

# 動物の進化 異時性とは何か？

理学部 海洋生物学研究室 遠藤広光

スジダラ(タラ目ソコダラ科)

BSKU 43409

ミスジオクメウオ(アシロ目オクメウオ科)

BSKU86066

114 mm SL



# 異時性と異座性は進化の重要な現象のひとつ

## 異時性・ヘテロクロニー Heterochrony

祖先に比べ成長の速度や量, 比, タイミングが変わる

★形態や生活史, 行動などに影響を及ぼす

## 異座性・ヘテロトピー Heterotopy

場所が変わる(相同性がわからなくなる)

★新しい形態が生じる

例: カメ類の甲羅, サボテン

# ヘテロトピーの例 ゴマフイカの発光器

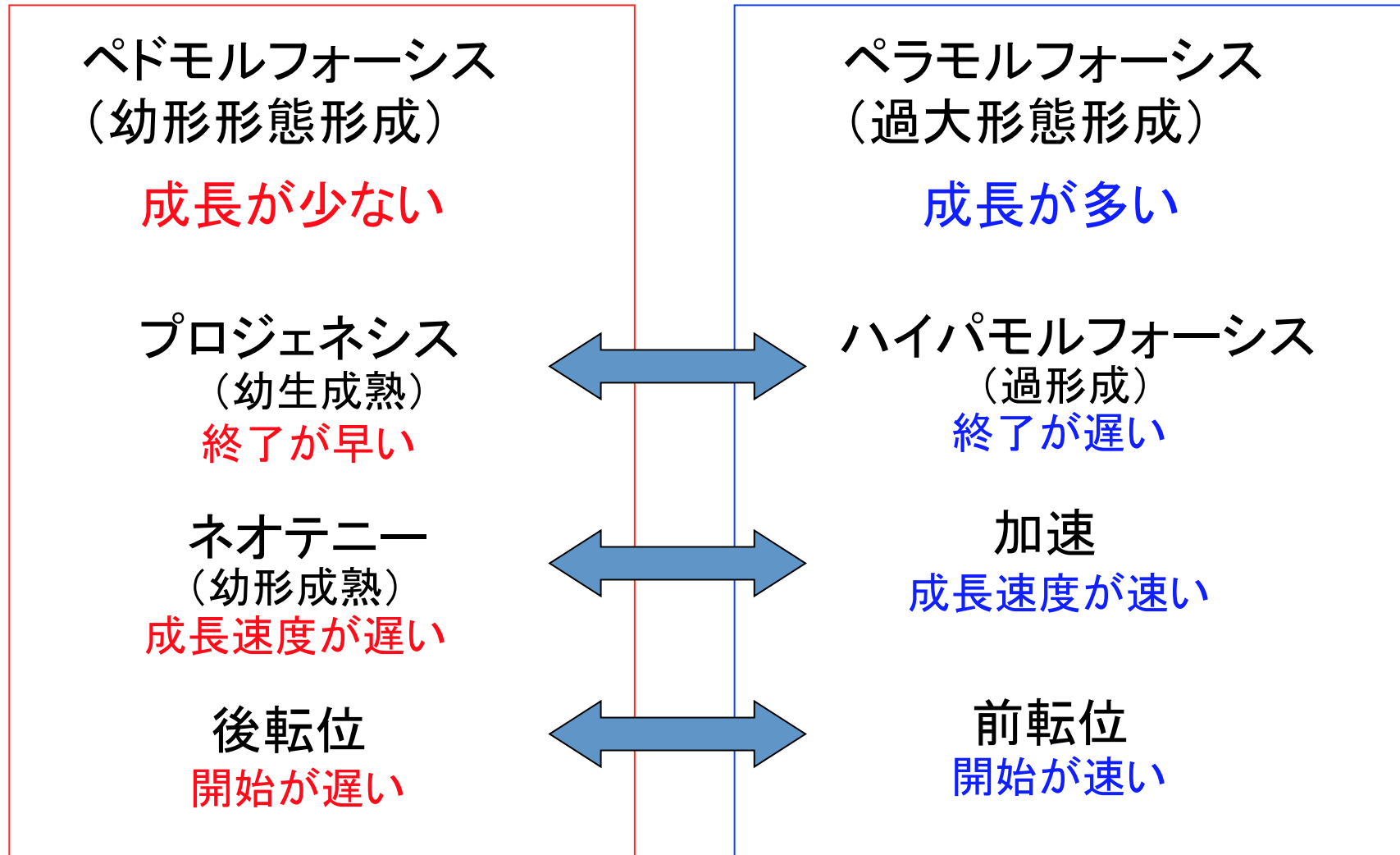


2005年1月6日 高知市御置瀬魚市場 町田吉彦先生撮影  
土佐の自然ギャラリー第201集より

# 異時性の影響は？

- 1) 大進化と小進化の両方に関係
- 2) アロメトリー・相対成長と関係
- 3) 性的二形に関係
- 4) 環境への適応と関係
- 5) 生活史戦略と関係
- 6) 行動の進化と関係

# 異時性・ヘテロクロニーの分類



ただし、複数の異時性がモザイク状に影響する

# 大局的ヘテロクロニー

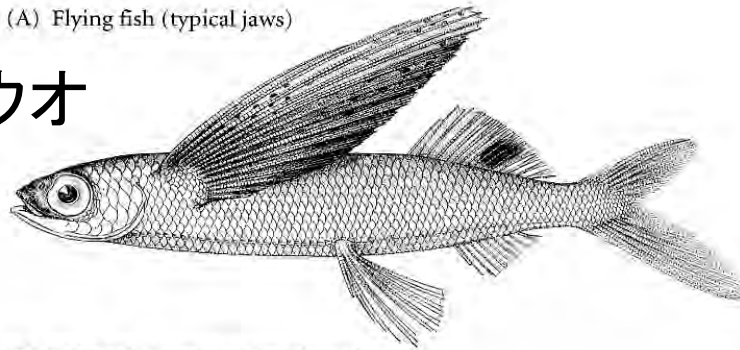


サンショウウオ類のペドモルフォーシス(ネオテニー)

# 局所的ヘテロクロニー

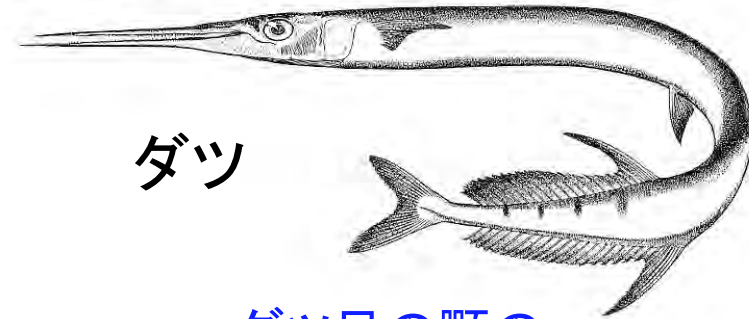
(A) Flying fish (typical jaws)

トビウオ



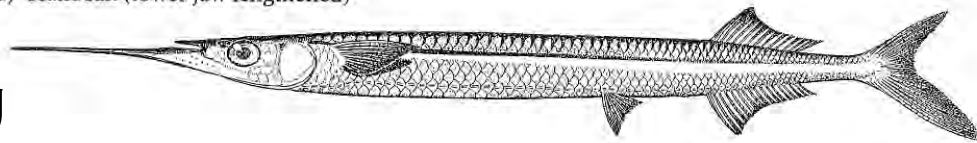
(C) Needlefish (both jaws lengthened)

ダツ



(B) Halfbeak (lower jaw lengthened)

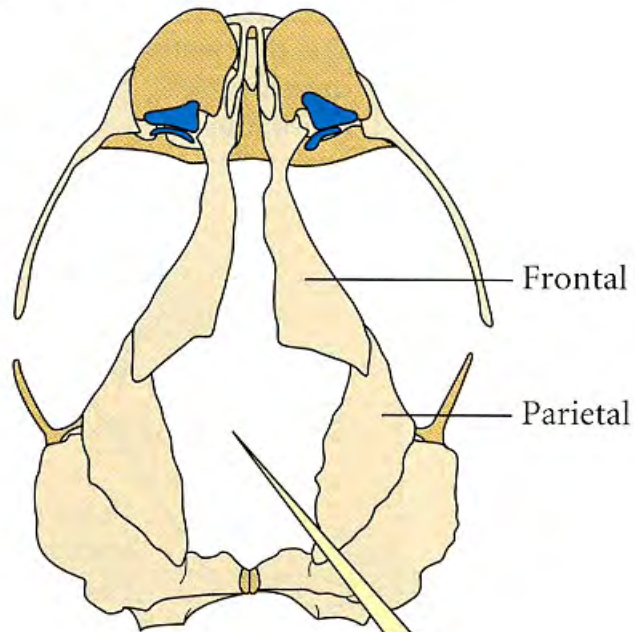
サヨリ



ダツ目の顎の  
ペラモルフォーシス  
(ハイパモルフォーシス)

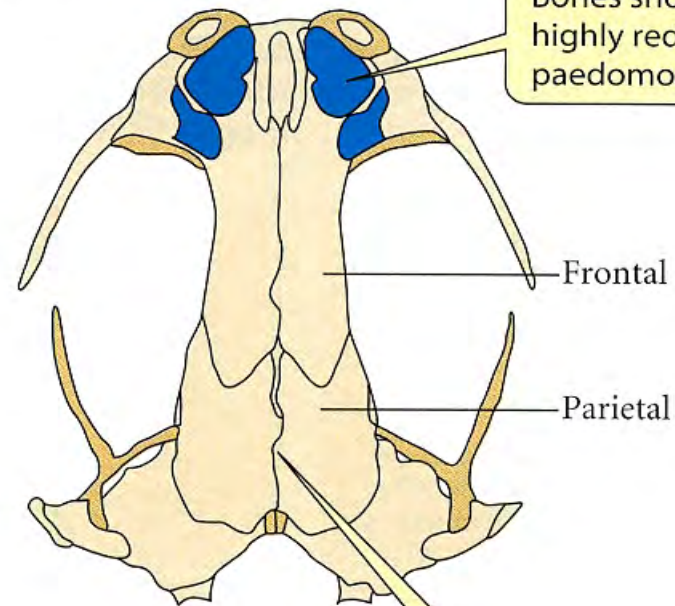
# ペドモルフォーシスの形態学的特徴は？

(A) Paedomorphic (*Thorius*)



The space between the paired frontal and parietal bones is a juvenile feature that is retained in adult *Thorius*.

(B) Nonpaedomorphic



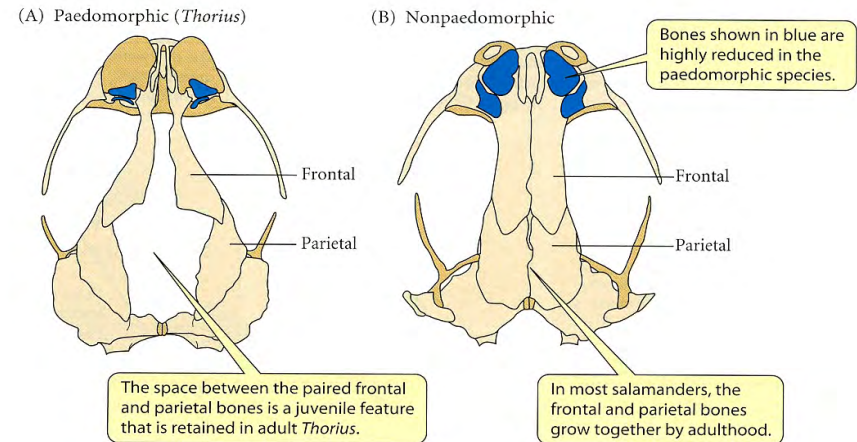
Bones shown in blue are highly reduced in the paedomorphic species.

In most salamanders, the frontal and parietal bones grow together by adulthood.

# サンショウウオ類のプロジェネシス

形態学的特徴は、

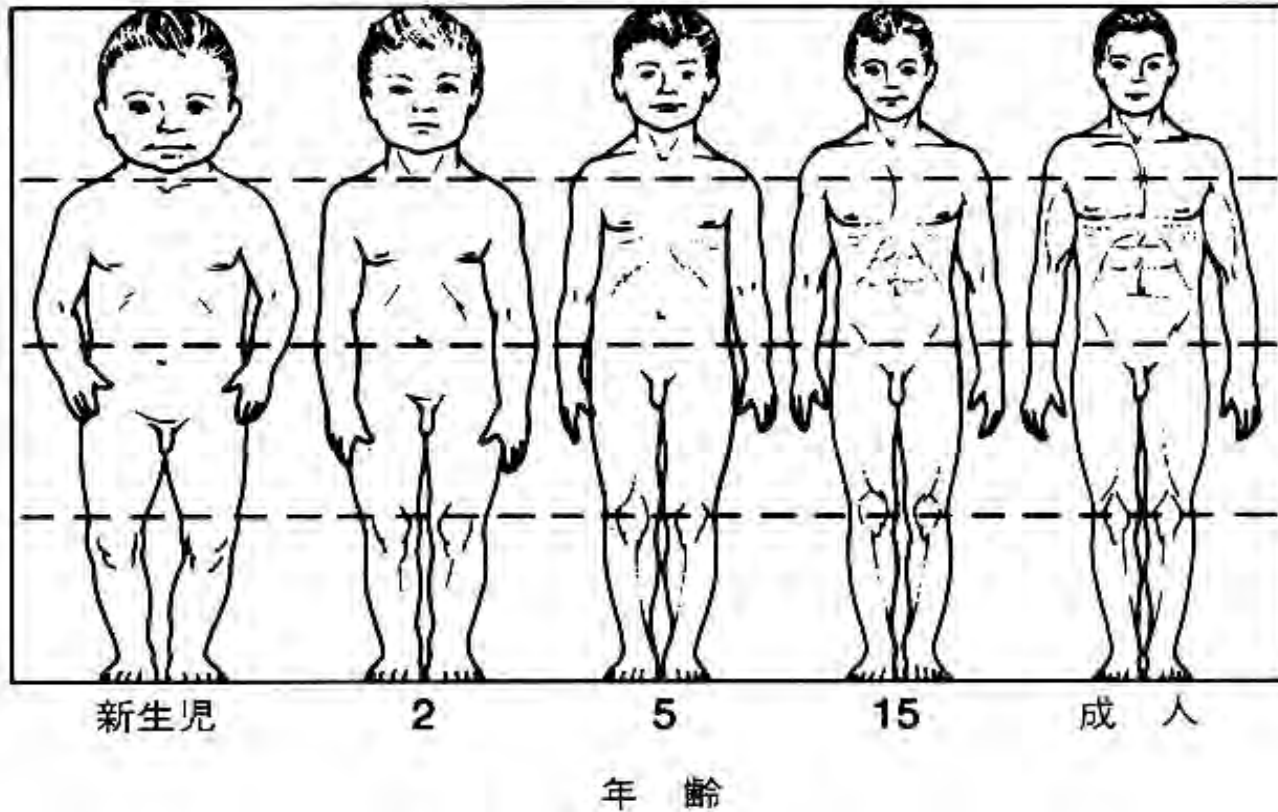
- 上顎の歯の退化または消失
- 骨化程度が低く、軟骨部が多い
- 個体発生後期に現れる骨が出現しない
- 眼や鼻(嗅球), 脳のプロポーションが大きい
- 手の骨(手根骨部)の変異が激しい





# ヒトにおける相対成長

フツイマ(1991)「進化生物学」より

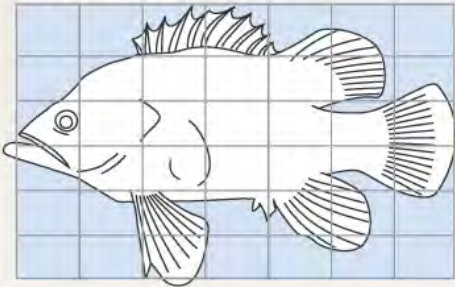


足の成長はペラモルフ的

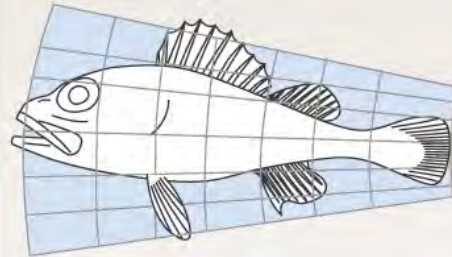
成長や成熟は様々なホルモンの調節により制御される

# グループ内の基本的な体型の変形により多様性がうまれる

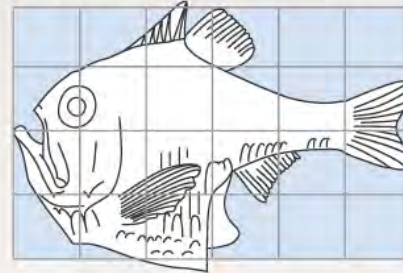
*Polyprion*



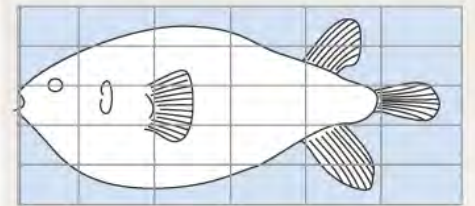
*Scorpaena*



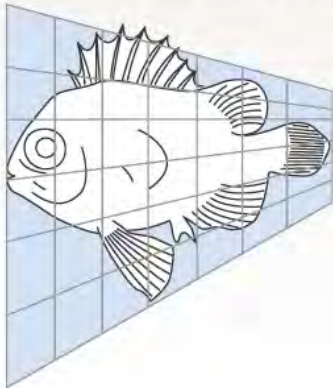
*Argyropelecus olfersi*



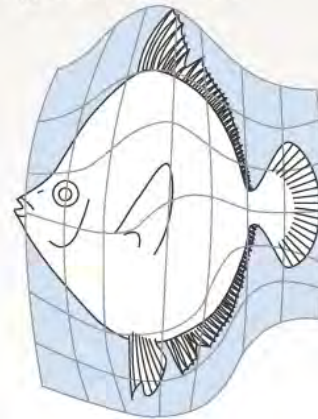
*Diodon*



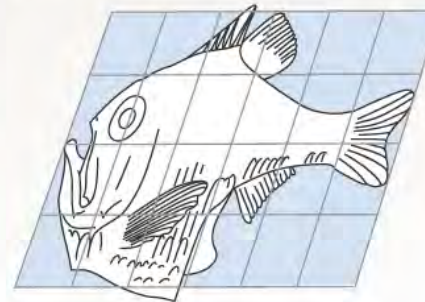
*Pseudopriacanthus altus*



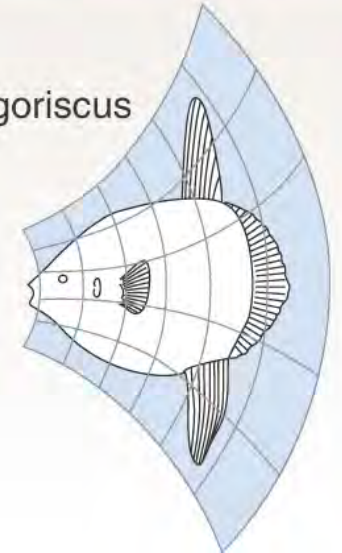
*Antigonia capros*



*Sternoptyx diaphana*



*Orthogoriscus*



スズキ目魚類

ムネエソ科魚類

フグ目魚類

Arthur, W. (2011) Evolution: a developmental approach より

# ペドモルフ(幼生)的な魚類

## 大局的ヘテロクロニーの例

シラウオ(サケ目シラウオ科)



短命で早熟  
産卵数が少ない  
生活史サイクルが早い

シラスウオ(ハゼ目シラスウオ科)

Watson & Walker: *Schindleria brevipinguis*—the smallest vertebrate 141

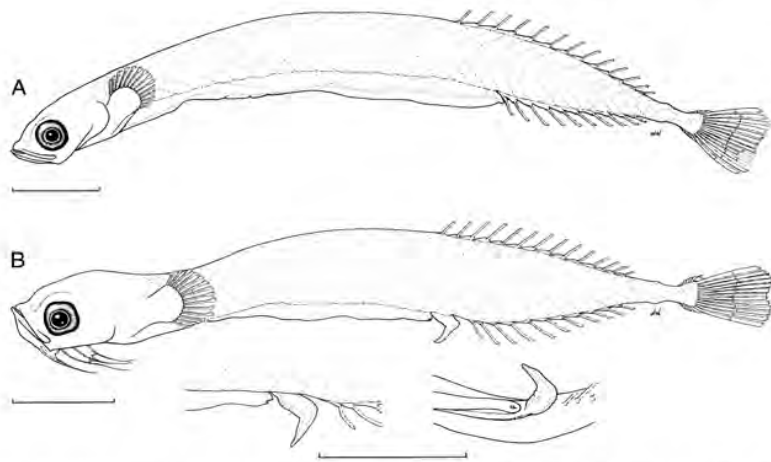


Fig. 1. *Schindleria brevipinguis* n.sp. (A) Holotype, AMS I.23552-006 (8.4 mm, female), from vicinity of Carter Reef, Great Barrier Reef, Queensland, Australia; (B) paratype, AMS I.26323-003 (6.6 mm, male; note that branchiostegal area is somewhat damaged) from Carter Reef vicinity, Great Barrier Reef. Enlarged lateral (left) and ventral (right) views of urogenital papilla are shown below paratype. Scale bar = 1 mm.

シロウオ(ハゼ目ハゼ科)



# 中深層に生息するプロジェネシス的な魚類

## 大局的ヘテロクロニーの例



A stomiatoid fish of the genus *Cyclothone*, the most widely and deeply represented of all deep-sea fish genera. Note the small eyes and light organs. Length about 6 cm.

例えば、オニハダカ属魚類

- 骨化の程度が低い
- 筋肉が少なく、退化的（代謝は低い）
- 体が半透明（色素が少ない）

# スジダラ(タラ目ソコダラ科)

大局的ヘテロクロニーの例



スジダラ属はソコダラ科では、もっとも小型でプロジェネシスの

# タラ目ソコダラ科魚類 4亜科約30属約380種

最大で全長20cm

スジダラ



BSKU 43409 *Hymenocephalus striatissimus*



アナダラ

全長40~50cm



全長40~50cm

オキナヒゲ



全長40cm

バケダラ

BSKU 51872



全長100cm

ズナガソコダラ



最大で全長150cm

ムネダラ

# 著しい性的二形を示すチョウチンアンコウ亜目魚類



Paxton and Eschmeyer (1998) Encyclopedia of Fishes, 2nd ed. より

# 現在，脊椎動物の中で最も小さな種

## ***Paedocypris*, a new genus of Southeast Asian cyprinid fish with a remarkable sexual dimorphism, comprises the world's smallest vertebrate**

**Maurice Kottelat<sup>1,2,\*</sup>, Ralf Britz<sup>3</sup>, Tan Heok Hui<sup>1</sup> and Kai-Erik Witte<sup>4</sup>**

<sup>1</sup>*Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore, Lower Kent Ridge Road, Singapore 119260, Singapore*

<sup>2</sup>*Route de la Baroche 12, Case Postale 57, 2952 Cornol, Switzerland*

<sup>3</sup>*Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK*

<sup>4</sup>*Max Planck Institute for Developmental Biology, Spemannstrasse 35/3, 72076 Tübingen, Germany*

*Paedocypris* is a new genus of paedomorphic cyprinid fish from highly acidic blackwater peat swamps in Southeast Asia. It includes two new species, one of which (*Paedocypris progenetica*) appears to be the smallest fish and vertebrate known, with the smallest mature female measuring a mere 7.9 mm. *Paedocypris* has many 'larval' features typically associated with paedomorphic fish (e.g. narrow frontals that leave the brain unprotected dorsally by bone and a precaudal larval-fin-fold), but, uniquely among fishes, males also possess highly modified pelvic fins with hypertrophied muscles and a keratinized pad in front of the pelvic girdle, which, we hypothesize, function together as a clasping or holding device, thereby suggesting an unusual reproductive mode. Unfortunately, habitat destruction jeopardizes the survival of these fishes and thus opportunities for further research.

**Keywords:** *Paedocypris*; Cyprinidae; peat swamps; smallest vertebrate; sexual dimorphism



# *Paedocypris progenetica* と *P. micromegethes* の2種

\* 酸性度の高い泥炭湿地に生息する

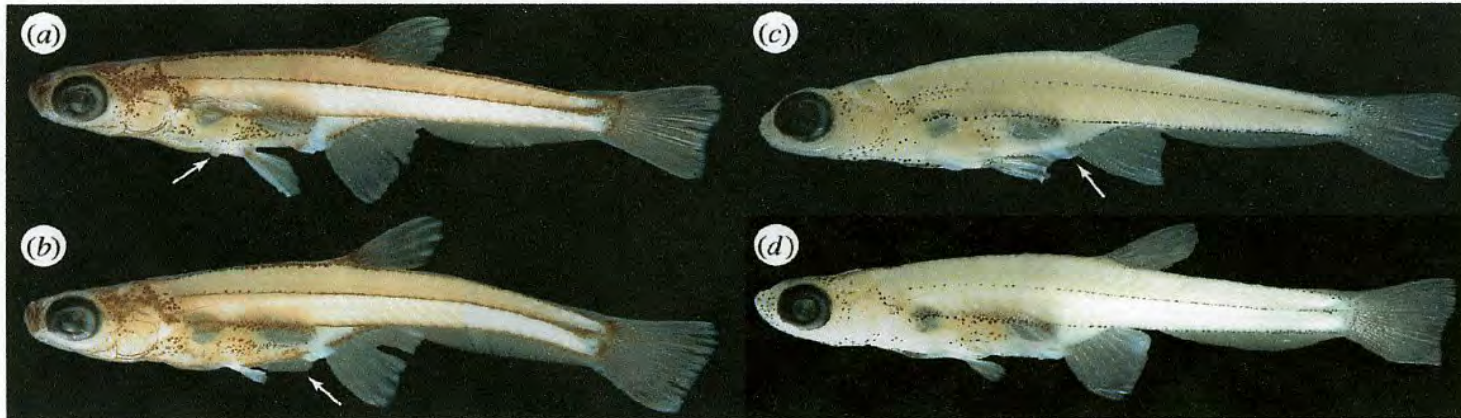


Figure 2. (a) *Paedocypris progenetica* holotype male, MZB 5998, 8.6 mm; arrow points to keratinized abdominal knob; (b) *Paedocypris progenetica* paratype female, ZRC 43199, 8.0 mm; arrow points to preanal larval-fin-fold; (c) *Paedocypris micromegethes* holotype male, ZRC 49869, 10.4 mm; arrow points to genital papilla; (d) paratype female, BMNH 2004.11.16.1-40, 10.0 mm.



Figure 1. Living *Paedocypris progenetica*, CMK 18496, (a, b) male, ca 9 mm; (c) female, ca 8.8 mm.

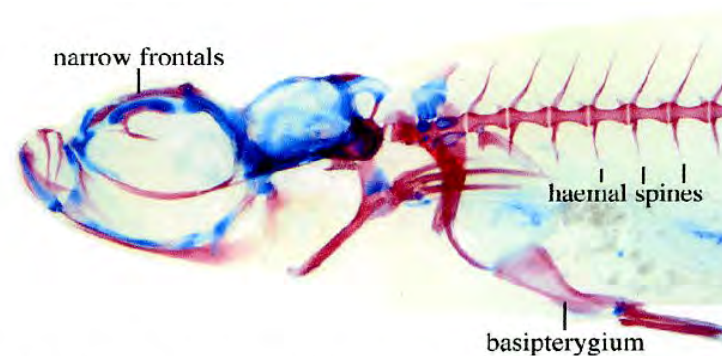
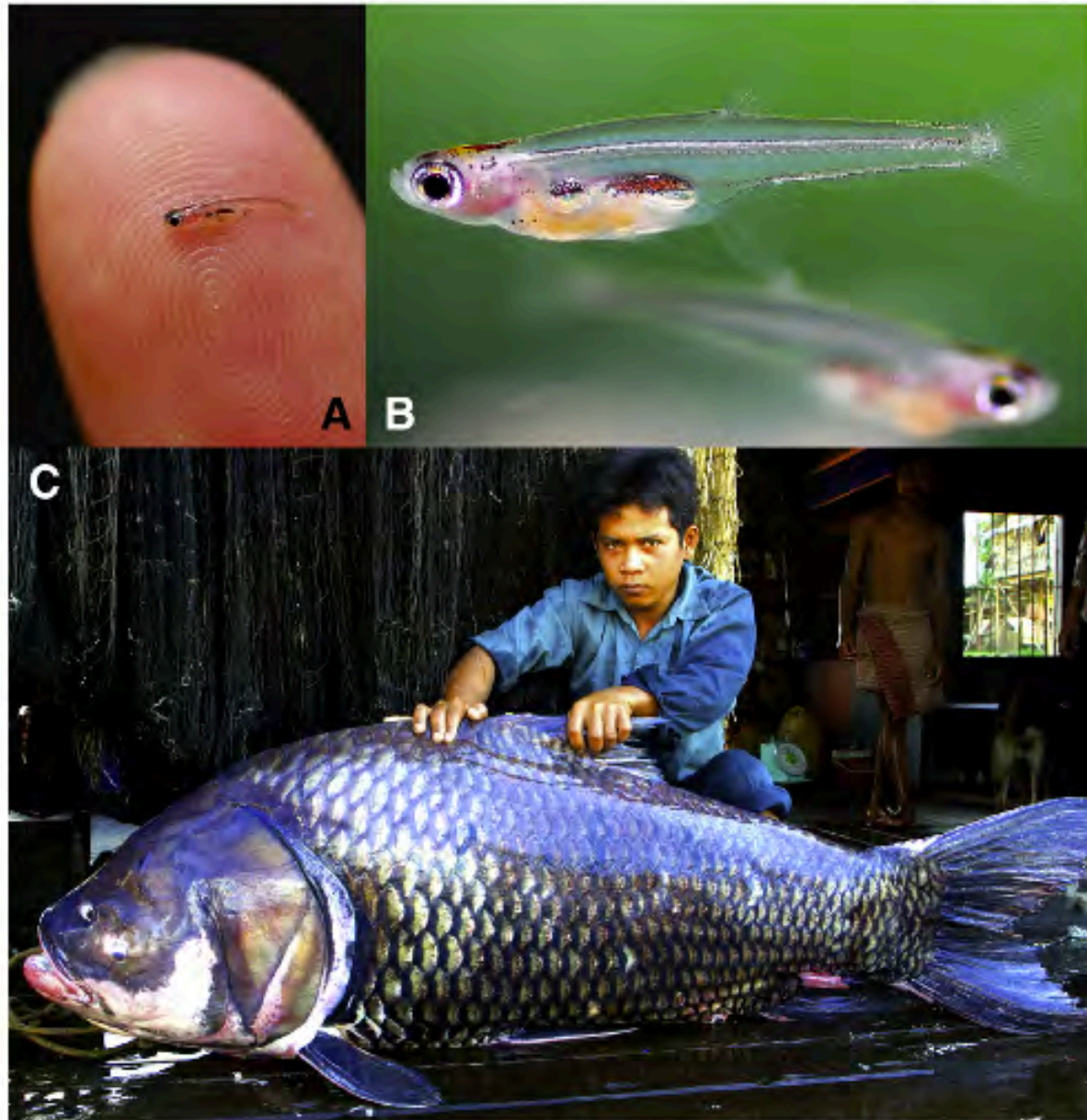


Figure 4. *Paedocypris micromegethes*, cleared and double stained paratype, male, BMNH 2004.11.16.41-60, 10.7 mm, cartilage in blue, bone in red, note largely cartilaginous roofless skull, haemal spines on abdominal vertebrae and hypertrophied basipterygium of pelvic girdle.



**Fig. 1.** Extremes in body size of adults of species of the Order Cypriniformes. (A and B) Adult specimen of *Paedocypris* ( $\leq 9$  mm SL) (photographs by Dr. Kobayashi and used with permission). (C) Adult specimen of *Catlocarpio siamensis*, one of the largest species of Cypriniformes (172 cm, 102 kg) (photograph by Dr. Zeb Hogan and used with permission).

Research article

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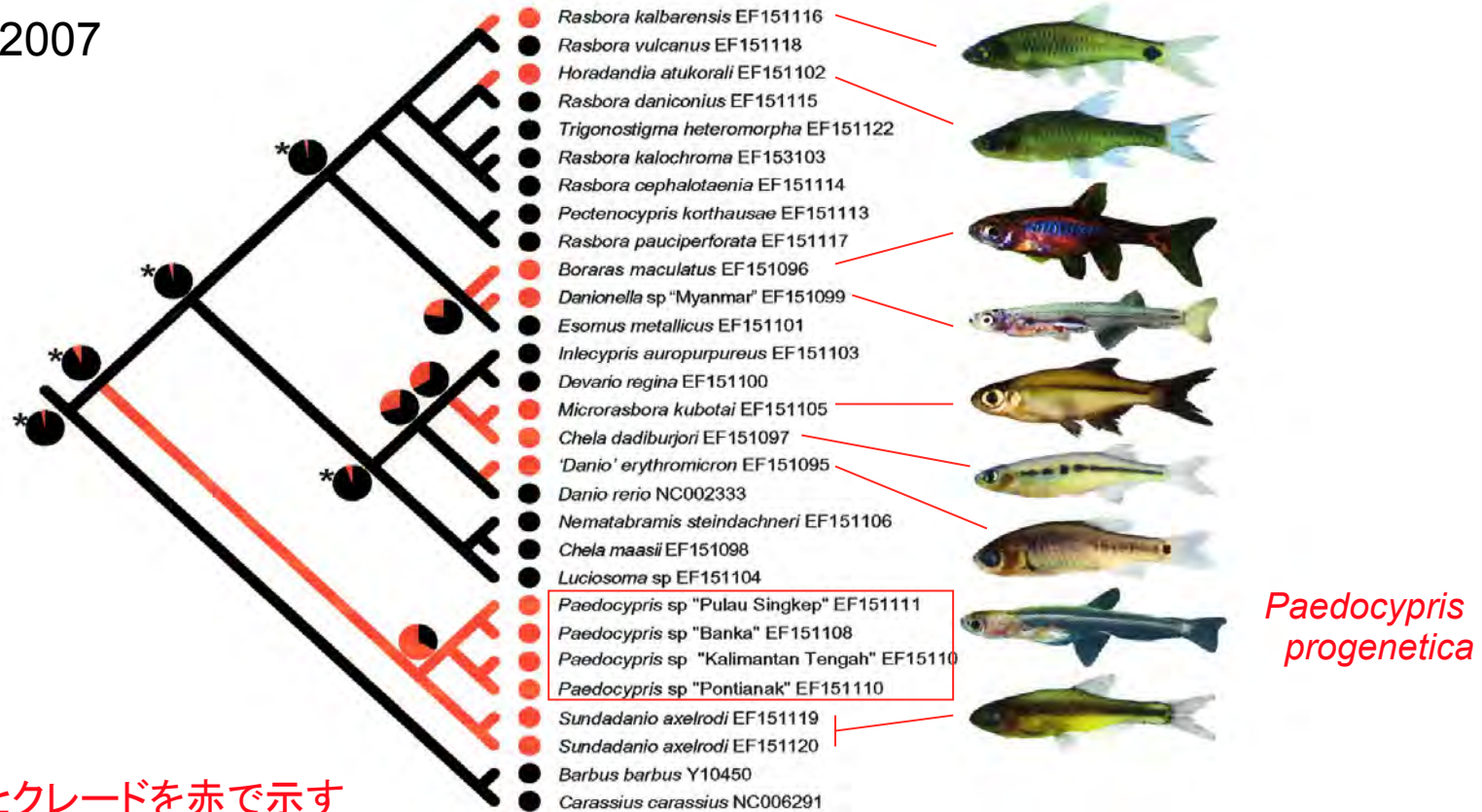
Evolution of miniaturization and the phylogenetic position of *Paedocypris*, comprising the world's smallest vertebrate

Lukas Rüber\*<sup>1</sup>, Maurice Kottelat<sup>2</sup>, Heok Hui Tan<sup>3</sup>, Peter KL Ng<sup>3</sup> and Ralf Britz<sup>1</sup>

www.biomedcentral.com/1471-2148/7/38

コイ科ラスボラ亜科内の分子系統仮説

Rüber et al. 2007



小型化した種とクレードを赤で示す

**Figure 3**  
**Evolution of miniaturization in the rasborine clade A.** Tracing the evolution of miniaturization on the ML topology (one of three ML topologies; choice of topology does not alter conclusions) of the rasborine data set (clade A). The state 'miniature' is given in red colour, whereas the state 'non-miniature' is given in black. Results from both, unweighted parsimony and ML (selected nodes only), are shown. Significant ML reconstructions are indicated with an asterisk. Photographs of selected miniature rasborines mentioned in the text are given behind taxon names: *Rasbora kalbarensis*, *Horadandia atukorali*, *Boraras brigittae*, *Danionella* sp 'Myanmar', *Microrasbora kubotai*, *Chela dadiburjori*, *'Danio' erythromicron*, *Paedocypris progenetica*, *Sundadanio axelrodi*.

# シラスウオ(スズキ目ハゼ科)

2004年

## The World's Smallest Vertebrate, *Schindleria brevipinguis*, A New Paedomorphic Species in the Family Schindleriidae (Perciformes: Gobioidae)

WILLIAM WATSON<sup>1\*</sup> AND H.J. WALKER JR.<sup>2</sup>

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8604 La Jolla Shores Drive, La Jolla, California 92037-1508, United States of America

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ABSTRACT. *Schindleria brevipinguis* n.sp., from the Lizard Island-Carter Reef vicinity of the Great Barrier Reef, Australia and from Osprey Reef nearby in the Coral Sea, is a small, unpigmented gobioid species distinctive in having fewer dorsal- and anal-fin rays and a deeper body with larger eyes than the other described species, *S. pietschmanni* and *S. praematura*. The urogenital papilla of male *S. brevipinguis* has a markedly different shape from those of the other two species. *Schindleria brevipinguis* apparently provides an even more extreme example of paedomorphosis than its congeners, and with males maturing by 7 mm and the largest specimen only 8.4 mm, it almost certainly is the world's smallest fish and smallest vertebrate.

WATSON, WILLIAM, & H.J. WALKER JR., 2004. The world's smallest vertebrate, *Schindleria brevipinguis*, a new paedomorphic species in the family Schindleriidae (Perciformes: Gobioidae). *Records of the Australian Museum* 56(2): 139-142.

# 世界で最も小さな脊椎動物は？

## *Trimmatom nanus*

シマイソハゼ属の一種



\* 1981年に新種記載された

写真は FishBaseより

## *Paedocypris progenetica*

\* 2006年



写真は FishBaseより

## *Schindleria brevipinguis*

Watson & Walker: *Schindleria brevipinguis*—the smallest vertebrate 141

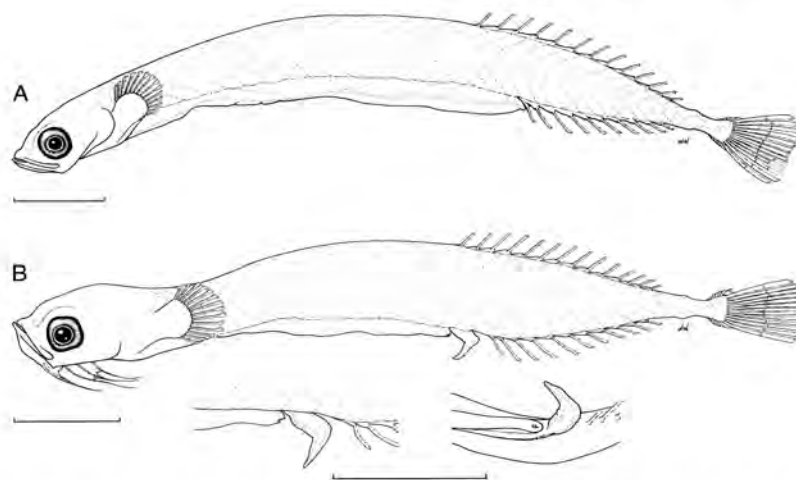


Fig. 1. *Schindleria brevipinguis* n.sp. (A) Holotype, AMS I.23552-006 (8.4 mm, female), from vicinity of Carter Reef, Great Barrier Reef, Queensland, Australia; (B) paratype, AMS I.26323-003 (6.6 mm, male; note that branchiostegal area is somewhat damaged) from Carter Reef vicinity, Great Barrier Reef. Enlarged lateral (left) and ventral (right) views of urogenital papilla are shown below paratype. Scale bar = 1 mm.

\* 2004年



Figure 1. Living *Paedocypris progenetica*, CMK 18496, (a, b) male, ca 9 mm; (c) female, ca 8.8 mm.

# 熟卵をもった雌の最小個体は...(Kottelat et al., 2006)

第1位 *Paedocypris progenetica* 7.9 mm (標準体長)



Figure 1. Living *Paedocypris progenetica*, CMK 18496, (a, b) male, ca 9 mm; (c) female, ca 8.8 mm.

第2位 *Trimmatom nanus* 8.0 mm



第3位 *Schindleria brevipinguis* 8.4 mm

Kottelat et al. (2006) によると...

\* 最小個体 7 mm は、雄の成熟個体とされたが、生殖突起を詳しく調べておらず、成熟個体であるかは怪しい

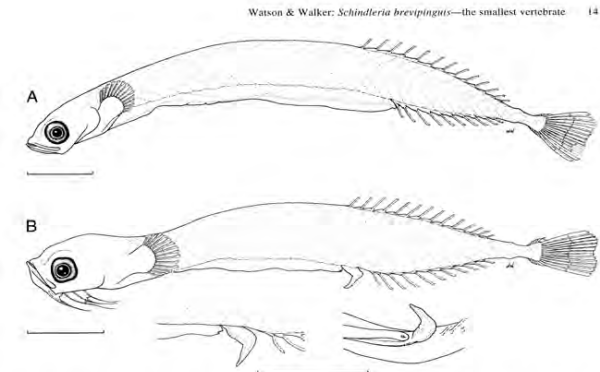


Fig. 1. *Schindleria brevipinguis* n.sp. (A) Holotype, AMS 1.23552-006 (8.4 mm, female), from vicinity of Carter Reef, Great Barrier Reef, Queensland, Australia. (B) paratype, AMS 1.26323-003 (6.6 mm, male; note that branchiostegal area is somewhat damaged) from Carter Reef vicinity, Great Barrier Reef. Enlarged lateral (left) and ventral (right) views of urogenital papilla are shown below paratype. Scale bar = 1 mm.

# オニハダカ属 (ワニトカゲギス目 ヨコエソ科)

Genus *Cyclothone*

現在13種を含む



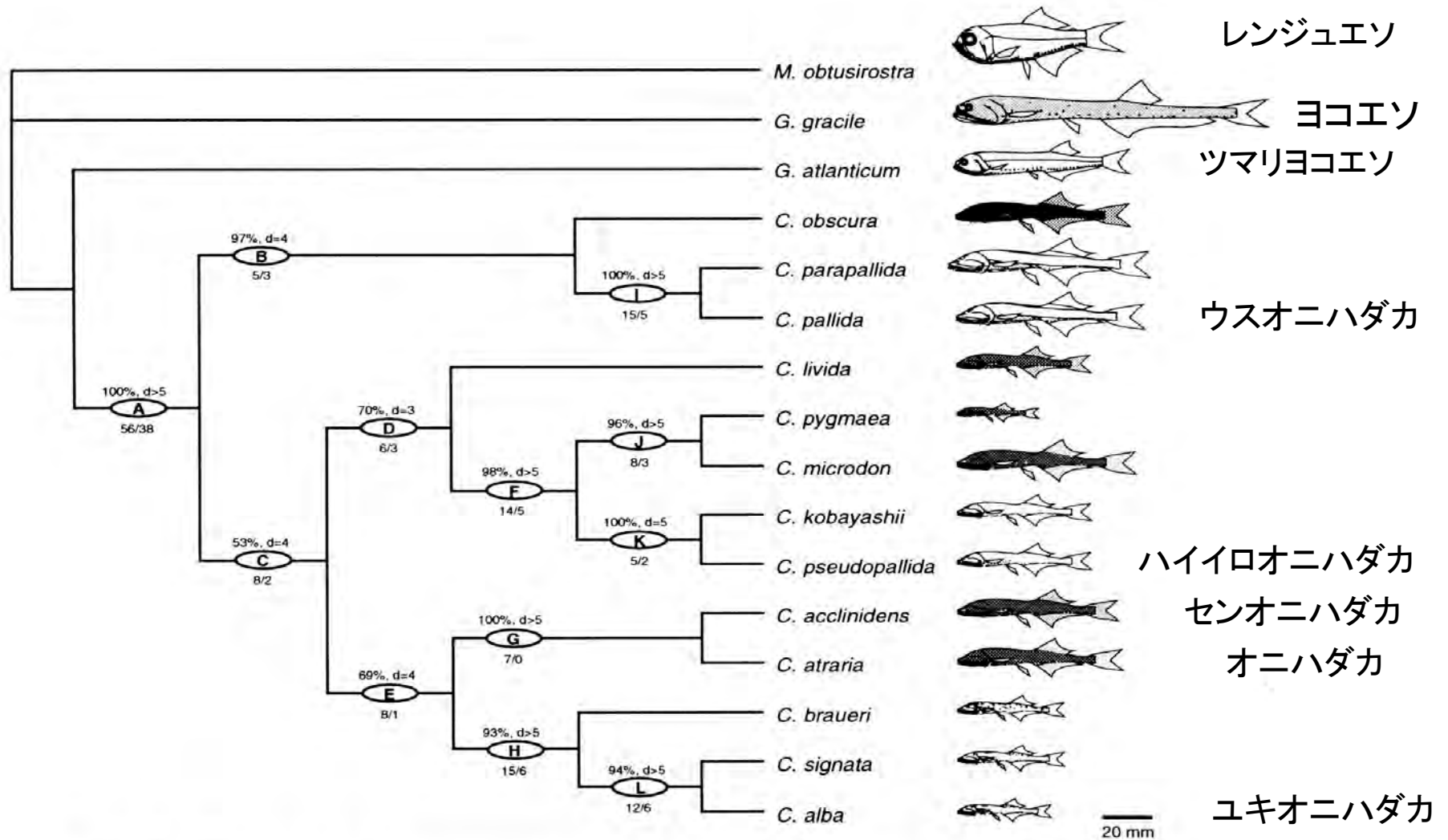
A stomiatoid fish of the genus *Cyclothone*, the most widely and deeply represented of all deep-sea fish genera. Note the small eyes and light organs. Length about 6 cm.

Marshall (1979) より

体長 25~75 mm の小型の中深層性魚類

\*世界で最も個体数の多い脊椎動物のグループ

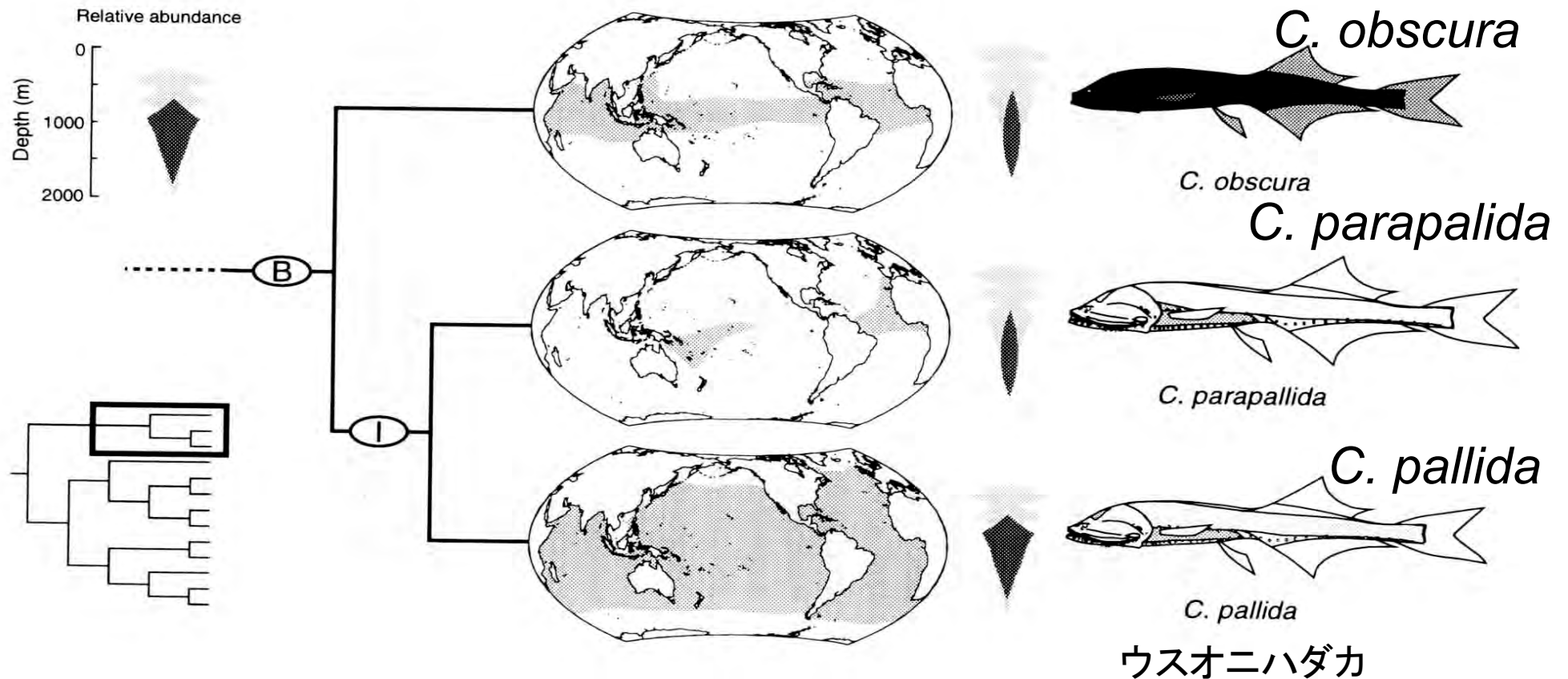
# オニハダカ属の分子系統



**Fig. 3.** The single most parsimonious tree of *Cyclothone* and outgroup taxa. Internal branches for the ingroup designated by capital letters A to L. Numbers above branches indicate bootstrap values obtained for 500 replicates and decay indices (d) up to five steps longer than the most parsimonious tree. Numbers below branches are unambiguous changes and unambiguous synapomorphies using ACCTRAN optimization. Size of fish illustrations proportional to the maximum size recorded (see Table 2).

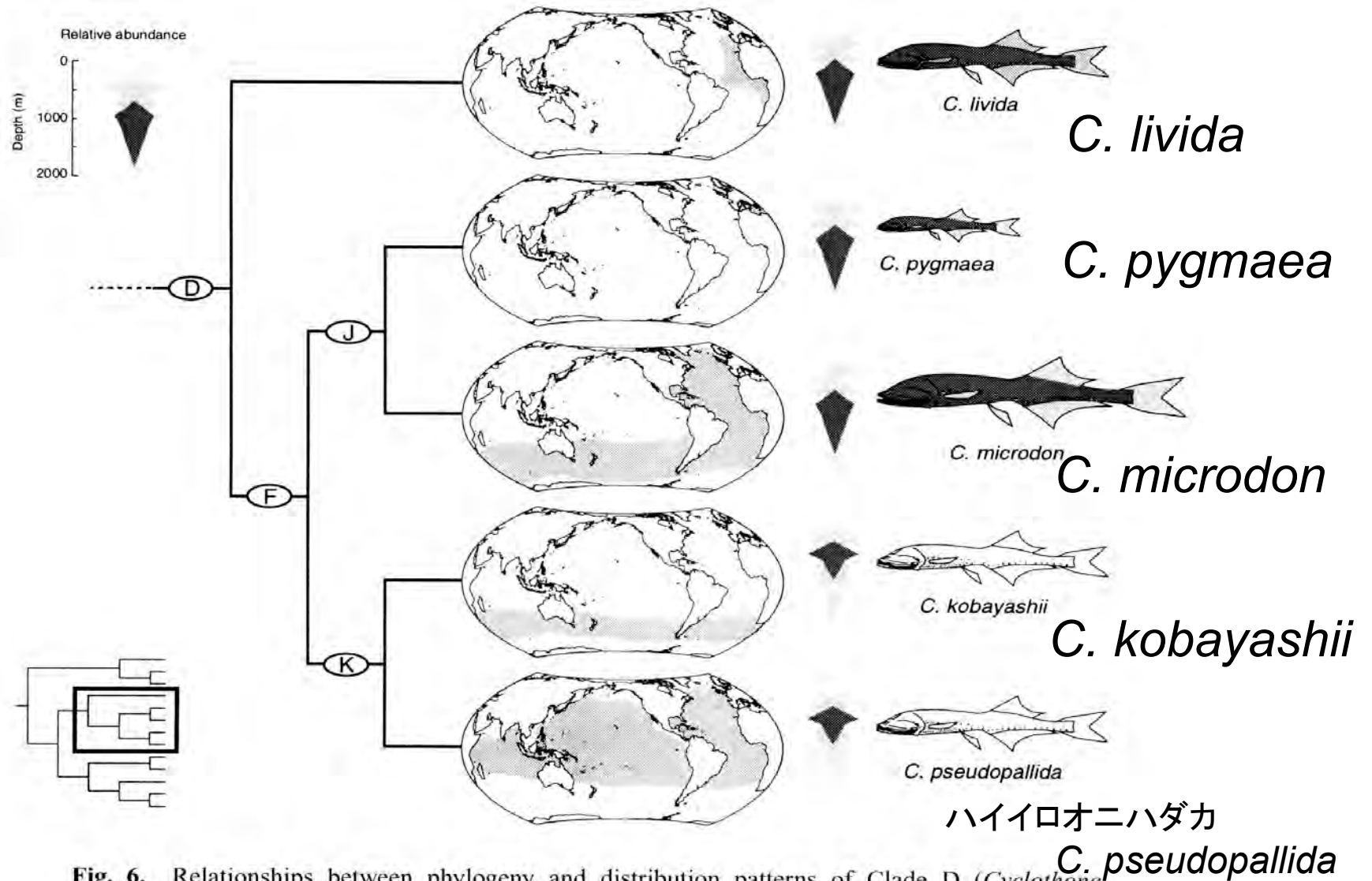


# オニハダカ属の分子系統



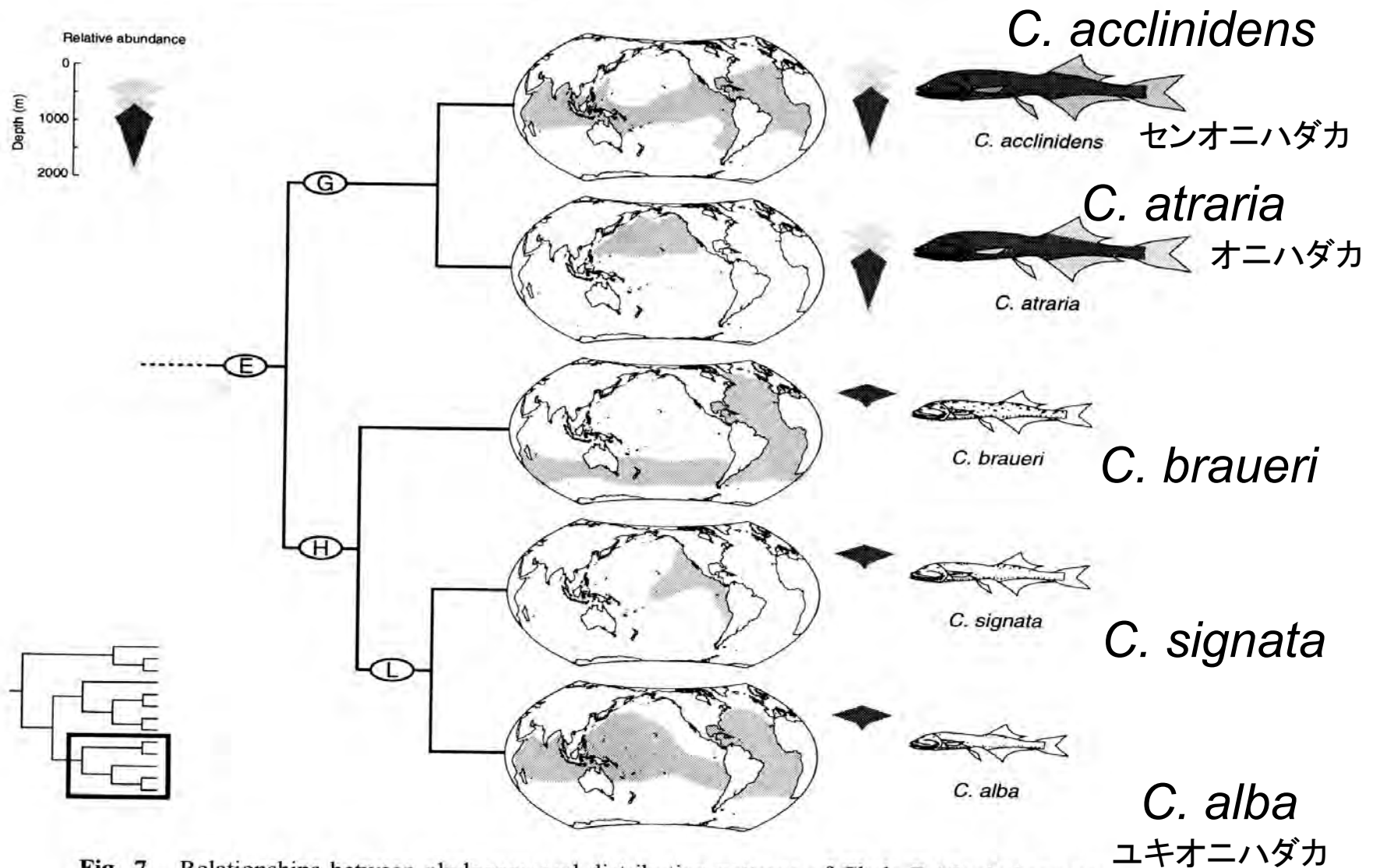
**Fig. 5.** Relationships between phylogeny and distribution patterns of Clade B (*Cyclothone obscura*, *C. parapallida* and *C. pallida*). Shaded portions of maps represent distributions based on literature (Mukhacheva, 1974; Badcock, 1982; Miya, 1994b) and unpublished records (Miya, unpubl. data). Vertical profiles of relative abundance indicated between maps and fish illustrations. Fish sizes proportional to largest size recorded.

# オニハダカ属の分子系統



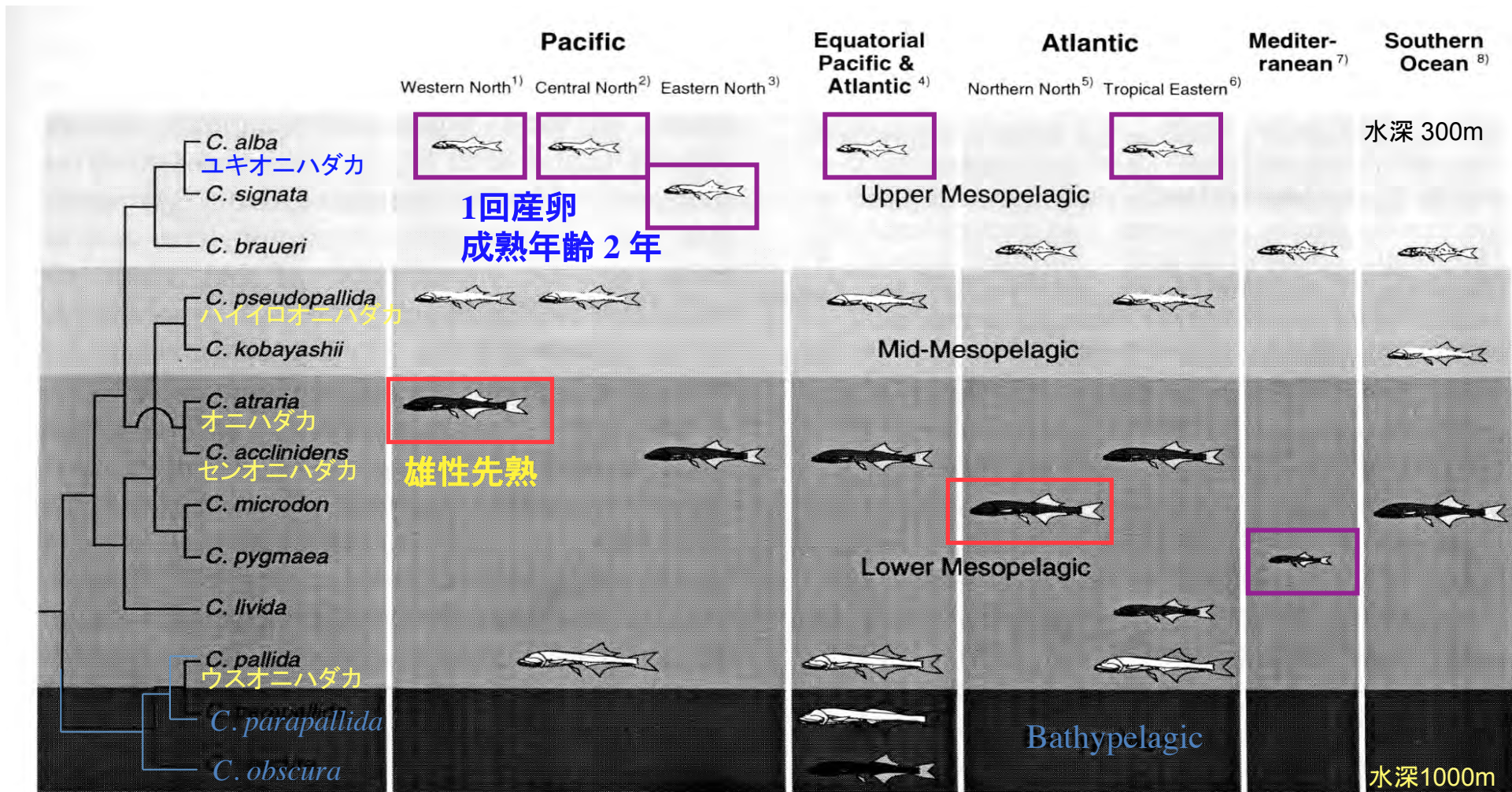
**Fig. 6.** Relationships between phylogeny and distribution patterns of Clade D (*Cyclothone livida*, *C. pygmaea*, *C. microdon*, *C. kobayashii* and *C. pseudopallida*). Shaded portions of maps represent distributions based on literature (Mukhacheva, 1974; Miya, 1994a) and unpublished records (Hartel, pers. comm.; Miya, unpubl. data). Vertical profiles of relative abundance indicated between maps and fish illustrations. Fish sizes proportional to largest size recorded.

# オニハダカ属の分子系統



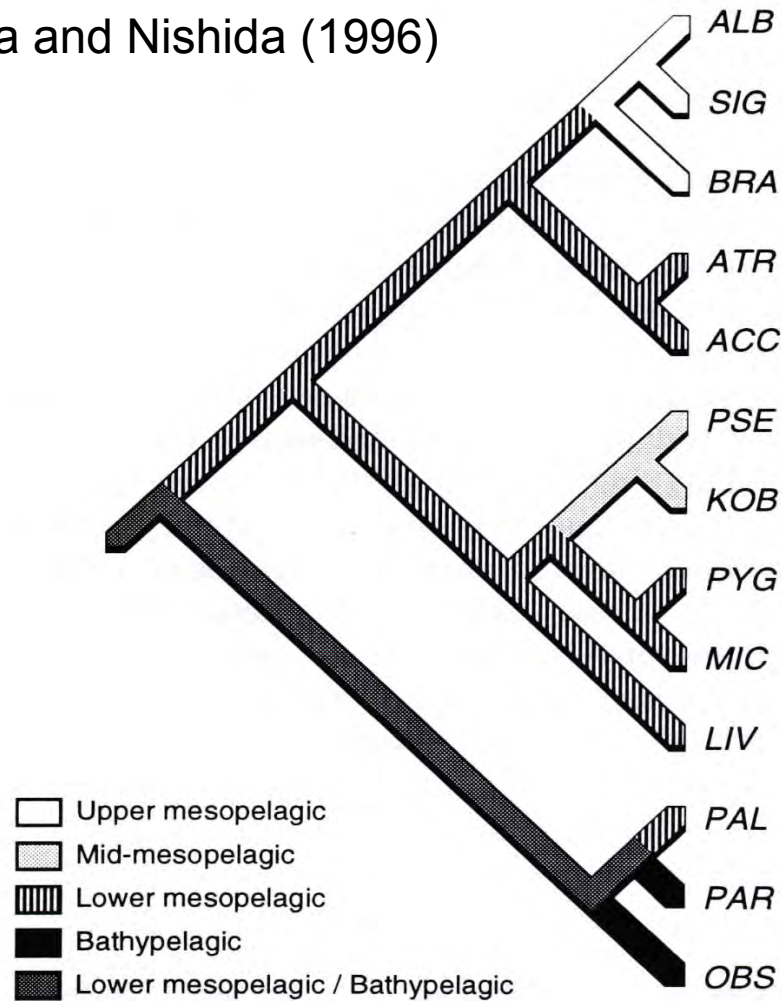
**Fig. 7.** Relationships between phylogeny and distribution patterns of Clade E (*Cyclothone acclinidens*, *C. atraria*, *C. braueri*, *C. signata* and *C. alba*). Shaded portions of maps represent distributions based on literature (Mukhacheva, 1974; Miya, 1994a) and unpublished records (Miya, unpubl. data). Vertical profiles of relative abundance indicated between maps and fish illustrations. Fish sizes proportional to largest size recorded.

# Miya and Nishida (1996): オニハダカ属の系統仮説と生息水深



**Fig. 9.** Combinations of co-dominant species in selected localities from the Pacific, Atlantic and Southern oceans and the Mediterranean Sea. No Indian Ocean data available. Vertical sequences of fishes within each depth category do not infer actual depth stratification. Fish sizes proportional to largest size recorded. Sources of information: <sup>1)</sup>Miya and Nemoto (1991); <sup>2)</sup>Maynard (1982); <sup>3)</sup>DeWitt (1972); <sup>4)</sup>Badcock (1982), Miya, unpubl. data; <sup>5)</sup>Badcock and Merrett (1976); <sup>6)</sup>Badcock and Merrett (1977); <sup>7)</sup>Goodyear et al. (1972); <sup>8)</sup>Miya (1994a).

Miya and Nishida (1996)



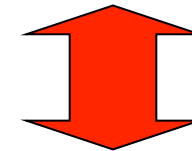
**Fig. 10.** The most parsimonious reconstruction of the four ecological groups on the molecular phylogenetic tree using MacClade ver. 3.02 (Maddison, W. P. and D. R. Maddison, 1992). Outgroup taxa used in the present study are upper-mid mesopelagic for *Margrethia obtusirostra* and *Gonostoma atlanticum* (Badcock, 1984) and lower mesopelagic for *G. gracile* (Kawaguchi, 1973). Specific names of *Cyclothone* abbreviated to first three letters.

## オニハダカ属の進化

### 浅層種

小型,早熟,1回産卵,  
産卵数が少ない

卵は300~1000個



しかし,例外も...

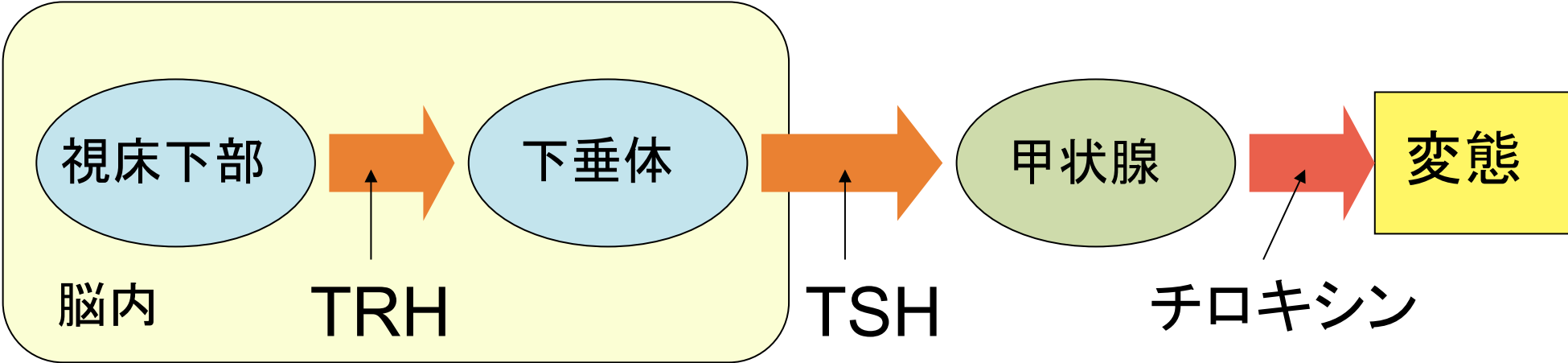
### 深層種

大型,晩熟,多数回産卵,  
産卵数が多い

卵は1500~4500個

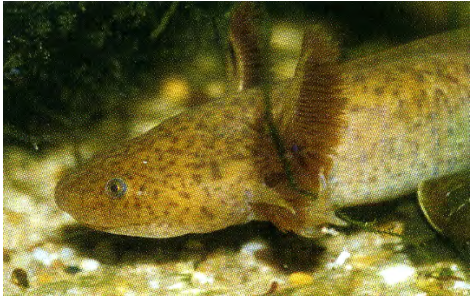
卵のサイズは0.5 mm

# アホロートルのネオテニー：変態の仕組み

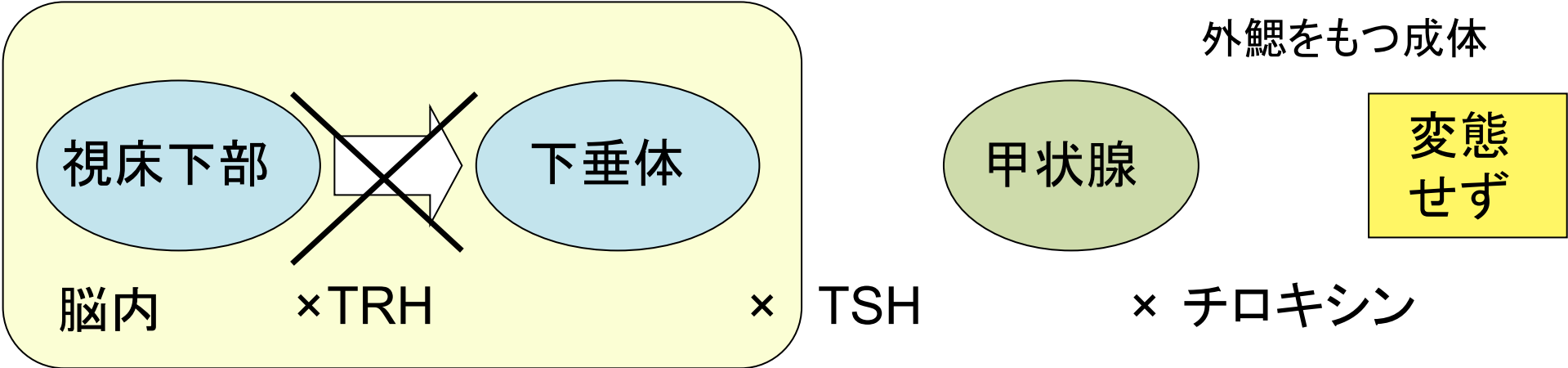


TRH=甲状腺刺激ホルモン放出ホルモン  
TSH=甲状腺刺激ホルモン

# アホロートルのネオテニー：変態の仕組み



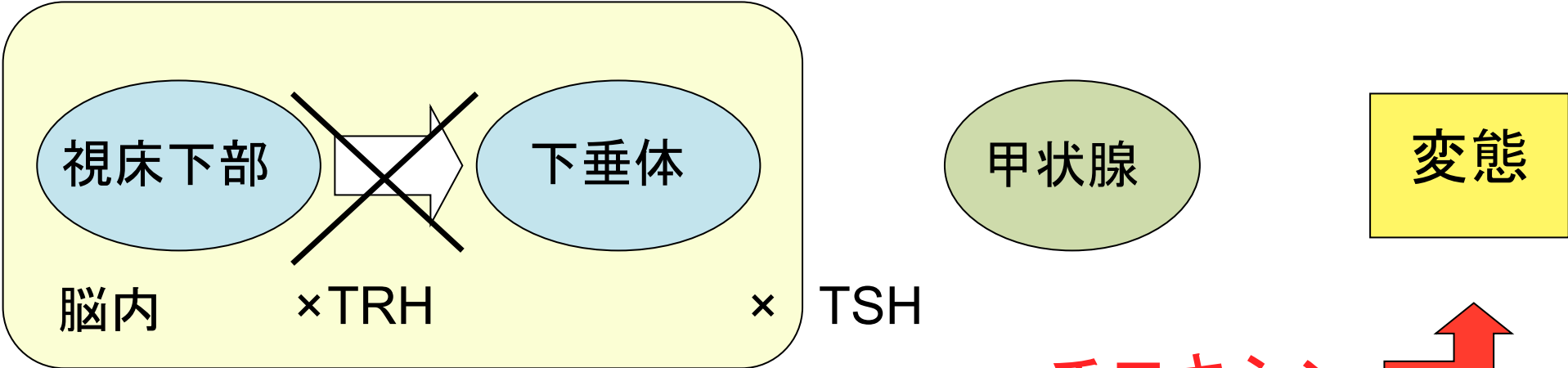
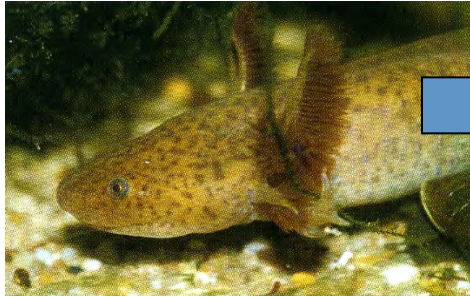
外鰓をもつ成体



TRH=甲状腺刺激ホルモン放出ホルモン  
TSH=甲状腺刺激ホルモン

最初のホルモンが放出されないために幼形化

# アホロートルのネオテニー：変態の仕組み



TRH=甲状腺刺激ホルモン放出ホルモン  
TSH=甲状腺刺激ホルモン

細胞のホルモン感受性は残っているため、変態できる

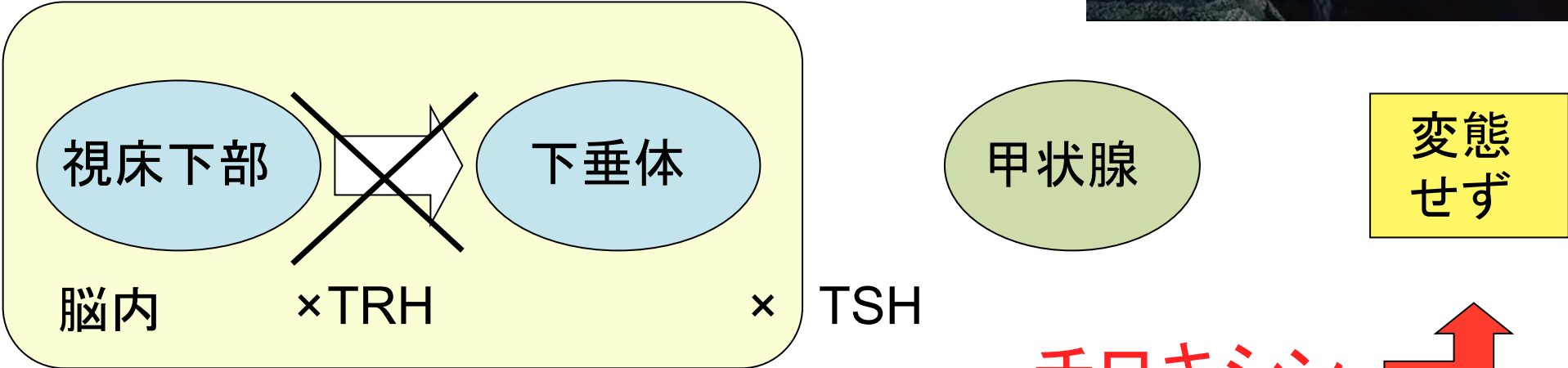




## ネオテニ一的な祖先から進化

- 1) 餌の乏しい洞窟内に生息
- 2) 極めて長期の絶食に耐える
- 3) 変態せずに10~12年後に成熟する
- 4) 寿命が極めて長い(80~100年?)
- 5) 稀に卵を産まず幼生を産む  
(通常は直径8~12ミリの卵を石の下などに産む)

# アホロートルのネオテニー：変態の仕組み



TRH=甲状腺刺激ホルモン放出ホルモン  
TSH=甲状腺刺激ホルモン

極めてネオテニーな祖先から進化  
細胞のホルモン感受性が失われた  
(環境「光」が影響)

# ペドモルフ型（ネオテニー）の動物

細胞サイズと発育速度の間に負の相関がある

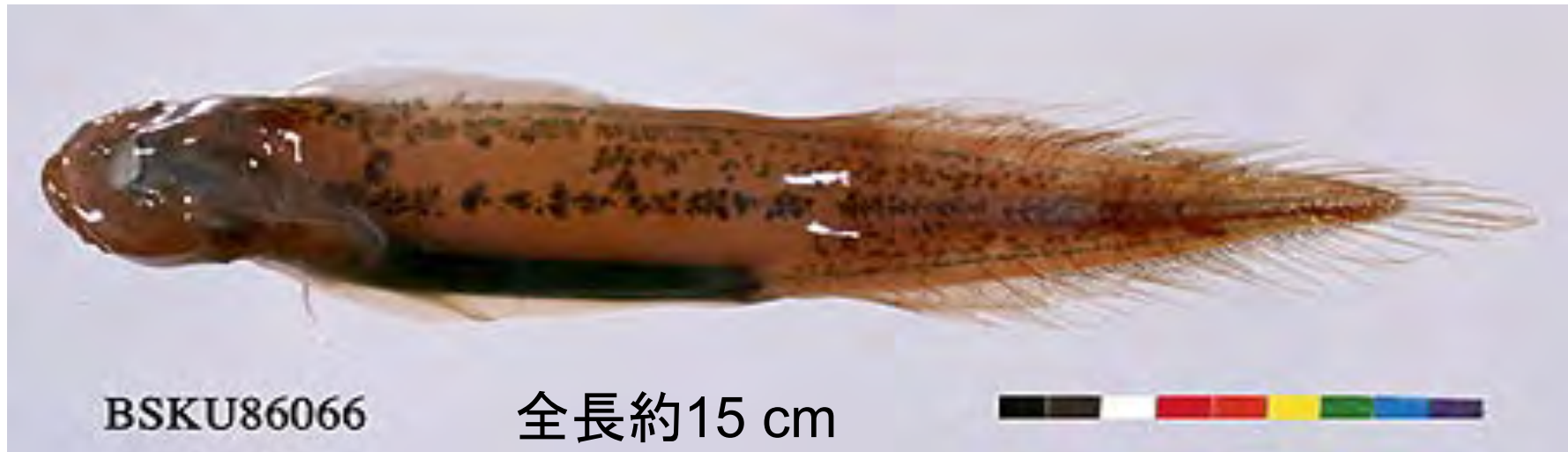
ペドモルフ型サンショウウオ類は例外的に大サイズのゲノムと高いDNA含有量をもつ

大きな細胞 → 低い呼吸量 → 経済的なエネルギー代謝

不活発であり、飢餓状態のもとで、長い時間を過ごす

# 極度にネオテニ一的な深海性魚類

ミスジオクメウオ(アシロ目オクメウオ科)



# 現生の肺魚類

レピドシレン  
(南米産)



any groups of fishes  
on can best be  
ontinental drift, lungfishes  
vater. The South  
th Lepidosiren paradoxa  
African species, such  
frican lungfish  
i (below), are more  
o one another than to  
ngfish.

プロトプテルス  
(アフリカ産)

ネオケラトドゥス  
(オーストラリア産)



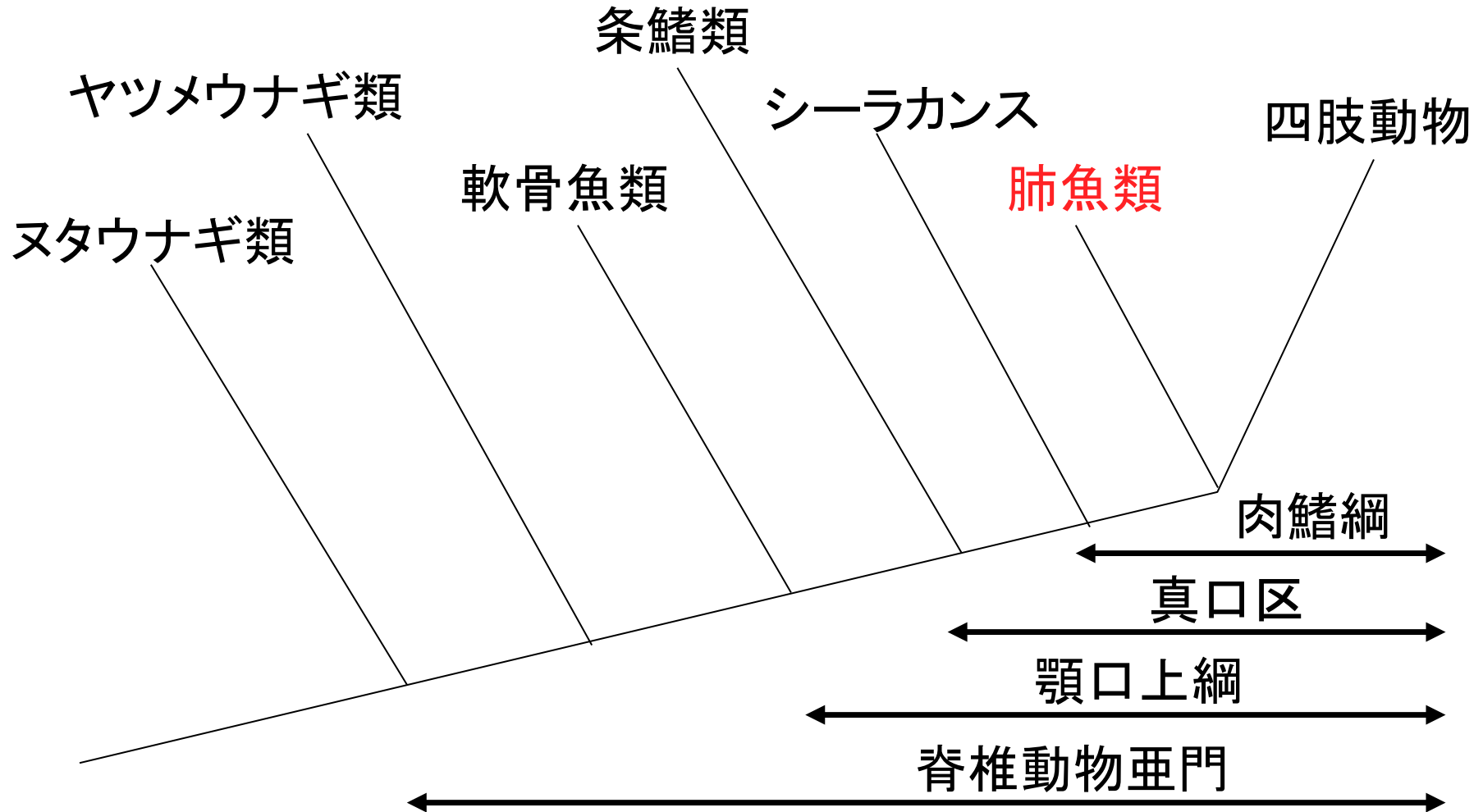
◀ Most primitive of the l  
the Australian lungfish N  
forsteri differs from the A  
American species in that  
scales, flipper-like fins, w  
gills and only one lung.  
this large species has a

Paxton and Eschmeyer (1998) Encyclopedia of fishes, 2nd ed.より

# 魚類

無顎類

硬骨魚類



# 肺魚のペドモルフ的な形態

- 1) 異形尾(歪形尾)が消失
  - 2) 前後2枚の背鰭が融合
  - 3) 鰭条数の全体的な減少
  - 4) 外骨格からコズミン質(象牙質の層)が消失
- ★現生ではシーラカンスのみがもつ
- 5) 鱗の形が菱形から円形に変化
  - 6) 全体に骨化が減衰
  - 7) 骨細胞の体積が次第に増加(化石のデータ)



極めてネオテニ一的な魚類  
低レベルの酸素中で生き延びることができる  
(鰓と肺で呼吸)

# 夏眠する肺魚

レピドシレン  
(南米産)

121ピコグラム



プロトプテルス  
(アフリカ産)

142ピコグラム



# ネオケラトドウス(オーストラリア産)



本属では化石のデータから過去2億5000万年の間、  
細胞サイズは増大しなかったことが判明

他の肺魚に比べ、細胞のゲノム当りのDNA量は少ない

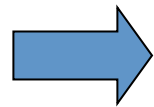
★夏眠しない

80ピコグラム

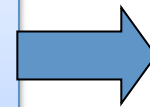
# 肺魚における細胞サイズの進化

- 魚類では最大の細胞体積をもつ
- ゲノム当りのDNA量が極めて多い
- 泥の中で夏眠する能力をもつ

成長速度  
の低下  
(ネオテニー)



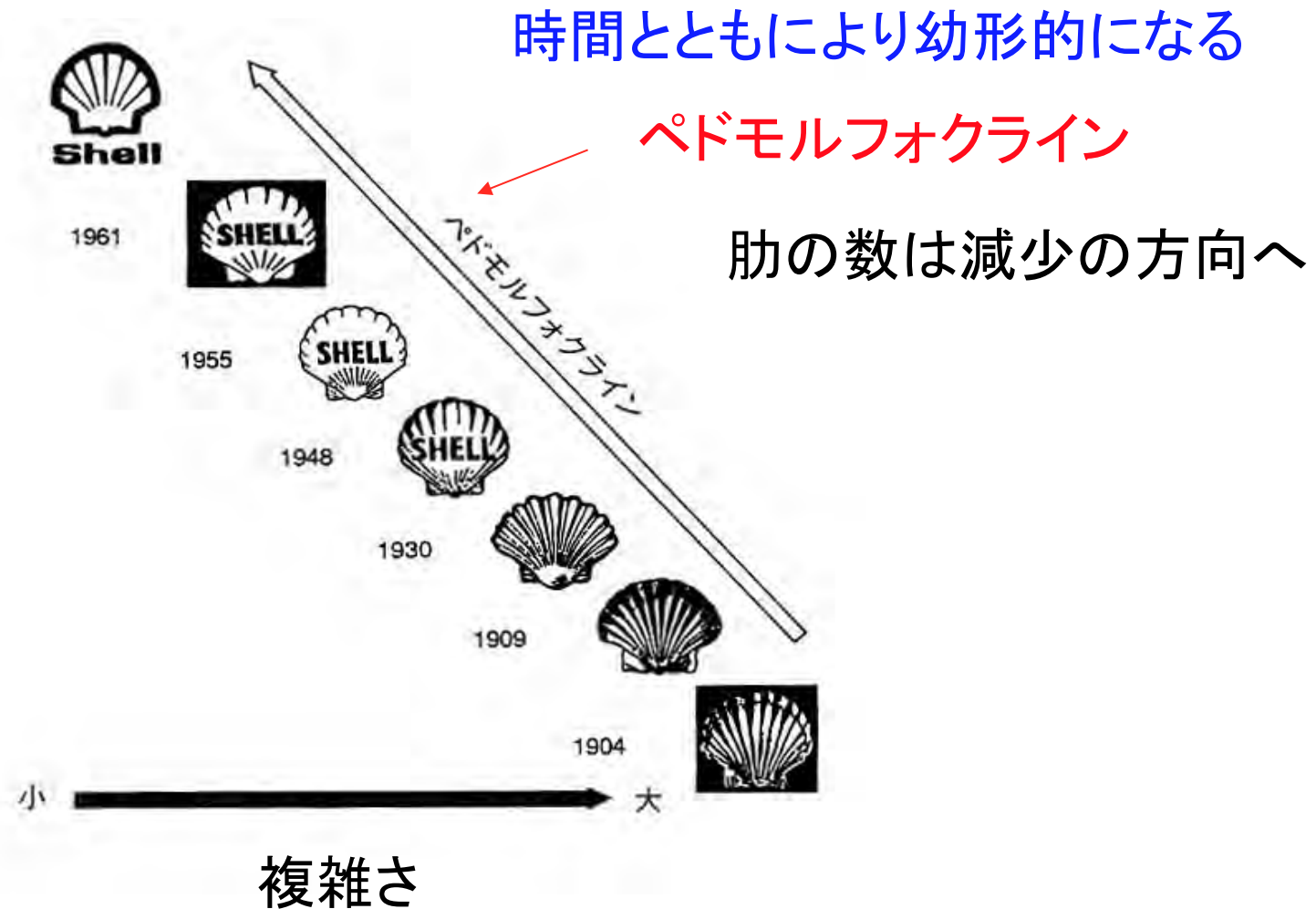
長い細胞周期による  
大きなサイズの細胞  
と大量のゲノムを獲得



呼吸速度  
が低い  
代謝が低い

淘汰・選択に有利？

# シェル石油のマークも進化した？



マクナマラ(2001)“動物の発育と進化”より



Mickey Mouse in the early 1930s (*far left*), looking in some amazement at his more juvenile-like namesake fifty years later (*far right*). “The Evolution of Mickey Mouse” © Disney Enterprises, Inc.

Snoopy today (*right*): a paedomorphic dog, little more than an overgrown puppy. Snoopy (*below*) not long after he was born in October 1950: a “normal”-looking dog.  
Snoopy: © 1958 United Feature Syndicate, Inc.



## 漫画も進化する？

時代とともに幼形的に...



McNamara (1997)  
“Shape of time”より