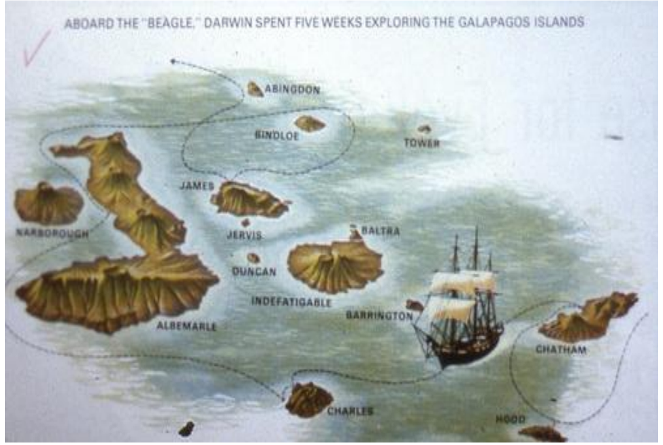
1. Аллопатрическое видообразование.
Причины дискретности видов с точки зрения
Биологической концепции вида

2. Симпатрическое видообразование
Причины дискретности видов с точки зрения
Морфологической концепции вида

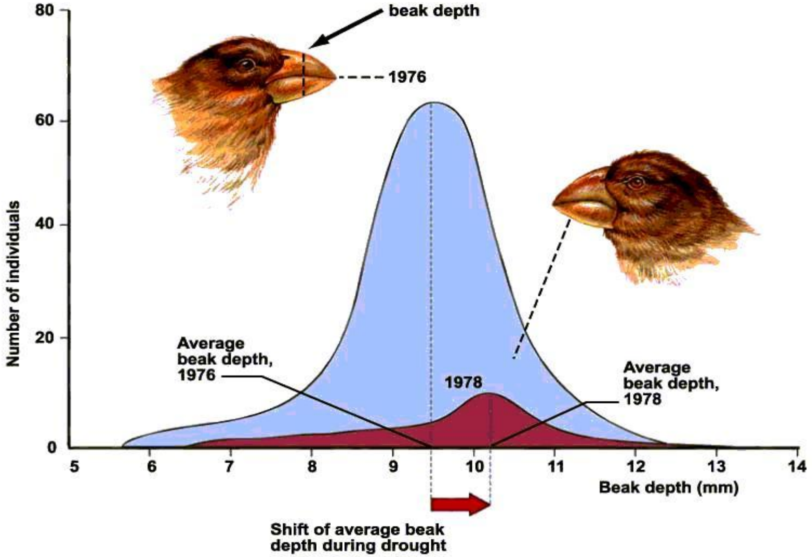
# Видообразование происходит “пучками”

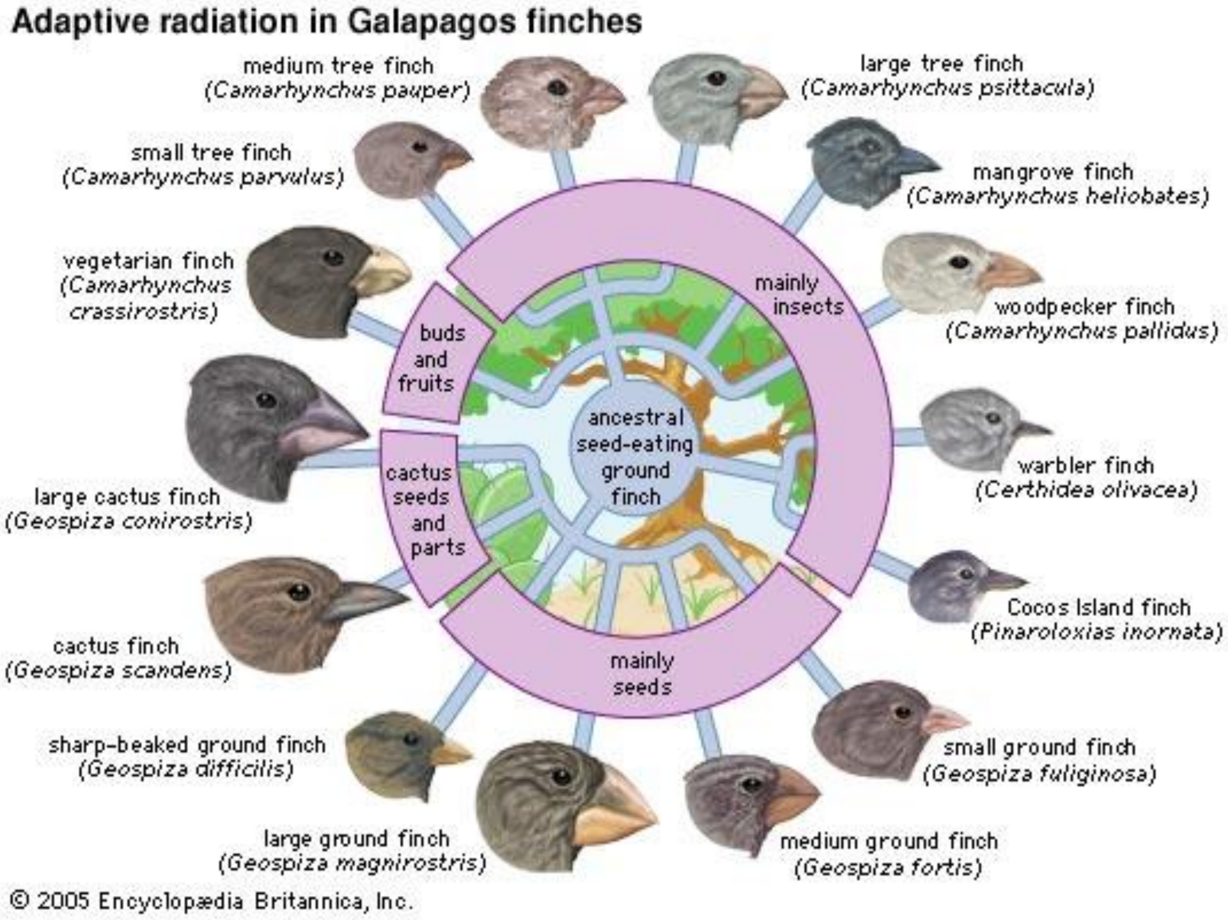
**Таблица V. Наши вьюрковые птицы:**
*1* — чиж; *2* — щегол; *3* — зяблик; *4* — снегирь.

Вопрос -
сколько генов
могут
это обеспечить

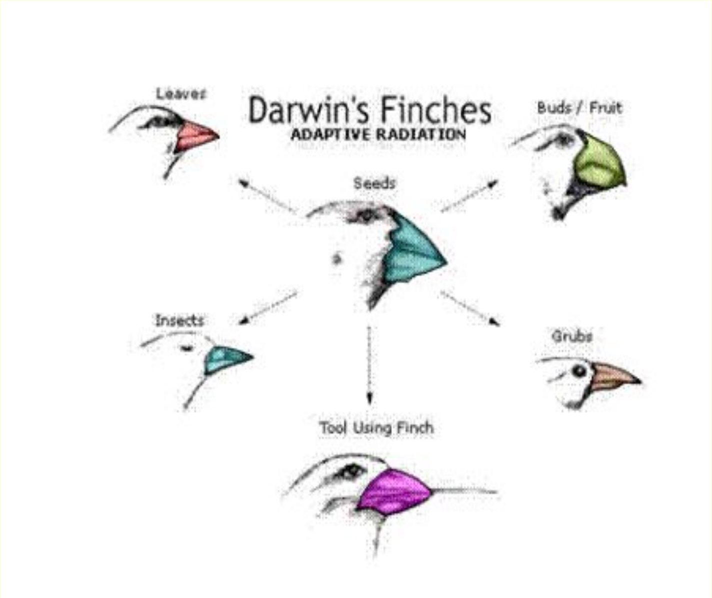


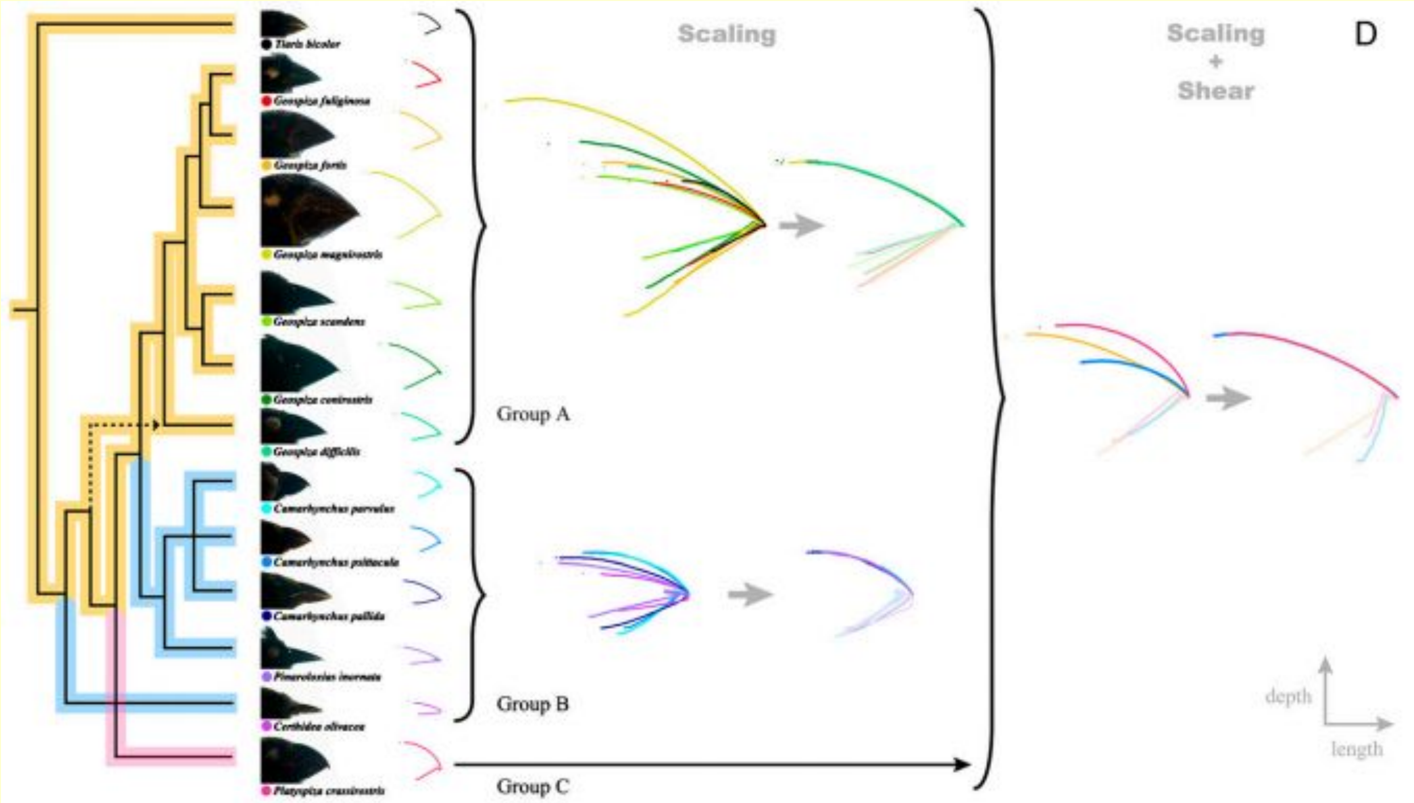
ABOARD THE "BEAGLE," DARWIN SPENT FIVE WEEKS EXPLORING THE GALAPAGOS ISLANDS



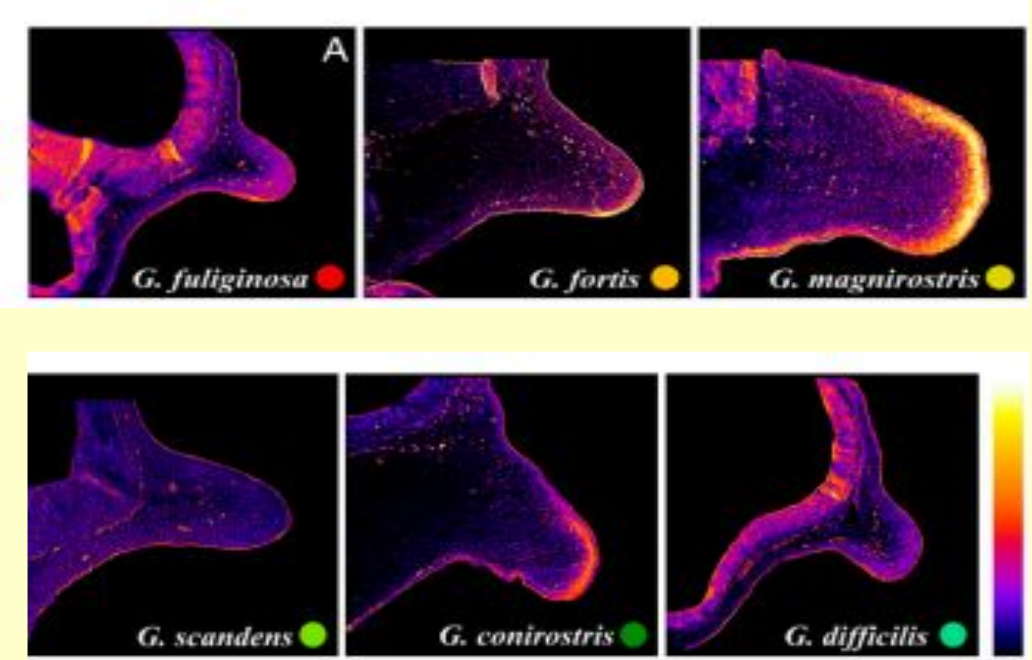


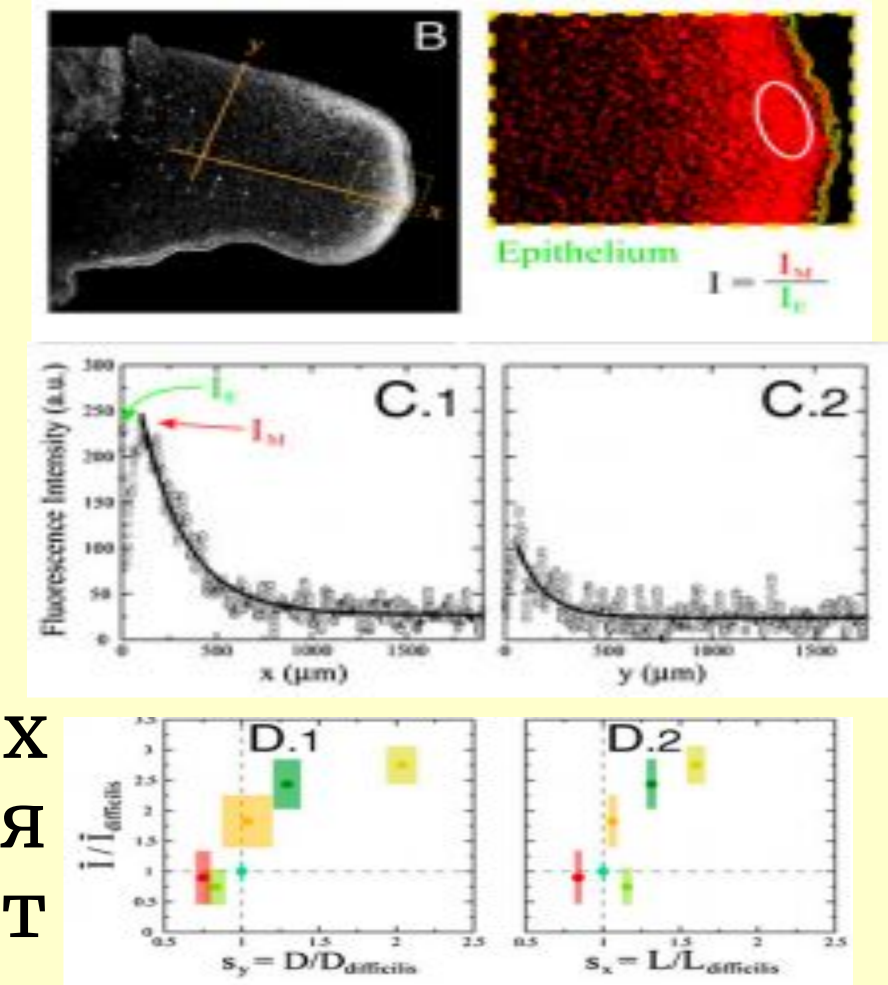
Adaptive radiation in Galapagos finches





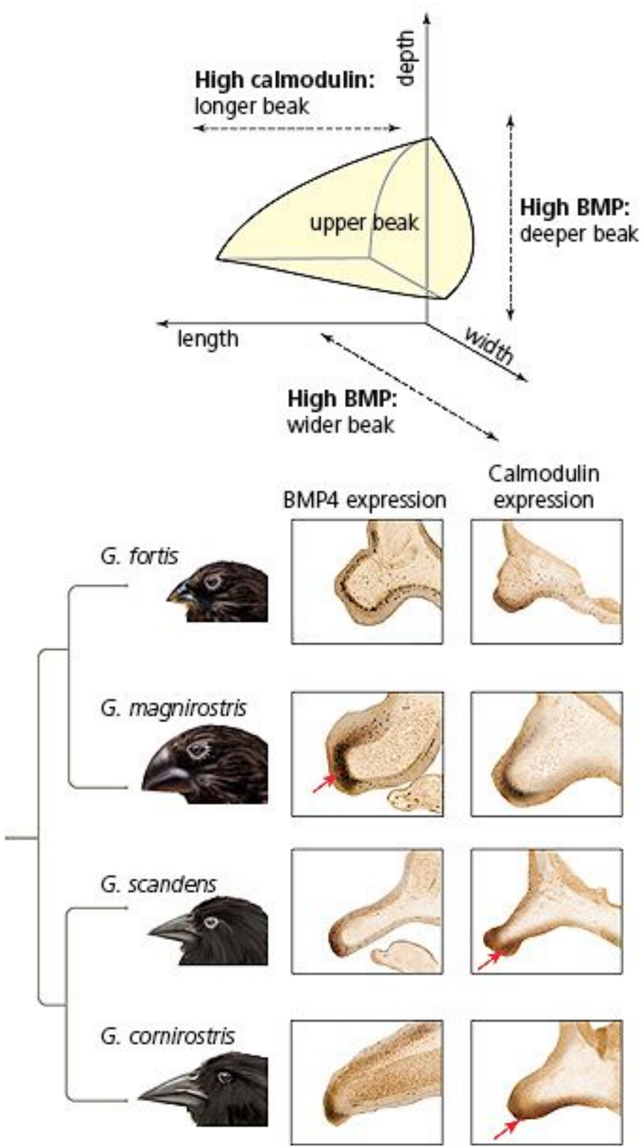
Формы клюва дарвиновских вьюрков внутри групп А и В переводятся друг в друга масштабированием, а между группами — масштабированием и срезающим преобразованием

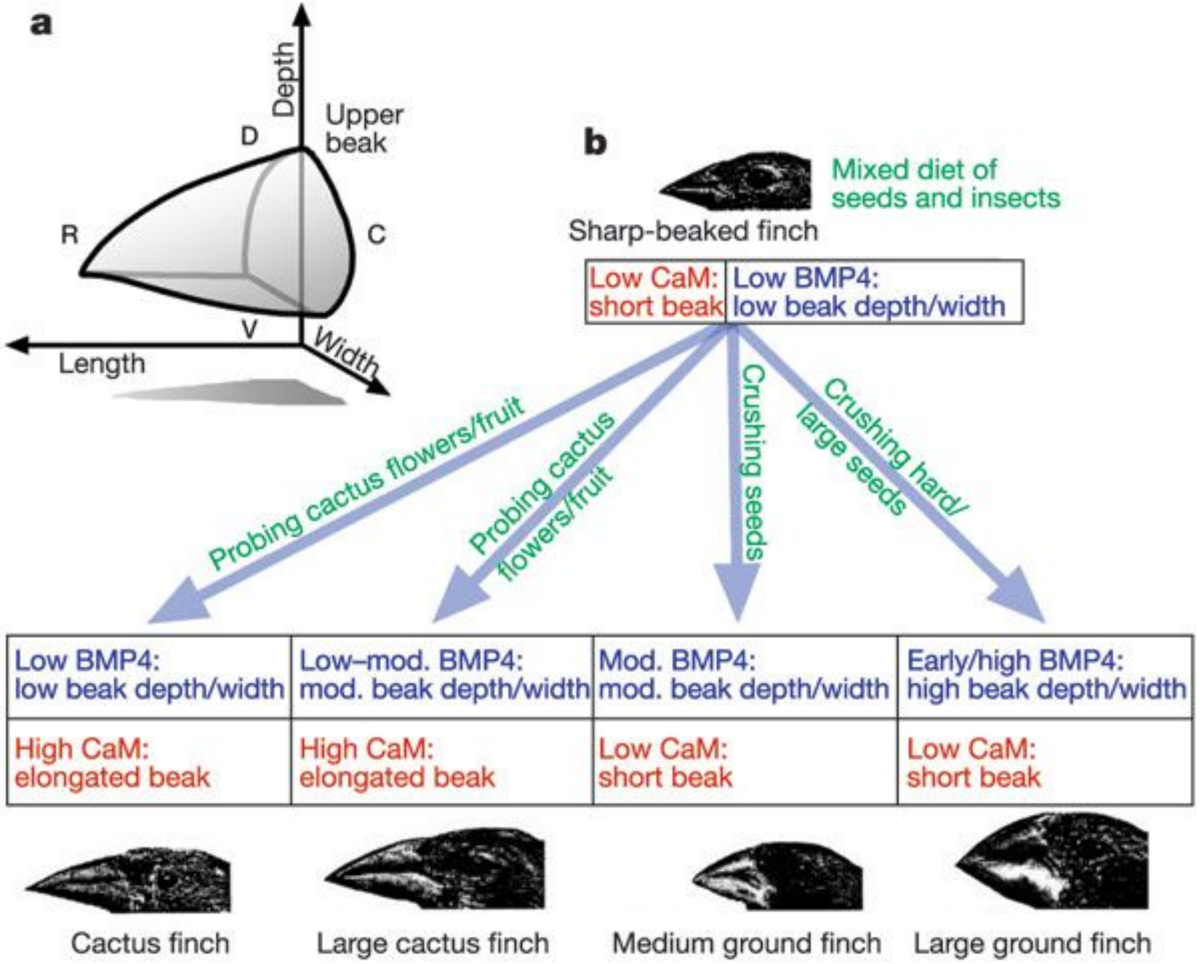




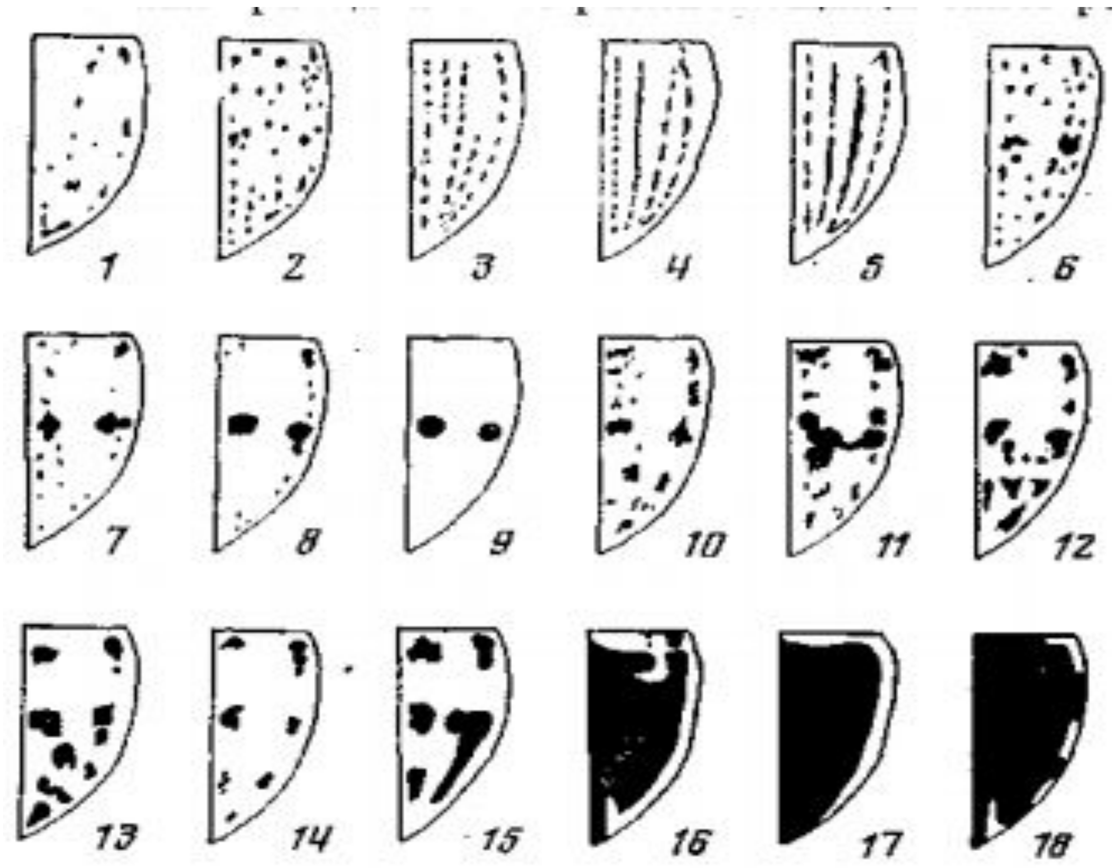
Форма клюва дарвиновских вьюрков *Geospiza* изменяется в зависимости от экспрессии*Bmp4*. *Bmp4* сильно коррелирует с

# А длина клюва – с экспрессией кальмодулина



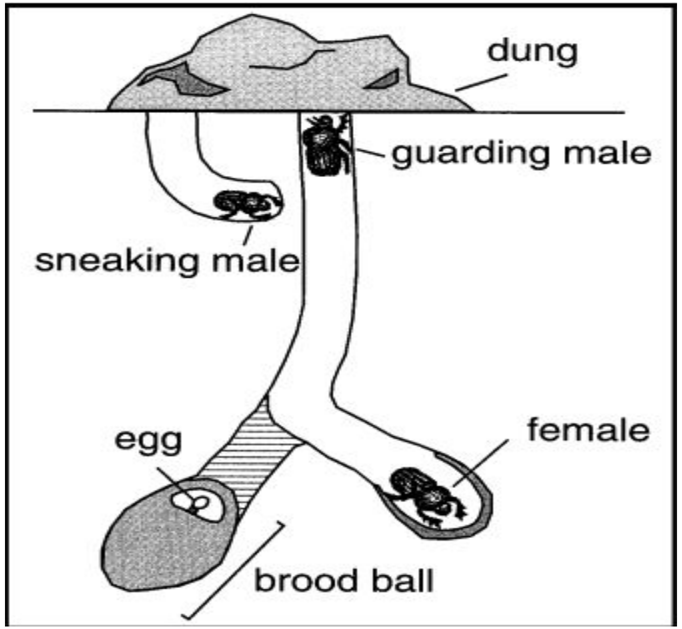


# Откуда берутся новые признаки?

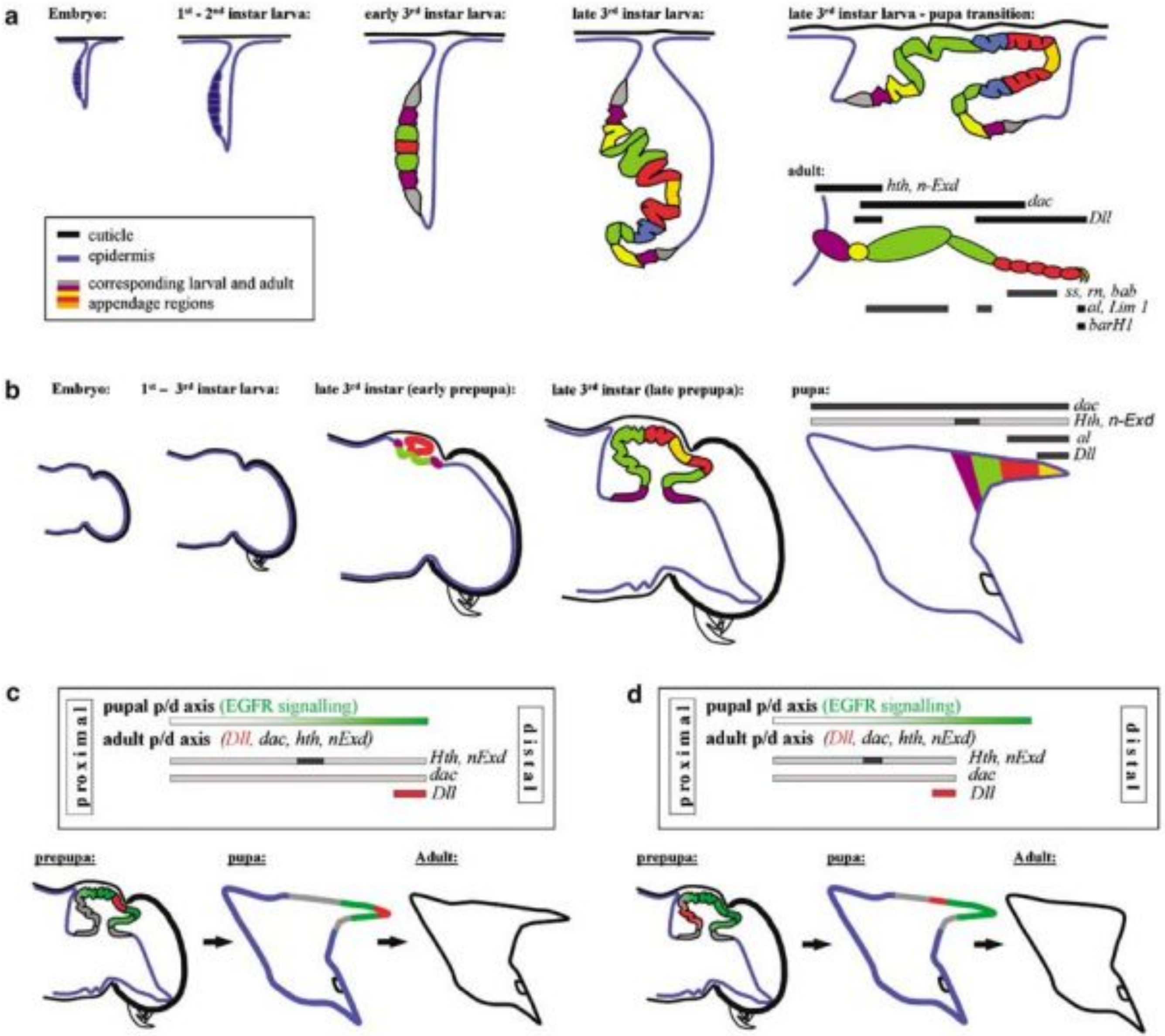


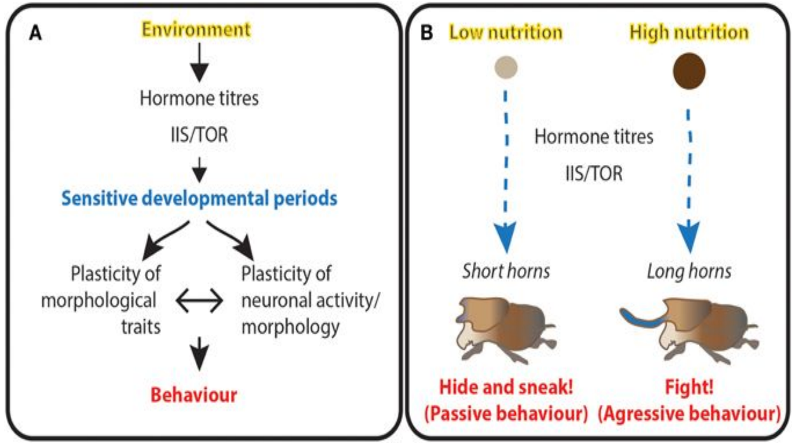
Некоторые признаки возникают в результате косвенных последствий отбора, другие — в результате самоорганизации

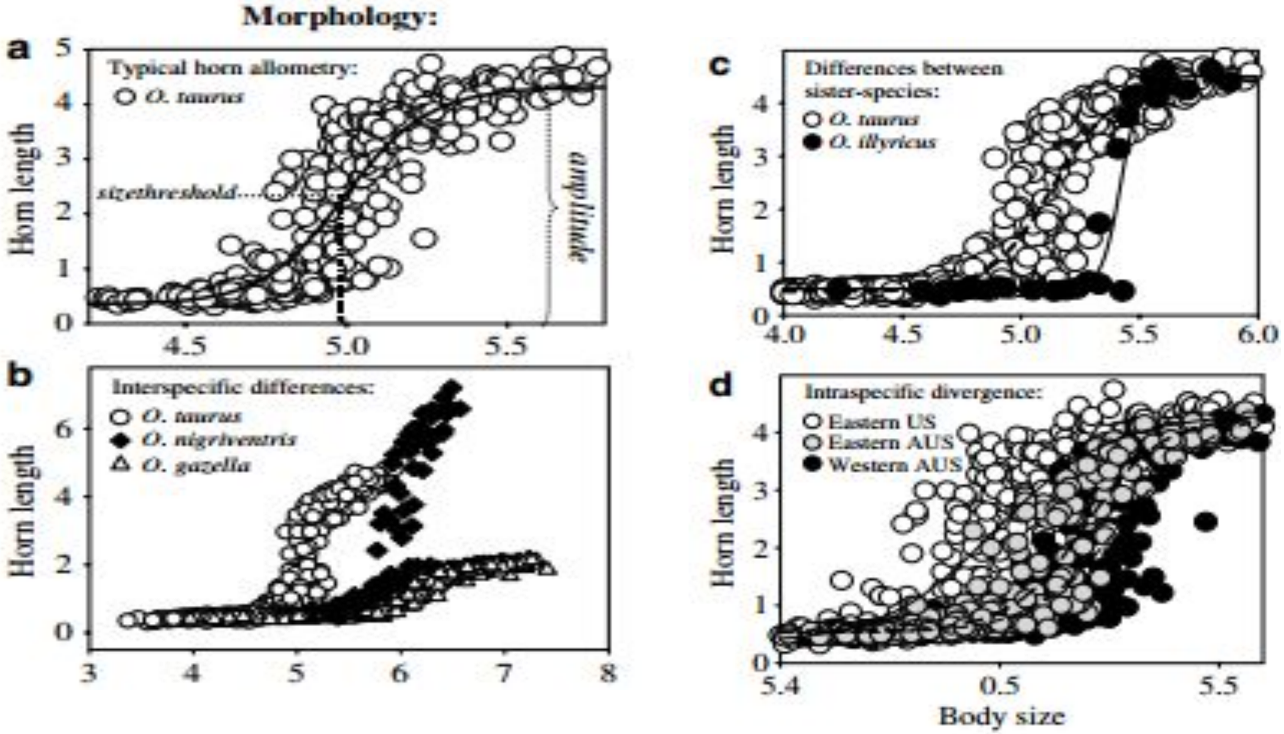
# Каких только рогов у жуков нет

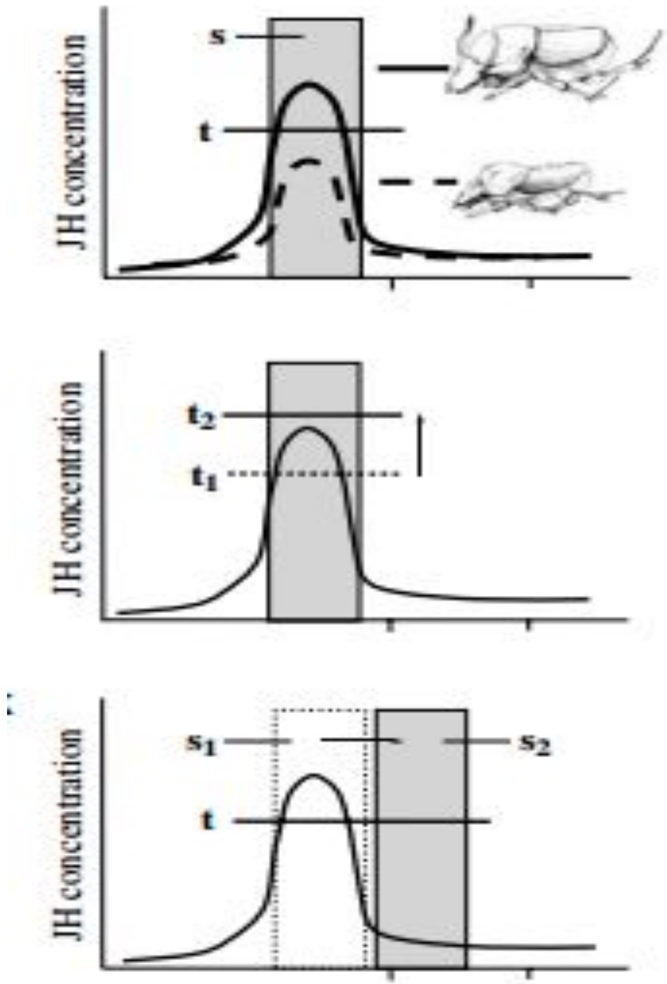


## Нога дрозофилы и рог жука-навозника - системы с одинаковой проксимо-дистальной разметкой

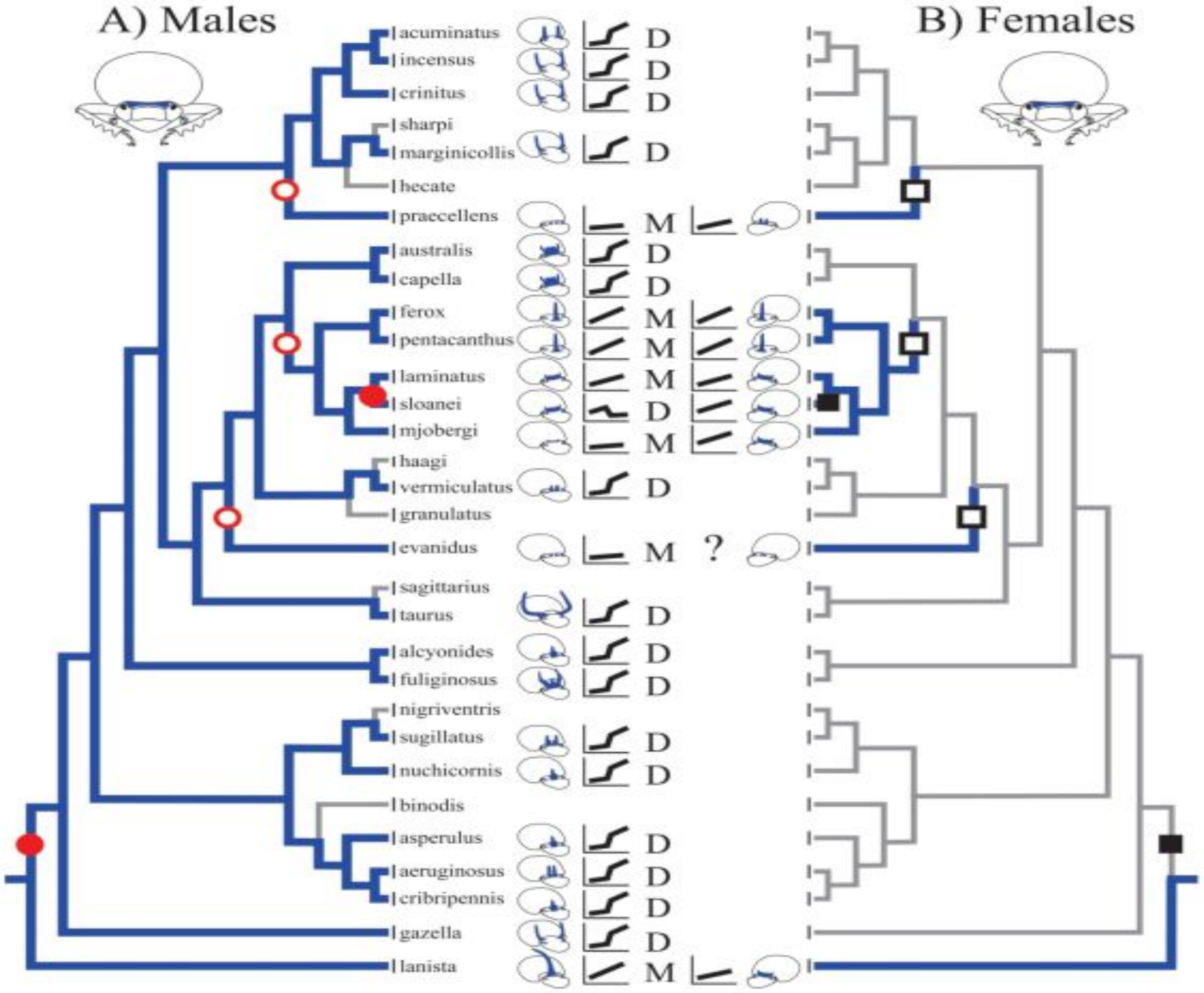






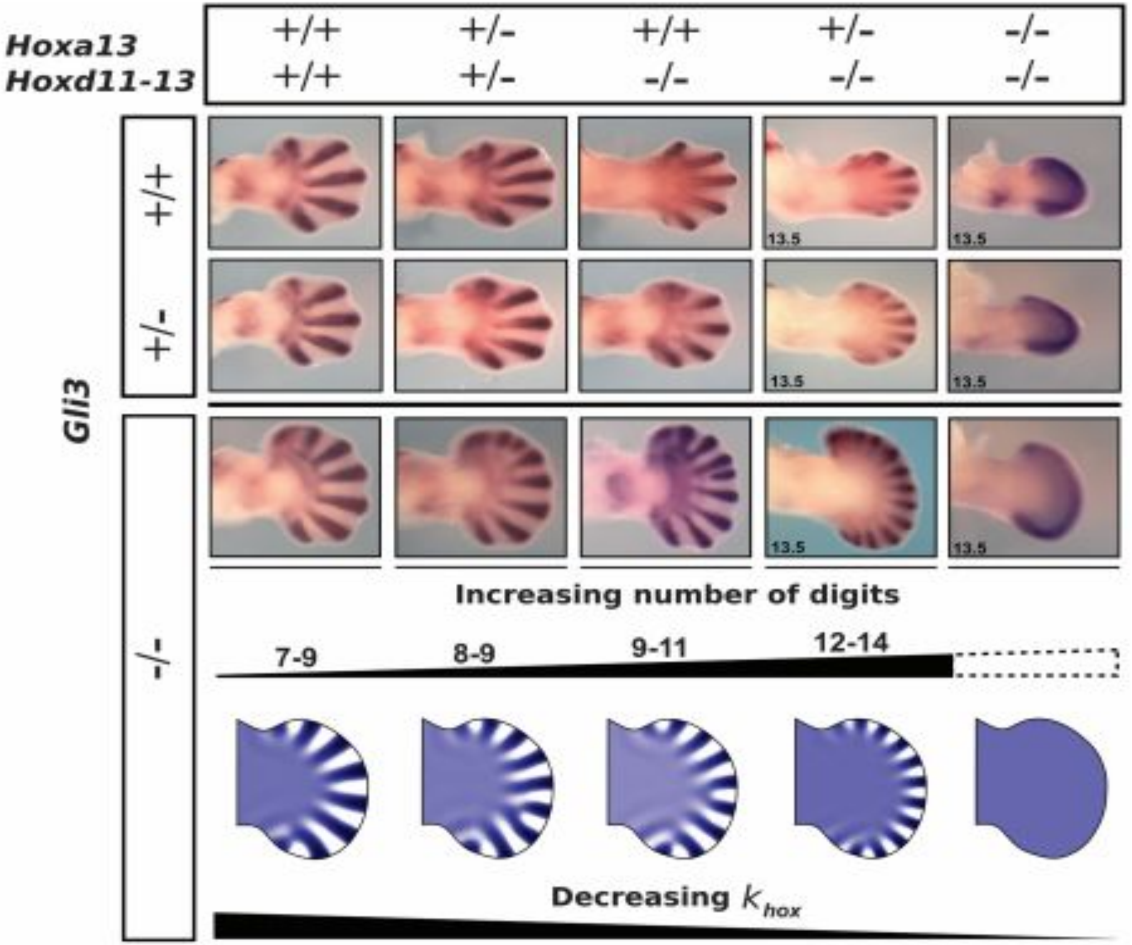


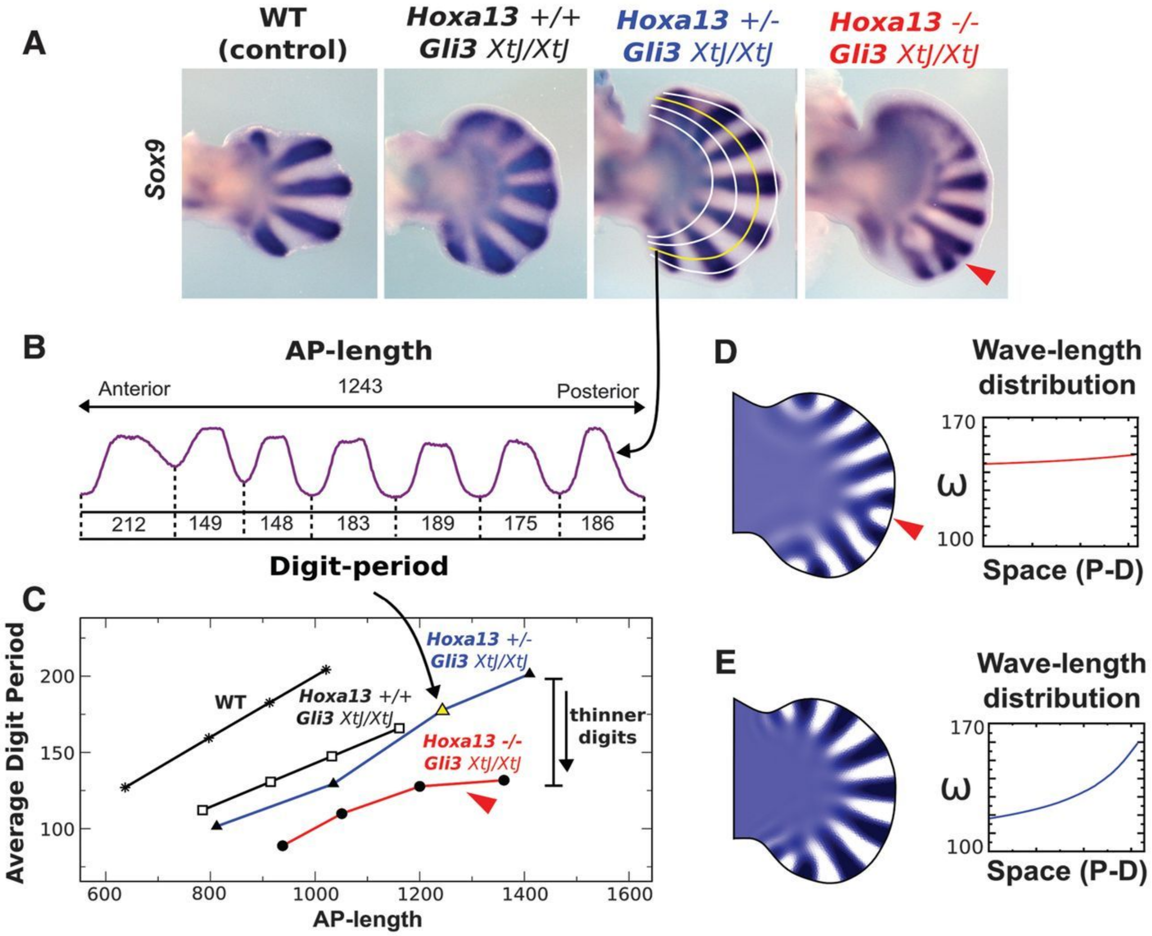
В зависимости от концентрации ювенильного гормона у жуков либо будут, либо не будет рогов. Изменения порога или периода чувствительности к ювенильному



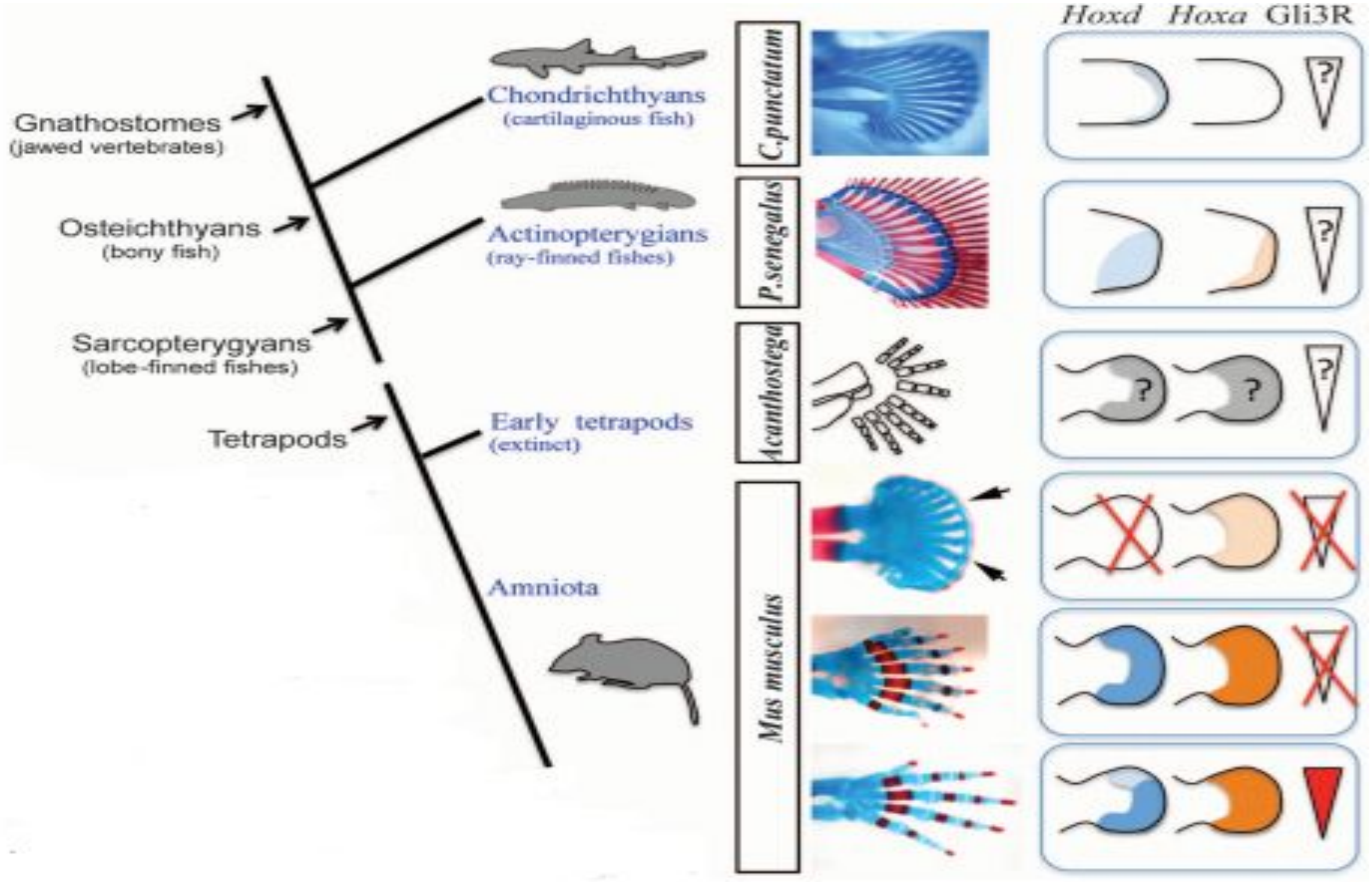
У жуков из рода *Onthophagus* несколько раз происходила потери и приобретения полового диморфизма, а также изменения формы рогов.

# Сколько пальцев?

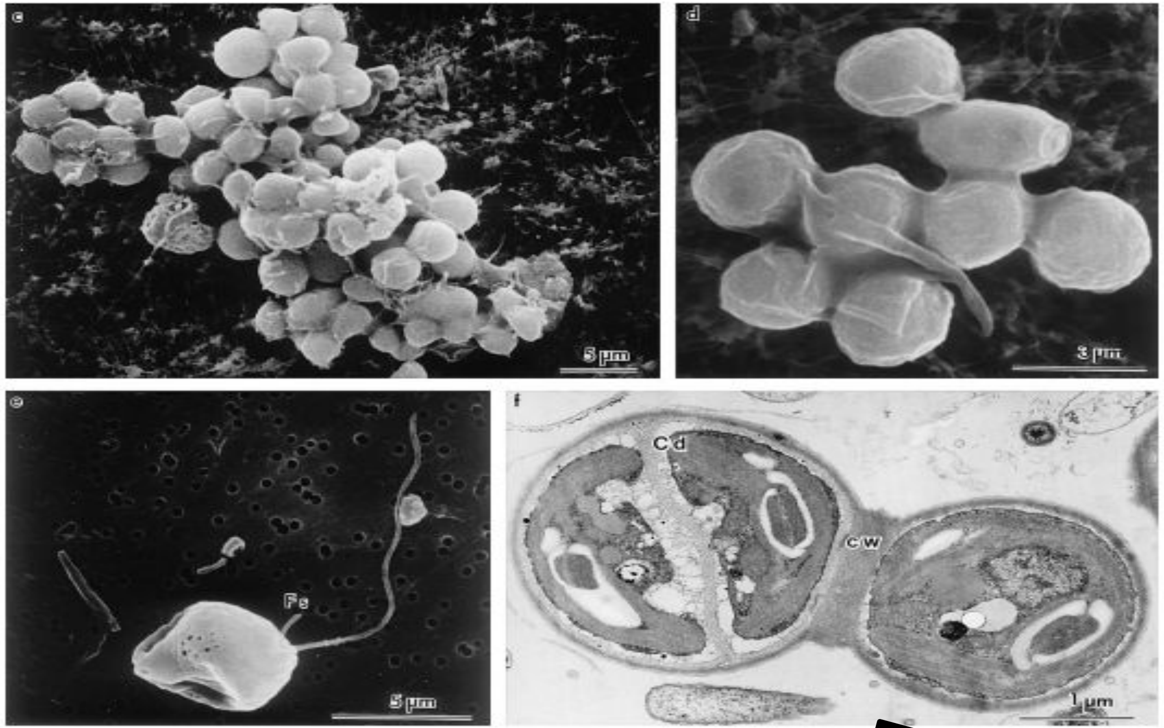




# Морфологическая эволюция

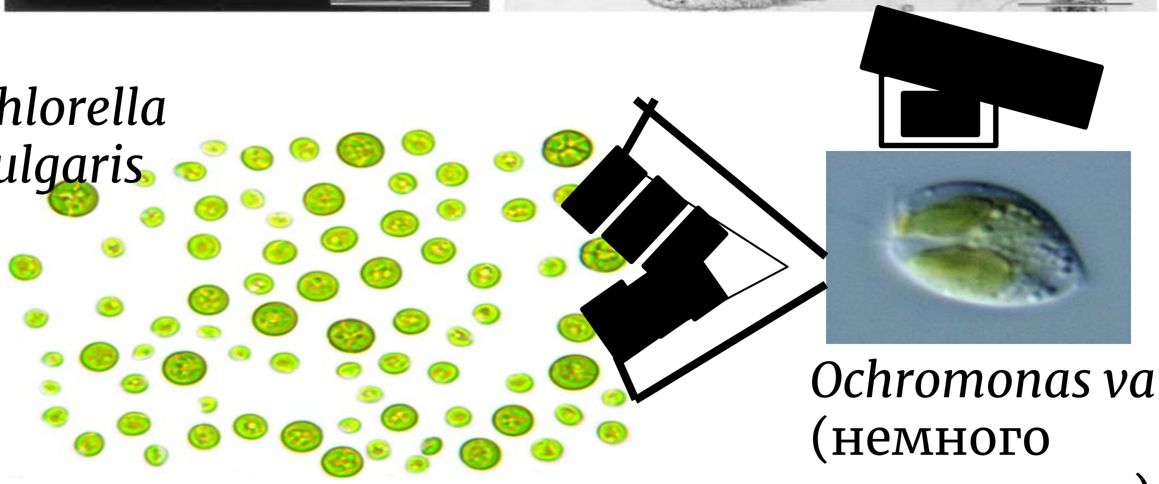


# Происхождение многоклеточности?



В присутствии хищника одноклеточные Chlorella стали формировать колонии, причём за 10–11 поколений большая часть хлорелл пребывала в виде 8-клеточных колоний, а через 100 — в виде больших многоклеточных самовоспроизводящихся колоний.

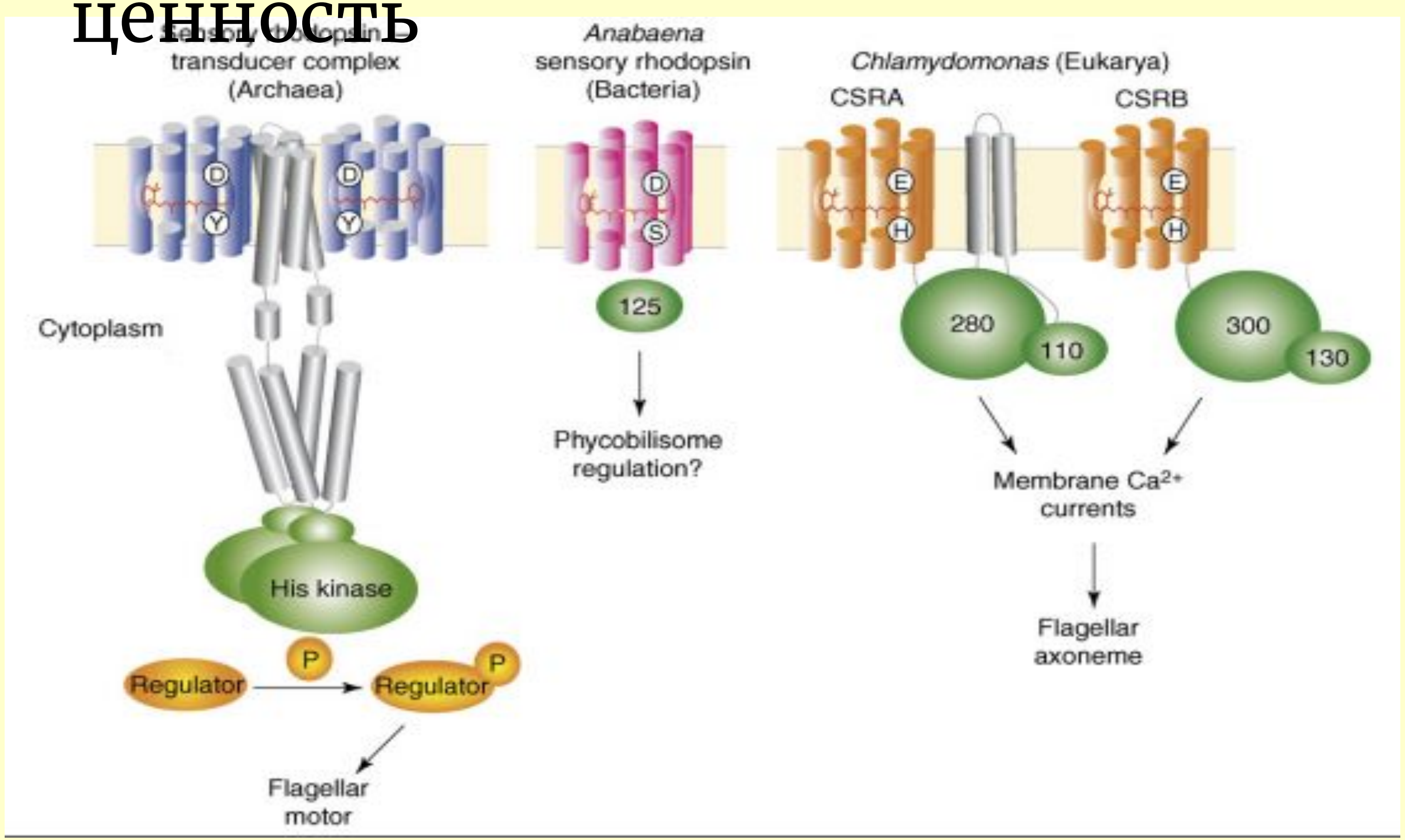
Ничто не мешает сформировать колониальность/многоклеточность, если уже есть клеточная стенка/другие механизмы агрегации после митоза.



*Chlorella vulgaris*

*Ochromonas vallescia* (немного прикрашен)

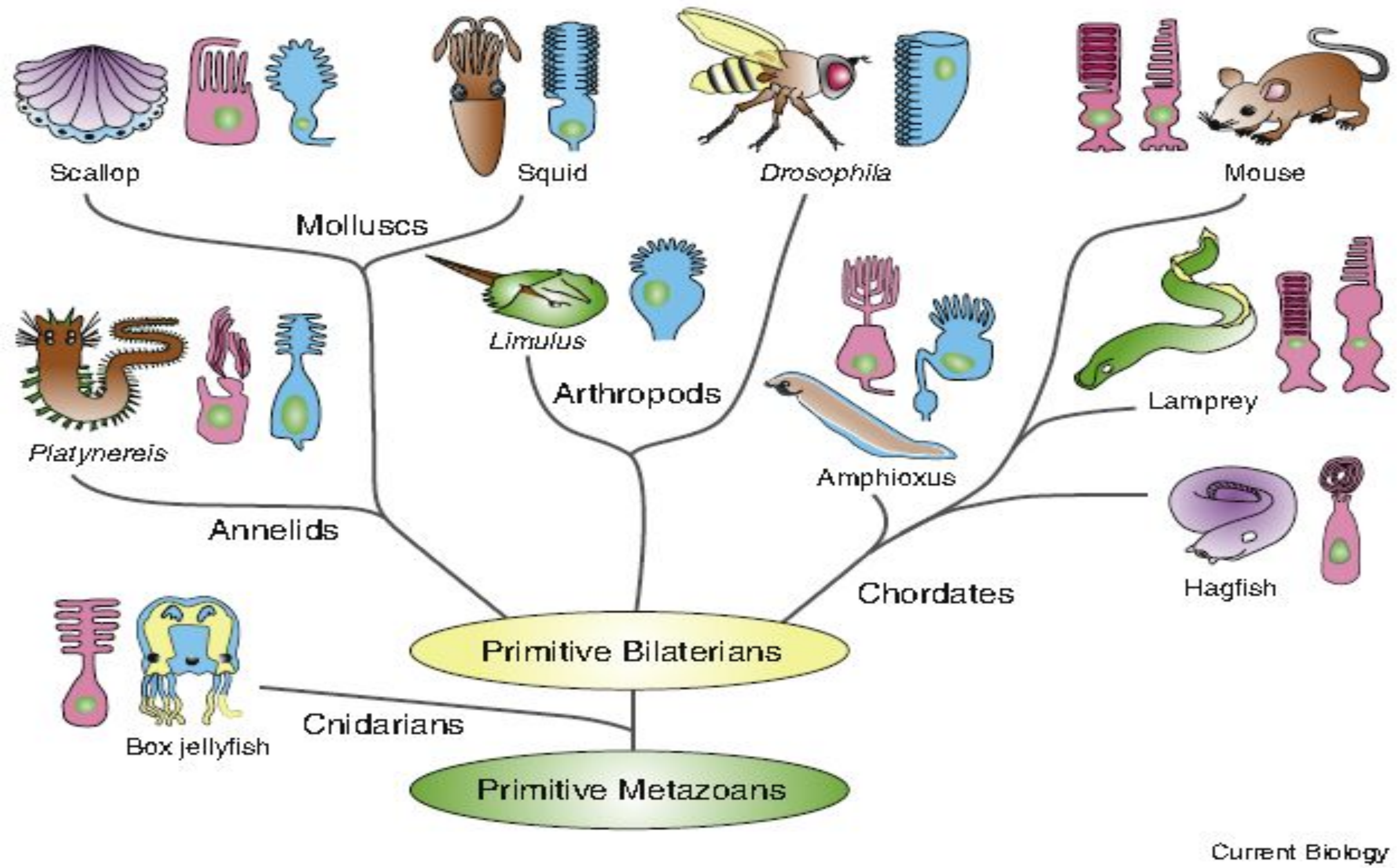
# Преадаптация — свойство или приспособление организма, потенциально имеющее адаптивную ценность



Родопсины присутствуют у всех трёх доменов живых организмов.

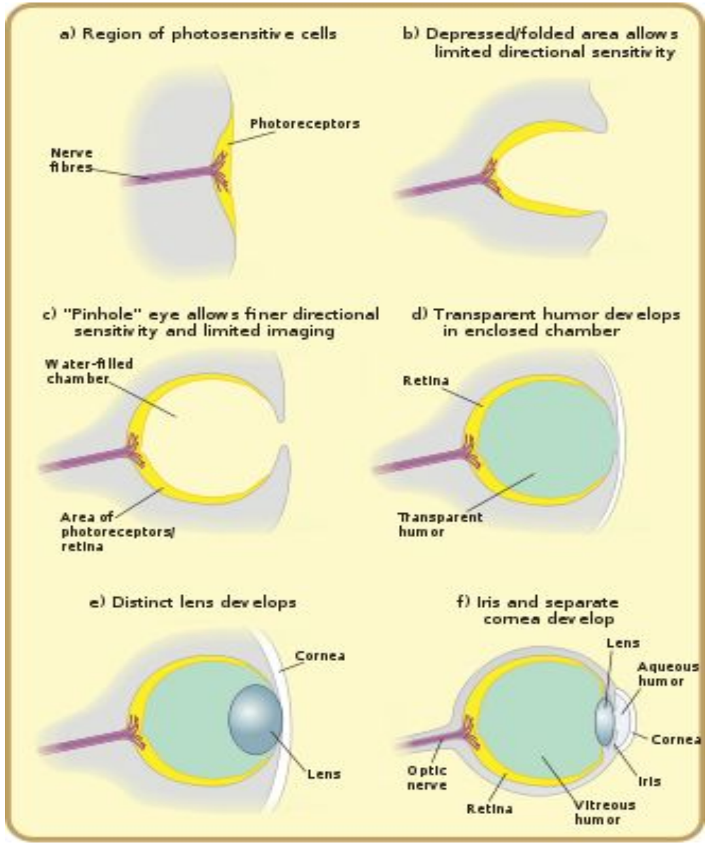
Есть предположения, что изначально они не выполняли сенсорную функцию, а применялись для использования солнечной энергии.

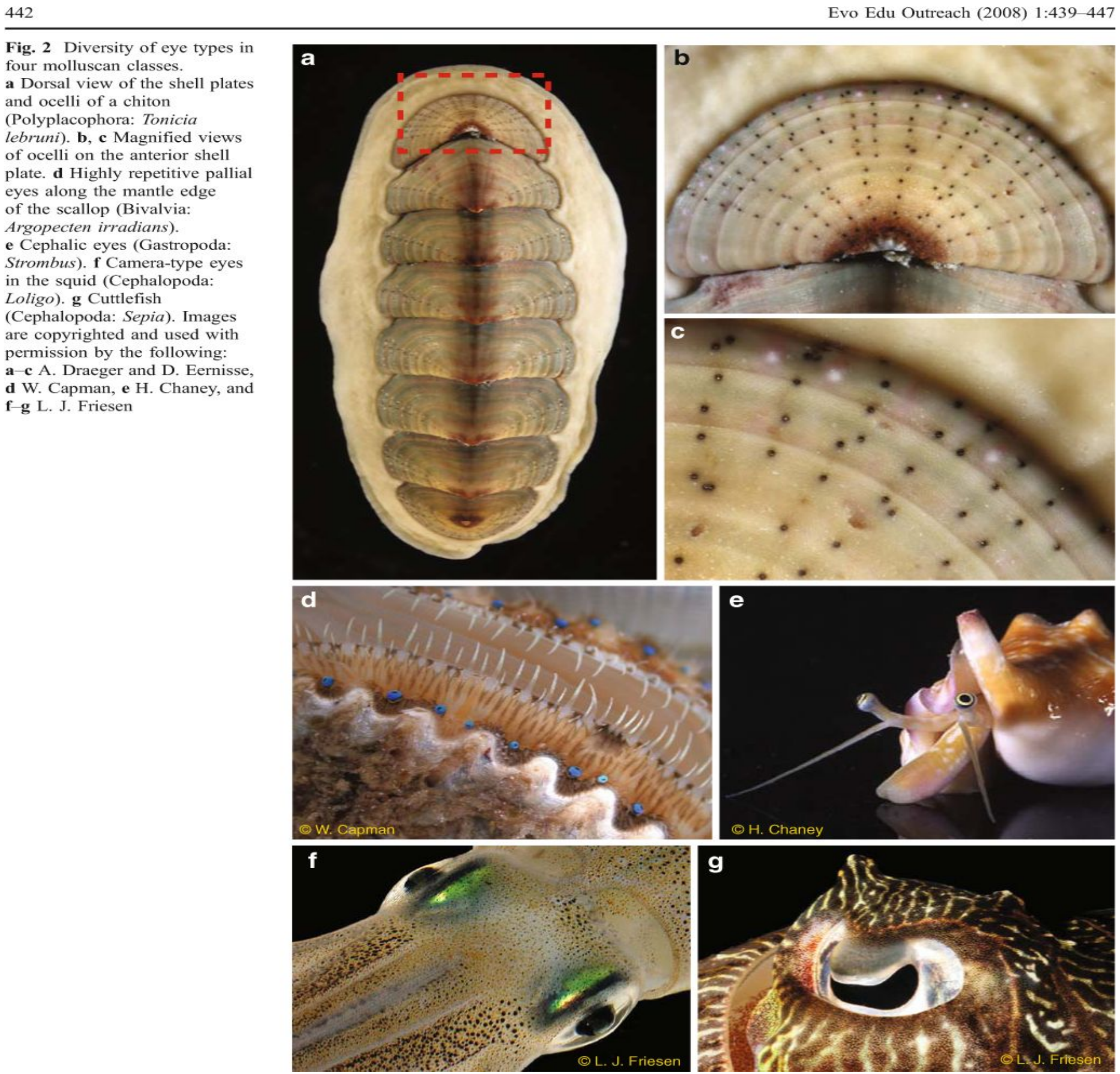
В таком случае их можно рассматривать как преадаптацию к фотосенсорной функции



ciliary (red) or microvillar (blue) photoreceptores.

# Моллюски. У них есть все

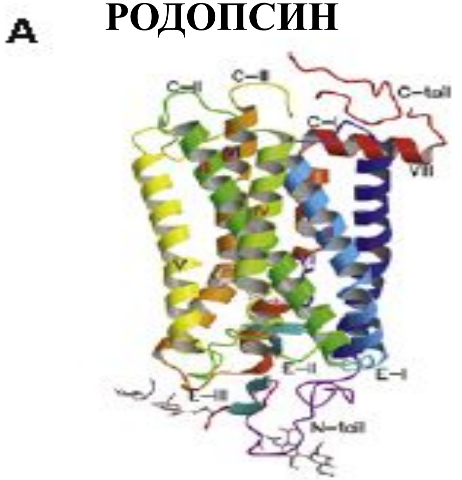


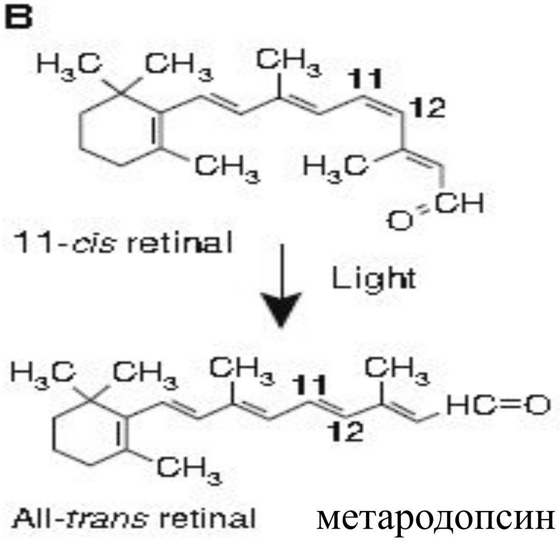


442 Evo Edu Outreach (2008) 1:439–447

**Fig. 2** Diversity of eye types in four molluscan classes. **a** Dorsal view of the shell plates and ocelli of a chiton (Polyplacophora: *Tonicia lebruni*). **b**, **c** Magnified views of ocelli on the anterior shell plate. **d** Highly repetitive pallial eyes along the mantle edge of the scallop (Bivalvia: *Argopecten irradians*). **e** Cephalic eyes (Gastropoda: *Strombus*). **f** Camera-type eyes in the squid (Cephalopoda: *Loligo*). **g** Cuttlefish (Cephalopoda: *Sepia*). Images are copyrighted and used with permission by the following: **a–c** A. Draeger and D. Eernisse, **d** W. Capman, **e** H. Chaney, and **f–g** L. J. Friesen

# РОДОПСИН

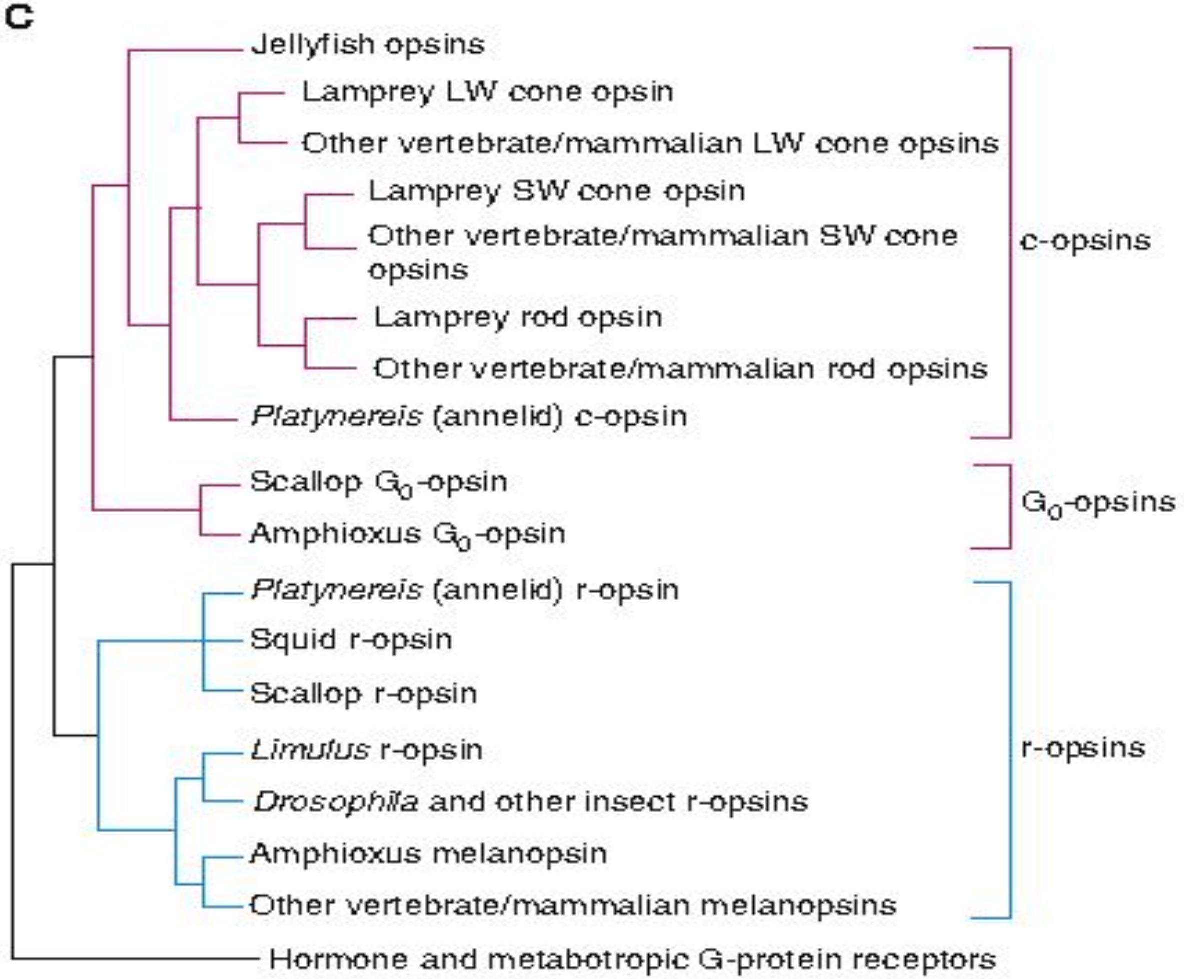




родопсин

метародопсин

**ФОТОИЗОМЕРИЗАЦИЯ**



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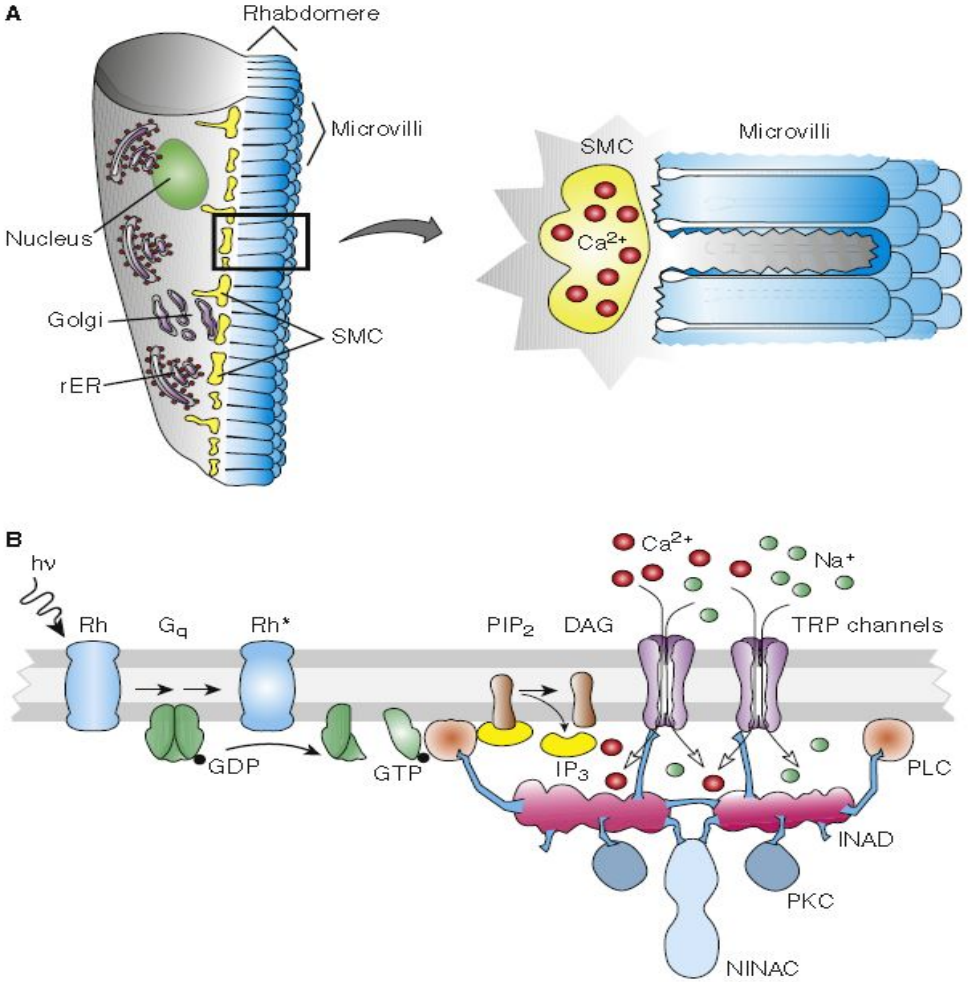
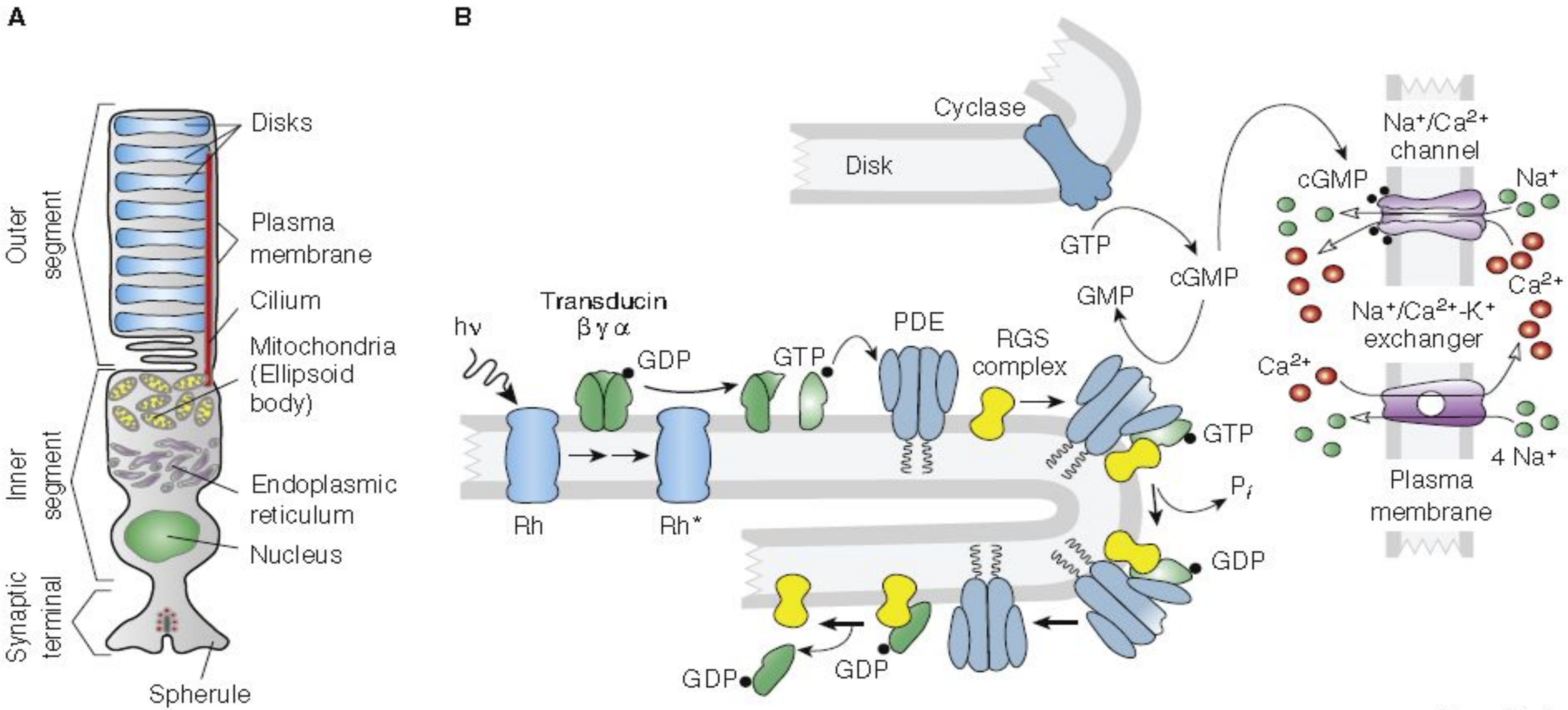


Current Biology

**Figure 3. Transduction scheme of microvillar photoreceptor.**

(A) Microvillar photoreceptor (left) and detail of microvilli with adjacent submicrovillar cisternae (SMCs) containing $Ca^{2+}$ (right). (B) Major proteins and mechanisms in microvillar transduction. Schema is based on results from fly. In other species, $IP_3$-induced $Ca^{2+}$ release from the SMCs (not shown in diagram) is known to make an important contribution to microvillar transduction. Abbreviations: hν, light; $Rh^*$, activated form of the photopigment rhodopsin; $G_q$, G protein containing $\alpha_q$ subunit; GDP, guanosine diphosphate; GTP, guanosine triphosphate; PLC, phospholipase C; $PIP_2$, phosphatidylinositol 4,5-bisphosphate; $IP_3$, inositol 1,4,5-triphosphate; DAG, diacylglycerol; PKC, protein kinase C; rER, rough endoplasmic reticulum; NINAC, class III myosin; and INAD, a protein containing PDZ binding domains responsible for forming the signaling complex in a fly microvillus.



Current Biology

**Figure 4.** **The vertebrate rod.**

(A) Schematic anatomy of representative vertebrate rod. (B) Major proteins and mechanisms in vertebrate rod transduction. Abbreviations: hν, light; Rh*, activated form of the photopigment rhodopsin; GTP, guanosine triphosphate; GDP, guanosine diphosphate; cGMP, guanosine 3′,5′-cyclic monophosphate; GMP, guanosine monophosphate; PDE, guanosine nucleotide phosphodiesterase; RK, rhodopsin kinase; RGS complex, group of three proteins including RGS9 which accelerate the hydrolysis of GTP by the alpha subunit of transducin; and $P_i$, inorganic phosphate.

*Cladonema radiatum*
(Cnidaria, Hydrozoa)

OCELLUS OF *CLADONEMA RADIATUM*

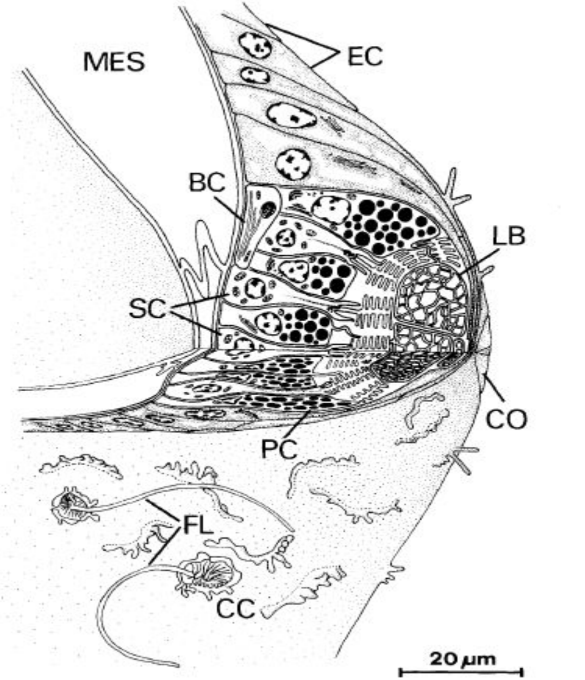
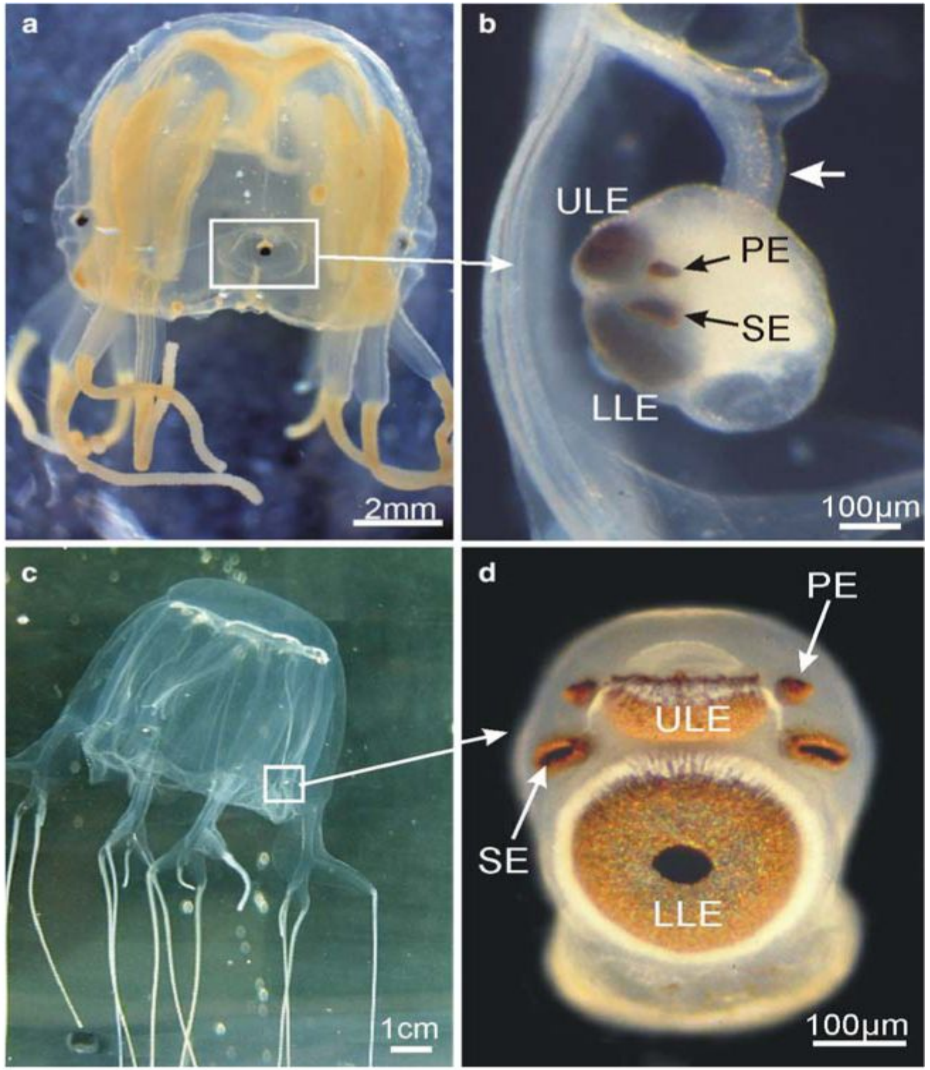


Fig. 1. Reconstruction of the cellular and subcellular architecture of the differentiated eye of *Cladonema radiatum* Duj. BC, basal cell; CC, cone complex; CO, cornea; EC, epithelial cell; FL, flagellum; LB, lens-body; MES, mesogloea; PC, pigment cell; SC, sensory cell.

*Tripedalia, Chiropsella* (Cnidaria, Cubozoa)



У хиропселлы нет мозга, что компенсируется ее близорукостью

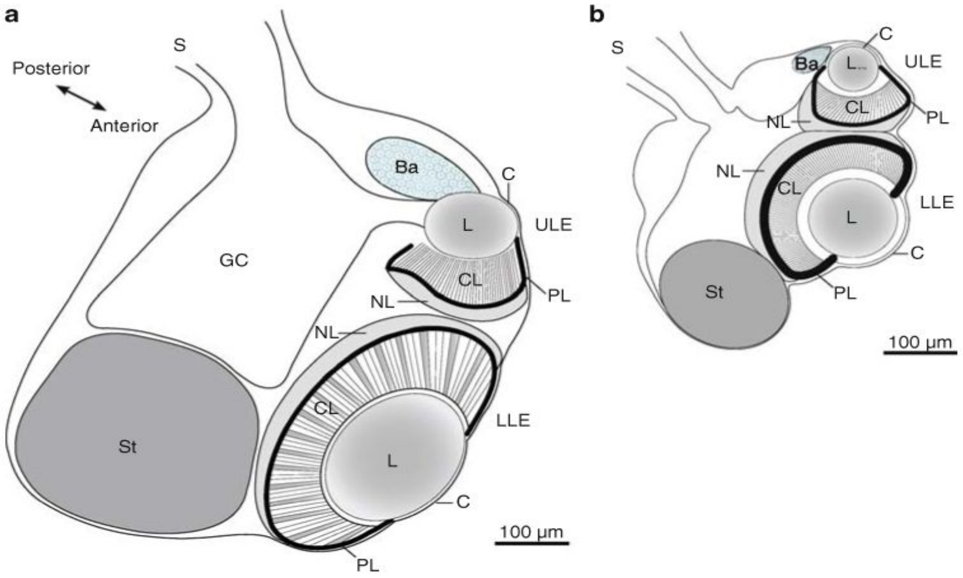
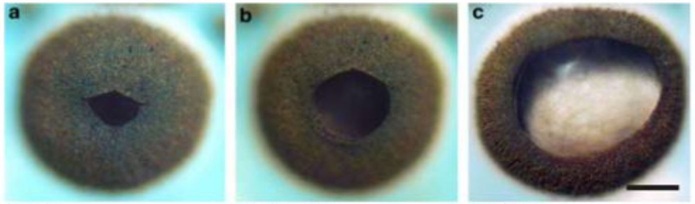


**Fig. 1** Schematic diagram of the sagittal plane through rhopalia of **a** *Chiropsella bronzie* and **b** *Tripedalia cystophora*. Box jellyfish have two different camera-type eyes, the upper lens-eye (*ULE*) and lower lens-eye (*LLE*), as well as two pairs of pigment pit eyes (not in the sagittal plane). Both the upper and lower lens-eyes contain the typical components of camera-type eyes: a cornea (*C*), a lens (*L*), and a retina consisting of a ciliary layer (*CL*), a pigment layer (*PL*) and neural layer (*NL*). In contrast to *T. cystophora*, the lenses of *C. bronzie* are not spherical. Additionally, in *C. bronzie*, the pigment layer of the upper lens-eye does not meet the lens at the posterior side of the rhopalium. At the peripheral end of the rhopalia, there is a crystalline weight (statocyst, *St*). The gastric cavity (*GC*) extends into the rhopalium via the stalk (*S*) and a mass of large cells, referred to as "balloon cells" (*Ba*), is covering part of the aperture of the upper lens-eye, and extending towards the rhopalial stalk



t = 0 t = 15 min t ≥ 1 h

**Fig. 4** Constriction and dilation of the pupil of the lower lens-eye of *Chiropsella bronzie* under different light adaptation states. **a** A fully light-adapted eye with constricted pupil, **b** after 15 min of dark adaptation and **c** after ≥1 h in total darkness. *Scale bar* 100 μm

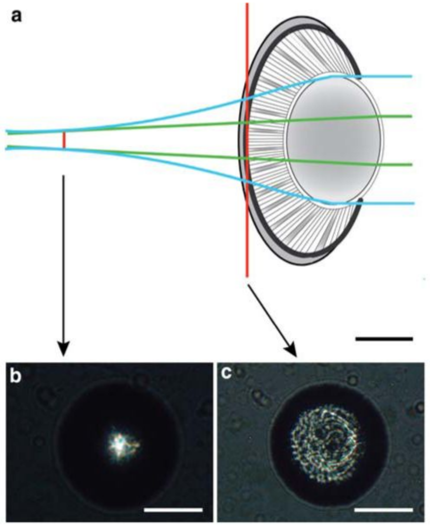


**Fig. 5** The severely under-focused optics of the lower lens-eye of *Chiropsella bronzie*. **a** A model of the eye showing the beam width (at 50% level) when parallel light enters the eye through a dilated pupil (*blue* beam width) and a constricted pupil (*green* beam width). The beam converges behind the lens, and reaches a minimum width at about 300 μm behind the back of the retina. The non-linear reduction of beam width is due to positive spherical aberration. Beam widths were measured by recording the light distribution behind isolated lenses illuminated by parallel light of 500 nm wave length. Examples of recorded beam profiles are given for the plane of the pigment layer (**c**), and for the plane of best focus (**b**). The lens does not bring light to a perfect focus at any distance, as indicated by the broad blur-spot at the plane of best focus (**b**). *Scale bars* 100 μm

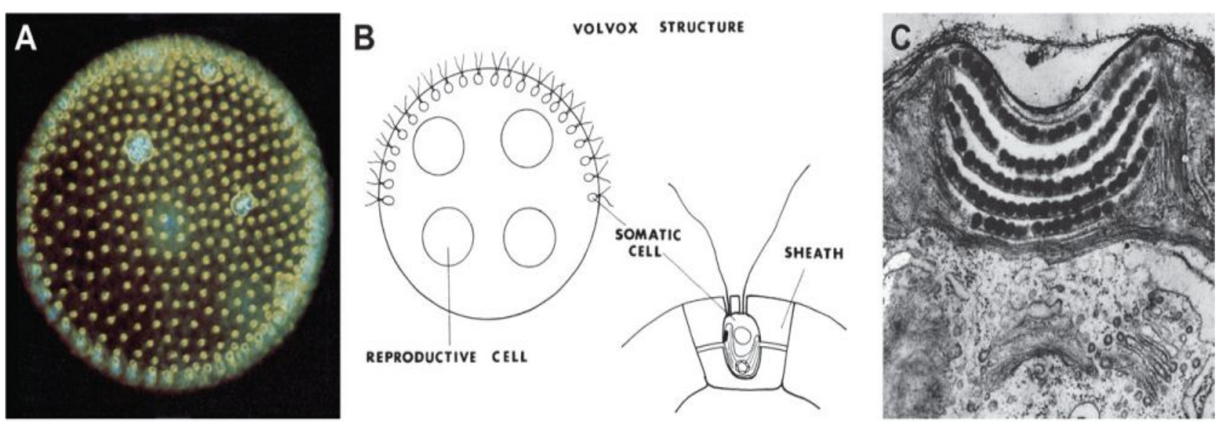


**Figure 12.** The colonial organization of *Volvox* and the structure of its photoreceptor organelle located in the chloroplast of *Eudorina*. (**A**) Colonial organization. (**B**) Structure of a single flagellate (somatic cell). (**C**) Ultrastructure of the photoreceptor organelle in the chlorplast (thylakoid membranes) of *Eudorina californica* (after Grell 1973).

Бывают и одноклеточные фоторецепторы и фоторецепторы одноклеточных

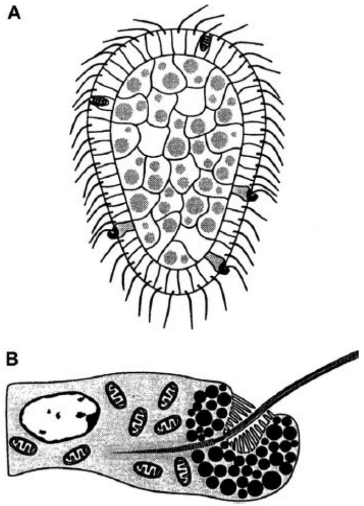


**Figure 10.** Unicellular photoreceptors in the planula larva of the box jellyfish *Tripedalia* (after Nordström et al. 2003). (**A**) Planula larva. (**B**) Unicellular photoreceptor with pigment granules, microvilli, and a flagellum.

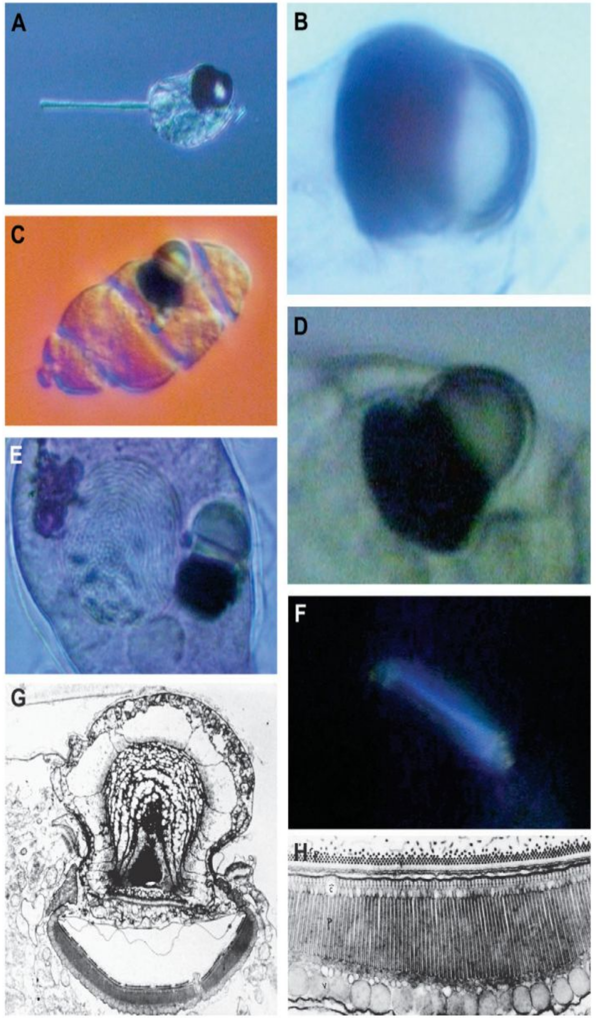
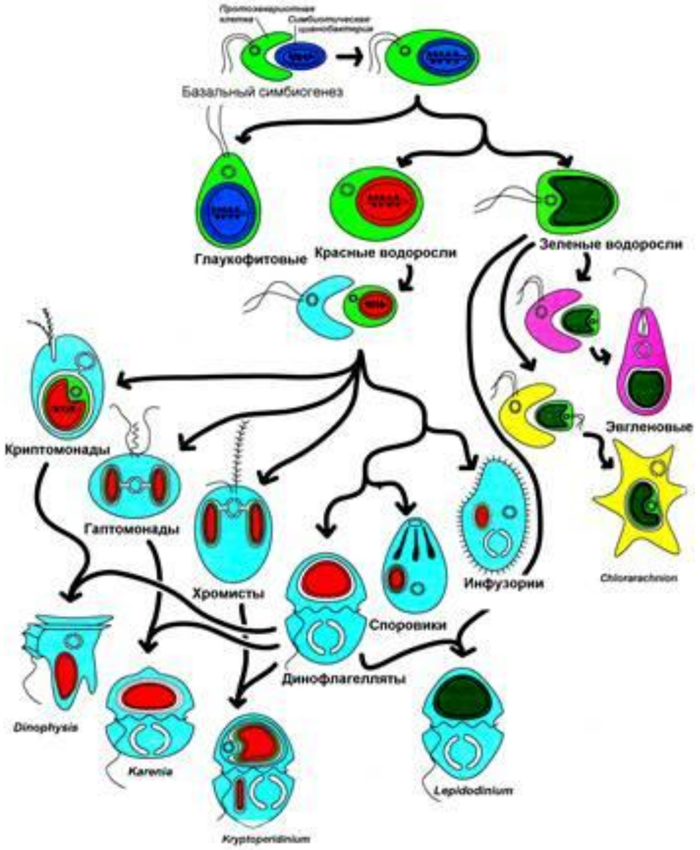


**Figure 13.** Eye organelle of the unicelllular dinoflagellates *Erythropsis* and *Warnowia*. (**A**) *Erythropsis*. (**B**) Eye organelle of *Erythropsis*. (**C**) *Warnowia*. (**D**) Eye organelle of *Warnowia*. (**E**) Nucleus and eye organelle of *Warnowia*. (**F**) Birefringence, the retina-like structure detected in polarized light in *Warnowia*. (**G**) Ultrastructure of the eye organelle of *Warnowia*. (**H**) Ultrastructure of the retina-like structure with stacked membranes and large pigment granules. A–F courtesy of Makiko Seimiya and Jean and Colette Febvre; G–H from Greuet 1969.

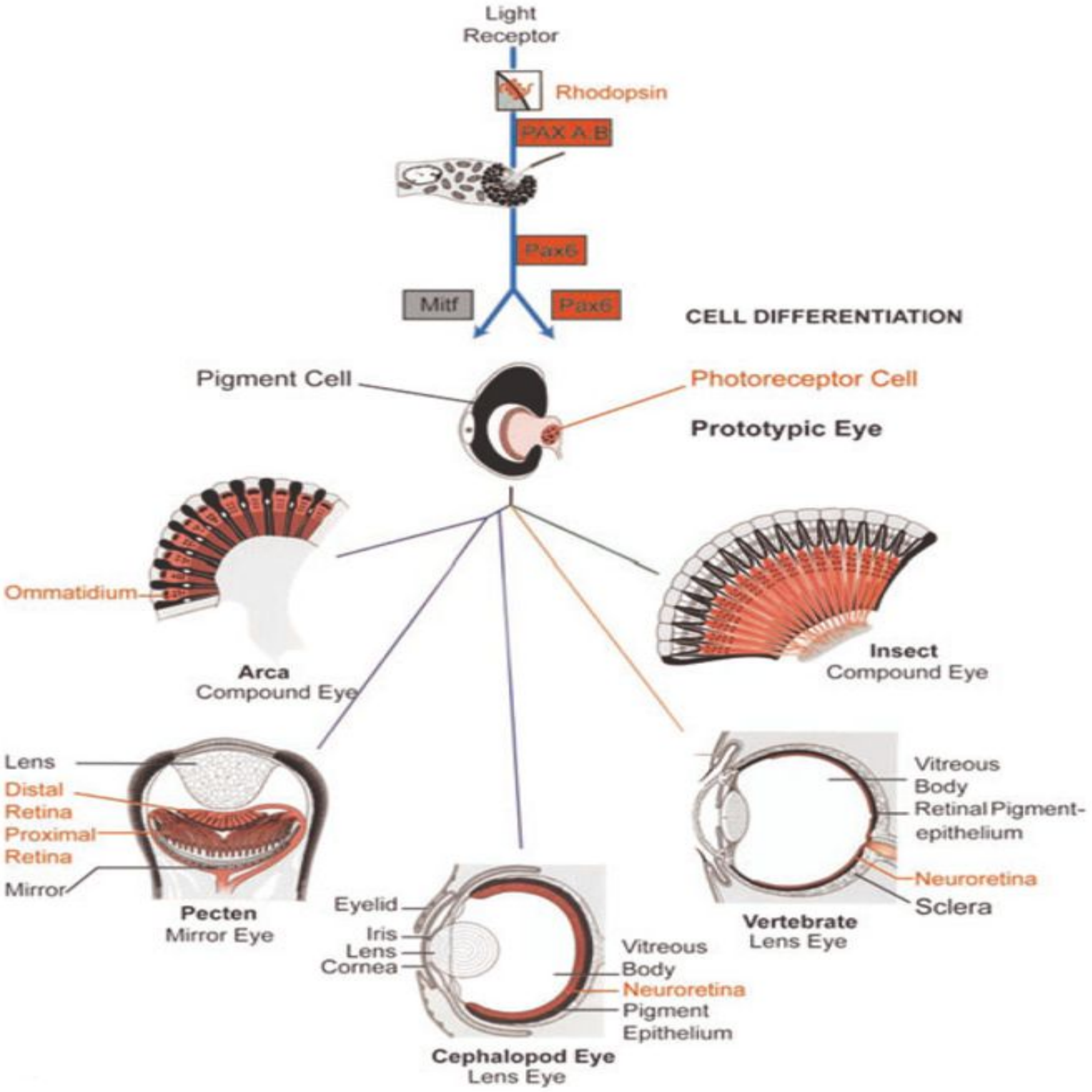


« ...... This symbiont hypothesis, which I call the Russian doll model, assumes that light sensitivity first arose in **cyanobacteria,** the earliest known fossils on Earth. These cyanobacteria were subsequently taken up by **eukaryotic red algae** as primary chloroplasts surrounded by an outer and inner bacterial membrane separated by a proteoglycan layer.

Subsequently, the red algae were taken up by **dinoflagellates** as secondary chloroplasts surrounded by an additional third membrane coming from the primary red algal host. In some species of dinoflagellates like *Erythropsis* and *Warnovia*, which do not have any chloroplasts, these secondary chloroplasts may have been transformed into elaborate photoreceptor organelles as suggested by Greuet.

Indeed, the sequencing of the complete genome of the cyanobacterium *Nostoc* has revealed the presence of a proteorhodopsin gene (Kaneko et al. 2001). A proteorhodopsin gene has also been found in the dinoflagellate *Pyrocystis* and shown to be controlled by the internal clock (Okamoto and Hastings 2003)......»

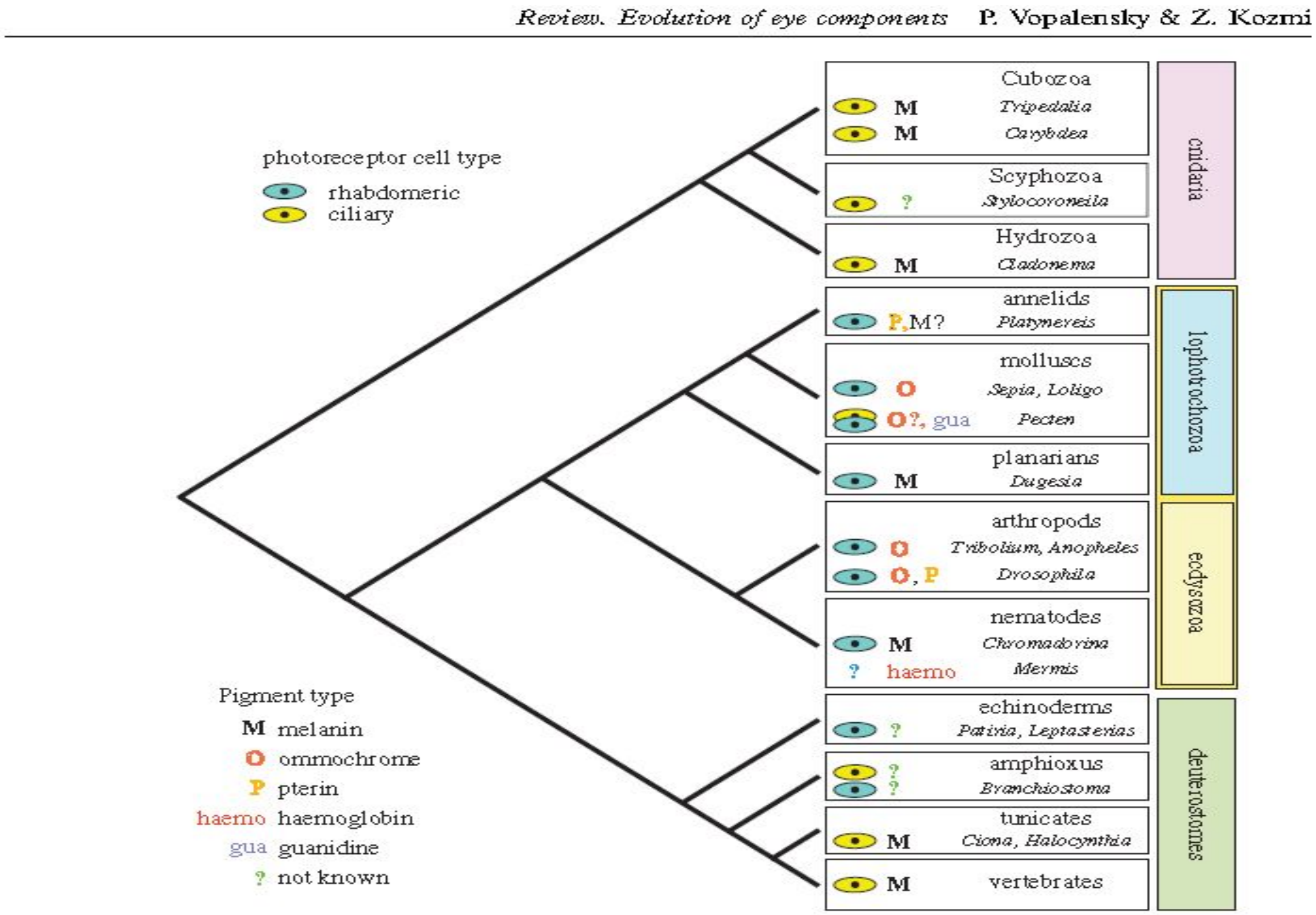
Gehring, 2005

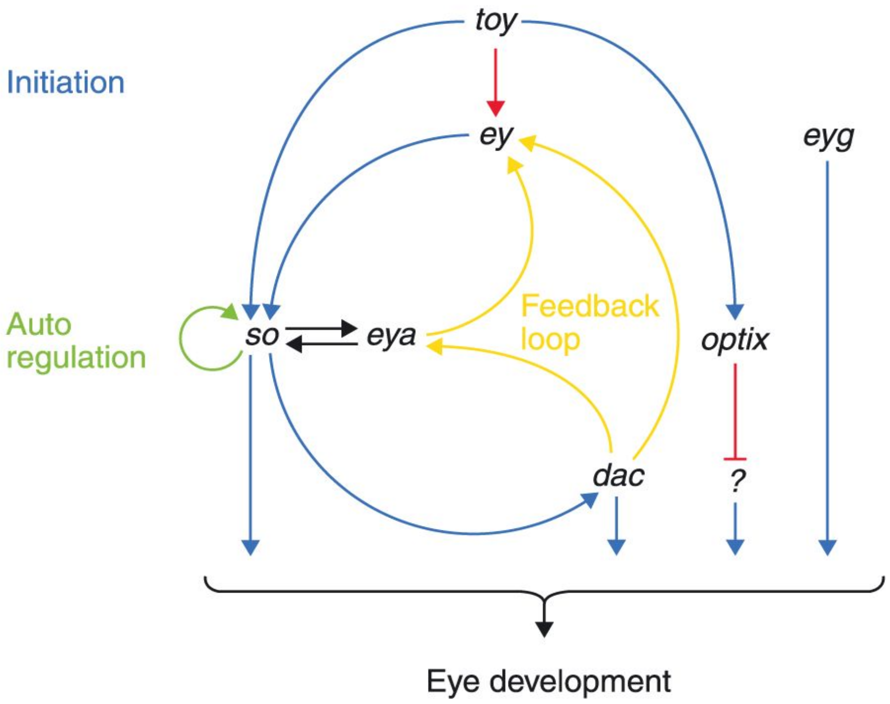


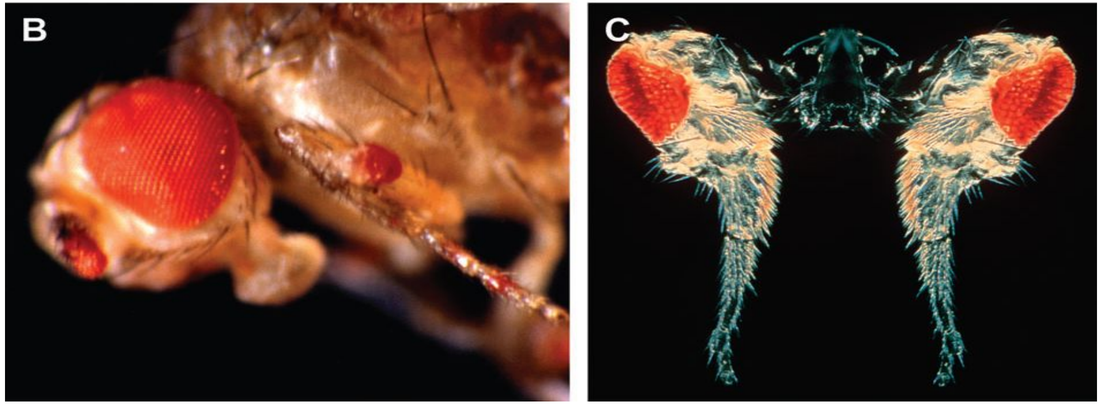
**General scheme of eye evolution.**

The first step in eye evolution is the evolution of a light receptor molecule which in all metazoans is rhodopsin. In the most ancestral metazoa, the sponges, a single Pax gene, but no opsin gene has been found. In the cubozoan jellyfish Tripedalia, a unicellular photoreceptor has been described in the larva. The adult jellyfish has complex lens eyes that form under the control of PaxB, whereas the eyes of a hydrozoan jellyfish (Cladonema) are controlled by PaxA. We propose that from the unicellular photoreceptor cell, the prototypic eye postulated by Darwin originated by a first step of cellular differentiation into a photoreceptor cell and a pigment cell, controlled by Pax6 and MITF, respectively. (Gehring, 2012).

Не сразу


Review. Evolution of eye components P. Vopalensky & Z. Kozmi
photoreceptor cell type
rhabdomeric
ciliary
Cubozoa
M Tripedalia
M Carybdea
Scyphozoa
? Stylocoronella
Hydrozoa
M Cladonema
cnidaria
annelids
P, M? Platynereis
molluscs
O Sepia, Loligo
O?, gua Pecten
planarians
M Dugesia
lophotrochozoa
arthropods
O Tribolium, Anopheles
O, P Drosophila
nematodes
M Chromadorina
? haemo Mermis
ecdysozoa
echinoderms
? Patiria, Leptasterias
amphioxus
? ? Branchiostoma
tunicates
M Ciona, Halocynthia
M vertebrates
deuterostomes
Pigment type
M melanin
O ommochrome
P pterin
haemo haemoglobin
gua guanidine
? not known





The top of the regulatory network is Pax 6 on the very top of the hierarchy. In *Drosophila*, Pax 6 has undergone a gene duplication and twin of *eyeless* (*toy*) activates *eyeless* (*ey*) initiating the developmental pathway. Together these two genes activate the subordinate homeobox transcription factor *sine oculis* (*so*) by binding to five *cis*-regulatory elements identified in the so enhancer. It is interesting to note that two of the subfamilies of Six genes control eye development, whereas the third subfamily is involved in muscle development. This shows clearly that there are no functional constraints on transcription factors to control a particular developmental pathway. The So protein interacts with the protein encoded *by eyes absent* (*eya*) forming a hetero-dimer. Eya serves both as a co-activator in the nucleus and as a protein phosphatase in the cytoplasm. The transcription factors are connected by positive feed-back loops to *dachshund* (*dac*). There are two additional genes involved; one is *optix* which like so is member of the six gene family, and the other is the Pax gene *eye gone* (*eyg*) which apparently acts independently of *ey* and *toy*. In order to block eye development in *Drosophila* completely, all three Pax genes *ey*, *toy*, and *eyg* have to be mutated. Interestingly, the top of the cascade involves mostly positive regulation (activation) and positive feed-back loops.

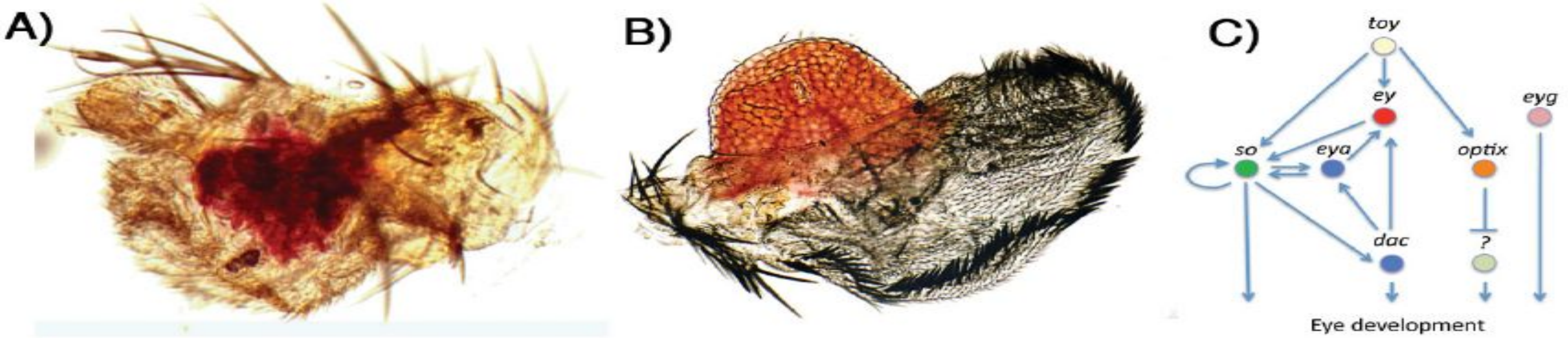


Figure 3. Ectopic expression of eye regulatory network genes in flies. A: Ectopic expression of optix in antennal discs leads to ectopic red pigment in adult antennae (photo courtesy of Makiko Seimiya and Walter Gehring). B: Ectopic expression of eyeless in wing discs leads to ectopic eyes [11] (photo courtesy of Georg Halder). C: The pattern of gene connections between several top regulatory genes in the eye network.

One possibility involves the co-option of the master regulator into a novel context, but at a different expression level from the endogenous eye context, leading to the activation of only those sub-networks that require lower levels of master gene expression to pass an activation threshold.

Previous work characterized the red pigments in Heliconius wings as ommochromes, and proposed that the ommochrome biosynthetic pathway originally deployed in the eye, had been co-opted to the wing. It appears that this was indeed the case, but the co-option was not done in a stepwise fashion.  Instead a single gene, that is known to regulate all the elements of this pathway as well as other eye components, optix, was co-opted to the wing.

## ПРЕДПОЛОЖИТЕЛЬНАЯ коопция молекулярно-генетических Каскадов, вовлеченных в морфогенез сложных глаз (ископаемое Diptera из Балтийского янтаря).

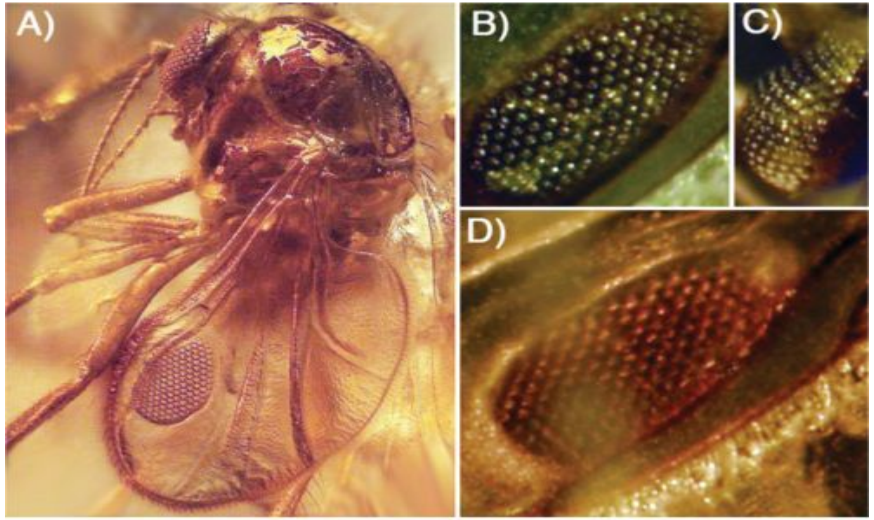


**Figure 1.** The extinct biting midge, *Eohelea petrunkevitchi*, with a unique wing organ that resembles the surface of its compound eye [7]. **A**: Photo courtesy of Volker Arnold. **B–D**: Photos courtesy of April Dinwiddie. **B**: The dorsal surface of the wing organ. **C**: The midge's compound eye. **D**: The ventral surface of the wing organ.

## Коопция гена *optix* в формирование красных пятен на крыльях *Heliconius*

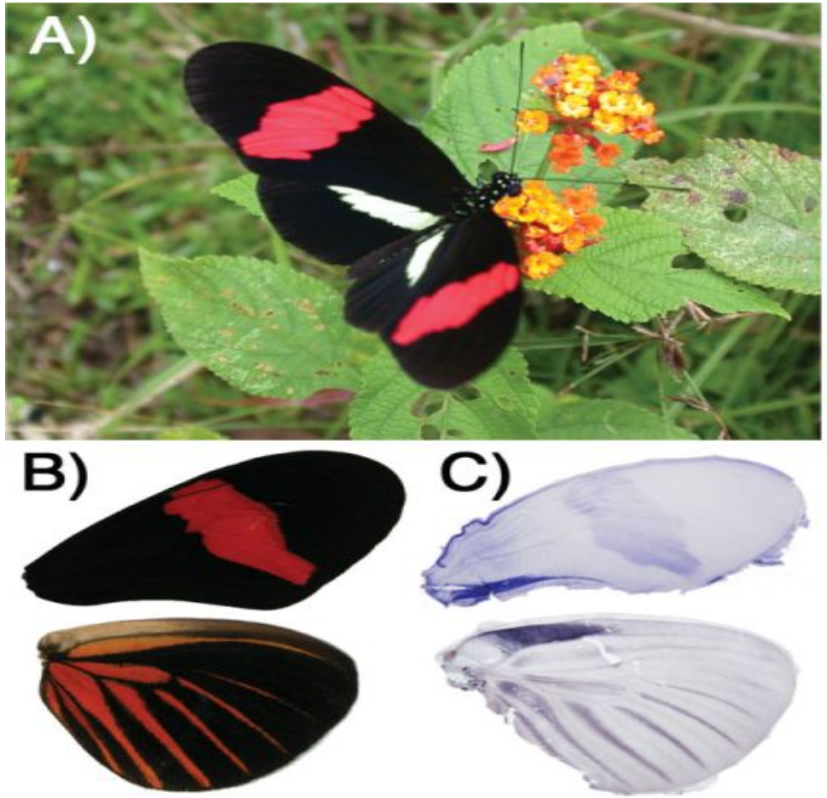
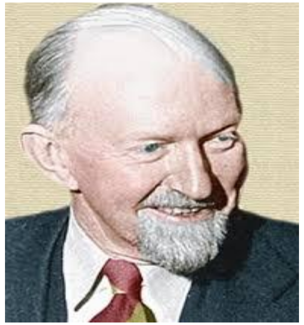


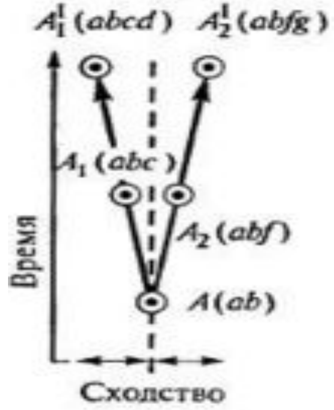
**Figure 2.** *Heliconius* butterflies express *optix* in wing epidermal cells that will produce red ommochrome pigments. **A**: *Heliconius erato*. **B**: Forewing and hindwing patterns from different races of *H. erato* (top: *H. e. petiverana*; bottom: *H. e. erato*). **C**: Pupal wings expressing *optix* mRNA in a pattern corresponding to the areas of red pigment in wings depicted in (B). Photos courtesy of Robert Reed.

Аналогичные органы могут возникать на основе разных планов строений в результате адаптации к одинаковым условиям.

Концепция адаптивной зоны Дж. Симпсона: адаптивная зона — комплекс условий внешней среды, определяющая тип адаптаций группы организмов.



George Gaylord Simpson
(1902 — 1984)



**Дивергентная эволюция:**
Эволюция на основе одного плана строения в разных адаптивных
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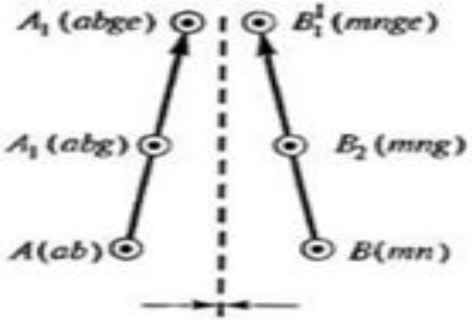
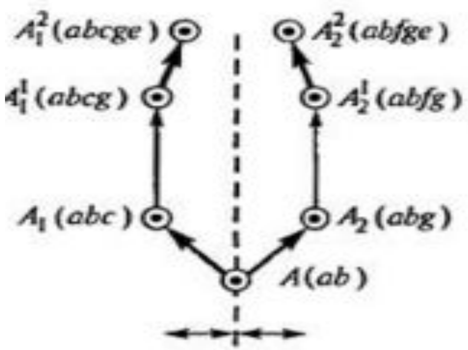


**Конвергентная эволюция:**
Эволюция на основе разных планов строения в одной адаптивной зоне



**Параллельная эволюция:**
Эволюция на основе одного плана строения в одной адаптивной зоне
ос

Для того, чтобы отличать **аналогичные** органы от **гомологичных** нужны критерии гомологии.