Of Fin and Mouth: the Evolution of Feeding and Locomotion in Seals, Sea Lions, and Walruses

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WHAT IS A MARINE MAMMAL?

- Any mammal with a primary dependence on the marine environment for existence.

Cetaceans

Sea Otter

Polar Bear

Pinnipeds

Sirenia

PROBLEMS FACING A MARINE MAMMAL:

- Respiration
- Insulation
- Pressure
- Buoyancy
- Sense organs
- Salinity
- **Locomotion**
- **Prey capture**

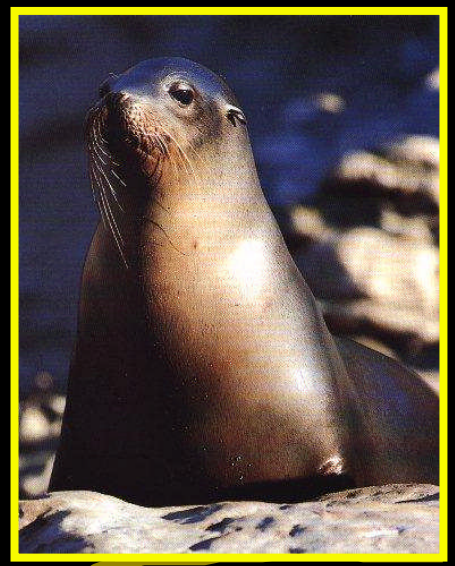
…others…

- Marine mammal research challenging:
  - observation difficult
  - animals are very large
  - boats/diving expensive

- Much of our knowledge about marine mammals comes from strandings and exploitation

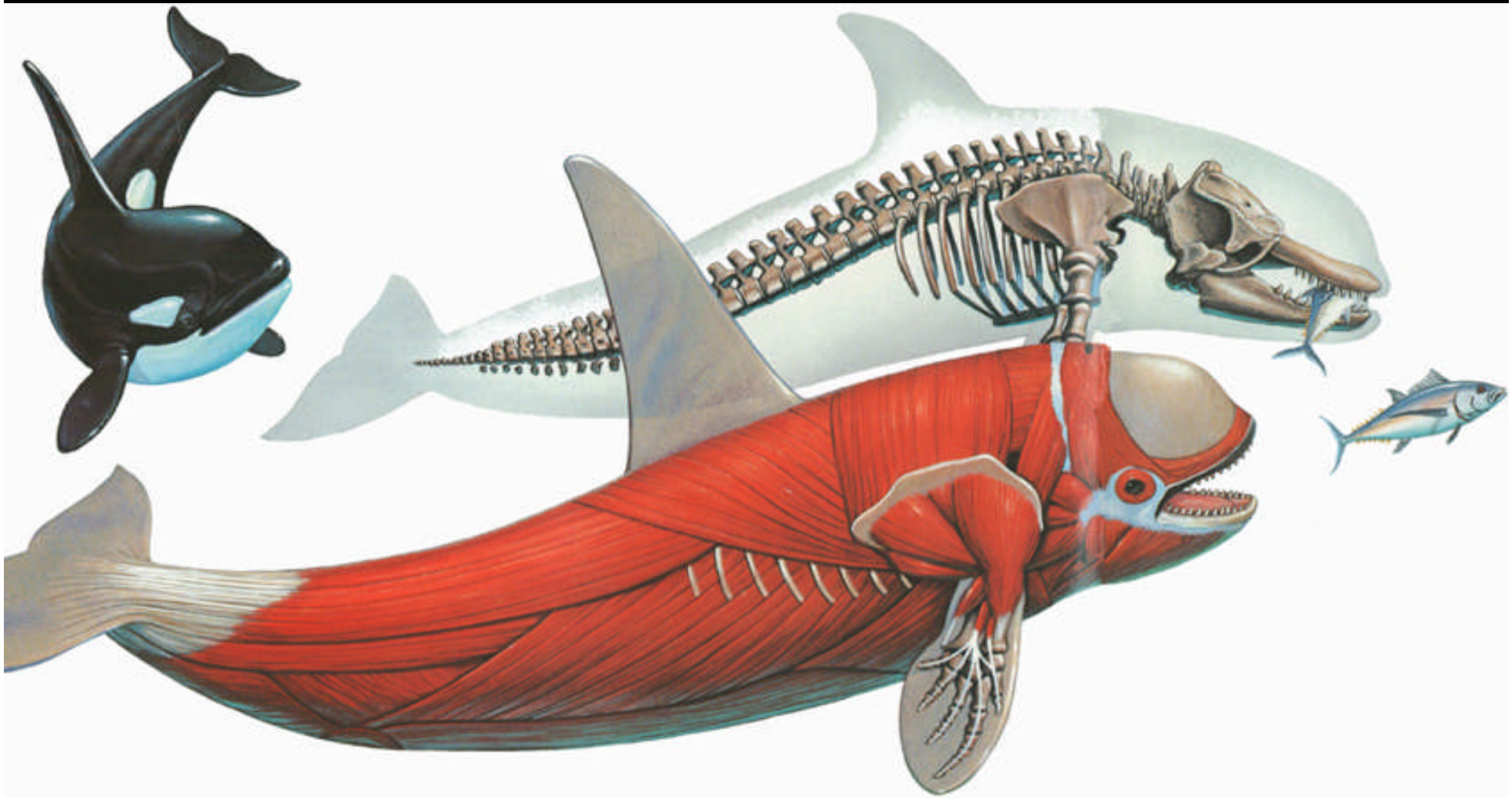
On Land 10-40% of Time

- resting
- molting
- raising young
- (mating)



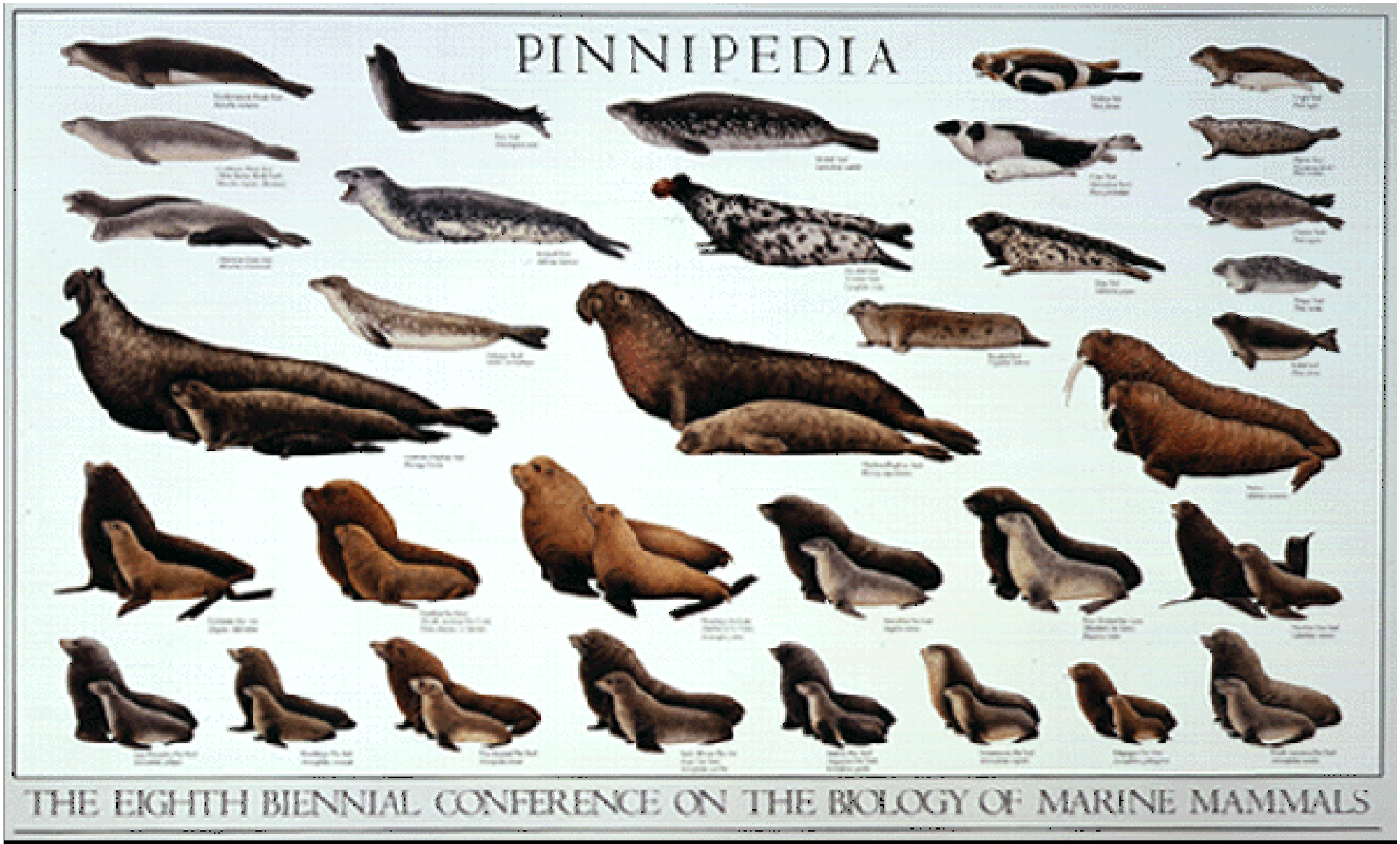
In Water 60-90% of Time

- foraging
- playing
- (mating)



OUTLINE

- What are pinnipeds?
    - Introduction
    - Phylogenetics
- Evolution of pinniped feeding
- Evolution of pinniped locomotion
- West Indian monk seal



- 34 species in 18 genera and 3 families

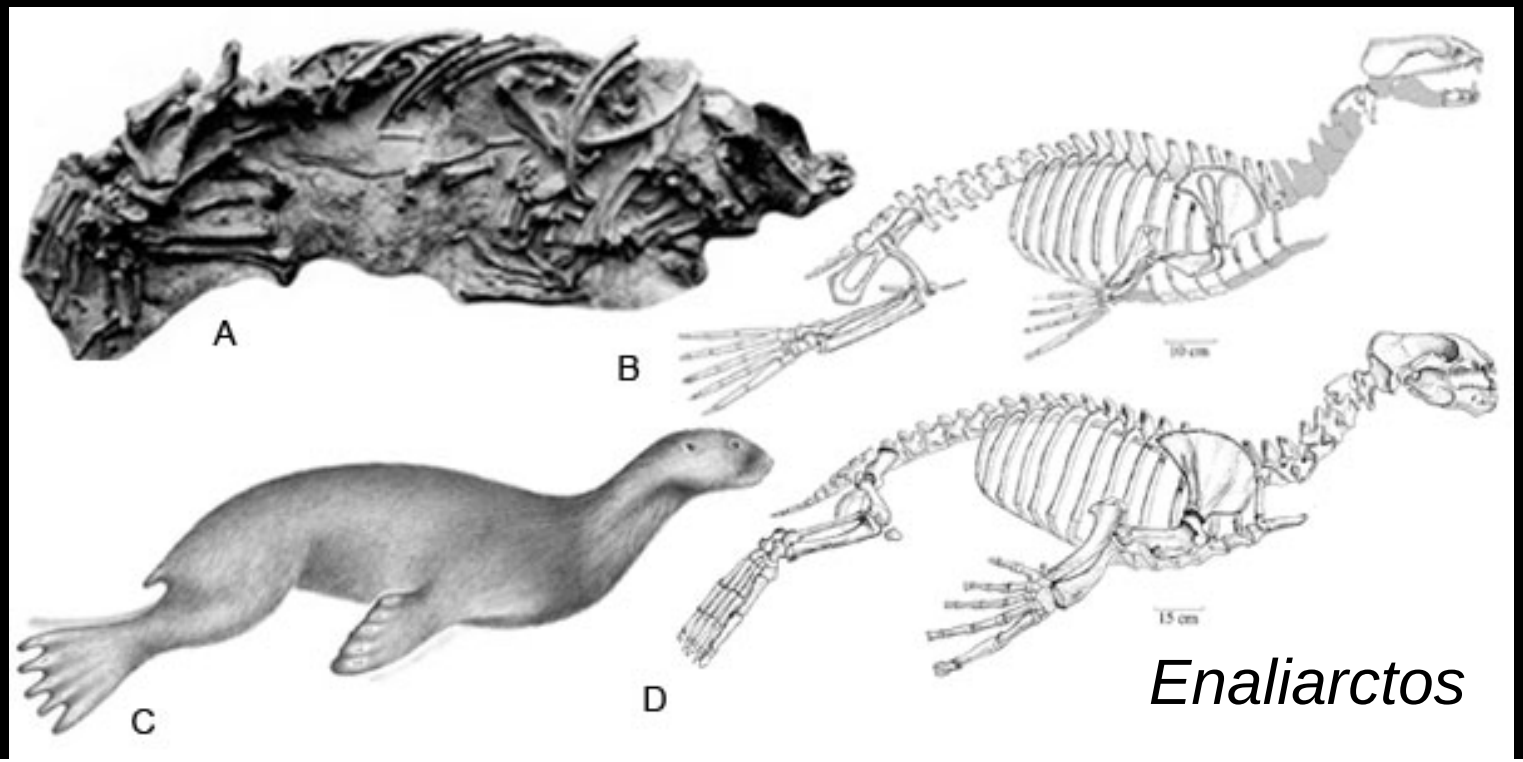
OTARIIDAE - SEA LIONS and FUR SEALS

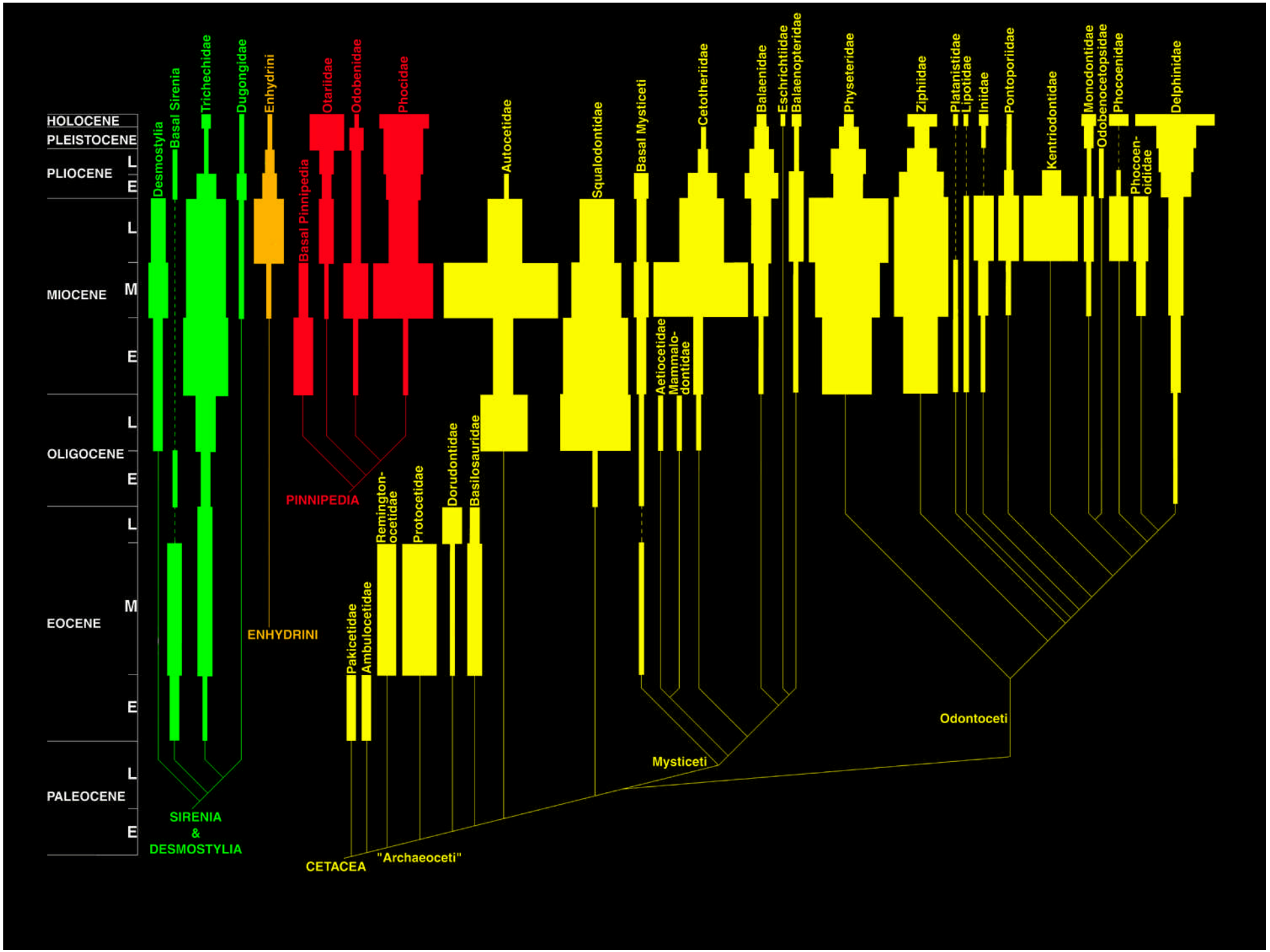
PHOCIDAE - HAIR or ‘TRUE’ SEALS

ODOBENIDAE - WALRUSES

Early Pinnipeds

- Early Miocene (37 mya) - present
- Cosmopolitan (N. Pacific origin)
- Seal-like bodies
- Amphibious




HOLOCENE
PLEISTOCENE
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MIOCENE
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OLIGOCENE
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EOCENE
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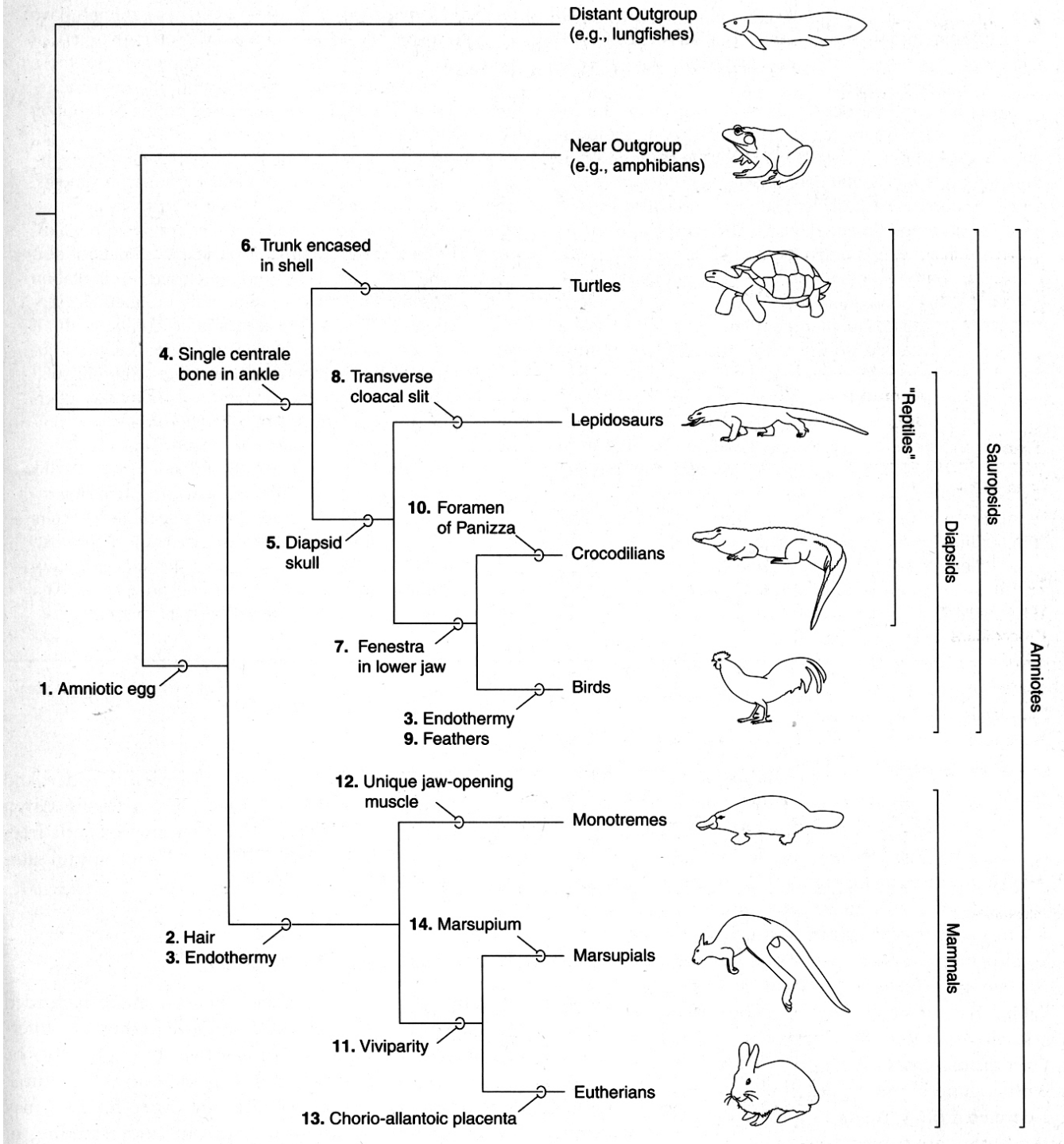
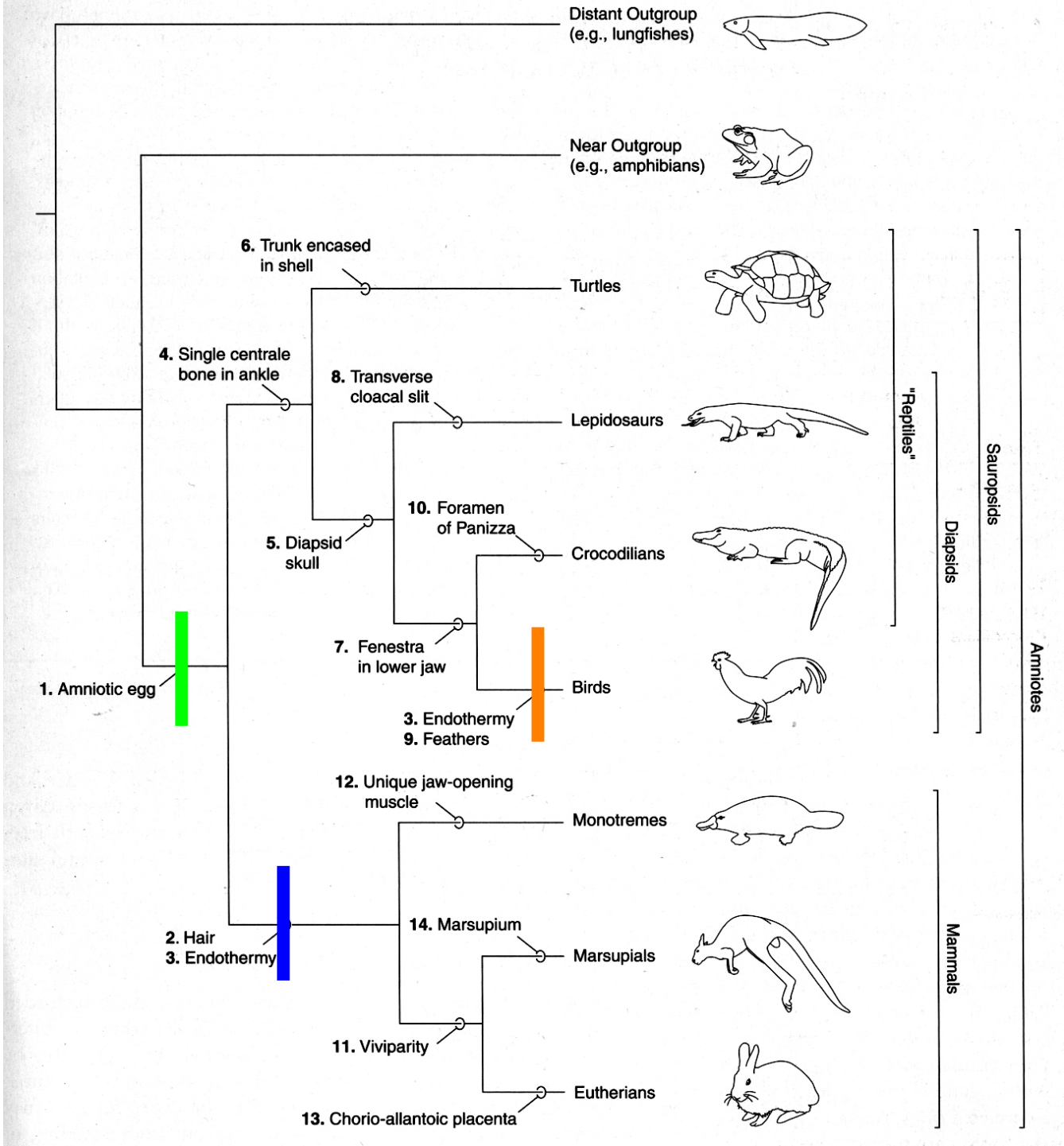
E
PALEOCENE
L
E
Desmostylia
Basal Sirenia
Trichechidae
Dugongidae
Enhydrini
Otariidae
Odobenidae
Phocidae
Basal Pinnipedia
Autocetidae
Squalodontidae
Basal Mysticeti
Cetotheriidae
Balaenidae
Eschrichtiidae
Balaenopteridae
Physeteridae
Ziphiidae
Platanistidae
Lipotidae
Iniidae
Pontoporiidae
Kentriodontidae
Monodontidae
Odobenocetopsidae
Phocoenidae
Phocoen-
oididae
Delphinidae
Aetiocetidae
Mammalo-
dontidae
PINNIPEDIA
Remington-
ocetidae
Protocetidae
Dorudontidae
Basilosauridae
Pakicetidae
Ambulocetidae
ENHYDRINI
Odontoceti
Mysticeti
SIRENIA
&
DESMOSTYLIA
CETACEA
"Archaeoceti"



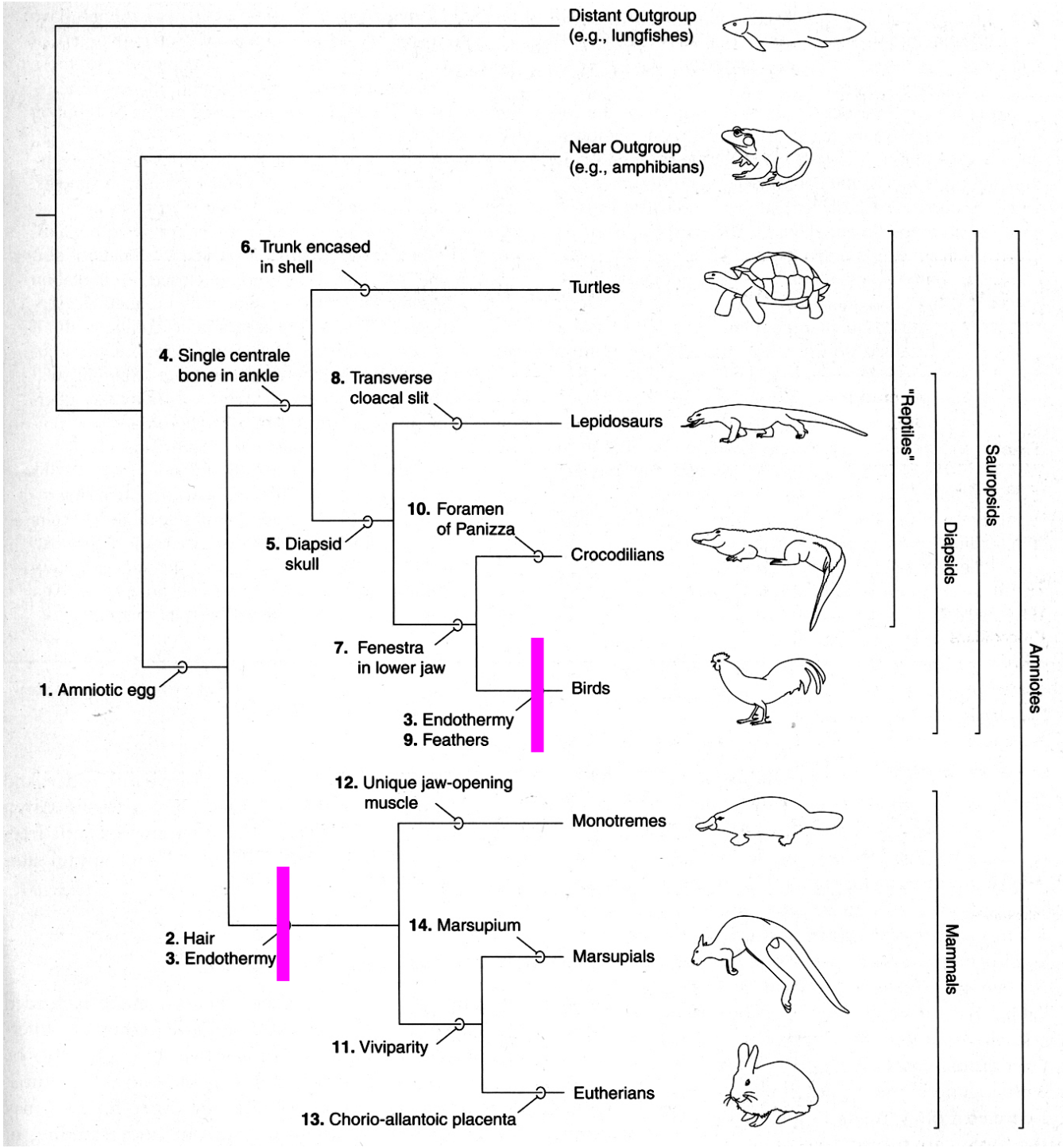
Phylogenies

- depict evolutionary relationships
- show relative timing of lineage divergences
- constructed using many "polar" characters



Phylogenies

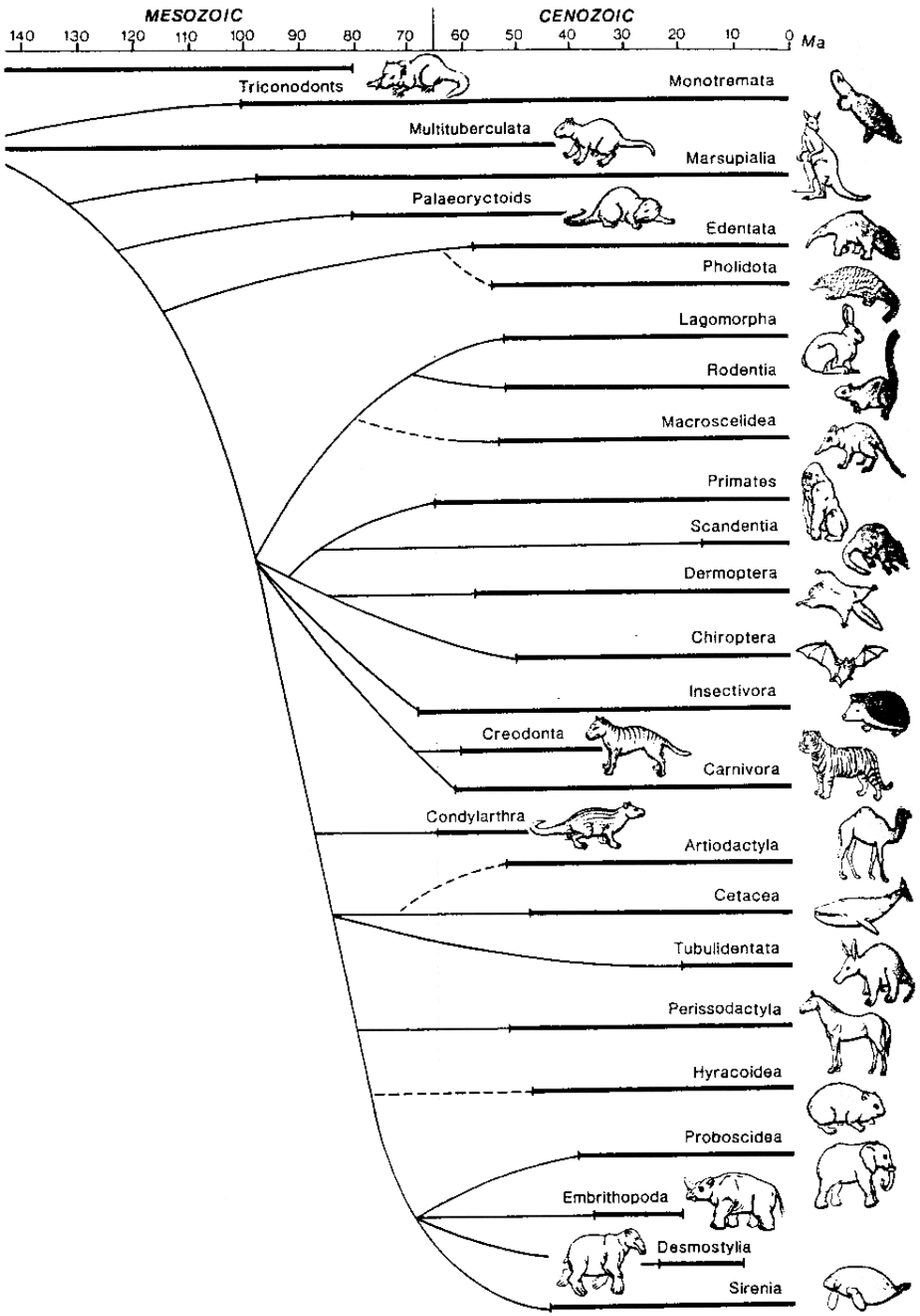
- useful for mapping the evolution of interesting traits:
- Amniotic egg in amniotes
- Feathers in birds
- Hair in mammals



Phylogenies

- useful for identifying incidence of convergence and other interesting evolutionary phenomena:

- Warm-bloodedness in birds and mammals



- Marine sloth (Pliocene)

Marine bear (Miocene)
- Pinnipedia (Oligocene)

Sea Otter (Miocene)

- Cetacea (Eocene)

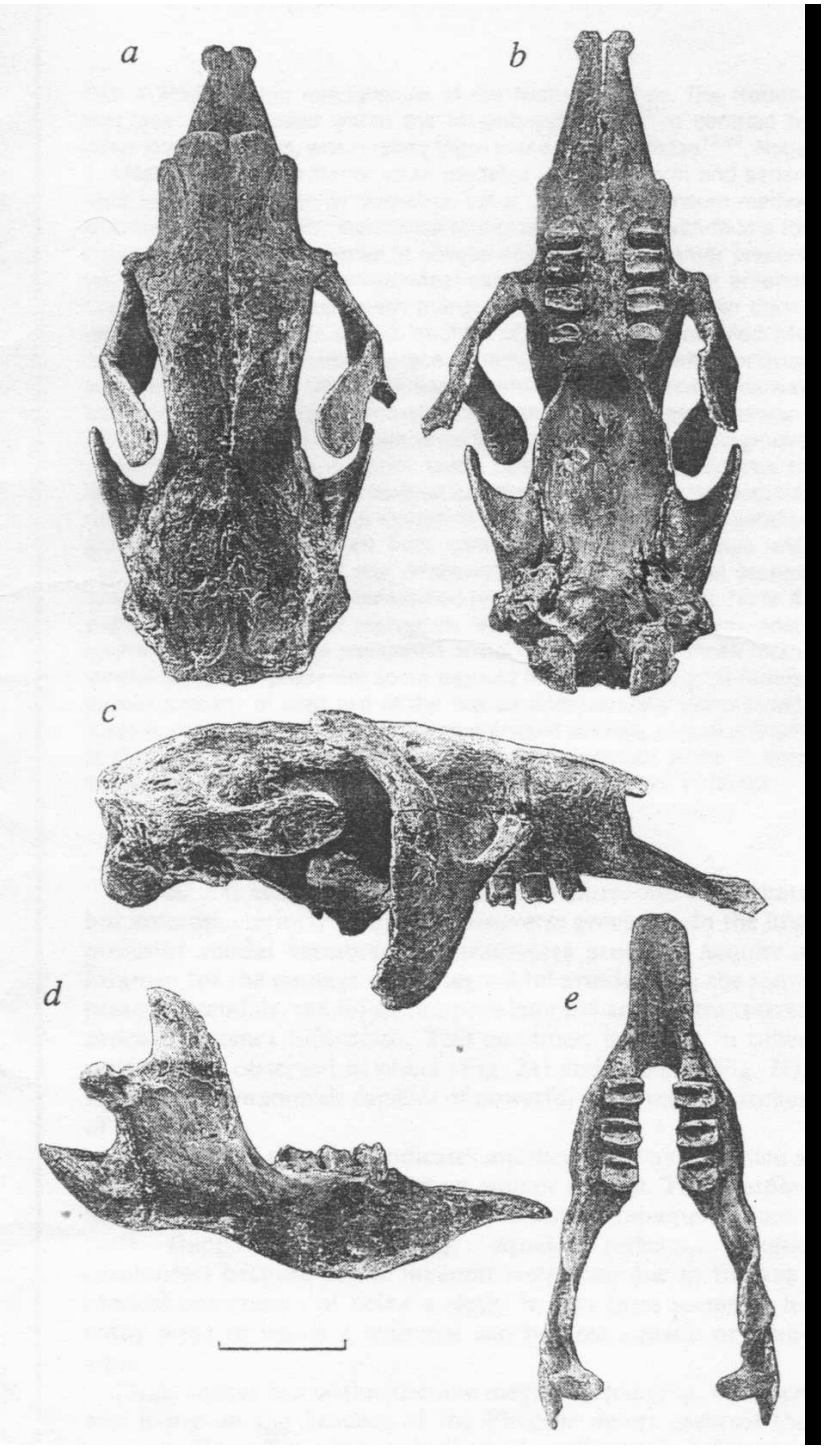
Desmostylia (Oligocene)
- Sirenia (Eocene)

Thalassocnus

- Marine sloth (5 spp.)
- Xenarthra
- Pliocene of Peru

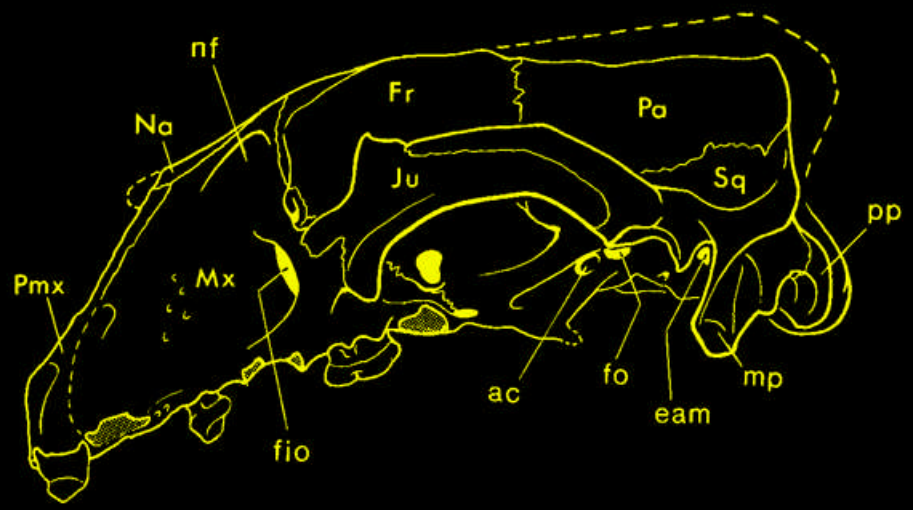
HABITS:

- herbivorous (algae)
- near-shore
- not a strong swimmer



Kolponomus

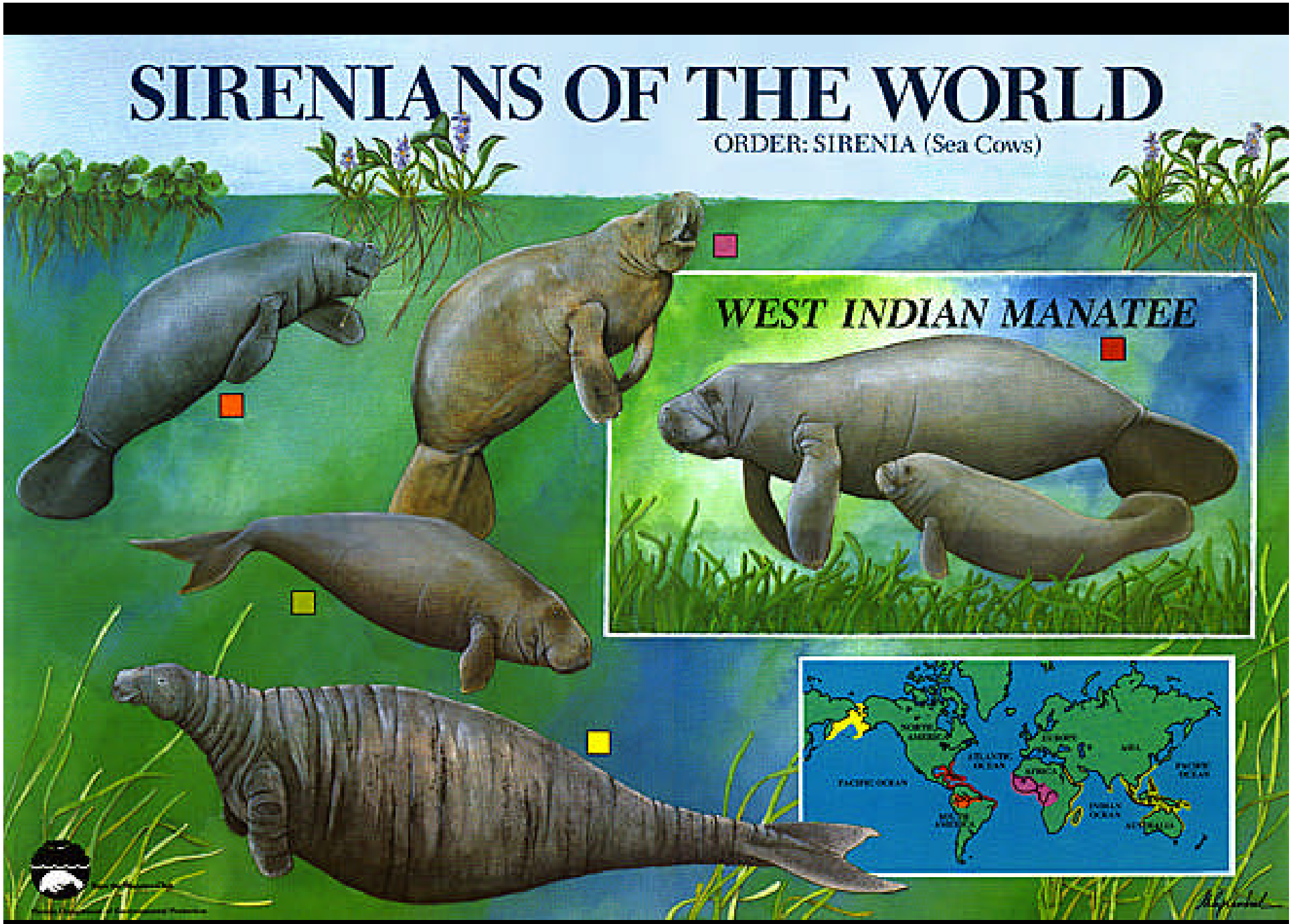
- Marine bear (4 spp.)
- Carnivora (Laurasiatheria)
- E. Miocene of NE Pacific



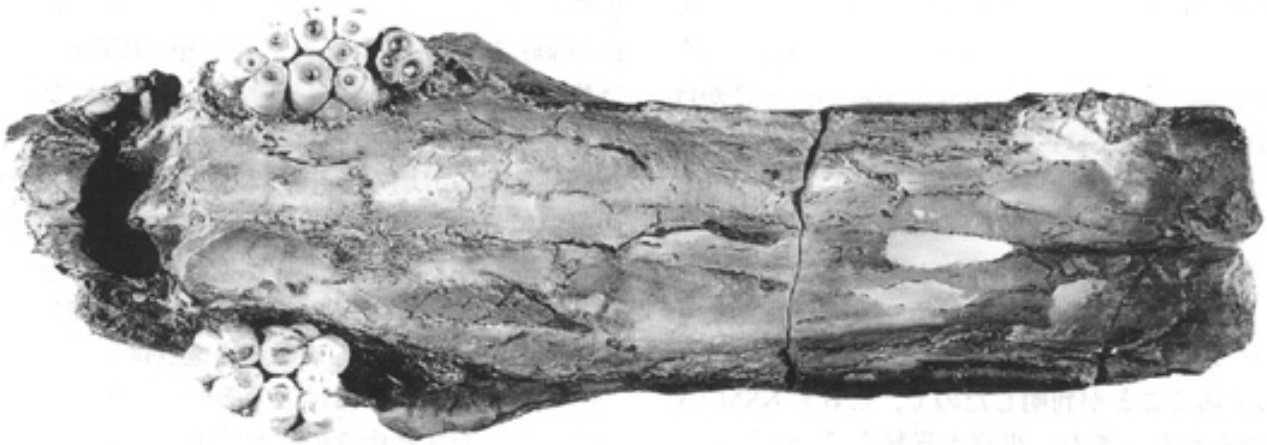
Kolponomus

HABITS:

- **carnivorous (inverts?)**
- **near-shore**
- **not a strong swimmer**

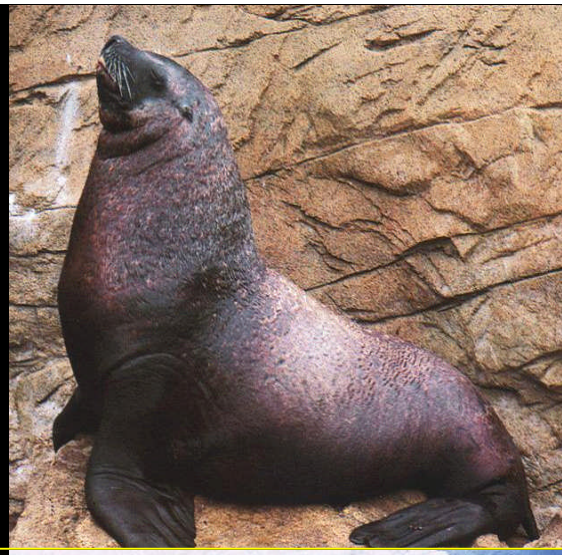

SIRENIANS OF THE WORLD
ORDER: SIRENIA (Sea Cows)
WEST INDIAN MANATEE

Desmostylus



OTARIIDAE - fur seals & sea lions

- 14 extant species
- ~10 fossil species



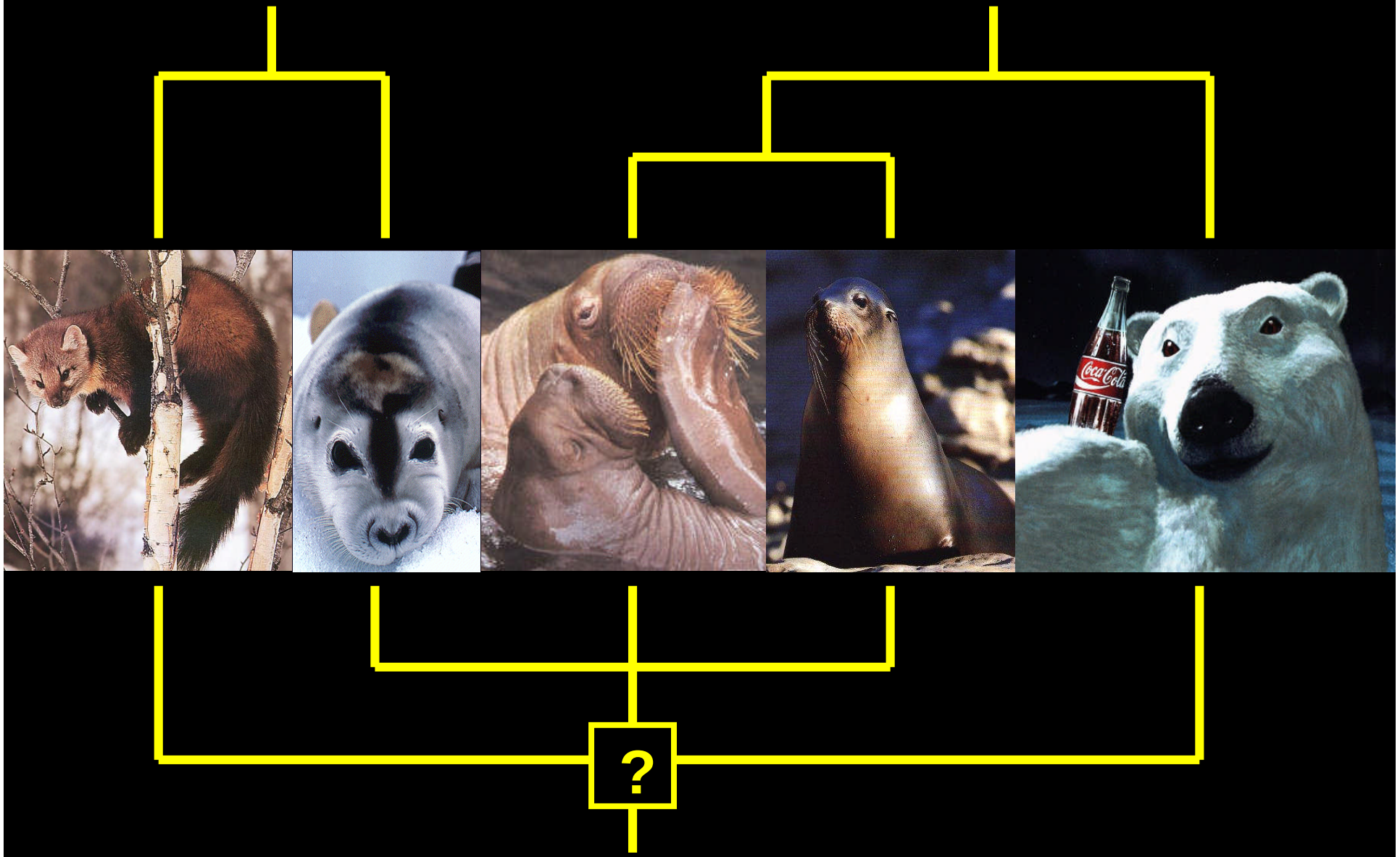
PHOCIDAE - “true” seals

- 19 extant species
- ~30 fossil species

ODOBENIDAE - walruses

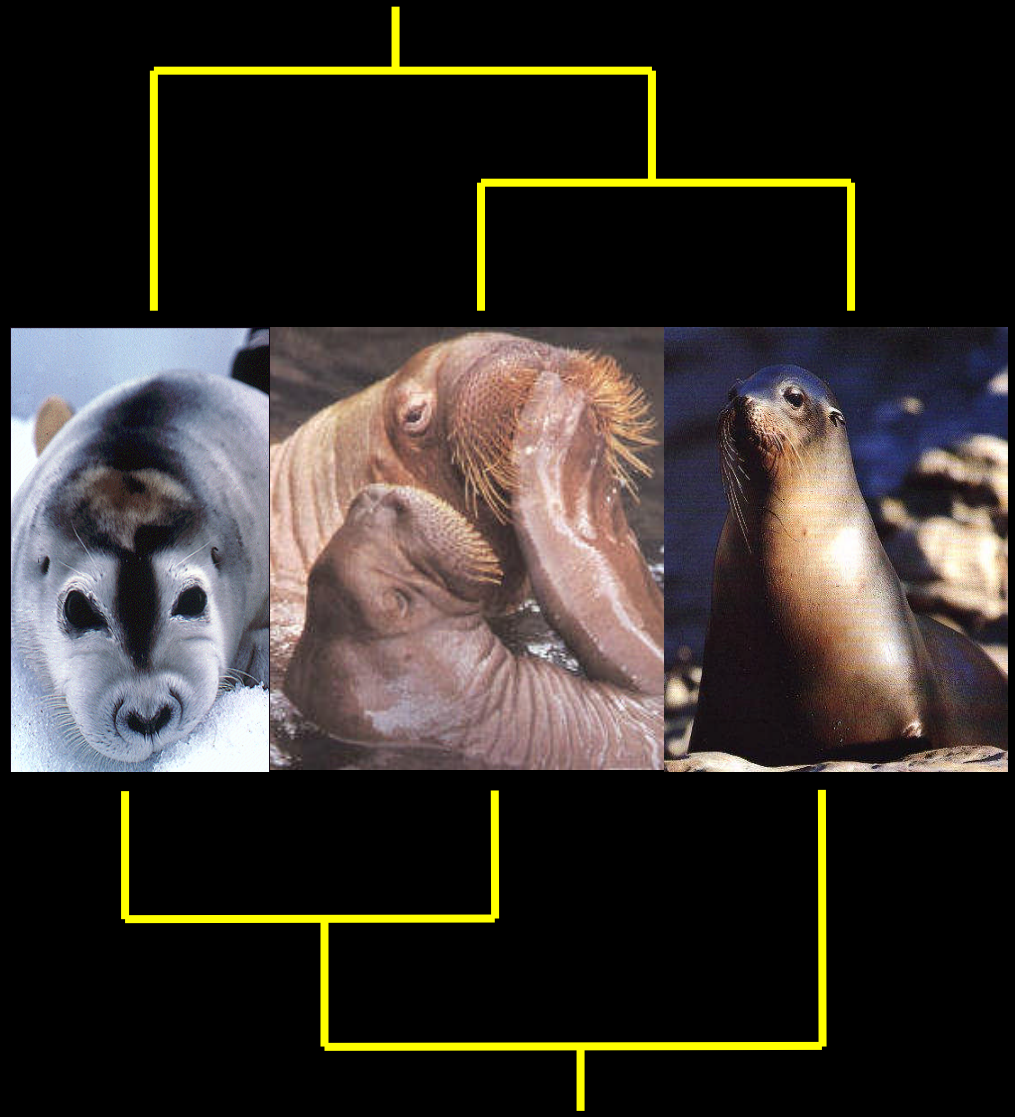
- 1 extant species
- ~15 fossil species

PINNIPED DIPHYLY



PINNIPED MONOPHYLY

“OTARIOIDEA”



“PHOCOMORPHA”

OVERVIEW

PURPOSE - examine evolutionary history of locomotion (terrestrial and swimming) & feeding strategies in pinnipeds

TOOLS - phylogenetic systematics & comparative/ functional anatomy

STEPS -

1. Establish phylogenetic hypothesis (“Total Evidence”)
2. Find functional osteological characters linked with locomotor & feeding strategies exhibited by extant species
3. Establish probable locomotor & feeding strategies of fossil taxa
4. Describe trends of these strategies

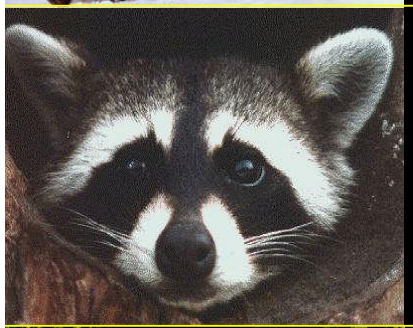
PHYLOGENETIC ANALYSIS - OUTGROUPS

Canidae

- *Canis lupus*
- *Dusicyon culpaeus*
- *Vulpes vulpes*

Ursidae

- *Ursus maritimus*
- *Tremarctos ornatus*
- *Selenarctos thibetanus*
- *Helarctos malayanus*
- *Ailuropoda melanoleuca*
- † *Kolponomos* sp.

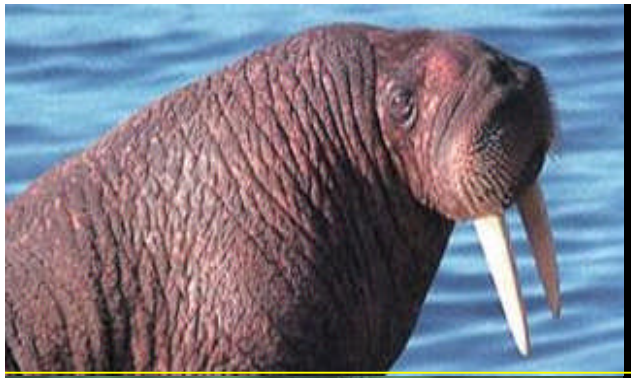


Procyonidae

- *Procyon lotor*
- *Ailurus fulgens*
- *Bassaricyon gabbii*
- *Nasua nasua*
- *Potos flavescens*

Mustelidae

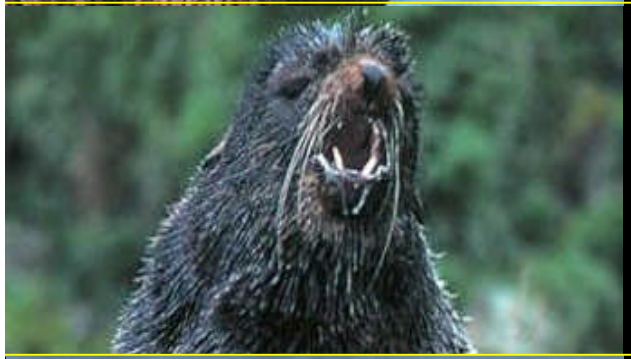
- *Mustela vison*
- *Mephitis mephitis*
- *Taxidea taxus*
- *Enhydra lutris*
- *Martes americana*
- *Lutra canadensis*
- *Lutra lutra*



Odobenid-like

- *Odobenus rosmarus*

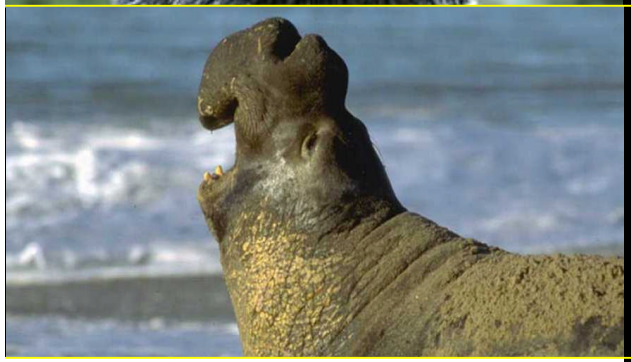
† *Aivukus cedroensis*
† *Alachtherium* n. sp.
† *Dusignathus seftoni*
† *Gomphotaria pugnax*
† *Imagotaria downsi*
† *Pontolis magnus*
† *Protodobenus japonicus*
† *Prototaria planicephala*
† *Pseudotaria* n. sp.
† *Valenictus chulavistensis*



Otariid-like

- 14 Extant Species

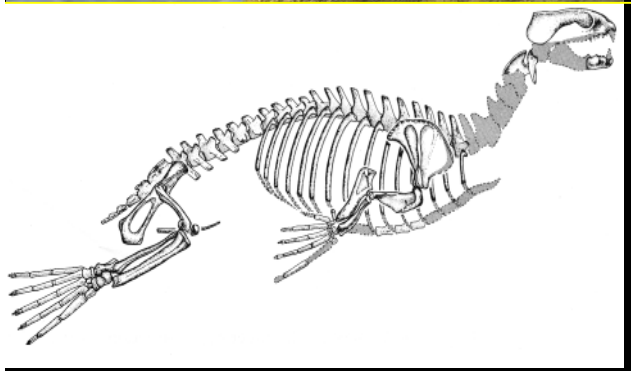
† *Thalassoleon macnalleyi*
† *Thalassoleon mexicanus*



Phocid-like

- 19 Extant species

† *Acrophoca longirostris*
† *Allodesmus courseni*
† *Allodesmus kernensis*
† *Desm. brachycephala*
† *Desm. oregonensis*
† *Homiphoca capensis*
† *Piscophoca pacifica*



Basal Pinnipeds

† *Enaliarctos mealsi*
† *Pinnarctidion rayi*
† *Pteronarctos goedertae*

PHYLOGENETIC ANALYSIS - CHARACTERS

IA. Morphological Characters (Sources):

- Barnes 1989
- Berta 1991
- Berta 1994a
- Berta 1994b
- Berta and Adam (in prep.)
- Berta and Deméré 1986
- Berta and Deméré (in press)
- Berta and Deméré (in prep.)
- Berta and Wyss 1994
- Bininda-Emonds and Russell 1996
- Deméré 1994
- Kohno 1994a
- Kohno 1994b
- Kohno 1996
- Kohno 1998
- Tedford 1994
- Wozencraft 1989
- Wyss 1987
- Wyss 1988
- Wyss and Flynn 1993
- New Characters (25)

IB. Morphological Characters (Numbers):

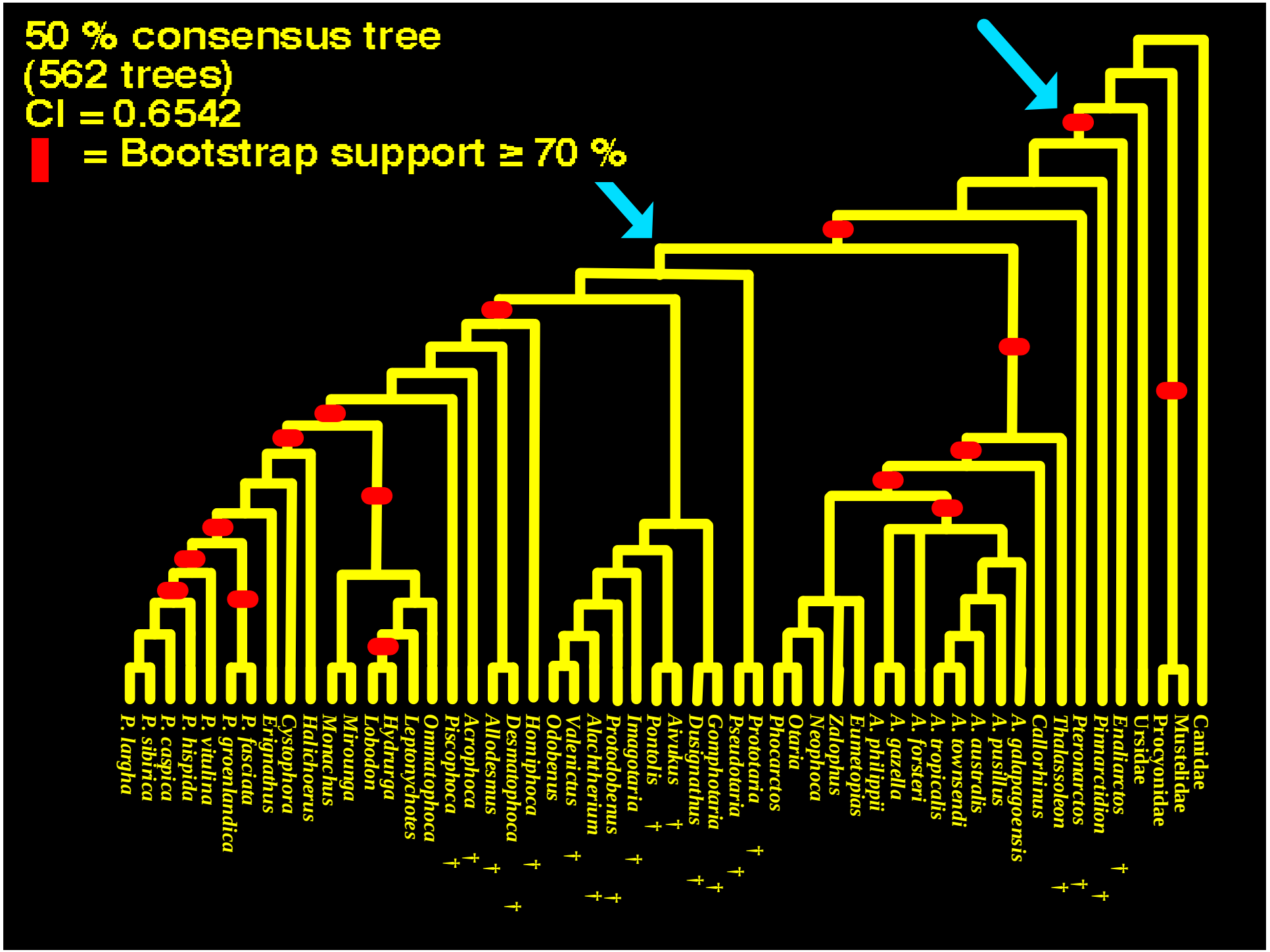
- Skull/Dentition - 384
- Mandible - 20
- Postcranial Skeleton - 112
- Soft Anatomy/Miscellaneous - 37

TOTAL - 553

MOLECULAR	SEQUENCE	INFORMATIVE
Cytochrome *b*	1140	963
12S rDNA	1004	308
16S rDNA	720	161
Valine (tRNA)	83	33
Aldolase *A*	484	16
Aldolase *C*	273	1
H2AF	368	7
H2AF (pseudogene)	316	3
Transthyretin	1088	336
Alpha Haemoglobin	141	31
Beta Haemoglobin	146	24
SUBTOTAL	5763	1883
MORPHOLOGICAL		553
TOTAL		2436

PAUP 4.0b2

- Equal weights, heuristic search, polymorphism enforced

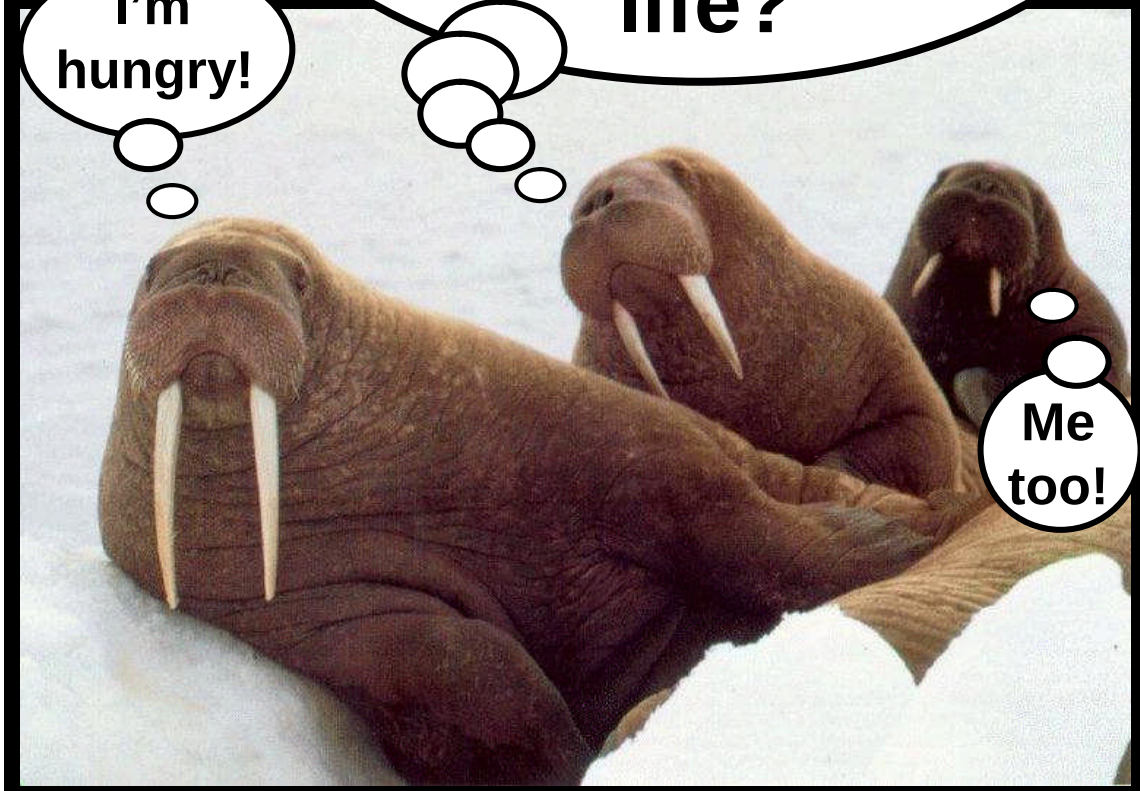

50 % consensus tree
(562 trees)
CI = 0.6542
= Bootstrap support ≥ 70 %
Canidae
Mustelidae
Procyonidae
Ursidae
Enaliarctos
Pinnarctidion
Pteronarctos
Thalassoleon
Callorhinus
A. galapagoensis
A. pusillus
A. australis
A. townsendi
A. tropicalis
A. forsteri
A. gazella
A. philippii
Eumetopias
Zalophus
Neophoca
Otaria
Phocarctos
Prototaria
Pseudotaria
Gomphotaria
Dusignathus
Aivukus
Pontolis
Imagotaria
Protodobenus
Alachtherium
Valenictus
Odobenus
Homiphoca
Desmatophoca
Allodesmus
Acrophoca
Piscophoca
Omnatophoca
Leptonychotes
Hydrurga
Lobodon
Mirounga
Monachus
Halichoerus
Cystophora
Erignathus
P. fasciata
P. groenlandica
P. vitulina
P. hispida
P. caspica
P. sibirica
P. largha

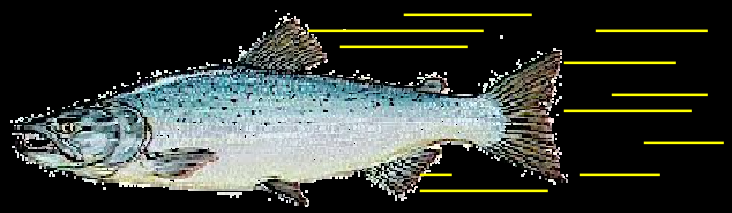
OUTLINE

- What are pinnipeds?
    - Introduction
    - Phylogenetics
- Evolution of pinniped feeding
- Evolution of pinniped locomotion
- West Indian monk seal

FEEDING IN WATER...

What specializations do pinnipeds have for feeding on marine life?





FEEDING TYPES



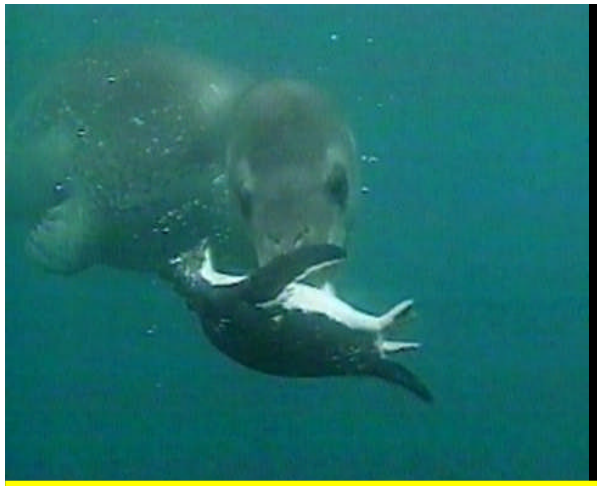
MASTICATORY FEEDING:

- **Most terrestrial carnivores**
- **Diet variable, but involves oral breakdown of food**

Kastelein & Mosterd (1989)

SUCTION FEEDING:

- **Walrus *(Odobenus).***
- **Diet consists primarily of benthic invertebrates.**

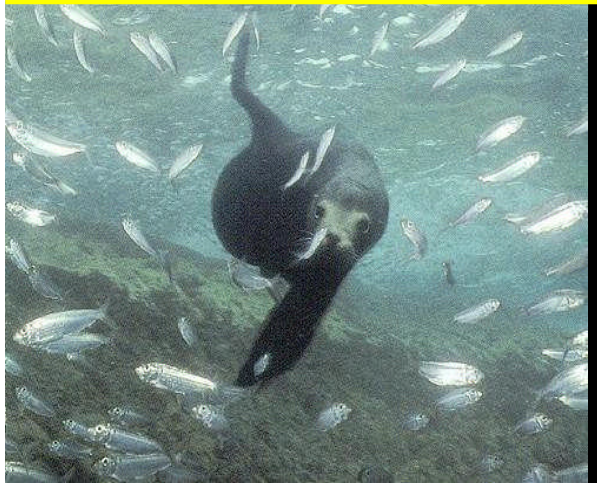


GRIP AND TEAR FEEDING:

- **Leopard Seal *(Hydrurga*).**
- **Diet consists primarily of large warm-blooded prey.**

FILTER FEEDING:

- **Crabeater Seal *(Lobodon*).**
- **Diet consists primarily of krill.**

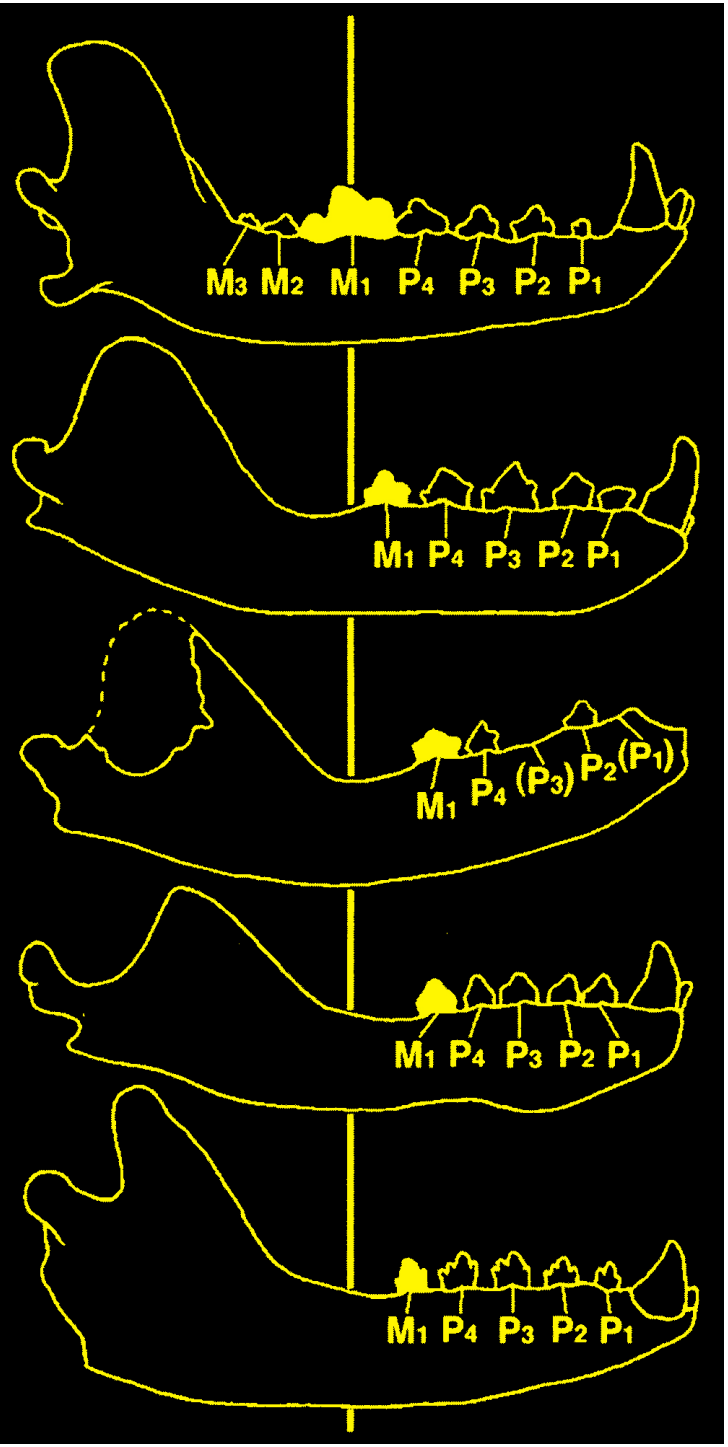


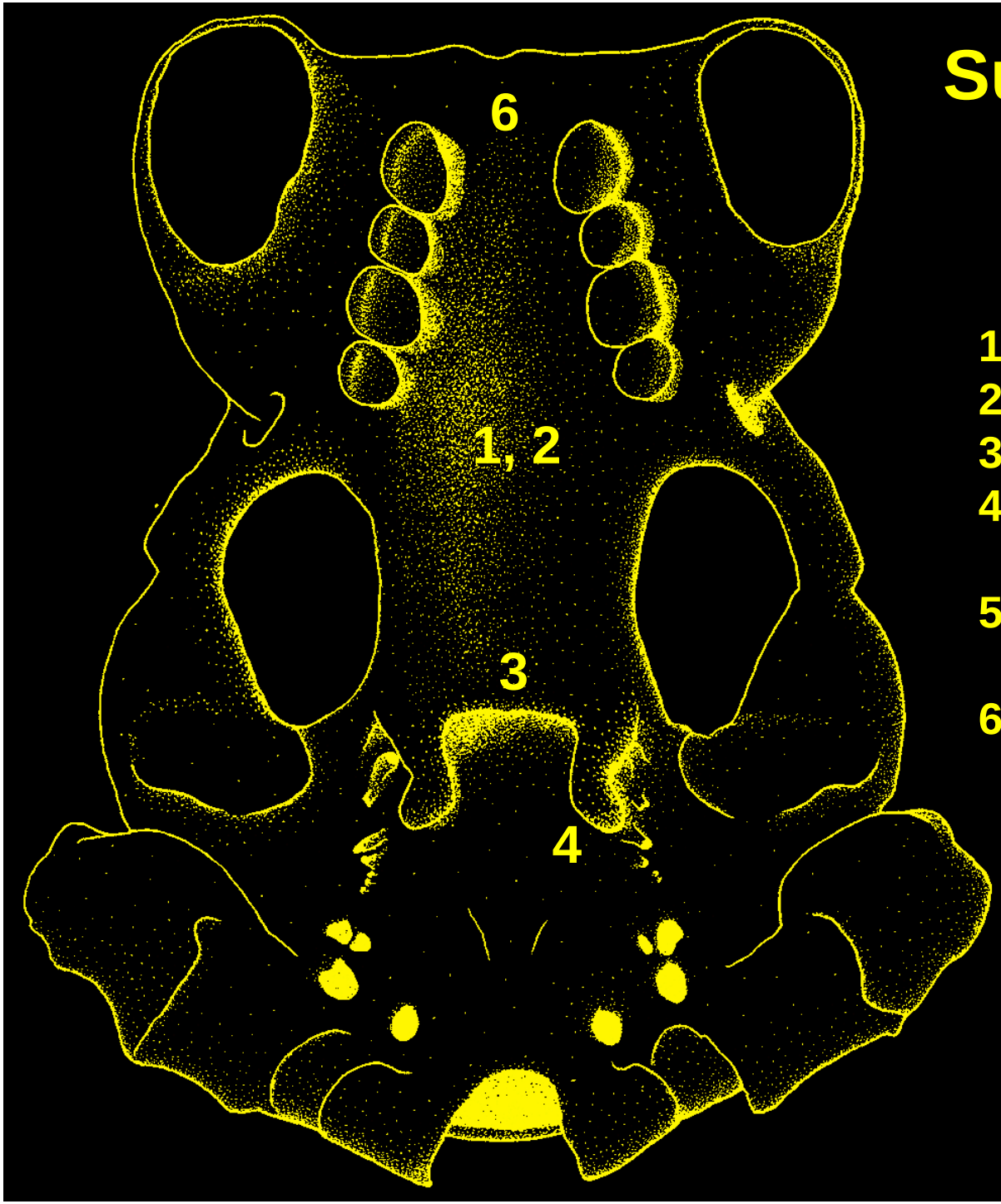
GENERALIST FEEDING:

- **Most pinnipeds.**
- **Diet consists primarily of fish and squid.**

Masticatory Feeding

1. Teeth with precise occlusion
2. Major molar located at or behind midpoint of jaw (where biting force is maximized)





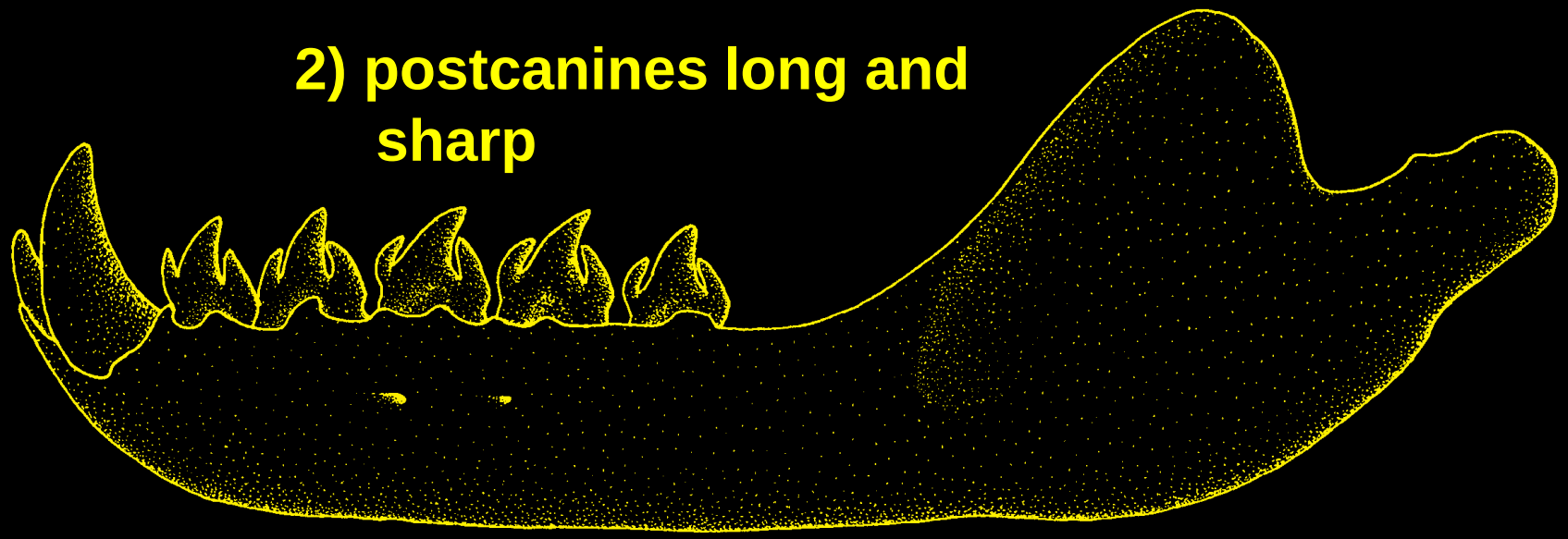
Suction Feeding

1. Palate, transverse arch
2. Palate, longitudinal arch
3. Palate, lengthening
4. Pterygoid hamuli, thickening
5. Fusion of mandibular symphysis
6. Incisors, loss

Grip and Tear Feeding

1) Incisors enlarged

2) postcanines long and sharp

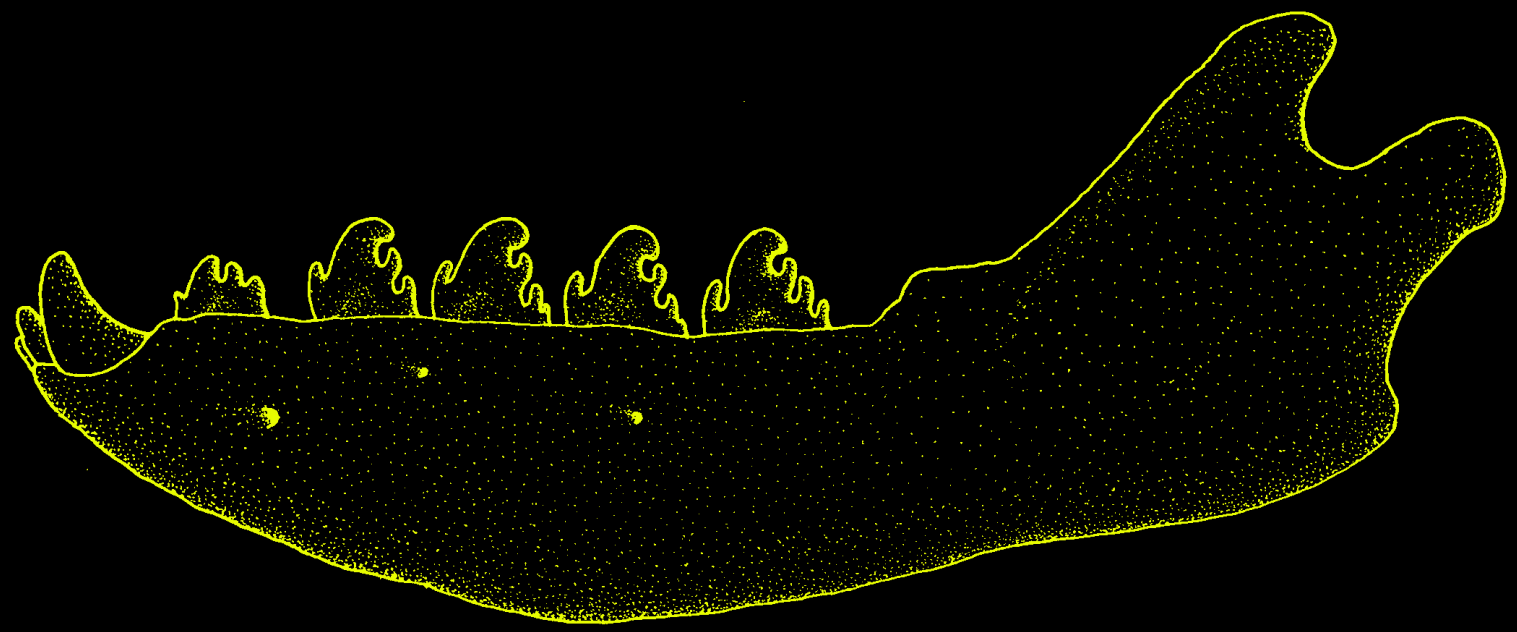


Filter Feeding

1) Lattice-like cusps on postcanines

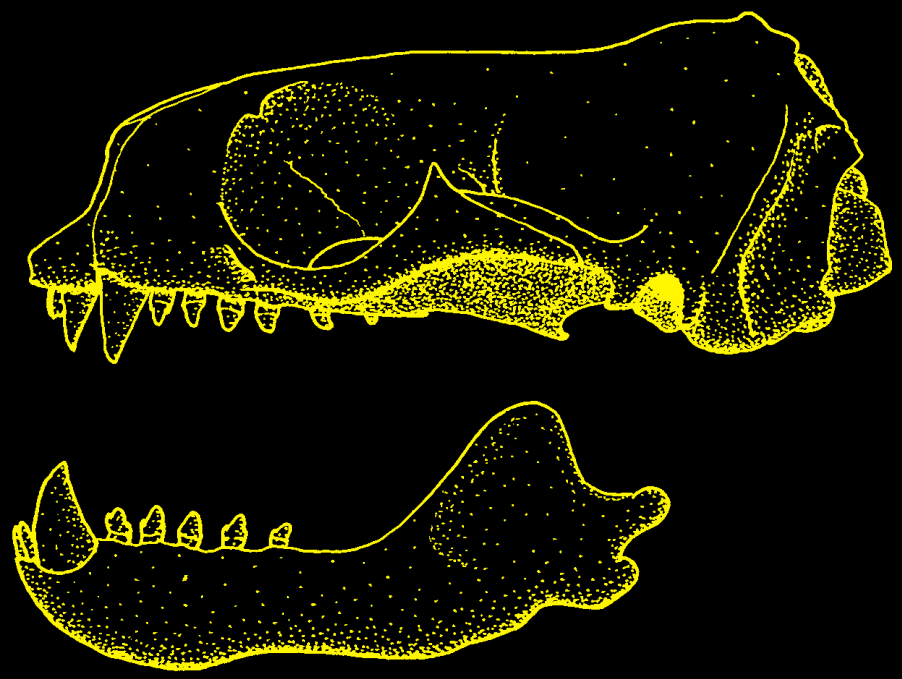
2) Postcanines interdigitate tightly in occlusion

3) Postdental ridge on mandible and skull



Generalist Feeding

Lack specializations of other feeding types



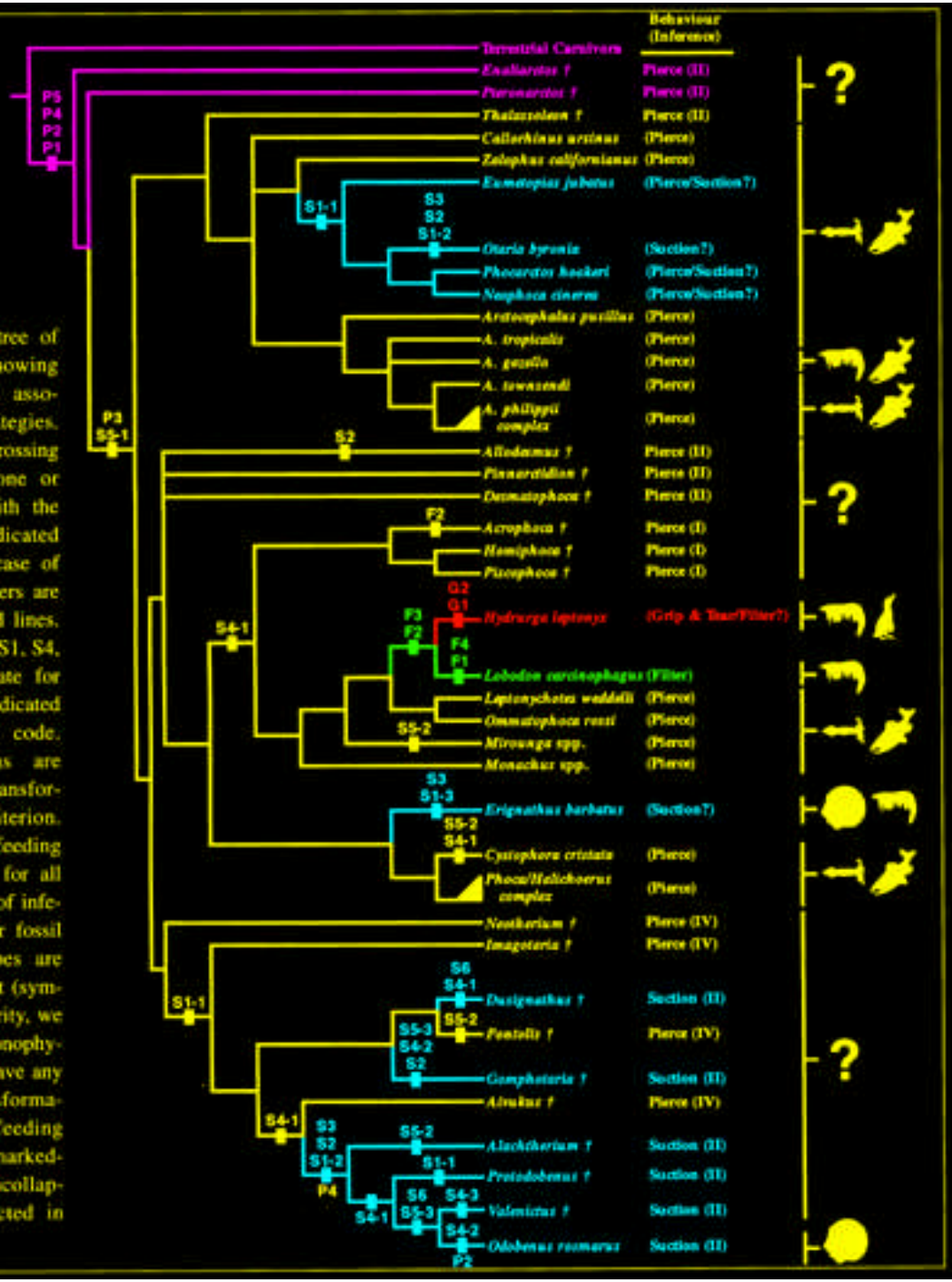
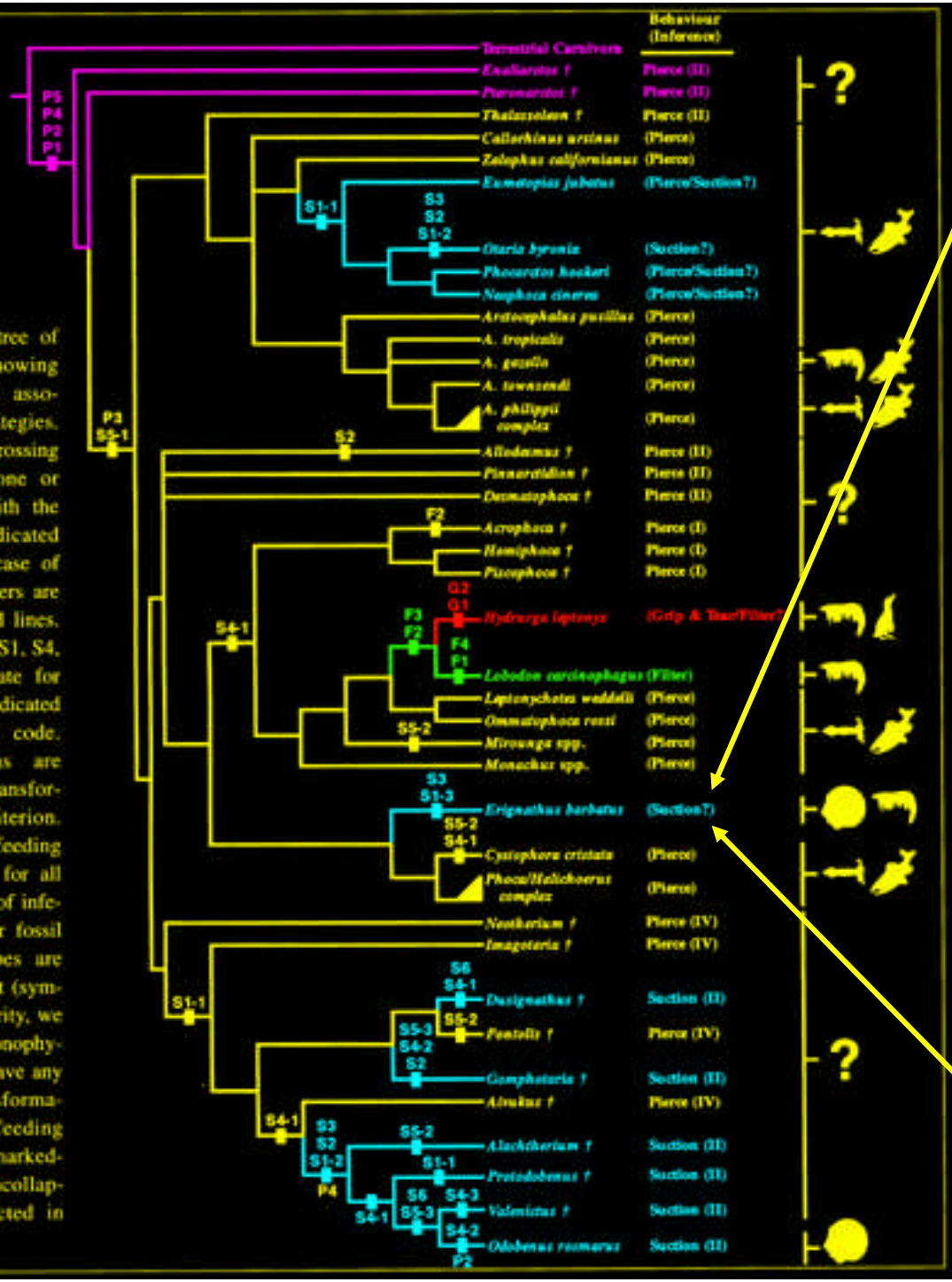


Figure 7.
Condensed phylogenetic tree of the Pinnipedimorpha showing character transformations associated with feeding strategies. Each thick vertical bar crossing an internode indicates one or more transformations, with the specific character indicated above each bar. In the case of reversals, specific characters are indicated below thickened lines. For multistate characters (S1, S4, and S5), the specific state for each transformation is indicated following the character code. Transformation positions are based on the delayed transformation (DELTRAN) criterion. Predicted and known feeding behaviours are indicated for all taxa, in addition to level of inference (in parentheses) for fossil taxa. Principle prey types are also indicated to the right (symbols as in fig. 1). For clarity, we have collapsed larger monophyletic groups that do not have any internal character transformations associated with feeding and which do not differ markedly in diet. A complete (uncollapsed) phylogeny is depicted in fig. 1.

Masticatory
Generalist
Grip and Tear
Filter
Suction (x5!!!)

(Adam & Berta 2002)



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SICB 2005:

Suction and Hydraulic Jetting Forces Produced by Feeding Bearded Seals (*Erignathus barbatus*)

Marshall, C. D. Texas A&M University at Galveston, USA marshalc@tamug.edu; **Kovacs, K. M.** Norwegian Polar Institute, Tromsø, Norway; **Lydersen, C.**, Norwegian Polar Institute, Tromsø, Norway

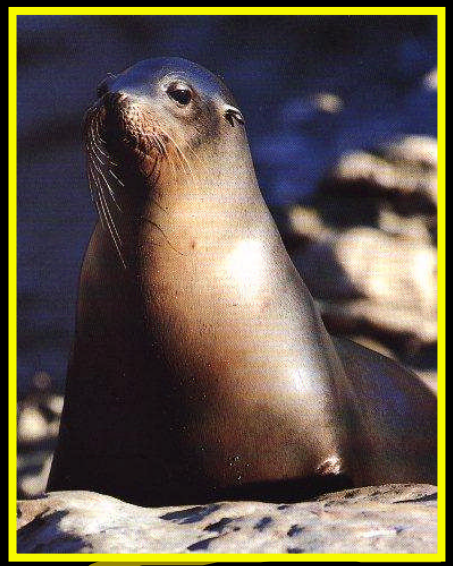
Bearded seals are thought to use suction as their primary feeding mode. This suggestion was, until recently, based only on anecdotal data. However, recent studies have confirmed that both suction and hydraulic jetting are important feeding behaviors of this species; the magnitude of these forces remained unknown. This study characterized suction and hydraulic jetting behaviors of bearded seals, and measured their magnitudes using a Millar MPC 350 pressure transducer inserted into a feeding apparatus. Pressure data from 70 feeding trials were collected with a portable electrophysiological recording system. Feeding behavior was videotaped and synchronized with physiological data using a pair of flashing LED lights whose optical pattern corresponded to a generated square wave pattern recorded as a separate channel. Bearded seals (N=2) used both suction and hydraulic jetting when feeding from the apparatus. The mean suction force recorded was -47.1 kPa (S.D.+ 25.7) and ranged from -3.2 to -108 kPa (N=392 suction events). The mean hydraulic jetting force recorded was 8.9 (S.D.+ 5.45) and ranged from 3.2 to 37 kPa (N=63 hydraulic jetting events). The mean duration of suction events (0.29 s, S.D.+ 0.12) was significantly greater ($p < 0.001$) than the mean duration of hydraulic jetting events (0.13 s, S.D.+ 0.07). Suction events were often preceded by a small increase in pressure (preparatory phase) followed by relatively large negative pressures (suction phase). Suction capability of bearded seals are comparable to walruses, and validate anecdotal data that bearded seals are suction foragers. However, hydraulic jetting is an important component of the feeding repertoire of bearded seals.

OUTLINE

- What are pinnipeds?
    - Introduction
    - Phylogenetics
- Evolution of pinniped feeding
- Evolution of pinniped locomotion
- West Indian monk seal

On Land 10-40% of Time

- resting
- molting
- raising young
- (mating)



In Water 60-90% of Time

- foraging
- playing
- (mating)

TERRESTRIAL LOCOMOTION



AMBULATION

- Both fore and hind limbs support the body.
- Movement by (modified) walking.

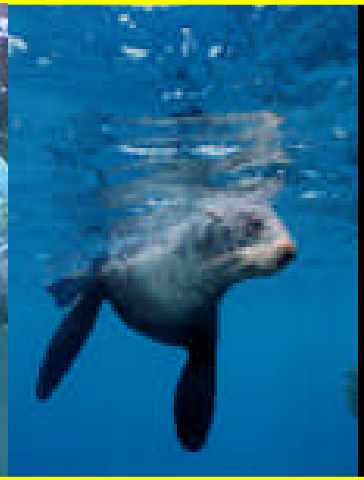
UNDULATION

- Hind limbs do not support the body.
- Movement by sagittal undulation of the spine.

SWIMMING LOCOMOTION

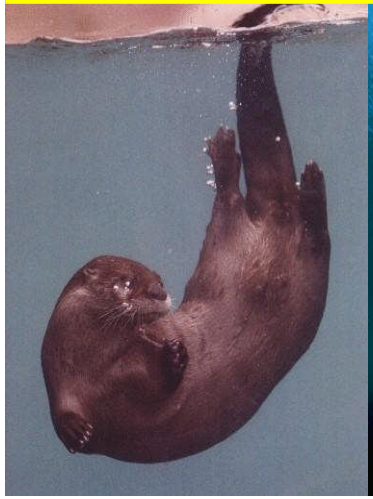
QUADRUPEDAL SWIMMING

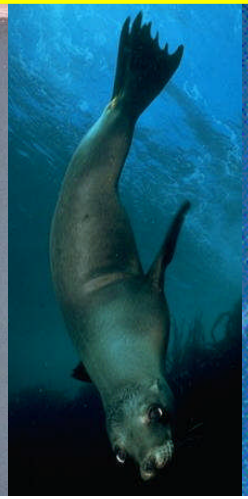
- All 4 limbs used to produce thrust (Canidae, Procyonidae)



PECTORAL OSCILLATION

- Forelimbs produce majority of thrust (Ursidae, Otariidae)



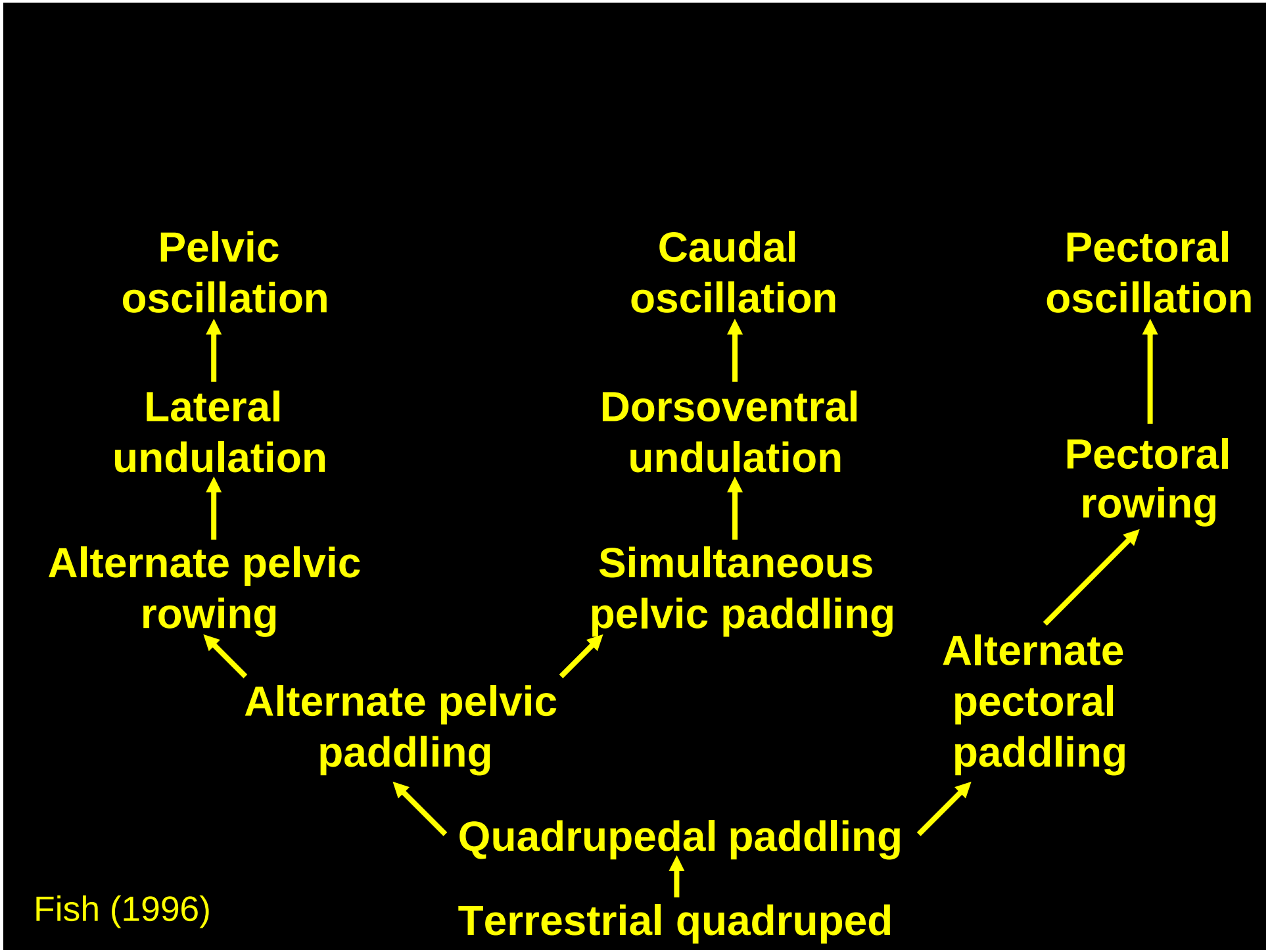


PELVIC OSCILLATION

- Hind limbs or lumbar region of spine produce thrust (Mustelidae, Phocidae, Odobenidae)

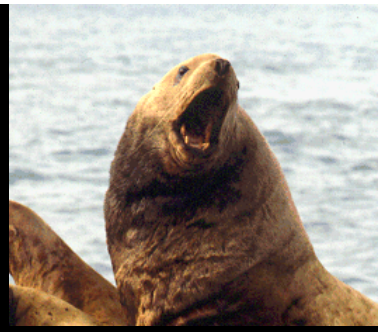
PECTORAL OSCILLATION

PELVIC OSCILLATION


Pelvic oscillation
Caudal oscillation
Pectoral oscillation
Lateral undulation
Dorsoventral undulation
Pectoral rowing
Alternate pelvic rowing
Simultaneous pelvic paddling
Alternate pectoral paddling
Alternate pelvic paddling
Quadrupedal paddling
Terrestrial quadruped

Fish (1996)





Pelvic oscillation

↑

Lateral undulation

↑

Alternate pelvic rowing

Caudal oscillation

↑

Dorsoventral undulation

↑

Simultaneous pelvic paddling

Pectoral oscillation

↑

Pectoral rowing

↗

Alternate pectoral paddling

↗

Alternate pelvic paddling

↖ ↗

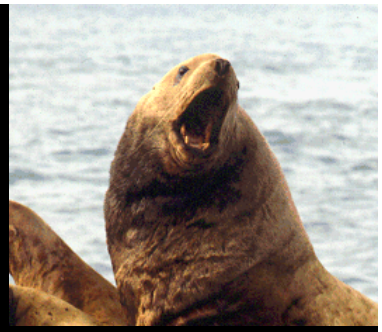
Quadrupedal paddling

↖

↑

Terrestrial quadruped

Fish (1996)



Pelvic oscillation

↑

Lateral undulation

↑

Alternate pelvic rowing

Caudal oscillation

↑

Dorsoventral undulation

↑

Simultaneous pelvic paddling

Pectoral oscillation

↑

Pectoral rowing

Alternate pelvic paddling

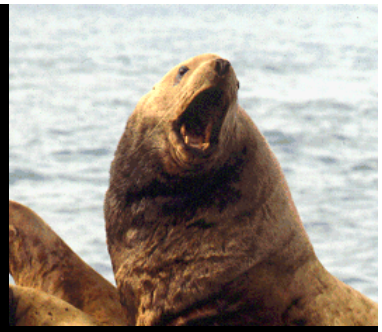
Alternate pectoral paddling

Quadrupedal paddling

↑

Terrestrial quadruped

Phylogeny not considered



Pelvic oscillation

Caudal oscillation

Pectoral oscillation

Lateral undulation

Dorsoventral undulation

Pectoral rowing

Alternate pelvic rowing

Simultaneous pelvic paddling

Alternate pelvic paddling

Alternate pectoral paddling

Intermediate stages not known

Quadrupedal paddling

Terrestrial quadruped

OBJECTIVES:

1) Establish functional osteological characters associated with each type of locomotion (terrestrial and swimming).

2) Map characters onto a phylogenetic framework to establish evolutionary patterns in pinniped locomotion (e.g., transitions, convergences).

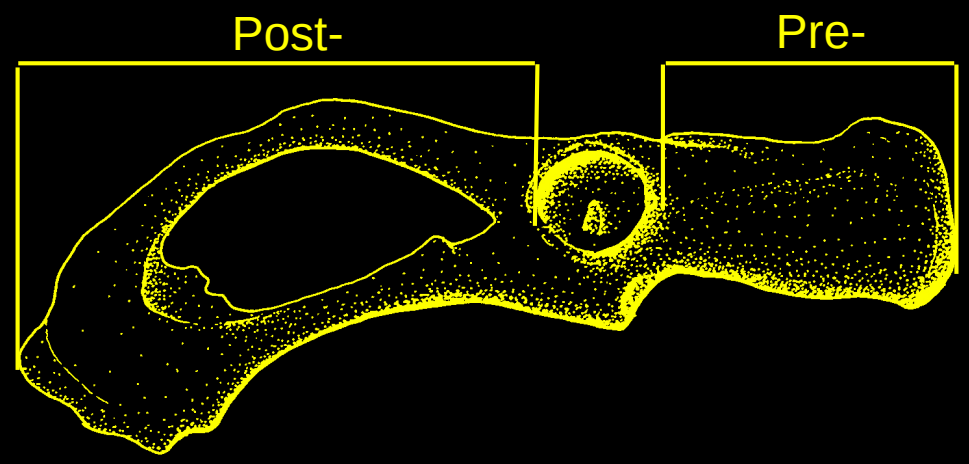
3) Test Fish's (1996) evolutionary hypothesis of swimming using a phylogenetic framework.

FUNCTIONAL CORRELATES OF TERRESTRIAL LOCOMOTION

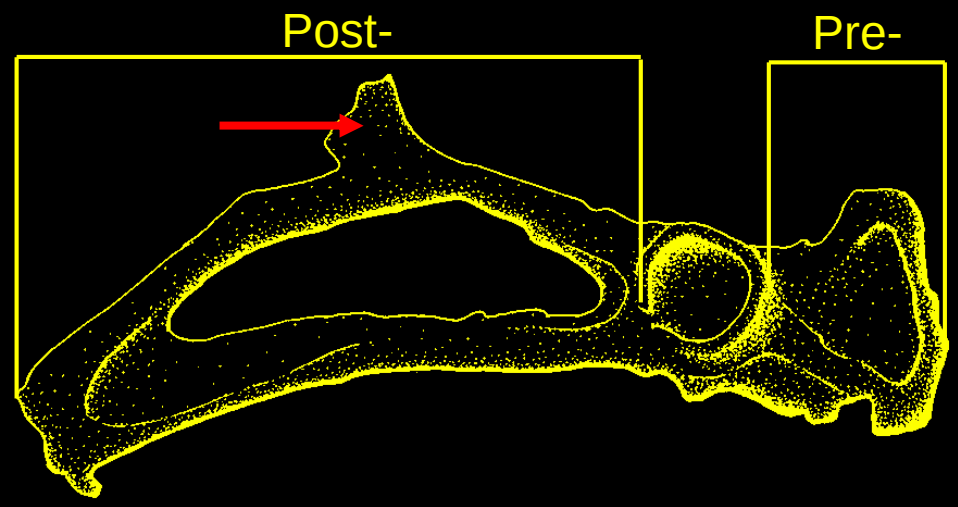
AMBULATION

UNDULATION

AMBULATION



UNDULATION



1) Pelvic girdle: length of post-acetabular region
2) Ischium: size of ischial tuberosity
3) Femur: inclination of femoral condyles
4) Astragalus: trochlear shape
5) Astragalus: presence of calcaneal process

AMBULATION

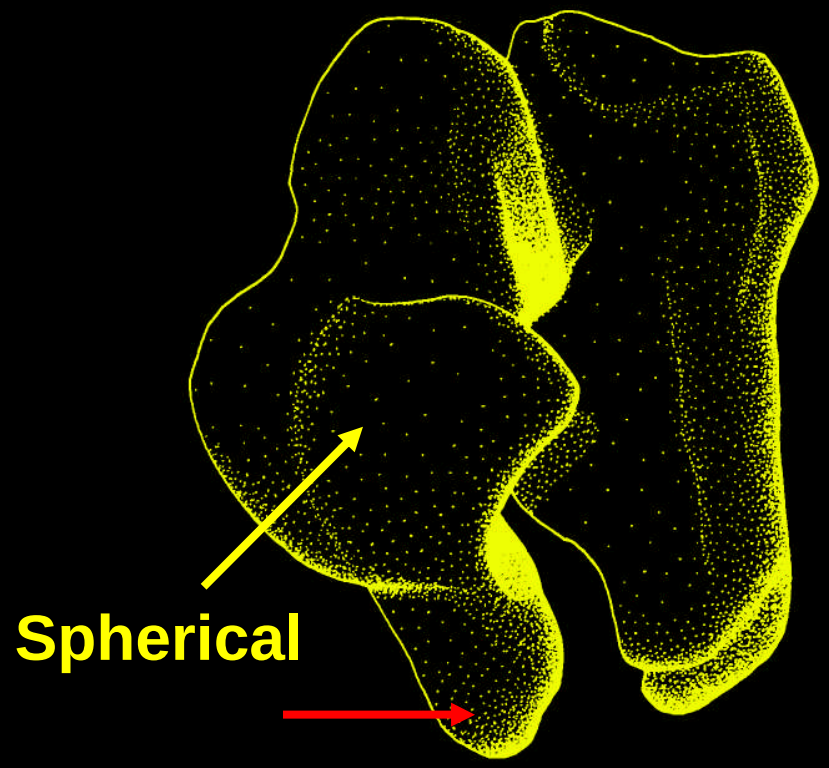
~ 90°

UNDULATION

< 80°

1) Pelvic girdle: length of post-acetabular region
2) Ischium: size of ischial tuberosity
3) **Femur: inclination of femoral condyles**
4) Astragalus: trochlear shape
5) Astragalus: presence of calcaneal process

AMBULATION



UNDULATION

1) Pelvic girdle: length of post-acetabular region
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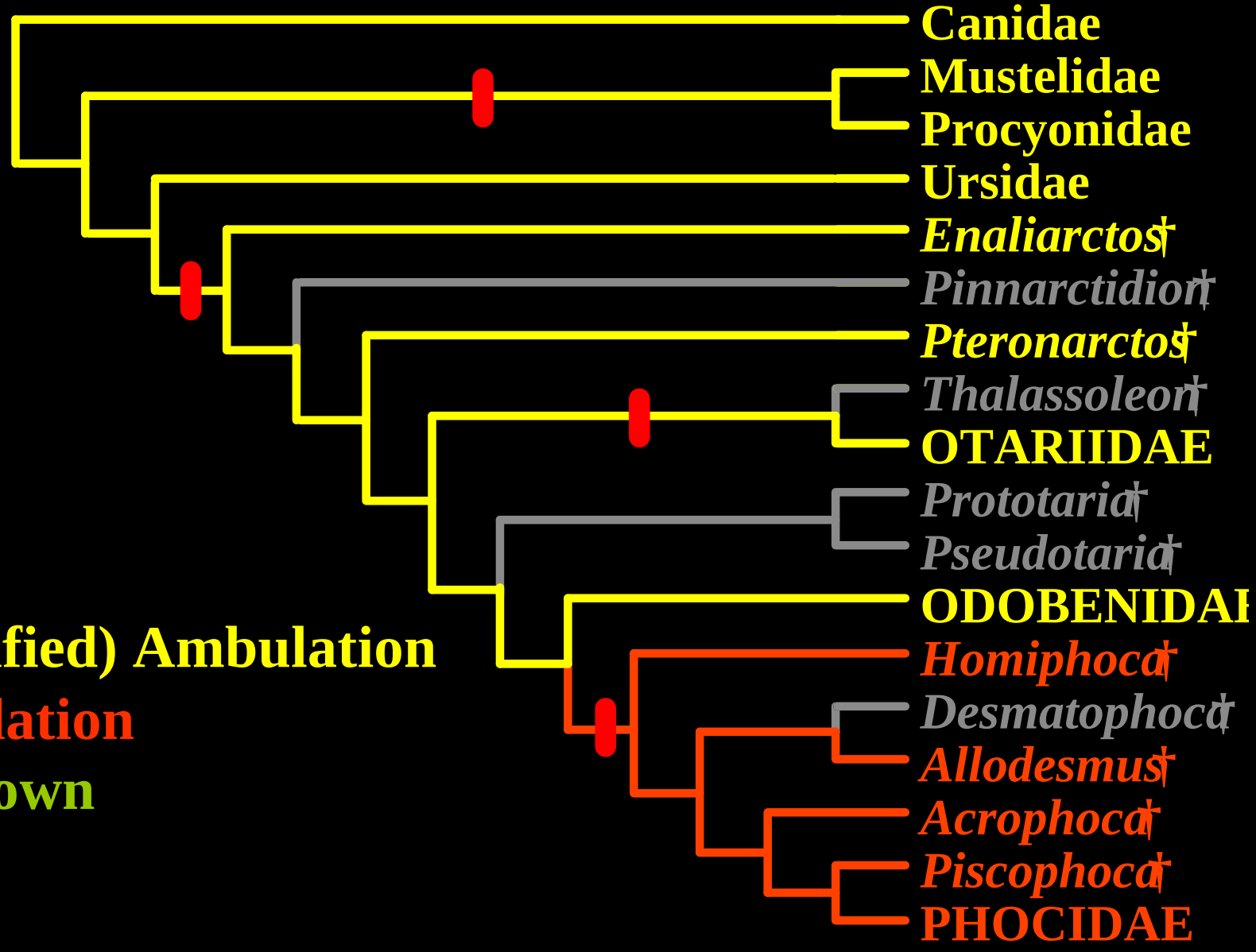
Evolution of Terrestrial Locomotion

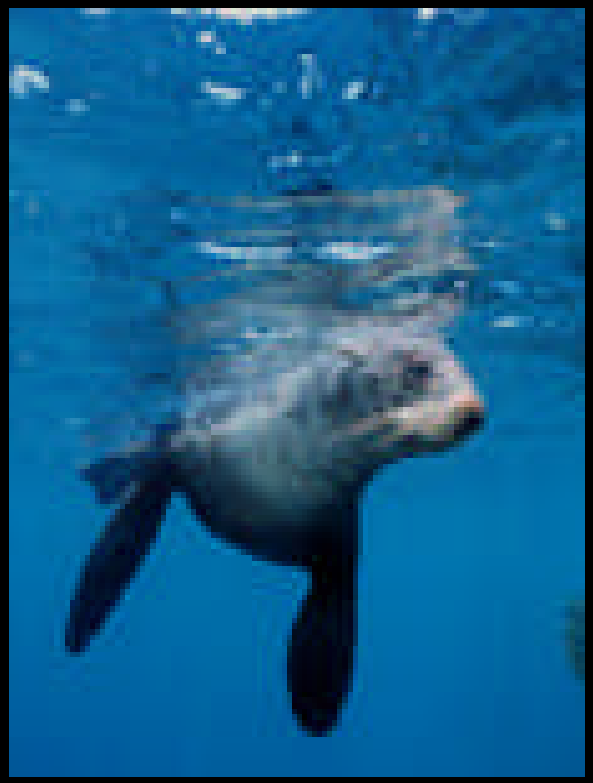


(Modified) Ambulation

Undulation

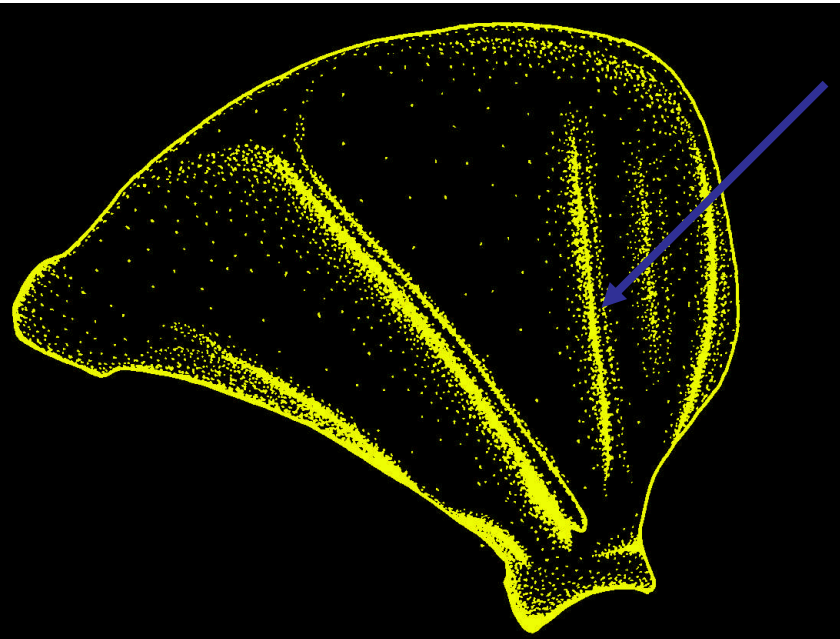
Unknown

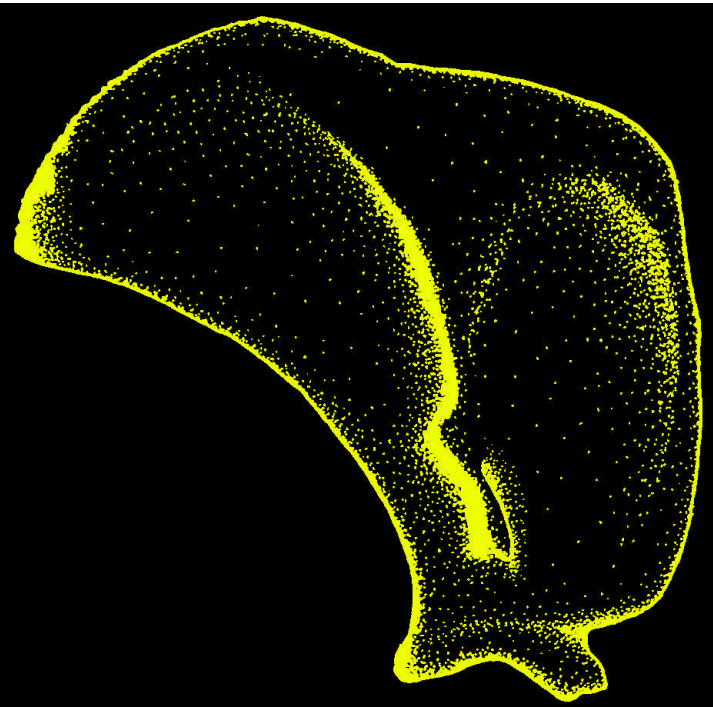
FUNCTIONAL CORRELATES OF SWIMMING LOCOMOTION



PECTORAL OSCILLATION

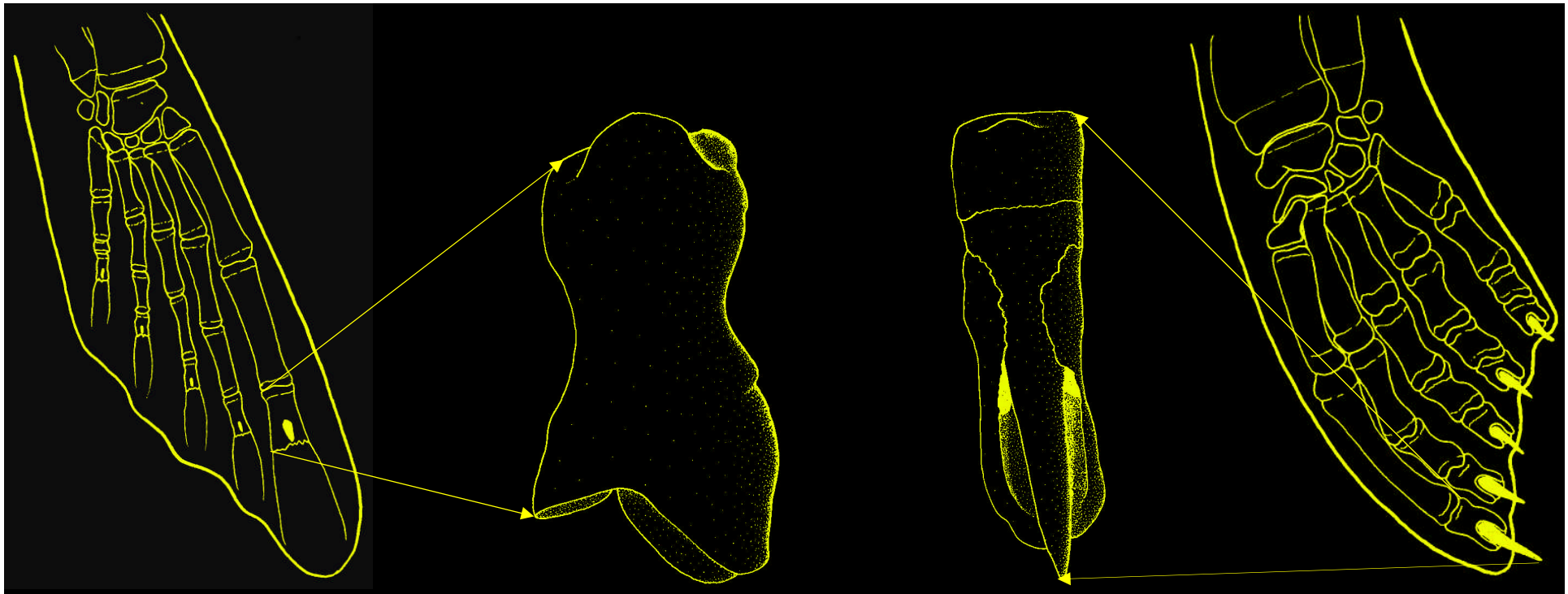
PELVIC OSCILLATION





Pectoral oscillator **Pelvic oscillator**

1) Scapula: relative sizes of supra- and infraspinous fossae
2) Scapula: development of accessory spines in supraspinous fossa
3) Scapula: eccentricity of glenoid fossa
4) Humerus: development of medial epicondyle
5) Ulna: dimensions of semilunar notch
6) Radius: relative position of pronator teres process
7) Manual phalanges: presence of distal cartilagenous extensions
8) Femur: presence of lesser trochanter
9) Tibia: development of medial malleolus
10) Pedal phalanges: shape of pes



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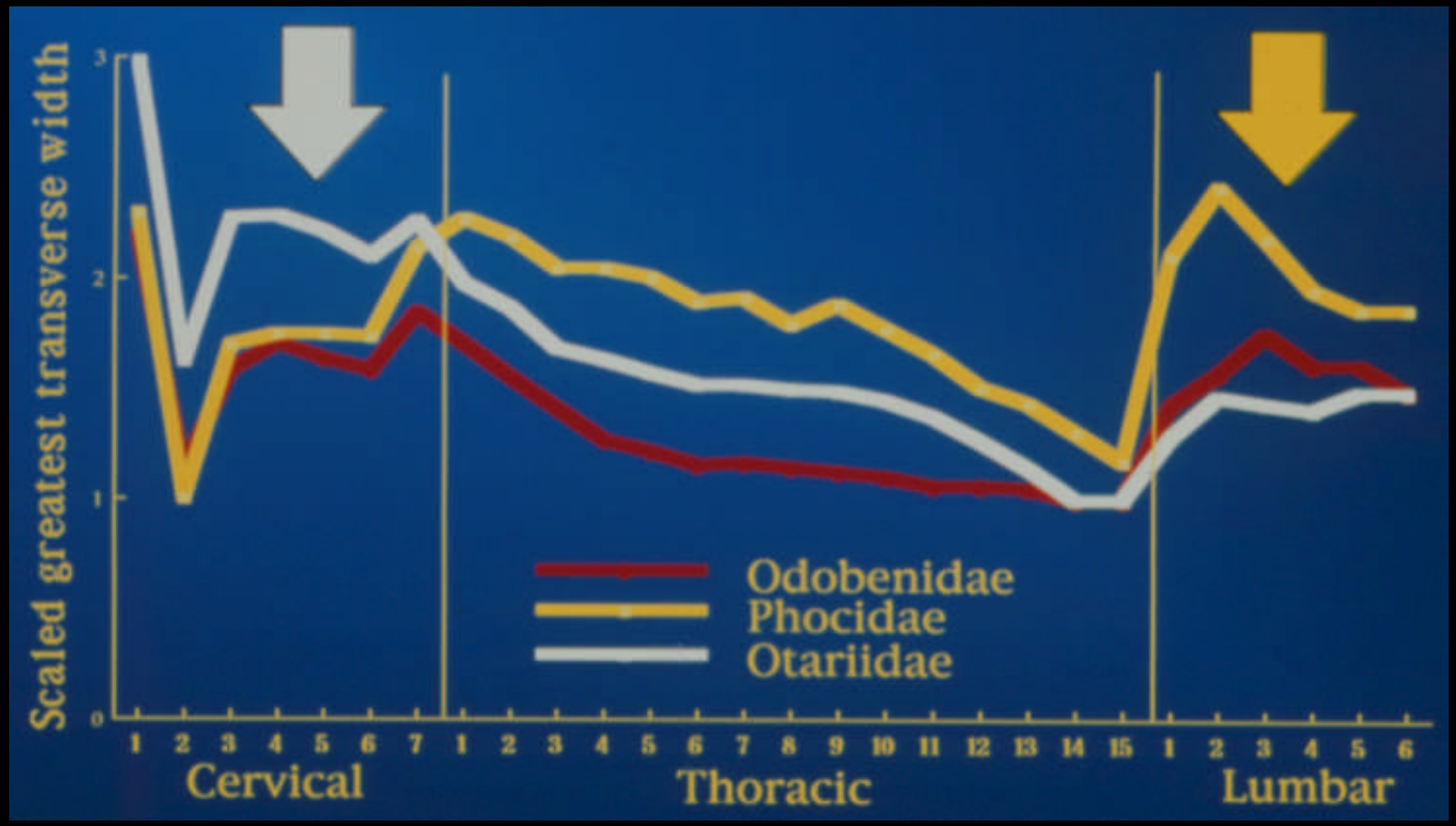
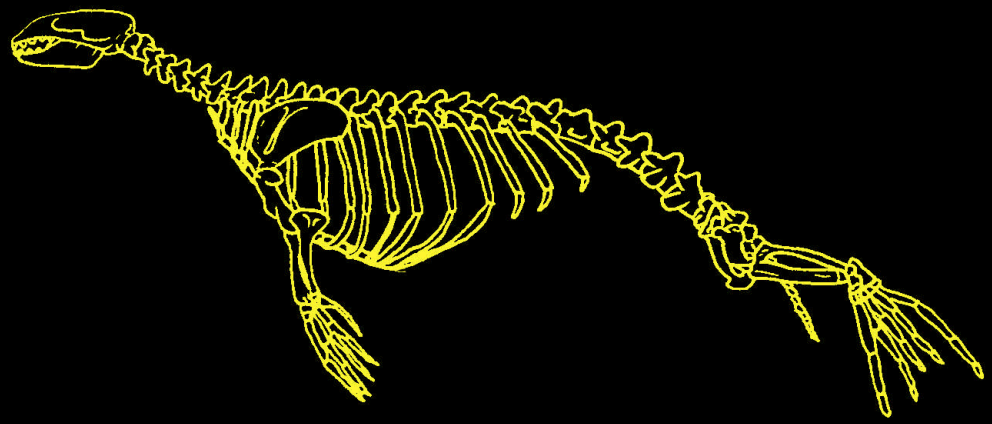
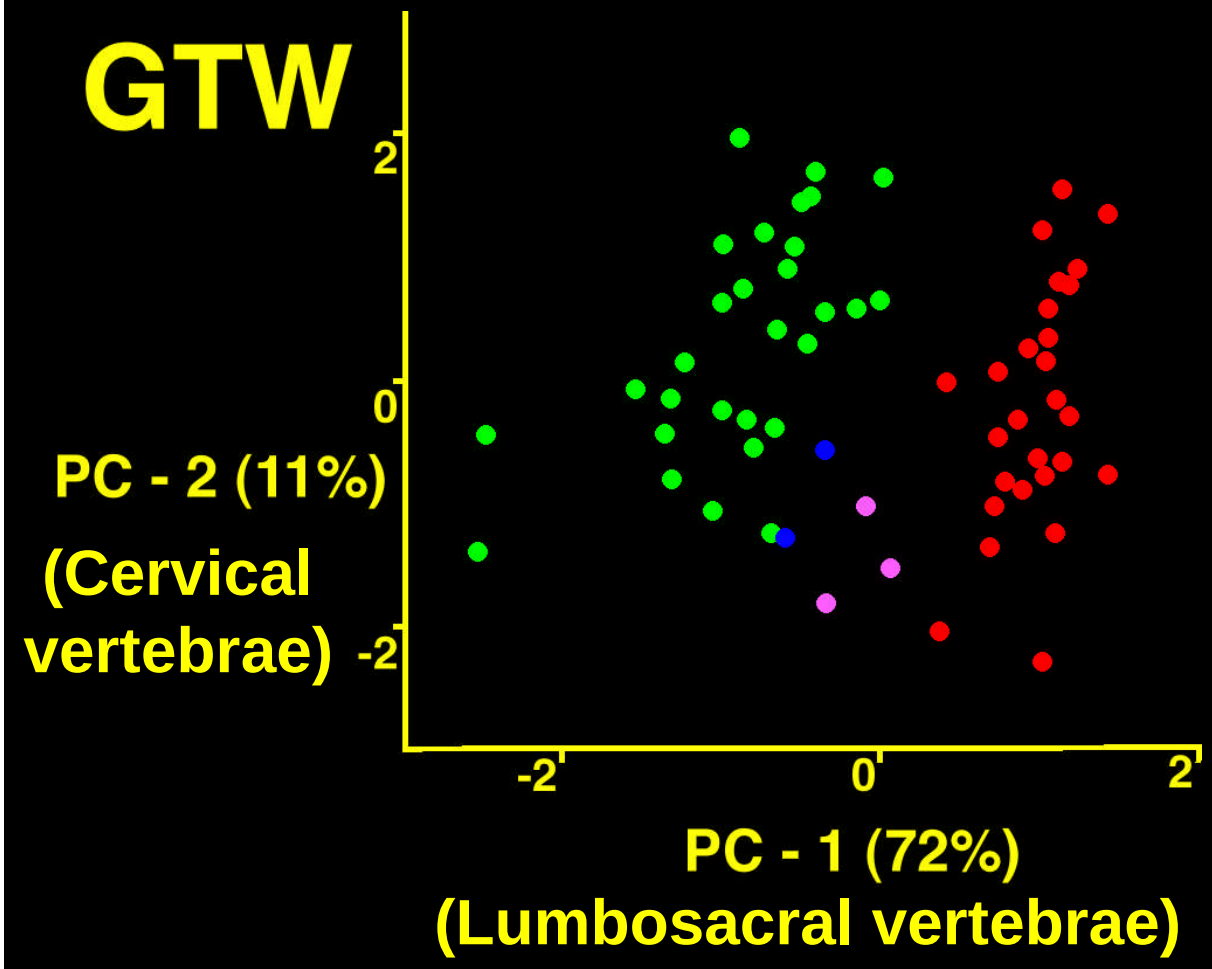
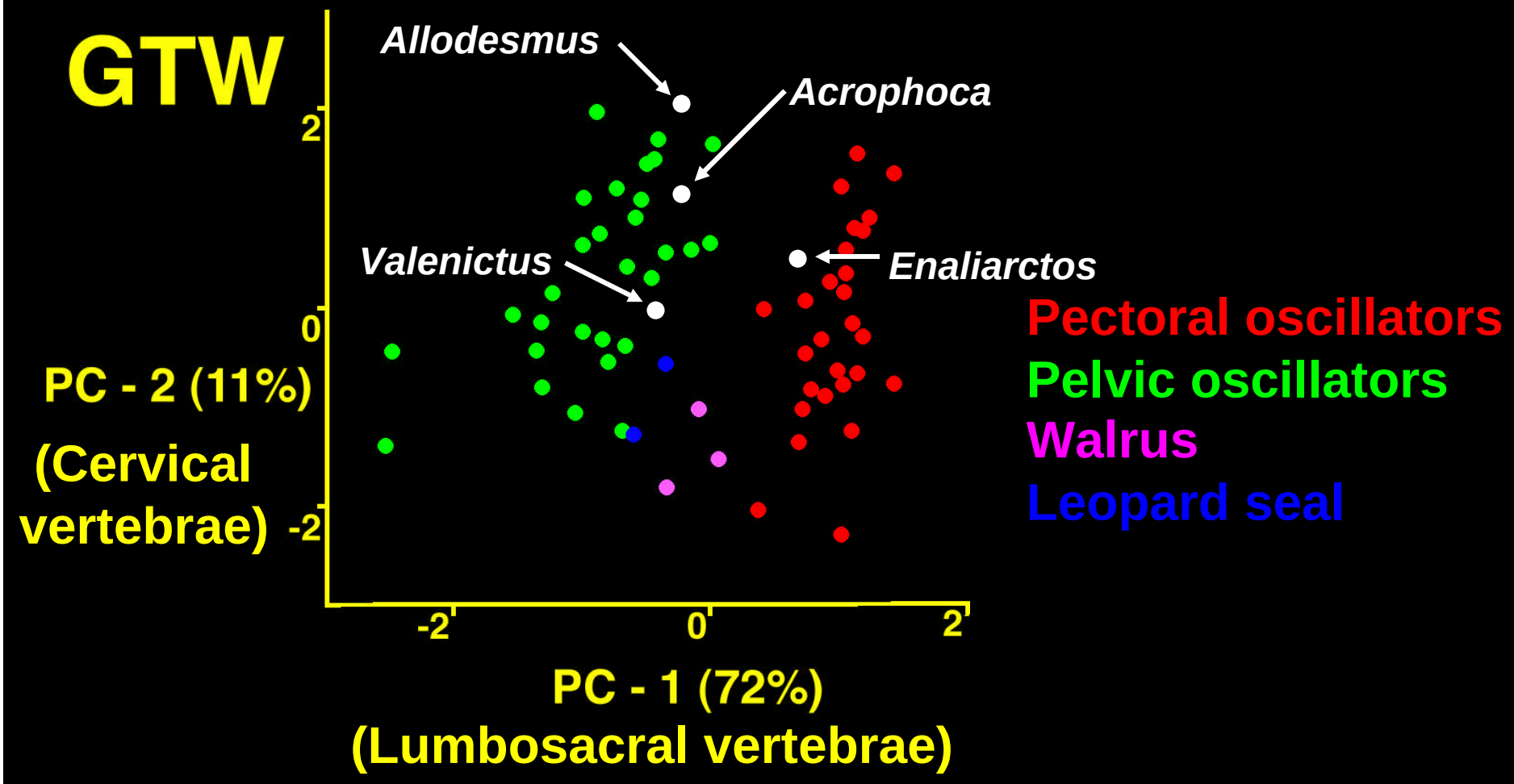
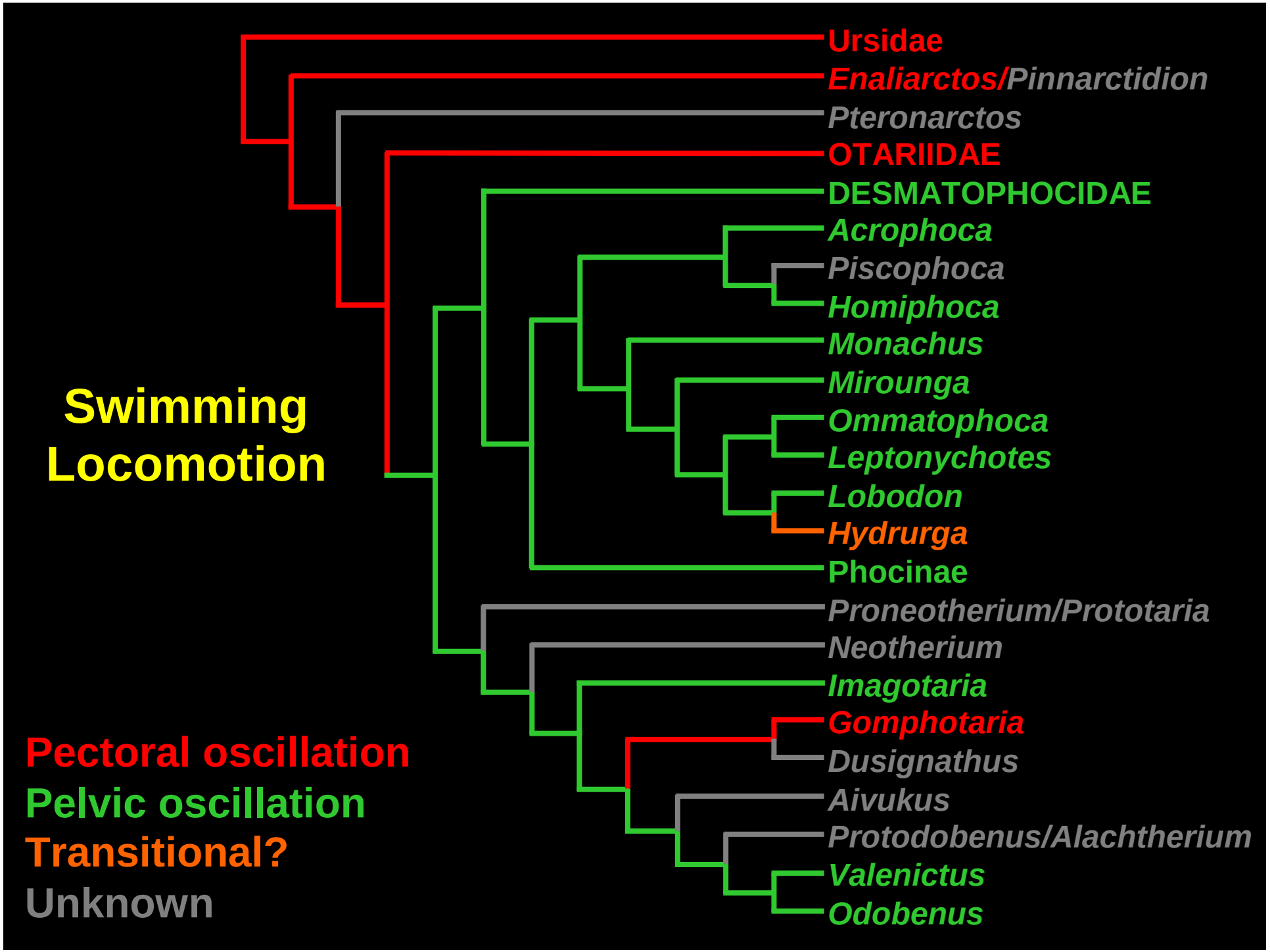

Scaled greatest transverse width
3
2
1
0
Odobenidae
Phocidae
Otariidae
1 2 3 4 5 6 7 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 1 2 3 4 5 6
Cervical
Thoracic
Lumbar



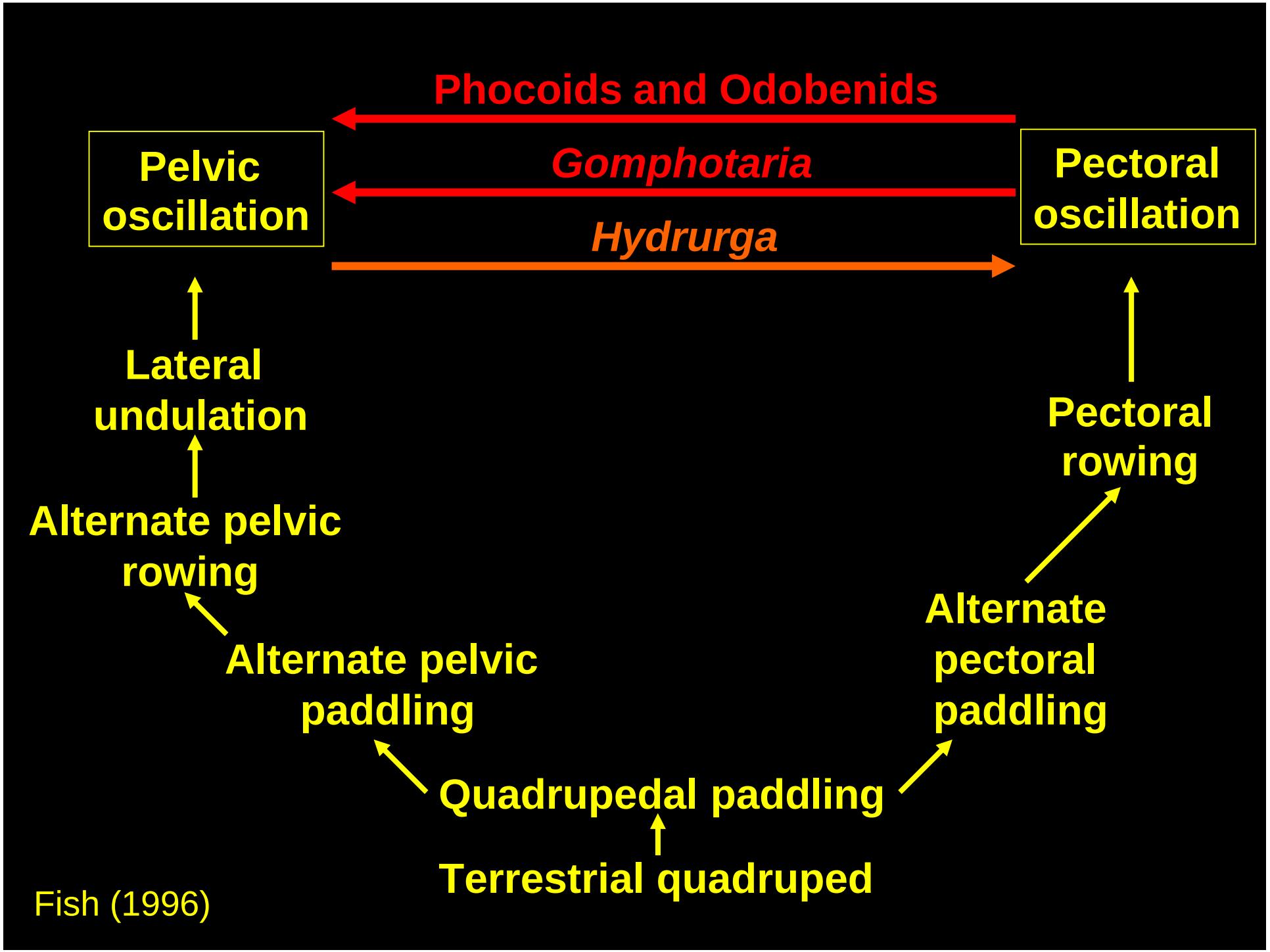


Pectoral oscillators
Pelvic oscillators
Walrus
Leopard seal


GTW
Allodesmus
Acrophoca
Valenictus
Enaliarctos
2
0
-2
PC - 2 (11%)
(Cervical vertebrae)
-2
0
2
PC - 1 (72%)
(Lumbosacral vertebrae)
Pectoral oscillators
Pelvic oscillators
Walrus
Leopard seal


Ursidae
Enaliarctos/Pinnarctidion
Pteronarctos
OTARIIDAE
DESMATOPHOCIDAE
Acrophoca
Piscophoca
Homiphoca
Monachus
Mirounga
Ommatophoca
Leptonychotes
Lobodon
Hydrurga
Phocinae
Proneotherium/Prototaria
Neotherium
Imagotaria
Gomphotaria
Dusignathus
Aivukus
Protodobenus/Alachtherium
Valenictus
Odobenus
Swimming Locomotion
Pectoral oscillation
Pelvic oscillation
Transitional?
Unknown

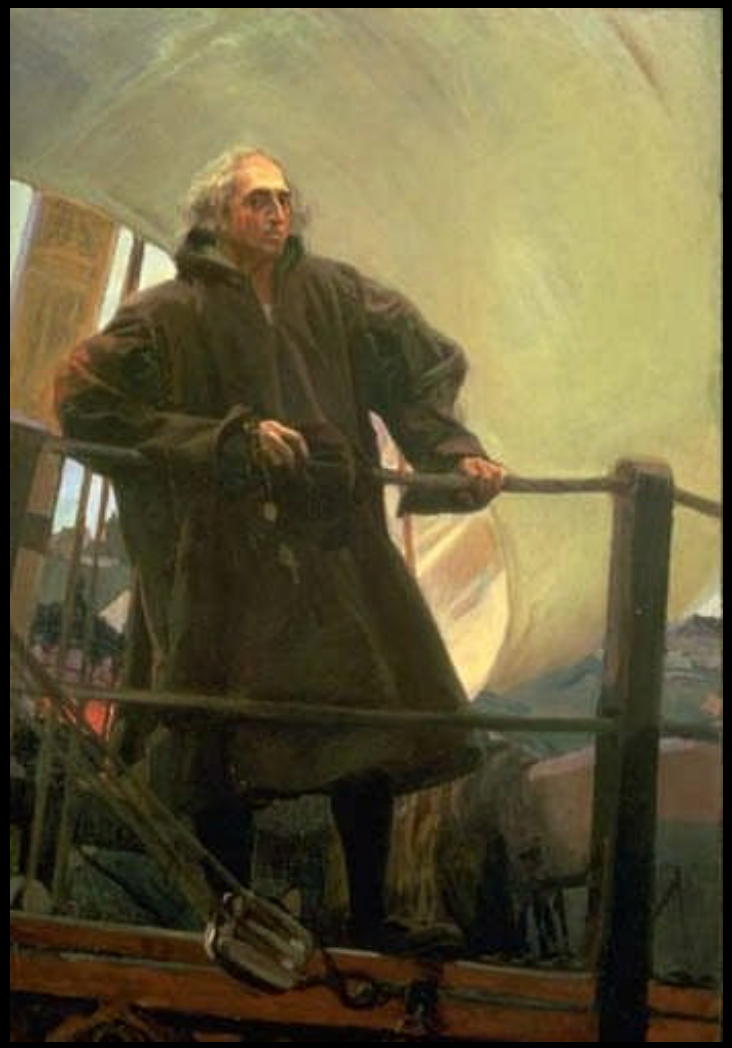
Transitional?


Phocoids and Odobenids
Gomphotaria
Hydrurga
Pelvic oscillation
Pectoral oscillation
Lateral undulation
Alternate pelvic rowing
Alternate pelvic paddling
Pectoral rowing
Alternate pectoral paddling
Quadrupedal paddling
Terrestrial quadruped

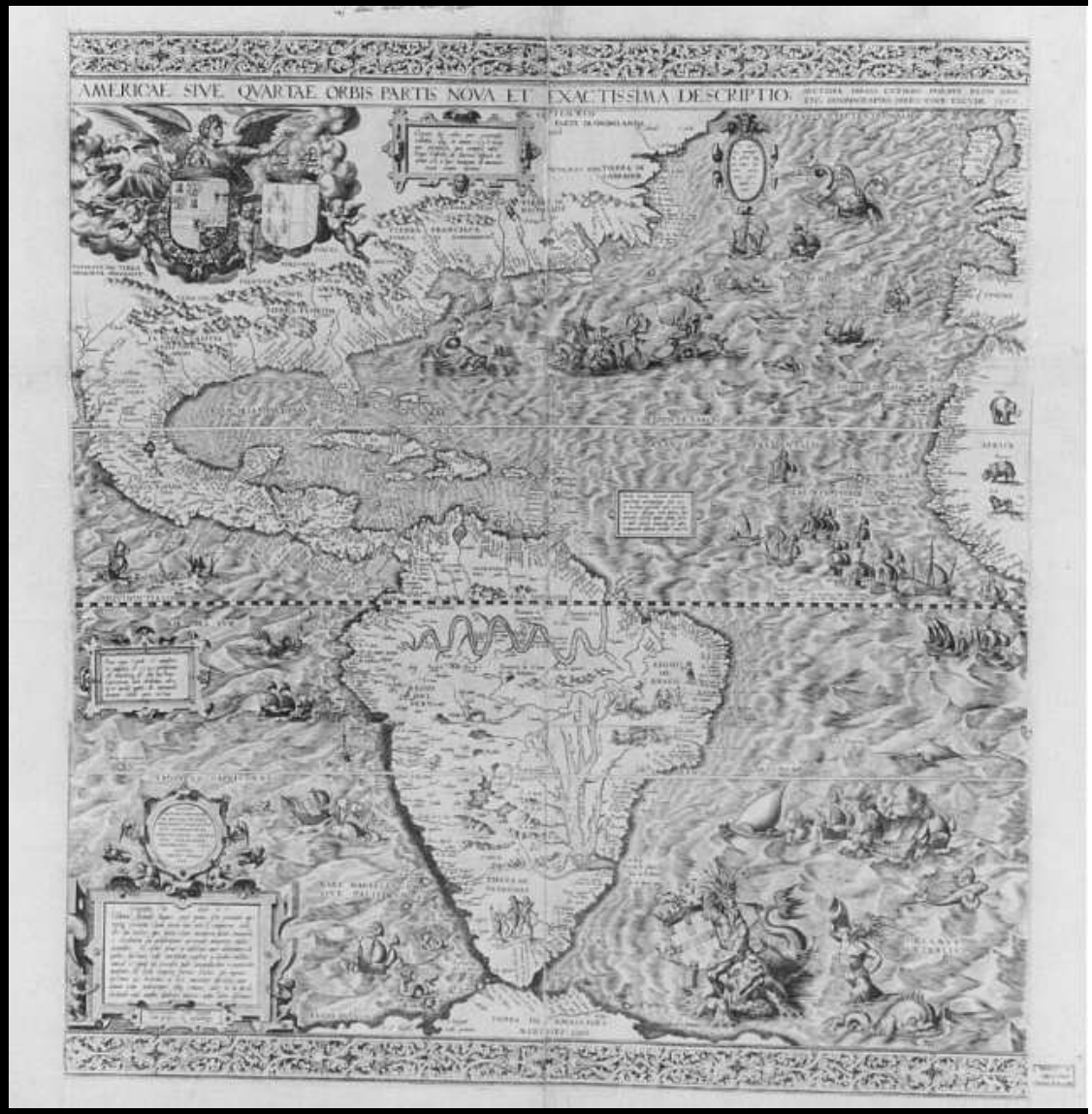
Fish (1996)

OUTLINE

- What are pinnipeds?
    - Introduction
    - Phylogenetics
- Evolution of pinniped feeding
- Evolution of pinniped locomotion
- West Indian monk seal



Christopher Columbus
1451-1506




CONQVISTA
MILAGRO DEL S. S.
hiago mayor apostol de cristo

"… the sea was thick with [turtles], … so numerous that it seemed that ships would run aground on them …"

- Columbus, 1494

"… [lost] vessels … have steered entirely by the noise which [turtles] make in swimming to attain the Cayman isles."

- Long, late 1600s

- estimated 1494 population based on hunting records: **660 000 000**
- current population: **ca. 2 000**

Source: Jeremy B.C. Jackson, 1997

Eight seals killed in August, 1494 during Columbus' second voyage...

"[There are many large seals in these lands]"

- Oviedo, 1520

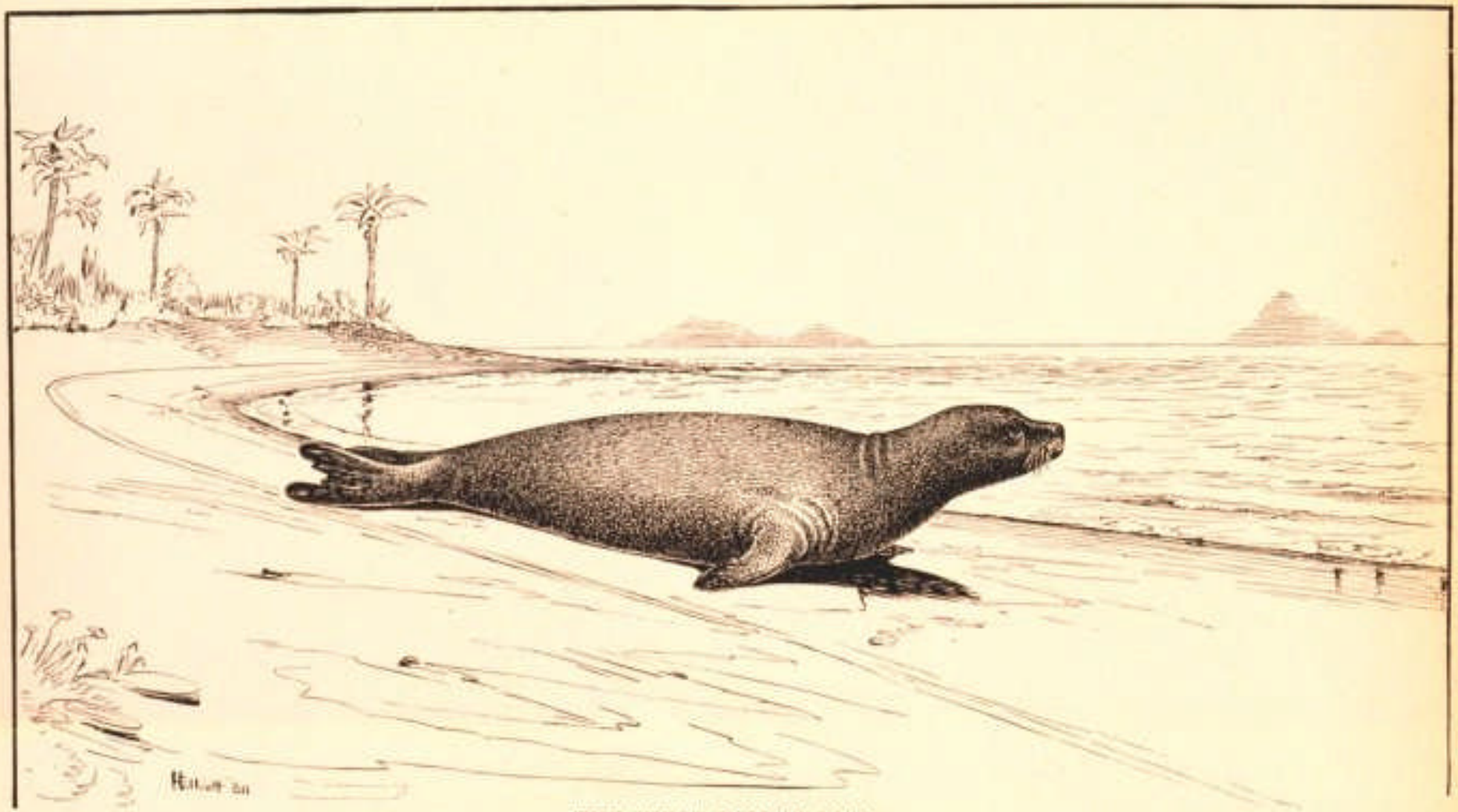
"The Bahama Islands are fill'd with seals, sometimes fishers will catch one hundred in a night."

- Sloan, 1707

Slaughtered in unknown numbers for oil to feed the needs of New World colonists

John Edward Gray
1800-1875

- provided first taxonomic description of the Caribbean monk seal in 1849.



THE WEST INDIAN SEAL.

Monachus tropicalis, Gray. (p. 67.)

Drawing by Henry W. Elliott, from specimen in U. S. National Museum, No. 2999, obtained by Professor Felipe Poey, at Matanzas, Cuba.

PLATE 19.

- Elliot, 1884

Henry Augustus Ward
1834-1906

Henry Levi Ward
1881-1943

- pupping restricted to early December
- newborn size 85 cm
- laguno black
- vocalizations
- no sexual dimorphism
- “docile and lazy”
- few marks of combat
- high parasite load
- no information on diet

- H.L. Ward, 1887

N.Y. Zoological Society, ca. 1910

- few data on captive animals
- last known sighting in 1952


Caribbean Monk Seal
45c
Antigua·Barbuda
CENTENARY OF DEATH OF CHARLES DARWIN
Antigua & Barbuda
$5
35
FOCA DEL CARIBE (Monachus tropicalis)
correos de colombia
Cuba
Correos 1980 30
Mamiferos Marinos
Monachus tropicalis
FOCA ANTILLANA
Grenada Grenadines
$6
CARIBBEAN MONK SEAL
Monachus tropicalis
300/.
TANZANIA
CARIBBEAN MONK SEAL
ST. VINCENT
50¢
TANZANIA
1994
MONACHUS TROPICALIS
250/.
COMMONWEALTH OF
DOMINICA
$1.00
MONK SEAL, Monachus Tropicalis
GRENADA
GRENADINES
75c
Seal
UMM AL QIWAIN
Grenada
10c
CARIBBEAN MONK SEAL Monachus tropicalis
Monk Seal
St. Vincent
90c

Is there more to know?

- distribution?
- unknown or unpublished accounts?
- information derived from the skeleton?
- extrapolation from the other two species of monk seal?

Distribution...

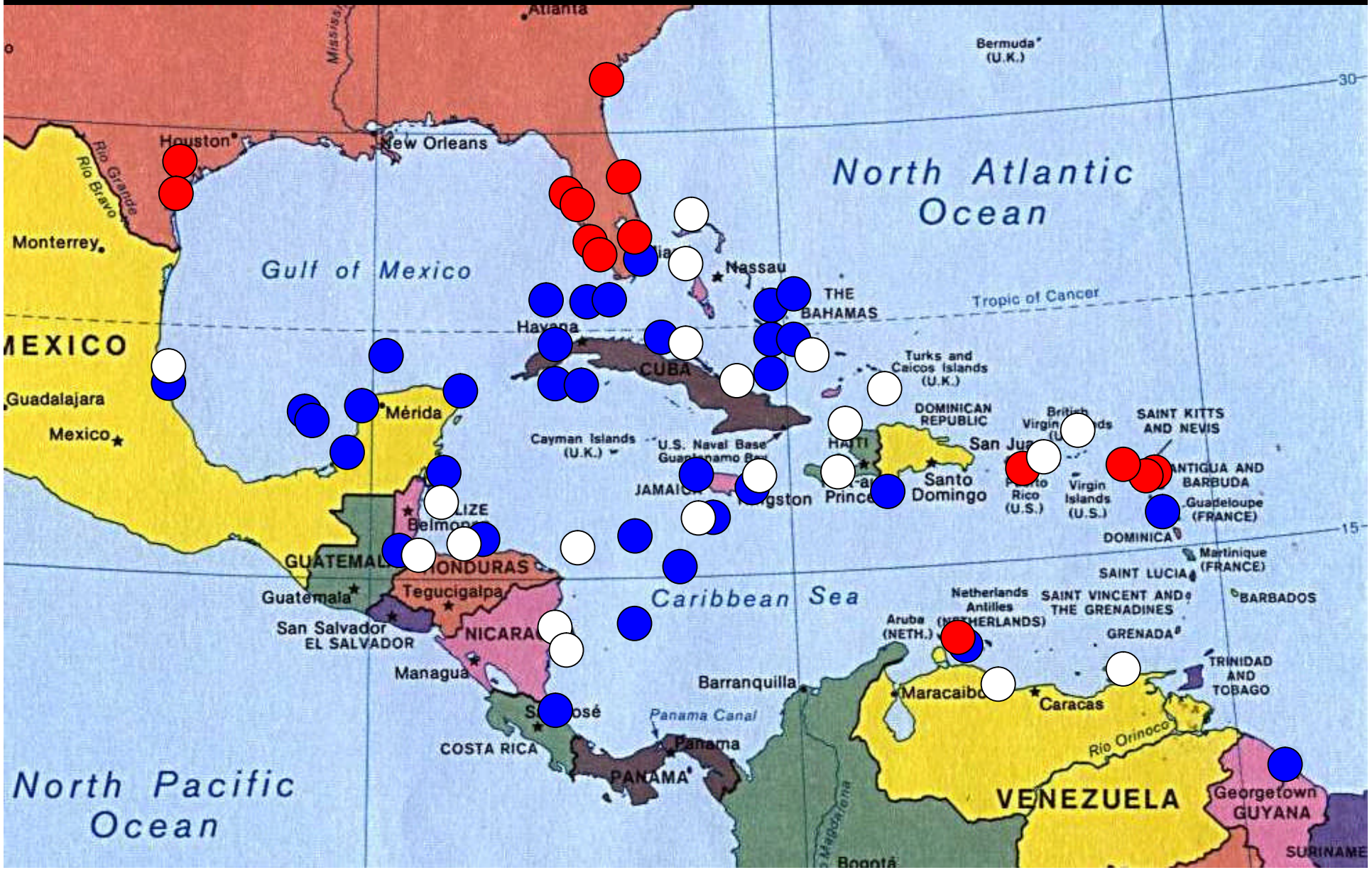
1) historical records

2) palaeontological/archaeological finds

3) place names suggestive of the species' former range (e.g. Seal Cay; Islas Lobos Marinos)

- searched using USGS and other geographic data banks

● = historical records
● = palaeontological/archaeological finds
● = place names



Edward William Nelson
1855-1934

Edward Alfonso Goldman
1873-1946

Hidden Accounts...

- pupping season long (at least June - December) due to lack of seasons in tropics
- seasonal migration to pupping areas unlikely
- segregation by age
- groups of up to 100
- behavioral thermoregulation
- diet of fish and crabs
- seal oil worth $0.16/L in late 1800s
- documented shark attacks on seals

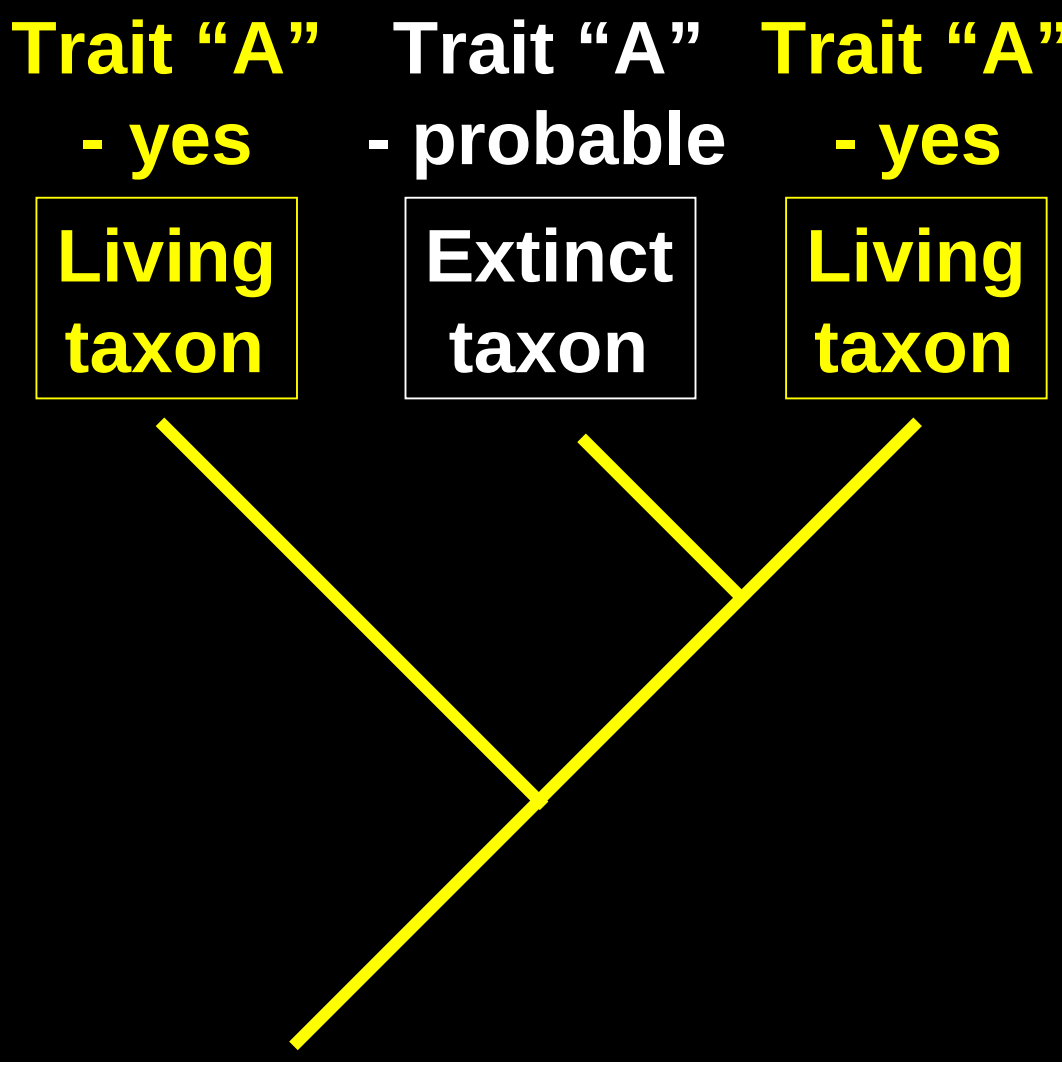
Information from the Skeleton...

1) Skull size is similar in males (*n* = 14) and females (*n* = 30), indicating no sexual size dimorphism

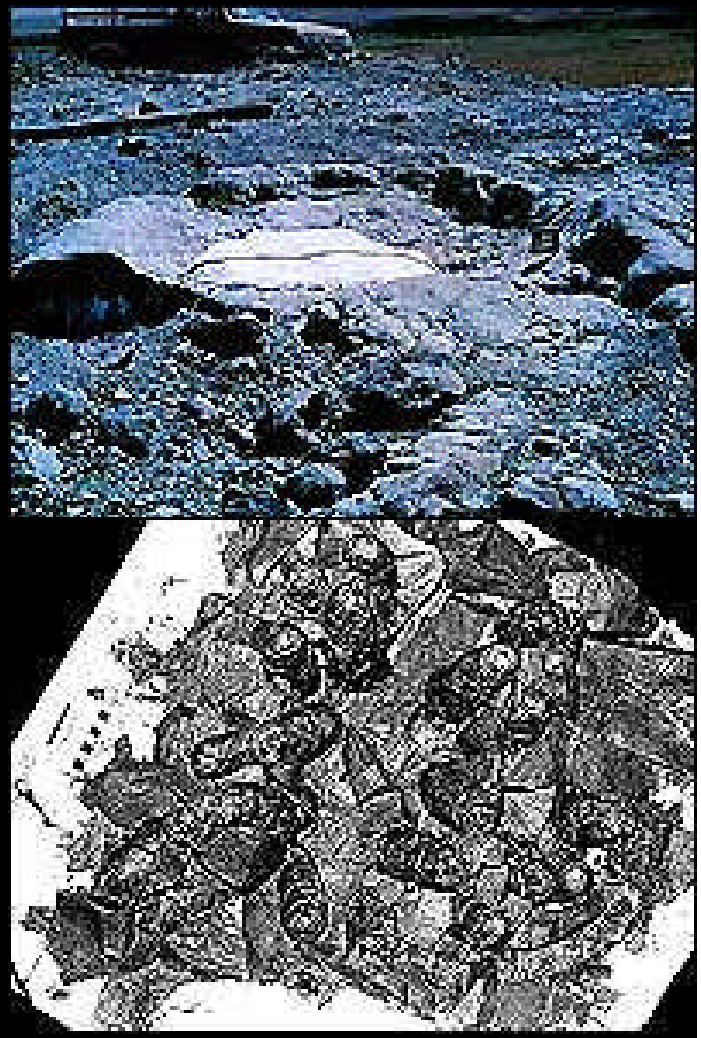
2) Two cases of carcinoma or histiocytosis X of the hard palate documented from the same population

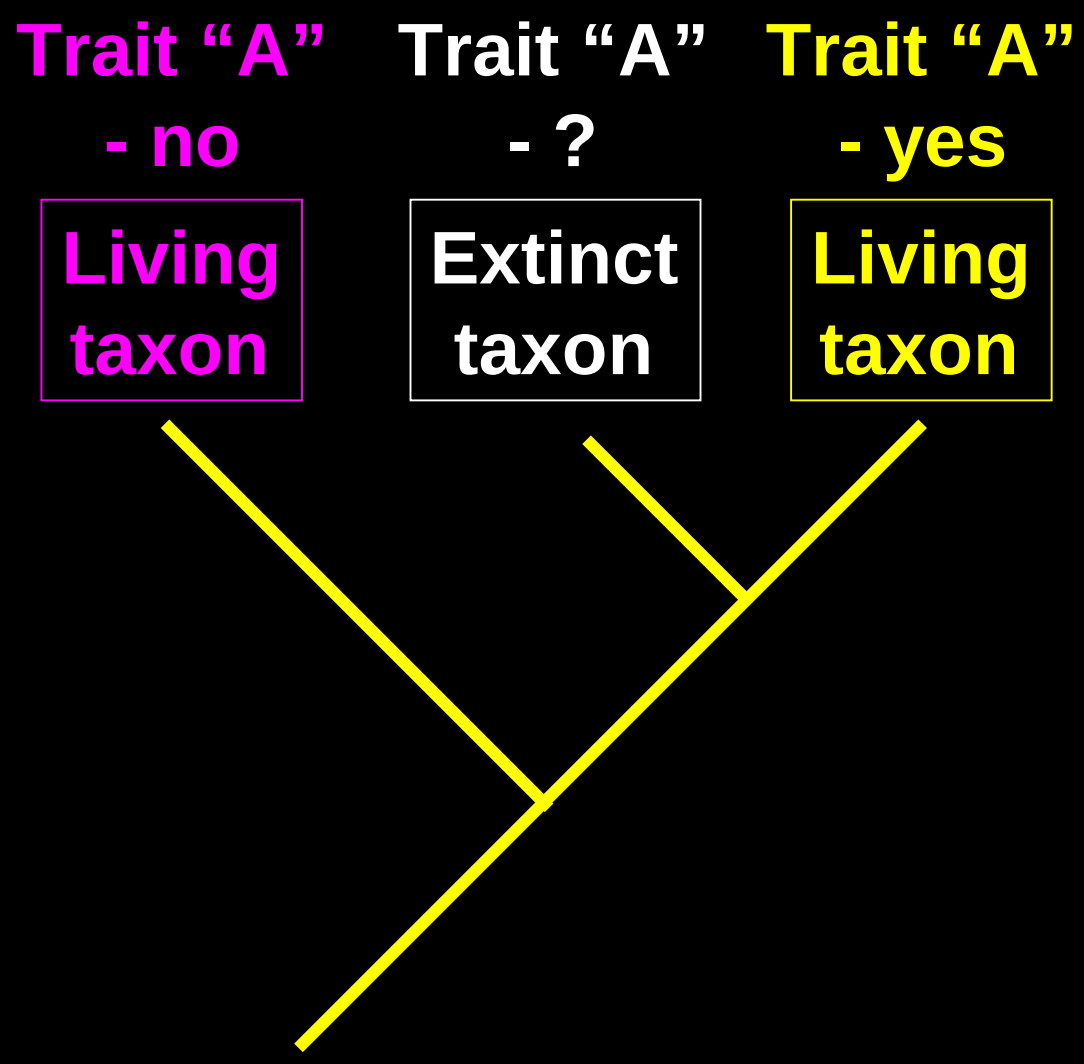
Phylogenetic Extrapolation...

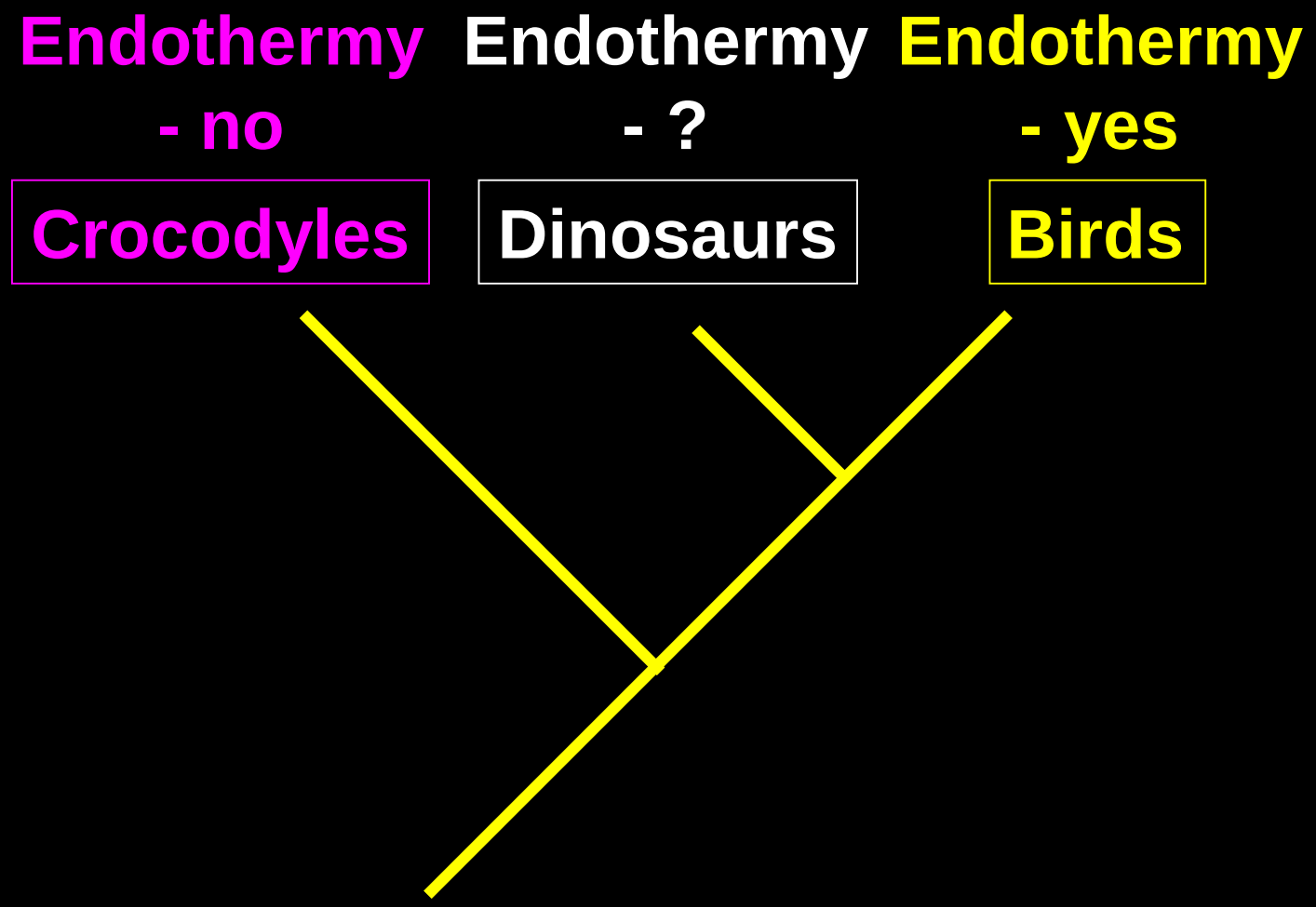
Method of crown group analysis:

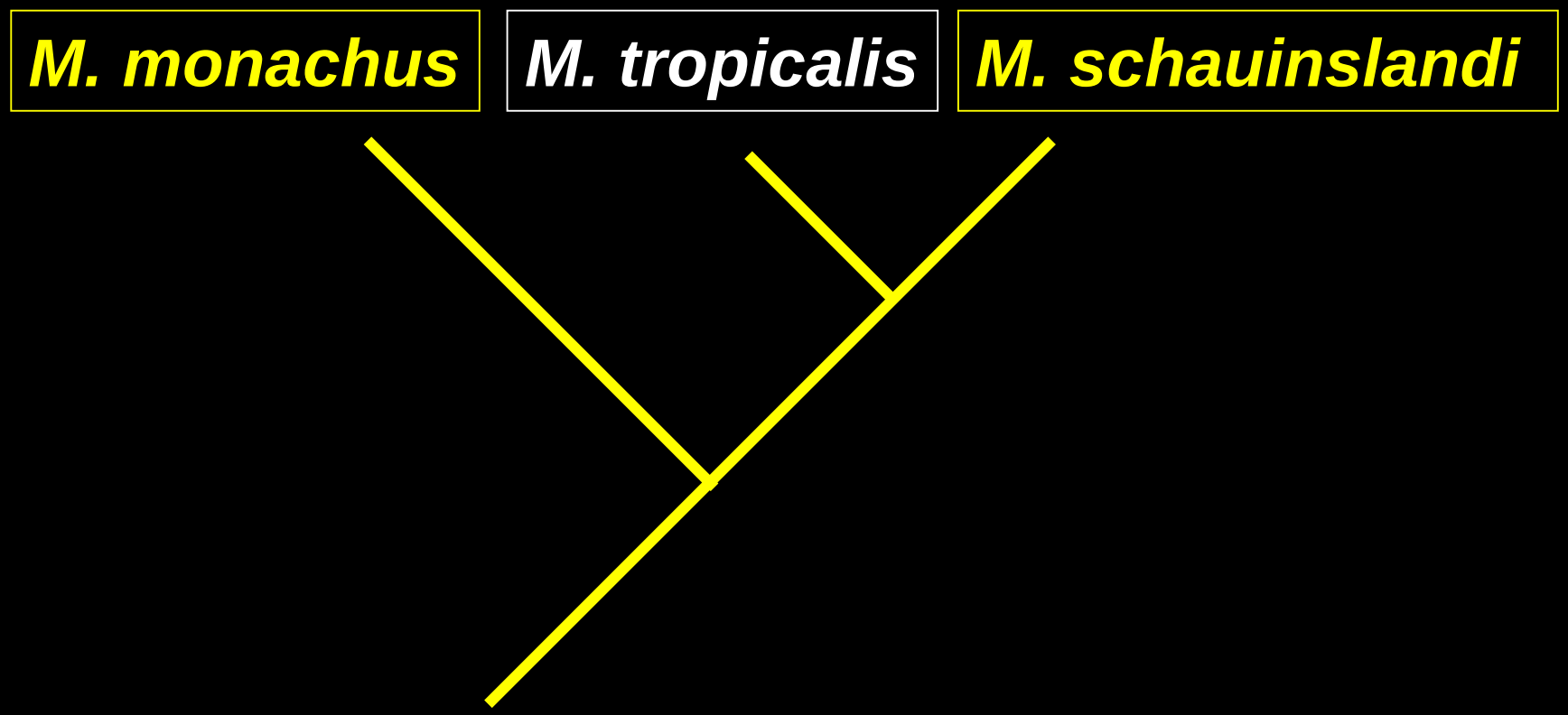


Parental care - yes	Parental care - probable	Parental care - yes
Crocodyles	Dinosaurs	Birds




Trait “A” - no
Trait “A” - ?
Trait “A” - yes
Living taxon
Extinct taxon
Living taxon


Endothermy - no
Endothermy - ?
Endothermy - yes
Crocodyles
Dinosaurs
Birds



- Adam et al., in progress

	Mm	Mt	Ms
Sexual maturity at 5 y.	Y	Y	Y
Reproductive cycle >1 y.	Y	Y	Y
1 y. gestation	Y	Y	Y
Lactation period 6 weeks	Y	Y	Y
Reniculate kidneys	Y	Y	Y
Single chambered stomach	Y	Y	Y
Aortic bulb for diving	Y	Y	Y

Acknowledgements

Specimen Access:

- AMNH: F. Brady, R. MacPhee
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- NMNH: D. Bohaska, L. Gordon, J. Mead, C. Potter, C. Ray
- UCLA: K. Molina
- ZMK: H. Baagøe
- CVM: C. Brown
- UofC: W. Fitch
- NMHN: C. de Muizon
- NHM: D. Hills

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- Central Puget Sound Stranding Network
- D. Duffield (PSU)
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- Ruth M. and George A. Bartholomew Fund
- Holmes-Miller Fund
- Sigma-Xi
- NMNH Lerner-Grey Fund
- Smithsonian Office of Fellowships & Grants

Thank You!