

Foods and Feeding Processes in Primates

Eighth International Congress of Vertebrate Morphology

July 16–21, 2007

Paris, France

This congress was mostly devoted to comparative anatomy and paleontology, but a large number of the studies presented were concerned with the masticatory apparatus. The relationship in humans between the temporomandibular joint and tooth shape has been emphasized in dentistry. This relationship has been considered as characteristic of different phyla and considered a part of scientific arguments in favor of certain prosthodontic theories. A different emphasis could be noted during this congress because the relationship between masticatory muscle structure and function and tooth shape was the topic of many communications. Several gave a deeper meaning to old knowledge.

Vegetable foods are commonly considered easy to chew in comparison to meat. This is supposed to explain the presence of powerful masticatory muscles in carnivores. This often unexpressed line of thought is a good example of how common sense may lead to an incorrect conclusion. Digestive enzymes have no difficulty in delivering nutrients from meat foods. Consequently, most carnivorous species do not really chew their food; instead, they usually cut it in rather big pieces before swallowing. On the contrary, plant-feeding animals find it much harder work to liberate the nutrients potentially available in grasses, leaves, and other types of vegetables. Ruminants, for instance, have developed a special digestive system which begins by having complex teeth adapted to a long period of crushing of food. In many herbivores, such as horses and rabbits, continuous growing of molar roots compensates for extensive dental wear. As well as the need to adapt to the dietary regimen of the different species, the masticatory muscles have to address a special need: they must be powerful in spite of the evident limitation of available space around the jaws. This space limitation was a difficult challenge for evolution. Decades ago, researchers publishing almost exclusively in German, Japanese, or French¹ believed that the pinnate organization of masticatory mus-

cles was the answer. They discovered that all the elevator masticatory muscles display an extensive fascial structure within which muscle fibers run from one fascia to another fascia instead of running in parallel along the whole length of the muscle. Since the fiber length is much shorter, the pinnate structure increases the number of muscle fibers contained in the same volume severalfold. Because the strength of a muscle is considered to be approximately proportional to the number of muscle fibers, this disposition helps increase the masticatory muscle strength. The reduction of fiber length due to the pinnate organization limits the shortening of the muscle during contraction since, usually, muscles can only be shortened by about one third of their fiber length. Of course, it also leads to a decrease in the muscle-stretching ability.

Usually the strength of a muscle is evaluated by considering its physiologic cross-sectional area. In the case of the masticatory muscles, however, a single cross section does not cut through all fibers and cannot therefore be used to estimate the muscle strength. Hartstone-Rose and Perry have solved this old problem by presenting 2 studies based on a method that measures the elevator masticatory muscles' cross-sectional areas by taking their pinnate structure into account. One study was performed in felids and the other in lemurs. In both cases the whole muscle was dissected and then heated in 10% sulphuric acid to obtain the total mass of muscle fibers. The whole muscle volume was then calculated. Since the authors could also measure the fiber length from these heated samples, the real cross-sectional area could be obtained, thus giving an estimate of the muscle strength, which could then be compared between species. Most of the results were similar within the 10 felid and within the 25 lemur species studied. The muscle volumes and cross-sectional areas were proportional to the body masses within the 2 phyla but in both, the muscle fiber length varied with the need for opening the mouth. Felid species that require large gapes (because they feed on large

prey) have relatively long temporalis and masseter fibers, while the felid species that target the smallest prey have relatively short fibers; similarly, among large-bodied lemurs, leaf-eaters have smaller muscle fiber lengths than fruit eaters.

The first plenary talk from H. Hoppeler also deserves description here, although it was related to muscles in general and was not restricted to the orofacial area. The speaker reported the results of many experiments carried out on muscle structure and function of trained sportsmen. He pointed out the aforementioned fact that parallel-fiber muscles and pinnate muscles perform differently with regard to speed of contraction, excursion, and force with respect to muscle cross-sectional area. He emphasized the malleability of skeletal muscle tissue. Massive changes in muscle structure and function can be induced rapidly using specific exercise regimes. Endurance training leads rapidly to a 2-fold increase in the mitochondrial and blood capillary masses. Eight weeks of training is enough to trigger changes that are significantly different at 1-week intervals. Structural modifications are different if training is oriented toward strength instead of endurance. Mitochondrial mass does not then change, but the muscle fibril mass increases. These changes involve adaptation of the ratio of type I to type II muscle fibers. This muscle plasticity typically results in the transcription of multiple early genes such as those in the *fos* and *jun* families as well as many other transcription factors. These kinds of muscle adaptation and training have been little explored for masticatory muscles, and this basic knowledge could well be useful to understanding mechanisms underlying painful or deficient masticatory muscles. Both strength and endurance training could have some clinical applications.

German et al. presented an interesting study in which they challenged the 1950s results of Doty and Bosma² about the chronological and standard sequence of activation of the muscles that participate in swallowing. Decerebrate infant pigs were fed with an accurately controlled milk source, assuring that all successive swallows were triggered by identical milk boluses. Electromyographic (EMG) activity was recorded from 16 muscles involved in swallowing and kinematic activity with a video-radiographic system. In spite of the use of modern techniques, results were strongly reminiscent of Doty and Bosma. The overall pattern among muscles was similar, and movements were highly stereotyped. However, the recorded EMG signals were variable between animals, between swallows in the same animal, and even when using different electrodes within the same muscle during

the same swallow. The origin of this variability triggered an extensive discussion, the outcome of which was that activation of different motor units may be responsible for the variability.

Finally, the congress included a workshop titled "The Physical Properties of Foods and the Evolution of the Primate Feeding Systems." The goal of the workshop, which was introduced by Callum Ross, the co-organizer with Peter Lucas, was to study the adaptation of the masticatory apparatus in response to changes at different time scales. The first level was the observed change in the masticatory apparatus from one species to another species through the different phyla, ie, evolution. The second level was the plasticity observed within a lifespan and could occur in reaction to aging or plastic changes to different external conditions. The third level was the adaptation induced in the masticatory function by immediate, day-to-day environmental changes, such as those occurring with change of food. All these changes can be induced by differences between available foods. Therefore, the masticatory apparatus could be affected through changes in the food availability related to climate modifications over centuries or millennia, to seasonal changes during 1 individual life, or simply to different available foods within a single meal or a single day. The workshop included 6 oral communications and 7 posters. In many of these works, the food properties were considered. Lucas and Darvell presented a panel of tests designed to characterize different foods and a theory that allowed better characterization of a number of foods based on the determination of simple physical properties.³ These principles were used in several other communications in the workshop. Certain studies documented some relationships between tooth shape and soft or hard diet (Wright, Yamashita et al, Dominy et al). Others studied the relationship between masticated foods and physiologic responses in man (Woda et al) and monkey (Reed and Ross).

Alain Woda
Associate Editor

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