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AN ANALYSIS OF MASTICATORY FORM AND FUNCTION IN THREE MUSTELIDS (*MARTES AMERICANA, LUTRA CANADENSIS, ENHYDRA LUTRIS*)

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ABSTRACT.—An analysis of the masticatory apparatus of three mustelids (*Martes, Lutra, Enhydra*) is presented. Descriptions are provided for dentition, cranial morphology, primary jaw musculature, and jaw mechanics. The most striking differences noted among the three genera are in the dentition, with the cheek teeth showing extreme modification toward grinding in the species examined. The cranium, jaw muscles, and jaw mechanics are more conservative. These results lend support to the hypothesis that the greatest variation in the components of the mammalian jaw apparatus is contributed by the shape of the teeth (Hiiemae, 1978).

It has been suggested that the basic pattern of mammalian mastication was established with the appearance of the temporal-mandibular joint. This pattern of mastication, although simple, had the flexibility to produce more complex chewing cycles through changes in tooth structure or muscle proportions, when the demands on the jaw apparatus changed (Hiiemae, 1978).

The present study examines the masticatory apparatus of three mustelids (*Martes americana, Lutra canadensis, Enhydra lutris*) representing a hypothetical lineage from an ancestral land dwelling omnivore to the extremely specialized aquatic sea otter. The three genera involved represent a spectrum of dietary adaptations that evolved from a single ancestor. Therefore, it should be possible to illustrate the primary changes in jaw morphology that resulted in new jaw movements.

Although the fossil record is fragmentary for mustelids, it generally is believed that they arose as an independent offshoot from an arctoid stock 35 million years ago (Hunt, 1974). Strong carnivorous dentition, short powerful jaws, and weak zygoma evolved quickly in the early mustelids (Ewer, 1973). Among modern genera, *Martes* is the least derived. Martens have an omnivorous diet consisting primarily of small mammals, some birds and fish, and a minor component of insects and fruit from July through October (McCowen and Mackay, 1950; Ewer, 1973). They kill their prey with a canine bite to the neck, slice the flesh with sharp carnassial blades, and swallow the pieces whole.

The lutrine branch of mustelids first appears in the fossil record in the upper Oligocene of Europe. The early species exhibited specializations for aquatic locomotion (Savage, 1957) but retained a 'primitive' dentition (Van Zyll de Jong, 1972), similar to that of extant *Lutra canadensis*, the river otter. *Lutra* is carnivorous; fish constitute 60–70% of its diet. Crayfish and amphibians are taken seasonally, and small mammals, waterfowl, mollusks, and aquatic insects make up a minor component of the diet (Ewer, 1973). River otters snatch swimming prey with a grasping bite and then return to the river bank to gnaw the flesh and bones with their posterior cheek teeth.

Another extant lutrine genus, *Enhydra*, has significantly different dentition and feeding habits. *Enhydra lutris*, the sea otter, is a marine species that remains in the littoral zone and has a crushing-type of tooth morphology in correlation with its diet of mollusks, crustaceans, and slow-swimming bottom fish (Kenyon, 1975).

Several authors have focused on the postcranial anatomy of the lutrine mustelids to illustrate intermediate stages of aquatic locomotor adaptations (Taylor, 1914; Tarasoff et al., 1971, 1972; Scapino, 1975, 1976, 1981). The present paper compares the masticatory apparatus of three mustelids, *Martes, Lutra*, and *Enhydra*, and describes the evolutionary changes in dentition,

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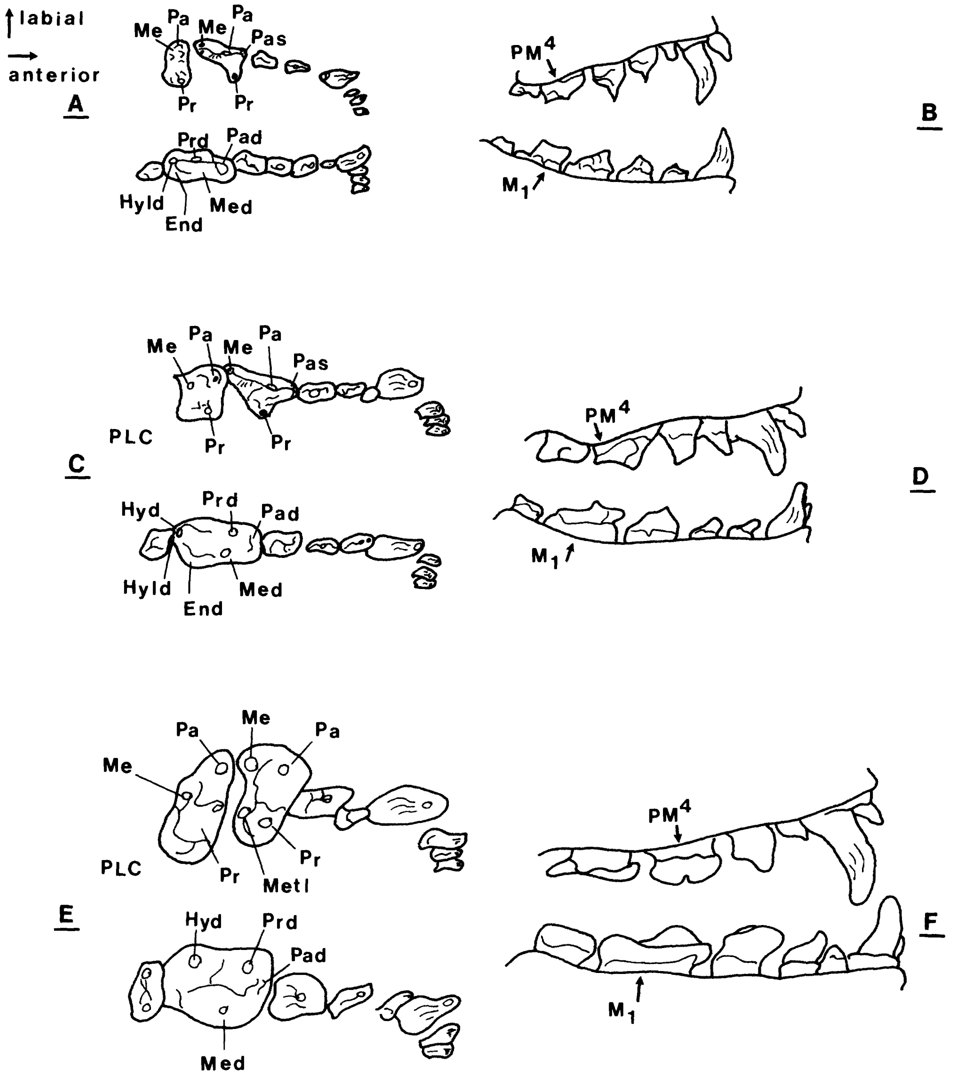

FIG. 1.—Dental comparisons for *Martes* (A + B), *Lutra* (C + D), and *Enhydra* (E + F). Pa = paracone, Me = metacone, Pr = protocone, Pas = parastyle, Metl = metaconule, Pad = paraconid, Prd = protoconid, Med = metaconid, End = entoconid, Hyd = hypoconid, Hyld = hypoconulid. A, C, E = right upper and left lower, occlusal view. B, D, F = right upper and right lower, lateral view.

cranial morphology, primary jaw musculature, and jaw mechanics that might have occurred in the transition from one adaptive zone to another.

METHODS

The dentition, skull, and mandible were examined in museum specimens (*Martes:* UMA 2579, 3680, 2324, 3389; *Lutra:* UMA 3385, 439, 2290, USNM 238257, 535046; *Enhydra:* UMA 3670, DC657, 438). Distortion grids were used to compare *Martes* and *Lutra* and *Lutra* and *Enhydra* (Colbert, 1935). Jaw muscle origins and insertions in *Martes americana* (Windle and Parsons, 1897; Hall, 1926; Poliakova, 1974) were used as the standard for comparisons of three specimens of *Lutra canadensis* (wild trapped in New Hampshire) and four specimens of *Enhydra lutris* (washed up on a beach in California). The primary jaw

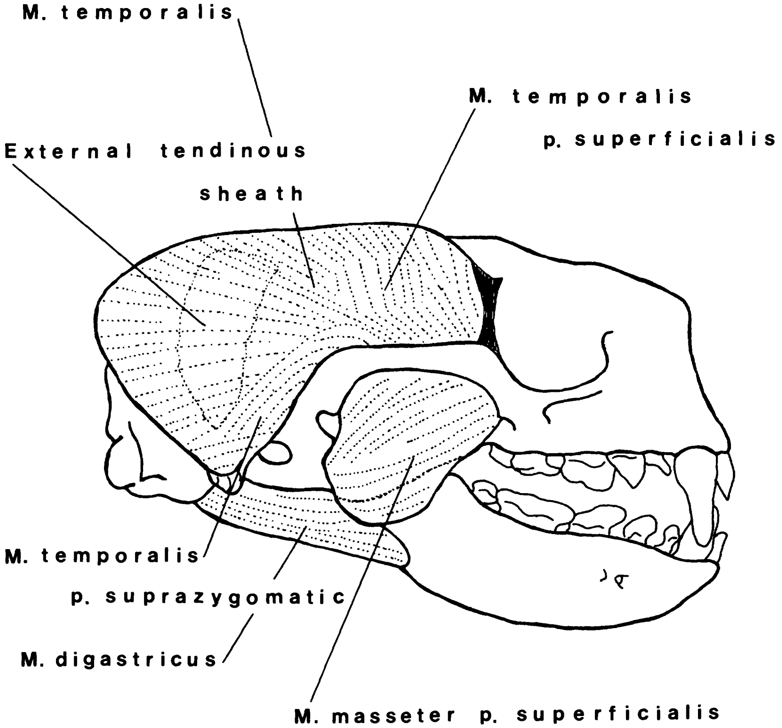

FIG. 2.—Primary jaw musculature of *Enhydra lutris,* lateral view, superficial aspect.

musculature was examined using standard morphological techniques; the muscles then were removed, blotted, and weighed.

Museum skulls of the three species were used for the mechanical analysis. The areas of origin and insertion of each jaw muscle were marked on the skulls and the center of each area was determined. The skulls then were mounted on a rat stereotactic apparatus with the jaw in the closed position, as described by Hiiemae (1971) and Weijs and Dantuma (1975). The origin and insertion points were recorded in a space coordinate system consisting of horizontal (h), vertical (v), and transverse (t) components. The readings were taken three times per side per animal and a mean was calculated for each species. These measurements represent a line of action (L) for each muscle and its breakdown into three planes by the formula $L = h + v + t$. The forces produced by the jaw muscles then were calculated using the formula $F = W/L$, with F equal to force, W equal to the % weight of the muscle and L equal to the line of action between the origin and insertion (see Hiiemae, 1971, for further details).

RESULTS AND DISCUSSION

Dentition.—The early mustelids evolved from miacid stock that had specialized carnassials, lacked M^2 and had a reduced M_2 (Butler, 1946). *Martes americana* retains this primitive dentition in a modified form. Dental illustrations for all three genera are provided in Fig. 1. *Martes* has a well-developed carnassial pair which provides shear between the lingual side of the paracone ridge of PM^4 and the labial edge of the paraconid-protoconid ridge of M_1. The M^1 inner lobe expands to provide crushing area with the basined talonid of M_1. The incisors, canines, and remaining cheek teeth preserve a simple and primitive cusp pattern. When viewed laterally the tooth structure appears as a well formed battery for tearing and slicing flesh with some evidence of crushing in the posterior molar region.

Lutra canadensis is intermediate and possesses a carnivorous dentition. In general, *Lutra* teeth appear more rounded and basined when compared to those of the marten. The M^1 lacks the hourglass shape characteristic of most mustelids and has a widened protocone and endostyle which adds a significant crushing area to the tooth. The carnassials have a slicing component as in *Martes*, although there are some differences. The protocone and endostyle of PM^4 is expanded to provide a crushing plate against the paraconid of M_1. Additionally, the talonid of M_1 is relatively larger than in *Martes* and has a fairly smooth surface for crushing against M^1 protocone, which also provides a shearing action against the posterior surface of the metaconid of M_1. The M_2 has an even rounder, smoother surface than is seen in *Martes*, and the remaining cheek teeth also have a more rounded appearance and are crowded in the jaw. The upper premolars are closely spaced, P^1 is squeezed between C^1 and P^2. The lower teeth also are crowded; P_1 is lacking.

Enhydra lutris exhibits extreme modifications for a crushing diet; PM^4 and M^1 lack shearing surfaces and are broad and flat. M^1 is the largest tooth; it provides a crushing plate against M_1 and M_2. M_1 lacks shearing potential and is a broad, smooth tooth. The remaining cheek teeth also are rounded and the anterior-most premolars are reduced; P^1 is lacking. The development of the crushing component in *Enhydra* has been achieved through the specialization of M^1 and M_1 (Butler, 1946). The protocone of M^1 expands with an accompanying increase in the posterior lingual cingulum. PM^4 loses its shear and adds lingual crush through the expansion of the protocone and the addition of a metaconule. When viewed laterally, the dentition of the sea otter appears as a sturdy crushing battery with some ability for puncture, but without shearing surfaces.

Cranial morphology.—The skull and mandible of *Martes* are recognizably mustelid in shape. The rostrum is typically long and the zygomatic arches are thin and curve dorsally and medially. The auditory bullae are inflated and extend to or slightly below the level of the tooth row. A ventral view illustrates a thin, straight row of teeth bordering the hard palate, which extends beyond the dentition and terminates in a short unpronounced pterygoid process. The cranium is smooth except for a slight lambdoidal crest. The mastoid processes are barely visible from the dorsal view and the postorbital processes are slight. The mandible has a typical carnivore form with an expanded coronoid process, distinct angular process, and a temporal-mandibular joint (TMJ) formed by a transverse, elongate mandibular condyle that fits into a trough-like glenoid fossa (Scapino, 1976).

The cranium of *Lutra* differs in several ways from that of *Martes*. The otter skull is roughly two times larger, has a relatively shorter rostrum and a relatively wider posterior cranium. The post orbital process is more pronounced and the lambdoidal crest continues from one mastoid process to the other. The auditory bulla are less inflated, the dorsal and medial arch of the thickened zygomatic arch has a slight depression and the pterygoid is flanged. A ventral view illustrates a widening of the cheek teeth and a crowding of the anterior premolars.

The sea otter skull is roughly twice the length of *Lutra* and generally appears more massive and sturdy. The mandible continues the trend of deepening and thickening the ramus. The coronoid process has a notable posterior-medial tilt, whereas the angular process has a dorsal tilt. The skull has a relatively short rostrum. The cranium is not as smooth as was noted for *Lutra* and *Martes*, because of the development of a sagittal crest that extends to the extensively widened and laterally flared mastoid processes. The auditory bulla are greatly inflated and the pterygoid flange is highly pronounced. The zygomatic arch appears thick and sturdy and the ventral view illustrates an even greater widening of the cheek teeth and crowding of the anterior molars.

Jaw musculature.—The three genera examined have a consistent pattern of primary jaw muscle morphology with only slight alterations. The primary jaw muscles of *Enhydra* are illustrated in Fig. 2. Table 1 presents the jaw muscle weights for the three genera, examined as percentages. *Martes* jaw musculature exhibits a fairly generalized carnivore plan. Descriptions of the marten jaw musculature are based on Windle and Parsons (1897), Hall (1926), and Poliakova (1974). The temporalis (M. Temporalis) makes up the bulk of the muscle mass and has an anteroventral fiber direction. The muscle originates from the entire temporal fossa, and

TABLE 1.—*Muscle weights (expressed as mean % total of jaw muscles), lines of action, force, moment.*

Genus	Muscle	Line of action (cm)					Force values (g)				Moment
Muscle	weights	H	V	T	L	L	Fh	Fv	Fl	Ft	(g·cm)
Martes											
Temporal	68.9	13.9	15.4	6.0	21.6	466.4					
Superf. mass.	12.7	13.8	10.4	6.4	18.4	339.6					
Deep mass.	5.2	9.0	6.8	2.9	11.6	134.6					
Digastric	8.6	25.6	10.7	5.6	28.3	800.9					
Lutra											
Temporal	50.9	29.7	11.0	6.2	32.3	1,043.3	1.51	0.54	0.31	1.58	15.8
Superf. mass.	10.01	33.9	16.7	3.4	37.9	1,436.4	0.24	0.12	0.02	0.26	1.8
Deep mass.	11.58	0.3	2.0	10.3	10.5	110.3	0.03	0.21	1.00	1.10	12.1
Digastric	19.11	46.0	9.5	4.3	47.2	222.5	0.40	0.08	0.04	0.41	5.3
Enhydra											
Temporal	61.06	34.2	15.1	11.9	39.2	1,536.6	1.36	0.60	0.47	1.60	28.8
Superf. mass.	10.87	23.6	21.5	9.8	33.4	1,115.6	0.23	0.21	0.10	0.33	5.3
Deep mass.	7.26	2.8	0.2	10.4	10.8	116.6	0.18	0.01	0.65	0.67	8.7
Diagastric	14.98	42.4	46.7	12.8	64.8	4,147.4	0.15	0.17	0.05	0.23	4.8

a strong aponeurosis inserts onto the coronoid process. No subdivisions within the muscle are discernable although one author, Poliakova (1974), does distinguish a small superficial piece (Pars Superficialis). When comparing *Martes* and *Lutra*, in *Lutra*, the fibers of the temporalis run more horizontally, the origin extends further anteriorly and ventrally, and the muscle bulges over the caudal edge of the cranium. The muscle insertion extends onto the lateral and anterior edge of the coronoid process via a strong tendinous attachment. *Enhydra* temporal muscle does not extend posteriorly to the same degree as in *Lutra*, but it does have a larger posterior-ventral portion that covers the expanded mastoid process with horizontally oriented fibers. The Pars Superficialis, although still vestigial, is more pronounced in *Enhydra*.

Martes masseter muscle (M. Massetericus) is divided into a superficial, medial and deep portion by Hall (1926) based on fiber direction but only into a superficial and deep portion by Poliakova (1974) and Windle and Parsons (1897). My observations on the closely related *Martes pennanti* also reveal that only two divisions are distinguishable. The superficial portion originates on the anterior half of the zygomatic arch and inserts on the angle of the lower jaw. The deep portion takes its origin on the posterior half of the zygomatic arch and has an insertion that fills the masseteric fossa of the lower jaw.

The superficial masseter of *Lutra* has an area of origin concentrated more anteriorly and an insertion that extends anteriorly, ventral to the deep portion. The deep masseter shows some evidence for a slight differentiation of a medial portion but the extensive fusion in the dorsal half of the muscle precludes the separation of medial and deep as has often been done (Fisher, 1942; Hall, 1926).

When *Enhydra* is compared to *Lutra*, the superficial masseter appears similar although the fibers take a less horizontally oriented angle, the tendinous insertion is more extensive and the distinction between superficial and deep is not as distinct as was noted for *Lutra*. The deep layer has an anteriorly expanded origin and there is a prominent tendon running from just anterior to the jaw joint anteroventrally three quarters of the way down the muscle.

The digastric muscle (M. Digastricus) consists of two bellies separated by a thin line of tendon. This tendon is superficial and does not functionally divide the muscle into two parts (Scapino, 1976). The digastric arises from the paraoccipital process and runs anteriorly to the posteroventral surface of the mandible.

The *Lutra* digastric muscle has an expanded area of origin, and the total muscle mass is remarkably large when compared to *Martes* but the area of insertion is reduced in *Lutra* when compared to other mustelids (Scapino, 1976). The digastric in *Enhydra* is a broad, thick muscle that exhibits no tendinous intersection between anterior and posterior bellies, although Scapino (1976) was able to distinguish a feeble line that seemed to be a remnant intersection which did not extend to the middle of the muscle. There are also slightly increased origin and insertion areas over that found in *Lutra*.

The pterygoid musculature is divided into medial (Pars Medialis) and lateral (Pars lateralis) components by Windle and Parsons (1897) although not by Hall (1926) or Poliakova (1974). Several authors note that these muscles are difficult to separate. My observations on *M. pennanti* reveal a condition as seen in dogs and bears, with a broad medial component originating on the alisphenoid bone just dorsal to the pterygoid bone and inserting on the medial surface of the mandible just ventral to the TMJ and a thin, tendinous lateral one which originates from the dorsolateral surface of the pterygoid hamulus and onto the lateral palatine bone and inserts on the posterior-medial edge of the angle, ventral to the Pars Lateralis. The lateral portion is very similar in *Lutra* although the insertion is slightly more anterior. It is an extremely small muscle and was hard to remove cleanly for weighing purposes. For *Enhydra* the lateral pterygoid appears very similar to *Lutra*.

The medial portion in *Lutra* has an extended area of origin along the pterygoid to the tip of the pterygoid flange. The medial portion in *Enhydra* is similar to *Lutra* although in *Enhydra* the separation between the Pars Lateralis and Pars Medialis is less clear and the area of origin appears more concentrated.

Jaw mechanics.—A simplified vector analysis of primary jaw muscles was undertaken using the approach described by Hiiemae (1971) and modified by Weijs and Dantuma (1975). As muscle weights for *Martes americana* were not available, the vector analysis presented by Smith and Savage (1956) was used as a baseline for comparison with *Lutra* and *Enhydra*. The medial and lateral pterygoids were excluded from the force analysis because I was unable to weigh the pterygoid muscles separately in *Enhydra* and because the stereotactic apparatus could not be used to measure pterygoid lines of action.

In the vector analysis of *Martes* jaw muscles produced by Smith and Savage (1956) they noted the following general characteristics of carnivore jaw lever systems. The temporal muscle is the largest muscle and has the largest moment, the pterygoids are weakly developed as adductors but function well in aligning the scissor-like carnassial blades. The jaw joint is in the form of a hinge, which tends to restrict movement to primarily the sagittal plane although there is enough lateral movement so both sides do not cut simultaneously. The tooth row is level with the TMJ. Pressure applied at the carnassials is diverted along the zygomatic arch because the carnassials are towards the back of the skull, under the buttressing of the zygomatic arch.

Table 1 presents the numerical results of the mechanical analysis and Fig. 3 illustrates the superficial masseter lines of action and forces for *Enhydra*. The temporal muscle in *Martes* exhibits what would be expected for a typical carnivore. The longest lines of action are in the vertical (43%) and horizontal (39%) planes, which produce a strong posterodorsal line of action. This line of action would result in a biting force being produced at the canines or the carnassials or both. In *Lutra* the horizontal component of the line of action is greater (63%), which might reflect the extensive muscular component overhanging the occipital ridge and having a nearly horizontal fiber direction. The largest component of temporal force is in the horizontal plane (1.5), which contributes 64% of the total temporal force. The moment of this muscle is 15.8 cmg, which makes it by far the most effective jaw adductor in *Lutra*.

Enhydra has an extensive horizontal component (56%), possibly reflecting the expansion of the mastoid ridge which increases the area of origin for the horizontally oriented portion of this muscle. The forces exhibited by *Enhydra* are comparable to those of *Lutra*, with the horizontal component contributing 57% of the total temporal force. The main difference between the two genera is the increase in the temporal moment to 28.8. This might reflect an increased force being produced at the canines or cheek teeth, or both, and also might be an effect of the larger size of the animal.

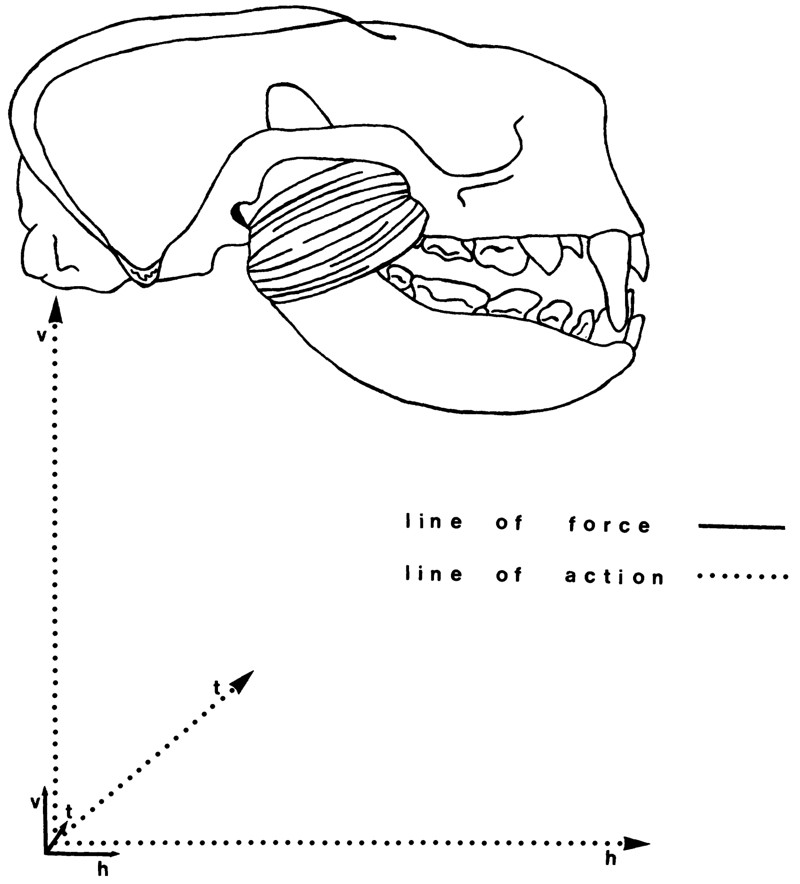

FIG. 3.—Forces and components of superficial masseter line of action in *Enhydra lutris* (line of action as percent of total: v = 39.2, h = 42.9, t = 18.0; force in g: v = 1.1, h = 1.2, t = 0.5).

The superficial masseter of *Martes* shows a fairly even division between the anteriorly directed horizontal (45%) and the vertical (34%) lines of action with a considerable medially-directed component (21%). This muscle exhibits lines of action suggesting that it acts as a couple with the temporalis to produce force at the carnassials with little resistance at the TMJ.

In *Lutra* the horizontal component of the line of action predominates (63%) and the transverse component contributes much less (6%). The total muscle force (0.26) and the moment (1.8) reflect the weak nature of this muscle when compared to the temporal.

Enhydra illustrates a situation more comparable to *Martes* than to *Lutra*. The force analysis indicates an even division of pull between the vertical and horizontal directions. This would create a slightly stronger anterodorsal force delivered in conjunction with the temporal force at the carnassials than was noted for *Lutra*. Whether this implies added resistance to torque created at the TMJ or more power at the molars, or both, is uncertain. The medially-directed force (0.1) represents 26.7% of the total jaw force, an increase over that in *Lutra*, which could be associated with either the aligning of the teeth as described for *Martes* or perhaps some other function associated with lateral grinding at the molars. The moment of the muscle (5.3), is the smallest component of adductor strength in *Enhydra*, but still is substantially greater than that observed in *Lutra*.

The deep masseter in *Martes* is the smallest of the three main jaw adductors. It has both a substantial horizontal (50%) and vertical (36%) line of action, and its transverse component (16%) is directed laterally. This muscle has not been analyzed in the literature but might be important to produce vertical force at the carnassials. The lateral component also might play a role in opposing the medial pull exerted by the temporal and superficial masseter and thereby might decrease the torque produced at the TMJ when these muscles contract simultaneously.

Lutra exhibits a more extensive transverse component (82%) in its deep masseter, which might be associated with the lack of medial curvature of the zygomatic arch. This muscle with such a dominant transverse component could effect carnassial biting as was postulated above for *Martes*. The force (1.10) exerted by the muscle is substantial, the transverse component is 81.8% of the total force produced. The deep masseter opposes the medial pull of the temporal and superficial masseter and also could produce vertical pull on the coronoid, in turn delivering force at the cheek teeth. The moment of this muscle (12.1) rivals that of the temporalis and its force should not be underestimated due to its relatively small size. Although its mass is quite close to that of the superficial masseter, its lever arm is longer and when coupled with a larger force it has a substantially increased ability to provide rotation at the TMJ.

In *Enhydra* the deep masseter is similar. The transverse line of action (78%) is substantially longer than the horizontal (21%) or the vertical (1%). These latter two have switched in their relative percentages from *Lutra* to *Enhydra*. The coronoid expands dorsally in *Enhydra* so that the center of the deep masseter insertion also is more dorsal; this might explain the decrease in the vertical component. The force provided by the muscle is primarily in the transverse plane (77.4%) and the moment (8.7) makes this muscle the second strongest jaw adductor in *Enhydra*.

The digastric is the primary jaw abductor in mammals. In *Martes* this muscle has a pronounced horizontal (61%) and vertical (26%) line of action. The transverse component (13%) is minor. In *Lutra* the lines of action are roughly comparable. The force supplied (0.41) is primarily in the horizontal plane and the moment is moderate (5.3). *Enhydra* has a tremendous increase in the vertical component (15%). The force delivered is roughly half that reported for the river otter and the major forces are applied in the vertical and horizontal directions in almost equal proportions.

Evolutionary and functional considerations.—Modern morphological techniques of recording jaw movement have provided data that establish a basic chewing cycle (Hiiemae, 1978). These data can be presented in the form of a loop, which shows the path through which a point on the lower jaw moves relative to a reference point in the skull. When loops of different mammals are compared a consistent pattern is evident with slight modifications among shearing, gnawing, and grinding classes. Within each major class, slight modifications have been demonstrated among the relatively few species examined thus far. Hiiemae (1978) attributes this variation in form of cycle to slight shifts in balance between pairs of muscles. In other words, there might be an adaptive response tending to enlarge one or other of the muscle vectors by alterations in their mass or fiber orientation or both. This would tend to produce slight changes in the chewing cycle without a major reorganization of the basic muscle plan.

A basic pattern of jaw movement apparently evolved with carnassial teeth. This carnivore chewing cycle seems to have been retained by the different groups within the Carnivora with only slight shifts in balance between pairs of muscles. These slight modifications in muscle capabilities combined with more extensive alterations in dentition appear to be associated with the variety of dietary specializations observed.

By focusing on these mustelids I was able to examine the jaw morphology of three closely related species which are ecologically divergent. The most striking differences in jaw morphology are those associated with the dentition, with the cheek teeth showing modification toward grinding. These differences primarily reflect a decrease in carnassial specialization, which involves a loss of all shearing surfaces, an increase in M^1/M_1 grinding components, a decrease in number of teeth, a crowding of the anterior premolars and incisors, and a shift from a shearing PM^4/M_1 to a crushing M^1/M_1. Among all the morphological characters examined, the dentition is most clearly relatable to the dietary differences.

The skulls also exhibit modifications that could be associated with the different diets of the animals. The most obvious of these are: 1) the increased width and depth of the mandibular ramus, which almost certainly reflects the need to resist strain along the jaw when crushing; 2) the thicker, expanded border of the zygomatic arch, which might also absorb strain imposed by the grinding molars situated directly ventral to it; and 3) the increased massiveness of the skulls, which could be involved in absorbing strain and providing larger, stronger areas for muscle attachment.

In contrast to the modifications observed in the dentition and skull, the jaw musculature of the three species examined is surprisingly conservative. Aside from the differences noted in the relative weights of the muscles and fiber orientation, the general carnivore plan has been retained. It then follows that the mechanics of the jaw apparatus might be fairly conservative and although there are some interesting differences reported in the series, on the whole the mechanics of *Enhydra* did not differ substantially from that of *Martes*. The basic plan of carnivore mechanics has been retained with only minor alterations and the analysis of Smith and Savage (1956) is confirmed by the present work.

Although the method of mechanical analysis employed has several limitations, it was able to provide a good summary of the general movements of each muscle at jaw closure. The temporalis is shown to serve primarily in elevation, retraction, and medial translation of the mandible. The superficial masseter is involved in protraction, elevation, and medial translation and the deep masseter is primarily responsible for elevation and lateral translation. The digastric serves in depression and retrussion of the jaw and perhaps also in tensing the floor of the mouth.

Given the set of complex jaw movements available, it is not surprising that evolution has altered vectors of some of the preexisting muscles (or muscle parts) to affect new jaw movements rather than altering the basic muscle plan. Major changes could be accomplished by either increasing or decreasing muscle mass or by changing fiber direction. This could result in slight changes in movement capabilities.

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