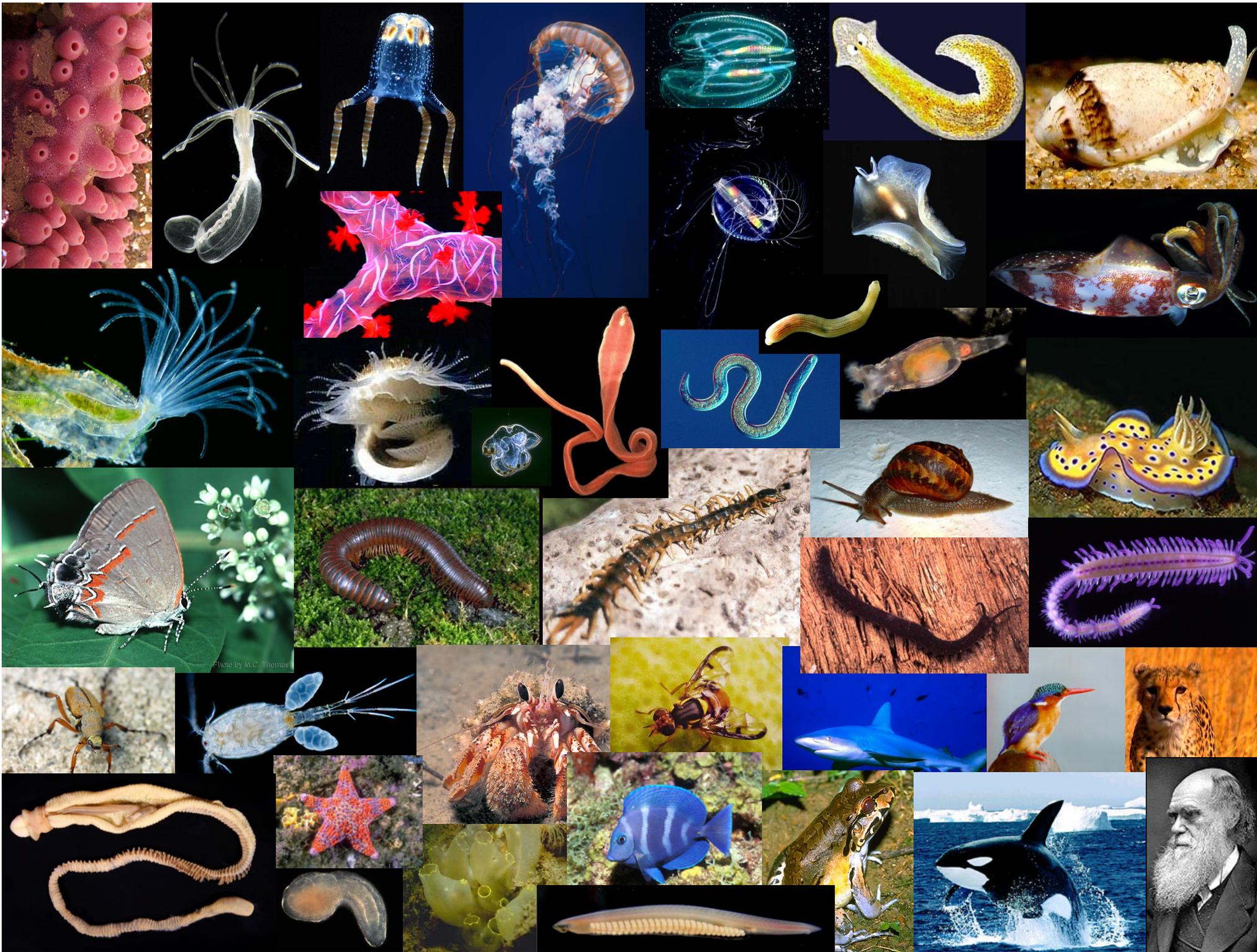


動物的演化

游智凱

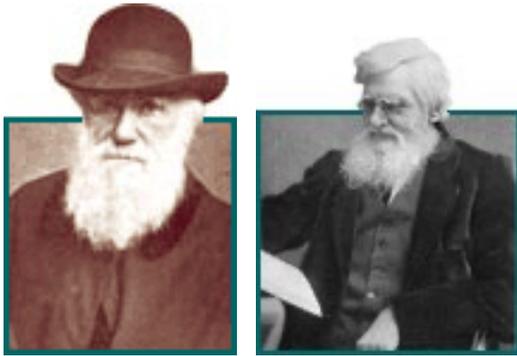
中研院細胞與個體生物學研究所
中研院宜蘭礁溪臨海研究站



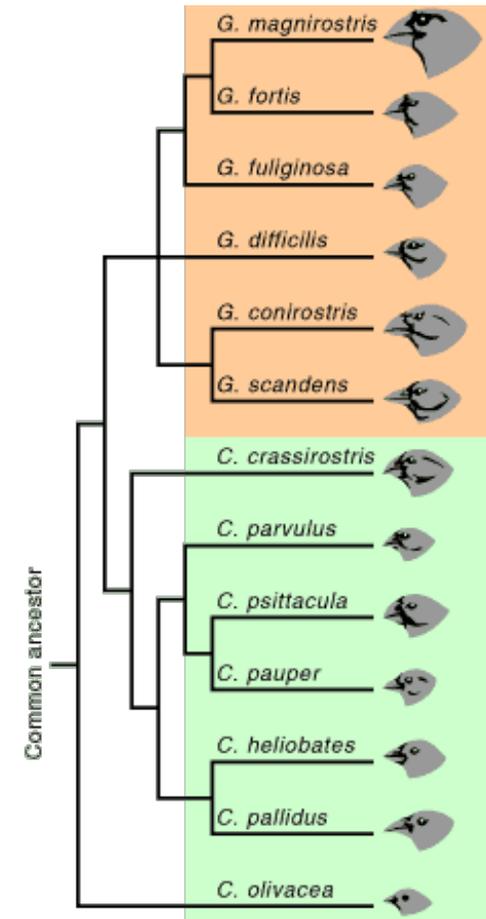
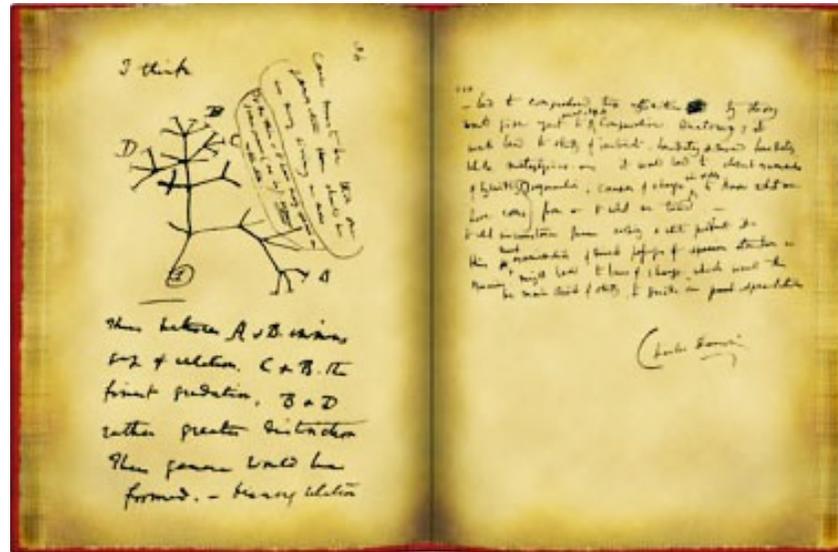
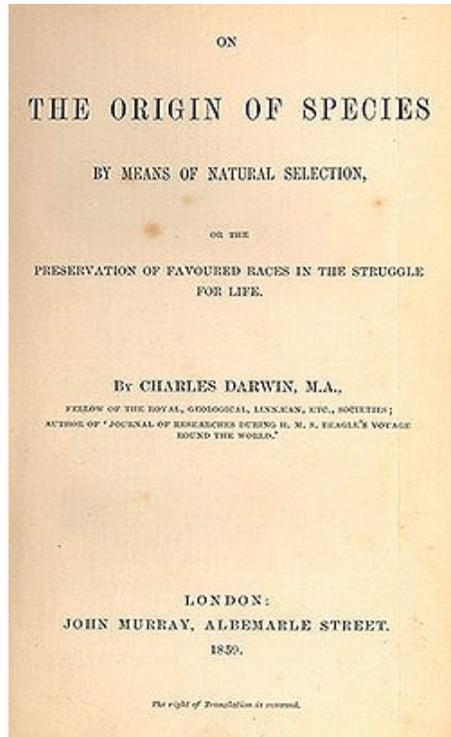
Nothing in Biology Makes Sense Except in the Light of Evolution
- T. G. Dobzhansky, 1973

演化生物學的研究一方面描述了生命的歷史；更重要的是要尋求答案來解釋**為什麼 (Why)** 生物及生命現象是我們現在所看到的狀況。

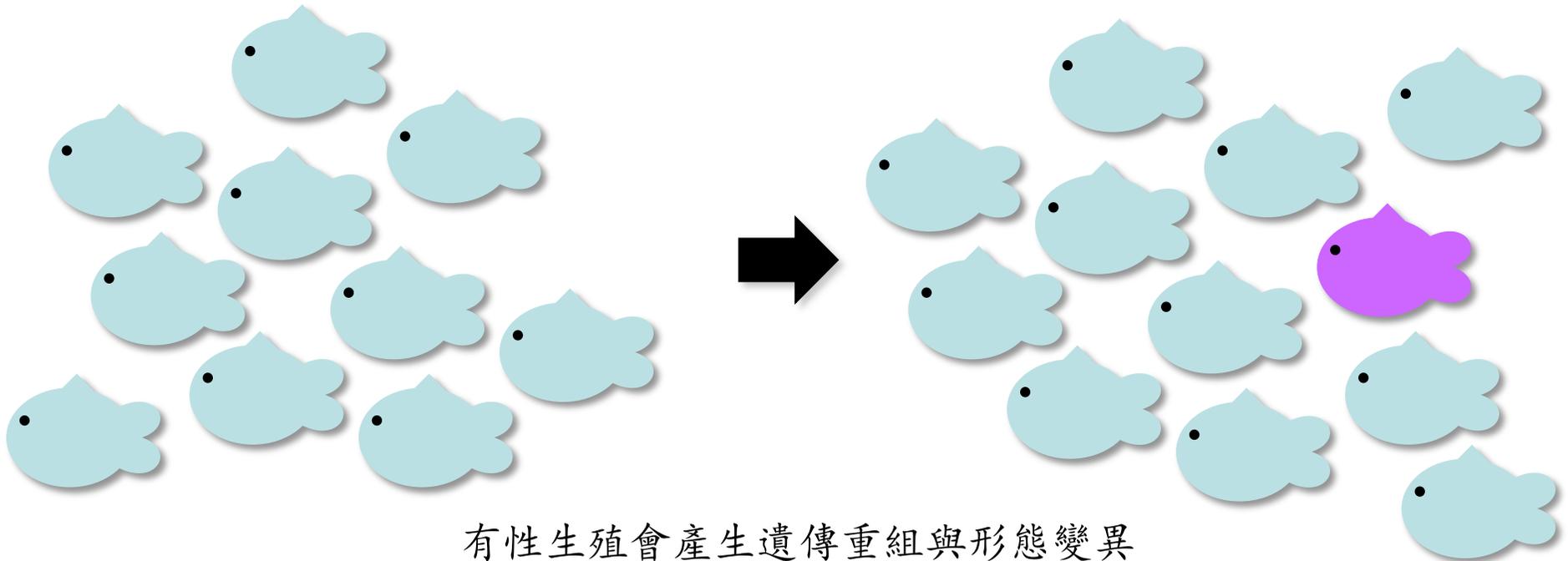
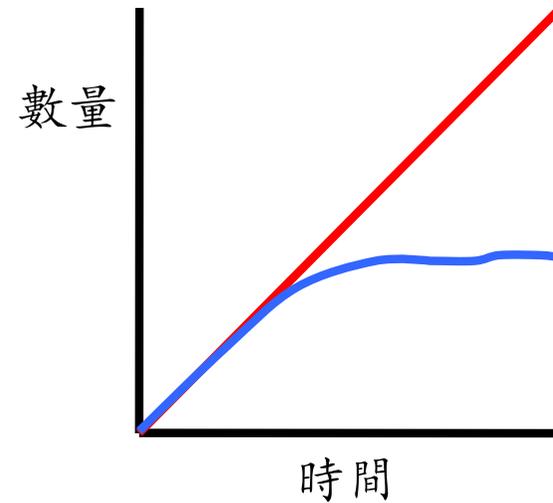
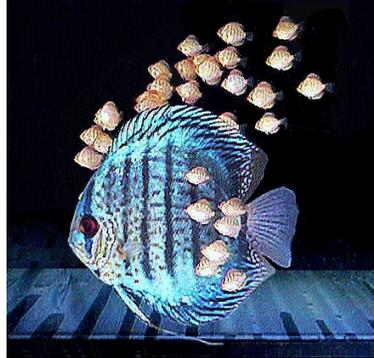
天擇造成生物特徵的適應演化



Charles Darwin 達爾文 Alfred Russel Wallace 華萊士 (1857, 1859):
 生物的共通性，起源於共同的祖先；傳統林奈式的分類系統所產生的
 物種階層關係，反應了不同物種間由此共同祖先分支出來的歷史。天
 擇 (nature selection) 為物種特徵演化的機制

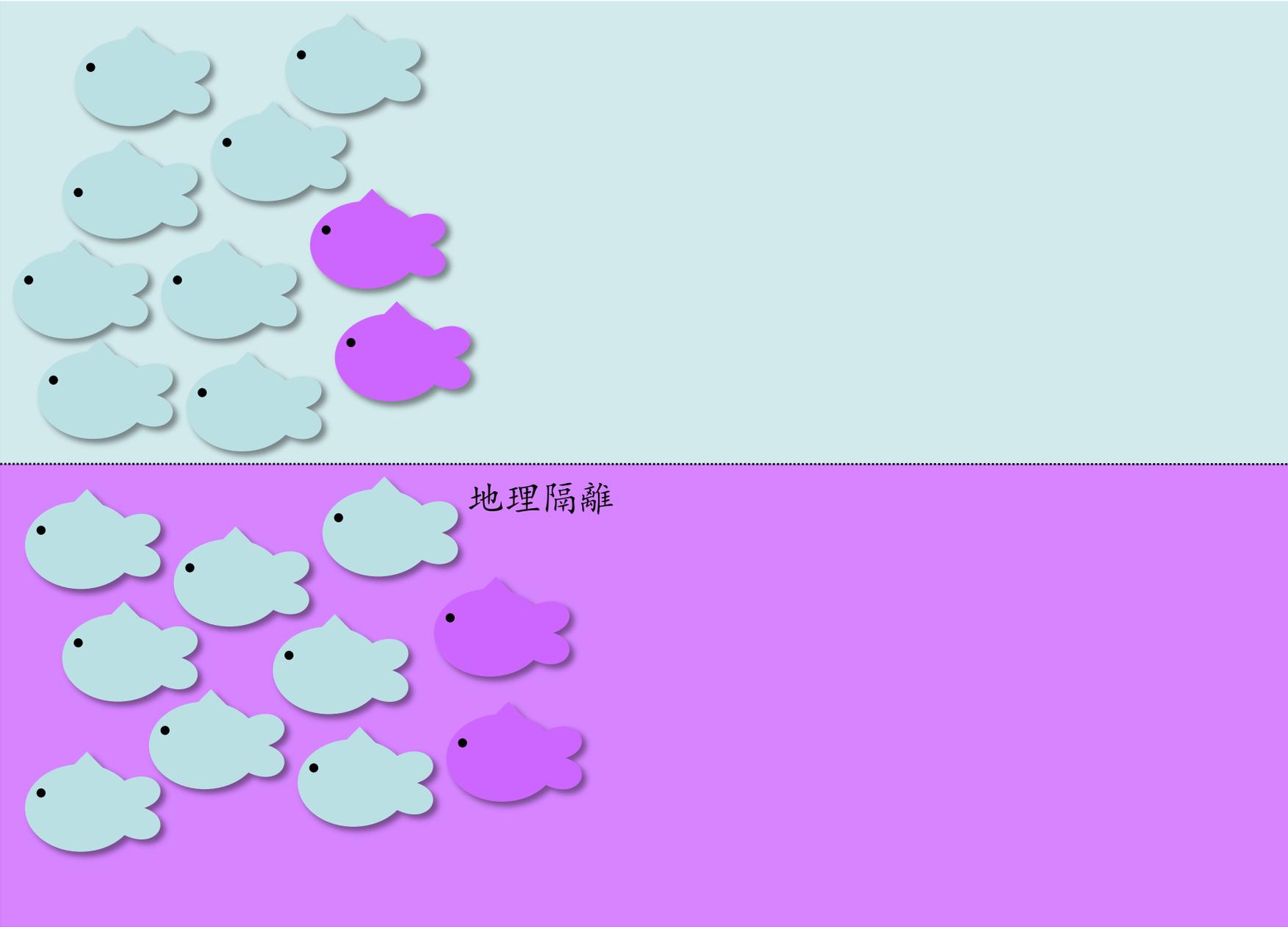


族群內個體間具有差異性



有性生殖會產生遺傳重組與形態變異

天擇與適應演化導致種化的發生



天擇與適應演化導致種化的發生

掠食壓力

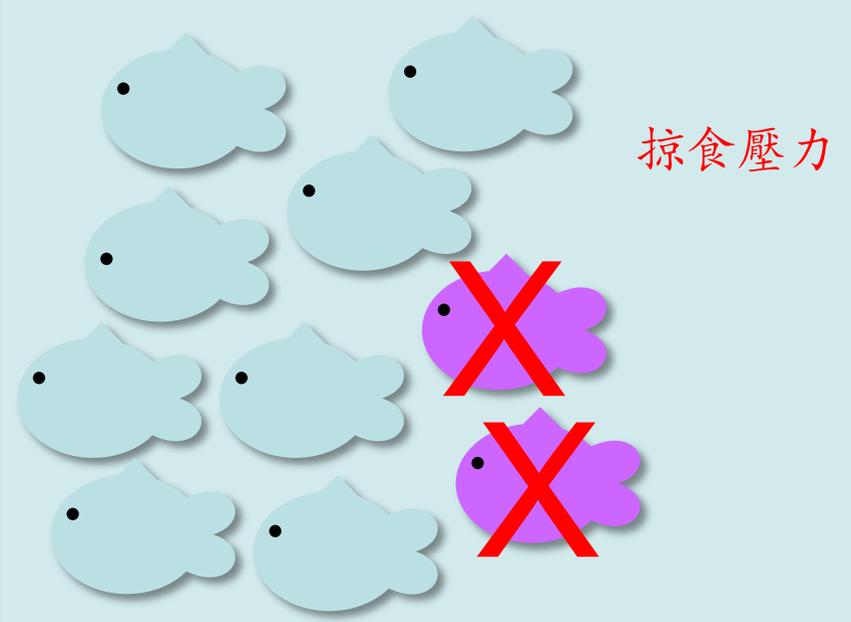


Diagram illustrating predation pressure. A group of light blue fish is shown, with two purple fish marked with red 'X's, indicating they are being targeted by predators.



A shark is shown spotting a purple fish, with a speech bubble saying "I see [purple fish]!".

地理隔離

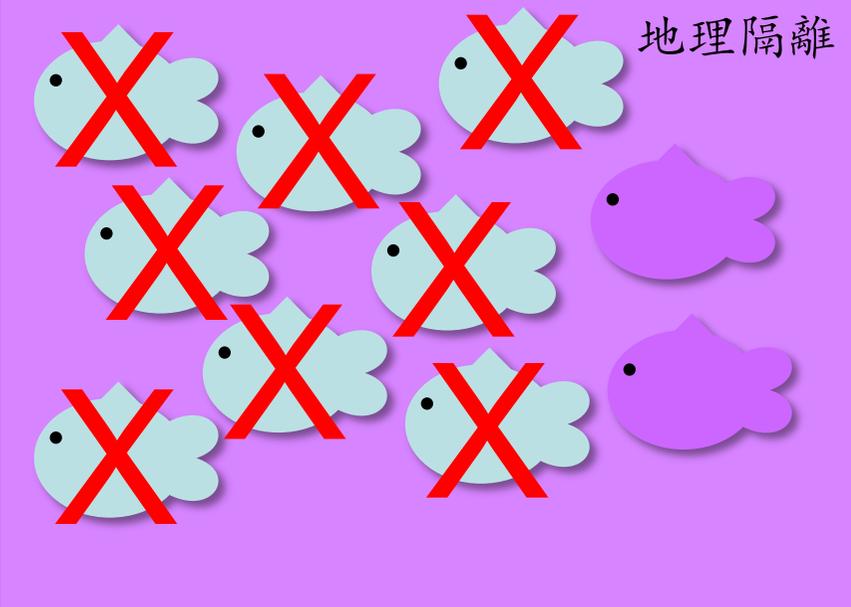
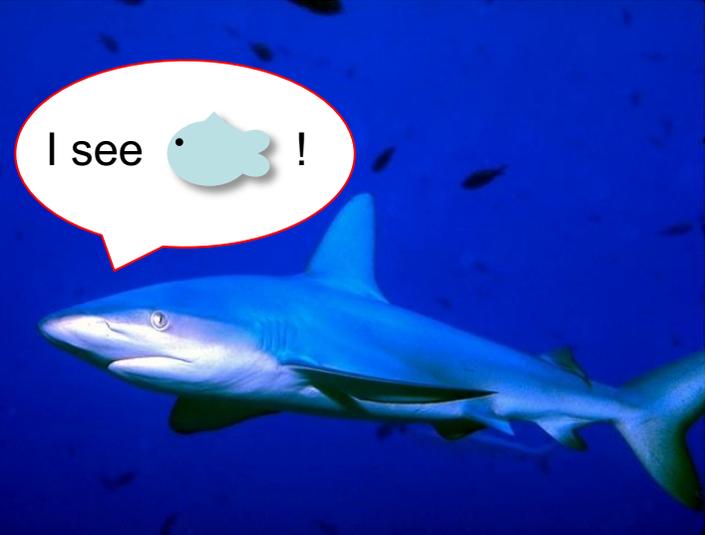
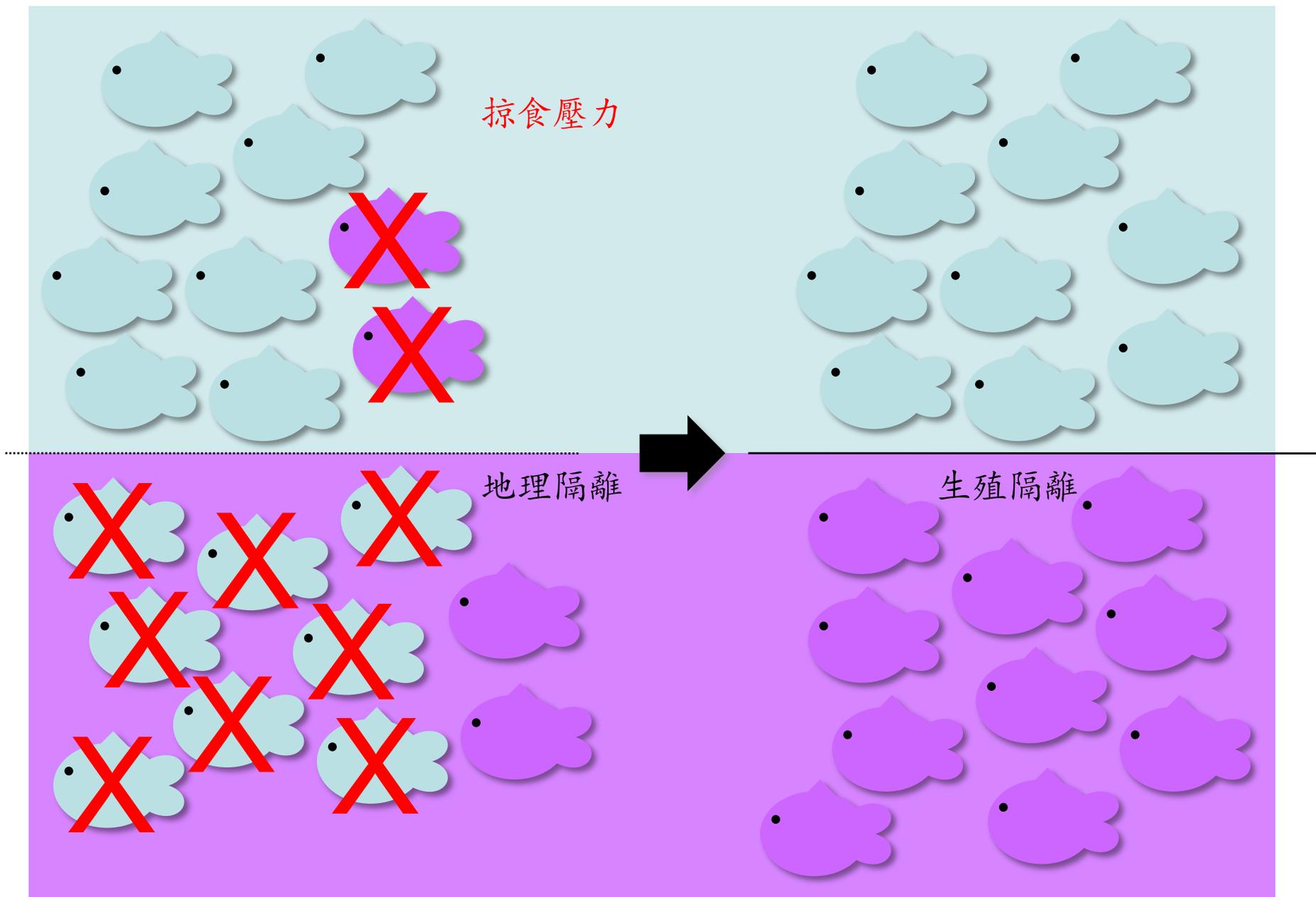


Diagram illustrating geographic isolation. A group of light blue fish is shown, with most marked with red 'X's, indicating they are being targeted by predators. Two purple fish are shown on the right, representing a separate population.

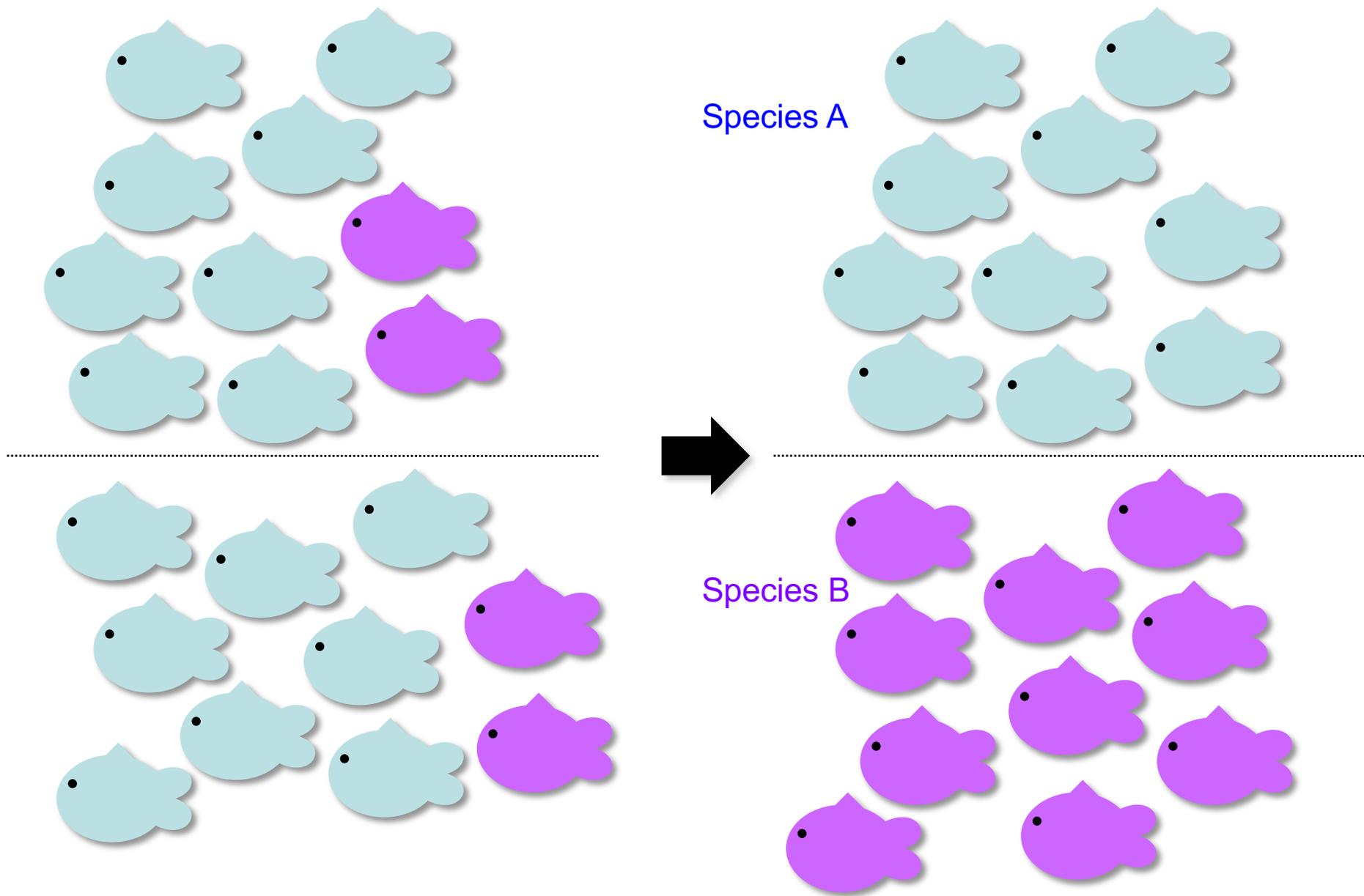


A shark is shown spotting a light blue fish, with a speech bubble saying "I see [light blue fish]!".

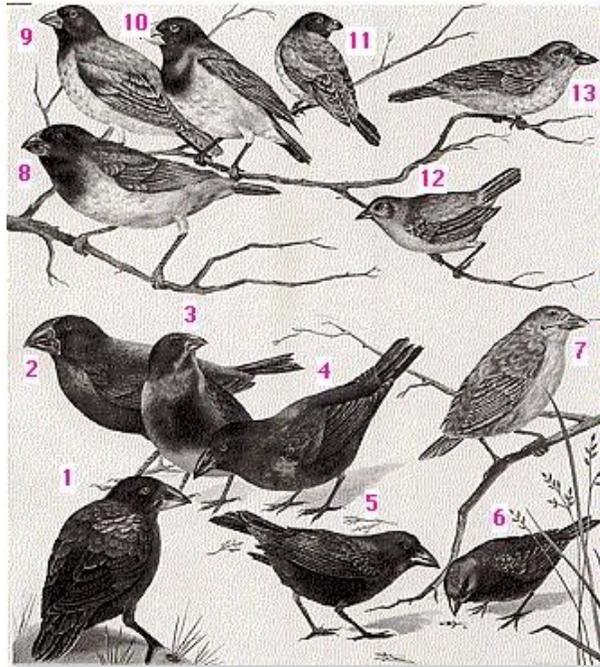
天擇與適應演化導致種化的發生



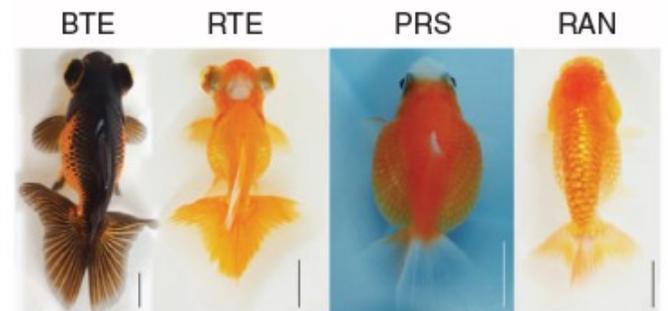
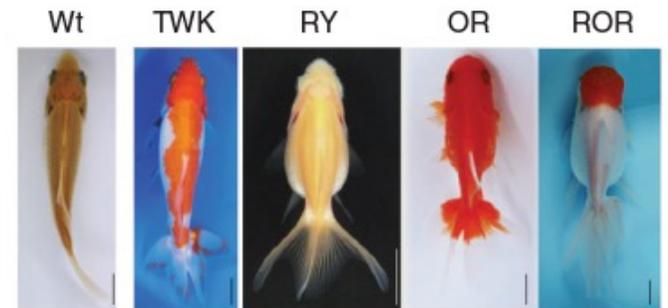
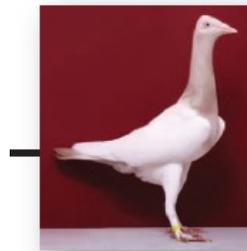
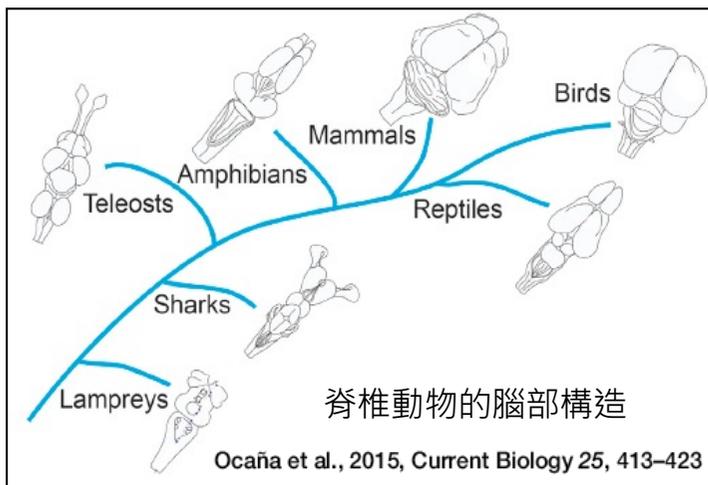
天擇與適應演化導致種化的發生



相近物種間或馴養家畜的形態變化



達爾文雀

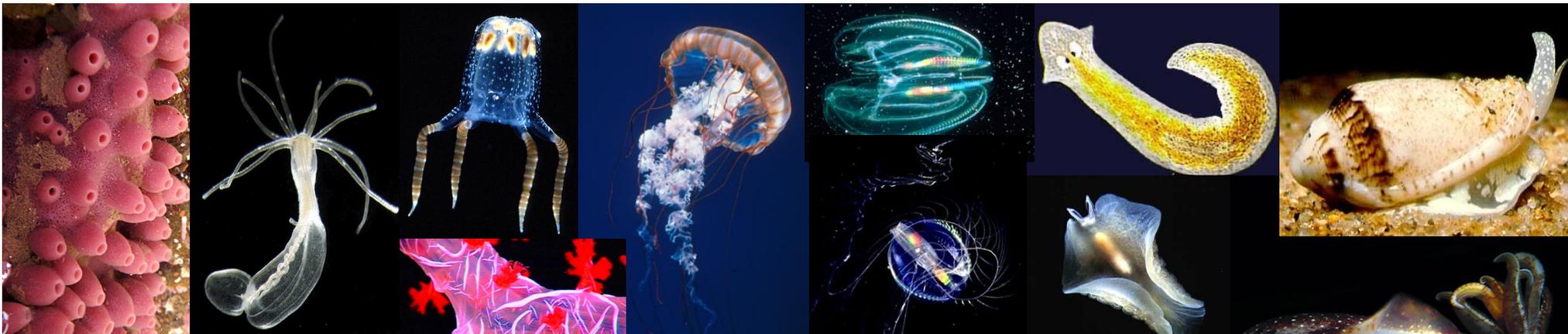


NATURE COMMUNICATIONS | 5:3360 |



Science 325, 995 (2009)

Science 339, 1063 (2013)



複雜多樣的動物形態是如何演化產生？

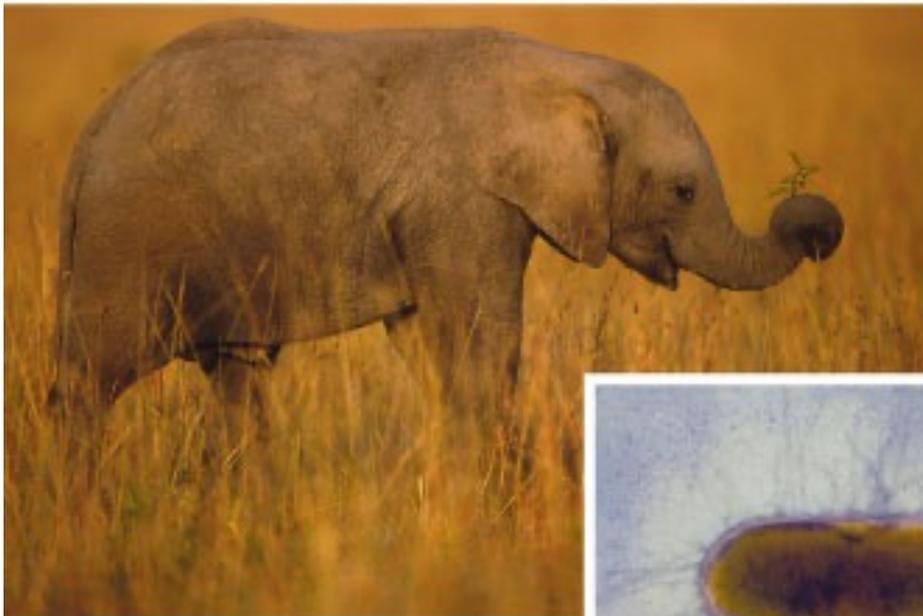


“Experiments ready prepared by Nature”

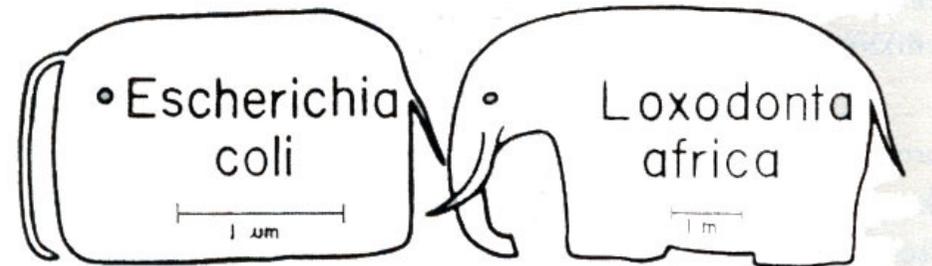


大腸桿菌與大象...

What is true for *E. coli* is also true for the elephant.
-*Jacques Monod*



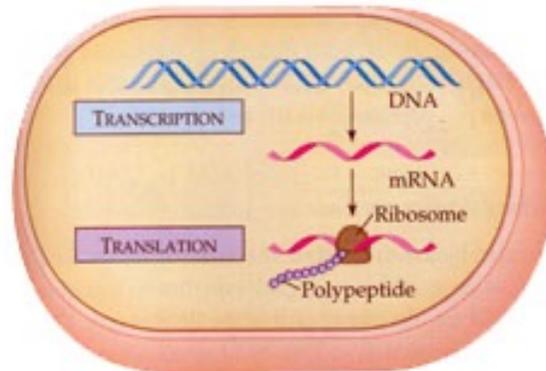
(Nature, 2002)



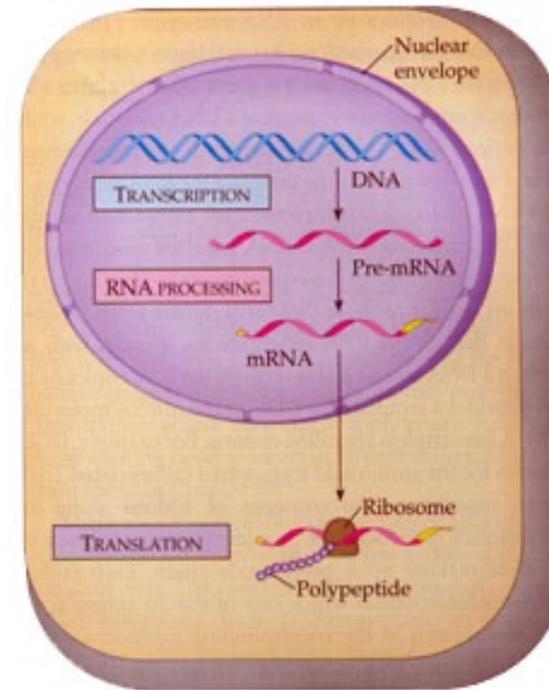
Whimsical representation of Monod's famous quip. COURTESY OF
DR. SIMON SILVER, UNIVERSITY OF ILLINOIS-CHICAGO

(Carroll, *Endless forms most beautiful*, 2005)

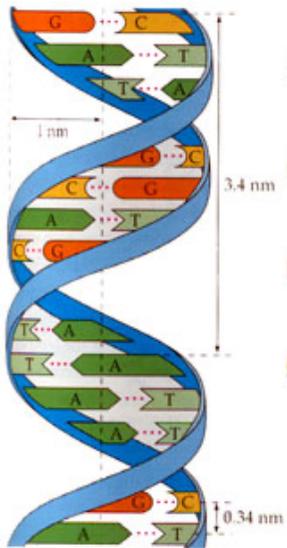
大腸桿菌與大象都有DNA



原核生物細胞

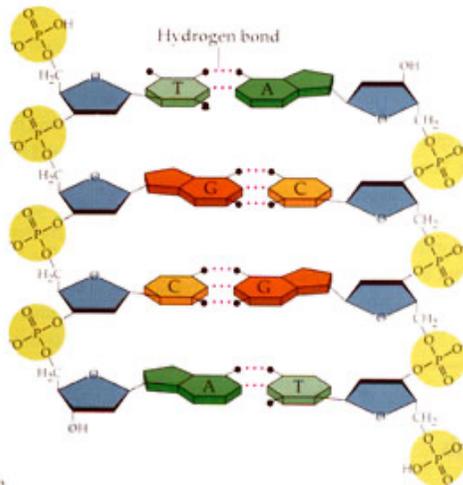


真核生物細胞

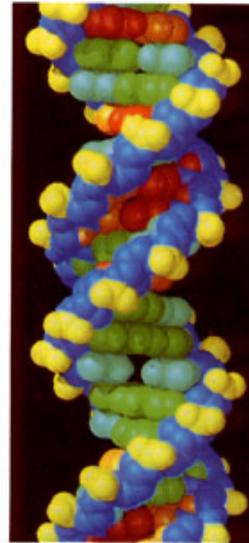


DNA雙股螺旋

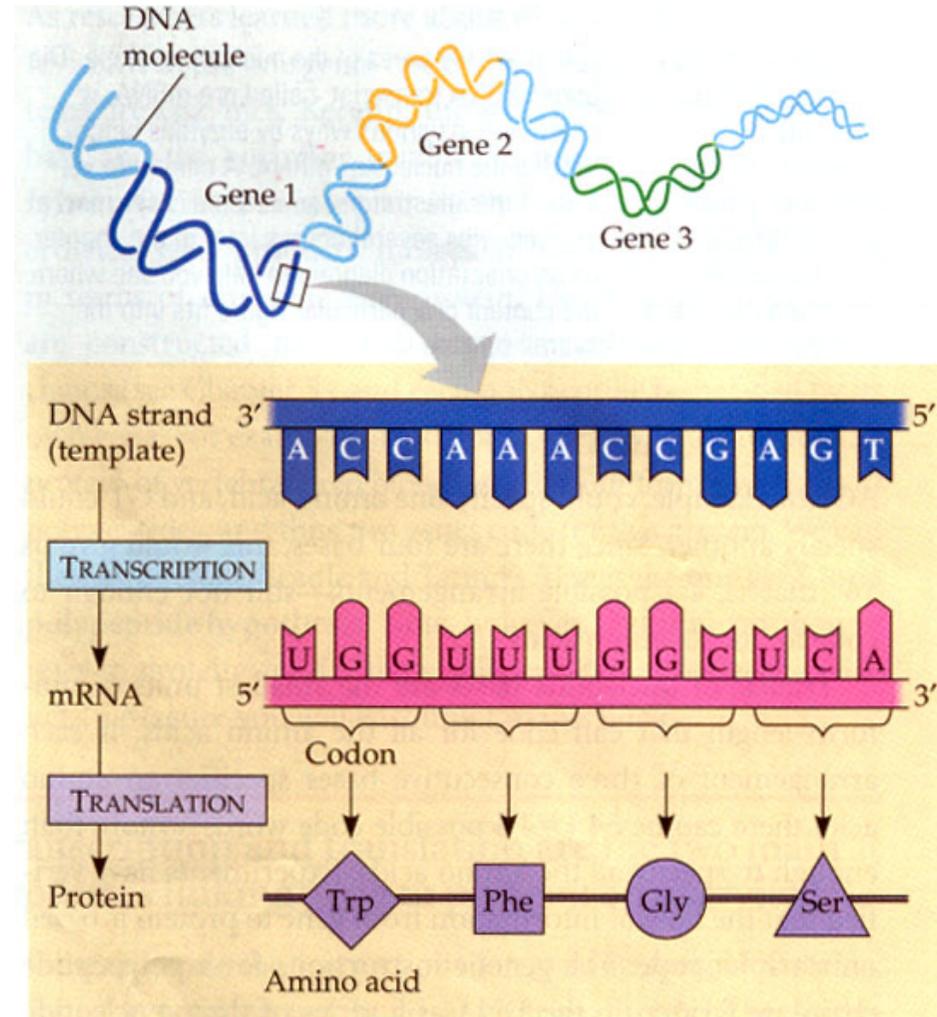
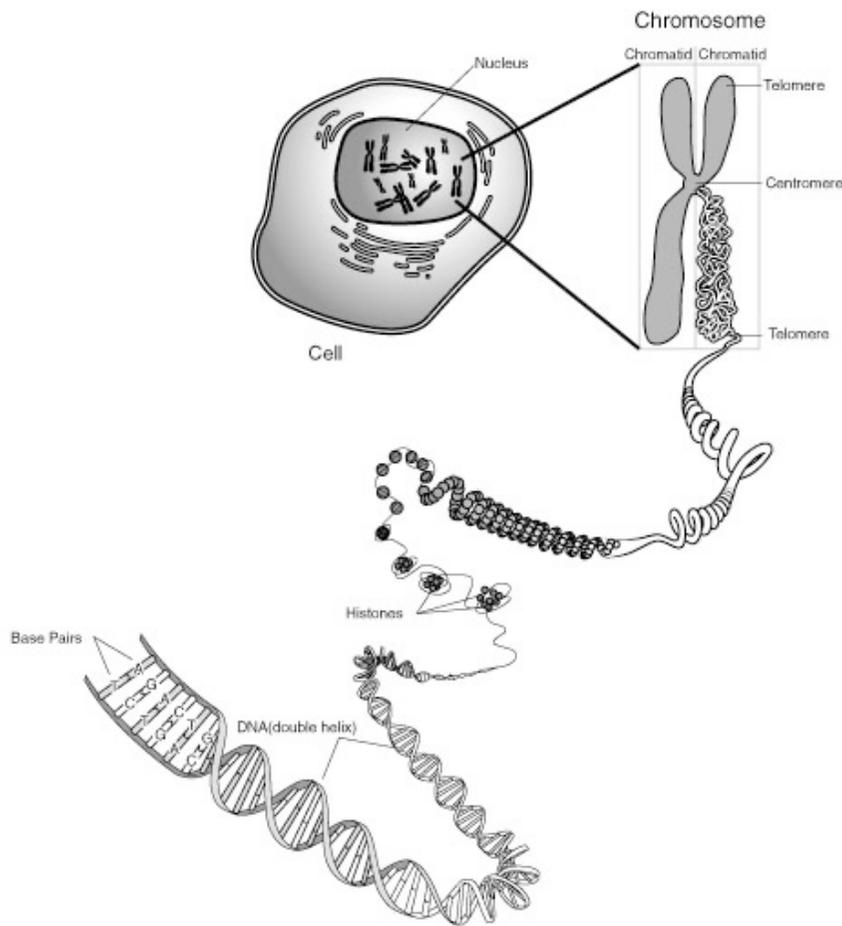
配對鹼基形成氫鍵



A - T
C - G



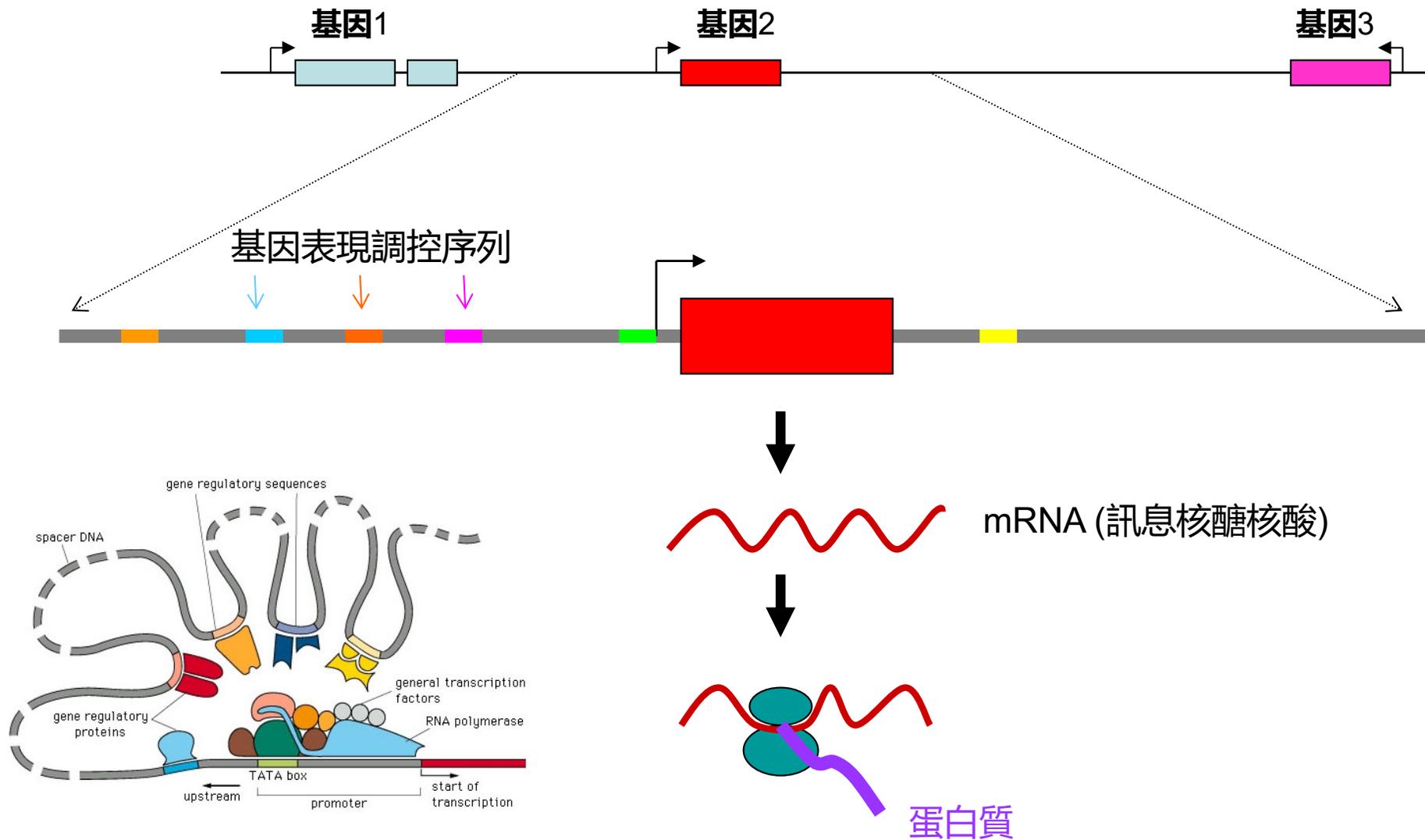
基因(Gene)- 遺傳的基本單位, 由片段的DNA組成



(National Genome Research Institute, USA)

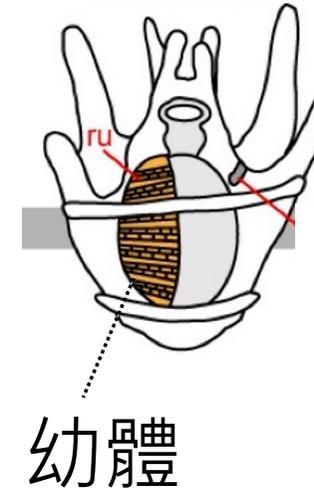
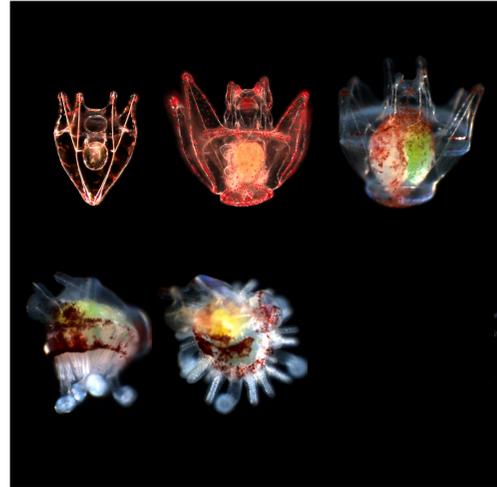
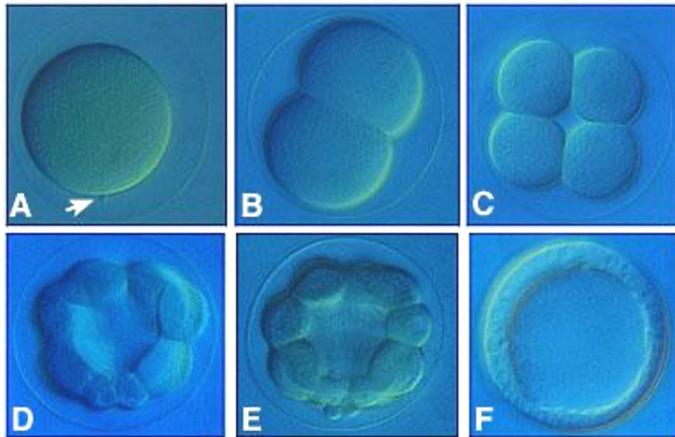
(Campbell, *Biology*)

基因的開啟與關閉- 時間與地點指令



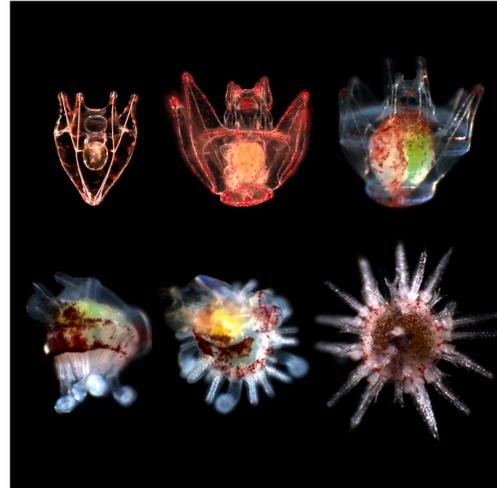
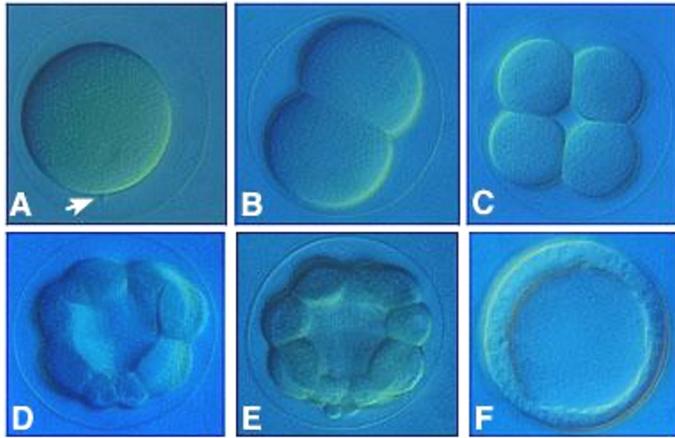
從單一細胞的受精卵發育到成體的過程受到基因表現的調控

動物的發育過程 - 從受精卵到成體



從單一細胞的受精卵發育到成體的過程受到基因表現的調控

動物的發育過程 - 從受精卵到成體

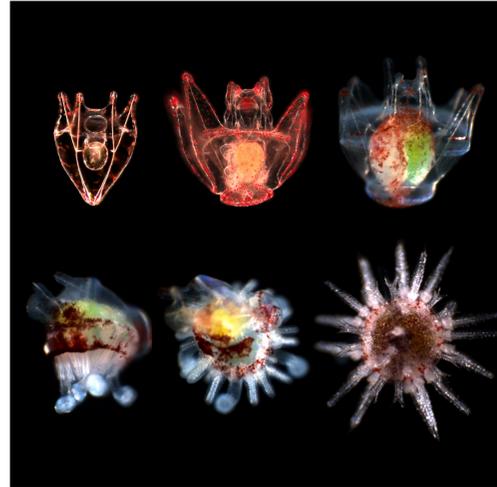
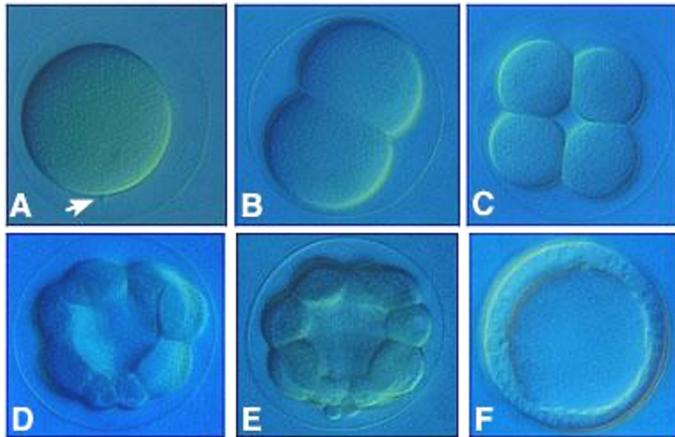


海膽



從單一細胞的受精卵發育到成體的過程受到基因表現的調控

動物的發育過程 - 從受精卵到成體



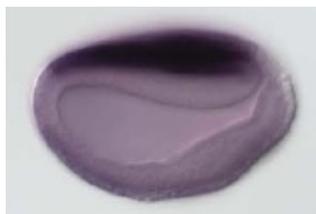
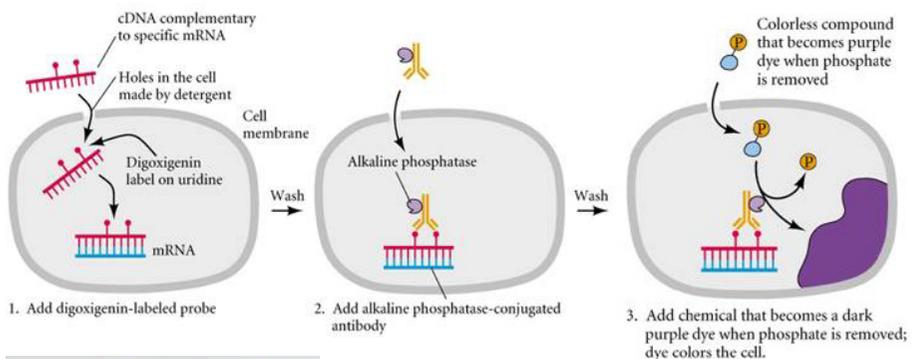
海膽



文昌魚

研究發育基因功能的方法：分析基因表現的時間與位置

1. 原位雜合 *In situ* hybridization: 分析 mRNA 表現



SoxB 基因表現在神經系統

2. 免疫化學染色: 分析蛋白質的分佈

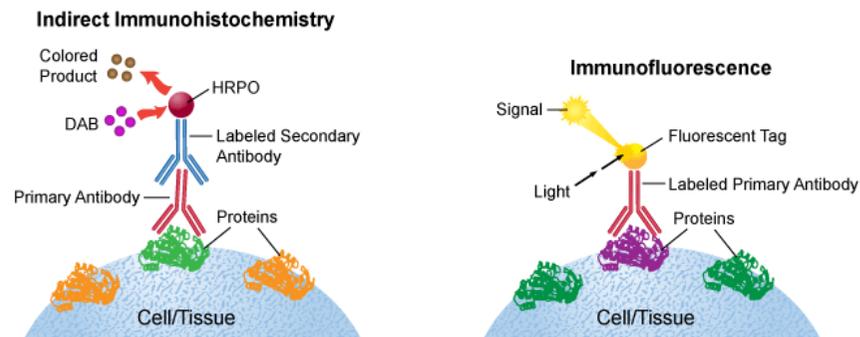
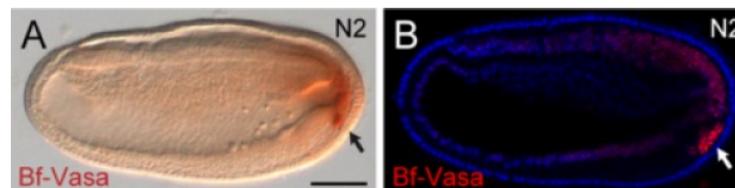
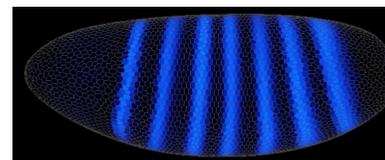
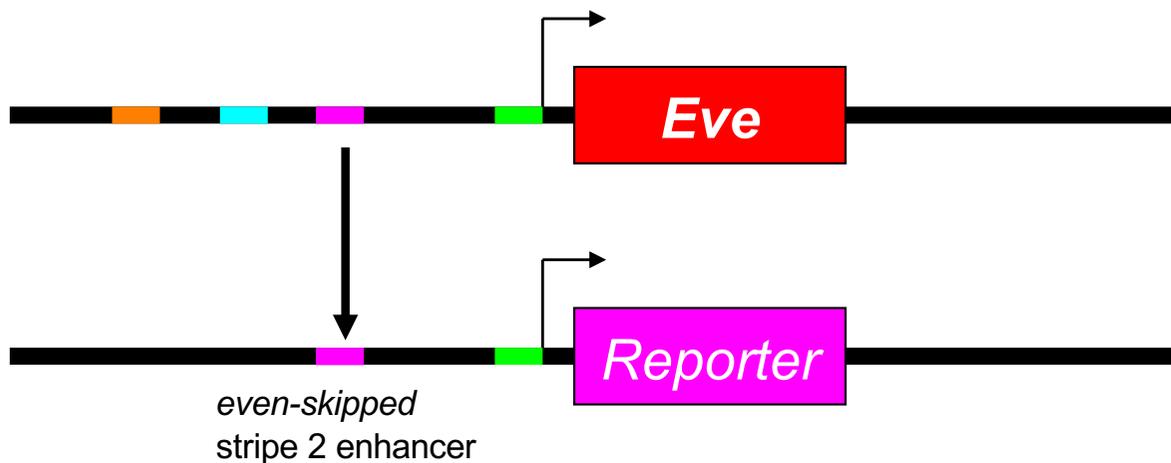


Diagram 1: Illustration of Indirect Immunohistochemistry and Immunofluorescence methods.

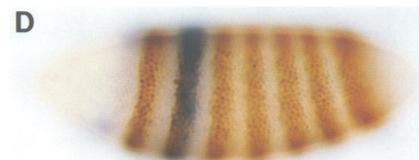


Vasa 蛋白質聚集在發育的生殖細胞中

3. 利用轉殖基因研究基因的調控機制與功能



Endogenous gene expression (*even-skipped* in fly embryo)

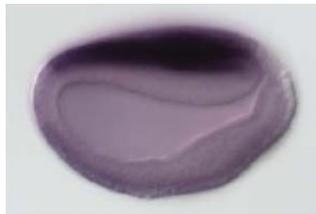
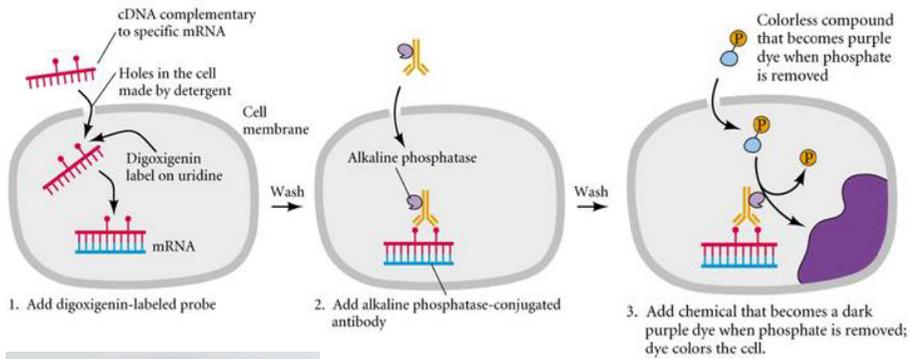


Reporter gene expression directed by tissue-specific enhancer (*even-skipped* stripe 2 enhancer)

(Modified from Small Blair & Levine, 1992)

研究發育基因功能的方法：分析基因表現的時間與位置

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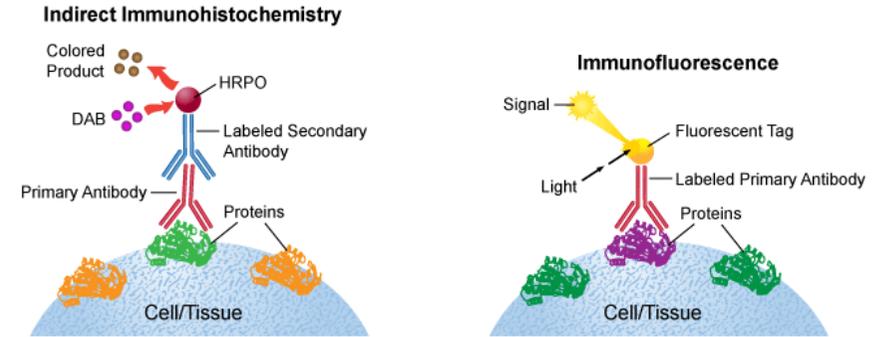
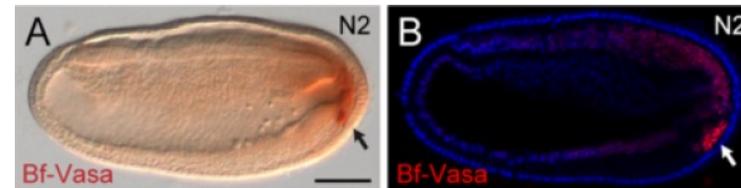
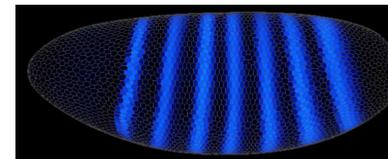
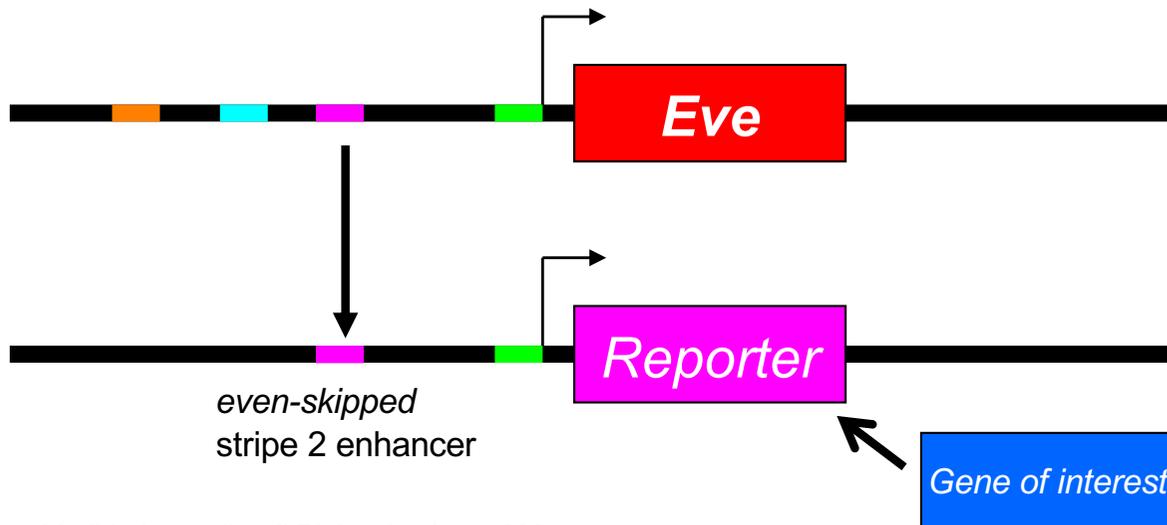


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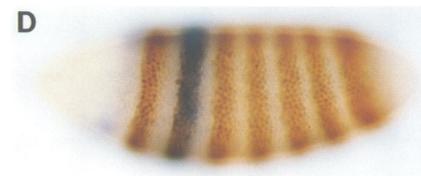


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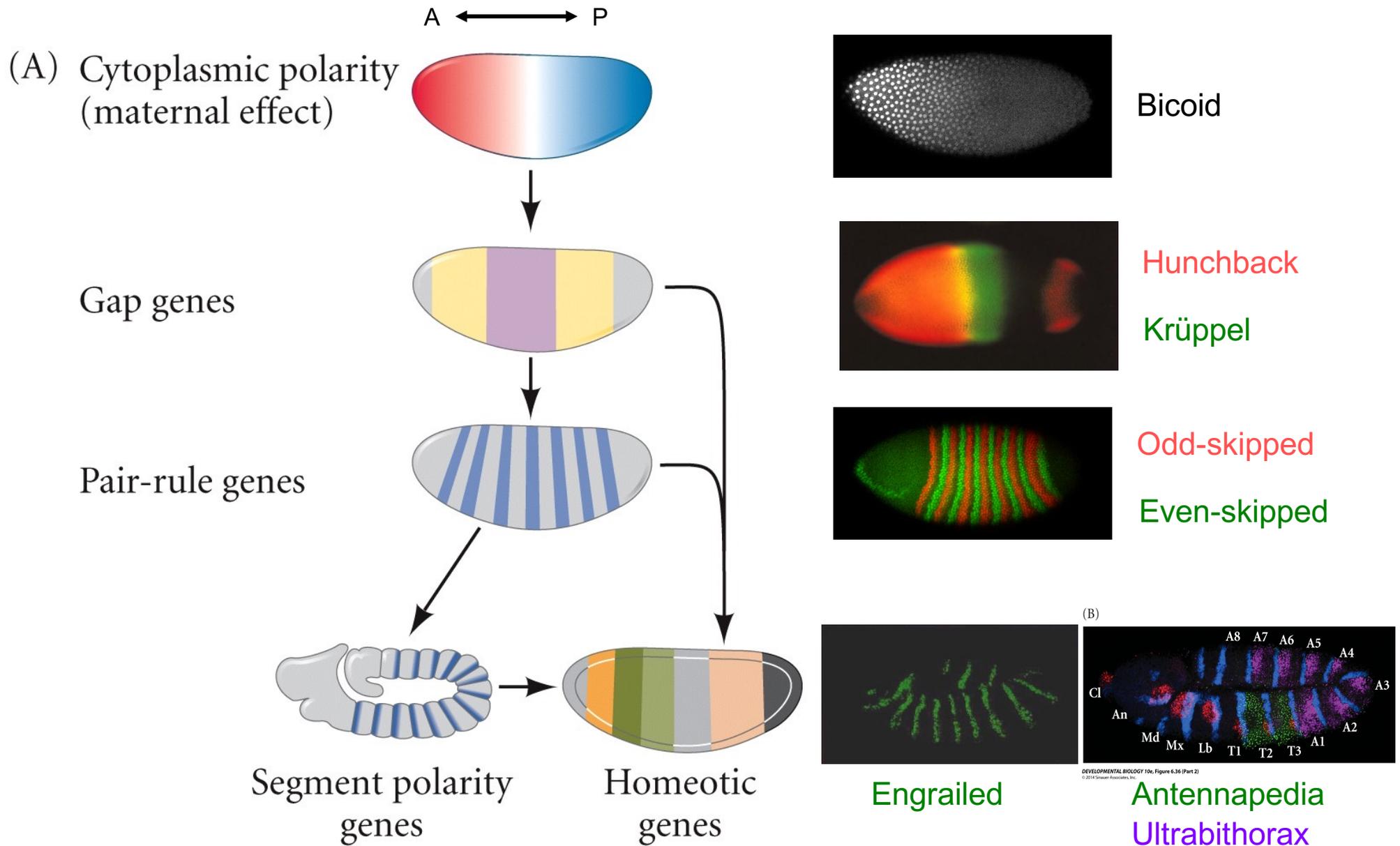
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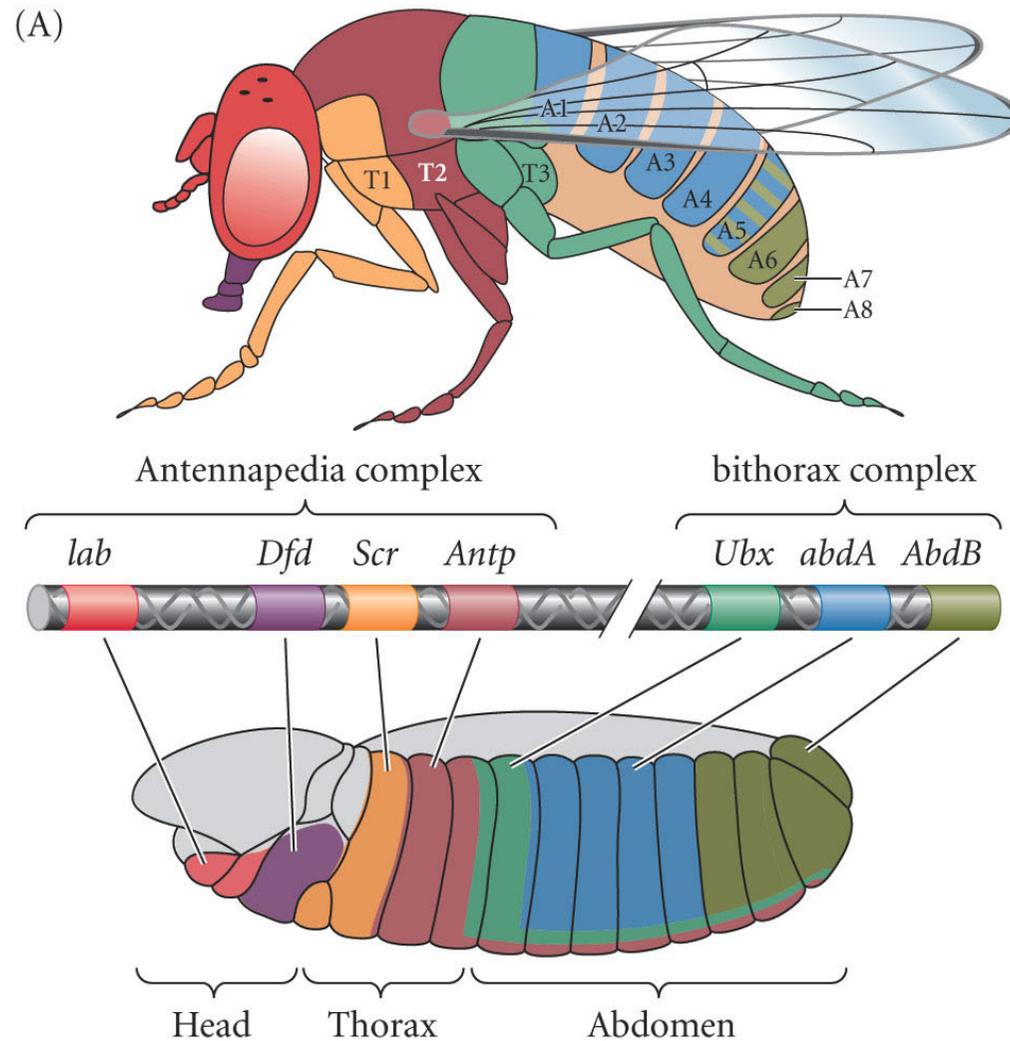
Reporter gene expression directed by tissue-specific enhancer (*even-skipped* stripe 2 enhancer)

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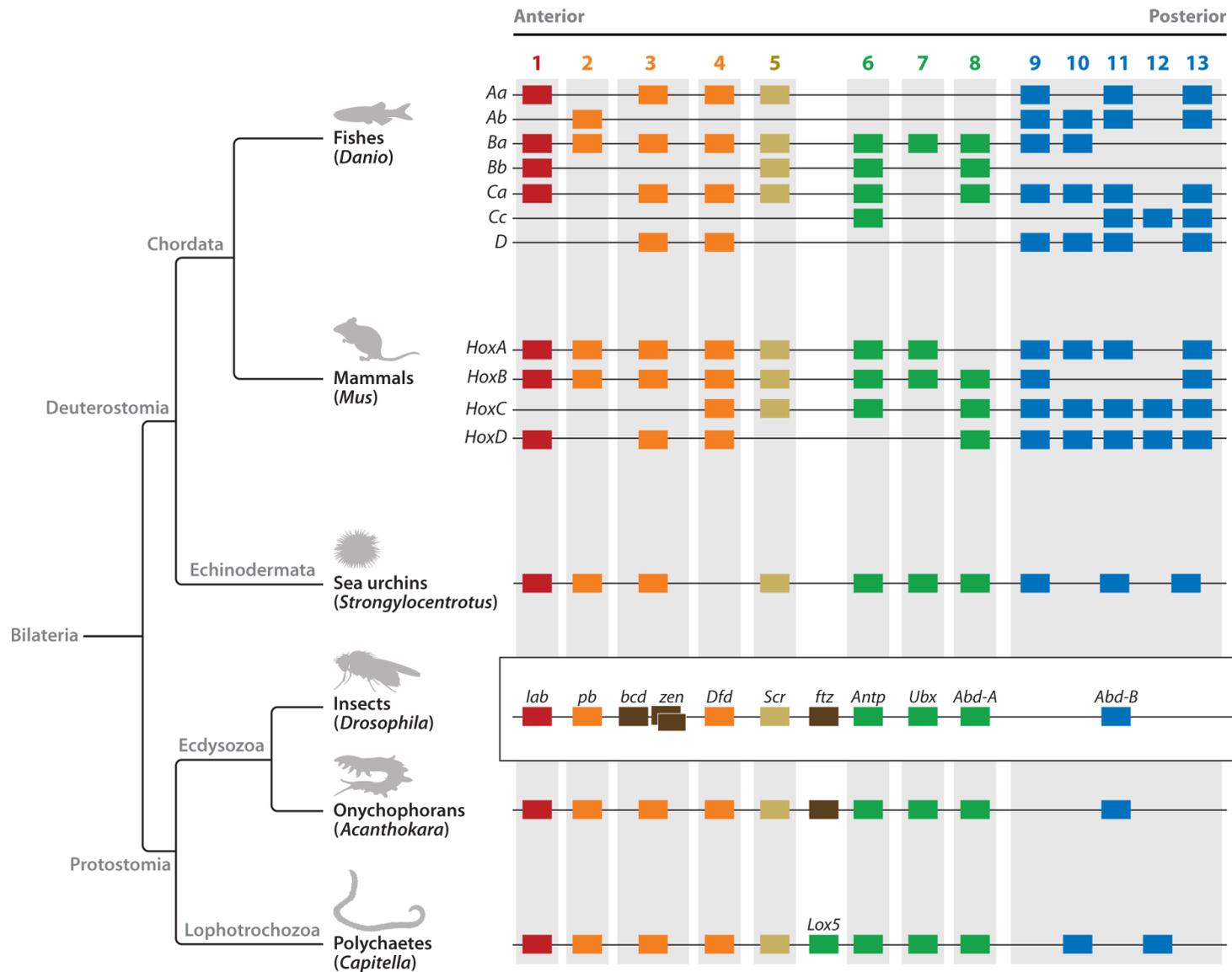
胚胎發育過程的基因邏輯-以果蠅為例



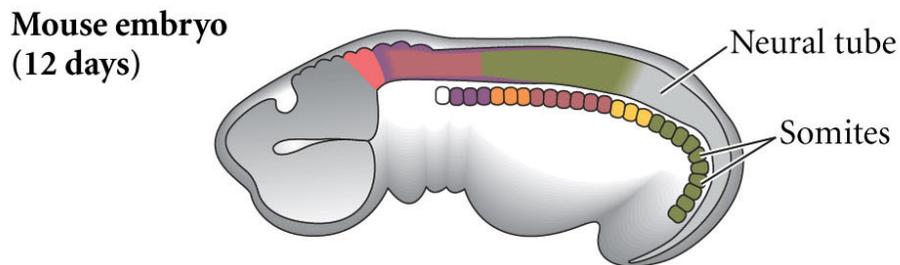
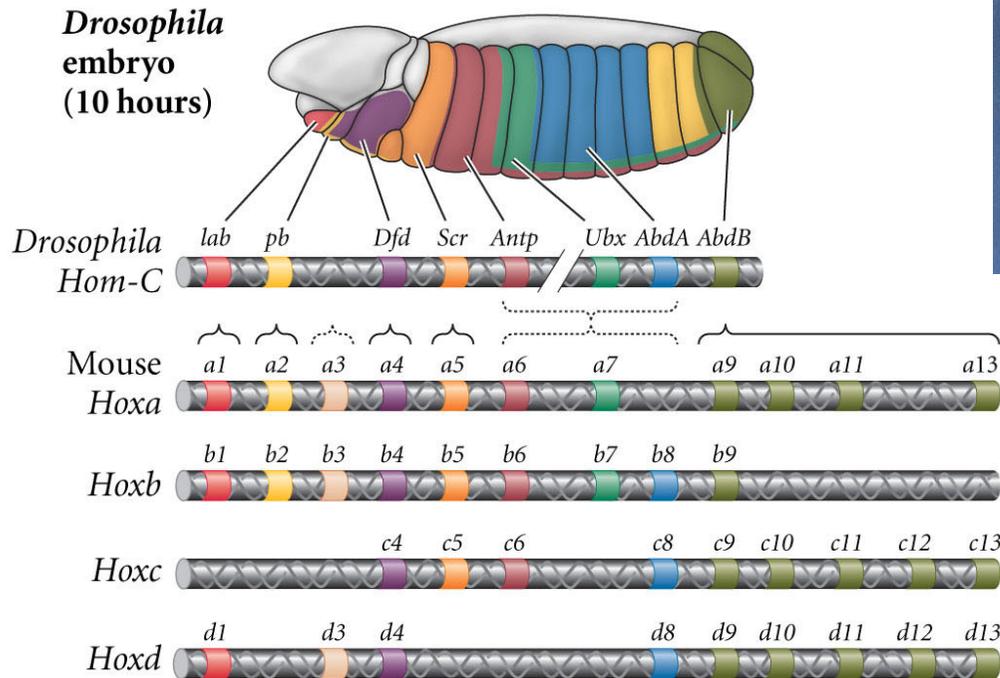
Hox 基因的表現位置決定前後體節的發育命運



Hox 基因廣泛存在於各類動物



Hox 基因調控動物前後體軸的發育

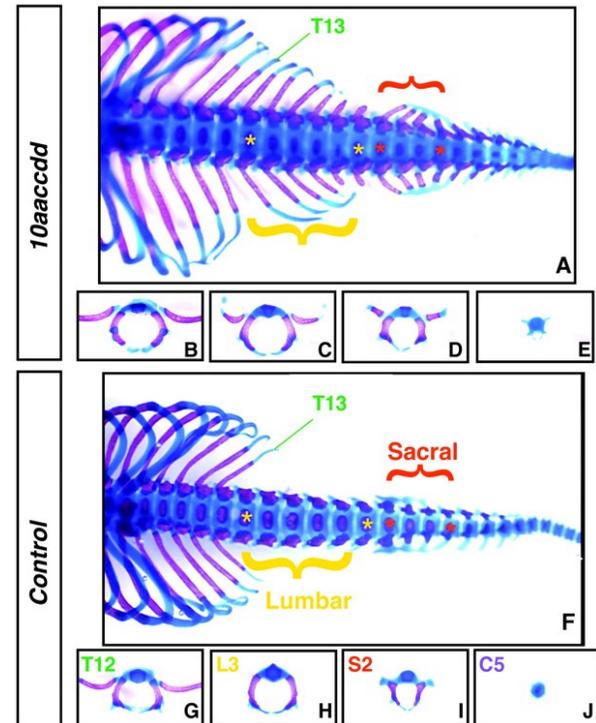


DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 11.42 © 2006 Sinauer Associates, Inc.



Mutations in cis-regulators of the *Ultrabithorax* gene
(Carroll et al, *From DNA to Diversity*, 2001)

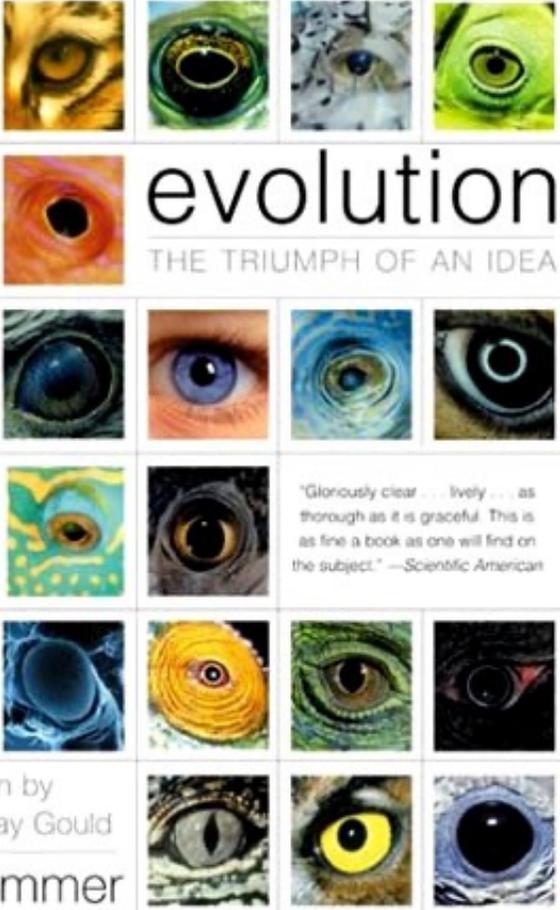
Hox10 triple mutant



(Wellik and Capecchi, *Science*, 301:363-367, 2003)

各式各樣的“眼睛”

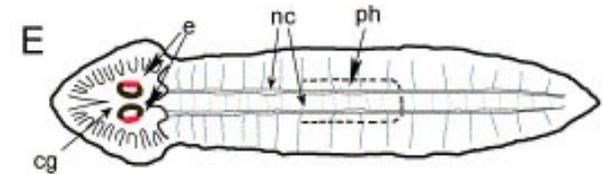
Companion
to the
PBS Series



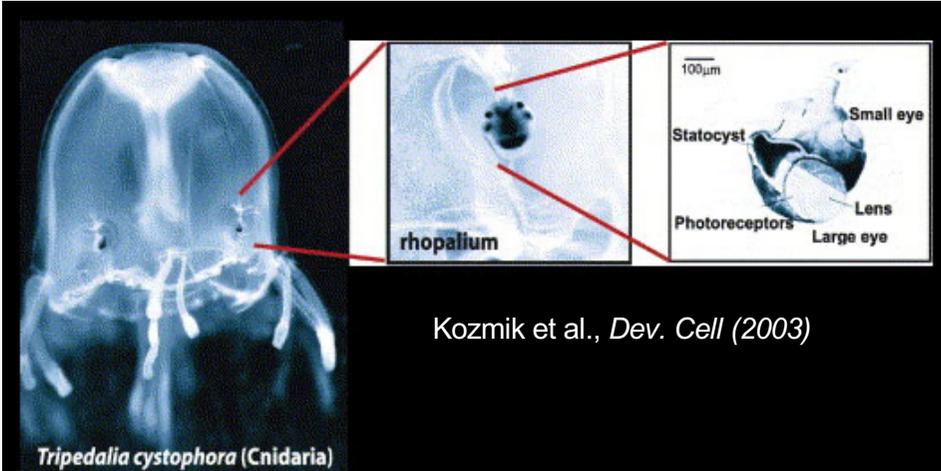
evolution
THE TRIUMPH OF AN IDEA

"Gloriously clear ... lively ... as thorough as it is graceful. This is as fine a book as one will find on the subject." —Scientific American

Introduction by
Stephen Jay Gould
Carl Zimmer



Mannini et al., *Dev. Biol.* (2004)



Tripedalia cystophora (Cnidaria)

rhopalium

100µm

Statocyst

Small eye

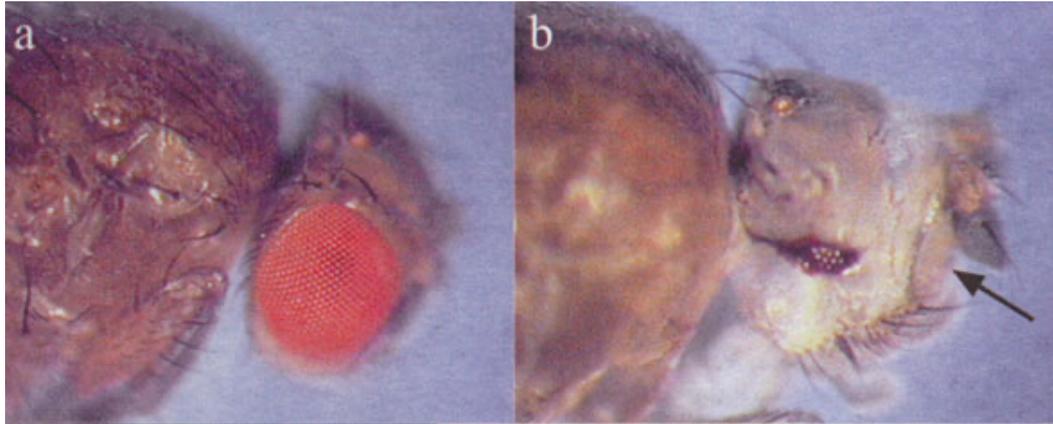
Photoreceptors

Large eye

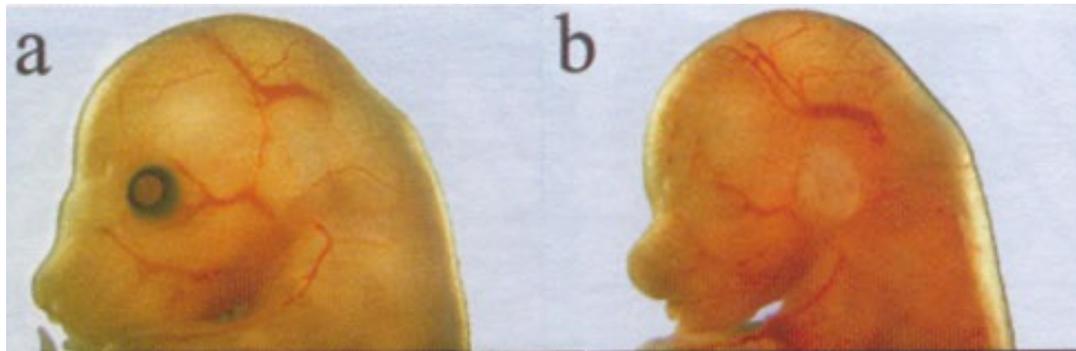
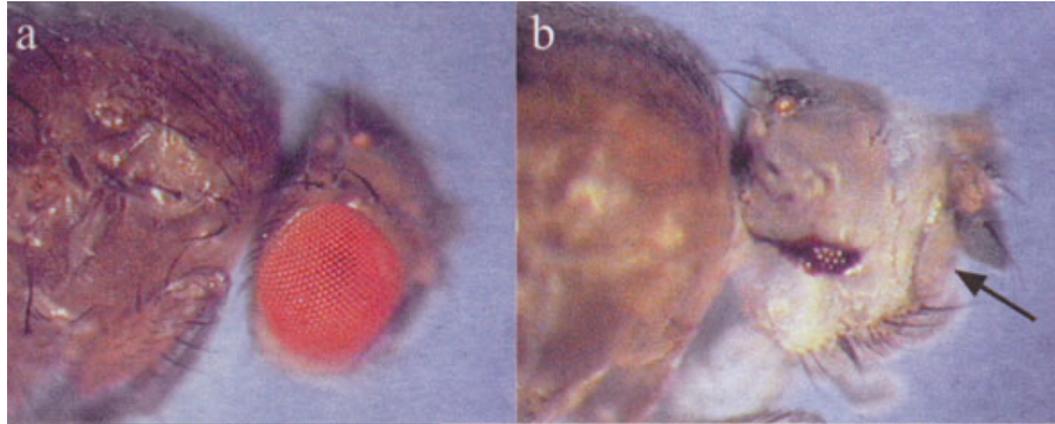
Lens

Kozmik et al., *Dev. Cell.* (2003)

Pax-6 基因調控動物眼睛的發育



Pax-6 基因調控動物眼睛的發育



(Carroll, *From DNA to Diversity*, 2001)



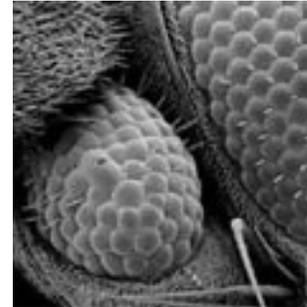
(Mouse Genome Database)

果蠅與老鼠的眼睛發育都受到這個同源基因的調控

果蠅的 *Pax-6* 基因誘導眼睛的發育



(Halder et al. 1995)



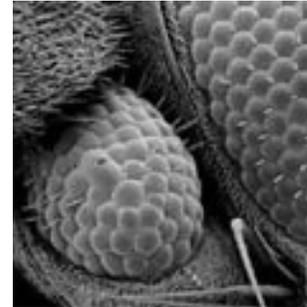
果蠅 *Pax-6*



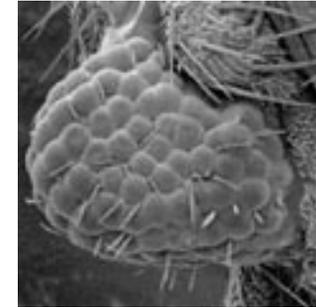
果蠅與老鼠的 *Pax-6* 基因在眼睛發育的功能上是可以互相置換



(Halder et al. 1995)



果蠅 *Pax-6*



老鼠 *Pax-6*

更多不同動物的 *Pax-6* 基因也可以在果蠅身體誘發眼睛發育



烏賊 *Pax-6*
(Tomarev et al. 1997)

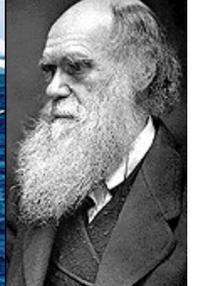


海鞘 *Pax-6*
(Gladon et al. 1997)

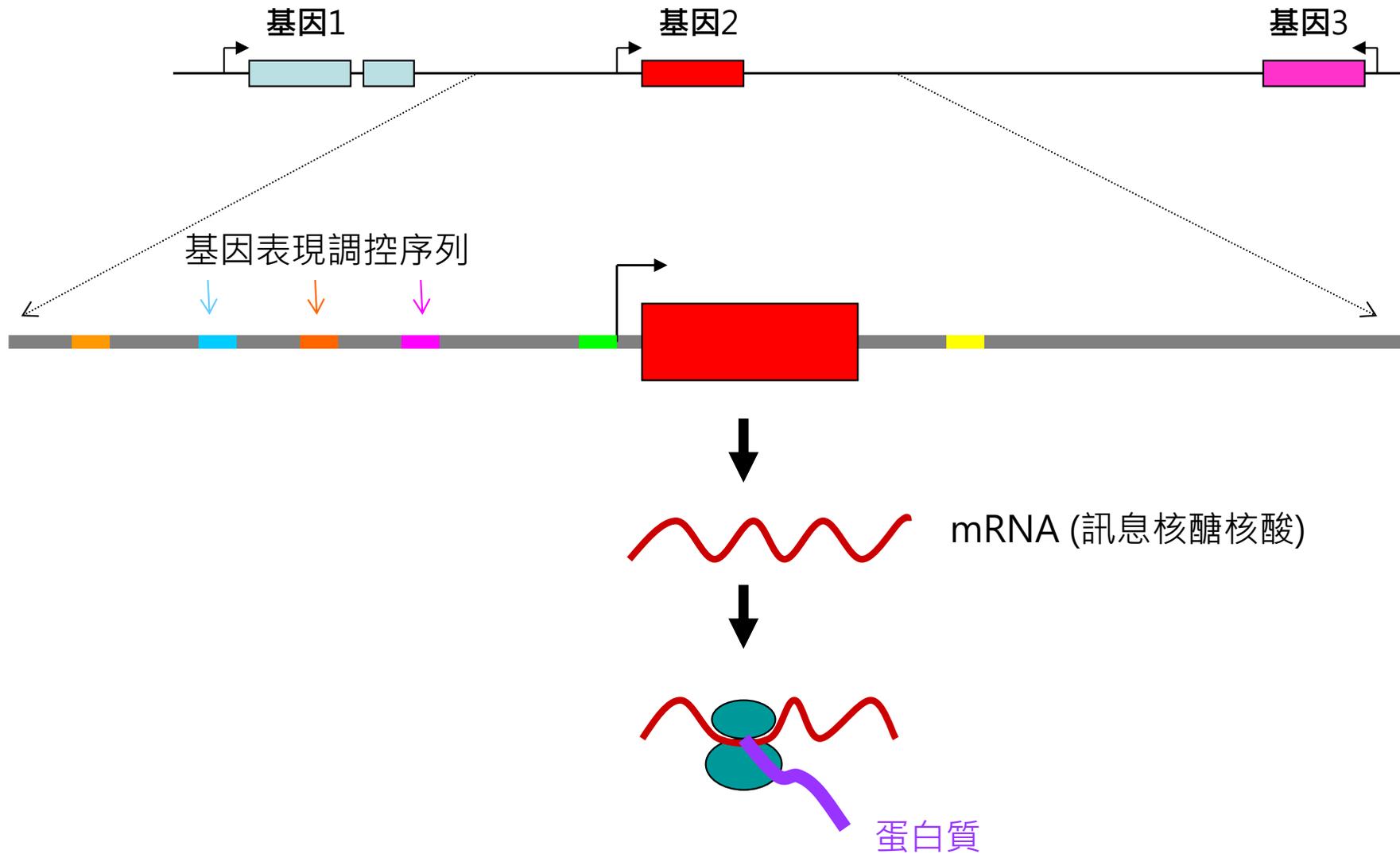


水母 *PaxB*
(Kozmik et al. 2003)

- 
- 如果不同動物的基本身體結構發育是由相似的同源基因來調控,動物如何演化出如此歧異的形態?
 - 我們是否能從發育基因與發育機制演化的角度來探討動物形態變異的起源?

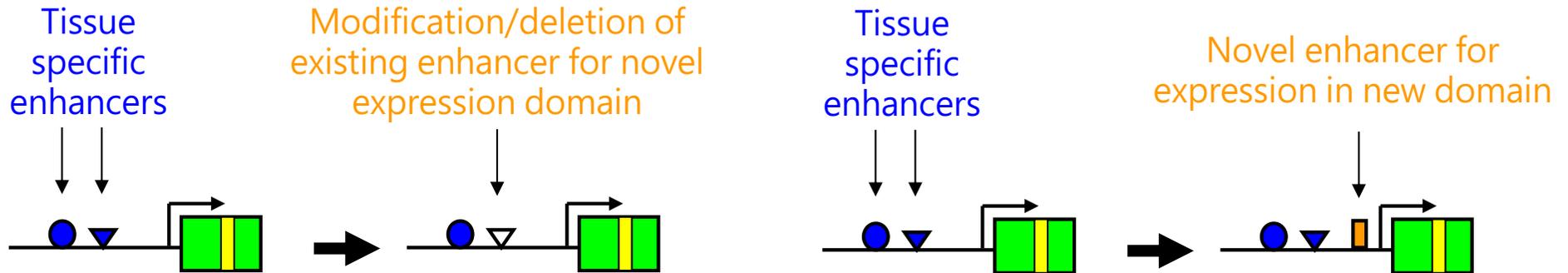


發育基因如何演化出新的功能？

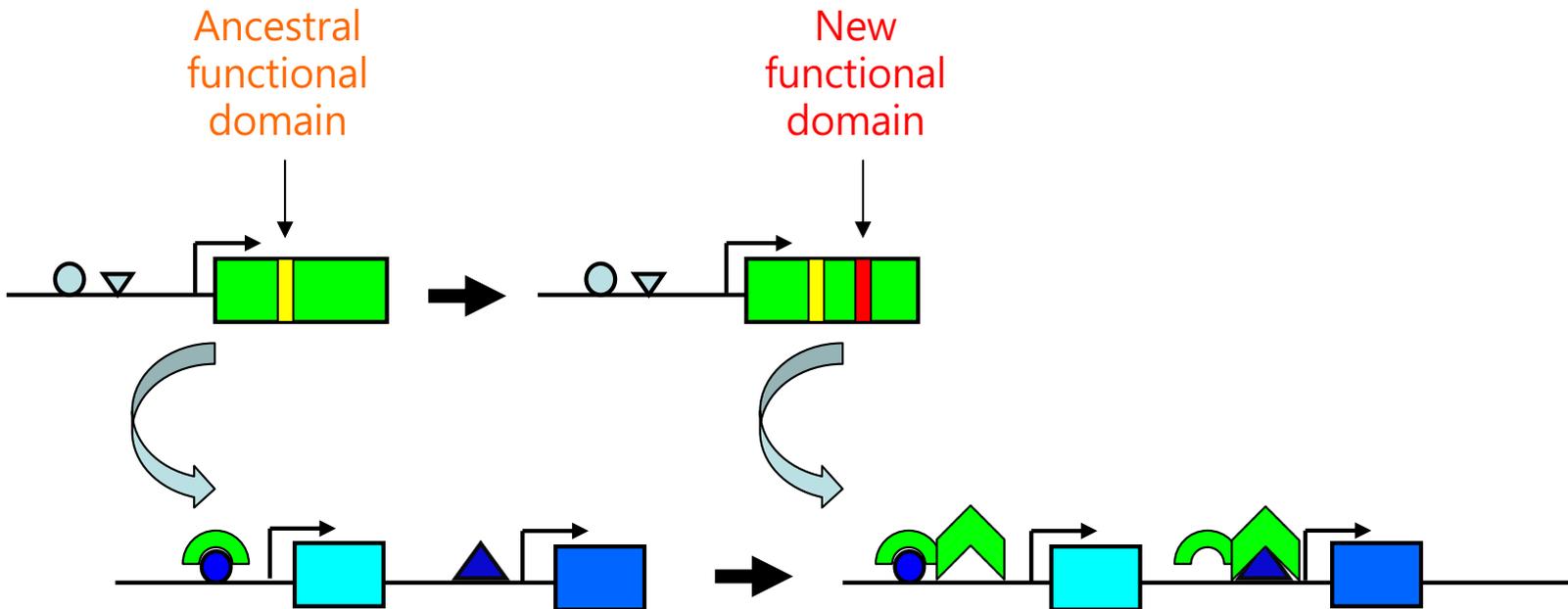


發育基因如何演化出新的功能？

1. 調控DNA序列的演化造成基因表現方式的改變

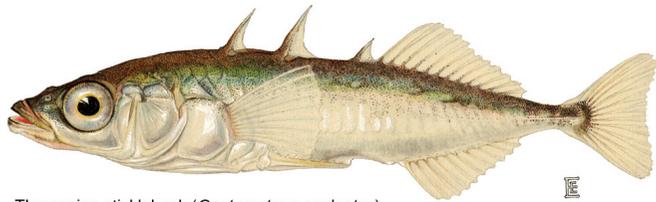


2. 蛋白質序列的演化造成基因功能的改變

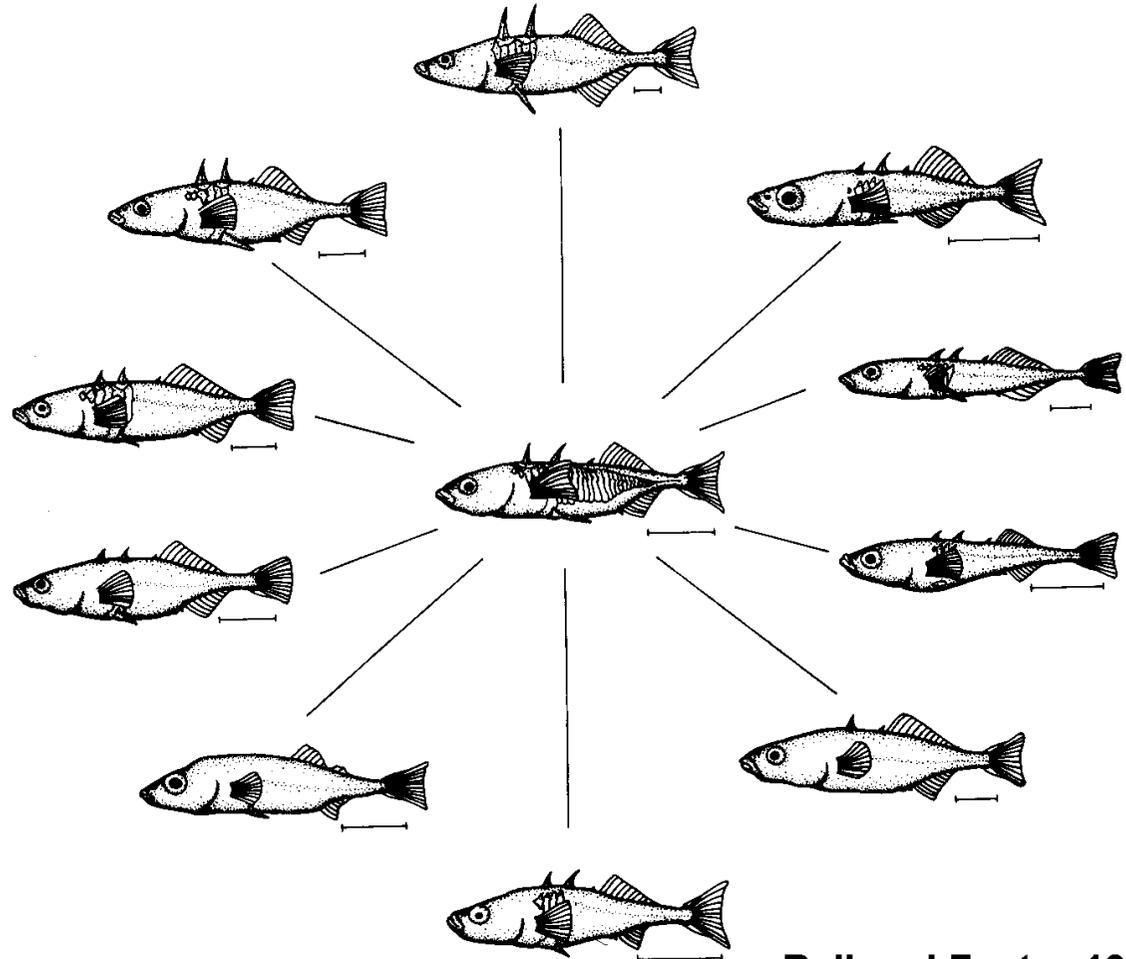
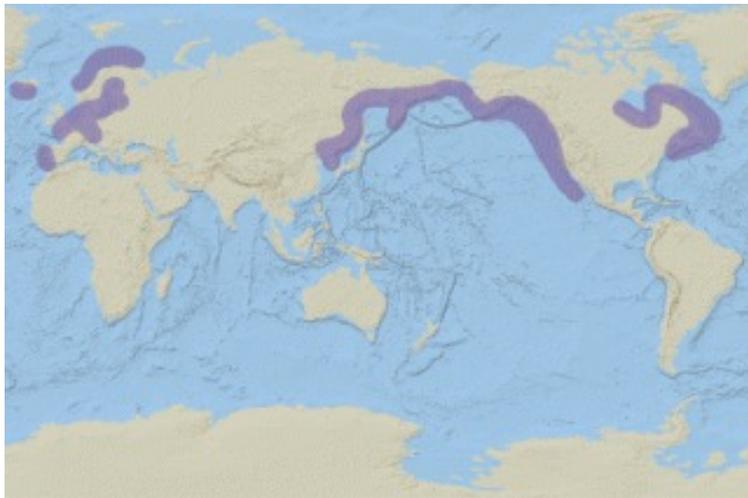


背棘魚形態的演化

在距今約 12,000 年前，一些原本在海水中生活的背棘魚進入淡水水域生活，並且演化出許多不同的形態，例如腹鰭的改變與消失

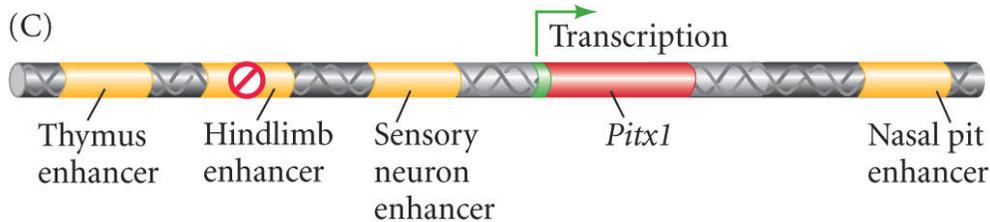
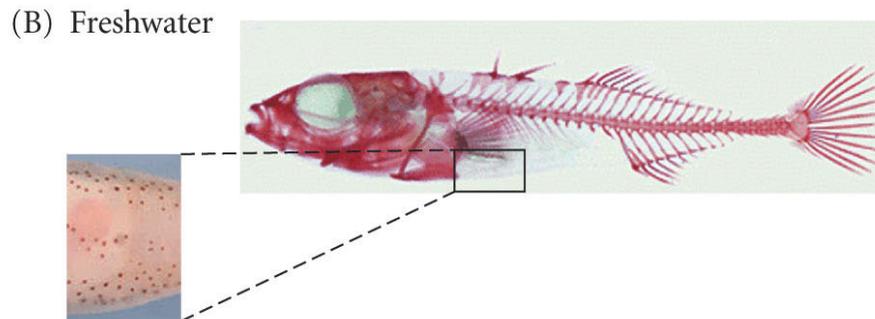
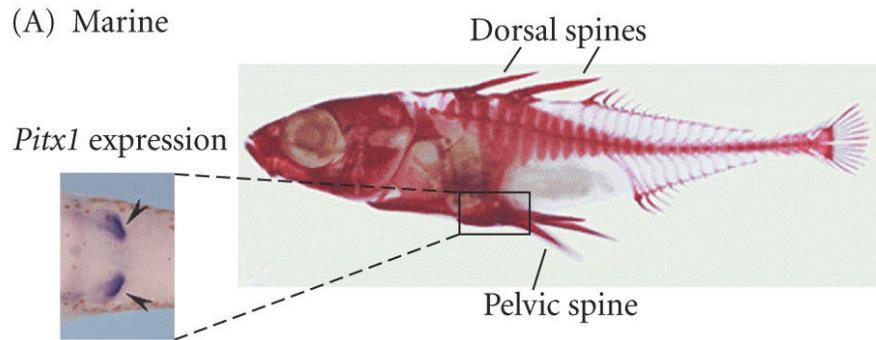


Threespine stickleback (*Gasterosteus aculeatus*)

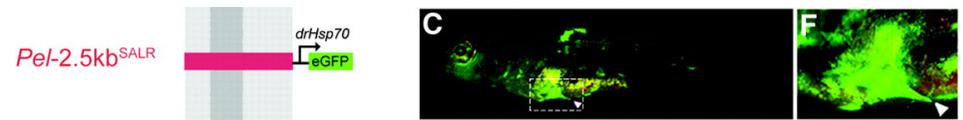


Bell and Foster 1994

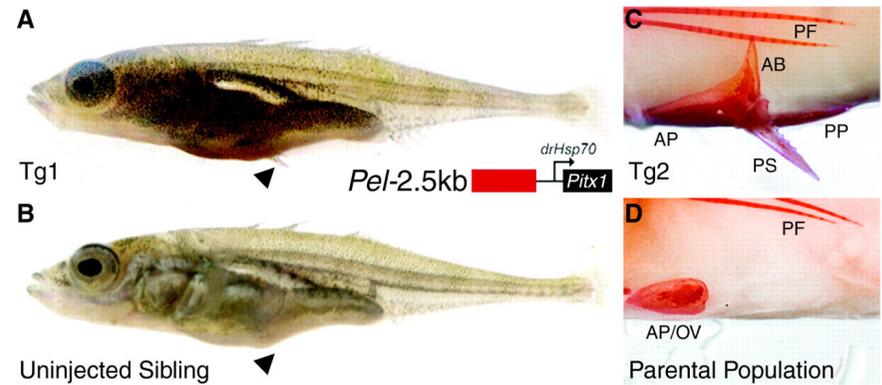
背棘魚腹鰭的消失與 *Pitx1* 基因的表現有關



研究人員從有腹鰭的海水背棘魚中找到一段 2.5-kb *Pitx1* intergenic DNA 可以調控腹鰭生長區域的基因表現



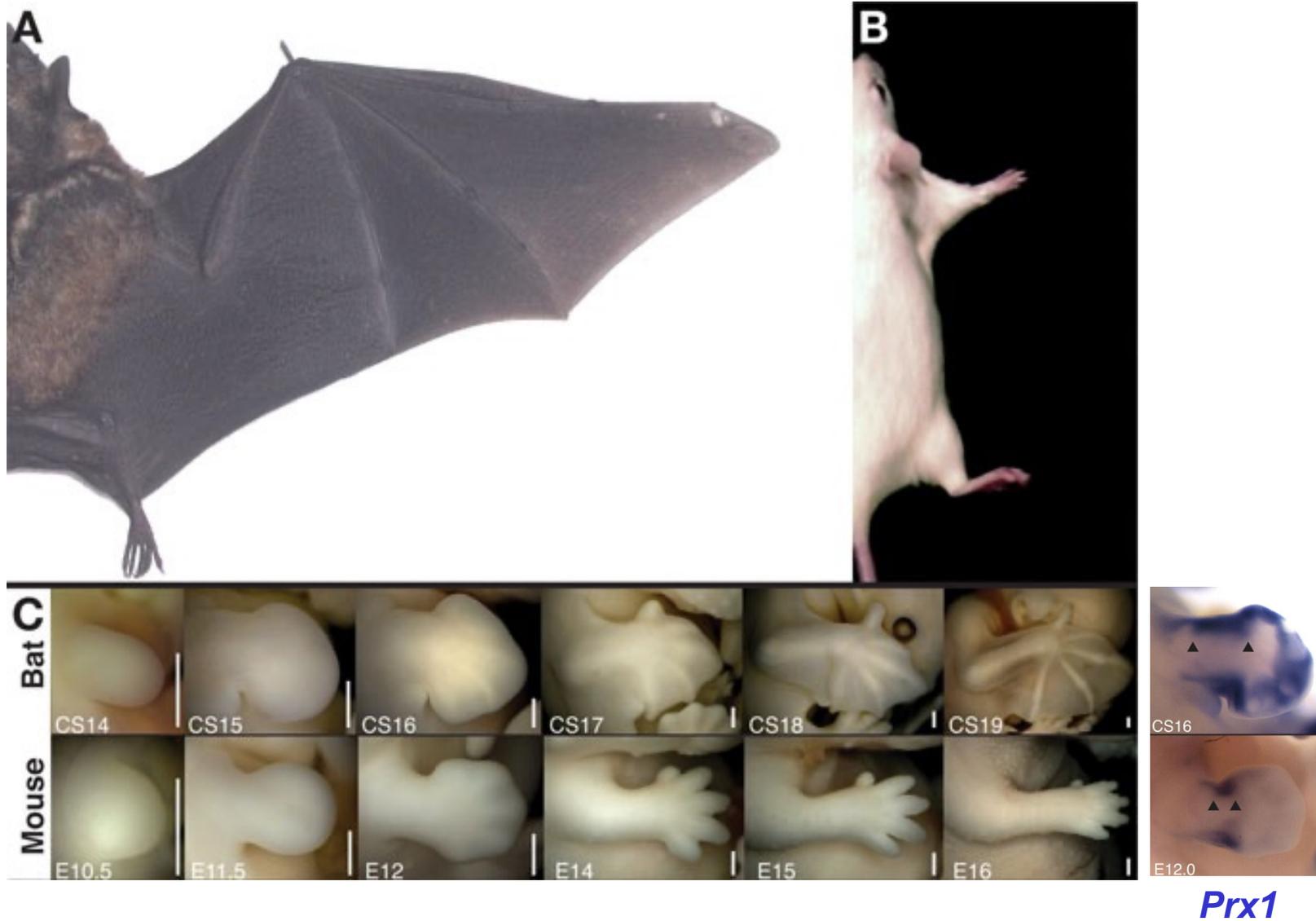
利用此片段調控序列可以強迫 *Pitx1* 基因在淡水背棘魚的腹部表現，並且在原本沒有腹鰭的魚誘發腹鰭的發育



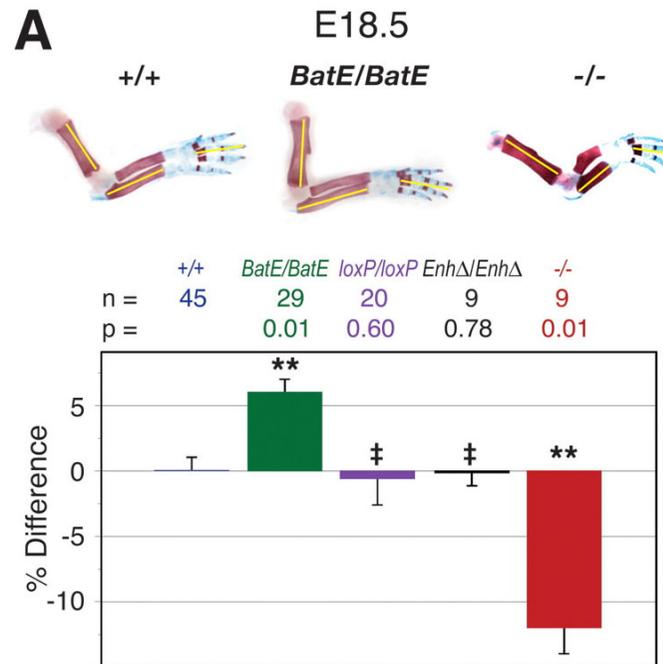
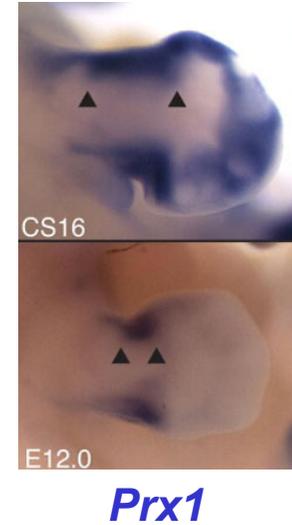
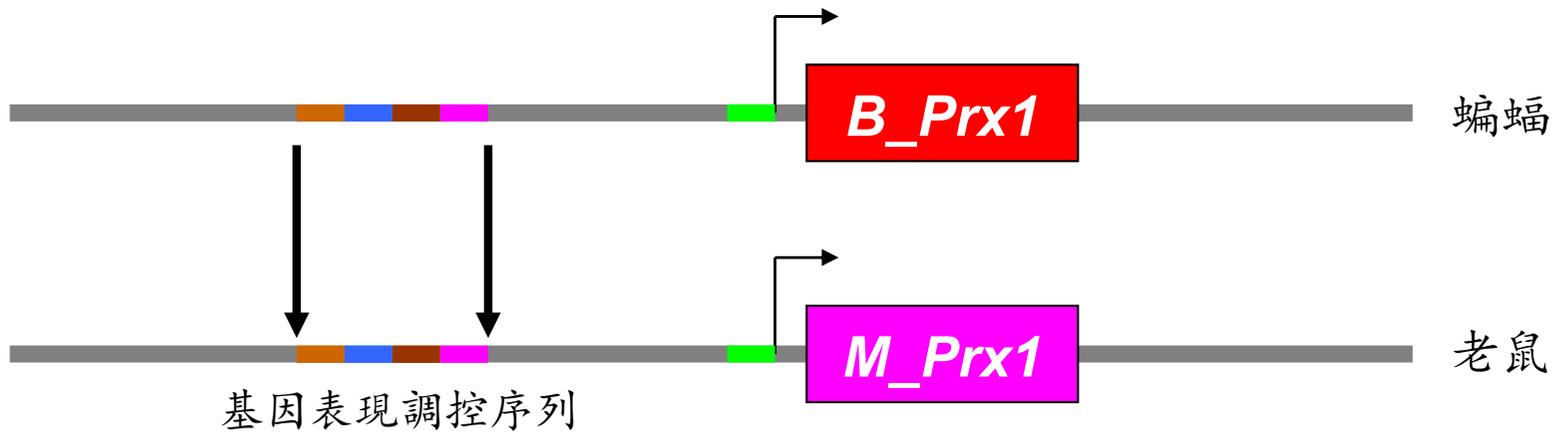
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(Chan et al., *Science*, 327, 302-305, 2010)

蝙蝠如何演化出翅膀？



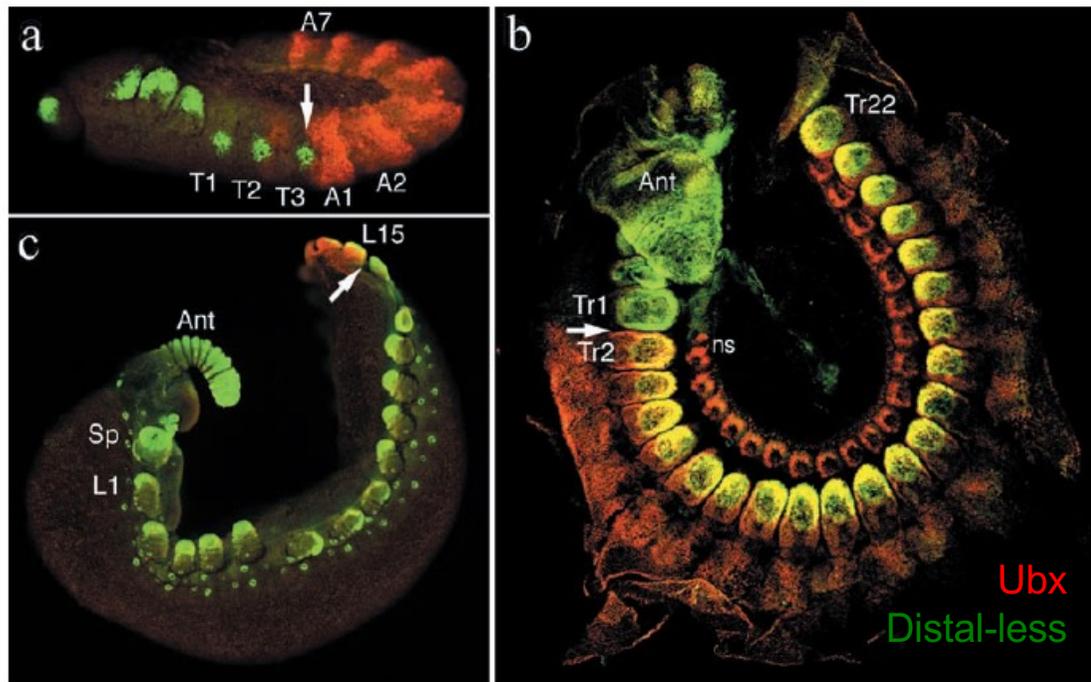
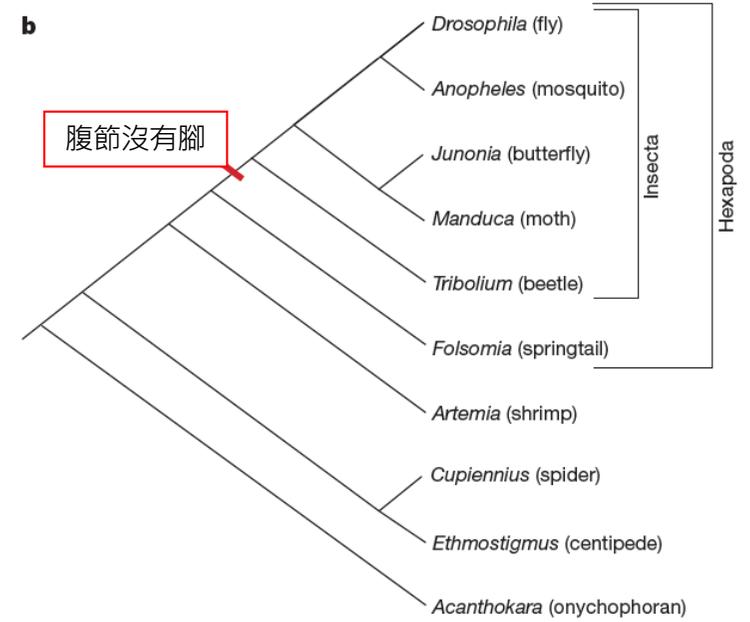
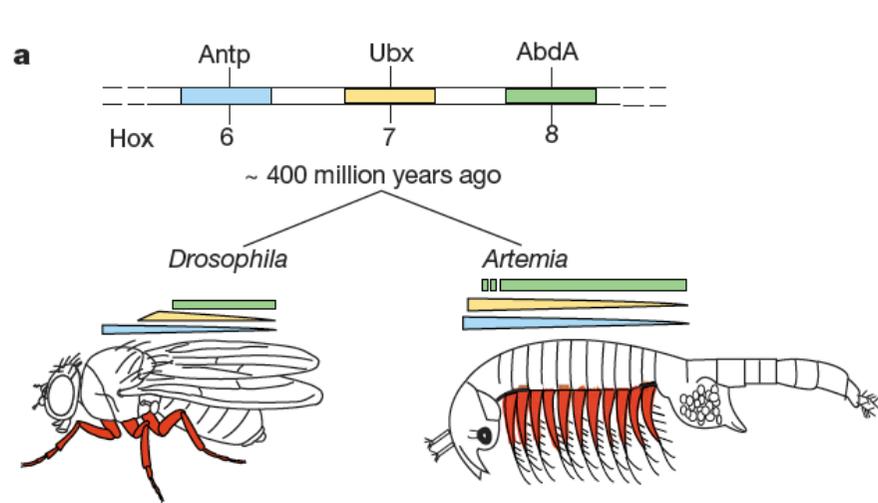
蝙蝠如何演化出翅膀?



蝙蝠的*Prx1*基因表現調控序列
會造成老鼠前肢增長6%

其他94%的變異要如何解釋?

- 為什麼昆蟲有六隻腳？

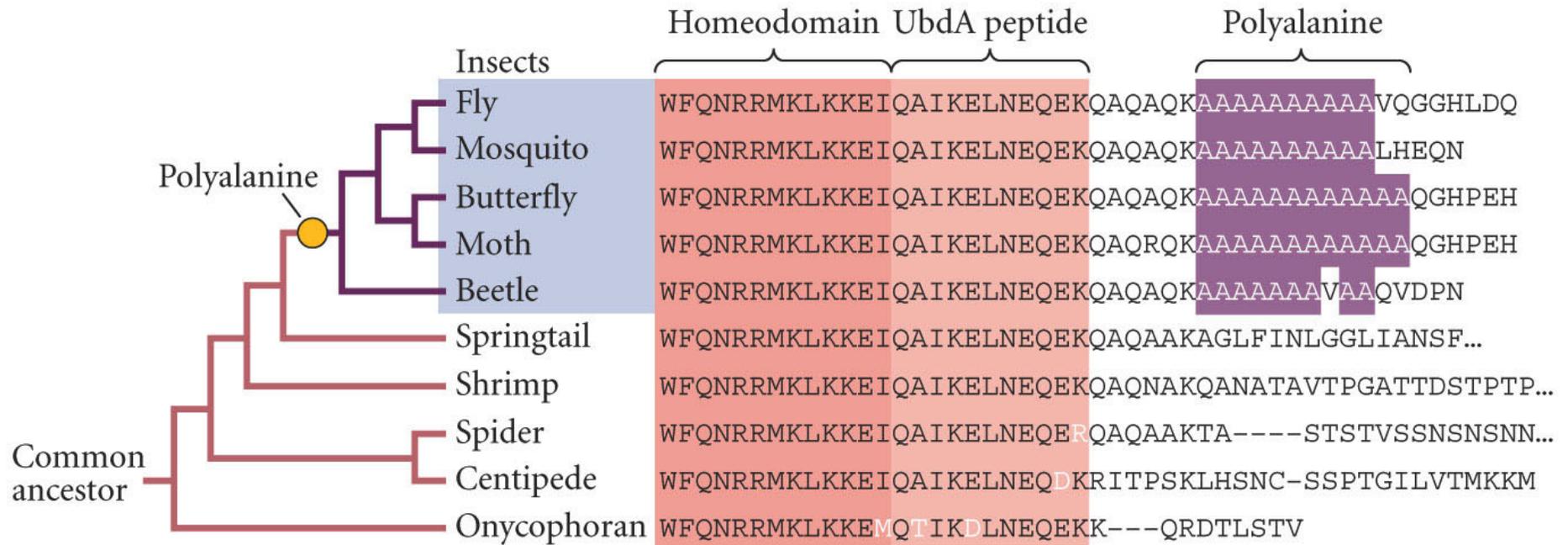


在大多數節肢動物中，Ubx 無法抑制與腳發育相關的基因 *Distal-less*

但是在昆蟲中Ubx 會抑制 *Distal-less* 基因的表現，因而昆蟲在後端的腹部體節不會有腳

Figure 5.8
Comparison of Ubx and Dll expression in arthropods and onychophora

昆蟲Ubx蛋白質序列的演化造成基因功能的改變



在昆蟲綱中，Ubx 蛋白質多了一段 poly-alanine 序列。這個新演化出來的功能性序列造成昆蟲 Ubx 蛋白質功能的改變。



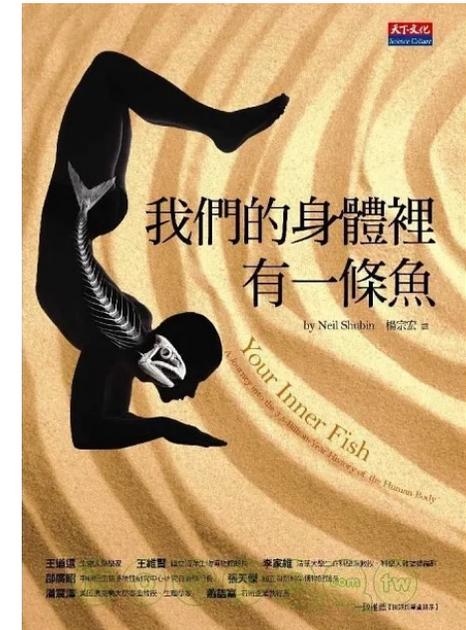
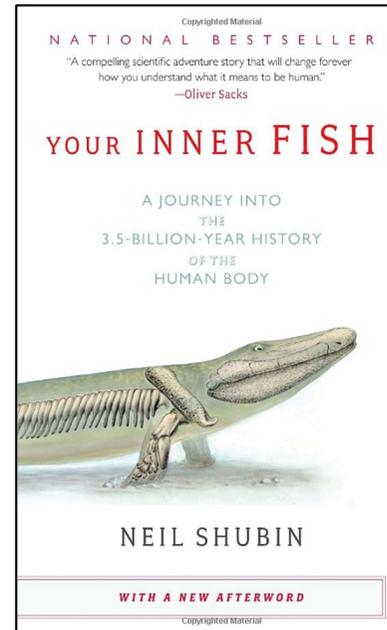
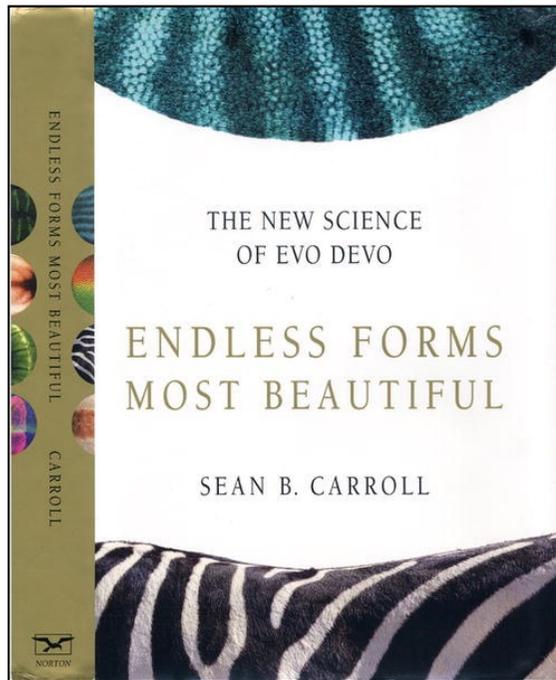
...from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

從如此簡單的起始
無止盡的奇妙形態
都可以被演化出來

-Charles Darwin, "*The Origin of Species*" (1859)
達爾文 "物種起源"



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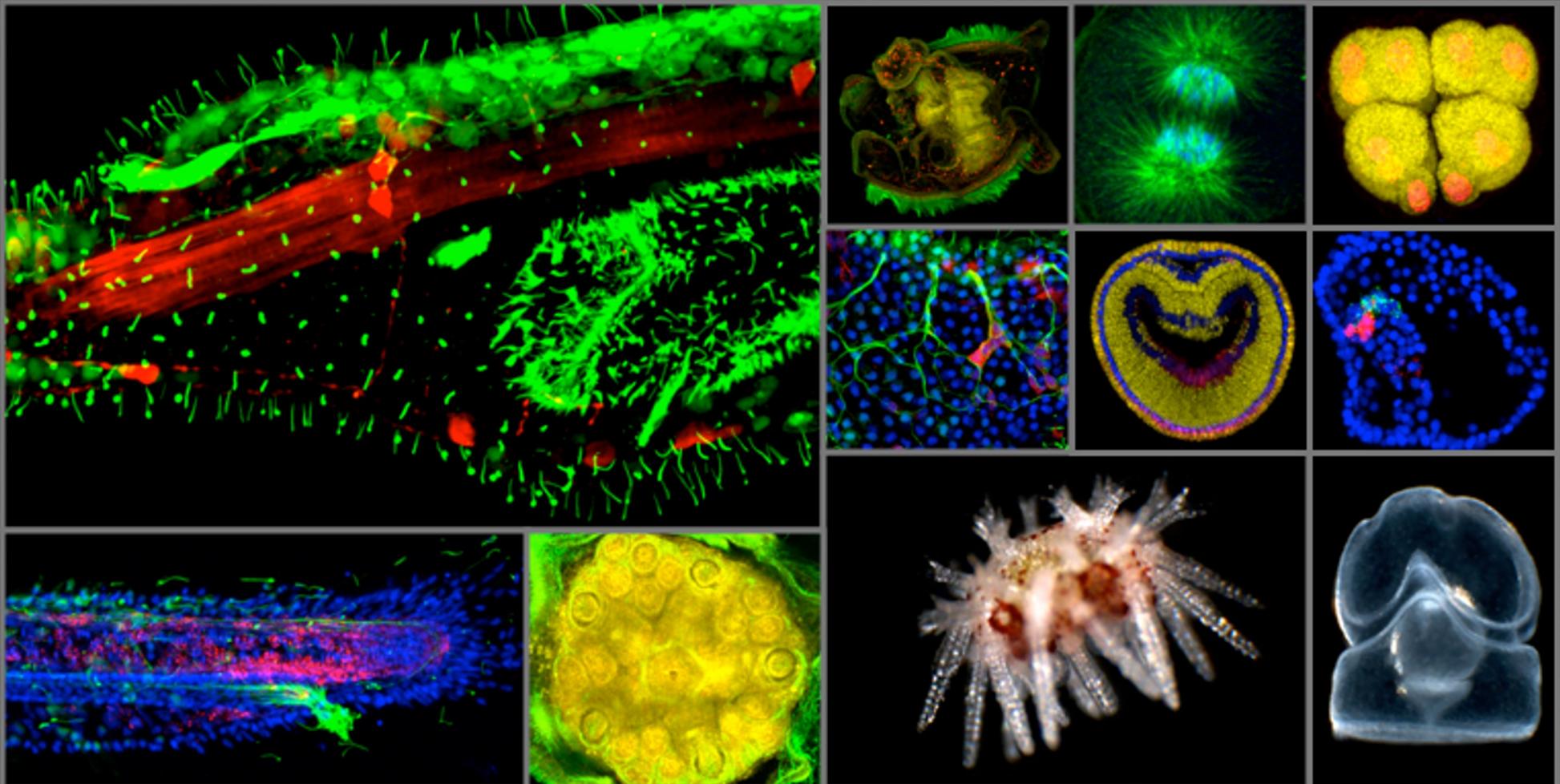
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