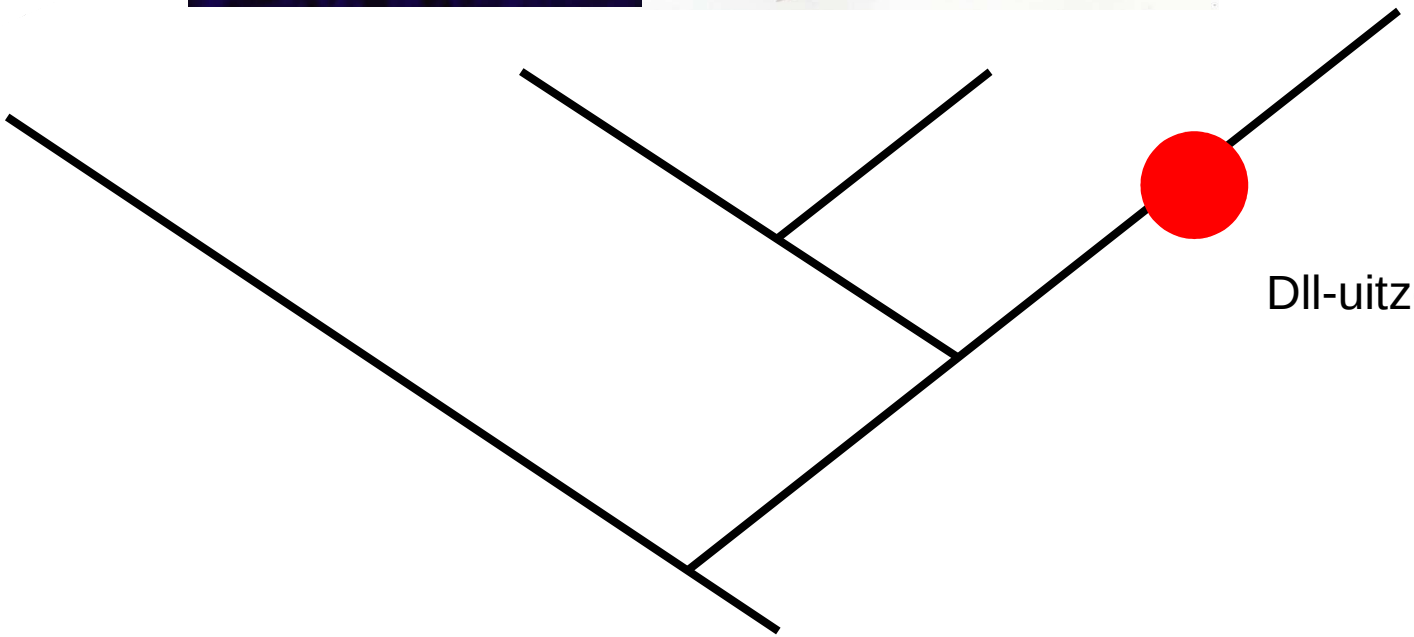
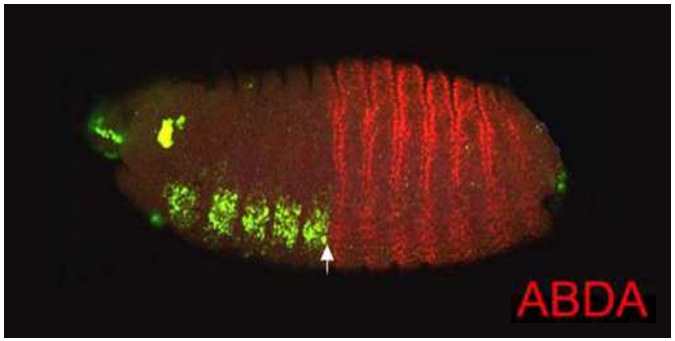


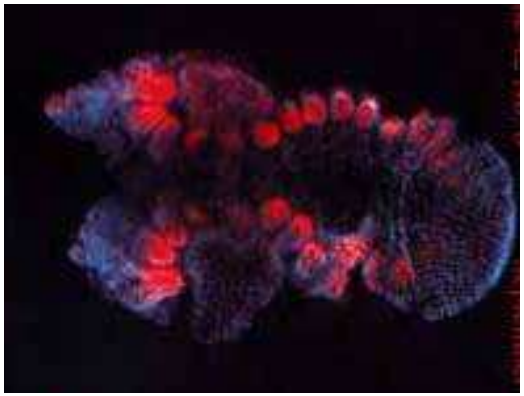


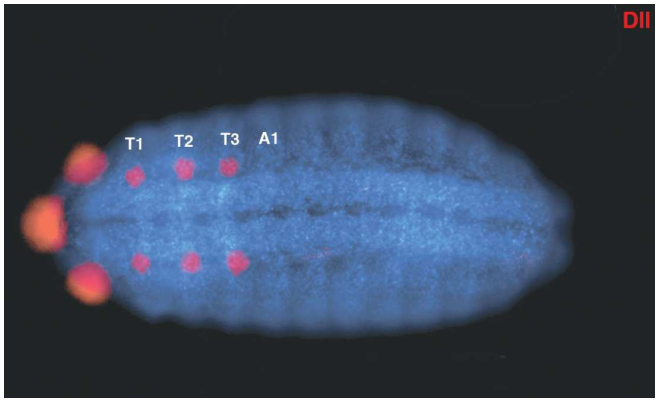


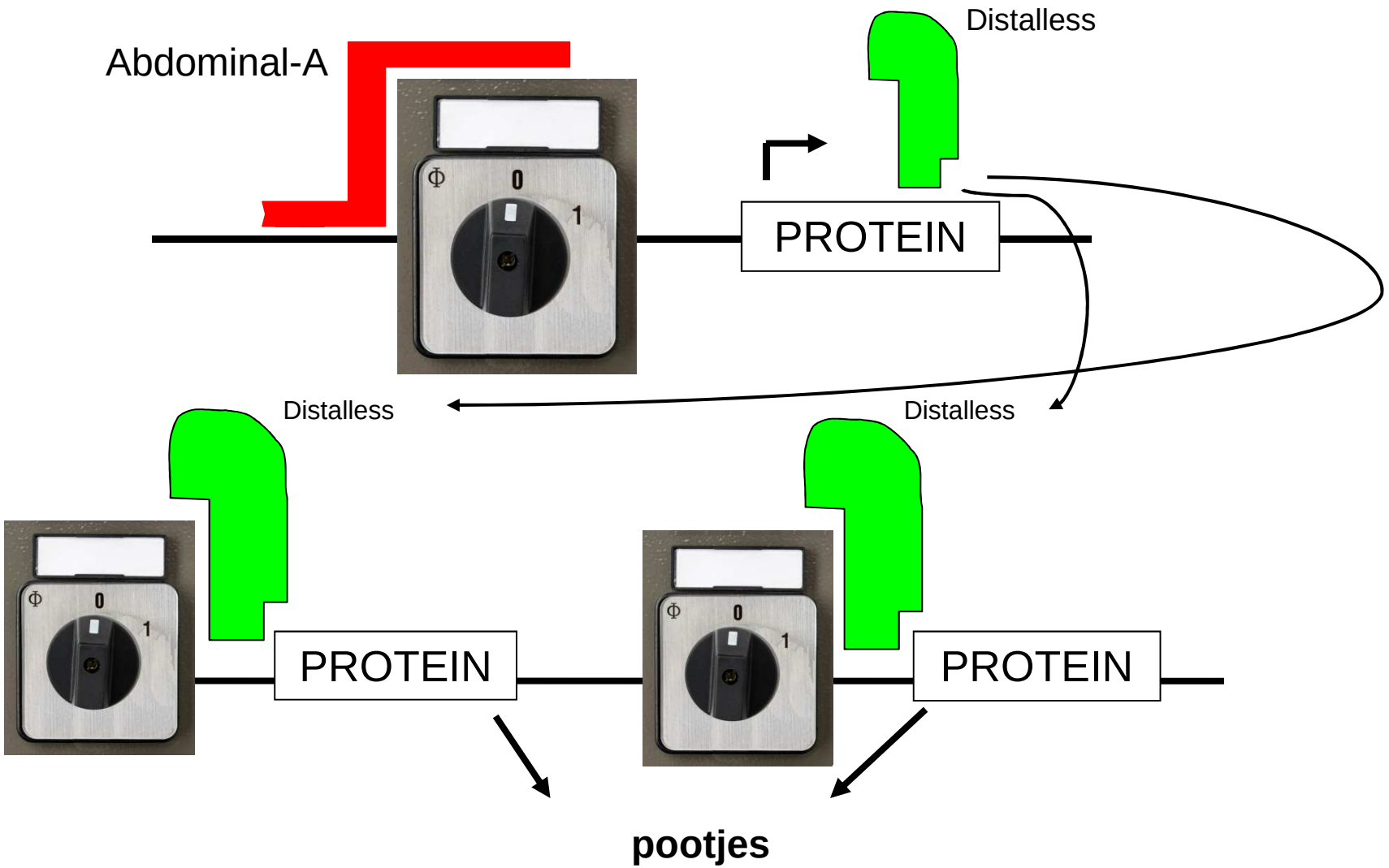
Dll-uitzetter

Abdominal-A








Abdominal-A
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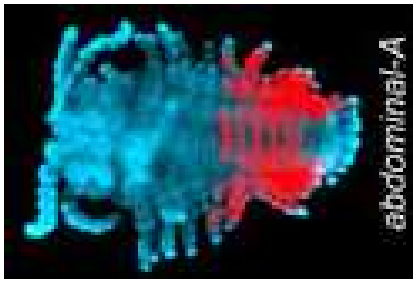
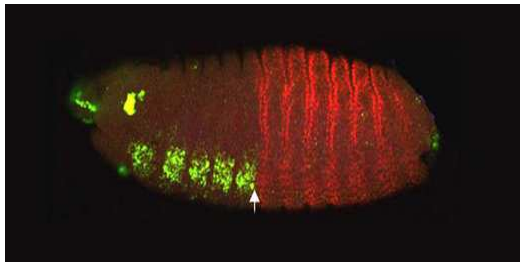
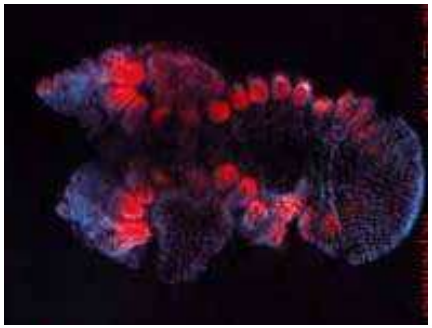
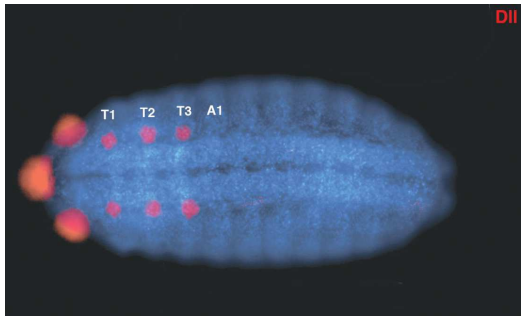

abdominal-A



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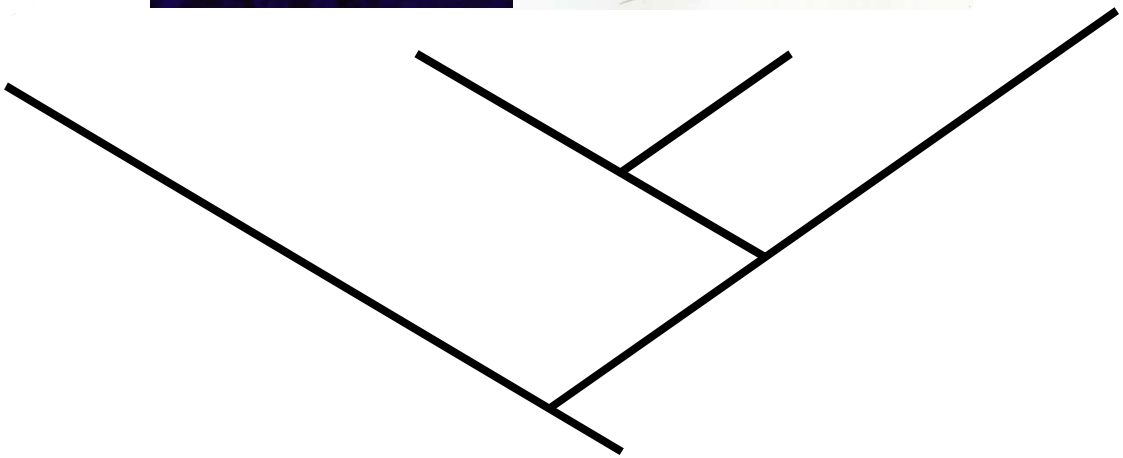

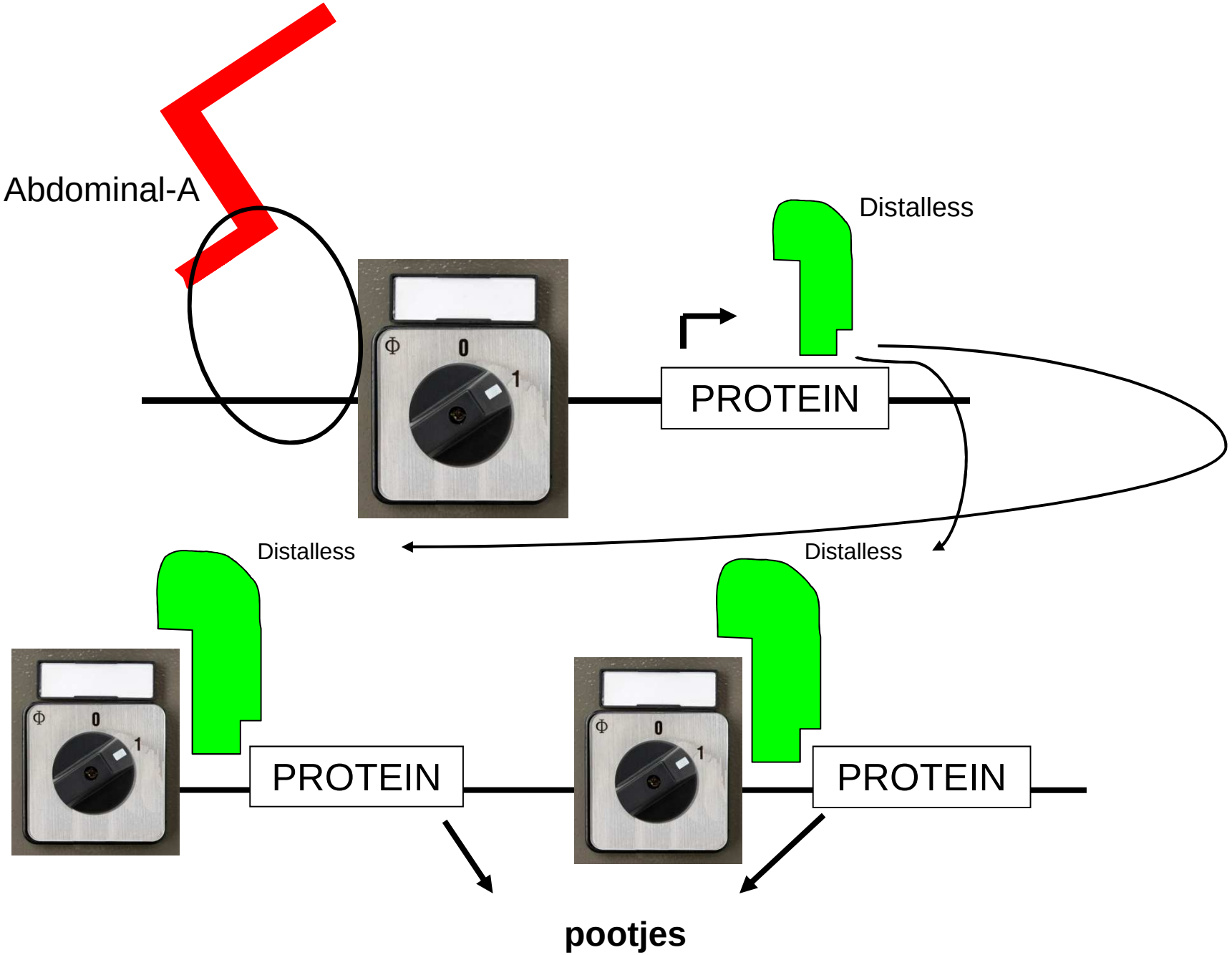
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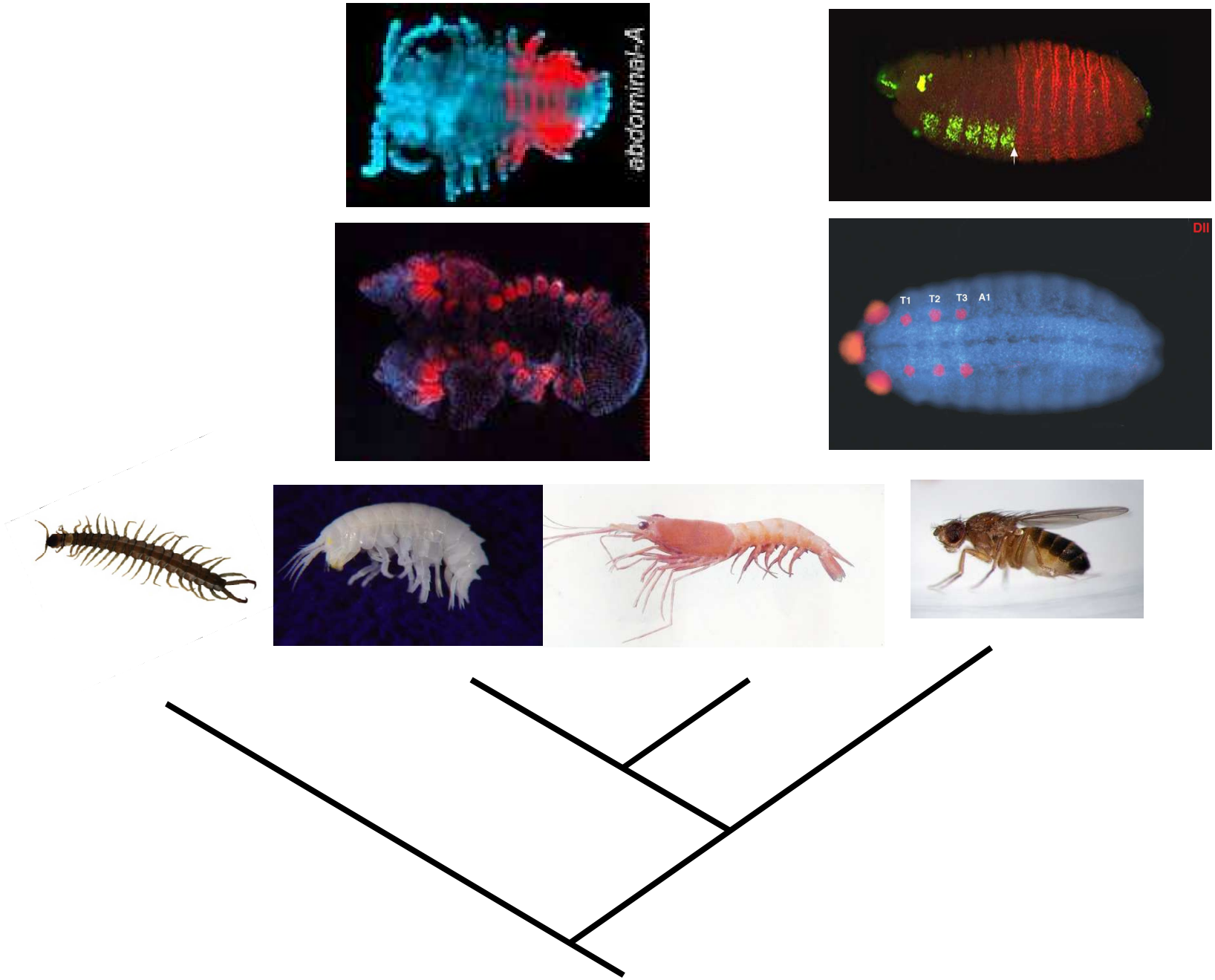
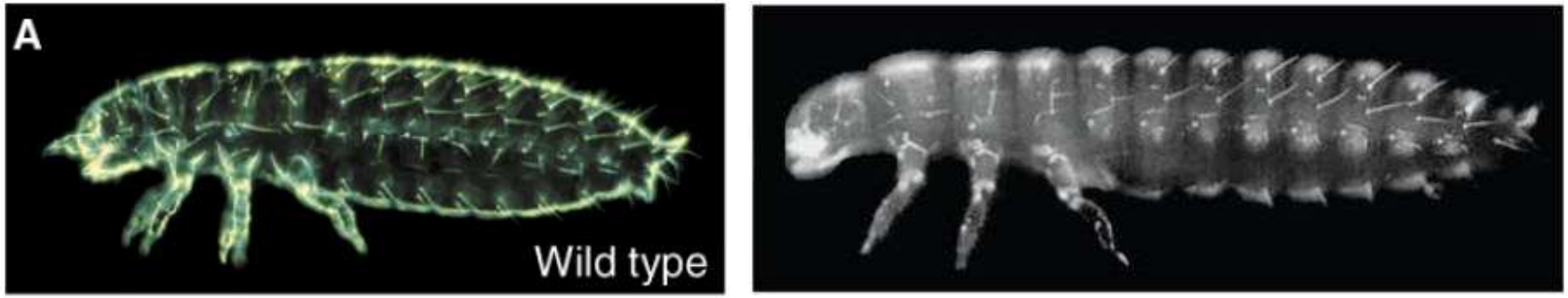


cis-regulatory evolution

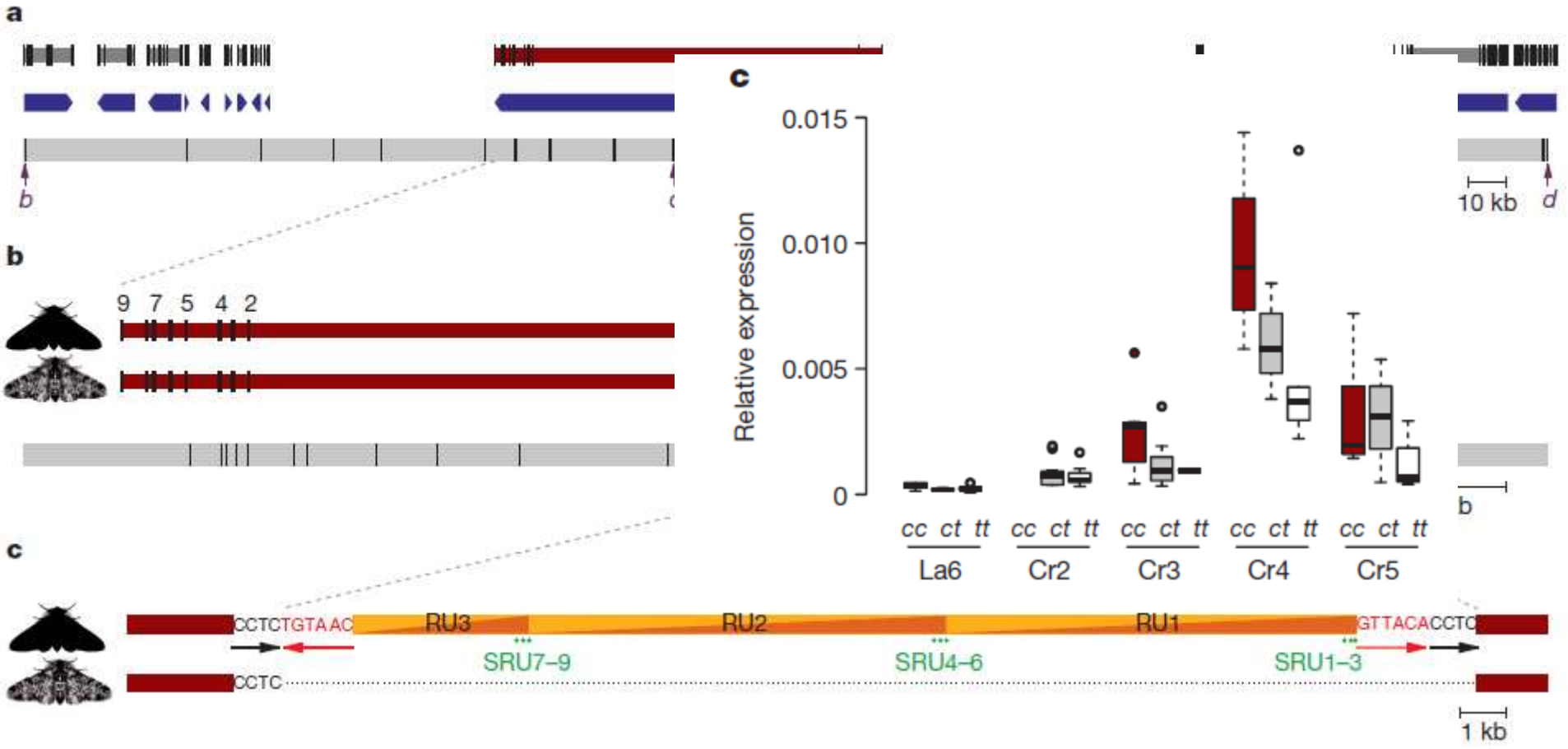

Tribolium castaneum


A
Wild type

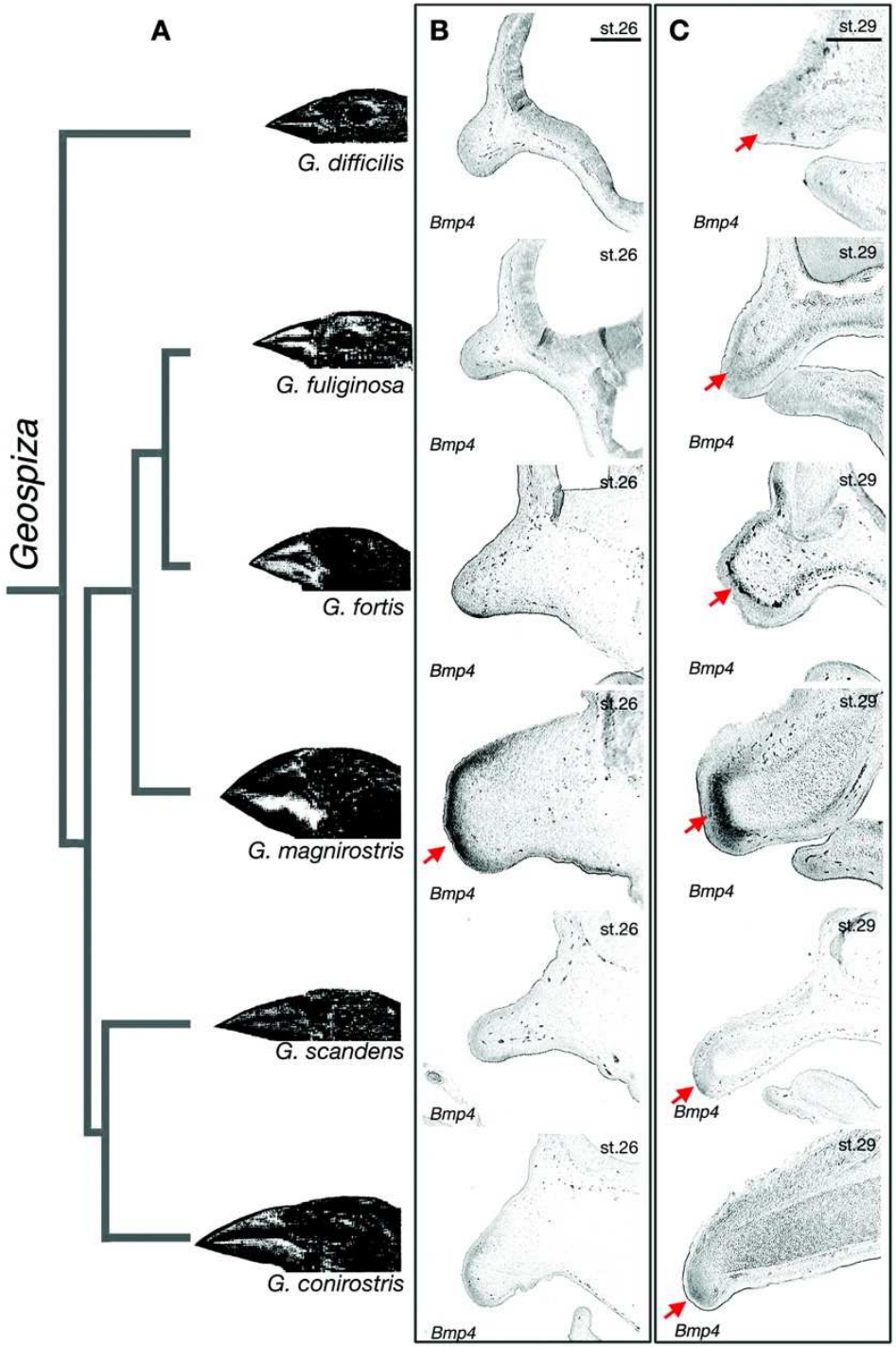
cis-regulatory evolution

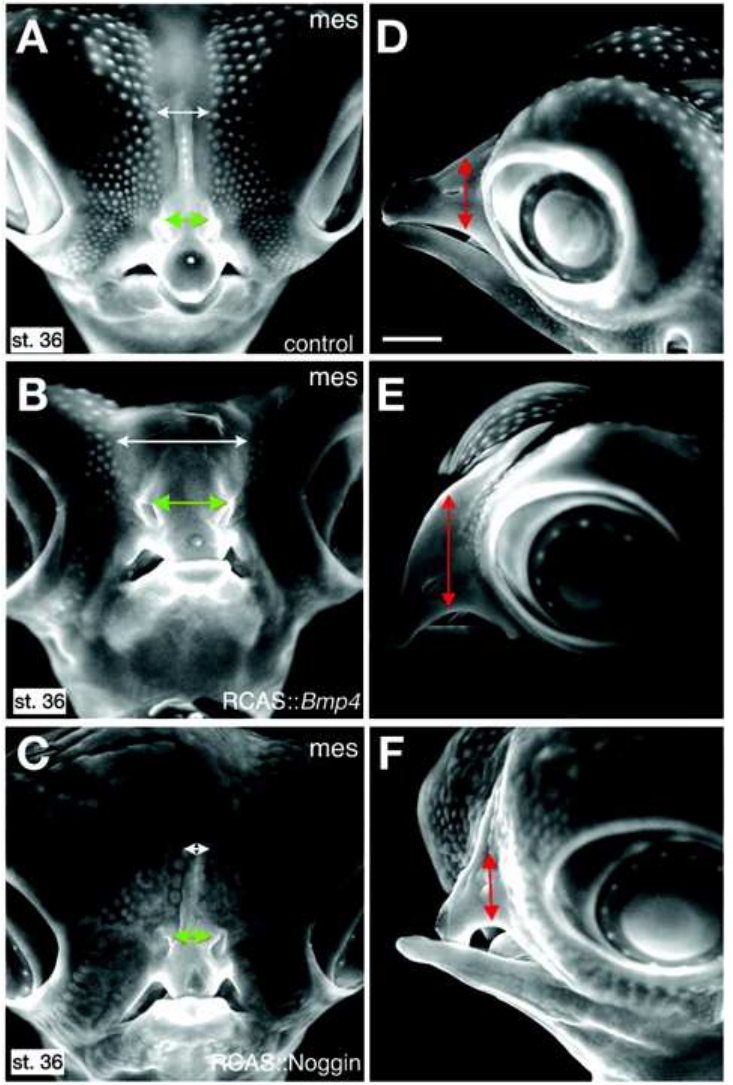
The industrial melanism mutation in British peppered moths

Arjen E. van't Hof[1]*, Pascal Campagne[1]*, Daniel J. Rigden[1], Carl J. Yung[1], Jessica Lingley[1], Michael A. Quail[2], Neil Hall[1], Alistair C. Darby[1] & Ilik J. Saccheri[1]

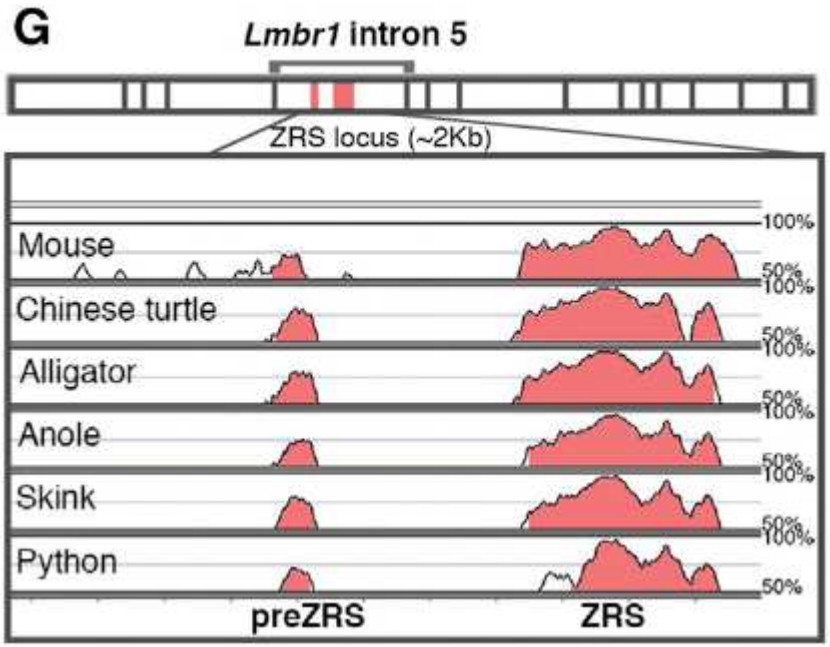


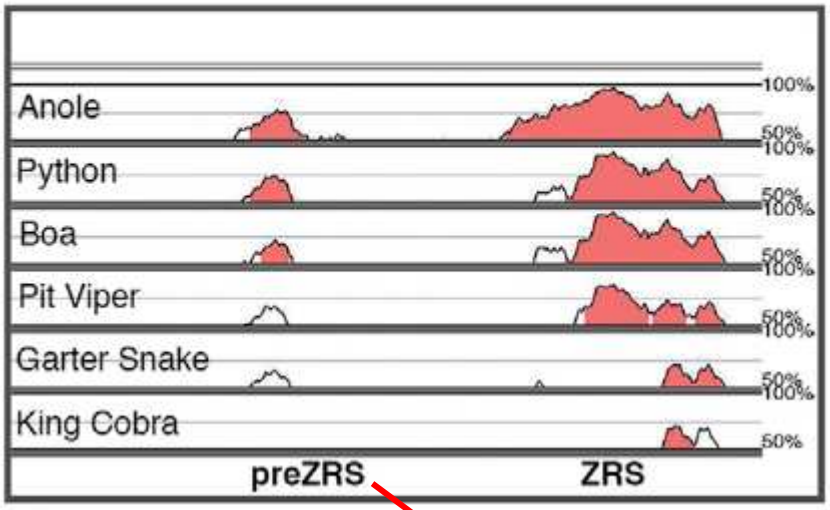
[1]Institute of Integrative Biology, University of Liverpool, Biosciences Building, Crown Street, Liverpool L69 7ZB, UK. [2]Wellcome Trust Sanger Institute, Wellcome Trust Genome Campus, Hinxton, Cambridgeshire CB10 1SA, UK.
*These authors contributed equally to this work.

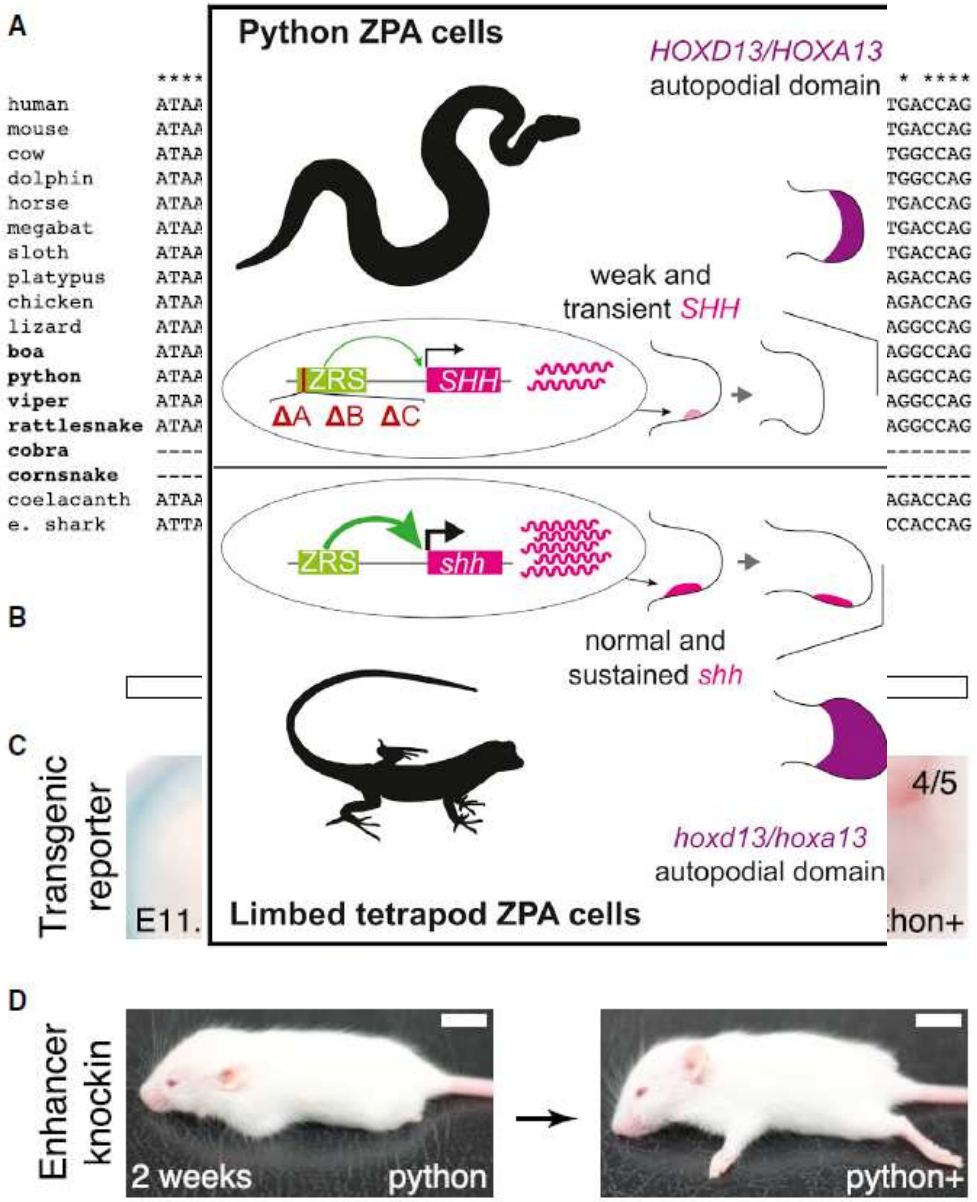




Abzahnov et al. *Science* 2004





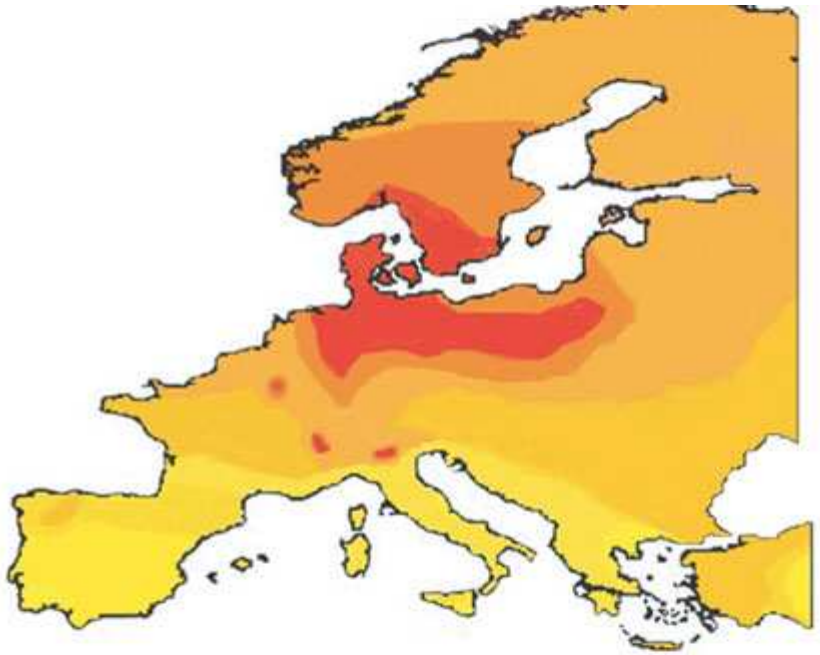


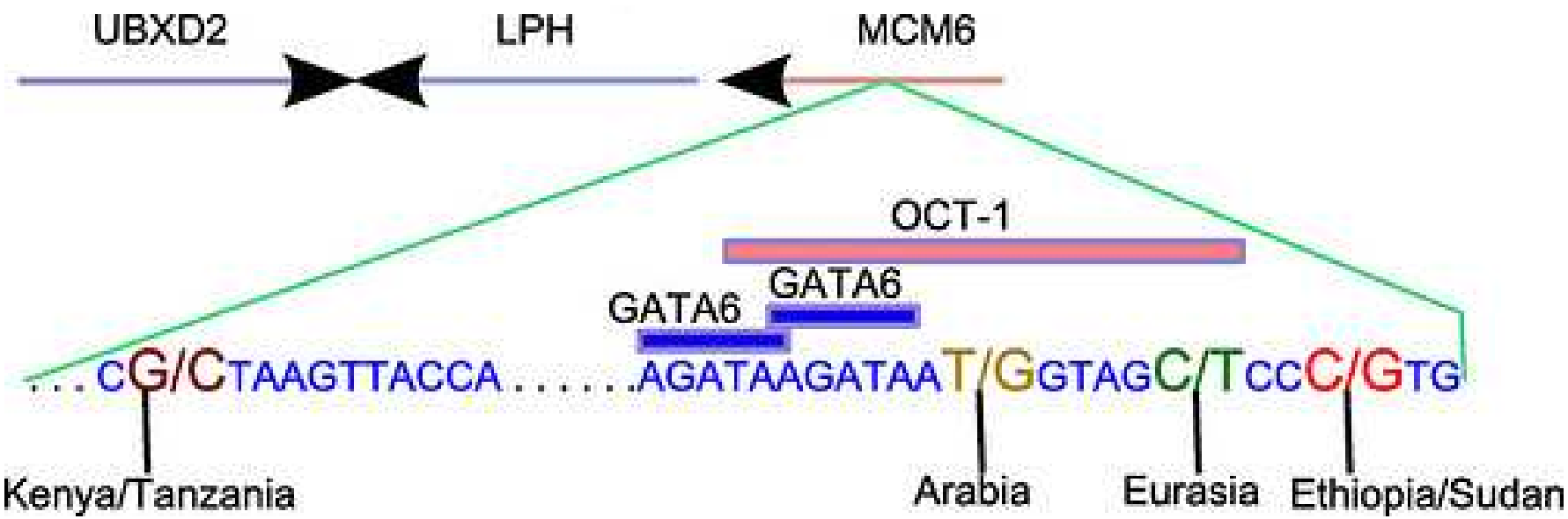
Leal & Cohen, 2014

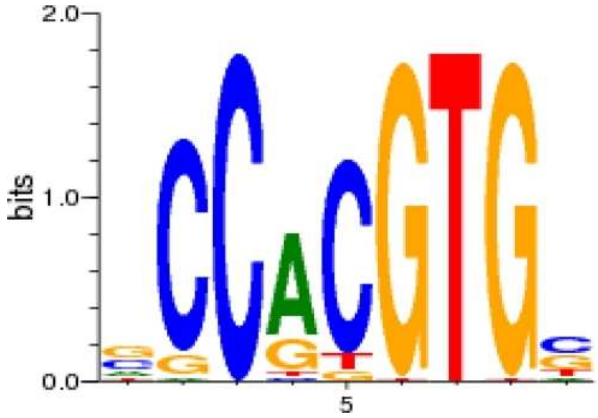
Kvon et al., 2014

ZPA Regulatory Sequence

Adulte lactose-tolerantie in mensen



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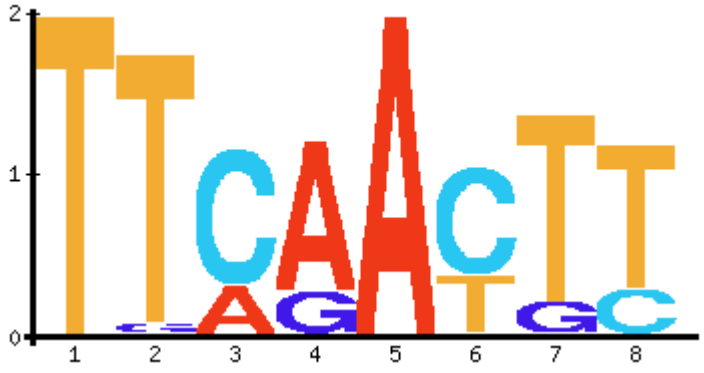
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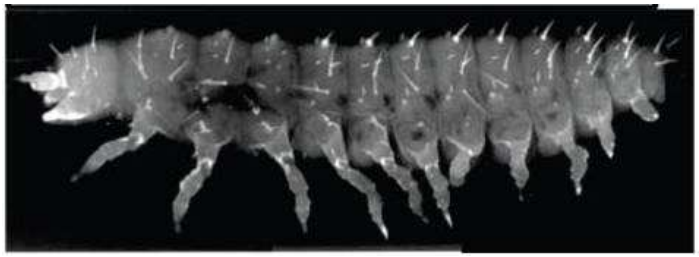


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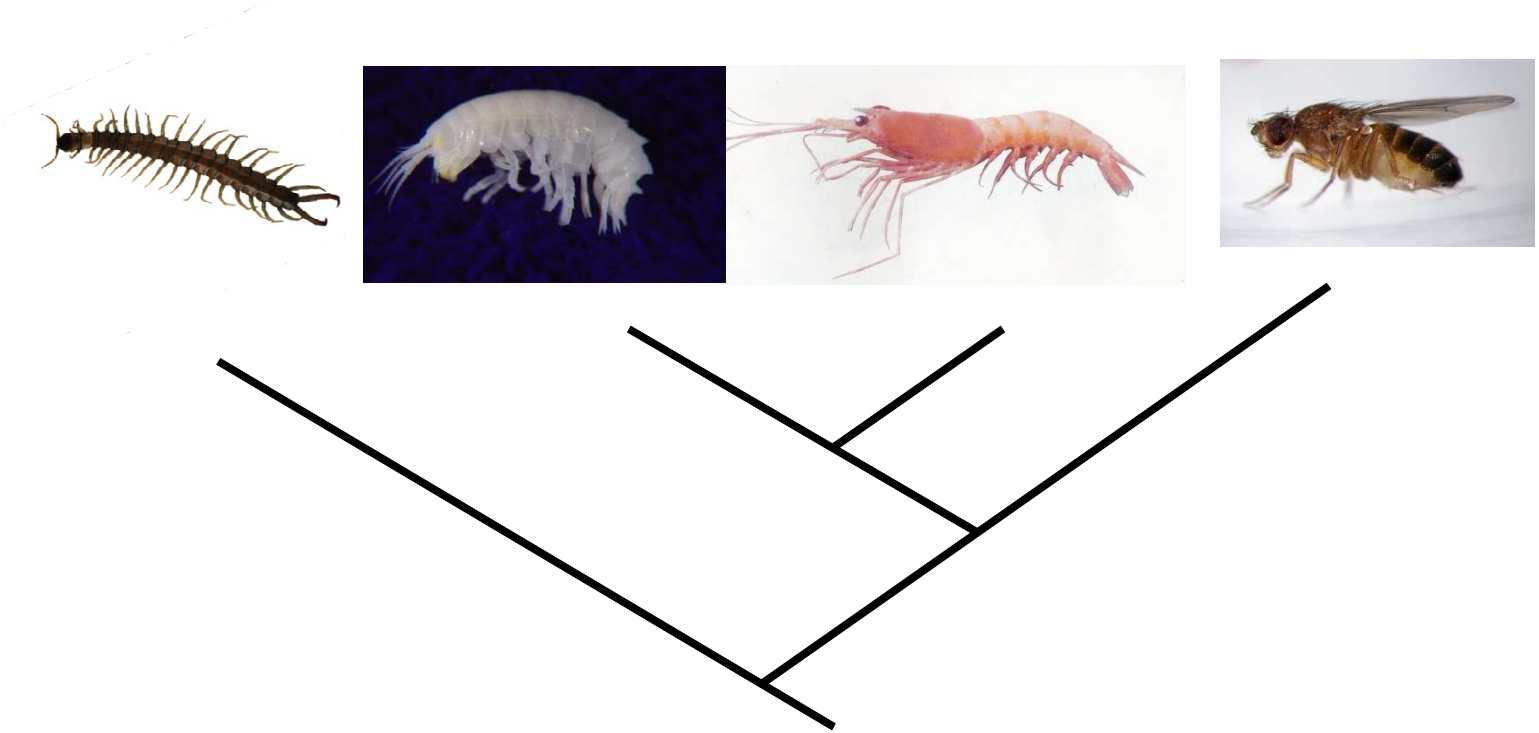

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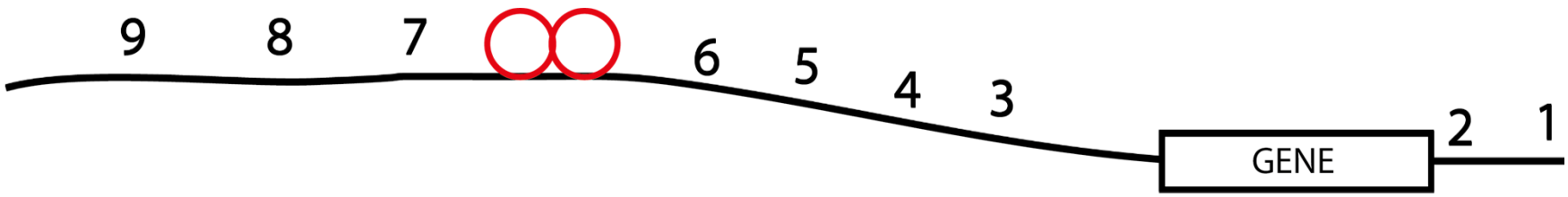

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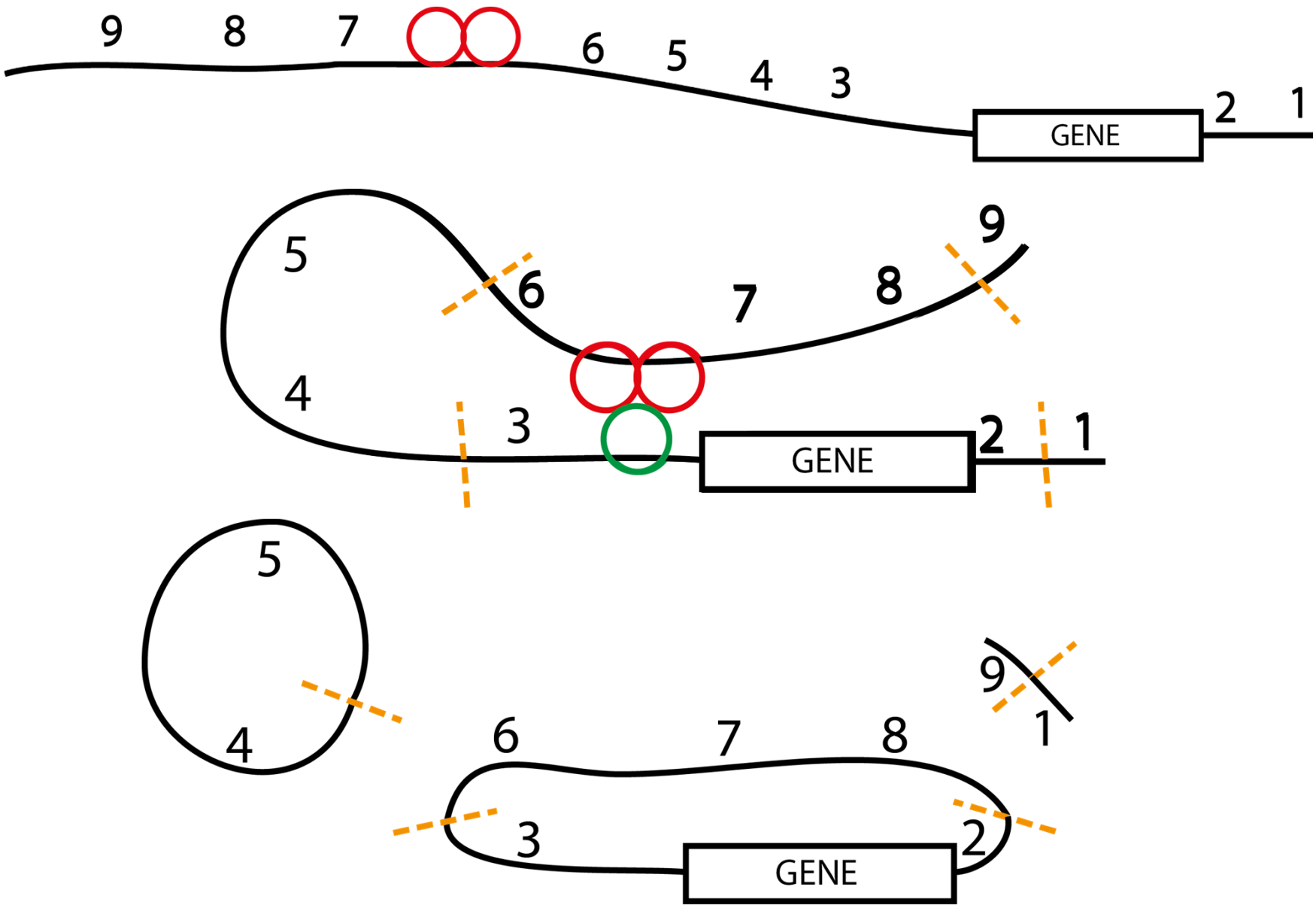

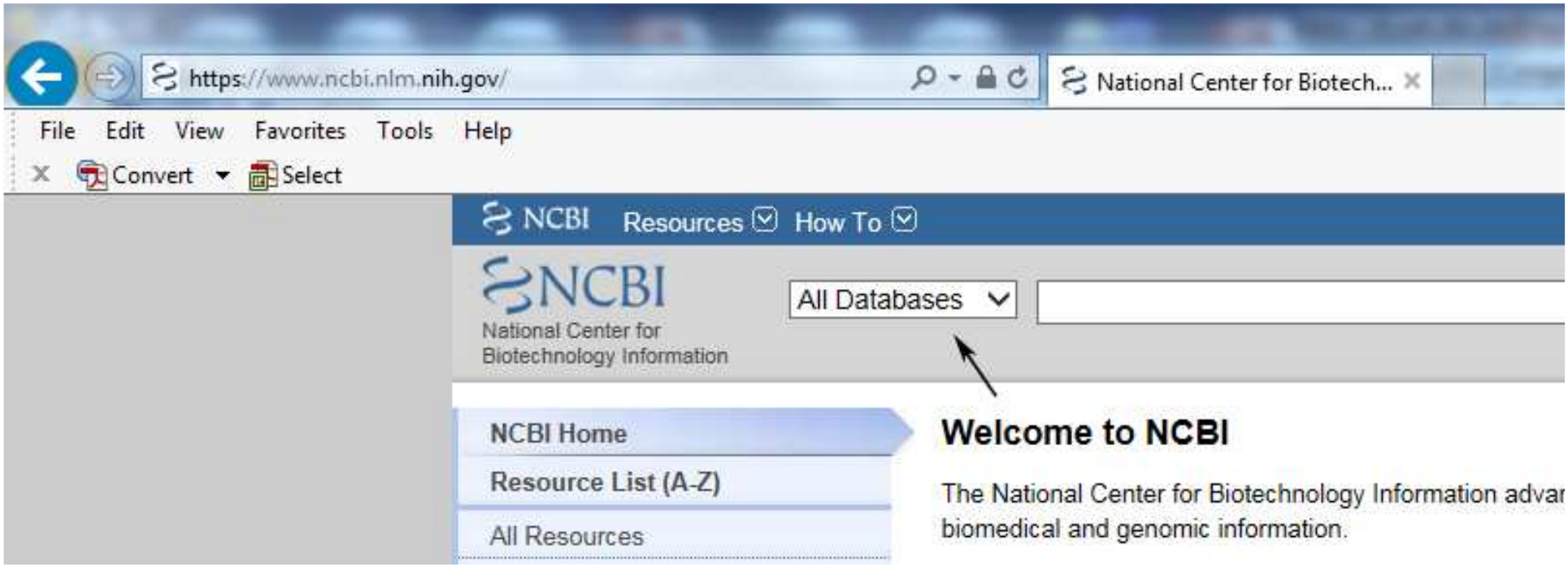
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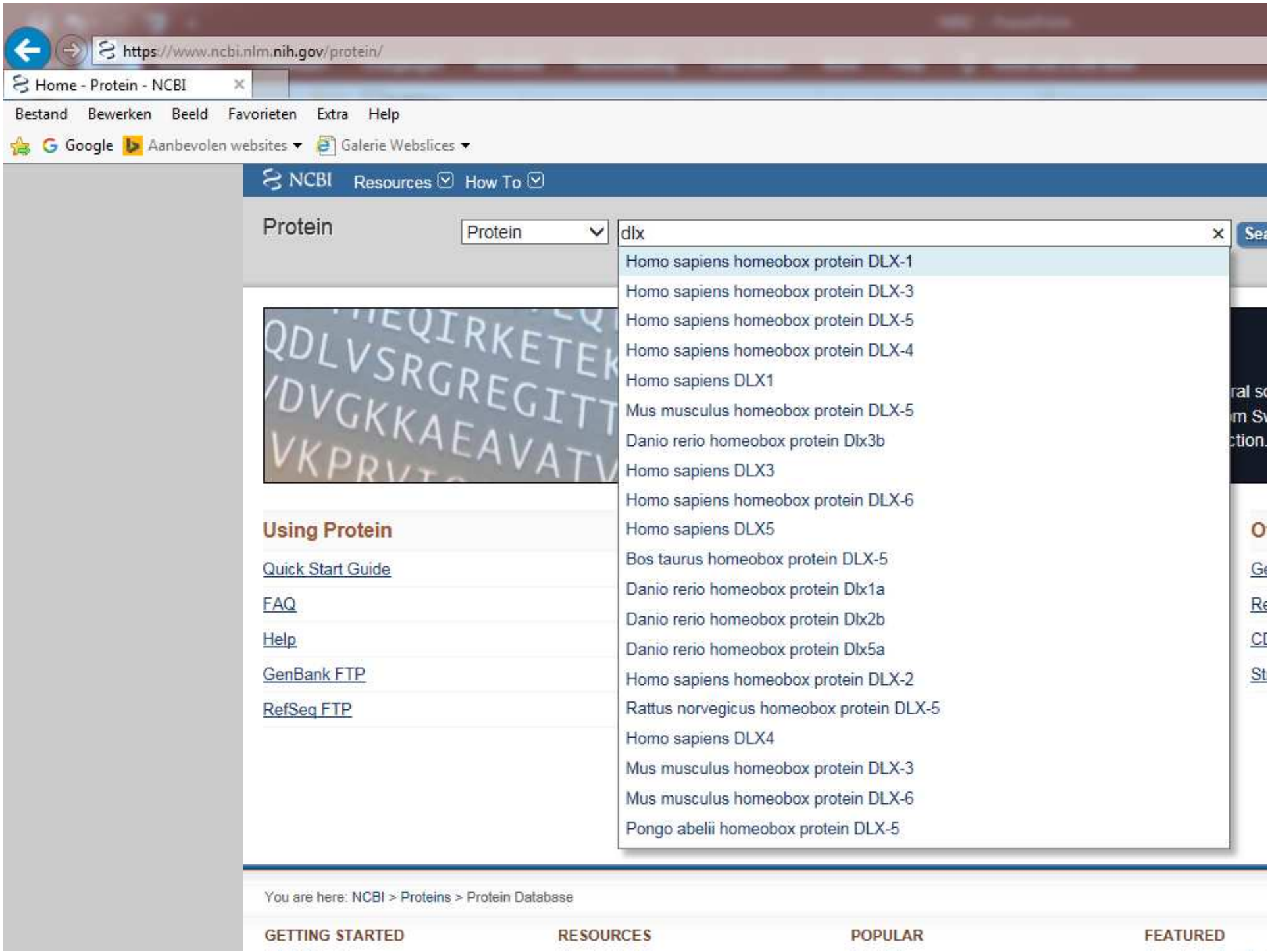
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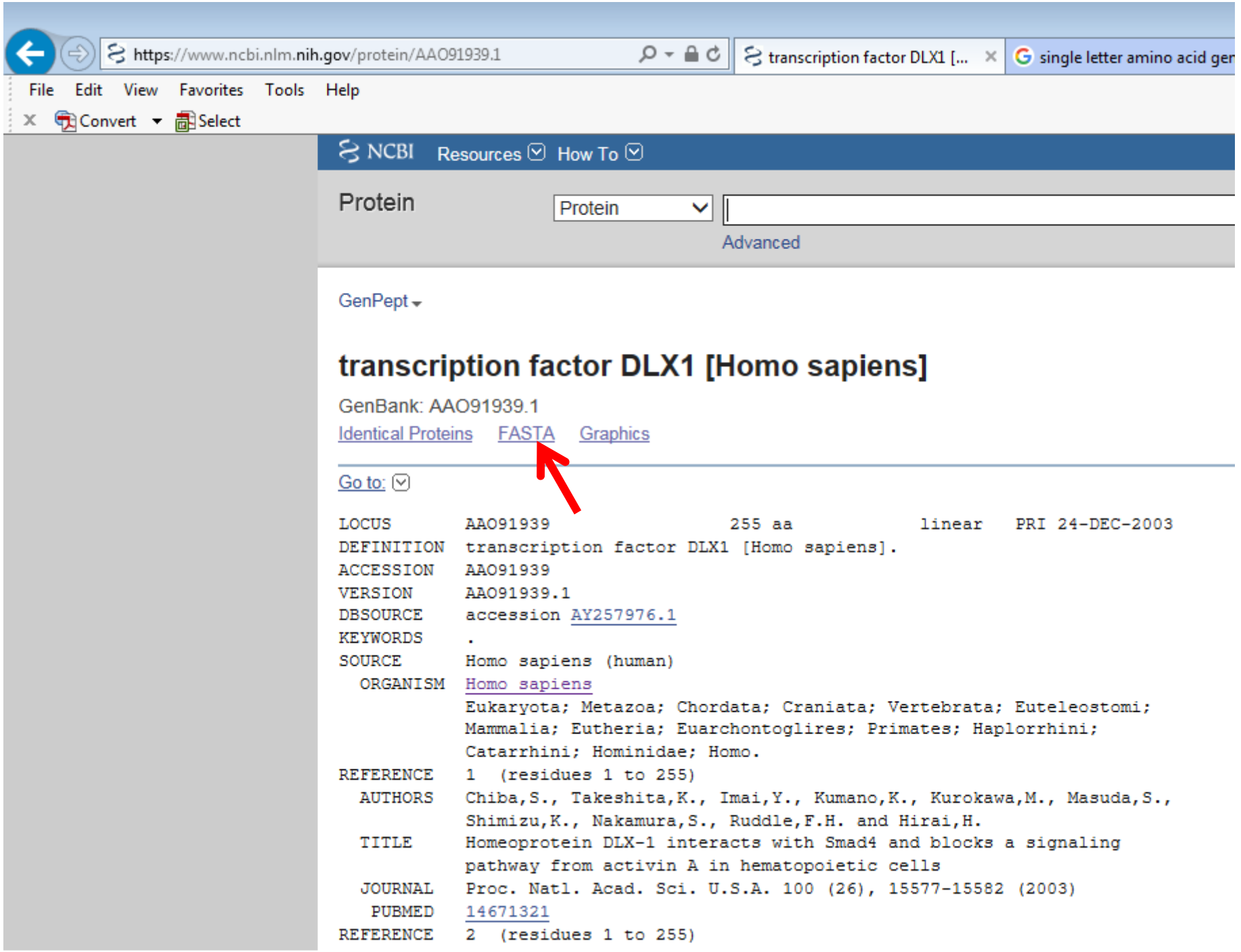
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Catarrhini; Hominidae; Homo.
REFERENCE 1 (residues 1 to 255)
AUTHORS Chiba,S., Takeshita,K., Imai,Y., Kumano,K., Kurokawa,M., Masuda,S.,
Shimizu,K., Nakamura,S., Ruddle,F.H. and Hirai,H.
TITLE Homeoprotein DLX-1 interacts with Smad4 and blocks a signaling
pathway from activin A in hematopoietic cells
JOURNAL Proc. Natl. Acad. Sci. U.S.A. 100 (26), 15577-15582 (2003)
PUBMED 14671321
REFERENCE 2 (residues 1 to 255)

unique identifier

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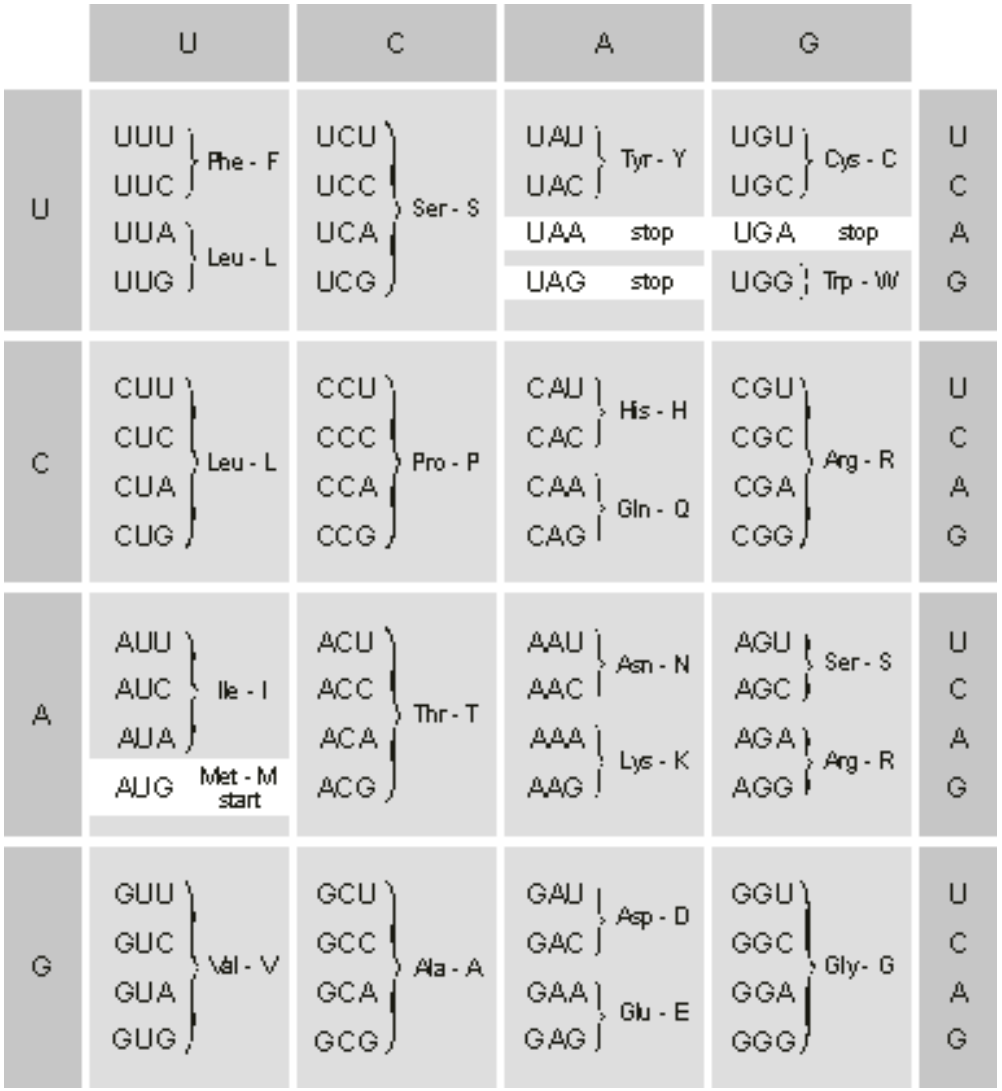
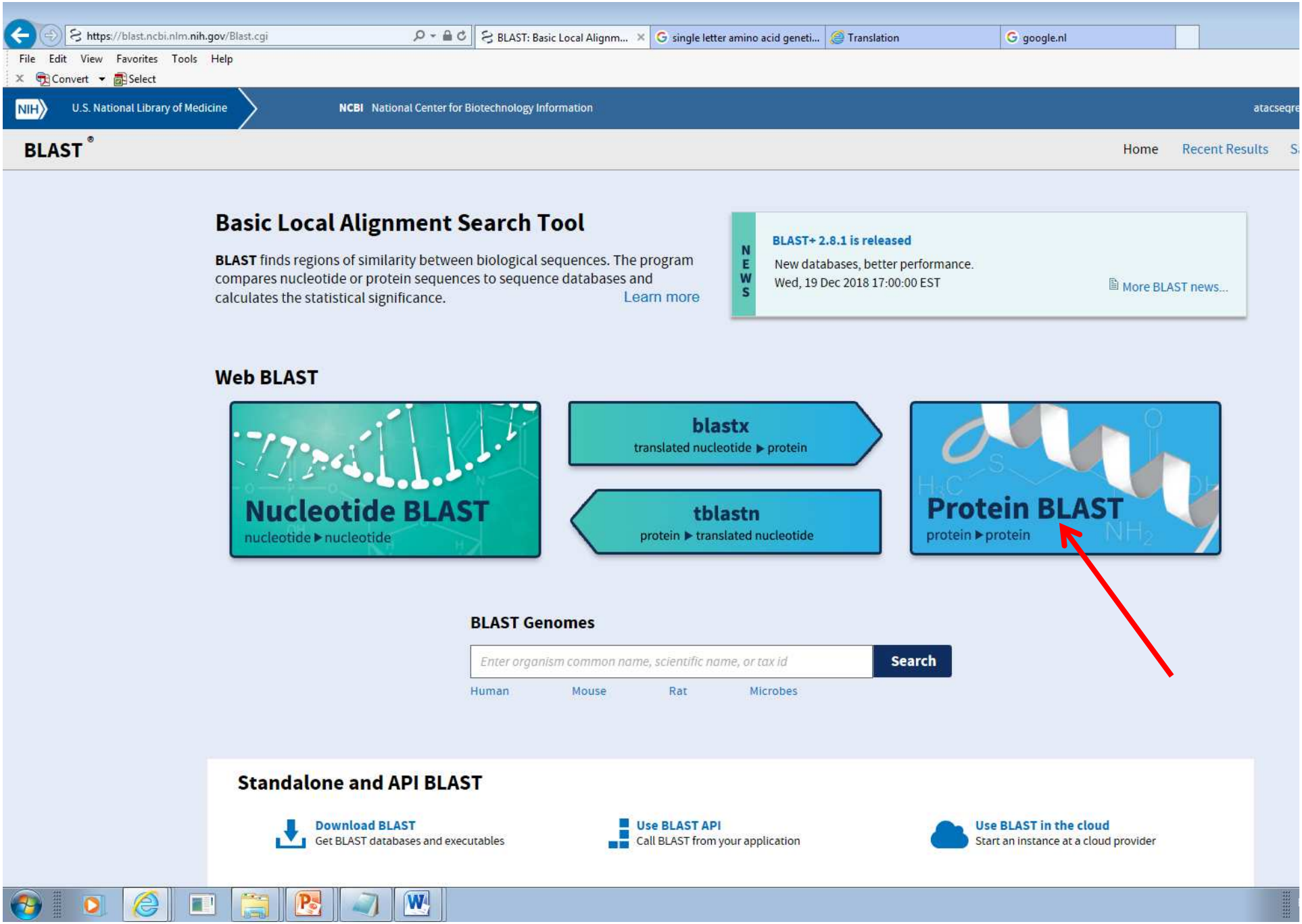


Abbreviations for amino acids

Amino acid	*Three-letter abbreviation*	*One-letter symbol*
Alanine	Ala	A
Arginine	Arg	R
Asparagine	Asn	N
Aspartic acid	Asp	D
Asparagine or aspartic acid	Asx	B
Cysteine	Cys	C
Glutamine	Gln	Q
Glutamic acid	Glu	E
Glutamine or glutamic acid	Glx	Z
Glycine	Gly	G
Histidine	His	H
Isoleucine	Ile	I
Leucine	Leu	L
Lysine	Lys	K
Methionine	Met	M
Phenylalanine	Phe	F
Proline	Pro	P
Serine	Ser	S
Threonine	Thr	T
Tryptophan	Trp	W
Tyrosine	Tyr	Y
Valine	Val	V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NIH U.S. National Library of Medicine
NCBI National Center for Biotechnology Information
BLAST®
Home Recent Results
Basic Local Alignment Search Tool
BLAST finds regions of similarity between biological sequences. The program compares nucleotide or protein sequences to sequence databases and calculates the statistical significance. Learn more
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New databases, better performance.
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Web BLAST
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nucleotide ▶ nucleotide
blastx
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tblastn
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protein ▶ protein
BLAST Genomes
Enter organism common name, scientific name, or tax id
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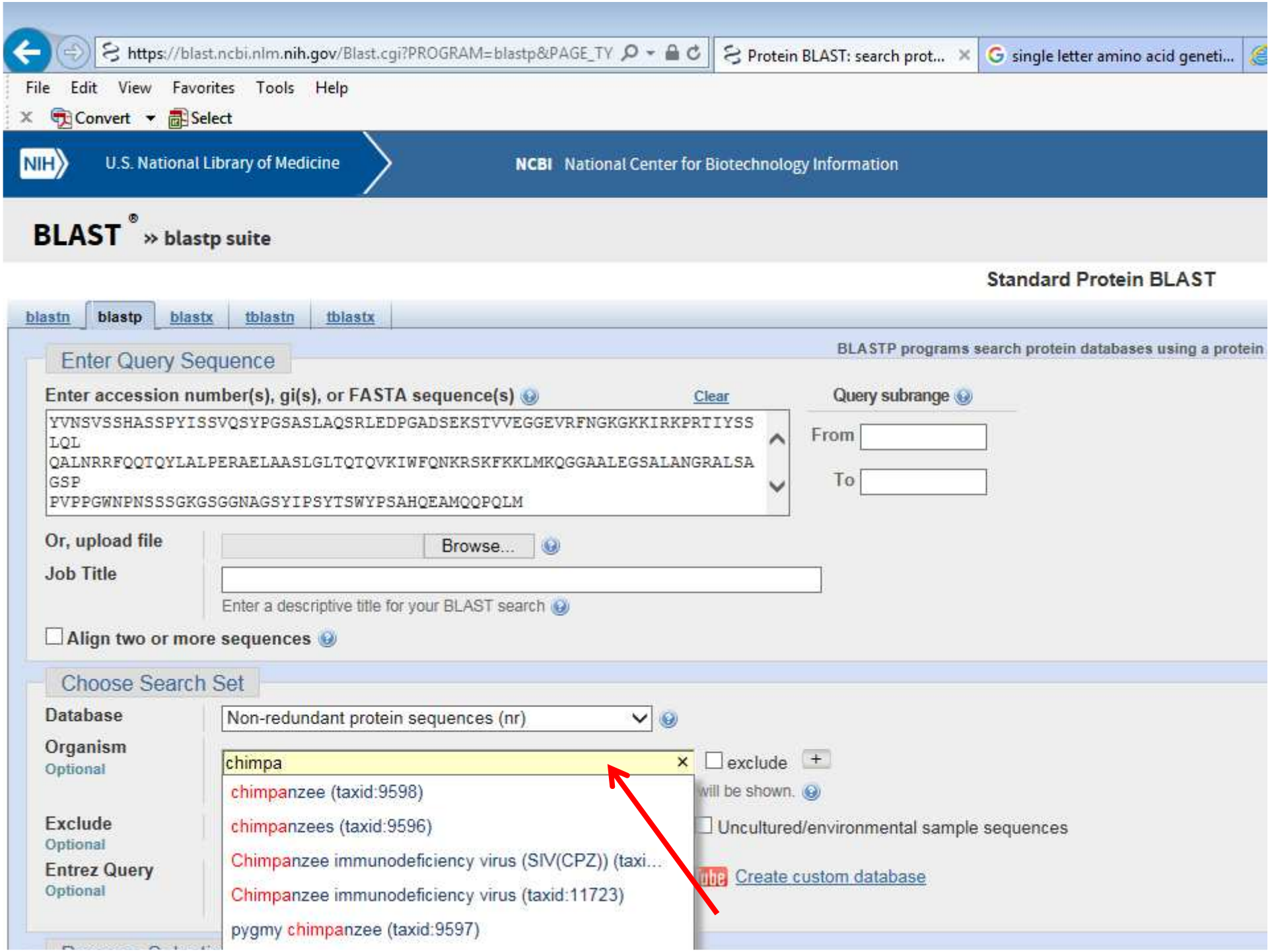
Download BLAST
Get BLAST databases and executables
Use BLAST API
Call BLAST from your application
Use BLAST in the cloud
Start an instance at a cloud provider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NCBI National Center for Biotechnology Information
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Standard Protein BLAST
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Enter accession number(s), gi(s), or FASTA sequence(s)
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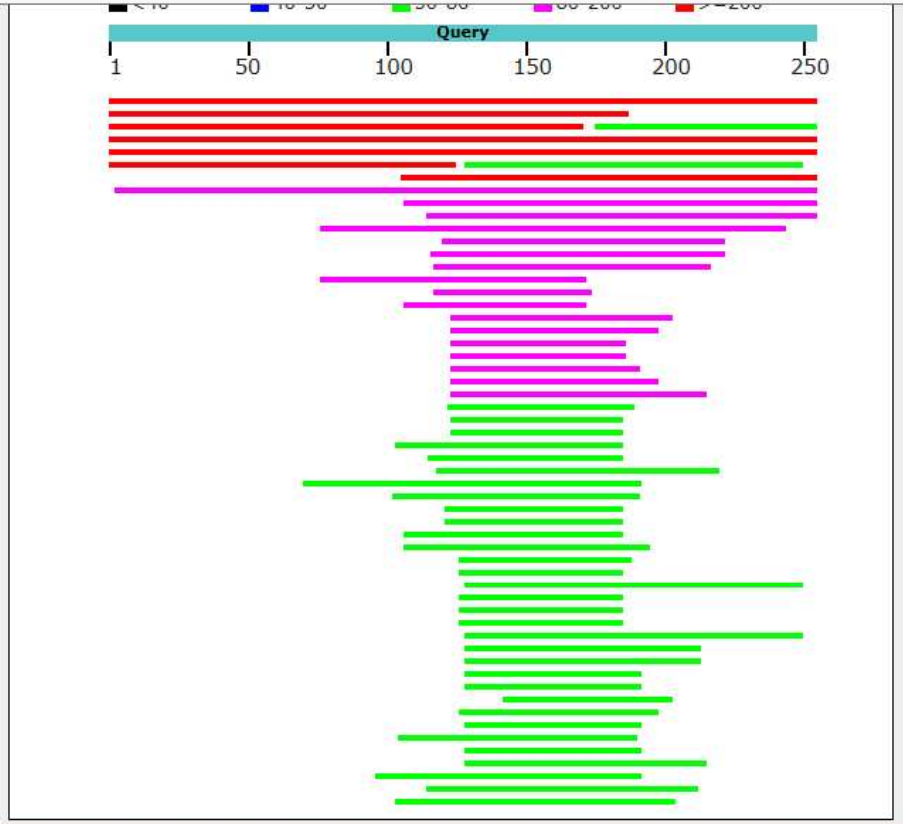

Descriptions

Sequences producing significant alignments:

Select: All None Selected:0

Alignments Download GenPept Graphics Distance tree of results Multiple alignment

Description	Max score	Total score
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DLX1 isoform 2 [Pan troglodytes]	384	384
DLX1 isoform 1 [Pan troglodytes]	348	348
DLX6 isoform 1 [Pan troglodytes]	231	231
homeobox protein DLX-6 [Pan troglodytes]	231	231

ventral anterior homeobox 1 isoform X1 [Pan troglodytes]

diencephalon/mesencephalon homeobox protein 1 isoform X1 [Pan troglodytes]

Alignments

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homeobox protein DLX-1 [Pan troglodytes]

Sequence ID: XP_009442039.1 **Length:** 255 **Number of Matches:** 1

See 1 more title(s)

Range 1: 1 to 255 GenPept Graphics Next Match Previous Match

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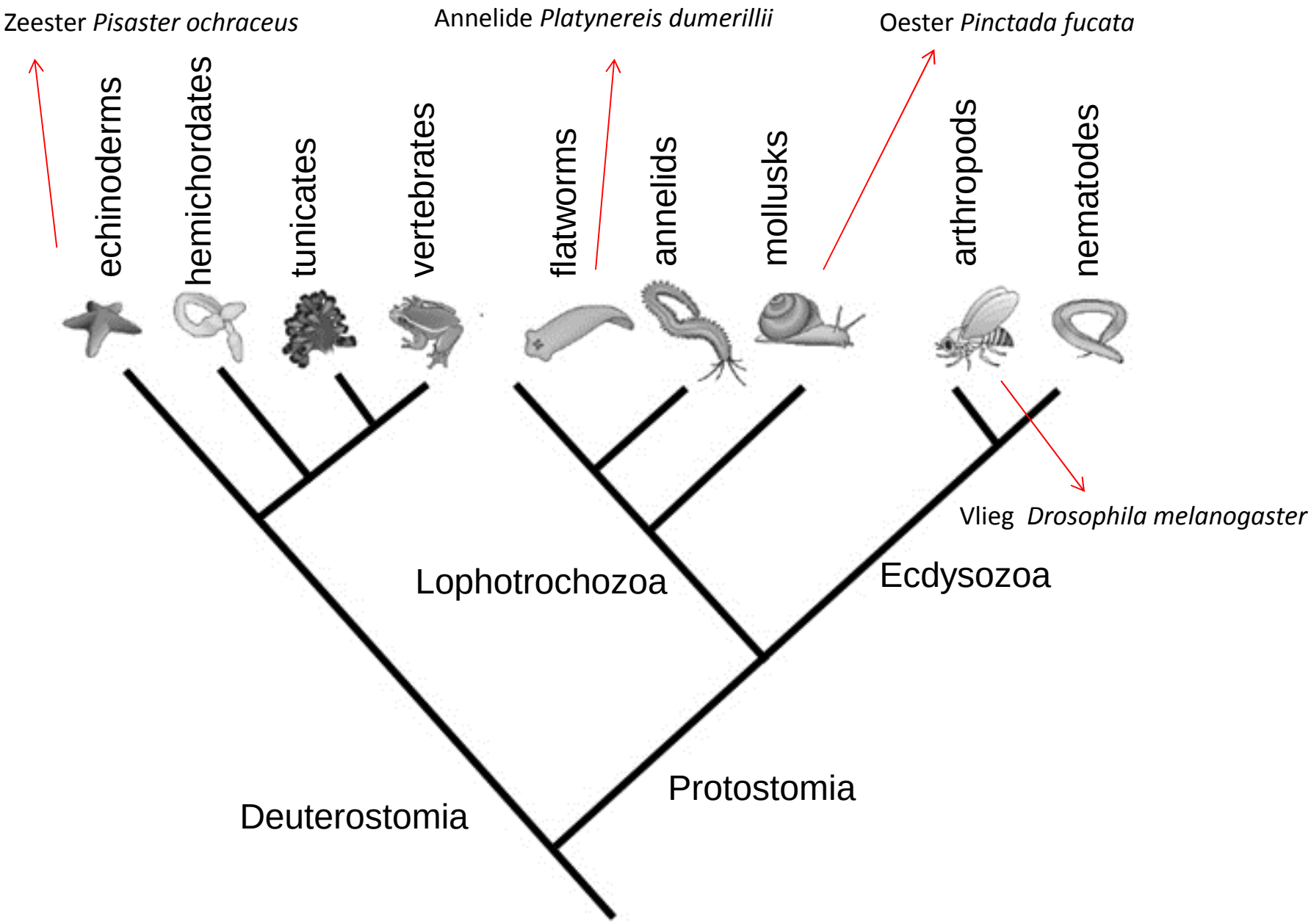
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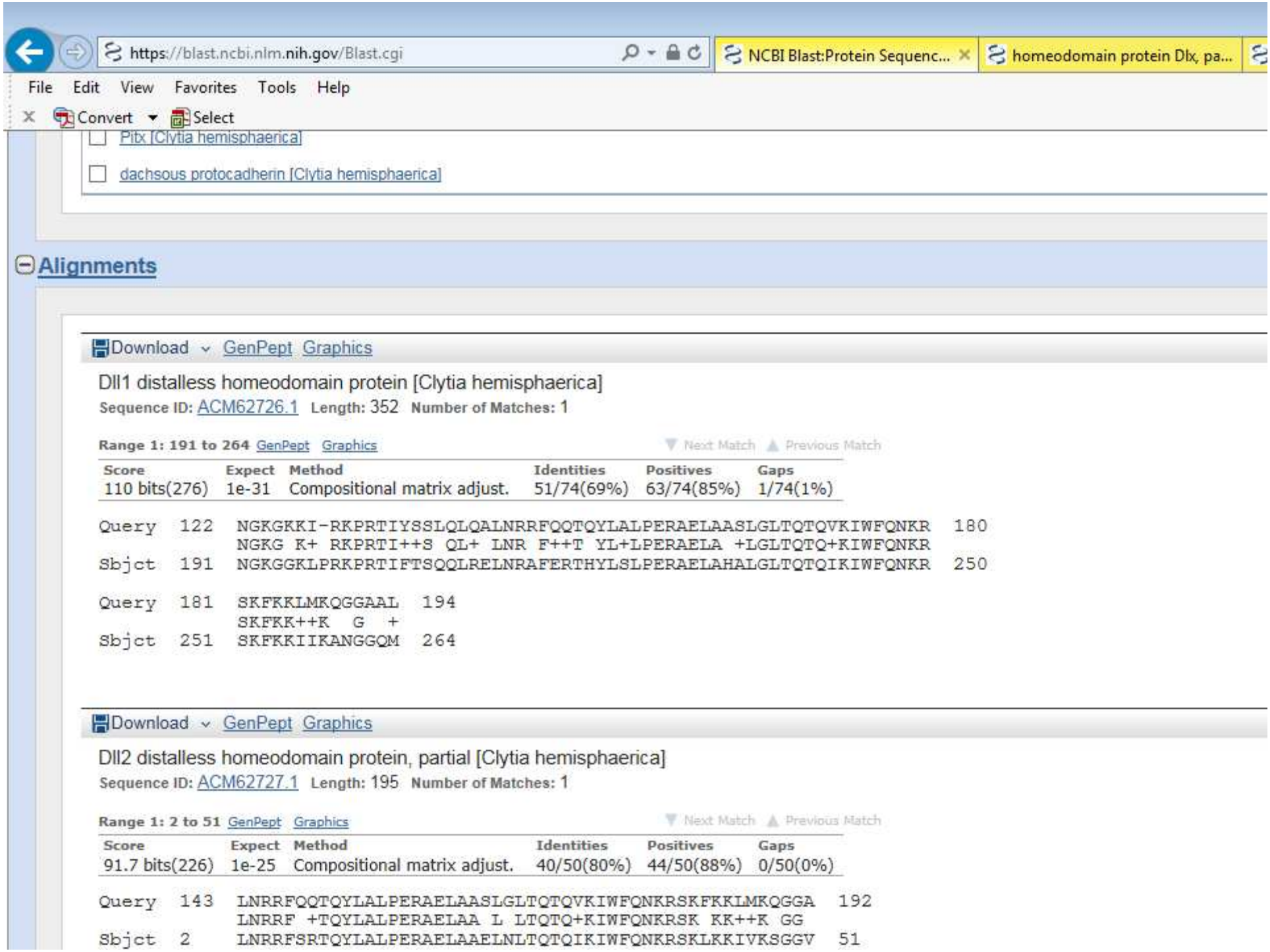
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>Zeester
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>Annelide
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>Oester
MLNVGSVEGMEQEMAGKSAFMELQQSGGMPMGHPAYPMRSSYQPPHHGGQHGESVFSNPQGRGPLAGYPFHMNAMSPTAYNPSSGHHFSMPPYQSPSPTRDDKSQMDELRINGKGKKMRKPRTIYSSLQLQQLNRRFQRT
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>Fruitvlieg
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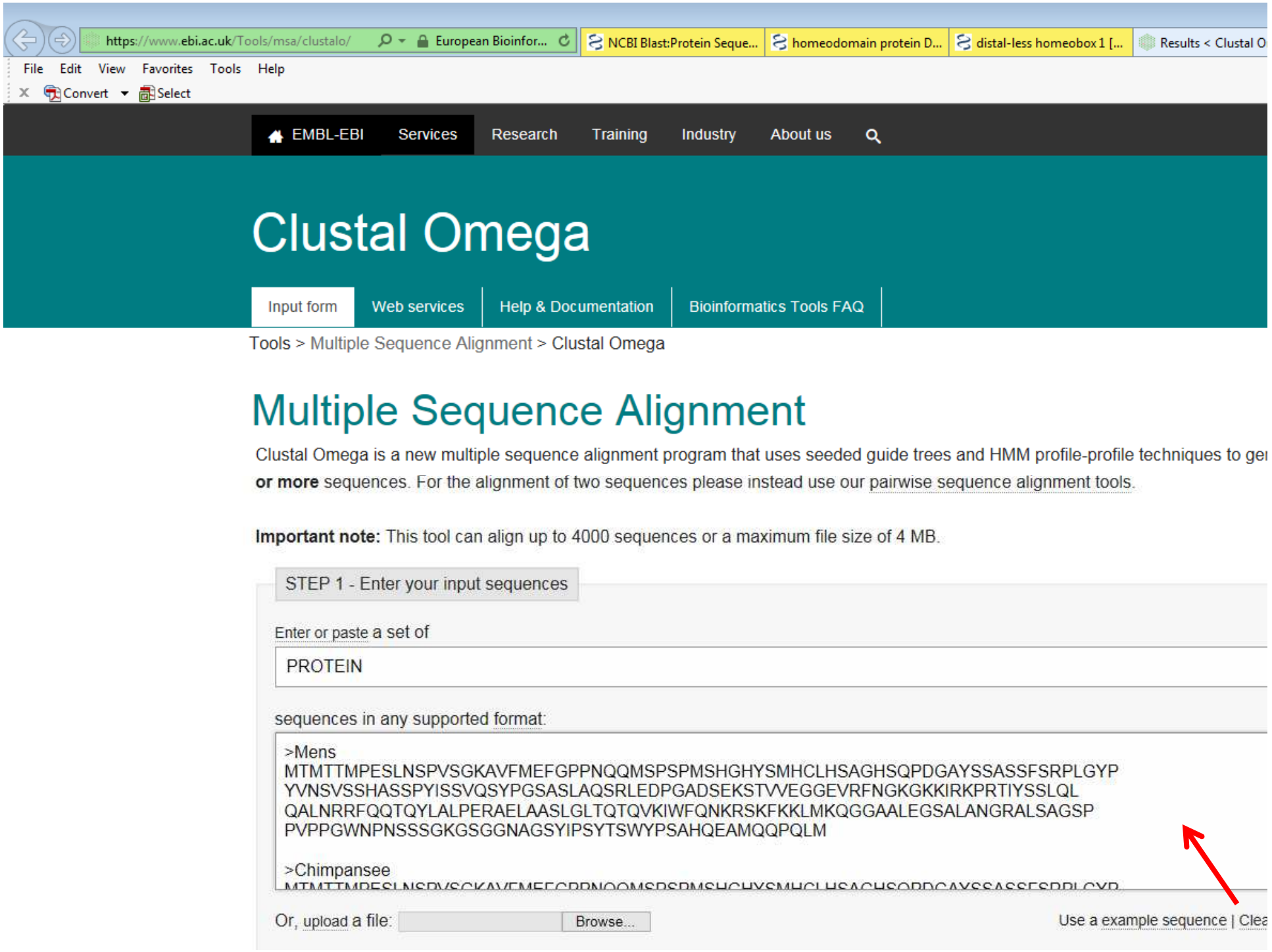
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Convert
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EMBL-EBI
Services
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Training
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Input form
Web services
Help & Documentation
Bioinformatics Tools FAQ
Tools > Multiple Sequence Alignment > Clustal Omega
Multiple Sequence Alignment
Clustal Omega is a new multiple sequence alignment program that uses seeded guide trees and HMM profile-profile techniques to ge
or more sequences. For the alignment of two sequences please instead use our pairwise sequence alignment tools.
Important note: This tool can align up to 4000 sequences or a maximum file size of 4 MB.
STEP 1 - Enter your input sequences
Enter or paste a set of
PROTEIN
sequences in any supported format:
>Mens
MTMTTMPESLNSPVSGKAVFMEFGPPNQQMSPSPMSHGHYSMHCLHSAGHSQPDGAYSSASSFSRPLGYP
YVNSVSSHASSPYISSVQSYPGSASLAQSRLEDPGADSEKSTVVEGGEVRFNGKGKKIRKPRTIYSSLQL
QALNRRFQQTQYLALPERAELAASLGLTQTQVKIWFQNKRSKFKKLMKQGGAALEGSALANGRALSAGSP
PVPPGWNPNSSSGKGSGGNAGSYIPSYTSWYPSAHQEAMQQPQLM
>Chimpansee
Or, upload a file:
Browse...
Use a example sequence | Clea

```
Oester          --MGHPAYPMRSSYQ--------PPHH---GGQHG-----ESVFSNPQ-GRG---PLAGY    68


Kwal            PEQDSISSSLQSFHSSGLPTSYTSSYNNNSMQTTLSSPSSITSN--------MS------    165
Zeester         ------------------------------------------------------------    0
Fruitvlieg      PFPPMHQNSYSGYHLG----------------SYAP----------------------PC    96
Kikker          PYMSH----------------------SQH-SPYLQ----------------------SC    93
Zebravis        PYVNSVGS-------------------HSS-SPYLS----------------------TV    87
Kip             PYVNSVSS-------------------HSG-NPYIS----------------------SV    87
Mens            PYVNSVSS-------------------HAS-SPYIS----------------------SV    87
Chimpansee      PYVNSVSS-------------------HAS-SPYIS----------------------SV    87
Koe             PYVNSVSS-------------------HAS-SPYIS----------------------SV    87
Annelide        PFSMTPMGSHGTYNPT--------SYHHFSAPGYQTSAPSVTPPTSRESMYDLPNYYSSY    124
Oester          PFHMNAMS-PTAYNPS--------SGHHFSMPPYQSP----------------------    96


Kwal            RSFSSSS-Y----V---KQESDEEDEGDLTQ-SKNGKGGKLPRKPRTIFTSQQLRELNRA    216
Zeester         ----------------------------------------GKKLRKPRTIYSSLQLQKLNHR    22
Fruitvlieg      AS-------------PPKDDFSISDKCEDSGLRVNGK-GKKMRKPRTIYSSLQLQQLNRR    142
Kikker          NS----NTTTQSRAE--EPDQQKTTVIENGEIRFNGK-GKKIRKPRTIYSSLQLQALNHR    146
Zebravis        QTYPNNSALAQTRLEDPAPESEKNTVVEGGEVRFNGK-GKKIRKPRTIYSSLQLQALNRR    146
Kip             QPYPNSSGLAQPRLEETGAESEKSTVVEGGEVRFNGK-GKKIRKPRTIYSSLQLQALNRR    146
Mens            QSYPGSASLAQSRLEDPGADSEKSTVVEGGEVRFNGK-GKKIRKPRTIYSSLQLQALNRR    146
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Koe             QSYPGSASLTQSRLEDPGADSEKSTVVEGGEVRFNGK-GKKIRKPRTIYSSLQLQALNRR    146
Annelide        DKLENKYIYRKGLFEDSPPNSD--EKPSMDELRVNGK-GKKMRKPRTIYSSLQLQQLNKR    181
Oester          -----------------SPTRD--DKSQMDELRINGK-GKKMRKPRTIYSSLQLQQLNRR    136
                                                    **  ******::* **: **:


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Zeester         FTKTQYLALPERADLAASLGLTQTQVKIWFQNRRSKYKKILKQHGSTPTSSTGSQDPE--    80
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Kikker          FQQTQYLALPERAELAASLGVTQTQVKIWFQNKRSKYKKLIKQGNNPLEIDQLAGTVALS    206
Zebravis        FQQTQYLALPERAELAASLGLTQTQVKIWFQNKRSKFKKLMKQGGGTIDTNALANGRGLS    206
Kip             FQQTQYLALPERAELAASLGLTQTQVKIWFQNKRSKFKKLMKQGGAALESGALSNGRALS    206
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Chimpansee      FQQTQYLALPERAELAASLGLTQTQVKIWFQNKRSKFKKLMKQGGAALEGSALANGRALS    206
Koe             FQQTQYLALPERAELAASLGLTQTQVKIWFQNKRSKFKKLMKQGGAALEGSALANGRALS    206
Annelide        FQRTQYLALPERAELAASLGLTQTQVKIWFQNRRSKYKKLMKQNPGIGGPGGAQNGPPMD    241
Oester          FQRTQYLALPERAELAASLGLTQTQVKIWFQNRRSKAKKIMKQGGTPPGPNQQ---PPT-    192
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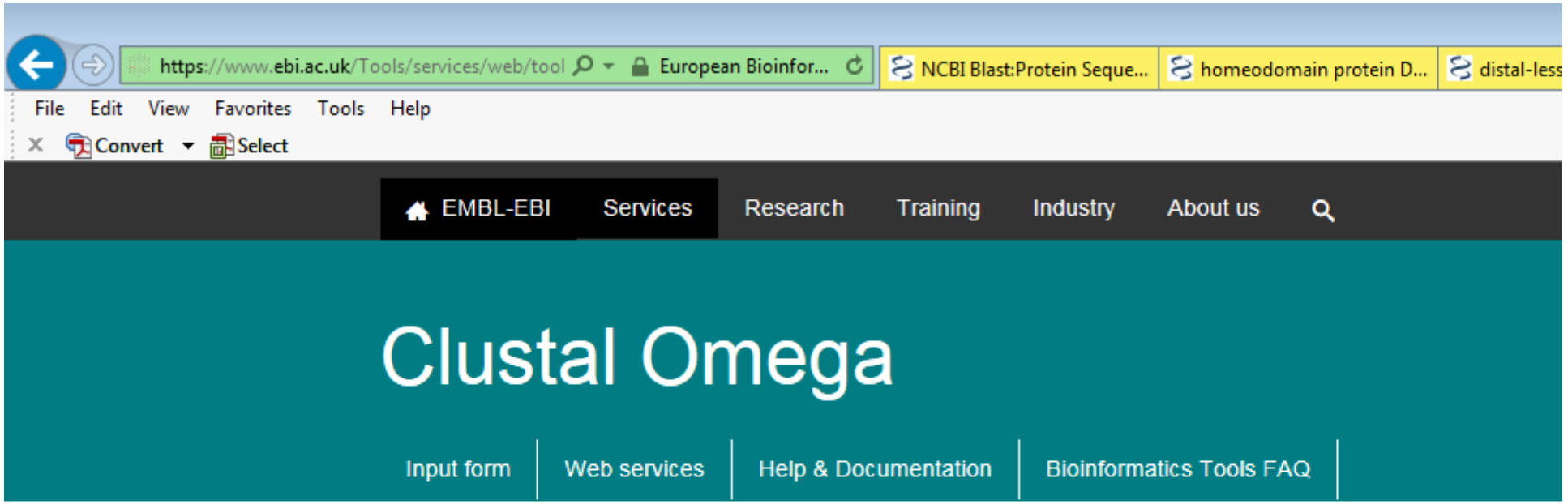

Tools > Multiple Sequence Alignment > Clustal Omega

Results for job clustalo-I20190109-142418-0795-79569343-p1m

Alignments | Result Summary | Phylogenetic Tree | Submission Details

Download Alignment File | Show Colors | View result with Jalview | Send to Simple Phylogeny | Sen

```
CLUSTAL O(1.2.4) multiple sequence alignment


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Zeester         ------------------------------------------------------------    0
Fruitvlieg      -MDAPDAPHTPKYMDGGN----TA---ASVTPG------INIPGKSAFVELQQHAAAG--    44
Kikker          ----------------------MMTMTTMADGLEA----QDSSKSAFMEFGQQQSHS--    31
Zebravis        ----------------------MTMSTIPESLNS----PVSGKSVFMEFGPPSQQ---    29
```

Results for job clustalo-I20190109-142418-0795-79569343-p1m

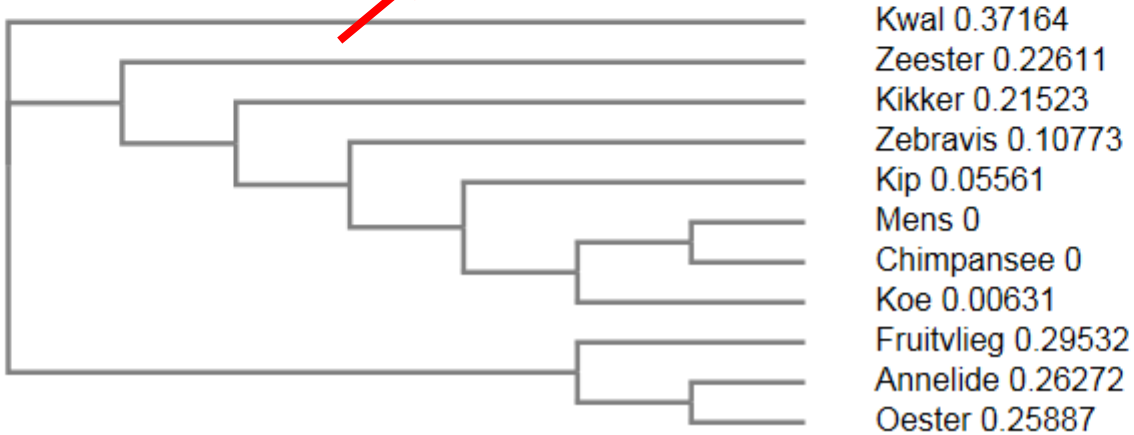
Alignments | Result Summary | Phylogenetic Tree | Submission Details

Phylogenetic Tree

This is a Neighbour-joining tree without distance corrections.

Download Phylogenetic Tree Data

Branch length: ◉ Cladogram ○ Real



Results for job clustalo-I20190109-142418-0795-79569343-p1m

Alignments | Result Summary | Phylogenetic Tree | Submission Details

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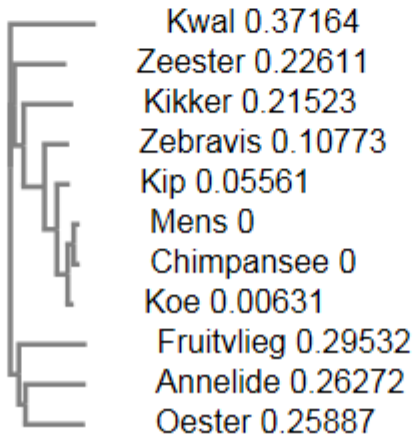
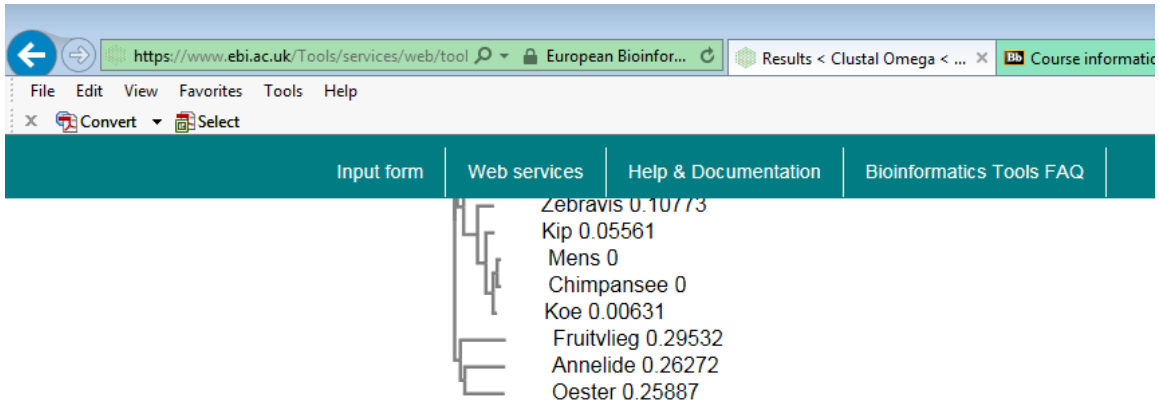
This is a Neighbour-joining tree without distance corrections.

Download Phylogenetic Tree Data

Branch length: ○ Cladogram ◉ Real





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Mens:0.00000,
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Koe:0.00631)
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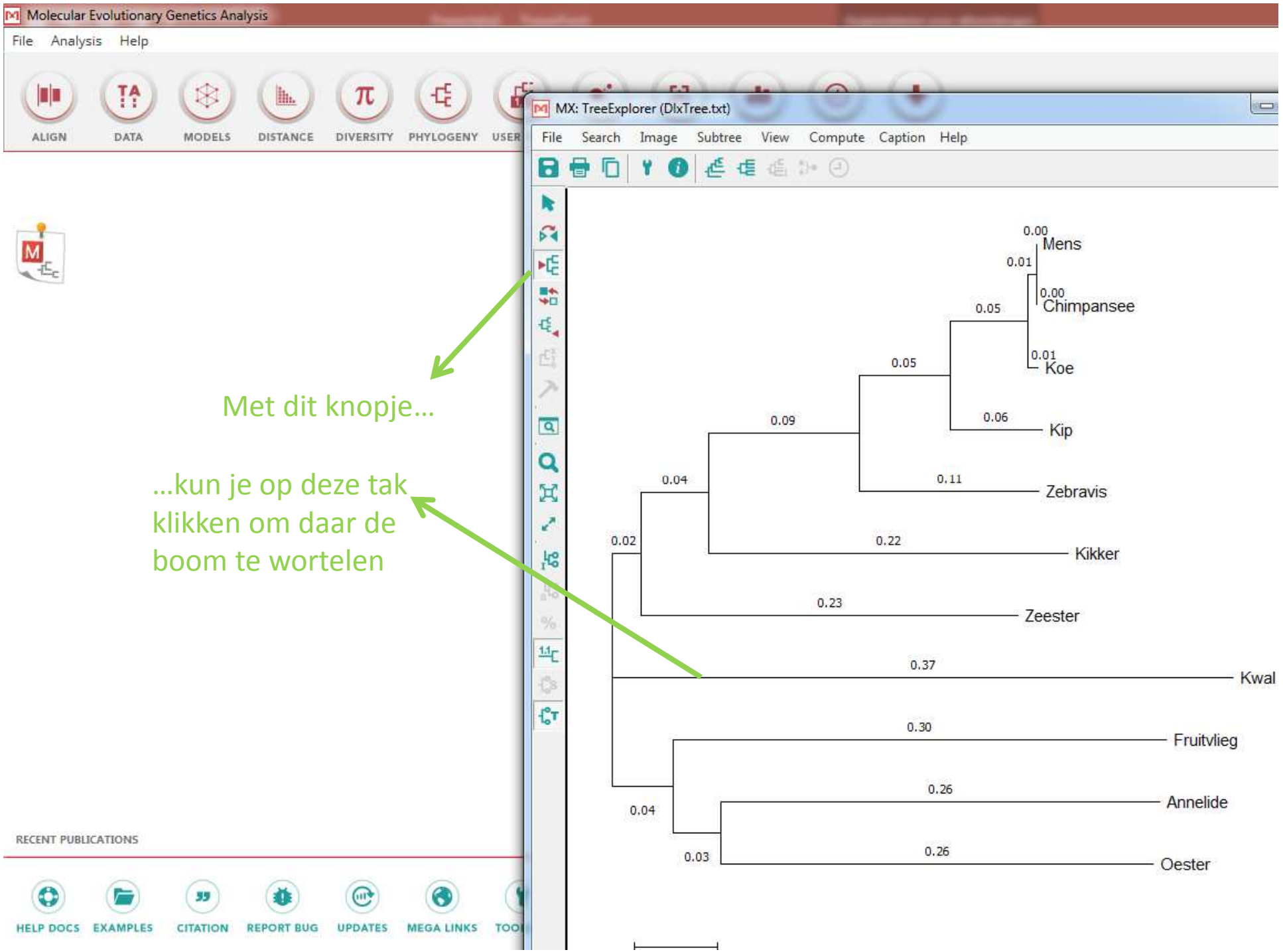
Molecular Evolutionary Genetics Analysis
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Met dit knopje…
…kun je op deze tak klikken om daar de boom te wortelen
0.00 Mens
0.01
0.00 Chimpansee
0.05
0.01 Koe
0.05
0.06 Kip
0.09
0.11 Zebravis
0.04
0.22 Kikker
0.02
0.23 Zeester
0.37 Kwal
0.30 Fruitvlieg
0.26 Annelide
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RECENT PUBLICATIONS
HELP DOCS EXAMPLES CITATION REPORT BUG UPDATES MEGA LINKS

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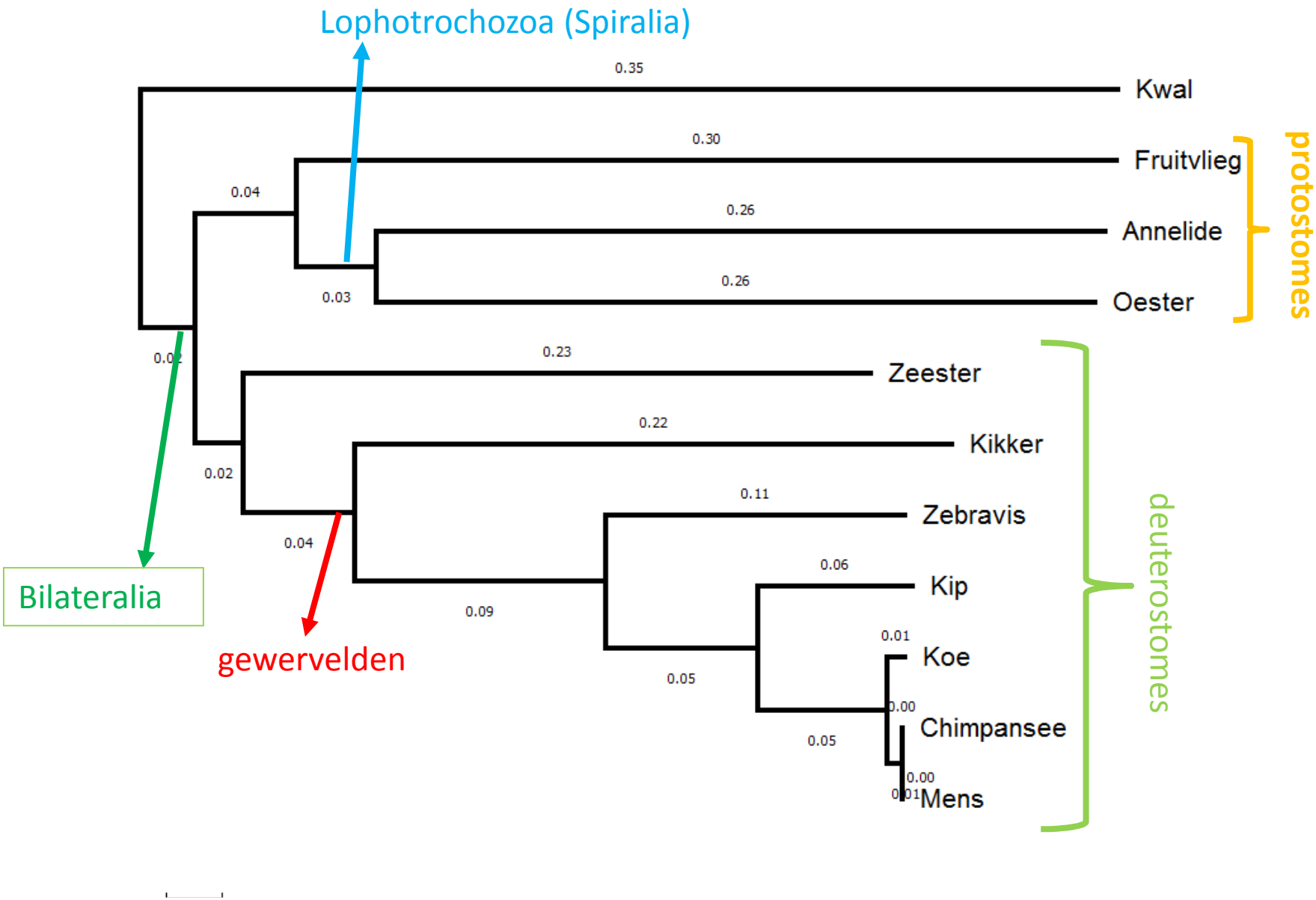

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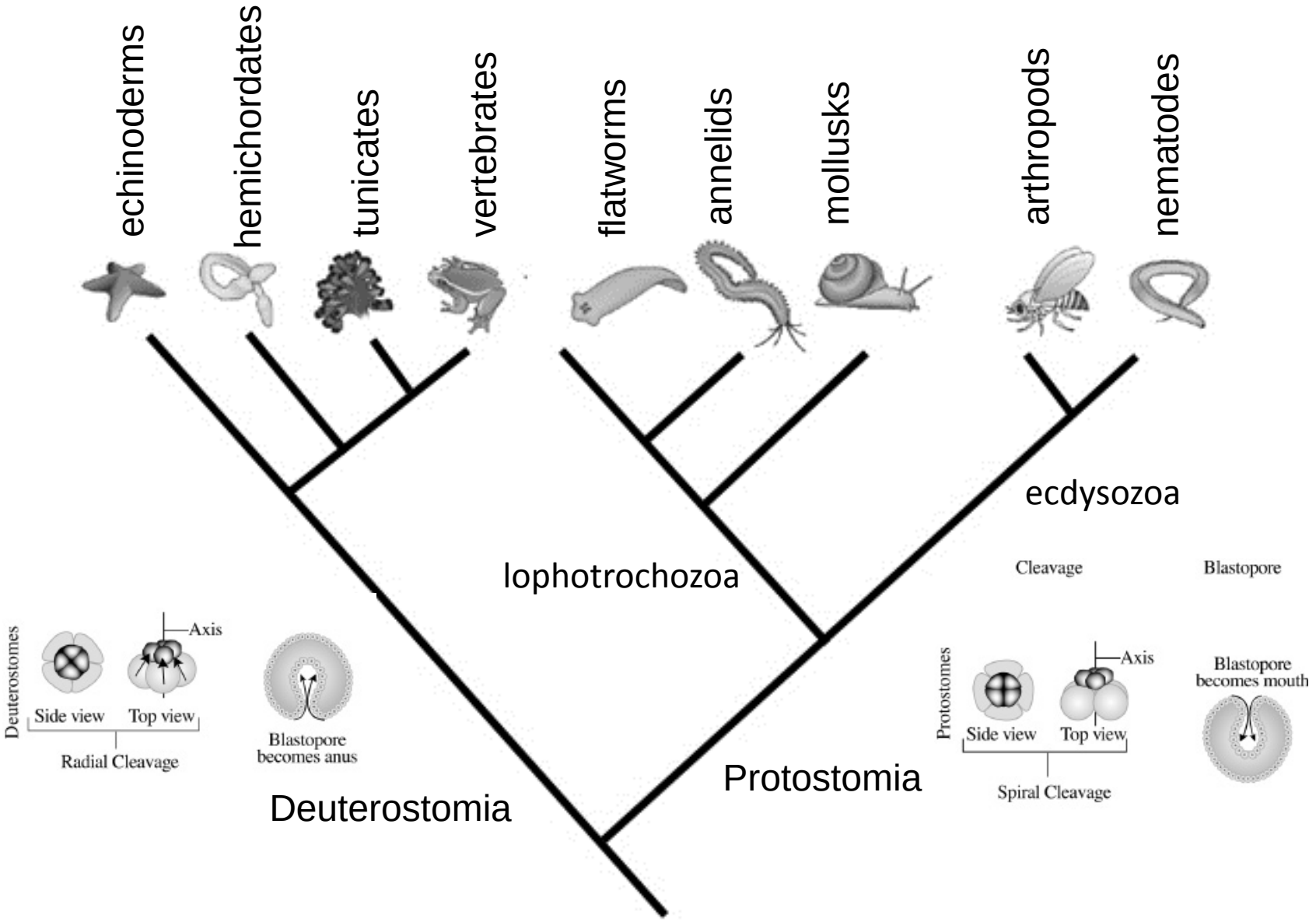

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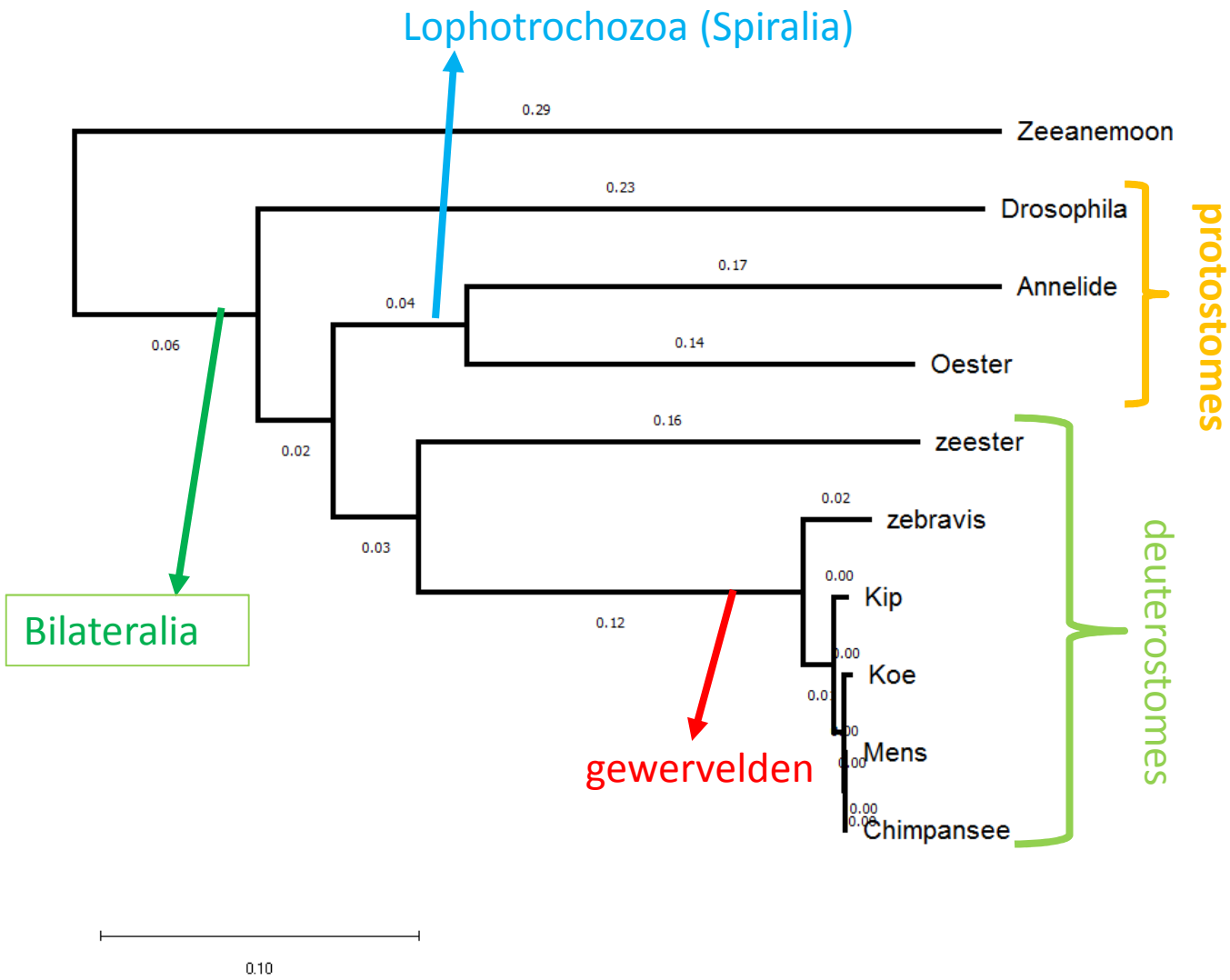

Waarom?

- Brengt leerlingen in contact met bioinformatica (databases, fasta-files, etc.)
- Laat zien hoe eiwitten in elkaar zitten (functionele domeinen)
- Doordringt leerlingen van de diepe verbondenheid van alle levende dieren die alleen maar door evolutie verklaard kan worden
- Laat een belangrijke fylogenetische methode zien (genetische afstand)
- Laat de taxonomische indeling van de dieren zien

Evolution and development

1. Embryo's vertellen je iets over evolutie.
2. Evo-devo onthult diepe homolgieën.
3. Evo-devo zoekt de genetische en ontwikkelingsbiologische basis van evolutionaire veranderingen.
4. Evo-devo bestudeert de oorsprong van *novelties*
5. Embryonale ontwikkeling kan de evolutie in bepaalde richtingen sturen.

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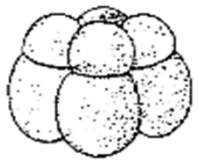
The origin of insect wings



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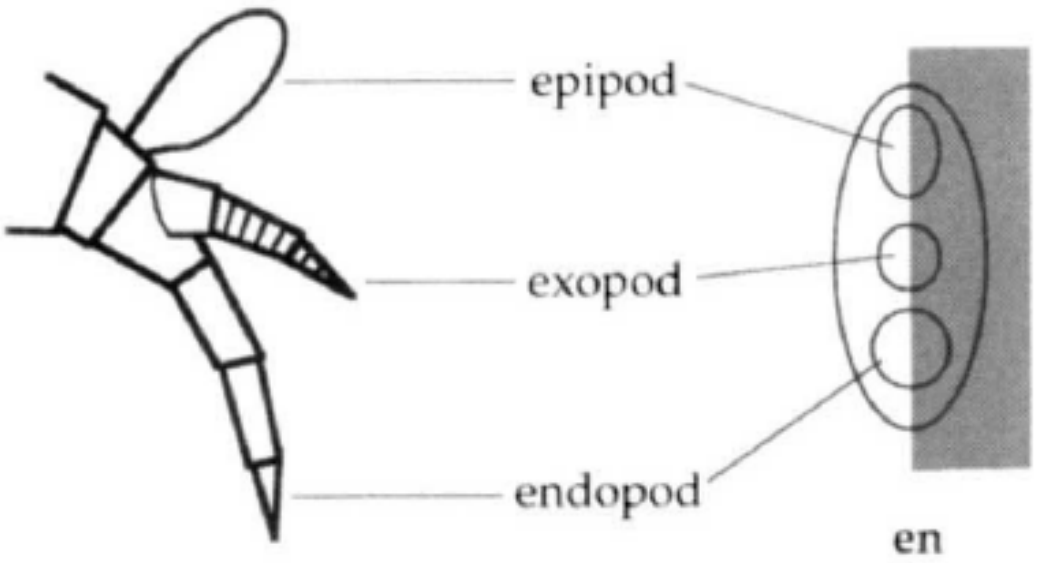


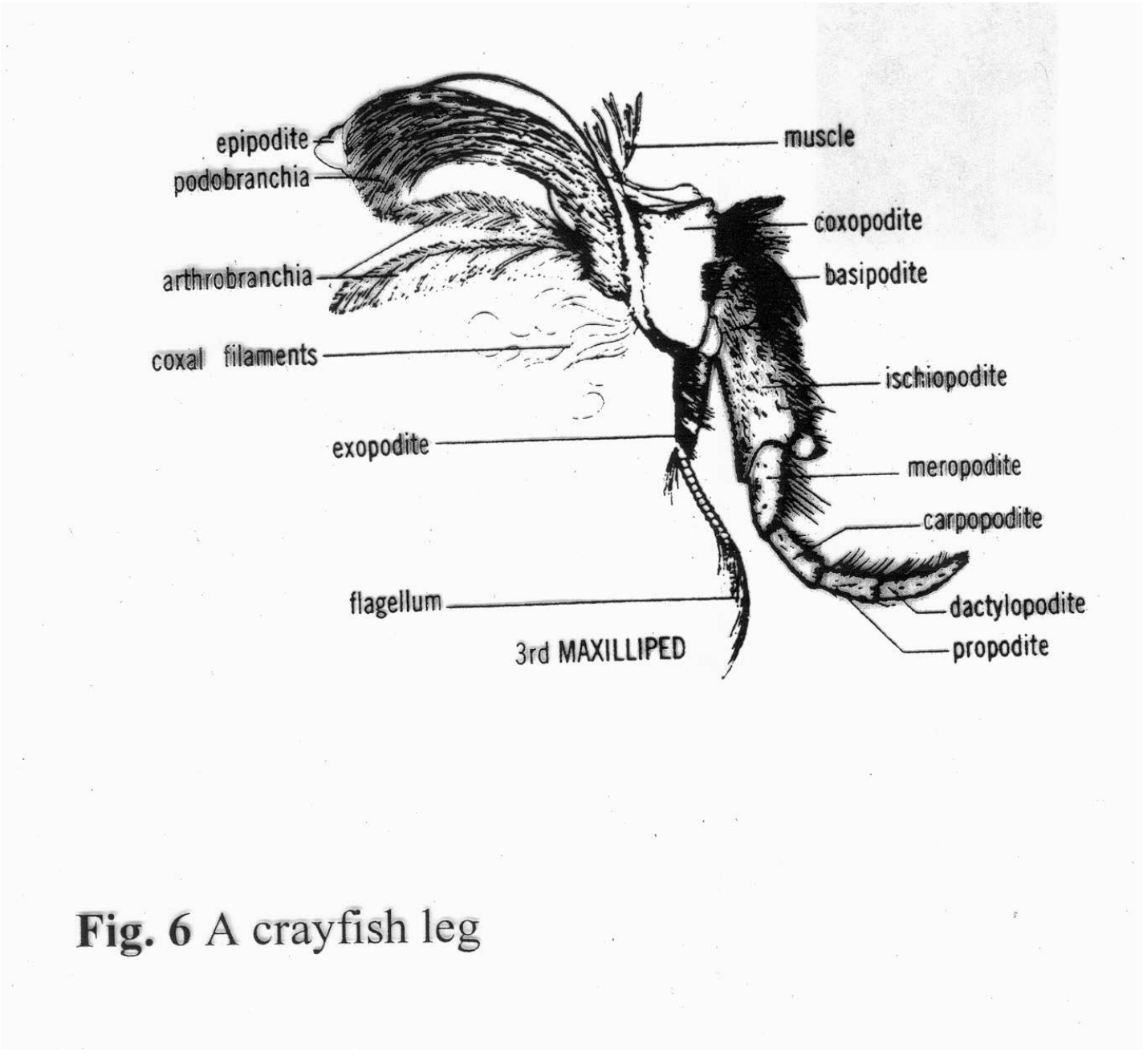


Fig. 6 A crayfish leg

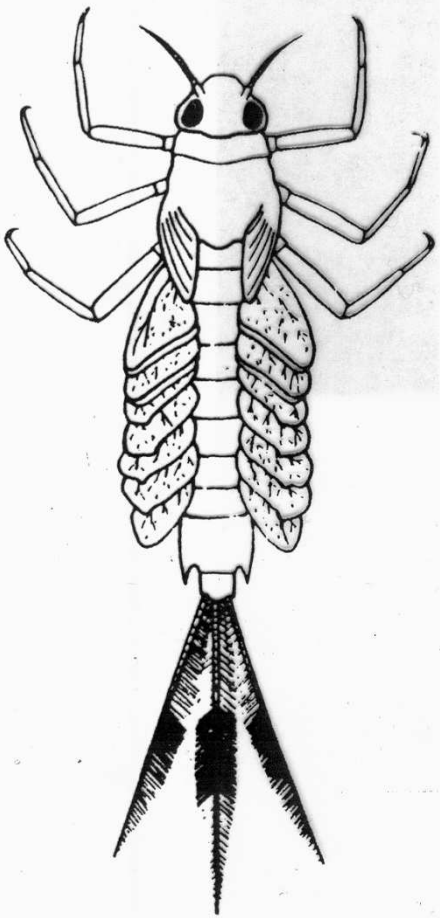
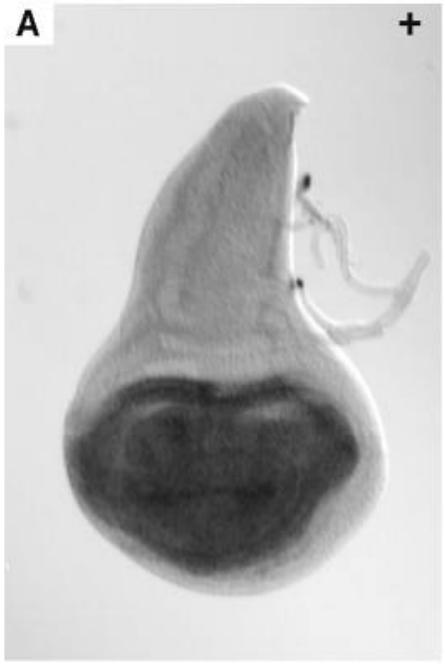
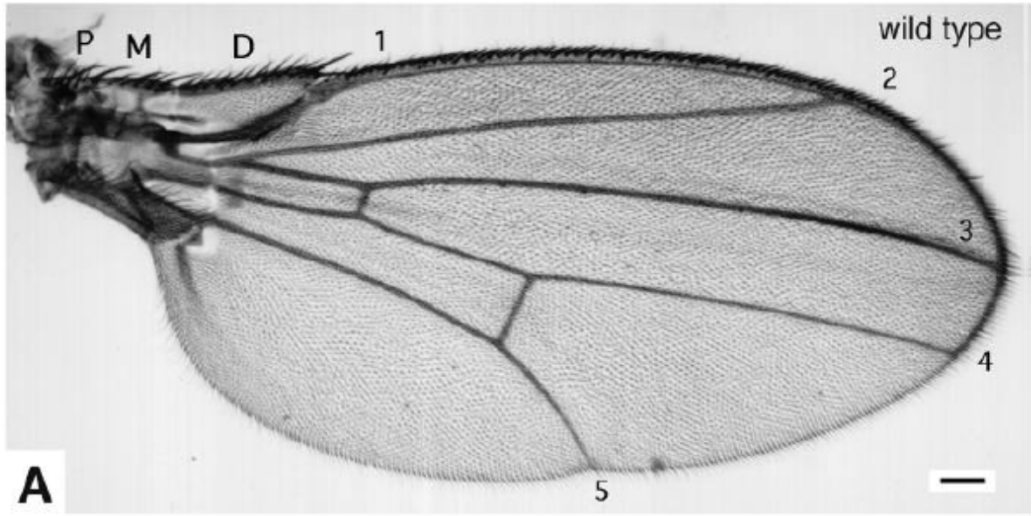
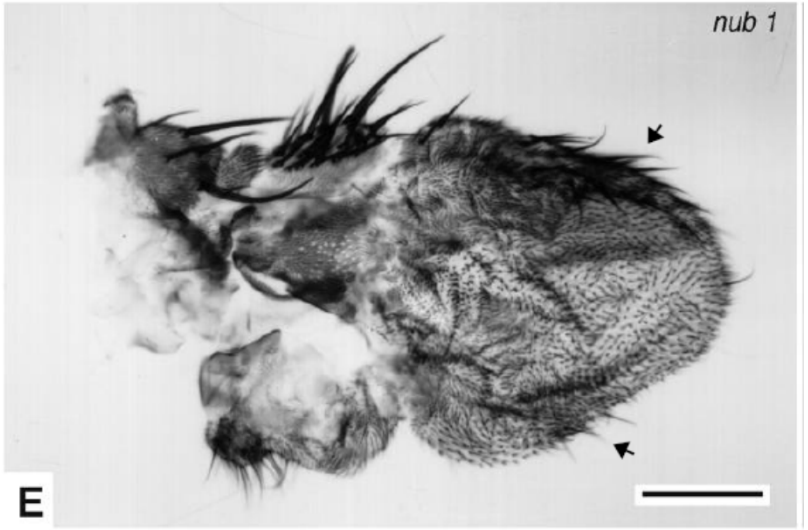


Fig. 1 *Siphlonorus sp.*

Nubbin (pdm) is required for wing development

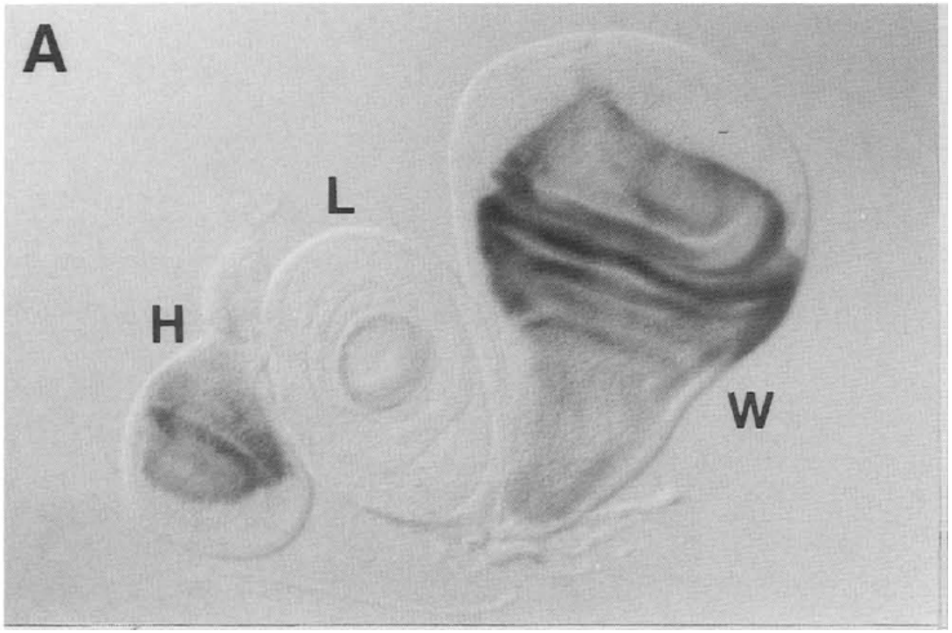






Ng et al., Development 1995

Apterous is required for wing development



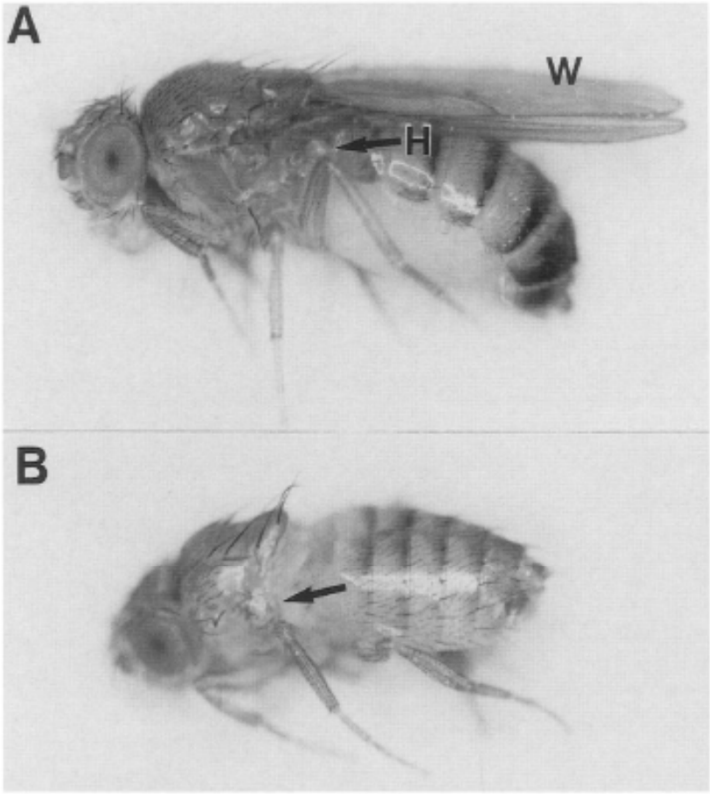
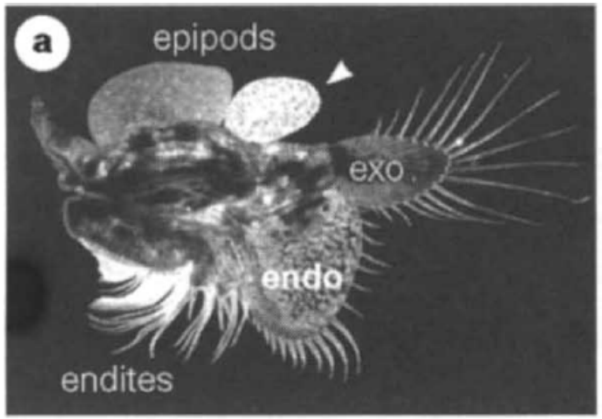
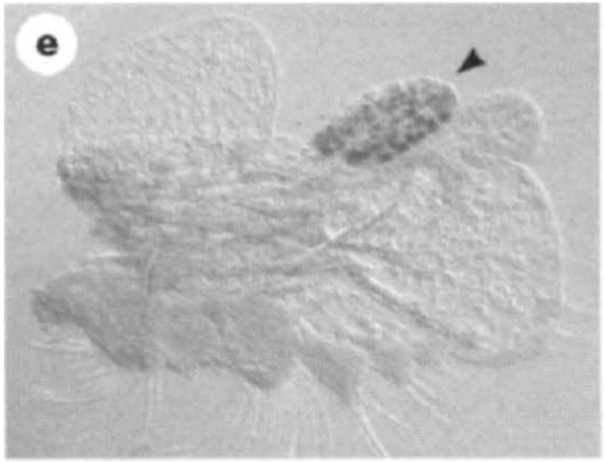


Figure 2. Morphological defects in *ap* mutants. (*A*) Side view of a wild-type fly, showing the normal appearance of the wing (W), haltere (H), and the pattern of bristles on the dorsal thorax. (*B*) Comparable view of an *ap* null mutant fly of genotype ap^{UGO35}/ap^{UGO35}. The wing is reduced to a small stump (arrow). The haltere is similarly reduced (not visible in the picture). A number of large bristles (machrochaetae) are missing from the thorax near the wing, and this region appears reduced in size relative to the rest of the thorax. These flies are short lived and females are nonvitellogenic.

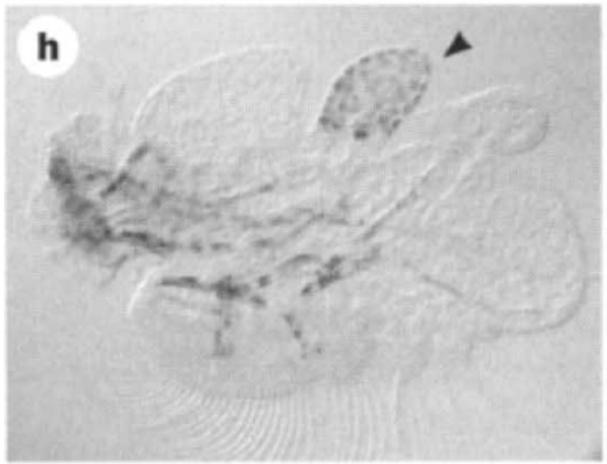
Cohen et al., Genes & Development, 1992



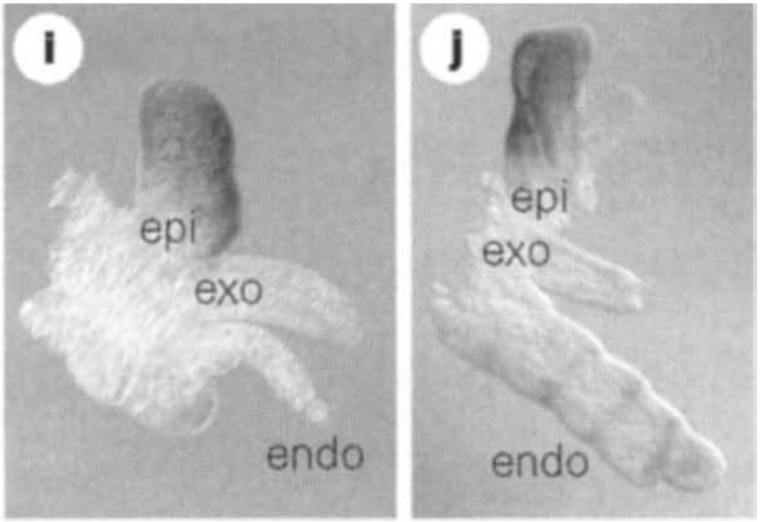
Nubbin and Apterous is expressed in the epipods in the shrimp *Artemia fransiscana*



Artemia pdm



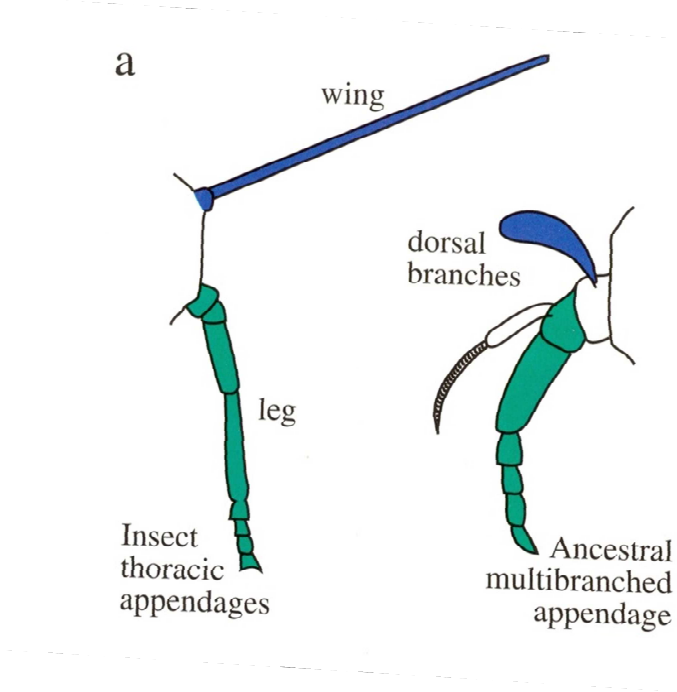
Artemia ap



As well as in the crayfish *Pacifastacus leniusculus*

Averof & Cohen, Nature 1997

Wings evolved from epipodites…



..that might have had a gill function

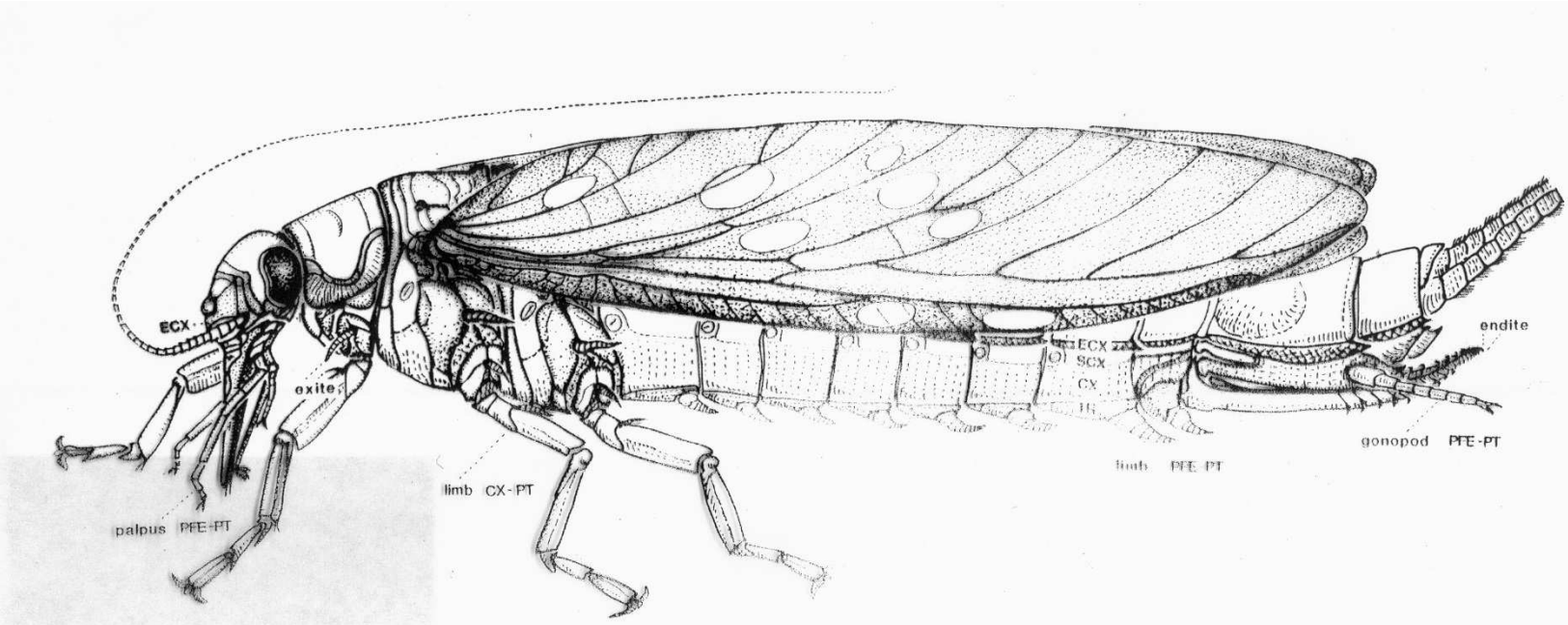


Fig.4 Reconstruction of a Pterygote insect from fossils (Kuckalova-Peck, 1982)

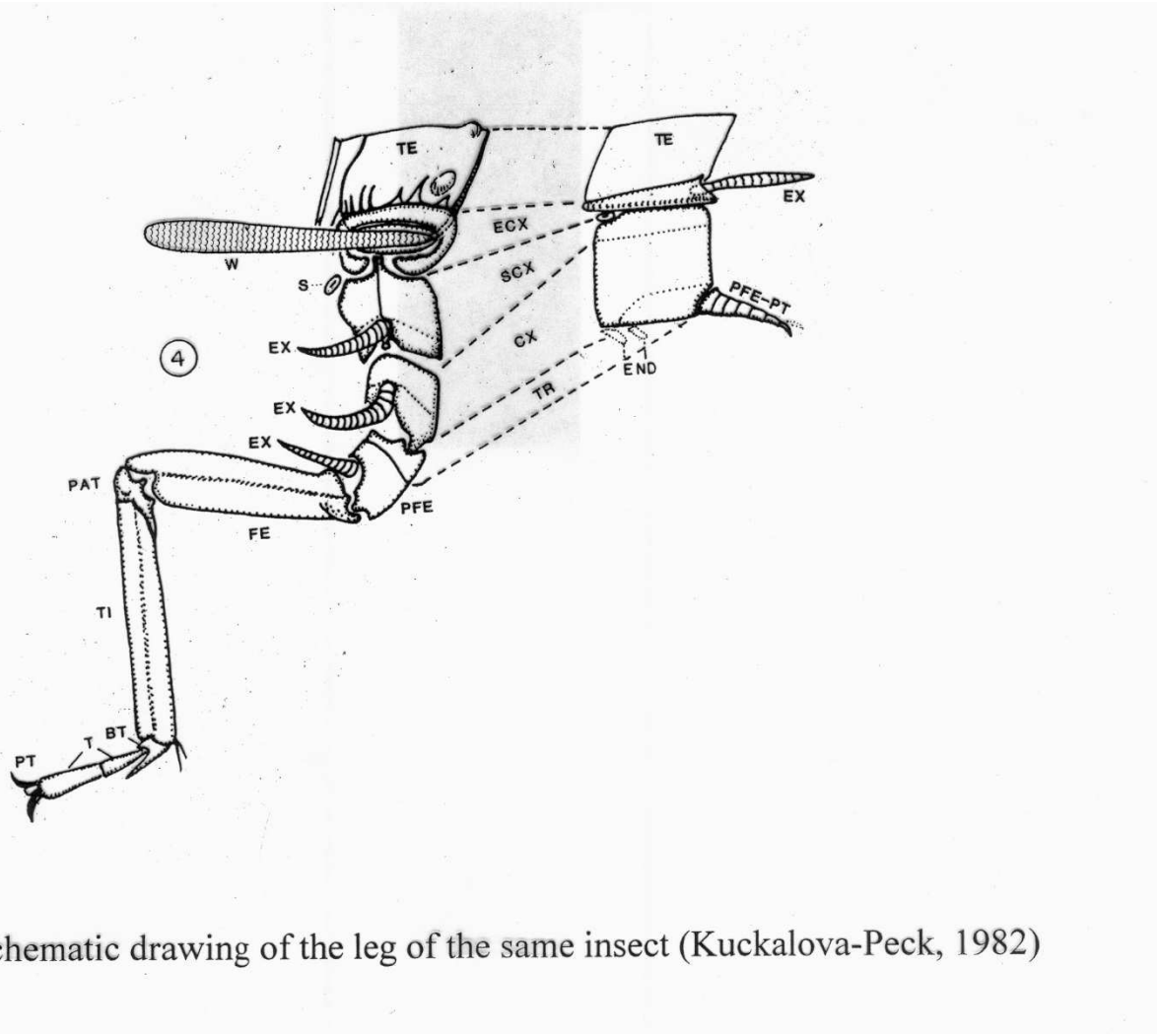
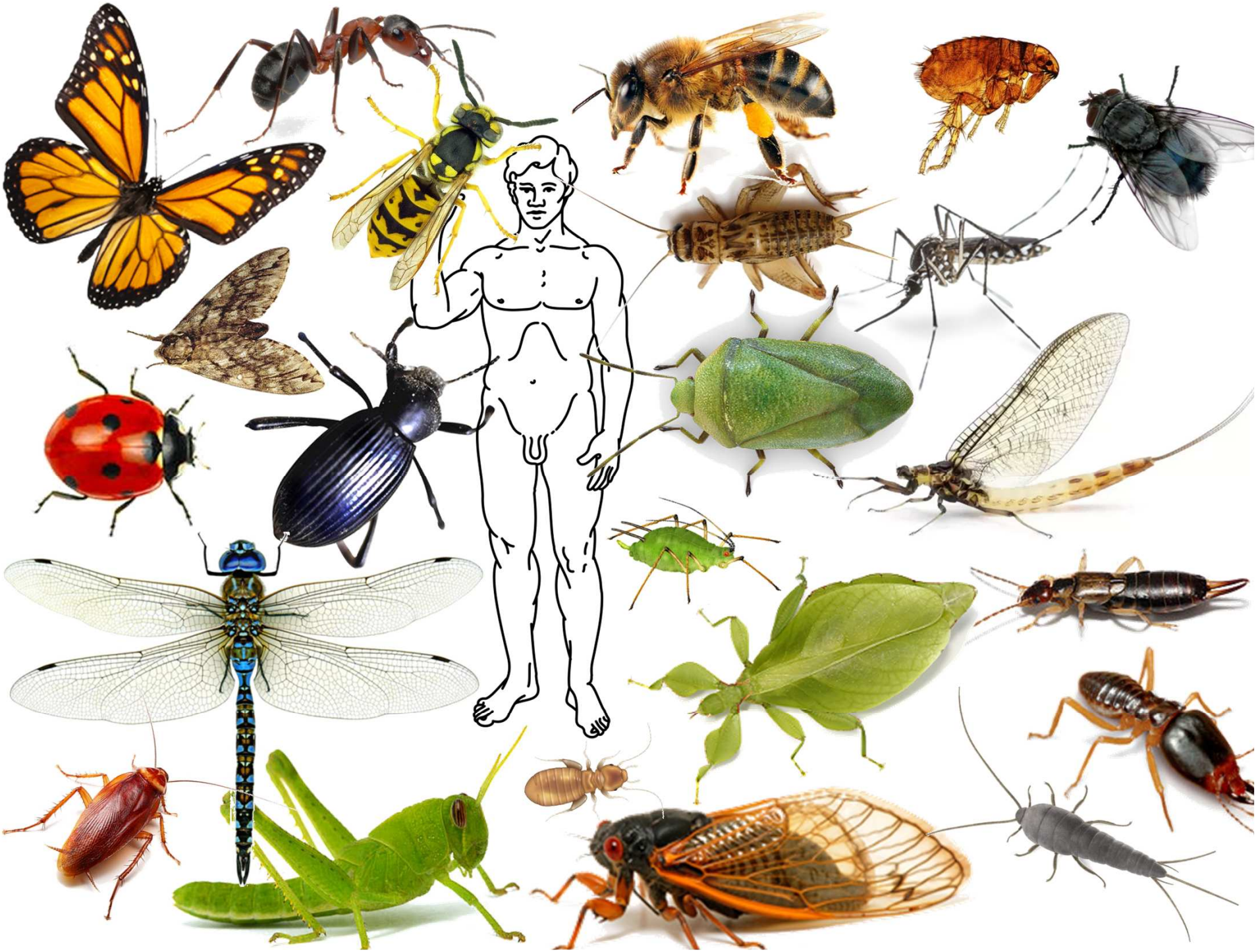
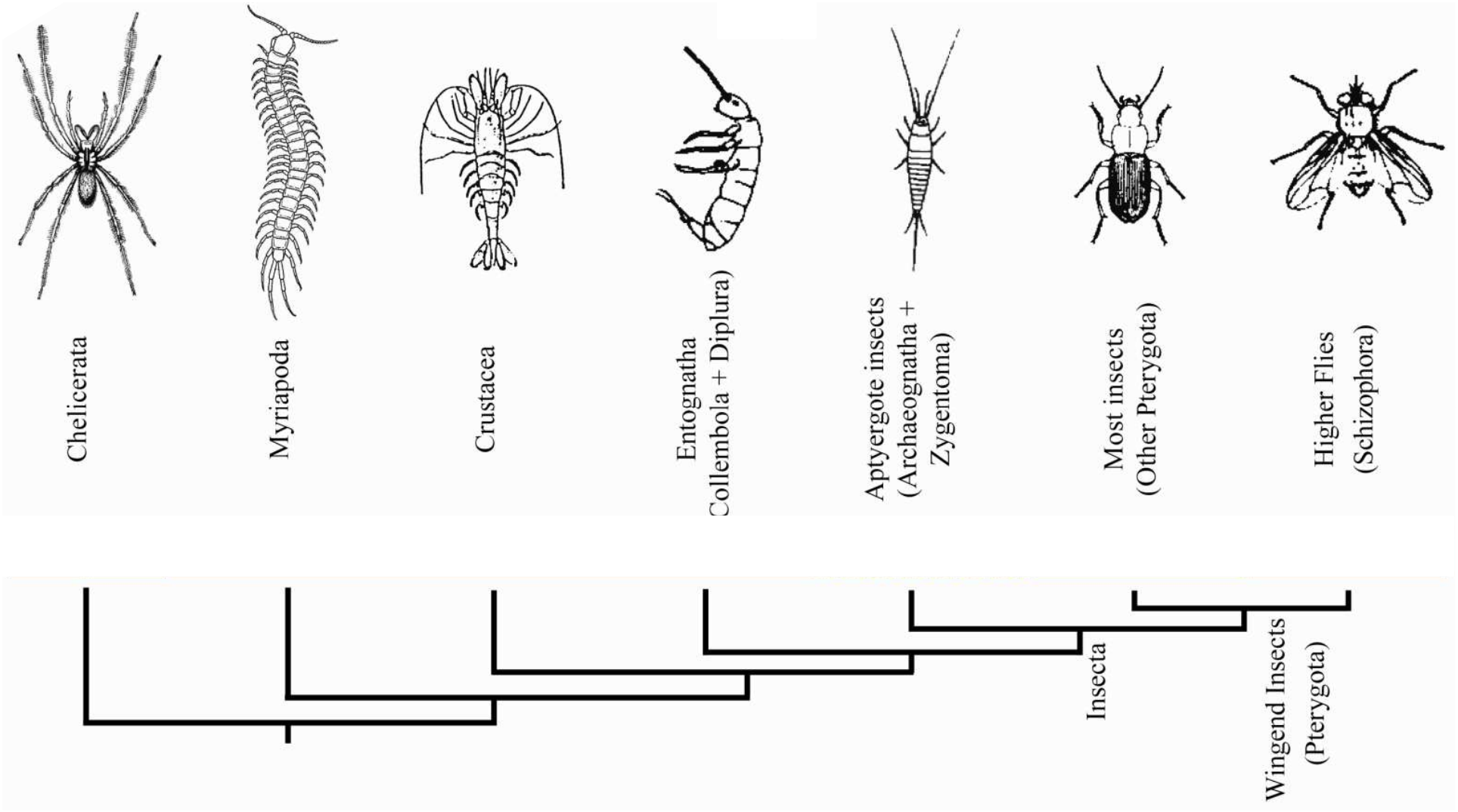
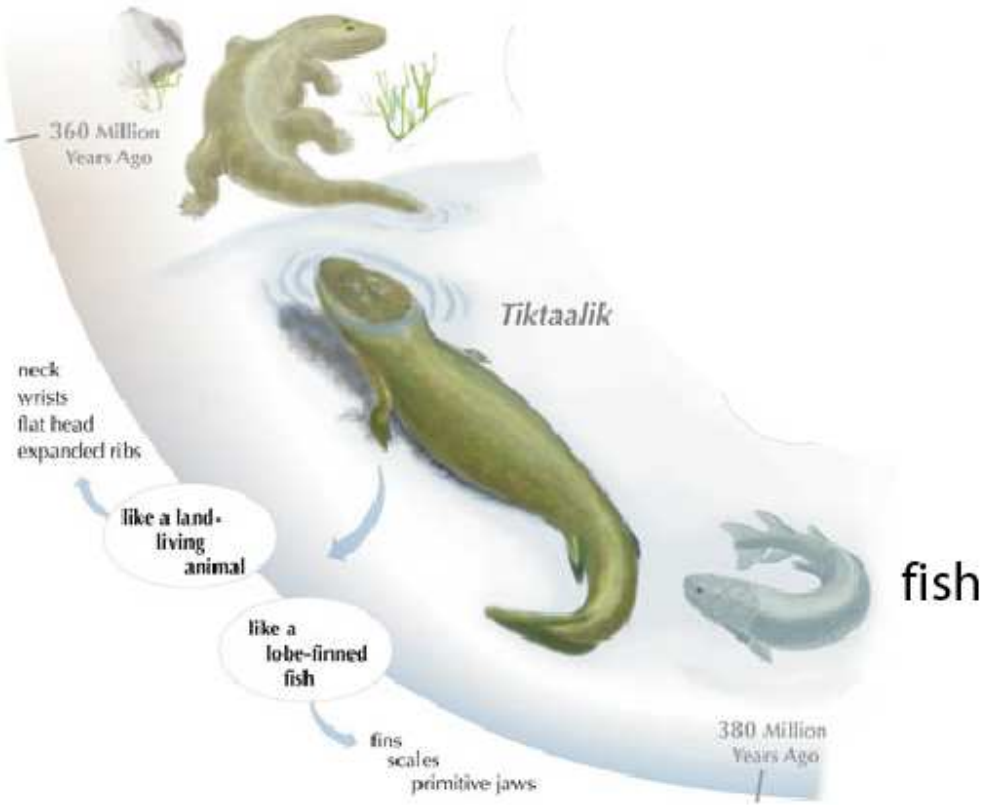


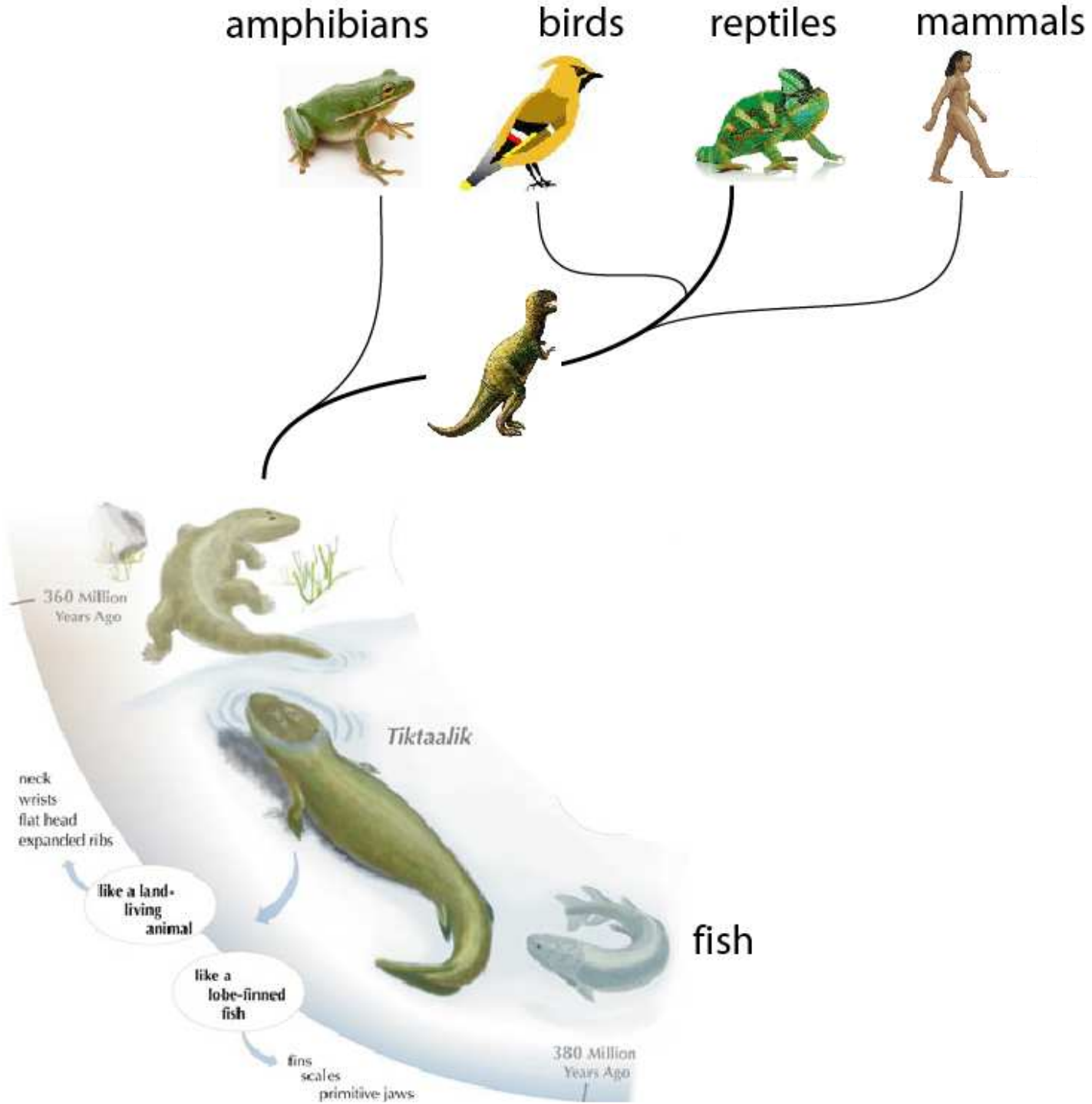
Fig. 5 Schematic drawing of the leg of the same insect (Kuckalova-Peck, 1982)

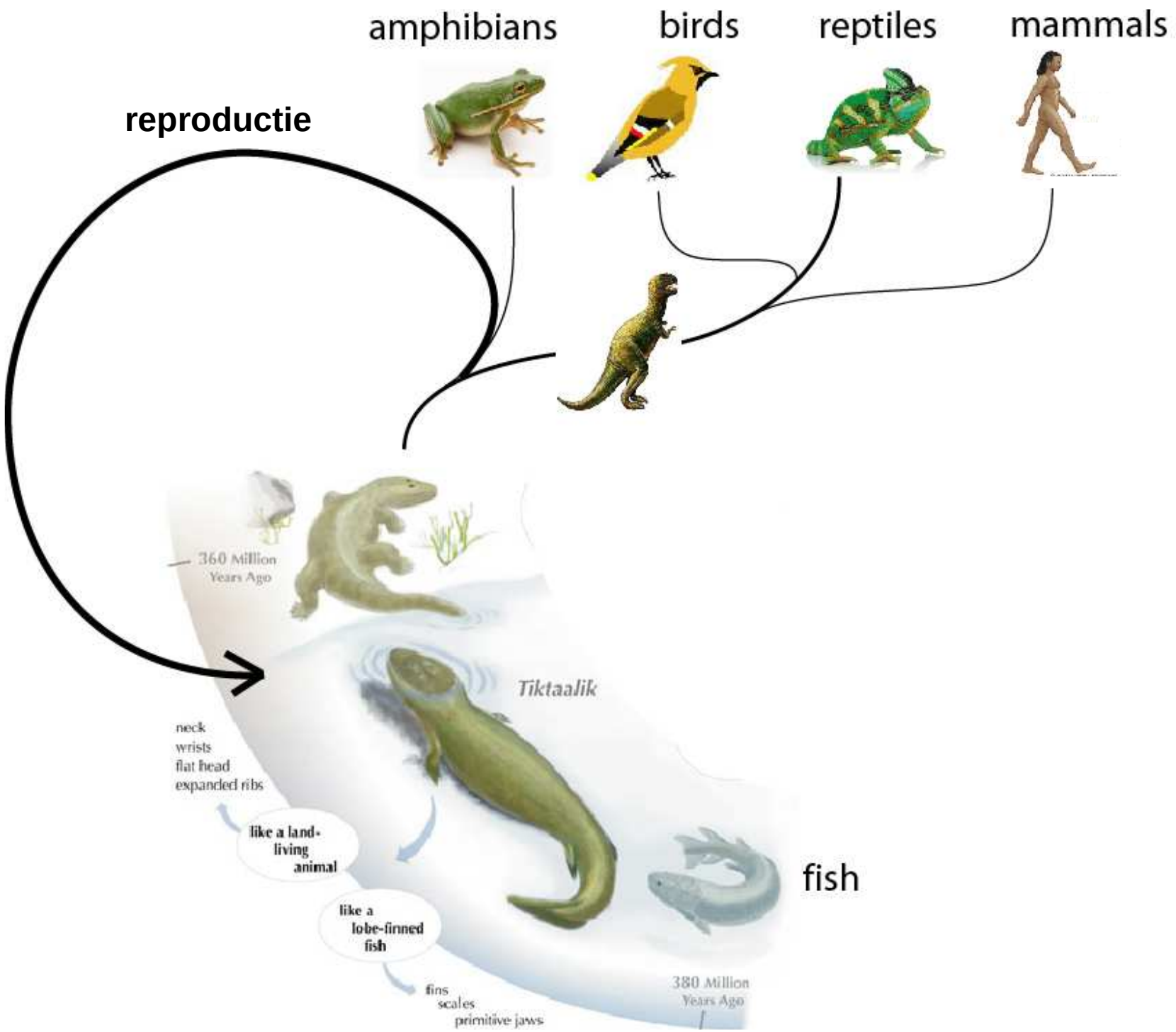


Insecten hebben massaal de stap naar het land gemaakt



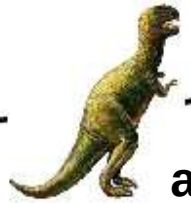

360 Million
Years Ago
Tiktaalik
neck
wrists
flat head
expanded ribs
like a land-
living
animal
like a
lobe-finned
fish
fins
scales
primitive jaws
380 Million
Years Ago
fish


amphibians
birds
reptiles
mammals
360 Million Years Ago
Tiktaalik
neck
wrists
flat head
expanded ribs
like a land-living animal
like a lobe-finned fish
fins
scales
primitive jaws
380 Million Years Ago
fish

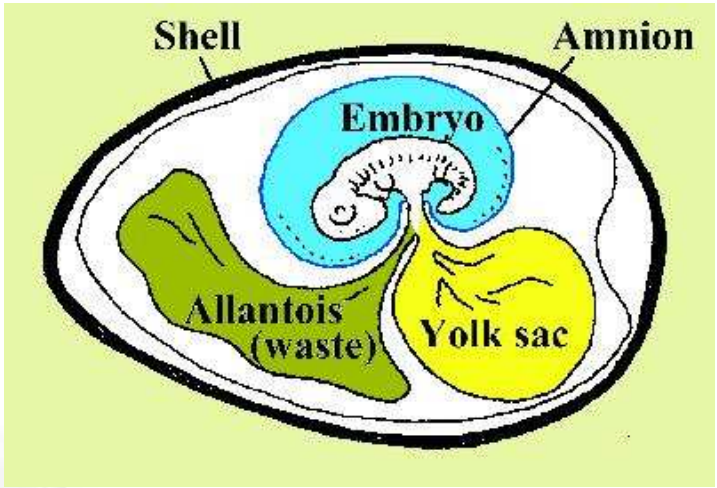

amphibians
birds
reptiles
mammals
reproductie
360 Million Years Ago
Tiktaalik
neck
wrists
flat head
expanded ribs
like a land-living animal
like a lobe-finned fish
fins
scales
primitive jaws
380 Million Years Ago
fish

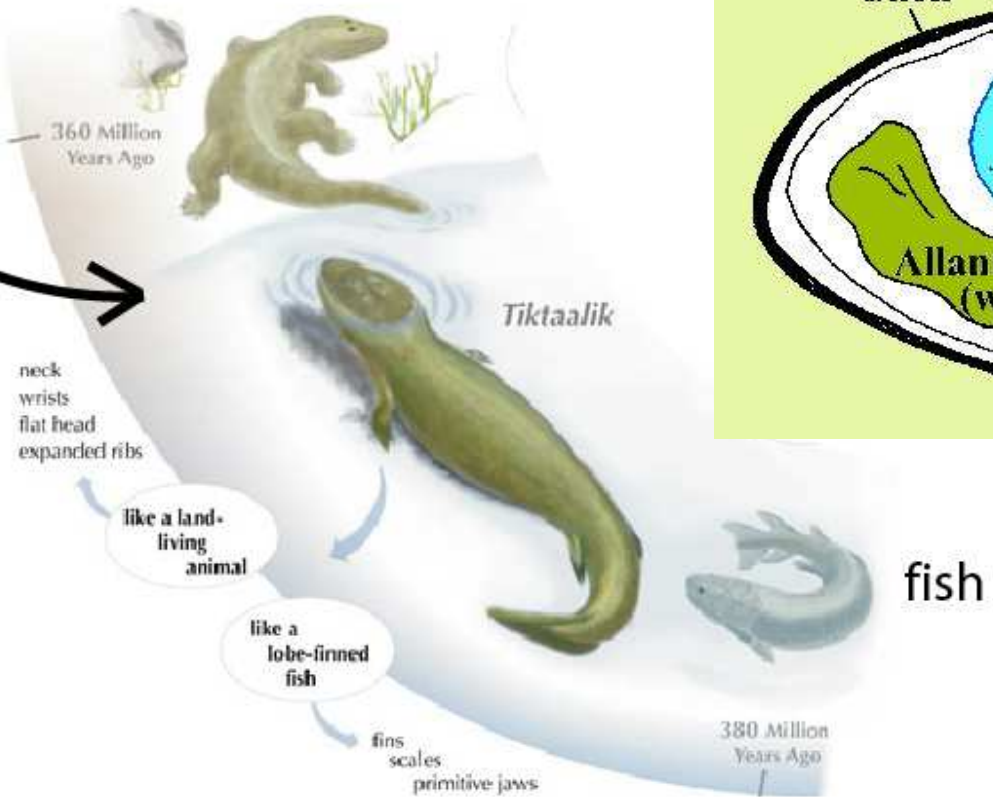
amphibians birds reptiles mammals

reproduction



amniote ei

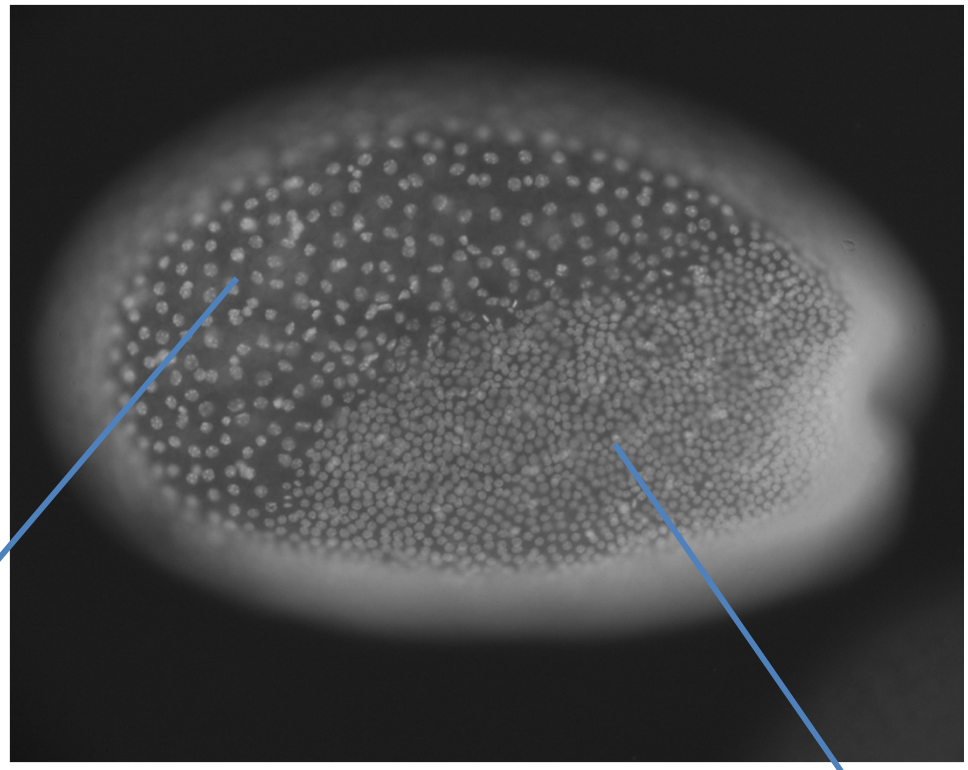




fish


Tribolium castaneum

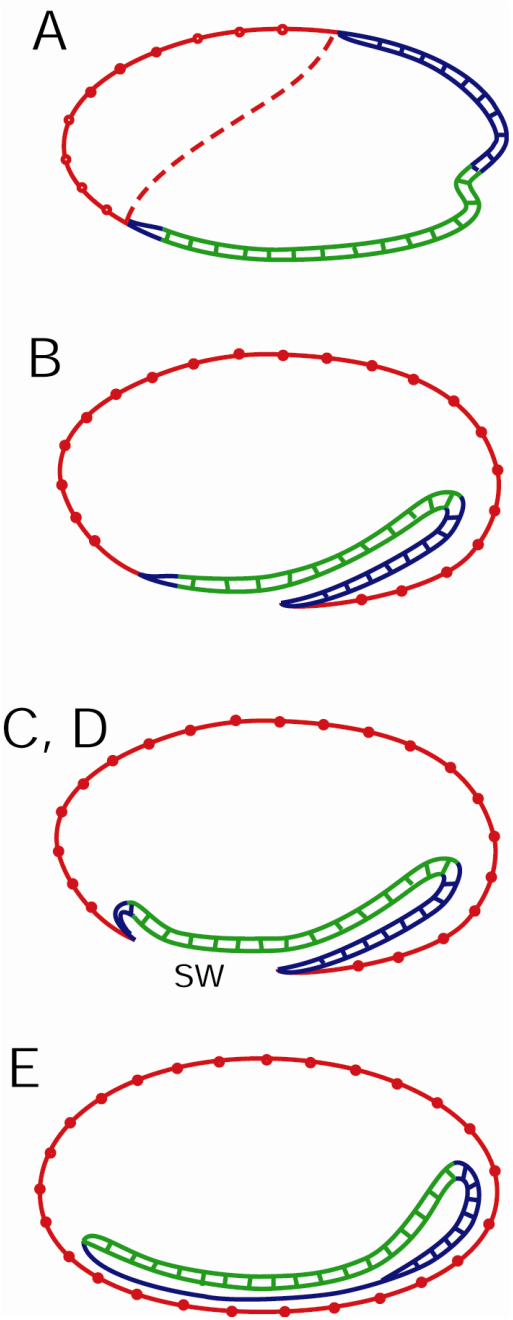
The serosa

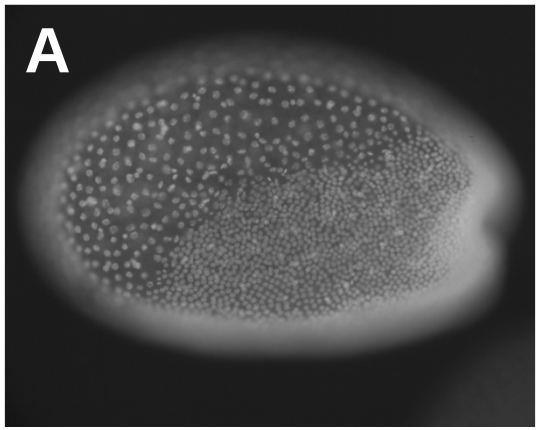


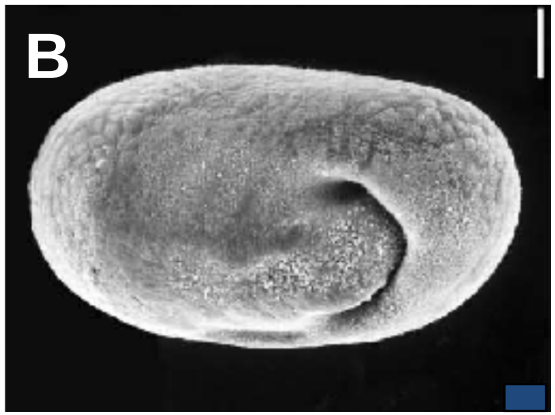
serosa

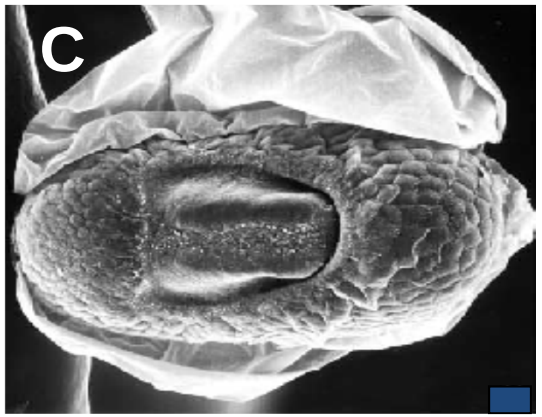
embryo

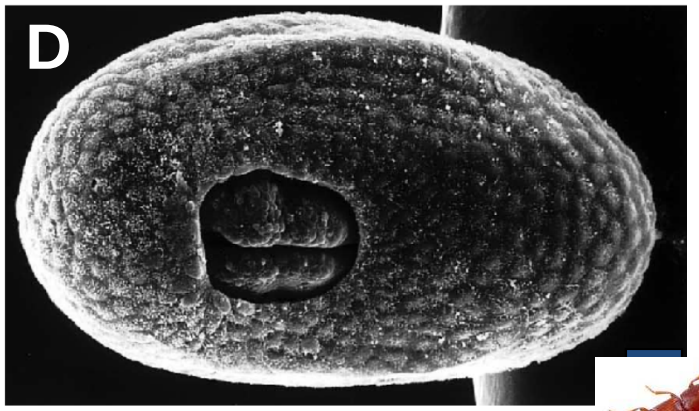
Development of the serosa









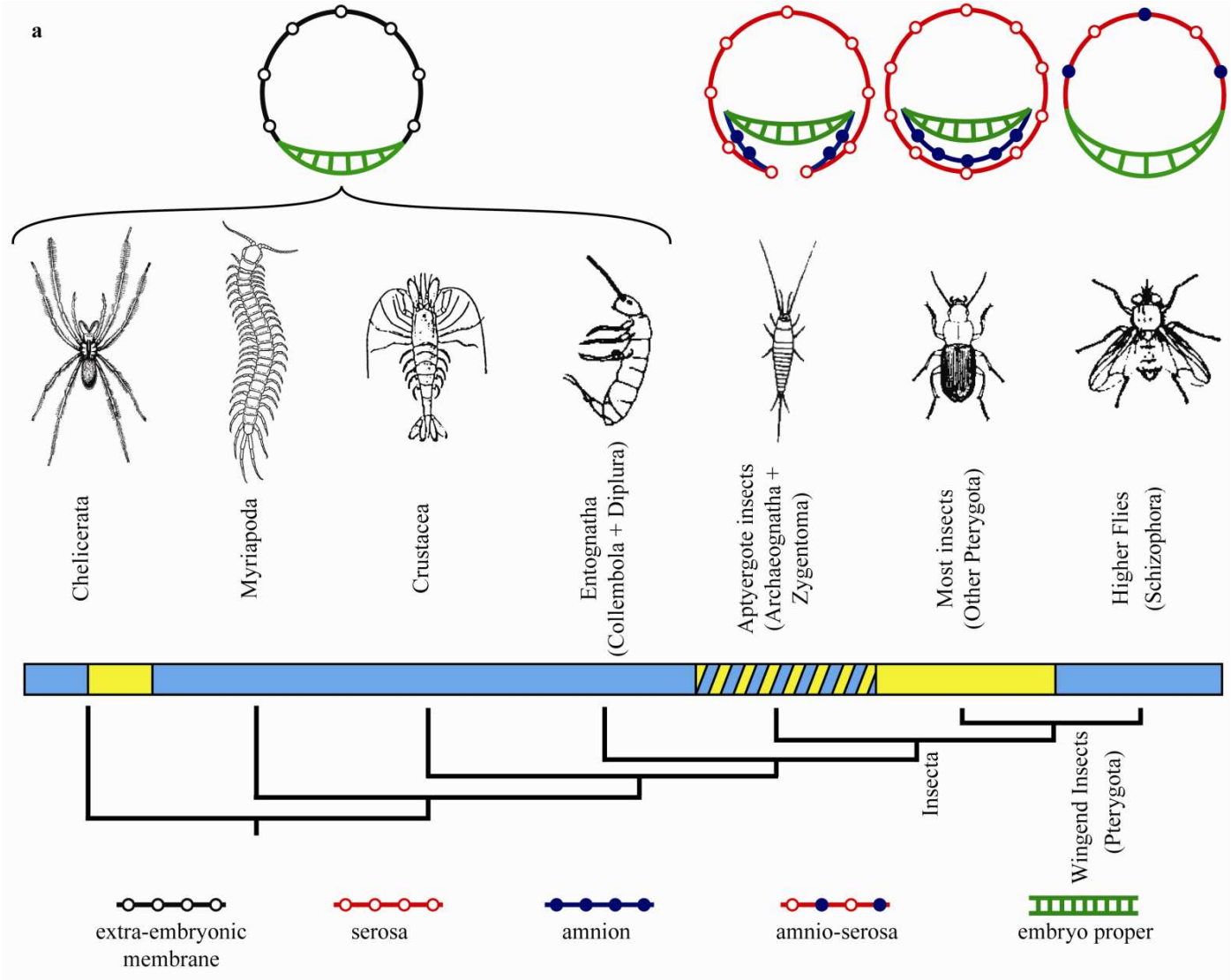


SEM: Handel et al., 2000

Development of the serosa

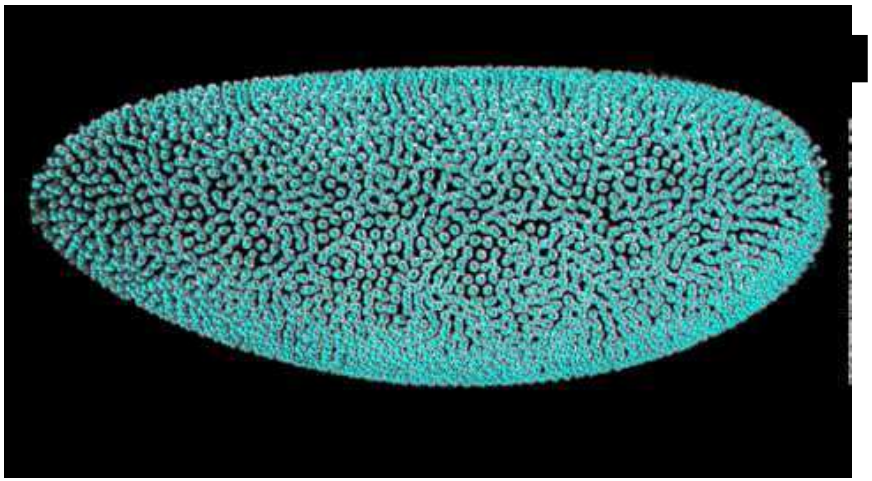
Tania Vazquez Faci

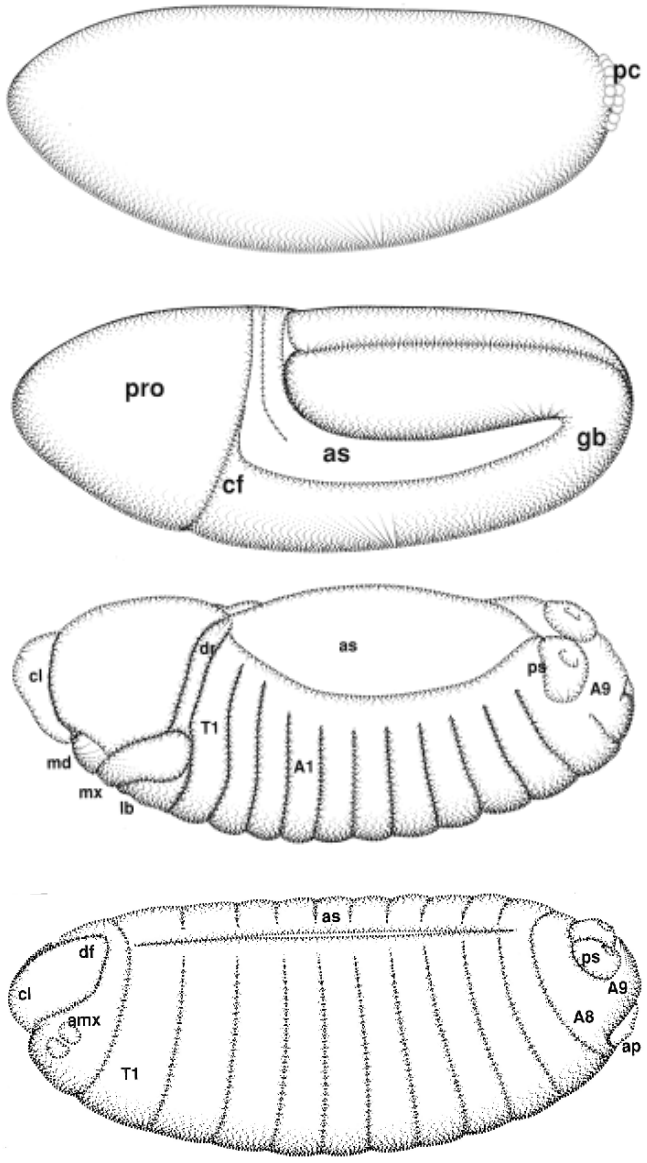
The serosa is an evolutionary innovation of the insects



Drosophila does not have a serosa

Drosophila melanogaster





Hartenstein, 1993

Drosophila eggs are very sensitive to desiccation

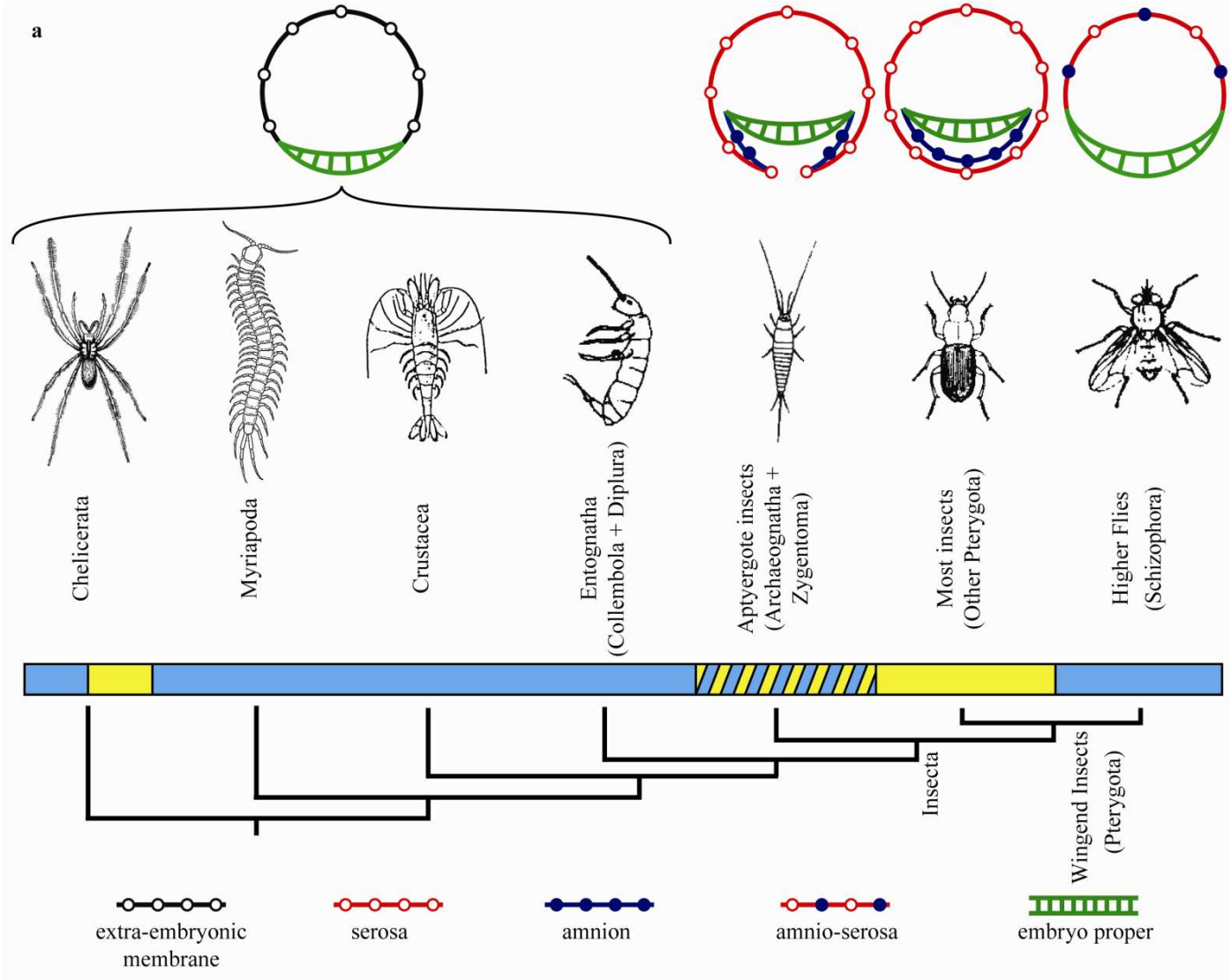
Table 1. The incubation periods of eggs of *D. melanogaster* (MDE) at different temperatures and humidities

Temperature (°C)	Relative humidity (%)	Vapour pressure deficit (hP)	Mean duration (h)	SE	Mortality (%)	N
25	100	0.0	24.59	0.29	15.8	189
	95	1.6	26.30	0.22	14.0	200
	90	3.2	27.88	0.25	15.7	140
	85	4.8	31.58	0.20	23.2	168
	80	6.4	31.65	0.20	41.6	233
	75	8.0	—	—	100	150

N = Number of eggs hatching. SE = Standard Error. hP = Hecto Pascal.

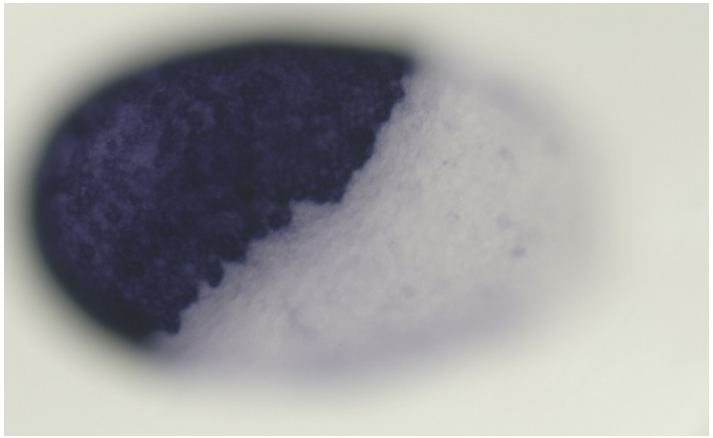
Al-Saffar et al., 1995

The serosa is an evolutionary innovation of the insects



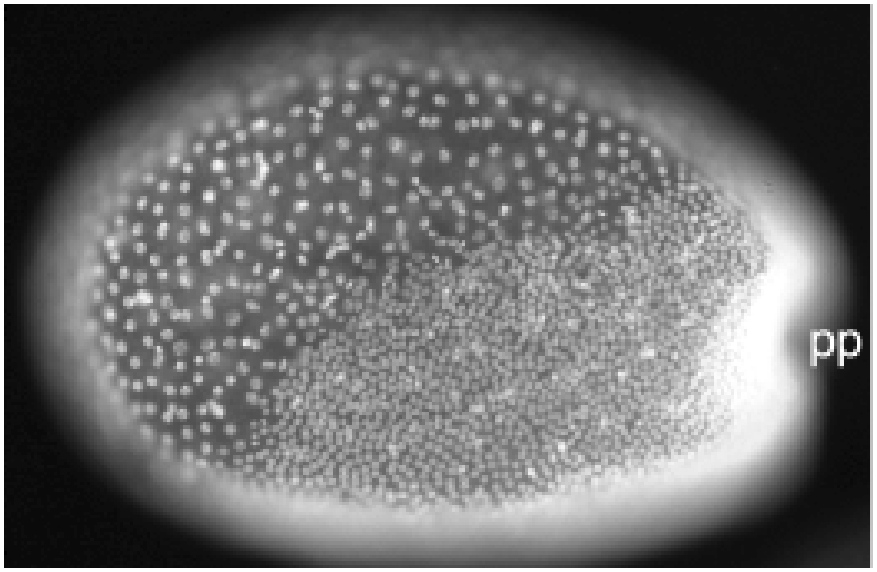
zerknüllt (*zen*) specificeert de serosa

Tribolium

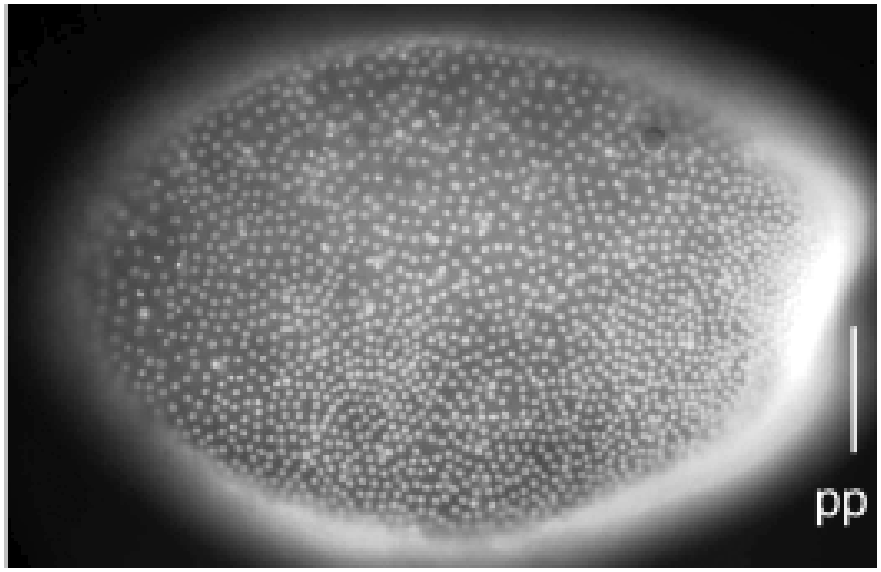


Tc-zen RNAi schakelt de serosa uit

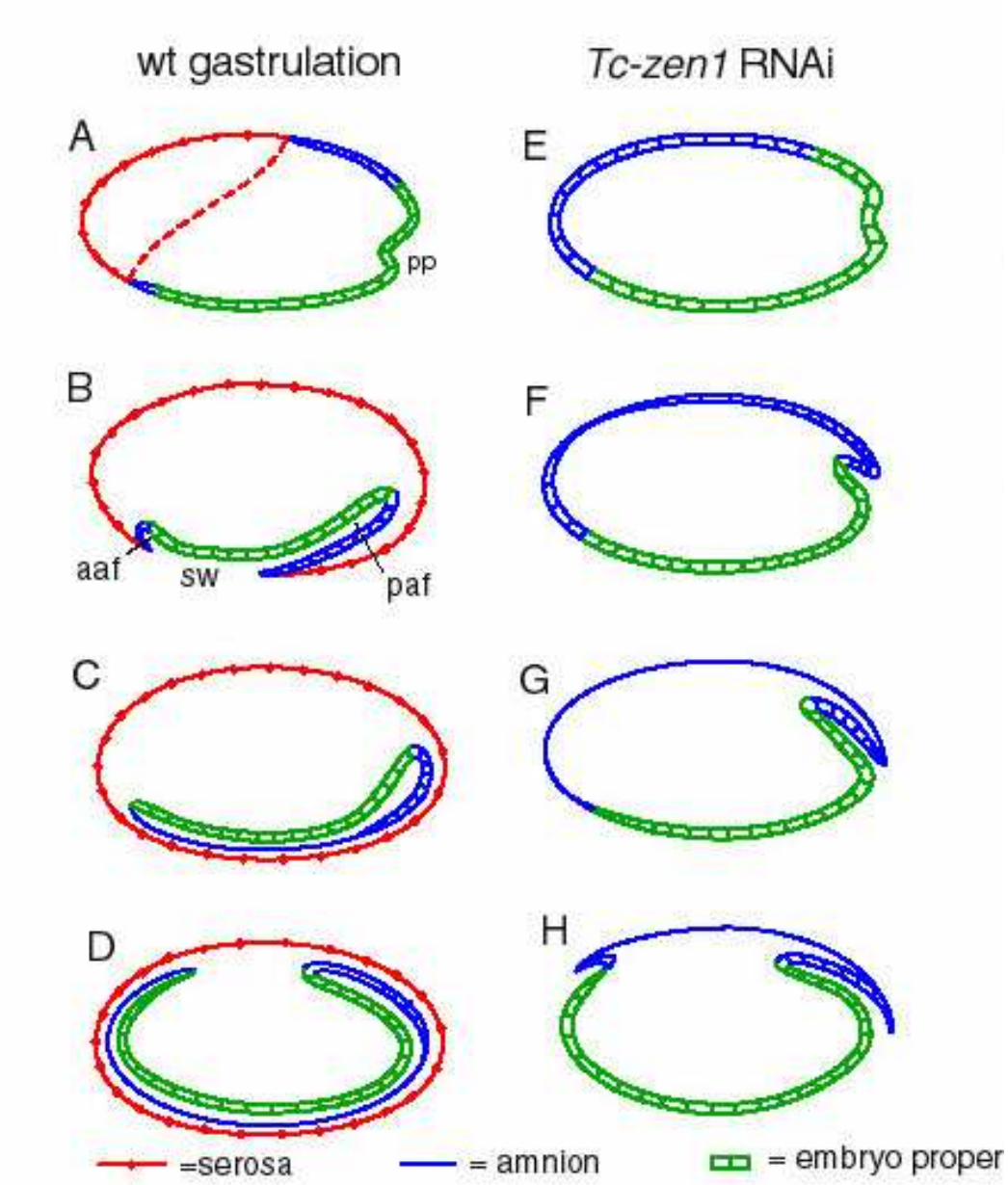
wild-type



Tc-zen RNAi



Ontwikkeling na *Tc-zen* RNAi



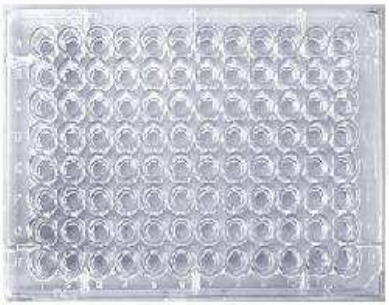
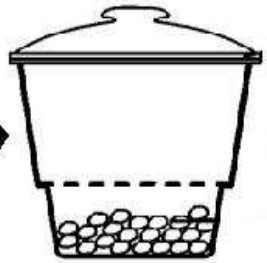
Setup

Treatments

-Wild type

-Control (non-targeting ds RNA)

-*Tc-zen1* RNAi

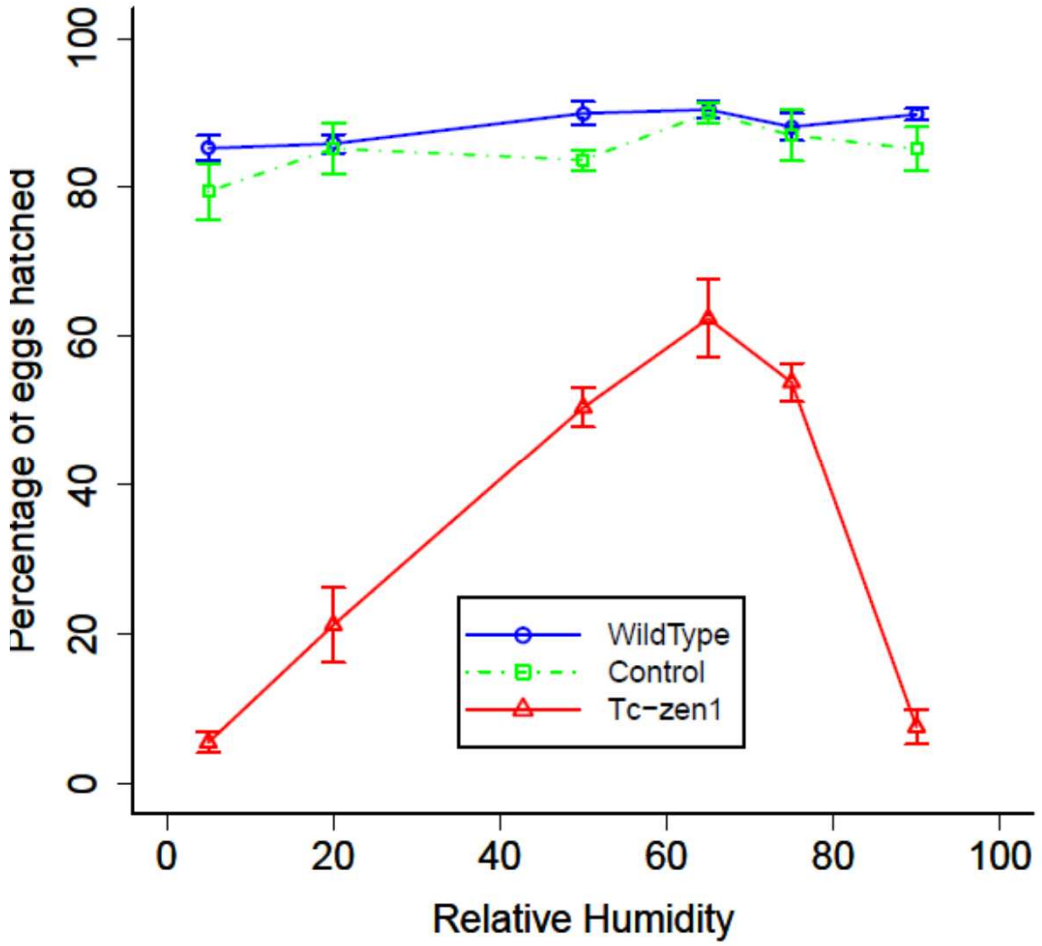
⇒ **Collect eggs** ⇒  ⇒  ⇒ **Count**

5%, 20%, 50%, 65%, 75% and 90% Relative Humidity

All experiments were repeated 2 to 9 times.

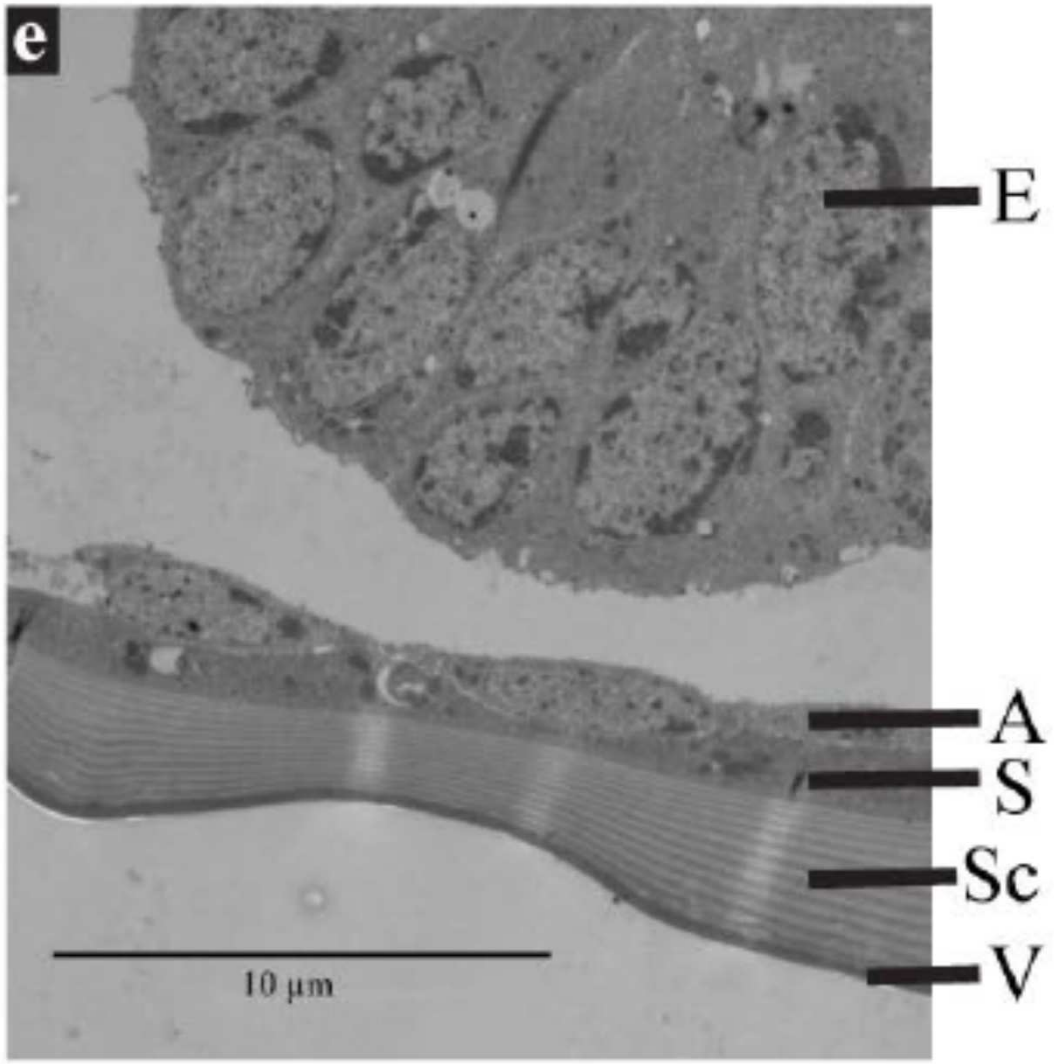
Chris Jacobs

Serosa-loze kevereieren drogen snel uit



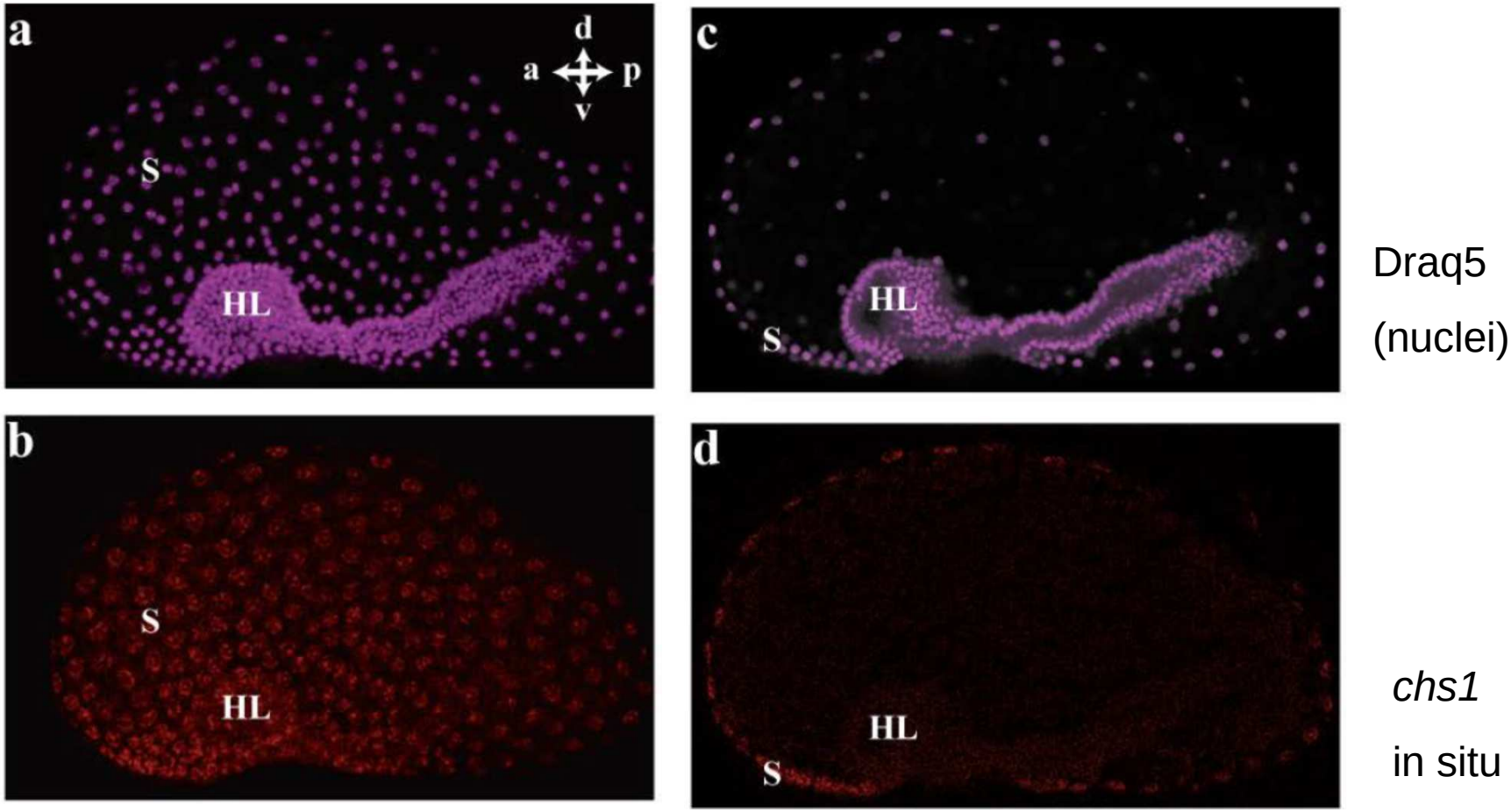
Jacobs, Rezende, Lamers and Van der Zee, *Proc R. Soc B.* 2013

De serosa scheidt een cuticula af



chitin synthase1 komt tot expressie in de serosa

Tc-chs1 in situ



Draq5

(nuclei)

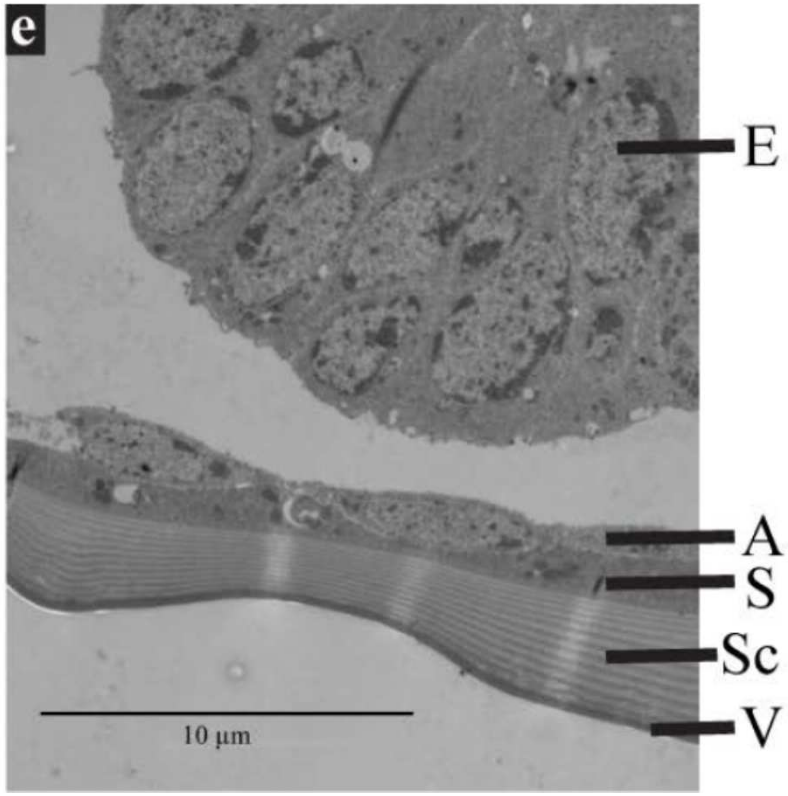
chs1

in situ

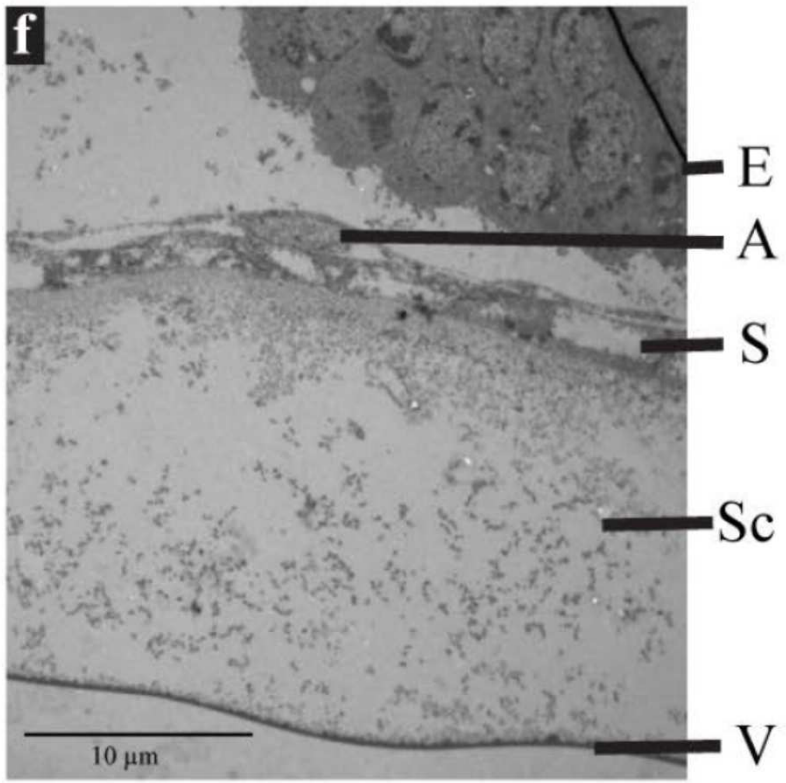
Gustavo Rezende

Tc-chs1 RNAi schakelt de cuticula uit

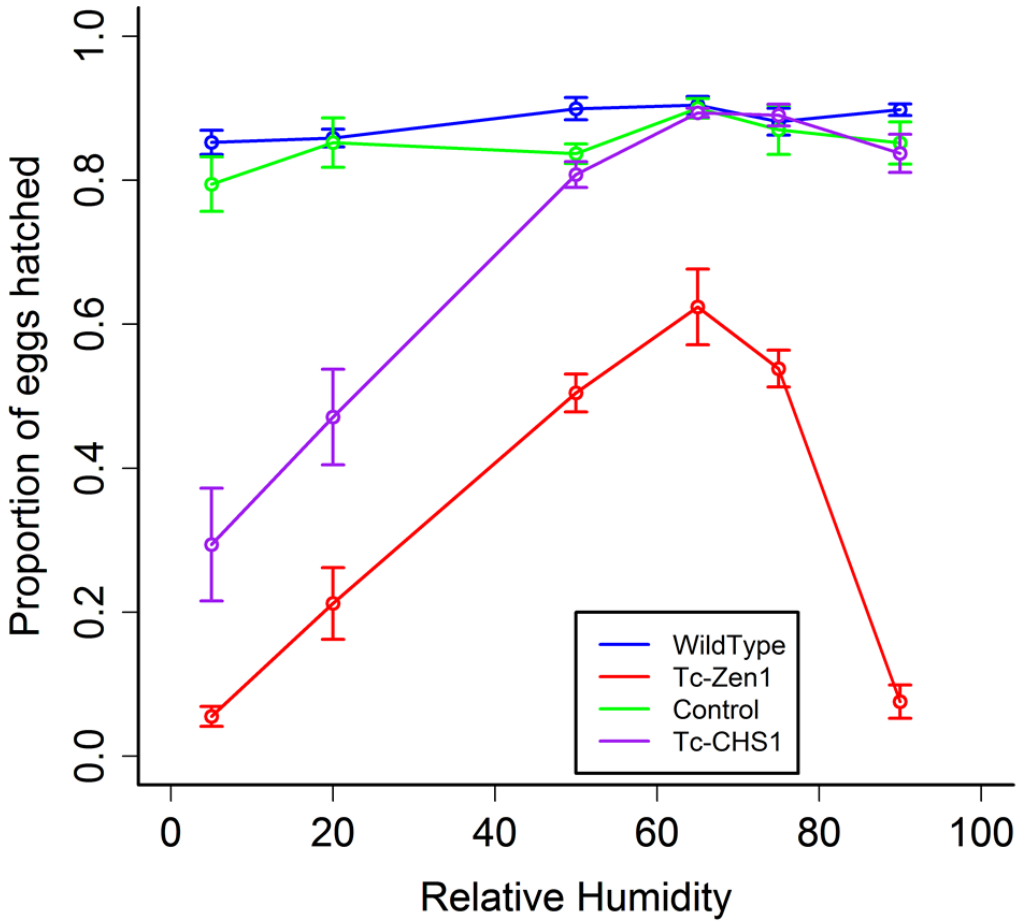
Wildtype



Tc-chs1 RNAi

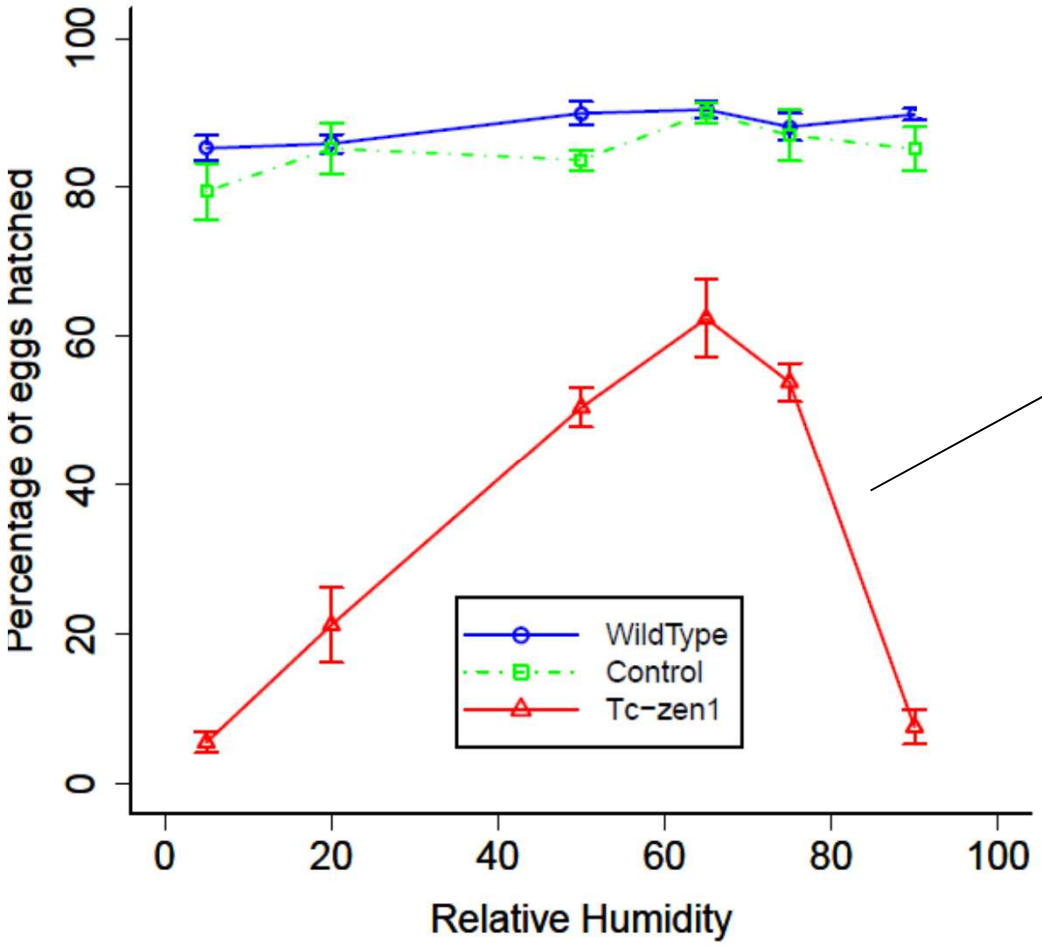


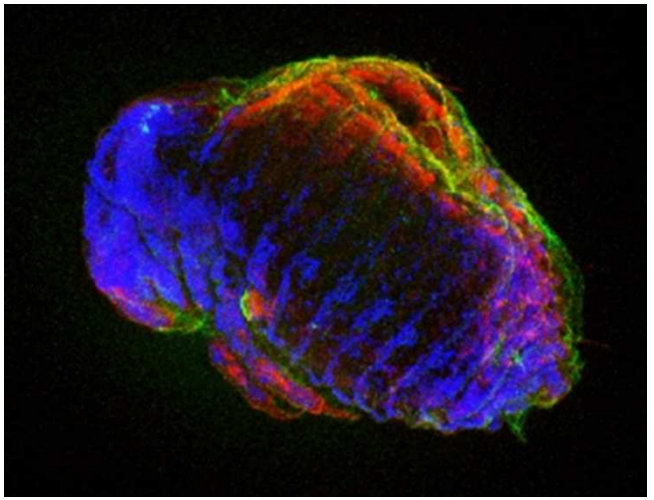
De cuticula beschermt tegen uitdroging



Chris Jacobs

Op hoge luchtvochtigheid, zijn de cellen van de serosa nodig voor dorsale sluiting.





- De serosa beschermt tegen uitdroging

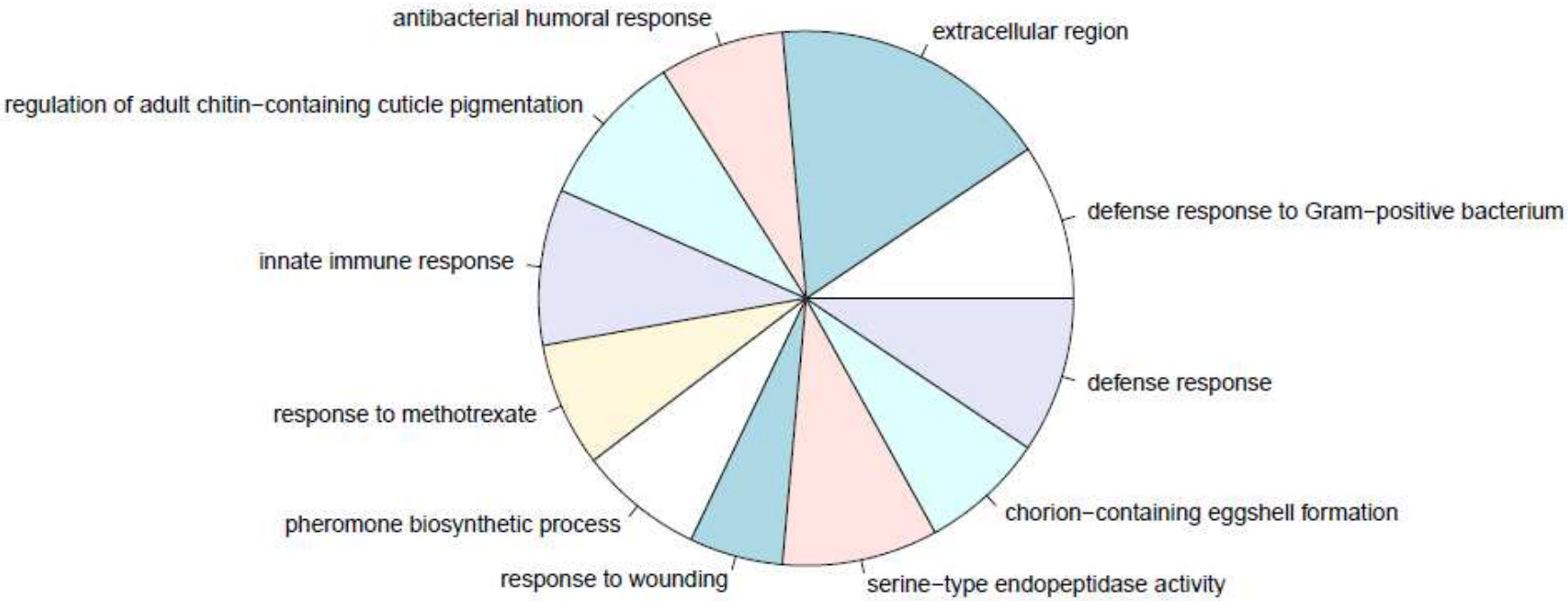
RNA sequencing

kind of eggs tested

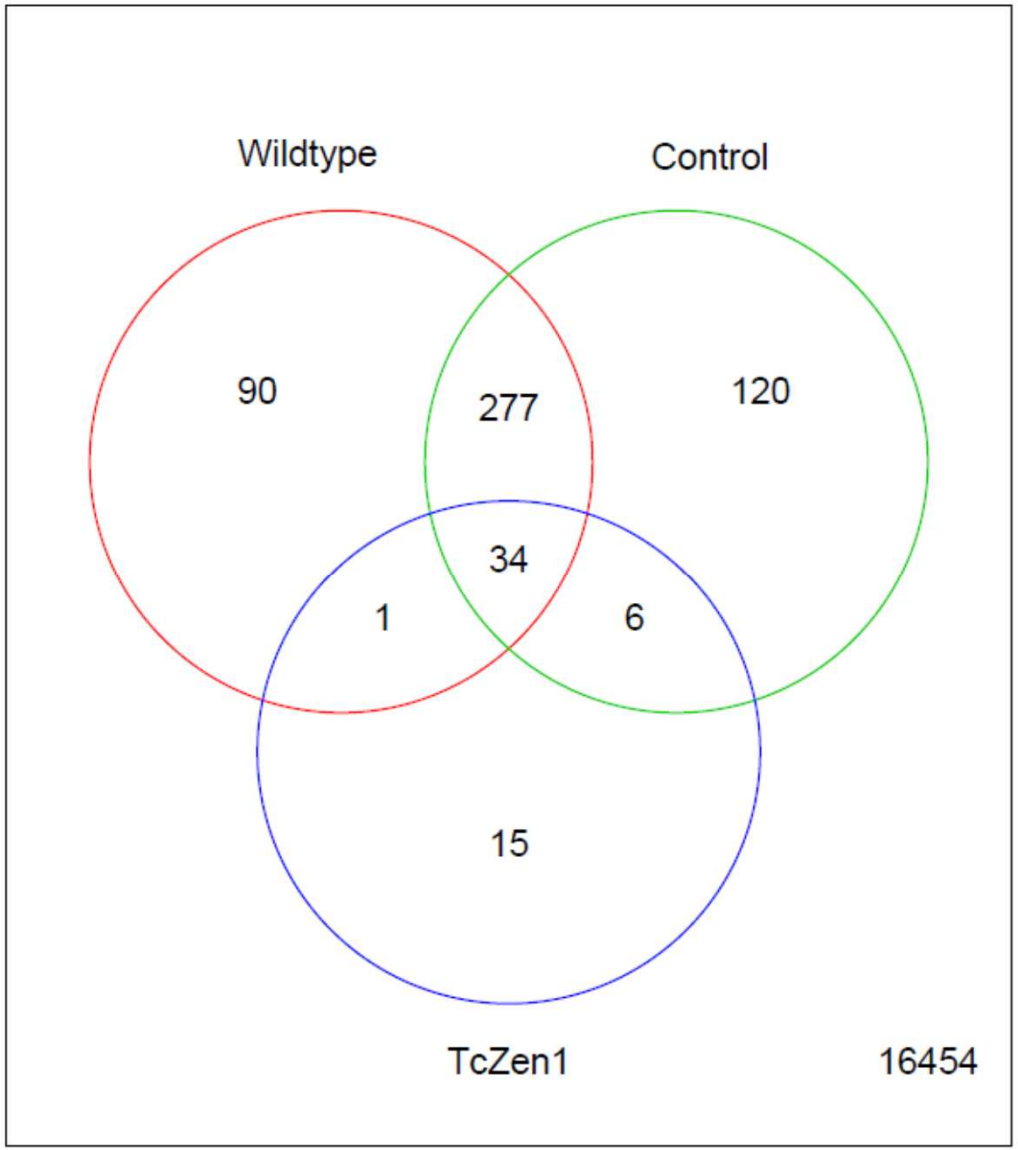
treatments

Wildtype non-treated	Control RNAi non-treated	*Tc-zen1* RNAi non-treated
Wildtype sterile injury	Control RNAi sterile injury	*Tc-zen1* RNAi sterile injury
Wildtype septic injury	Control RNAi septic injury	*Tc-zen1* RNAi septic injury

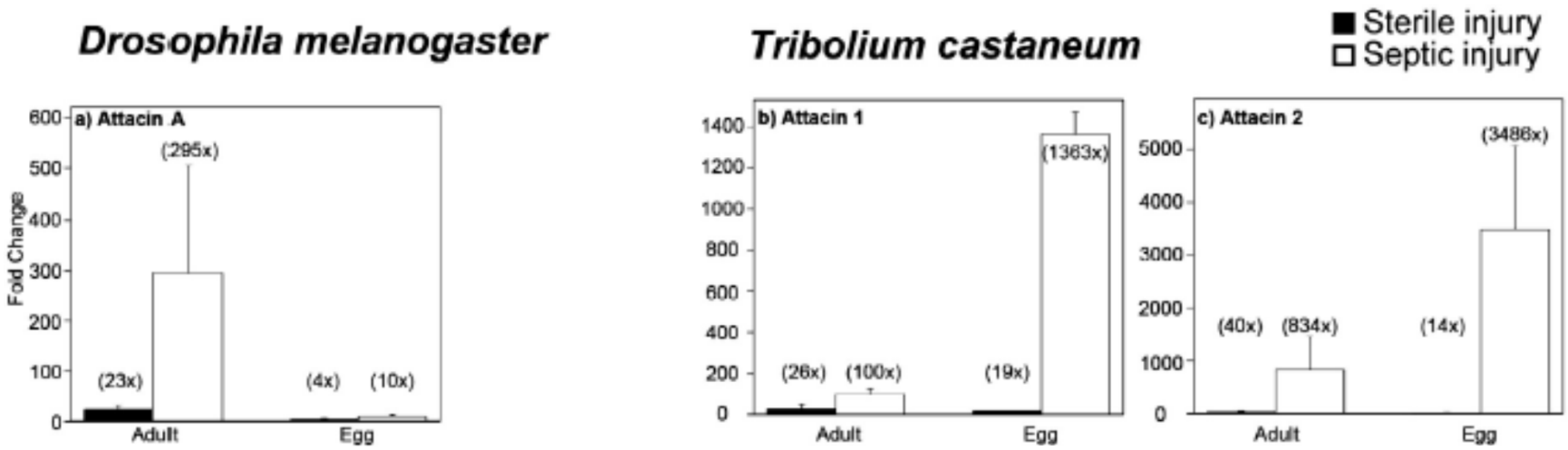
Significantly overrepresented categories after septic injury in wild-type eggs



Genes significantly (p<0.01) upregulated after septic injury



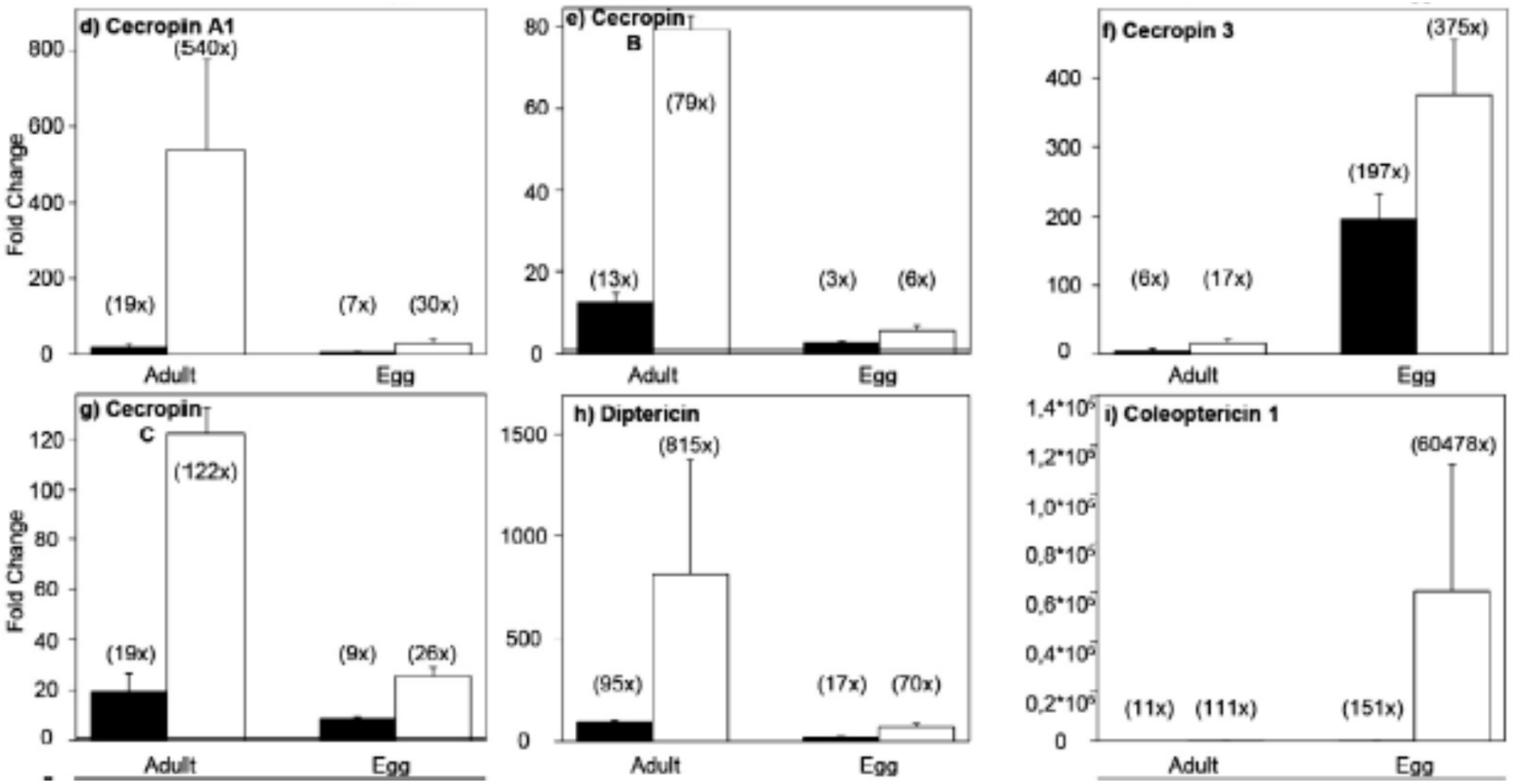
Upregulation of antimicrobial peptides upon septic injury



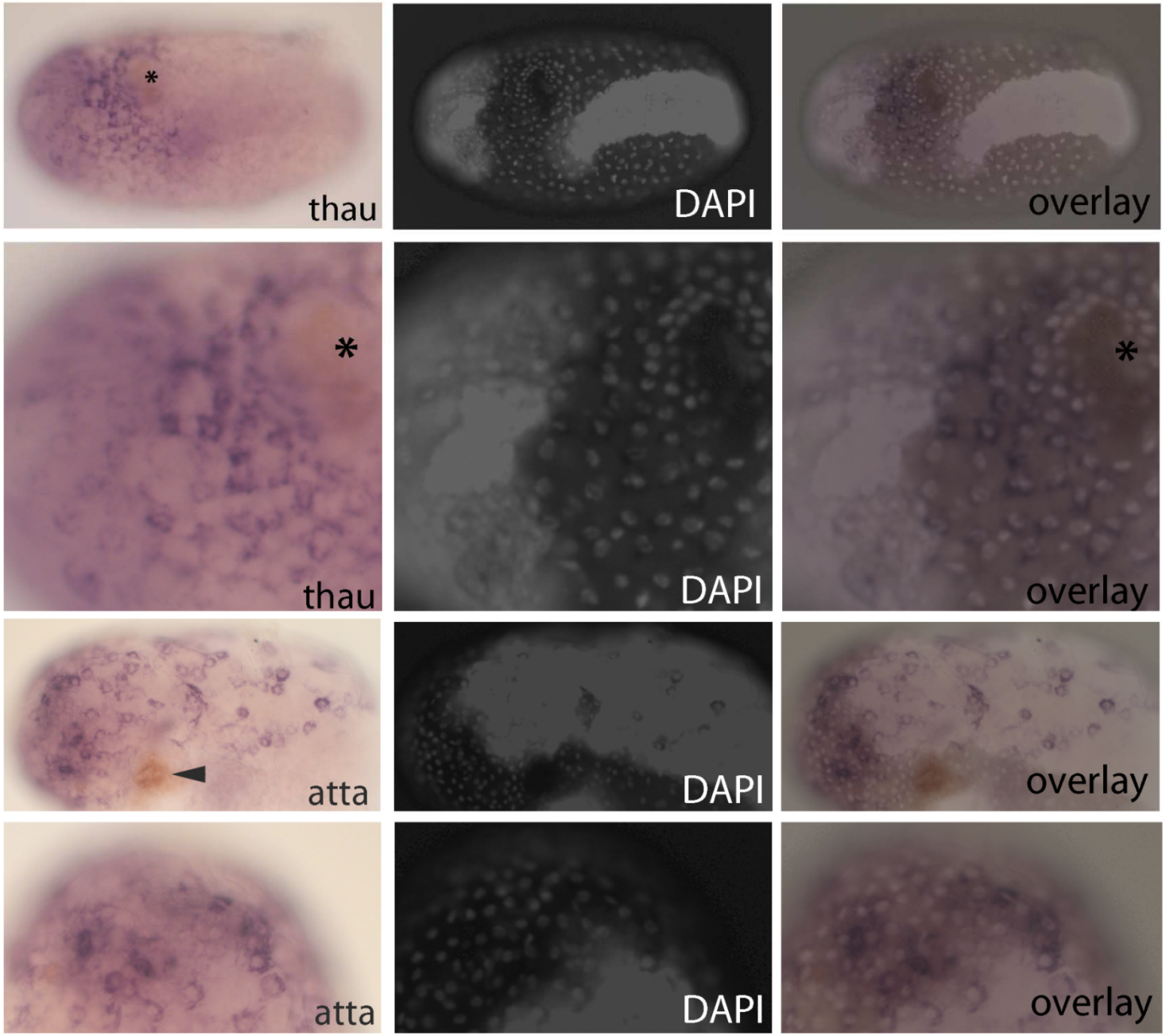
Chris Jacobs

Upregulation of antimicrobial peptides upon septic injury

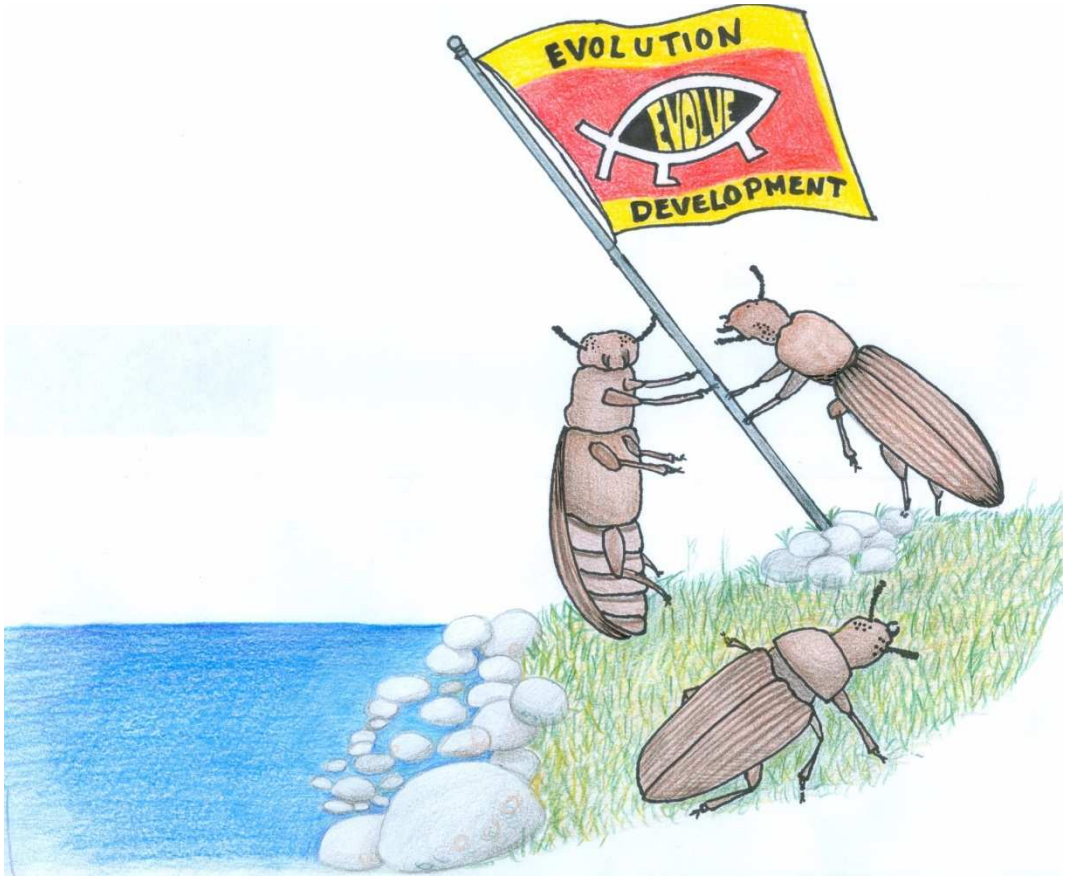
Drosophila *Tribolium*



Antimicrobial peptides are expressed in the serosa upon septic injury



- De serosa beschermt tegen uitdroging en bacterien en zou wel eens een belangrijke rol kunnen hebben gespeeld bij de verovering van het land.



Leidse bioloog brengt spectaculaire stap evolutie in beeld door onderzoek met eitjes meelkevers

Hoe insecten te land kwamen

nature International weekly journal of science

bionieuws 22 juni 2013 | jaargang 23

Insecten op land dankzij nieuw ei

NATURE | NEWS

Waterproof eggs let insects conquer dry land

Membrane that protects eggs from drying out freed critters from need to stay close to water.

Ed Yong

19 June 2013

Insects were among the first animals to invade the land around 400 million years ago, and they have diversified so greatly that they now account for three-quarters of all animal species.

This success, according to a new study, depended to a great extent on the serosa — a membrane that makes insect embryos waterproof as they develop inside the eggs. By genetically removing the serosa from embryos of the red flour beetle (*Tribolium castaneum*), Maurijn van der Zee at

20 juni 2013 · Mare 7

Wetenschap

Insecteneitjes

Rondom de eitjes van veel insecten zit aan de binnenkant van de eischaal een speciaal laagje, de zogeheten serosa. De eieren van andere geleedpotige dieren hebben niet zo'n serosa. Als je met wat biotechnologisch knutselwerk zorgt dat een kever eitjes legt zonder serosa, komen die in het laboratorium nog steeds

3. 'Corkscr
Nature | 2

Membraan om ei was grote troef insecten

Door onze redactie wetenschap

AMSTERDAM. Eén genetische verandering heeft het enorme evolutionaire succes van insecten mogelijk gemaakt. Insecten waren de eerste dieren die het land veroverden, 400 miljoen jaar geleden en nog steeds behoort driekwart van alle diersoorten tot de orde van insecten. De Leidse bioloog Maurijn van der Zee heeft nu, samen met zijn promovendus Chris Jacobs en twee Braziliaanse biologen, vastgesteld dat dit mede te danken is aan een unieke eigenschap van het insectenei. Het embryo in het ei droogt niet uit, dankzij de serosa. Dat is een membraan dat het embryo zelf produceert en dat andere geleedpotigen (zoals krabben en duizendpoten) missen.

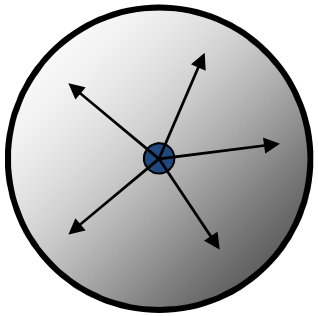
In de *Proceedings of the Royal Society B* van deze week beschrijft Van der Zee hoe hij erin slaagde om in eitjes van de kastanjebruine rijstmeelkever het gen Tc-zen1 uit te schakelen, dat verantwoordelijk is voor de serosa. Bij lage luchtvochtigheid droogden de eitjes snel uit en kwamen ze niet uit. Onverwacht, trouwens, bleken de serosa-loze eitjes ook slecht uit te komen in hoge luchtvochtigheid, omdat het ei dan juist te veel vocht opnam. Ook ontdekte Van der Zee dat het keratinelaagje van de membraan cruciaal was voor de overleving in la-

Evolution and development

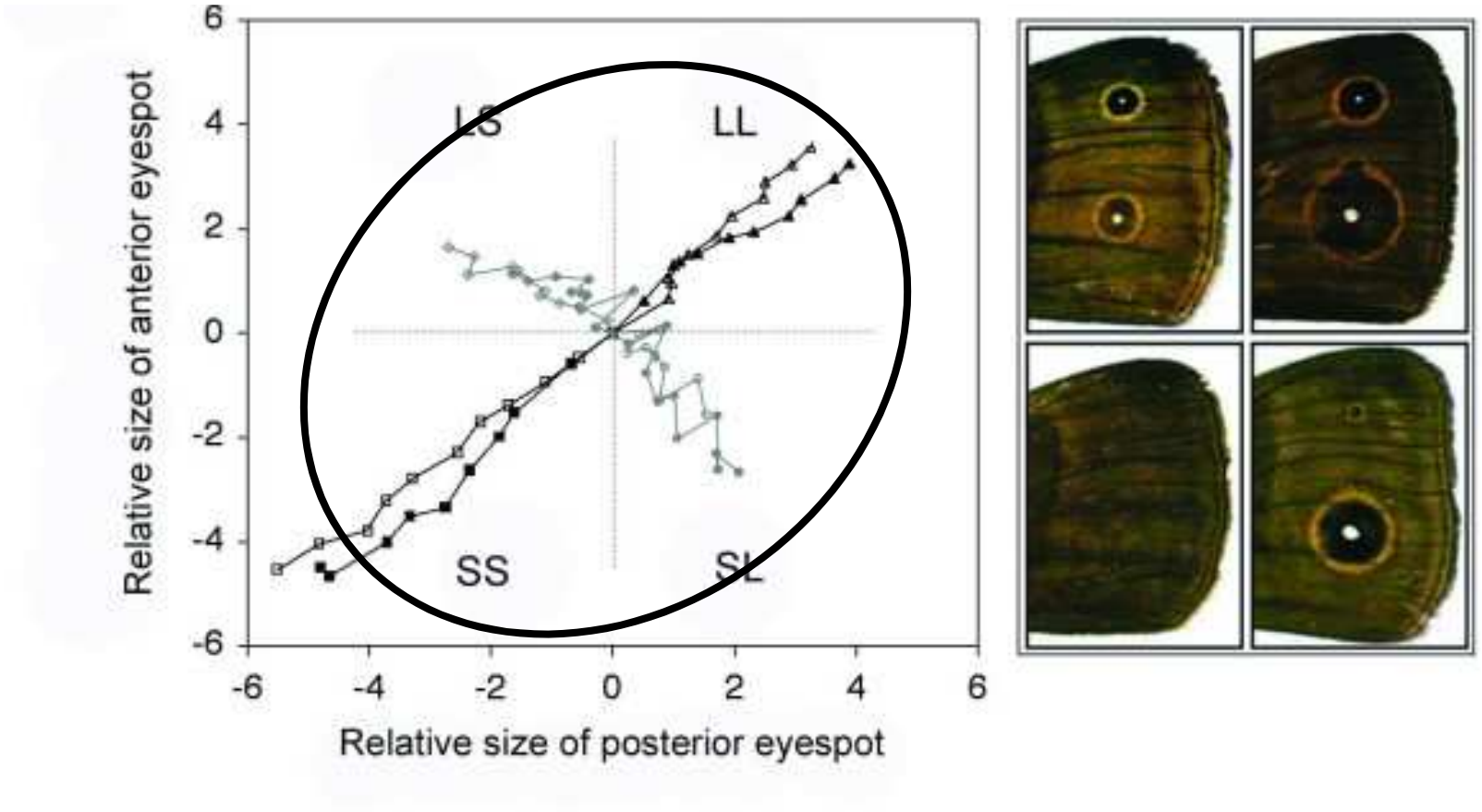
1. Embryo's vertellen je iets over evolutie.
2. Evo-devo onthult diepe homolgieën.
3. Evo-devo zoekt de genetische en ontwikkelingsbiologische basis van evolutionaire veranderingen.
4. Evo-devo bestudeert de oorsprong van *novelties*
5. Embryonale ontwikkeling kan de evolutie in bepaalde richtingen sturen.

Darwin:

- Variation is isotropic (random and in every direction)

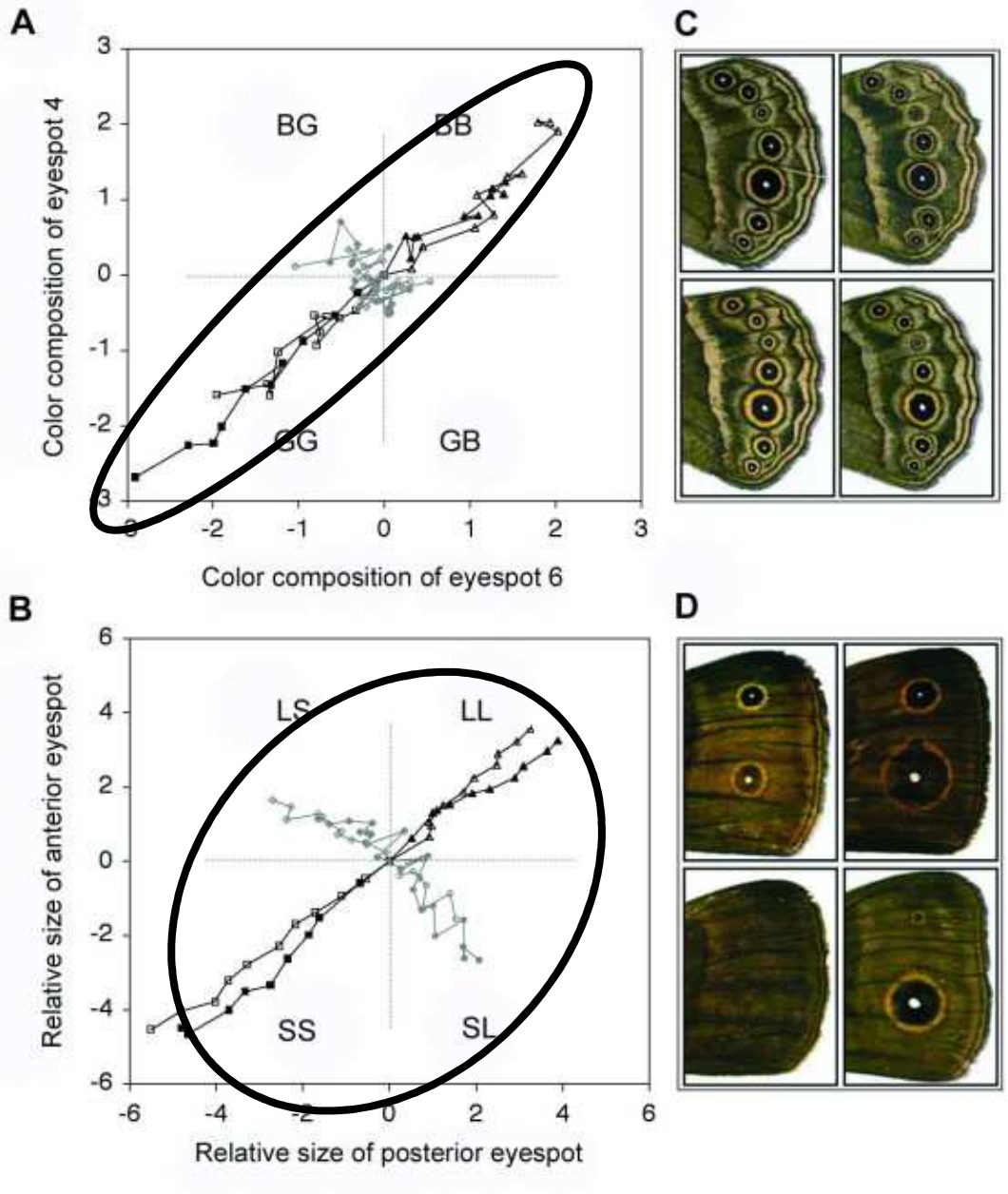


Variation and selection seems to be possible in every direction

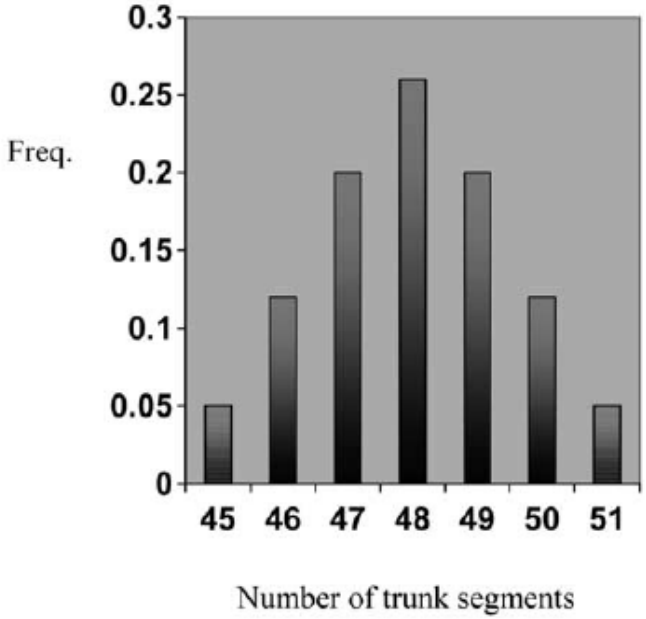


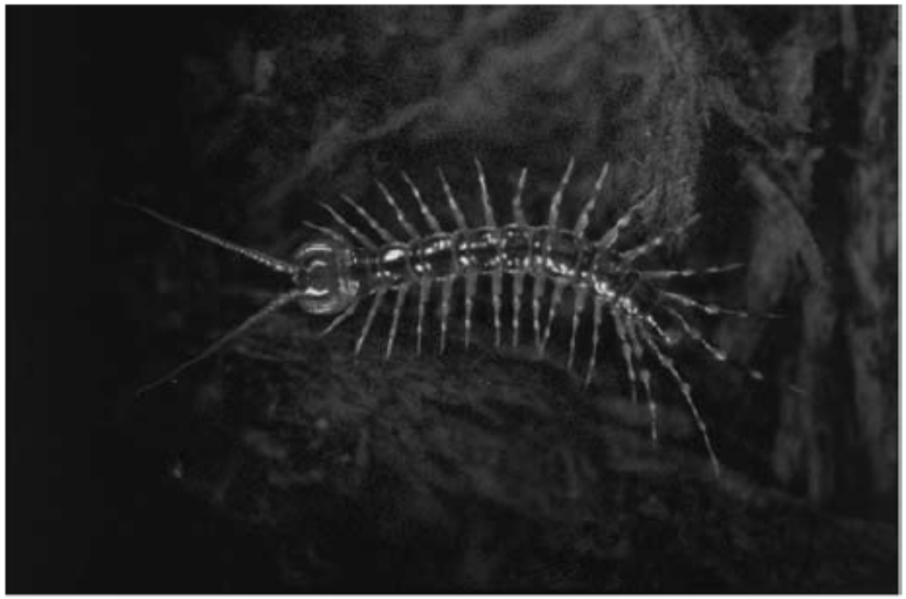
Beldade et al., *Nature* 2002

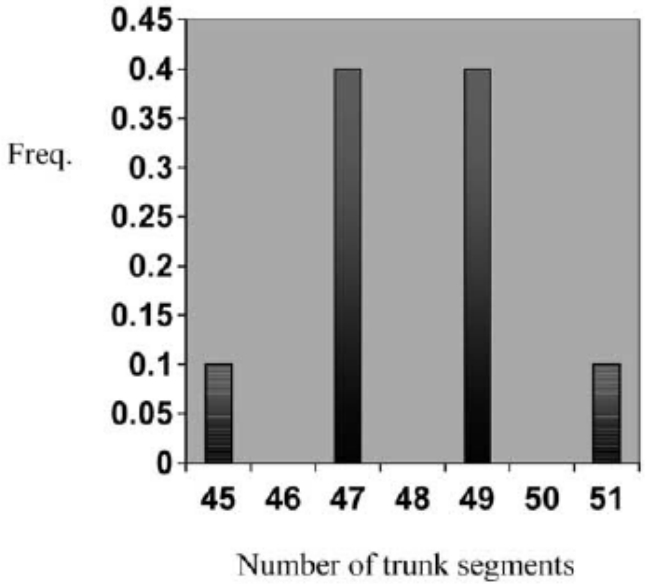
…but not for eyespot color!

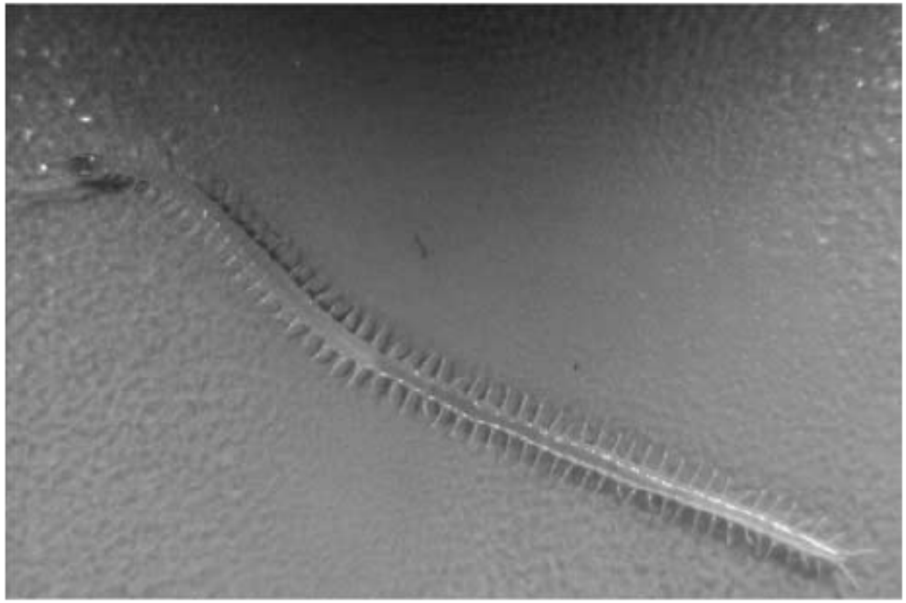


Beldade et al., *Nature* 2002

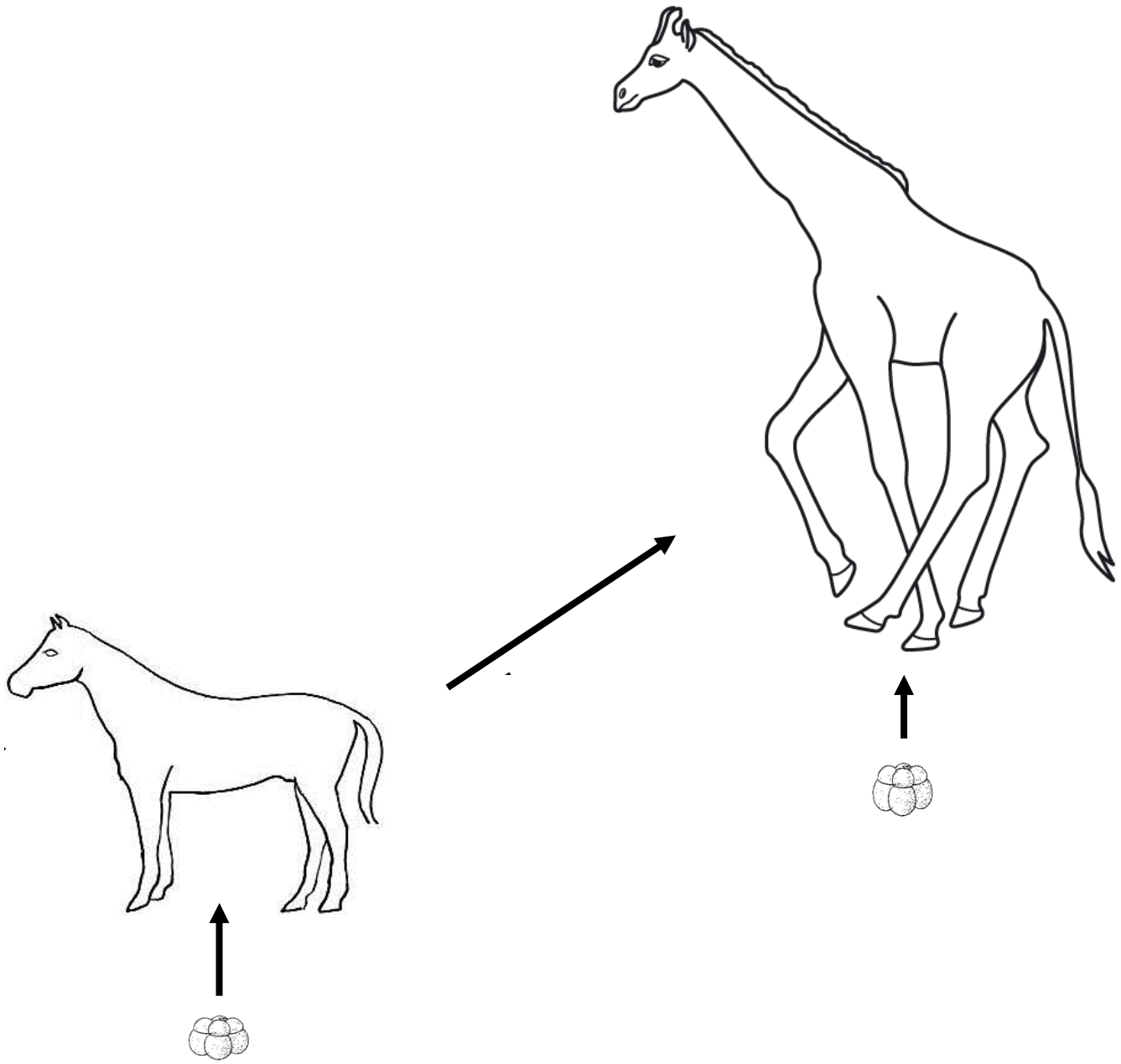


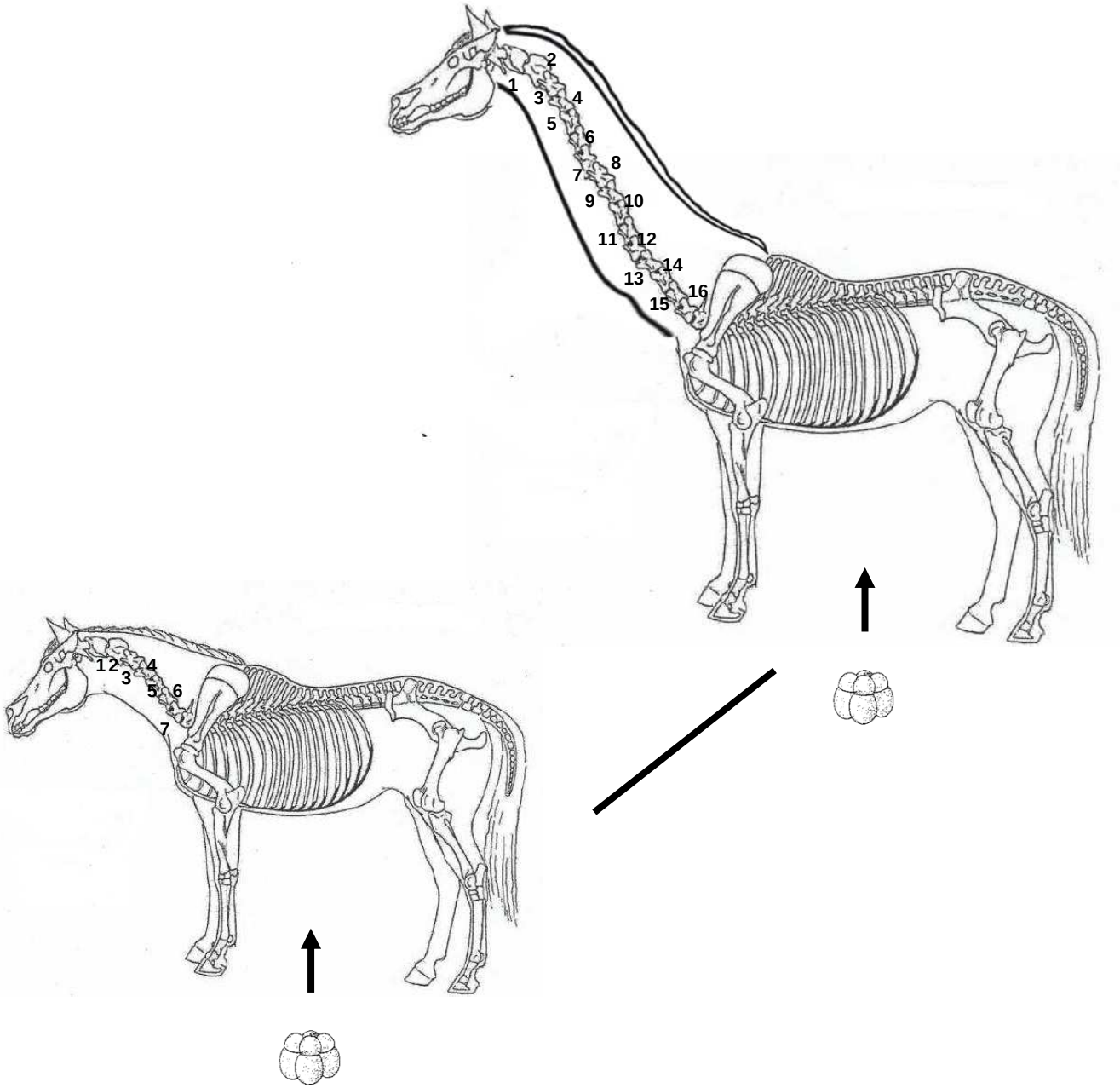






Arthur, *Heredity*, 2002

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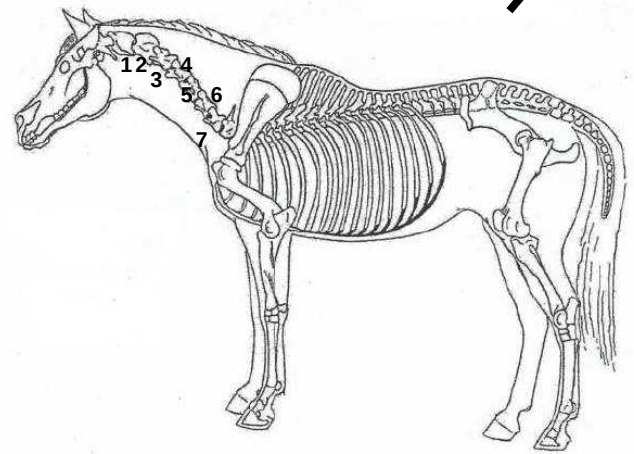
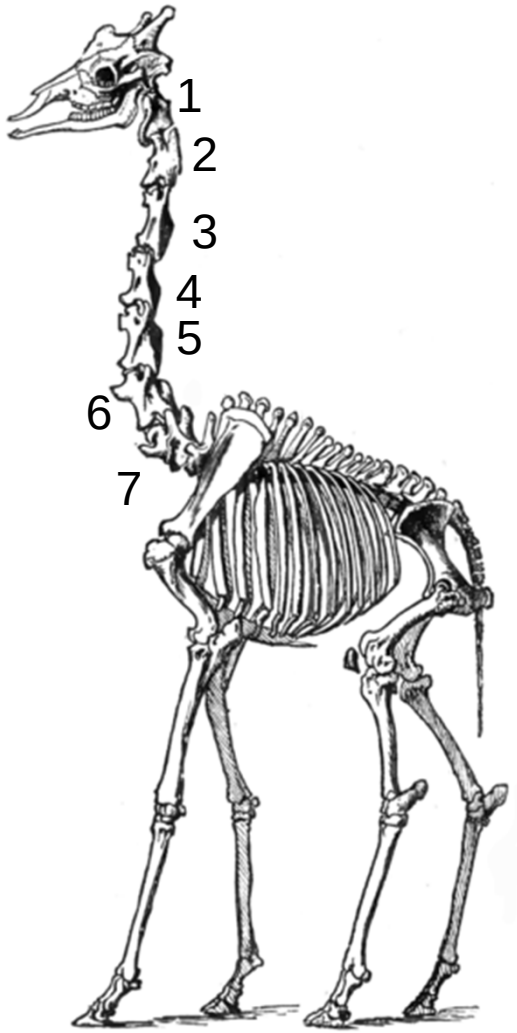
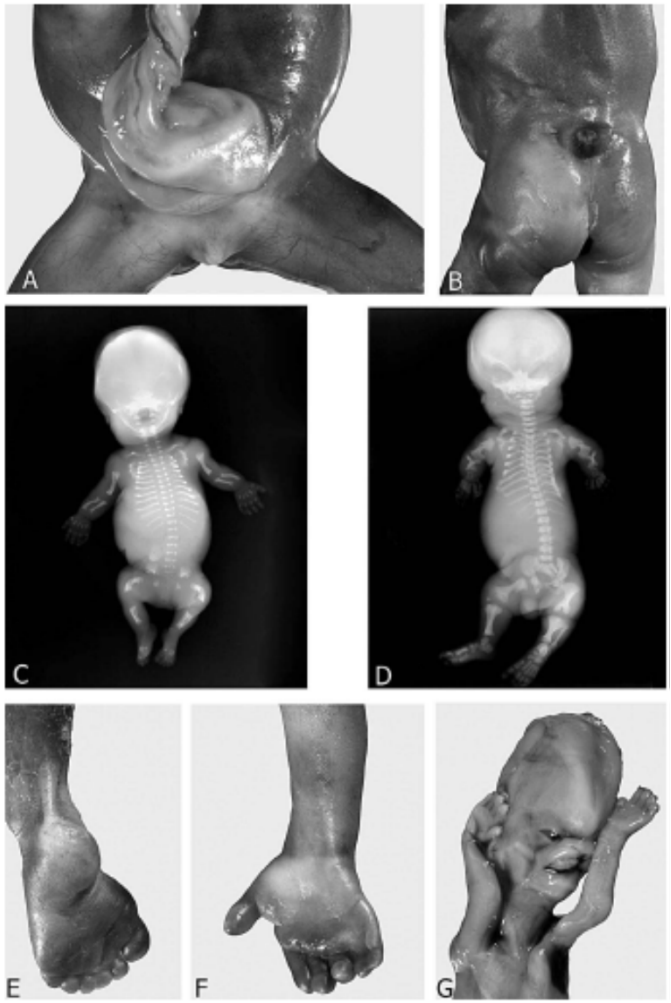




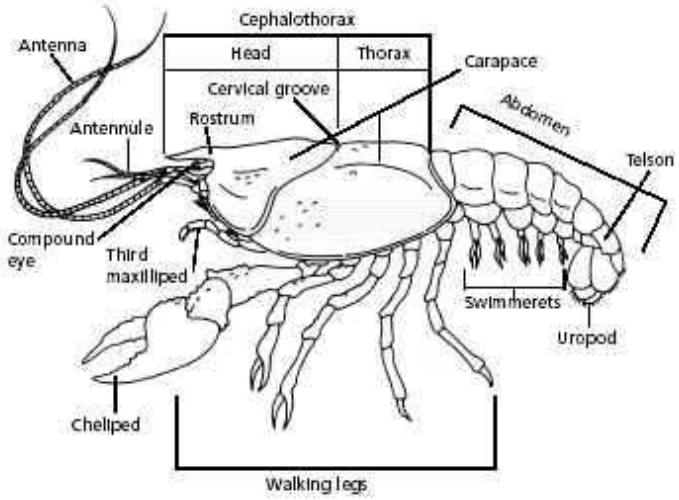
SKELETON OF GIRAFFE.

Human embryos lacking a cervical vertebrum



→ Pleiotropy

Galis



Facilitated variation = positive bias

(Kirschner and Gerhart)

-compartmentation/uncoupling/modularity

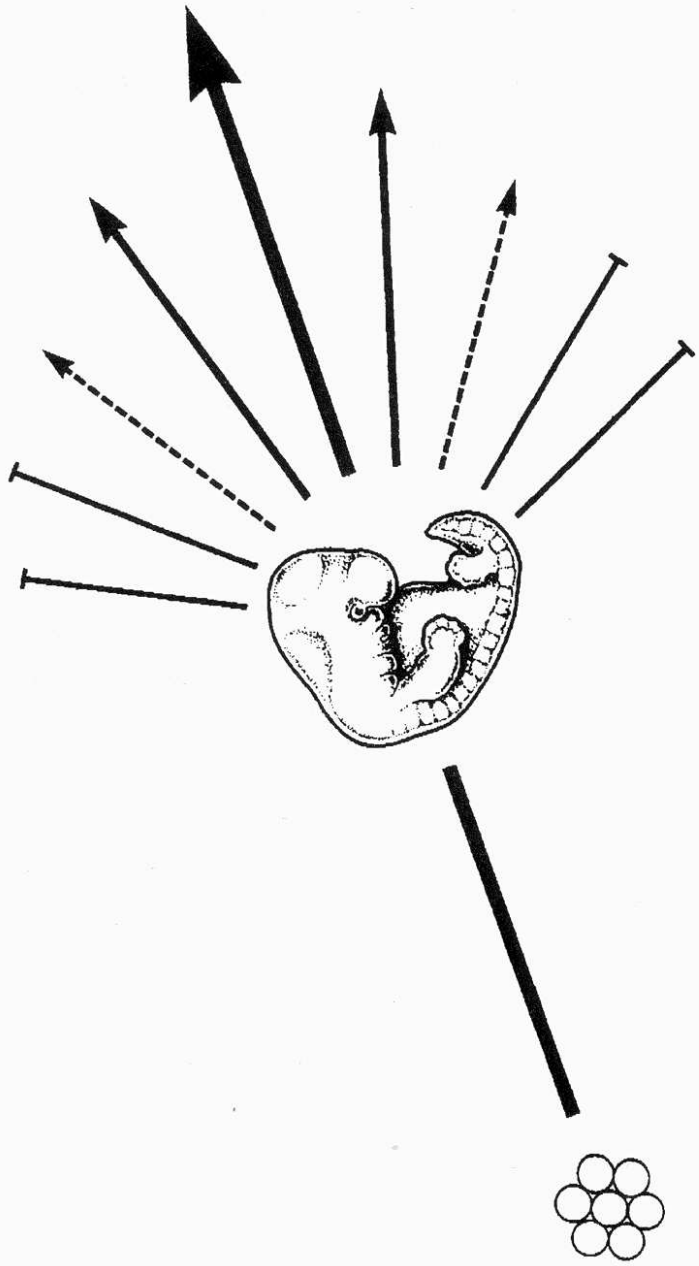
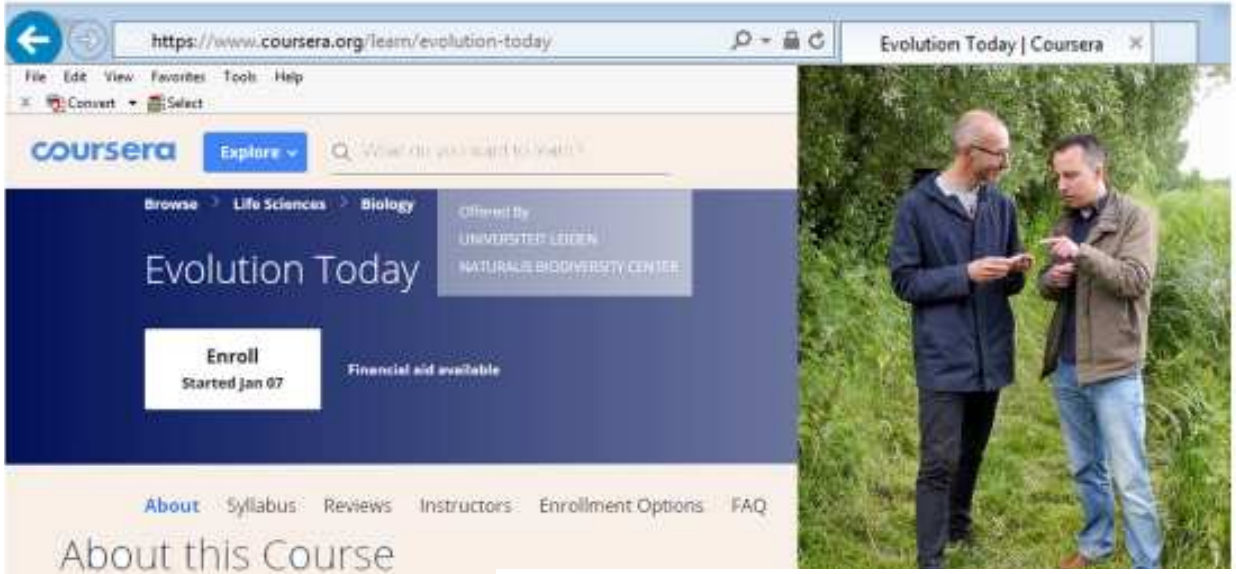


FIGURE 3 Developmental bias, represented by different probabilities of reprogramming an embryo's trajectory in different ways. Large arrow, original trajectory; solid arrow, easy; dashed arrow, difficult; blunt-ending lines, impossible.

Arthur, 2004

Evolution and development

1. Embryo's vertellen je iets over evolutie.
2. Evo-devo onthult diepe homolgieën.
3. Evo-devo zoekt de genetische en ontwikkelingsbiologische basis van evolutionaire veranderingen.
4. Evo-devo bestudeert de oorsprong van *novelties*
5. Embryonale ontwikkeling kan de evolutie in bepaalde richtingen sturen.



Evolution Today

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Dr.
Leiden University

Rutger Vos
Dr.
Naturalis Biodiversity Center

Krijg inspiratie of volg de cursus op:
https://www.coursera.org/learn/evolution-today
Engels met Nederlandse ondertiteling
Of bekijk en gebruik de kennisclips op ons YouTube-kanaal:

https://www.youtube.com/playlist?list=PLzugOrS2Z8ooypVJNuUxp5xelqATlhp3i

https://www.youtube.com/watch?v=ydqReeTV_vk

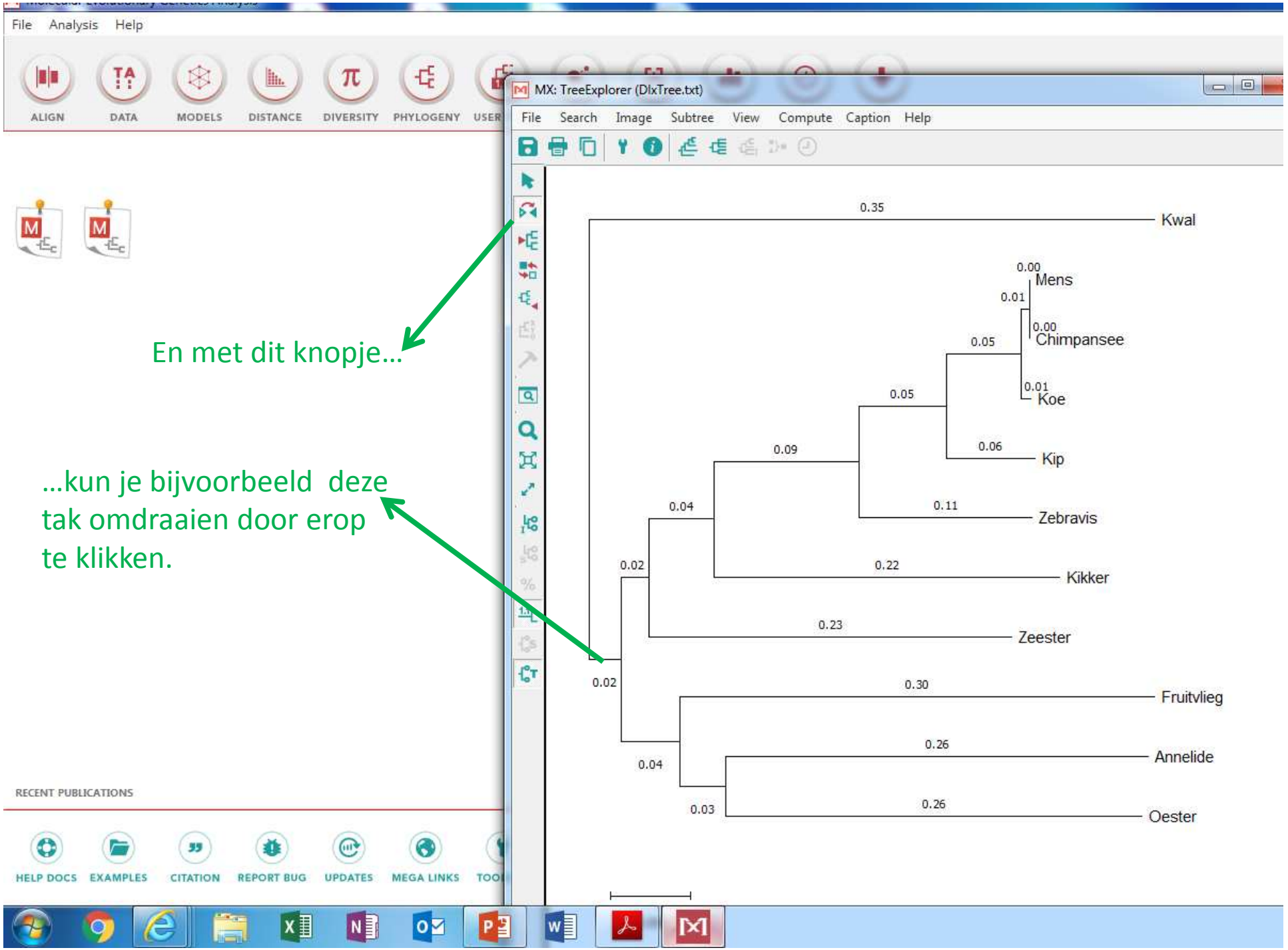
Universiteit Leiden

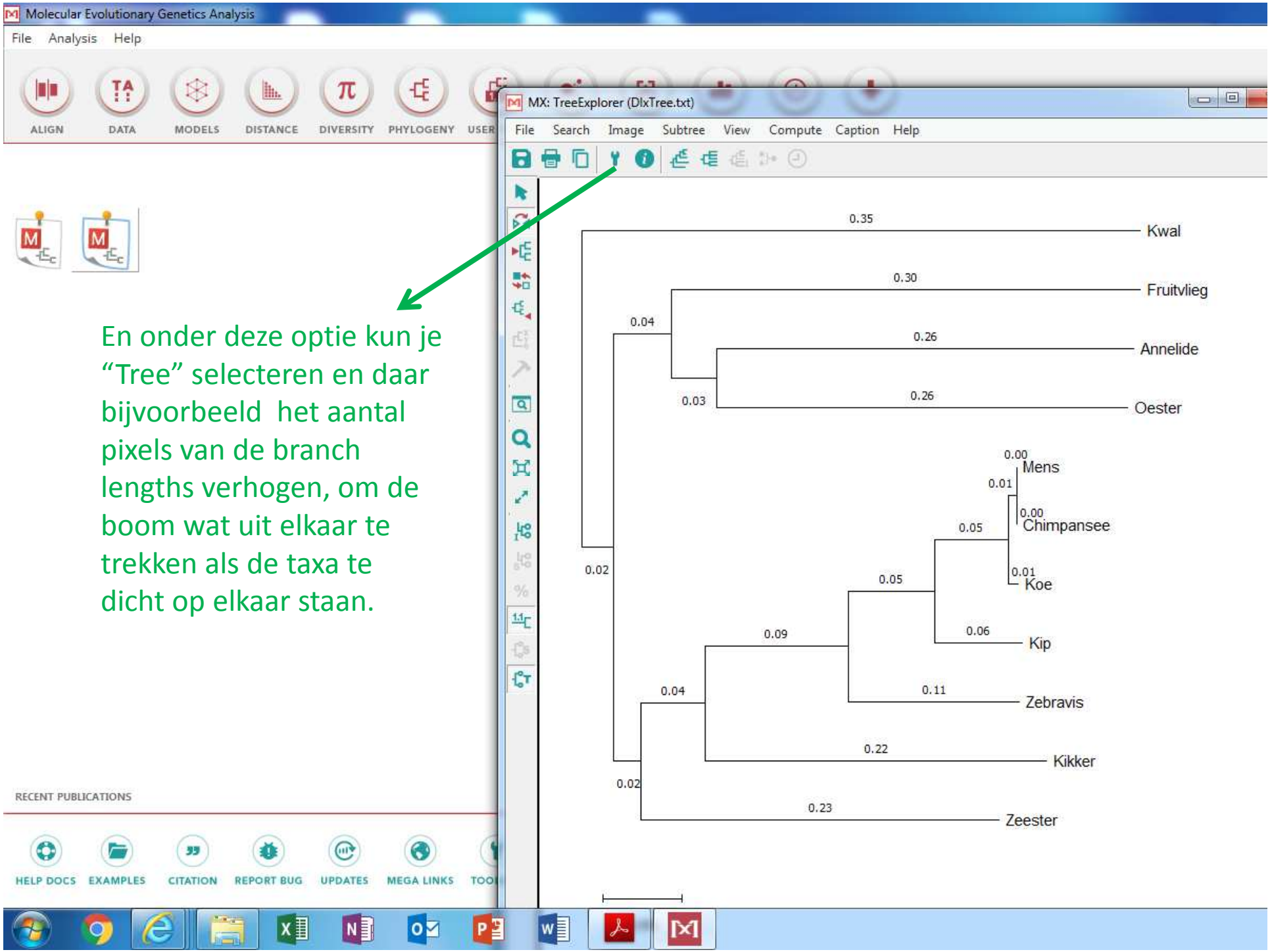
Generade
Applied Genomics for Life

EMBO

UNIVERSITIES COIMBRA GROUP

NWO
Netherlands Organisation for Scientific Research


File Analysis Help
ALIGN
DATA
MODELS
DISTANCE
DIVERSITY
PHYLOGENY
MX: TreeExplorer (DlxTree.txt)
File Search Image Subtree View Compute Caption Help
En met dit knopje…
…kun je bijvoorbeeld deze tak omdraaien door erop te klikken.
0.35
Kwal
0.00
Mens
0.01
0.00
Chimpansee
0.05
0.01
Koe
0.05
0.09
0.06
Kip
0.04
0.11
Zebravis
0.02
0.22
Kikker
0.23
Zeester
0.02
0.30
Fruitvlieg
0.26
0.04
Annelide
0.03
0.26
Oester
RECENT PUBLICATIONS
HELP DOCS
EXAMPLES
CITATION
REPORT BUG
UPDATES
MEGA LINKS



En onder deze optie kun je “Tree” selecteren en daar bijvoorbeeld het aantal pixels van de branch lengths verhogen, om de boom wat uit elkaar te trekken als de taxa te dicht op elkaar staan.

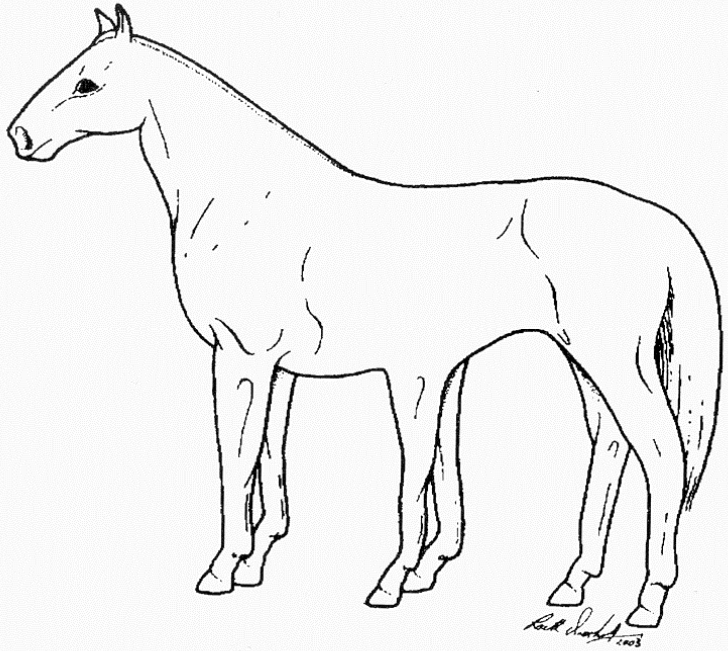
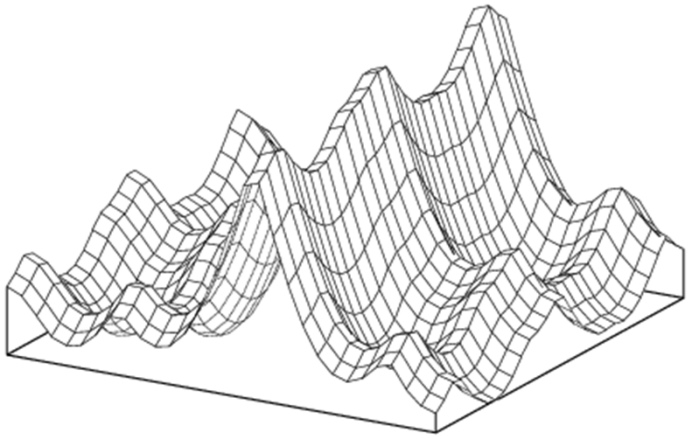


FIGURE 2 The fictitious but potentially viable six-legged horse.



Arthur