

Morphology and Function of the Feeding Apparatus of *Pelusios castaneus* (Chelonia; Pleurodira)

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ABSTRACT Feeding mechanics of vertebrates depend on physical constraints of the surrounding media, water or air. Such functions are inseparably combined with form. The aim of this study is to show this linkage for the pleurodiran freshwater turtle *Pelusios castaneus* and, additionally, to point out the major functional and biomechanical distinctions between aquatic and terrestrial feeding turtles as well as several intermediate forms. Gross morphological investigations of skull, hyoid, tongue, and connected musculature, as well as scanning electron microscopy of the tongue surface, show typical features of an aquatic feeder, e.g., strongly developed hyoid apparatus vs. a small tongue with only moderate papillae, and massive jaw and hyoid musculature. Additionally, the special

function of the esophagus during feeding is investigated to elucidate the problems of a bidirectional feeder. The esophagus is highly distensible in order to store the excess water sucked in during feeding until the prey is fixed by the jaws. The distension is probably achieved by a coincidence of active (branchial horn) as well as passive (water) components. *P. castaneus* is a feeding generalist, and is well adapted to the aquatic medium in terms of its functional as well as morphological features. *J. Morphol.* 244: 127–135, 2000. © 2000 Wiley-Liss, Inc.

KEY WORDS: anatomy; hyoid movements; scanning electron microscopy; skull, tongue

The feeding mechanics of vertebrates depend on physical constraints of the surrounding media, water or air. Since aquatic feeding is the primitive mode of prey capture in vertebrates, it is of special interest in the study of vertebrate evolution. The existence of many aquatic-feeding turtles provides morphologists with a group of vertebrates that has evolved aquatic feeding convergently with anamniote feeding systems. Since this theory has been based primarily on studies of fish and amphibians (for review, see Lauder, 1985; Lauder and Shaffer, 1993), there are few data for corroboration of the hypothesis of kinematic similarities based on hydrodynamic constraints about chelonids (Lauder and Prendergast, 1992; Lemell and Weisgram, 1997; Summers et al., 1998; Van Damme and Aerts, 1997).

Most aquatic feeding turtles utilize a “pharyngeal” mechanism that exploits the relatively high density and viscosity of water (Bramble, 1973). This mechanism relies primarily on the generation of large negative pressure within the buccopharyngeal chamber through rapid expansion of the chamber by the hyoid apparatus—the so-called suction feeding. When coupled with high-speed inertial feeding movements of the head, such negative pressure effectively aspirates water and food into the mouth. The esophagus probably functions as a temporary reservoir of water to delay the reversal of flow (Lauder and Shaffer, 1993).

The aim of this article is to demonstrate the relation of form and function for the pleurodiran fresh-

water turtle *Pelusios castaneus* and, additionally, to point out the major functional and biomechanical distinctions between aquatic- and terrestrial-feeding turtles, which stem mainly from morphological differences reflecting adaptation to the physical properties of the two media.

MATERIALS AND METHODS

For three subadult specimens of the pleurodiran West African mud turtle *Pelusios castaneus* Schweigger 1812, the morphology of the feeding apparatus—skull, hyoid, jaw, and hyoid musculature, as well as tongue surface topography—were studied. The animals (3 males; specimen 1: 10.5 cm carapace length, 230 gm; specimen 2: 11 cm carapace length, 257 gm; specimen 3: 12.5 cm carapace length, 286 gm) were obtained commercially and identified by Richard Gemel of the Museum of Natural History in Vienna (pers. comm.). They were kept in a glass aquaterrarium (100 × 35 × 40 cm, 10 cm water level, about 25°C water temperature) with a 12/h light/dark cycle. *Pelusios castaneus* is a

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semiaquatic freshwater turtle that lives in a variety of habitats, such as rivers, marshes, swamps, lakes, and shallow ponds; it is omnivorous and feeds mainly on fish, large pulmonate snails, and floating water lettuce (Ernst and Barbour, 1989).

The animals were killed by an intraperitoneal injection of sodium pentobarbital and fixed in a 8% formaldehyde solution for 3 days prior to dissection. Drawings were made of all stages of the dissection using a WILD M5A dissecting stereomicroscope. The morphological findings were compared with other data available in the literature on osteology and myology of skull and hyoid of chelonids (Bramble, 1974; Carroll, 1993; Fürbringer, 1922; Gräper, 1932; Poglayen-Neuwall, 1953; Romer, 1956; Schumacher, 1953-54, 1973; Siebenrock, 1898).

For scanning electron microscopy (SEM) of the lingual surface, tongues were removed and immediately fixed overnight with modified Karnovsky solution (2% paraformaldehyde and 2.5% glutaraldehyde containing 0.1M cacodylate buffer, pH 7.4 [Karnovsky, 1965]). After rinsing in 0.1M cacodylate buffer, tissue samples were postfixed in a cacodylate-buffered solution of 1% osmium tetroxide at 36°C for 2 h. Mucus was removed from the surface of the epithelium by treating these samples with 8 N hydrochloric acid at 60°C for 30 min. This procedure was followed by dehydration in a graded ethanol series, critical-point-drying, and gold-coating. The specimens were observed on a PHILLIPS XL20 scanning electron microscope.

RESULTS

Osteology

Skull (Fig. 1). The skull of *Pelusios castaneus* has a strong temporal emargination that allows a stronger development of more deeply positioned adductors. The jugal bar is well developed; deep to it, the strong quadrato-squamoso-jugo-maxillare membrane is unfolded to enlarge the width of the jugal bar. As known for all pleurodiran turtles, the pterygoid exhibits a prominent pterygoid process, which curls upward in the region of the subtemporal fenestra and forms a partial septum between the external and internal jaw adductors. However, the most important function of this process is its application as a trochlear process for the Cartilago transiliens of the external adductors (see below). The supraoccipital is only slightly enlarged to caudal—other aquatic turtles have much more enlarged supraoccipitals except for all marine turtles (Romer, 1956)—the high median ridge serves as the insertion area for the external adductor.

The jaw articulations are placed far laterally and well anterior of the occiput. Contrary to cryptodiran turtles, in which the articular surface on the quadrate exhibits two rounded antero-posterior ridges separated by a depression, here the whole surface of the quadrate bone is concave.

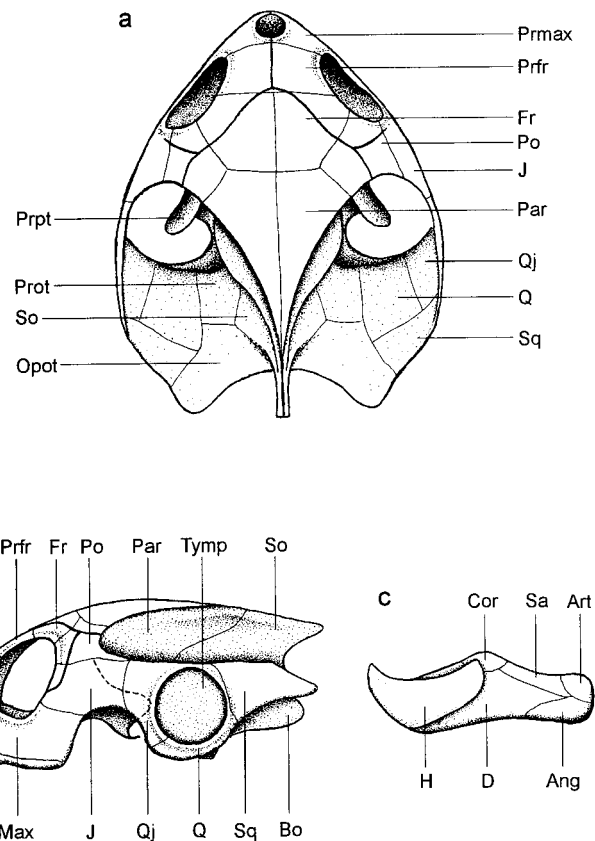


Fig. 1. Dorsal (a) and lateral (b) view of the skull, and lateral view (c) of the lower jaw of *Pelusios castaneus*. Ang, Os angularis; Art, Os articulare; Bo, Os basioccipitale; Cor, Os coronoideus; D, Os dentale; Fr, Os frontale; H, horny beak; J, Os jugale; Max, Os maxillare; Opot, Os opisthoticum; Par, Os parietale; Po, Os postorbitale; Prfr, Os praefrontale; Prmax, Os praemaxillare; Prot, Os prooticum; Prpt, Processus pterygoideus; Q, Os quadratum; Qj, Os quadratojugale; Sa, Os surangulare; So, Os supraoccipitale; Sq, Os squamosum; Tymp, tympanic membrane.

Hyolaryngeal skeleton (Fig. 2). The hyoid apparatus of *Pelusios castaneus* is well developed, as it is in all aquatic-feeding turtles. It consists of a longish ossified plate, the hyoid body (Corpus hyoidei) with its reduced process (Processus lingualis) and three pairs of visceral arches (strongly reduced Cornu hyale—Ch, Cornu branchiale I—CbI, and Cornu branchiale II—CbII). Both ceratobranchials articulate via a plane hinge with the hyoid body. Taut ligaments provide for firm articulations. The CbI is almost circular in cross-section. Its second half is a strongly bent, ossified rod. It runs posterolaterally from the articulation and turns up at the level of the squamosal. In the middle of the tympanic membrane it turns caudally again. There, it is fixed with a tendon coming from the squamosum. This tendon forms a loop holding the CbI in a rather fixed position. The CbII is a bit shorter than CbI. It is flattened and relatively wide. It runs parallel to the CbI. Its second half leans against the wall of the pharynx, functioning as a dilatator. The hyoid ap-

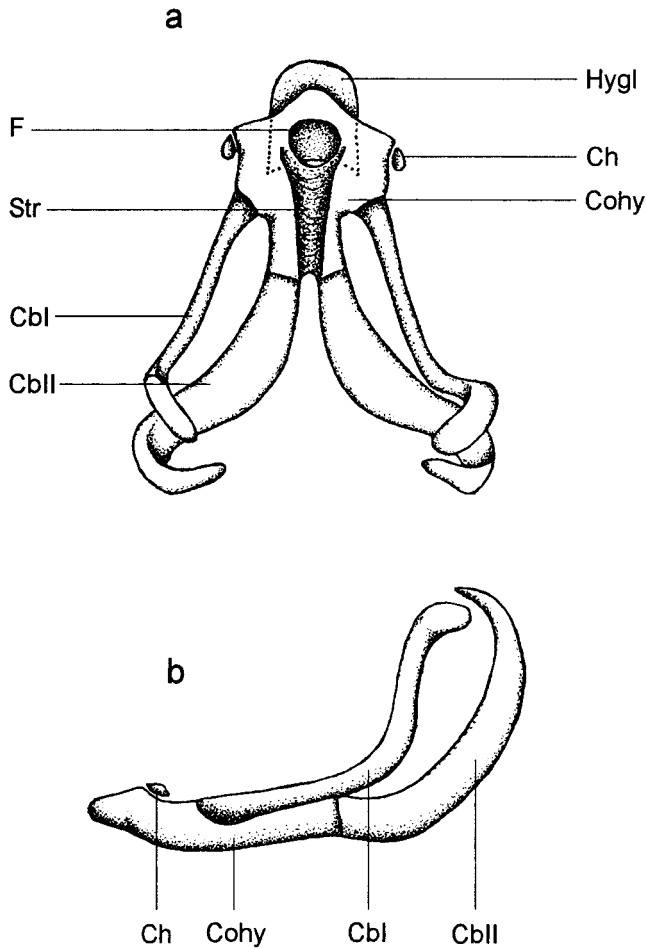


Fig. 2. Dorsal (a) and lateral (b) view of the hyoid apparatus of *Pelusios castaneus*. CbI, Cornu branchiale I; CbII, Cornu branchiale II; Ch, Cornu hyale; Cohy, Corpus hyoideus; F, Fenestra hyoidei; Hygl, Hypoglossum; Str, Sulcus tracheae.

paratus as a whole is a quite rigid frame and functions as a depressor of the floor of the mouth to generate a large negative pressure within the buccopharyngeal chamber. In doing so, it is supported by the hypoglossum, a skeletal element unique for turtles, that is developed ventrally to the hyoid body. It is a flat, slightly vaulted, cartilaginous disc, that nearly fills the whole space between the mandibles.

Myology and Function

Jaw musculature (Fig. 3). Since they derive from the mandibular arch, the jaw muscles are of visceral nature. Their principal function is to close the jaws, so they are also called jaw adductors. As is common for all sauropsids, the Musculus (M.) adductor mandibulae is divided into three adductors: the external, the posterior, and the internal. A centrally located tendon (Bodenaponeurose sensu Lakjer, 1926; Binnensehne sensu Poglayen-

Neuwall, 1953; external tendon sensu Schumacher, 1973) serves for the insertion of most fibers of this muscle and attaches by a broad base to the bones of the coronoid process (coronoid, surangular, prearticular). At the transition from the lower to the upper temporal fossa, this tendon exhibits the Cartilago transiliens, whose articular surface reflects the form of the trochlear process of the pterygoid. The cartilage substantially increases the effective height of the trochlear process, thus causing the muscle to insert on the jaw in a more vertical plane than would otherwise be the case. This results in a greater upward force applied to the mandible. The pinnate structure of the external adductor with its fibers inserting on all sides of the tendon enlarges the muscles physiological cross-section and force.

The posterior adductor is semicircle-shaped and lies within the lower temporal fossa and extends with almost all of its fibers into the caudal margin of the "internal tendon" (sensu Schumacher, 1973).

The M. pterygoideus is the most anteriorly located part of the internal adductor. Its fibers run from the orbital region into a groove formed by the internal side of the pterygoid process and then passes into the internal tendon. After joining the parts of the posterior adductor behind the trochlear process of the pterygoid, it extends to the inner side of the mandible (surangular, prearticular).

The adductors are typically arranged within the temporal fossae; the external lies in the upper, the

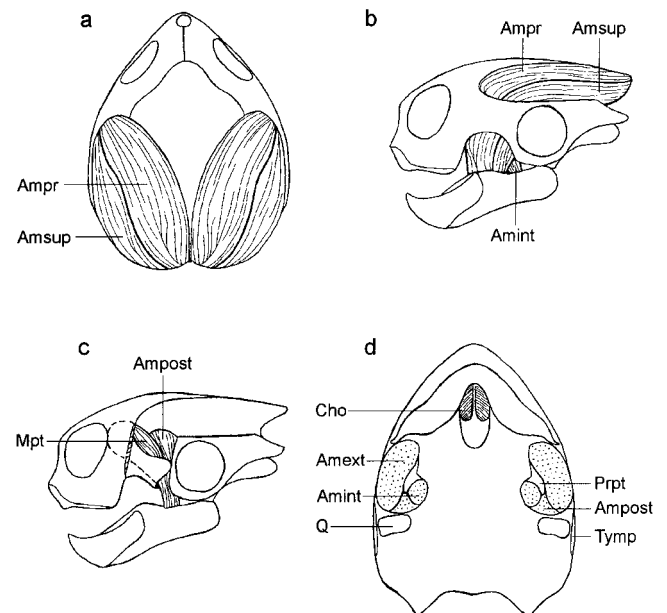


Fig. 3. *Pelusios castaneus*; dorsal (a) and lateral (b) view of the external adductors; lateral view (c) of the internal and posterior adductors, and ventral view (d) of distribution of all three adductors within the lower temporal fossa. Amext, external adductor; Amint, internal adductor; Ampost, posterior adductor; Ampr, Pars profunda of ext. add.; Amsup, Pars superficialis of ext. add.; Cho, choanae; Mpt, pterygoid muscle; Prpt, Q, Tymp, as in Figure 1.

internal and posterior muscles in the lower fossa. In all cases, the muscles of the external complex are larger than those of the internal and posterior adductors together. For an optimum functioning of the jaw adduction all three muscles have to work together. The external complex lies horizontally and thus is not able to exert a lifting effect on the lower jaw. Here, the external tendon comes into play by transforming the horizontal traction into a vertical one. In pleurodires, it runs up to the trochlear process of the pterygoid, which is used as a fulcrum. Thus, the horizontal tendon is prolonged, and the tendon's declination enlarged. In *Pelusios castaneus*, this angle reaches up to 150°.

The muscles of the posterior and internus adductor complex form a muscular crescent in the lower temporal fossa. Here, the muscles of the posterior part run vertically, and those of the pterygoid muscle run from antero-medial to postero-lateral to the lower jaw. The fibers of the posterior adductor act as a lift for the lower jaw; the fibers of the pterygoid muscle have another special function: they form the topographic equivalent to the externus complex. The result of these muscles is a protraction by the internal, and a retraction by the external adductors, producing together a huge lifting effect to the lower jaw (Fig. 4). Protraction and retraction components act synergistically in closure, reducing horizontal stresses at the jaw articulation. Additionally, there is a medial traction resulting from all the jaw adductors.

As an antagonist to the adductors, the M. depressor mandibulae, being a derivate of the second visceral arch, functionally belongs to the jaw musculature. It bows from postero-dorsal to antero-ventral with an inclination of about 50° (the degree of the inclination depends principally on the height of the skull as well as the posterior extent of the squamosal).

To complete the major musculature of the first and second visceral arches, the M. intermandibularis has to be mentioned. It extends ventrally between the two mandibles and belongs topographically to the muscles of the floor of the mouth. Its fibers run from the dentaries as well as the angulars to a median connective tissue raphe, which continues posteriorly within the M. constrictor colli. Its major function is to reduce the volume of the buccal cavity before mouth opening as well as to expel excess water sucked in during feeding.

Other important visceral muscles (Fig. 5). The constrictor colli, anteriorly connected with the intermandibularis, forms the posterior part of the floor of the mouth. The larger part of this muscle envelops the esophagus along the long neck, where it plays a major part in swallowing. The third visceral arch is developed rudimentarily in sauropsids, but here the M. branchiomandibularis is of major importance for the hyoid apparatus. It runs parallel to the depressor mandibulae extending from the end

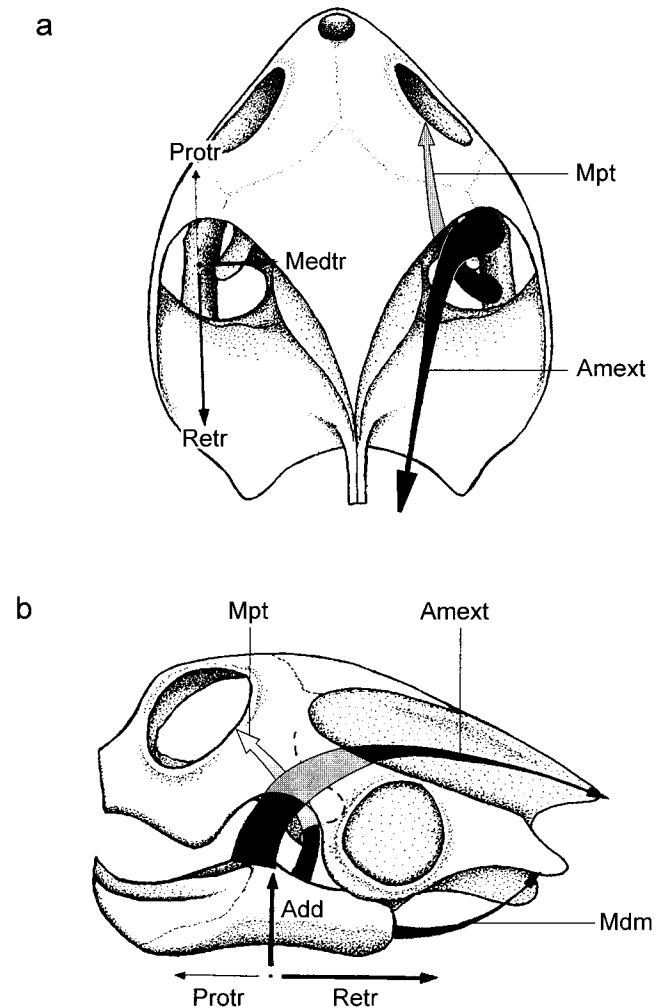


Fig. 4. Dorsal (a) and lateral (b) view of *Pelusios castaneus*. Arrows indicate the direction of forces, appearing during contraction of the jaw adductors; the tendons positions are shown on the right (a), and dorsal (b), the resulting forces on the left (a), and ventral (b) side, respectively. Length and thickness of arrows reflect the relative forces. Amext, Mpt as in Figure 3; Add, adduction; Mdm, depressor mandibulae; Medtr, medial traction; Protr, protraction; Retr, retraction.

of the CbI, which is sheathlike, to the medial side of the mandible. From the fourth visceral arch, only two muscles are noteworthy. The M. geniohyoideus, belonging to the muscles of the floor of the mouth, extends just above the intermandibularis muscle. It lies along the ventral surface of the hyoid apparatus, originating from the medial face of the lower jaw and a median raphe, and inserting at both branchial arches. When contracted, it pulls the hyoid forwards. The same is true for the M. genioglossus, which runs median from the mandible symphysis to the anterior part of the hyoid body.

Another very important muscle of the feeding apparatus is the M. coracohyoideus, belonging to the hypobranchial longitudinal muscles. Its fibers run from the coracoid antero-ventrally from the CbII to

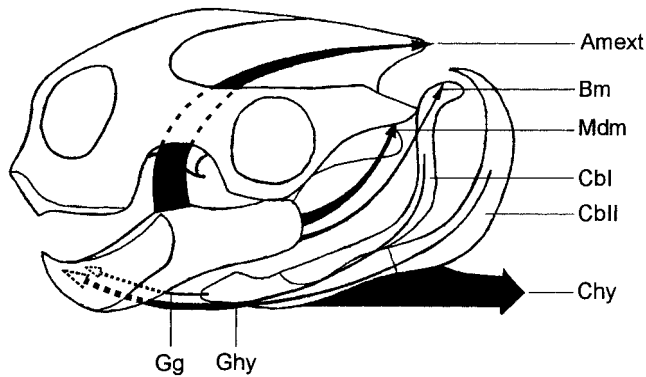


Fig. 5. Schematic drawing of the jaw-hyoid-apparatus of *Pelusios castaneus*. The course of the major jaw and hyoid muscles is shown by arrows. Length and thickness of arrows reflect the relative forces. Amext, Mdm as in Figures 3 and 4; Cbl, CbII as in Figure 2; Bm, Musculus (M.) branchiomandibularis; Chy, M. coracohyoideus; Gg, M. genioglossus; Ghy, M. geniohyoideus.

the hyoid body and the Cbl. When contracted, it pulls the hyoid apparatus backwards.

Functional Aspects

Looking at a typical feeding cycle, the special functions of the different muscles become more obvious. According to Bramble and Wake (1985), the feeding cycle of *Pelusios castaneus* can also be subdivided into four phases—slow open (SO), fast open (FO), fast closing (FC), slow closing-power stroke (SC-PS) (Fig. 6)—which is not the case for all turtles (for details of the feeding kinematics of *P. castaneus*, see Lemell and Weisgram, 1997).

During the SO-phase, the lower jaw is slightly depressed by the depressor mandibulae. The internal adductor complex must also be active in order to prevent the entire opening of the mouth. The hyoid is depressed by the branchiomandibularis and at the same time pulled anteriorly by the geniohyoideus and genioglossus. Through contraction of the intermandibularis musculature the hyolingual complex is additionally pressed dorsally; so at the end of this phase, it is at its most antero-dorsal point. During the SO-phase the volume of the buccal cavity is strongly reduced to achieve a good suction force in the following phase. Additionally, the esophagus is compressed to reduce the intraoral volume of water.

During the FO-phase the mouth is rapidly opened to its maximum gape. The depression of the jaw is achieved by the depressor mandibulae. Additionally, the geniohyoideus and genioglossus muscles remain contracted and hold the hyoid at a certain distance to the tip of the mandible. The simultaneous action of the coracohyoideus, which is withdrawing the hyoid, assists in depressing the lower jaw. Thus, the velocity of mouth opening is enormously increased. Therefore, depression of the hyolingual complex postero-ventrally starts, and suction is generated.

The acceleration of head and neck toward the prey is also begun.

In the FC-phase the mouth is closed rapidly and grasps the prey. The external and internal adductors lift the lower jaw, the coracohyoideus musculature retracts the hyoid, and the geniohyoideus and genioglossus relax. Only the hyolingual complex is moved because the rigid connection to the lower jaw no longer exists. At the end of the phase, this complex is at its most postero-ventral position. Head and neck are also retracted. Through the beginning of the esophageal distension, water is sucked further backwards.

During the SC-PC-phase, only the adductors are active. When the coracohyoideus is relaxing, the hyoid apparatus returns to its starting position through its own elasticity and through the contraction of the overstretched geniohyoideus and genioglossus muscles to normal. Esophageal expansion reaches its maximum at the beginning of the phase. When the jaws are closed or the prey is fixed, the process of expelling excess water starts. Through the craniad peristaltic wave of the constrictor muscles, and by lifting the hyoid, water is expelled at the end of the SC-PC-phase and at the beginning of the following SO-phase.

Tongue

Tongue musculature. Like many other aquatic lower vertebrates, the intrinsic musculature of the tongue of *Pelusios castaneus* is only weakly developed.

Surface topography. The tongue of *Pelusios castaneus* lies anterior to the pharynx. It is somewhat triangular in shape with a round apex in dorsal view (Fig. 7a), and appears flat in lateral view. Lingual papillae are widely distributed all over the dorsal surface. At low magnification, very moderate papillae are visible (Fig. 7a,b). They are ridge-like, with interspersed columnar parts; all papillae seem to be interconnected. However, the shapes and widths of the papillae are not constant. The interpapillar epithelium is sunken (Fig. 7c). At higher magnification, dome-shaped bulges can be discerned all over the surface of the papillae, each resembling the surface of a single cell. Cell borders between adjacent cells are clearly visible (Fig. 7d). Short microvilli are abundant on the surface of each cell (Fig. 7e).

DISCUSSION

Evaluation and comparison of the morphology of *Pelusios castaneus* with that of other chelonids makes it very obvious that it must be an aquatic feeder. The model of correlated anatomy with aquatic vs. terrestrial feeding modi, developed for vertebrates (Bramble and Wake, 1985), also holds true for *P. castaneus*. Comparing anatomical fea-

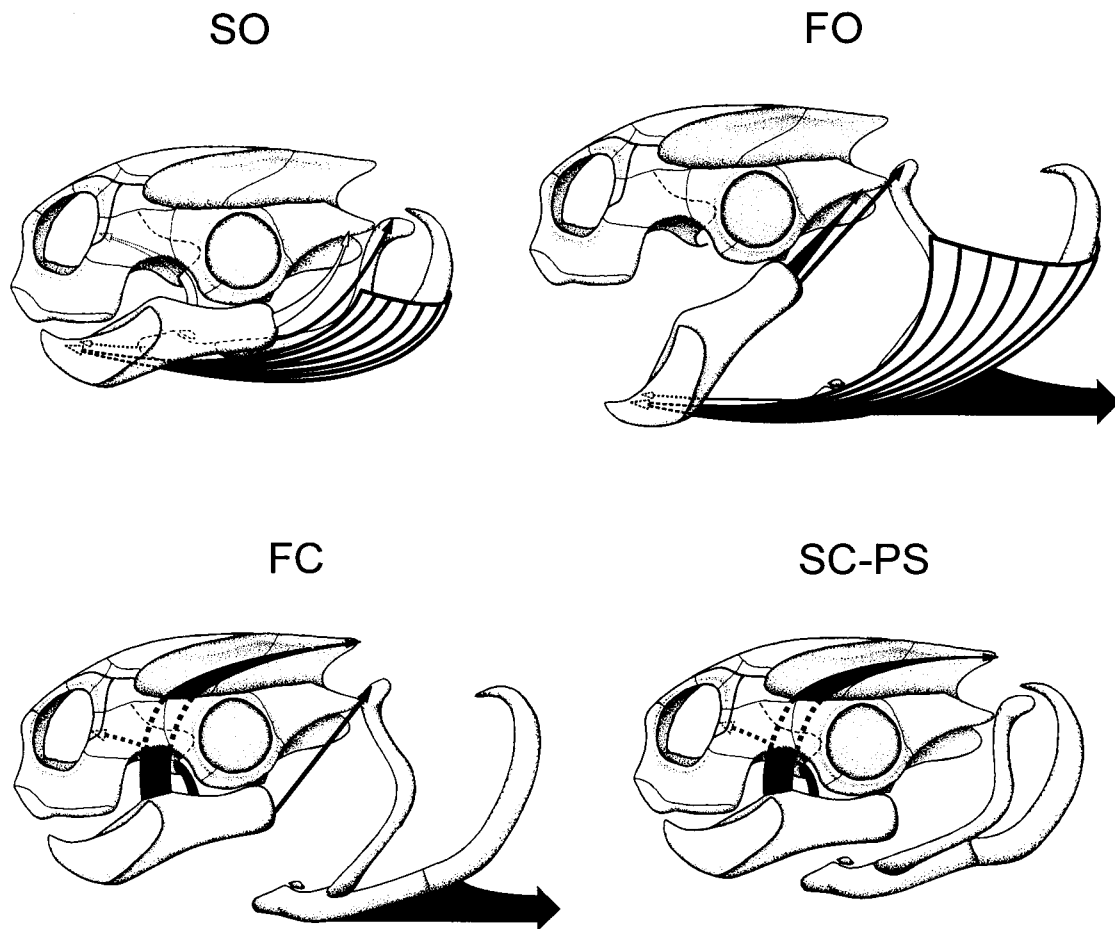


Fig. 6. Supposed muscle activity during the four phases of a typical feeding cycle of *Pelusios castaneus*. Arrows show the active (black) and quite active (white) musculature of the jaw and hyoid apparatus.

tures of *P. castaneus* with some semiaquatic (Fürbringer, 1922; Gräper, 1932; Romer, 1956; Schumacher, 1973) and purely terrestrial species (Romer, 1956; Schumacher, 1973; Wochesländer and Weisgram, 1999), the following differences are found. The skull of *P. castaneus* exhibits limited specializations. Comparing the jaw musculature, some specific features, typical for pleurodires on the one hand, and typical for aquatic feeders on the other hand, become obvious. The function of the pterygoid process as a fulcrum for the tendon of the external adductor is a pleurodiran character. Thus, the horizontal part of the tendon is much longer than in cryptodires, in which the tendon turns ventrad at the anterior edge of the upper temporal fossa. The longer the horizontal part of the adductor, the more muscle fibers may insert on the tendon, resulting in a larger muscle force. Additionally, the tendinous declination is larger (150° in *Pelusios*, only about 100° in *Testudo*). A larger angle means a larger adduction force, and both together are absolutely necessary for aquatic turtles feeding in a medium 900 times as dense as air and 80 times as viscous. The inclination of the

depressor mandibulae is also a typical distinguishing feature: while it is almost vertical in some terrestrial species (*Gopherus*, *Testudo*, and also *Caretta*), it is quite transversal in many aquatic species like trionychids, *Cuora*, *Clemmys*, and pelomedusids (*Podocnemis*, *Pelusios*) (Schumacher, 1973). Drawing a conclusion, in water it appears to be much more efficient to utilize a double muscle system (depressor and coracohyoideus) for mouth opening than a single muscle system only using the depressor, as occurs in terrestrial-feeding turtles.

Within the hyolingual complex, there is an inverse relationship between the relative development of the hyoid apparatus and the tongue. The bigger the hyoid, the less developed the tongue, and vice versa. The hyoid skeleton of aquatic feeders is much larger than in terrestrial feeders; the branchial horns especially are more developed and also well ossified (Siebenrock, 1898). The organization of the hyolingual complex in tortoises reflects the dependence on lingual transport of food. The more a turtle feeds on land, the more flexible the skeleton has to be, since the tongue is much more involved in terrestrial feed-

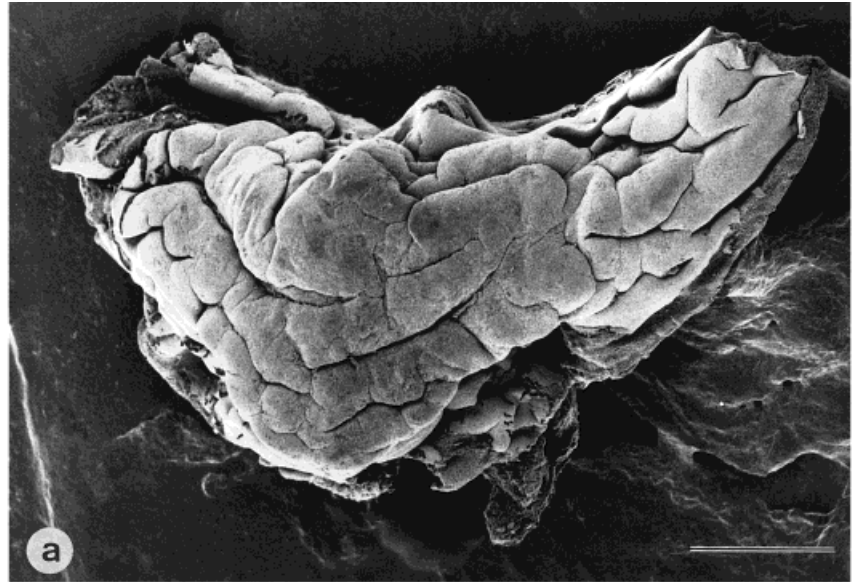
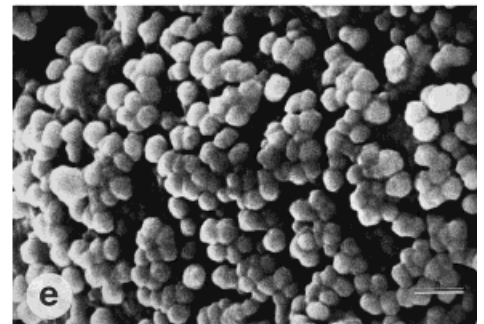
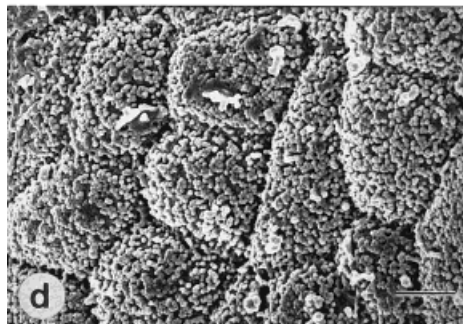


Fig. 7. *Pelusios castaneus*, tongue. SEM. **a**: Total view of the tongue. Moderate papillae cover the whole surface of the tongue; all of them correspond with each other. Scale bar = 1,000 μm . **b**: Higher magnification of the lingual apex. Here, the papillae seem to be of a more columnar shape than in posterior regions of the tongue. Scale bar = 250 μm . **c**: Dorsal surface. Between the lingual papillae, the epithelium is sunken; single cells are already visible. Scale bar = 50 μm . **d**: Higher magnification of the dorsal surface of the tongue. Dome-shaped bulges give the epithelium a cobblestoned appearance; each of these "stones" corresponds to a single cell. Cell borders between adjacent cells are visible. Scale bar = 2.5 μm . **e**: High magnification micrograph of the surface of a single cell. Short microvilli cover the surface. Scale bar = 0.5 μm .



ing. Therefore, a greater range of motion is allowed (Bels et al., 1997; Wochesländer and Weisgram, 1999). Furthermore, the tongue is relatively small, with very moderate papillae. A large tongue would impede the suction of water and prey by occupying too much space, space that could otherwise be utilized for volumetric expansion, and also by producing turbulences during suction (Bramble and Wake, 1985). The presence or formation of lingual papillae is also correlated with the adaptation of species to their habitat and feeding behavior: turtles living permanently in water have a typically small tongue, with no or very moderate lingual papillae (Bramble and Wake, 1985; Winokur, 1988). Turtles belonging

to this group are pleurodires (e.g., *Platemys pallidipectoris* [Beisser et al., 1995]) as well as many species of cryptodires. To the contrary, purely terrestrial adapted species, which exclusively use terrestrial feeding mechanisms, have high and complex papillae (e.g., *Testudo hermanni* [Kochva, 1978]). Between them, a few chelonids can be seen as intermediate forms; they live in and around water and are able to feed on land as well as under water, e.g., *Geoclemys reevesii* (Iwasaki, 1992), *Clemmys japonica* (Iwasaki et al., 1992), and *Trachemys scripta elegans* (Beisser et al., 1998).

The function of the esophagus raises some questions. For aquatic feeders it is obvious that excess

water sucked in during feeding must be stored because of the problems faced by a bidirectional feeder (see Lauder and Shaffer, 1993). Therefore, the esophagus of aquatic turtles is highly distensible. The expulsion of some residue of water during the SO-phase is done by compressing the esophagus with the constrictor colli muscles. But how does the distension work? Three possibilities seem likely. Bramble found that in *Chelydra serpentina* some tendinous insertions extend from the coracohyoideus to the wall of the esophagus (Lauder, 1985). Thus, whenever the latter is contracted, the wall is expanded. Hereby, the esophagus would actively aspirate some water. In *Pelusios castaneus* no such tendons could be found.

Another possibility is a totally passive distension: when water is sucked in by the large hyoid depression, the constrictor muscles relax and the water would fill the esophagus to its maximum volume.

As a third possibility, the CbII, which are closely related to the wall of the esophagus, could play a major role: whenever the hyoid is brought to its most ventral point, the branchial horns are at their most lateral position, and the anterior part of the esophagus would be expanded actively. Afterwards, water again fills up the rest of the distensible esophagus. In our opinion, the last solution seems quite plausible, a coincidence of active as well as passive components would be a rather simple way to achieve maximal efficiency.

In tortoises the esophagus is less distensible. Food is swallowed by caudally directed contraction waves of the constrictor colli. But also in terrestrial-feeding turtles, the esophagus serves as storage. Food stuff remains in the anterior part of the esophagus, like in a crop, until no more food is available. Afterwards it is swallowed (personal X-ray observations).

For turtles that are able to feed in water as well as on land, these features lie between the two extremes: the hyoid is often more adapted to aquatic feeding, the quite large tongue is more typical in terrestrial feeding. The esophagus is not that distensible other than in aquatic feeders, but is also able to store some excess water and produce contraction waves for swallowing. Thus, all these semiaquatic turtles are typical feeding generalists. In our opinion, the ancestor of all recent turtles must have been a probably emydid-like amphibious turtle, from which the specializations to purely aquatic on the one hand as well as terrestrial on the other hand evolved.

Taking all morphological data of *Pelusios castaneus* into account, it can finally be stated that this species' feeding apparatus is well adapted to the aquatic habitat. The feeding apparatus exhibits strong adductors with a good lever system for generating large forces and high velocities, which is absolutely necessary in an aquatic medium; a strong depressor supported by the coracohyoideus

muscle for fast mouth opening; a large and rigid hyoid apparatus combined with strong musculature for an optimal (fast and wide) enlargement of the mouth cavity; a small tongue with moderate surface topography to lower turbulences and increase the volume of the mouth cavity; and, finally, a distensible esophagus to store a large amount of water until the jaws are closed. With all these well-developed structures all important functional demands of an aquatic feeder are fulfilled.

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