

Kinematics and Functional Morphology of Aquatic Feeding in Australian Snake-Necked Turtles (Pleurodira; *Chelodina*)

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ABSTRACT Head kinematics during aquatic feeding of the Australian long-necked turtle (*Chelodina*) were studied by means of high speed video recordings. Buccal expansion was assessed by calculation of elliptical cross-sectional surfaces. Further, displacements of head, carapace, and prey in the earth bound frame, of the prey relative to the center of the gape, and of the head relative to the carapace were determined. Rates of change (velocities) of all these variables were calculated. These data are combined with information on the osteology and myology of the head. The robust development of the large hyobranchial apparatus, the massive intercornuatus muscle, and the presence of the branchiosquamosus muscle were related to aquatic feeding skills. Head kinematics are variable in amplitude and relative timing, but proceed always in a rostrocaudal sequence. According to their effect on the prey, two components are distinguished in the process of expansion. The first compensates for head/body movements (compensatory suction). The second causes distinct acceleration of water and prey (inertial suction). The latter component is mainly driven by the abduction of the second branchial arch. In spite of largely different structural solutions, optimal feeding conditions as deduced for suction in feeding fishes are also employed by *Chelodina*. This further promotes the assumption that hydrodynamics constrain evolutive solutions for aquatic feeding. *J. Morphol.* 233:113–125, 1997. © 1997 Wiley-Liss, Inc.

Contrary to fishes and salamanders, aquatic feeding in turtles is poorly studied to date (for an overview of the literature on fish feeding see Aerts, '90, '91, '92; Aerts and De Vree, '93; for salamander feeding see Lauder and Reilly, '94). Apart from some general and qualitative descriptions (e.g., Belkin and Gans, '68; Bramble, '73, '78; Lauder, '85; Parmenter, '76; Weisgram, '82, '85), only one paper by Lauder and Prendergast ('92) presents quantitative data focusing on the kinematics of aquatic feeding in turtles. The latter authors studied the cryptodiran snapping turtle *Chelydra serpentina*. The paper concentrates upon differences and similarities in kinematic patterns when feeding on distinct prey types and compares the obtained results with those formerly found for fishes and salamanders. Bels and Renous ('91) give preliminary quantitative data about functional and behavioral characteristics of the feeding apparatus and its relationship with the locomotor apparatus in marine turtles.

The present paper is the first to deal with the feeding kinematics of a pleurodiran turtle: the long-necked Australian *Chelodina longicollis*. General strike kinematics of head, body, and prey (displacements and velocities) and the kinematics of the head parts elicited by aquatic feeding on slowly sinking food items are determined (3D) and integrated with the morphology of the hyobranchial apparatus. Kinematics and morphology are discussed in the context of basic principles of aquatic feeding.

MATERIALS AND METHODS

For two adult specimens of *Chelodina longicollis* (specimen I: female, 0.75 kg, 0.18 m carapace length, 0.14 m neck length; specimen II: male, 0.53 kg, 0.15 m carapace length, 0.12 m neck length) aquatic feeding trials were recorded by means of a NAC-

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1000 high speed video system (500 frames/s; illumination: TRILITE, Cool Light Co., Inc., Hollywood, CA). The animals were obtained with the help of the Antwerp Zoo, and were housed in a glass aquaterrarium on a 12 h light/dark cycle. The water temperature was kept at 28°C. During the experiments unrestrained turtles were feeding on slowly sinking pieces of meat above a mirror placed at an angle of 45°. This allowed simultaneous registration of lateral and ventral views.

Forty-eight relevant points (Fig. 1) were digitized frame by frame using a NAC X-Y coordinator. Thus obtained numerical data were combined into 3D-coordinates. These were scaled and transformed to an orthogonal frame of reference as presented in Figure 2. The origin of this frame coincides with the center of the gape just prior (2 ms) to the onset of fast mouth expansion. Orientation and direction of the X-axis are then defined by the position of the center of the gape when the mouth is closed again. In this way changing X-coordinates point at displacements parallel to the strike direction.

For the quantitative part of the present study eight feeding sequences of specimen I were analyzed in detail. They were selected on the basis of their quality: horizontal strike, in a plane perpendicular to the camera. Only the points marked by black dots on Figure 1 were retained in the analysis. Displacements in direction of prey, snout, and carapace during the strike (Fig. 1, points A, B, C) were considered in a fixed frame of

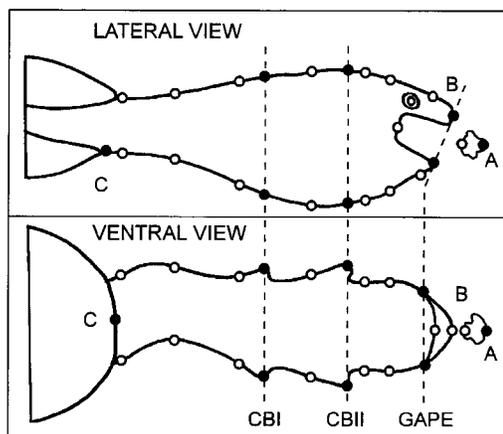


Fig. 1. *C. longicollis*. Schematic representation of a video frame. Dots mark the digitized points (for details see Materials and Methods).

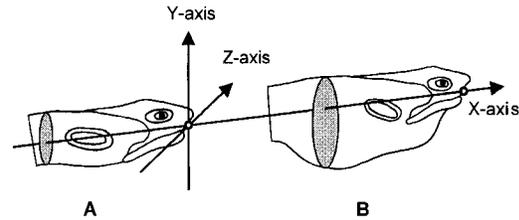


Fig. 2. *C. longicollis*. Definition of the turtle bound frame of reference (tbfr). Positions of the head just prior to the onset of mouth opening (A) and just after mouth closure (B). Stippled areas illustrate the elliptical cross-sectional surface used to assess buccal expansion (for details see Materials and Methods).

reference. Prey movements relative to the center of the gape, and gape movements relative to the carapace were also deduced. Further, height and width of the gape and of the head at the level of the first and second ceratobranchials (CBI, CBII) were calculated for each frame. These values were used to determine the corresponding "elliptical" cross-sectional surface (Fig. 2). Changing surfaces were considered a measure for the local volume increase/decrease of the buccal cavity (cf. Drost and Van Den Boogaert, '86). First and second derivatives to time were calculated for all eight variables after they had passed a Fourier filter on the second derivative (i.e., smooth acceleration profiles; see Wood, '82; routines supplied by G.A. Wood, Department of Movement Studies, University of Western Australia). One of these eight sequences (trial 3 in Table 2) is used to describe and to explain which kinematic variables are used to characterize the strikes (see Table 1). For a number of additional strikes ($n = 12$) only the maximal linear accelerations of the head were determined.

A preserved adult male specimen of *C. longicollis* (0.15 m carapace length) was dissected and stained to characterize all jaw and hyobranchial muscles (Bock and Shear, '72). For discussion, this information was compared with data obtained from dissecting a preserved adult specimen of the red-eared slider *Trachemys scripta* (Cryptodira, 0.25 m carapace length). Drawings were made of all stages of the dissection using a Wild M5 dissecting microscope, provided with a camera lucida.

Skeletal features are deduced from the prepared skull of a large specimen of *Chelodina* (carapace length: 0.31 m). Morphological findings were compared with data avail-

TABLE 1. *C. longicollis*: Mean and standard deviation of the kinematic variables¹

Kinematic variable	Mean	SD	N
Maximal gape surface (cm ²)	2.07	0.36	8
Delay [max. V _{GAP} - max. V _{CBI}] (ms)	20	7	8
Delay [max. V _{CBI} - max. V _{CBII}] (ms)	11	3	8
Duration total gape cycle (ms)	110	15	8
max. V _{PREY} in EBFR (m/s)	-0.78	-0.40	8
max. V _{CARAPACE} (m/s)	0.071	0.054	8
max. V _{NECK EXTENSION} (m/s)	0.240	0.126	8

¹The substantial variation in feeding kinematics in spite of the single food type used is shown. N, number of trials considered; V, velocity; EBFR, earth bound frame of reference.

able in the literature on osteology (Gaffney, '72; Fürbringer, '22; Schumacher, '73) and myology (Gräper, '32; Gnanamuthu, '37; Kesteven, '44; Poglayen-Neuwall, '53; George and Shah, '54, '55; Schumacher, '54, '55a,b; Shah, '63) of the head of turtles.

RESULTS

General description of the strike

Figure 3 illustrates some representative outline drawings based on video frames of a typical strike by *C. longicollis*. Lateral and simultaneous dorsoventral views are shown. Frame numbers also refer to time in milliseconds. Prior to mouth opening, head and body slowly approach the food item (stalking) and no conspicuous volume changes of the buccal cavity can be observed. Sometimes a little pushing on the food item occurs (i.e., food slightly moves in the same direction as the head does). At frame 726, the mouth opens slowly, but volume increase further back in the mouth cavity is not obvious. The extension of the neck starts. The food particle remains stationary in the earth bound frame of reference. At frame 742, the fast mouth

opening is now succeeded by the expansion of the anterior part of the buccal cavity. The head protrudes fast, mainly as a result of neck extension. The prey is stationary relative to the fixed background. At frame 750, maximal gape is combined with maximal expansion of the anterior part of the buccal cavity. The more posterior region of the buccal cavity starts to expand. Forward head movements diminish. The food position is still unchanged. At frame 756, the head has stopped its fast forward movement. With the anterior part kept maximally extended, the posterior part of the buccal cavity forcefully expands. The food particle starts moving backward relative to the fixed background. At frame 766, the backward flow caused by the maximal expansion rate of the posterior part of the buccal cavity has already drawn the food item into the pharynx. The last two frames show that the mouth closes (mainly by depression of the head; cf. Lauder and Prendergast, '92) with the buccal cavity still largely expanded. The esophageal sack bulges to accommodate the backward flowing water (inertial effect; see Discussion).

Osteological correlates of the buccal expansion

The hyobranchial apparatus plays a very important role in buccal expansion (Fig. 4). In *Chelodina* this apparatus is strongly elongated and firmly ossified in comparison with other turtles (Fig. 4A; cf. Schumacher, '73). Even the second branchial arch (CBII), which is cartilaginous in most turtles (e.g., *T. scripta*; see Fig. 8), is completely ossified. Both ceratobranchials articulate via a hinge with the hyoid body. Figure 4B shows schematically two cross-sections through the hyoid apparatus (caudal view). The first one is at the level of the articulation between CBI-hyoid body. The second one is at the CBII-hyoid body articulation. Due to the different orientations of the rotation axes (solid lines, Fig. 4B), the first branchial arch (CBI) rotates laterodorsally (arrows, Fig. 4B), whereas CBII abducts lateroventrally relative to the hyoid body (arrows, Fig. 4B). The hypoglossum, usually a small, rather floppy plate ventral to the hyoid body, is very large and stiff (see Fig. 6B), and supports the entire buccal floor whenever the hyoid is depressed (Fig. 4A).

Kinematic analysis

The points retained from the video analysis (see Materials and Methods) permit accu-

TABLE 2. *C. longicollis*: Maximal linear head acceleration (m/s²) of 20 feeding strikes¹

Trial 1	7.56	Trial 11	17.43
Trial 2	18.23	Trial 12	8.29
Trial 3	9.71	Trial 13	39.59
Trial 4	14.72	Trial 14	31.30
Trial 5	18.95	Trial 15	15.63
Trial 6	25.06	Trial 16	14.83
Trial 7	17.52	Trial 17	44.23
Trial 8	19.98	Trial 18	18.23
Trial 9	15.33	Trial 19	22.30
Trial 10	20.92	Trial 20	38.16

¹The highly variable participation of neck extension in feeding is shown. Trials 1-10: specimen I; trials 11-20: specimen II. The strike illustrated in Figures 3 and 5 corresponds to trial 3.

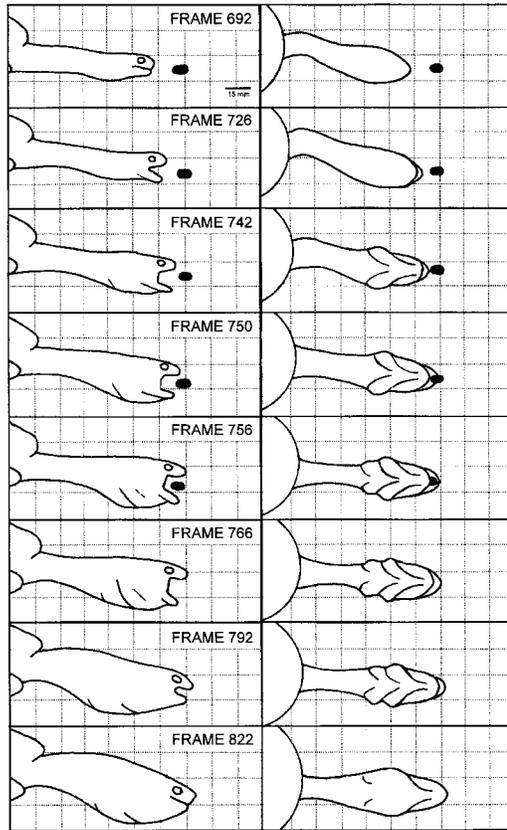


Fig. 3. *C. longicollis*. Outline drawing of lateral and ventral views of a representative strike. The frame numbers are indicated and refer to milliseconds (see text). Black dot: food item. The mesh size of the fixed background equals 1.5 cm.

rate assessment of the expansion movements (via the “elliptical cross section”) of the gape, CBI, and CBII. (Notice that for the latter two, the hyoid is also depressed.) Figure 5A,B shows the results (Fig. 5A: surface areas; Fig. 5B: rates of change of surface area) for the strike presented in Figure 3. Especially the velocity graphs document the occurrence of a rostrocaudal expansion wave. The expansion velocity peaks first, then for CBI and finally for CBII. This sequence of expansion events occurs for all analyzed trials, but the degree of maximal expansion and relative timing of the three components are very variable. For instance, maximal gape surface ranges from 1.6 and 2.7 cm². The delay between maximal gape velocity and maximal CBI velocity varies from 8 to 30 ms. The delay between CBI and CBII is

always smaller than the corresponding gape-CBI delay but still varies between 6 and 14 ms. The total gape cycle takes 90–132 ms.

Figure 5C,E shows linear displacements. Figure 5D,F gives velocities in strike direction for body and food item, respectively, in a fixed frame of reference [Fig. 5C,D, earth bound frame of reference (ebfr)] and in a frame moving with the turtle [Fig. 5E,F, turtle bound frame of reference (tbfr)]; see Materials and Methods]. In this particular sequence, the food item is slightly pushed forward by the oncoming expanding head (cf. increasing “prey” position; initial positive prey velocity). Apparently, this pushing can usually be avoided as it is not found for all sequences. However, the onset of backward movements of the food item in the earth bound frame always coincides with the start of the expansion of CBII, and the prey disappears in the gaping mouth when the expansion rate of CBII reaches its maximum. This usually coincides with maximal gape (cf. velocity profiles of Fig. 5B and Fig. 5D; gape profile crosses zero at the instance of prey capture). For some sequences, the maximal gape is maintained for a longer period until the prey is captured. Ultimate prey velocities induced by backward flow (i.e., in the earth bound frame) range from -0.41 to -1.24 m/s. Maximal velocities of the turtle (carapace; Fig. 5D) and of neck extension (neck; Fig. 5F) remain small compared to this, respectively, 0.006–0.15 and 0.03–0.48 m/s. Table 1 illustrates the means and standard deviations of the kinematic variables.

Myology

In view of the importance of ceratobranchial abduction for buccal expansion, the muscle groups of *Chelodina* which are associated with the first and second branchial arches are relatively large. The jaw and hyobranchial muscles are briefly described. Drawings are shown in Figure 6. Frequently used synonyms are added. Figure 7 shows a schematic representation of the most important jaw and hyobranchial muscles for buccal expansion. The thin *M. intermandibularis* (MIM; *M. mylohyoideus*) arises from the inner surface of the mandible. Posteriorly its fibers insert into a median raphe (Fig. 6A). Anteriorly the fibers insert at some distance of the midline on a tendinous plate (Fig. 6A). The *M. adductor mandibulae* complex (MAM) is powerful and consists of two

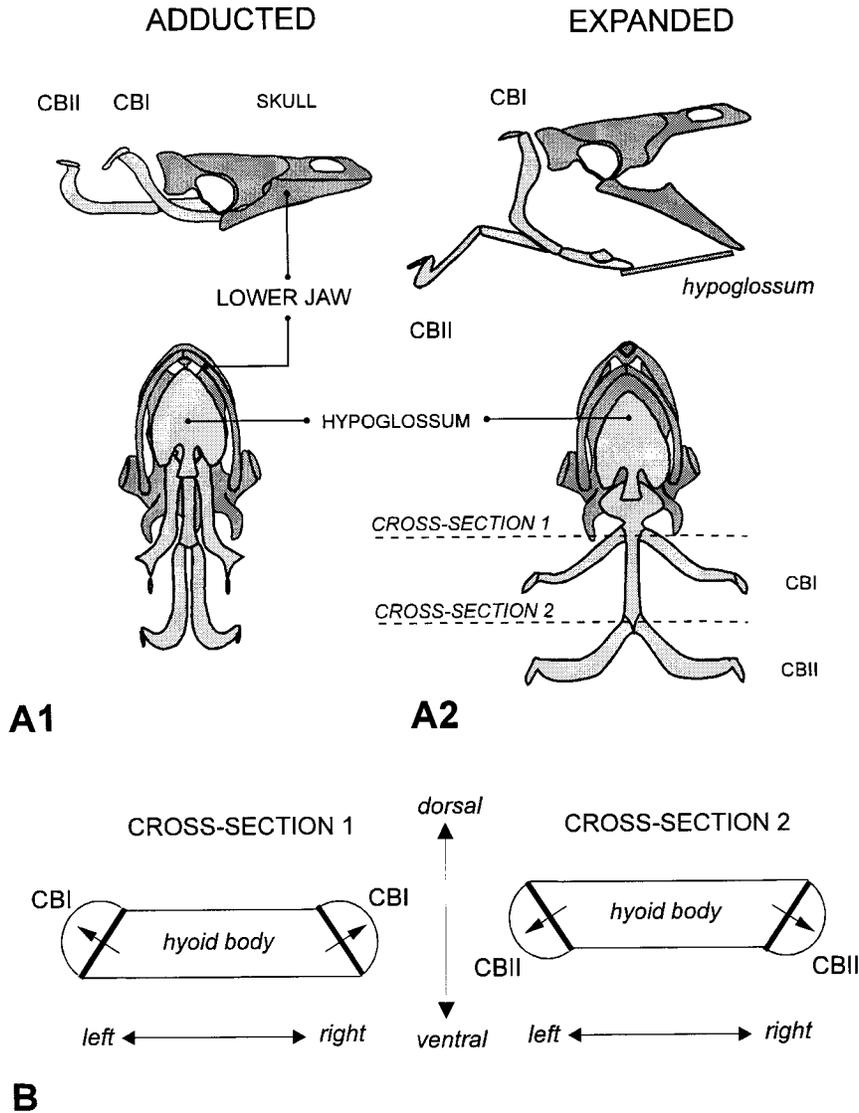


Fig. 4. **A1:** *C. longicollis*. Lateral and ventral views of the skull and hyobranchial apparatus in adducted situation (based on skeletal preparations). **A2:** Contribution to gape of skull and jaw motion as seen on high speed video images. **B:** Schematic representation of a caudal view on cross sections through the hyoid at the

level of the articulation between CBI-hyoid body (section 1, A2) and CBII-hyoid body (section 2, A2). Heavy solid lines indicate the orientation of the rotation axis. Arrows show the direction of movement of the ceratobranchial relative to the hyoid body.

main parts: the *M. adductor mandibulae externus* and the *M. adductor mandibulae internus*. The fibers of each part differ in direction and have separate insertions (for a more detailed description of this muscle complex see Schumacher, '55b). The *M. depressor mandibulae* (MDM) arises from the outer border of the squamosal and the posterior

border of the tympanic capsule and inserts on the posterior end (retroarticular process) of the lower jaw. The thin *M. sphincter colli* (MSC; *M. constrictor colli*) forms a superficial sheet on the neck. Its fibers run from the dorsal fascia and dorsomedial side of the neck to the ventral side of the neck forming a median raphe.

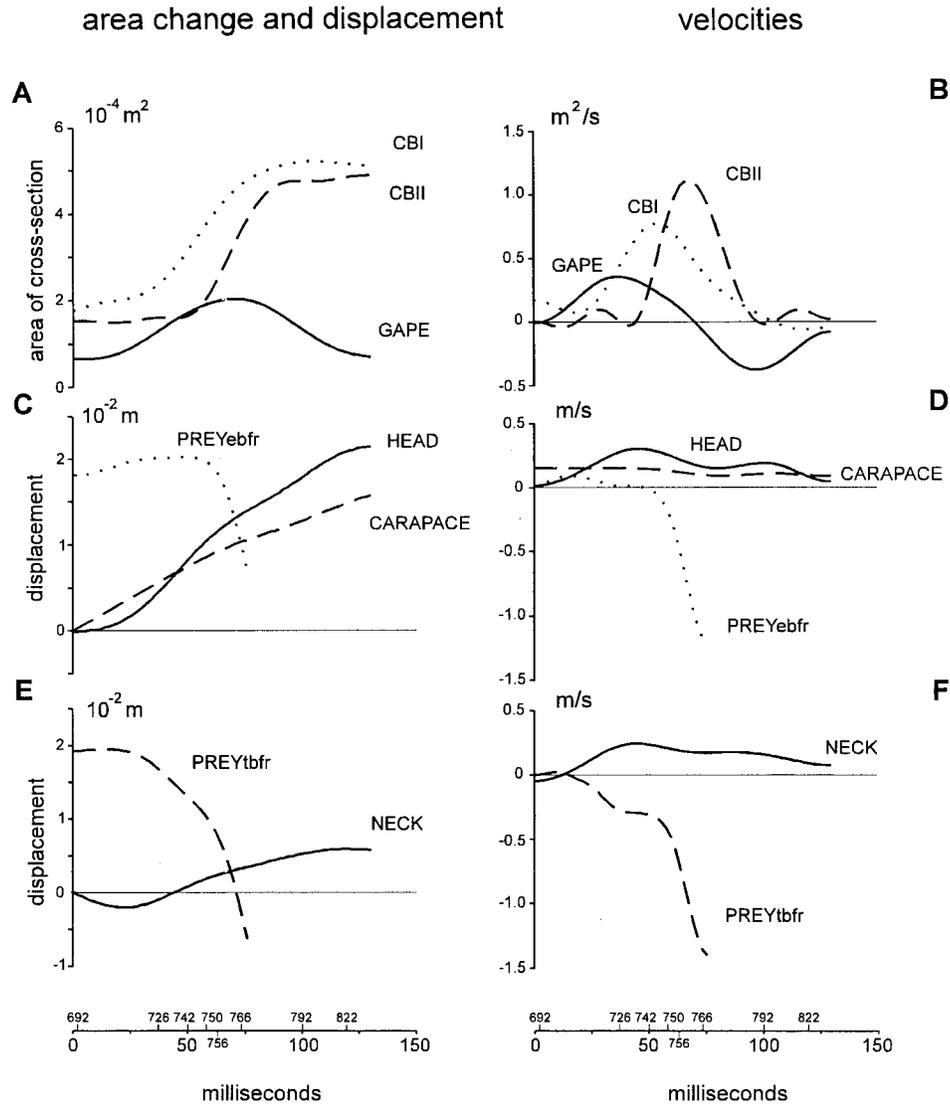


Fig. 5. *C. longicollis*. Kinematic profiles of the representative strike shown in Figure 3. Time scale (in milliseconds) is shown below the graphs (bold numbers). Zero time refers to the frame just before the mouth opens. The frame numbers shown in Figure 3 are also indicated on the time axis (small font number). **A**: Elliptical cross-sectional surface area at the level of the gape and first and second branchial arches (CBI, CBII). **B**: Rate of change of the surface areas represented in A. **C**: Displacement in strike direction of food item, head, and carapace

in the earth bound frame of reference (ebfr). **D**: Velocities in the earth bound frame of food item, head, and carapace. **E**: Displacement in strike direction of the food item relative to the center of the gape and of the head relative to the carapace. **F**: Velocities of the food item in the turtle bound frame of reference (tbfr) and of the head relative to the carapace. The curves describing displacement and velocity of the food item stop at the instant the food particle disappears into the buccal cavity. Total gape cycle takes about 75 ms.

The tongue of *Chelodina* contains very little intrinsic musculature. The small *M. genioglossus* (MGG) originates from the dentary and inserts on the lateral and ventral sides of the anterior part of the hyoid body.

The *M. geniopharyngeus* (MGH) arises from the inner side of the mandibular symphysis and inserts on the posterior part of the first branchial arch, ventrally of the hypoglossum and the *M. branchiohyoideus*.

The *M. hyoglossus* (MHG) originates from a connective tissue sheet between the hyoid and the lower jaw and inserts on the anterior part of the first branchial arch, adjacent to the articulation with the hyoid body. The *M. hypoglossohyoideus* (MHGH) is a special muscle associated with the hypoglossum (Fig. 6C1). It originates from the dorsal surface of the posterior part of the hypoglossum and inserts on the hyoid body at the level of the lingual process. The well-developed *M. branchiomandibularis* (MBM) originates on the posterior end of the mandible and inserts on the distal part of the first branchial arch. The *M. branchiohyoideus* (MBH) originates from the anterior lateral protuberances of the hyoid (anterior lateral process; Fürbringer, '22) and inserts along the entire length of the first branchial arch. It is the largest hyolingual muscle in *Chelodina*. The highly developed *M. intercornuatus* (MIC) attaches to the second branchial arch and has a ligamentous insertion on the proximal part of the first branchial arch. It is the only muscle running between both branchial arches. In *Chelodina*, the *M. branchiosquamosus* is a muscle running from the distal part of the first branchial arch to the back of the skull (squamosal). The muscle fibers originate from the fascia covering the proximal part of the MBM and inserting on the posterior border of the squamosal.

Two other muscles inserting on the hyoid originate more posteriorly in the neck or on the pectoral girdle. The very long, slender *M. coracohyoideus* (MCH; *M. rectus cervicis*) originates from the coracoid bone of the pectoral girdle and runs ventrally in the neck, closely adjacent to the trachea and connected to the esophagus. In the middle of the neck, the muscle fuses with the most ventral fibers of the *M. omohyoideus* and runs forward to insert mainly on the ventral side of the posterior part of the hyoid body. The *M. omohyoideus* (MOH; *M. constrictor hyoideus*) originates from the lateral process of the sixth cervical vertebra and runs obliquely forward. The ventral part of the muscle joins the MCH. The dorsal fibers insert on the mid and distal parts of the first branchial arch.

DISCUSSION

For feeding on aquatic prey with a density equivalent to that of water, animals have to generate a backward flow *relative* to the buccal cavity. Two components can contribute to this: 1) water and the food item may be accelerated backward by a sudden expan-

sion of the buccal cavity (i.e., inertial suction; continuity principle), and 2) the buccal cavity can be moved toward and/or over the food item; however, this is only possible whenever the displacements of the feeding animal give no significant food-directed momentum to the water [otherwise the induced flow inevitably carries the food item in the same direction as the head moves, thus hindering uptake; for a treatise on the physical necessity to eliminate the stagnation point at the mouth see Osse and Muller ('80) and Muller and Osse ('84)]. In fishes, this "pushing" can be avoided by swimming with both the mouth and the opercula wide opened and the gill arches expanded; this permits a nearly unrestrained flow of water and entrained food through the buccal cavity. To our knowledge, this technique only occurs in filter feeding fishes. A similar effect is obtained by protrusion of the mouth toward the prey; however, this mechanism only rarely produces most of the *relative* backward flow (cf. *Epibulus*: Westneat and Wainwright, '89; Westneat, '91).

Nevertheless, in the earth bound frame of reference most fishes do show displacements in the direction of the food item during the final phase of the feeding act. However, they compensate the risk for induction of adverse velocity to the food by highly coordinated expansion of the buccal, pharyngeal, and opercular cavities, simultaneously with body movements. (Ultimately, opening of the opercular slits may allow through-flow of some of the water.) In other words, the head cavities act as expanding reservoirs that ensure the inward flow *relative* to the moving gape (i.e., a moving sink; notice that ideally the water remains motionless in the earth bound frame). Without such relative flow, uptake of freely moving particles is hardly possible. If the rate of volumetric change of the head cavities is too low, the fish still pushes on the food particles (i.e., pushing; see Van Leeuwen, '84). If the rate of change is higher than strictly required to avoid pushing, water and entrained food are accelerated in the earth bound frame toward the moving gape (inertial suction). [In the latter case, part of the translation of the feeding animal derives from the suction act (i.e., momentum conservation theorem).]

Some studies (e.g., Lauder and Liem, '81; Lauder and Prendergast, '92; Norton and Brainerd, '93) only refer to suction when predator-directed prey movements in the

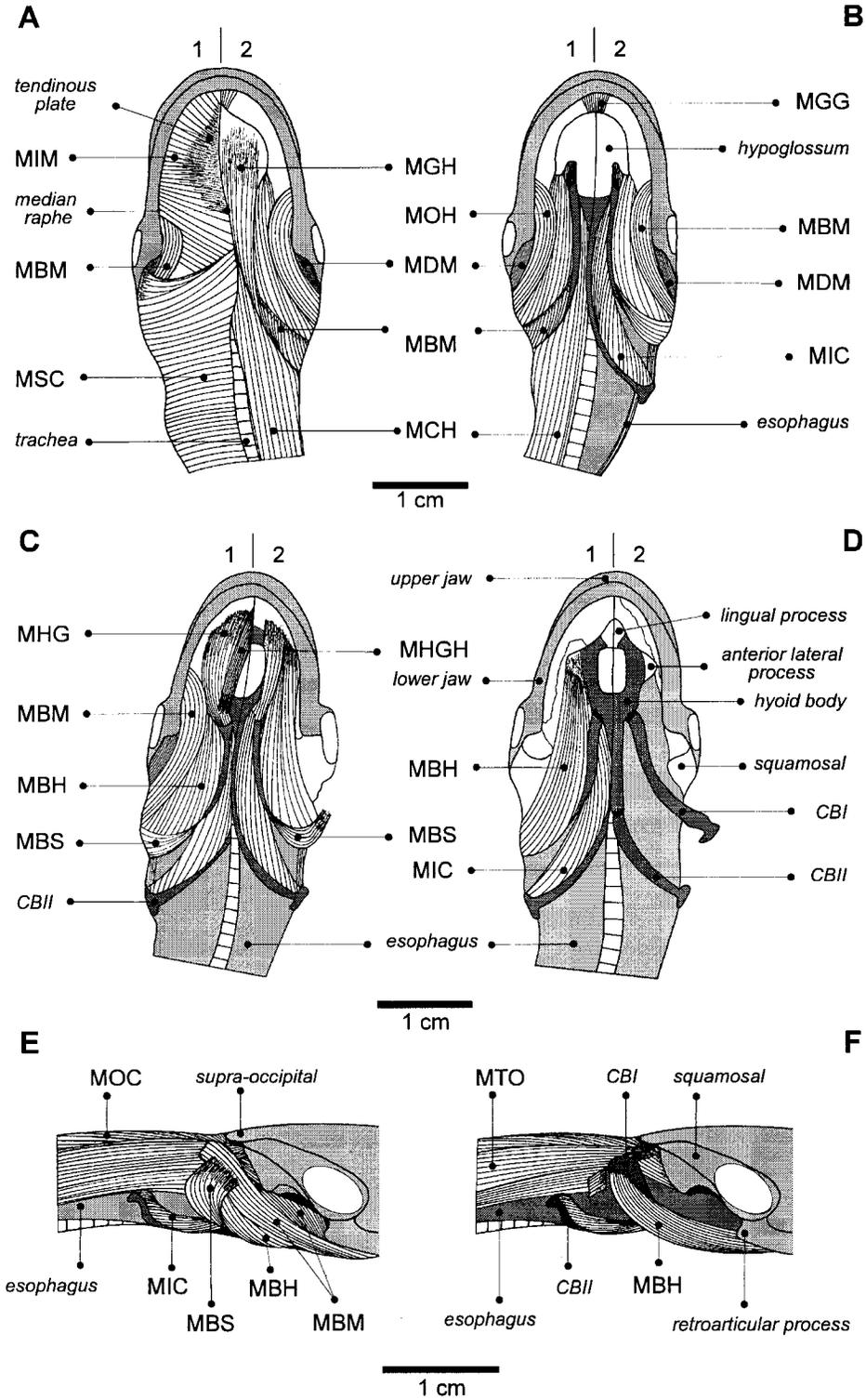


Figure 6

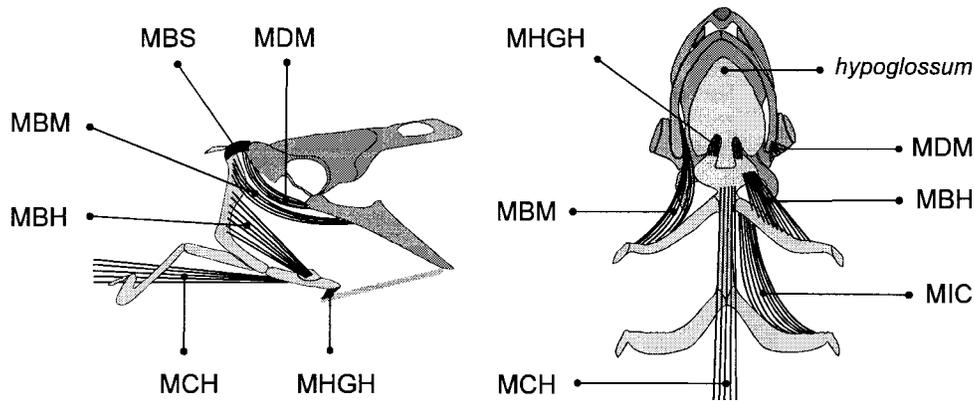


Fig. 7. *C. longicollis*. Schematic representation of the most important jaw and hyobranchial muscles for buccal expansion. See Figure 6 for abbreviations.

earth bound frame are obvious. If the predator moves toward the prey, these studies speak about a ram-feeding component. However, as no water can enter the gaping mouth unless the head cavities are expanded coincidentally, we prefer to call this “compensatory suction” (vs. inertial suction) and to reserve the term “ram-feeding” for feeding events with a nearly unrestrained through-flow (see above). Moreover, apparent lack of prey movement in an earth bound frame during any part of the strike does not necessarily imply the absence of inertial suction (i.e., backward acceleration of water in front of, or in the mouth). Muller et al. ('82; modeling and flow visualization) and Muller and Osse ('84; modeling and flow visualization), but also Lauder and Clark ('84; flow visualization), showed that the effect of inertial suction readily decays with distance in front of the gape. [For all these reasons we do not support the ram-suction-index as it is defined by Norton and Brainerd ('93).]

Turtles lack opercular slits. Therefore, movements of the head toward the prey must

be accompanied by compensatory suction in order to avoid pushing the prey. Yet, head movements are clearly important for feeding by long-necked species such as those of the genus *Chelodina*. These strike very fast, extending the neck from its initially flexed S-shape. Table 2 lists the linear head accelerations of the head as the neck is extended (range: 8–45 m/s^2).

Chelydra (Cryptodira) also shows fast neck extension during prey capture (Lauder and Prendergast, '92). Logically, compensatory expansion movements of jaw and hyobranchial apparatus are present. However, expansion movements in *Chelydra* apparently only contribute slightly to inertial suction as prey movements in the earth bound frame prior to engulfment are small (Lauder and Prendergast, '92). This contrasts with our results for *Chelodina*. In the latter species, prey movements are manifest in all strikes and ultimate prey velocities (i.e., at the instant of uptake) are largely determined by the inertial flow (see Results). For the strike represented in Figures 3 and 5, 75% of the ultimate prey velocity relative to the head derives from inertial suction (i.e., the velocity of the prey when entering the mouth as given in Fig. 5D amounts to 75% of this mentioned in Fig. 5F).

As in fishes, salamanders and *Chelydra* (e.g., Aerts, '91; Lauder and Reilly, '94; Lauder and Prendergast, '92), the head movements in *Chelodina* proceed in a rostro-caudal sequence (see Results). Basically, the kinematics of the strikes of *Chelydra* and *Chelodina* are similar. Yet, our results show

Fig. 6. *C. longicollis*. A–D: Ventral views of jaw and hyobranchial muscles. Left and right sides of each figure show a different level of the dissection (A1 most superficial level, after removal of the skin). E, F: Lateral views. MBH, M. branchiohyoideus; MBM, M. branchiomandibularis; MBS, M. branchiosquamosus; MCH, M. coracohyoideus; MDM, M. depressor mandibulae; MGG, M. genioglossus; MGH, M. geniohyoideus; MGH, M. hyoglossus; MHGH, M. hypoglossohyoideus; MIC, M. intercornuatus; MIM, M. intermandibularis; MOC, M. obliquus capitis; MOH, M. omohyoideus; MSC, M. sphincter colli; MTO, M. testis-occipitis.

that, in spite of the single food type used, the feeding kinematics of *Chelodina* vary substantially (Table 1). Amplitudes, relative timing of the expansion components, and velocities thereof change from one trial to the next (see Results; Table 1). Perhaps, peripheral feedback (most likely depending upon visual clues; cf. binocular vision and prey fixation prior to the strike) allows subtle modulation of the strike behavior. This contrasts with the behavior of *Chelydra*. Lauder and Prendergast ('92) give very small standard deviations of the kinematic variables in their table 1, revealing highly stereotyped kinematic patterns whenever using a single food. However, different food types elicit differences in head kinematics (Lauder and Prendergast, '92).

In *Chelodina*, the food displacements in the earth bound frame coincide with the onset of expansion of CBII (see Results; Fig. 5B–D). This suggests that the buccal expansion could be split into two components: jaw and hyoid depression and CBI abduction compensate for the forward movement of the head, whereas the inertial suction component is mainly driven by the abduction of CBII. Notice, however, that inertial flow might occur close to or in the mouth without affecting the food item (see above). CBII can fulfill an important role in inertial suction because of its strength and size (see Figs. 6, 7) and because the esophageal wall is very strongly connected to the flattened surface of CBII. The specific orientation of its rotational axis with the hyoid body (see Fig. 4) determines that CBII abduction distends the anterior part of the esophagus, thus expanding its volume as necessary for inertial suction. According to Bramble (personal communication in Lauder, '85), the snapping turtle (*Chelydra*) has tendon slips of the *M. rectus cervicis* (i.e., the *M. coracohyoideus* in *Chelodina*; see Fig. 6) that help to expand the esophagus sack. *Chelodina* lacks such connections. As this muscle is intimately connected to the esophagus it seems obvious that its action, in depressing and retracting the hyoid body (see further), will also assist ventrally directed expansion of the anterior part of the esophagus. The posterior part of the esophageal sack likely bulges passively due to the momentum of the backward flowing water, because the ceratobranchials are kept abducted and the volume change due to mouth buccal closure is too small to cause the substantial bulging by pressing water

backward. This temporary water storage in the esophagus can be compared with the inertial outward flow through the opercular slits after these are opened at the end of the expansion phase of feeding fishes (Alexander, '67; Osse, '69).

In spite of the fact that aquatic feeding in turtles evolved de novo from an apparatus adapted for terrestrial feeding (Lauder and Prendergast, '92), their feeding kinematics show some striking similarities to those observed for primary aquatic feeding animals. This has already been reported by Lauder and Prendergast ('92) and points at hydrodynamical constraints on evolutive solutions for aquatic feeding. Several kinematic components are similar, but the buccopharyngeal expansion of turtles is performed by distinct skeletal units: the role of the hyoid rami in fishes and salamanders is taken over by CBI in turtles and the opercular and branchiostegal abduction observed in fishes (i.e., caudal expansion) is replaced by the abduction of CBII. The significance of hydrodynamic constraints is further supported by the fact that optimal feeding conditions as deduced for fishes apparently also occur (at least) in *Chelodina*. Van Leeuwen and Muller ('84: pp. 156, 160) deduced that prey sucking fish should expand their opercular cavities at the maximal rate at the instance of the maximal mouth aperture, whenever this instance coincides with the moment of prey capture and that "a fish gains more if it tries to optimize the ultimate velocity, than it would gain in optimizing the initial prey distance." In all analyzed trials, the rate of CBII expansion is maximum at the instant the prey enters the buccal cavity (e.g., see Fig. 5B,D,F). Moreover, at this instant, the prey velocity (in both the moving and the earth bound frame) is maximal. This is inferred as the calculated prey acceleration always reaches zero (with a clear tendency toward change in sign; i.e., onset of deceleration) once the prey passes the mouth.

All of the above considerations attribute an important role to CBII and the musculature for pharyngeal expansion. To evaluate this, muscle masses of the jaw and hyobranchial muscles of *Chelodina* will be compared with those of *T. scripta* (common slider). Contrary to *Trachemys*, the head of *Chelodina* is much flattened and elongated and the construction of the hyobranchial apparatus is much larger and much more rigid; this likely makes the construction more suitable

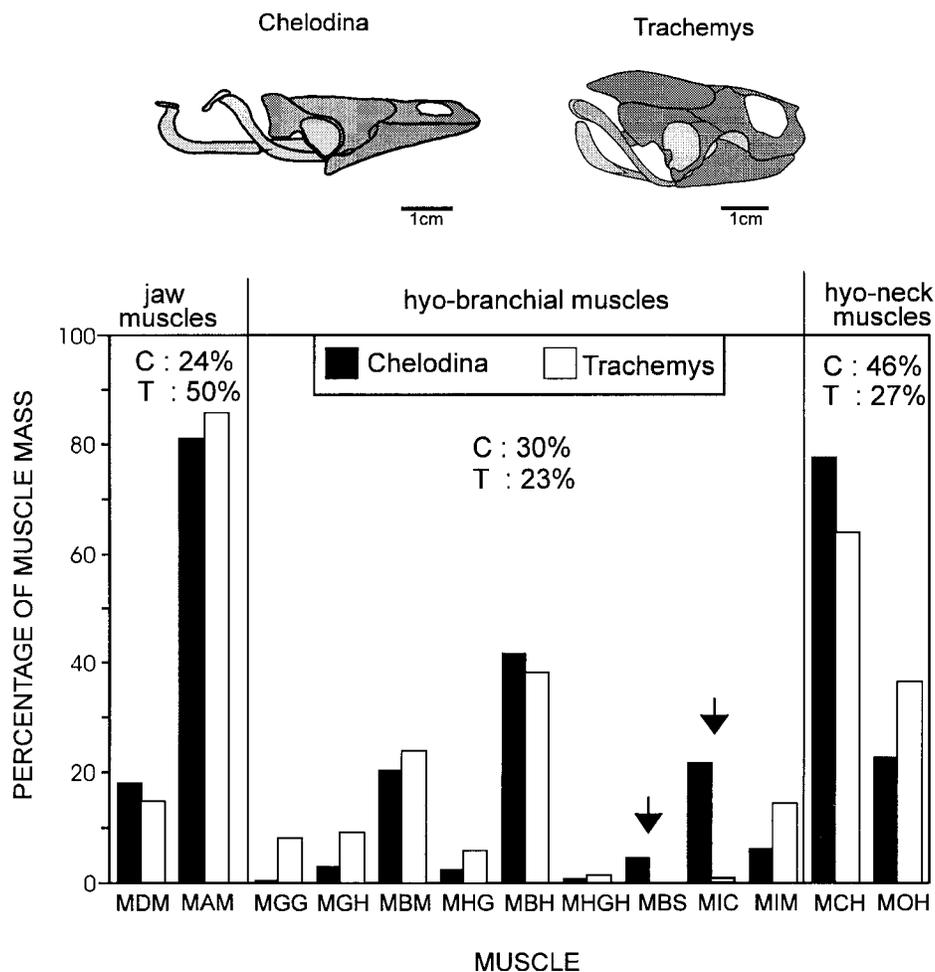


Fig. 8. Comparison of muscle masses between *C. longicollis* and *T. scripta*. Three groups are considered (jaw muscles, hyobranchial muscles, and neck muscles connected to the hyoid = hyo-neck muscles). Muscle mass within each group is set to 100%. The numbers for each group give the percentile contribution of this group to the total muscle mass. Arrows indicate important differences between *Chelodina* and *Trachemys*. MAM, M.

adductor mandibulae complex; MBH, M. branchiohyoideus; MBM, M. branchiomandibularis; MBS, M. branchiosquamosus; C, *Chelodina*; MCH, M. coracohyoideus; MDM, M. depressor mandibulae; MGG, M. genioglossus; MGH, M. geniohyoideus; MHG, M. hyoglossus; MHGH, M. hypoglossohyoideus; MIC, M. intercornuatus; MIM, M. intermandibularis; MOH, M. omohyoideus; T, *Trachemys*.

for inertial suction. These differences in skull and hyobranchial morphology are also reflected in a difference in aquatic feeding ability between both turtle species. Slider turtles (Emydidae) are a group of rather generalized, short-necked, mainly aquatic turtles. They are omnivorous and opportunistic feeders, eating what is available or most easily obtained. They seldom pursue any prey (Moll and Legler, '71). Turtles of the genus *Chelodina* (Chelidae) are carnivorous (Parmenter, '76). These turtles actively pur-

sue agile prey and their fast extension of the neck ensures proximity of the prey to the mouth at the moment of grasping.

The hyobranchial muscles and neck muscles connected to the hyoid (participating in buccal expansion) contribute much more to the total mass of head muscles in *Chelodina* than in *Trachemys* (Fig. 8). In the latter species, the jaw muscles are more prominent (Fig. 8). Within the functional group of the hyobranchial muscles, the M. branchiohyoideus, abducting CBI (Figs. 6,

7), is the most massive muscle in both species. *Trachemys* has better-developed tongue muscles (MGG, MGH, and MHG in Fig. 6). *Trachemys* lacks a M. branchiosquamosus (first arrow in Fig. 8). In *Chelodina*, this muscle is important for expansion because it fixes the dorsal tip of CBI to the neurocranium (Figs. 7, 8). Consequently, contraction of the coracohyoideus muscle (inserting on the hyoid body; Figs. 7, 8) results in the large depression of the buccal floor. The M. intercornuatus (connecting both branchial arches; Figs. 7, 8) is only a thin ligamentous sheet in *Trachemys*. In *Chelodina*, this muscle is strongly developed (Figs. 7, 8) and assumed to be the primary abductor of CBII (in concert with the retractive force of the neck muscles), thus being responsible for the distinct inertial suction component in feeding *Chelodina*.

Preliminary observations on feeding *Trachemys* (with the reduced intercornuatus muscle) support the above-formulated thoughts. Prey displacements in the fixed frame of reference are less obvious, pointing at a smaller inertial suction component. Electromyographic studies could expose the role of the head muscles in turtle feeding more decisively.

In conclusion, it can be stated that *Chelodina*, when feeding on small slowly sinking particles, combines compensatory and inertial suction. The latter component contributes significantly to prey capture. Further studies must reveal whether the present findings can be generalized (e.g., changing feeding conditions, elusive prey, bottom feeding, etc.) and how neck movements interact with head kinematics.

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