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
- Pinnipeds
- Polar Bear
- Sirenia
- Sea Otter

Pinnipeds
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
Early Pinnipeds

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

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

Phylogenies depict evolutionary relationships, show relative timing of lineage divergences, and are constructed using many "polar" characters.

1. Amniotic egg
2. Hair
3. Endothermy
4. Single centrale bone in ankle
5. Diapsid skull
6. Trunk encased in shell
7. Fenestra in lower jaw
8. Transverse cloacal slit
9. Feathers
10. Foramen of Panizza
11. Viviparity
12. Unique jaw-opening muscle
13. Chorio-allantoic placenta
14. Marsupium

Distant Outgroup (e.g., lungfishes)
Near Outgroup (e.g., amphibians)
Turtles
Lepidosaurus
Crocodilians
Birds
Monotremes
Marsupials
Eutherians
Mammals
Amniotes
Sauropterygia
Diapsids
"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
SIRENIA 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
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
<table>
<thead>
<tr>
<th>Family</th>
<th>Members</th>
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<tbody>
<tr>
<td>Canidae</td>
<td>Canis lupus, Dusicyon culpaeus, Vulpes vulpes</td>
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<tr>
<td>Ursidae</td>
<td>Ursus maritimus, Tremarctos ornatus, Selenarctos thibetanus, Helarctos malayanus, Ailuropoda melanoleuca, † Kolponomos sp.</td>
</tr>
<tr>
<td>Procyonidae</td>
<td>Procyon lotor, Ailurus fulgens, Bassaricyon gabbii, Nasua nasua, Potos flavescens</td>
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<tr>
<td>Mustelidae</td>
<td>Mustela vison, Mephitis mephitis, Taxidea taxus, Martes americana, Lutra canadensis, Lutra lutra, Enhydra lutris</td>
</tr>
<tr>
<td>Odobenid-like</td>
<td>Otariid-like</td>
</tr>
<tr>
<td>---------------</td>
<td>--------------</td>
</tr>
<tr>
<td>† Odobenus rosmarus</td>
<td>† Thalassoleon macnalleyi</td>
</tr>
<tr>
<td>† Aivukus cedroensis</td>
<td>† Thalassoleon mexicanus</td>
</tr>
<tr>
<td>† Alachtherium n. sp.</td>
<td></td>
</tr>
<tr>
<td>† Dusignathus seftoni</td>
<td></td>
</tr>
<tr>
<td>† Gomphotaria pugnax</td>
<td></td>
</tr>
<tr>
<td>† Imagotaria downsi</td>
<td></td>
</tr>
<tr>
<td>† Pontolis magnus</td>
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</tr>
<tr>
<td>† Protodobenus japonicus</td>
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</tr>
<tr>
<td>† Prototaria planicephala</td>
<td></td>
</tr>
<tr>
<td>† Pseudotaria n. sp.</td>
<td></td>
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<tr>
<td>† Valenictus chulavistensis</td>
<td></td>
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</table>

<table>
<thead>
<tr>
<th>Phocid-like</th>
<th>Basal Pinnipeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>† Desm. brachycephala</td>
<td>† Enaliarctos mealsi</td>
</tr>
<tr>
<td>† Desm. oregonensis</td>
<td>† Pinnarctidion rayi</td>
</tr>
<tr>
<td>† Homiphoca capensis</td>
<td>† Pteronarctos goedertae</td>
</tr>
<tr>
<td>† Piscophoca pacifica</td>
<td></td>
</tr>
</tbody>
</table>

**Odobenid-like**
- *Odobenus rosmarus* (†)
- *Aivukus cedroensis* (†)
- *Alachtherium n. sp.* (†)
- *Dusignathus seftoni* (†)
- *Gomphotaria pugnax* (†)

**Otariid-like**
- 14 Extant Species
  - *Thalassoleon macnalleyi* (†)
  - *Thalassoleon mexicanus*

**Phocid-like**
- 19 Extant species
  - *Acrophoca longirostris* (†)
  - *Allodesmus courseni* (†)
  - *Allodesmus kernensis* (†)

**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
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<th>MOLECULAR SEQUENCE</th>
<th>INFORMATIVE</th>
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<tr>
<td>12S rDNA 1004</td>
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<tr>
<td>16S rDNA 720</td>
<td>161</td>
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<tr>
<td>Valine (tRNA) 83</td>
<td>33</td>
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<tr>
<td>Aldolase A 484</td>
<td>16</td>
</tr>
<tr>
<td>Aldolase C 273</td>
<td>1</td>
</tr>
<tr>
<td>H2AF 368</td>
<td>7</td>
</tr>
<tr>
<td>H2AF (pseudogene) 316</td>
<td>3</td>
</tr>
<tr>
<td>Transthyretin 1088</td>
<td>336</td>
</tr>
<tr>
<td>Alpha Haemoglobin 141</td>
<td>31</td>
</tr>
<tr>
<td>Beta Haemoglobin 146</td>
<td>24</td>
</tr>
<tr>
<td><strong>SUBTOTAL</strong> 5763</td>
<td><strong>1883</strong></td>
</tr>
</tbody>
</table>

| MORPHOLOGICAL                      | 553         |

| TOTAL                               | 2436        |

**PAUP 4.0b2**
- Equal weights, heuristic search, polymorphism enforced
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?

I’m hungry!

Me too!
MASTICATORY FEEDING:
• Most terrestrial carnivores
• Diet variable, but involves oral breakdown of food
SUCTION FEEDING:

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

Kastelein & Mosterd (1989)
GENERALIST FEEDING:
• Most pinnipeds.
• Diet consists primarily of fish and squid.

FILTER FEEDING:
• Crabeater Seal (*Lobodon*).
• Diet consists primarily of krill.

GRIP AND TEAR FEEDING:
• Leopard Seal (*Hydrurga*).
• Diet consists primarily of large warm-blooded prey.

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

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.

(Adam & Berta 2002)
Figure 7. Condensed phylogenetic tree of the Pinnipedia pomorpha 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 behaviors 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.

SICB 2005:
Suction and Hydraulic Jetting Forces Produced by Feeding Bearded Seals (Erignathus barbatus)
Marshall, C.D. Texas A&M University at Galveston, USA marshall@tamu.edu; Kursar, K. M. Norwegian Polar Institute, Tromsø, Norway. 1

Bearded seals are thought to use suction as their primary feeding mode. This suggestion was until recently, based only on anecdotal data. More recent studies have confirmed that both suction and hydraulic jetting are important feeding behaviors of this species; the magnitude of these forces remains 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 while feeding from the ice. The mean suction force recorded was -47.1 kPa (S.D. +25.7) and ranged from -3.2 to -108 kPa (N=50) suction events). The mean hydraulic jetting force recorded was 3.3 (S.D. 3.45) and ranged from 3.2 to 37 kPa (N=52 hydraulic jetting events). The mean duration of suction events (0.29 s; S.D. 0.12) was significantly greater (p<0.051) 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 a delivery large negative pressures (suction phase). Suction capability of bearded seals is 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

Lateral undulation

Alternate pelvic rowing

Alternate pelvic paddling

Quadrupedal paddling

Terrestrial quadruped

Caudal oscillation

Dorsoventral undulation

Simultaneous pelvic paddling

Alternate pectoral paddling

Alternate pectoral rowing

Pectoral oscillation

Pectoral rowing

Fish (1996)
Pelvic oscillation

Lateral undulation

Alternate pelvic rowing

Alternate pelvic paddling

Pelvic paddling

Quadrupedal paddling

Terrestrial quadruped

Caudal oscillation

Dorsoventral undulation

Simultaneous pelvic paddling

Pectoral oscillation

Pectoral rowing

Alternate pectoral paddling

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
- Lateral undulation
  - Alternate pelvic rowing
  - Alternate pelvic paddling
- Intermediate stages not known

Caudal oscillation
- Dorsoventral undulation
  - Simultaneous pelvic paddling
  - Alternate pelvic paddling
  - Quadrupedal paddling
  - Terrestrial quadruped

Pectoral oscillation
- Pectoral rowing
  - Alternate pectoral paddling

Quadrupedal paddling
- Simultaneous pelvic paddling
- Intermediate stages not known
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
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
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
Evolution of Terrestrial Locomotion

(Modified) Ambulation
Undulation
Unknown

Canidae
Mustelidae
Procyonidae
Ursidae
Enaliarctos†
Pinnarctidion†
Pteronarctos†
Thalassoleon†
OTARIIDAE
Prototaria†
Pseudotaria†
ODOBENIDAE
Homiphoca†
Desmatophoca†
Allodesmus†
Acrophoca†
Piscophoca†
PHOCIDAE
FUNCTIONAL CORRELATES OF SWIMMING LOCOMOTION

PECTORAL OSCILLATION

PELVIC OSCILLATION
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 cartiligenous extensions
8) Femur: presence of lesser trochanter
9) Tibia: development of medial malleolus
10) Pedal phalanges: shape of pes
Pectoral 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
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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
Allodesmus, Acrophoca, Enaliarctos, Valenictus, Pectoral oscillators, Pelvic oscillators, Walrus, Leopard seal,

PC - 1 (72%) (Lumbosacral vertebrae)

GTW

PC - 2 (11%) (Cervical vertebrae)
Transitional?
Pelvic oscillation

Lateral undulation

Alternate pelvic rowing

Alternate pelvic paddling

Quadrupedal paddling

Terrestrial quadruped

Phocoids and Odobenids

Gomphotaria

Hydrurga

Pectoral oscillation

Pectoral rowing

Alternate pectoral paddling
OUTLINE

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• West Indian monk seal
Christopher Columbus
1451-1506
“... 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
• provided first taxonomic description of the Caribbean monk seal in 1849.

John Edward Gray
1800-1875
THE WEST INDIAN SEAL.

Monachus tropicalis, Gray. (p. 67.)

Drawing by Henry W. Elliot, from specimen in U. S. National Museum, No. 12395, obtained by Professor Felipe Poy in Matanzas, Cuba.

- Elliot, 1884
• 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
- few data on captive animals
- last known sighting in 1952
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
• 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:

- Trait “A” - yes
  - Living taxon

- Trait “A” - probable
  - Extinct taxon

- Trait “A” - yes
  - Living taxon
Parental care - yes
Crocodyles

Parental care - probable
Dinosaurs

Parental care - yes
Birds
Trait “A” - no
Living taxon

Trait “A” - ?
Extinct taxon

Trait “A” - yes
Living taxon
- Adam et al., in progress
<table>
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<th>Feature</th>
<th>Mm</th>
<th>Mt</th>
<th>Ms</th>
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</thead>
<tbody>
<tr>
<td>Sexual maturity at 5 y.</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Reproductive cycle &gt;1 y.</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
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<tr>
<td>1 y. gestation</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
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<tr>
<td>Lactation period 6 weeks</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
</tr>
<tr>
<td>Reniculate kidneys</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
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<tr>
<td>Single chambered stomach</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
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<tr>
<td>Aortic bulb for diving</td>
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Acknowledgements

Specimen Access:
- AMNH: F. Brady, R. MacPhee
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- UofC: W. Fitch
- NMHN: C. de Muizon
- NHM: D. Hills

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