

Embryonic and post-embryonic hourglass patterns of plant development



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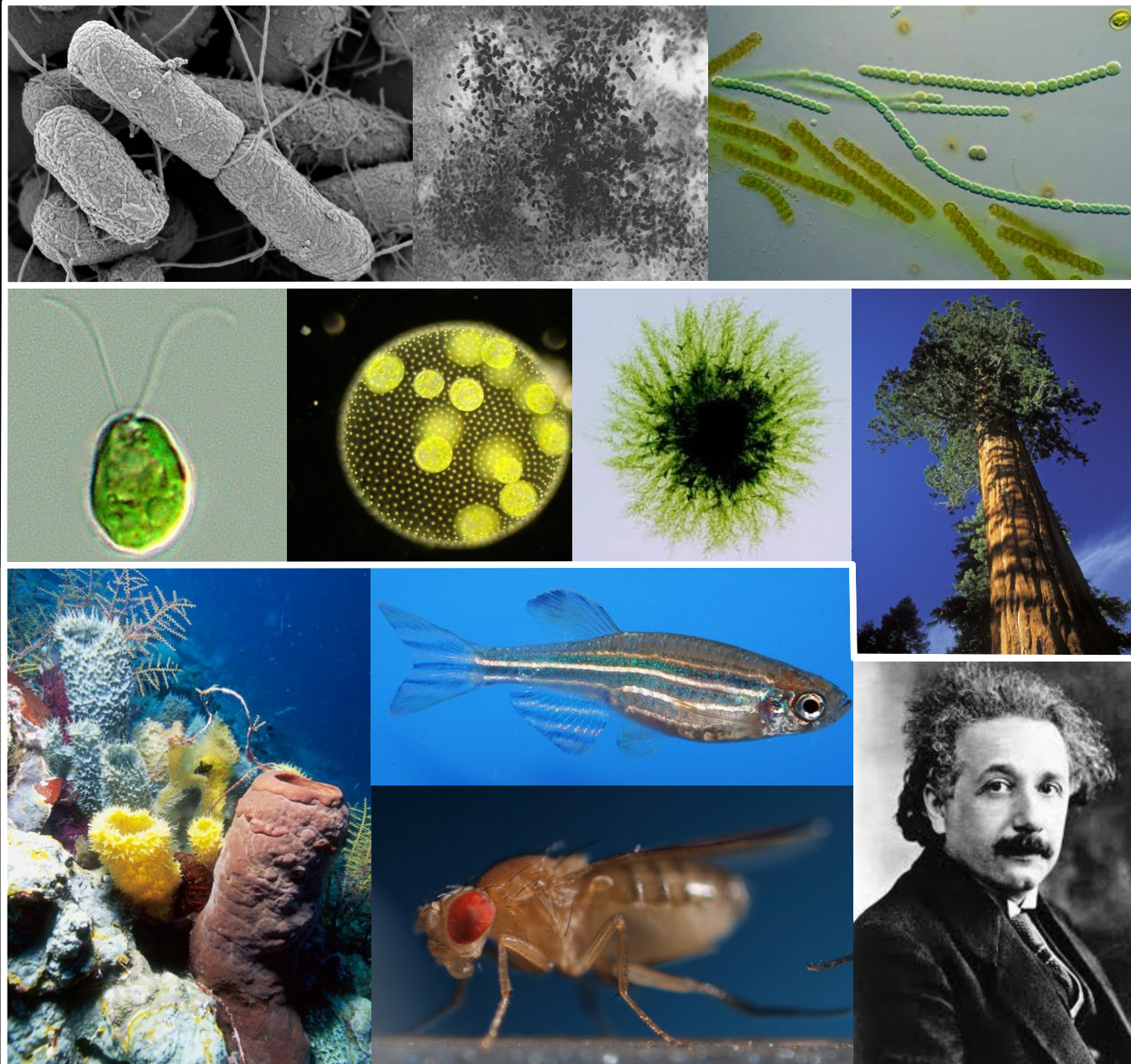
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Trinity College Dublin**

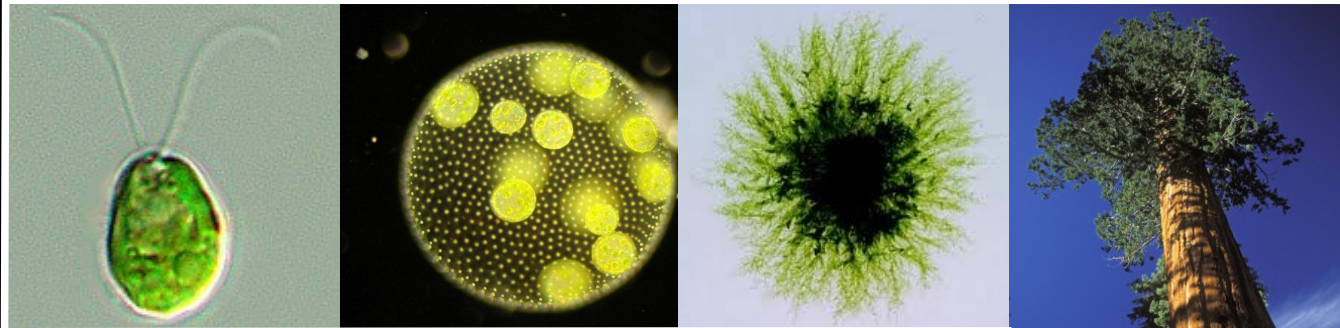
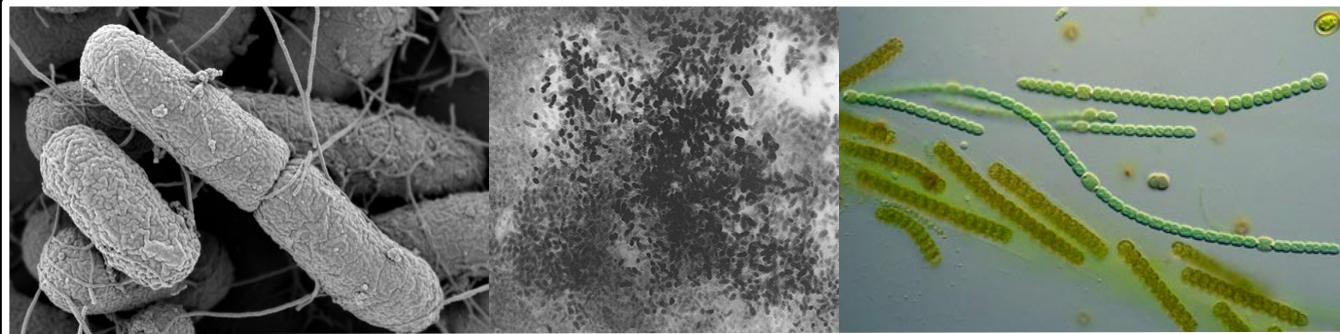
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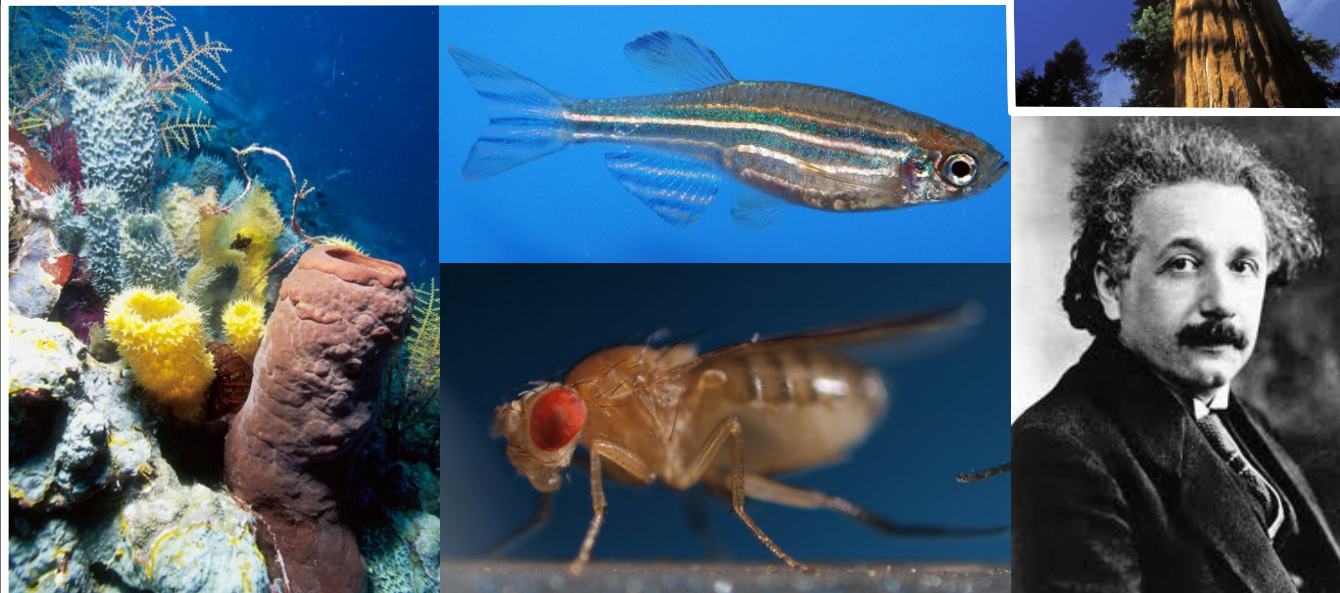
How did **complex life** emerge?



How did **complex life** emerge?

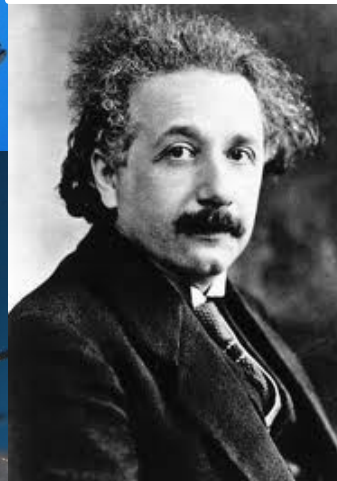
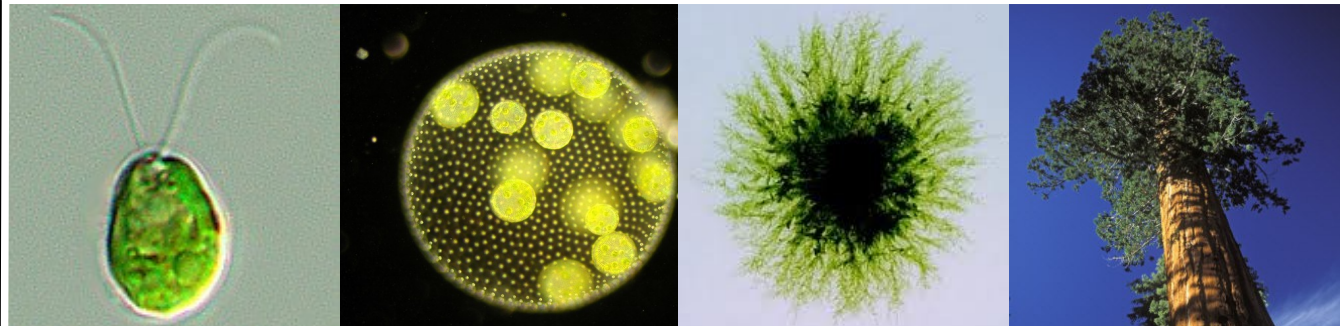
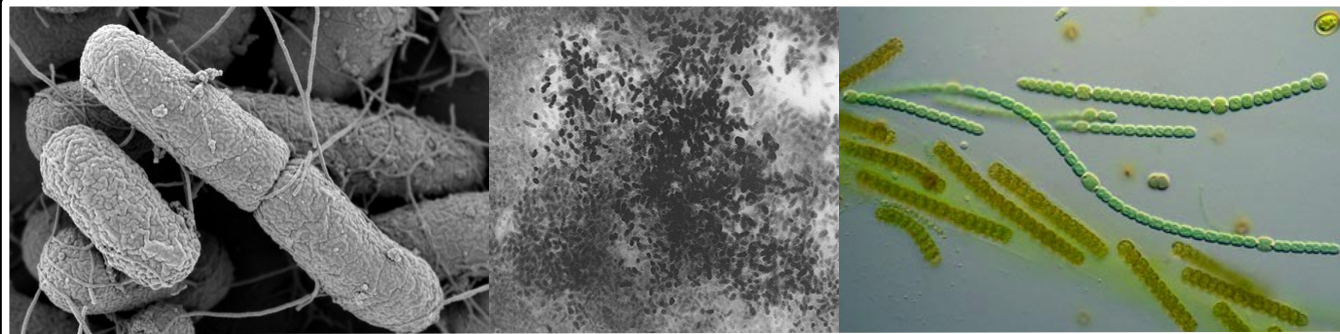


on the
evolutionary
level



on the
developmental
level

How did **biodiversity** emerge?

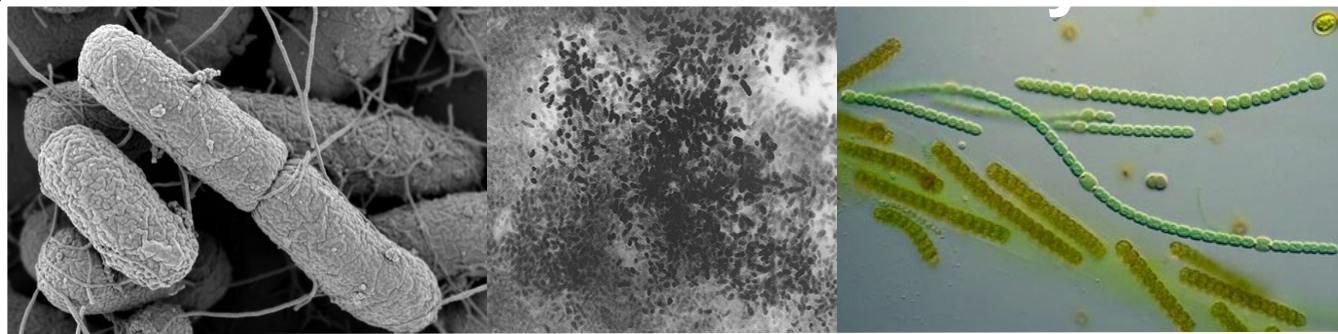


on the
evolutionary
level

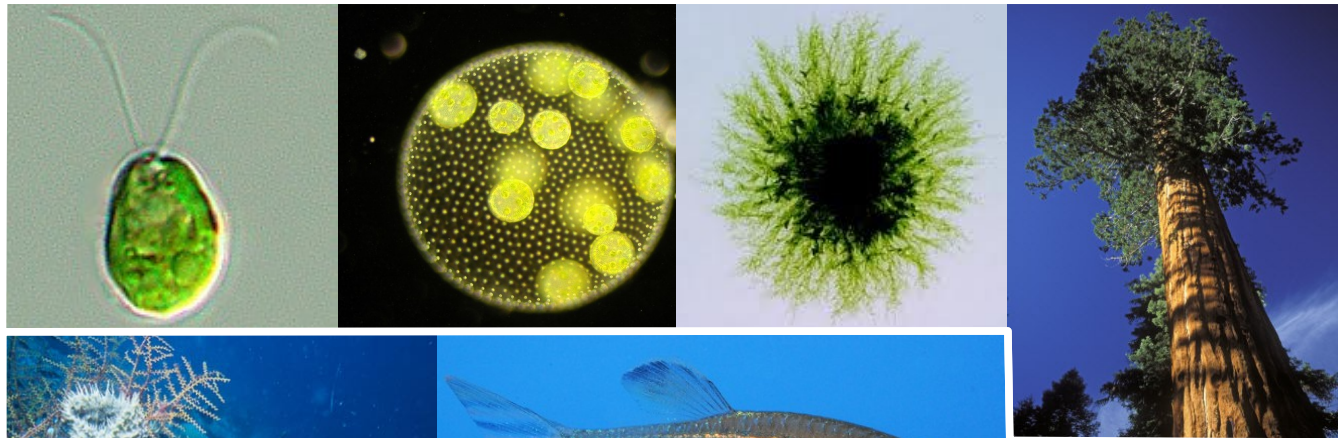
on the
developmental
level

Gradual evolution of complex life and biodiversity

Bacteria



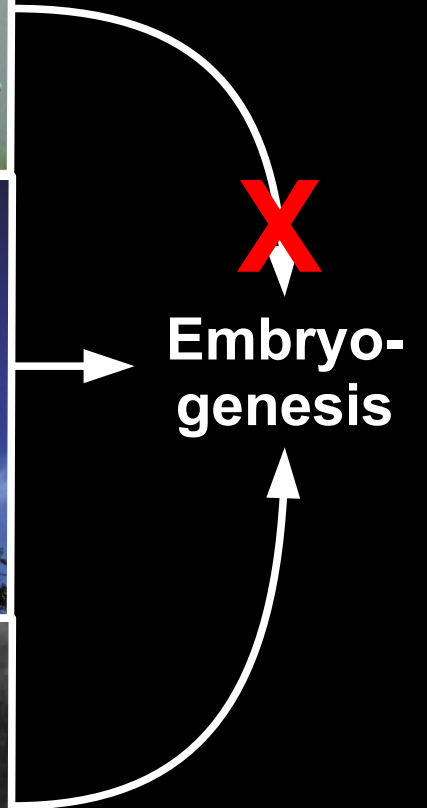
Plants



Animals

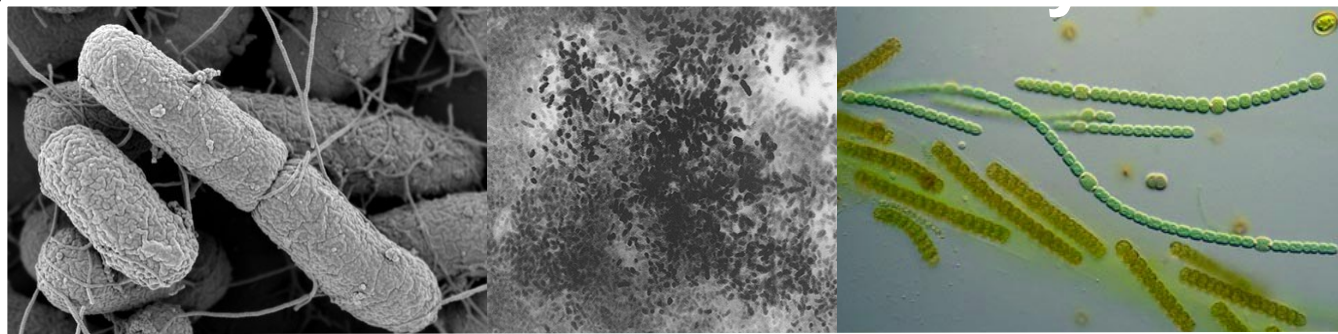


X
Embryo-
genesis

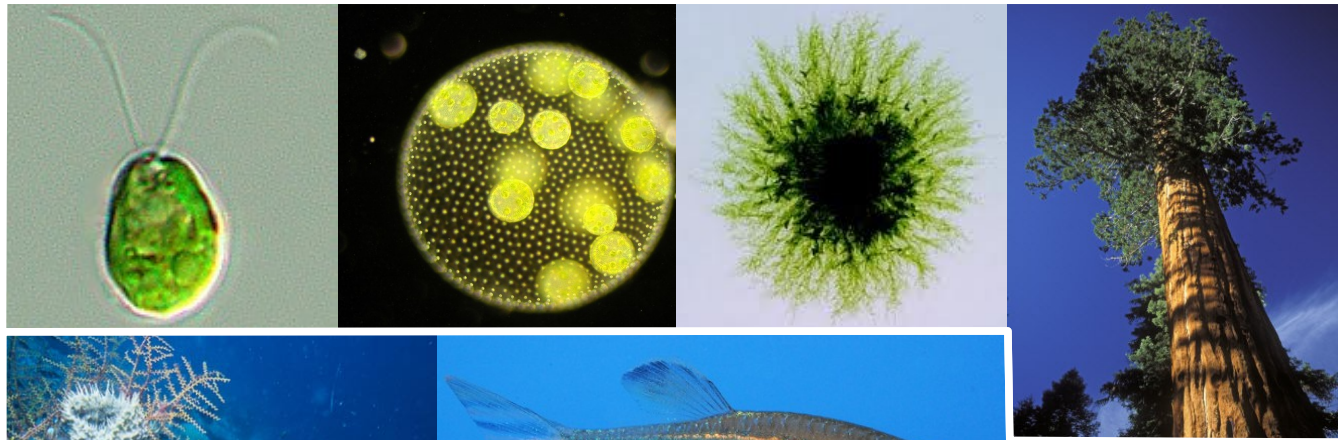


Gradual evolution of complex life and biodiversity

Bacteria



Plants



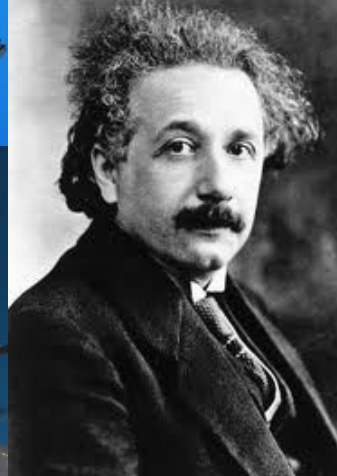
Animals

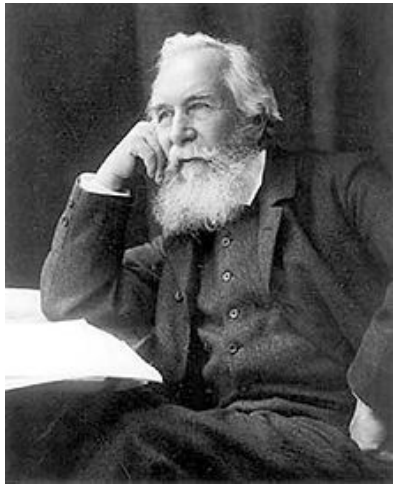


Comparative embryology

Evolutionary embryology

Evo-devo

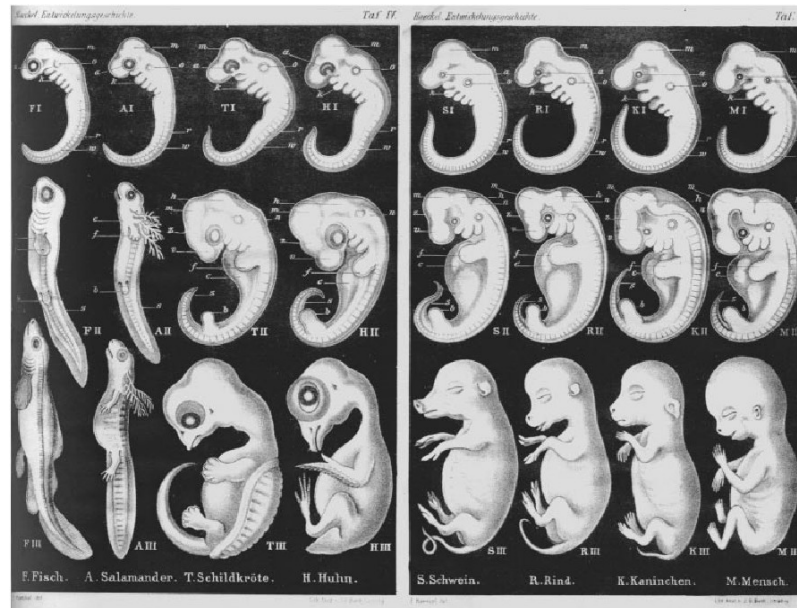




Ernst Haeckel
1834 - 1919

Haeckel's biogenetic law (1866):

“Die Ontogenese ist die kurze und schnelle Recapitulation der Phylogenese”



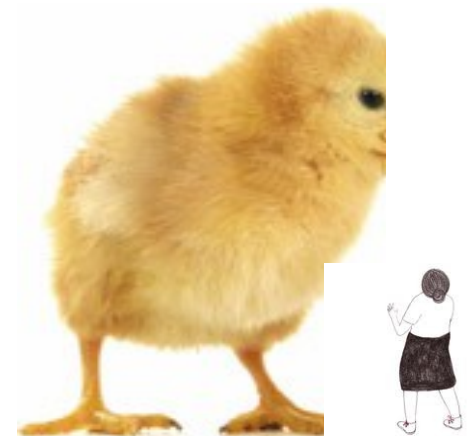
Comparative embryology - Baer's laws of embryology

Gedankenexperiment K.E. von Baer, 1828:

“Stellen wir uns vor, dass Vögel ihre eigene Entwicklung studieren und dass sie es waren, die die Struktur adulter Säugetiere und des Menschen untersucht haben. Würden ihre Physiologiebücher nicht folgendes lehren?

'Diese vierbeinigen Tiere weisen viele Ähnlichkeiten zu unseren eigenen Embryonen auf. Ihre Schädelknochen sind nur lose zusammengefügt und sie haben keinen Schnabel, genauso wie wir in den ersten fünf oder sechs Tagen unserer Brutzeit; ihre Extremitäten sind sich alle sehr ähnlich, so wie unsere in demselben Stadium; bis auf dünne Federschäfte haben sie keine wirklichen Federn an ihrem Körper, sodass wir als Küken im Nest bereits weiter entwickelt sind als sie es jemals sein werden ... Darüber hinaus können sich diese Säugetiere noch lange nach der Geburt nicht selbständig ernähren, sie können sich niemals eigenständig von der Erde erheben und sehen sich selbst als weiter entwickelt als wir?' “

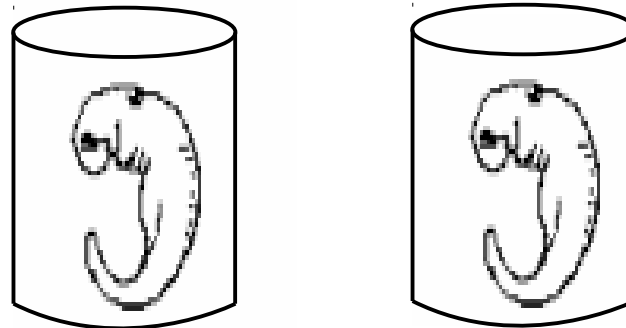
- von Baer, 1828, *Entwicklungsgeschichte der Thiere*



Comparative embryology - Baer's laws of embryology



Karl Ernst von Baer
1792-1876

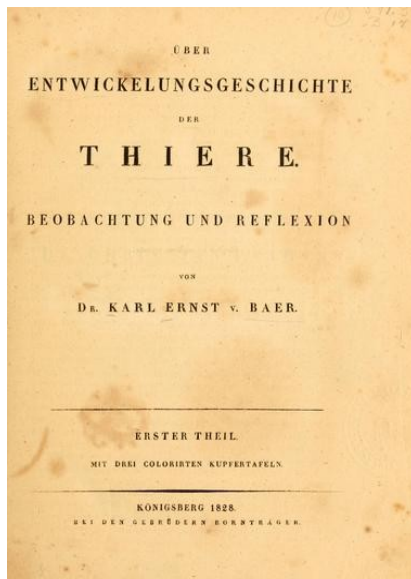


„Ich besitze zwei kleine Embryonen in Weingeist, für die ich versäumt habe die Namen zu notieren, und ich bin jetzt durchaus nicht im Stande, die Klasse zu bestimmen, der sie angehören. Es können Eidechsen, kleine Vögel oder ganz junge Säugetiere seyn. So übereinstimmend ist die Kopf- und Rumpfbildung in diesen Thieren.“

- K.E. von Baer, (1828), *Entwicklungsgeschichte der Thiere* (S. 221)

- (1) General features of the embryo appear earlier than special features
- (2) Special characters develop from general characters
- (3) Embryos of different species progressively diverge from one another during ontogeny**
- (4) Embryos of one animal can never resemble the adult form of another animal, but only its embryo

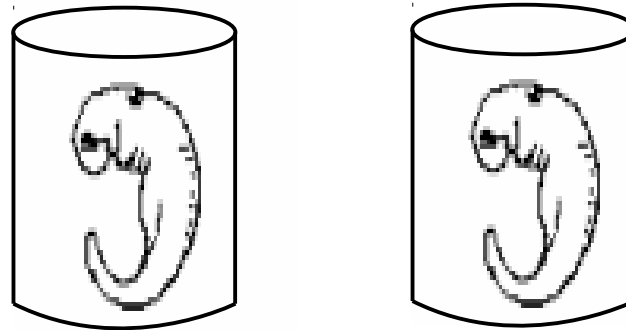
- Existence of a stage in which embryos of different vertebrate species could not be distinguished
- One of the milestone discoveries in developmental biology!



Comparative embryology - Baer's laws of embryology



Karl Ernst von Baer
1792-1876

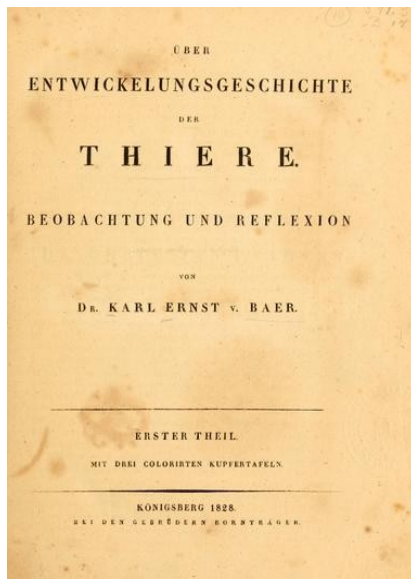


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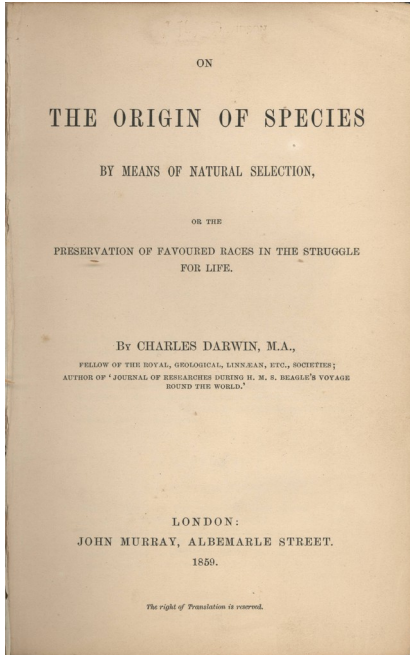
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→ **Pre-Darwin** → **no connection to Darwinian evolution**



Post-Darwin



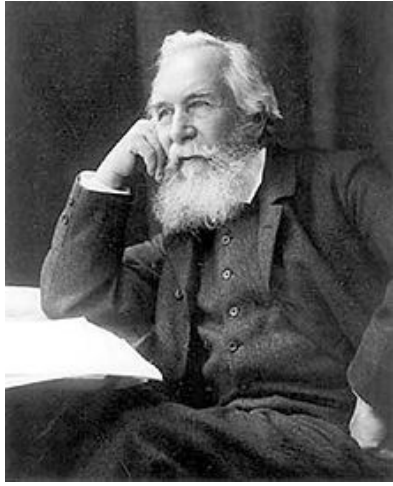
Darwin delivered the connection of:

- Theory of evolution
- Common origin of species

} Mechanism:
} Natural Selection

Connection between origin / descent, systematics, and ontogeny?

Post-Darwin - Ernst Haeckel

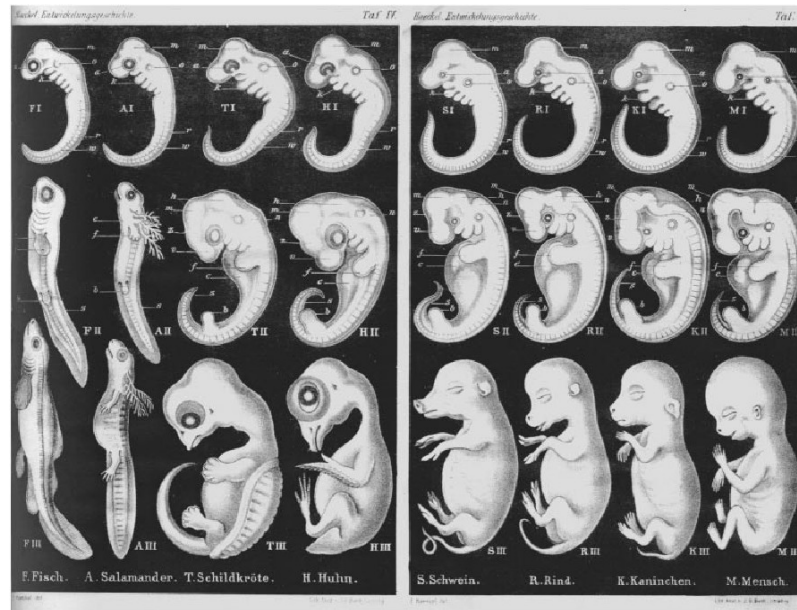


Ernst Haeckel
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Haeckel's biogenetic law (1866):

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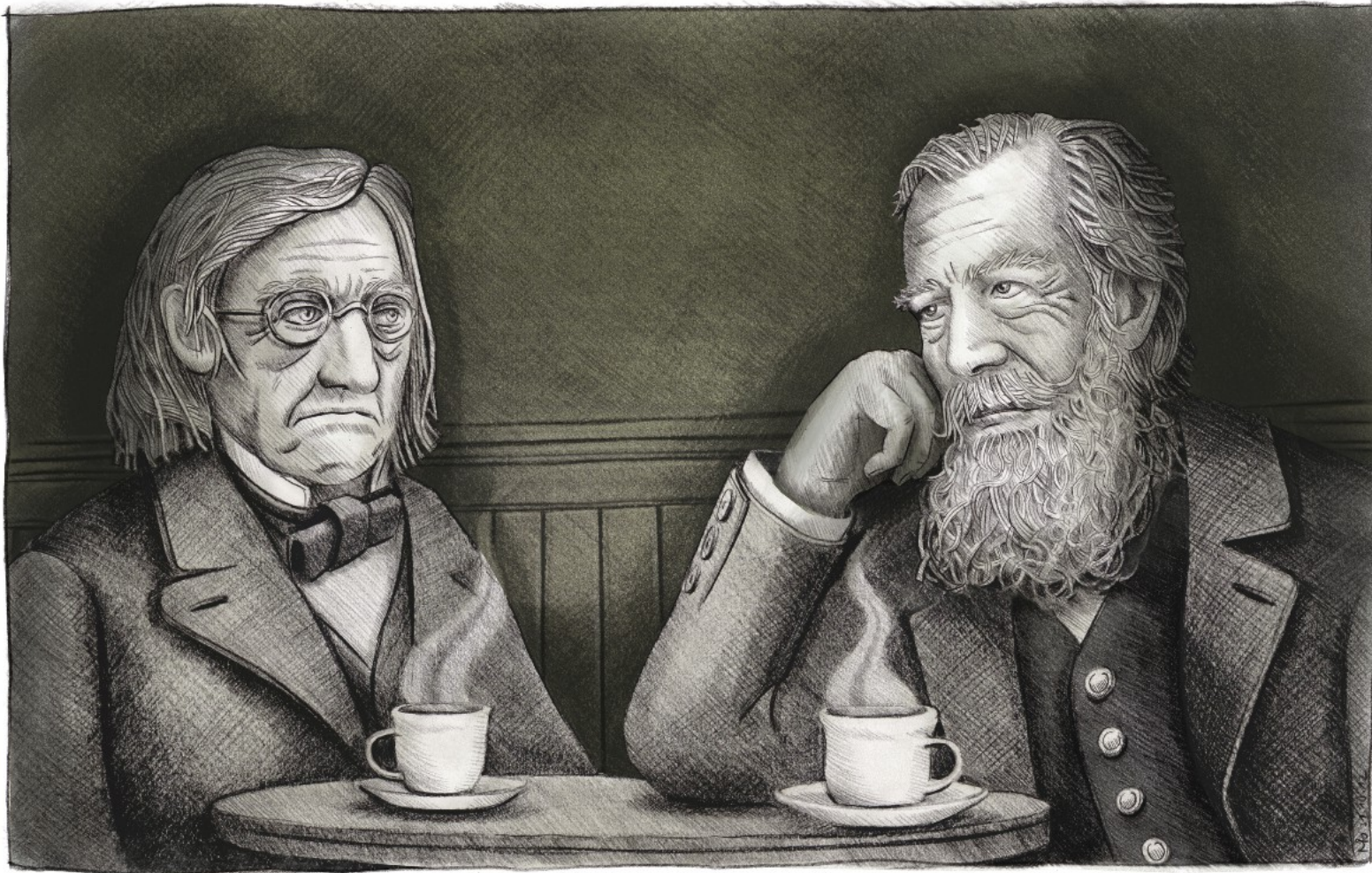
- Mostly wrong and based on purposely falsified data:



- Groundwork for social darwinism and nazi racial ideology

BUT: for the first time approaching developmental biology from an evolutionary perspective

Comparative embryology – 19th century



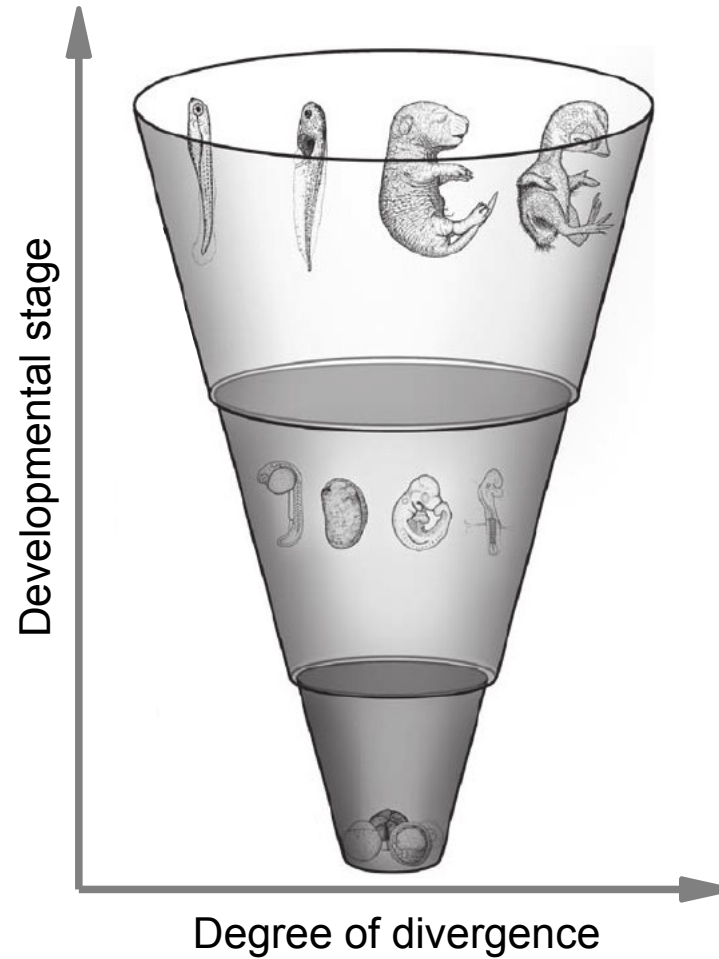
von Baer's contribution

- Existence of a stage of max. morphological conservation during embryogenesis of different vertebrate species

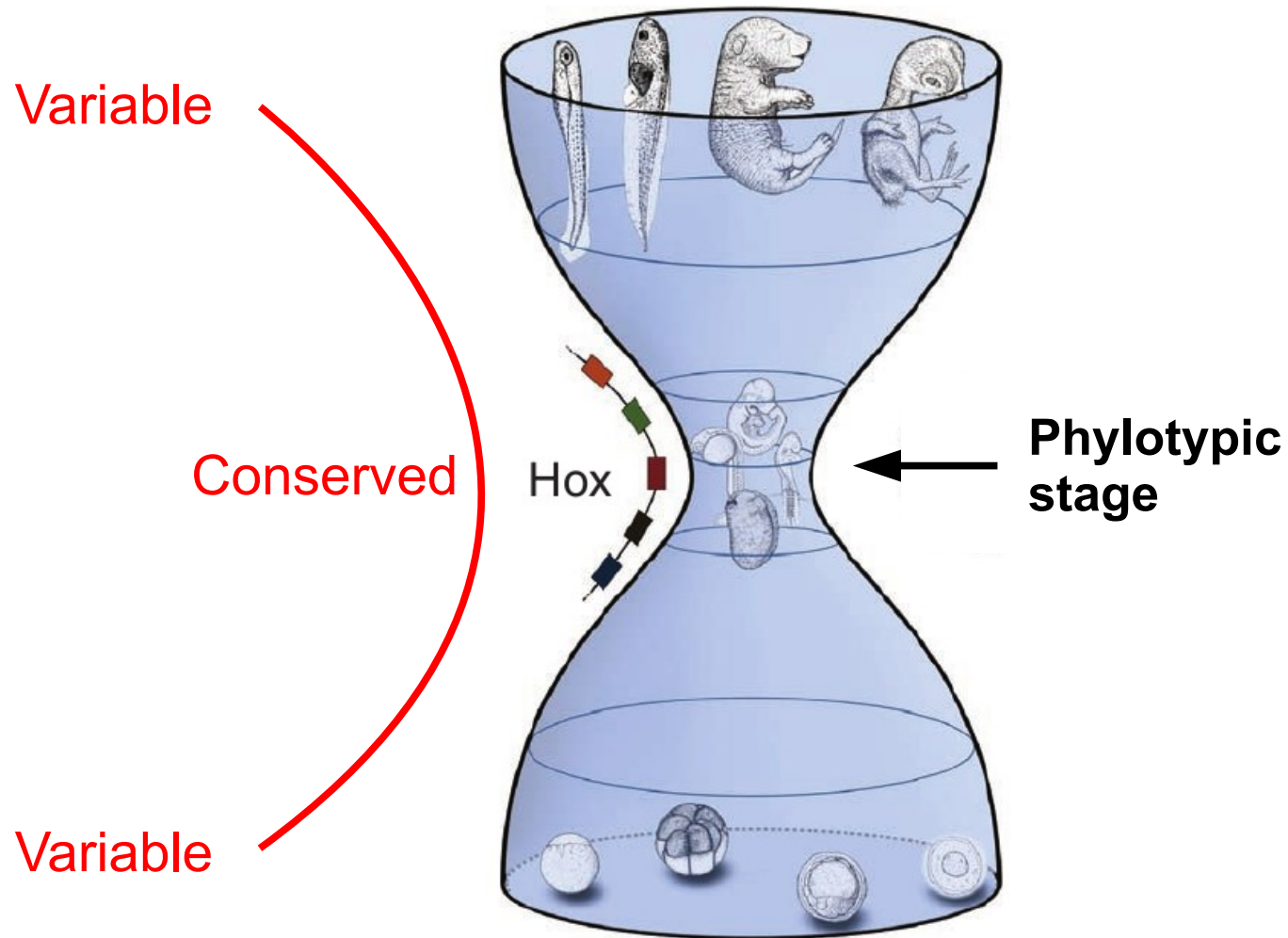
Haeckel's contribution

- Integration of different disciplines, such as taxonomy and embryology, into the then new Darwinian framework
- Use of such data for phylogeny reconstruction

Comparative embryology – The funnel model



Comparative embryology – The hourglass model



- 21st century – the genomic level

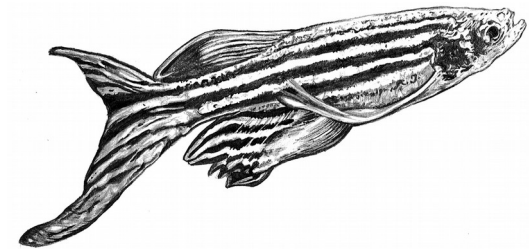
LETTER

doi:10.1038/nature09632

A phylogenetically based transcriptome age index mirrors ontogenetic divergence patterns

Tomislav Domazet-Lošo^{1,2} & Diethard Tautz¹

Nature (2010)



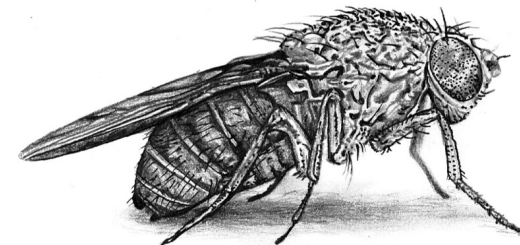
LETTER

doi:10.1038/nature09634

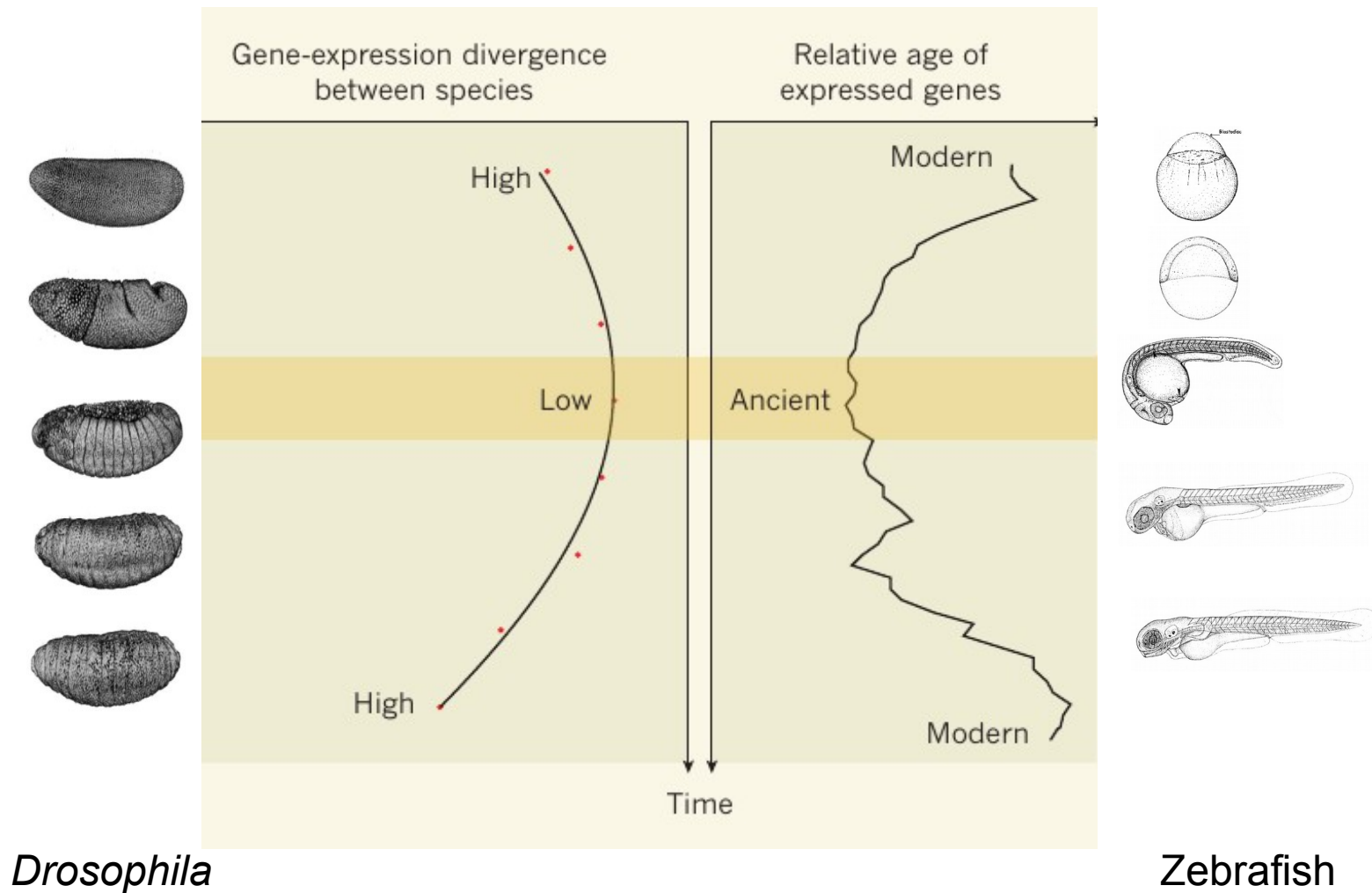
Gene expression divergence recapitulates the developmental hourglass model

Alex T. Kalinka^{1*}, Karolina M. Varga^{1*†}, Dave T. Gerrard², Stephan Preibisch¹, David L. Corcoran³, Julia Jarrells¹, Uwe Ohler³, Casey M. Bergman² & Pavel Tomancak¹

Nature (2010)

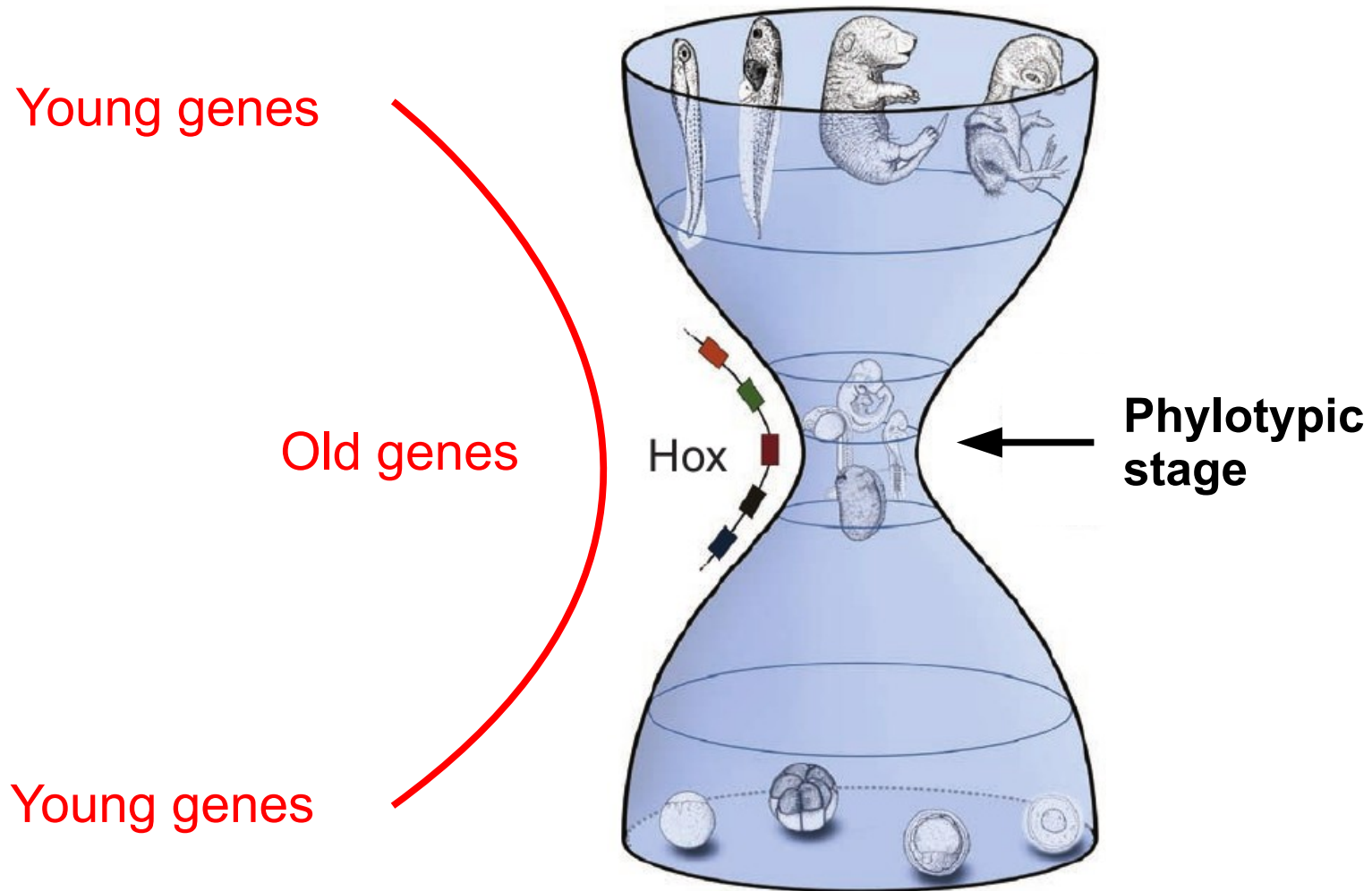


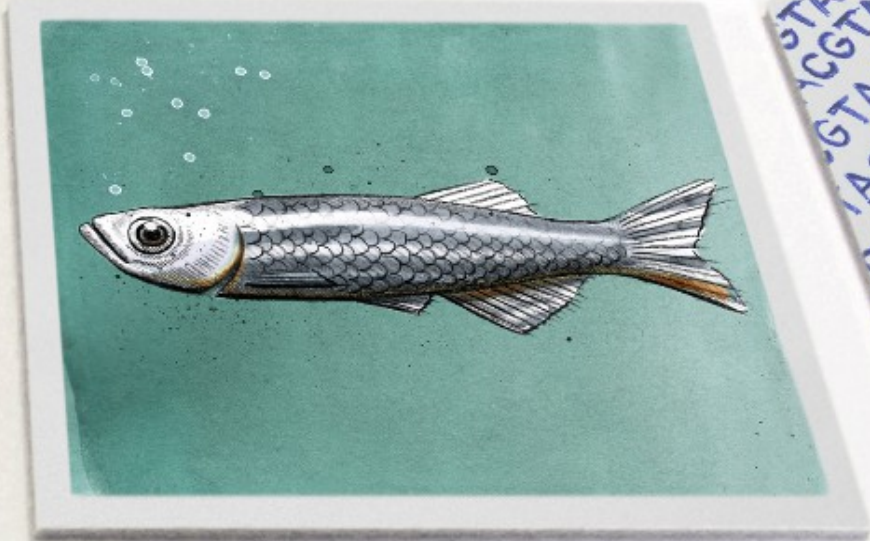
21st century – the genomic level



1. Morphology AND transcriptomes follow an hourglass pattern!
2. Max. conservation of the transcriptomes observed at the morphological phylotypic stage!

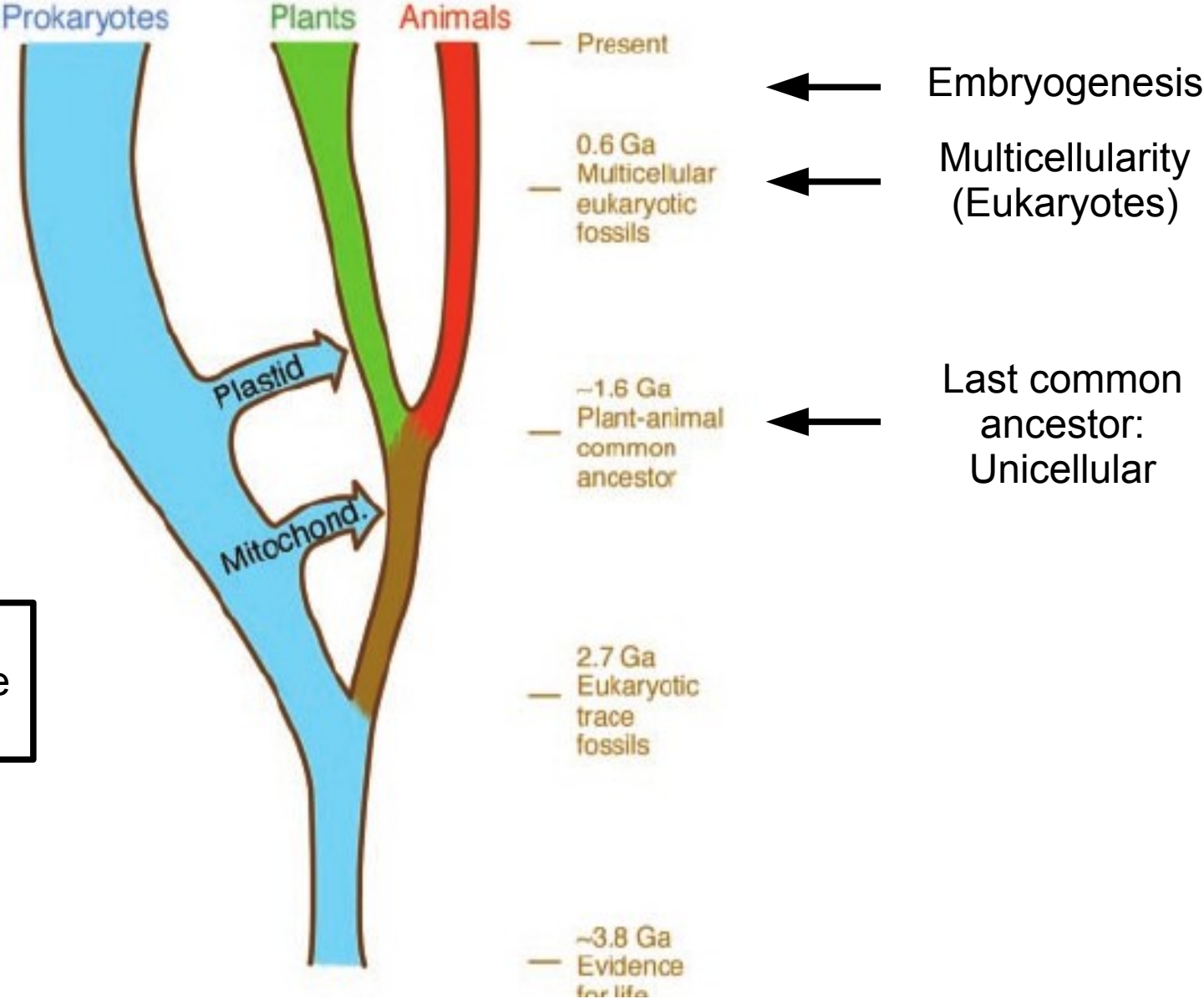
21st century – the genomic level





Evolution of embryogenesis

Unicellular life → Multicellular life → Embryogenesis → Complex life



Embryogenesis evolved at least twice and independently

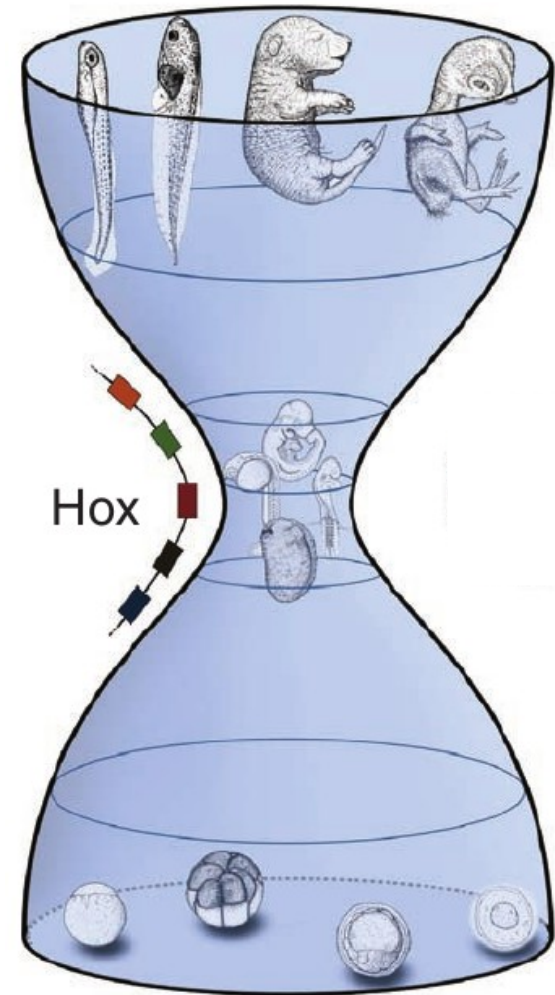
What about plants?

Young genes

- Is there a transcriptional hourglass in plants?

Old genes

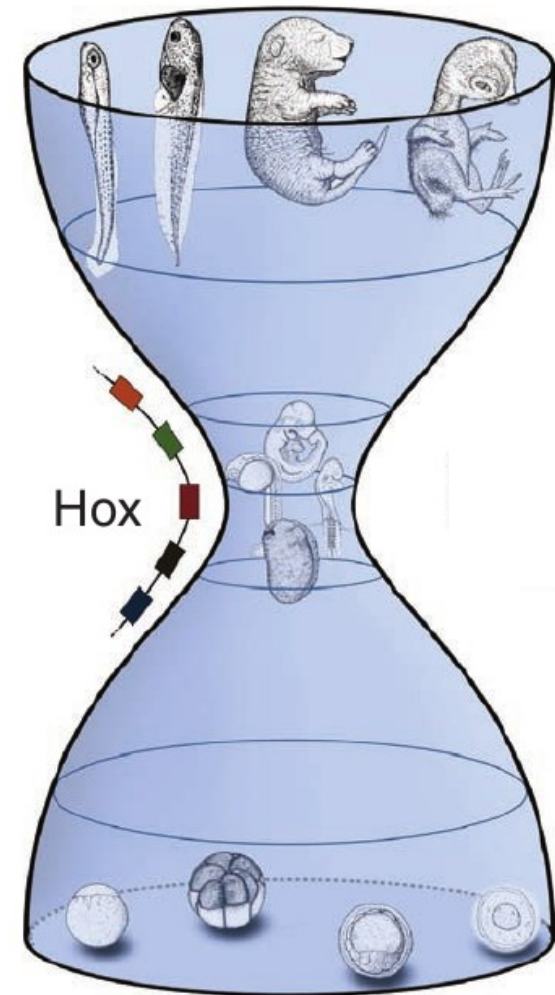
Young genes



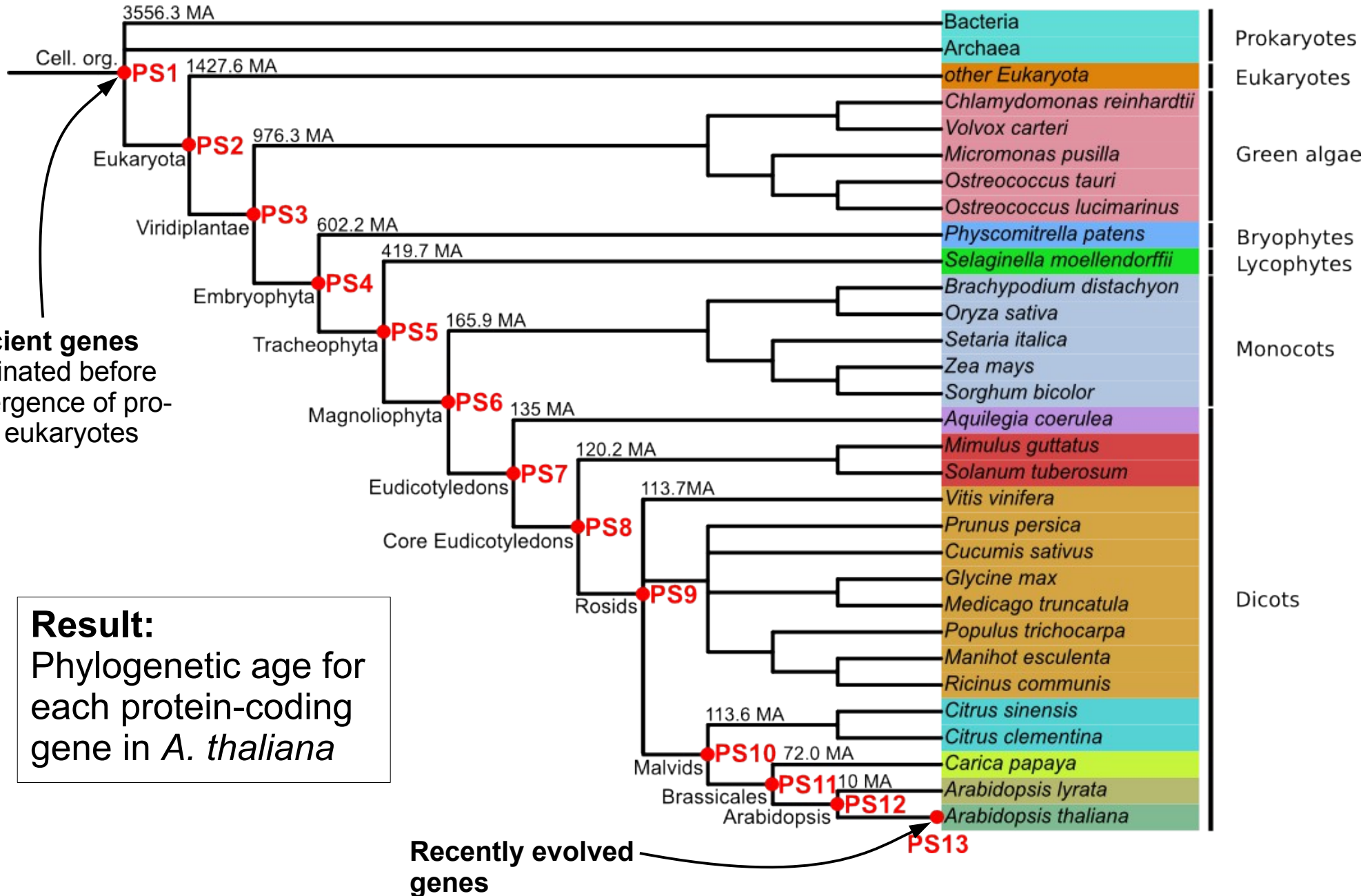
What about plants?

Two pieces of information:

1. Evolutionary age for each gene
2. Transcriptomes of various embryo stages



Phylostratigraphic map of *A. thaliana*



- based on completely sequenced species (n = 1452)

Step 2: How can we apply phylostratigraphy to transcriptional data?

adapted from Domazet-Lošo and Tautz, 2010, *Nature*



Introduce expression intensity
of a gene as a weight for its
phylogenetic age



Sum over all genes

=

← **Transcriptome Age Index
(TAI)**



Definition TAI:

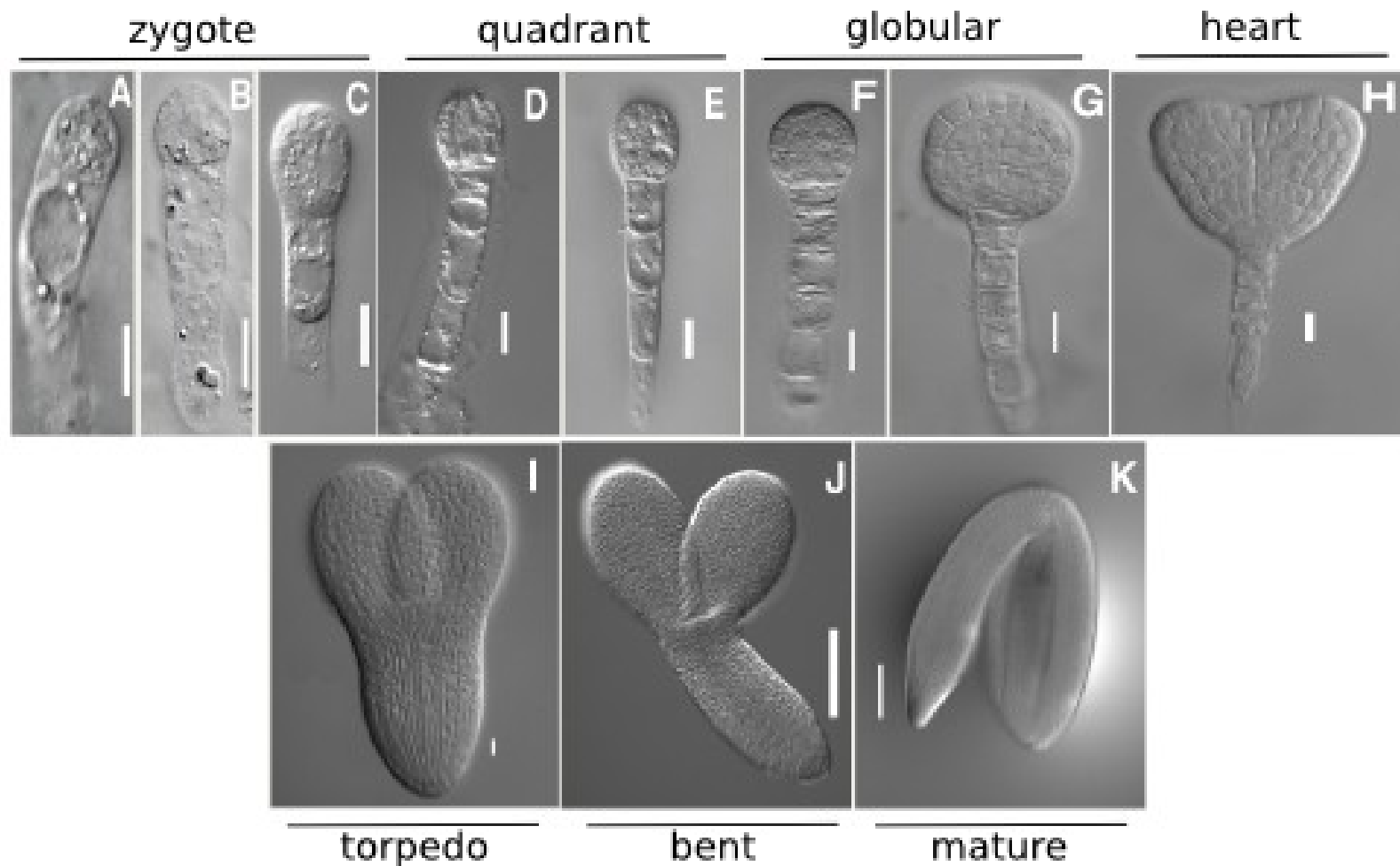
The mean evolutionary age of a transcriptome, where the evolutionary age (PS) of each gene is weighted by its expression level.

Goal:

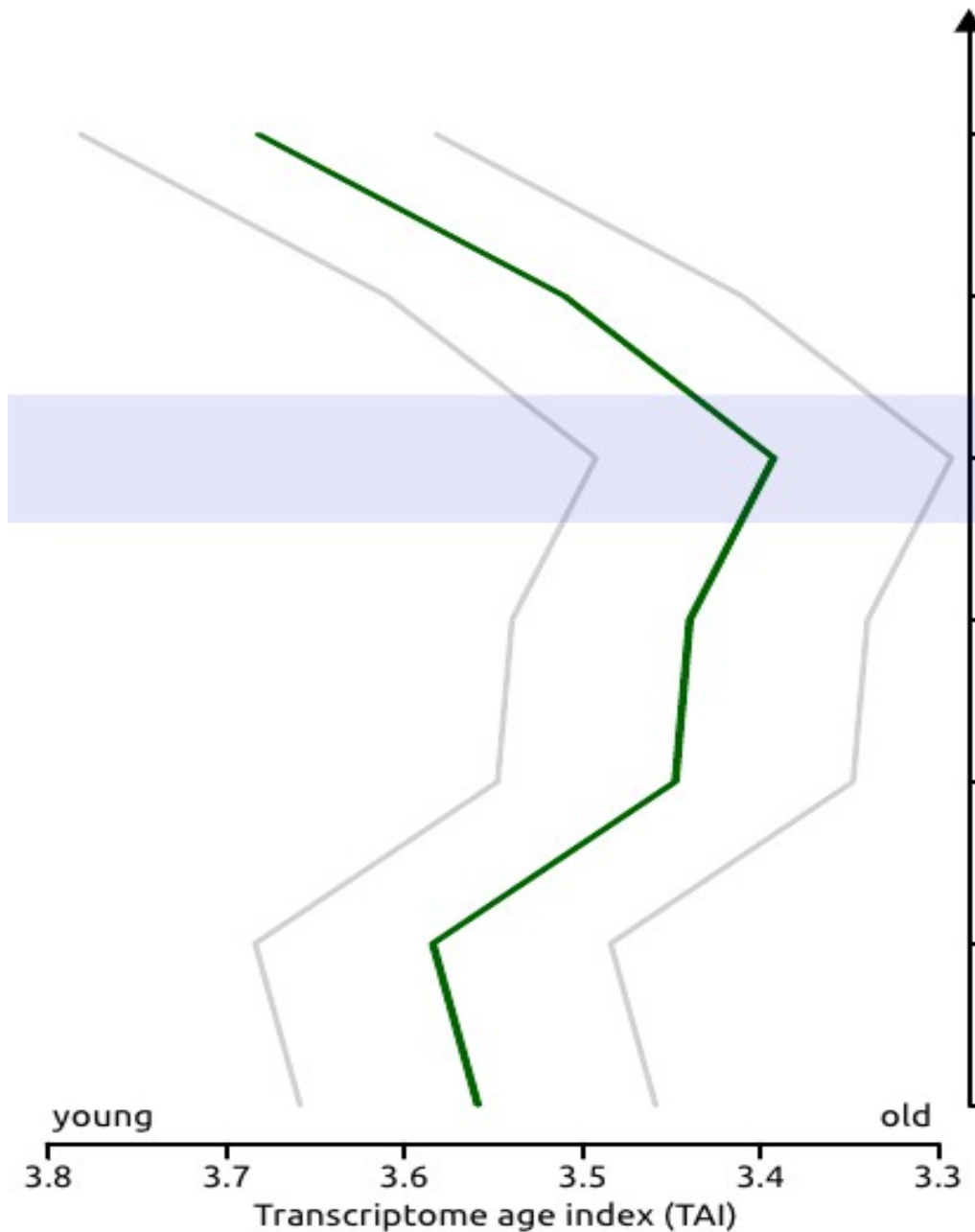
Compute TAI across multiple embryo stages

→ compare TAI profile to hourglass pattern

Embryogenesis in *Arabidopsis thaliana*



TAI pattern of *A. thaliana* embryogenesis is reminiscent of the developmental hourglass

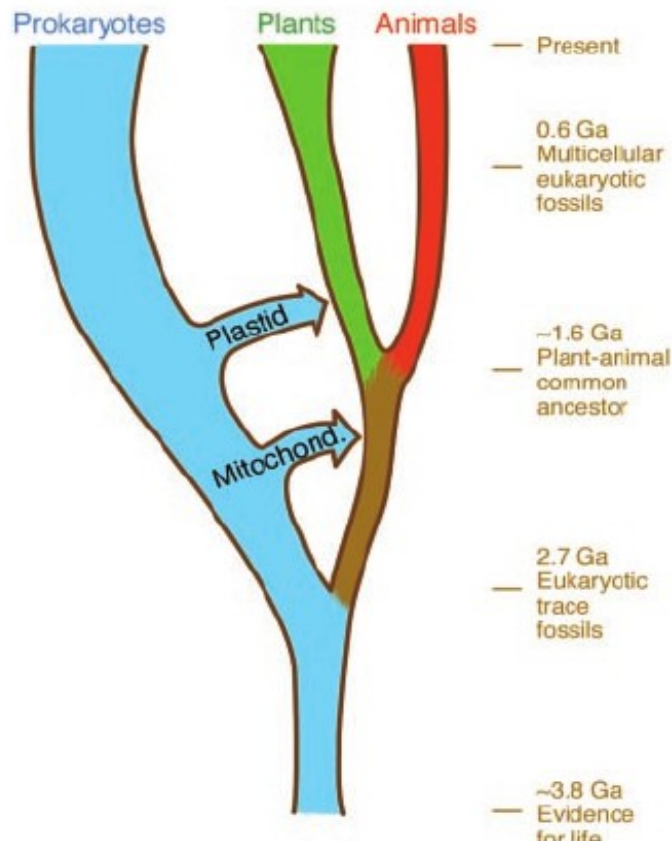


Intermediate conclusions

Embryogenesis evolved twice and independently in animals and plants

Embryogenesis morphologically and genetically different in animals and plants

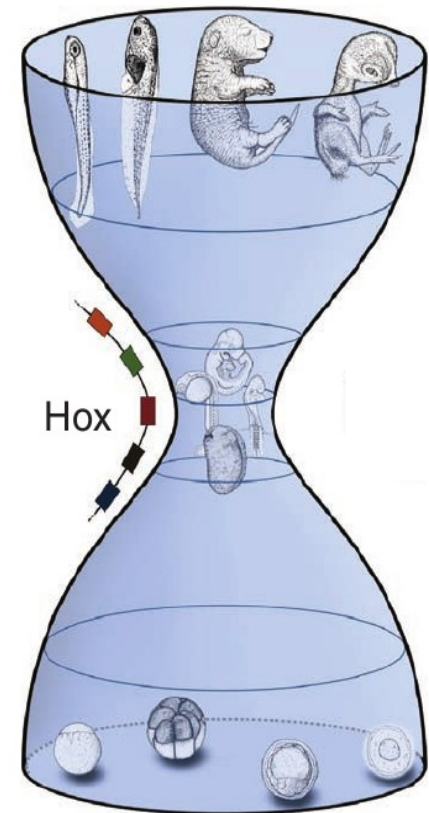
But transcriptomes of animals and plants show the same hourglass pattern



Young genes

Old genes

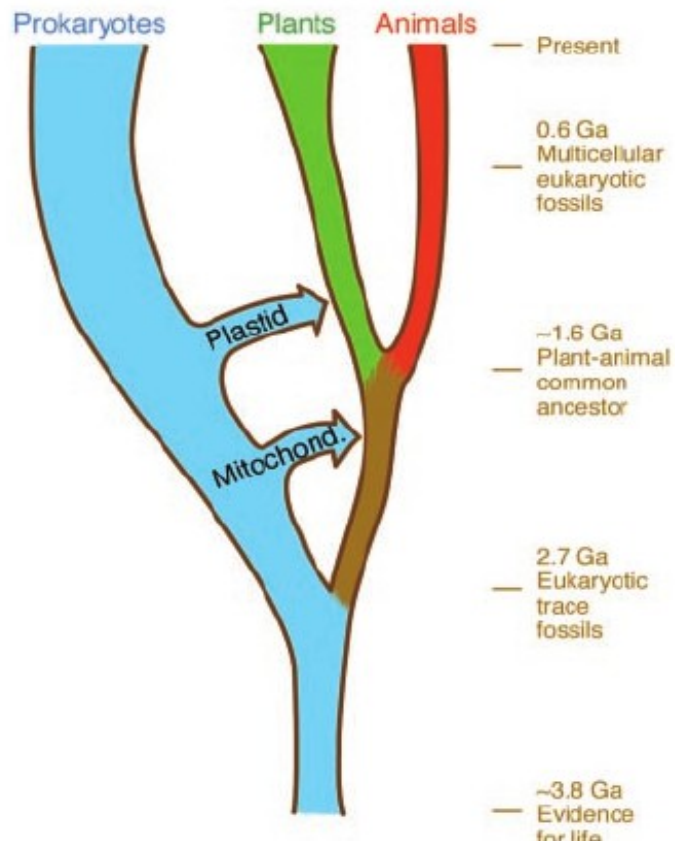
Young genes



Fundamental question

Is the hourglass pattern

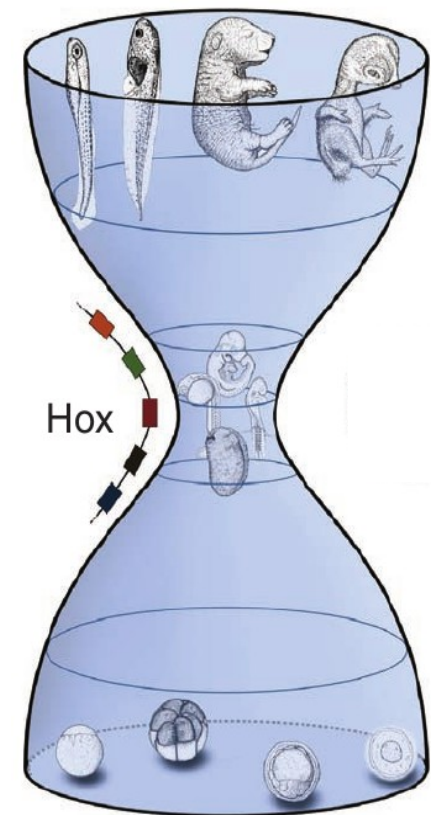
- **an evolutionary relic** and possibly not functional anymore?
- **or actively maintained** and possibly still functional?



Young genes

Old genes

Young genes



Transcriptome divergence index - TDI

TDI based on sequence divergence



Sequence comparison of orthologous genes in related species



Sequence divergence = Ka/Ks

Ka = nonsyn. mutations
 Ks = syn. mutations

Evolutionary conserved genes
→ sequence divergence small

Evolutionary variable genes
→ sequence divergence large



Genome-wide → Ka/Ks ratios for all orthologous gene pairs

A. thaliana vs. *A. lyrata*

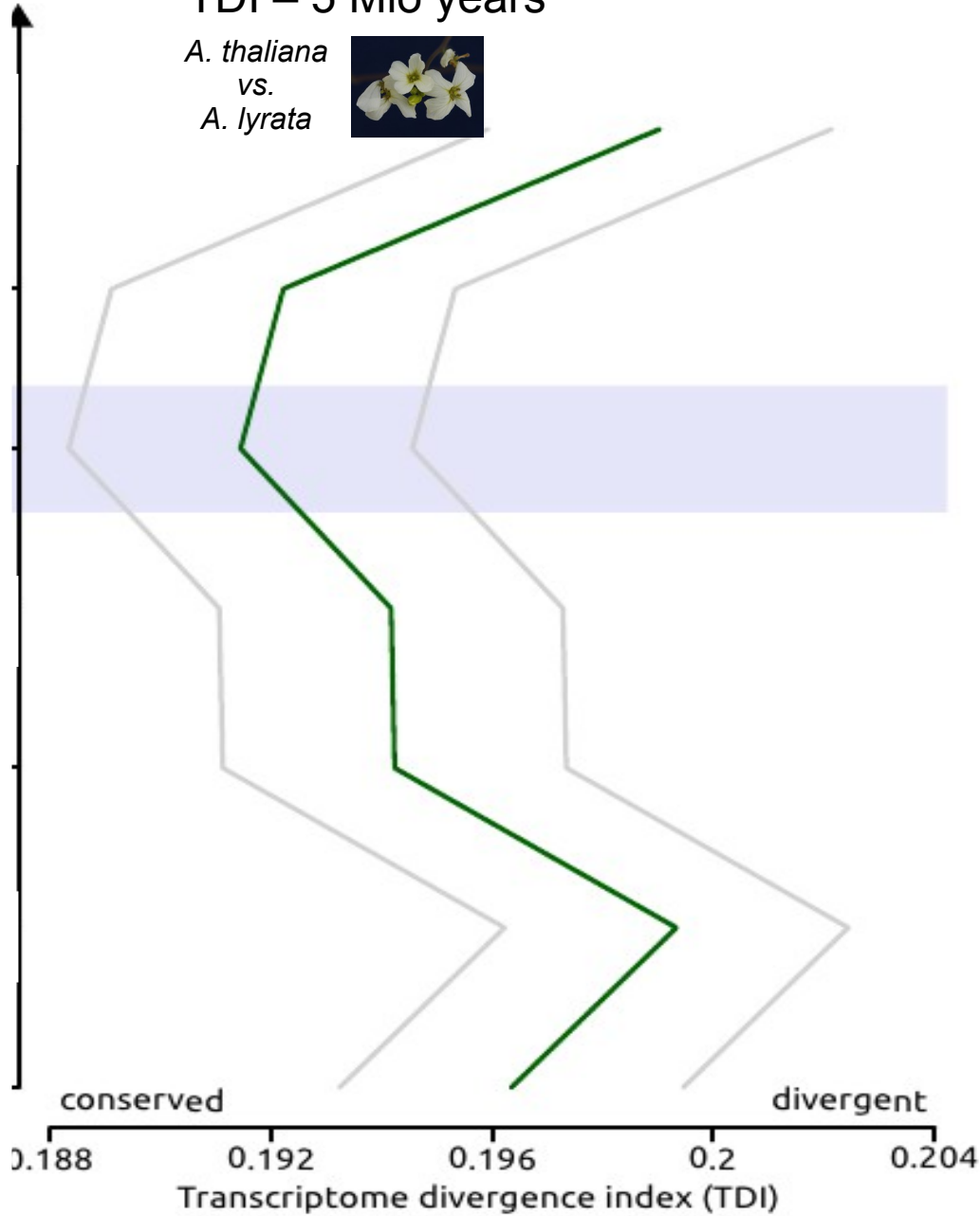


**Ka/Ks
instead of PS**

TDI patterns

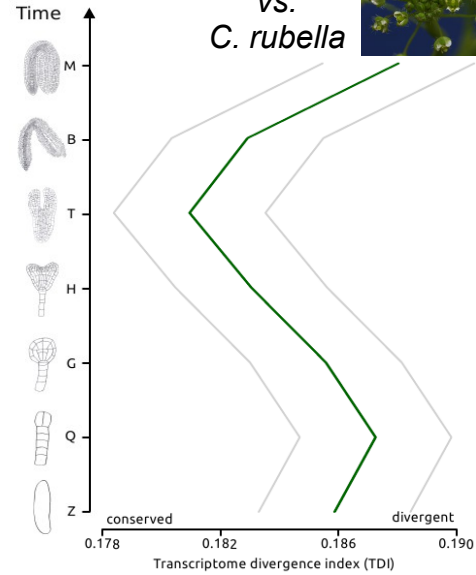
TDI – 5 Mio years*

A. thaliana
vs.
A. lyrata



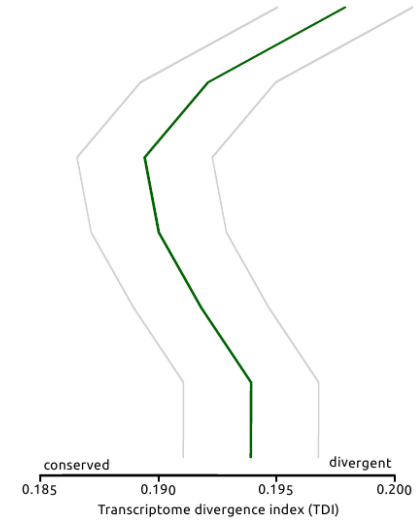
TDI – 10 Mio years*

A. thaliana
vs.
C. rubella



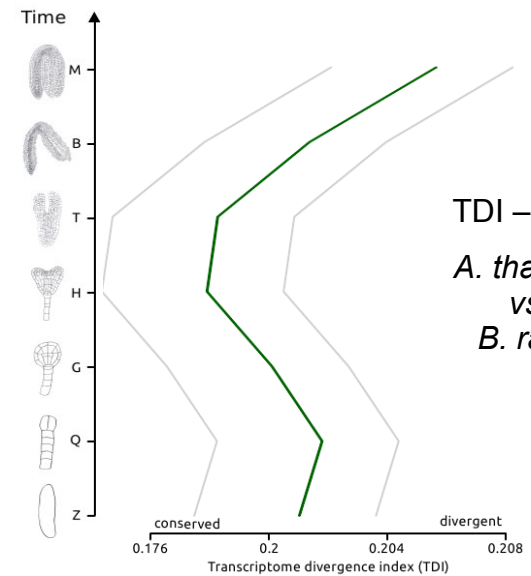
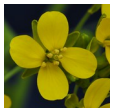
TDI – 12 Mio years**

A. thaliana
vs.
T. halophila

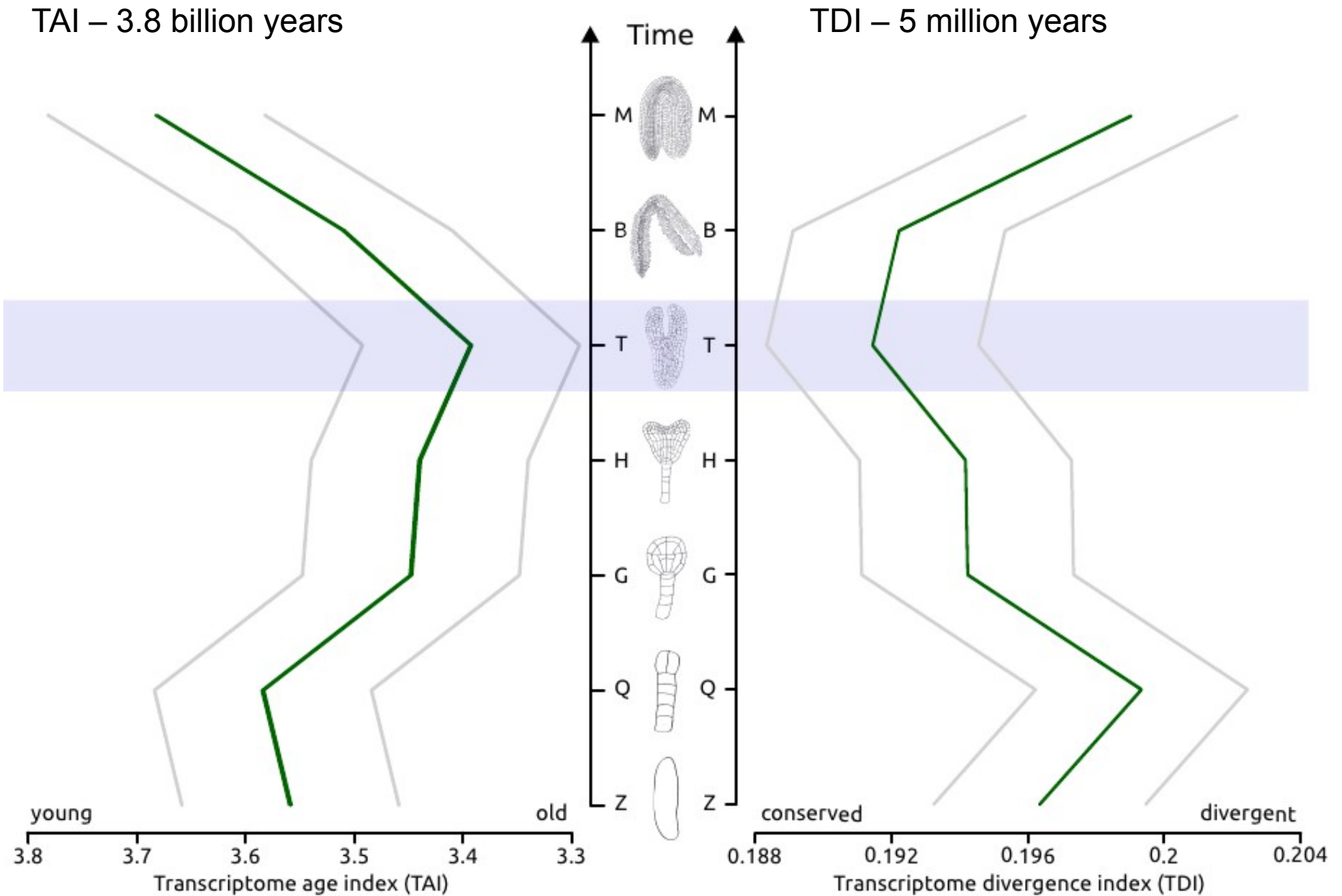


TDI – 16 Mio years*

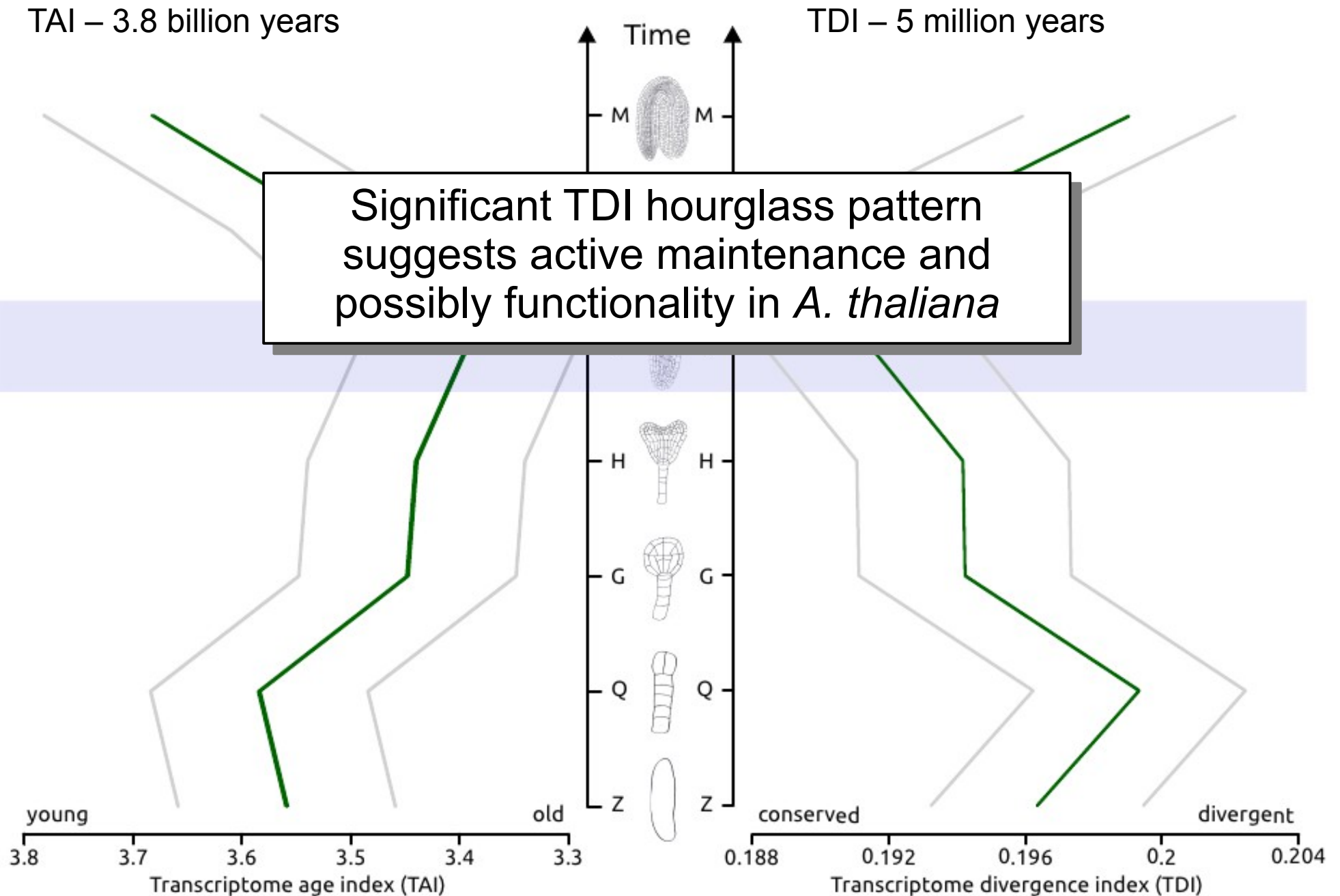
A. thaliana
vs.
B. rapa



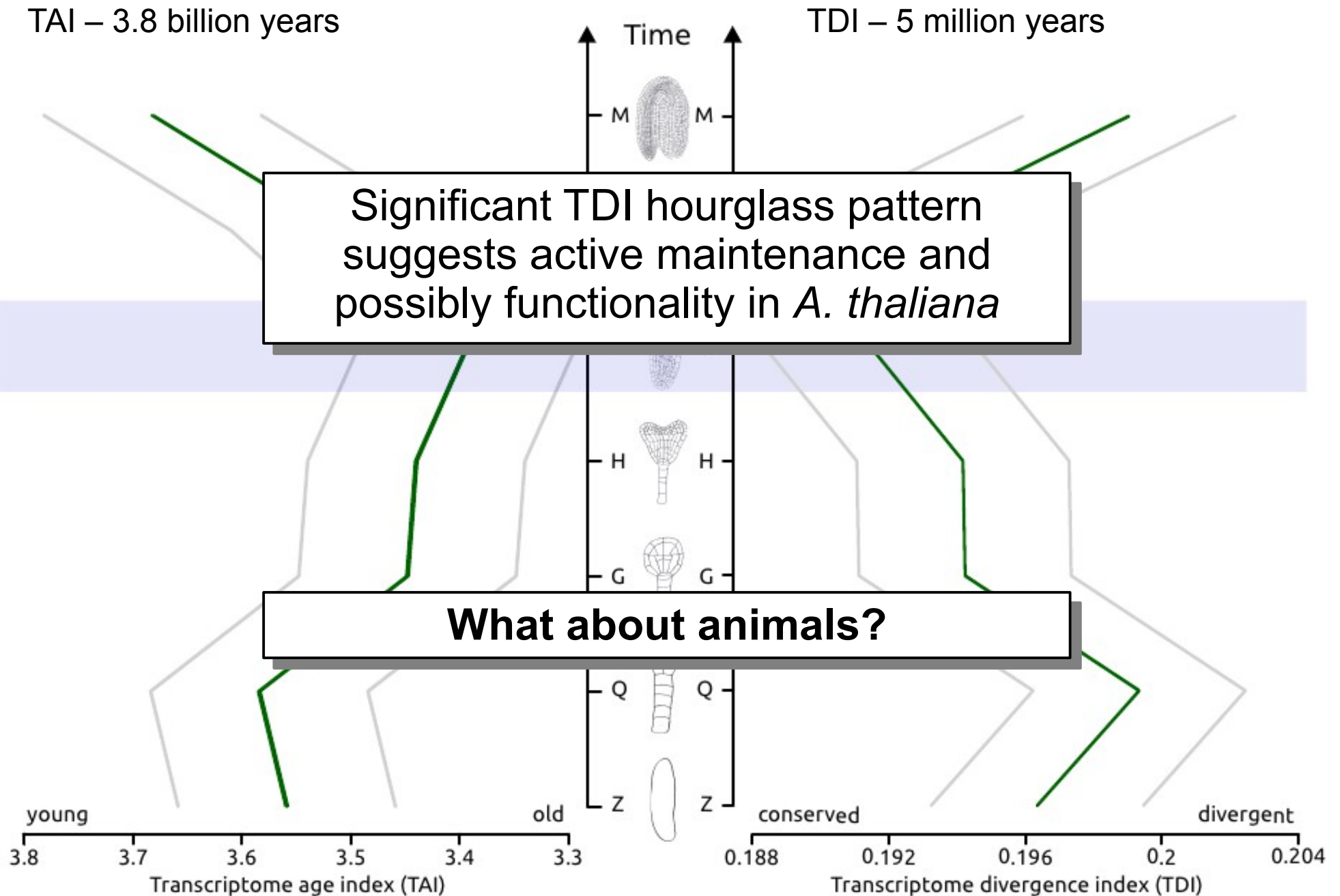
Developmental hourglass for *A. thaliana* embryogenesis



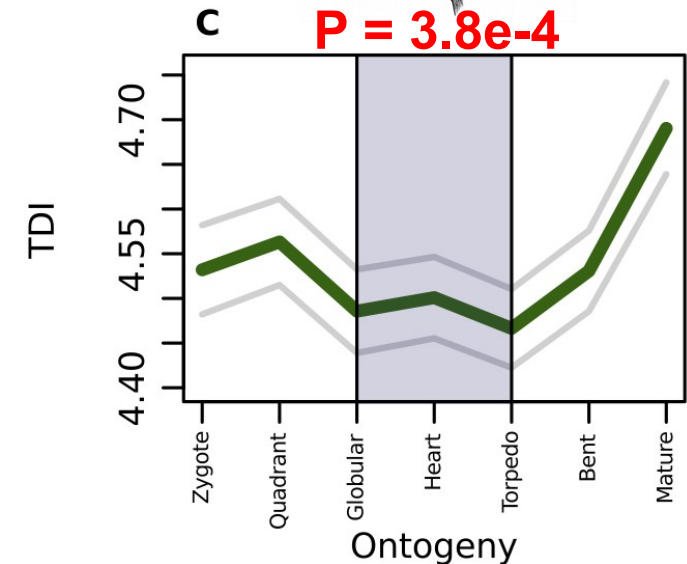
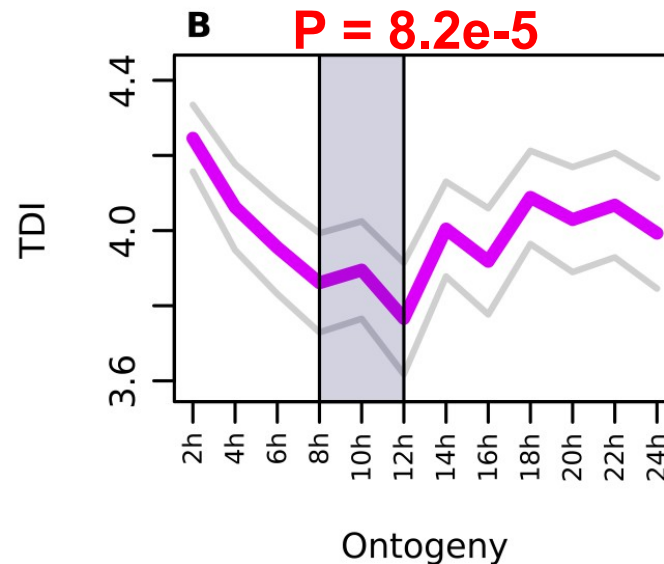
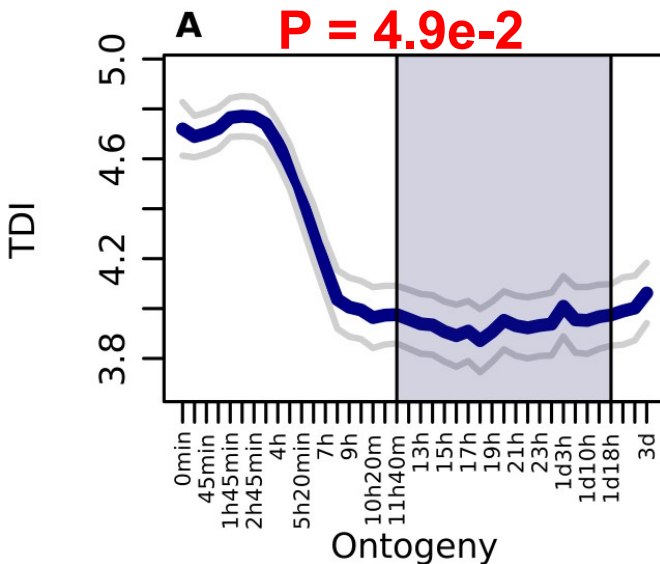
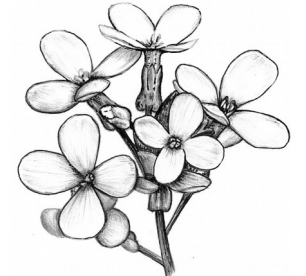
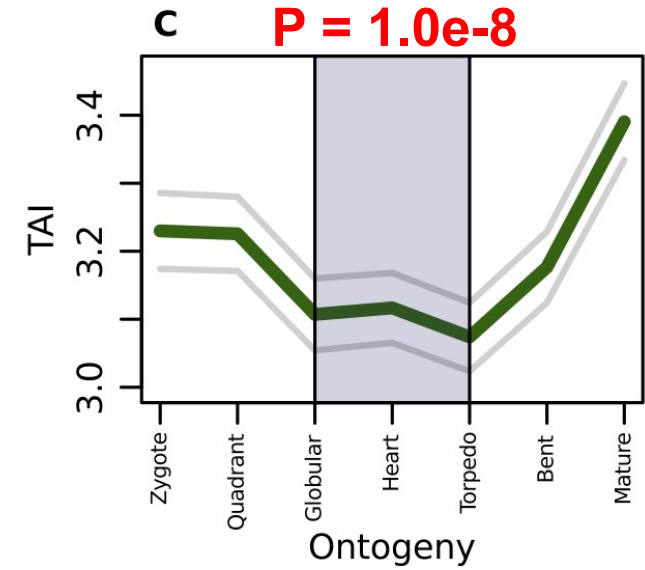
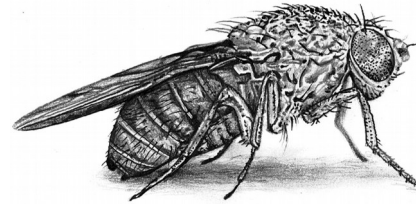
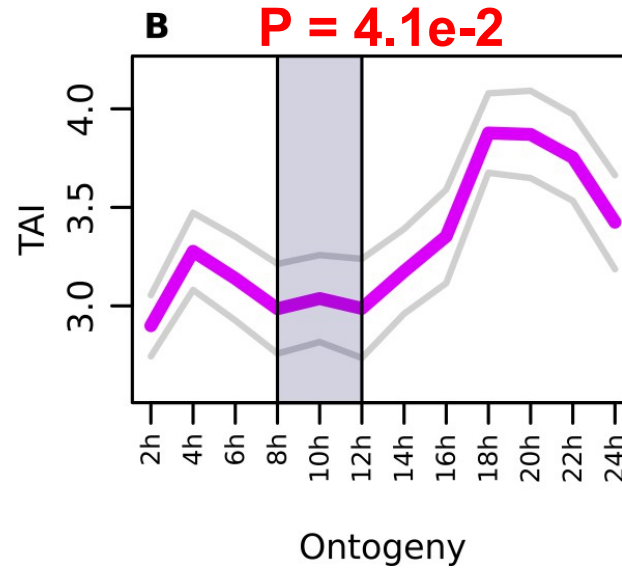
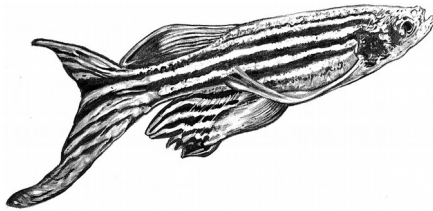
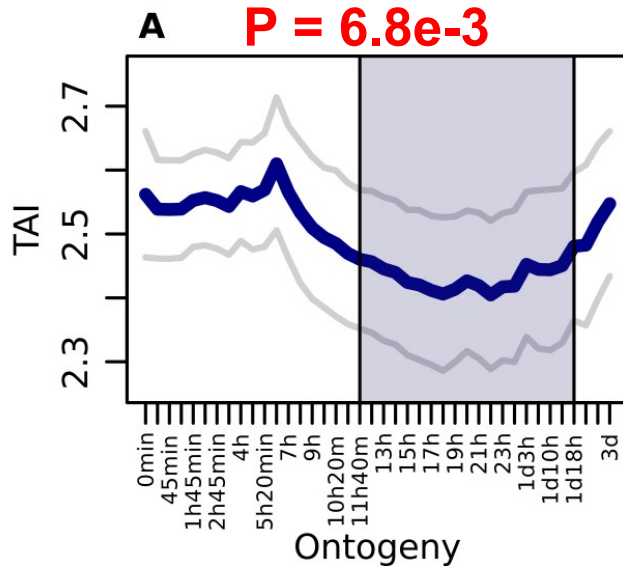
Developmental hourglass for *A. thaliana* embryogenesis



Developmental hourglass for *A. thaliana* embryogenesis

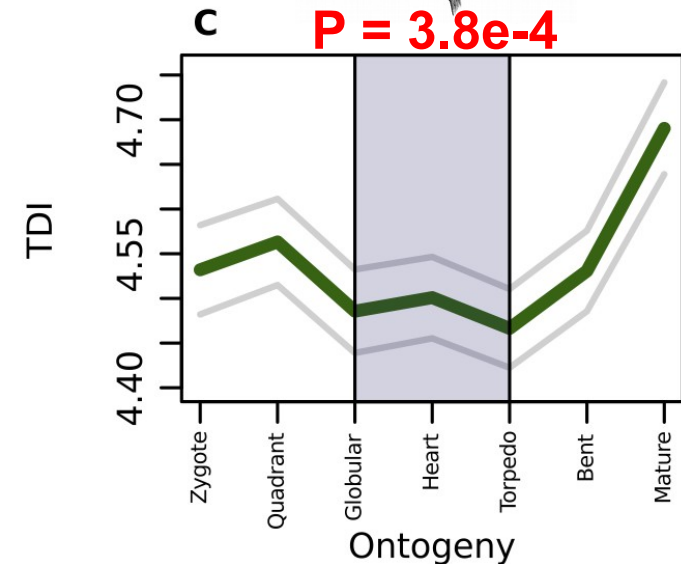
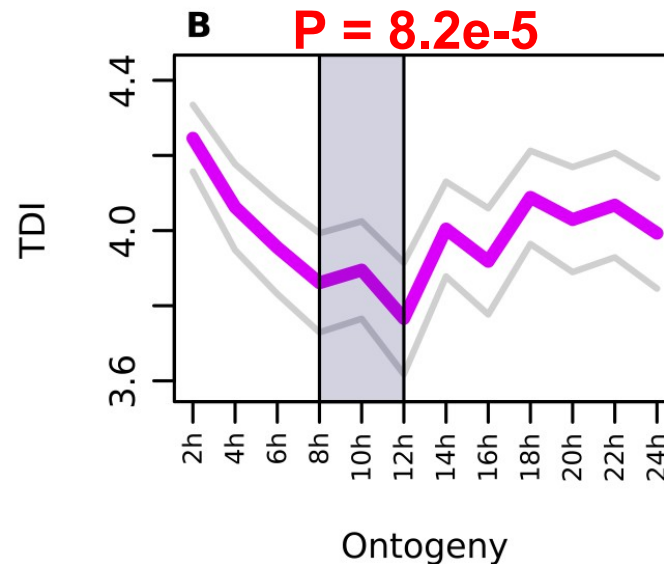
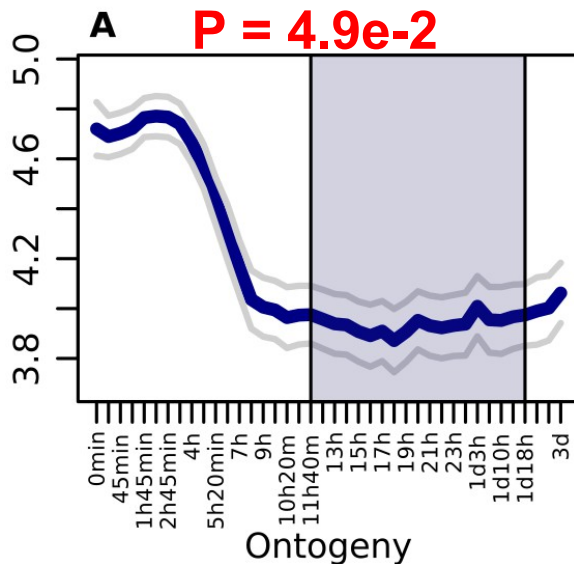
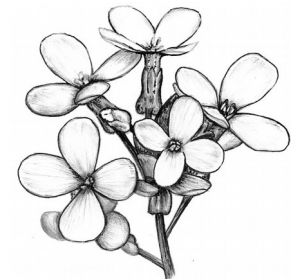
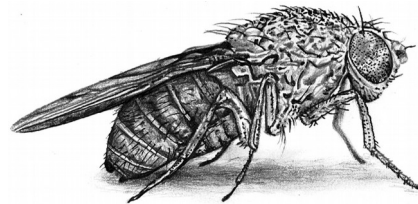
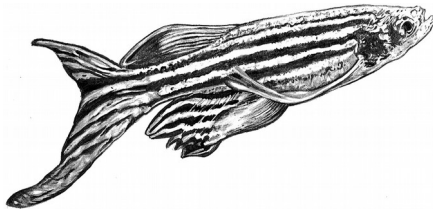


TAI and TDI for embryonic transcriptomes across kingdoms



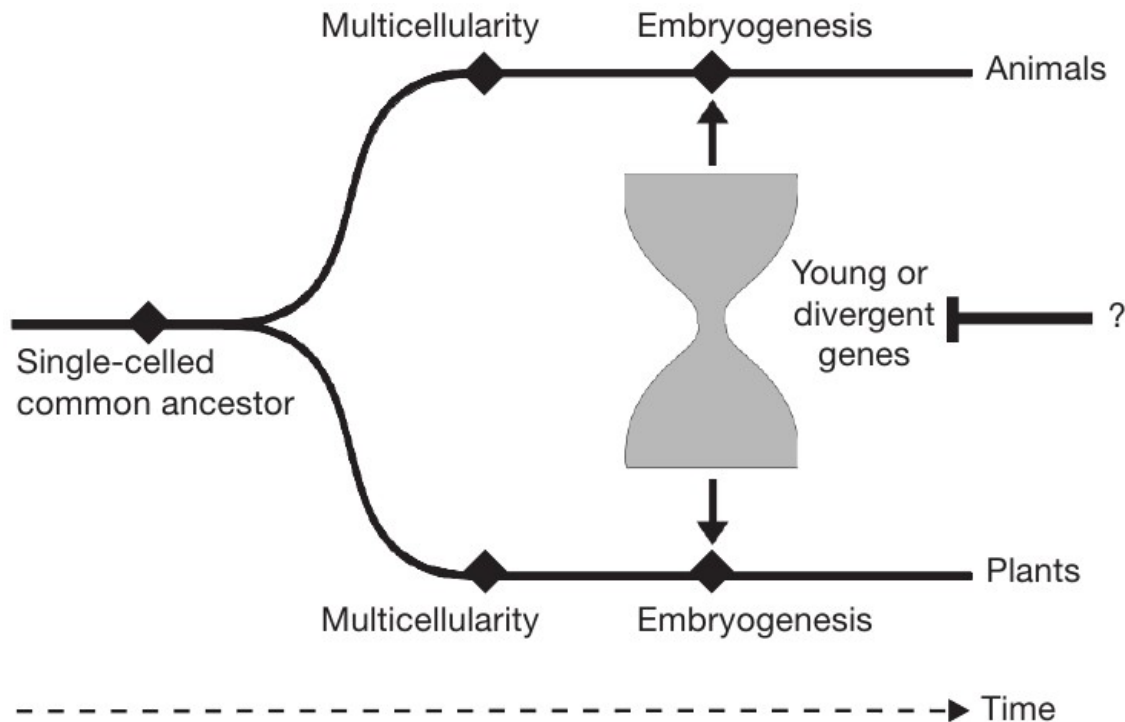
TAI and TDI for embryonic transcriptomes across kingdoms

Significant TDI hourglass patterns suggest active maintenance and possibly functionality in both animals and plants

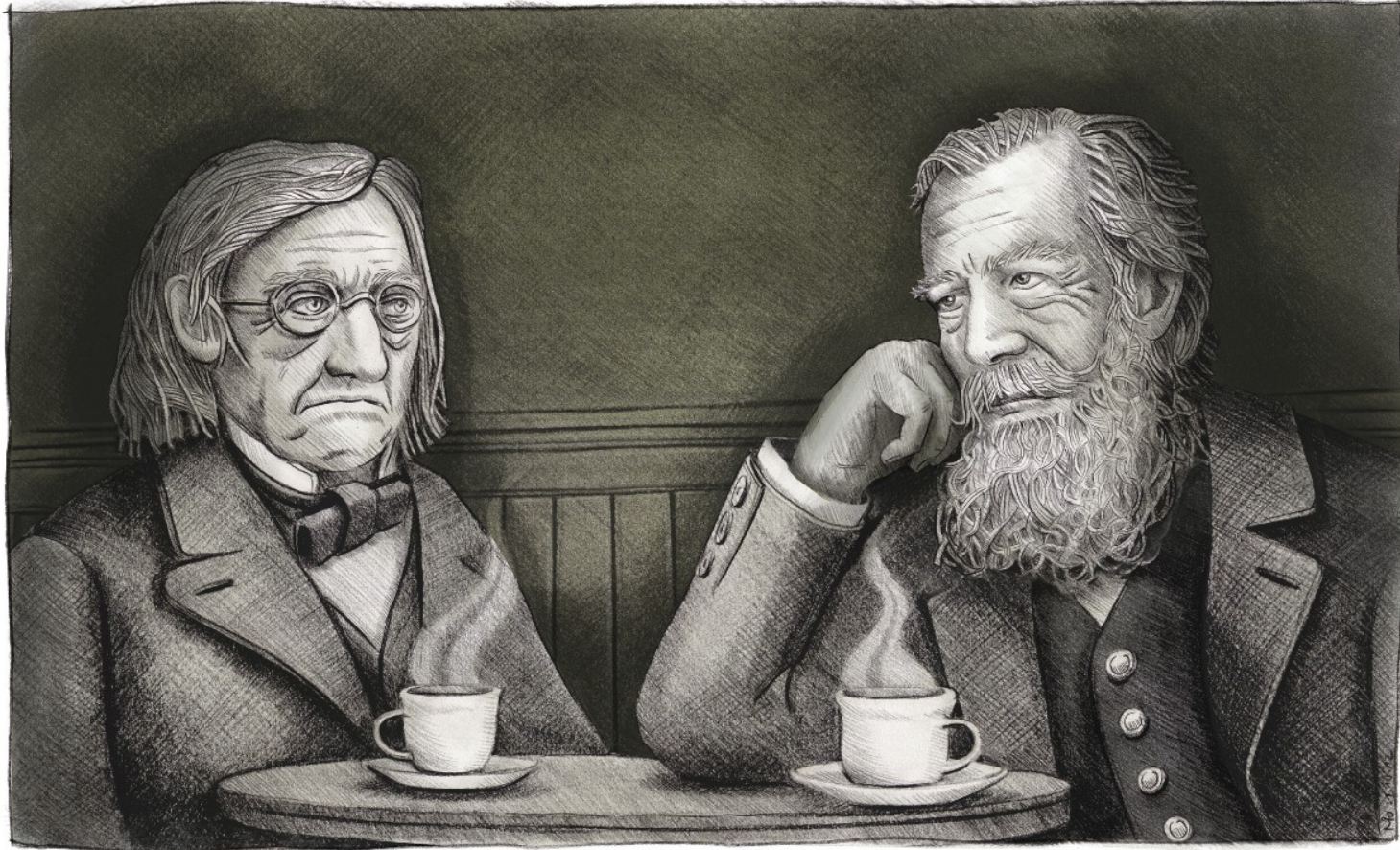


Intermediate conclusions

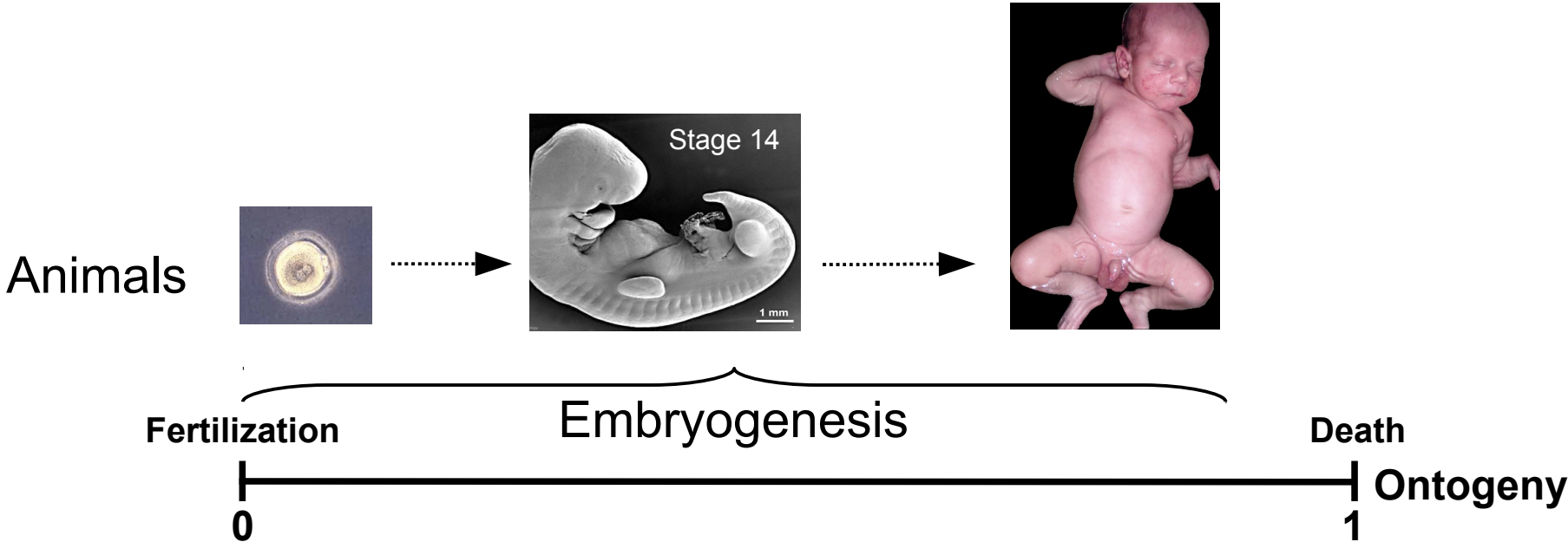
- Nature invented embryogenesis twice and independently
- Embryogenesis very different in plants and animals
- Developmental hourglass seems to be
 - essential
 - actively maintained
 - possibly still functional?



Is the hourglass pattern specific for embryogenesis?



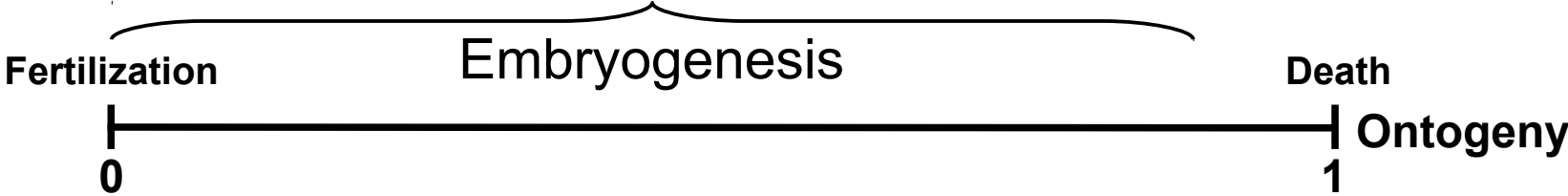
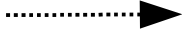
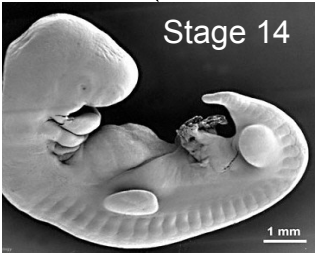
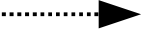
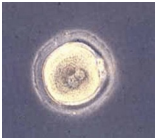
Ontogeny / organ development: animals vs. plants



Ontogeny / organ development: animals vs. plants

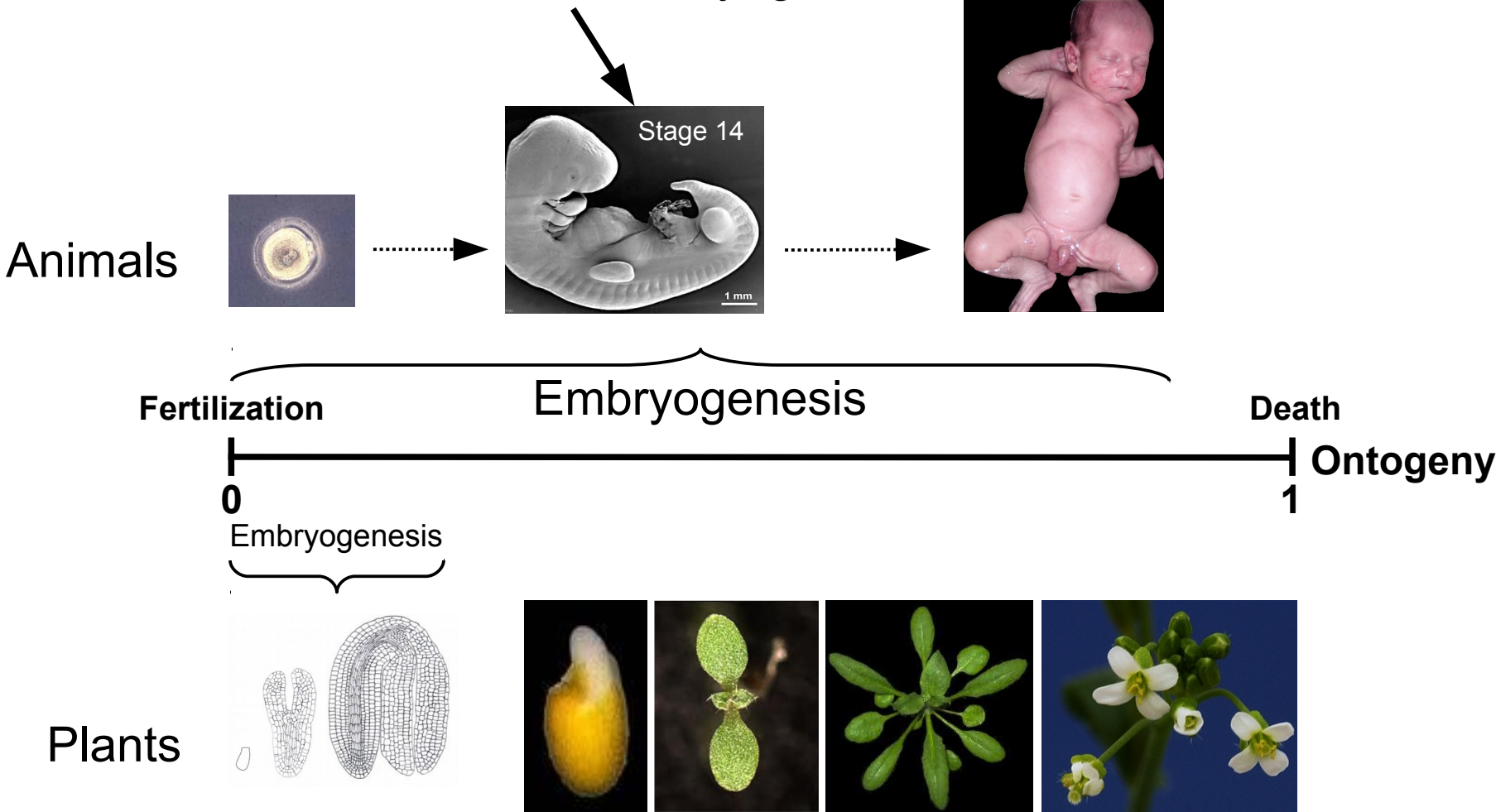
simultaneous & embryonic

Animals

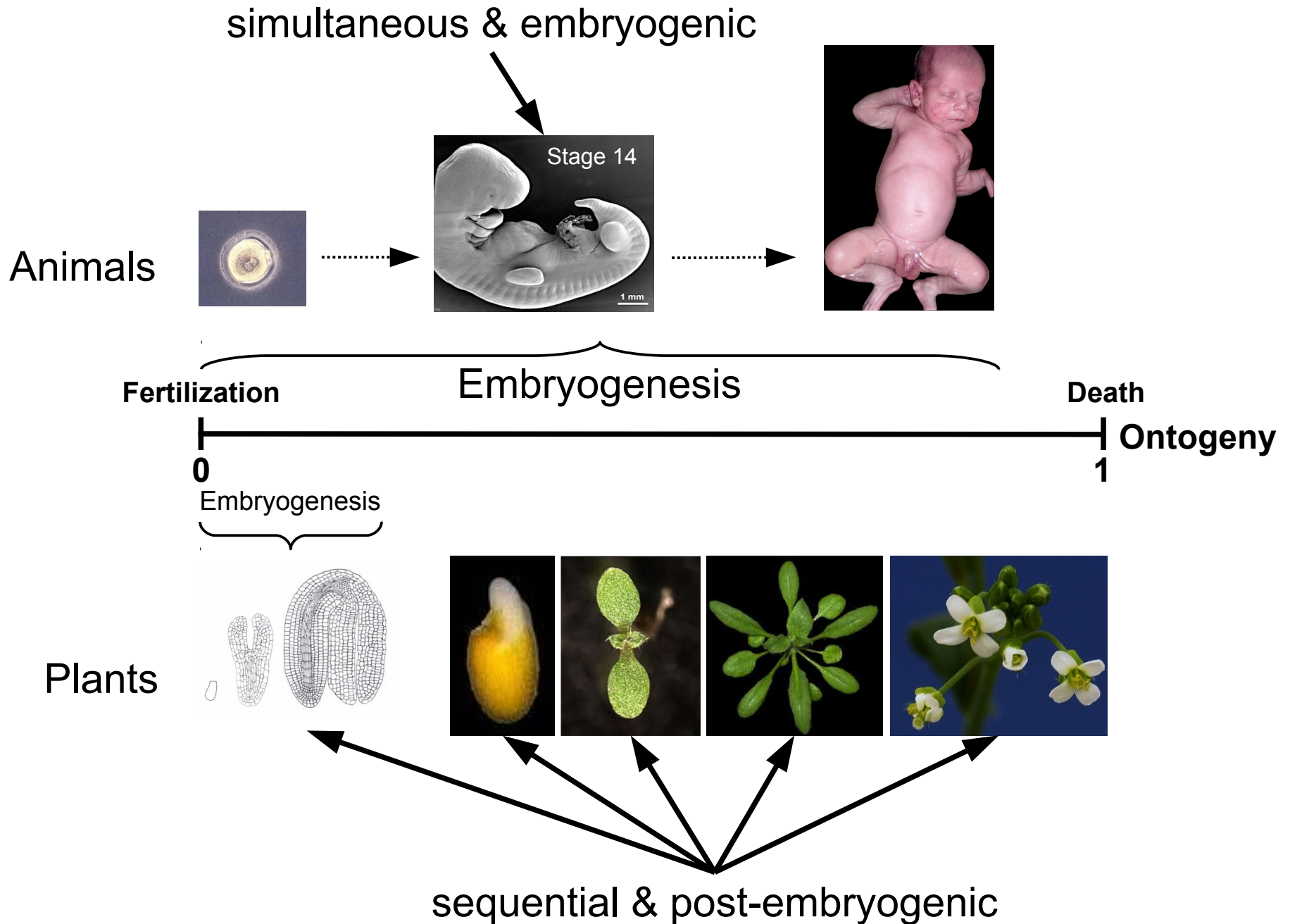


Ontogeny / organ development: animals vs. plants

simultaneous & embryonic



Ontogeny / organ development: animals vs. plants



Are transcriptomic hourglasses unique to embryogenesis?

Are they possibly a general feature of developmental transitions?

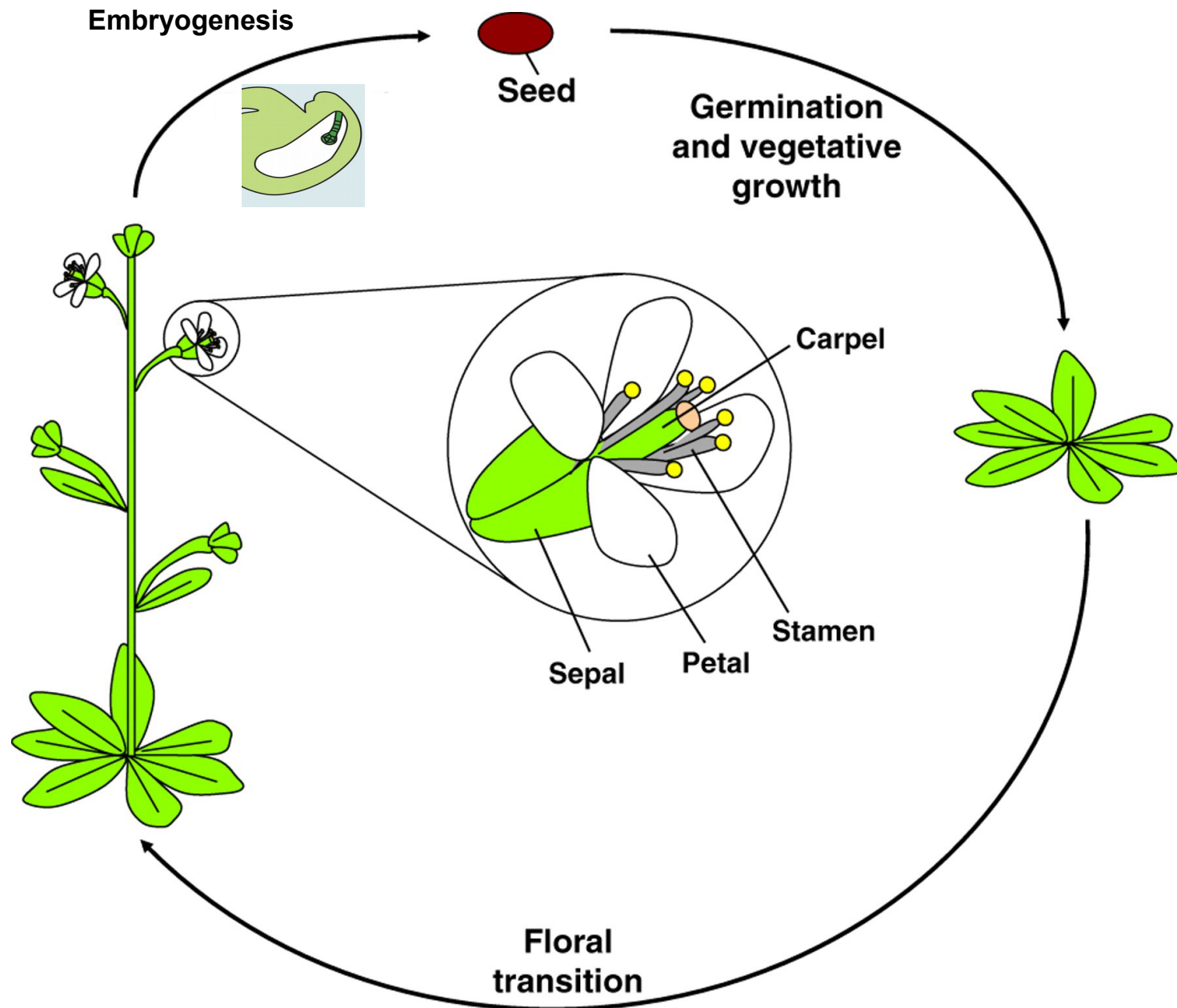


Difficult to address in most animals
→ development largely embryonic

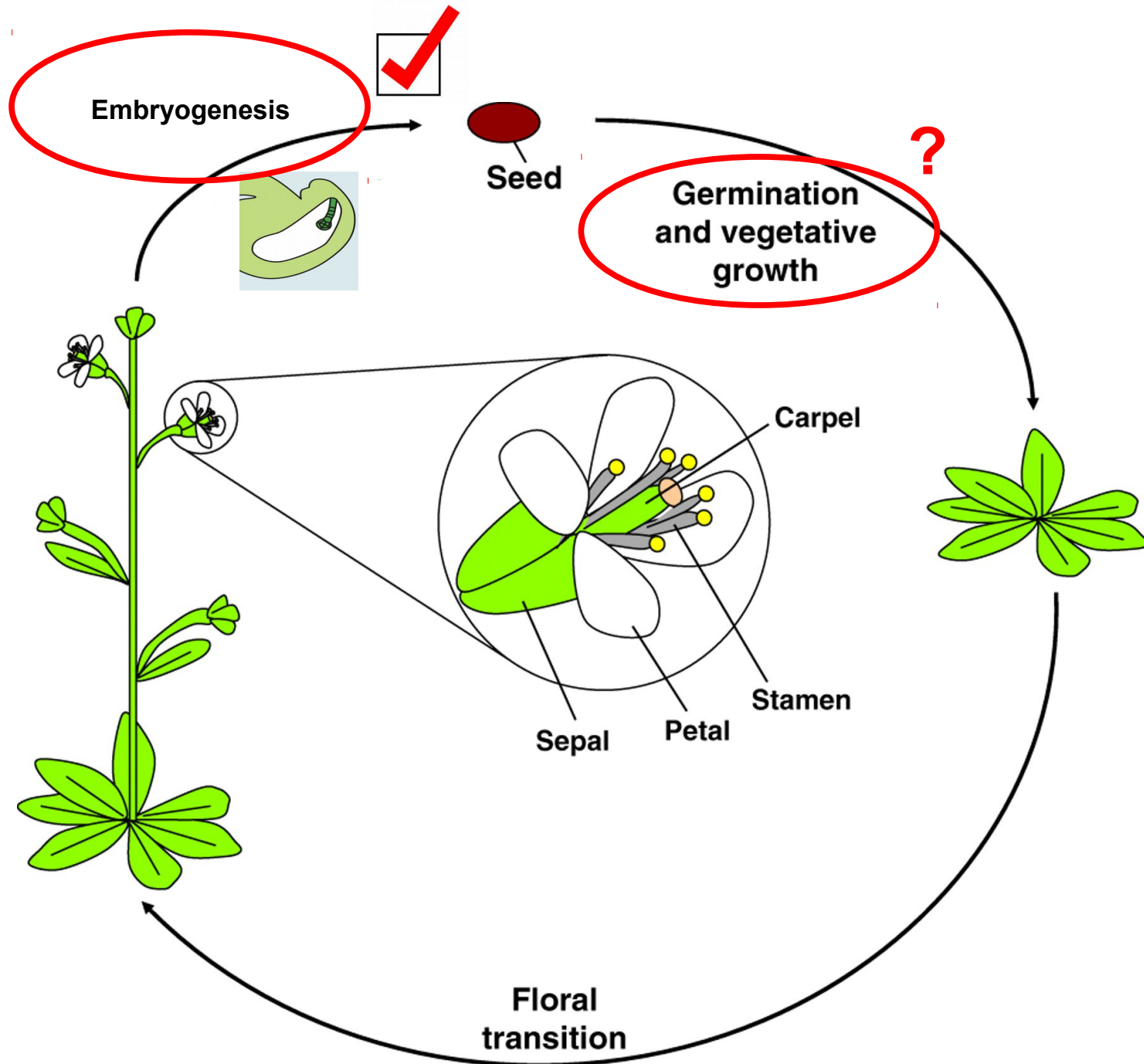


Straight-forward to address in plants
→ development largely post-embryonic

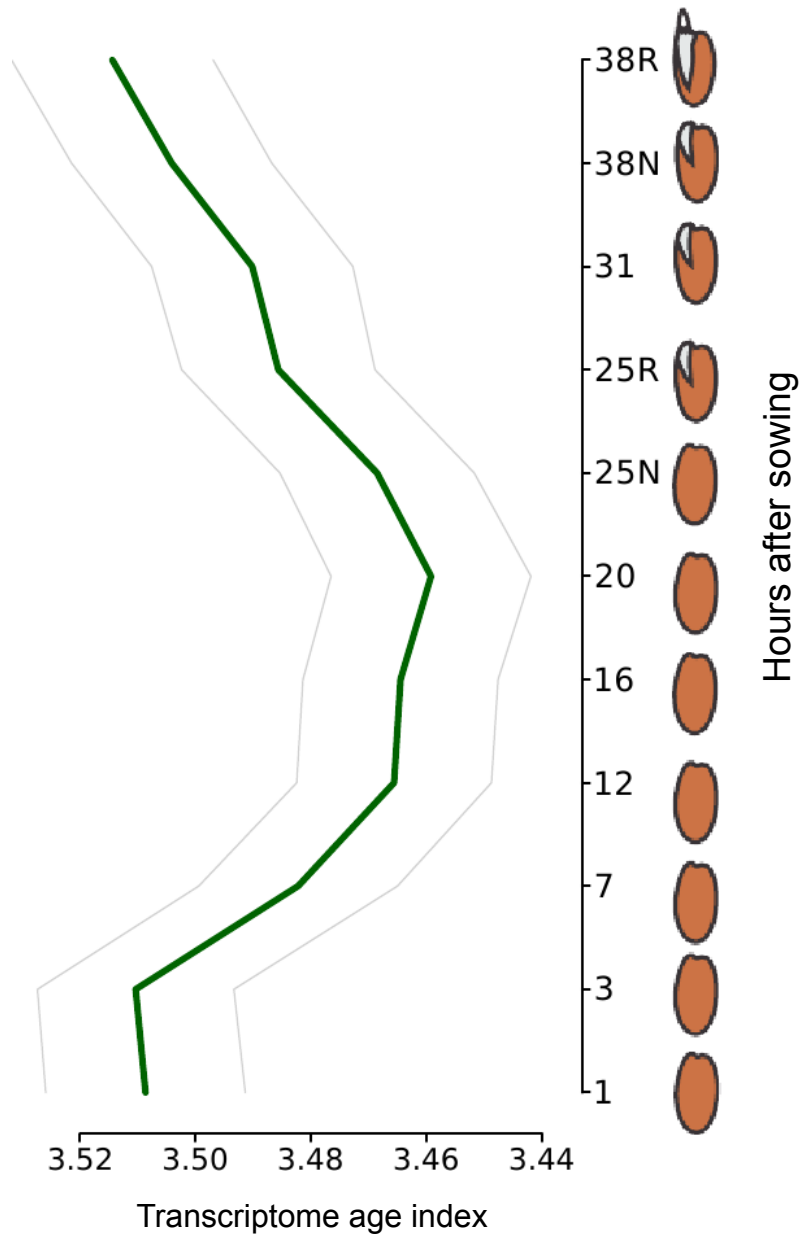
Major developmental transitions in the *A. thaliana* life cycle



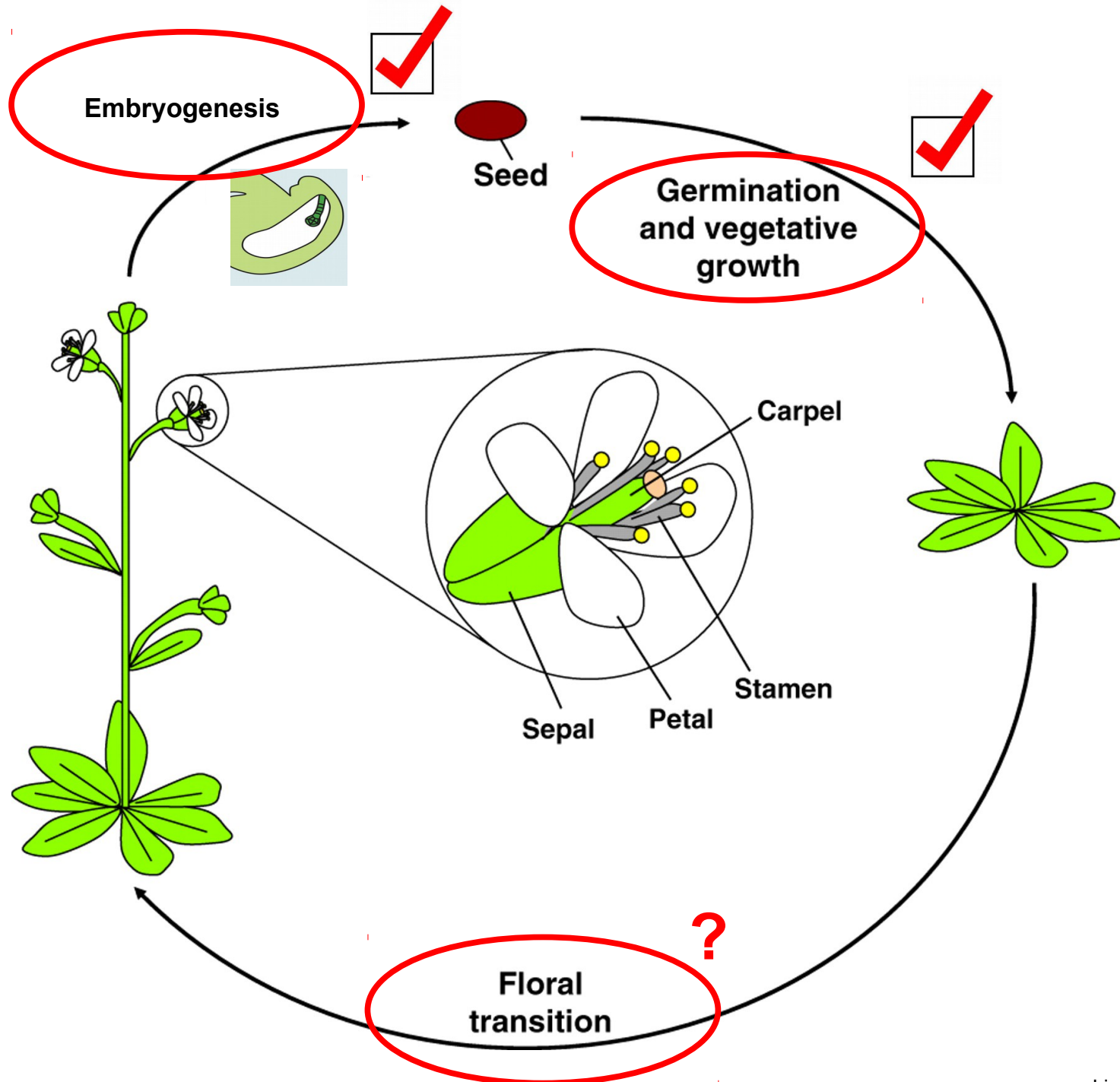
Major developmental transitions in the *A. thaliana* life cycle



A developmental hourglass for germination

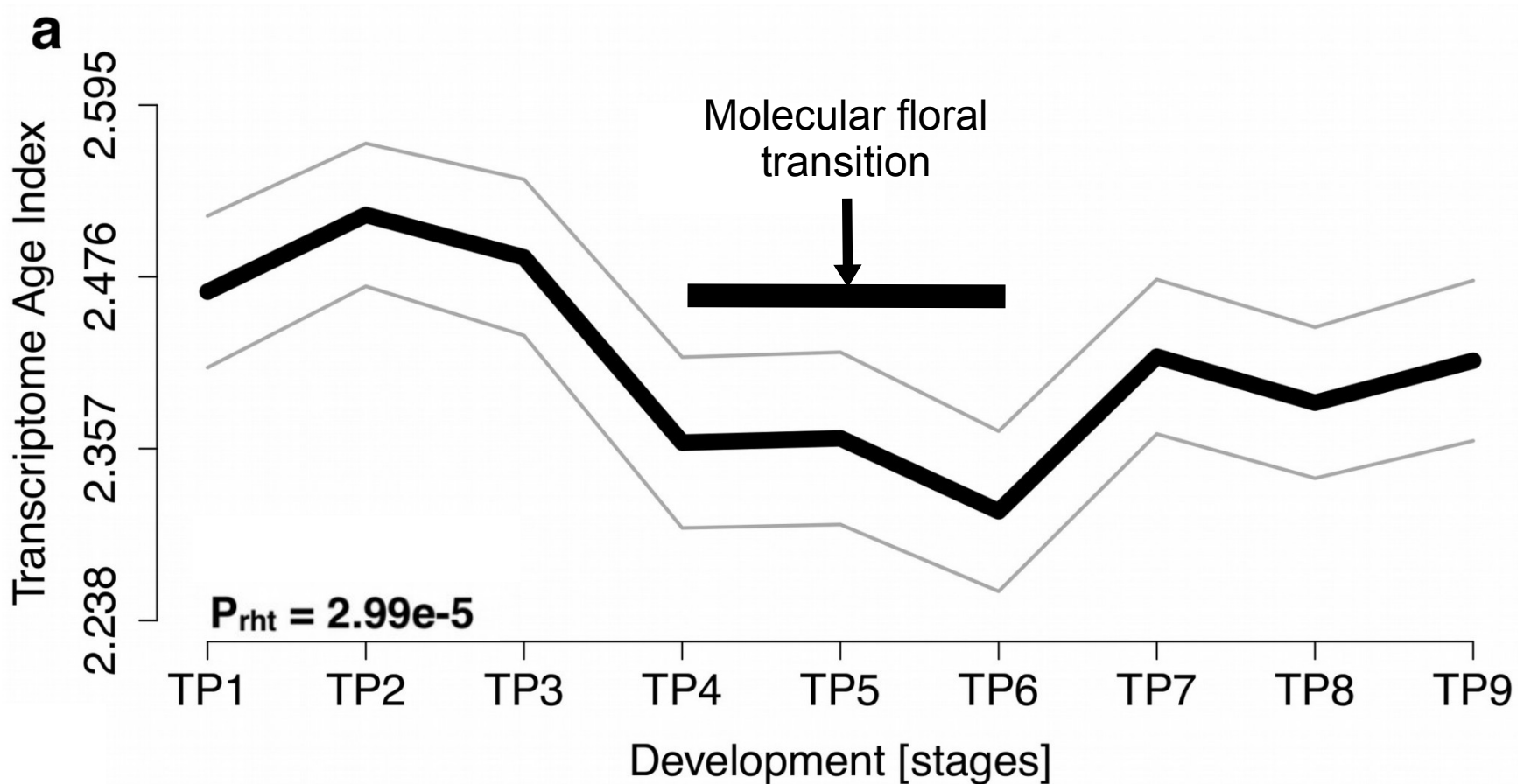


Major developmental transitions in the *A. thaliana* life cycle



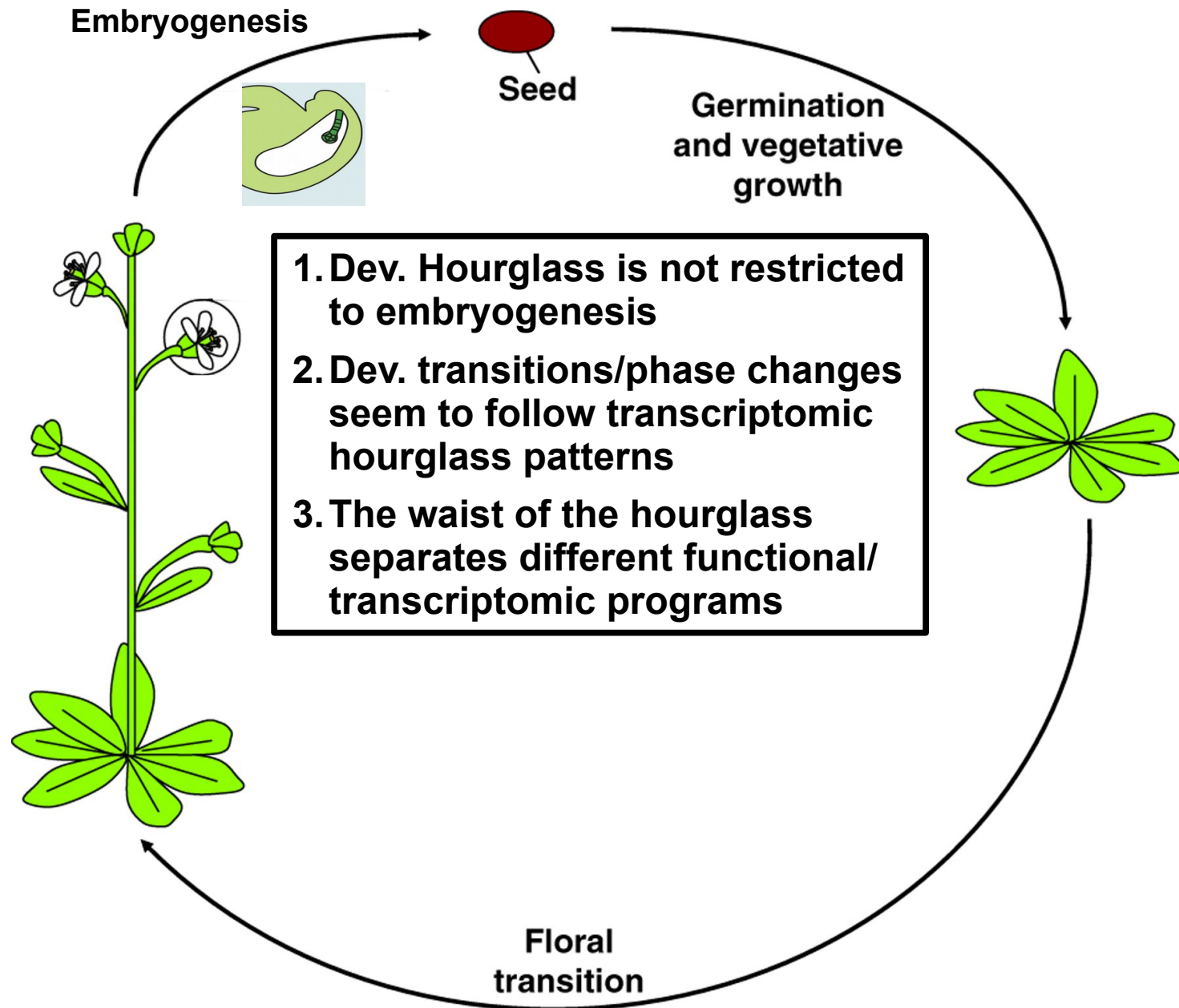
Vegetative to reproductive transition aka floral transition

- SPP1530 – PP24, Quint, Grosse, Weisshaar



- Highly significant TAI hourglass for vegetative-reproductive phase change
- Waist of the hourglass pattern marks molecular floral transition
- TAI pattern separates two transcriptional programs

Conclusions and outlook so far



1. Developmental hourglass specific for animals?

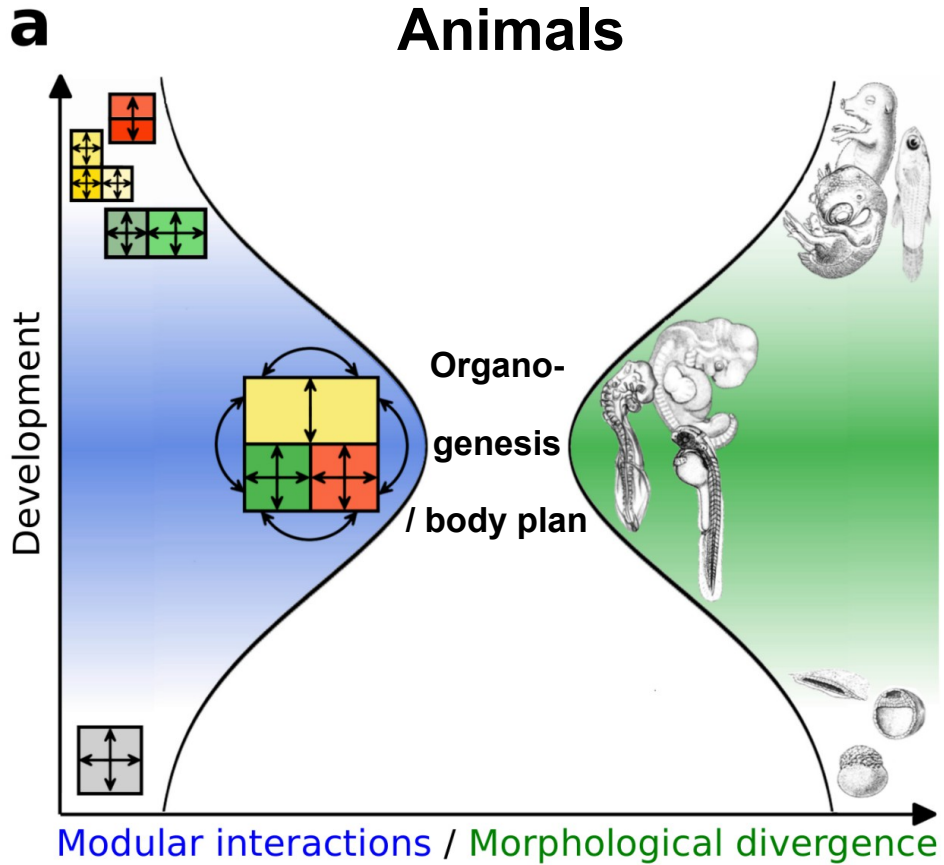


2. ... specific for embryogenesis?

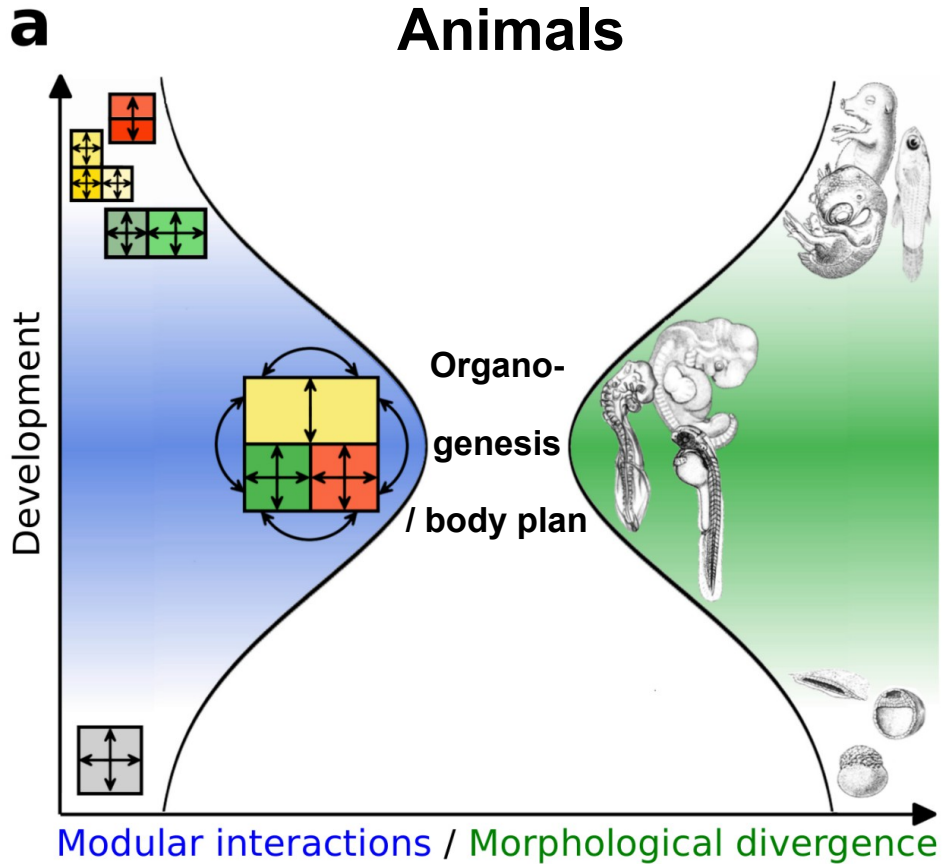


3. ... related to organogenesis?

Concurrence of plant hourglass patterns with organogenesis hypothesis



Concurrence of plant hourglass patterns with organogenesis hypothesis



Plants

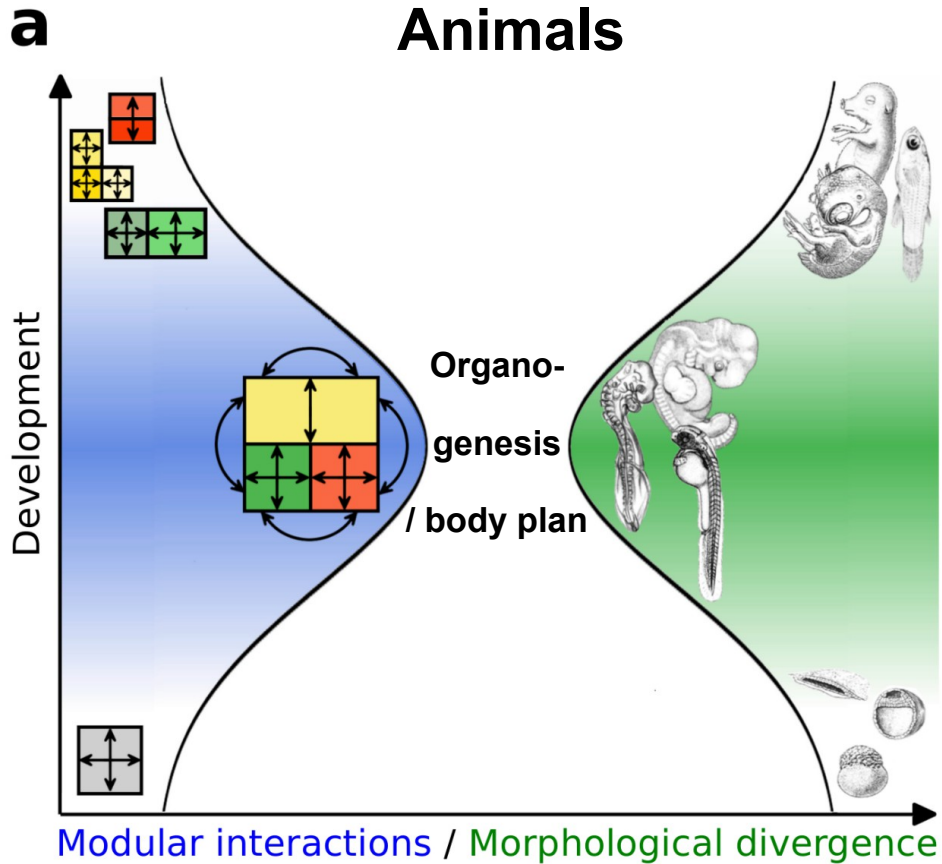
Hourglass for:

- Embryogenesis
- Germination
- Floral transition

Organogenesis?

- Yes
- Hardly
- No

Concurrence of plant hourglass patterns with organogenesis hypothesis

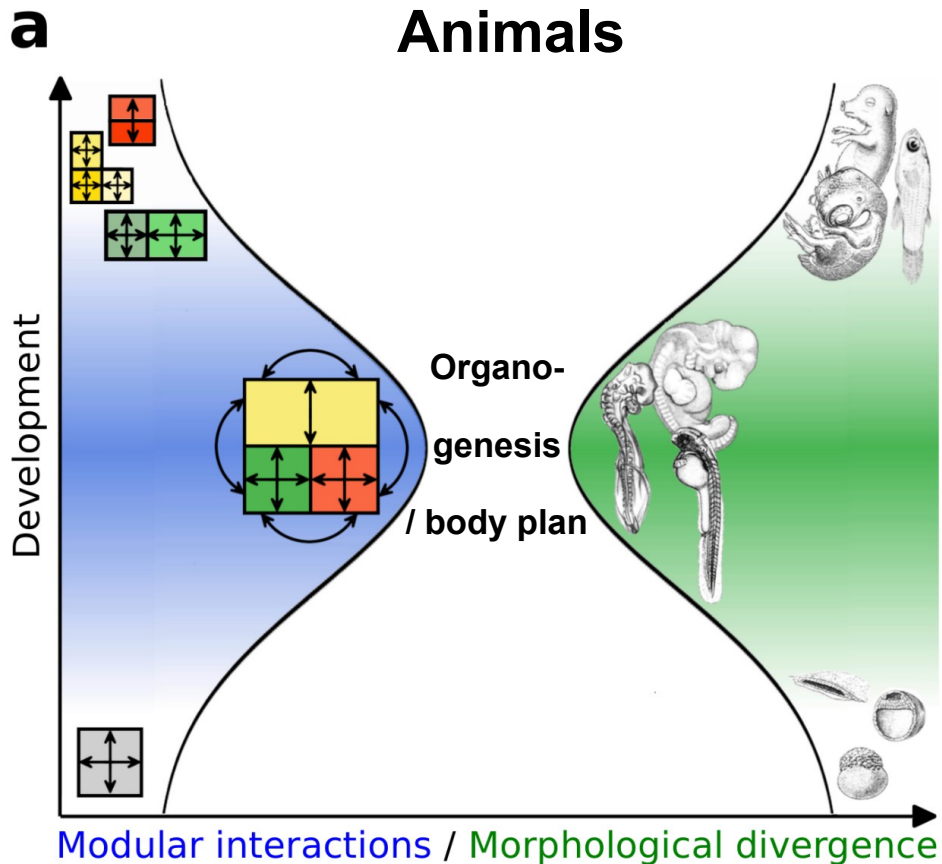


Plants

Hourglass for:	Organogenesis?
• Embryogenesis	• Yes
• Germination	• Hardly
• Floral transition	• No

Data largely disagree with the favored explanation for animal hourglass patterns

Concurrence of plant hourglass patterns with organogenesis hypothesis



Plants

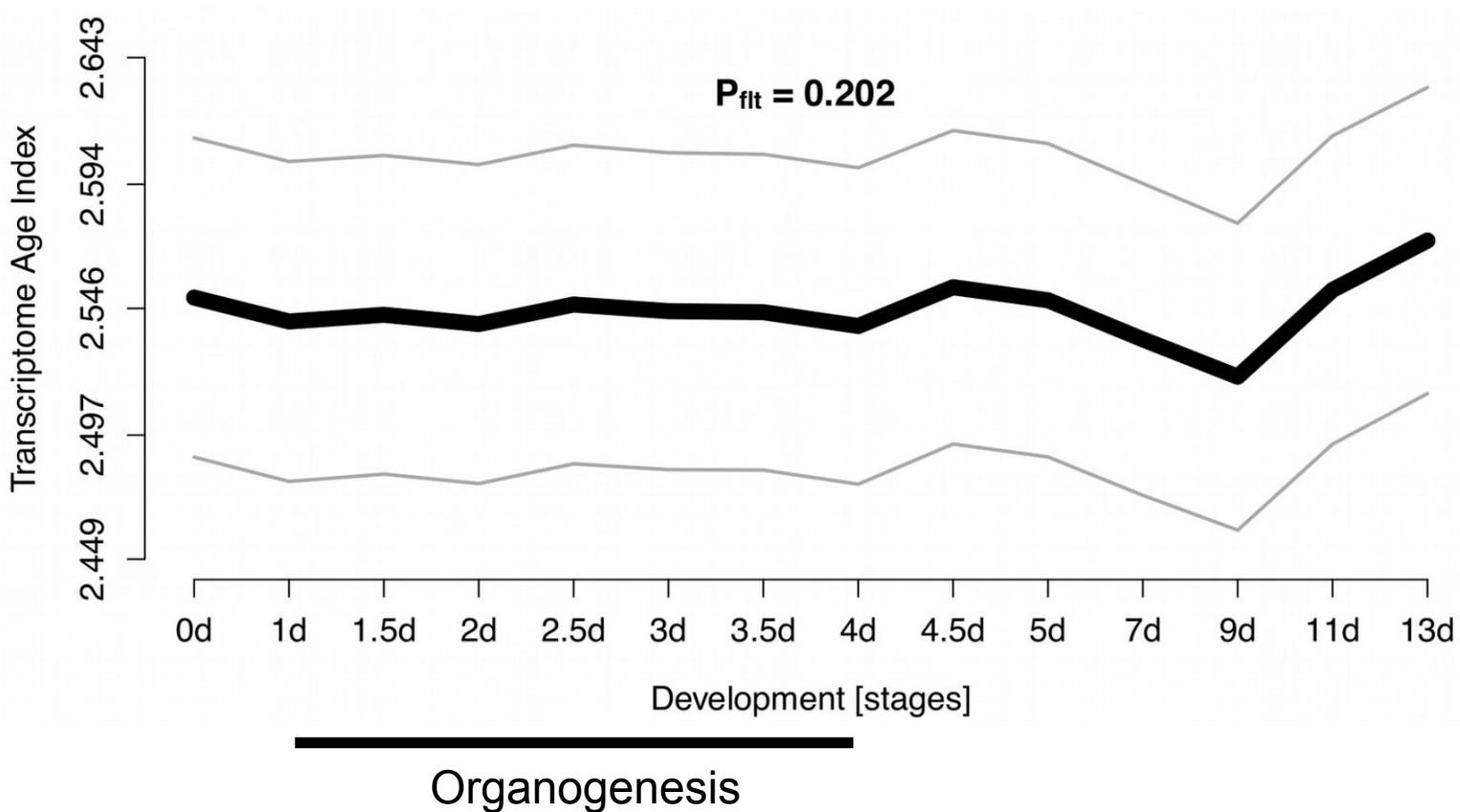
Hourglass for:	Organogenesis?
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Negative control:
→ Flower development

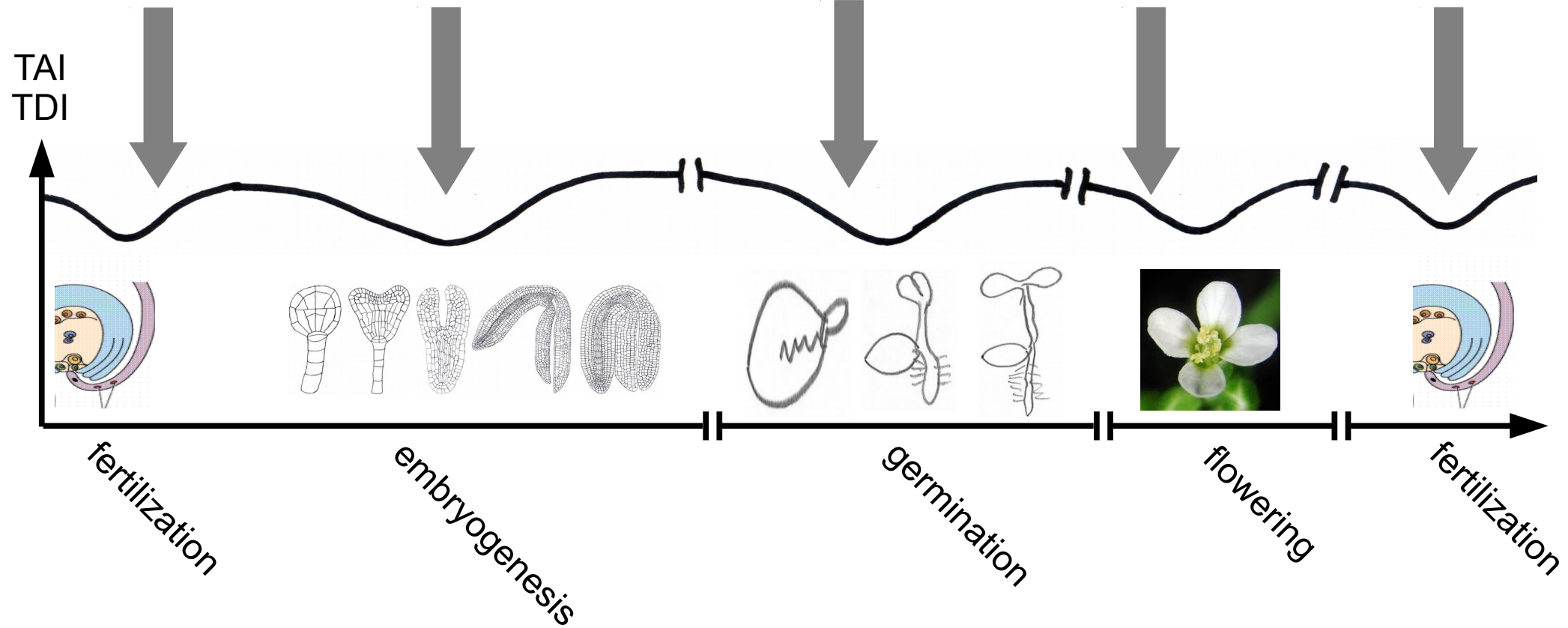
Flower development as negative control

- Collaboration with Frank Wellmer, Dublin



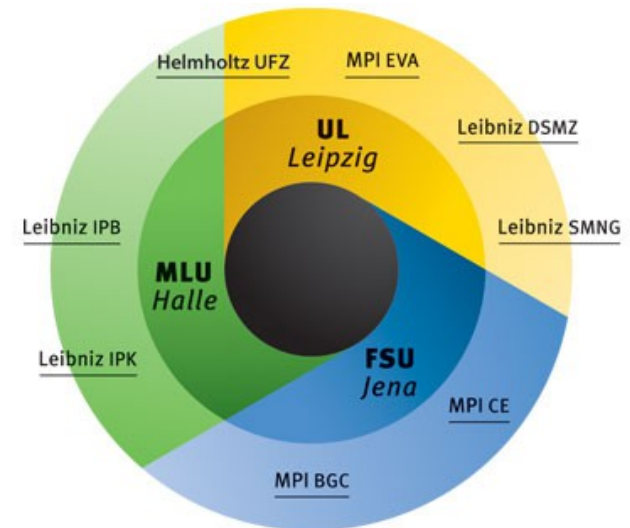
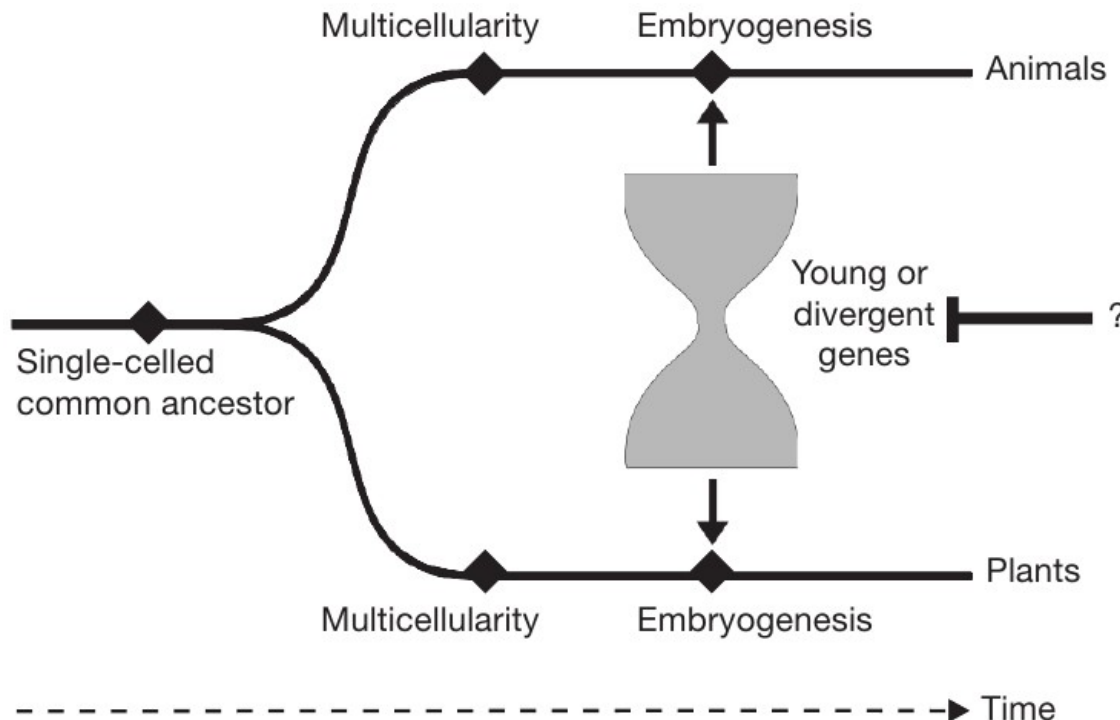
The absence of conserved transcriptomes during organogenesis stages of flower development further refutes the association of organogenesis as the driving force of the developmental hourglass

Many hourglasses? Checkpoint hypothesis



Conclusions

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