

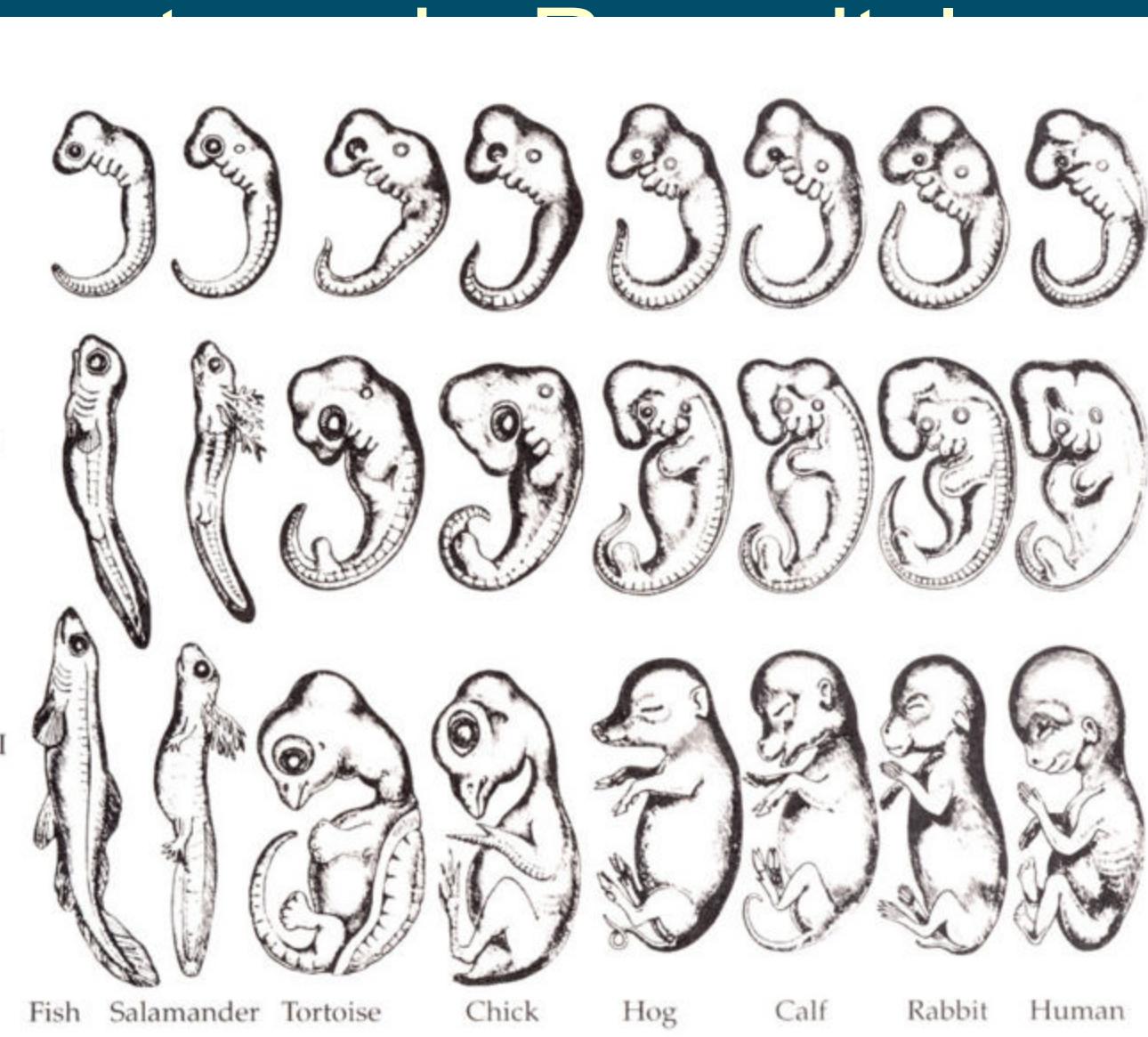
Desenvolvimento – Heterocronia, Alometria e Macroevolução

Macroevolução – usualmente estudada nos fósseis.
Isto porque a morfologia é preservada, mas reações
bioquímicas, cromossomos, fisiologia não.

Ora, a morfologia é produzida pelo crescimento e sua
forma emerge do processo de desenvolvimento.

Assim, as mudanças evolutivas na forma de um orgão
ou parte do corpo são frequentemente ontogenéticas

“Lei Biogenética” – Ernest Haeckel (1866) – A Filogenia



Estágios do desenvolvimento de um organismo correspondem a história filogenética da espécie, recapitulando um estágio ancestral na história evolutiva de um grupo.

Ex. O aparecimento transitório de “branquias” no desenvolvimento de humanos e outros mamíferos – Logo, mamíferos evoluíram de um peixe ancestral e suas branquias embrionárias recapitulam esta ancestralidade pisciana...

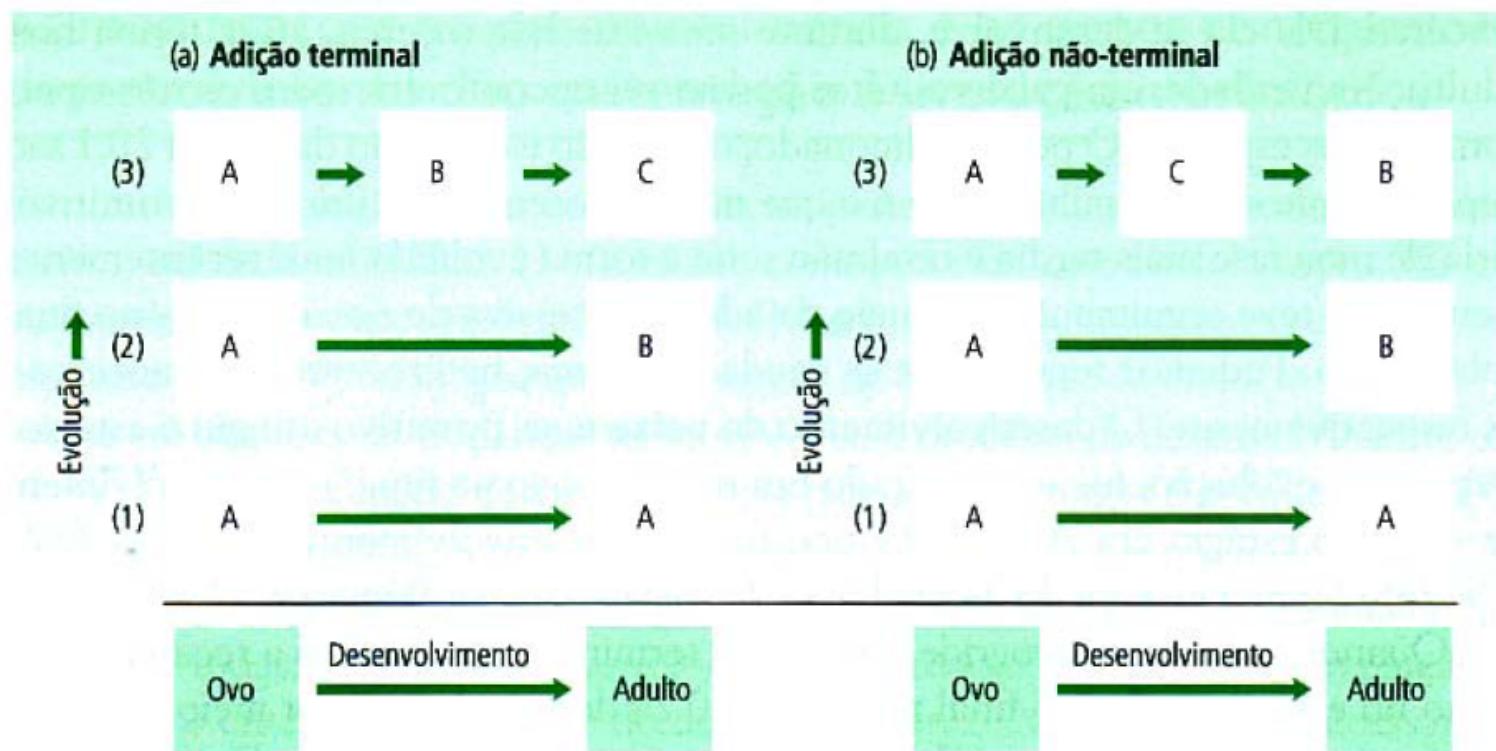


Figura 20.2

(a) Evolução por adição terminal. As etapas do desenvolvimento de um indivíduo estão representadas pelas letras. Página acima, o (1), o (2) e o (3) representam três estágios evolutivos sucessivos. Nas adições terminais, novos estágios só são acrescentados ao final do ciclo vital. (b) Evolução por adição não-terminal. Um novo estágio evolutivo foi acrescentado no início do desenvolvimento, e não no final do ciclo vital do adulto.

Como pode o desenvolvimento de um embrião mudar quando este processo de desenvolvimento é tão finamente ajustado e complexo? Como pode tal mudança ocorrer sem destruir o organismo inteiro?

No passado acreditava-se que para a evolução ocorrer novos passos tinham que ser adicionados ao final do desenvolvimento.

Hoje sabemos que mesmo estágios precoces do desenvolvimento podem ser alterados e produzir novidades evolutivas.

Razão pra isto = MÓDULOS!

Módulos

Mapa Genotípico-Fenotípico

ADAPTATION AND EVOLVABILITY

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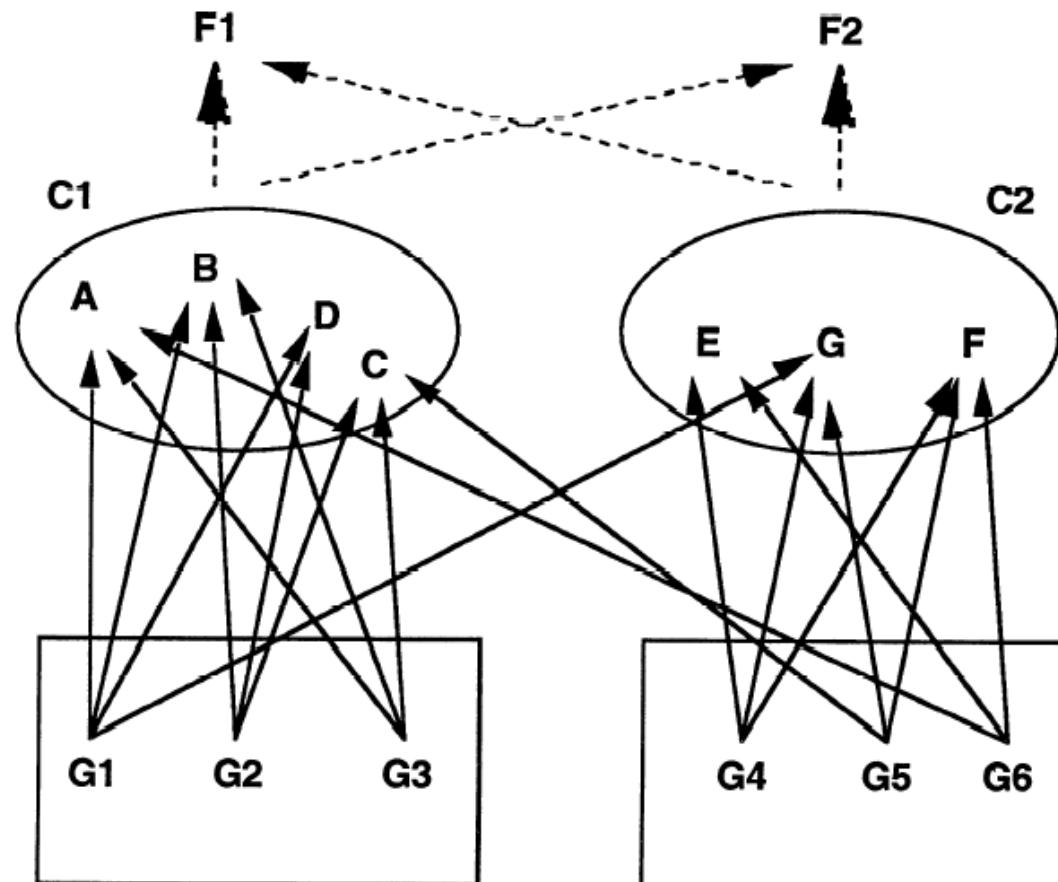
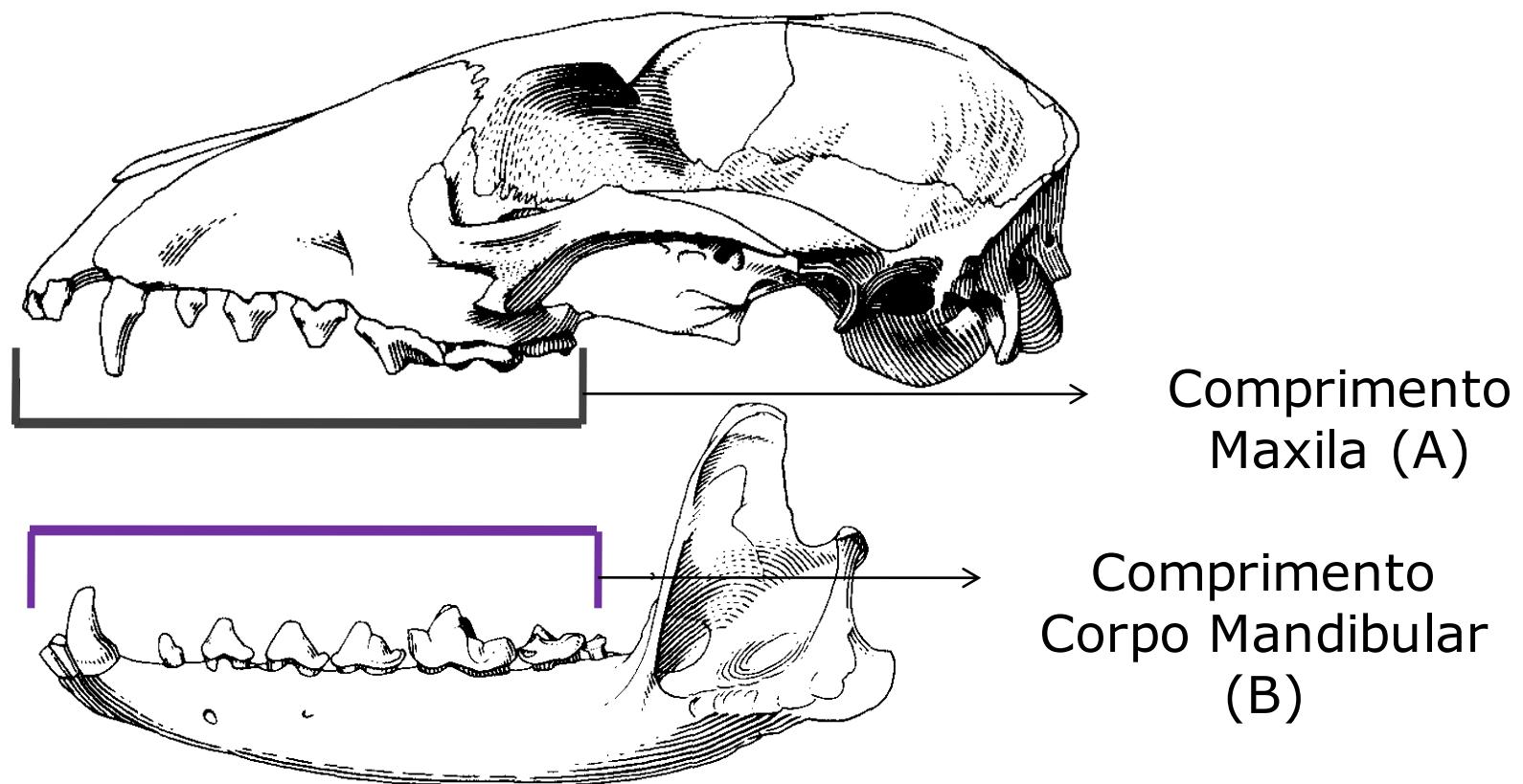
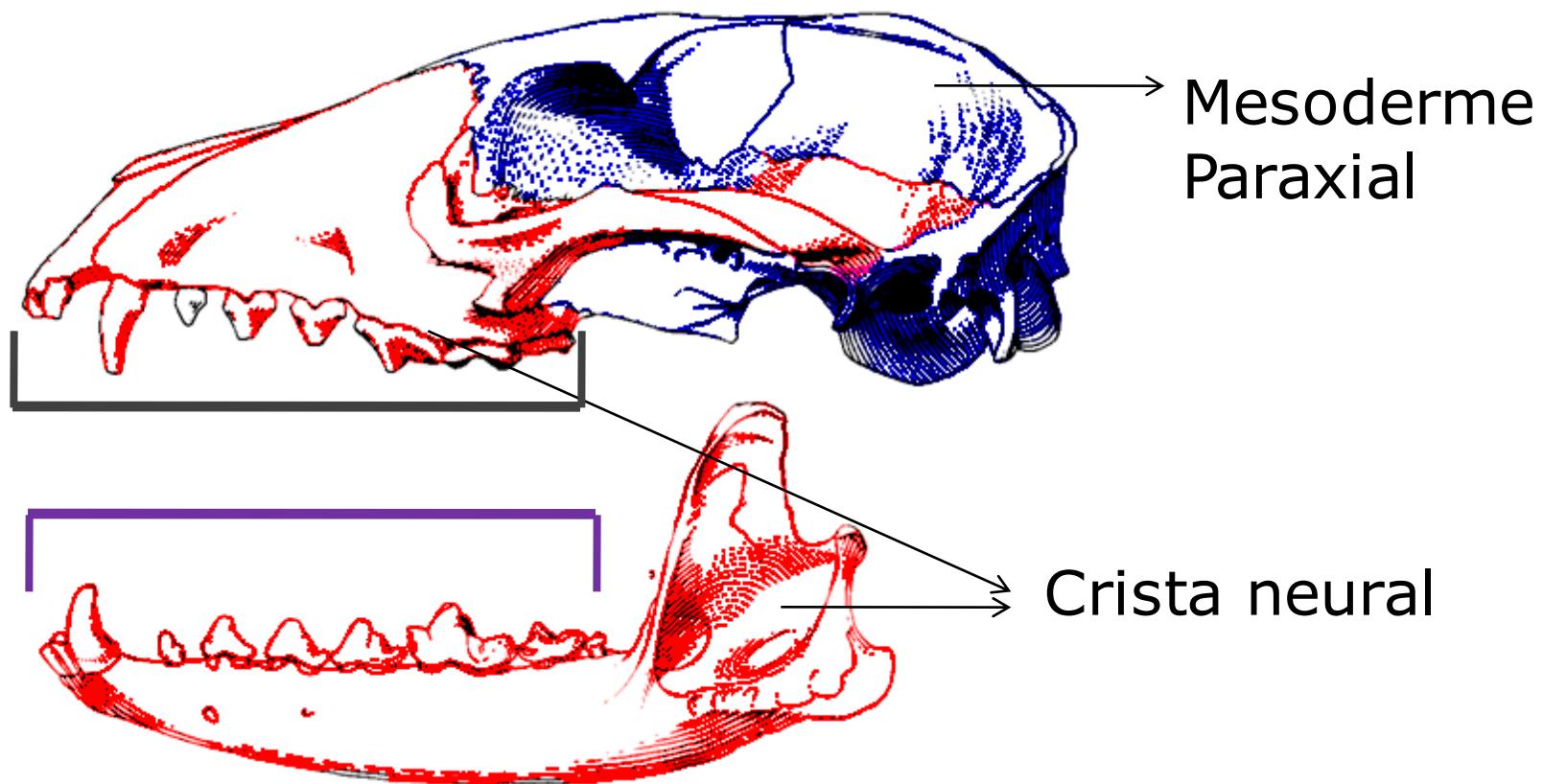


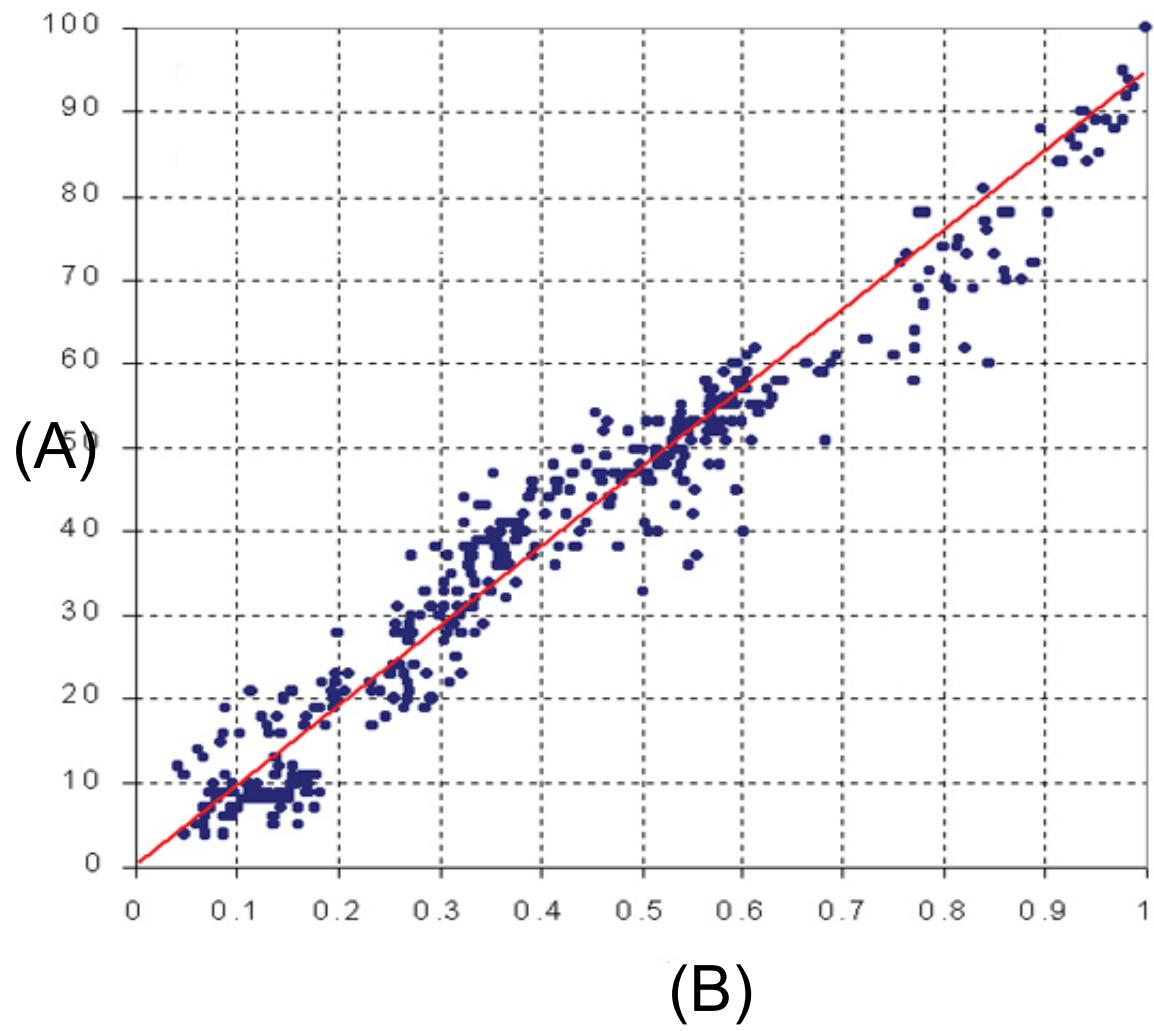
FIG. 1. Example of a modular representation of the character complexes $C_1 = \{A, B, C, D\}$ and $C_2 = \{E, F, G\}$ which serve to functions F_1 and F_2 . Each character complex has a primary function, F_1 for C_1 and F_2 for C_2 . Only weak influences exist of C_1 on F_2 and vice versa. The genetic representation is modular because the pleiotropic effects of the genes $M_1 = \{G_1, G_2, G_3\}$ have primarily pleiotropic effects on the characters in C_1 and $M_2 = \{G_4, G_5, G_6\}$ on the characters in complex C_2 . There are more pleiotropic effects on the characters within each complex than between them.

Visualizando



Origem comum no desenvolvimento

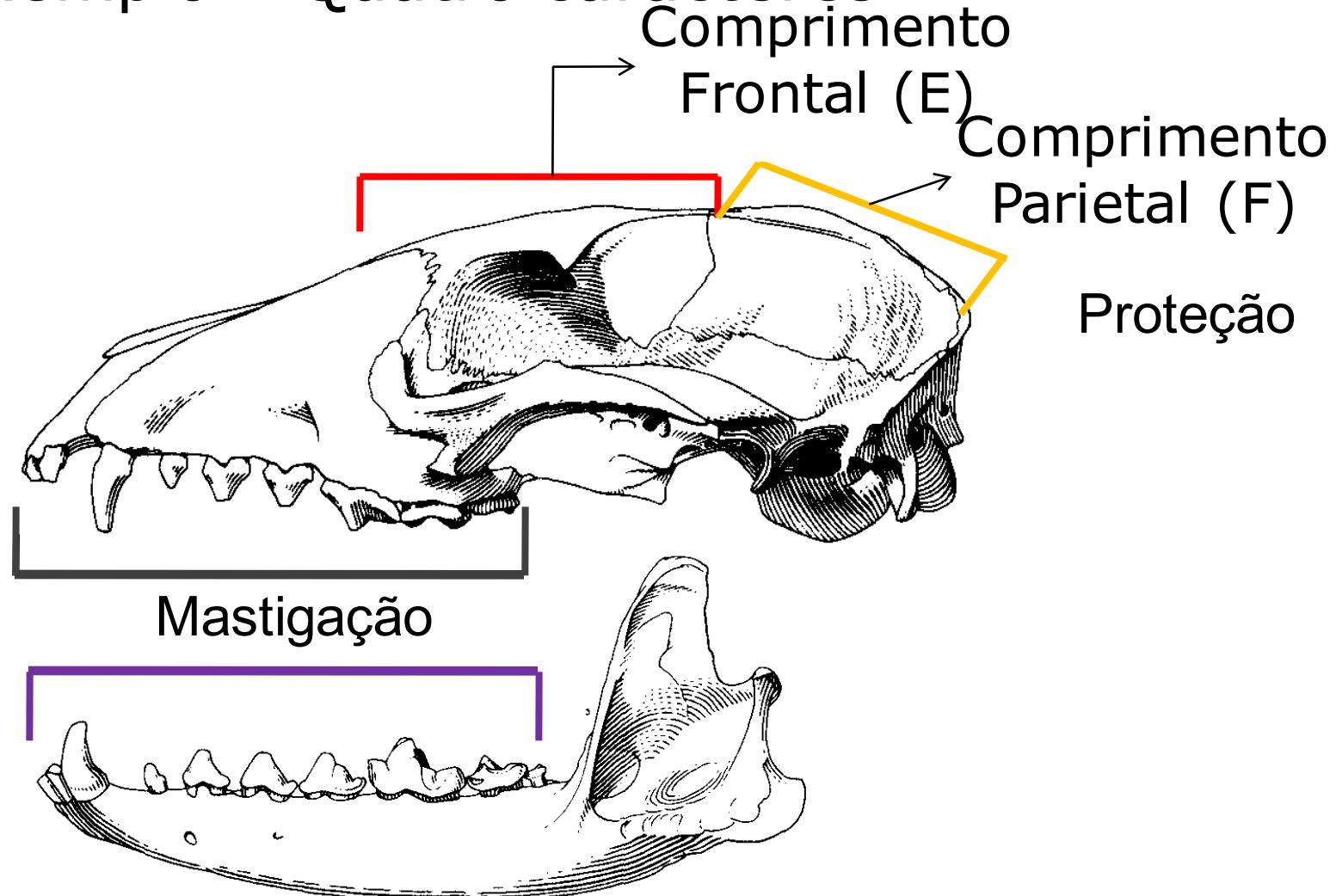




Comprimento
Maxila (A)

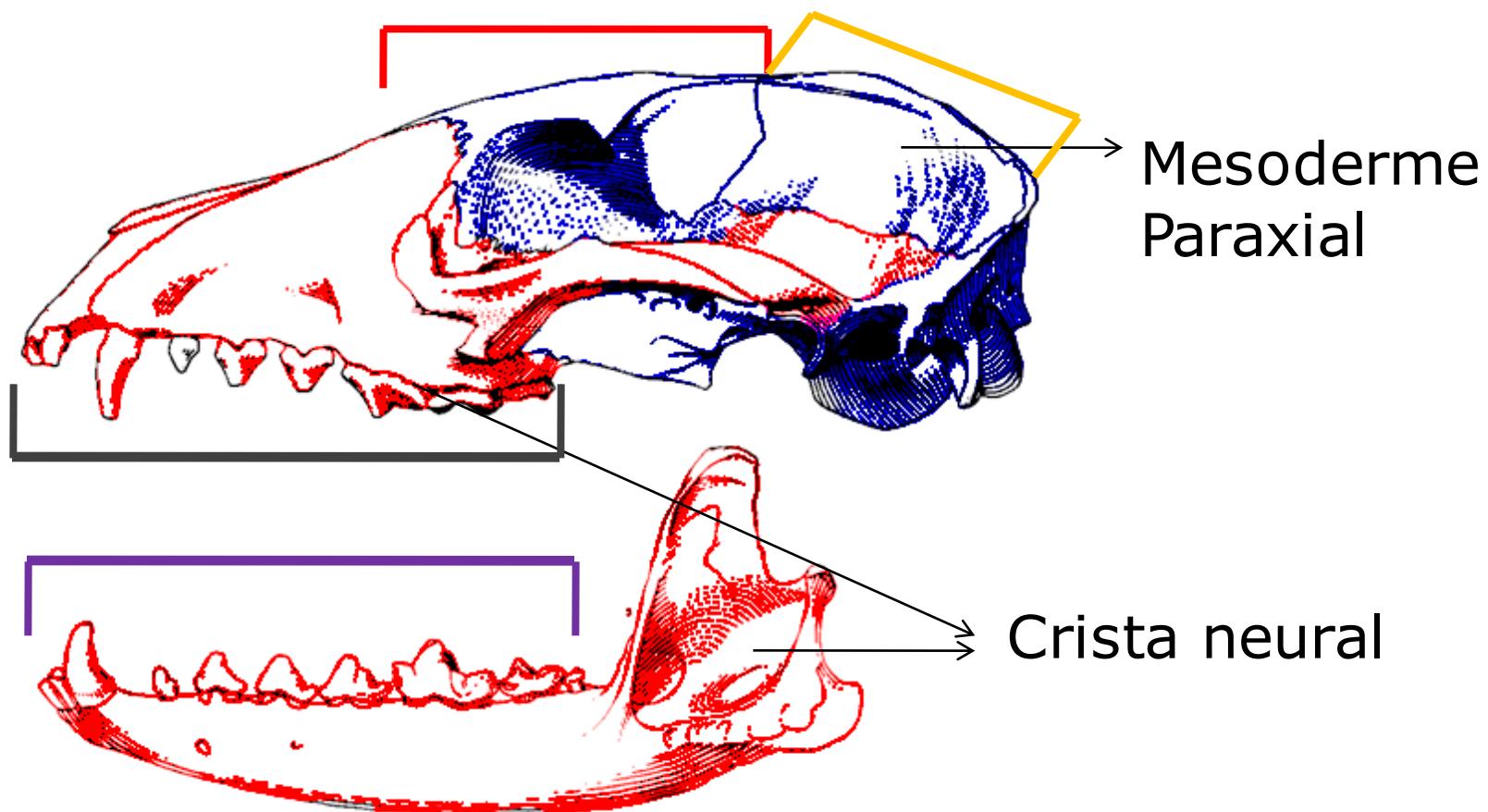
Comprimento
Corpo
Mandibular
(B)

Exemplo – Quatro caracteres

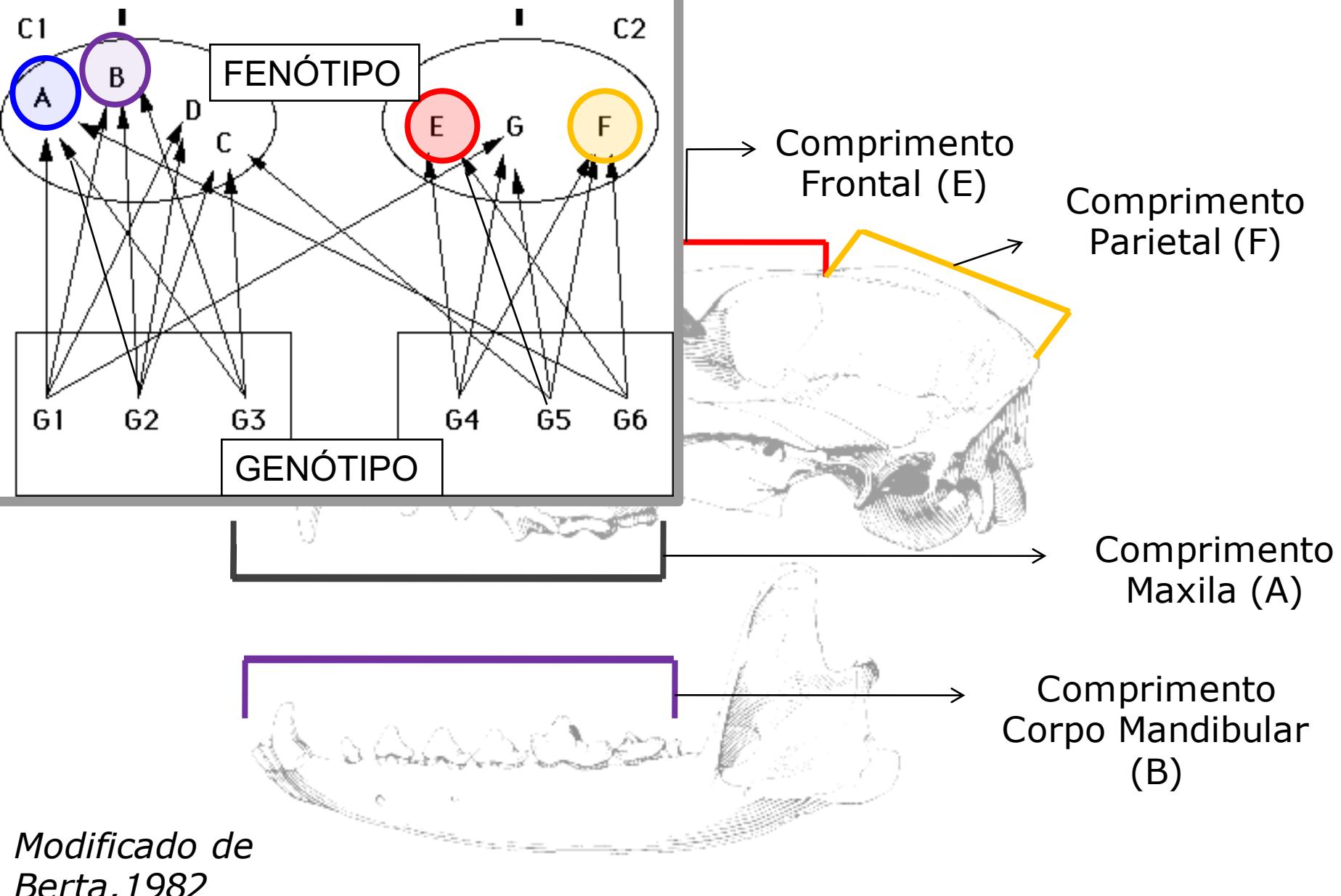


Modificado de Berta, 1982

Origem comum no desenvolvimento

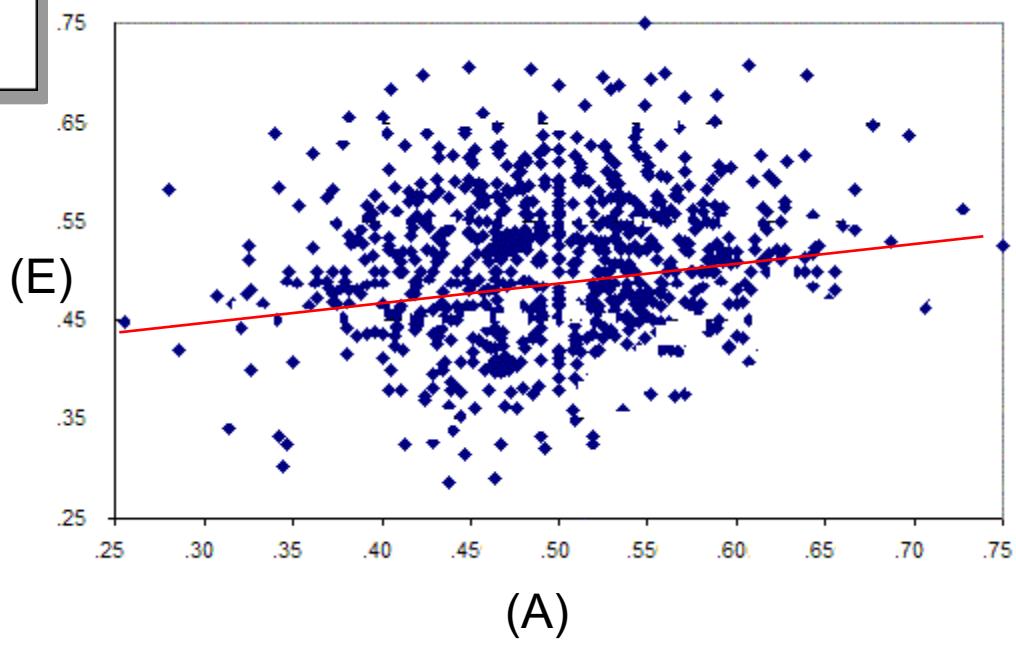
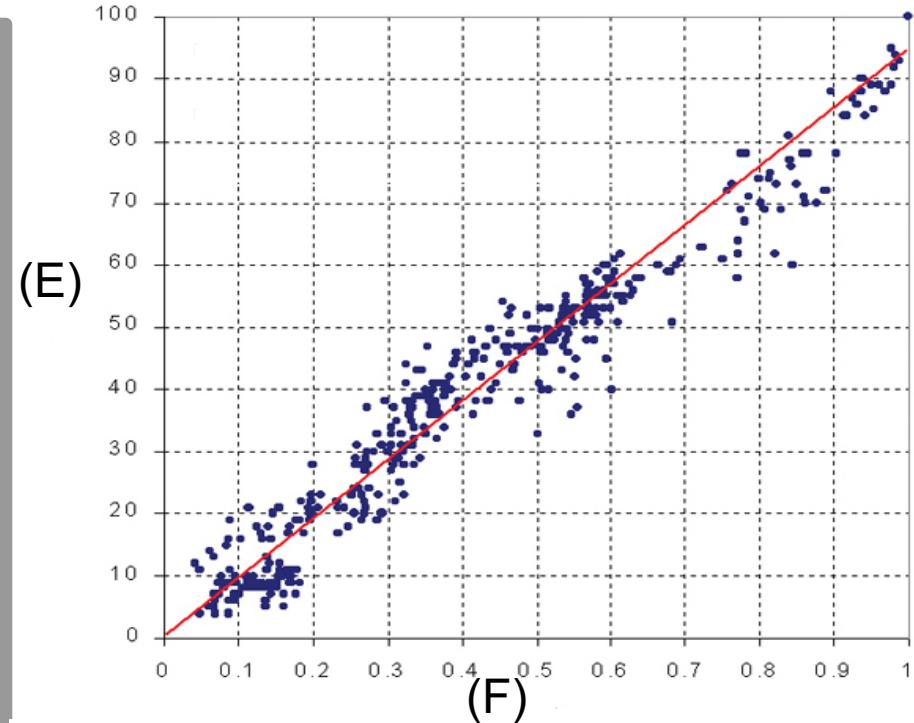
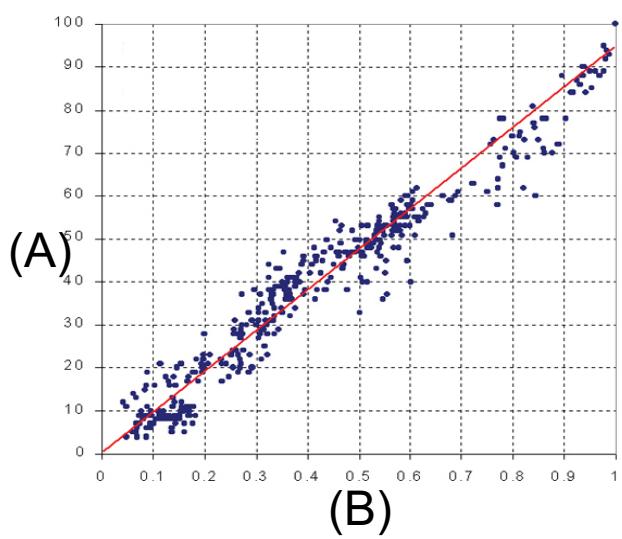
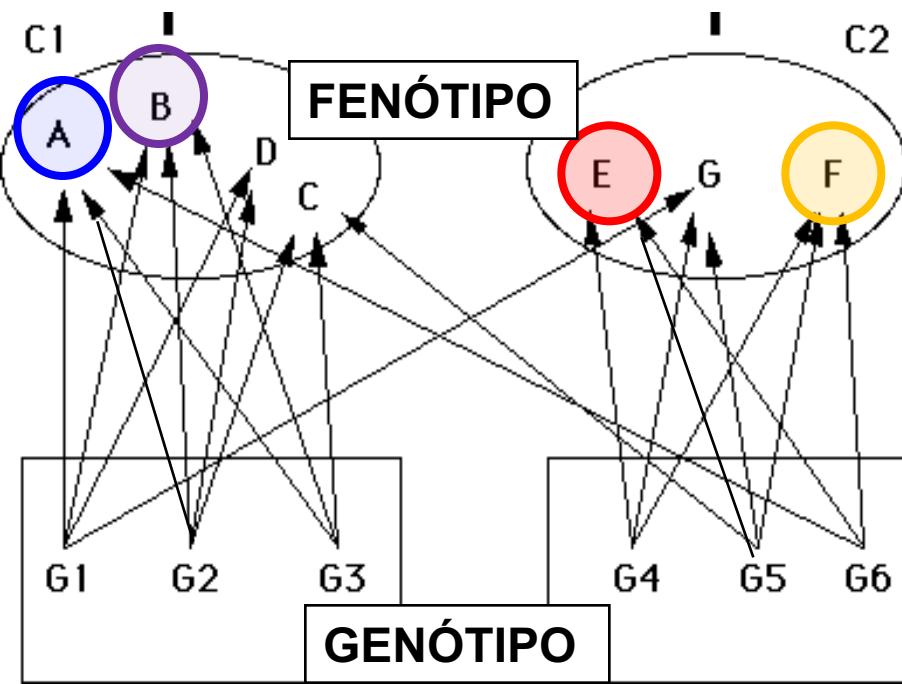


MASTIGAÇÃO



MASTIGAÇÃO

PROTEÇÃO



Evolução da modularidade – Note que o conceito de módulos se aplica a vários níveis na hierarquia biológica (do molecular ao organismal)

ADAPTATION AND EVOLVABILITY

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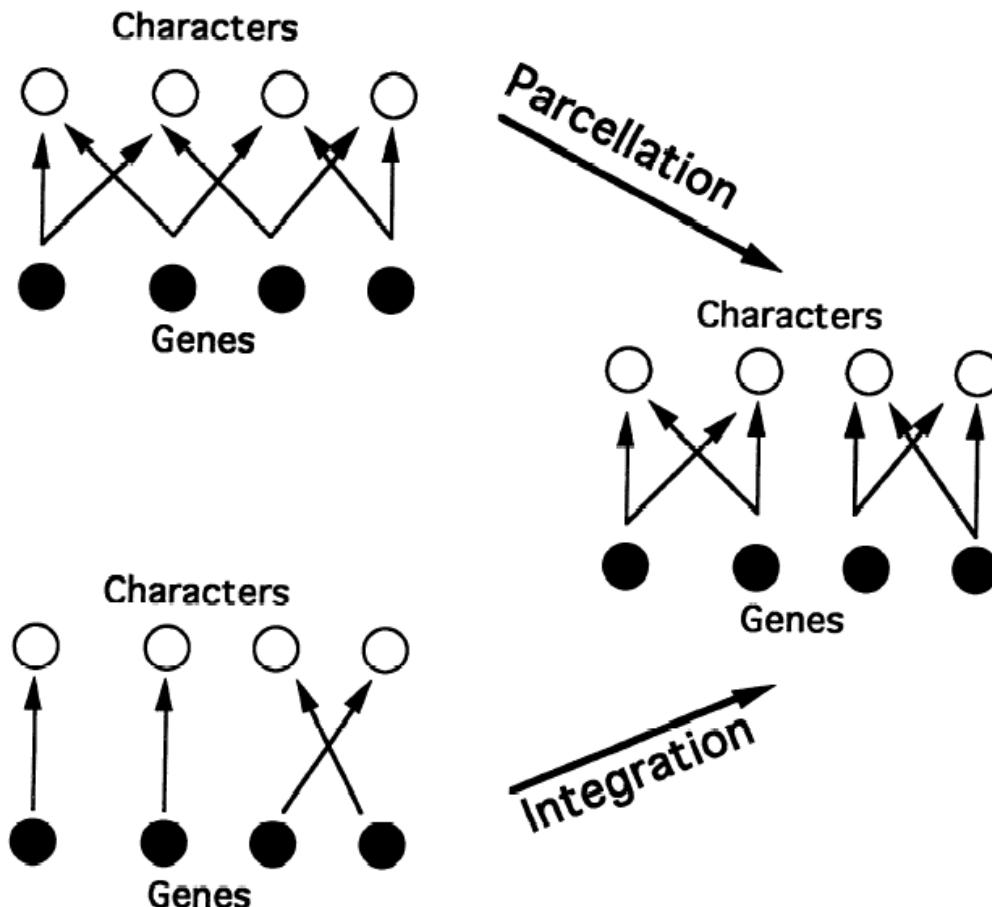


FIG. 2. Two ways of obtaining modularity. Parcellation consists of a differential suppression of pleiotropic effects between groups of characters. Modularity through integration consists in the selective acquisition of pleiotropy among characters from the same group.

Desenvolvimento ocorre através de uma série de módulos discretos que interagem.

Organismos são construídos de unidades que são coerentes dentro delas mesmas (correlacionadas) e ainda assim fazem parte de uma unidade maior (células em tecidos, tecidos em órgãos, órgãos em sistemas, ...) –

BIOLOGIA É HIERÁRQUICA

No desenvolvimento estes módulos incluem campos morfogenéticos (formação de membros), vias metabólicas, linhagens celulares, discos imaginais, segmentos dos insetos etc.

Modularidade permite que certas partes do corpo mudem sem interferir com outras partes

Modularidade permite 3 processos de alteração do desenvolvimento:

Dissociação, duplicação e divergência, e recrutamento (cooptação).

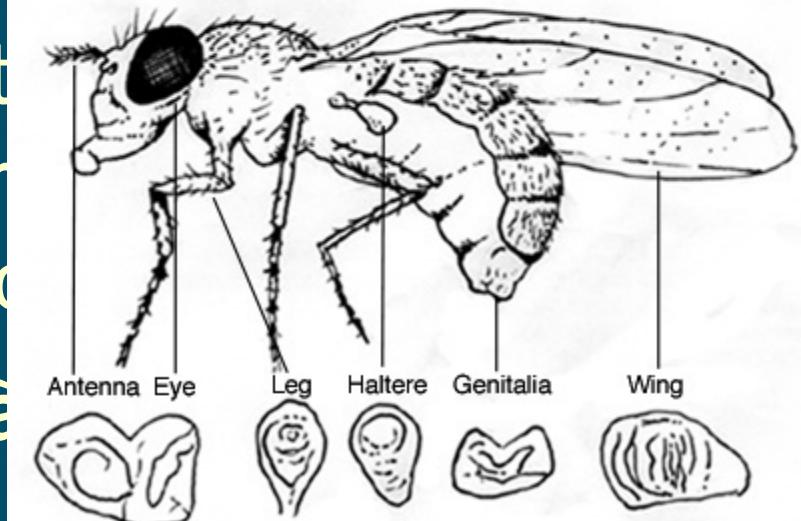
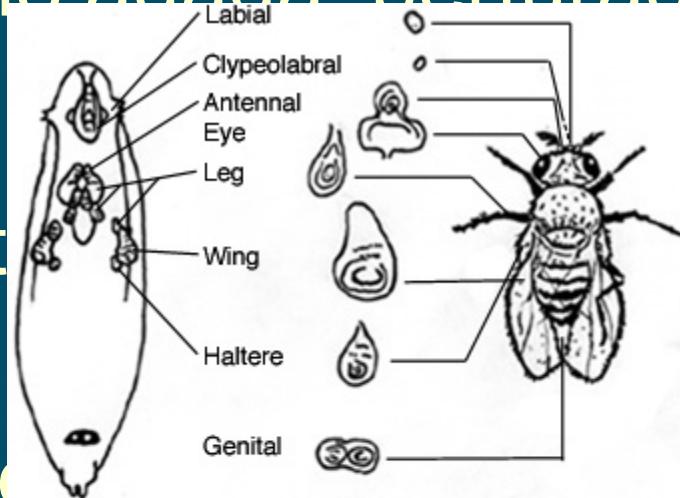
Duplicação e divergência = duplicação gera redundância permitindo divergência – duplicação gênica e divergência das funções após a duplicação (globinas, genes *hox*)

Co-optação (recrutamento) – um lápis pode servir para escrever, batucar, palitar o dente (eca_1!), limpar a orelha (eca_2!), como adaga perfurador

Mensagem: Nenhuma estrutura tem um propósito particular!

Ex. O gene “*engrailed*” é usado no embrião de *Drosophila*, mais tarde especificar os neurônios destinados a mais tarde ainda é usado para definir anterior/posterior para os discos

Adh no fígado e na formação



Em outras palavras, unidades pre-existentes podem ser recrutadas para novas funções (esta por sinal foi a solução de Darwin para a origem e evolução de caracteres morfológicos complexos e hoje é conhecida com pré-adaptação ou exaptação).

Algumas vezes caminhos metabólicos inteiros podem ser cooptados de um sistema para outro.

Transição réptil-mamíferos – cooptação de partes da mandíbula embrionária para criar os ossos do ouvido médio.

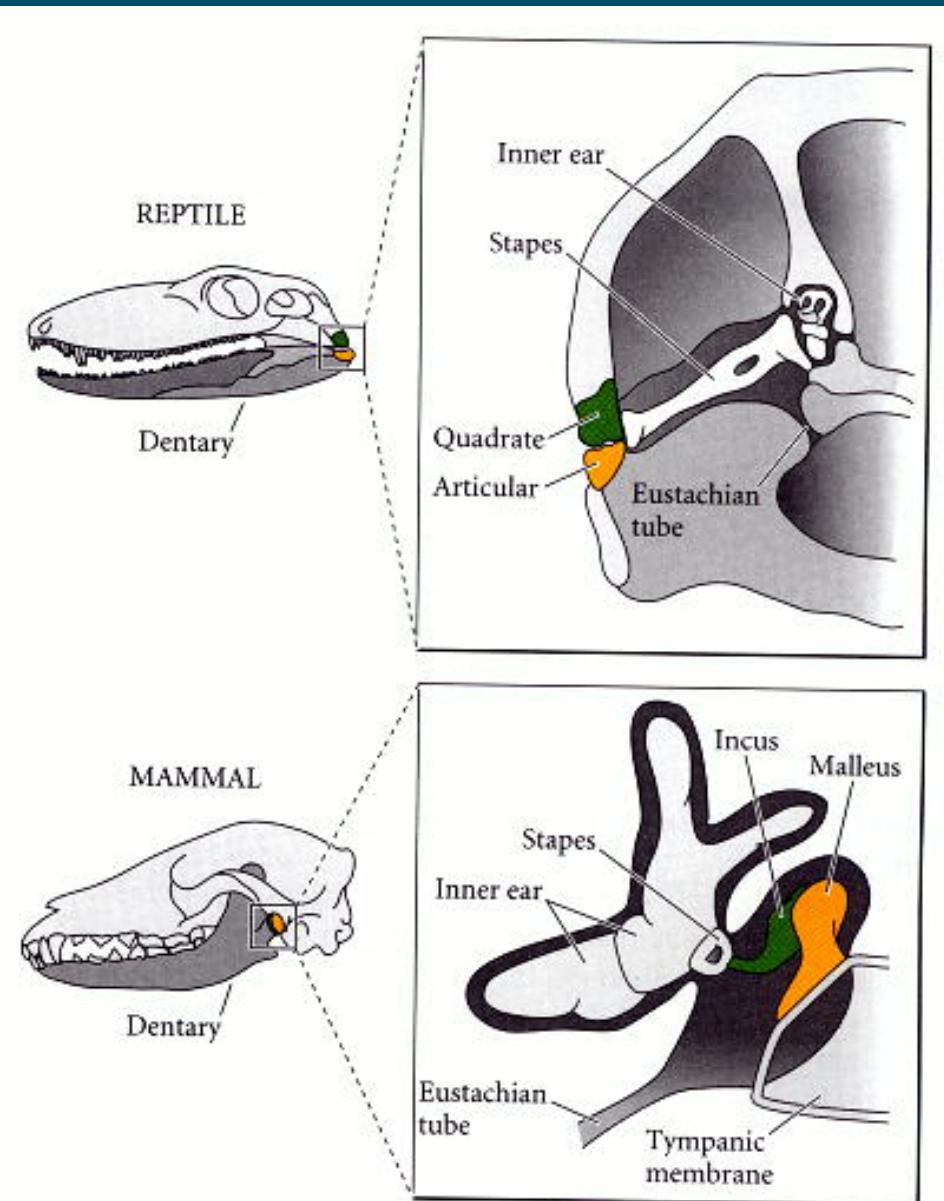


Figure 22.21. Evolution of the mammalian middle ear bones from the reptilian jaw. The quadrate and articular bones of reptiles were part of the lower jaw. Sound could be transmitted from these bones via the large stapes. When the dentary bone grew and took over the jaw functions of these two bones, the articular bone became the malleus (Martelo) and the quadrate bone became the incus (Bigorna). (After Romer 1949)

Primeiro os arcos branquiais dos peixes sem mandíbula tornaram-se as mandíbulas dos descendentes; milhões de anos depois os elementos (ossos) da parte superior da mandíbula foram transformados em martelo (malleus) e bigorna (incus), os ossos do ouvido médio dos mamíferos enquanto o dentário passou a ser a mandíbula dos Theria.

biologia:



Evolução do vôo em insetos

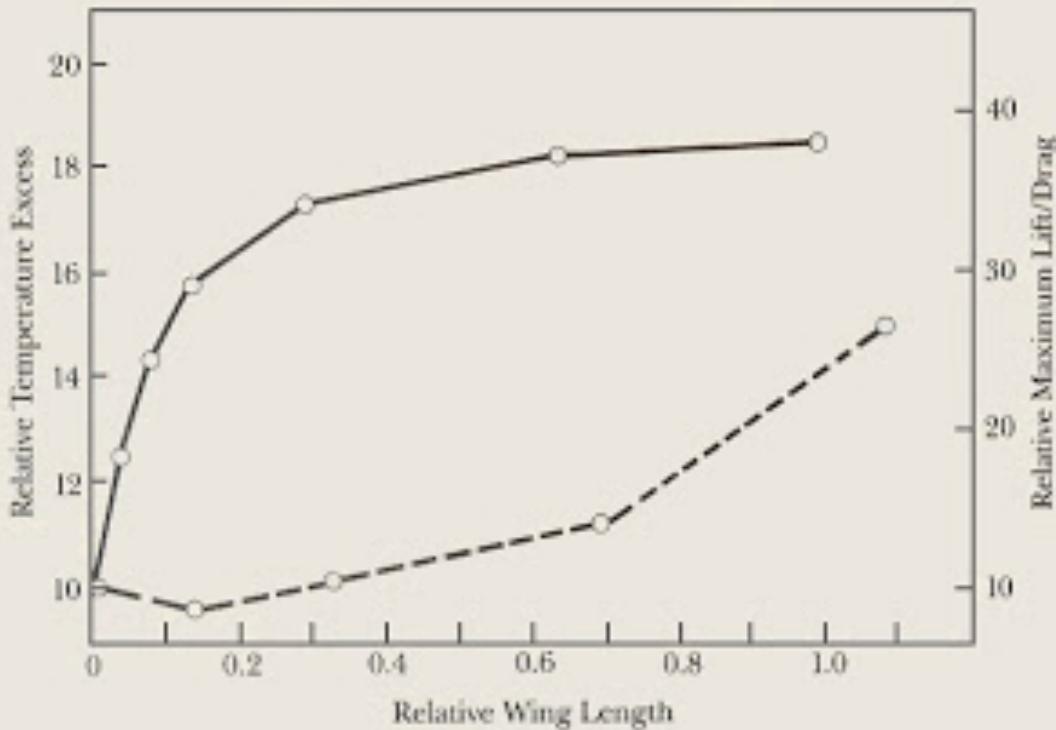
Evolution, 39(3), 1985, pp. 488–504

AERODYNAMICS, THERMOREGULATION, AND THE EVOLUTION OF INSECT WINGS: DIFFERENTIAL SCALING AND EVOLUTIONARY CHANGE

JOEL G. KINGSOLVER¹ AND M. A. R. KOEHL

Department of Zoology, University of California, Berkeley, CA 94720

The Evolution of Insect Wings



Summary.—We examine several aerodynamic and thermoregulatory hypotheses about possible adaptive factors in the evolution of wings from small winglets in insects. Using physical models of Paleozoic insects in a wind tunnel, we explore the potential effects of wings for increasing gliding distance, increasing dispersal distance during parachuting, improving attitude control or stability, and elevating body temperatures during thermoregulation. The effects of body size and shape, wing length, number, and venation, and meteorological conditions are considered. Hypotheses consistent with both fixed and moveable wing articulations are examined.

Short wings have no significant effects on any of the aerodynamic characteristics, relative to wingless models, while large wings do have significant effects. In contrast, short wings have large thermoregulatory effects relative to wingless models, but further increases in wing length do not significantly affect thermoregulatory performance. At any body size, there is a wing length below which there are significant thermoregulatory effects of increasing wing length, and above which there are significant aerodynamic effects of increasing wing length. The relative wing length at which this transition occurs decreases with increasing body size.

These results suggest that there could be no effective selection for increasing wing length in wingless or short-winged insects in relation to increased aerodynamic capacity. Our results are consistent with the hypothesis that insect wings initially served a thermoregulatory function and were used for aerodynamic functions only at larger wing lengths and/or body sizes. Thus, we propose that thermoregulation was the primary adaptive factor in the early evolution of wings that preadapted them for the subsequent evolution of flight. Our results illustrate an evolutionary mechanism in which a purely isometric change in body size may produce a qualitative change in the function of a given structure. We propose a hypothesis in which the transition from thermoregulatory to aerodynamic function for wings involved only isometric changes in body size and argue that changes in body form were not a prerequisite for this major evolutionary change in function.

Por último - Dissociação = Heterocronia e alometria

Heterocronia - (do Grego "hetero" significando “outro” ou “diferente” e “chronos” significando “tempo”) descreve a mudança no tempo dos eventos ontogenéticos ou nas taxas de desenvolvimento entre duas linhagens quaisquer.

“Alterando as taxas de desenvolvimento somático e reprodutivo”

Por último - Dissociação = Heterocronia e alometria

Heterocronia –

Estas mudanças podem ser resultado de mudanças genéticas relativamente pequenas, incluindo mudanças que não sejam nem mesmo na sequência do DNA, mas no tempo de um gene ser ligado ou desligado durante o desenvolvimento por exemplo via metilação das bases



quente

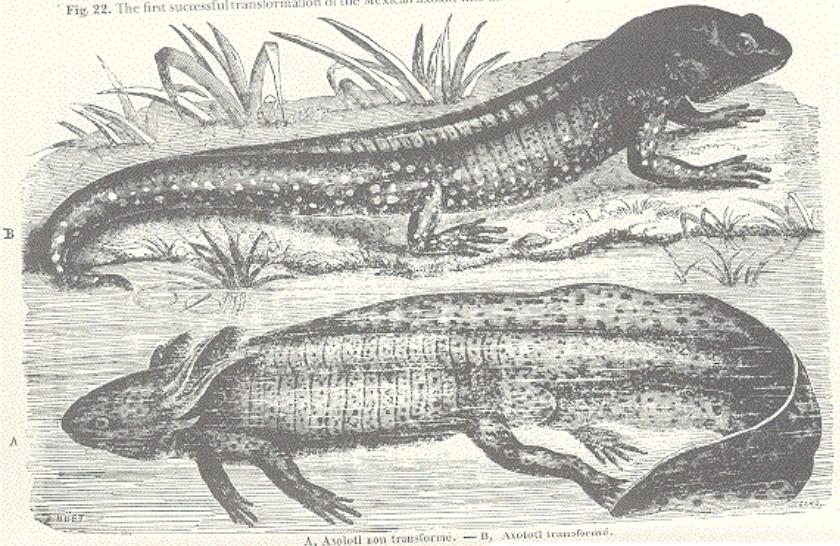
eastern tiger salamander (*Ambystoma tigrinum*) - depende do ambiente

frio

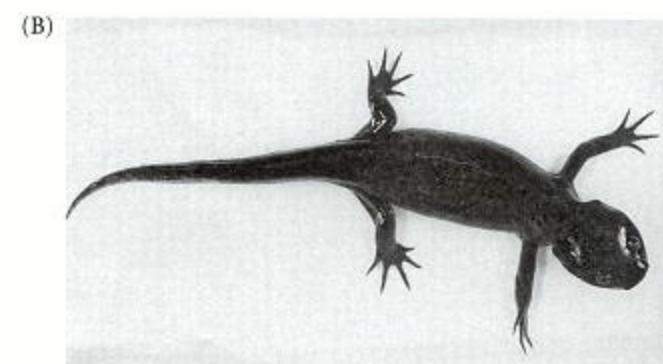
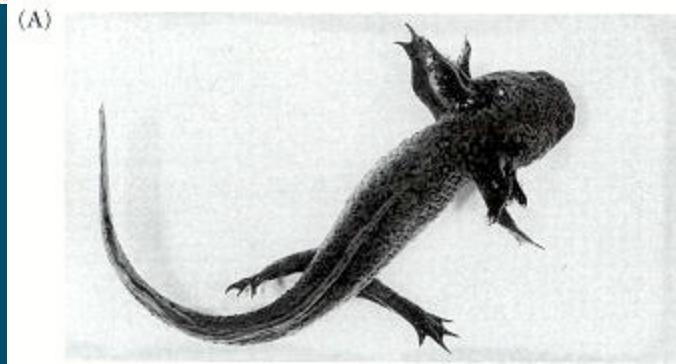
**Neotenia –
somático
retardado,
reprodutivo
inalterado**



Fig. 22. The first successful transformation of the Mexican axolotl into an adult *Ambystoma*. (From Duméril, 1867.)



Ambystoma mexicanum
Não secreta mas
responde a tirotropina

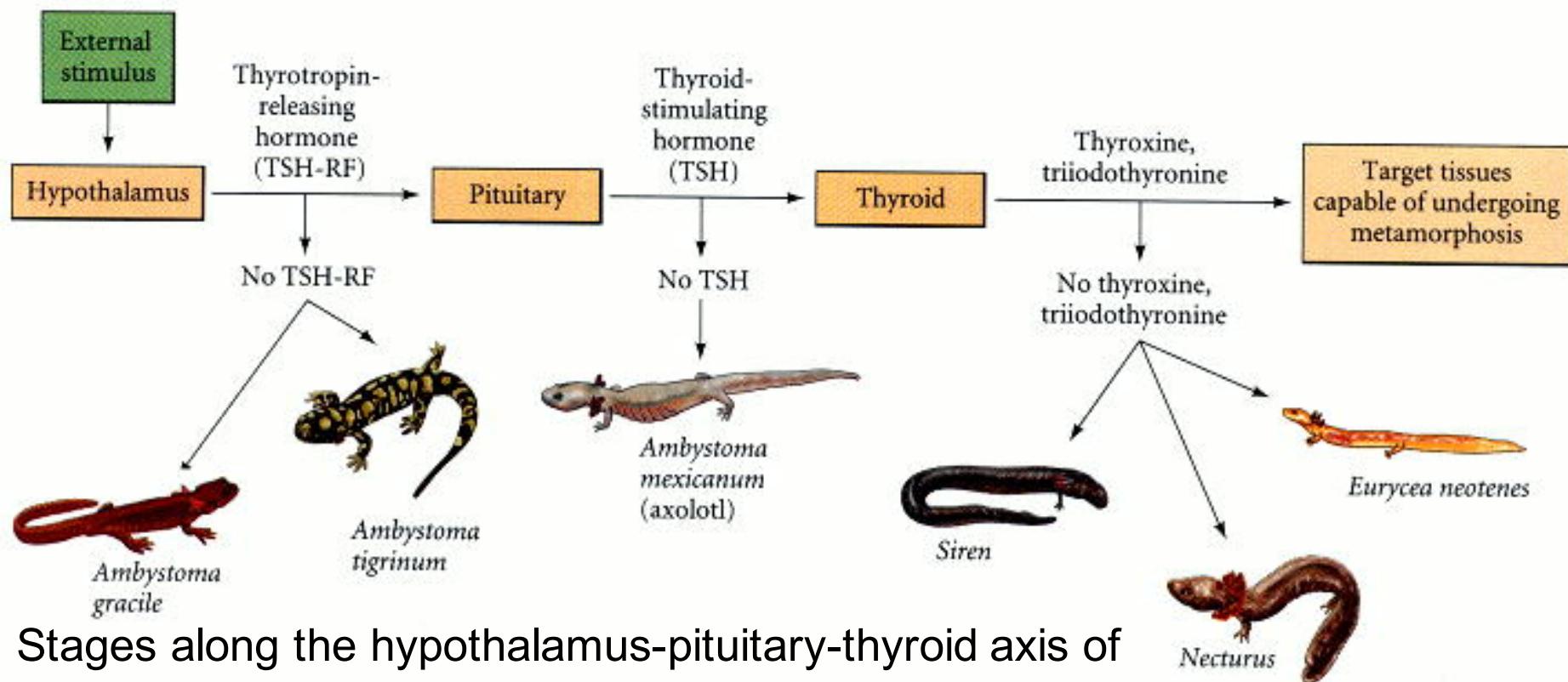


Siren
Não responde



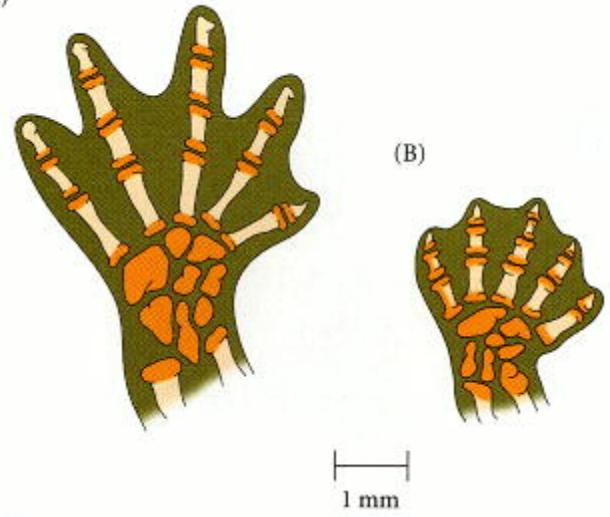
Necturus
Não responde





Stages along the hypothalamus-pituitary-thyroid axis of salamanders at which various species are thought to have blocked metamorphosis. Normally, thyrotropin-releasing factor from the hypothalamus causes the release of thyrotropin from the pituitary. Thyrotropin causes the thyroid gland to synthesize and release T₃ and T₄. These thyroid hormones bind to their receptors in competent tissues. *Ambystoma tigrinum* and *A. gracile* have defects in thyrotropin-releasing hormone, while *A. mexicanum* has a defect in thyrotropin production. *Eurycea*, *Necturus*, and *Siren* appear to have a receptor defect in the thyroid hormone-responsive tissues. *Eurycea* will metamorphose when exposed to extremely high concentrations of thyroxine, while *Necturus* and *Siren* do not respond to any dose. (After Frieden 1981.)

(A)



(B)

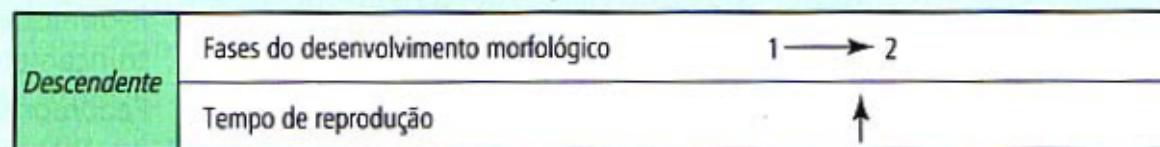
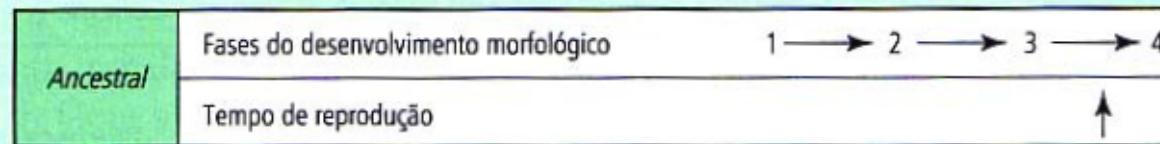
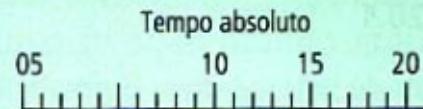


© 1980 David Wake

PROGÊNESE – somático normal, reprodutivo acelerado

Figure 22.17. Salamander heterochrony. The progenesis of limb development in *Bolitoglossa* can create a tree-climbing salamander. (A) Foot of an adult *B. rostratus*, a terrestrial salamander. (B) Foot of an adult *B. occidentalis*, an arboreal salamander. The feet, skull, and body size of *B. occidentalis* adults resemble those of juvenile *B. rostratus*. Since the digits have not expanded past the webbing, the feet can produce suction to climb trees. (After Alberch and Alberch 1981.)

(a) Progênese, causando pedomorfose (por truncamento)



(b) Neotenia, causando pedomorfose (por retardamento)

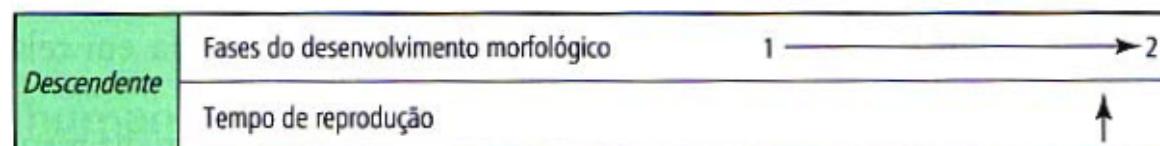
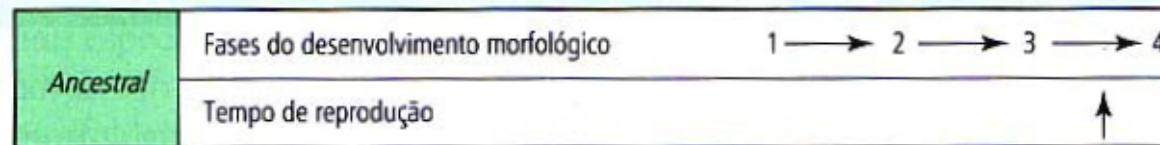
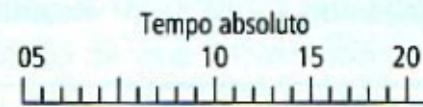


Figura 20.3

Pedomorfose é quando uma espécie descendente reproduz em uma fase morfológica que era juvenil em seus ancestrais, e pode ser causada por (a) progênese, em que a reprodução ocorre mais cedo em tempo absoluto ou (b) neotenia, em que a reprodução ocorre na mesma idade, mas o desenvolvimento somático fica retardado.

Heterocronia

Tempo do desenvolvimento	Nome do processo evolutivo	Resultado morfológico
Somático	Reprodutivo	
Acelerado	Inalterado	Aceleração
Inalterado	Acelerado	Progenesis
Retardado	Inalterado	Neotenia
Inalterado	Retardado	Hipermorfose

Pedomorfose = Presença de características larvares ou juvenis na fase adulta de um organismo

Desenvolvimento direto

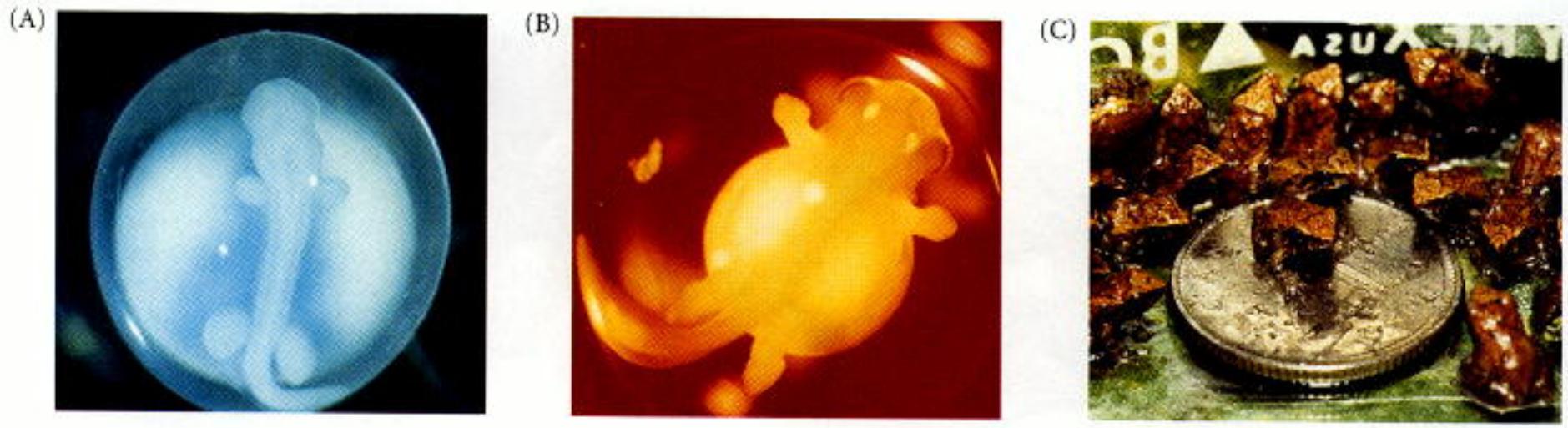
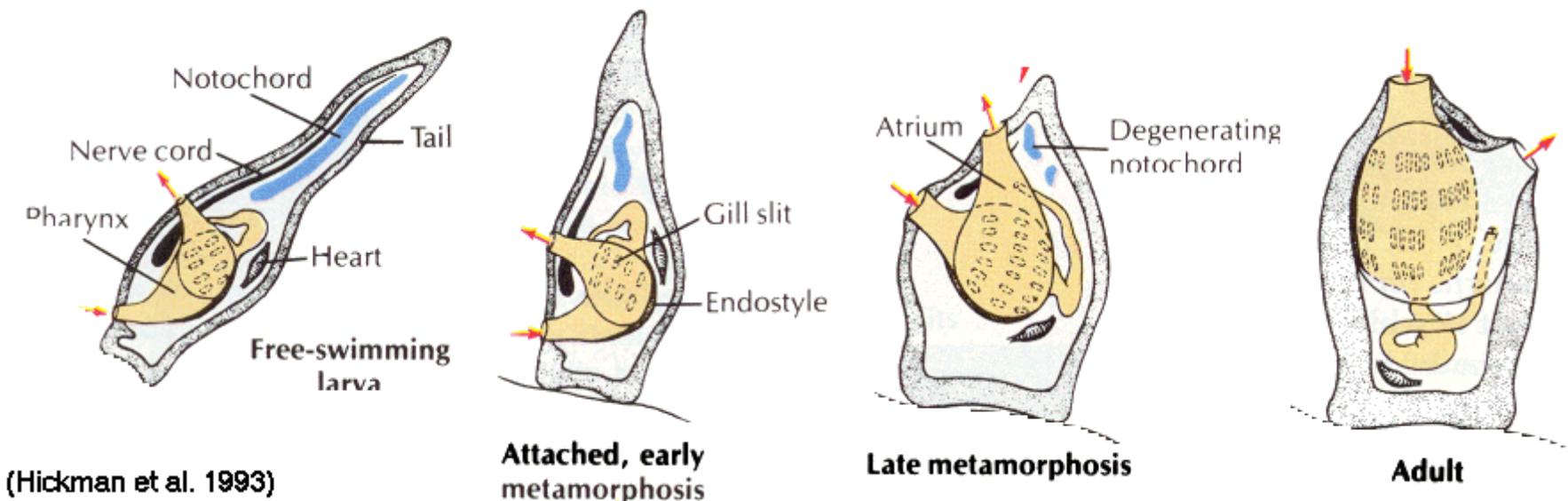
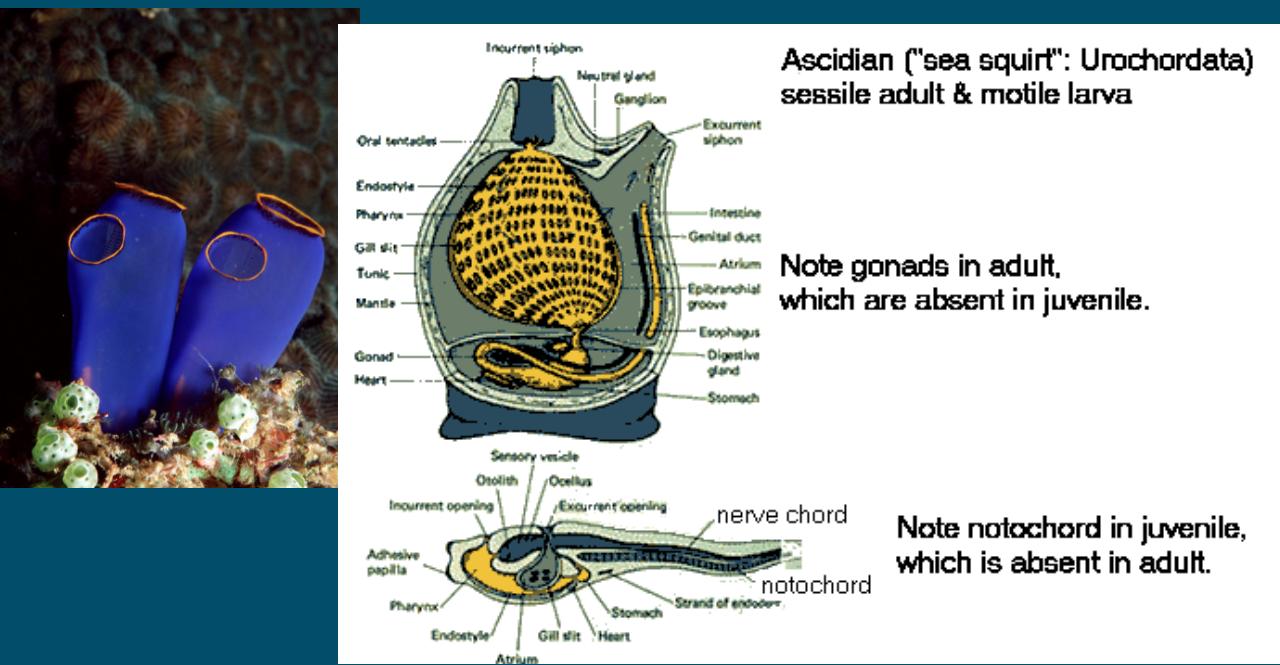


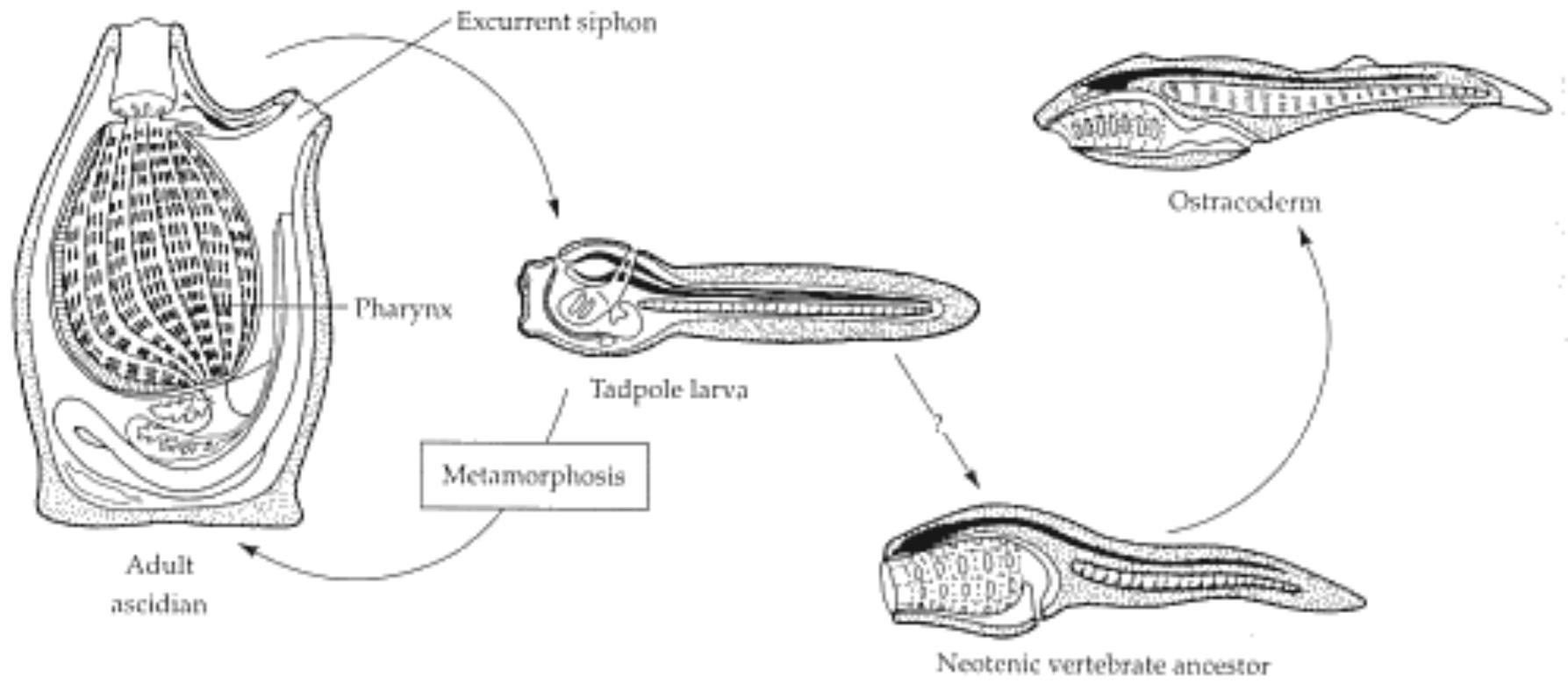
Figure 18.10. Direct development of the frog *Eleutherodactylus coqui*. (A) Limb buds are seen as the frog develops on the yolk. (B) As the yolk is used up, the limb buds are easily seen. (C) Three weeks after fertilization, tiny froglets hatch. They are seen here in a petri dish and on a Canadian dime. (Photographs courtesy of R. P. Elinson.)



Urochordados – ascídeos



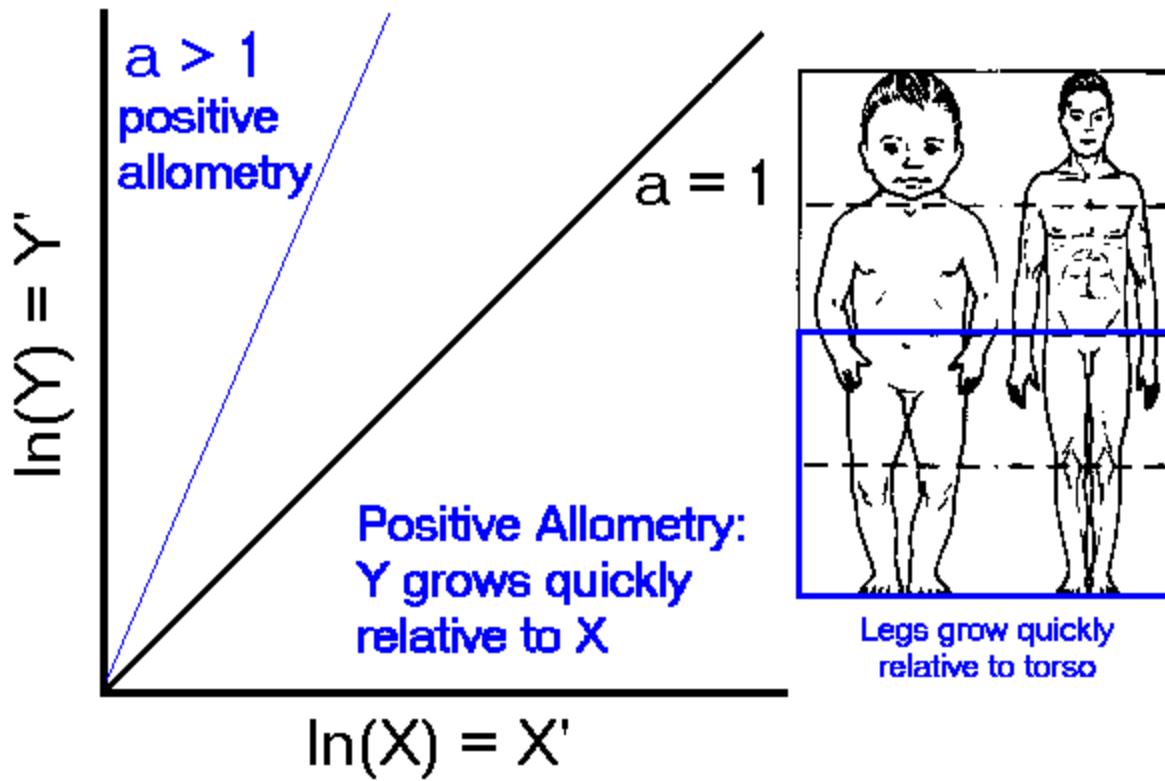
Hipótese de Garstang - Cordados teriam evoluído das larvas móveis de urocordados (com notocorda) através de um processos heterocrônico (progenese)



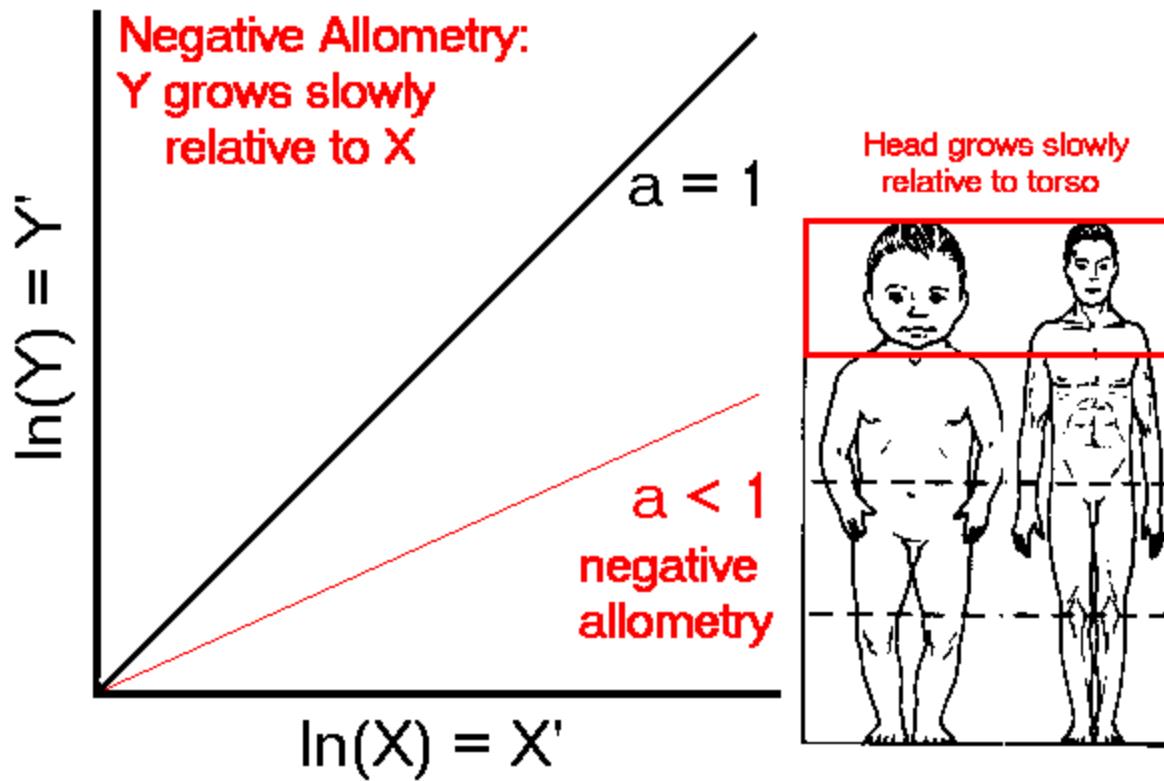
Hipótese de Garstang - Ascidias atuais (Subphylum Urochordata) tipicamente têm uma larva móvel que sofre metamorfose para a vida séssil adulta. Esta larva tem características dos Chordata, incluindo uma notochorda, branquias faríngicas, e uma cauda pós-anal. Garstang sugeriu que o desenvolvimento de maturidade sexual em uma linhagem não metamorfoseada de tunicados pode ter dado origem ao ancestral proto-chordado de cordados típicos como os *Amphioxus* (Subfilo Cephalochordata), ou mesmo dos primeiros Vertebrata (Ostracodermos).

Alometria – ocorre quando diferentes partes de um organismo têm taxas de crescimento diferentes

$y = b x^a$, (onde X e Y são dois caracteres mensuráveis, b é o valor de Y quando $x = 0$ (note que se a regressão parte da origem isto quer dizer que $X=0$ então $Y= 0$ tb.). Esta relação entre duas características é frequentemente não linear, tanto que a equação acima pode ser transformada para uma escala logarítmica: $\log y = a(\log x) + \log b$ ($a = 1$, isometria; $a < 1$, alometria negativa; $a > 1$, alometria positiva)



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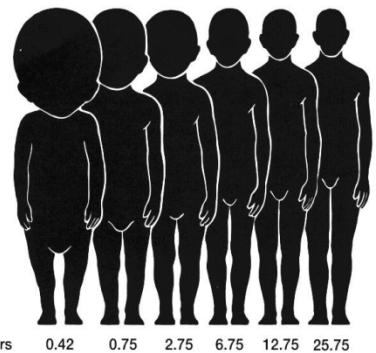
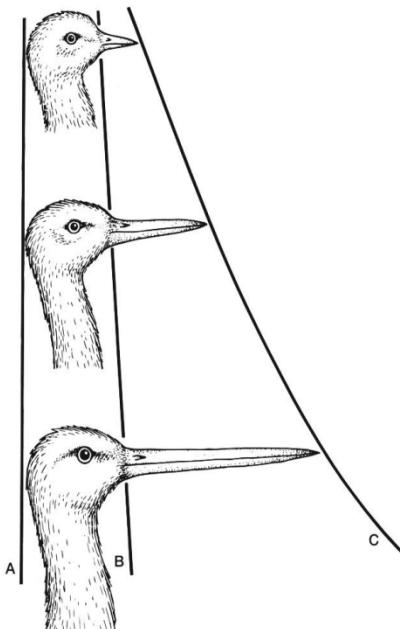


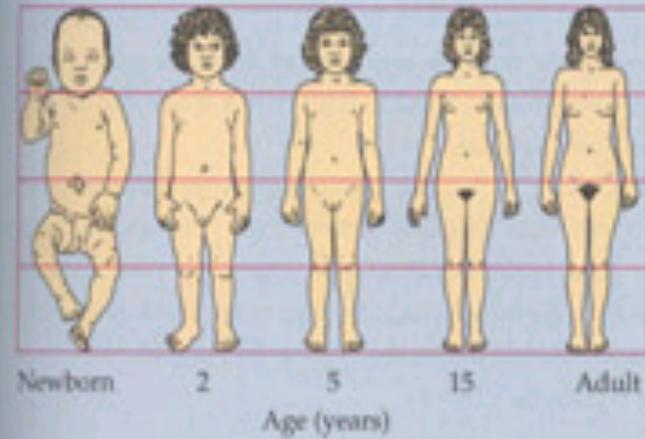
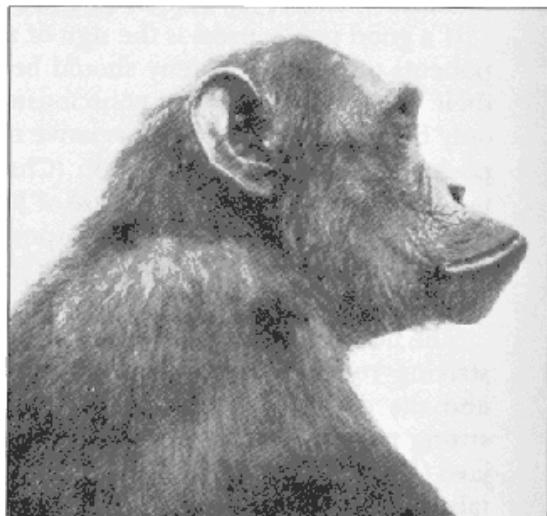
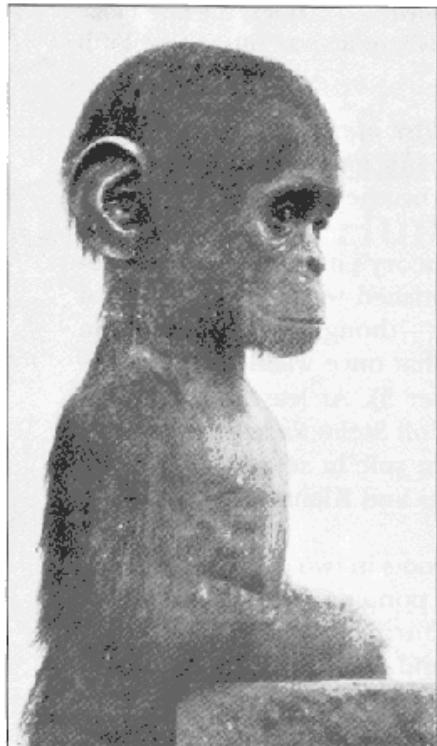
FIGURE 4.9 Allometry in human development. During growth, a person changes shape as well as size. As an infant grows, its head makes up less of its overall height and its trunk and limbs make up more. Ages, in years, are indicated beneath each figure.

From McMahon and Bonner; modified from Medawar.

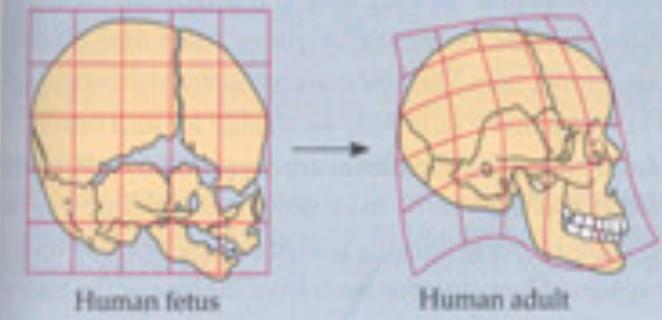
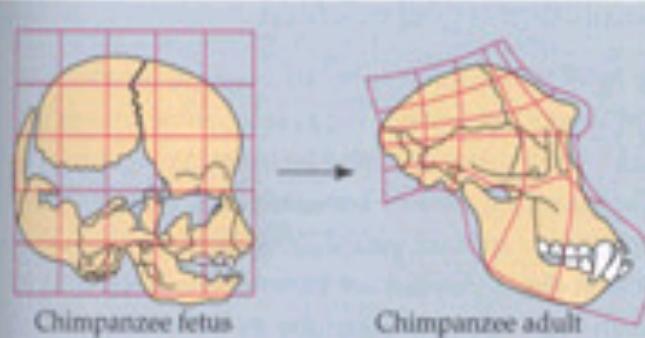


head of a black-tailed
tween skull length (lines
are compared. Notice
bill grows in length as
the skull is shorter than the
adult

"Of all animal pictures known to me,
this is the most manlike." (Naef, 1926)



(a) Differential growth rates in a human



(b) Comparison of chimpanzee and human skull growth

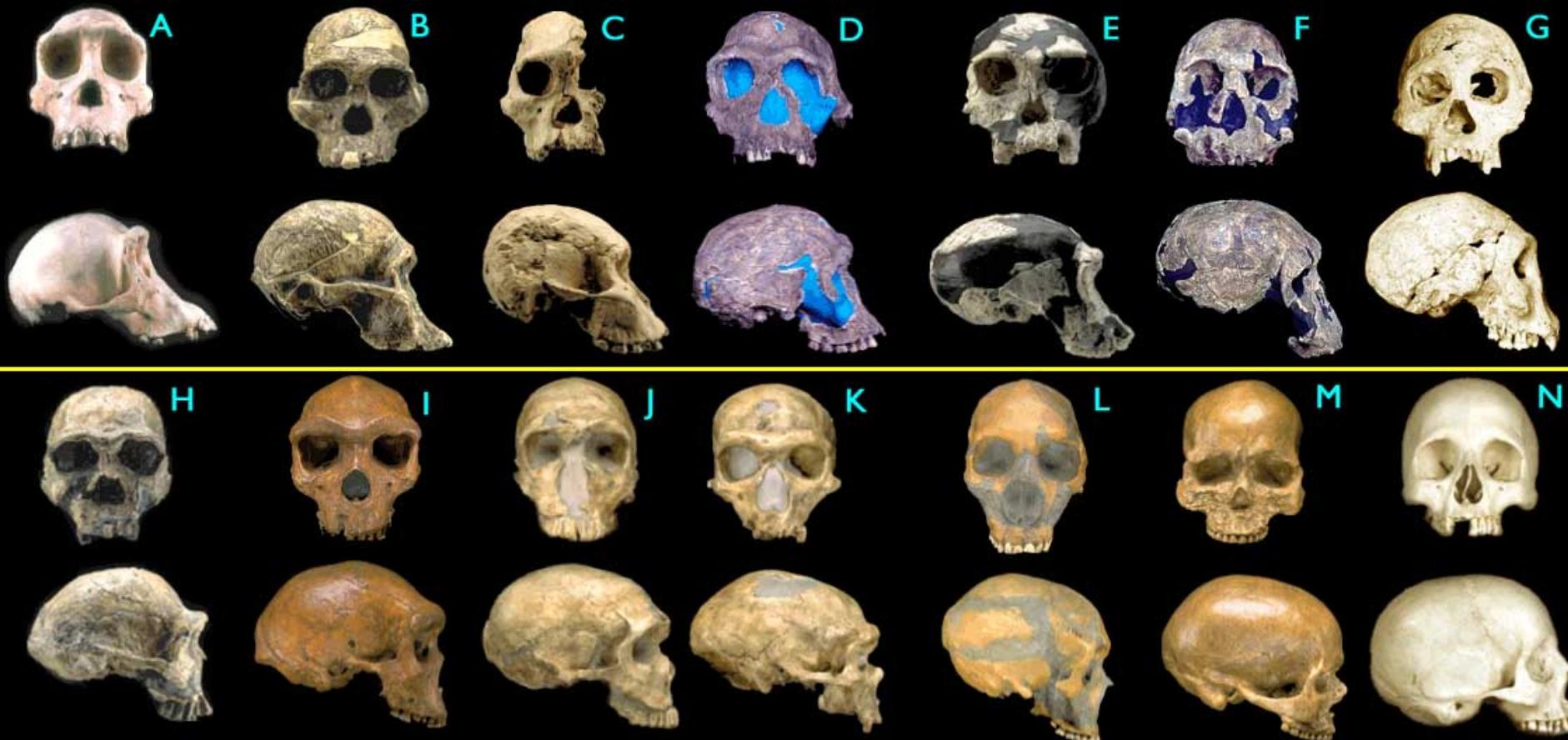


Figure 1.4.4. Fossil hominid skulls. Some of the figures have been modified for ease of comparison (only left-right mirroring or removal of a jawbone). (Images © 2000 Smithsonian Institution.)

(A) *Pan troglodytes*, chimpanzee, modern; (B) *Australopithecus africanus*, STS 5, 2.6 My; (C) *Australopithecus africanus*, STS 71, 2.5 My; (D) *Homo habilis*, KNM-ER 1813, 1.9 My; (E) *Homo habilis*, OH24, 1.8 My; (F) *Homo rudolfensis*, KNM-ER 1470, 1.8 My; (G) *Homo erectus*, Dmanisi cranium D2700, 1.75 My; (H) *Homo ergaster* (early *H. erectus*), KNM-ER 3733, 1.75 My; (I) *Homo heidelbergensis*, "Rhodesia man," 300,000 - 125,000 y; (J) *Homo sapiens neanderthalensis*, La Ferrassie 1, 70,000 y; (K) *Homo sapiens neanderthalensis*, La Chappelle-aux-Saints, 60,000 y; (L) *Homo sapiens neanderthalensis*, Le Moustier, 45,000 y; (M) *Homo sapiens sapiens*, Cro-Magnon I, 30,000 y; (N) *Homo sapiens sapiens*, modern

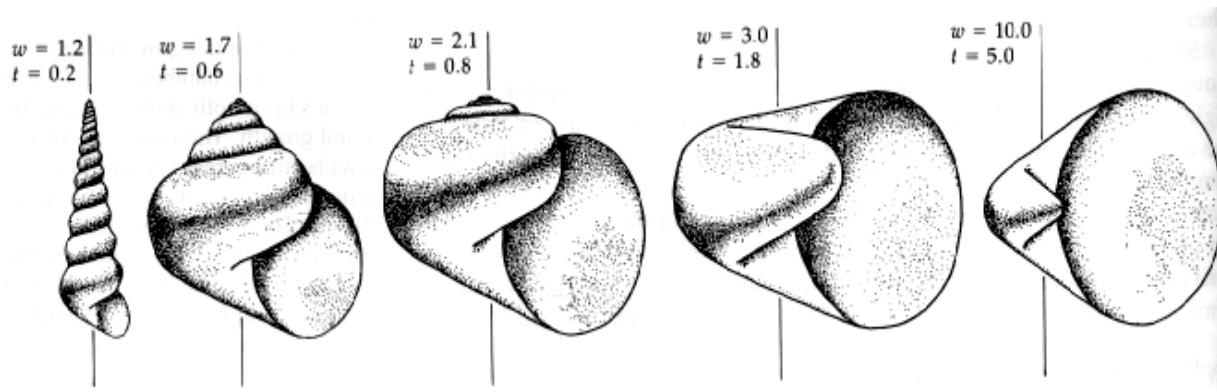


FIGURA 1. Hypothetical snail shells drawn by computer. Only two of the four parameters, the rate of curve enlargement (w) and the rate of curve translation (t) are varied in this series. (From Raup, 1962.)



FIGURA 3. Specimens of the fiddler crab, *Uca pugnax*. The allometric growth occurs only in one of the male claws. In females (not shown), both claws retain isometric growth. (From Swarthmore College Marine Biology laboratory).

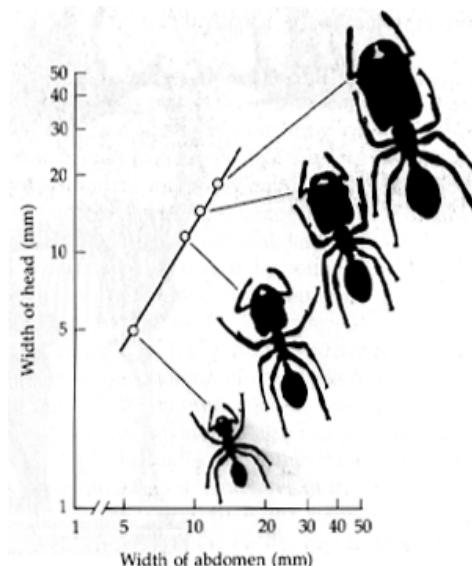


FIGURE 4. Allometric relationship between head size and body size in the ant *Pheidole instabilis*. Note the logarithmic axes of the graph. (After Raff and Kaufman, 1983.)

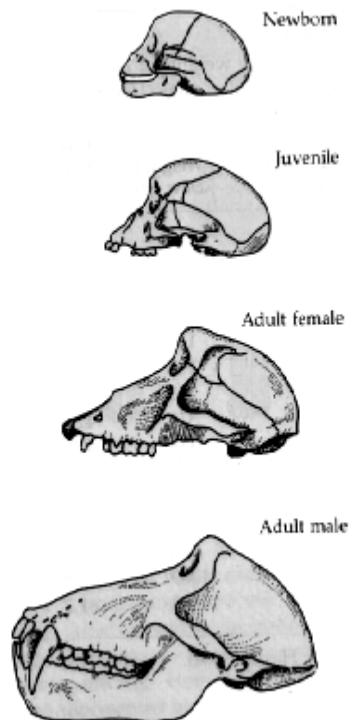


FIGURA 2. Allometry in the baboon head. Skulls from individuals of various ages show the enormous increase of facial structures relative to those of the head. (After Huxley, 1932.)

Pode-se mostrar que o coeficiente alométrico é variável, herdável e portanto pode ser selecionado - adaptativo

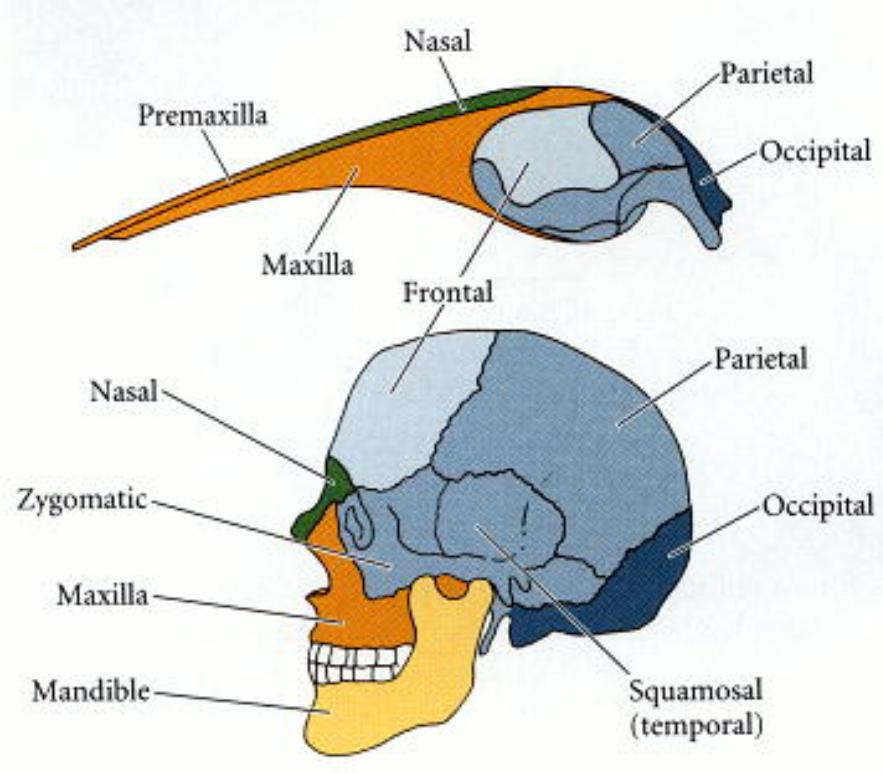


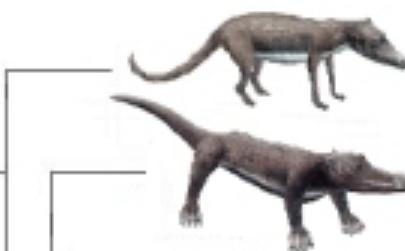
Figure 22.18. Allometric growth in the whale head. An adult human skull is shown for comparison. The whale's upper jaw (maxilla) has pushed forward, causing the nose to move to the top of the skull. (The premaxilla is present in the early human fetus, but it fuses with the maxilla by the end of the third month of gestation. The human premaxilla was discovered by Goethe, among others, in 1786.) (After Slijper 1962.)

65 60 55 50 45 40 35 30 million years ago

Palaeocene Eocene Oligocene Miocene-Recent

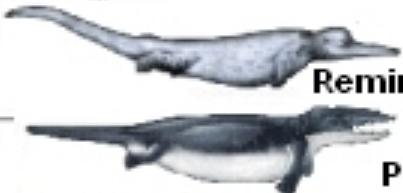
Artiodactyla

Pakicetidae



Ambulocetidae

Remingtonocetidae



Protocetidae



Basilosauridae



Dorudontidae

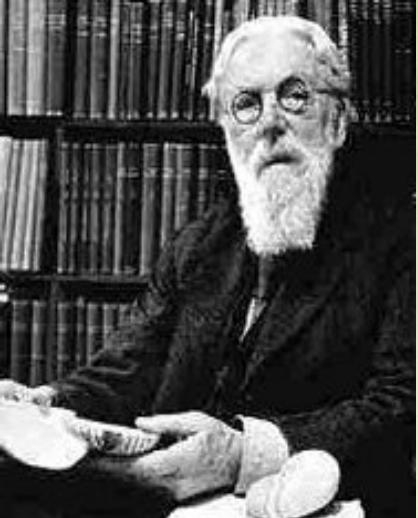


Mysticeti



Odontoceti





ON GROWTH AND FORM

The Complete Revised Edition



D'Arcy Wentworth Thompson

1917

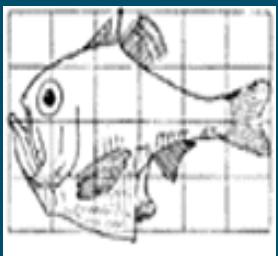
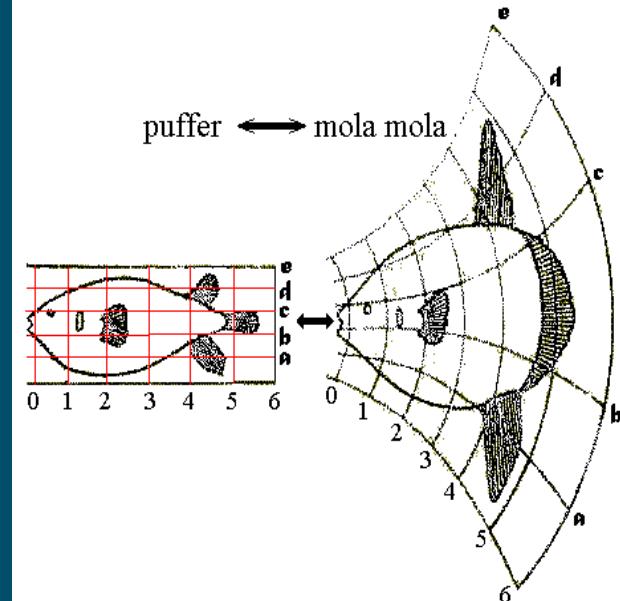


Fig. 517. *Aggregationus Olfersii*.

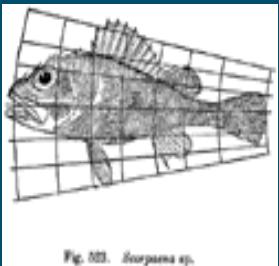


Fig. 518. *Sternoptyx diaphana*.

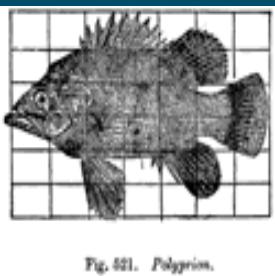


Fig. 519. *Scarus sp.*

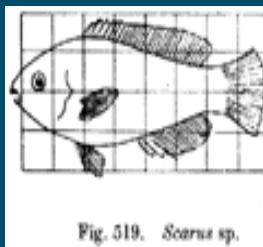


Fig. 520. *Pomacanthus*.



Fig. 521. *Polyprion*.

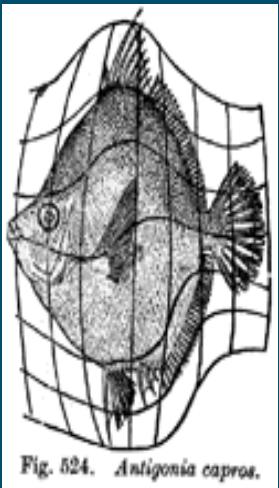


Fig. 522. *Pseudoprionotus altus*.

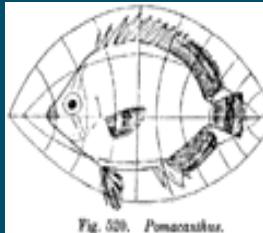
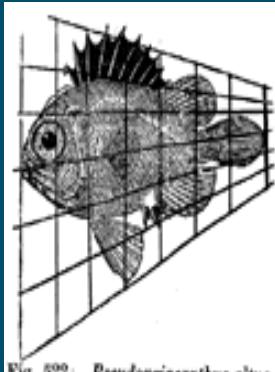
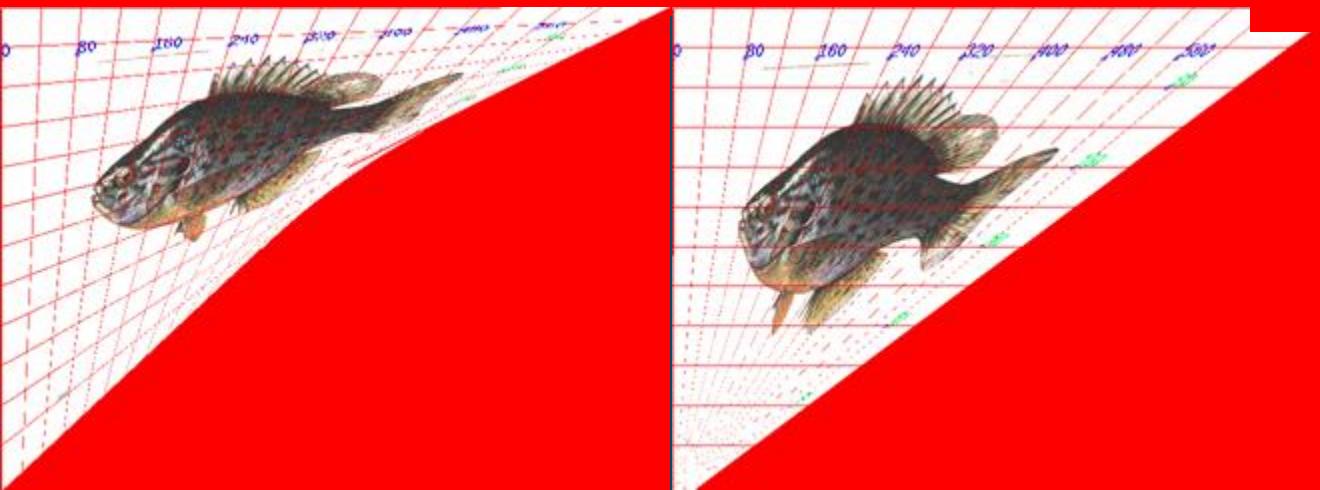
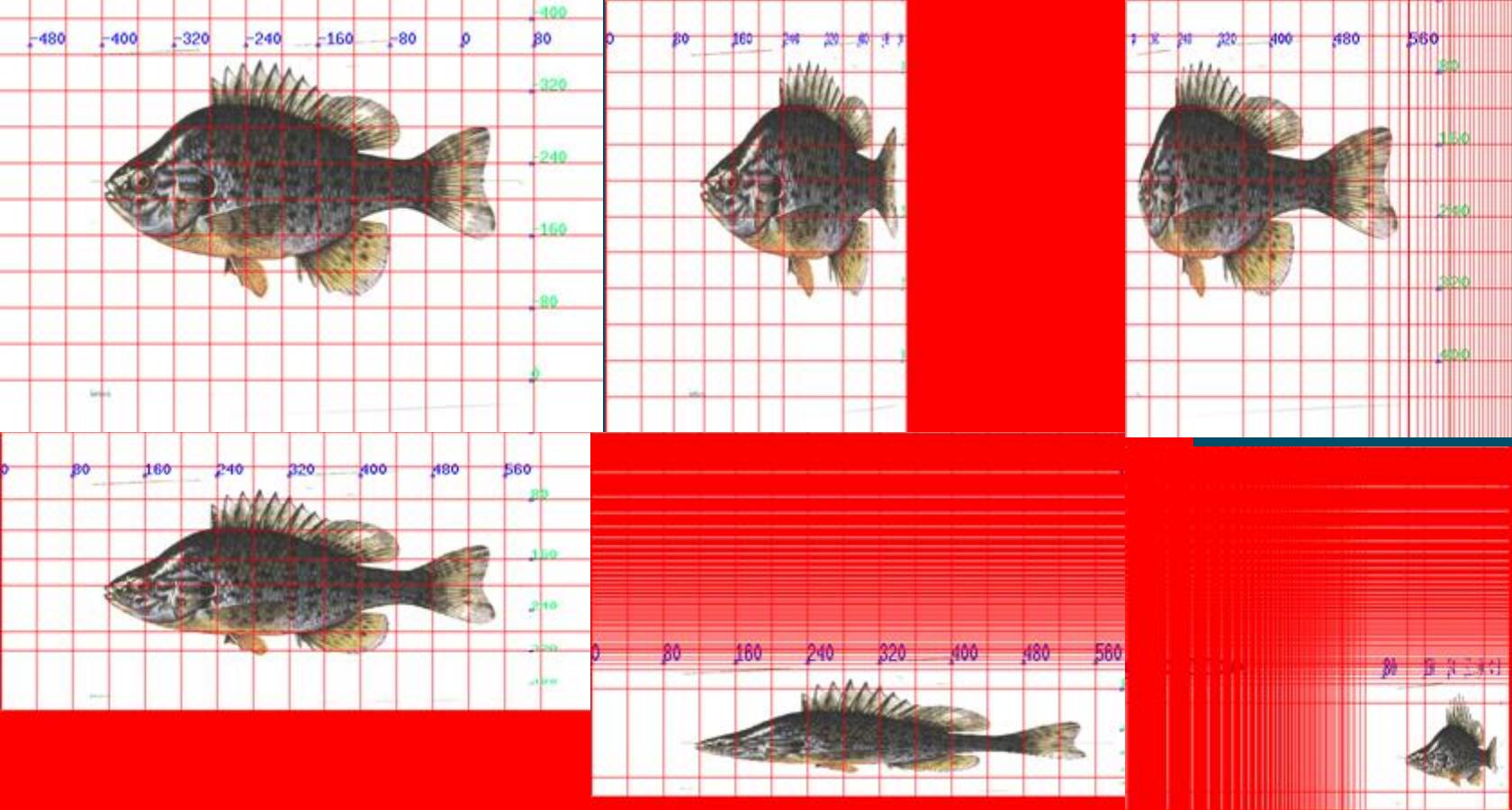


Fig. 524. *Antigonia capros*.





Restrições evolutivas = Qualquer limitação no curso ou resultado da evolução

podem ser relativas (a variação/covariância genética) ou absolutas

Físicas, mecânicas, químicas, dos materiais,

Um estudo de caso – Evolução morfológica em macacos Neotropicais

BMC Evolutionary Biology



Research article

Open Access

When size makes a difference: allometry, life-history and morphological evolution of capuchins (*Cebus*) and squirrels (*Saimiri*) monkeys (Cebinae, Platyrhini)

Gabriel Marroig*

Address: Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, CP 11.461, CEP 05422-970, São Paulo, Brasil

Email: Gabriel Marroig* - gmarroig@usp.br

* Corresponding author

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Cebus (macaco prego)

2 kg até 6 kg



Jardin Zoologique
de la Ville de Lyon

Saimiri (macaco de cheiro)

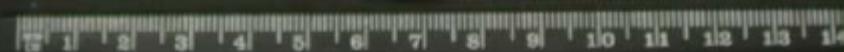
Cerca de 900 g



AB 4312
Saimiri



AB 4312
Saimiri



AB 4312



AB 5211
Saimiri



Saimiri Adult

Mini series – 3 Saimiri + 1
Cebus



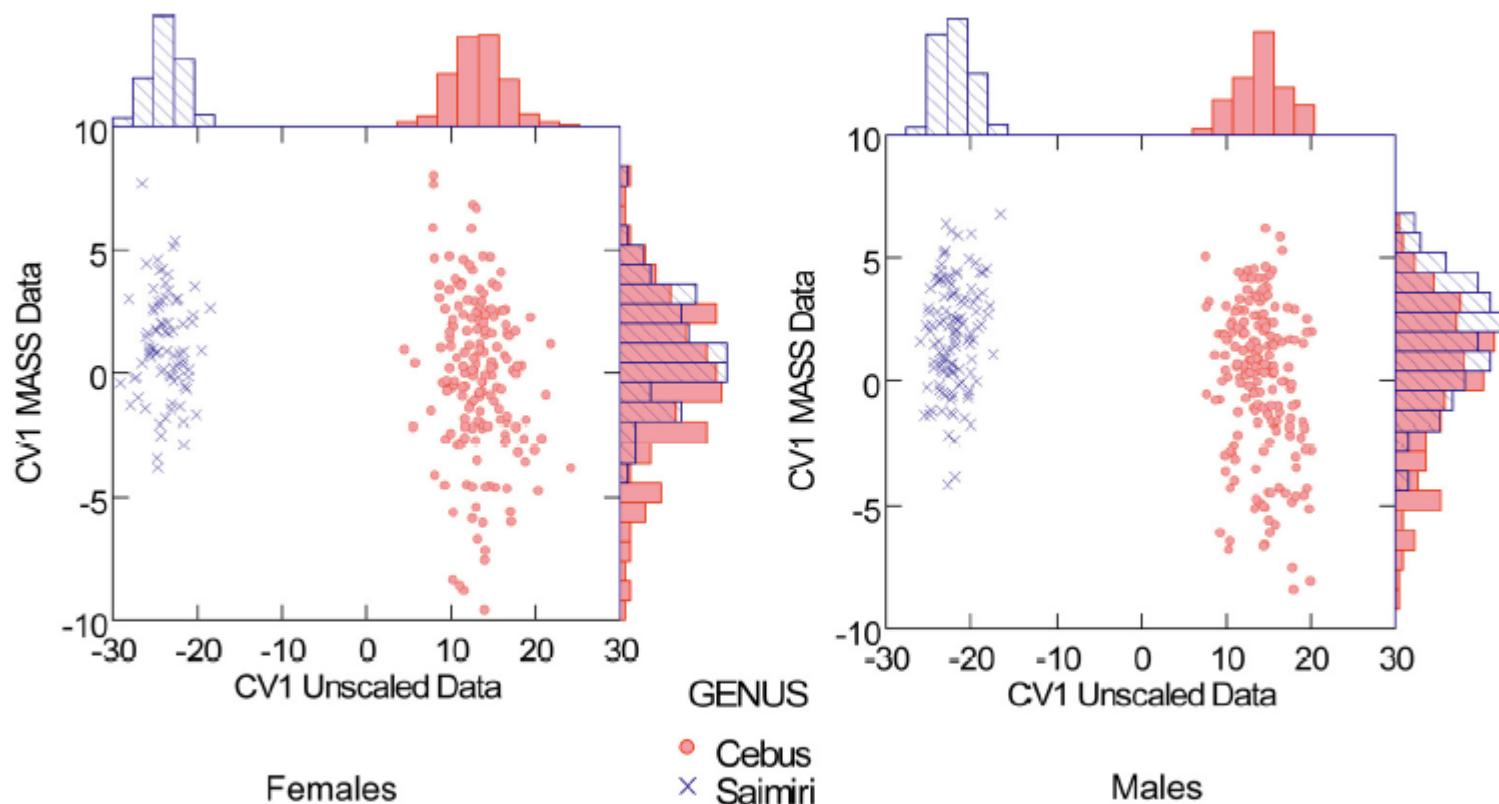
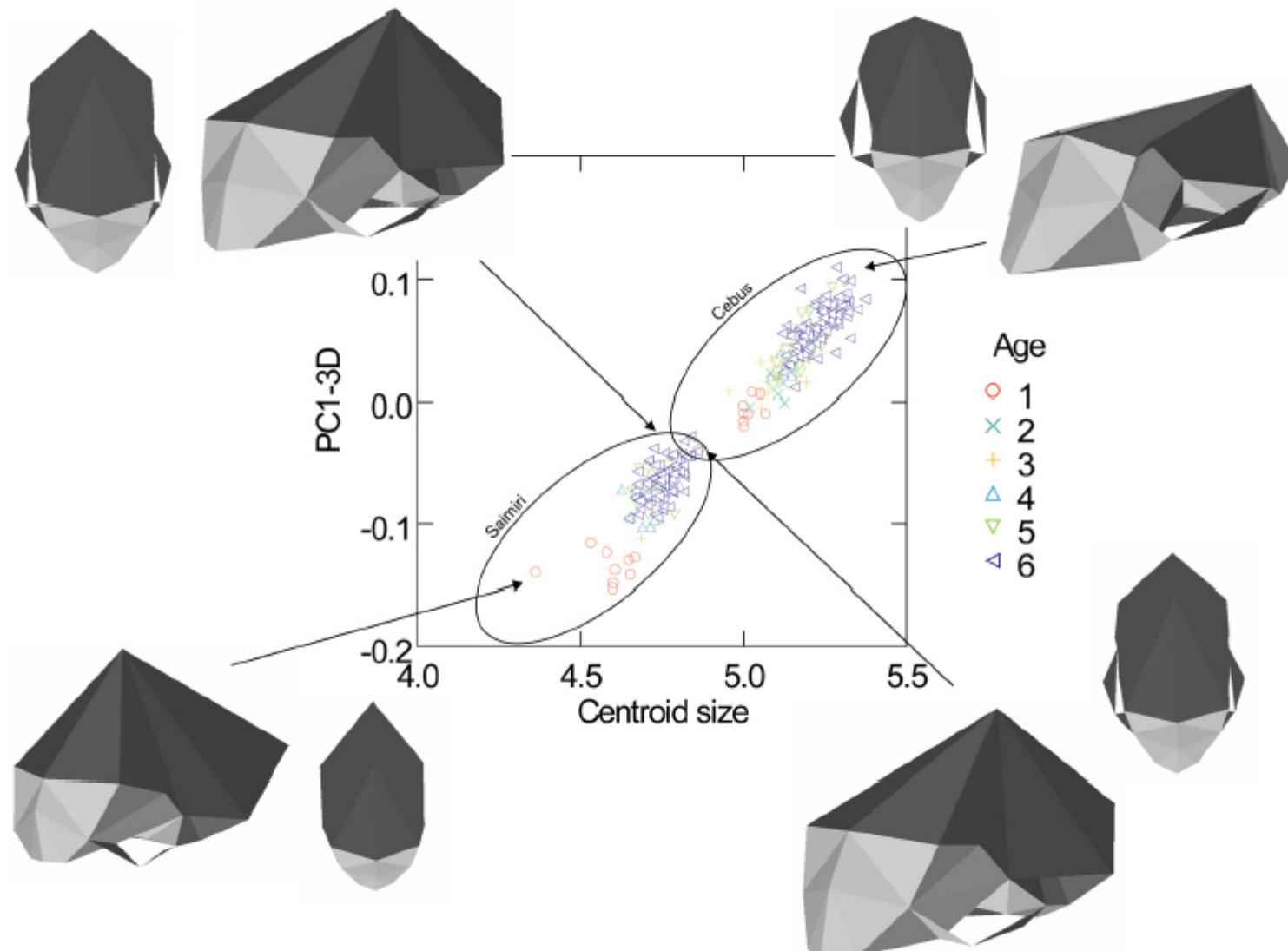
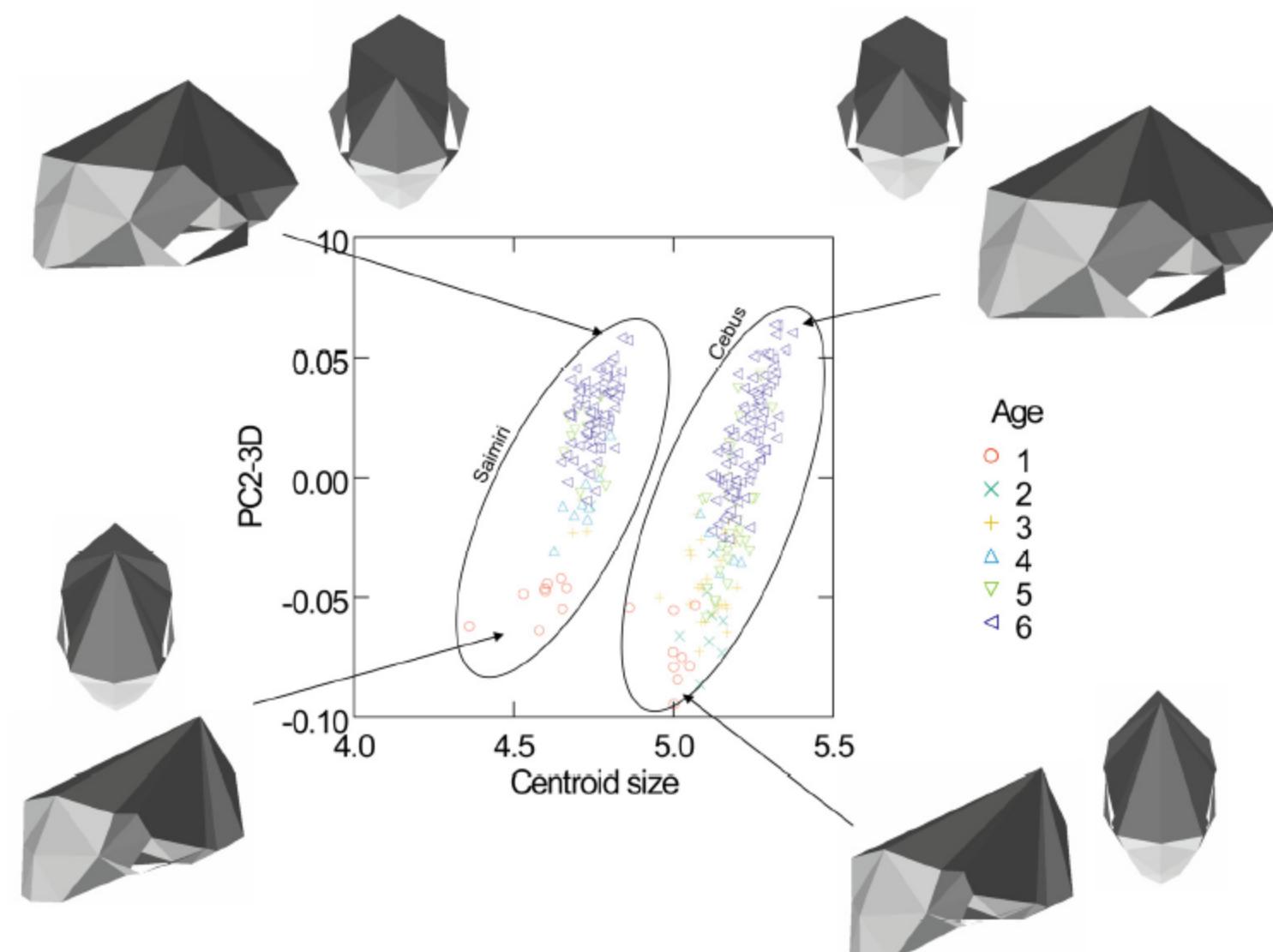


Figure 1

Canonical variates. Canonical variate I (CV1) obtained separately for males and females with frequency distribution of CV1 scores on the margin. On the x-axis is shown the CV1 obtained from the unscaled data and on the y-axis the CV1 from the MASS corrected data.

**Figure 7**

Geometric Morphometrics – size and evolutionary shape allometry. Plot of the PC1-3D against centroid size (ln). Specimens with different ages are show in different colours and symbols and skull 3D reconstructions are show in oblique and dorsal views.

**Figure 8**

Geometric Morphometrics – size and ontogenetic shape allometry. Plot of the PC2-3D against centroid size (ln). Specimens with different ages are show in different colours and symbols and skull 3D reconstructions are show in oblique and dorsal views.

Table 7: Correlation between absolute size, evolutionary and ontogenetic allometry

	SIZE	PC1-3D	PC2-3D
SIZE	1	$P < 10^{-5}$	0.320
PC1-3D	0.972	1	0.872
PC2-3D	-0.060	0.009	1
Cebus	SIZE	PC1-3D	PC2-3D
SIZE	1	$P < 10^{-5}$	$P < 10^{-5}$
PC1-3D	0.864	1	$P < 10^{-5}$
PC2-3D	0.809	0.768	1
Saimiri	SIZE	PC1-3D	PC2-3D
SIZE	1	$P < 10^{-5}$	$P < 10^{-5}$
PC1-3D	0.723	1	$P < 10^{-5}$
PC2-3D	0.699	0.868	1

The Pearson correlation and associated probability between absolute size, PC1-3D and PC2-3D are show for a conjoint analysis (both genera) and for each of the two genera.

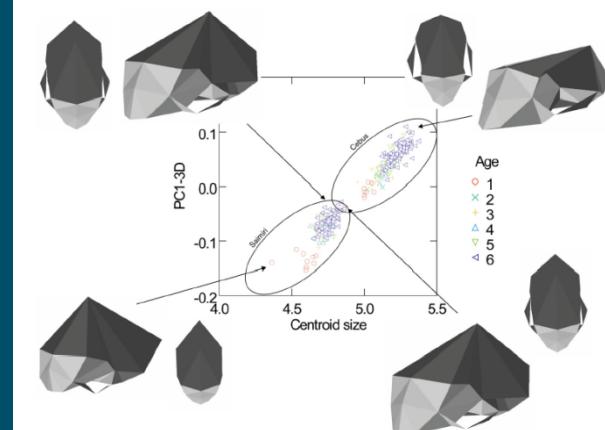


Figure 7
Geometric Morphometrics – size and evolutionary shape allometry. Plot of the PC1-3D against centroid size (ln). Specimens with different ages are show in different colours and symbols and skull 3D reconstructions are show in oblique and dorsal views.

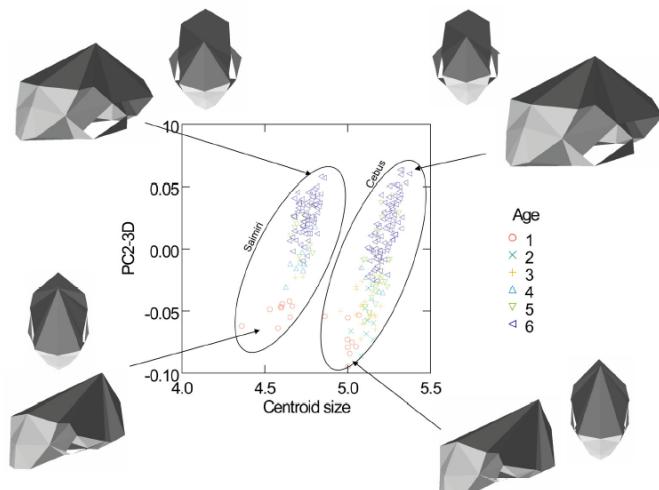
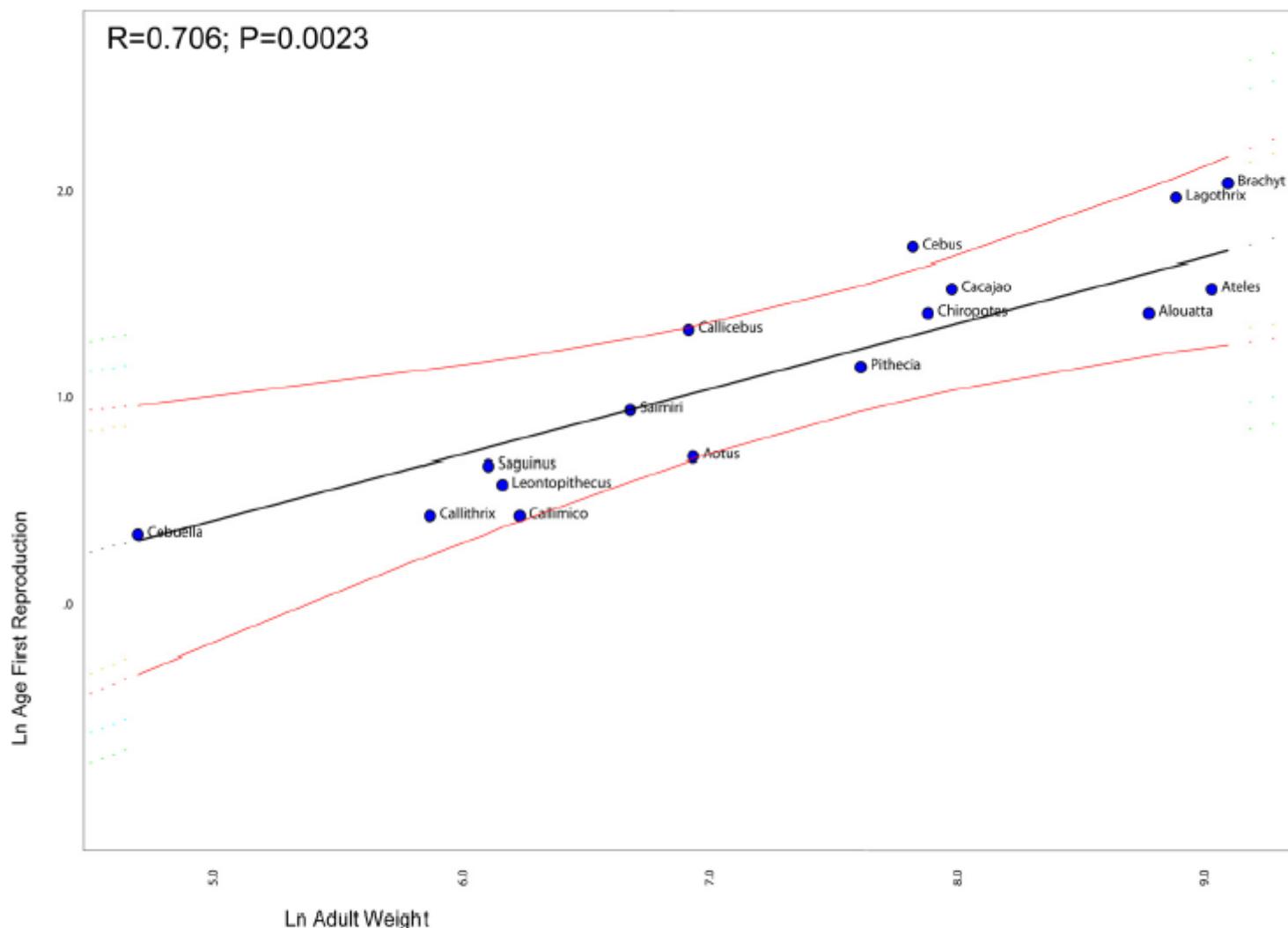


Figure 8
Geometric Morphometrics – size and ontogenetic shape allometry. Plot of the PC2-3D against centroid size (ln). Specimens with different ages are show in different colours and symbols and skull 3D reconstructions are show in oblique and dorsal views.

**Figure 2**

Comparative phylogenetic regression of life-history traits. Plot of the age of first reproduction against adult weight in New World Monkeys controlling for shared history (phylogeny). The regression line and 95% confidence limits were obtained from the method described in Garland and Ives (2000) and implemented in package PDAP in MESQUITE.

Um estudo de caso – Evolução morfológica em macacos Neotropicais

Evolution, 59(5), 2005, pp. 1128–1142

SIZE AS A LINE OF LEAST EVOLUTIONARY RESISTANCE: DIET AND ADAPTIVE MORPHOLOGICAL RADIATION IN NEW WORLD MONKEYS

GABRIEL MARROIG^{1,2} AND JAMES M. CHEVERUD^{3,4}

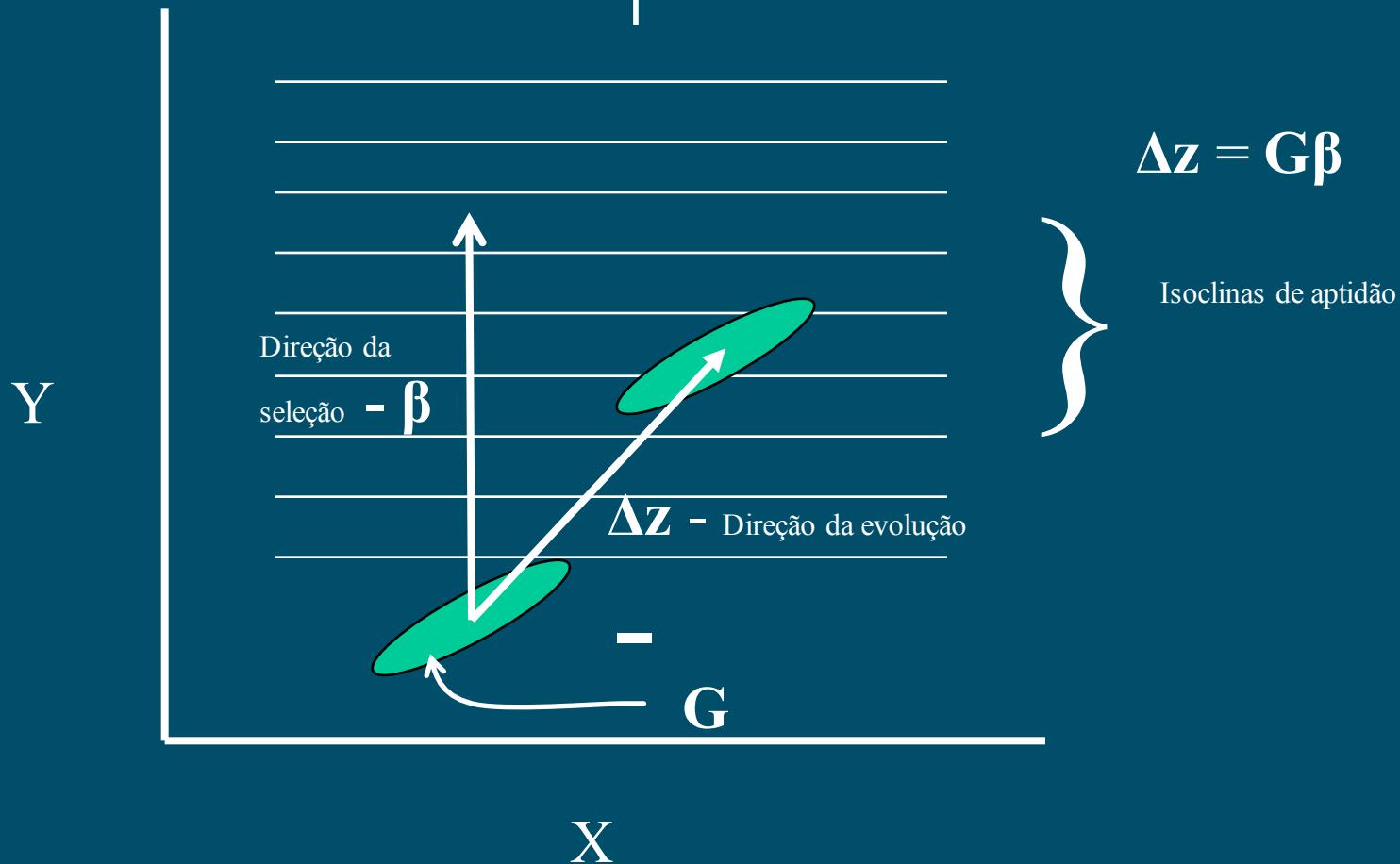
¹*Departamento de Genética e Biologia Evolutiva, Instituto de Biociências, Universidade de São Paulo, CP 11.461, CEP 05422-970, São Paulo, SP, Brazil*

²E-mail: gmarroig@ib.usp.br

³*Department of Anatomy and Neurobiology, Washington University School of Medicine, 660 South Euclid Avenue, Campus Box 8108, Saint Louis, Missouri, 63110*

⁴E-mail: cheverud@pcg.wustl.edu

- Resposta evolutiva à seleção (Δz) desvia da direção da seleção (β) por causa do padrão da matriz de variância/covariância genética (G = faz o papel da h^2 na equação univariada $R = h^2 S$, e portanto é devido primordialmente aos efeitos dos alelos em todos os genes individuais afetando os caracteres em questão)



Evolução via deriva genética

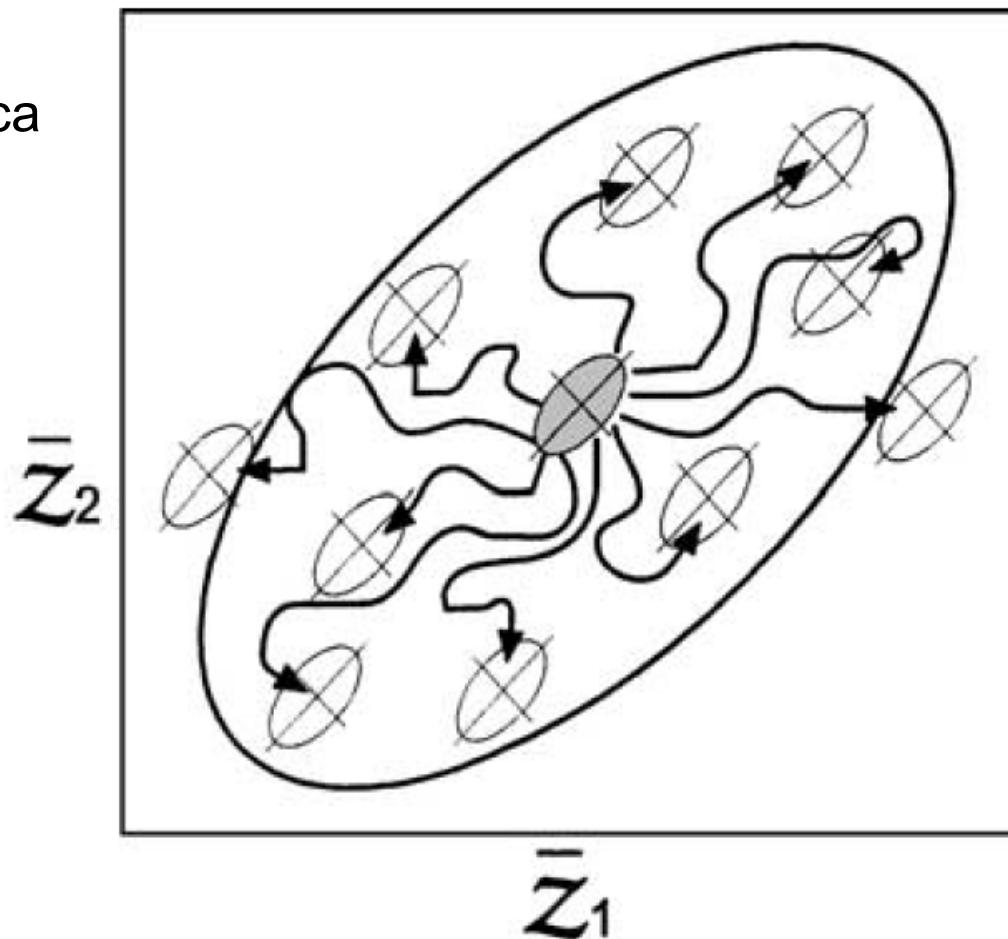
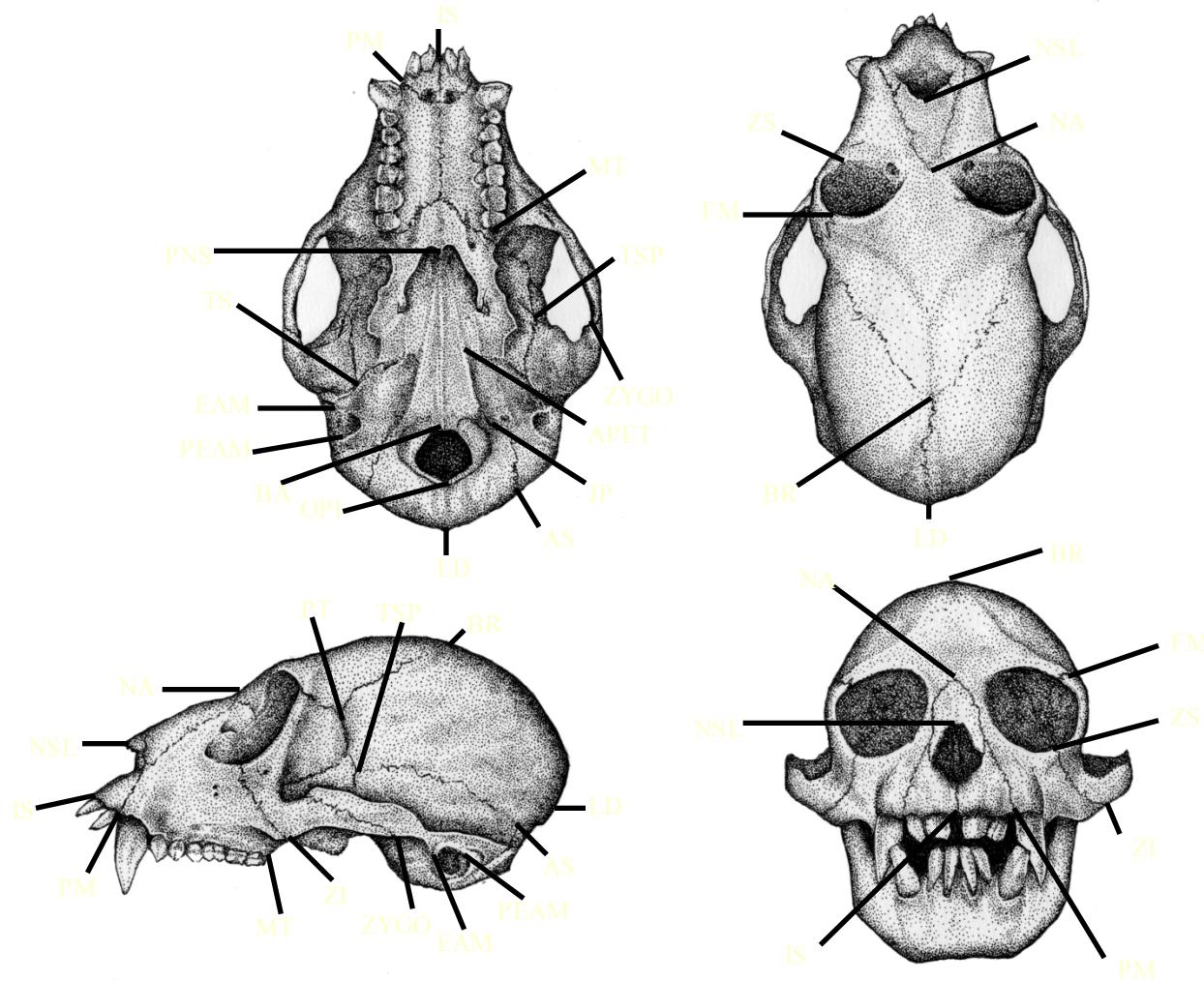
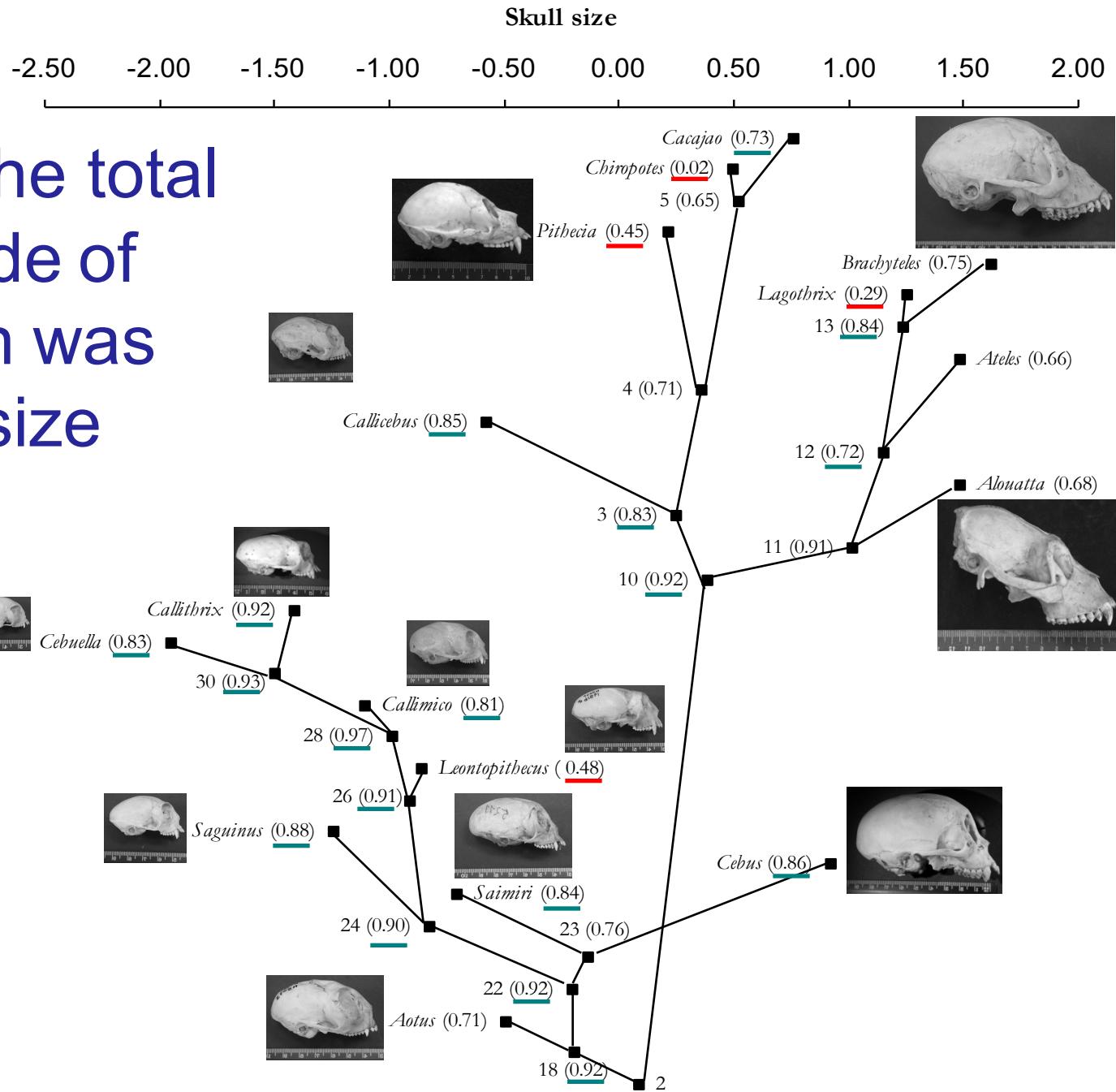


Figure 6. Bivariate drift on a flat adaptive landscape. The small ellipse at the center represents the **G**-matrix of the ancestral population. The large, outer ellipse represents 95% confidence ellipse for the means of replicate, descendant populations. Solid curved lines show representative evolutionary trajectories. Other conventions as in Figure 5.

* 5222 crânios medidos em vários museus



93% of the total
magnitude of
evolution was
aligned size



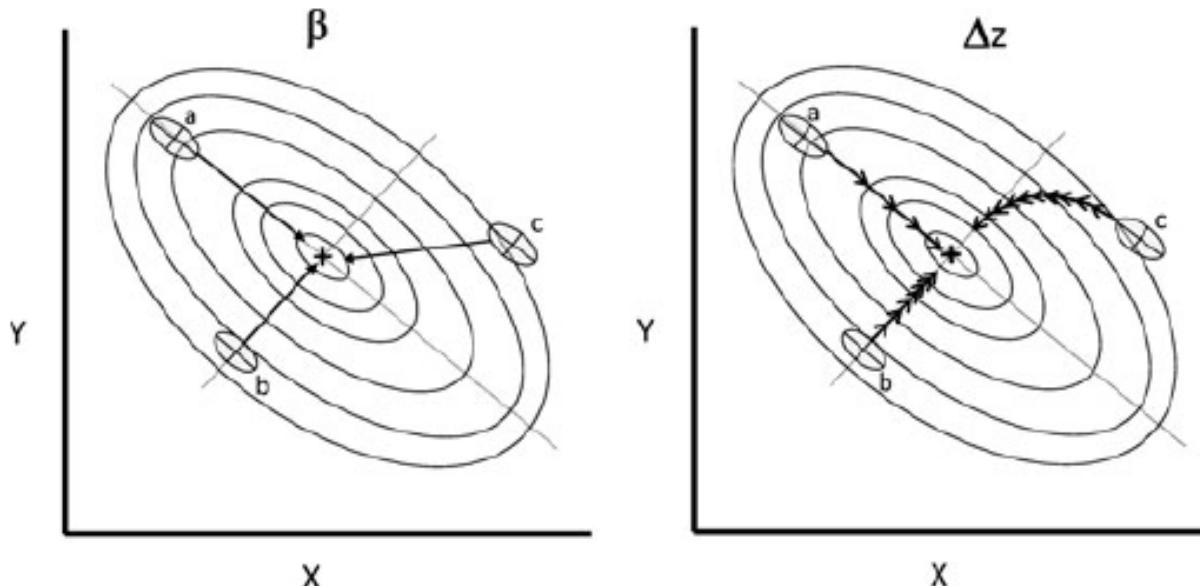
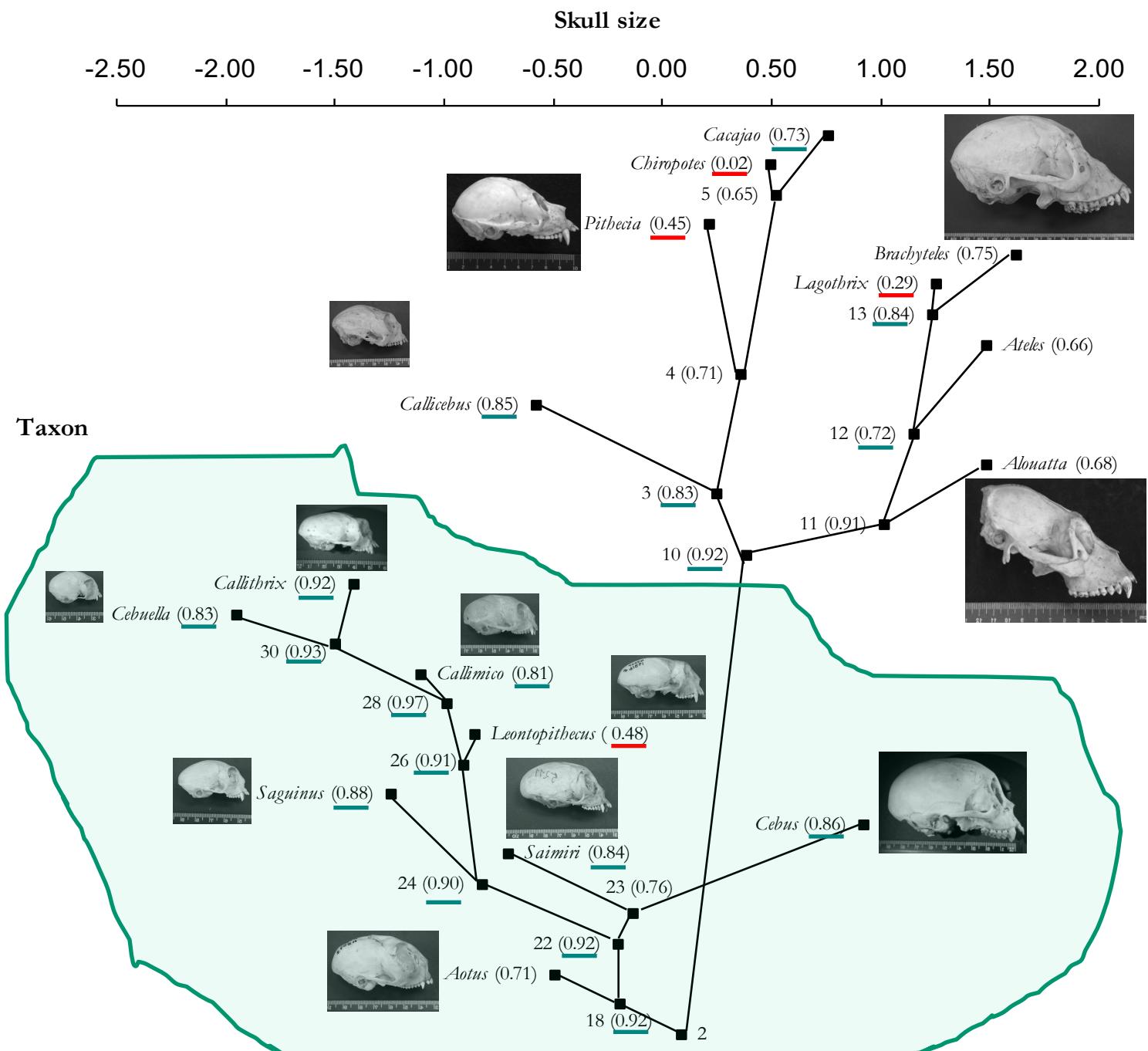


Figure 1. A hypothetical adaptive landscape for two characters with the cross marking the adaptive optima (peak) and oval lines indicating isolines of subsequent smaller height (fitness). Three populations (A, B, C) are show with their corresponding variance/covariance pattern (gray small ellipses) and averages for both traits (the ellipse center corresponding to the crossing of the two major axes of variation). The long and short axes within the gray ellipses represent the first (g_{\max}) and second (g_2) lines of least resistances or the two largest eigenvalues of the G-matrix. On the left the selection gradients (β) operating upon these three populations are show. On the right side the evolutionary responses (Δz) are shown, with the arrows indicating the direction and magnitude of those responses.

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Evolution 64:5: 1470–1488

SIZE AS A LINE OF LEAST RESISTANCE II: DIRECT SELECTION ON SIZE OR CORRELATED RESPONSE DUE TO CONSTRAINTS?

Gabriel Marroig^{1,2} and James Cheverud³



Chapter 3

Paleogeography of the South Atlantic: a Route

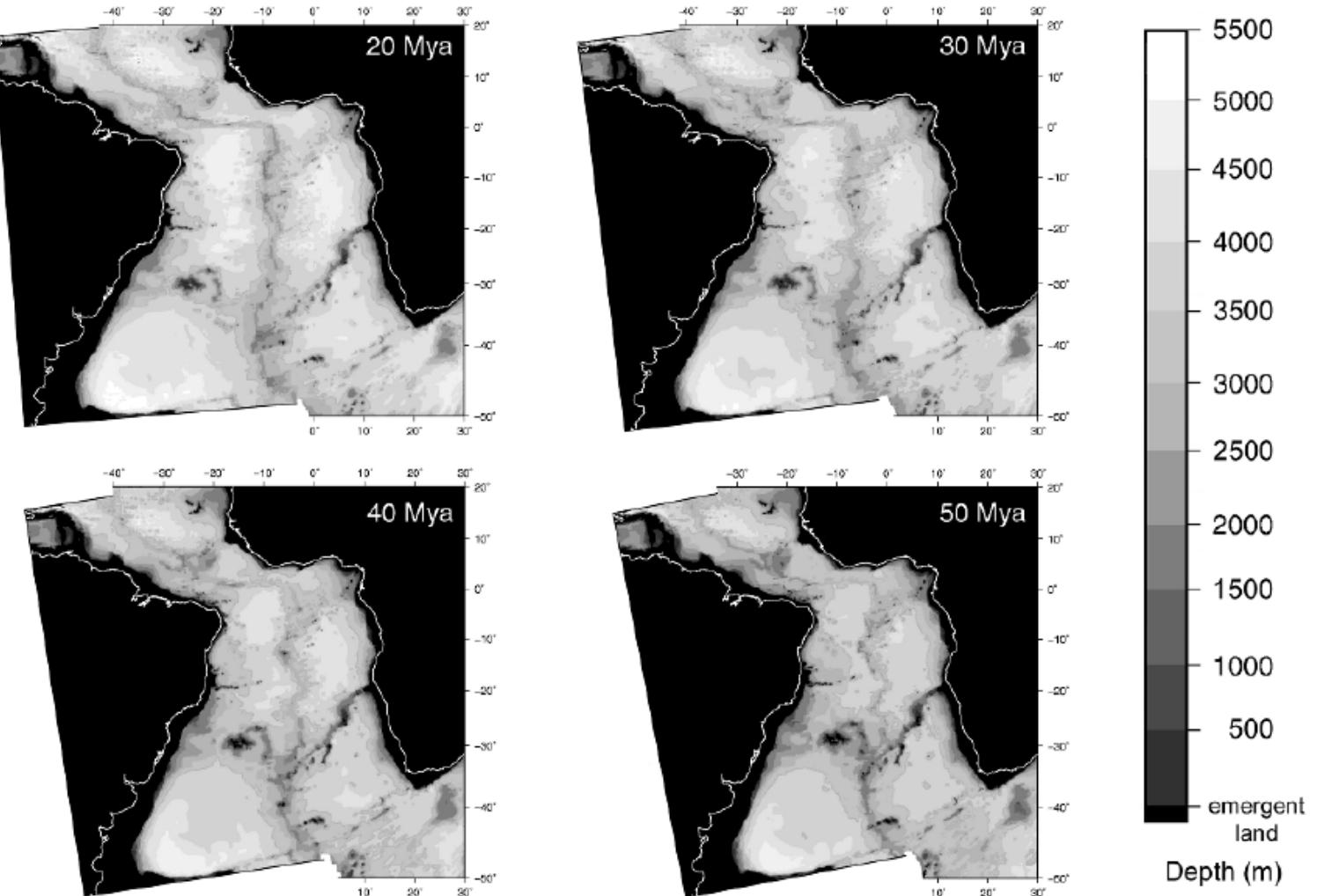
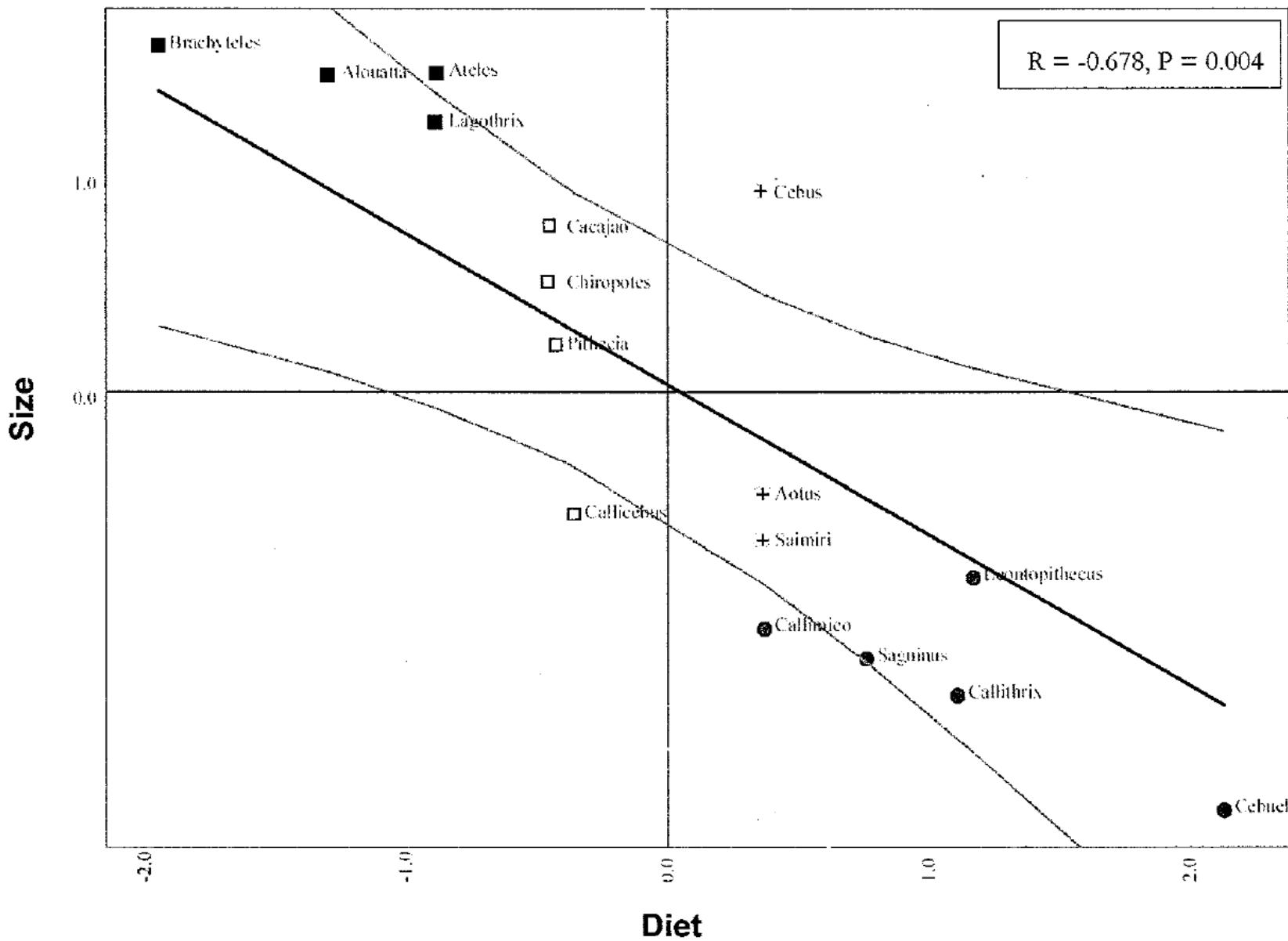


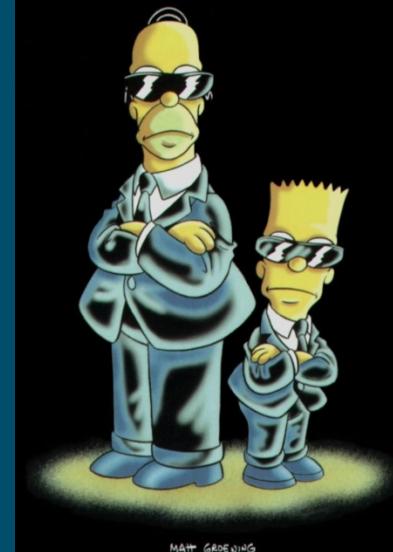
Fig. 3.1 Reconstruction of South America and Africa configuration and Atlantic Ocean bathymetry at 20, 30, 40 and 50 million years ago. Present day coastlines are represented by a white continuous line. At the equator, 10° are approximately 1,100 km

ALLOMETRY AS A LINE OF LEAST RESISTANCE



Visão Simpsoniana da macroevolução

“Life is like a donut, round and empty inside”



– Invasão e diversificação de zonas adaptativas



George G. Simpson