
7 Cervical Anatomy and Function in Turtles

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7.1 INTRODUCTION

Being mobile is an essential requirement for any animal. Not only do animals need to move about to find food or partners, they also need to be able to escape potential predators (Irschick & Garland, 2001). Interestingly, some vertebrate groups appear to have sacrificed part of their mobility in response to predation pressure by the development of a robust armored body (e.g., pangolins, glyptodonts, turtles, and so on). Although body armor can provide an animal with an adequate protection against predators, it also dramatically reduces its locomotor ability and overall agility (Wren et al., 1998; Zani et al., 2005). Thus, many armored vertebrates have specialized on eating non-mobile food items like plants, or clumped food sources such as ants or termites (King, 1996). However, some groups have developed an alternative strategy for capturing elusive prey by developing long, mobile appendages such as projectile tongues (Deban et al., 1997; Herrel et al., 2000) or a long neck (Gans, 1992). For instance, many semi-aquatic and aquatic turtles have developed remarkably long necks that are used to capture elusive prey under water (Pritchard, 1984).

Although the turtle carapace provides an excellent defense against predators, it is imperative that the long neck and head can be protected as well. To do so, the head-neck system needs to be withdrawn within the margins of the bony shell. This can be done in one of two ways: in the

mid-sagittal plane (vertically), which involves the retraction of the head and neck within the bony shell, or laterally (in the horizontal plane), where the neck is folded between the dorsal and ventral rim of the bony shell. In this case, the head and neck do remain partially exposed in the outer carapacial chamber in front of the pectoral girdle (Van Damme et al., 1995). This difference in the mode of neck retraction in turtles has often been used as an important character for the subdivision of the class Testudines into the subclasses Cryptodira and Pleurodira. Whereas cryptodires retract their head-neck system in the vertical plane, pleurodires do so in the horizontal plane (Figure 7.1).

Accurate control of the neck during rapid movements associated with escape head retraction and prey capture appears crucial for turtles. However, the turtle neck is a highly complex multi-jointed system, consisting of eight cervical vertebrae, the head, and the body and a large number of muscles that span anywhere from one to over eight joints. The control of such a multi-joint system with a large number of degrees of freedom appears inherently complex. Although some ways to facilitate the control of the system have been identified previously (Aerts et al., 2001), a better understanding of the detailed structure and function of the musculo-skeletal elements of the cervical system is essential to gain better insight into the control of the cervical system. Moreover, large differences in vertebral structure, in the morphology of associated musculature, and in the control of the cranio-cervical system can be expected for turtles that retract their necks predominantly in either the horizontal or vertical plane. Unfortunately, previous authors have described differences in vertebral structure between cryptodiran and pleurodiran turtles predominantly from a taxonomic standpoint (Vaillant, 1881; Williams, 1950; but see Weisgram & Splechtna 1990, 1992). Thus, it remains presently unclear whether different functional capacities (i.e., ranges of mobility) are associated with either morphology. Without this type of information, our understanding of the control of the cranio-cervical system in cryptodiran and pleurodiran turtles must, unfortunately, remain limited.

The aim of the present chapter is to give a detailed morphological description of the cervical system in pleurodiran and cryptodiran turtles. In doing so, our emphasis will be on the functional consequences of differences in morphology in the two groups. Additionally, some previously unpublished data on the actual kinematics of neck movement will be presented to highlight the consequences of morphological differences in the two groups. As our type representatives for cryptodiran and pleurodiran turtles we have chosen the genera *Chelodina* and *Apalone*. The Australian pleurodiran turtles of the genus *Chelodina* are renowned for their extreme elongated neck. Because the neck is longer than the carapace, these turtles are also known as snake-necked turtles. These animals use their elongated neck both for quick strikes at prey and for snorkeling, thus aspirating air from the surface without exposing more than the tip of the snout. Species from this genus will be used as a typical representative of the pleurodiran condition. Turtles of the genus *Apalone*, also known as the soft-shelled turtles, represent the cryptodiran counterpart of *Chelodina*. These animals are also characterized by an extremely elongated neck, often longer than the carapace itself (Ernst & Barbour, 1989). Soft-shell turtles typically live in shallow water and will use their elongate neck to breathe at the water surface with minimal movement. Moreover, just like *Chelodina*,

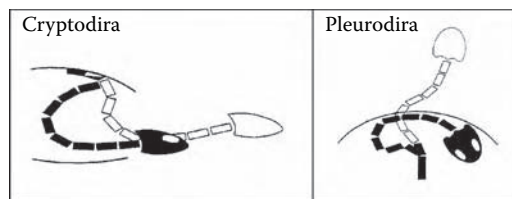


FIGURE 7.1 Schematic representation of the two major modes of head retraction in turtles. Left, lateral view on the cervical system in a cryptodire. In cryptodires, the head is retracted in the vertical plane. Right, dorsal view on the cervical system in a pleurodire. Here the head is retracted in the horizontal plane.

members of the genus *Apalone* are voracious predators that will actively strike at elusive prey under water (Dalrymple, 1977; Ernst & Barbour, 1989).

7.2 MATERIALS AND METHODS

7.2.1 ANATOMICAL STUDIES

The anatomy of the cervical vertebrae, joint structures, and cervical musculature of *Chelodina longicollis* was studied by means of dissection of a preserved specimen (K.B.I.N., R.G.nr.4566). Additionally, an adult *C. reimani* (cadaver obtained through the commercial pet trade) was used to study the cervical anatomy. One individual of the species *Apalone ferox* and one *A. spiniferus* were dissected to investigate the anatomy of the cervical system in a typical cryptodire. Animals were obtained through the commercial pet trade, sacrificed by means of an overdose of Nembutal and preserved in a 10% aqueous formaldehyde solution for 24 hours. Next, animals were rinsed extensively and transferred to a 70% aqueous ethanol solution.

Cervical morphology was studied by means of dissections. In the morphological descriptions, vertebrae are indicated by capital C or D (cervical and dorsal vertebrae, respectively) followed by their serial number. C1 is closest to the head. Joints are labeled by the number of the adjacent vertebrae: C(n)-($n - 1$), with n the number of the more caudal vertebra and ($n - 1$) the number of the more cranial one as suggested by Heidweiller (1991). For example, the joint between vertebra 5 and 6 is defined as “joint C6-5.”

7.2.2 KINEMATIC ANALYSES

To study the kinematics of snorkeling, two live adult specimens of *Chelodina longicollis* were used for the experiments (one female of 730 g, 18 cm carapace length and one male of 520 g, 15 cm carapace length). The animals were obtained with the help of the Antwerp Zoo and were housed in a glass aqua-terrarium on a 12-hour light/dark cycle. One live *Apalone ferox* and one live *A. spiniferus*, obtained through the commercial pet trade, were used to study the mobility of the cervical vertebrae in these long-necked cryptodires. The water temperature was kept at 28°C for all species. Twice a week, the turtles were fed with meat, mice, and small invertebrates (crickets, grasshoppers).

Snorkeling movements (neck movements in the vertical plane) of *C. longicollis* were recorded by means of cineradiography in lateral view using a Polydoros 80S generator equipped with a Siemens Siregraph D40 x-ray flash apparatus at 66 kV. The digital cineradiographic recordings (depending on the sequence 4 or 6 frames per second, Fluorospot H) were printed on Scopix laserfilm (35 × 43 cm) by means of an Agfa laser printer. During the recordings, the animals were restrained by means of a body-shaped corselet. This corselet was mounted under the water surface on a fixed frame.

The sequences were projected frame by frame and digitized. Digitization of the position of the joints allowed the calculation of several kinematical parameters (joint angles, elevation of the head, head position) in a turtle-bound frame. The same terminology of joint rotations is used as described for the neck movements in the horizontal plane, i.e., clockwise rotations are defined as positive.

Mobility of the cervical vertebrae in *A. ferox* and *A. spiniferus* was studied by means of CT scanning. The animal was anesthetized by means of intramuscular injection of Ketamine (150 mg/kg body mass). CT scans were recorded using a CT-highlight Advantage scanner at the University of Antwerp Hospital. Of 10 different static neck positions, ranging from fully extended to fully retracted, 3-s long recordings resulting in 1.5 mm thick slices through the vertebral column were made at 140 kV, 140 mA. Scans were printed on Scopix LT2B-100 NIF x-ray film.

7.3 RESULTS

7.3.1 OSTEOLOGY

The cervical column in all recent turtles consists of eight elongated vertebrae (C1 to C8) and nine joints. The most important element of the vertebrae is the vertebral centrum, which is positioned right below the spinal cord. From the centrum, the neural arch rises and covers the spinal cord (Figure 7.2). The neural spines are positioned midventrally on the neural roof and are reduced in most turtles (Figure 7.2). The articulation of the different vertebrae occurs by means of the vertebral centra and the zygapophyses (Figure 7.2). The prezygapophyses of the vertebra articulate with the postzygapophyses of the more cranially situated vertebra. Whereas the articular facets of the prezygapophyses are positioned dorsally, those of the postzygapophyses are oriented ventrally. Vertebral centra can be biconvex (C5 and C8 in *Chelodina*), biconcave or amphicoelous (C1 in both species; C7 in *Chelodina*), procoelous (C6 in *Chelodina*) or opisthocoelous (C2, C3, and C4 in *Chelodina*; C2 to C8 in *Apalone*).

In a transverse section, the vertebral centrum of *Chelodina* is saddle-shaped (Figure 7.3 and Figure 7.4). The vertebral centrum is well developed only at the level of the anterior and posterior articulations. The neural spine is reduced to an inconspicuous longitudinal rim. The anterior zygapophyses are clearly separated from each other (Figure 7.3 and Figure 7.4). Their articular facets are mainly oriented in the medio-dorsal direction. The posterior zygapophyses are fused to each other except those of C1 (Figure 7.3), but the articular facets remain separated and face mainly ventrally and slightly laterally (Figure 7.3 and Figure 7.4). The elevation of the posterior zygapophysis gradually increases from distal to proximal (Figure 7.3 and Figure 7.4). The transverse processes are strongly developed, especially those on the more proximal vertebrae (Figure 7.3 and Figure 7.4).

The cervical vertebrae in *Apalone* are relatively gracile and elongated (Figure 7.5 and Figure 7.6). They bear well-developed and well-separated pre- and post-zygapophyses (Figure 7.5 and

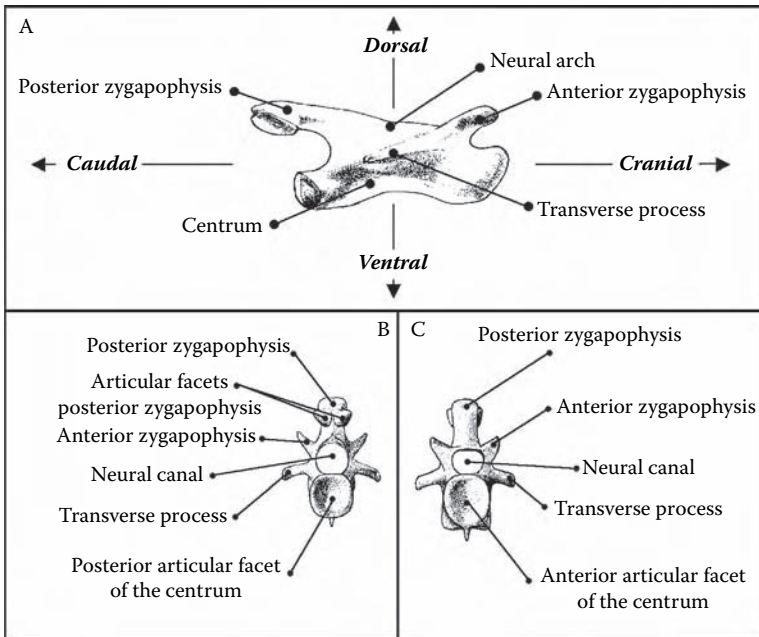


FIGURE 7.2 *Chelodina longicollis*. Terminology of the most important structural elements of a cervical vertebra (C7). (A) Lateral view, (B) posterior view, and (C) anterior view (terminology after Romer & Parsons, 1977).

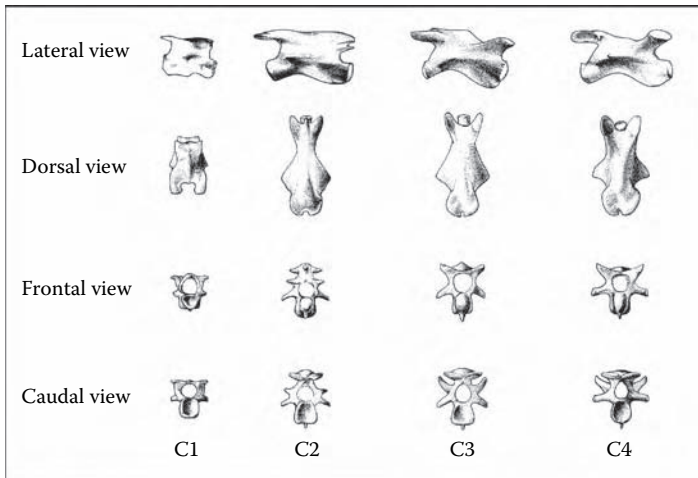


FIGURE 7.3 Lateral, dorsal, frontal, and caudal views of the first four cervical (C1-C4) vertebrae in *C. longicollis*.

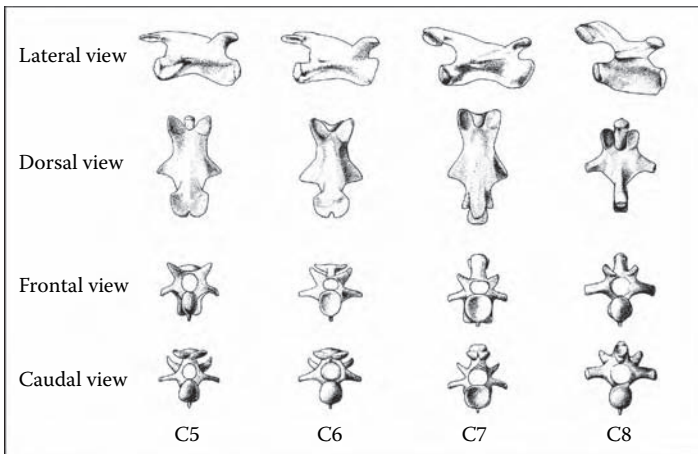


FIGURE 7.4 Lateral, dorsal, frontal, and caudal views of the last four cervical (C5-C8) vertebrae in *C. longicollis*.

Figure 7.6). The orientation of the zygapophyses is variable throughout the neck. Because of the absence of the iliocostalis and logissimus groups (discussed later), the transverse processes are only poorly developed (Figure 7.5 and Figure 7.6). Because of the strong divergence of the post-zygapophyses and the absence of a well-developed neural spine, a hiatus intervertebralis (Bojanus, 1821) is created. In *Apalone*, this hiatus is covered by a thick membrane (Ogushi, 1913).

7.3.2 CERVICAL JOINTS

Joint S(kull)-C1 (occipito-cervical joint). This procoelous ball-and-socket type joint allows the skull to move independently from the neck. The occipital is spherical. The ridges of the congruent cotyle on C1 are well developed. C1 lacks anterior zygapophyses. The connection between the

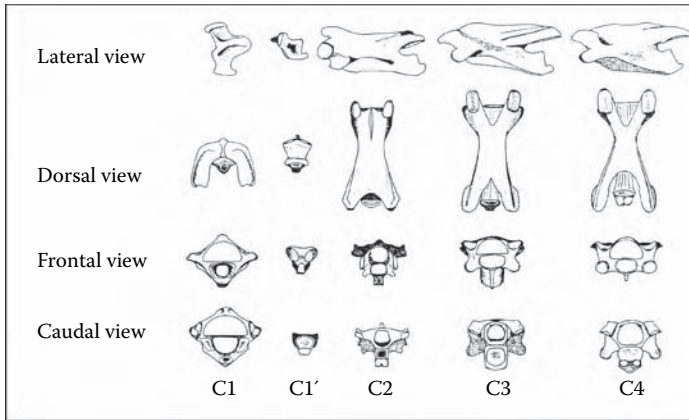


FIGURE 7.5 Lateral, dorsal, frontal, and caudal views of the first four cervical (C1-C4) vertebrae in *A. spinifera*. C1' is the intercentrum of the atlas.

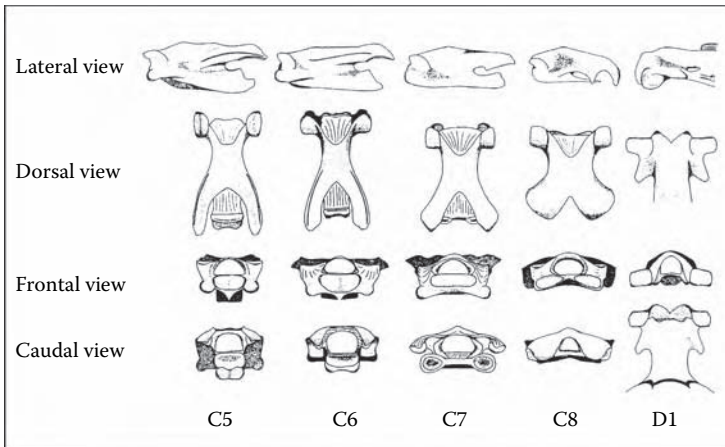


FIGURE 7.6 Lateral, dorsal, frontal, and caudal views of the last four cervical (C5-C8) and the first dorsal vertebra (D1) in *A. spinifera*.

neural arch of C1 and the base of the skull is ligamentous. The joint is similar in both *Apalone* and *Chelodina*.

Joints C2-1, C3-2, C4-3, C5-4 (anterior part of the neck). The articulation facets of vertebrae composing these joints are very similar. The vertebral centra are all opisthocelous and have an anterior elliptical cotyle, of which the long axis is oriented vertically in *Chelodina* and horizontally in *Apalone*, and a posterior condyle with enlarged lateral ridges. The articular facets of the zygapophyses of the most cranial joint of this group (C2-1) are less strongly developed. The elongated neural spine of C2 extends anteriorly beyond the articular facets of the posterior zygapophyses of C1 in both groups. The posterior zygapophyses of C1 are clearly separated. In the more caudal joints, the zygapophyses are elongated and slightly elevated (Figure 7.3). The articular facets of the anterior zygapophyses are slightly concave and their outline is kidney-shaped. They are oriented in a dorso-medial direction. The posterior zygapophyseal facets are ventrolaterally inclined. Lateral mobility is strongly reduced in *Apalone* compared to *Chelodina* because of the paired post-zygapophyses.

Joints C6-5 and C7-6. The central joints C6-5 and C7-6 are procoelous in *Chelodina* but opisthocoelous in *Apalone*. In posterior view, the posterior condyle of C5 in *Chelodina* has the shape of a raindrop. Alternatively, in *Chelodina* the condyle of C6 is almost spherical. The congruent cotyle on the anterior side of C6 and C7 has pronounced lateral and ventral ridges. The articular facets of the posterior zygapophysis are well developed and also have a kidney-shaped outline. The bilateral posterior zygapophyseal facets contact each other medially, forming a semicircular or horseshoe-shaped articular surface. The articular facets of the anterior zygapophyses are more oval (almost circular) as compared to the more distal joints. In *Apalone*, the articular facets of the post-zygapophyses are positioned horizontally. The post-zygapophyses themselves are nearly in line with the long axis of the vertebrae (less than 6°).

Joint C8-7. C8-7 is opisthocoelous and the shape of its condyle and cotyle resemble previously described opisthocoelous joints in both groups. The cotyle has enlarged lateral ridges in *Chelodina* and is fully split in *Apalone*. The posterior zygapophysis of C7 is elongated, inclined in dorsal direction in both groups (Figure 7.4). The articular facets are clearly distinguishable from those of the remainder of the zygapophyses and are laterally oriented in *Chelodina*. The rather short but strongly elevated anterior zygapophyses of C8 tend to incline dorsomedially in *Chelodina* but more laterally in *Apalone*.

Joint D1-C8 (cervico-dorsal joint). D1-C8 is procoelous in *Chelodina*. In *Apalone*, this joint lacks a central articulation. In *Chelodina*, the rather flattened condyle on the posterior part of C8 is almost circular. The articular facet faces caudo-ventrally. The circular congruent cavity on the anterior part of D1 is shallower than those on the more anterior joints. The elongate posterior zygapophysis in *Chelodina* is more elevated in the dorsal direction than that of joint C8-7 (Figure 7.4). The articular facets of the zygapophyses are more inclined than those in the previously described joints. On C8, the articular facets of both sides fuse and are clearly distinguishable from the posterior zygapophysis. Their appearance is that of a vertically positioned cylinder (approximating a vertical hinge joint). The anterior zygapophyses on D1 are rather short and present an increased dorsomedial inclination of the articular facets. In *Apalone*, the post-zygapophyses of C8 are extremely well developed and wider than those of the more anteriorly situated vertebrae (Figure 7.6). The articular facets are strongly concave. The pre-zygapophyses of D1 have been rearranged to horizontally oriented cylinders. Only ventroflexion is possible at this joint.

7.3.3 MUSCULATURE

The following short description of the cervical musculature is based on the terminology of Shah (1963) for *Chelodina* and that of Ogushi (1913) for *Apalone*. Other morphological accounts on the cervical musculature in turtles (Bojanus, 1819; George & Shah, 1954, 1955; Scanlon, 1982) were consulted to clarify the position of certain muscles where needed.

7.3.3.1 *Chelodina*

m. constrictor colli. This is a thin sheet-like muscle which covers the first two thirds of the neck. The muscle has a dual origin: some fibers originate on the squamosal and the dorsal connective tissue associated with the occipital spine and others originate on the neural spines of C2-C6. The fibers run ventrally and insert midventrally on a central connective tissue sheet (median raphe).

m. retrahens capitis et collicae (Figure 7.7). This muscle consists of a number of well-developed and individualized bundles that connect the carapace to the neck and head. The first bundle is the longest and originates at the lateral aspect of D8 and the adjacent part of the carapace. The muscle runs cranially and inserts by means of a long tendon at the basioccipital. A number of fibers from the first bundle insert on the lateral aspect of C1-C5. The second bundle originates at the level of D5. The muscle runs cranially and inserts tendinously at the lateral aspect of C5. The third bundle

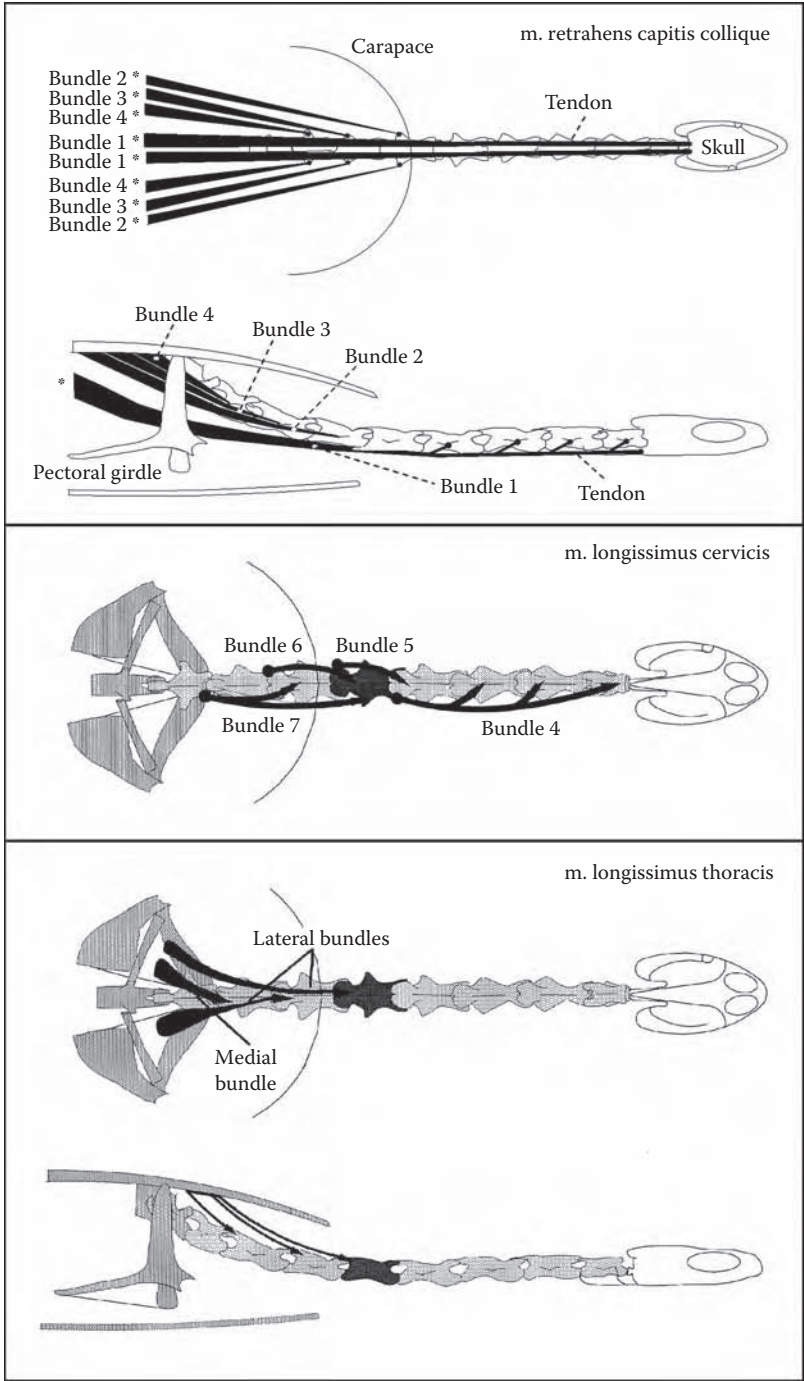


FIGURE 7.7 Schematic representation of the *m. retrahens capitis colliq*, the *m. longissimus cervicis*, and the *m. longissimus thoracis* in *C. longicollis*.

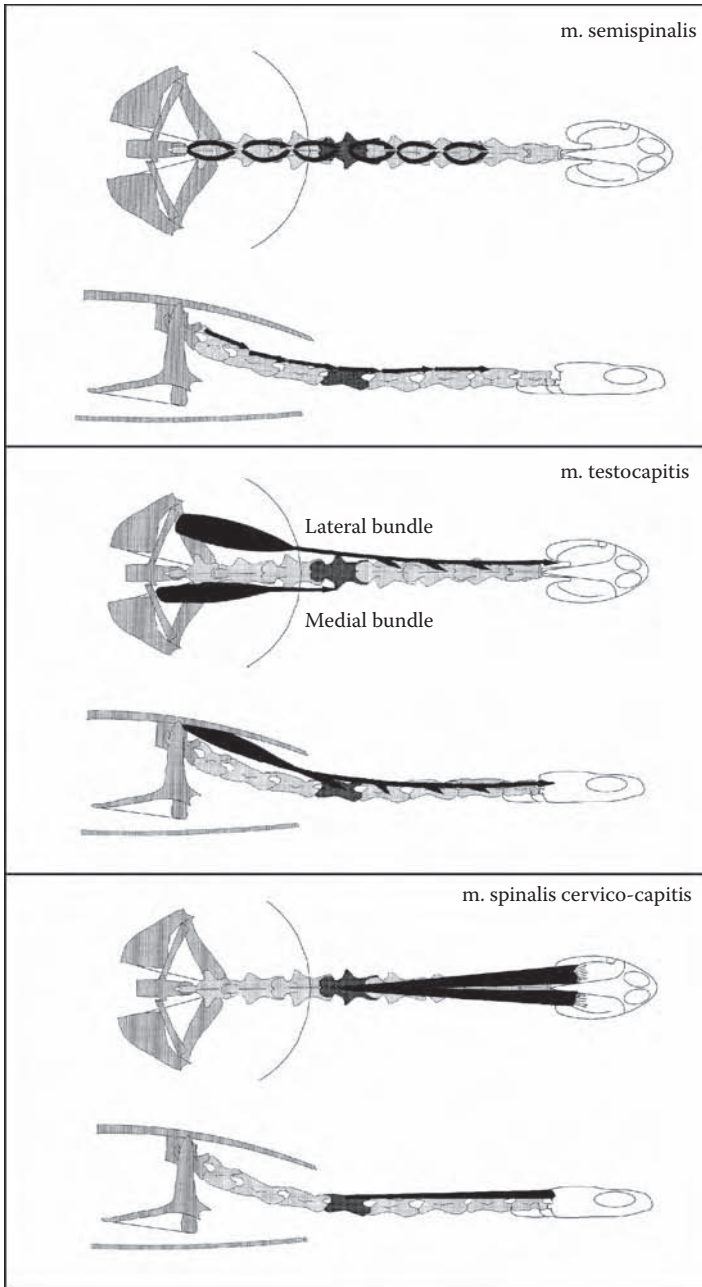


FIGURE 7.8 Schematic representation of the m. semispinalis, the m. testocapitis, and the m. spinalis cervico-capitis in *C. longicollis*.

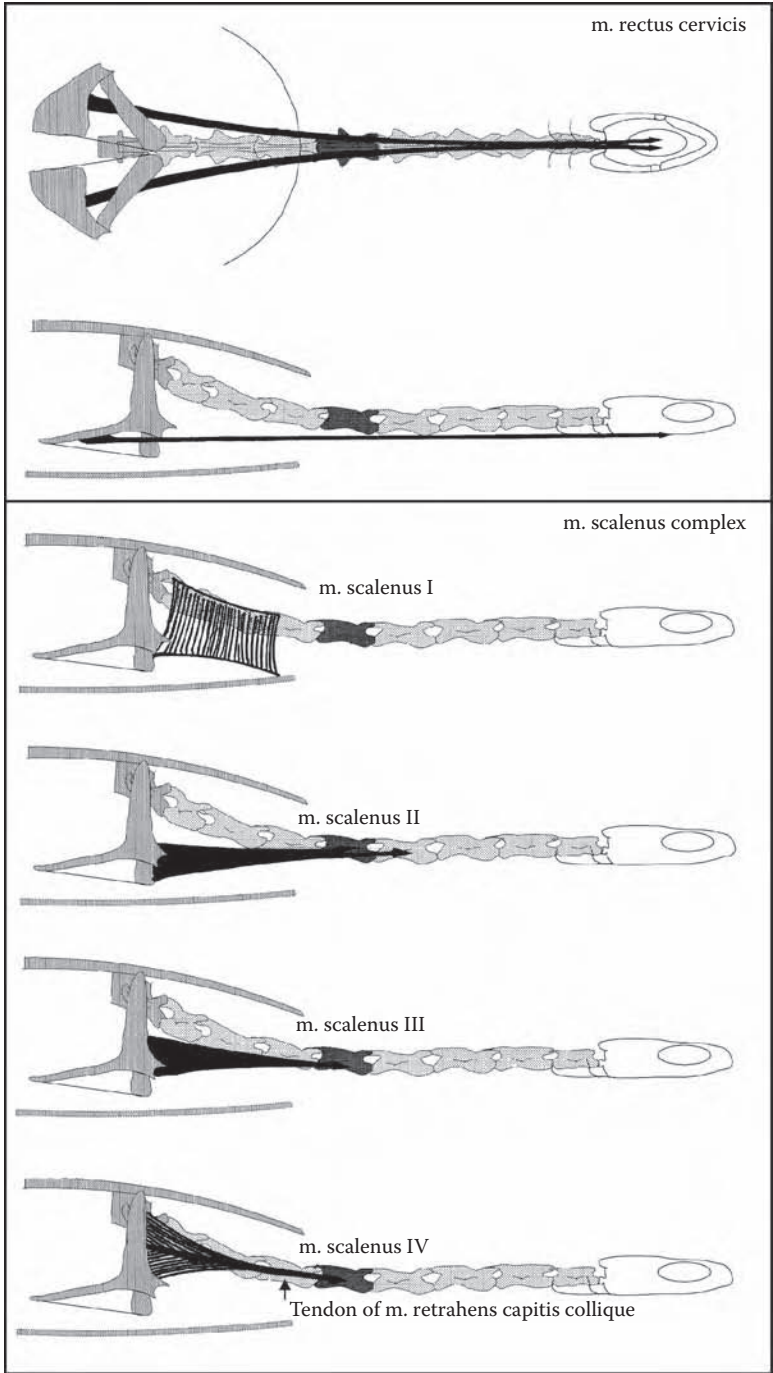


FIGURE 7.9 Schematic representation of the m. rectus cervicis and the m. scalenus complex in *C. longicollis*.

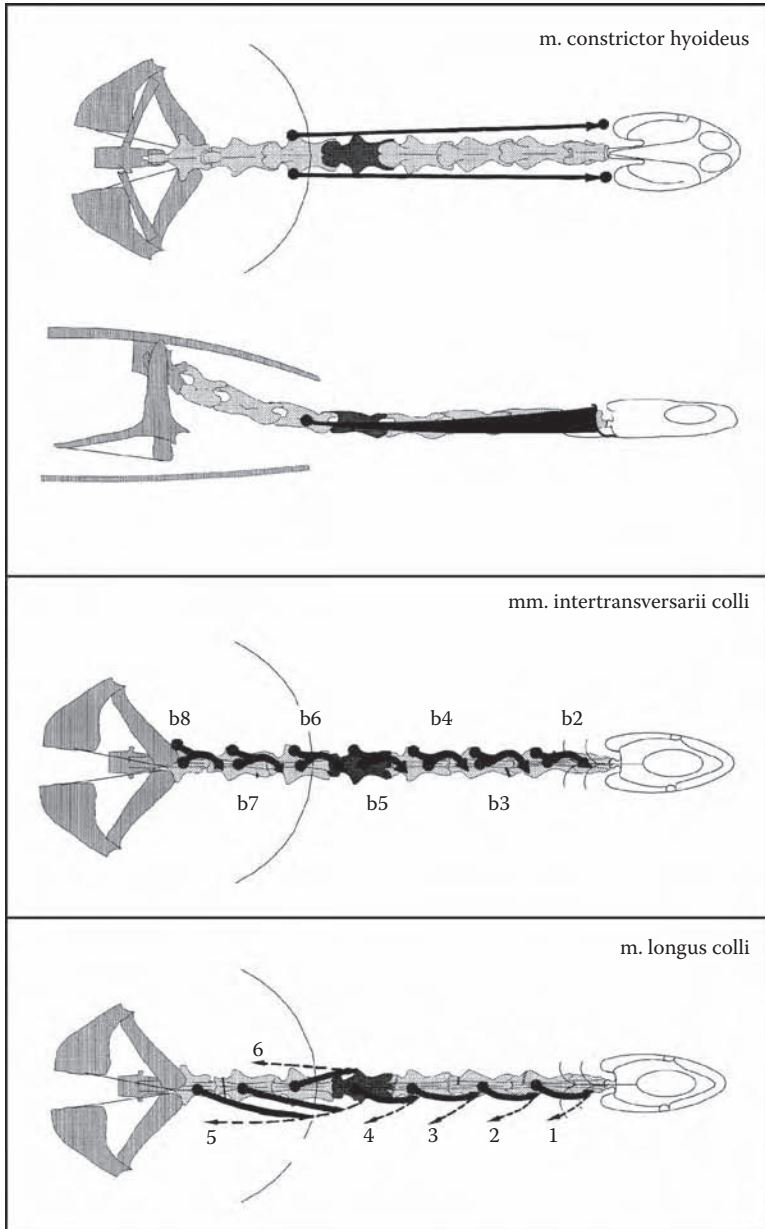


FIGURE 7.10 Schematic representation of the m. constrictor hyoideus, the mm. intertransversarii colli, and the m. longus colli in *C. longicollis*.

originates at D4 and inserts at the lateral aspect of C7. The fourth bundle originates at D3 and inserts at the transverse process of C8.

m. longissimus cervicis (LC, Figure 7.7). This is a segmentally arranged muscle with a more complex arrangement. The LC of C7 originates on the pre-zygapophysis of C8. The muscle belly runs anteriorly and divides into a more medial and a lateral bundle. The lateral bundle inserts on the post-zygapophysis of C6 and the medial on the lateral aspect of C5. The LC 6 originates on the pre-zygapophysis of C7 and inserts on the post-zygapophysis of C5. The LC 5 originates on the pre-zygapophysis of C6 and inserts on the post-zygapophysis of C4. The LC 4 originates on the pre-zygapophysis of C5 and inserts mainly on the neural arch of C1. During the course of the muscle, fibers diverge and insert on the post-zygapophyses of C3 and C2 as well.

m. longissimus thoracis (Figure 7.7). This muscle is responsible for lateral flexion of the posterior part of the neck and consists of one medial and two lateral bundles. All bundles originate at the ventral aspect of the carapace, cranial to the origin of the *m. testocapitis*. The medial bundle inserts at the lateral aspect of C8. The first lateral bundle inserts by means of a tendon on C6 at the level of the post-zygapophysis. The fibers of the lateral most bundle run initially ventral to the previous bundle but run more laterally at the level of C7. The muscle bundle inserts tendinously at the level of the post-zygapophysis of C5.

mm. semispinalis (Figure 7.8). This is a series of short serially arranged muscles that span adjacent vertebrae and run from C2 to C8. The muscles originate at the neural spine of the more posterior vertebra and run anterolaterally to insert on the post-zygapophysis of the anterior vertebra.

m. testocapitis (Figure 7.8). This is a very long muscle that consists of two distinct muscle bundles that connect the carapace to the head and neck. Both bundles originate at the ventral aspect of the carapace, lateral to the scapula. The fibers of the medial bundle converge onto a strong tendon that inserts at the lateral aspect of C5. The lateral bundle inserts through a complex arrangement of tendons in the anterior part of the neck at the lateral aspect of C4-C2.

m. spinalis cervico-capitis (Figure 7.8). This is superficial dorsal cervical muscle bundle. The muscle originates at the neural spines of C3-C5 and runs obliquely anteriorly. The more medially positioned fibers insert on the lateral aspect of the occipital spine and the more lateral fibers on the dorsal aponeurosis covering the *m. adductor mandibulae*.

m. rectus cervicis (Figure 7.9). This is a very long and ventrally positioned muscle that connects the pectoral girdle with the ventral aspect of the hyobranchium. The muscle originates at the mid-dorsal aspect of the coracoid. The fibers run ventrally and join the fibers of the *m. constrictor hyoideus* of the same side. At the level of the hyobranchium, the two muscles separate again and the fibers of the *m. rectus cervicis* insert partially on the second ceratobranchial and partially on the basibranchium.

m. scalenus complex (Figure 7.9). This is a series of four muscles that connect the pectoral girdle with the lateral aspect of the posterior neck. The most superficial bundle is very thin and runs between the acromion, the dorsal aspect of the plastron, and the posterior most cervical vertebrae (C6-C8). The second and ventral most bundle of the scalenus complex originates on the acromion but distally to the first bundle. The fibers insert at the ventrolateral aspect of C4 and C5. The third bundle originates partly on the scapula and partly on the acromion. The fibers converge on a flat tendon that inserts at the ventrolateral aspect of C5. The fourth part is the shortest and originates across the entire width of the scapula. The muscle inserts on the proximal aspect of the tendinous insertion of the second bundle of the *m. retrahens capitis et collique*.

m. constrictor hyoideus (Figure 7.10). This muscle originates at the lateral aspect of C6, runs cranially and inserts at the posterior aspect of the first ceratobranchial. Although its primary function is presumably related to the abduction and retraction of the ceratobranchial, it presumably also plays a role during lateral bending of the neck.

mm. intertransversarii colli (Figure 7.10). This is another segmentally arranged muscle that has a dual origin. The lateral bundle originates at the ventral aspect and the medial bundle at the

diapophysis of the cervical vertebra. Both bundles join and insert at the posterior aspect of the vertebral centrum of the more cranially positioned vertebra.

m. longus colli (Figure 7.10). This muscle consists of a series of segmentally arranged small muscle bundles that run in close association to the *m. retrahens capitis et collique*. The longus colli bundles of the first five vertebrae originate at the ventral aspect of the respective vertebrae. Insertion takes place by means of the tendinous insertion of the second bundle of the *m. retrahens capitis et collique* on the lateral aspect of C4-C1. The muscles in the more posterior part of the neck are somewhat more complex. The *m. longus colli 8* originates on the ventral side of C8 and inserts on the tendon of the second bundle of the *m. retrahens capitis et collique*. The longus colli 7 originates at the ventral aspect of C7 and inserts by means of the insertion of the tendon of the second bundle of the *m. retrahens capitis et collique* at the lateral aspect of C5. The longus colli 6 originates at the ventral aspect of C6 and inserts at the lateral aspect of C5.

7.3.3.2 *Apalone*

Notable in *Apalone* is the strong reduction of the epaxial musculature (Hofstetter & Gasc, 1969), the absence of the longissimus system, and the absence of the iliocostalis system that is characteristic for all turtles.

m. constrictor colli (*m. sphincter colli*, Ogushi, 1913). This muscle is poorly developed in *Apalone* and consists of two discrete parts. The anterior part covers the lateral and ventral aspect of the anterior neck region. It originates on the dorsal connective tissue associated with the occipital spine and runs ventrally to insert on the median raphe. The posterior part is often difficult to discern and originates more posteriorly in the neck on the nuchal connective tissue associated with the neural spines and inserts ventrally on the median raphe.

m. rectus cervicis (*m. coraco-hyoideus*, Ogushi, 1913). This is the ventral-most muscle in the cervical region. The muscle has a dual origin—one part originates on the dorsal aspect of the proximal part of the procoracoid, and the other part originates at the dorsal aspect of the epicoracoid. The muscle runs anteriorly and inserts at the posterior aspect of the basibranchium.

m. carapaco-basioccipitis (Figure 7.11). This is a very long muscle that runs from the pelvic girdle to the cranium. Three distinct origins on the crista mediana ventralis of the first, second, and third caudal vertebrae are present. In addition, three accessory sites of origin can be discerned: on the proximal aspect of the fifth rib, across the entire length of the sixth costal plate, and along the entire seventh rib and associated costal plate. The fibers of this last bundle initially run at an angle of at most 90° to the long axis of the remainder of the muscle.

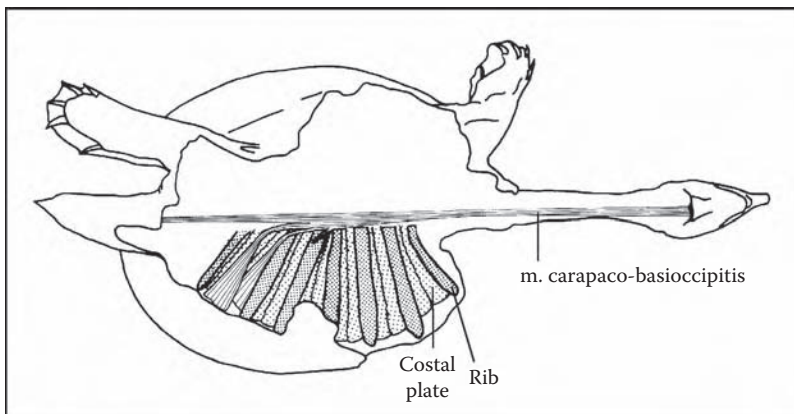


FIGURE 7.11 Schematic representation of the *m. carapaco-basioccipitis* in *A. spinifera*.

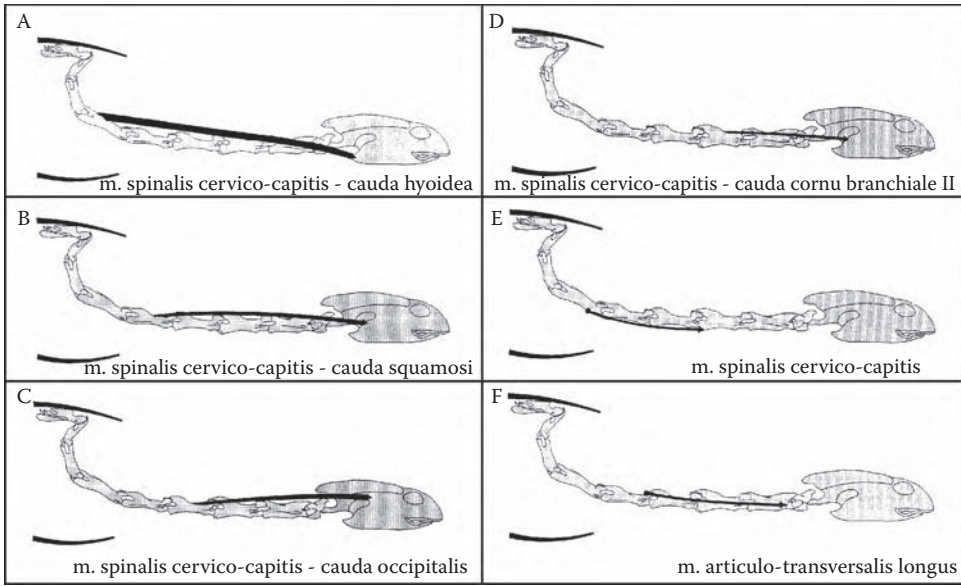


FIGURE 7.12 Schematic representation of the m. spinalis cervico-capitis complex (A–D), the m. cervico-spinalis (E), and the m. articulo-transversalis longus (F) in *A. spinifera*.

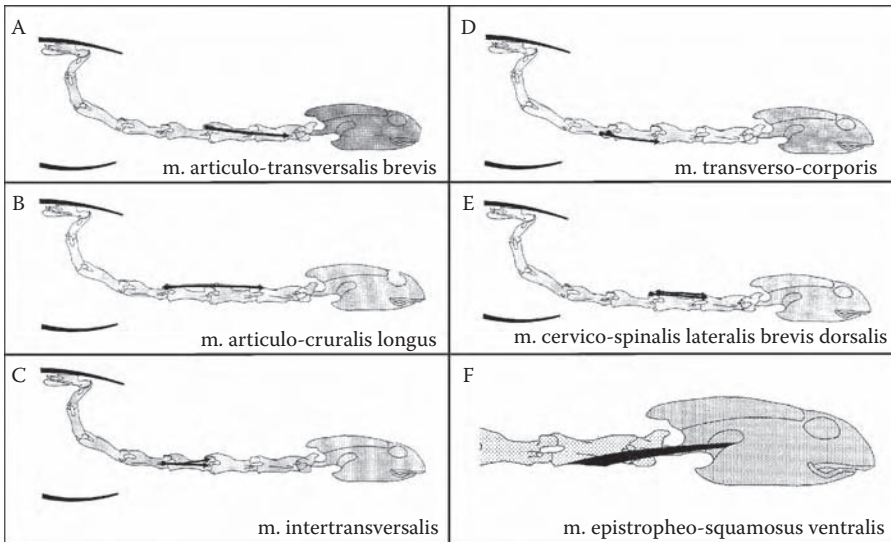


FIGURE 7.13 Schematic representation of the m. articulo-transversalis brevis, the m. articulo-cruralis longus, the m. intertransversalis, the m. transverso-corporis, the m. cervico-spinalis lateralis brevis dorsalis, and the m. epistropheo-squamosus ventralis in *A. spinifera*.

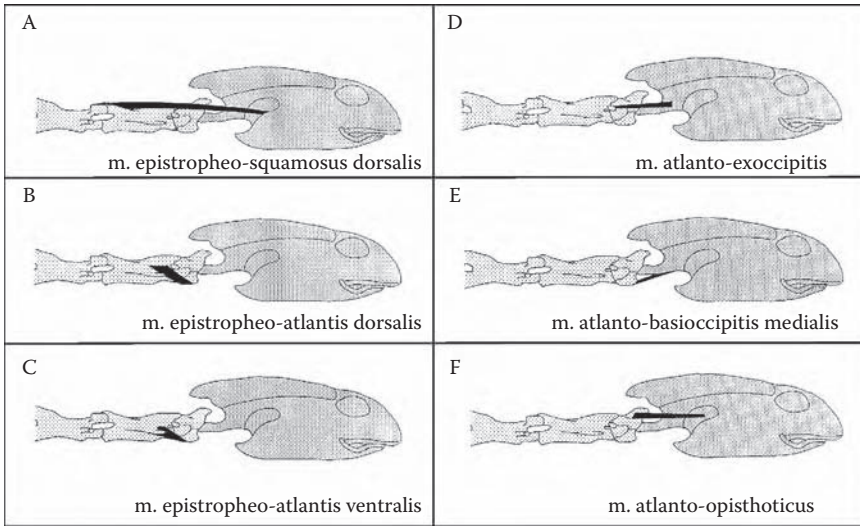


FIGURE 7.14 Schematic representation of the m. epistropheo-squamosus dorsalis, the m. epistropheo-atlantis dorsalis and ventralis, the m. atlanto-exoccipitis, the m. atlanto-basioccipitis medialis, and the m. atlanto-opisthoticus in *A. spinifera*.

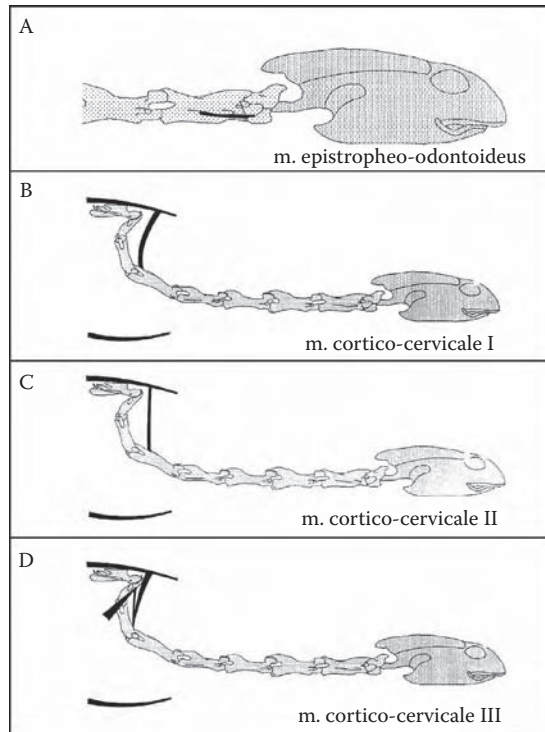


FIGURE 7.15 Schematic representation of the m. epistropheo-odontoideus and the m. cortico-cervicale group in *A. spinifera*.

m. *spinalis cervico-capitis* (*cervico-hyo-capitis*, Ogushi, 1913; Figure 7.12). This is a large muscle that consists of four distinct muscle bellies—the cauda hyoidea, the cauda squamosi, the cauda occipitalis, and the cauda cornu branchiale II. The cauda hyoidea (Figure 7.12A) originates at the neural roof of C6, runs anteriorly and merges with the fibers of the m. *rectus cervicis*. The cauda squamosi (Figure 7.12B) part originates at the neural roof of C5, runs cranially, and inserts by means of a broad aponeurosis at the posterior aspect of the squamosum. The cauda occipitalis (Figure 7.12C) originates at the neural roof of C4, runs cranially, and inserts on the external fascia covering the external adductor. The cauda cornu branchiale II (Figure 7.12D) originates at the neural roof of C3, runs cranially, and inserts at the connective tissue associated with the tip of the second ceratobranchial.

m. *cervico-spinalis medialis* (Figure 7.12E). This is a segmentally arranged muscle. The muscles originate tendinously at the anterior aspect of the crista mediana ventralis, run anteriorly, and insert tendinously at the posterior aspect of the crista mediana ventralis of the third more cranially positioned vertebra. The muscles originating on the C2-C4 merge and insert jointly at the ventral aspect of the basioccipital by means of a well-developed tendon.

m. *cervico-spinalis lateralis longi* (Figure 7.12 & Figure 7.13). This consists of three long, superficial muscles that originate at the lateral aspect of the zygapophyses of C5 through C8:

- The m. *articulo-transversalis longus* (Figure 7.12F) originates on the lateral aspect of the pre-zygapophyses of the last five cranial vertebrae. The muscle runs cranially across the ventral aspect of the two more cranially situated vertebrae and inserts on the transverse process of the following vertebra.
- The m. *articulo-transversalis brevis* (Figure 7.13A) runs across three vertebrae. It originates at the dorsal aspect of the pre-zygapophyses and inserts jointly with the m. *articulo-transversalis longus*.
- The m. *articulo-cruralis longus* (Figure 7.13B) originates tendinously at the dorsal aspect of the pre-zygapophyses, runs cranially, and inserts directly at the dorsal aspect of the post-zygapophyses of the third more cranially positioned vertebra.

mm. *cervico-spinalis lateralis breves ventrales* (Figure 7.13). This consists of two distinct muscle groups, the more laterally positioned mm. *intertransversales* (Figure 7.13C) and the more medially positioned mm. *transverso-corporis* (Figure 7.13D). The former originates tendinously at the transverse process, runs cranially, and inserts directly on the posterolateral aspect of the pre-zygapophysis and the posterior aspect of the transverse process of the more cranially situated vertebra. The m. *transverso-corporis* originates on the ventral aspect of the transverse process and the vertebral body, runs cranially, and inserts on the condyle of the more cranially situated vertebra.

mm. *cervico-spinalis lateralis brevis dorsales* (Figure 7.13E). This is a segmentally arranged muscle running from C7 to C3. Each segment consists of two distinct parts. The medial part originates at the lateral aspect of the crista lateralis of the post-zygapophysis and inserts at the dorsal aspect of the base of the post-zygapophyses on the more cranially positioned vertebra. The lateral part originates tendinously on the connective tissue surrounding the zygapophyseal articulation and inserts at the dorsolateral aspect of the post-zygapophysis of the more cranially situated vertebra.

m. *epistropheo-squamosus ventralis* (Figure 7.13F). The muscle originates aponeurotically at the posterior aspect of the crista mediana ventralis of the axis. The muscle runs anterodorsally to insert at the processus mastoideus (Ogushi, 1913) of the squamosal.

m. *epistropheo-squamosus dorsalis* (Figure 7.14A). This originates fleshy at the neural arch and the posterior aspect of the neural roof of the axis. The muscle runs anteriorly and inserts at the processus mastoideus of the squamosal and the posterior edge of the opisthoticum.

m. *epistropheo-atlantis dorsalis* (Figure 7.14B). This originates at the anterior aspect of the neural arch of the axis. The muscle runs anteriorly and inserts tendinously at the processus articularis transversalis ventralis of the atlas.

m. epistropheo-atlantis ventralis (Figure 7.14C). This lies ventral to the previous muscle. It originates fleshy at the lateral aspect of the axis, both dorsal and ventral to the transverse process, and inserts by means of a short aponeurosis at the processus articularis transversalis of the atlas.

m. atlanto-exoccipitis (Figure 7.14D). This originates at the tendinous insertion of the m. rectus lateralis on the atlas and inserts fleshy at the exoccipital.

m. atlanto-basioccipitis medialis (Figure 7.14E). This originates by means of a short tendon at the processus articularis ventralis of the atlas. The muscle runs cranially and diverges toward its origin on the basioccipital.

m. atlanto-opisthoticus (Figure 7.14F). This originates at the dorsolateral aspect of the atlas and inserts at the dorsal surface of the opisthoticum.

m. epistropheo-odontoideus (Figure 7.15A). This originates at the lateral aspect of the atlas, just dorsal to the crista mediana ventralis, and inserts by means of a narrow tendon at the processus odontoideus.

m. cortico-cervicale I (Figure 7.15B). This originates fleshy at the anteromedial aspect of the nuchal plate and inserts musculously at the lateral aspect of the post-zygapophysis of C6.

m. cortico-cervicale II (Figure 7.15C). This originates at the nuchal plate, just posterior to the origin of the m. cortico-cervicale I. The muscle inserts fleshy at the neural roof of C6, just posterior to the insertion of the cauda hyoidea of the m. cervico-hyo-capitis.

m. cortico-cervicale III (Figure 7.15D). This has a dual origin. The lateral part of the muscle originates at the lateral aspect of the ventral side of the nuchal plate by means of a narrow and long muscular head. The medial head originates posterior to the origin of the m. cortico-cervicale II. Both heads merge toward the origin on the neural roof of C7, lateral to the insertion of the m. cervico-spinalis lateralis brevis dorsalis.

m. spinalis dorso-lumbalis. This segmentally arranged muscle is positioned in the canalis collateralis vertebralis (Vallois, 1922). The origin is partly on the inner aspect of the canal and partly on the dorsal aspect of the capitulum of the rib. The muscle leaves the canalis collateralis vertebralis right posterior to the rib associated with D1 and inserts directly at the post-zygapophysis of C8.

7.3.4 NECK MOVEMENTS

Neck movements in *Chelodina* are described in detail by Van Damme et al. (1995, 2002), Aerts et al. (2001), Weisgram et al. (1992), and Van Damme and Aerts (1997). Previously unpublished information on neck movements in *Apalone* and *Chelodina* are presented here.

7.3.4.1 Neck Retraction and Cervical Mobility in *Apalone ferox*

In the extended configuration, joints C9-8, C8-7, and C7-6 show the largest initial angles. The more cranially positioned joints are all in the extended configuration. The retraction of the neck in *Apalone* is characterized by relatively small angular changes in the first three (C3-2, C2-1, and S-C1) and the last cervical joint (C9-8). The largest

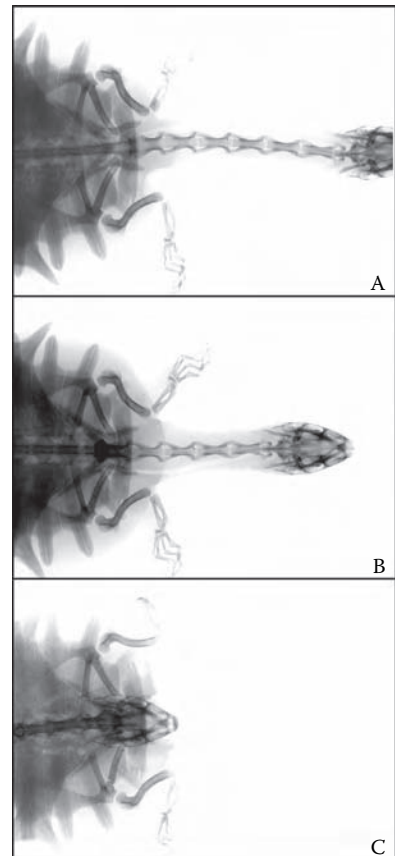


FIGURE 7.16 Static cineradiographs recorded in dorso-ventral view, showing the configuration of the cervical vertebrae in (A) fully extended, (B) relaxed, and (C) fully retracted positions of the neck in *Apalone spinifera*.

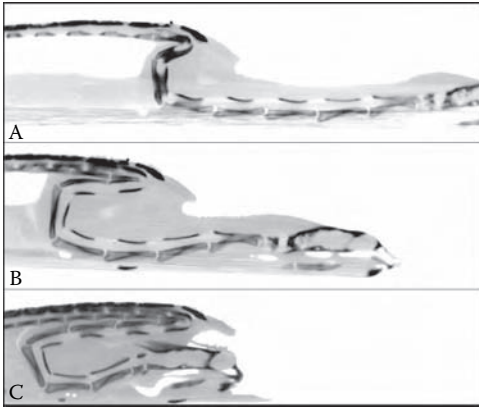


FIGURE 7.17 CT-scan showing the configuration of the neck and the cervical vertebrae of *A. spinifera* in fully extended, relaxed, and fully retracted positions.

of the neck in *A. spinifera* is also surprisingly high, with the more proximal joints being the ones allowing most movement in the horizontal plane. In contrast, the last three cervical joints allow almost no lateral movements.

7.3.4.2 Kinematics of Snorkeling in *C. longicollis*

Neck movements during snorkeling in *C. longicollis* are much slower in comparison with those involved during feeding behavior (Aerts et al., 2001; Van Damme et al., 2002) and escape retraction (Van Damme et al., 1995). The total duration of a typical ventroflexion followed by a dorsiflexion is about 6 s. Each component of the movement takes about 3 s. The representative example of a snorkeling movement in *C. longicollis* is represented by successive stick diagrams in Figure 7.19. Starting from an extended configuration in which head and neck are slightly depressed, the animal initially balances its neck around this configuration. This configuration is characterized by very small starting angles in all joints (with exception of D1-C8). Minor changes in joint angles occur during the first phase of the movement mainly in the posterior part of the neck (Figure 7.20). During this phase, no conspicuous changes of the elevation of the head and head position are observed. After approximately 3 s, a conspicuous, rather steady increase in the elevation of the head is observed, mainly as a result of changes in the angle of joints C4-3 to C7-6. In patterns observed in C8-7 and D1-C8 in the most posterior part of the neck and S-C1 and C2-1 in the most anterior part of the neck, changes in vertebral joint angle

angular changes during retraction occur in the middle region of the neck. Joints C8-7 and C7-6 extend during the course of the retraction. The situation for joints C6-5, C5-4, and C4-3 is more complex. C6-5 initially flexes during the retraction but extends again toward the latter part of neck retraction. The two more cranially situated joints start with an initially extended configuration. During retraction, the angle of these joints gradually increases.

The potential range of movement in the dorso-ventral direction is relatively large in most vertebral joints but largest in joints C8-7, C5-4, C4-3, and C3-2. However, joint angles during a simulated snorkeling movement are most pronounced at the most posterior cervical joints (D1-C8, C8-7, and C7-6). The anterior joints are kept relatively constant throughout the movements, as is observed during neck retraction (Figure 7.16 and Figure 7.17). Lateral mobility

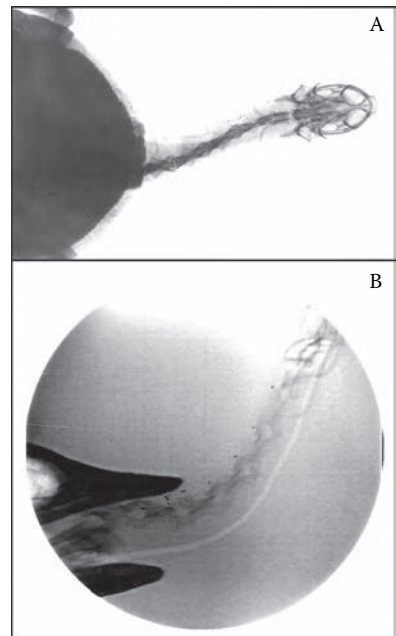


FIGURE 7.18 (A) Static cineradiographs recorded in dorso-ventral view illustrating the position and shape of the cervical vertebrae in *C. longicollis*. (B) Lateral view of the cervical system in *C. longicollis* during snorkeling. Note the radio-opaque markers inserted onto the cervical vertebrae to facilitate the analyses of vertebral movements.

appear less conspicuously related to the observed movements, show less overall change, and display a generally more irregular movement pattern. At very high degrees of elevation—at which also head position is also starting to change—changes in joint angle are mainly occurring in joints C5-4, C6-7, and especially C4-3 (more than 30° of dorsiflexion). This is not the case for C6-5. This joint reaches up to 20° of dorsiflexion and then levels off. Figure 7.21 illustrates the absolute range of movement (expressed in degrees of flexion) of each joint during the whole sequence. Notice the relatively minor joint rotations in the anterior (S-C1, C2-1, and C3-2) and posterior parts (C8-7, D1-C8) of the neck. As mentioned previously, the most conspicuous changes in joint angle are observed in the middle part of the neck, especially in joints C4-3, C5-4, and C7-6.

In summary, the range of mobility in the vertical plane of the cervical joints is limited, especially in comparison with the changes of joint angle in the horizontal plane. Dorsiflexion of the joints is more conspicuous than ventroflexion. Ventroflexion in the joints is nearly non-existent. The dominant changes in joint angle are observed in the middle part of the neck.

7.4 DISCUSSION

7.4.1 VERTEBRAL STRUCTURE

The nature of retraction of the head-neck system in turtles (in the vertical plane as in *Apalone* or in the horizontal plan as in *Chelodina*) has profound implications on the morphology of the cervical system. Although in both species the cervical vertebrae are markedly elongated, in *Chelodina* the vertebrae are rather narrow and tall. However, in *Apalone* the situation is reversed and the vertebrae are wide and rather shallow. Another marked difference is the presence of a pronounced ventral vertebral crest in *Chelodina*. In *Apalone*, these crests are only present in the most anterior vertebrae. The transverse processes that serve as insertion sites for the muscles of the longissimus are well developed in *Chelodina* and are positioned laterally at the border between the neural roof and the vertebral centrum. Because the longissimus system is absent in *Apalone*, the transverse processes are poorly developed and positioned more cranially. Also, the structure of the posterior zygapophyses is markedly different between the two species. Whereas in *Chelodina* there is only a single basal element carrying the two horizontally oriented articular facets, in *Apalone* two separate post-zygapophyses are present. Additionally, the articular facets are much more curved in *Apalone* compared to those in *Chelodina*. However, in both species the structure of the zygapophyses limits ventroflexion considerably.

7.4.2 CERVICAL MUSCULATURE

The differences in retraction mode in the two groups are also reflected in the structure and differentiation of the cervical musculature. As mentioned previously, for example, the longissimus system appears to be completely absent in *Apalone*. As head-neck movements typically occur in the vertical plane in these animals, this is not unexpected. Alternatively, in *Chelodina* the longissimus system is strongly developed. Notable in the cryptodires is the cortico-cervical muscular system that

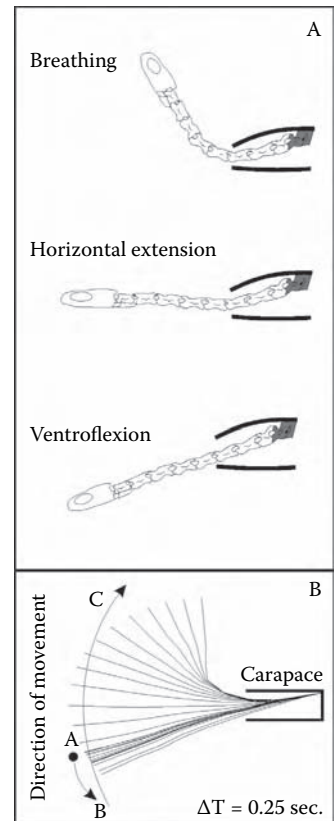


FIGURE 7.19 (A) Schematic illustration of the neck configuration in *C. longicollis*. (B) Stick diagram representing an actual snorkeling movement in *C. longicollis*.

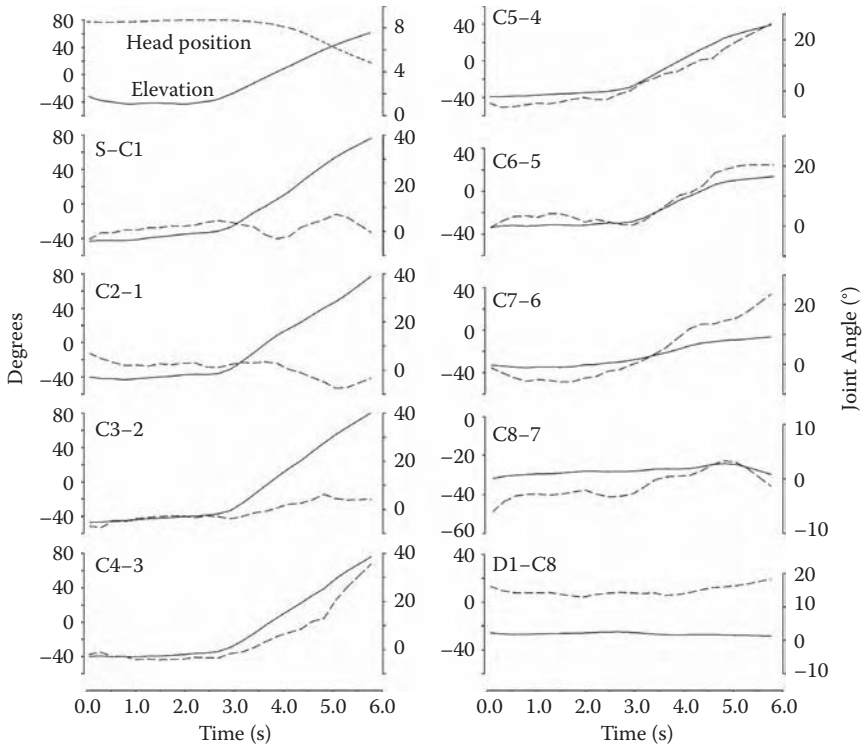


FIGURE 7.20 Kinematic plots illustrating time profiles of joint angle (dashed curves, right vertical axis) and elevation angle with respect to the horizontal of the more distal of the segments constituting the joint (solid curve, left vertical axis) during a snorkeling movement in *C. longicollis*. The first panel represents elevation of the head segment and the rectilinear distance (right axis in cm) between head and carapace.

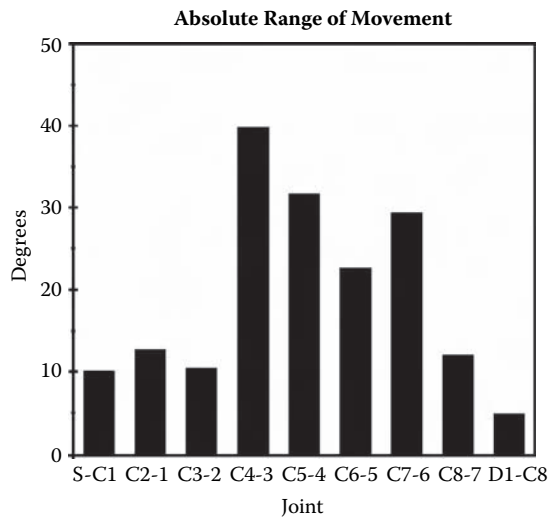


FIGURE 7.21 Movement range of the cervical joints in *C. longicollis* in the vertical plane.

presumably functions to protract and retract the neck. Preliminary electromyographic data for the cryptodire *T. scripta elegans* (Van Damme, unpublished) support this hypothesis. In pleurodires like *Chelodina*, this system is absent. Rather unexpectedly, the m. sphincter colli is poorly developed in *Apalone*. In *Chelodina* and most other pleurodires, this muscle appears much better developed and may actually play a role in aligning the cervical muscle bundles along the cervical column during neck movements. However, this remains speculative and must be tested by electromyography. Also, the dominant head retractor muscle, the m. retrahens capitis et collicque in *Chelodina* (Shah, 1963) and the m. carapace-basioccipitis in *Apalone* (Ogushi, 1913), is notably different in the two species. In *Apalone*, this muscle consists of a paired massive muscle bundle running from the first caudal vertebra to the back of the skull. In *Chelodina*, this muscle is more complex and consists of several discrete bundles that insert on specific sites along the cervical column.

However, a striking similarity among the two groups is the extreme length of the head retractor muscle. Presumably, elongation of the retractor muscle allows for more sarcomeres to be placed in series, which may considerably increase the contraction speed of the muscle (Josephson, 1975). Moreover, by increasing the number of sarcomeres in series, each individual sarcomere has to contract less and may thus potentially operate continuously on the plateau of its length-tension relationship. However, for an extremely elongated muscle to contract efficiently, all parts must contract simultaneously. The polyneuronal, polysegmental innervation of the m. carapace-basioccipitis in turtles (Guthe, 1981) may allow for this. Unexpectedly, the m. carapace-basioccipitis consists not only of fast twitch fibers but also has a considerable population of tonic fibers (Guthe, 1981), which may help control the position of the head and neck during slow movements or near-stationary behaviors such as snorkeling.

7.4.3 MOVEMENT PATTERNS

The cranio-cervical system in turtles can be characterized as an open kinematic chain of eight vertebrae and nine joints. Because each joint theoretically has three rotational degrees of freedom (and to a limited extent also three translational degrees of freedom), and because the positioning of the vertebrae must be achieved by the combined actions of roughly 50 symmetrical muscle bundles, the control of the position of the head in space obviously presents a challenging control problem (Aerts et al., 2001). However, the control of the system is largely simplified by a number of morphological constraints limiting the mobility at each joint. For example, in *Chelodina* the horizontal nature of the zygapophyseal articular facets and the vertical orientation of the articular facets of the condyle and the vertebral centrum will facilitate movements in the horizontal plane. Additional simplification of the control of the neck in *Chelodina* is achieved by the presence of distinct areas of rotation along the neck (Van Damme et al., 1995). For instance, the joint between cervical vertebrae 7 and 8 and the joints between cervical vertebrae 6-5 and 5-4 typically show the greatest range of angular change. Moreover, the resting position of the neck is characterized by a distinct bend at these locations, facilitating the correct retraction of the neck using only a simple activation of the m. retrahens capitis et collicque (Aerts et al., 2001). Dorso-ventral mobility is greatest at the joints C3-2 through C6-5. The joints surrounding the bi-convex articular centrum of C5 show the greatest angular change during dorsiflexion.

The cervical system in *Apalone* is notably divergent and the kinematic patterns are also markedly different from those observed in *Chelodina*. Upon retraction of the neck, the more caudally positioned vertebrae are the first to start their rotation around a transverse axis. The angular changes in all vertebrae are negative during retraction, suggesting that the neck is retracted as a safety-linked bicycle chain. Cervical vertebrae 5, 6, and 7 undergo an angular change of nearly 180°, which implies that these vertebrae end up with their ventral aspect alongside the ventral aspect of the immobile dorsal vertebrae. This is made possible by the nearly complete reduction of the ventral crest of these vertebrae. It is also striking that C8 remains in a near-vertical position at the moment of full protraction. The more anterior vertebrae (C1 to C4) do not contribute to neck retraction at

all. The bicycle-chain-like retraction pattern observed for *Apalone* is in contrast to the retraction patterns suggested in other cryptodires such as *Testudo* or *Trachemys* (Scanlon, 1982; Weisgram & Splechtina, 1990). In the latter species, as well as in *Chelodina*, distinct rotation centers are present where the majority of the angular rotation takes place. Thus, the extremely elongated neck and associated morphology of *Apalone* may not be representative for the cryptodiran condition in general but provide an excellent example of a highly specialized cervical system that can be compared to the condition in *Chelodina*. Clearly, further investigation into the morphology and function of the cervical system in turtles is needed to increase our understanding of the evolution of the cervical system and its control in turtles. Especially insightful would be studies exploring cervical structure and function in a broader sample of turtles including short-necked representatives of both cryptodires and pleurodires. Functional approaches including electromyography of the cervical muscles, albeit challenging, are essential to further our understanding of the evolution of the cervical system in turtles.

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8 Functional Evolution of Feeding Behavior in Turtles

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8.1 INTRODUCTION

Turtles have one of the most unusual body plans among the amniotes, with a carapace that constrains their behavioral activities differently from all other tetrapods (Gaffney, 1979; Reisz & Laurin, 1991; Laurin & Reisz, 1995; Lee, 1997; Schaffer et al., 1997; Pough et al., 2001; Cebras-Thomas, 2005; Kear & Lee, 2006; Shedlock et al., 2007). Although the origin and evolution of this clade of vertebrates is still unclear despite thorough discussion (Joyce & Gauthier, 2004; Hill, 2005; Nagashima et al., 2005), such a body plan appears to be conservative. However, reduction of the shell has been reported in relation to chelonian life strategies, especially in aquatic turtles (Pritchard, 1979). Evolutionary transformations of the locomotor system in aquatic turtles enable them to display highly adapted mobility and maneuvering, presumably for optimizing searching for food, sexual partners, and areas for egg laying (Davenport & Clough, 1986; Renous & Bels, 1989; Wyneken, 1997; Chapter 5). Although some sea turtle populations nest and feed in the same general areas, others (species or populations within a species) can migrate over great distances. Leatherbacks have probably the

longest migration of all sea turtles because they can be found more than 7000 km from their nesting beaches (Hughes et al., 1998).

Despite their “armored tank” shape, turtles have adopted specialized foraging and feeding strategies derived from those of the stem reptiles that have provided enduring advantages while simultaneously imposing basic restrictions. The living species of turtles, distributed among 99 genera and 14 families (Ernst & Barbour, 1989), inhabit a large number of various ecological niches in marine, freshwater, and terrestrial habitats from temperate and tropical regions of all continents except Antarctica, and in all oceans. It is well known that turtles are either specialized or generalized in their diet, with possible ontogenic dietary shifts being common (Pritchard, 1979). Foraging and feeding behaviors have been generally described for almost all families of turtles (Pritchard, 1979). Dietary preferences and ontogenic changes during the life cycles of turtles have been reported in numerous species, particularly in marine turtles. Most chelonians show dietary fluctuations during their lives and can shift from carnivorous to omnivorous and herbivorous diets as they age (Harless & Morloch, 1979; McCauley & Bjorndal, 1999; Bouchard & Bjorndal, 2006). Briefly, true terrestrial turtles (Testudinidae) are the only species able to ingest and swallow food on land, so are subject to the same constraints as all other truly terrestrial vertebrates. Apart from these turtles, a large number of species make forays into terrestrial habitats for feeding and drinking (e.g., Emydidae). Some other species are wholly water-feeders and chase their food by using various strategies from active foraging to sit-and-wait predator behavior (e.g., softshells, Tryonichidae). Some species can capture live food on land but swallow it in water. Several herbivorous species (e.g., Bataguridae) can feed on plant material at the surface of the water or can drag terrestrial vegetation into the water (Davenport et al., 1992). Some species can feed on land or in water, completing the process from food capture to swallowing in either medium (e.g., *Terrapene carolina*, Emydidae). Although basking on land has been reported in a few cases, marine turtles are generally found on land only in two situations: when adult females return to the land for egg laying and when hatchlings must travel from the nest down the beach to the sea. Marine turtles always forage and feed in the water.

A series of phylogenetic studies have demonstrated significant relationships between various characteristics of the trophic system and corresponding ecological specializations in some groups of turtles (Gaffney, 1975, 1979; Claude et al., 2004). From these data, there have been several hypotheses generated to demonstrate a relationship between feeding performances and the phylogenetic hypotheses. For example, the morphological variation of the superfamily Testudinoidea relates to both diet and habitat (Claude et al., 2004). These authors suggest that aspects of the feeding mode (e.g., diet) can be a key factor in determining morphological evolution and diversification of turtle skulls. Phylogeny appears to constrain only localized features of the skull and remains of minor influence.

8.2 OBJECTIVE

There are substantial problems in providing a complete overview of the feeding behavior of turtles using aquatic and terrestrial habitats based only on previously published data: kinematic and functional analyses of complete feeding mechanisms are relatively rare, and feeding behavior has been studied using non-standardized methods and techniques. In his comprehensive volume of evolution of feeding behavior in tetrapods, Schwenk (2000) provides an exhaustive list of literature describing feeding behavior and mechanisms in turtles. The present chapter provides the first comparative analysis of feeding behavior in turtles. Though aquatic feeding has been studied in several very different representative species drawn from fresh water families, few data are available concerning the feeding behavior of marine turtles or of terrestrial turtles. Consequently, this chapter will not only provide information from the literature but will also present data collected by the chapter's authors, together with their analyses of feeding behavior in terrestrial and aquatic species. All of these data are considered from a comparative viewpoint. When necessary, a rapid survey of the methods used

for collecting data is provided for each of the feeding modes, terrestrial and aquatic. The mechanism of neck movements that play a key role in feeding in turtles is discussed in Chapter 7.

8.3 FEEDING STRUCTURES

Detailed analyses have been made of the skull, hyobranchium, and tongue in turtles (Lindeman, 2000; Schwenk, 2000; Claude et al., 2004). When needed, we provide morphological data that are necessary to explain the functional and biomechanical aspects of feeding behavior. Some functional analyses demonstrate how structures are used in various phases of feeding in aquatic turtles (Schwenk, 2000; Lemell et al., 2002).

8.4 OVERVIEW OF FEEDING AND DRINKING BEHAVIORS

A rapid survey of the evolution of turtles and their diet show that turtles use two main feeding strategies to gain water, energy, and nutrients: feeding/drinking on land and feeding in water. Drinking water is a particular problem for terrestrial turtles and for some turtles living in saline/marine habitats. All of these turtles need to drink water (when available) to maintain the hydric balance that is essential to welfare and survival. Water intake rates and frequencies are highly variable among turtles. For example, some desert turtles are able to consume a large amount of water in one intake, thereby increasing body mass by up to 40%. Drinking in aquatic turtles has been rarely described. A recent study demonstrated that hatchling sea turtles can osmoregulate effectively and gain mass by drinking sea water (Reina et al., 2002). Although well reported in the literature, drinking behavior has been quantified only in *Malaclemys terrapin* (Davenport & Macedo, 1990; Bels et al., 1995). This species is able to modulate its drinking posture in relation to the water source; it can drink from very thin films of fresh water either on the sea surface or on the surface of intertidal mud, and can even drink directly from falling rain or from water droplets on vegetation (Davenport & Macedo, 1990). *Malaclemys* can also forcibly expel water out of the bucco-pharyngeal cavity when disturbed during the drinking sequence, or when the volume of water within this cavity is too great. *Malaclemys* can expel water very quickly (less than 1 s) by a sudden gape increase accompanied by throat elevation and neck retraction (Bels et al., 1995).

As recognized for all vertebrates, feeding behavior in turtles is a modal-action-pattern (MAD), involving movements of the trophic elements integrated with neck displacements, sometimes associated with complex limb movements, sometimes not. All of these coordinated sensori-motor movements define the feeding strategy of turtles. Any food item consumed by turtles (from plant material to fast-moving mobile prey) must be located and ingested by a rhythmic series of head, jaw, and hyolingual movements. There are three major successive phases in terrestrial turtles (Schwenk, 2000): ingestion (capture), transport and intrabuccal manipulation, and swallowing. A fourth phase called pharyngeal packing occurs at the end of several feeding sequences but does not involve any jaw opening-closing cyclic movement (Figure 8.1). Since the earliest functional studies of vertebrates, a clear difference has been demonstrated between feeding strategies in water and on land (Liem, 1990). Incompressible water can be used to drive a mobile food item (living prey) into the buccal cavity by producing negative pressure inside that cavity. When food is caught, it must be transported and swallowed.

All feeding phases are based on rhythmic coordinated series of movements of the trophic elements (e.g., jaws, tongue, hyobranchium) associated with neck movements producing whole displacement of the head (Figure 8.1). These movements are probably the result of rhythmic jaw movements generated by a central neuronal population called the central pattern (or rhythm) generator (CPG) (Schwenk, 2000). All rhythmic jaw opening-closing activities are modulated by sensory feedback generated by various structures within the buccal cavity. For example, taste buds have been described in the buccal and tongue epithelium of several species of turtles (Iwasaki, 1992, 2002; Iwasaki et al., 1996a, 1996b, 1996c, 1996d; Beisser et al., 2001). Although a large number of

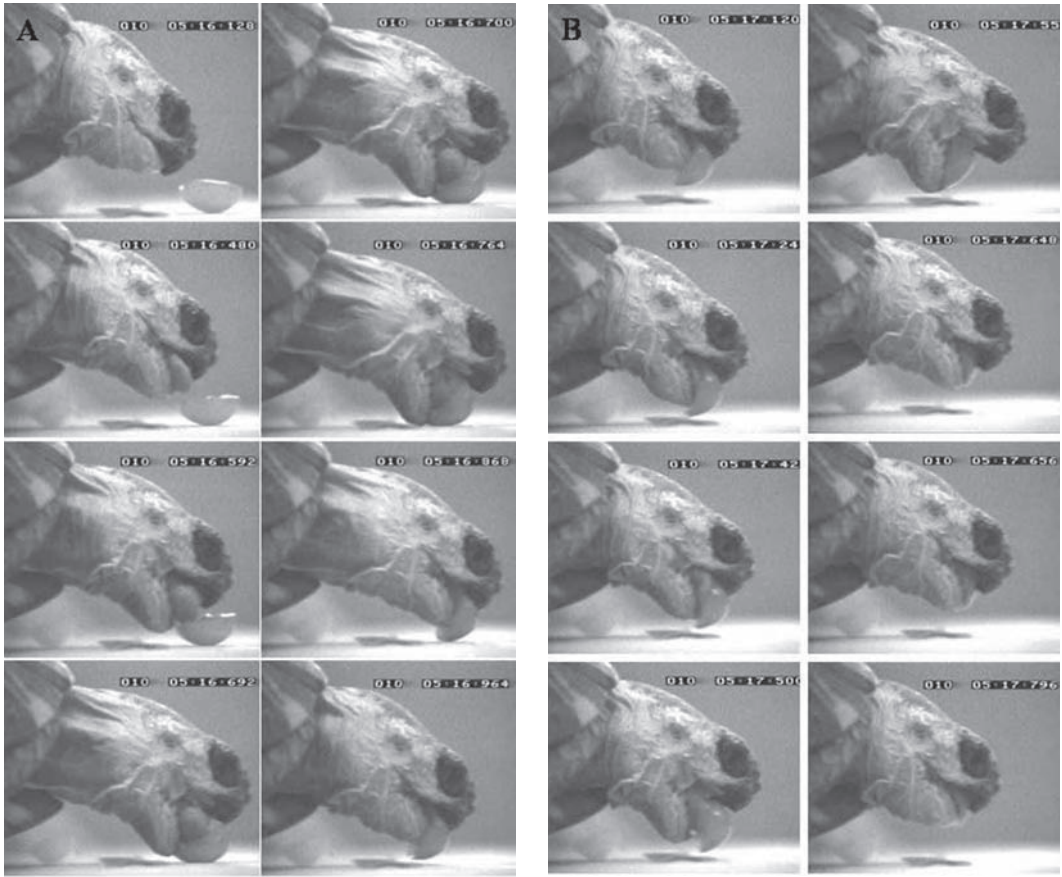


FIGURE 8.1 Series of frames depicting the successive events of a typical feeding sequence in *Geochelone radiata* eating a piece of grape. (A) Ingestion cycle, (B) transport cycle, (C) swallowing or pharyngeal packing, and (D) pharyngeal compression. Food ingestion always involves contact by the tongue prior to surrounding by the jaws for grasping. Food ingestion and transport involve rhythmic cyclic jaw and tongue movements. In transport, the forward movement of the tongue is modulated by the position of the food in the buccal cavity. In swallowing, the mouth is opened and the food moved toward the pharynx. In pharyngeal compression, the jaws always remain closed. The timing of each frame is provided in ms (last three numbers recorded on the frames).

studies provide information on the foraging behavior of turtles, no quantitative analysis has actually demonstrated the effect of food properties (i.e., texture, volume, size) on the modulation of the movements of the trophic system (e.g., jaws, tongue, and hyobranchium). In the majority of studies, turtles have been fed in the laboratory on standardized prey items (e.g., live fish as elusive prey) or plant material (e.g., fruits and lettuce items for terrestrial species, available plants for aquatic species) for herbivorous species.

For aquatic turtles mainly living on the substratum, hunting strategies usually involve immobility while awaiting prey proximity before striking, or moving slowly toward the prey. For example, a very slow (0.4 cm s^{-1}) stalking motion is reported in the highly camouflaged pleurodiran *Chelus fimbriatus* that moves toward its prey until the tip of the snout is close to the prey itself (Lemell et al., 2002). Lemell and Weisgram (1997) described the feeding sequence in the aquatic *Pelusios castaneus* while catching prey on the substratum by associating movements of the turtle and the use of the trophic system. Lauder and Prendergast (1992) described a preparatory phase in

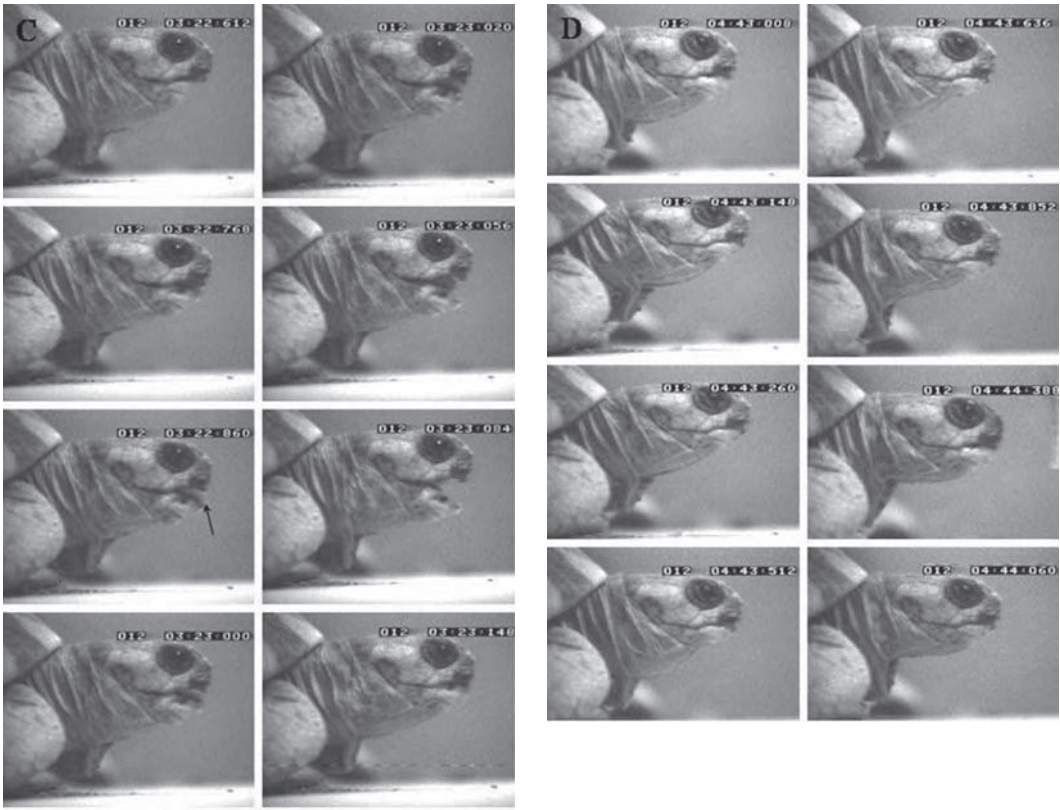


FIGURE 8.1 (continued)

Chelydra serpentina feeding on various prey types that consists of a slow, voluntary stalking movement with little horizontal body and neck movement before a fast opening of the mouth associated with a sudden neck extension (see Chapter 7). Slow stalking movement prior to mouth opening was also reported in *M. terrapin* eating food on the substratum (Bels et al., 1998).

From a functional point of view, it is rather difficult to determine the integration between locomotor and trophic systems for these turtles because in the laboratory, food is often presented at too short a distance from the head to measure the kinematic and hydrodynamic characteristics of the feeding behavior. However, it is clear that the neuromotor integration between both systems plays a particularly key role when turtles are hunting in the water column, or when the prey items show specialized behavior or physical texture (e.g., shells in mollusks and crustaceans). Many aquatic turtles must associate complex limb movements with neck movements and rhythmic movements of the trophic system to support the complex maneuvering ability that improves food capture success (Figure 8.2). Davenport and Clough (1985) report an apparently unique feeding behavior that involved the use of the fore flippers to gain food in the marine turtle *Caretta caretta*. These authors observed the role of “pseudoclaws” (sharp-pointed scales) on the proximal portions of the forelimbs of young specimens to allow the combined use of foreflippers and beak to tear food items that are otherwise too large to be swallowed whole or readily bitten into chunks (thus mimicking the feeding behavior of freshwater turtles such as emydids that use true claws and the beak to achieve a similar goal) and allowing food morsels adhering to the pseudoclaws to be ingested by the turtle.

Feeding behavior in the brackish-water emydid *M. terrapin* is the best example currently available in the literature to demonstrate plasticity in neuromotor integration of limb, neck, and trophic systems during prey capture (Bels et al., 1998). Capturing immobile prey (e.g., mussels) on

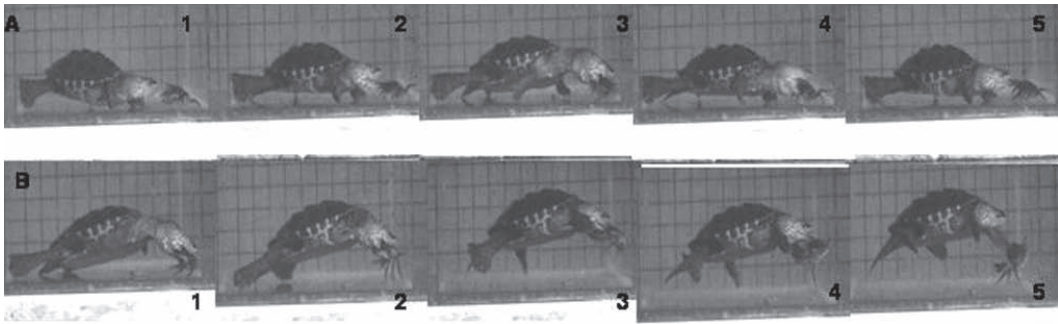


FIGURE 8.2 Two typical feeding sequences of *Malaclemys* attacking a defending crab. These sequences show the complex interaction between the turtle and the living prey. However, images show the stereotyped pattern of neck extension, gape cycle, and throat depression for both attempts to ingest parts of the crab. The arrow shows the jumping behavior of the crab attacking the turtle that defends by biting (corresponding to ingestion cycle).

the substratum is mainly achieved by coordinated neck extension and jaw opening with relatively small inertial suction (Van Damme & Aerts, 1997; see following for discussion). Capturing mobile and aggressively defensive prey in the water column (e.g., living crabs) requires coordination of neck extension and jaw opening with the limb cycles used for swimming. In all cases, the neck is extended to place the opening jaws close to the prey during limb retraction, to increase the thrust of the turtle toward the prey (Figure 8.2). Another sort of coordination of limb, neck, and jaws has also been described. Bels and Renous (1992) and Bels et al. (1998) demonstrated that feeding on soft, slowly swimming prey (jellyfish) by young leatherback turtles always involves placement of the long foreflippers alongside the body during the catching cycles. They suggest that this strategy strongly decreases the possibility of limb movements displacing jellyfish away from the buccal cavity. In terrestrial habitats, turtles often approach food slowly and stop all movements before capturing the prey or biting the plant material.

The use of the limbs in all other feeding phases remains relatively poorly understood. For turtles feeding in the water column (e.g., Emydidae), the limbs play a major role in optimizing food transport (Bels et al., 1998); typically, the forelimb claws are used to tear large food items into smaller pieces. However, for turtles that feed in terrestrial habitats, the limbs only play an occasional role by stabilizing the position of a food item on the substratum or aiding the seizure of “difficult” hard food items between the jaws (e.g., Testudinidae eating living prey such as snails). All of these examples show that functional studies must be ecologically relevant to yield a full understanding of turtle feeding strategies and their plasticity that plays a key role in the overall fitness of the organism.

8.5 KINEMATICS

8.5.1 TERRESTRIAL FEEDING

8.5.1.1 Ingestion

Two modes of food prehension have been reported for terrestrial turtles: lingual prehension and jaw prehension (Figure 8.1 & Figure 8.3). A clear difference in ingestion cycles has been reported for *Terrapene* sp. feeding on insects and *Geochelone* sp. feeding on plant material. *T. carolina* and *T. ornata* never use lingual prehension but only jaw prehension when catching insects (e.g., Bels et al., 1997). *Geochelone* sp. and *Testudo* sp. always use lingual prehension for feeding on plant material. For mobile prey (mealworms, as used in *Terrapene* studies), *Kinixys* also uses lingual prehension. However, no quantitative comparative analyses of the modulatory effects of food items

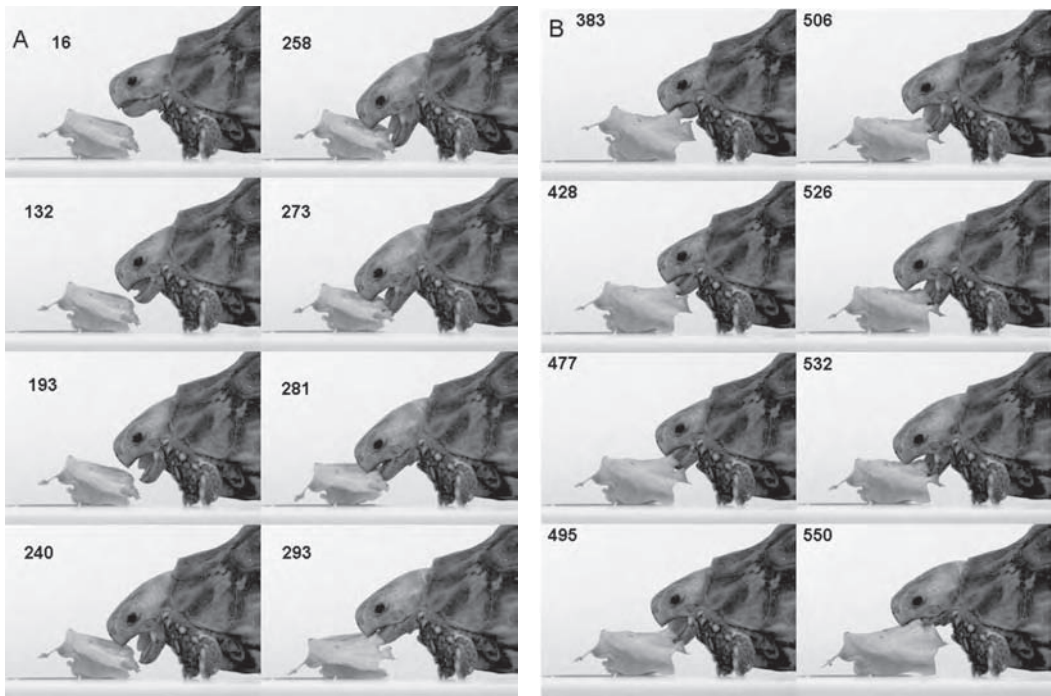


FIGURE 8.3 Series of frames depicting the successive events of a typical feeding sequence in *Kinixys beliana* eating a piece of lettuce: (A) ingestion cycle and (B) transport cycle. Food prehension does not involve contact by the tongue outside the buccal cavity. Food transport involves rhythmic cyclic jaw and tongue movement. Contact between tongue and food occurs within the buccal cavity. In transport, the forward movement of the tongue that plays the key role is modulated by the position of the food in the buccal cavity. The timing of each frame is provided in ms (last three numbers recorded on the frames).

on kinematic and motor variables have yet been reported in these representative tortoises of Testudinidae. In cases of living prey (e.g., insects), only one ingestion cycle is used to catch the food and drive the food item into the front of the buccal cavity. In *Terrapene* sp. studied with this food item, the jaw moves quickly around the prey and the tongue is never used for prehension of insects (Bels et al., 1997). For plant material, the ingestion (capture) cycle is more complex and depends on the size of the food item because the feeding bout is a continuous process that does not terminate at one particular phase. Two examples demonstrate this complexity. For relatively large food items such as grapes, *G. radiata* contacts the food with the tongue and retracts the food item within the buccal cavity while the jaws are moving around the food. The turtle usually uses one to three ingestion cycles to bring the food material successfully into its buccal cavity. Similar behavior has been reported for the herbivorous lizard *Uromastix* fed on endive (Herrel et al., 2002). The *G. radiata* head is then placed in an approximately horizontal position during the immediately subsequent cycles, allowing transport and intrabuccal manipulation; for “long” food items such as lettuce leaves that are drawn into the mouth by rhythmic jaw cycles, the food items are caught by the tongue and the jaws move the piece of food around several times before the food partly or completely enters the buccal cavity. It is rather difficult to separate food ingestion and transport because at each tongue cycle (Figure 8.1 and Figure 8.3), the food within the buccal cavity is moved by the mid and posterior portions of the tongue while the foretongue moves to adhere to the parts of the food item that are still outside of the buccal cavity. When a piece of food is cut off, the turtle can stop to ingest the rest of the food item, which continues to be acted upon only by transport cycles. Such a continuous

process of ingestion-transport is strongly influenced by the size of the food material. When a short piece of lettuce is provided to turtles, only one or two ingestion cycles are used to deal with the food. The effect of the size of the food item on the continuous process involving the foretongue to catch the food item and the mid- and hindtongue portions for transporting the food has been clearly demonstrated in all herbivorous mammals feeding on long pieces of hay (Bels, 2006), so this process is not unusual in vertebrates. As soon as the food is within the buccal cavity of *G. radiata*, a series of integrated head (neck), jaw, and hyolingual cycles termed transport-intrabuccal manipulation move the food posteriorly toward the pharynx. At the end of a complete sequence, cycles determining the swallowing phase typically show a different gape profile as has been noted in herbivorous lizards (Herrel & De Vree, 1999).

In both modes of food prehension, turtles always use combined movement of the jaws, the head, and the neck that may or may not be associated with displacements of the hyolingual apparatus. All ingestion cycles in all terrestrial turtles are accompanied by neck extension, moving the opening jaws toward the food item (Figure 8.4). During the next extension, the head is positioned relative to the food item depending on the properties of the food and its proximal cues (i.e., size, volume, texture, mobility), showing a complex sensory-motor mechanism controlling the initiation of this feeding phase. At each ingestion cycle, the turtle rotates the head in various positions to be able to take hold of the plant material. The sensory-motor mechanisms underlying such functional plasticity during ingestion remain understudied. In terrestrial turtles, the question of positioning the head together with a neck extension remains an open question. Probably differences in the speed of head movements toward the food are key parameters that permit these reptiles to modulate head rotation during food ingestion. This difference can be seen as a functional consequence of diet selection in terrestrial turtles.

Two main types of ingestion cycles have been reported: jaw prehension and lingual prehension. In both modes of food prehension, turtles always use combined movements of the jaws, the head, and the neck, associated or not with displacements of the hyolingual apparatus. In all prehension, the mouth is opened in slow (SO) and fast (FO) stages (Figure 8.4). However, the duration of SO stage is variable. In *T. carolina* and *T. ornata*, a clear distinction between SO and FO stage was not always easy to determine because the gape increases rather regularly, and often the mean duration of FO stage is longer than that of the fast closing (FC) stage. The tongue always moves forward within the buccal cavity during gape increases and retracts during the beginning of the FO stage. Upon protrusion, the tongue bulges and the tongue tip curves ventrally, so that the foretongue makes contact with the food item. During the SO phase, the tongue is protruded from the mouth and contacts the food. Next, the tongue continues to be extended and pushed against the food item. The food is then maintained in contact with the tongue because of strong mucous adhesion between the tongue surface and the food. Once the tongue has been retracted within the jaw margins, the jaws are closed quickly, and the slow closing/power stroke phase started. The mean duration of the FO stage is longer than that of the FC stage. During the decrease in gape size, the lower jaw arrives under the beak formed by the upper jaws as in transport cycles. The tongue moves forward while the gape increases and contacts the food before maximal gape is achieved. Retraction of the tongue occurs during the beginning of the FO stage. After closing the jaws on the prey, the head retracts and rotates in reverse. Timing of kinematic events of *G. elephantopus* (lingual prehension) and *T. carolina* (jaw prehension) is similar in these different species (Figure 8.4). For example, peak hyoid retraction occurs just after peak gape angle and maximum throat depression occurs 30 to 100 ms after maximum gape angle. The successive six events in both turtles can be summarized as follows:

- Neck extension to drive the head toward the food
- Opening of the mouth (SO and FO stages)
- Retraction of the tongue during the beginning of the FO stage
- Depression of the throat immediately following the tongue retraction

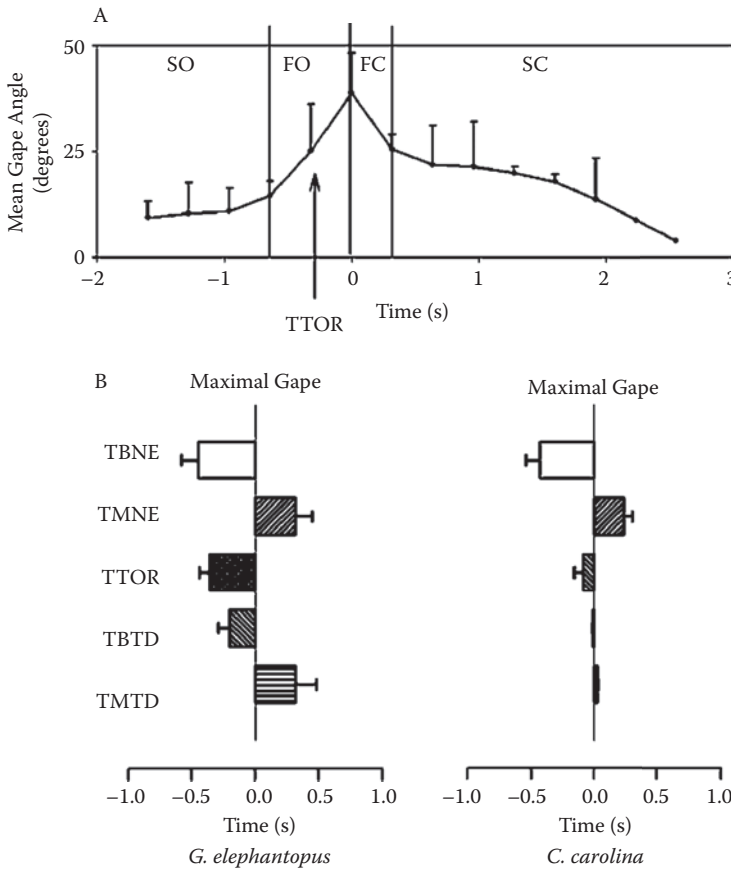


FIGURE 8.4 (A) Mean gape profile (\pm standard deviation) from 10 lateral ingestion cycles in one specimen of *Geochelone elephantopus*. The arrow indicates the mean time of tongue retraction. (B) Comparison between timing events in *G. elephantopus* and *T. carolina* (data from Bels et al., 1997). Timings were calculated from the time to peak gape angle (time 0). Gape is divided into slow opening (SO), fast opening (FO), fast closing (FC), and slow closing (SC). TBNE: time to beginning of the neck extension, TMNE: time to maximal neck extension during ingestion cycle, TTOR: time to tongue retraction, TBTD: time to beginning of throat depression, TMTD: time to maximum throat depression.

- Closing of the mouth on the food
- Retraction of the head toward the carapace.

8.5.1.2 Intra-oral Transport Cycle

As soon as the food (e.g., living prey, plant material) enters the buccal cavity, transport of the food toward the pharynx begins. For example, after ingestion of a mealworm, the prey is not completely held within the buccal cavity and is reduced (i.e., partially crushed) by the jaw margins at each transport cycle (Figure 8.3 and Figure 8.5). Because the mealworm enters the buccal cavity progressively, successive portions of the mealworm are reduced at the closing stage of each transport cycle.

The slow opening of the mouth during transport is composed of the SO I (opening) and often SO II (stationary stage) stages. The FO stage corresponds to a rapid increase in the vertical displacement of the jaws (Figure 8.5). The FO stage begins after a slight decrease in gape angle at the end

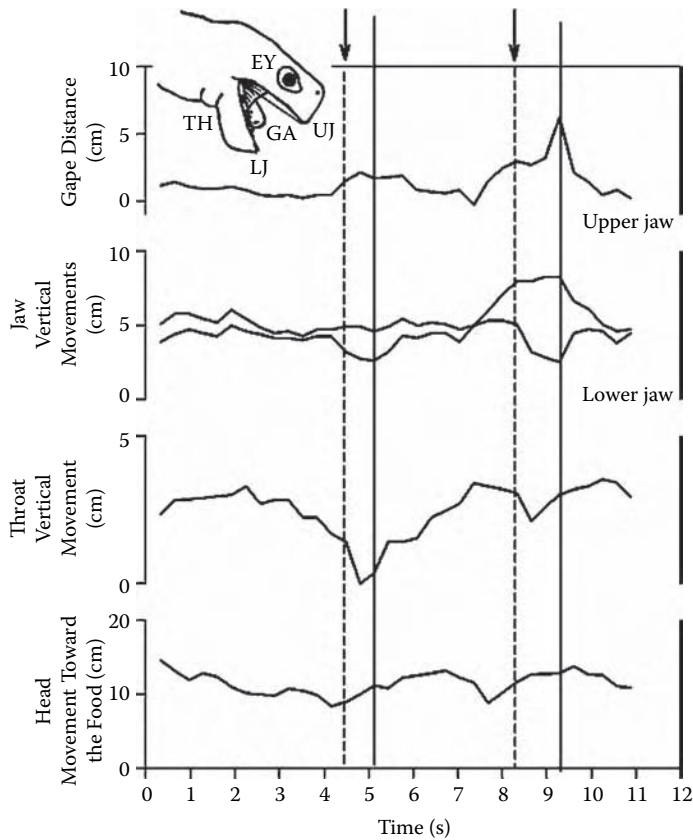


FIGURE 8.5 Kinematic profiles of two successive intraoral food transport cycles in *G. elephantopus*. Throat vertical movement (TH) associated with tongue retraction shows the cyclic depression and elevation of the throat. Head movement toward the food was measured by the horizontal displacement of the eye (EY). This movement shows the cyclic displacement of the jaws toward the food associated with gape angle (GA) produced by combination of vertical movement of the upper (UJ) and lower (LJ) jaws. The arrows indicate the first frame of tongue retraction with the food adhering to the tongue surface and the line indicates peak gape angle for each of the gape cycles.

of SO stage. The closure of the mouth is divided into fast closing (FC) and slow closing (SC) stages. The FC stage corresponds to a rapid decrease in the vertical displacement of the jaws. The SC stage corresponds to the elevation of the lower jaw under the beak of the upper jaw. The horizontal distance between the tip of the upper jaw and lower jaw decreases during the FC stage because vertical displacement of the lower jaw produces an arc, and the upper jaw moves little. The SC stage is not reflected in recordable gape angle and gape vertical distance changes because the lower jaw moves under the edges of the upper jaw. However, during this stage the horizontal distance between the tip of the upper jaw and the most anterior point of the lower jaw increases just after FC stage in the gape cycle, indicating that the lower jaw continues to close against the upper jaw. When gape increases during the SO stage of the next cycle, this horizontal distance decreases again.

In the transport cycle, during the SO stage the tongue is protracted as illustrated by a decrease of the horizontal distance between the tips of the tongue and the lower jaw (Figure 8.3B and Figure 8.5). At the same time, the tongue is slightly elevated. In the transport cycle, the forward displacement of the tongue into the buccal cavity is strongly correlated with the vertical displacement of the lower jaw during the SO stage. When the tongue moves forward, the lower jaw depresses

(SO I), and when the tongue is stationary prior to moving backward during the FO stage, the lower jaw does not move and the gape angle remains stationary (SO II). The head extends during the FO stage and the beginning of the FC stage, and depresses during the SO, FO, and the beginning of FC stages. During half of the duration of the SO stage, the head rotates downward as showed by the vertical displacement of the head. Preliminary analysis of food transport by using x-ray video (250 Hz) in a typical plant feeding turtle, *K. belliana*, shows that the food is accumulated within the pharynx and the rear part of the buccal cavity (Figure 8.6). Subsequently, swallowing of the alimentary bolus begins.

8.5.1.3 Swallowing

According to Schwenk (2000), we can divide swallowing in terrestrial turtles into pharyngeal packing (opening of mouth) and pharyngeal compression (no gape cycle). Figure 8.3 and Figure 8.6 show typical swallowing cycle in two *T. carolina* (Figure 8.3) and *K. belliana* (Figure 8.6) feeding on different food items (mealworms in *T. carolina* and lettuce leaves in *K. belliana*). Probably based on the sensory-motor feedbacks from properties of the alimentary bolus (i.e., volume, size, toughness), the turtle either enters into a new feeding sequence that drives more food into the pharynx,

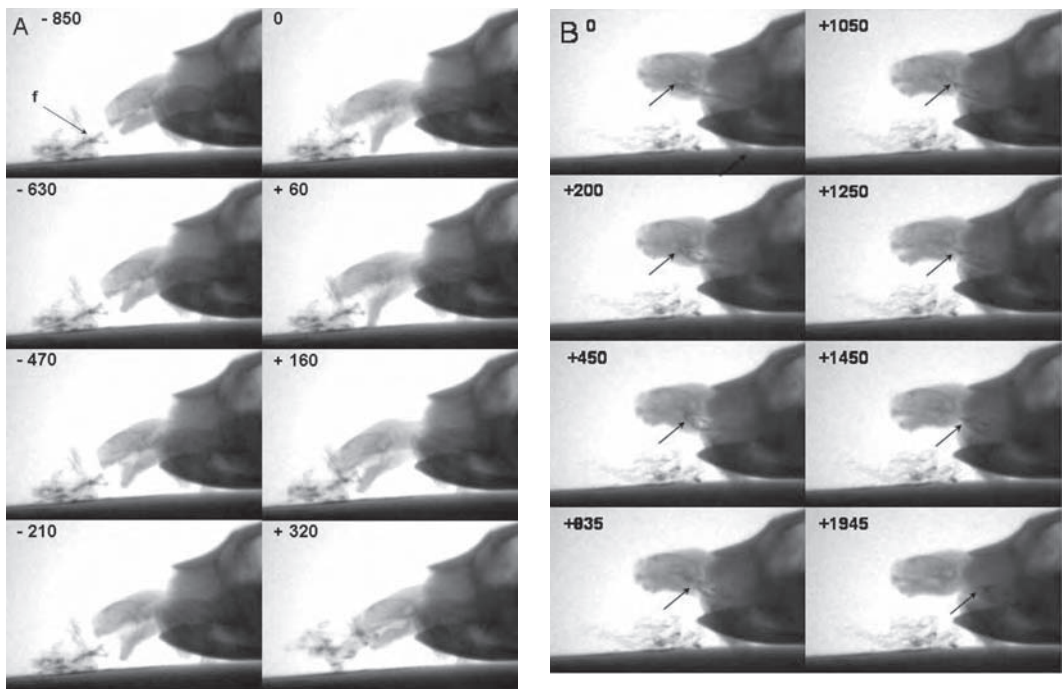


FIGURE 8.6 (A) Typical ingestion cycle of a piece of lettuce in *K. belliana* filmed by x-ray videofluorography (100 Hz), showing the tongue contacting the food whereas the jaws moved to surround the food material (leaf of lettuce). The contact between the tongue and the food occurs within the buccal cavity at time 0. (B) Typical swallowing cycle filmed by x-ray fluoroscopy (200 Hz) involving mouth opening to show the combined movement of the food associated with the swallowing cycle, demonstrating the key role of the tongue and throat in the posterior displacement of the food toward the esophagus. Peristaltic activity of the esophagus helping movement of the food within the esophagus is also shown. The displacement of the food along pharyngeal packing is shown by the arrow on each frame. Time 0 corresponds for this cycle to the first frame of mouth opening. f: markers (the lettuce was covered with a thin film of water charged with barium powder).

or moves the bolus into the esophagus, which structure drives the bolus directly to the stomach by peristaltic movement. For emptying the pharynx, the turtles produce either jaw cycles or pharyngeal compression (Figure 8.6).

8.5.2 AQUATIC FEEDING

Feeding in aquatic turtles has received more attention than that of terrestrial turtles, although relatively few species have been studied. However, robust experimental conditions with more-or-less similar environmental constraints have been employed. Since the first quantitative analysis of feeding mechanism in *Chelydra* (Lauder & Prendergast, 1992), turtles have been used for testing hypotheses and generalizations regarding morphological and functional patterns associated with aquatic feeding in lower vertebrates.

The large number of species and foraging strategies in aquatic-feeding turtles probably reflects a rather unique group of vertebrates that has evolved aquatic feeding convergently with anamniote feeding systems and with amniotes that have returned secondarily to aquatic environment such as several mammals. Many food resources can be exploited in aquatic habitats. Plant material constitutes a first source of food. This material can be firmly attached to the substrate and must be bitten and extracted or pulled out before being transported and swallowed. Other plant material can be floating and must be bitten and caught from beneath (Davenport et al., 1992). Living prey can be exploited by rapid strikes if they have elusive abilities (e.g., fishes) or must be approached slowly to avoid their movement away of the buccal cavity (e.g., jellyfish). Since the earliest analyses of feeding mechanisms in water, the question of importance of suction has remained paramount (Aerts et al., 2001; Figure 8.7).

8.5.2.1 Ingestion Cycle

Aquatic turtles all show much the same pattern of head, jaws, and hyobranchium movements. To our knowledge, the tongue is not used for capturing aquatic prey. Typical capture cycles for some aquatic turtles (*C. longicollis*, *C. fimbriatus*, *C. serpentina*) involve a sudden forward thrust of the head by neck extension (see Chapter 7). In contrast, other species strike less rapidly (mean duration between 250 and 300 ms in *M. terrapin*, Bels et al., 1998; 400 ms in *T. carolina*, Summers et al., 1998; and up to 800 ms in *D. coriacea*, this chapter), opening the mouth either by using SO and FO stages or regularly without the SO stage. All kinematic profiles available in the literature provide classical examples of neck extension producing a sudden thrust of the opening mouth associated with large depression of the hyobranchium. Depression of the hyobranchium occurs 30 to 50 ms after maximum gape (Lauder & Prendergast, 1992; Bels & Renous, 1992; Van Damme & Aerts, 1997; Bels et al., 1998; Summers et al., 1998; Lemell et al., 2002).

The problem of approaching the food in aquatic environment always remains the same: any flow of water produced by the turtle must be compensated for in efficient capture. Lauder and Prendergast (1992) were the first to stress the hydrodynamic constraints on aquatic prey capture resulting in kinematic similarities among predators such as fish, amphibians, and turtles. Their findings were supported by other analyses of ingestion in turtles from freshwater and marine habitats. All of the aquatic turtles can generate a backward water flow relative to the buccal cavity (called suction) to acquire the food (Van Damme & Aerts, 1997). Van Damme and Aerts (1997) discussed in depth the question of compensatory and inertial suction in prey capture by aquatic turtles. The term “compensatory suction” indicates suction used to maintain food immobile during the strike, and permits engulfing of the food as the jaw apparatus surrounds it. The term “inertial suction” is used to describe suction in which food and water move toward the buccal cavity whereas the head of the predator remains essentially immobile (Van Damme & Aerts, 1997; Aerts et al., 2001). Aerts et al. (2001) state that probably food capture in various aquatic turtles is related to a combination of both modes of suction, as demonstrated by displacements of various food items recorded in different aquatic turtles. For example, inertial suction plays a major role in *Chelodina longicollis*

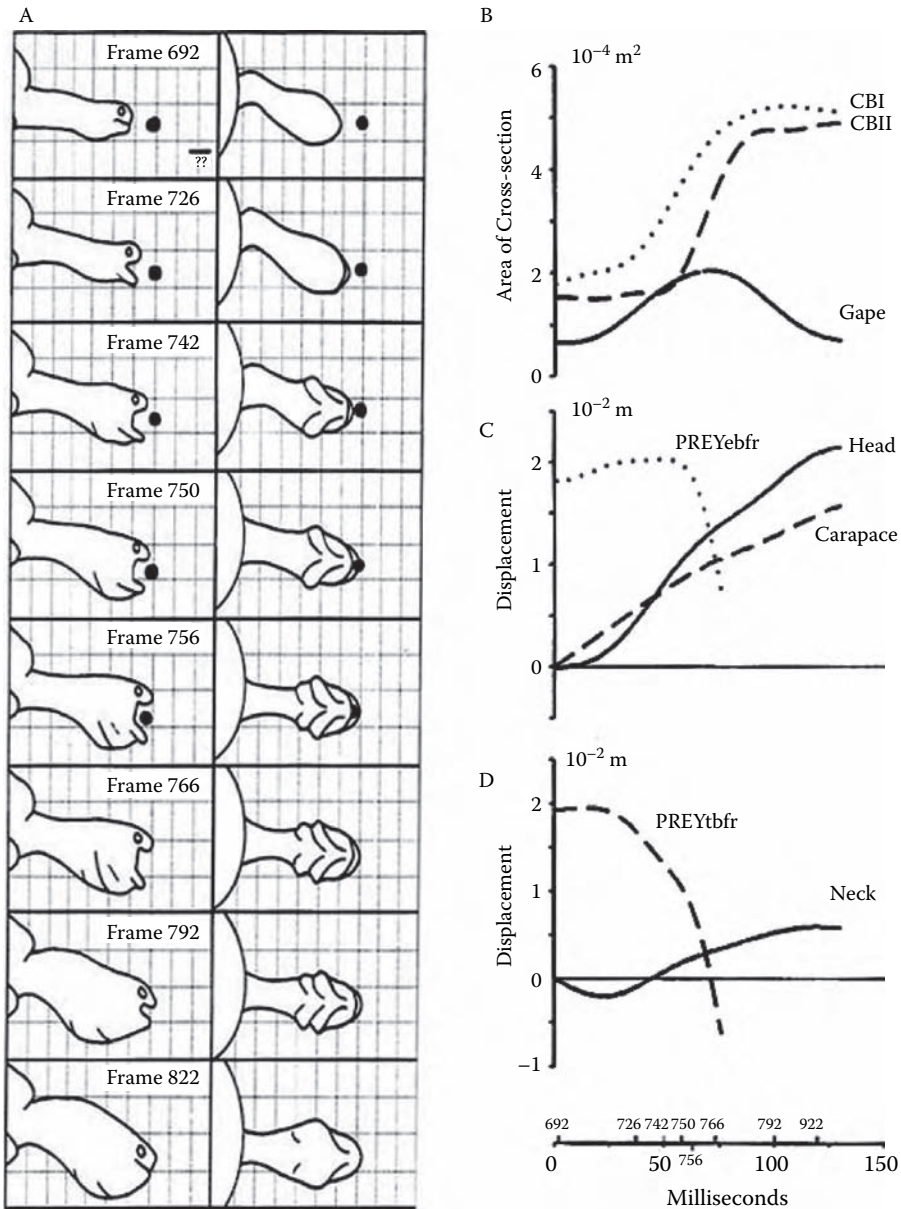


FIGURE 8.7 (A) Drawings of lateral and ventral views of the strike used for illustrating the kinematic profiles. (B–D) Kinematic profiles of one representative strike in *Chelodina longicollis* to show (B) the modification of areas of cross sections through three successive levels on the head of the turtle (Van Damme & Aerts, 1997): the mouth (gape) and at the level of ceratobranchial I (CB I) and II (CB II), the displacement, of the prey, the head, and the carapace of the turtle in the earth bound frame of reference (ebfr = fixed frame of reference). Time scale is given in ms and numbers of the upper time scale correspond to the number of the sequences presented at the left of the figure. (Modified from Van Damme & Aerts, 1997.)

but compensatory suction is dominant in *C. serpentina* (Van Damme & Aerts, 1997). Van Damme and Aerts (1997) and Summers et al. (1998) do not agree with the use of the ram/suction index (RSI) proposed by Norton and Brainerd (1993) to describe the feeding mechanisms of fishes. In their recent study, Lemell et al. (2002) applied this index to capture of by *C. fimbriatus*. The equation for RSI is

$$RSI = \frac{D_{predator} - D_{prey}}{D_{predator} + D_{prey}}$$

where $D_{predator}$ and D_{prey} are the net distances moved by the predator and the prey between the moment the mouth first begins to open and the moment the prey disappears or is seized by the jaws). RSI ranges from +1, indicating a pure ram strike in which only the predator moves, to -1, indicating a pure suction strike in which only the prey moves. The calculated RSI during prey (fish) capture in *P. castaneus* varies between 0.36 and 0.55, and in *C. fimbriatus* was always positive (mean = 0.36 \pm 0.23, range = 0.071 to 0.664; prey = fish; $N = 20$). However, these authors think that the equation used for RSI tends to overestimate the ram component.

Whatever the terms used for describing food capture (e.g., suction, RSI), and whatever the hydrodynamic calculations or other considerations involved, all aquatic turtles must expand the oropharyngeal cavity for successful food capture. Summers et al. (1998) demonstrate clearly that prey capture in water involves greater hyoid depression in *T. carolina* feeding in water compared with feeding on land. These authors and Bels et al. (1998) show that hyoid depression is modulated not only from land to water but also in water feeding in relation to food type and behavior (e.g., crabs capable of defensive behavior). It is evident that this expansion plays a key role in the successful capture of elusive prey by any mode of prey displacement toward the buccal cavity (inertial suction) or of maintaining the prey immobile in the water column (compensatory suction). Aerts et al. (2001) suggest that functional demands related to feeding in water always relate to expansion of the area posterior to the jaw apparatus that opens to allow prey and water to enter partly or completely into the oropharyngeal cavity. However, the role of this expansion becomes less important in turtles feeding upon plant material floating at the surface, pulling material out of the substratum, or attacking a vigorously defending prey. In the latter case, biting performance by the jaws probably plays the key role because it allows the turtle to obtain food and also defend against the attack of the self-protecting potential prey (Herrel et al., 2002). Despite large structural variations, the expansion of the oropharyngeal cavity is mainly produced by movement of the hyobranchium as nicely demonstrated by x-ray films (Aerts et al., 2001; Lemell et al., 2002). For illustrating the motor control of throat expansion in *Chelonida*, few data are available. Aerts et al. (2001) provided the first description of motor sequences that show depression and retraction of the hyoid body (Figure 8.8). Lemell et al. (2002) report that the esophagus is filled with the large amount of water sucked in during the gape cycle until the mouth is closed. These authors provide a complete x-ray analysis of prey movement within the bucco-pharyngeal cavity (Figure 8.9). In all turtles, the prey is either sucked inward (inertial suction) or bitten by closing jaws (compensatory suction). In the meantime, the throat is laterally expanded by rotation of lateral elements (ceratobranchials I) of the hyobranchium. The displacement of the elements of the hyoid apparatus has always been assumed to produce throat expansion in all studied aquatic turtles (Lemell & Weisgram, 1997; Van Damme & Aerts, 1997; Lemell et al., 2002), and now there is clear confirmatory evidence. The posterior part of the throat is expanded by rotation of the posterior lateral elements of the hyobranchium (cetarobranchials II; Van Damme & Aerts, 1997; Lemell et al., 2002). The mouth is then again opened slightly to expel the excess water by returning the hyoid apparatus to its starting position, and the prey is retained on the floor of the buccal cavity.

All major data on food ingestion in aquatic turtles have been collected in environmental conditions (e.g., temperature, salinity) close to the classical relevant ecological conditions determined for the studied species. For example, Bels et al. (1998) recorded feeding behavior in *M. terrapin* at 25°C in water with salinity of 33 psu. Leatherback turtles were filmed at 26°C in classical artificial seawater (Bels & Renous, 1992). However, performances in turtles (as in all reptiles) can be modulated in relationship to temperature. It would be expected in ectothermic turtles that speeds of jaw action would increase with higher temperatures within the physiological range of a species, and vice versa.

Given the different thermal conditions of their natural ranges, we compared gape performances of three aquatic species (Figure 8.10). In this study, it was necessary to study jaw action at a range of realistic temperatures for each species. Data were obtained for *Trachemys* (Emydidae) at 18, 24 and 30°C. *Cuora* (Emydidae) and *Siebenrockiella* (Bataguridae) would not feed at 18°C; they were filmed at 24, 28, and 30°C (three specimens of each species were held overnight for more than 14 hours at each study temperature before being filmed). Figure 8.3 and Figure 8.4 respectively show the effects of temperature on bite time (i.e., time to contact food) and jaw opening time (i.e., time to maximum gape) for adults of all three species. It is evident that the two emydid species were both less affected by temperature changes than *Siebenrockiella*, which showed a steep decline in bite time and jaw opening time between 24 and 30°C (at 24 and 30°C, one-way ANOVA comparisons among the three species revealed highly significant differences, $p < 0.005$). *Trachemys* showed no change in bite time and jaw opening between 24 and 30°C; even at 18°C there was relatively little slowing of jaw action in comparison with 30°C (bite time by 24%, jaw opening time by 55%). Tukey post hoc tests showed that *Trachemys* was significantly faster (shorter bite/jaw opening times) than *Cuora* at common temperatures (24 and 30°C; $p < 0.05$ in all cases) and also significantly faster ($p < 0.05$) than *Siebenrockiella* at 24 but not at 30°C. Data for bite time were more variable than for jaw opening time; this possibly reflects variation in food morsel size and the positioning of the jaws relative to food during jaw closure. Jaw opening time appears to be more useful for comparisons and is solely presented for the rest of the results. Differences between the two emydid species were particularly marked, with jaw opening time being 227% longer in *Cuora* than in *Trachemys* at 24°C, and 200% longer at 30°C; clearly, *Trachemys* bites far faster than its Asian relative.

These results provide the first relevant functional data to explain the role of feeding performances in the success of invasion of *Trachemys* turtles throughout the aquatic habitats of the world.

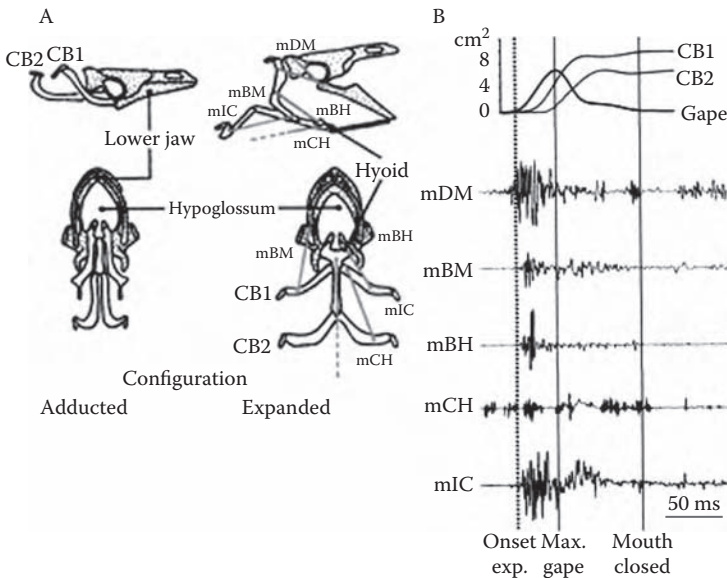


FIGURE 8.8 (A) Schematic representation of the head skeleton of *C. longicollis* in the adducted and expanded configurations. (B) Results of electromyographical analysis during expansion of the hyobranchium in *C. longicollis* (from Aerts et al., 2001). The graph represents the change of the cross sectional surface of the oropharyngeal cavity at the level of the gape and through the throat at the level of ceratobranchials I and II. Arrows indicate position and orientation of the major expansion muscles. CB1: ceratobranchial I; CB2: ceratobranchial II; mBH: m. branchiohyoideus; mBM: m. branchiomandibularis; mCH: m. coracohyoideus; mDM: m. depressor mandibulae; mIC: m. intercornuatus., exp.: throat expansion (Aerts et al., 2001).

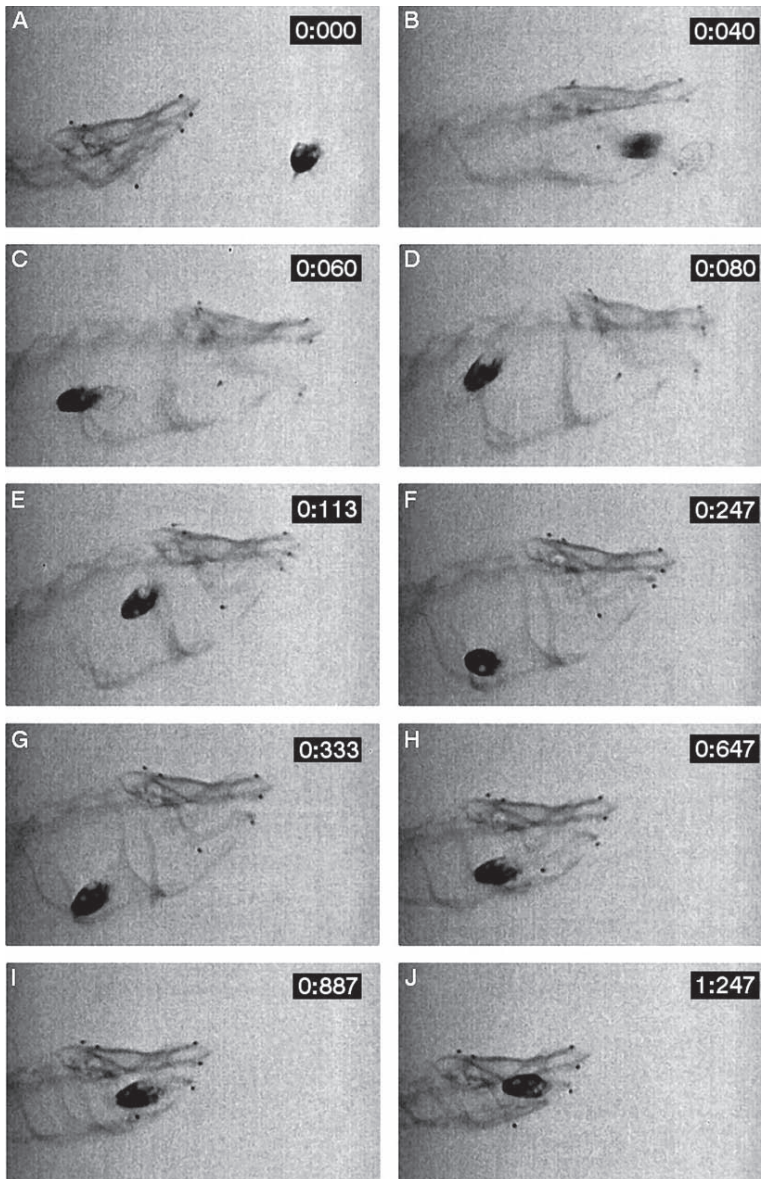


FIGURE 8.9 Successive frames of a high-speed x-ray film sequence (150 frames/s) showing a lateral view of *C. fimbriatus* during food capture. The time (s:ms) is provided for each frame. The prey item appears dark because of the x-ray contrast medium. Lead markers were also positioned on the skull of the turtle. (From Lemell et al., 2002.)

We demonstrate too that the invasive *Trachemys* bites faster over a wide range of temperatures relative to the two Asian species (*Cuora*, *Siebenrockiella*) whose habitat it now shares. This suggests that it can deal more effectively with elusive or dangerous prey as well as feeding on carrion or vegetation more quickly. The thermal data also indicate that *Trachemys* is capable of effective feeding over a wider temperature range than the two native species, allowing it to continue feeding under cooler conditions. The introduction of an omnivorous, highly effective competitor to an ecosystem is clearly undesirable, but the situation is made worse by the unusual characteristics of

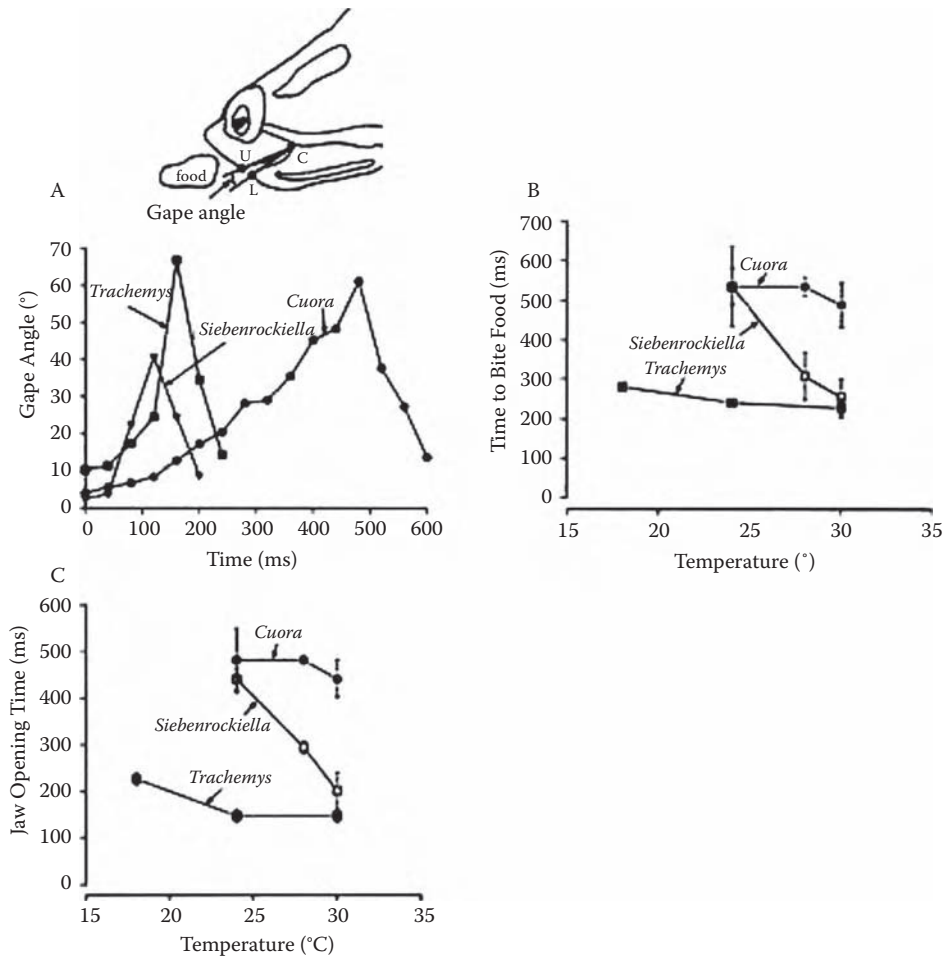


FIGURE 8.10 (A) Examples of gape angle sequences in the three study species at 30°C. The body masses of the three specimens filmed were as follows: *Trachemys* (492 g), *Siebenrockiella* (701 g), and *Cuora* (1041 g). (B) Effect of temperature on bite times (time to contact with food) in adult *Trachemys*, *Cuora*, and *Sieberockiella*. Symbols represent mean values ($n = 3$) and standard deviations. (C) Effect of temperature on jaw opening times (time to maximum gape) in adult *Trachemys*, *Cuora*, and *Sieberockiella*. Symbols represent mean values ($n = 3$) and standard deviations.

Trachemys introductions. Most invasive species do not become established in new habitats because they fail to reproduce, or do not have immunity to pathogens present in their new habitat. Whereas feral *Trachemys* have been shown to breed in Japan, Israel, Germany, and France (Ernst et al., 1994; Cadi et al., 2004), the great bulk of their numbers in Asia (as elsewhere) stem from repeated and continuing large-scale introductions. To some extent, their ability to breed/not breed is irrelevant, particularly as they are very long lived, often surviving 30+ years in the wild (Kuhrt & Dewey, 2002). According to the Turtle Conservation Fund (2002), Asia is “the geographic region that warrants the highest priority if we are to avoid losing [chelonian] species in the near future.” The results of our comparative biomechanical study provide further indication of the necessity for trapping and removing this highly competitive introduced turtle from non-native ecosystems.

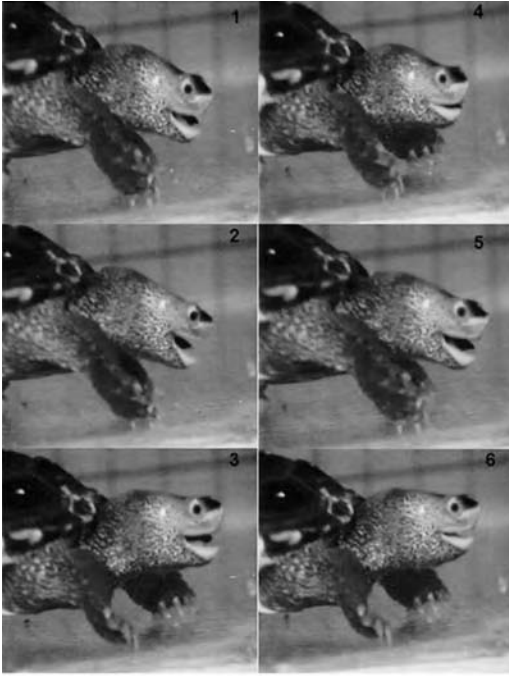


FIGURE 8.11 Typical stages of food (entire mussel) manipulation in *M. terrapin*. The tongue plays a major role in moving food from one side of the jaws to the other. The food is partially crushed at each closing of the jaws. Time between frames: 0.08 s.

8.5.2.2 Manipulation and Transport Cycle

Although poorly analyzed, transport of the food is more complex because it involves two main types of use of both elements of the hyobranchium: the tongue and the hyoid apparatus. In *M. terrapin*, the tongue plays a key role in manipulating food in association with the depression of the hyobranchium (Figure 8.11). For transporting the food, the tongue is also clearly associated with classical depression of the hyobranchium in helping backward displacement of the food within the oropharyngeal cavity. In other species, the food can be sucked in without any action of the tongue. Based on differences in movement of the hyobranchium in *C. fimbriatus*, Lemell et al. (2002) described two modes of transport cycles involving slow suction effects on the prey within the buccal cavity (Figure 8.12). In the first mode, the hyoid is depressed slightly and the mouth is open enough to facilitate the release of the prey from the jaws, with the fish being held at the end of the ceratobranchials. In the second mode, hyoid depression is of the same extent as during prey capture. The volume of the anterior part of the esophagus increases slowly and the prey is held between the ceratobranchials. The turtle expels the water very slowly and the prey remains at the end of the hyoid apparatus.

8.5.3 FEEDING IN *DERMOCHELYS CORIACEA*: A TYPICAL EXAMPLE OF A MARINE TURTLE WITH A HIGHLY SPECIALIZED DIET

8.5.3.1 Materials and Methods

Four young leatherback turtles (80 to 500 g) have been filmed at 200 to 300 Hz using 16 mm films. The turtles from French Guiana were incubated at 30.5°C and kept in an aquarium of 2.3 to 5.0 m³ at 25°C in sea water (pH = 8.0 to 8.1; salinity = 32 g/l). The animals were filmed under 500 W when fed with crude mussels (Bels et al., 1988). The food was presented gently in front of the turtles. Only true lateral sequences were kept for the analysis using the typical method detailed previously (Bels et al., 1998) and points were digitized to compare movements of the jaws, the hyobranchium, and the limbs during the successive phases of the feeding behavior (Figure 8.12 and Figure 8.13).

8.5.3.2 RESULTS

Feeding bouts in *D. coriacea* consist of successive jaw and hyolingual cycles from prey capture to its transport into the esophagus. During the feeding bouts, the turtles stabilize the body by slow displacements of the forelimbs that are not related to the successive gape openings. Two types of jaw cycles were observed: ingestion (including biting of the smooth material that is cut at each cycle) and transport cycles. We did not record any specific swallowing cycles with the type of soft

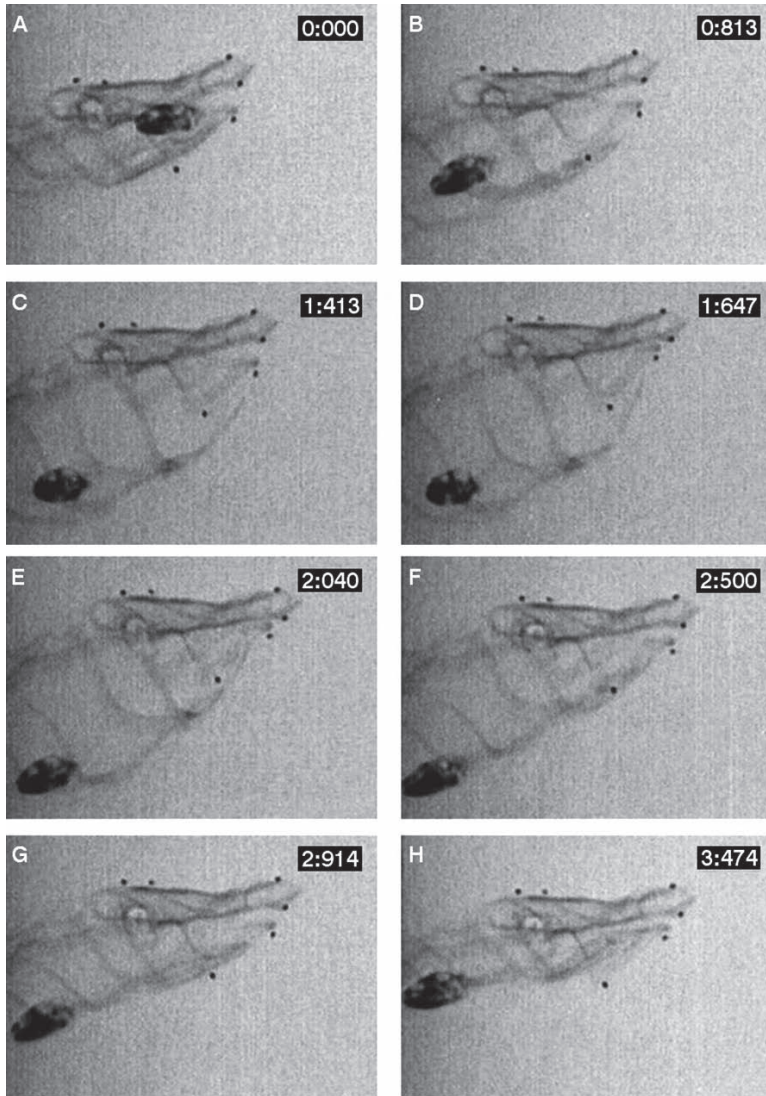


FIGURE 8.12 Successive frames of a high-speed x-ray film sequence (150 frames/s) showing a lateral view of *C. fimbriatus* during food transport. The time (s:ms) is provided for each frame. The prey item appears dark because of the x-ray contrast medium. Lead markers were also positioned on the skull of the turtle (figure from Lemell et al., 2002).

food used in this study (pieces of mussel flesh). In successive ingestion cycles, the food enters the buccal cavity and is reduced between the closing jaws. However, in some of these ingestion cycles, transport also occurs when the food is maintained in front of the turtles. In true transport cycles (Schwenk, 2000), the food is taken completely into the buccal cavity and then moves posteriorly to the esophagus without any reduction between the jaws. However, the food may be reduced between the hard palate and the tongue. Such reduction and biting cycles produce small particulate matter that is ejected from the mouth during the slow opening of the next jaw cycle. Throat elevation during the time between the two FO stages of successive cycles produced movement of water (and particulate matter) out of the buccal cavity (Figure 8.13).

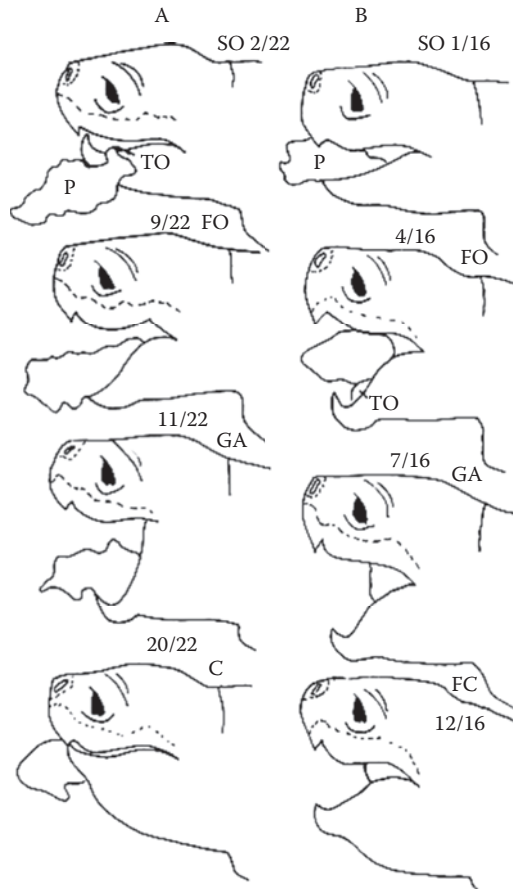


FIGURE 8.13 Successive frames showing (A) ingestion and (B) transport cycles in *D. coriacea* (high-speed 16-mm films at 100 Hz). The gape is divided in slow opening (SO), fast opening (FO), and closing (C) stages—the division in fast closing (FC) and slow closing (SC) stages was not always clear during the ingestion cycle. Inertial suction plays a key role in both feeding phases. The duration of the ingestion cycle is 0.22 s (22 frames) and the duration of the transport cycle is 0.16 s (16 frames). The numbers indicated at each drawing correspond to the number of frames relative to the total number of the cycle. Time to peak gape is indicated by GA. Contact between the food and the tongue was always observed and tongue retracts with the food as the throat is depressed. TO: tongue.

Kinematically, each gape cycle of the biting and transport phases involves a slow opening (SO), fast opening (FO), and closing (C). The SO stage of both cycle types is highly variable in duration and amplitude. In some cycles, it involves a “stationary stage” (SO II) prior to the sudden increase of the FO stage; in others, it does not. The SO stage may be also completely absent in some cycles. From high-speed cinematographic films, it was not possible to record clear relationships between the presence and duration of this SO stage, with the cycle function or the tongue-food position. The mean duration of SO stage in biting cycle was significantly longer than of SO stage in the transport cycle (Kruskall-Wallis ANOVA, $T = 4.7$; $df = 18$; $P < 0.05$), whereas FO and C stages were not significantly different.

The mouth is opened by a combination of ventral depression of the lower jaw and dorsal elevation of the upper jaw. Typically, the hyoid-tongue displacements are not different in ingestion and transport cycles. During the SO stage and the first half of the FO stage, the hyoid-tongue complex

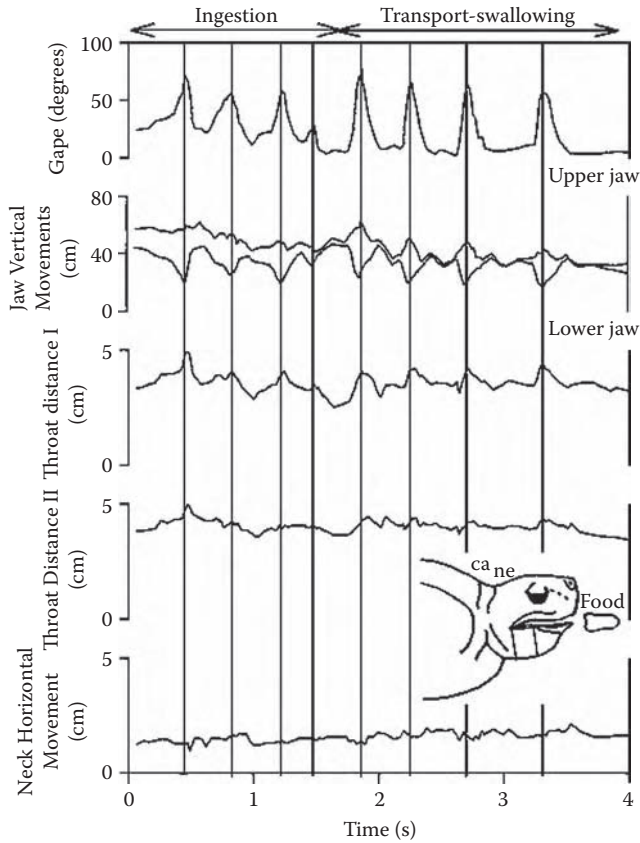


FIGURE 8.14 Kinematic profiles of ingestion and transport cycles in *D. coriacea* feeding on soft material (pieces of mussels) with properties close to the material caught in the natural environment (jellyfish). We categorize ingestion cycles as all cycles used for moving food into the buccal cavity, and transport cycles as all cycles that take place with food inside the buccal cavity. Gape cycles in both phases are divided into slow opening (SO), fast opening (FO), and fast closing (FC). Division between closing in fast closing (FC) and slow closing (SC) is not yet clear. However, at the end of the closing stage the angular acceleration of the gape angle decreases slightly. The kinematic profiles illustrating the throat displacement follow a similar pattern during biting and transport cycles. The throat distances I and II were calculated as the distance corresponding to the line traced from one point on the throat to the horizontal line passing through the edge of the mandible at each frame at an angle of 90°. The throat distance I corresponds to the hyoid body and the throat distance II to the region of the ceratobranchials I. During the SO and first half of the FO stages of each cycle, the throat distance I is elevated 0.01 s before the throat distance II (posterior). Retraction of the hyoid-tongue system begins during the FO stage and occurs during the closing stage. Peak hyoid retraction begins with or just before (0.01 s) fast closing. The hyoid apparatus is maximally retracted until the fast closing (FC) is achieved. The neck distance was calculated as the distance between point NE (end of the skull) and CA (carapace).

is elevated and protracted as illustrated by decreasing of the throat angle. The distance between the mandible and the hyoid body visible through the throat skin decreases strongly during SO stage and is 0.07 ± 0.01 s prior to maximal gape amplitude (end of FO stage). The throat expansion then occurs during 0.14 ± 0.05 s at the end of FO and FC stages. In cases of a stationary stage prior to a SO stage or very slow opening stage, the hyoid-tongue distance does not change greatly prior decreasing. There was no significant difference between displacements of the hyoid point on the throat during biting and transport cycles (Figure 8.14).

During SO and FO stages, water moves into the buccal cavity simultaneously as the prey that moves either to the buccal cavity (biting) or posteriorly into the buccal cavity (transport). An additional inertial suction mechanism helps displace prey toward the pharyngeal cavity; this is mainly produced by tongue retraction in biting and transport cycles. Strong contacts between prey surface and tongue dorsal surface were observed in both cycles.

8.6 EVOLUTION OF FEEDING BEHAVIOR IN TURTLES

Discussion of evolution of feeding behavior in turtles remains controversial. Based on their study of prey capture in *T. carolina*, Summers et al. (1998) state that “the currently accepted hypothesis is that the ancestor to recent turtles was terrestrial (Gaffney et al., 1987), but that an aquatic lifestyle evolved early in the history of the clade and is probably primitive for all extant turtles (Gaffney et al., 1987, 1991; Carroll, 1988).” These authors concluded that terrestrial feeding in turtles is a derived behavior (Bels et al., 1997; Summers et al., 1998). Here we provide some discussion that highlights the need for future quantitative kinematic and motor analyses in terrestrial and aquatic turtles.

8.6.1 INGESTION

Terrestrial feeding modes include lingual and jaw prehension. Both modes are used for various food items. Except in *Terrapene* (Bels et al., 1997; Summers et al., 1998; Bels, 2003), lingual prehension is the main mode for all studied turtles of the Testudinidae. The food adheres to the tongue either in (e.g., *Kinixys*) or out (e.g., *Geochelone*) of the buccal cavity. Summers et al. (1998) suggest that *T. carolina* uses a terrestrial feeding mode in water because the velocities of all skull elements during food capture by generalists are slower than those of specialists. From available data, three hypotheses can be suggested. First, the ingestion cycle has been derived in the “true” terrestrial chelonians (i.e., Testudinidae) showing a tongue-based intraoral feeding behavior from food transport and reduction to swallowing. Ingestion can be viewed as an evolutionary transformation of a tongue-based feeding mechanism for efficient procurement of food. The coordination of the tongue movement has not changed greatly, with the tongue moving slightly toward the food during jaw opening and retracting the food after contact; alternatively, the jaw apparatus can simply surround the food item and the tongue makes contact with the food within the buccal cavity prior to being retracted. Second, both modes of prehension (lingual and jaw prehensions) were present in ancestors of turtles and can be used in various ways determined by the properties of the food. Such modulation in food prehension has been reported for squamates (Schwenk, 2000). Third, terrestrial turtles derived from aquatic ancestors have “reinvented” the key role of the tongue for improving efficiency of food procurement together with their conquest of terrestrial habitats. In this case, we must admit that lingual prehension is a derived pattern constrained by the properties of the food resources becoming available during the evolution of terrestrial turtles. In *Terrapene*, which belongs to a primitively aquatic clade, terrestrial feeding is a secondarily derived mode in which the jaw prehension that plays a key role in aquatic feeding has been conserved. Summers et al. (1998) suggest that *T. carolina* would use tongue prehension on prey that is larger than mealworms. We have not yet confirmed this suggestion by examining prehension of various types of food in *Terrapene* (Bels, personal observation).

8.6.2 TRANSPORT (AND OTHER FEEDING PHASES)

The evolution of feeding behavior and motor control of turtles still remains difficult to fully understand. First, the origin of turtles continues to be largely problematic. Second, only a few species have been extensively studied, mainly in terms of feeding mechanisms and not from an evolutionary perspective. However, available data can provide some insight, particularly with respect to the likelihood of some possible hypotheses concerning the evolution of feeding behavior in chelonians.

A comparative analysis of all feeding phases—except food capture—appears interesting. Lauder and Gillis (1997) compared transport kinematics and mechanisms of truly aquatic vertebrates (e.g., fishes and amphibians), first with those of amphibians that feed in both terrestrial and aquatic habitats, and second with those of truly terrestrial Amniota (e.g., squamates). They suggest that several traits recorded for squamates are novel features of the feeding mechanism that appeared with the conquest of terrestrial habitats and can therefore be considered as plesiomorphic for tetrapods. These traits include diversity of intraoral processing, the presence of a SO stage prior to sudden gape increase (FO stage), and hyoid and tongue protraction during SO produced by a unique pattern of hyoid muscle contraction (Lauder & Gillis, 1997). These suggestions agree with the evolutionary approach to feeding behavior proposed by Reilly and Lauder (1990), who advocate a single generalized model of food transport in tetrapods. More recently, McBrayer and Reilly (2002) do not support all the features of Bramble and Wake's (1985) general model (i.e., presence of SO I and SO II in slow opening). These two models have been proposed to describe the generalized gape pattern and tongue movement during food transport in terrestrial vertebrates. Based on available data in 1985, Bramble and Wake (1985) presented a hypothetical generalized model for ancestral tetrapods with gape being divided into slow opening (SO), fast opening (FO), fast closing (FC), and slow closing (SC-PS) stages. Before FO, the gape increase is divided into slow opening I (SO I) involving "a comparatively low gape angle" (Bramble & Wake, 1985) while the tongue slides beneath the food and a slow opening II (SO II), that "is recognized by a distinct decline in the rate of change of gape" (Bramble & Wake, 1985). This latter stage is represented in the model by a plateau in the gape cycle. Then during FO, the food is moved posteriorly by action of the tongue. After FO, the mouth closes rapidly (FC) and then more slowly as the jaws contact the prey during SC-PS stages.

Reilly and Lauder (1990) proposed another generalized model for amniotes. These authors divide the increasing stage of the gape cycle (opening of the mouth) only into slow opening (SO) and fast opening (FO), with no SO II stage. This difference in gape increase is highly significant because it emphasizes a difference in tongue movement during transporting of the food—see McBrayer & Reilly (2002) for a discussion based on quantitative data in a large set of squamates. According to Lee (1997), the development of the shell and rather flattened body of turtles could be linked to an ancestral herbivorous diet. It may be assumed that ancestral forms were terrestrial and fed on plant material (and perhaps small, slowly moving prey or carrion), as is the case for a large number of extant species studied to date (e.g., *Geochelone* sp., *Kinixys* sp.). Based on this hypothesis, we may conclude that available data support the conclusion that the characteristics of transport cycles are plesiomorphic for terrestrial feeding in turtles, although there is a large variety in diet and specialization of the hyobranchium, yielding the presence of a SO stage before FO of the mouth, a movement of the tongue under the food during the SO, and retraction of the food by the tongue at SO-FO transition or at the beginning of SO stage.

In their quantitative analysis, Bels et al. (1997) compared their data in terrestrial feeding by *T. carolina* with the two previously described generalized models for tetrapods. Available data do not permit categorical conclusions. However, a rapid survey of kinematics facilitates the comparison of aquatic and terrestrial transport phases. In all turtles, with all types of food, the jaw cycle is often divided into SO, FO, and closing stages. The SO stage is always present in all terrestrial turtles. This stage has also been reported in a large number of aquatic turtles (*P. castaneus*, Lemell & Weisgram, 1997; *T. carolina*, Bels et al., 1997; Summers et al., 1998; *M. terrapin*, Bels et al., 1998; *D. coriacea*, Bels et al., 1998; *C. fimbriatus*, Lemell et al., 2002). We suggest that there is an intra-oral transport cycle that is similar for all terrestrial turtles. It is also evident that the tongue is used in a large number of aquatic turtles to transport food items, just as in terrestrial turtles. Its protraction occurs during the SO stage and it retracts with the food at the boundary between SO and FO stages or early during FO stage. We may call this mechanism *intra-oral aquatic lingual transport*. In contrast, suction plays the dominant role for transporting food in some species such as *C. fimbriatus* (Lemell et al., 2002). We may call this mechanism *intra-oral aquatic hyoid transport*. Probably, the relative size of the tongue is the limiting morphological factor in determining use of tongue-based

intra-oral transport or hyoid-based intra-oral transport. The slowly opening mouth can generate low pressure within the mouth cavity because of protraction of the hyoid during this stage in both cases. However, this is rapidly compensated for by suction that occurs during throat expansion after maximum gape. During the FO stages, rapid mouth opening is immediately followed by a posteroventral movement of the hyoid apparatus; high negative pressure occurs within the oropharyngeal cavity, which is produced by peak hyoid depression following peak gape in all studied turtles. During the FC phase, the hyoid apparatus remains depressed until the mouth is closed.

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