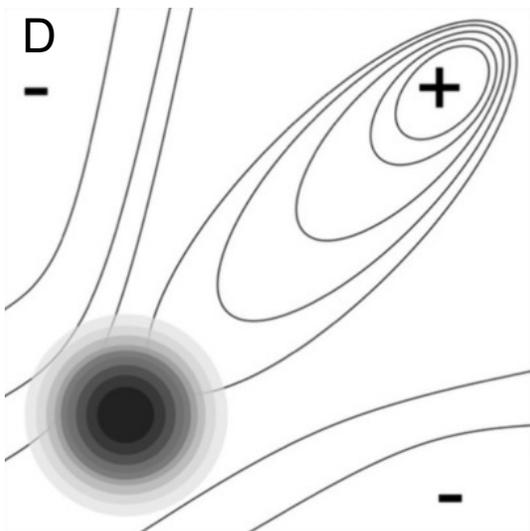
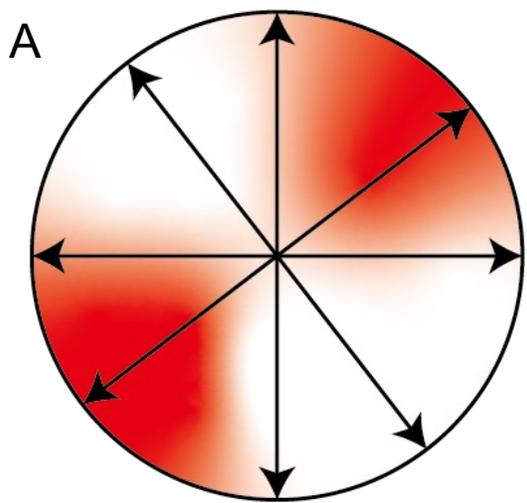
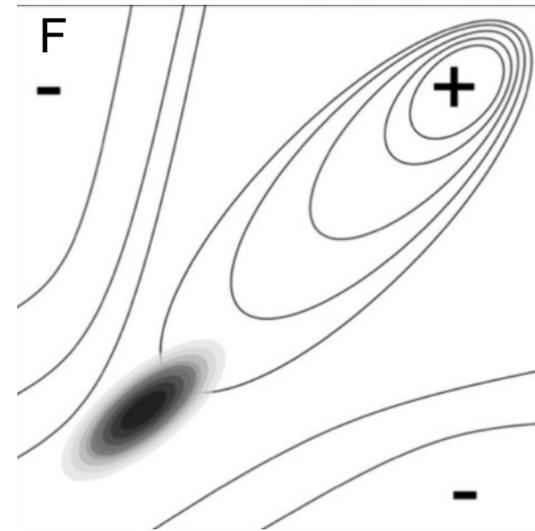
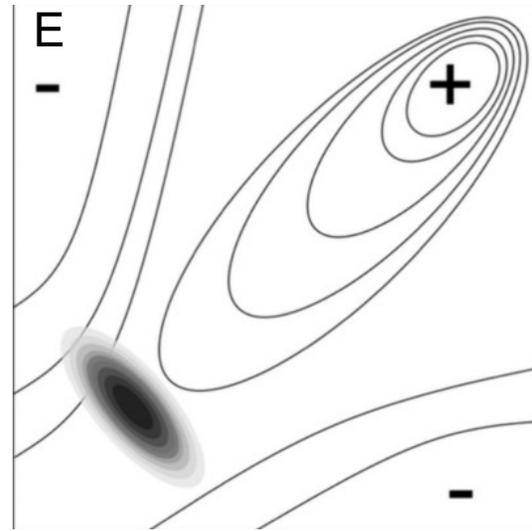
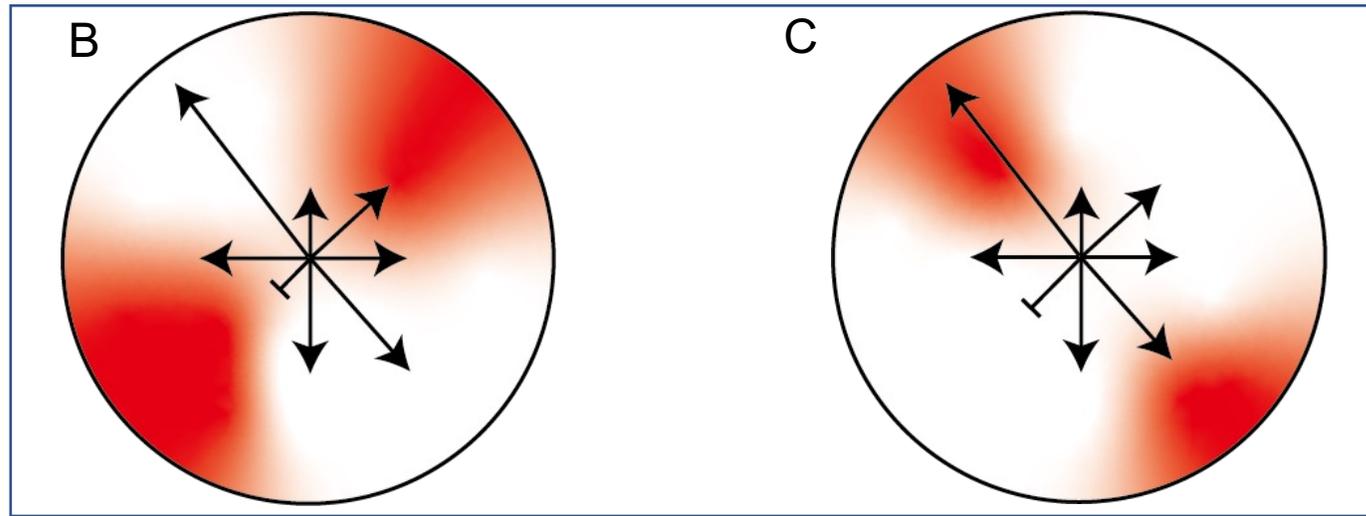


自然选择与发育偏好模型

MS



EES

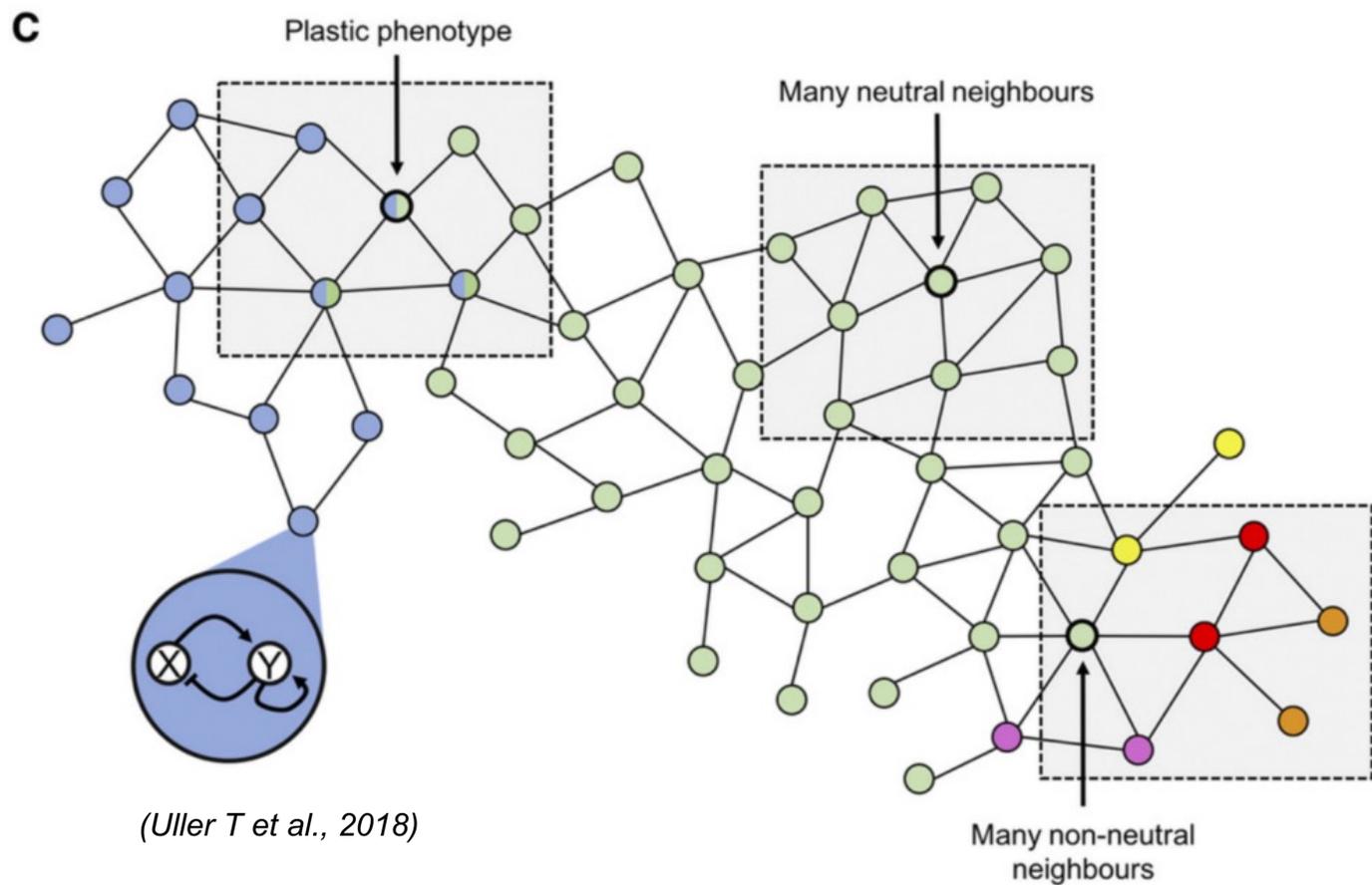
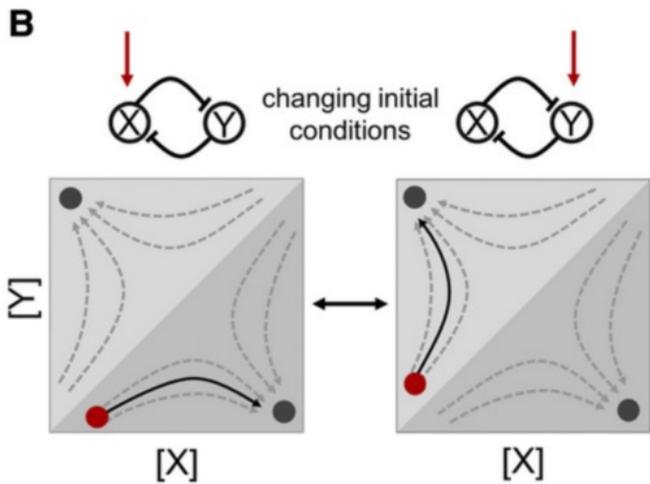


(Uller T et al., 2018)

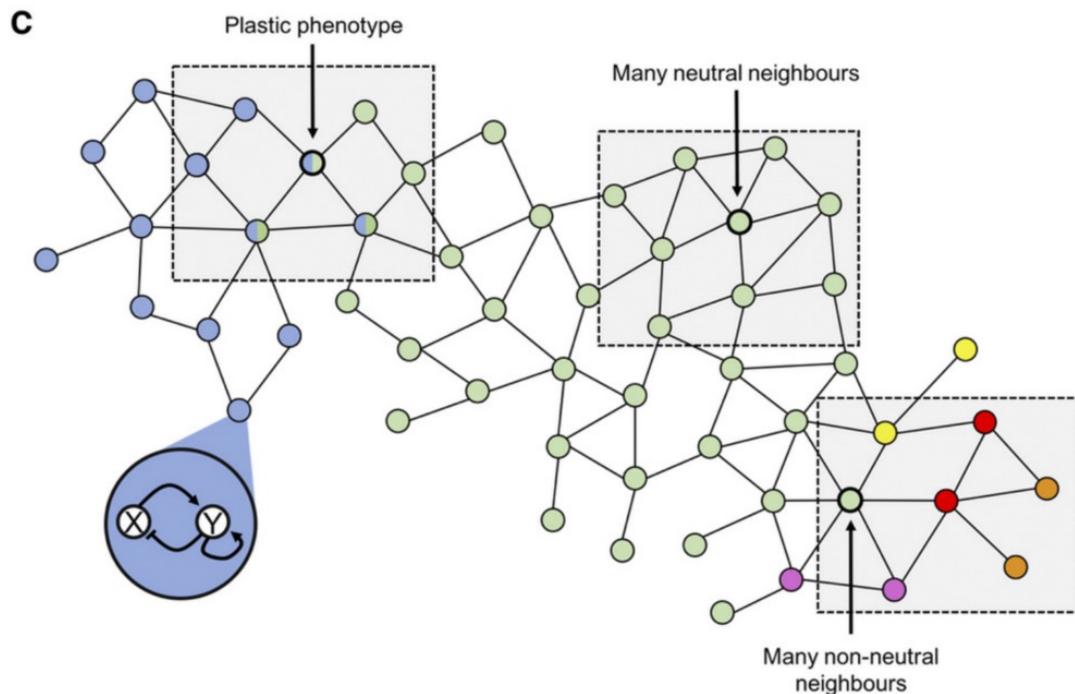
- 自然选择 不是决定进化方向的唯一要素
- 发育偏好 可能限制也可能促进适应性进化

调控网络 Regulatory networks

注：调控网络并不局限于基因的相互作用，细胞、组织间的相互作用也可以纳入其中



调控网络 Regulatory networks



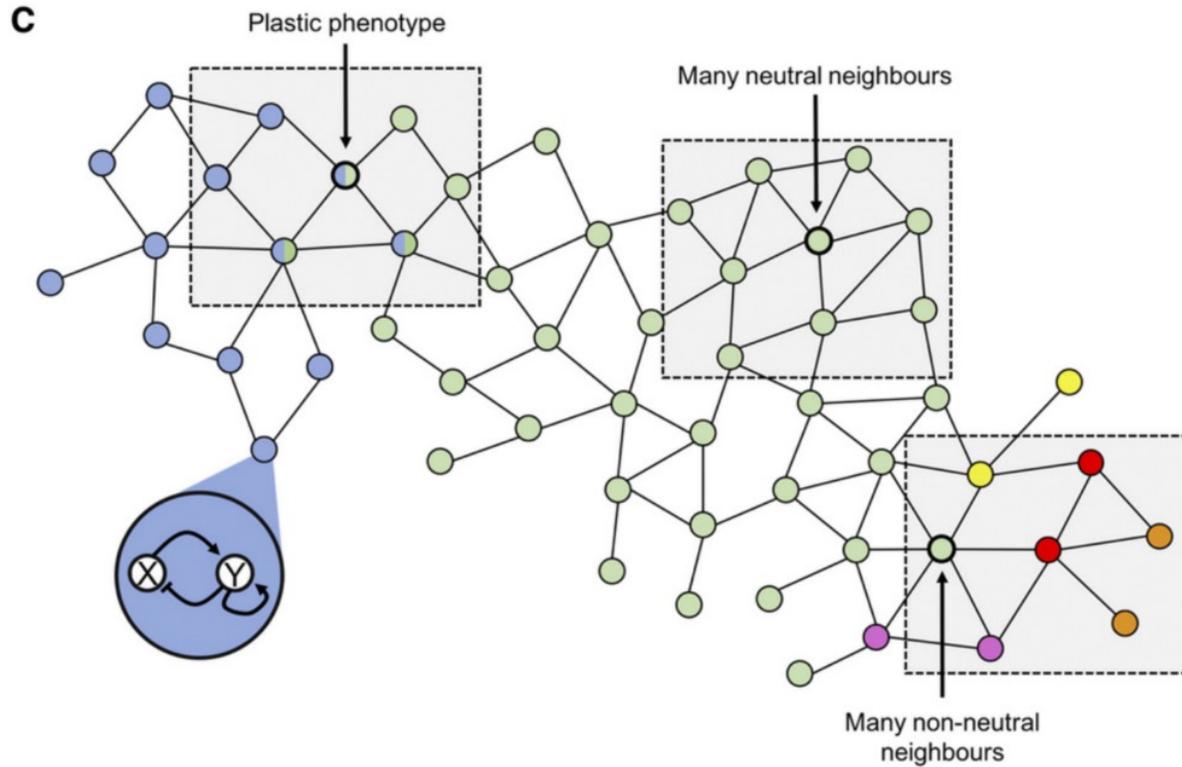
调控网络的特性：

1. 基因型的数量要远远多于表型数量
 - 表达相同表型的基因型数量并不一致
 - 具有相同表型的基因型往往在拓扑上相似，但其相邻的表型可能完全不同
2. 几乎任何一种表型的多种基因型构成了一个巨大的相连的网络
 - 典型的基因型可能具有大量相同表型的邻居
3. 即使距离非常远的基因型，也可能产生相同的表型
 - 这意味着表达相同表型的调控网络可能没有相同的调控元件
4. ...

一些推论：

1. 表型之间的可及性是有差异的，且是不对称的
2. 随机突变/环境扰动也能被调控网络引导偏向某些表型
3. 群体进化新的功能表型的能力随着相同表型的基因型数量的增加而增加；
4. 不同的选择将群体推向网络的不同区域（如在稳健的选择下，种群将朝着特定表型的网络中心进化，而在不停变化的选择下，种群将朝着不同表型的边界进化）；
5. 更高维的网络（表型之间具有相关性）、模块化使得网络可以具有学习能力，可以加速适应性进化。
6. ...

发育偏好能帮助理解自然选择难以解释的问题



The explanatory value of developmental bias is that it can help to explain biological features that are difficult to account for assuming that selection acts on unbiased variation.

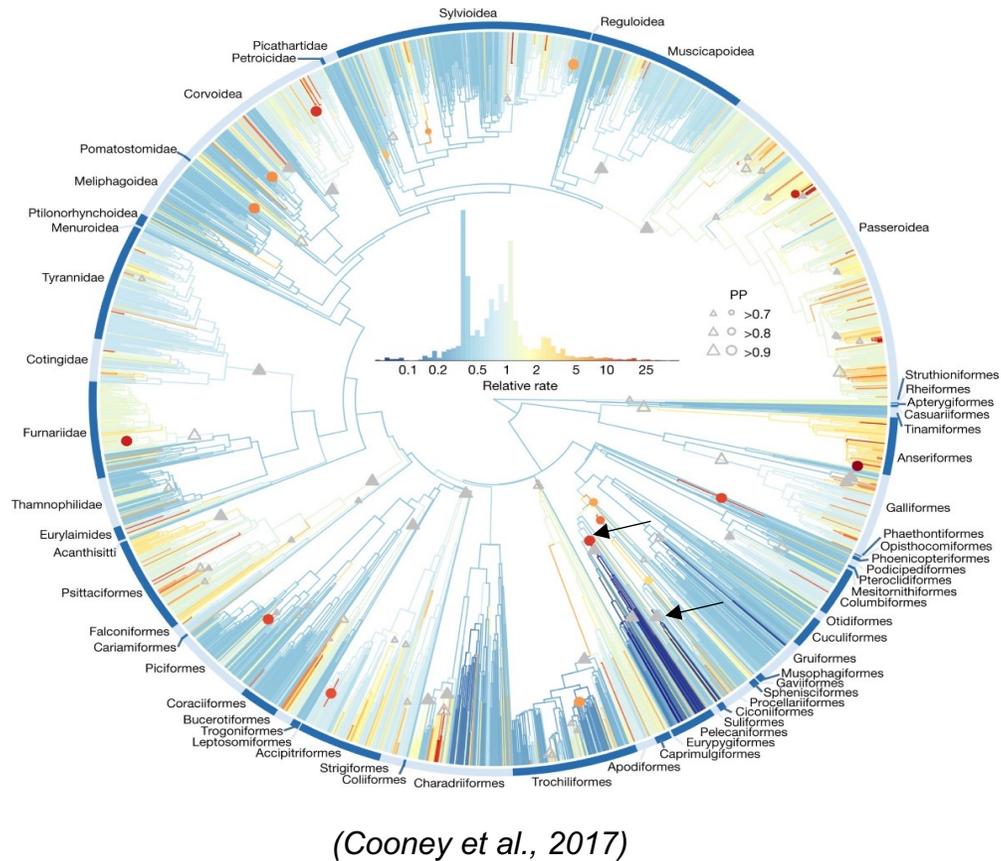
Such features include

- the rapid adaptation of complex phenotypes,
- why some lineages continue to diversify while others do not,
- and why some features evolve repeatedly, oftentimes using the same developmental pathways, whereas others are one-offs.

发育偏好研究有助于回答的进化问题

Question	Answer with key reference
Why is the influence of genetic and environmental change on phenotypes not uniform?	The feedback, modular structure, and nonlinear interactions of regulatory networks allow developmental systems to exhibit both robustness (<i>i.e.</i> , no or small phenotypic change even under large perturbation) and innovation (<i>i.e.</i> , large yet functionally integrated phenotypic change even under small perturbation) (Wagner 2011).
How can regulatory networks facilitate the expression of functional phenotypes when populations are exposed to novel environments?	As regulatory interactions evolve, they discover underlying structural regularities of the environments to which they become adapted, including through modular structure, making it possible to reach new adaptive combinations of characters through a small number of mutations (Watson and Szathmary 2016).
Why did a great deal of morphological variation evolve early in the history of multicellular life?	Simple, low-dimensional ancestral regulatory networks will tend to produce greater disparity among the set of common phenotypes than derived high-dimensional networks because ancestral genotypes are less constrained by regulatory epistasis (Borenstein and Krakauer 2008).
Why do phenotypes occupy only a small region of possible phenotype space?	Chance and the adaptive demands of natural selection combine with regulatory epistasis in evolving networks to leave only a fraction of possible phenotypes reachable (Wagner 2011).
How can developmental processes influence the direction of phenotypic evolution?	Evolution of regulatory networks illustrate that the phenotypic variation available for natural selection will typically be biased, sometimes in a functional manner, even when mutations are randomly distributed (Watson and Szathmary 2016).
How does developmental bias contribute to evolvability?	Developmental bias increases the recurrence and fitness of new phenotypes, thereby reducing the amount of genetic change needed to convert them into adaptive phenotypes (Watson and Szathmary 2016). Developmental bias may thus increase evolvability by making it more likely that adaptive phenotypes arise.
How does developmental bias shape macro-evolutionary patterns?	Analyses of regulatory networks reveals that stabilizing selection will push evolving populations to regions of genotype space where changes in topology do not affect the phenotype (generating stasis), while disruptive selection shifts populations to regions in which rapid change can ensue (Wagner 2011).

尝试用调控网络来理解鸟喙的演化



- 鸟喙表型的变化和许多极端转变(shift) (例如火烈鸟、鸬鹚、夜鹰等) 发生在鸟类辐射的基础上, 与早期**快速量子进化**进入新的适应区的想法一致。
- 在某些情况下(例如, 左图黑色箭头所指的分支), 极端喙形状的演化与**随后的喙形演化速度减慢**有关;
- 鸟喙在不同支系存在**演化速率异质性**

尝试用调控网络来理解这些现象

1. 稳定选择下基因型的累积, 破坏性选择下种群转移到发生快速变化的区域
2. 新事物的进化将现有的发育元件连接到新的调控网络
3. 不同表型的基因型数量不同 (稳健性不同)

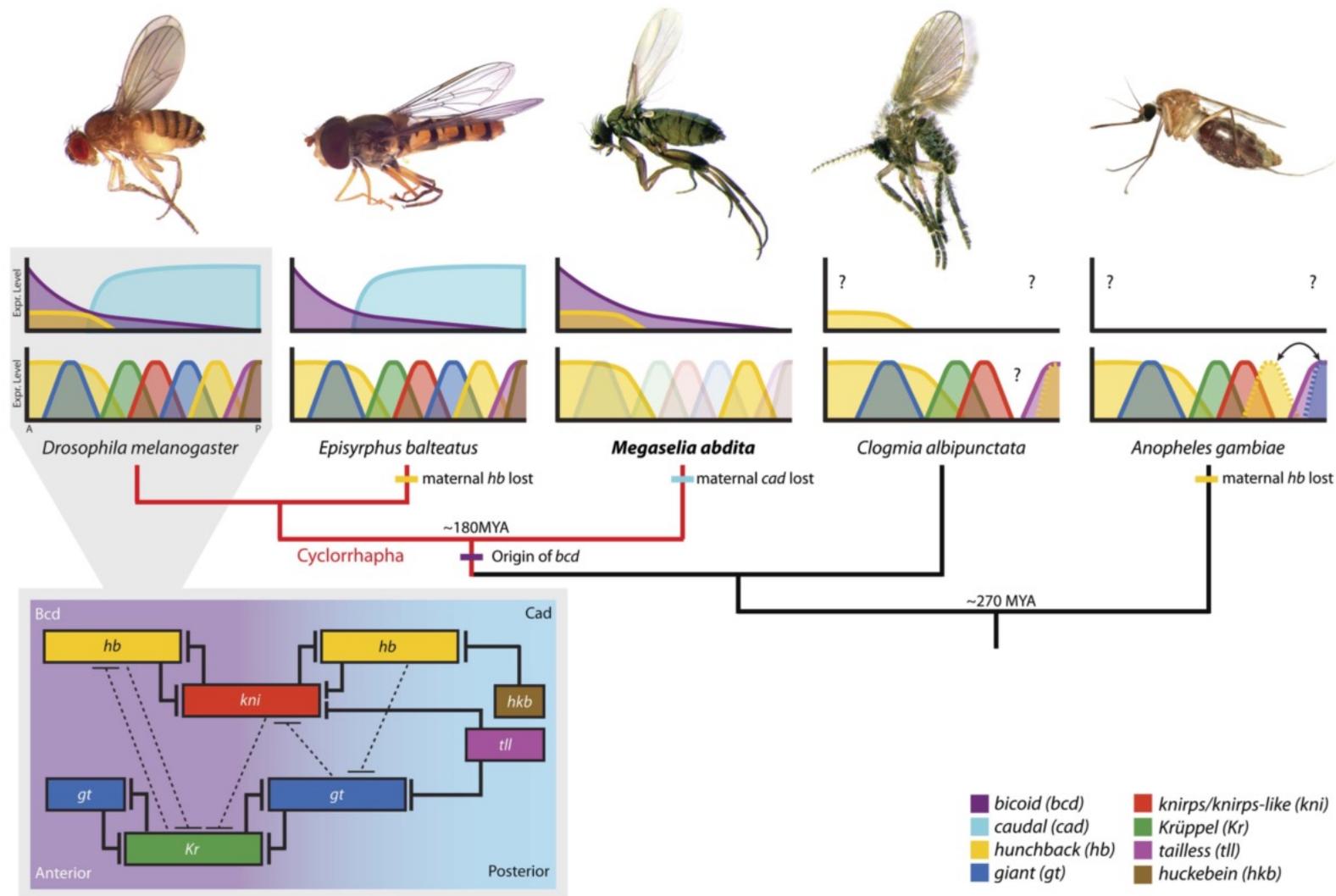


鸬鹚



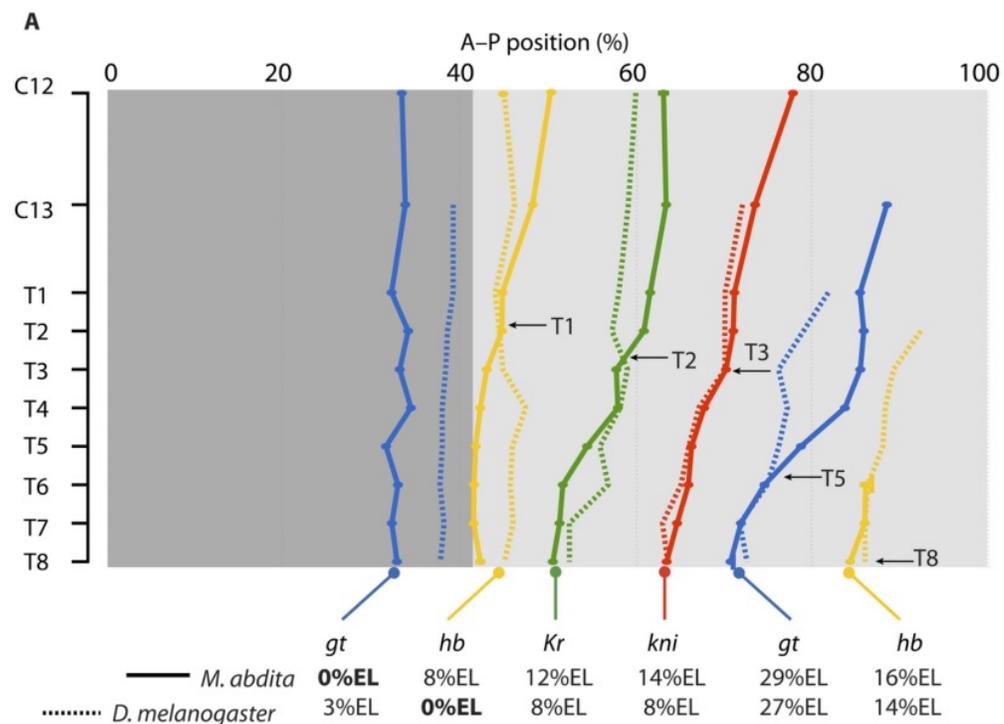
鹳

昆虫分节——segmentation gene network

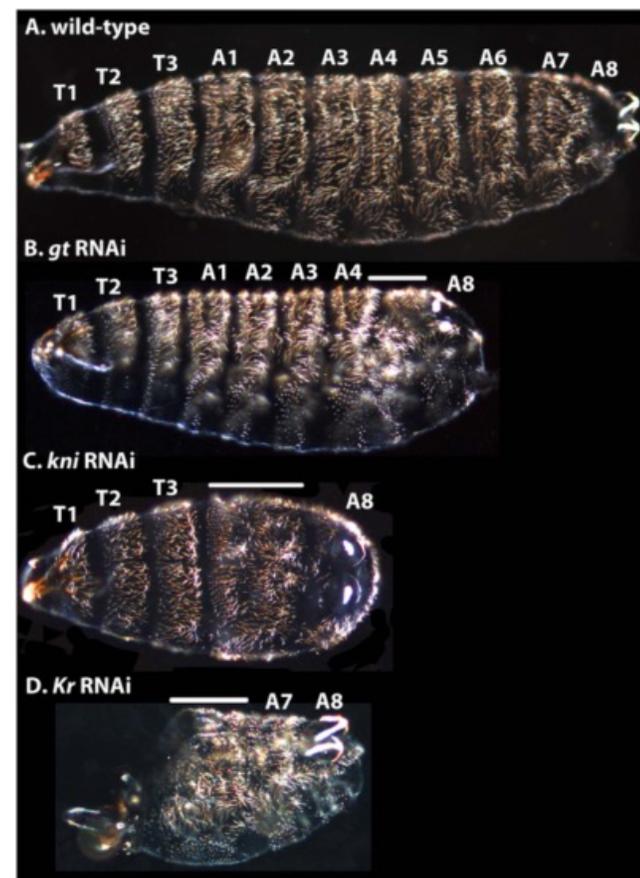
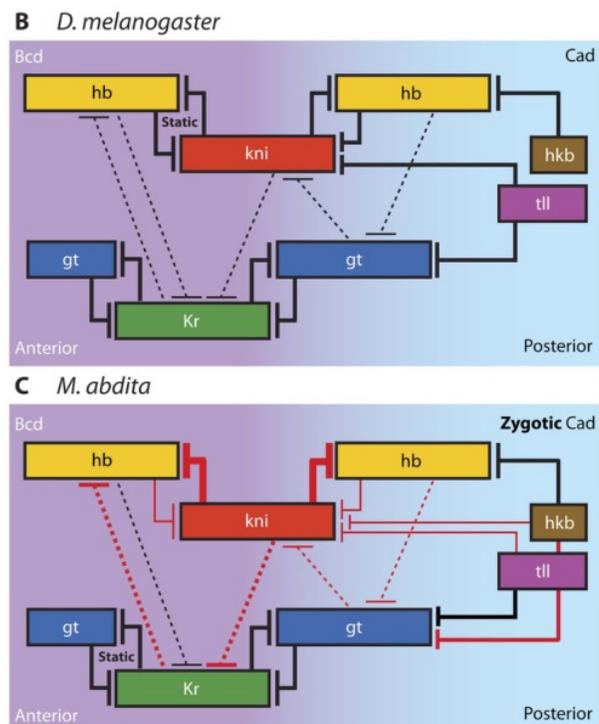


(Wotton K R et al., 2015)

昆虫分节——segmentation gene network



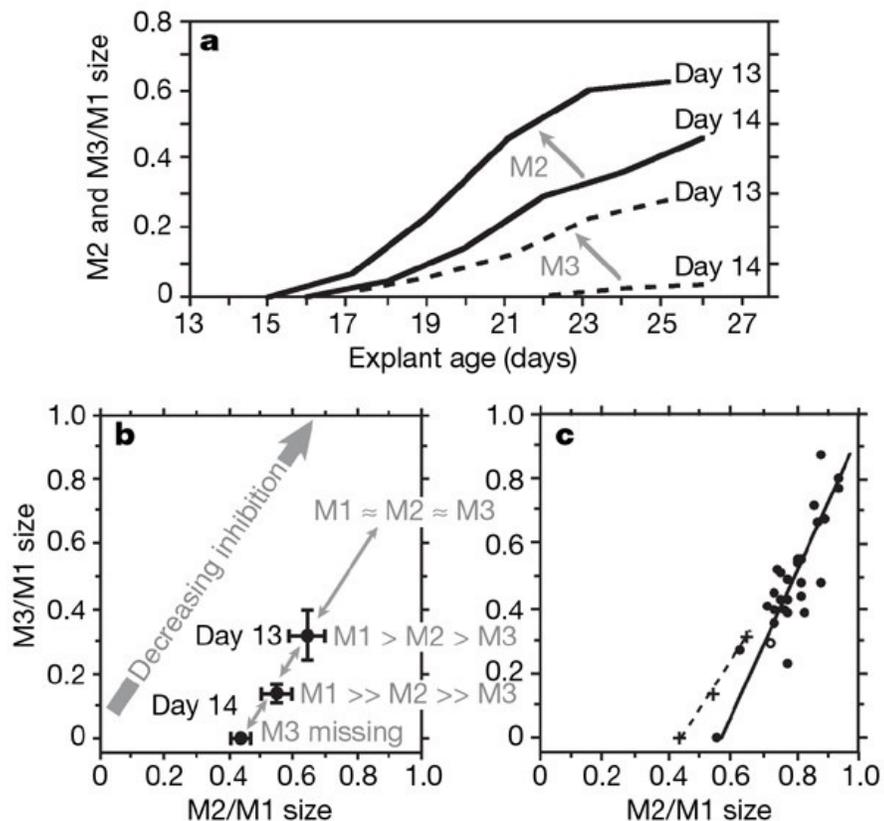
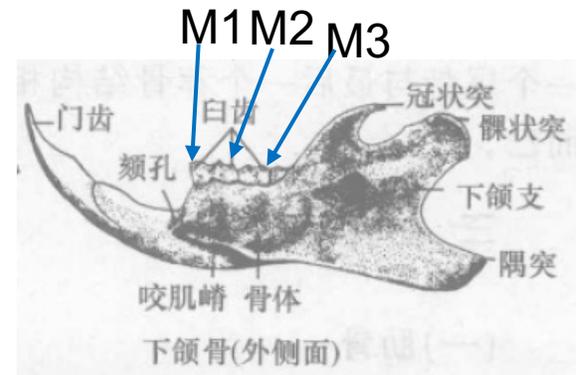
(Wotton K R et al., 2015)



(Wotton K R et al., 2015)

发育过程补偿可变的环境、信号或调节输入以产生恒定的表型结果

啮齿动物牙齿相对大小的数学模型



(Kavanagh K D et al., 2007)

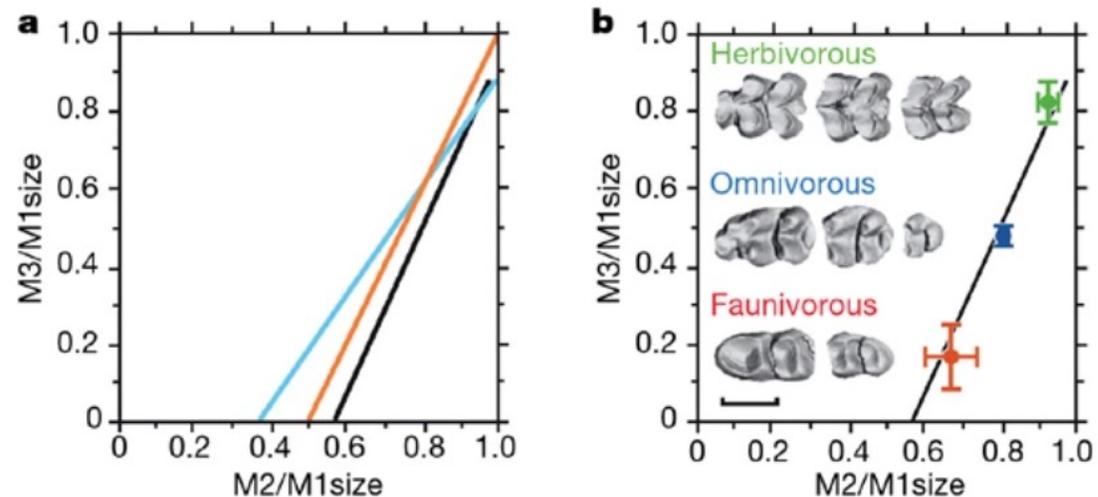
假设激活剂和抑制剂比率对牙齿比例有线性影响

$$molar\ size = 1 + [(a - i)/i](x - 1)$$

a = effect of activator,

i = effect of inhibitor,

x = the position of molar



$$M1 = 1, M2 = a/i \text{ and } M3 = 2a/i - 1$$

$$\text{Molar proportions: } M1 = i/3a, M2 = 1/3 \text{ and } M3 = (2a - i)/3a$$

磨牙比例可能不反映功能本身，但可能通过影响牙齿的变化特性来体现发育对功能特征（如复杂性和整体大小）的选择的反应方式。

哺乳动物牙齿发育的计算模型

- 整合基因型、发育和表型
- 通过发育偏好进行模拟、预测

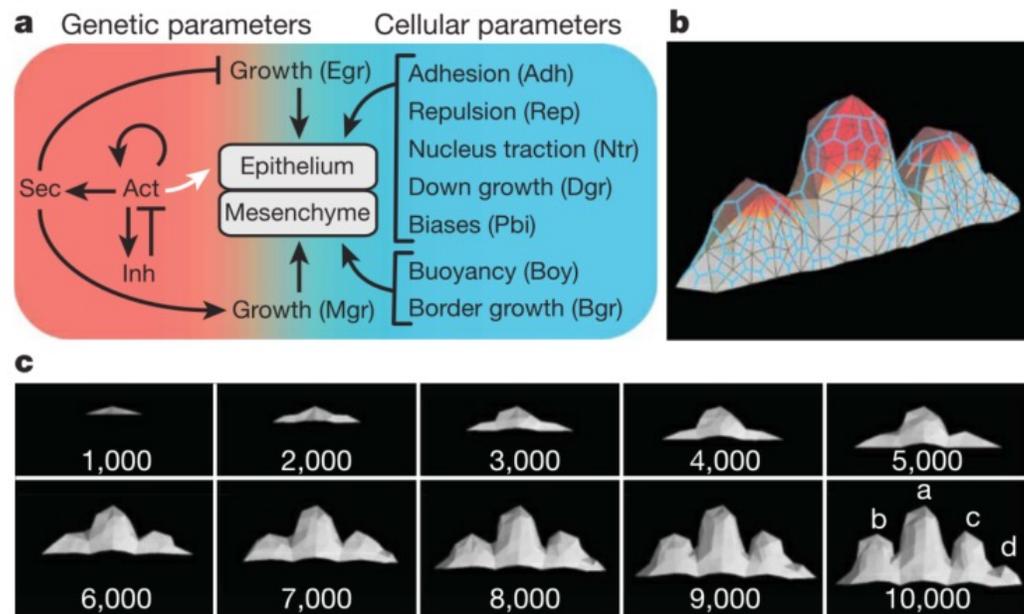


图1

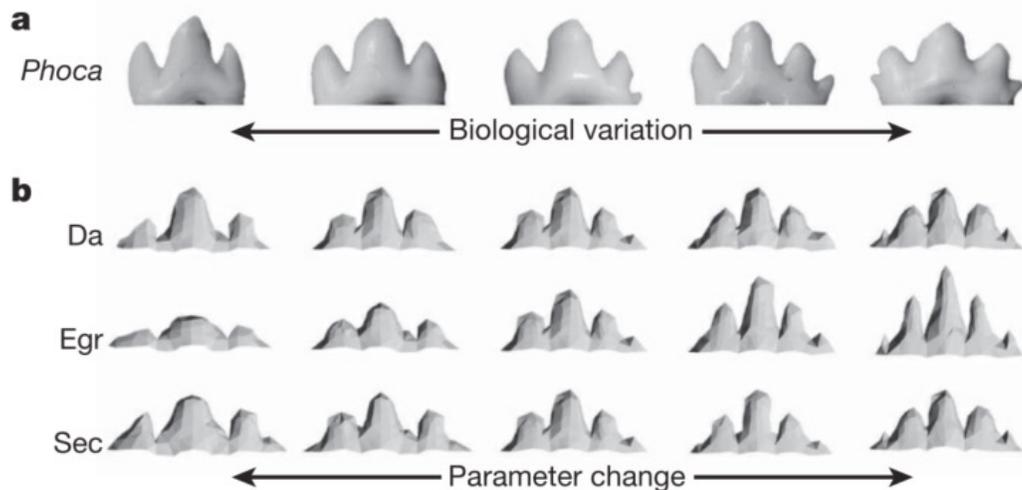


图2

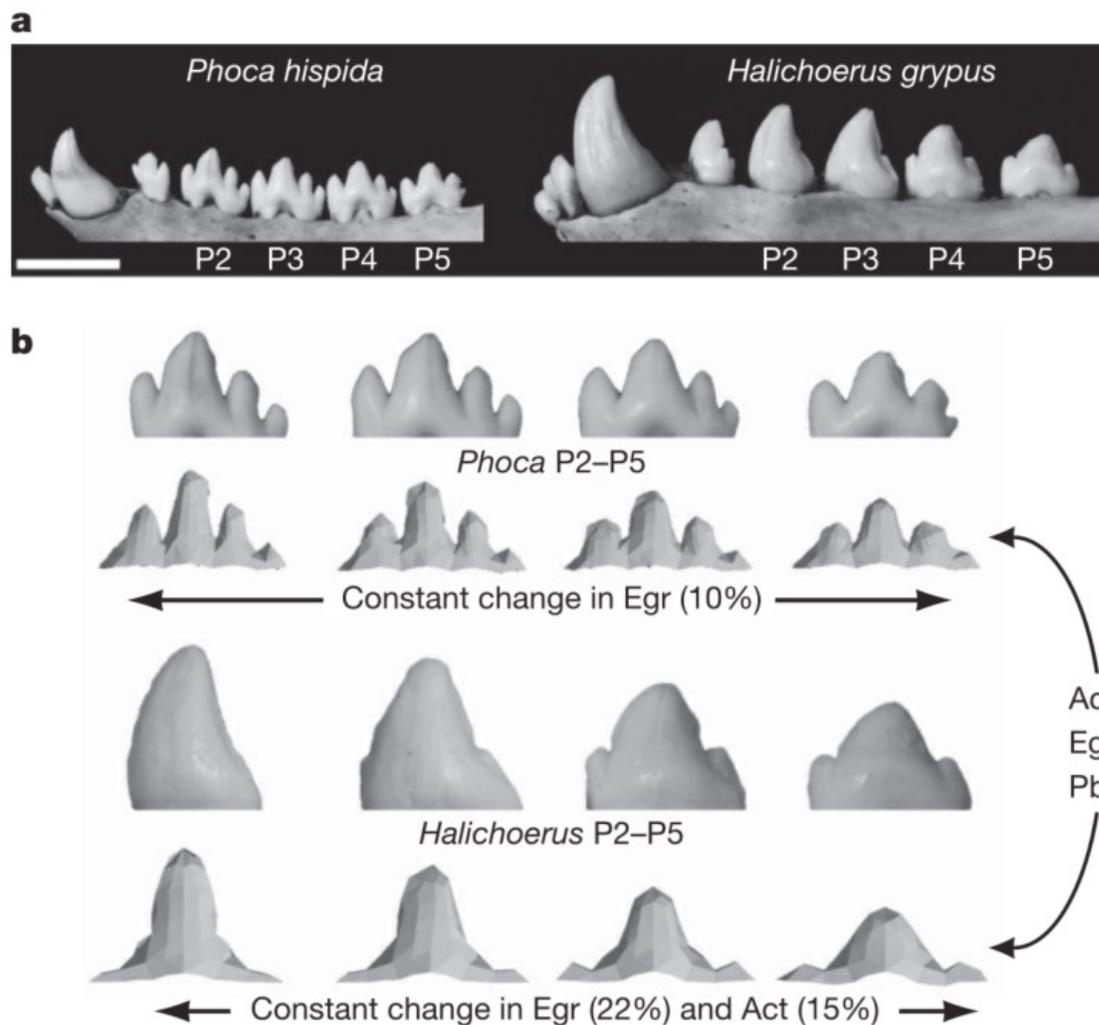
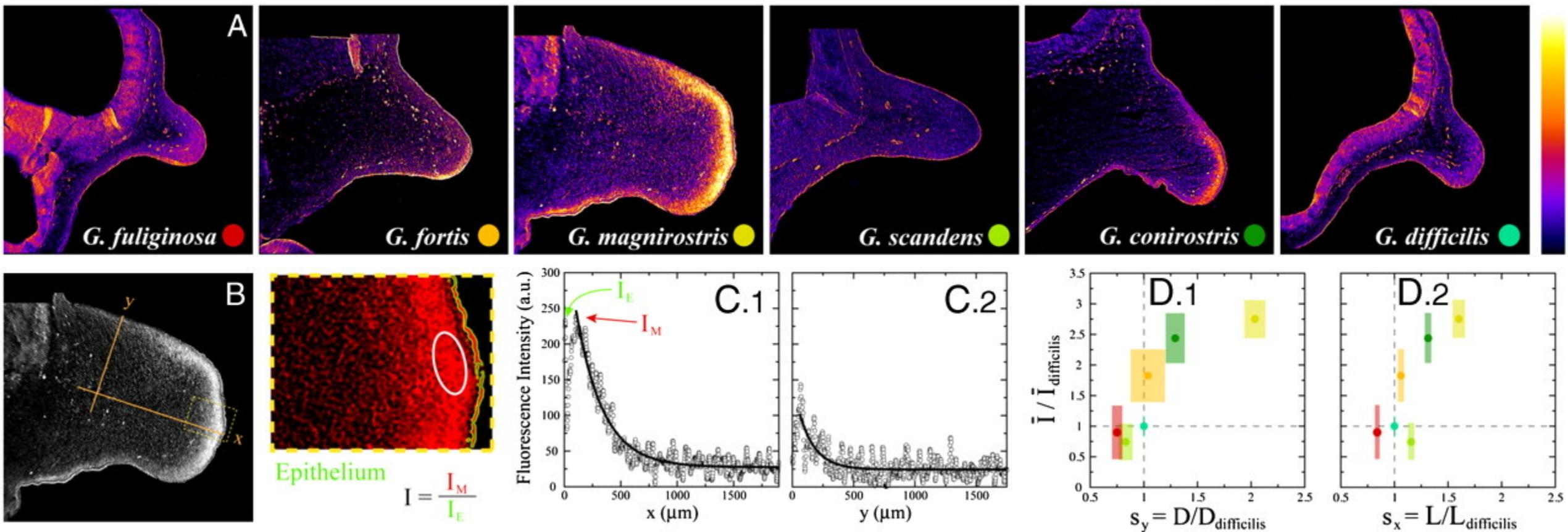


图3

(Salazar-Ciudad I et al., 2010)

Geospiza 属中喙形态变化与 *Bmp4* 表达的关系



(Campàs O et al., 2010)

如果弄清楚了喙的发育机制，可能可以像哺乳动物牙齿一样构建一个计算模型