FUNCTIONAL ANATOMY

Functional analysis of the manatee's entire myology is beyond the scope of this paper, which is intended as a source of morphological data for future studies. However, some observations made in the course of the dissections call for discussion going beyond pure description; this is presented below.

BRISTLES OF THE UPPER LIP

A key element in the manatee's feeding apparatus is the distinct set of large, stiff, white bristles found at the anteromedial corner of each of the lobes of the upper lip. These have been well illustrated for *T. manatus* by Vrolik (1852: fig. 5), Murie (1872: fig. 7), and Garrod (1877: pl. 28: figs. 1, 2), and for *T. inunguis* by Stannius (1845: fig. 2). As noted by Pereira (1944: 38, 40), these bristles can be withdrawn into the skin or extended at will to serve in grasping and manipulating food. The mechanism of this action has apparently never been studied and would probably repay a microscopic examination, though its main features seem sufficiently clear in gross dissection. The roots of the extrusible bristles are surrounded by muscle fibers slightly darker than those of the rest of the snout. Such fibers as were grossly visible appeared to run lateroventrad; however, external pressure applied in any direction to this region in a dead specimen causes the bristles to extrude to a startling degree. On relaxation of the pressure (or of the muscle fibers, in a live animal) the bristles are elastically retracted into their sheaths.

OPENING OF THE NOSTRILS

There has been some confusion in the literature over the mechanism of opening and closing the nostrils in sirenians; however, a clear and correct description of the process has been given by Genschow (1934: 433-435, fig. 24). The floor of the narial passage is strongly convex dorsad and lightly pigmented for about 5 cm inside the nostril of a juvenile animal; *i.e.,* a distance equivalent to the fore-and-aft length of the portion of the lateralis nasi arising from the side of the rostrum. This muscle's vertical fibers insert into the floor of the passage throughout this distance and act to depress it, perhaps assisted by the maxillonasolabialis. Upon relaxation of the lateralis nasi, this entire portion of the floor of the narial passage, and not just the small part visible at the nostril itself, springs back against the roof elastically, closing the passage. As in cetaceans and pinnipeds, there are no muscles which serve to close the nostrils; this is done entirely automatically by elastic tissue, and only the opening is voluntary. The latter seems to be the chief function of the lateralis nasi, contrary to my earlier supposition (Domning, 1977a) that it helped to manipulate the snout and upper lip.

JAW MUSCLES

Turnbull (1970) has provided both a simple, standardized framework for basic analysis of mammalian jaw mechanics and a large amount of data on jaw musculature of diverse mammals for comparative purposes, with which we can briefly examine some features of the manatee's jaw apparatus.

Jaw muscle weights of four juvenile *T. inunguis* are given in Table 3. With these, and with the muscle maps of Figs. 10-15, we can estimate the static useful power (E) of any muscle or set of muscles helping to close the jaw, from Turnbull's formula

$$E = M \times F_L \times F_X \times r$$

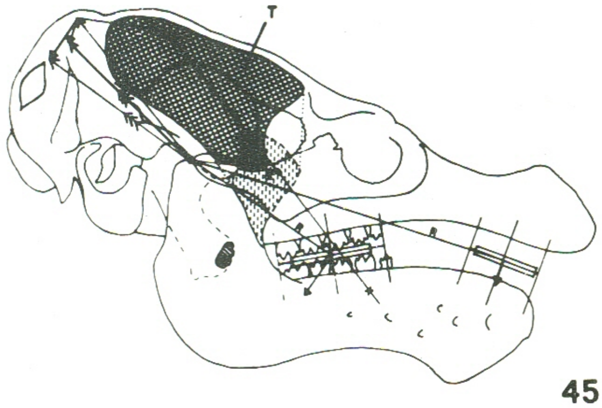
where M is the weight of the muscle group expressed as a percentage of the total jaw-closing musculature; F_L is a correction **factor** for the muscle's angle of pull on its effort lever arm, projected into the (parasagittal) plane of jaw closure; F_X is a correction factor for the divergence from the vertical, in a vertical transverse plane, of the muscle's direction of pull; and r is the ratio of the muscle's effort lever arm to the resistance lever arm of the system. The rationale, derivation, use, and limitations of this formula are explained in more detail by Turnbull (1970: 281-296).

TABLE 3. Weights and percentages of masticatory muscles in juvenile Trichechus inunguis; left and right sides combined.

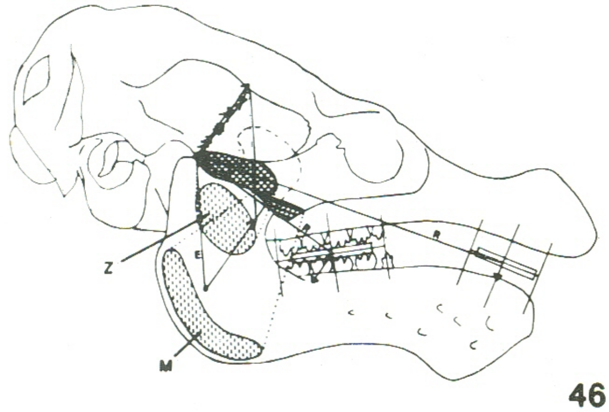
Muscle	Weight (g)	%	% (omitting digastricus)
INPA-PB 6:			
Masseter	9.3	16.6	17.7
Zygomaticomandibularis	4.1	7.3	7.8
Temporalis	27.0	48.1	51.4
(Superficial temporalis)	(9.0)	(16.0)	(17.1)
(Deep temporalis)	(18.0)	(32.1)	(34.3)
Pterygoideus internus	7.7	13.7	14.7
Pterygoideus extenus	4.4	7.8	8.4
Digastricus	3.6	6.4	...
Totals	56.1	99.9	100.0
INPA-PB 8:			
Masseter	16.3		
Zygomaticomandibularis	6.6		
Temporalis	...		
Pterygoideus internus	13.2		
Pterygoideus externus	5.2		
Digastricus	9.8		
INPA-PB 9:			
Masseter	12.4	16.9	19.2
Zygomaticomandibularis	4.0	5.5	6.2
Temporalis	34.6	47.2	53.6
(Superficial temporalis)	(11.7)	(16.0)	(18.1)
(Deep temporalis)	(22.9)	(31.2)	(35.5)
Pterygoideus internus	8.9	12.1	13.8
Pterygoideus externus	4.6	6.3	7.1
Digastricus	8.8	12.0	...
Totals	73.3	100.0	99.9
INPA-PB 169:			
Masseter	14.7	17.3	18.5
Zygomaticomandibularis	6.5	7.7	8.2
Temporalis	40.4	47.6	50.9
(Superficial temporalis)	(14.6)	(17.2)	(18.4)
(Deep temporalis)	(25.8)	(30.4)	(32.5)
Pterygoideus internus	12.6	14.8	15.8
Pterygoideus externus	5.3	6.2	6.7
Digastricus	5.4	6.4	...
Totals	84.9	100.0	100.1

To analyze the manatee's jaw-closing musculature, we first divide the weights of the adductor muscles in Table 3 into three groups: the weights of the temporalis (Mt), of the masseter plus zygomaticomandibularis (Mm), and of the pterygoideus internus (Mpti). As the pterygoideus externus of the manatee is not an adductor, it is excluded here, although Turnbull included it in his analyses of other mammals. (Only the muscle-weight data on INPA-PB 6, 9, and 169 are complete enough to use here.).

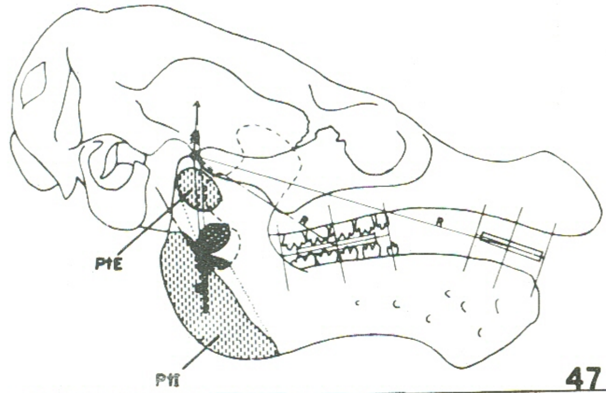
Next, maps of the attachments of each of these muscle groups are constructed in lateral view (Figs. 45-47). Functional centers of resistance to jaw-closing in the rostral and molar regions (corresponding to Turnbull's incisor-canine and premolar-molar regions, respectively) are visually estimated and lines are drawn connecting these points with the temporal condyle; these are the resistance lever arms for orthal motion around the condyle. The functional midpoints of the origin and insertion fields for each muscle group are estimated and plotted, taking into account the form, structure, and average fiber direction of the muscles. A line from the functional midpoint of each insertion field to the condyle is the muscle's effort lever arm. The angle between this and a line joining the origin and insertion midpoints is measured with a protractor, and the resulting value is compared with Turnbull's diagram (1970: fig. 41) to determine the value of the correction factor F_L for that muscle group. The effort and resistance lever arms are measured directly from the diagrams to calculate r. The average directions of muscle pull are likewise projected into a transverse vertical plane (Fig. 48), and their divergences from the vertical measured and compared with Turnbull's diagram to obtain the values of F_X. The values of these factors for the adductor muscles are given in the top part of Table 4.



45



46



47

Figs. 45-47 — Lateral views of skull and mandible of juvenile **Trichechus inunguis**, for analysis of jaw-closing forces (see text). Resistance lever arms (R) shown for rostral and molar regions; resistance vectors (solid-headed arrows) are proportioned to estimated useful power of each muscle group. Dots indicate estimated functional midpoints of origin and insertion fields of temporalis (Fig. 45), masseter + zygomaticomandibularis (Fig. 46), and pterygoideus internus (Fig. 47). Lines from insertion midpoints to jaw joint are effort lever arms (E). Polygons show resolution of forces at jaw joint; effort vectors (open-headed arrows) are proportional to weight of muscle group; feathered arrows mark unresolved translational force vectors. Dotted lines show outlines of muscles. Dashed lines show outlines of concealed coronoid and pterygoid processes. Cross-hatched area in Fig. 45 is pterygoid-mandibular articular surface; extension of temporalis effort vector through molar resistance field marked by X. Outline and attachments of pterygoideus externus shown in Fig. 47, but vector analysis of this muscles not shown. Unresolved vector of pterygoideus internus is proportional to Mpti only, since Epti = 0.0.

In Table 5 are given the values of M for each muscle group in each specimen, as percentages of the total weight of the three groups together. These values are used with those from Table 4 to calculate the useful power (E) according to the above formula; each E is then converted again to a percentage of the sum of all Es. These figures express the proportion of the total jaw-closing force contributed by each muscle group, which may be greater or less than that group's share of the total adductor muscle weight. The difference, shown in the next two columns of Table 5, results from the relative advantageousness of the group's angle of pull on its lever arm and the mechanical advantage of the lever arm itself. The results of similar calculations are shown for both the molar and the rostral resistance fields.

It must be emphasized that the estimate of useful power thus obtained applies only to orthal motion of the jaw. Especially in an animal like the manatee, this is not the only or even the most important aspect of jaw motion; so the values of E in Table 5 hardly begin to reflect the true functions of the muscles. This is most obvious from the zero values obtained for Epti, indicating that the pterygoideus internus, one of the major jaw muscles, plays no significant role at all in rotating the jaw parasagittally about the condyle. Chewing in the manatee, as in most other "ungulates", appears to have a large transverse component; accordingly I have adapted Turnbull's method to analyze the muscle actions in the occlusal plane.

In Fig. 49A the average directions of muscle pull are projected into the horizontal plane, as was done for the sagittal plane in Figs. 45-47. Here, however, we are concerned with the muscles producing transverse motion, so the weights of the pterygoideus externus (Mpte) from Table 3 are included. The percentage values of M are accordingly recalculated and shown in Table 6. Again using the condyle as the assumed center of rotation of the mandible, effort and resistance lever arms are plotted and values of r and F_L measured as before (Table 4, third part; only the molar region is considered). To obtain F_X, the

TABLE 4. Constants for use in calculation of jaw-closing useful power in juvenile *Trichechus inunguis*.

Muscle Group	Angle of pull on lever arm (parasagittal)	F L	Angle of pull on lever arm transverse)	F X	r (molar) region)	r (rostral region)
ORTHAL MOTION: FULCRUM AT TEMPORAL CONDYLE						
T	44°	0.71	49°	0.71	0.54	0.28
M+Z	40°	0.71	38°	0.71	0.79	0.40
PtI	5°	0.00	36°	0.71	0.92	0.47
FULCRUM AT PTERYGOID-MANDIBULAR JOINT						
T	71°	1.00	17°	0.27	0.91	
M+Z	5°	0.00	40°	0.71	0.47	
PtI	20°	0.27	29°	0.50	0.66	
PtE	13°	0.27	38°	0.71	0.63	
TRANSVERSE MOTION: FULCRUM AT TEMPORAL CONDYLE						
T	84°	1.00	41°	0.71	1.46	
M+Z	89°	1.00	55°	0.87	0.16	
PtI	5°	0.00	49°	0.71	0.27	
PtE	50°	0.71	59°	0.87	0.15	
FULCRUM AT POINT B, POSTEROMEDIAL TO PTERYGOID PROCESS						
T	67°	0.87	41°	0.71	1.08	
M+Z	62°	0.87	55°	0.87	0.61	
PtI	30°	0.50	49°	0.71	0.48	
PtE	29°	0.50	59°	0.87	0.64	

directions of pull are projected into the vertical transverse plane (Fig. 48A); but their angles with a horizontal line are measured, rather than with a vertical line as was done before. The resulting values of E are given on the left side of Table 6. Once again we obtain a zero value for Epti; moreover, the directions of Em and Epte on the active side are such that they would counteract Et and tend to move the mandible laterad rather than mediad as is normally the case in transverse chewing. So we are still far from a realistic approximation of the manatee's jaw mechanics.

One of the characteristic features of sirenian jaw structure, and a highly unusual one among mammals, is the extremely massive pterygoid process. The anterolateral and ventrolateral (palatine) surface of this pillar-like process is actually an articular surface of sorts, lying parallel to a corresponding surface on the posteromedial and dorsomedial side of the coronoid arch of the mandible, with a cushion of fascia between (Figs. 45, 48, 50). If a skull and mandible are properly manipulated, it is at once apparent that the mandible can be retracted against the pterygoid processes and then rotated about a median point lying somewhat abaft the processes, in a manner strongly resembling normal transverse jaw movement. In fact, actual chewing is almost certainly asymmetrical; the mandible is probably in close contact with the pterygoid process only on the active side, so that the center of rotation is offset toward that side. From careful manipulation it appears that point B in Figs. 48 and 49 may be close to the true center of rotation.

If the calculations are redone using this point rather than the condyle as the fulcrum (Tables 4, bottom; 6, right), a much more

TABLE 5. Jaw-closing useful power (efficiency) data for juvenile *Trichechus inunguis*, calculated for orthal motion with fulcrum at temporal condyle.

Muscle Mass (M) as %	MOLAR RESISTANCE REGION				ROSTRAL RESISTANCE REGION			
	E	% total adductor power (comp. w/muscle mass)	Change in % from direct muscle proportion %	Proportionate change	E	% total adductor power (comp. w/muscle mass)	Change in % from direct muscle proportion %	Proportionate change
INPA-PB 6:								
Mt =56.1	Et =15.3	58.0	+ 1.9	3% gain	7.9	58.5	+ 2.4	4% gain
Mm =27.9	Em =11.1	42.0	+14.1	51% gain	5.6	41.5	+13.6	49% gain
Mpti =16.0	Epti= 0.0	0.0	—16.0	100% loss	0.0	0.0	—16.0	100% loss
Totals 100.0	26.4	100.0			13.5	100.0		
INPA-PB 9:								
Mt =57.8	Et =15.7	59.0	+ 1.2	2% gain	8.2	59.9	+ 2.1	4% gain
Mm =27.4	Em =10.9	41.0	+13.6	50% gain	5.5	40.1	+12.7	46% gain
Mpti =14.9	Epti= 0.0	0.0	—14.9	100% loss	0.0	0.0	—14.9	100% loss
Totals 100.1	26.6	100.0			13.7	100.0		
INPA-PB 169:								
Mt =54.4	Et =14.8	56.5	+ 2.1	4% gain	7.7	57.0	+ 2.6	5% gain
Mm =28.6	Em =11.4	43.5	+14.9	52% gain	5.8	43.0	+14.4	50% gain
Mpti =17.0	Epti= 0.0	0.0	—17.0	100% loss	0.0	0.0	—17.0	100% loss
Totals 100.0	26.2	100.0			13.5	100.0		

believable set of figures results. Though dominated by the masseter group, the pterygoidei do play detectable roles, and all pull the mandible mediad with the ipsilateral side active, as expected. Overshadowing all of these, however, is the enormous contribution of the contralateral temporalis, which appears to be the most important factor in transverse chewing, in accord with the fact that the temporales alone constitute more than half the adductor muscle weight, a most unexpected condition for an "ungulate" with transverse chewing. It must of course be remembered that no one diagram can show all the important functions of any of these muscles; the masseter, for instance, has major roles in both orthal and transverse movements, and the contralateral pterygoideus externus and ipsilateral temporalis are probably important in the recovery stroke.

The significance of the hypothesized position of the fulcrum can be further demonstrated by vector analysis of the forces acting at the fulcrum. In Fig. 49, the temporalis, masseter, and pterygoideus effort vectors, scaled to the weights of the respective muscle groups (but not corrected for the muscle alignment factors), are summed sequentially, with the hypothetical fulcrum (A or B) serving as origin of the temporalis vector in each case. Both vector sums leave large unresolved forces (marked by feathered arrows) tending to translate the fulcrum posteromediad. With the fulcrum at A there is no means of resisting this force; but with the fulcrum at B, an extension (marked by X) of the corresponding force vector through point B almost precisely intersects the pterygoid-mandibular articulation perpendicular to its surface. This shows that this joint is properly located to resist translation of the center of rotation, and independently confirms the assumption that the pterygoid process and mandible are closely appressed on the active side in transverse chewing.

With respect to orthal motion, if we resolve the parasagittal forces at the jaw joint as is done in Figs. 45 and 46, we find large unresolved posterodorsad forces of the temporalis which are only partly counteracted by the masseter-zygomaticomandibularis. In mammals such as carnivores, a force of this sort would be resisted by a stout postglenoid process. In sirenians, however, the postglenoid process is very small and located behind a distinct mandibular fossa, much as in humans, and it seems not to come into contact with the mandible or play any apparent role in chewing. Thus, since the unresolved force of the temporalis cannot be resisted at the temporal joint, it must be resisted either at the pterygoid-mandibular joint or at the only other point of contact between the skull and mandible, *i.e.*, the food between the teeth.

Under the former assumption, the contraction of the temporalis would first retract the mandible, sliding the condyle back into the mandibular fossa and bringing the coronoid arch against the pterygoid process, as noted earlier in regard to manipulation of the bones. Subsequent contraction would rotate the jaw upward around the pterygoid-mandibular joint as fulcrum, as shown in Fig. 50. If we resolve the forces acting at this joint, using values of E calculated with this point considered as fulcrum (Table 4, second part; Table 7), we find the unresolved force aligned posterodorsad, nearly parallel to the long axis of the pterygoid process and against the pterygoid-mandibular joint surface — clearly a favorable arrangement for resisting the force. This force also has a laterad component (not illustrated) tending to separate the pterygoid process and mandible, but thanks to the solidly fused mandibular symphysis this component is either cancelled by the equivalent force on the opposite side (if the jaw muscles on both

TABLE 6. Masticatory useful power (efficiency) data for juvenile Trichechus inunguis, **calculated for molar resistance region and transverse motion.**

	FULCRUM AT TEMPORAL CONDYLE				FULCRUM AT POINT B			
Muscle Mass (M) as %	E	% total adductor power (comp. w/muscle mass)	Change in % from direct muscle proportion %	Proportionate change	E	% total adductor power (comp. w/muscle mass)	Change in % from direct muscle proportion %	Proportionate change
INPA-PB 6:								
Mt =51.4	Et =53.3	92.4	+41.0	80% gain	34.3	67.4	+16.0	31% gain
Mm =25.5	Em = 3.6	6.2	—19.3	76% loss	11.8	23.2	— 3.1	12% loss
Mpti =14.7	Epti = 0.0	0.0	—14.7	100% loss	2.5	4.9	— 9.8	67% loss
Mpte= 8.4	Epte= 0.8	1.4	— 7.0	83% loss	2.3	4.5	— 3.9	46% loss
Totals 100.0	57.7	100.0			50.9	100.0		
INPA-PB 9:								
Mt =53.6	Et =55.6	93.0	+39.4	74% gain	35.8	69.0	+15.4	29% gain
Mm =25.4	Em = 3.5	5.9	—19.5	77% loss	11.7	22.5	— 2.9	11% loss
Mpti =13.8	Epti = 0.0	0.0	—13.8	100% loss	2.4	4.6	— 9.2	67% loss
Mpte= 7.1	Epte= 0.7	1.2	— 5.9	83% loss	2.0	3.9	— 3.2	45% loss
Totals 99.9	59.8	100.1			51.9	100.0		
INPA-PB 169:								
Mt =50.9	Et =52.8	92.5	+41.6	82% gain	34.0	66.8	+15.9	31% gain
Mm =26.7	Em = 3.7	6.5	—20.2	76% loss	12.3	24.2	— 2.5	9% loss
Mpti =15.8	Epti = 0.0	0.0	—15.8	100% loss	2.7	5.3	—10.5	66% loss
Mpte= 6.7	Epte= 0.6	1.1	— 5.6	84% loss	1.9	3.7	— 3.0	45% loss
Totals 100.1	57.1	100.1			50.9	100.0		

sides contract together) or resisted by the contralateral pterygoid process (if the muscles on only one side contract). Using the pterygoid-mandibular joint as fulcrum might seem to have the additional advantage of lowering the functional jaw joint almost to the level of the tooth row, giving the temporalis a great mechanical advantage as in carnivores; this, however, is more than cancelled out by the reduced mechanical advantage in the transverse plane (FX, Table 4), so that the absolute useful power of the temporalis is reduced despite its gain relative to the other adductors. Moreover, the pterygoideus internus opposes rather than assists the temporalis, and the large unresolved force of the temporalis is wasted in compression of the pterygoid process.

These problems are avoided if the point of skull-mandible contact is considered to be the food itself, as described by Gingerich (1971). In this model, the contraction of the temporalis retracts the mandible as above, but this force is resisted by the food rather than the pterygoid process; thus virtually the entire force of the temporalis is used directly in mastication without any lever systems being involved. This is indicated in Fig. 45 by the extension (marked by X) of the temporalis effort vector through the molar resistance field; compare fig. 3 of Gingerich (1971). The mandible acts merely as a link between the temporalis (acting at the coronoid process) and the teeth. This is made possible by the sliding jaw joint, which has a very similar structure in sirenians and in man (the example

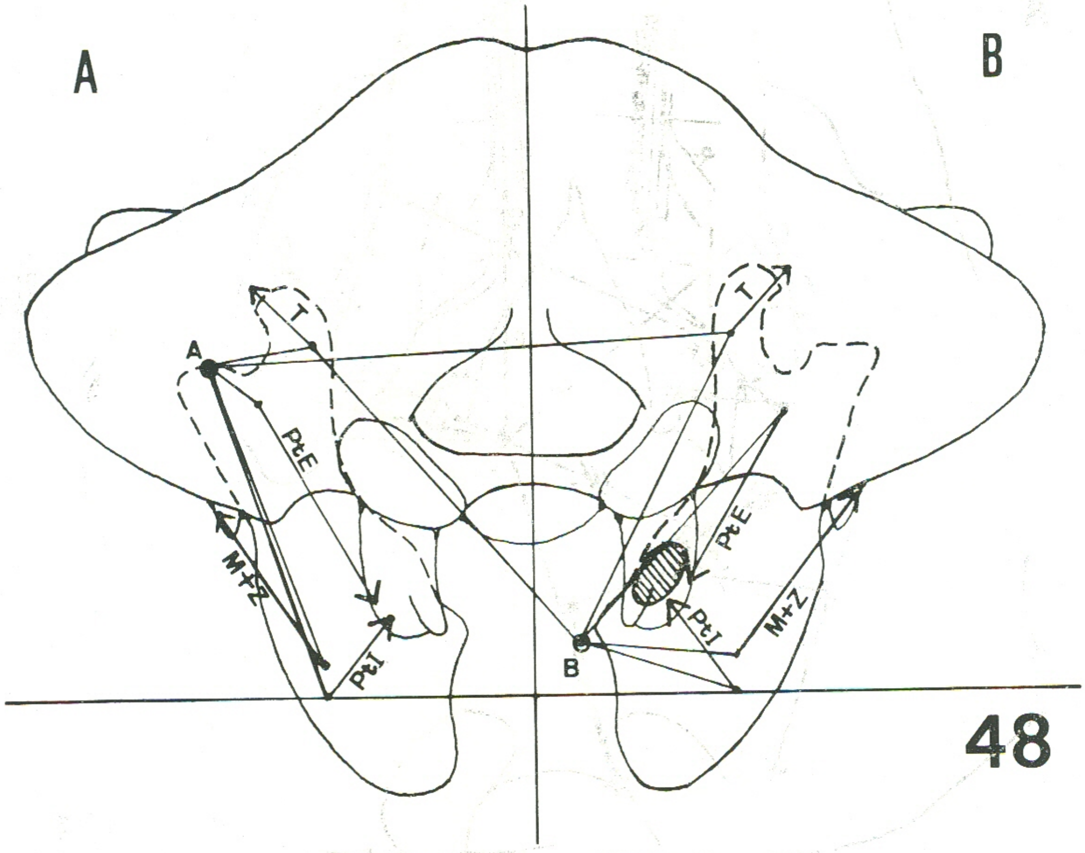


Fig. 48 — Posterior view of articulated skull and mandible, for analysis of orthal and transverse jaw movements. On each side, arrows connect functional midpoints of attachment fields of temporalis, masseter + zygomaticomandibularis, pterygoideus internus, and pterygoideus externus and show average directions of pull. On side A, effort lever arms are drawn to the temporal condyle (A) as fulcrum; on side B, to a point (B) ventromedial to pterygoid process, here considered the center of rotation in transverse chewing. Effort lever arms are shown for both ipsilateral and contralateral temporales. Bertical and horizontal lines are used to measure muscles' angles of pull and estimate F_X (see text). Cross-hatched area is pterygoid-mandibular articular surface. Dashed lines show outlines of concealed ascending rami of mandible.

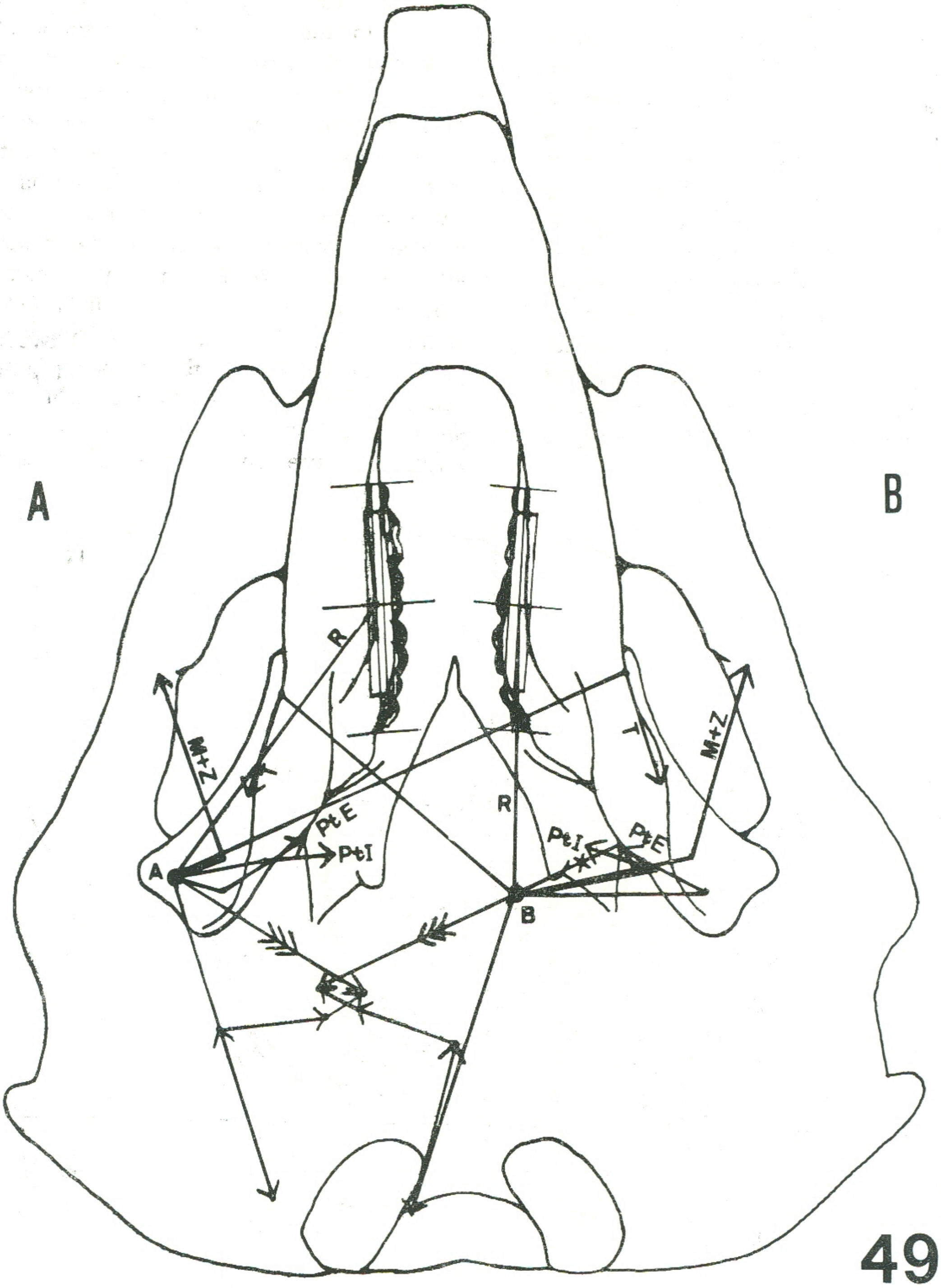


Fig. 49. — Ventral view of articulated skull and mandible, illustrating two hypotheses of transverse jaw movement. On each side, arrows connect functional midpoints of attachment fields of temporalis, masseter + zygomaticomandibularis, pterygoideus internus, and pterygoideus externus and show average directions of pull. On side A, resistance (R) and effort lever arms are drawn to the temporal condyle (A) as the hypothetical fulcrum; on side B, to a point (B) posteromedial to pterygoid process. In lower part of figure, effort vectors, proportioned to muscle weights, for each of the two hypothetical lever systems are summed, with origins at the fulcra; unresolved translational force vectors are marked by feathered arrows, and an extension through point B of the vector on side B is marked by X. Force vector resolutions for individual muscle groups not shown.

TABLE 7. Jaw-closing useful power (efficiency) data for juvenile Trichechus inunguis, calculated for molar resistance region and orthal motion with fulcrum at pterygoid-mandibular joint. Pterygoideus internus included for comparison though it does not act as an adductor; see Fig. 50.

Muscle Mass (M) as %	E	% total adductor power (comp. w/ muscle mass)	Change in % from direct muscle proportion %	Proportionate change
INPA-PB 6:				
Mt =51.4	Et =14.8	86.5	+35.1	68% gain
Mm =25.5	Em = 0.0	0.0	—25.5	100% loss
Mpti =14.7	Epti = 1.3	7.6	— 7.1	48% loss
Mpte= 8.4	Epte= 1.0	5.8	— 2.6	31% loss
Totals 100.0	17.1	99.9		
INPA-PB 9:				
Mt =53.6	Et =13.2	86.3	+32.7	61% gain
Mm =25.4	Em = 0.0	0.0	—25.4	100% loss
Mpti =13.8	Epti = 1.2	7.8	— 6.0	43% loss
Mpte= 7.1	Epte= 0.9	5.9	— 1.2	17% loss
Totals 99.9	15.3	100.0		
INPA-PB 169:				
Mt =50.9	Et =12.5	85.0	+34.1	67% gain
Mm =26.7	Em = 0.0	0.0	—26.7	100% loss
Mpti =15.8	Epti = 1.4	9.5	— 6.3	40% loss
Mpte= 6.7	Epte= 0.8	5.4	— 1.3	19% loss
Totals 100.1	14.7	99.9		

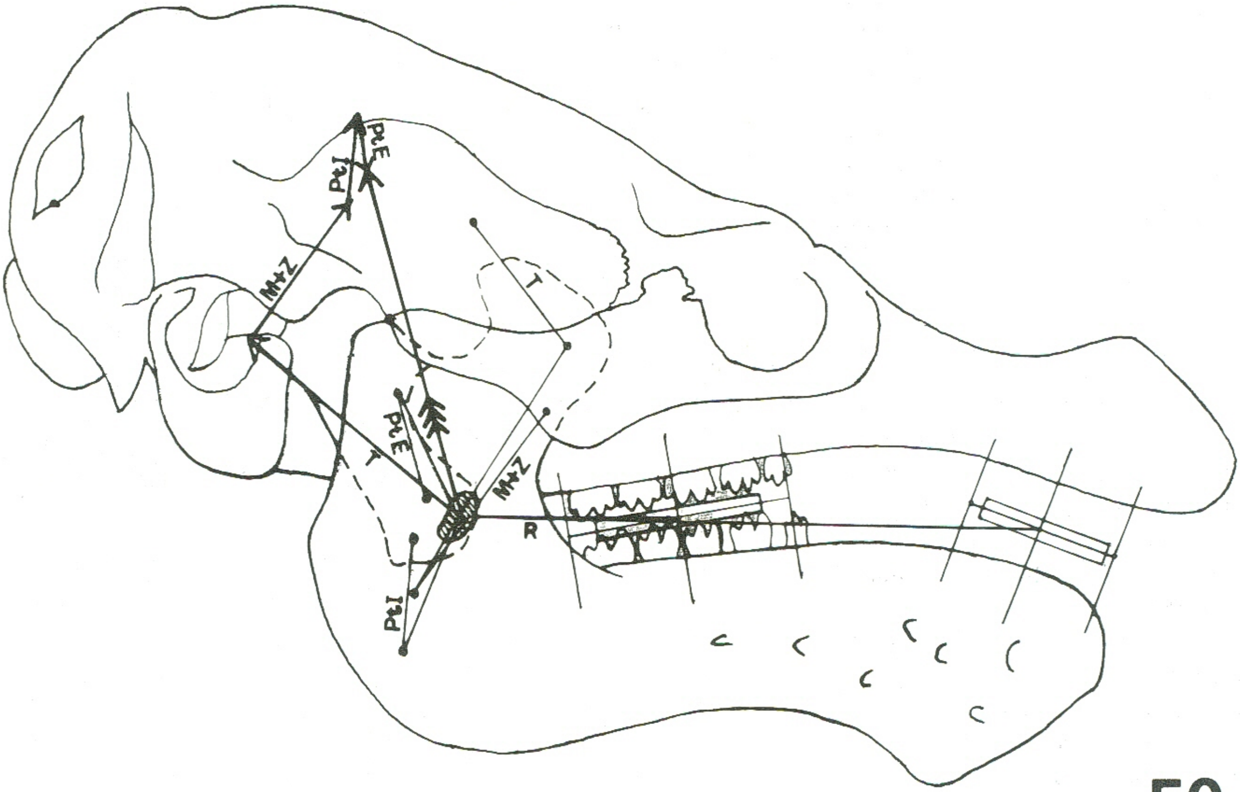
used by Gingerich). It is also in accord with the fact that the initially-formed wear facets on the teeth, especially as seen in juvenile animals, lie in posterodorsad-sloping planes, indicating a large amount of jaw movement in this direction.

This appears to be the most likely mechanism of orthal motion, in which the temporalis provides the main adductive force and the pterygoideus externus acts to slide the jaw joint downward and forward on the return stroke. The pterygoideus internus and masseter-zygomaticomandibularis seem to play no role, unless the latter serve to rotate the mandible about the condyle at the beginning of a bite. The anterad lengthening of the coronoid process seen in *Trichechus* in contrast to other sirenians is advantageous to the temporalis under any of the above models, and is evidently an adjustment to the unusual length of the tooth row in this genus.

It is in transverse chewing that the masseter and pterygoideus internus probably play their principal roles, though in subordination to the contralateral temporalis, as described above. The pterygoideus internus is probably much more efficient than Table 6 would suggest, as it can to some degree act directly (anteromediad) against the food, in a manner analogous to the temporalis in orthal motion. The contralateral temporalis adds to this a larger posteromediad component. It is questionable whether the posteromediad resultant can be completely absorbed by the food; if not, it would be resisted at the pterygoid-mandibular joint as demonstrated above, and this seems to be the best explanation of the massive pterygoid process.

These hypotheses of sirenian jaw mechanics need to be tested further by examination of the orientation of wear surfaces on the teeth, in order to independently locate the center of mandibular rotation (cf. Kay and Hiiemae, 1974). For determining its location in the horizontal plane, at least, *Dugong* might be an ideal animal, as its teeth have flat occlusal surfaces marked by striations which should be concentric to the center of rotation. The entire picture also needs to be reevaluated in more detail than space here permits, and in less artificially simplified fashion; in particular, the role of the zygomaticomandibularis, which is undoubtedly distinct from that of the masseter, needs to be clarified. The present results should be regarded as no more than a first approximation.

How, then, do the jaw mechanics of the manatee compare with those of the other mammals described by Turnbull (1970)? I had earlier (Domning, 1977a) supposed that *Dugong* and other sirenians would fit into the "ungulate-grinding" category (Specialized Group II) of Turnbull. This is now seen, at least for *Trichechus*, to be very far from the truth. In terms of adductor muscle mass (M), the manatee is most comparable to the forms of Turnbull's Generalized Group, especially the primates (including *Homo*). In terms of useful power (E), however, it more resembles the carnivores (Specialized Group I), and indeed is more extreme in this direction than any carnivore because of the negligible contribution of the pterygoidei to orthal jaw-closing about the condyle. Clearly the Sirenia must be placed in a separate, specialized group of their own, which can be characterized as



50

Fig. 50 — Lateral view of skull and mandible, illustrating effort and resistance lever arms of jaw muscles and resultant forces for molar resistance region in orthal movement when fulcrum is considered to lie at pterygoid-mandibular articulation (cross-hatched area). Summed vectors (open-headed arrows) shown are unresolved forces produced at fulcrum by each muscle group, determined as in Figs. 45-47; feathered arrow marks resultant vector of total unresolved force at fulcrum.

follows: the temporalis is very large (constituting more than half of the adductor muscle mass), and gains significantly in useful power over the other muscles; the masseter and zygomaticomandibularis are well-developed, and important both in orthal chewing when the condylar joint acts as fulcrum, and in transverse chewing; the pterygoideus internus is probably important mainly in transverse chewing; the pterygoideus externus serves not as an adductor but more probably in an auxiliary role, such as in recovery strokes; a pterygoid-mandibular articulation is developed and probably of major importance in transverse chewing, where it serves to absorb otherwise unresolved resultant forces.

NECK MUSCLES

(Note: Wet weights of some neck, limb, and other muscles which were taken in the course of this study are presented in Table 8; however, vector analysis of these muscle systems will not be attempted at this time).

TABLE 8. Weights of some muscles of juvenile Trichechus inunguis **(grams). Left and right sides combined; asterisk (*) marks weights which pertain to only one side; e = estimated.**

Muscle	INPA-PB 6	INPA-PB 9
Platysma pars jugularis + cutaneus trunci	523.2	
Sphincter colli profundus pars auris	115.5	
Mandibularis	2.6	
Mentalis	4.7	
Sternohyoideus	2.9e	
Thyrohyoideus	0.7e	
Geniohyoideus	2.6	
Splenius	19.2	
Semispinalis capitis	50.3	
Semispinalis	139.8	
Longissimus dorsi	353.0	
Iliocostalis dorsi	50.0	
Rectus capitis dorsalis intermedius	10.3e	
Rectus capitis dorsalis minor	6.5e	
Rectus capitis lateralis	7.0	
Rectus capitis ventralis	1.0	
Sternothyroideus	3.3e	
Scalenus (superficial)	7.2	
Scalenus (deep)	1.1	
Longus capitis	6.8	
Longus colli	2.3	
Intercostales externi and interni	175.0	
Intercartilaginei	2.4	
Sternocostalis	2.5	
Diaphragm	89.7	
Obliqui abdominis externus and internus	73.4	
Transversus abdominis	82.6	
Rectus abdominis	79.2	
Intertransversarius coccygeus	40.6	
Sacrococcygeus ventralis lateralis	75.8e	
Sacrococcygeus ventralis medialis	239.5e	
Trapezius	36.6	
Rhomboideus	6.9*	
Serratus magnus	20.7*	
Latissimus dorsi	22.6	
Pectoralis major	35.2	25.0*
Pectoralis minor	12.6	
Deltoideus	16.1	13.6*
Supraspinatus	28.3	44.0
Infraspinatus	23.0	26.4
Subscapularis	52.0	60.8
Teres major	19.9	16.2*
Coracobrachialis	6.2	6.8
Biceps brachii	0.7	1.9
Triceps brachii, long head	9.0	11.8
Triceps brachii, lateral head	4.1	4.6
Triceps brachii, medial head	3.5	5.0
Brachialis	9.6	12.3
Brachioradialis	2.4	1.9
Extensor carpi radialis	1.9	1.7
Extensor digitorum communis	2.8	3.5
Extensor digiti quinti	1.7	1.4
Extensor carpi ulnaris	1.5	1.9
Extensor pollicis	1.8	2.3
Flexor carpi radialis	2.3	1.8
Palmaris longus		0.1*
Flexor digitorum	6.2	8.3
Flexor carpi ulnaris	5.7	3.7*
Abductor digiti quinti	1.8	0.3*
Flexor digiti quinti brevis	0.7	0.2*
Flexor pollicis brevis	0.2	0.1*
Lumbricalis III	0.7	0.3*
Lumbricalis IV	1.3	0.4*
Lumbricalis V	1.8	1.0*
Interosseus II	1.2	0.5*
Interosseus III	1.1	0.6*
Interosseus IV	1.1	0.8*
Interosseus V	0.4	0.4*

The Amazonian manatee is characterized by several striking features of the occipital region of the skull. There is a well-developed sigmoid ridge on the squamosal, as in other living and in primitive sirenians. The supraoccipital, however, is swollen to a unique degree, so that its posterior surface is roughly perpendicular to the dorsal side of the cranium, in contrast to the 50°-60° parietal-supraoccipital angles seen in other manatees. A distinct, rugose and posteriorly overhanging flange is developed on the dorsolateral border of the exoccipital, and shallow fossae just dorsal to the occipital condyles are often present on one or both sides. The former feature is developed, though to a much lesser degree, in some *T. senegalensis,* and not at all in *T. manatus;* while the latter feature is not seen in other manatees although it is better developed in *Dugong* than in *T. inunguis.* The development of supracondylar fossae, which receive the dorsal edges of the atlas cotyles at maximum extension of the atlantooccipital joint, is accompanied by a very slight but distinct anterodorsal and inward curvature of the dorsal part of the occipital condyle, whereas in sirenians lacking supracondylar fossae, such as *T. manatus,* the dorsal part of the condylar articular surface is nearly vertical and its dorsal edge stands well out from the surface of the occiput. (These differences are epitomized in the fact that an adult skull of *T. inunguis* can always be balanced upright on its occiput on a horizontal surface, in contrast to *T. manatus* and most *T. senegalensis.).*

The sigmoid ridge serves for the insertion of the splenius, which turns the head laterally. The supraoccipital bears the insertions of the semispinalis capitis and rectus capitis dorsalis muscles, levators of the head; its thickened condition in *T. inunguis* (seen in the adult but not the young) suggests an unusually high degree of activity of these muscles, producing stress on the bone surface and causing deposition of additional bone. The exoccipital border receives part of the insertion of the semispinalis capitis in *Dugong* (Domning, 1977a) and apparently in *T. manatus,* but in *T. inunguis* it receives the rectus capitis lateralis instead, as noted above. As the latter muscle arises only from the atlas, the extension of the neck produced by the muscles inserting on the exoccipital border has, in *T. inunguis,* become restricted to the atlantooccipital joint. The details of this joint just noted, together with the development of a prominent flange at the rectus lateralis insertion, further corroborate the emphasis on atlantooccipital extension which has evolved in *T. inunguis.* We may further note that the longissimus capitis, which turns the head laterally in *Dugong* and *T. manatus,* is completely absent in *T. inunguis.*

Elsewhere (Domning, 1977b) I have proposed the hypothesis that degree of rostral deflection in sirenians is inversely proportional to degree of specialization for feeding on floating or other near-surface vegetation. The living species of *Trichechus* provide an opportunity to test this hypothesis, as they differ significantly (at the .001 level) in degree of deflection of the rostrum from the palatal plane, with mean values of 38.2° in T. *manatus* (observed range = 24°-52°, N = 72), 30.4° in *T. inunguis* (OR = 25°-36°, N = 35), and 25.8° in *T. senegalensis* (OR = 15°-40°, N = 20).

Trichechus manatus is known to feed both in fresh water, where it takes plants located anywhere between the bottom and the surface (Hartman, 1971), and in salt water, where the available food plants are for the most part seagrasses growing on the bottom (Hartman, 1974). In the Amazon basin, where submerged aquatic plants are relatively scarce (Sioli, 1968), *T. inunguis* feeds predominantly on the "floating meadows" and other natant and near-surface vegetation (Pereira, 1944). The food habits of *T. senegalensis* are practically unknown, but should be more similar to those of *T. inunguis* than *T. manatus* due to its largely riverine habitat.

At least for the former two species, then, there appears to be a correlation between rostral deflection and location of principal food plants, *T. manatus* being quite generalized while *T. inunguis* is more specialized for surface-feeding. The condition of the neck joint and muscles clearly support this conclusion, indicating that the Amazonian manatee's adaptations to surface-feeding include habitual sharp bending upward of the head to reach floating plants. As *T. inunguis* normally assumes an oblique rather than horizontal attitude of the body axis while feeding at the surface (personal observation), the mechanism I proposed for elevation of the head in *Hydrodamalis,* involving reduced rather than increased extension of the atlantooccipital joint and permitting the body axis to remain horizontal (Domning, 1977b), need not be invoked here. It remains to be seen whether *T. senegalensis*, with a very slight rostral deflection but a more *manatus*-like occiput, is merely intermediate between the other two manatee species or is divergently specialized.

A large exoccipital flange is also found in the extinct *Hydrodamalis* and its Late Miocene ancestors, where I interpreted it, by analogy with *Dugong,* as an expanded attachment for the semispinalis capitis (Domning, 1977b). I went on to suggest that this was an adaptation for more effective lateral bending of the neck. In *Hydrodamalis,* however, unlike *T. inunguis,* the sigmoid ridge, and presumably the splenius, were very reduced, so that compensating modification of another muscle, such as the semispinalis capitis, to take over part of its function might be reasonably expected. If, however, the exoccipital flange in hydrodamalines was occupied by the rectus capitis lateralis as in *T. inunguis,* this would only strengthen my argument that *Hydrodamalis,* like *T. inunguis,* was specialized for surface-feeding. The fact that it lacked supracondylar fossae and a swollen supraoccipital, and the fact that supracondylar fossae are present in Dugong (a highly specialized bottom-feeder), only emphasize that adaptation to "surface-feeding" (for example) has proceeded in different ways in different lineages. Certainly the "surface-feeding" of *Hydrodamalis,* a large animal in a high-energy environment, imposed different functional requirements than that of *T. inunguis,* a small animal feeding in quiet waters. Specialization of sirenians to such a nich is a complex phenomenon in which the roles and relative importance of the anatomical modifications are not yet fully understood.

FORELIMB MUSCLES

Like other anatomical and functional differences between the species of *Trichechus,* the differences seen in the forelimb have not received adequate attention, although one major study (Bahrdt, 1933) has documented some of the skeletal and ontogenetic aspects. It has been recognized (*e.g.,* by Hatt, 1934) that the forelimbs (particularly the metacarpals and phalanges) of *T. inunguis* are proportionately longer than in the other species, and of course lack nails. The presence of a bicipital groove on the humerus of *T. inunguis* was demonstrated long ago by Cuvier (1809: pl. 19: fig. 17; the specimen illustrated, though said to be "from Cayenne", has been recognized to be *T. inunguis* at least since Stannius, 1845: 25-26) This, however, was forgotten by later writers *e.g.,* Howell, 1930: 228; Simpson, 1932: 490; Domning, 1977a: 31), who apparently assumed from the conditions in *T. manatus* that all manatees lack a bicipital groove. Bahrdt (1933: 200, 202, 204) noted that it is present though very weakly developed in *T. senegalensis,* and, moreover, even observed it in a 13.6 cm embryo of *T. manatus* (1933: 198), which suggests that its absence in adults is a derived condition. The possible significance of these differences, however, has never been explored.

The contrast in proportions of limb segments between *T. inunguis* and the other species is startling; compare the illustrations of *T. inunguis* and *T. senegalensis* in figs. 9 and 11 of Bahrdt (1933). Even in these immature specimens, the digits of *T. inunguis* are strikingly elongated and make the limb truly finlike, bearing little resemblance to the stubby fingers of *T. senegalensis* (likewise *T. manatus).* The humerus and forearm, respectively, in this *T. inunguis* make up 31% and 22% of the total limb length, compared to 39% and 27% in the *T. senegalensis* (Bahrdt, 1933: 269). As the latter animal was smaller and presumably younger than the former, and as the proximal limb segments increase in relative length during growth (Bahrdt, 1933:206), the difference might be even greater at maturity.

If an analogy can be made with terrestrial mammals, the long distal elements of *T. inunguis* certainly give its flipper a "cursorial" appearance compared to the more "gravigrade" limb proportions of the other species. But we need not go so far afield; Howell (1930: 232) has shown that in aquatic mammals in general the proximal limb segments tend to become shortened with increasing aquatic specialization. If we then take as a working hypothesis the proposition that the flipper of *T. inunguis* is in some sense a more refined swmming organ than those of other manatees, we can try to interpret the other observed differences in this light.

In addition to the bicipital groove, the proximal humerus of *T. inunguis* is distinguished by a greater tuberosity which extends well proximad of the head of the humerus. This process provides the supraspinatus, the principal extensor of the forelimb, with a much more effective lever arm than it has, for example, in *T. manatus,* where the greater tuberosity hardly extends proximad of the head. Moreover, the insertion of the infraspinatus has become elongated proximomediad to a point almost or quite level with the proximal side of the head and almost reaching the supraspinatus insertion, thereby giving the infraspinatus additional advantage in extending the humerus as well as rotating it laterally. All this would lead us to expect strong movements of extension at the shoulder joint of *T. inunguis*. Coupled with the drag produced by the elongated manus, this would tend in turn to force passive extension of the elbow. It is, however, precisely in *T. inunguis* that we find the peculiar accessory tendon of the biceps, whose apparent action as a "check ligament" to resist extension of the elbow has already been noted. Such forceful extensional movements would most likely be recovery strokes, made with the flipper feathered, and alternating with backward propulsive strokes made with the elbow abducted, the humerus being simultaneously adducted, elevated (flexed), and medially rotated. The muscular portion of the biceps, stretched over the bicipital groove during this power stroke, might aid in quickening the recovery stroke by its elasticity.

In *T. manatus*, on the other hand, these features are lacking, so we might expect extension of its shoulder to be less forceful, though why the bicipital groove should be lost is unclear; perhaps the biceps has become specialized as an adductor.

Thus the conditions in *T. inunguis* result in a more oarlike flipper with its fulcrum at the shoulder joint and with extra stiffening to counter drag on recovery strokes; and this is clearly a step in the direction of greater aquatic specialization. Why *T. inunguis* should use the flippers for such forward propulsion more than the other species, however, is far from clear. One possibility is that *T. inunguis,* in a habitat with few bottom plants, seldom has occasion to travel for any distance in close proximity to the bottom, or, consequently, to use the flippers for traction on the bottom; accordingly its flippers have adapted to a more "pelagic" life. *T. manatus,* on the other hand, may more frequently propel itself by pushing against the bottom, as Hartman (1971) has described. The difference may thus lie not in the degree of use of the flippers for propulsion, but in the absence or presence of a solid substrate. This could explain both the stubby, "gravigrade" digits and the retention of nails in *T. manatus* and *T. senegalensis*, the latter structures serving to protect the edge of the flipper against abrasion; it might also call for the extra strength in adduction that the specialized biceps of *T. manatus* may provide. This hypothesis, of course, suffers from the dearth of knowledge of the ecology of *T. senegalensis,* as well as the fact that nails are lacking in *Dugong*, which travels extensively along the bottom in feeding.

In *Dugong,* we find a shoulder structure very different from that of the manatees, and, as I suggested previously (Domning, 1977a: 31), the dugong has apparently evolved a strong emphasis on parasagittal movements of the limb. The long insertion and separate cephalic portion of the trapezius and the peculiar platysma pars scapularis, together with the rhomboideus and divided serratus magnus, seem well adapted to rotate the elongated and falciform scapula and scapular cartilage on the side of the rib cage. Apart from the extra leverage of the trapezius' attachment to the elongated acromion process, *Trichechus* has no such specializations for scapular rotation; even its scapular cartilage is much abbreviated, despite the similarity in shape of the scapula itself to that of *Dugong.* The olecranon of *Dugong* is much better developed than that of *Trichechus*, giving the triceps much greater leverage in extending the elbow. The biceps is large and muscular, clearly playing an active rather than a passive role in movements of the limb. The much more distal insertion of the pectoralis minor makes it an adductor rather than an abductor and gives it a role in forward propulsion. The latissimus dorsi, by inserting with the pectorales rather than the teres major, may be able to rotate the humerus medially through a greater arc during a propulsive stroke; perhaps more importantly, its origin from the cutaneus trunci rather than the ribs may extend its effective fiber length over much of the length of the trunk, giving it a tremendous fore-and-aft excursion at its insertion. The manatee, on the other hand, may be better adapted for abductive and adductive movements; its elongate acromion porcess may aid the deltoideus in its role as an abductor and possibly an extensor, and the broadened manubrium suggests an increase in the adductive power of the pectoralis major.

Thus it is clear that the dugong is better equipped than the manatees for fore-and-aft sweeping movements of the whole limb, including the scapula. This accords with its greater degree of overall specialization for swimming (Domning, 1977a: 28-30). Its limb proportions, however, are more comparable to those of *T. senegalensis* and *T. manatus* than *T. inunguis*, the humerus and radius respectively forming 36% and 24% of the forelimb length (measured from photograph of adult specimen in Kaiser, 1974: pl. 60); so it is also clear that not all the factors influencing the form of the sirenian flipper have yet been taken into account. The need for systematic observations on the behavior and locomotion of live sirenians, in both field and laboratory, remains as great as ever; without such data the questions posed by the anatomist will remain unanswered.