REMARKS ON CORRELATIONS AND IMPLICATIONS
OF THE MANDIBULAR STRUCTURE AND DIET
IN SOME SEALS (MAMMALIA, PHOCIDAE)

I. A. Koretsky[1], S. J. Rahmat[1*], N. Peters[2]

[1] *Laboratory of Evolutionary Biology, Department of Anatomy, College of Medicine,*
 Howard University, 520 W St. NW, Washington, DC 20059 USA
[2] *Oertijdmuseum De Groene Poort, c/o Markt 11, 5492 AA Sint-Oedenrode, The Netherlands*
[*] *E-mail: sulman.rahmat@howard.edu*

Remarks on Correlations and Implications of the Mandibular Structure and Diet in Some Seals (Mammalia, Phocidae). Koretsky, I. A., Rahmat, S. J., Peters, N. — The diverse representatives of Recent seals within the three extant subfamilies (Cystophorinae, Phocinae, Monachinae) of the family Phocidae exhibit dietary variations among species, feeding on invertebrates and a diversity of prey depending on the season and availability. To explain this variability, an introductory morphological examination of the mandibular structure of Recent seals from each subfamily was performed, focusing on: heights of the mandibular ramus and condyloid process; measurements of the masseteric fossa; and attachments of muscles of mastication. After measuring the condyloid angles (the inclination of the condyloid process in relation to the axis of the alveolar row) among the examined species, a correlation between the size of the angle, function, and diet was recognized. Seals with a tall mandibular ramus and greater condyloid angle (Cystophorinae) feed on larger-sized prey, while seals with a shorter ramus and lesser condyloid angle feed on small (Monachinae) to medium-sized (Phocinae) prey, regardless of the overall size of the seal. This study focused on the mandibular morphology of some living and fossil representatives of Phocidae, providing an association between functional and ecological interpretations of modern seals in general and extrapolating this knowledge for fossil dietary preference.

K e y   w o r d s: Phocidae, mandibular ramus, carnivore, mammal, feeding, condyloid angle.

Заметки по взаимосвязи челюстной структуры и диеты некоторых тюленей (Mammalia, Phocidae). Корецкая И. А., Рахмат С. Дж., Петерс Н. — Различные представители современных тюленей в рамках трёх сохранившихся подсемейств (Cystophorinae, Phocinae, Monachinae) семейства демонстрируют вариации в диете между видами, питаясь беспозвоночными и самой разнообразной добычей в зависимости от сезона и её доступности. Чтобы объяснить эту вариабельность, было выполнено вводное морфологическое исследование нижнечелюстной структуры современных тюленей каждого подсемейства и уделено особое внимание: высоте челюстной ветви и бугорков мыщелка; измерению жевательной ямки и прикреплению жевательных мышц. После измерения углов мыщелка (углу наклона бугорка мыщелка по отношению к оси альвеолярного ряда) среди исследованных видов была признана корреляция между размером угла, функцией и диетой. Тюлени с высокой ветвью нижней челюсти и большим углом мыщелка (Cystophorinae) питаются добычей большего размера, в то время как тюлени с более короткой ветвью и меньшим углом мыщелка питаются добычей небольших (Monachinae) и средних (Phocinae) размеров, независимо от общего размера тюленей. Это исследование было сосредоточено на морфологии нижней челюсти некоторых живых и ископаемых представителей Phocidae, обеспечивая связь между функциональными и экологическими интерпретациями современных тюленей в целом и экстраполяцией этих знаний на диетические предпочтения ископаемых тюленей.

К л ю ч е в ы е   с л о в а: Phocidae, ветви нижней челюсти, хищник, млекопитающее, питание, угол мыщелка.

Introduction

Due to the controversial taxonomic relationships within Phocidae (Koretsky, Rahmat, 2013), this study will continue with the more classical classification of seals as the family Phocidae includes carnivorans divided

into three extant subfamilies (Phocinae, Monachinae, Cystophorinae) in addition to the recently described extinct subfamily Devinophocinae. Morphologically, true seals are easily distinguishable from other carnivores due to unique adaptations to aquatic life. Previous studies have demonstrated that the mandibular condyloid process is located superior to the tooth row in herbivores and is typically inferior to or at the same level as the tooth row in carnivores (Greaves, 1998). However, different condyloid process heights occur in species of Phocidae: while some species appear similar to herbivores (significantly superior to the tooth-row level), others closely resemble carnivores (almost at the level of the tooth-row). Furthermore, there are variations in the heights of the condyloid process among representatives of the three extant phocid subfamilies, highlighting potentially interesting relationships between form and function, which can be extrapolated to fossil members of all four subfamilies. Here, we discuss the correlations of the mandibular ramus with dietary adaptations of some Recent seals and their potential implications for fossil species.

There is a functional significance in the position of the mandibular ramus of mammals compared to the axis of the alveolar row, the shape and location of the coronoid and condyloid processes, and the depth and size of the masseteric fossa. Among these features, the physical characteristics of the masseteric fossa are especially noteworthy since they correspond to the power of mastication (Jones et al., 2013). The inclination of the condyloid process in relation to the axis of the alveolar row, measured from the posterior edge of M1, also has particular implications for the functional morphology of the mandible. Specifically in Phocidae, this feature, which we term the condyloid angle (fig. 1), provides tangible measurements and is used to define the size of gape. While some aspects of the mandible have been examined in a functional light in relation to diet (Adam, Berta, 2002; Jones et al., 2013), the ecological interpretation of the condyloid angle in Phocidae has not previously been examined.

The mandibular ramus includes the sites of attachment for two major mastication muscles: the masseter and temporalis. The masseter originates from a large area of the zygomatic arch and inserts onto the masseteric fossa, while the temporalis muscle originates from the lateral side of the temporal and parietal bones and inserts onto the coronoid process (Endo et al., 1998). The masseter can be divided into superficial and deep portions, with the former mostly inserting into the inferior edge of the labial side of the ramus closer to the mandibular angle and the latter mostly inserting into the superior edge of the ramus closer to the coronoid process (Muizon, 1981). In our comparison of the osteology and myology of these phocids, it is assumed that a larger bony surface area provides more attachment sites for muscle fibers. The masseteric fossa extends across the entire ramus length in all species mentioned except for *Lobodon carcinophagus*, likely due to its specialized filter-feeding behavior.

Phocidae is one of the most diverse and widespread families of marine mammals, meaning that their diets exhibit an assortment of interesting variations among species. All phocids are carnivorous and most eat a rather broad range of animals, but there are certain dietary specializations and preferences that depend on diving depths, seasonal changes, and availability. While most phocids catch prey with their teeth and swallow them whole, some species (*Erignathus barbatus*) use suction-feeding (Adam, Berta, 2002) or filter-feeding (*Lobodon carcinophagus*) techniques (Berta, Sumich, 1999; Croll et al., 2008, Jones et al., 2013). We will attempt to explain the dietary implications of some representatives of each subfamily of Phocidae by examining variations in the degree of the condyloid angle in relation with the size and type of prey consumed. Also, we examine the significance of the location of the condyloid process at a lower level than the coronoid process in the mandibles of phocids. This positioning would help maximize the force of bite at larger gape angles, which is an important objective in the feeding of carnivorans such as phocids. This study focused on the mandibles of living representatives of Phocidae, providing useful information for the dietary separation of seals in general and extrapolating this knowledge to fossil taxonomy.

Abbreviations — Specimens from the following institutions have been examined for this study:
CMM — Calvert Marine Museum, Solomons, Maryland, USA;
NMNH — National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

Material and methods

A study of 25 mandibles (table 1) from the osteological collection of the NMNH and CMM of Recent and fossil seals was performed. For each mandible, the following measurements/descriptions were demonstrated from photographs, creating two-dimensional figures (instead of a three-dimensional bone): 1) the condyloid angle (the inclination of the condyloid process in relation to the axis of the alveolar row as seen in fig. 1); 2) the width of the coronoid process at the level of the mandibular notch (measured from the widest part of the cranial portion of the coronoid process) and the height (measured from the tip of the process to the ventral edge of the mandibular notch); 3) the masseteric fossa height (h) from the base of the coronoid process to the inferior edge of the fossa and 4) the masseteric fossa width (w) at its widest portion (indicated by arrows in fig. 2–6).

Specifically, the condyloid angle can be identified by the joining of a horizontal axis parallel to the base of the mandible, starting from the lower alveolar edge of the canine (as indicated by line a in fig. 1), a vertical axis from the posterior edge of m1 to the base of the mandible (line b in fig. 1) and an oblique axis from the intersection of lines a and b to the tip of the condyloid process (line c in fig. 1).

T a b l e 1. Measurements of the condyloid angle in Phocidae

Т а б л и ц а 1. Результаты измерения угла мыщелка у Phocidae

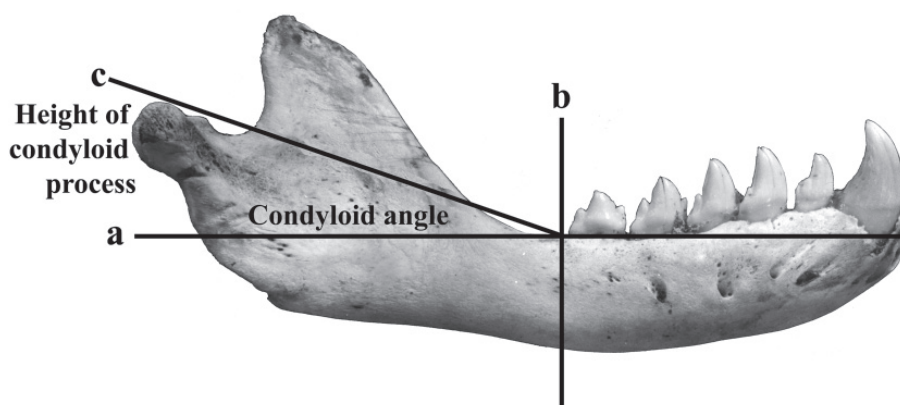| Subfamily	Species	Width (cm) of masseteric fossa	Coronoid process base width (cm) — measured at level of alveolar line	Coronoid process height (cm) — measured perpen-dicular to alveolar line	Condyloid angle
Cystophorinae	*Mirounga angustirostris* n = 5	♂10.0	♂7.0	♂3.0	♂18°
		♀4.5	♀2.5	♀2.5	♀31°
	Cystophora cristata n = 4	4.5	4.5	4.5	♀28°
					♂33°
Phocinae	*Halichoerus grypus* n = 2	5.5	4	4.4	20°
	Phoca largha n = 3	3	2.2	1.8	25°
	† *Leptophoca lenis* n = 2				26°
Monachinae	*Monachus tropicalis* n = 3	5	4	3	♀16°
	Lobodon carcinophagus n = 2	4	2	2	20°
	† *Pliophoca etrusca* n = 4				24°
Devinophocinae	† *Devinphoca sp n?* n = 1				20°
Incerta sedis	† *Miophoca vetusta* n = 1				9°

Fig. 1. Right mandible of Recent Gray seal (*Halichoerus grypus*, NMNH 51488) in labial view with measured condyloid angle based on the inclination of the condyloid process to the alveolar line. The condyloid angle can be identified by the joining of a horizontal axis parallel to the base of the mandible, starting from the lower alveolar edge of the canine (as indicated by line a), vertical axis from the posterior edge of m1 to the base of the mandible (line b) and an oblique axis from the intersection of lines a and b to the tip of the condyloid process (line c).

Рис. 1. Правая челюсть серого тюленя (*Halichoerus grypus*, NMNH 51488) с губной стороны, с измеренным углом мыщелка на основе наклона отростка мыщелка к альвеолярной линии. Угол мыщелка может быть идентифицирован путём соединения горизонтальной оси, параллельной основанию нижней челюсти, начиная от нижнего альвеолярного края клыка (как показано линией b), вертикальной оси, от заднего края m1 к основанию челюсти (линия b) и косой оси, от пересечения линии a и b на вершине отростка мыщелка (линия c).

Remarks on mandibular morphology of some phocids

The abundance of seals occupying the same niches and competing for similar prey likely forced ecological adaptations, including change of diet, diving depth and habitat. Numerous studies have shown the strong correlation between phocid diet and diving depth (Le Boeuf et al., 1985; Schreer, Kovacs, 1997). The morphology of seals likely changed as a direct result of the two-way interaction between ecological and morphological adaptations to feeding competition and availability of prey. Seals with increased diving capabilities are able to feed on types of prey not accessible at shallower levels, resulting in the ability to feed on larger prey or krill living in deeper waters.

Subfamily CYSTOPHORINAE
Mirounga angustirostris Gill, 1866 (fig. 2, table 1)

In female *Mirounga angustirostris*, the ramus of the mandible extends very high above the tooth row, is directed caudally, and yields a condyloid angle that is rather wide at about 31°, indicating a large gape. The coronoid process rises slightly above the level of the condyloid process posterodorsally. The mandibular notch is inferior to the condyloid process (in females, not in males). There is a distinct inferior notch on the posterior border of the ramus, a fossa for the masseteric muscle on the labial surface, and a small angular process that marks the location of the mandibular angle. The masseteric fossa covers almost
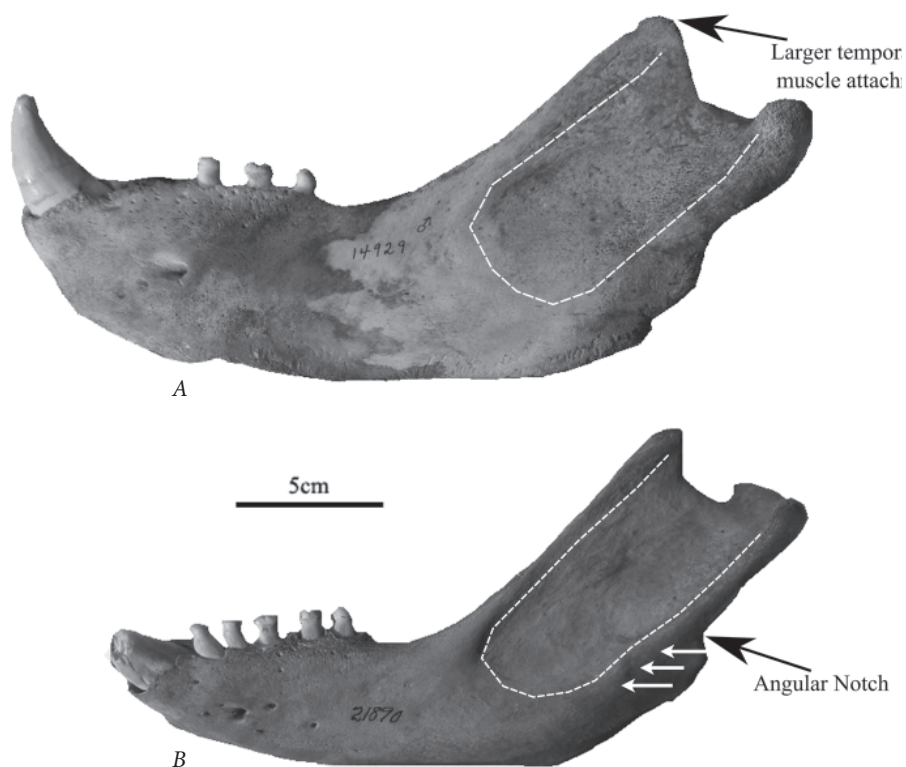

Fig. 2. Subfamily Cystophorinae: left mandible of *Mirounga angustirostris* in labial view: *A* — ♂, NMNH 14929; *B* — ♀, NMNH 21890.

Рис. 2. Подсемейство Cystophorinae: левая челюсть *Mirounga angustirostris*, вид с губной стороны: *A* — ♂, NMNH 14929; *B* — ♀, NMNH 2189.

the entire labial surface of the ramus and extends down at an oblique angle towards the body (fig. 2). The deepest portion of the fossa is along its posterior border. The outline for the masseter muscle is distinct and well developed. Located in the inferior half of the fossa are a few bony ridges or grooves for attachment of mostly superficial masseter tendons (fig. 2). The widest portion of the fossa is approximately 4.5 cm (table 1). The coronoid process is a short broad triangle about 2.5 cm high and 2.5 cm wide at the base (width and height of the coronoid process is measured at the level of the mandibular notch).

The male *M. angustirostris* mandibular ramus is dissimilar to that of females in most aspects and shows very well-defined sexual dimorphism and overall larger size (condyloid angle: ♀ — 31° and ♂ — 18°; table 1). The mandibular notch in males is slightly inferior than the condyloid process. The masseteric fossa of males is considerably wider and shallower than females (table 1). The antero-inferior border of the fossa is less defined compared to female *M. angustirostris*, but it appears to be at the same level. Despite the lack of fossa depth, the breadth alone indicates a larger masseter muscle than female. The base of male coronoid process is more than twice the width of that of female (7.0 cm : 2.5 cm), but the heights are similar (3.0 cm : 2.5 cm). The larger surface area of the coronoid process in male suggests a larger and more prominent temporalis muscle than in female, indicating sexual dimorphism within this particular species.

Throughout the year, northern elephant seals (*Mirounga angustirostris)* feed on rockfish, squid, midshipman, octopus, Pacific lamprey, hagfish and small sharks (Heptner et al.*, 1976; Riedman, 1990; Stewart, Huber, 1993). More recent examinations of the stomach contents of female *M. angustirostris* suggest that the diet consists of more mesopelagic squid and less fish (Le Boeuf et al., 2000). Both male and female *M. angustirostris* show noticeably weak teeth and according to Stewart and Huber (1993) they have similar diets. Diet is strongly determined by diving depth. As shown by Le Boeuf et al. (1985) and Schreer and Kovacs (1997), the preferred average diving depth for female *M. angustirostris* is 350–650 m, but they may dive up to 1273 m, while males range from 450–1250 m, with a maximum depth of 1530 m.

Cystophora cristata Erxleben, 1777 (fig. 3, table 1)

The mandibular ramus is considerably superior to the tooth row, directed posterodorsally and is slightly wider than the body. The posterior border of the coronoid process takes on a hook-shape and slopes slightly toward the condyloid process in both sexes. The condyloid process is located slightly superior to the level of the mandibular notch in females, while in males it is significantly higher (black arrows in fig. 3). Overall, the mandibular notch is considerably wider in males than in females. A relatively small depression is present on the caudal border of the ramus (fig. 3). The angular process is rather weak, creating a distinctly smooth and rounded mandibular angle. The condyloid angle (♂33° and ♀28°; table 1) is wide and shows a large gape.

The masseteric fossa is less distinctly outlined than that of female *Mirounga angustirostris*, and the width measures approximately the same (4.5 cm in both sexes of *Cystophora cristata*), even though the overall size of the body is much smaller. Like in *M. angustirostris*, the fossa seems to extend the entire length of the ramus (fig. 3). The masseteric fossa is relatively smooth in the middle, with no obvious significant ridges or grooves for muscle attachment. The *C. cristata* coronoid process is much narrower, especially towards the base, but the height is approximately the same as that of female *M. angustirostris*. The overall size of the *C. cristata* mandible is smaller than that of male and female *M. angustirostris*, and both the masseter and temporalis muscle attachments are weaker and less defined in *C. cristata*. Similar to *Mirounga*, the *C. cristata* mandible has weak teeth.

The stomach content of hooded seals (*C. cristata*) describes diets consists of halibut, Greenland cod, herring, flounder, octopus, shrimp, squid and mussels (Kovacs, Lavigne,
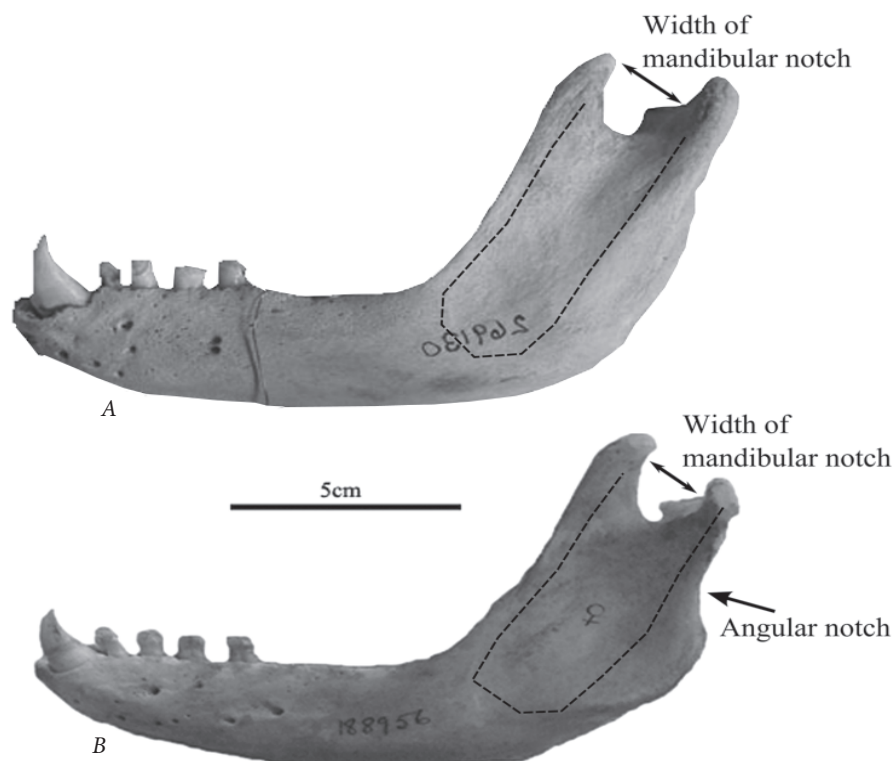
Fig. 3. Subfamily Cystophorinae: left mandible of *Cystophora cristata*: *A*— ♂, NMNH 269130, reversed; *B* — ♀, NMNH 188956, in labial views.

Рис. 3. Подсемейство Cystophorinae: левая челюсть *Cystophora cristata*: *A* — ♂, NMNH 269130, развёрнута; *B* — ♀, NMNH 188956, вид с губной стороны.

1986). The average diving depth of young pups is 75 m (Scholander, 1940) while adults have been known to dive to 180 m in order to obtain food (King, 1983).

Subfamily PHOCINAE
Halichoerus grypus Fabricius, 1791 (fig. 4, *A*, table 1)

The mandibular ramus is noticeably thicker than the body. The condyloid process is approximately at the same level as the mandibular notch and has a large round head. On the anterior surface of the condyloid process is a well-defined depression for the attachment of the lateral pterygoid muscle. The coronoid process is a large broad triangle with a rounded apex located superior to the condyloid process. The posterior edge of the coronoid process ends as a strong vertical slope towards the mandibular notch. Along the posterior border of the ramus is a small inferior notch and a slight angular process. In *H. grypus* the condyloid angle of 20° (table 1) is considerably smaller than in most cystophorines.

The masseteric fossa is well defined with a width of about 5.5 cm and located in the inferior portion of the fossa are small oblique ridges for the attachment of superficial masseter tendons (black arrows in fig. 4, *A*; similar to *M. angustirostris*). These features are either less defined or absent in the fossa of the other species presented in this paper. The masseteric fossa is especially deep along both its anterior and posterior borders, where the ramus meets with the body. The coronoid process is quite broad and provides significant surface area for the attachment of temporalis muscle fibers. The taller coronoid process is located about 4.5 cm superior to the mandibular notch.

Gray seals (*H. grypus*) feed mostly on salmon, cod, herring, skates, squid and octopus (Bonner, 1981). The diving depth ranges from 70–225 m (Scronce, Ridgway, 1980; Thompson et al., 1987).

Phoca largha Pallas, 1811 (fig. 4, *B*, table 1)

The mandibular ramus is directed posterodorsally and the mandibular body is noticeably thinner than the body of *Halichoerus grypus*. The condyloid process is situated superior to the tooth row (similar to *H. grypus*) and the mandibular notch. The coronoid process is a slender triangle with the apex sloping towards the condyloid process. The area of attachment for the temporalis muscle on the coronoid process is marked by a small ridge that is directed towards the labial side of the ramus (black asterisks in fig. 4, *B*). Along the posterior border of the ramus is a small knob-shaped angular process. The condyloid angle of 25° is larger than *H. grypus*, but is smaller than the cystophorines *C. cristata* and female *M. angustirostris*.

The entire labial surface of the ramus is covered by the masseteric fossa (fig. 4, *B*), which is very smooth and devoid of ridges or grooves for attachment of masseter tendons.

Fig. 4. Subfamily Phocinae: *A* — mandible of *Halichoerus grypus*, left, NMNH 51488; in labial view showing masseteric fossa (dashed outline) and arrows indicating ridge for attachment of superficial masseter tendons; *B* — mandible of *Phoca largha*, right, reversed, NMNH 290654; in labial view showing width (w) and height (h) of the masseteric fossa and the small ridge on the coronoid process (black *) for attachment of the temporalis muscle.

Рис. 4. Подсемейство Phocinae: *A* — нижняя челюсть *Halichoerus grypus*, слева, NMNH 51488, вид с губной стороны; показана жевательная ямка (пунктирная линия), стрелки указывают на гребень для крепления поверхностных жевательных сухожилий; *B* — нижняя челюсть *Phoca largha*, справа, развернута, NMNH 290654, вид с губной стороны; показана ширина (w) и высота (h) жевательной ямки и малый гребень на венечном отростке (отмечены звёздочками) для прикрепления височной мышцы.

The fossa is much deeper along the anterior and posterior borders when compared to the shallower inferior border. The fossa width (3.0 cm) is noticeably narrower than in *H. grypus*, suggesting that the masseter is likely to be slightly smaller and weaker. The coronoid process height (about 1.8 cm) is smaller than the one of *H. grypus*. Along with the difference in height, the much narrower *P. largha* coronoid process apex indicates less attachment area for the temporalis muscle. The diminished sizes of the *P. largha* masseter and temporalis correspond to an overall smaller mandible than in *H. grypus*.

Spotted seals (*P. largha*) are mostly piscivorous, feeding on available fish including flounder, herring, anchovy, trout, salmon and others as well as squids, crabs and clams (Bigg, 1981; Dehn et al., 2006). The maximal dive depth for *P. largha* was thought to be 206 m (Harrison, Kooyman, 1968; Kooyman, 1981), but it has been noted more recently that they can dive up to 508 m (Schreer, Kovacs, 1997).

Subfamily MONACHINAE
Monachus tropicalis Gray, 1850 (fig. 5; table 1)

The mandibular ramus does not strongly project dorsally and is broader than the body. The condyloid process is situated slightly superior to the alveolar border of the mandible. The condyloid process is approximately at the level of the mandibular notch and is directed more posteriorly than vertically, yielding a rather deep mandibular notch. The condyloid process in males has a distinct crest and a well-defined masseteric fossa (fig. 5). The posterior edge of the coronoid process is to some extent directed toward the condyloid process, more so in males. The coronoid process is a large broad triangle with a markedly round apex located superior to the condyloid process. On the lingual surface of the coronoid process is a well-defined depression that marks the site of attachment of some temporalis muscle fibers. Additional attachment is provided by a small overhang on the labial surface of the coronoid process. There is a slight angular process at the mandibular angle. The condyloid angle (♀16°; table 1) is significantly smaller than that of cystophorines and phocines, suggesting smaller gape.

It is difficult to determine how far down the inferior border of the masseteric fossa extends, but it appears to cover the entire length of the ramus (fig. 5). The fossa width measures about 5.0 cm and indicates a relatively well-developed masseter muscle. The surface within the fossa is rather smooth and is not marked by ridges or grooves for masseter tendon attachment. The height of the coronoid process height is 3.0 cm and the width is
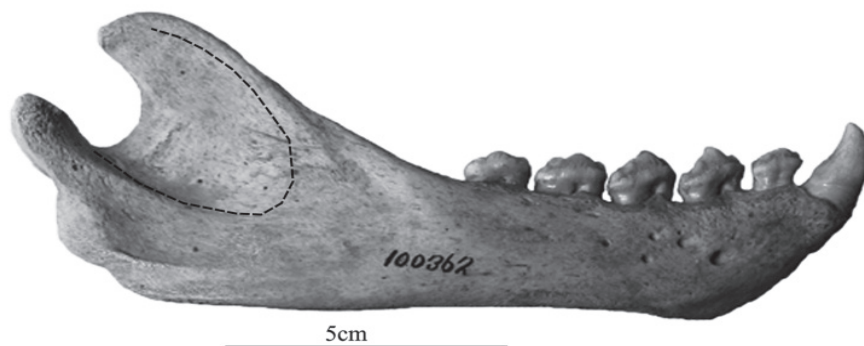

Fig. 5. Subfamily Monachinae: mandible of *Monachus tropicalis* in labial view (♀, right, NMNH 100362); showing masseteric fossa (dashed outlines).

Рис. 5. Подсемейство Monachinae: челюсть *Monachus tropicalis,* вид с губной стороны (♀, справа, NMNH 100362); показана жевательная ямка (пунктирная линия).

4.0 cm, providing a large surface area for the attachment of temporalis muscle fibers.

Very little is known about the natural diet of the extinct Caribbean monk seals (*Monachus tropicalis*), but they likely exhibited a generalized feeding strategy similar to most phocids (Adam, 2004). Presumably, the diet was similar to *Monachus monachus* and *M. shauinslandi*, the two species of monk seals that are still alive today. Evidence from stomach contents and fecal deposits reveal that monk seals feed primarily on lobster, eels, larval fish and octopus (Kenyon, 1981). It has been noted that monk seals can dive up to about 615 m, but the estimated preferred feeding niche is less than 100 m (Kenyon, 1981). Studies of *Monachus schauinslandi* (Hawaiian monk seals) show that the average diving depth is 10–40 m, with maximum ranging from 121–175 m (Kooyman et al., 1983).

Lobodon carcinophagus Hombron et Jacquinot, 1842 (fig. 6, table 1)

The lesser degree of the condyloid angle is likely due to the short height of the mandibular ramus (table 1). The short condyloid process extends slightly superior to the tips of the teeth, specifically the canine, with a narrow mandibular notch. The short coronoid process is a slender triangle with a rounded apex. The anterior border of the coronoid process is slightly thicker, marking the site for attachment of the temporalis and masseter muscles. On the labial surface of the ramus is a rather weak, narrow masseteric fossa (fig. 6). Between the posterior border of the molar and the coronoid process is a bony protuberance that fills in what would otherwise be a triangular gap when the mouth is closed. There is a medium-sized condyloid angle of 20°, which is smaller than most cystophorines and phocines, but larger than *M. tropicalis*.

The width of the masseteric fossa (4.0 cm) of *Lobodon carcinophagus* covers only 1/2 to 3/4 of the ramus length and is very shallow. The diminished size and lack of depth of the fossa indicates a significantly reduced and less developed masseter than in *Monachus tropicalis* and most of the other species discussed in this paper. The coronoid process, with a width and height of 2.0 cm is slightly smaller than in *M. tropicalis* and suggests that the temporalis muscle is either similar or smaller in size.

The common name "crabeater seal" is confusing because unlike most seals, the preferred prey of *L. carcinophagus* is small shrimp-like crustaceans known as krill belonging to the genus *Euphausia* (King, 1961). However, they do eat fish, squid and the occasional crab (Burns et al., 2004). Studies on *L. carcinophagus* confirm that the average diving depth is up to 528 m (Schreer, Kovacs, 1997).

Fig. 6. Subfamily Monachinae: left mandible of *Lobodon carcinophagus* (NMNH 28538) in labial view showing masseteric fossa (dashed outline).

Рис. 6. Подсемейство Monachinae:. левая челюсть *Lobodon carcinophagus* (NMNH 28538), вид с губной стороны; показана жевательная ямка (пунктирной линией).

Discussion

These preliminary results demonstrate that the three extant subfamilies of Phocidae can be divided morpho-functionally based on the size and shape of the mandible. The noted differences are as follows:

Subfamily CYSTOPHORINAE

Both species of the Subfamily Cystophorinae have very weak teeth, which could be the reason that representatives of this subfamily possess a superior-positioned mandibular ramus, very much elevated above the tooth-row. The bigger condyloid angle demonstrates the ability of these seals to eat large sized prey. Furthermore, the very well-developed masticatory muscles, such as the masseter and temporalis, could be the result of compensation for weak teeth. Thus, the powerful actions of the muscles of mastication would allow for a stronger bite and more forceful tearing of large prey. On the other hand, weakened teeth could be a direct result of the strong mastication muscles, with increased muscular force influencing the unnecessary need of strong teeth due to their ability to swallow prey whole. Future morphological studies would benefit greatly by examining the causal relationship between weak teeth and strong mastication muscles to determine exactly which structures dominate and which are the result of compensation. In addition, the condyloid angle and its measurements suggest a degree of sexual dimorphism among Cystophorinae, but few or no significant differences between the sexes of representatives in the other subfamilies. *Mirounga* is the only genus of Phocinae where sexual dimorphism is clearly displayed, mainly in size, color and cranial and postcranial skeletal elements. Therefore, sexual dimorphism in mandibular anatomy likely corresponds to cranial dimorphism.

Subfamily PHOCINAE

The members of this subfamily also have well-developed muscles of mastication (similar to the subfamily Cystophorinae), but without sexual dimorphism and with much smaller overall sizes. They have smaller teeth, a small mandibular ramus, a condyloid process that is superior to the tooth-row (but not as high as in Cystophorinae) and a condyloid angle that lies between Cystophorinae and Monachinae, suggesting that Phocinae diets consist of mostly medium-sized prey (larger than monachine and smaller than cystophorine prey). Therefore, the subfamily Phocinae is located in an intermediate position among the three extant subfamilies.

Subfamily MONACHINAE

Members of this subfamily have large teeth and a lower mandibular ramus. The condyloid process is situated at about the level of the tooth-row and these seals possess the smallest condyloid angles of the three extant subfamilies examined, demonstrating the smallest gape and diets consisting of small-sized prey. Lobodontini are unique phocids that are specialized filter-feeders, inferring a smaller condyloid angle and gape than Cystophorinae and Monachinae. The masseter and temporalis muscles in Monachinae are weak compared to those in Cystophorinae.

Previous studies have shown direct association between the power of bite force and food processing with the mandible (Hylander, Johnson, 1994). Thus, functional implications can be found by examining the mandibular morphology of primates (Hylander, 1979; Daegling, Grine, 1991) and some carnivorans (Therrien, 2005). Also, in carnivores, Greaves (1985, 2000) showed that jaw length is related to gape. Despite numerous carnivoran mandibular studies and the examination of the jaw morphology of pinnipeds (Jones et al.,

2013), no one has detailed the correlation of specific mandibular characteristics to dietary adaptations in seals. As an initial study, we specifically narrowed our attention on: 1) the morphological variations of the masseteric fossa; 2) the measurement of the condyloid angle with 3) correlating known dietary studies of different true seals.

Due to the dietary preferences of seals (i. e. hard shells, fish, and krill), the ratio between the condyloid process height and the level of the alveolar row (= the condyloid angle) can be correlated to the type/size of prey consumed by each of the three extant subfamilies. Examinations of the mandibles in this study demonstrate that the condyloid angle does not change due to age. A lower condyloid process reduces the muscle stretching and therefore maximizes the bite force at a given gape angle (Herring, Herring, 1974). Male *Mirounga angustirostris* (Cystophorinae) has a significantly lower condyloid process depth than in Phocinae and Monachinae, minimizing the muscle stretch while maximizing the bite force. Having a more powerful bite is of crucial importance to *M. angustirostris* because their diet includes larger and stronger prey such as small sharks (Stewart, Huber, 1993). Despite being the largest phocid in terms of body size, male *Mirounga* possess one of the smaller condyloid angles, indicating potential dietary preferences as a suction/bottom feeder. This would correlate with species such as walruses, which are extremely large yet are suction feeders. This initial finding must be further investigated to determine the diet of male *Mirounga*, as previous studies show that both male and female *Mirounga* prefer similar diets of fish and small sized sharks (Heptner et al.*,* 1976; Riedman, 1990; Stewart, Huber, 1993).

For modern Phocinae and Monachinae, the position of the condyloid process in relation to the alveolar row is generally taller than in Cystophorinae as evidenced in *H. grypus*, *P. largha*, *L. carcinophagus*, and *M. tropicalis*. Thus, Phocinae and Monachinae seals feed on primarily fish and invertebrates, which include smaller-sized and weaker prey, and therefore require a less powerful bite.

Therefore, species such as *Cystophora cristata* and female *Mirounga angustirostris* (Cystophorinae) possess the largest condyloid angles, directly correlating to their diet of larger prey, despite the presence of weak teeth. In contrast, seals with smaller condyloid angles limit the stretch of masticatory muscle fibers, allowing for more forceful contractions and a smaller gape, correlating with a diet consisting of small to medium-sized prey, as in *Lobodon carcinophagus*. The extinct *Pliophoca etrusca* (Koretsky, Ray, 2008: fig. 42) has a relatively large condyloid angle (24˚), suggesting that they ate medium to large sized prey and were deep divers. A large condyloid angle in this fossil could represent a plesiomorphic trait for all monachines.

Ecological and morphological adaptations may partly explain the differing dietary capabilities of the three extant subfamilies of seals. Female *Mirounga* have the greatest diving depth (up to 1270 m), correlating with the ability to obtain larger prey that live in deeper waters and having one of the largest condyloid angles. Phocinae, who eat medium sized prey, have the second deepest diving depths (up to 225 m) and second largest condyloid angles, while Monachinae have the shallowest diving depths (up to 175 m) and eat small-sized prey. The highly specialized monachine filter-feeder *Lobodon* is the second deepest diver (up to 520 m), despite eating the smallest prey of any phocid. Despite the general opportunistic feeding habits of seals, there appears to be a strong correlation between degree of condyloid angle, size of teeth and types of prey.

The Recent seals from the three extant subfamilies examined here show two different basic morphologies of the mandible: 1) high ramus with a condyloid process superior to the alveolar plane (as in herbivores) and 2) low ramus with condyloid process just at or inferior to the alveolar plane (as seen in other carnivores). The varying heights of the mandibular ramus and condyloid process, both between and within each subfamily, suggest strong association of the function, morphology and diet of true seals. Seals with a high mandibular ramus and greater condyloid angle feed on larger-sized prey, while seals with a low ramus

and lesser condyloid angle feed on small to medium-sized prey regardless of the overall size of the animal.

Thus, our results demonstrate differences in morphological features of the mandible and their correlation with taxonomy between the three extant subfamilies and with further extrapolation to fossil representatives. The importance of these findings to future phocid studies is extremely evident when considering the shortage of published material on this vital region for modern and fossil seals.

The limited sampling of representatives from each extant subfamily of true seals used in this preliminary study demonstrates significant variation in the condyloid angle. Despite this shortcoming, this study can be used as the basis for future extrapolative examinations of fossil seal mandibles in order to determine potential dietary implications. For example, the extinct phocine *Leptophoca lenis* (late-early Miocene ~18 Ma, Calvert County, Maryland, USA; Koretsky, 2001: fig. 42), representing the Phocinae subfamily, has a condyloid angle of 26°, which is similar to the fossil *Pliophoca etrusca* (Pliocene ~5.2–3.4 Ma, Western Europe and Eastern United States), representing the Monachinae subfamily, with a condyloid angle of 24° (Koretsky, Ray, 2008: fig. 42). It should be noted that the overall morphology

Fig. 7. Subfamily Phocinae: right mandible of fossil *Leptophoca lenis*, CMM–V 2021 in labial view from Calvert Formation, late-early Miocene (~18 Ma), Calvert County, Maryland, USA (*A*); subfamily Devinophocinae: reversed right mandible of fossil sp. n. ? (NMNH 553687) in labial view from Badenian Formation, early–middle Miocene (~16 Ma), Central Paratethys, Vienna Basin of Western Slovakia, Europe. Masseteric fossae are shown by dashed outlines (*B*).

Рис. 7. Подсемейство Phocinae: *A* — правая челюсть ископаемого *Leptophoca lenis*, CMM–V 202, вид с губной стороны, из формации Калверт, поздний–ранний миоцен (~18 млн. л.), Калверт Каунти, штат Мэриленд, США; подсемейство Devinophocinae: развернута правая челюсть ископаемого sp. n. ? (NMNH 553687), *B* — вид с губной стороны, из формации Бадениан, ранний–средний миоцен (~16 млн. л.), Центральный Паратетис, Венский бассейн Западной Словакии, Европа (жевательные ямки показаны пунктирными контурами).

of *Leptophoca lenis* (fig. 7) has mixed characters of Phocinae and Monachinae as well. Thus, fossil *L. lenis* was probably a shallow to deep diver with a diet consisting of small to medium-sized prey due to the medium condyloid angle and morphology of dentition and muscle attachment, similar to Recent Phocinae and Monachinae. The condyloid angle of a new fossil Devinophocinae (sp. n. ?) is 20° (table 1), which is smaller than most cystophorines and larger than most monachines, suggesting that this extinct seal was a medium-depth diver and ate medium sized prey, despite the small size of this seal as compared to other Phocidae. The fossil skulls and mandibles of Devinophocinae share characters with all three extant subfamilies. The first fossil record representing the subfamily Cystophorinae recently described by Koretsky and Rahmat (2013) did not include mandibular descriptions due to the lack of preserved material. The mandible of the fossil *Miophoca vetusta* (Zapfe, 1937), a possible fossil Cystophorinae, has been described, but there remains questionable classification of this seal and therefore, presently is situated in an uncertain taxonomic position. The condyloid angle of the extinct *M. vetusta* (9°, table 1) is the smallest of any seal examined, suggesting that they fed on small sized prey, perhaps even as a suction/bottom feeder.

While the morphology of the mandibular ramus of some Recent seals has been discussed, future studies are needed to accurately describe mandibular biomechanics. These examinations would need to include: distinguishing the comparative sizes of different types of teeth (cheek, incisors, and canines); specifying lines of actions of the muscles of mastication; and estimating vector inclination and joint locations. Although not included in this paper, we realize the importance of such studies and the potential for extrapolating the findings to determine the functional, morphological, and dietary correlations for modern and possibly fossil seals.

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