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DIVERSITY OF MANDIBULAR MORPHOLOGY IN SOME CARNIVORANS

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Diversity of Mandibular Morphology in Some Carnivorans. Rahmat, S. J. Koretsky, I. A. — Comparison of mandibular morphology of some aquatic (seals, walruses, and sea otters) and terrestrial (hyenas and pandas) carnivorans demonstrates a rather general pattern correlating size of condyloid angle, size of gape, and diet. Structural differences of carnivoran jaws reveal morphological and ecological adaptations that are directly correlated with availability of prey, diving depth, feeding competition and specialized feeding methods. Specifically, the inclination of the condyloid process relative to the axis of the alveolar row (= condyloid angle) can be used to determine dietary preferences, including size of prey. Generally, carnivorans with a large condyloid angle feed on larger prey, while a low condyloid angle suggests feeding on small prey or can be an advantageous feeding mechanism. *Mirounga angustirostris* (Northern elephant seal) displays sex-specific characters in cranial and postcranial elements. Likewise, significant sexually dimorphic differences in the size of condyloid angle imply that deeper-diving male Northern elephant seals have a feeding niche dissimilar to that of females. Morphological assessment of male *M. angustirostris* suggests they are bottom-feeding seals that utilize a suction-feeding mechanism to capture small prey and crush shells with their teeth, which become weaker as they age.

Key words: marine mammal, seal, mandibular morphology, carnivoran, gape, condyloid angle.

Разнообразие в морфологии челюстей некоторых хищных животных. Рахмат С. Й., Корецкая И. А. — Сравнение морфологии нижней челюсти некоторых водных (тюлени, моржи и морские выдры) и наземных хищников (гиены и панды) демонстрирует довольно общую картину корреляции между величиной мышечкового угла, расстоянием между открытыми челюстями и характером питания. Структурные различия челюстей хищников выявляют морфологические и экологические адаптации, прямо связаны с доступностью добычи, глубиной погружения, конкуренцией за ресурсы и специализированными методами кормления. В частности, угол наклона мышечкового отростка по отношению к оси альвеолярного ряда (= мышечковый угол) может быть использован для определения трофических предпочтений, в том числе размера добычи. Как правило, хищники с большим мышечковым углом челюсти охотятся на крупную добычу, в то время как небольшой мышечковый угол предполагает питание мелкой добычей или может быть эффективным трофическим механизмом. *Mirounga angustirostris* (северный морской слон) демонстрирует признаки полового диморфизма черепных и посткраниальных элементов. Кроме того, значительные половые различия в размерах мышечкового угла означают, что экология питания самцов северных морских слонов, способных к глубоководному погружению, существенно отличается от таковой у самок. Морфологическая оценка самцов *M. angustirostris* позволяет предположить, что они являются тюленями, которые кормятся на глубине и используют механизм кормления всасыванием, захватывая мелкую добычу и разрушая раковины зубами, которые с возрастом становятся слабее.

Ключевые слова: морские млекопитающие, тюлени, морфология нижней челюсти, хищники, расстояние между открытыми челюстями, мышечковый угол.

Introduction

It is common knowledge that carnivorous mammals can be terrestrial or aquatic predators/scavengers with powerful jaws and sharp teeth adapted for tearing. Few carnivores are obligate, with nutrition based solely

on animal flesh (i. e. polar bear, cat), and many are omnivores, eating both animal and non-animal foods (i. e. bears). Pandas are unique carnivores that are exclusively herbivorous, with mandibles adapted to chewing plants and large molars designed to grind.

Extant pinnipeds are semi-aquatic marine carnivorans that can stay on land/ice for extended periods of time. The three families of so-called pinnipeds are: phocids (seals), otariids (sea lions) and odobenids (walruses). The finding of the Oligocene seal demonstrates that true seals have maintained an aquatic lifestyle for over 24 million years (Koretsky, Sanders, 2002), similar in geological time to the earliest Enliarctinae, which first appeared in the late Oligocene approximately 24 million years ago (Koretsky, Barnes, 2006; Barnes, 2007). According to Rycbczynski et al. (2009), a large, transitional mammal resembling sea otters (*Puijila darwini*) re-entered the marine environment approximately 20–25 million years ago. Sea lions (~23 Ma; late Oligocene) are of similar age to seals and walruses (~16 Ma; Middle Miocene) appear significantly later than seals (Barnes, 2007). Although phocids and otariids appear to have comparable early origins, they have separate ancestries (Koretsky, Barnes, 2006), with phocids in the North Atlantic (resembling otter-like animals) and otariids in the North Pacific (resembling walruses and bear-like animals). Despite separate origins of true seals, walruses and otariids, their adaptation to aquatic environments is analogous, resulting in the formation of the order “Pinnipedia.”

Extant odobenids (walruses) are much larger in size than most seals. They show a combination of traits (Riedman, 1990) found in phocids and otariids; e. g., they can rotate their hind flippers forward to walk on land like otariids and have a swimming pattern like true seals. Walruses have tusks and use suction feeding to eat shellfish from the ocean floor.

Molecular and morphological analyses of seals result in contradictory subfamilial taxonomic relationships. This study maintains the traditional classification of seals as the family Phocidae, including carnivorans divided into three extant subfamilies (Phocinae, Monachinae, and Cystophorinae) in addition to the recently-described extinct subfamily Deviniophocinae (Koretsky, Holec, 2002; Koretsky, Rahmat, 2013; 2015).

Mandibular morphology in terrestrial carnivores (Greaves, 1998; 2000) shows a condyloid process on the mandibular ramus inferior to or at the same level as the tooth row, which contrasts with terrestrial herbivores where the mandibular ramus (and both coronoid and condyloid processes) are very high, superior to the tooth row. In marine carnivorans, specifically true seals, the mandibular ramus (including the condyloid process) has differing heights (Koretsky et al., 2014), with some species appearing similar to herbivores (significantly superior to the tooth-row level) and others closely resembling carnivores (almost at the level of the tooth-row). Greaves (2000) described the importance of the location of the resultant force during mastication in animals, detailing the correlation between dominant musculature and force direction. A dominant temporalis muscle has fibers inclined posteriorly, resulting in a resultant force directed posteriorly, while a dominant masseter/pterygoid complex is anteriorly inclined, shifting the resulting force anteriorly. Overall, larger muscle size, altering muscle architecture and even increasing the size of the animal can increase muscle force.

The masseter and temporalis muscles (both vital for mastication) attach on the mandibular ramus. The Jones et al. (2013) study on bite force demonstrated differing morphology and biomechanics of the pinniped jaw. There is a difference in the shape of the mandible in predaceous and non-predaceous carnivores due to the pressure of capturing and holding live prey (Meloro et al., 2011). Also, the shape of the carnivoran mandible and location/size of dentition are important indicators of feeding behaviors (Meloro, 2012). From a preliminary study on the osteology and myology of phocids (Koretsky et al., 2014), it appears there exists variation in the surface area of the masseteric fossa, where muscles of mastication attach. Also, between seal taxa, there are differences in the size and shape of the coronoid process, where the temporalis muscle attaches.

Our previous publication (Koretsky et al., 2014) examined morphological differences of the mandibular ramus and condyloid angle in true seals. The condyloid angle is the inclination of the condyloid process relative to the axis of the alveolar row (fig. 1). The results showed a strong discrepancy between the condyloid angle of male and female *Mirounga angustirostris* (Subfamily Cystophorinae; Koretsky et al., 2014; table 1). While *Mirounga* does display sexual dimorphism in cranial and postcranial elements, the significantly dissimilar condyloid angles needed to be examined further in relation to diet. Additionally, we compared the association between mandibular morphology, degree of condyloid angle and average diving depths of seals and some other aquatic carnivorans such as sea otters and walruses (fig. 2).

Previous studies (Stewart, Huber, 1993) have stated that male and female *Mirounga* feed on similar prey. However, the strong correlation between size of gape, condyloid angle and diet in seals from our previous study (Koretsky et al., 2014) indicated that the degree of the condyloid angle can be used to determine specific diets of extant seals and can be extrapolated to predict diet and feeding behaviors in fossil representatives. Thus, we correlate this measured angle with size of gape and dietary adaptations of some terrestrial (hyena and panda) and aquatic (pinnipeds and sea otter) carnivorans to test our hypothesis that male *Mirounga angustirostris* seals utilize a specialized feeding mechanism and eat smaller sized prey than their female counterparts.

For this comparative survey, we use species with known diets (hyena, panda, walrus, sea otter) to test whether the degree of inclination of the condyloid process can indeed be a predictor of dietary preference across a wide range of taxa. These terrestrial and marine carnivorans were chosen due to their unique dietary specializations, ranging from bone crushers (hyena), completely herbivorous carnivorans (panda) and suction-feeders (walrus). This study will test our hypothesis that *Mirounga angustirostris* has sexually dimorphic diets, resulting from significantly different condyloid angles, diving depths and mandibular morphology.

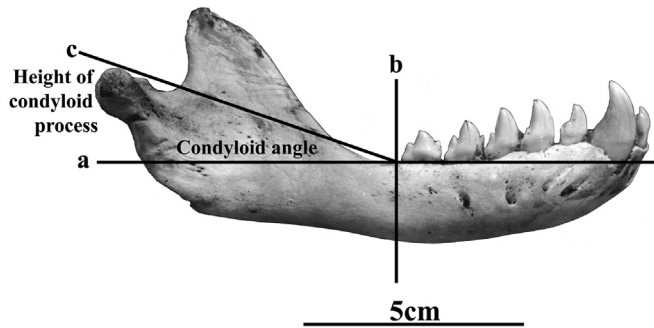


Fig. 1. Right mandible of Gray seal (*Halichoerus grypus*, USNM 51488) in labial view showing the condyloid angle (= inclination of condyloid process to the alveolar line). The intersections of a horizontal axis starting from the lower alveolar edge of the canine through the posterior edge of the m1 alveolus (as indicated by line a), vertical axis from the posterior edge of m1 perpendicular to line a (line b) and an oblique axis from the junction of lines a and b to the tip of the condyloid process (line c) were used to define the condyloid angle.

Рис. 1. Правая челюсть серого тюленя (*Halichoerus grypus*, USNM 51488) с губной стороны показывает мышелковый угол (= наклон мышелкового отростка по отношению к альвеолярной линии). Пересечения горизонтальной оси, начиная с нижнего альвеолярного края клыка через задний край m1 альвеолы (как показано линией а), вертикальной оси от заднего края m1, перпендикулярной к линии а (линия б) и косой оси от пересечения линий а и б на вершине мышелкового отростка (линия с) использовалась для определения мышелкового угла.

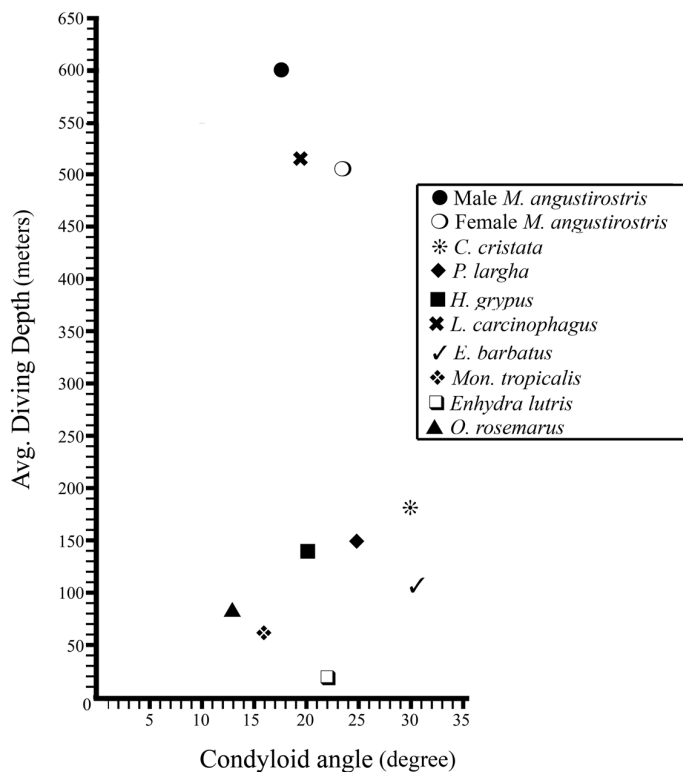


Fig. 2. Chart comparing median degree of condyloid angle with average diving depths among aquatic carnivorans.

Рис. 2. График сравнивающий средний уровень мышелкового угла со средней глубиной погружения водных хищных.

Table 1. Measurements of the condyloid angle in some carnivorans

Таблица 1. Промеры мышелкового угла у некоторых хищных животных

Taxa	Species	Condyloid angle (M)	
sub. Cystophorinae	<i>Mirounga angustirostris</i> n = 8	♂ 17°	
		♀ 23°	
	<i>Cystophora cristata</i> n = 4	♀ 28°	
		♂ 33°	
sub. Phocinae	<i>Halichoerus grypus</i> n = 2	20°	
		<i>Phoca largha</i> n = 3	♂, ♀ 25°
			<i>Erignathus barbatus</i> n = 5
sub. Monachinae	<i>Monachus tropicalis</i> n = 3	♀ 16°	
		<i>Lobodon carcinophagus</i> n = 2	♂, ♀ 20°
Sea Otter	<i>Enhydra lutris</i> n = 9		♂ 22°
		♀ 23°	
Walrus	<i>Odobenus rosmarus</i> n = 7	♂ 13°	
		♀ 13°	
Hyena	<i>Crocuta crocuta</i> n = 2	♂ 19°	
		♀ 10°	
Giant Panda	<i>Ailuropoda melanoleuca</i> n = 1	32°	

Methods

Mandibular morphology of some modern aquatic (seals, sea otters and walruses) and terrestrial carnivorans (hyenas and pandas) were studied (tables 1, 2) from the osteological collection of the NMNH (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA). Some comparative diagnostic mandibular characters of the carnivorans surveyed in this study were also detailed, including condition of dentition (table 2). The mandibular morphology of aquatic carnivorans studied was correlated with preferred diving depths (fig. 2) to examine dietary preferences.

For each mandible, measurements of the condyloid angle were recorded from photographs, creating two-dimensional figures from a three-dimensional bone. As described by Koretsky et al. (2014), the condyloid angle can be defined by the intersection of a horizontal axis starting from the lower alveolar edge of the canine through the posterior edge of the m1 alveolus (as indicated by line a in fig. 1), a vertical axis at the posterior edge of m1 perpendicular to line a (line b in fig. 1), and an oblique axis from the junction of lines a and b to the tip of the condyloid process (line c in fig. 1).

Abbreviations: ang. pr. = angular process; cond. pr. = condyloid process; cor. pr. = coronoid process; mand. n. = mandibular notch; mf = masseteric fossa.

Comparative analysis

Due to the diversity of terrestrial and aquatic carnivorans inhabiting similar niches and competing for comparable prey, ecological specializations including change of diet, diving depth and habitat became necessary. Some workers (Adam, Berta, 2002; Jones et al., 2013) have examined the functional relationship of the mandible and diet, but prior to Koretsky et al. (2014), none examined the correlations between the condyloid angle, size of gape and diet these animals consume. Structural differences of carnivoran jaws reveal

adaptations (both ecological and morphological) that are directly influenced by availability of prey, prey capture techniques, feeding competition and specialized feeding mechanisms.

True Seals (Phocidae), fig. 3–4, table 1

Phocidae are very diverse marine mammals and have varying diets that depend on seasonal changes, diving depths, mandibular morphological characteristics and availability of prey. Depending on the taxa examined and seasonal availability of foods, seals feed on various crustaceans, krill, squid, fish and even some small sharks (Koretsky et al., 2014). The condyloid angle (fig. 1) in Phocidae provides physical measurements that can be used to define the size of gape.

Members of the subfamily Cystophorinae have the largest condyloid angle among the seals examined in this study (table 1). Male *Cystophora cristata* (Hooded seal) have an angle of 33° and females 28°. Adult *C. cristata* have been shown to have an average diving depth of 180 m in order to obtain food (King, 1983). These large condyloid angles and similar diving depths suggest comparable diets of larger-sized prey. The mandibular ramus of *C. cristata* extends considerably superior to the tooth row and the coronoid process has a hook-shape in both sexes. The base of the coronoid process is narrow and the masseteric fossa is not very well outlined, but extends the entire length of the ramus (Koretsky et al., 2014; fig 3).

The extremely large cystophorine *Mirounga angustirostris* (Northern elephant seal; fig. 3) shows obvious sexually dimorphic characters in postcranial and cranial elements, including mandibular morphology. The mandible of male *M. angustirostris* differs from females by having: 1) a wider snout; 2) a longer mandibular symphysis; 3) a broader anterior portion of the mandible; and 4) longer, more robust canines (Briggs, Morejohn, 1974). The masseteric fossa of males (mf; fig. 3 A) is wider and shallower than in females, with females having a more well-developed outline for the masseter muscle (Koretsky et al.,

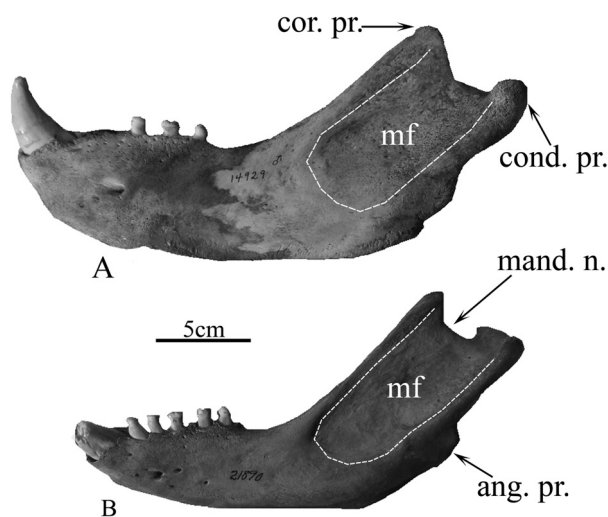


Fig. 3. Left mandibles of (A) ♂, USNM 14929 and (B) ♀, USNM 21890 Northern elephant seal (*Mirounga angustirostris*) in labial view. Dashed lines indicate the outline of the masseteric fossa. Abbreviations: ang. pr. = angular process; cond. pr. = condyloid process; cor. pr. = coronoid process; mand. n. = mandibular notch; mf = masseteric fossa.

Рис. 3. Левые челюсти (A) ♂, USNM 14929 и (B) ♀, USNM 21890 северного морского слона (*Mirounga angustirostris*) с губной стороны. Пунктирная линия указывает на контур жевательной ямки. Аббревиатуры: ang. pr. = угловой отросток; cond. pr. = мышечковый отросток; cor. pr. = клювовидный отросток; mand. n. = челюстная выемка; mf = жевательная ямка.

2014, table 1). While the mandibular ramus in females (fig. 3 B) extends very high above the tooth row, in males it is larger and not as high. The base of the coronoid process (cor. pr.), the attachment site of the temporalis muscle, is significantly wider in males than females. Similar to *C. cristata*, *Mirounga* seals have weak postcanine teeth. Sexual dimorphism is also evident in the condyloid angle of these seals, as males have a significantly smaller angle (17°) than females (23°), indicating potential sex-specific dietary differences.

Phocine seals exhibit intermediate condyloid angles (suggesting a diet of medium-sized prey) among the three extant subfamilies, ranging from 20° in *Halichoerus grypus* (Gray seal) to 25° in *Phoca largha* (Spotted seal). The mandibular ramus of *H. grypus* is extremely thick and the masseteric fossa is very well-defined and deep. A broad coronoid process implies a large attachment site for the temporalis muscle. The mandibular ramus of *P. largha* is noticeably thinner than *H. grypus* (Koretsky et al., 2014; fig. 4), with the masseteric fossa extending over the entire labial surface. The narrow coronoid process of *P. largha* suggests a less powerful temporalis muscle, while the overall smaller mandible implies a weaker masseter muscle as well. These phocines feed on squid, octopus and fish such as salmon, trout and cod (Bonner, 1981; Bigg, 1981; Dehn et al., 2006). Gray seals dive between 70 to 225 m, while Spotted seals have been noted to be able to dive up to 508 m (Schreer, Kovacs, 1997).

The phocine *Erignathus barbatus* (Bearded seal) has a much larger condyloid angle (ranging from 27° to 33°) than other taxa in this subfamily and are known benthic feeders. Bearded seals favor shallow coastal waters, preferring to dive less than 200 m, and utilize their whiskers to feed on small-sized prey such as clams, squid and crustaceans (Burns, 1981) in soft bottom sediments on the ocean floor. *E. barbatus* has a deep, narrow and well-defined masseteric fossa (indicating a well-developed masseter muscle) that does not extend the full length of the labial surface of the ramus (fig. 4). The coronoid process extends slightly superior to the condyloid process and is rather broad and flattened, suggesting a large surface area for attachment of the temporalis muscle. The condyloid process is relatively thin with the presence of a minute tubercle on the caudal surface, likely for attachment of lateral pterygoid

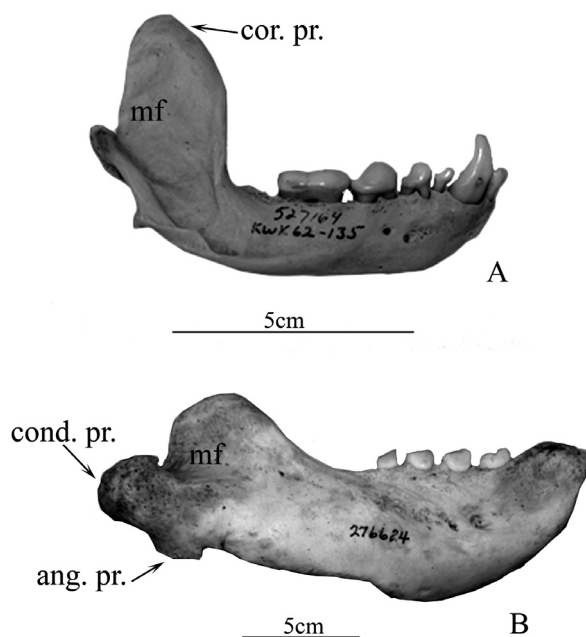


Fig. 4. Right mandible of Bearded seal (*Erignathus barbatus*; ♂; USNM 396801) in labial view.

Рис. 4. Правая челюсть морского зайца (*Erignathus barbatus*; ♂; USNM 396801) с губной стороны.

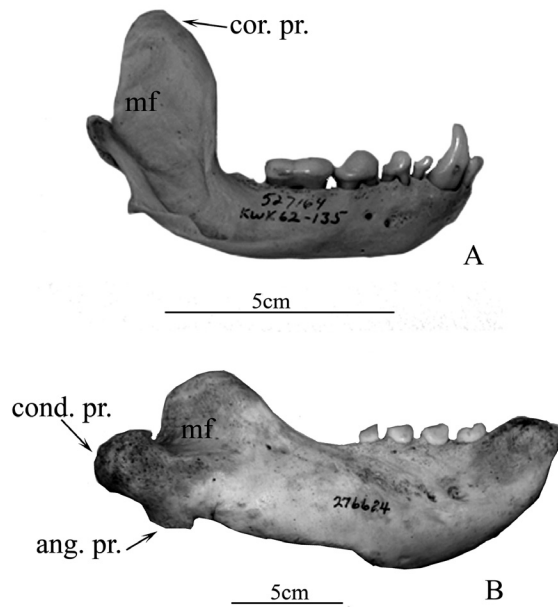


Fig. 5. Right mandibles of (A) Sea otter (*Enhydra lutris*; ♀; USNM 527164) and (B) Atlantic walrus (*Odobenus rosemarus*; ♀; USNM 276624) in labial views.

Рис. 5. Правые челюсти (А) морской выдры (*Enhydra lutris*; ♀; USNM 527164) и (В) атлантического моржа (*Odobenus rosemarus*; ♀; USNM 276624) с губной стороны.

fibers. There is a very prominent mandibular angle in all specimens examined for attachment of the medial pterygoid muscle. In contrast to *Phoca*, where the medial pterygoid attaches from the angular process to the condyle (Piérard, 1971; Howell, 1929), in Bearded seals the medial pterygoid attachment is very well-outlined along the mandibular angle.

Lastly, monachine seals exhibit the smallest condyloid angles of 16° in *Monachus tropicalis* and 20° in *Lobodon carcinophagus* (Koretsky et al., 2014). *Mon. tropicalis* (Caribbean monk seal) has a wide mandibular ramus, a large, broad coronoid process and a deep, well-defined masseteric fossa extending the length of the ramus, indicating a well-developed masseter muscle (Koretsky et al., 2014; fig. 5). *L. carcinophagus* (Crabeater seal) has a very short mandibular ramus and coronoid process. The shallow masseteric fossa is not well-defined, extends a little more than half the length of the ramus and is rather narrow, suggesting a reduced masseter muscle (Koretsky et al., 2014; fig. 6).

Sea Otter (*Enhydra lutris*), fig. 5 A, table 1

Enhydra lutris is the largest species of sea otters and adults have a wide skull and short nasal bones (Wilson et al., 1991). Adult molars are round and flattened in order to crush food rather than tear it (Love, 1992). The mandibular ramus extends significantly high above the tooth row and is directed almost vertically. The masseteric fossa is well-defined and extends the length of the ramus. The coronoid process is short, rounded and very broad, indicating attachment of a well developed temporalis muscle. The posterior edge of the coronoid process terminates as an almost completely vertical slope towards the mandibular notch. The mandibular notch is extremely narrow and small. A short, well-defined angular process extends caudally. The angular process is much more prominent than in pinnipeds, suggesting a more powerful medial pterygoid muscle.

The very short, oval-shaped condyloid process is directed caudally and yields a mean ($n = 9$) condyloid angle of 22° in males and 23° in females. These measurements are similar to phocine seals and imply a diet of medium-sized prey compared to the overall small

size of these animals. Sea otters are known to have a wide ranging diet of marine animals, including: clams, mollusks, crustaceans, sea urchins, various fish and crabs (VanBlaricom, 2001). They utilize short dives to hunt on the sea floor in shallow water less than 40 m deep (Love, 1992). They possess a unique loose pouch of skin under each forelimb that can be used to hold tools to open shells and to carry food back to the surface to feed (VanBlaricom, 2001). They are one of the few mammals that use tools such as rocks to hunt and feed (i. e. open shells) and have forepaws that can be used to hold and manipulate tools as well as dig and gather prey (Kenyon, 1981).

Atlantic Walrus (*Odobenus rosmarus*), fig. 5 B, table 1

Walruses have robust mandibles with a larger symphysis and lower jaw joints than other pinnipeds (Jones et al., 2013). The thick ramus has a narrow, yet very deep masseteric fossa. The mandibular coronoid process is positioned almost directly above the angular process, in contrast to phocids, where the coronoid process is positioned slightly caudal to the angular process (Jones et al., 2013). The broad coronoid process is a wide triangle with a rounded apex and indicates a strong temporalis muscle attachment. The very robust, round condyloid process extends caudally in a horizontal manner and is located at the level of the tooth row. On the anterior surface of the condyloid process is a well-defined depression for attachment of the lateral pterygoid muscle. A rather broad, flattened angular process for the attachment of the medial pterygoid muscle is also present.

The most distinguishing feature of walruses is their unique suction-feeding mechanism. Their specialized vibrissae help identify prey and they use their flippers to clear sediments in order to vacuum-feed in mostly shallow waters (Levermann et al., 2003). The average condyloid angle of male and female Atlantic walruses (*Odobenus rosmarus*) is 13°, which is close to the measured angle in *Mon. tropicalis*, and supports a diet of small-sized prey despite the enormous size of these animals. Walruses dive to depths of about 90 m and have an opportunistic diet, foraging on the sea floor to feed on mollusks, clams, shrimp, crabs, sea cucumbers, and even parts of other pinnipeds (Sheffield et al., 2001).

Spotted Hyena (*Crocuta crocuta*), fig. 6 A, table 1

The Spotted hyena (*Crocuta crocuta*) is the largest member of the Hyaenidae and is native to Sub-Saharan Africa. *C. crocuta* generally live in large groups and have a unique social structure based on competition. Females control clans and males are forced to compete with each other for food and mating opportunities (Holekamp, 2007), unlike other carnivores. While most modern hyenas are scavengers, Spotted hyenas can be both hunters and scavengers, increasing rates of survival. A unique dentition allows Spotted hyenas to crush bones without dulling teeth and digest all parts of prey (flesh, skin, bones). Also, Spotted hyenas possess the strongest jaw muscles among terrestrial mammals, having stronger bone-crushing ability than even brown bears (Tanner et al., 2008).

Examination of the mandibular morphology of hyenas reveals a thick, high mandibular ramus with a deep masseteric fossa, suggesting a powerful masseter muscle (fig. 6 A). The masseteric fossa is very well-defined and extends the length of the ramus. The coronoid process curves caudally back towards the condyloid process and is wide, implying a strong temporalis muscle, which supports the feeding habits of hyenas. The short, round condyloid process extends slightly above the alveolar row, at the level of the tips of the teeth in males and females. The angular process, for attachment of the medial pterygoid muscle, is extremely well defined in both sexes and extends further caudally than in any other carnivoran examined in this study. There is a well-defined, elongated tuberosity extending along the caudal border from the base of the condyloid process, a rare morphological character demonstrating strong attachment of the lateral pterygoid muscle. Both these pterygoid muscles aid in raising the mandible. As a known bone-crusher, the Spotted

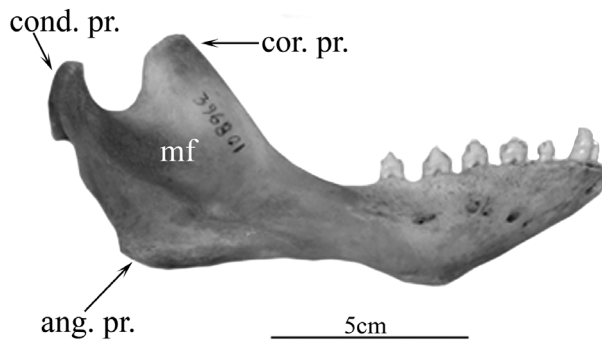


Fig. 6. Right mandibles of (A) Spotted hyena (*Crocota crocota*; ♂; USNM 367384) and (B) Giant panda (*Ailuropoda melanoleuca*; ♀; USNM 259403) in labial views.

Рис. 6. Правые челюсти (А) пятнистой гиены (*Crocota crocota*; ♂; USNM 367384) и (В) гигантской панды (*Ailuropoda melanoleuca*; ♀; USNM 259403) с губной стороны.

hyena has powerful muscles of mastication (masseter, temporalis, pterygoids). There is also a substantial mid-sagittal crest running along the top of the skull and a robust zygomatic arch below the orbit. These cranial features allow hyenas to have greater leverage during feeding and catching prey and larger attachment surface areas to accommodate sizeable masseter and temporalis muscles.

The condyloid angle in *C. crocota* is 19° for males and 10° for females (table 1), suggesting a diet of small-sized prey. However, Spotted hyenas are active hunters who eat medium-sized ungulate prey, including wildebeests, zebras, and gazelles. Kruuk (1972) noted that a single Spotted hyena can eat at least 14.5 kg of meat per meal, and they have also been found to catch young elephants, fish, rhinos, hippo calves, and pythons. Although hyenas appear not to follow our proposed pattern as they should feed on small-sized prey due to their small condyloid angle, this issue will be discussed in detail below.

Giant Panda (*Ailuropoda melanoleuca*), fig. 6 B, table 1

While the giant pandas (*Ailuropoda melanoleuca*) are classified as terrestrial carnivores, they are completely herbivorous, eating bamboo. Their genetic makeup makes it difficult for these carnivores to extract protein and energy from bamboo (Li et al., 2010), leading to consumption of a large quantity to meet their enormous energy requirements.

One clearly prominent cranial adaptation in the giant panda is the significant lateral expansion of the zygomatic arch, increasing the size of the temporal fossa and limiting horizontal movement of the mandible (Davis, 1964). The expanded temporal fossa allows for increased attachment of the temporalis muscle. The masseter muscle also has an extensive attachment site on the enlarged zygomatic arch. Larger mastication muscles and limited jaw movements would allow giant pandas to increase bite force during crushing of bamboo. Biomechanics of the Giant panda skull show that they are capable of resisting high stresses and utilize quick, discrete bite and swallow feeding techniques when breaking down bamboo trunks (Figueirido et al., 2014).

The posterior part of the Giant panda jaw looks like a typical herbivorous mandible with a broad mandibular ramus extending high above the tooth row. There is a well-defined, deep masseteric fossa that covers the length of the ramus. In contrast to hyenas, the masseteric fossa reaches the inferior edge of the mandible (fig. 6 B). The masseteric fossa provides a very large surface area for attachment of a strong masseter muscle, vital for pandas during feeding. The narrow coronoid process curves caudally at its tip almost like a hook. The round and robust condyloid process rises high above the tooth row and yields a condyloid angle of 32° (table 1), indicating a large gape. The mandibular notch is much wider than found in hyenas and a well-defined angular process is present, but

not as prominent as observed in hyenas. The medial pterygoid, responsible for raising the mandible and lateral movement of the jaw in herbivores, attaches to the angular process. Overall, parts of the skull not directly associated with mastication are compressed (Davis, 1964), resulting in increased area for masticatory function.

Morphometric analysis of the Giant panda demonstrates a significantly more developed mandibular structure than other carnivores such as bears and tigers (Zhang et al., 2007). The Giant panda mandible is extremely dense and weighs twice as much as the mandible of the larger Brown bear (*Ursus arctos*, Davis, 1964). According to Zhang et al. (2007), mandibular structure is strongly influenced by dietary preferences in carnivores. Thus, the unique mandibular morphology of Giant pandas would be the result of adaptations to the tough, thick fibers in bamboo that these pandas consume.

Discussion

Examination of the mandibular morphology of seals, walruses, sea otters, hyenas and pandas confirms results in the Koretsky et al. (2014) study and demonstrates a correlative pattern between degree of condyloid angle, size of gape and dietary preferences among terrestrial and aquatic carnivorans. It appears that only the Bearded seal (a specialized suction-feeding carnivoran) and the Giant panda (a unique herbivorous carnivoran) do not fit the general trend. Specifically, this survey reveals that the significantly smaller condyloid angle in male *Mirounga angustirostris* (Northern elephant seal) suggests that their diets are not the same as those of females as stated previously (Stewart and Huber, 1993; Le Boeuf, 2000). The much deeper diving depths of male Northern elephant seals likely result in different feeding niches than females and supports our idea that males are bottom feeders who utilize a suction-feeding mechanism to capture prey and crush shells with their teeth.

Seals

Monachine seals (*Mon. tropicalis* and *L. carcinophagus*) have very large teeth and the smallest condyloid angle of the extant seals examined. Mandibular morphology shows monachine seals have a lower mandibular ramus and a condyloid process at about the level of the tooth-row, similar to other carnivorans (Koretsky et al., 2014; fig. 5–6). The small gape implies that these seals eat smaller-sized prey, with *L. carcinophagus* being a known specialized filter-feeder that gulps water and filters out krill, and grabs squid, fish and sometimes crabs. The filtering mechanism in Crabeater seals correlates with having an unusual shape and position of teeth (Adam and Berta, 2002). The mandibular ramus of *L. carcinophagus* and *Mon. tropicalis* extends above the tooth row, similar to other carnivores, but not as high as in *M. angustirostris*. In contrast to Northern elephant seals (*M. angustirostris*), Crabeater seals (*L. carcinophagus*) have a very narrow masseteric fossa that covers about half of the ramus, implying a less-developed masseter muscle (Koretsky et al., 2014; fig. 6). The presence of a narrow coronoid process in the Crabeater seal suggests a weaker temporalis muscle as well. Similar to male *M. angustirostris*, the Crabeater seal and the monachine *Mon. tropicalis* have less-developed angular processes, indicating weaker medial pterygoid musculature. Morphology and myology demonstrate that monachine seals have weak muscles of mastication, have small gapes and feed on small prey.

Most phocine seals have small teeth, well-developed mastication muscles and a medium-sized condyloid angle, implying that they mostly eat medium-sized prey and have an intermediate size of gape amongst the three extant true seal subfamilies. However, *E. barbatus* (fig. 4) does not follow this pattern and has the weakest teeth of any Phocinae, with a very large condyloid angle (table 1). This specialized suction feeder is an obvious outlier as the very similar suction-feeding walrus has a small condyloid angle. It is our belief that the mandibular morphology of *E. barbatus* is unique, as a typical suction feeder vacuums food in through the mouth and would not need a large gape. On the other hand, it

is possible that Bearded seals cannot form as tight a vacuum around their prey as walruses can. Thus, a larger gape in Bearded seals would be advantageous for sucking in larger volumes of food. Examination of mandibular morphology shows a well-outlined area for attachment of the medial pterygoid muscle (function: raises the mandible; Miller et al., 1964) on the mandibular angle, supporting the unique *E. barbatus* suction and crushing feeding behavior.

The mandible of *E. barbatus* (fig. 4) is much more slender than the robust mandibles of *M. angustirostris*. Similar to both sexes of *M. angustirostris*, the masseteric fossa of *E. barbatus* covers most of the mandibular ramus, but does not extend to the inferior edge of the mandible. The masseteric fossa is clearly deeper and better defined in Bearded seals than in Northern elephant seals, suggesting more powerful masseter muscles to aid in suction feeding. The round and flat shape of the coronoid process and the wider base of the coronoid process in Bearded seals is comparable to male *M. angustirostris*, while in female Northern elephant seals the coronoid process is thinner and triangular in shape. The wider coronoid process in Bearded seals and male Northern elephant seals implies a strong temporalis muscle, likely to also aid in suction-feeding behaviors. While the condyloid process of *E. barbatus* is flattened and curves towards the mandibular notch, it is not as large as the round condyloid process found in male *M. angustirostris*. The angular process is not very prominent in *E. barbatus* or in male *M. angustirostris*, but is slightly more pronounced in female Northern elephant seals (fig. 3, 4). This suggests comparably less developed medial pterygoid muscles in Bearded seals and male Northern elephant seals. Although there are vast differences in the overall size of the mandibles, morphological similarities support our idea that male *M. angustirostris* utilize a feeding mechanism different than females, likely as a suction feeder similar to *E. barbatus* and walruses. These results directly contradict those of Stewart and Huber (1993) and Le Boeuf (2000) who state that male and female *M. angustirostris* have the same diet.

Although the suction-feeding mechanisms of *E. barbatus* differs significantly from the grab-and-tear feeding of cystophorine seals, the degree of condyloid angle, preferred diving depth, and geographical distribution strongly correspond to those found in *C. cristata*, suggesting a close ecological resemblance between these taxa. In addition, *E. barbatus* has very specific serological and cytogenetic characteristics, with a diploid number of chromosomes (34) similar to *C. cristata*, *M. angustirostris* and *Monachus schauinslandi*, instead of 32 as in other Phocinae (Anbinder, 1980). Heptner et al. (1976) suggested that *E. barbatus* may have separated from the main branch of Phocinae much earlier in geological time and could be the one of the most basal morphotypes among Recent phocids.

Cystophorine seals have weak teeth, large condyloid angles and powerful mastication muscles, allowing them to eat larger prey than seals in the other subfamilies. *Mirounga* is the only genus of true seals in which sexual dimorphism is clearly displayed, both in cranial and postcranial skeletal elements. Previous studies (Stewart, Huber, 1993; Le Boeuf et al., 2000) describe similar diets for male and female *M. angustirostris*, which would contradict our hypothesis that there is a strong correlation between degree of condyloid angle, size of gape and diet (including size of prey). However, studies on diving behaviors of *M. angustirostris* have detailed a preferred diving depth of 350–650 m for females and 450–1250 m for males (Le Boeuf et al., 1985; Le Boeuf, Laws, 1994; Schreer, Kovacs, 1997), supporting our proposal that sex-specific diving capabilities allow males to access different prey than their female counterparts, resulting in dietary variations.

Observations of stomach contents by Antonelis et al. (1987, 1994) showed that female *M. angustirostris* feed mainly on fish and squid while males feed primarily on smaller cephalopods and crustaceans, supporting our belief of differing diets for males and females. The types of prey mentioned in these studies appear to strongly correlate with our measured condyloid angle and size of gape hypothesis, as females have the larger gape and therefore should be eating larger prey.

Male Northern elephant seals have deeper diving abilities and migrate farther north and west to specific foraging areas, while females have a wider dispersal in the open ocean and forage en route (LeBeouf et al., 1994). More in-depth examinations of the stomach contents of male and female *M. angustirostris* are necessary to determine the degree of sex-specific dietary differences. A recent study on the functional implications of tooth size and spacing by Churchill and Clementz (2015) further supports our hypothesis that male *M. angustirostris* relied on suction feeding techniques, in contrast to the pierce feeding strategy stated by Adam and Berta (2002). Furthermore, Churchill and Clementz (2015) also showed that *M. angustirostris* has severe reduction and wear in crown morphology. Thus, their results support our suggestion that there are sexually-specific dietary differences in *M. angustirostris*, with males likely being a suction feeder, similar to *E. barbatus*.

The smaller condyloid angle in male *M. angustirostris* (17°) than in females (23°) and deeper diving depths support our suggestion that males may be bottom feeders who use a type of suction-feeding mechanism. This would correlate with species such as walruses, which are extremely large in size yet have low condyloid angles and are known suction feeders. Male *M. angustirostris* dentition shows noticeable crown erosion in adults, likely due to crushing prey over a lifetime, further supporting a bottom-feeding ecology, similar to *E. barbatus* and walruses. Overall, these results support the claim by Koretsky et al. (2014) that although seals are opportunistic feeders with habitual dietary preferences, there exists a strong correlation among the type of prey eaten, diving depth, size of teeth and degree of the condyloid angle.

Sea Otters

The condyloid angle of male sea otters ranged from 21° to 23° , while females ranged from 20° to 26° , both very similar to the measurements reported for phocine seals. Like the phocine *H. grypus* (with a condyloid angle of 20° ; table 1), sea otters have a well-defined, deep masseteric fossa that extends the length of the ramus and a broad coronoid process (fig. 5 A). Both these similarities suggest well-developed masseter and temporalis mastication muscles in these taxa. Additionally, both sea otters and phocines eat medium-sized prey (crustaceans, mollusks, fish, crabs) compared to their overall size and appear to be moderate divers.

The mandibular ramus in male *M. angustirostris* extends high above the tooth-row (characteristic for herbivores; fig. 3 A), while the level of the sea otter ramus is more typical of carnivores (at the level of the tooth row; fig. 5 A). The masseteric fossa of sea otters is deeper and better defined than that of male *M. angustirostris* and extends to the inferior edge of the mandible. Both taxa have wide coronoid processes for attachment of the temporalis muscle. While male Northern elephant seals have an unimpressive angular process, in sea otters it is well developed, meaning a stronger medial pterygoid muscle. A pronounced angular process is observed in herbivores, as they require lateral jaw movement to grind and chew food. Thus, sea otters maintain powerful medial pterygoid musculature to aid in crushing their prey. These muscles are a necessary adaptation as sea otters have a larger condyloid angle than male *M. angustirostris* and eat/crush medium-sized prey rather than small prey.

While morphology of dentition differs significantly as most seals tear food with their teeth and sea otters crush prey, the degree of condyloid angle, size of gape and examination of mandibular characters support our hypotheses that: 1) condyloid angle size can be used to determine dietary preferences; and 2) male Northern elephant seals likely utilize a unique feeding behavior (suction/crushing).

Walruses

Walruses have the most distinctive pinniped mandible, with robustness consistent with pachyosteosclerosis (fig. 5 B) and a low jaw joint relative to the tooth row (Jones et

al., 2013). The condyloid angle of the Atlantic walrus (*Odobenus rosmarus*) examined in this study range from 10° to 16° in both males and females, with an average angle of 13° for both sexes (table 1). As suction feeders, walrus create a vacuum seal around their prey, creating more force to suck meat directly out of shells using their piston-like tongue (Levermann et al., 2003). The unique suction feeding of walrus makes a large gape unnecessary and therefore supports our idea that a small condyloid angle implies feeding on small prey. The specialized diet and feeding behaviors of walrus are similar to those of *L. carcinophagus*, a filter-feeding monachine seal. Both *L. carcinophagus* and walrus have smaller condyloid angles than the other taxa examined, supporting the presence of a small gape. This correlative pattern was extrapolated to fossil seals in the Koretsky et al. (2014) study, with the extinct *Miophoca vetusta* (Badenian, ~13.6 Ma) having the smallest condyloid angle (9°) of seals examined, suggesting a diet of small prey and a likely suction/bottom-feeding habitat (similar to walrus). Thus, with the addition of other terrestrial and aquatic carnivorans, the results from this survey directly support those in our previous study.

While the mandibular ramus of male *M. angustirostris* extends high above the tooth row, the walrus ramus is short, rising marginally above the tooth row. Walrus and male *M. angustirostris* have well-developed masseteric fossae that cover most of the mandibular ramus, but do not extend to the inferior edge of the mandible (fig. 5 B). Both taxa appear to have: a strong masseter muscle, important for crushing; prominent, rounded condyloid processes; and a wide coronoid process base, for the attachment of a well-developed temporalis muscle. The angular process in walrus is more robust than in male *M. angustirostris*, meaning a more powerful medial pterygoid muscle (raising the mandible). Although walrus and male Northern elephant seals likely have similar feeding habits as a suction feeder, walrus use a unique muscular vacuum-like suction on their prey. The known diet of small-sized prey of walrus, low condyloid angle in walrus and Northern elephant seals (compared to their enormous overall body size) and morphological similarities in mandible thickness, size and characteristics suggest that male *M. angustirostris* feed on smaller prey than their female counterparts, contrasting with previous studies (Stewart and Huber, 1993; Le Boeuf, 2000).

Hyenas

The mandibular ramus of hyenas extends above the tooth-row (fig. 6 A), but significantly less than in male Northern elephant seals. Hyenas have an extremely prominent angular process for attachment of the medial pterygoid muscle (raising the mandible), which aids in crushing thick bone. Similar to male *M. angustirostris*, the masseteric fossa of *C. crocuta* covers the majority of the mandibular ramus, but does not extend to the inferior edge of the mandible. Compared with Northern elephant seals, the masseteric fossa is substantially deeper and more well-defined in hyenas, implying more powerful masseter muscles. As bone-crushing carnivores, hyenas would need significantly stronger mastication muscles than the bottom-feeding male Northern elephant seals.

Female *C. crocuta* have a condyloid angle of 10°, while males have an angle of 19°, similar to male *M. angustirostris*. The low condyloid angle means a small gape for these carnivores, suggesting that they should eat small-sized prey. However, hyenas are known to eat available medium to large prey, suggesting a likely morphological advantage to having a small to medium condyloid angle. Due to their well-developed mastication muscles and ability to crush and digest thick bones (not just the marrow), we believe the small condyloid angle suggests that they take quick, powerful bites. Thus, having a large gape would be burdensome for hyenas and reduce the amount of force their jaws could exert to tear through thick bone. Also, due to feeding competition, taking several small, fast, and powerful bites has become a necessary adaptation and creates an advantage in being able to consume large amounts of food rapidly (Tanner et al., 2010).

Unlike the unworn, strong teeth used for tearing and crushing bone in hyenas, male Northern elephant seals have very weak teeth (table 2) due to crushing shells over a lifetime. While similar condyloid angles (table 1) in hyenas and male *M. angustirostris* may appear ambiguous due to their obvious differences in feeding habits and dietary preferences, these results remain consistent with our hypothesis. Thus, the low condyloid angles in hyenas are a morphologically and ecologically advantageous adaptation (greater force and faster bites); whereas the small angles in male *M. angustirostris* suggest feeding on smaller-sized prey.

Recently, Amson and Muizon (2014) described the mandibular/dental morphology and mastication musculature of the monachine seal *Hadrokirus martini* (Late Miocene to Early Pliocene). Their conclusion that a large, wide coronoid process suggests the presence of a powerful temporalis muscle is further supported by this present study. Additionally, a large-sized mandibular ramus indicates a large insertion area for a powerful masseter muscle and a well-developed angular process indicates strong pterygoid musculature, similar to our findings in hyenas. The dentition of *Hadrokirus martini* reveals massive premolars similar to *Crocota* and considerably greater pressure during bite force (Amson, Muizon, 2014).

Pandas

Their unique herbivorous diet and specialized mandibular morphology make pandas different than any other carnivoran examined in this study. The condyloid angle of 32° in the giant panda suggests a large gape and the mandibular ramus extending high above the tooth row (fig. 6 B) is a typical feature of herbivores (also seen in male *M. angustirostris*). Pandas require powerful forces to crush and grind extremely strong, fibrous bamboo. The high cranium and deep mandibular body help disperse torsional forces generated during chewing on tough foods (Biknevicius, Ruff, 1992). Giant pandas have higher bite forces than omnivores, insectivores and even carnivores who consume small prey, with forces matched only by bone-crushing carnivores that feed on ungulate prey significantly larger than themselves (Christiansen, Wroe, 2007).

Table 2. Comparative diagnostic characters of the manibule of some Carnivorans
(+ character present; - character absent; +/- character variable)

Таблица 2. Сравнительные диагностические признаки челюстей некоторых хищных животных
(+ признак присутствует; - признак отсутствует; +/- признак изменчивый)

Character	<i>Mirounga angustirostris</i>	<i>Cystophora cristata</i>	<i>Halichoerus grypus</i>	<i>Phoca largha</i>	<i>Erignathus barbatus</i>	<i>Lobodon carcinophagus</i>	<i>Monachus tropicalis</i>	<i>Enhydra lutris</i>	<i>Odobenus rosmarus</i>	<i>Crocota crocuta</i>	<i>Ailuropoda melanoleuca</i>
Defined angular process	-	-	-	-	-	-	-	+	+	+	+
Hook shaped coronoid process	-	+	-	-	-	-	-	-	-	+	+
Broad coronoid process	+♂/-♀	-	+	-	+	-	+	+	+	+	-
Mandibular ramus high above toothrow	+♀/-♂	+	+	+	+	-	-	+	-	-	+
Deep masseteric fossa	+♀/-♂	-	+	+	+	-	+	+	+	+	+
Tubercle on mandilloid process	-	-	-	-	+	-	-	-	-	+	-
Coronoid process much higher than condyloid process	-	-	+	-	-	-	-	+	-	+	+
Weak teeth	+	+	-	+	+	+	-	-	+	-	-

Specifically, powerful masseter and pterygoid musculature is essential for herbivores (Asher, Muller, 2012). Although the pterygoid musculature is not as important in the Giant panda for mastication as the masseter and temporalis muscles are (Davis, 1964), pandas have a prominent angular process (for medial pterygoid attachment) and masseteric fossa (for masseter attachment). Unlike in Northern elephant seals, the masseteric fossa in the giant panda extends to the inferior edge of the mandible (fig. 6 B), providing larger surface area for attachment of the masseter muscle.

The temporalis muscle is poorly developed in typical herbivores, but is very large in Giant pandas, with fibers running much more vertically than in any other carnivoran (Greaves, 2000). This seems a bit odd as pandas have the presence of a narrow, unimpressive coronoid process, suggesting a weaker temporalis muscle attachment. In contrast, the male *M. angustirostris* has a broad, triangular coronoid process, suggesting a more well-developed temporalis muscle for this cystophorine seal. The prominent angular process and powerful dentition seen in Giant pandas are not present in Northern elephant seals, which is not surprising considering these seals suction small prey from the ocean floor, crush shells to extract meat and have gradual degradation of teeth over time due to crushing. Overall, Giant pandas utilize more powerful masseter and medial pterygoid musculature for eating bamboo, while male *M. angustirostris* require well-developed masseter and temporalis muscles to crush their diet of small prey.

The dentition of Giant pandas differs from hyenas significantly as pandas are grinders and hyenas tear and crush prey. As a result, pandas may require a larger gape in order to deeply insert the bamboo within their oral cavities and allow their grinding molars to begin chewing. Additionally, because bamboo is low in energy, pandas need an enormous quantity to obtain necessary energy requirements. Thus, a larger gape would allow not only more, but thicker trunks of bamboo to be chewed. Lastly, the skull of the giant panda is modified more extensively than any other carnivore due to the high demands of the masticatory apparatus (Davis, 1964).

Conclusion

In general, there appears to be a strong correlation between mandibular morphology, size of gape and diet in both terrestrial and aquatic carnivorans. While each taxonomic group surveyed has specific identifiable morphological features (table 2), the condyloid angle is a vital character that can be used to determine dietary preferences. Even taxa with specialized suction (walrus) and filter (Crabeater seal) feeding behaviors follow the common correlative pattern.

The major taxa that seem to depart from the general trends discussed in this study are the Bearded seal, a known suction-feeding phocine, and the Giant panda, a unique herbivorous carnivoran. As suction feeders, Bearded seals should have a small condyloid angle paralleling that of walruses. However, they possess large condyloid angles similar to Hooded seals. The close relationship between Bearded and Hooded seals explains the similarities of overall morphology, genetics and geographical distribution. The large condyloid angle and large gape in Giant pandas are necessary to aid in grinding their distinctive diet and for their requirement of large quantities of food. Thus, dietary preferences do indeed influence ecological and morphological adaptations in terrestrial and aquatic carnivorans.

Overall, this survey on carnivoran mandibles reveals evidence consistent with our previous hypothesis that: 1) species with a large condyloid angle have a larger gape and diets consisting of larger sized prey (except for the highly specialized Bearded sea land Giant panda); and 2) species with small condyloid angles have lesser gapes and diets of smaller prey (monachine seals) or are powerful crushers (Spotted hyena) who need smaller gapes for increased bite force.

Morphological examination of mandibles in the compared taxa reveals a correlation between strength of dentition and positions of the coronoid and condyloid processes. In

taxa where the coronoid process sits much higher than the condyloid process (i. e. Spotted hyena and Giant panda), the teeth are stronger. However, in those taxa where the coronoid and condyloid processes are at about the same level (i. e. Northern elephant seal and Crabeater seal), dentition is significantly weaker (table 2).

Our previous paper on correlations between mandibular structure and diet of seals (Koretsky et al., 2014) interpreted how ecological and morphological adaptations may influence dietary capabilities of extant seals. We extrapolated this methodology to predict the likely diet of some extinct seal taxa as well. Recently, similar approaches inferring diet from morphological assessment of fossil cranial material has been used by other scientists (Amson, Muizon, 2014). While Churchill et al. (2014 a, b) examined whole or fragmented mandible and cranial fossil material to predict the body size of seals and sea lions, potential biases in their data analysis exist, and were mentioned, as many mandibles were unassociated and some fragmented material was not easily discernible as juvenile or adult. The fragmented material was applied to predictive equations in order to estimate body size of extinct seals. Thus, the basic premise of recent studies supports our approach as the morphological examination of cranial (and postcranial) material, correlated with ecology, can reveal not only the size of extinct seals, but can also infer diet, habitat and functional interpretations.

There appears to be no correlation in the chart (fig. 2) comparing the median degree of condyloid angle with average diving depths among aquatic carnivorans. This lack of correlation infers that although diving depth does not influence the degree of condyloid angle, it does impact dietary specialization. For example, seals with medium to large condyloid angles can obtain medium to large sized prey from either deeper waters or close to the surface (fig. 2). The varying diets of different species of seals are supported by this data, as the availability of prey can be found in different ecological niches.

It is known that not every seal taxon has obvious sexual dimorphism. Although sexual dimorphism in the condyloid angle is not evident in all of the species examined (table 1), there exists significant sexual variation in the subfamily Cystophorinae (*M. angustirostris* and *C. cristata*) and in the hyena (*C. crocuta*). The dominant sex of *M. angustirostris* (male) and *C. crocuta* (female) possess smaller condyloid angles than their counterparts. These differ from taxa such as the walrus, where despite obvious sexually dimorphic size disparities, the condyloid angles of male and female walruses are the same (table 1). Additionally, male *C. cristata* (dominant sex) have a larger condyloid angle than females, opposite to the condition seen in *M. angustirostris*. Thus, the dietary specializations of *C. cristata* must be examined more in depth to account for this discrepancy.

While the results from this survey largely support our hypothesis that male *Mirounga angustirostris* have dietary preferences that differ from females, we can conclude that the condyloid angle alone cannot fully determine sexual dimorphism in mandibular morphology. Thus, the condyloid angle measurement must be correlated with dental and mandibular morphology and lines of action for muscles of mastication to determine dietary preference for both sexes of *M. angustirostris*.

In addition, due to the discrepancy of condyloid angle measurements between sexes, the diet of the cystophorine *M. angustirostris* must be closely examined as our results propose that males utilize a suction-feeding mechanism and eat smaller prey than females. During the revision process for this manuscript, a newly published study (Churchill, Clementz, 2015) strongly supported our hypothesis that male *M. angustirostris* are likely suction feeders similar to *E. barbatus* and that their diets can be influenced by differences in ecology (diving depths).

While the morphology examined in this investigation supports our hypothesis, we want to make clear that this manuscript is an initial study of some aquatic and terrestrial carnivorans, with results used as the foundation for future projects combining the size of the condyloid angle, dentition, mandibular biomechanics, myology of muscles of mastication

and their attachments. We plan on expanding the taxonomic sample, including extant and extinct carnivorans, and broadening the biomechanic framework, accounting for the lines of action for each muscle.

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