

**KINEMATICS
OF THE ESCAPE HEAD RETRACTION
IN THE COMMON SNAKE-NECKED TURTLE,
CHELODINA LONGICOLLIS (TESTUDINES :
PLEURODIRA : CHELIDAE)**

by

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SUMMARY

Cervical movements during the fast escape head retraction in the pleurodiran turtle *Chelodina longicollis* were studied by means of x-ray cinematography. Radio-opaque markers were inserted near the cervical joints to allow calculation of joint rotations between the successive vertebrae expressed as a function of time and head position. Head retraction as a percentage of the extended neck configuration and angular and linear velocities were also calculated. A combination of muscular organisation and kinematics shows that the neck is divided into two functional regions, anterior and posterior to the biconvex fifth cervical vertebra respectively. Head retraction proceeds in two phases. During the first phase the animal retracts the head very fast underneath the carapace but leaves the neck partially exposed. This phase (with exception for C3-2 and C5-4) shows no significant differences in the timing of the peak-velocities. During the second phase rotations occur mainly in the proximal joints leading to the maximally retracted configuration. Left and right head retractions are mirror images. Retractions never start from a completely extended neck configuration. Initial angles always occur in C6-5 (joint between vertebrae 5 and 6) and C8-7. These joints are also the major bending sites for full retraction of the neck. Peak-velocities of these joints strongly correlate with each other but also with head retraction. When expressed as functions of head position, the rotation patterns of the proximal joints are particularly stereotyped. It is hypothesized that both initial angles and stereotypical retraction patterns are required to allow a fast (escape) retraction powered by a simple motor pattern.

Keywords : neck, kinematics, reptiles, *Chelodina*.

INTRODUCTION

Reptiles, birds and mammals possess a distinct cervical region which gives the head great mobility with respect to the trunk. The benefit to the animal is manifold : e.g. mobile prey can be captured easily, the environment can be scanned

effectively and the head can be retracted close to the trunk, protecting it against negative environmental stimuli (GANS, 1992).

Over the past decade, there has been considerable advance in the knowledge of the kinematics of the avian cervical system (ELSHOUD and ZWEERS, 1987 ; KOOLOOS and ZWEERS, 1989 ; ZWEERS *et al.*, 1977 ; ZWEERS, 1982 ; HEIDWEILLER *et al.*, 1992). The kinematics of the cervical system of turtles, however, has not yet been studied in great detail.

In turtles, the potential for morphological differentiation is largely influenced by the presence of the bony shell. Few changes occur at the level of the trunk, but body parts outside the bony shell are very susceptible to functional changes. Therefore, it is not surprising that the neck of testudinians has shown several conspicuous modifications during the course of turtle evolution (WILLIAMS, 1950 ; HOFSTETTER and GASC, 1969). Starting from a nearly rigid cervical region (with unspecialized cervical vertebrae), two basic patterns of mobile neck configurations evolved independently (GAFFNEY, 1975). Cryptodiran turtles retract the head by bending their neck in the vertical plane. Pleurodirans or side-necked turtles withdraw the head by bending the neck in the horizontal plane ; they fold it back between the dorsal and ventral rim of the bony shell. The neck remains partially exposed in the outer carapacial chamber in front of the pectoral girdle.

In all species of recent pleurodiran turtles, the cervical system can be described as an open kinematic chain of ten links : the body, the head and eight cervical vertebrae. This system has, within certain limits, 27 degrees of freedom, and more than 50 mono- and polyarticular muscles (SHAH, 1963) are present to steer a variety of movements in which speed (*e.g.* escape retraction, feeding strikes) as well as accuracy (*e.g.* feeding strikes) are important. It is obvious that such a system must move the constituent links in concert, which presumably requires a high level of neuromotor control. Anatomical studies of the neck muscles and vertebrae of several turtle species are available (*e.g.* BOJANUS, 1819, 1821 ; VAILLANT, 1881 ; OGUSHI, 1913 ; VALLOIS, 1922 ; WILLIAMS, 1950 ; GEORGE and SHAH, 1954 ; GEORGE and SHAH, 1955 ; HOFSTETTER and GASC, 1969 ; SCANLON, 1982). However, only WEISGRAM and SPLECHTNA (1992) have discussed the integration of morphology and kinematics of the neck system.

This paper is the first in a series dealing with the functional anatomy and cervical kinematics of the Common snake-necked Turtle, *Chelodina longicollis*. The neck in these turtles is very long. This allows the head to be displaced through an extensive volume of space, effectuating a whole range of movements. Slow movements in any direction are performed while scanning the environment. The head can be projected and retracted very rapidly during feeding strikes (see VAN DAMME *et al.*, in prep.). The displacement range usually remains small. The long neck also permits the animal to maintain the trunk deep below the surface, and to extend the neck for breathing (snorkelling ; VAN DAMME *et al.*, in prep.).

The fast escape head retraction has a protective function and must be feasible at any time and from any starting position. In contrast to feeding and snorkelling movements, fast escapes induce the largest joint rotations of the movement reper-

toire in *Chelodina*, and will be discussed in the present paper. Retractions following upon a feeding strike are excluded as they form an integrated part of the feeding behaviour and remain always limited to a much smaller displacement range. They will be dealt with in a subsequent paper.

The fast escape retraction of the head is analyzed by means of cineradiography. These data permit discussion of the dominant kinematical patterns associated with rapid cervical retraction. It also permits hypothesizing about the functional significance of specific initial neck configurations of this mechanism.

MATERIAL AND METHODS

Three live adult specimens of *Chelodina longicollis* were used for the experiments : Chelo #1 (female, 0.73 kg, 0.18 m carapace length, 0.12 m neck length), Chelo #2 (male, 0.52 kg, 0.15 m carapace length, 0.11 m neck length), Chelo #3 (female, 0.70 kg, 0.18 m carapace length, 0.12 m neck length). The animals were obtained with the help of the Antwerp Zoo, and were housed in a glass aqua-terrarium on a 12h light/dark cycle. The water temperature was kept at 28°C. Twice a week the turtles were fed mainly with meat (carved heart muscle), mice and small invertebrates (crickets, grasshoppers).

Head retraction movements (=cervical movements in the horizontal plane) of Chelo #1 and Chelo #2 were recorded cineradiographically (dorsoventrally) using a Siemens Tridoros Optimatic 800 x-ray generator equipped with a Sirecon-2 image intensifier. An integral Arriflex 16 mm camera recorded movements on 7231 Eastman negative film at 50 frames per second. Tube voltage was 50 kV (400mA), the exposure time of the x-ray flashes 1 ms and the distance between tube and image intensifier 1 m. In order to keep the animal above the image amplifier the animals were restrained by means of a body-shaped corset made of thermoplastic material (Orthoplast ; Johnson and Johnson Orthopaedics). To improve the accuracy of the image analysis, radio-opaque lead markers pinched out of a 1mm thick lead sheet were inserted under the periosteum by hypodermic needles in Chelo #1 and Chelo #2 under radiographic control. Because Chelo #3 belonged to the Antwerp zoo, no invasive experiments were allowed on this animal. The animals were anaesthetized with an intramuscular injection of 147 mg/kg Ketamine hydrochloride. The markers were inserted in 12 locations ; one dorsally on the caudal part of the skull, one near each of the cervical joints (dorsal on the posterior zygapophysis of the vertebrae), one on the first dorsal vertebra, and two into the anterior part of the carapace (Fig. 1A). The position of these markers was checked on dorsoventral and lateral radiographs. For Chelo #2 the marker at the level of joint C2-1 was not inserted properly, and therefore could not be used in the analyses (*i.e.* joint angles S-C1 and C2-1 are missing for this specimen). Sequences were projected frame by frame on a Hipad Digitizer (Houston Instruments) connected to a 80386-DX IBM-compatible computer. The position of the markers was digitized and converted to a turtle bound frame defined by the carapace markers (ref 1 and ref 2 on Fig. 1A).

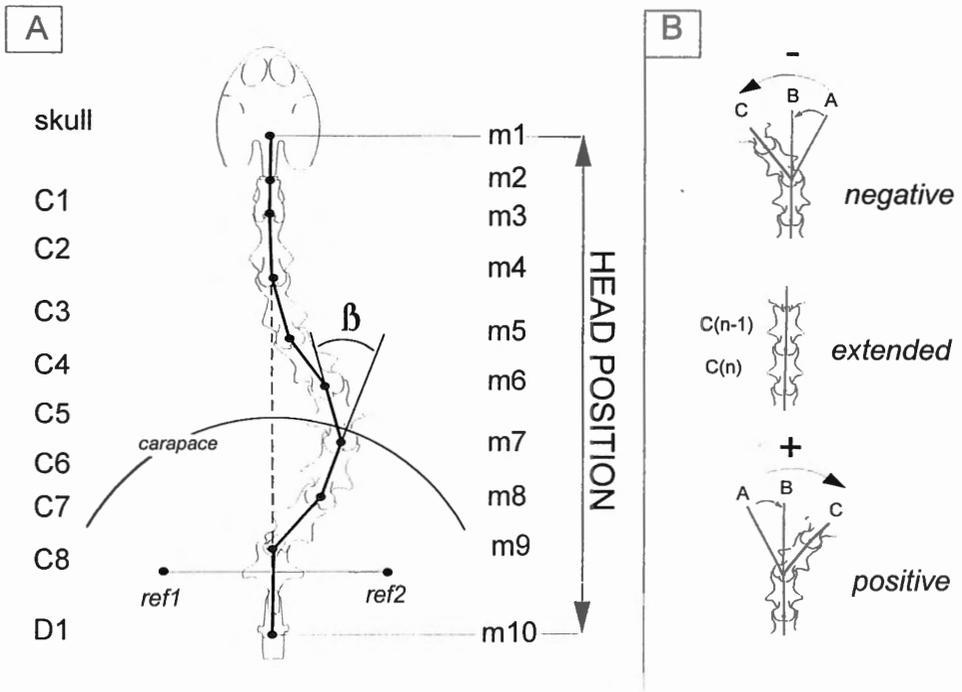


Fig. 1. — *Chelodina longicollis* — A. Position of the radio-opaque markers (black dots, m1–m10) on a schematic representation of a neck configuration from which a retraction can start. The black solid line represents a stick diagram as constructed based on the position of these markers. The length of the dashed line gives the head position. ref 1 and ref 2 are the carapace markers. β represents a starting angle (e.g. C6–5). — B. Terminology of joint rotation. Starting from the extended configuration (middle), counter clockwise rotations (above) result in a negative joint angle. Clockwise rotations (below) result in a positive joint angle. Distance A–C represents the total joint excursion. Distance A–B the contralateral joint excursion.

The degree of head retraction is defined by the rectilinear distance between the cranial-most (m1) and the caudal-most (m10) marker (Fig. 1A), and is expressed as the percentage of the maximum possible distance between these two markers. Thus, a completely extended neck coincides with a head position of 100 %, whereas maximal retraction equals 25 %. Left and right head retractions stands for movements in which the final retraction of the head occurs to that particular side of the body. Twenty head retractions were analyzed in detail (5 left and 5 right trials for each specimen). Left and right movements were compared within and between both specimens. For each movement, stick diagrams were constructed in order to obtain a schematic representation of the observed cervical movement (Fig. 3B).

Special attention was paid to changes in angles between successive vertebrae (*i.e.* joint angles), both as a function of time and as a function of the degree of head retraction. These changes are defined as rotations about a vertical axis of ver-

tebra $n-1$ with respect to the more caudal one (vertebra n ; see Fig. 1B). Starting from the extended position (= 0 degrees of lateral flexion) a positive joint angle is defined as a displacement of the anterior vertebra to the right (clockwise rotation, Fig. 1B).

Slow head displacements were induced by luring the animal with a prey item. When the head was positioned approximately in the midsagittal plane, a fast escape head retraction was initiated by suddenly touching the tip of the snout with a plastic tube. In most cases however, retraction began from an obviously bent neck, and all joints showed a starting angle. When during a retraction a joint angle crosses the extended configuration of the joint, the starting angle is defined as contralateral (with respect to the joint angle at maximal head retraction), and the rotation up to the fully extended position is called a contralateral change of joint angle. Retraction movements were never observed to start from the 100 % head position, because the cineradiographs of an extended neck always revealed initial angles being present in a few specific joints (see further).

Angular velocities (rad.s^{-1}) in the joints and the linear velocity of the head (percentage.s^{-1}) were obtained by differentiation of the smoothed displacement data of the cineradiographical recordings (WOOD, 1982). This procedure emphasizes the relationships in timing and relative importance of the centres of motion (= joints). A Quintic spline routine (supplied by G.A. WOOD, Department of Movement Studies, University of Western Australia) was used, and the accuracy of fit (least-square criterion) was adjusted until the velocity profile was free of any biologically irrelevant oscillations (*i.e.* oscillations in the acceleration profiles occurring at frequencies above the ones expected from the displacement pattern itself). For each trial, peak-velocities and the corresponding times at which these peaks occurred were determined for the joints and the head (Table 1). Kinematic variables were statistically analyzed as follows. Times of peak-velocities among joints were compared within trials using a Friedman Two-way Anova. Pairwise comparison of the relative times of the joints with the head were analyzed with Wilcoxon Matched-pairs Signed-rank tests (NORUSIS, 1986). To determine multivariately which peak-velocities of joints were correlated with the head, a canonical correlation analysis (SAS v6.07) was carried out.

Static radiographs (50 kV) were made of all three specimens with the neck forced to maximal retraction. Figure 5 is based on such a radiograph of Chelo #3.

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 labelled by the number of the adjacent vertebrae: $C(n)-(n-1)$, with n the number of the more proximal (caudal) vertebra and $(n-1)$ the number of the more distal (cranial) one. For example, the joint between vertebra 5 and 6 is defined as « joint C6-5 ».

RESULTS

Morphology

The cervical column in all recent turtles consists of eight elongated vertebrae (C1-C8) and nine joints. Fig. 2 (part A, B, C) illustrates the terminology of the

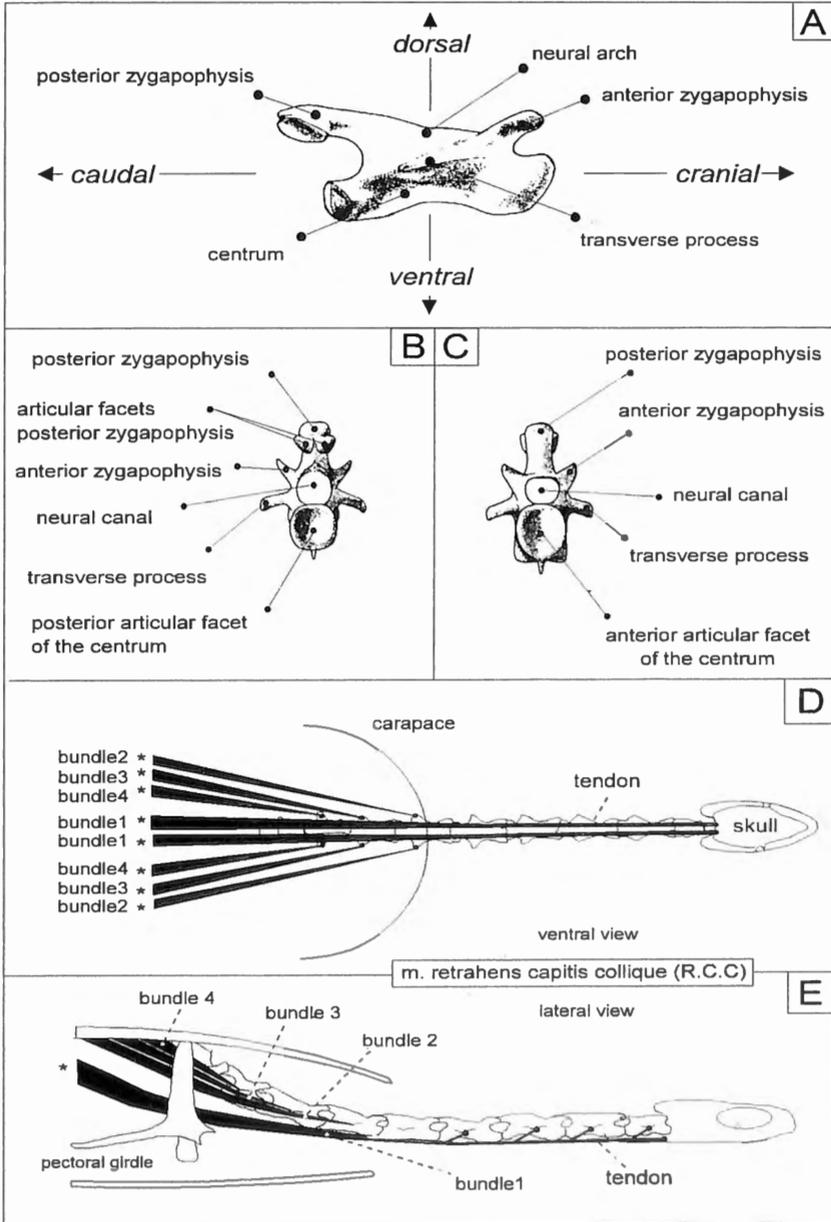


Fig 2. — *Chelodina longicollis* — Upper half : Terminology of the most important structural elements of a cervical vertebra (e.g. C7). A. lateral view, B. posterior view, C. anterior view (terminology after ROMER and PARSONS, 1977). — Lower half : organisation of the m. retrahens capitis collicae. D (ventral view) and E (dorsal view). «*» indicates that the place of origin is not shown (see description for more details). Each bundle is numbered according to its site of insertion in the neck. Bundle 1 has the rostral most insertion.

most important structural elements of a cervical vertebra (e.g. C7) in *Chelodina*. The neural spine is reduced to a inconspicuous longitudinal rim. The anterior zygapophyses are clearly separated from each other. Their articulation facets are mainly oriented in the medio-dorsal direction. The posterior zygapophyses are fused to each other except those of C1, but the articulation facets remain separated and face mainly ventrally and slightly laterally. The elevation of the posterior zygapophysis gradually increases from distal to proximal. The transverse processes are strongly developed, especially those on the more proximal vertebrae (for a more detailed description of the vertebrae of *Chelodina* see VAILLANT, 1881). Vertebral centra can be biconvex (C5, C8 : two condyles), biconcave or amphicoelous (C1, C7 : two cotyles), procoelous (C6 : anterior cotyle, posterior condyle) or opisthocelous (C2, C3, C4 : anterior condyle, posterior cotyle).

The muscular organisation of the neck in *Chelodina* is very complex. There are short monoarticular and longer polyarticular muscles. The most important muscle powering fast head retraction (based on position and morphology) is the m. retrahens capitis collique (Figs 2D, 2E). It consists of four well developed muscle bundles on each side of the trunk. Bundle 1 (RCC₁) is the longest muscle observed in the whole turtle body. It originates from the lateral sides of the eighth dorsal vertebra immediately anterior to the pelvic girdle, and from the carapace adjacent to this vertebra. The muscle bundle runs ventrally to the other bundles of the RCC-complex and the cervical vertebrae, lying dorsal to the oesophagus and trachea. At the level of C5 the muscle fibres of RCC₁ insert on a large tendon which extends anteriorly to the base of the skull attaching to the basioccipital. Small tendon slips split off from this large tendon and insert on the transverse processes of the first four cervical vertebrae. Bundle 2 (RCC₂) originates on the ventral side of the neural plate of the carapace, adjacent to D5. It runs anteriorly, parallel and dorsal to bundle 1 and inserts by means of a large, flat tendon on the transverse processes of C6. Bundle 3 (RCC₃) originates from the ventral side of the neural plate adjacent to the fourth dorsal vertebra. The tendon inserts on the lateral side of C7. The muscle fibres of the smallest bundle (bundle 4, RCC₄) originate at the level of D3 and insert on the transverse processes of C8.

Kinematics

Detailed description of an escape retraction movement

A representative example of a left head retraction movement of Chelo #1 is illustrated in Figure 3. Starting from a nearly extended neck configuration (90 % position, Fig. 3A), retraction takes about 0.6 s. The displacement range is large, but retraction is still incomplete (retracted head position equals 35 %, versus 25 % for maximal retraction). The actual movement is represented by the stick figures of Fig. 3B (1) (time interval : 20 ms.). Figure 3B (2) shows the path of the joints during the retraction. The four proximal joints displace latero-caudally to the right. The more distal (=cranial) joints move mainly in caudal direction (=in the direction of the carapace). Because the spatial displacement of a joint represents the summed

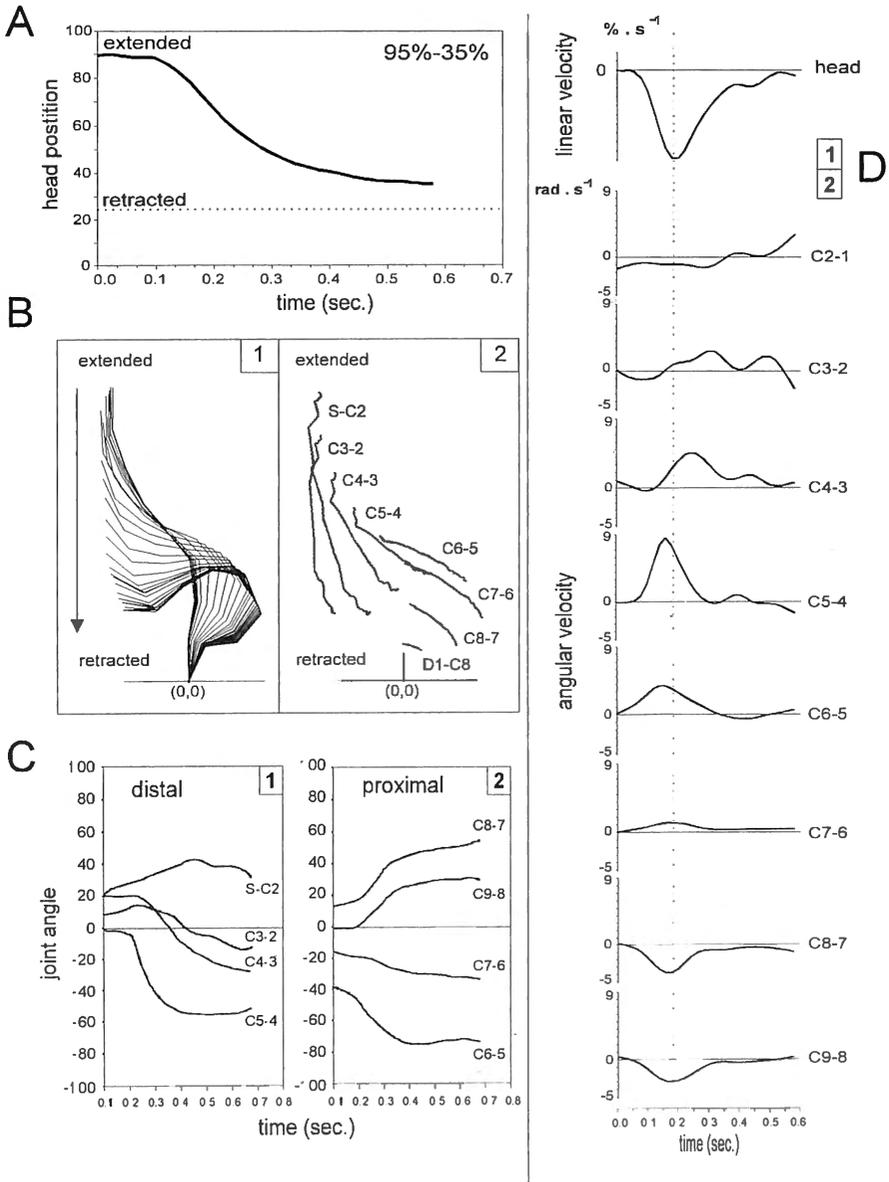


Fig 3. — *Chelodina longicollis* : Kinematics of a left head retraction movement. — A. head position in function of time. — B. stick diagrams, B1. sticks illustrating schematically the retraction movement, B2. path followed by individual joints. The arrow indicates the direction of movement. — C. changes in joint angle as function of time. C1. anterior neck region. C2. posterior neck region. — D. velocity profiles of head retraction (D1) expressed in percentage head position. s^{-1} , and of changes in joint angles (D2) expressed in $rad.s^{-1}$. Dashed line coincides with maximal head velocity.

effect of all rotations in the more proximal joints, the lengths of the paths increase from proximal to distal. Figure 3C gives the changes of joint angle as a function of time. Because the retraction movement initiates from an already partly retracted head position (90%), starting angles (*i.e.* diverging from zero) exist in several joints. In the posterior part of the neck, the largest starting angles occur in C6-5 (negative) and C8-7 (positive). All joints, with exception of the first (C2-1) and the last two (D1-C8 and C8-7) show changes of joint angle in the negative direction. In the distal part of the neck the fastest changes in joint angle occur in C5-4 (see also the velocity profile of C5-4 in Figure 3D (2)). In the proximal part of the neck, rotations in C7-6 remain restricted.

The velocity profiles of the head retraction and joint rotations are illustrated in Fig. 3D (1) and 3D (2) respectively. The peak velocity of head retraction equals $-281 \text{ \%} \cdot \text{s}^{-1}$, which accords to an actual velocity of -0.35 m s^{-1} (retractions result in negative velocities). The angular velocity profiles of the first two joints (C2-1 and C3-2) are rather flattened and irregular. From C4-3 on, a distinct peak in the profile is apparent which tends to coincide with the peak velocity of head retraction. From C4-3 to C7-6 the peak velocities are positive (clockwise rotation). In the last two joints the peak velocities are negative (counter clockwise rotation). The greatest peak amplitude is observed in C5-4 (approximately $9 \text{ rad} \cdot \text{s}^{-1}$). Velocities in C7-6 remain very low throughout neck retraction.

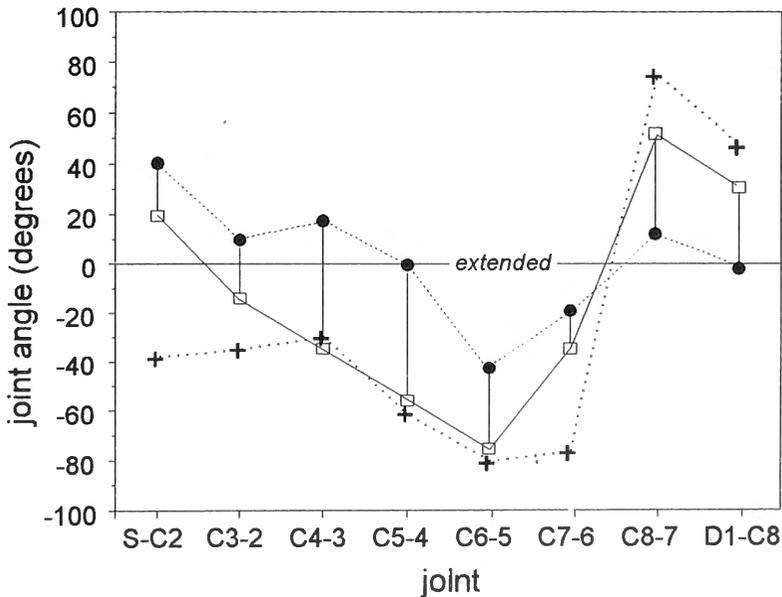


Fig. 4. — *Chelodina longicollis*: Kinematics of a left head retraction movement. Filled dots: starting angles. Filled squares: final angles for this particular sequence. Plus signs: final joint angles occurring in a complete left head retraction.

Fig. 4 summarizes the range of motion in the different joints for this specific left head retraction movement. Differences between the final joint angles observed in this trial (open boxes in Fig. 4), and the final joint angles occurring at maximal head retraction (« + » in Fig. 4) are observed in the three proximal most joints (especially C7-6) and the two anterior most joints (C2-1 and C3-2).

Neck configuration at maximal retraction

Fig. 5 illustrates the final neck configuration when head and neck are completely retracted (example given for a right head retraction of Chelo #3). This figure is based on a static radiograph of a living specimen forced to retract its head maximally. The values of the final joint angles are indicated. Left and right configurations are mirror imaged (final joint angles for a right retraction : S-C1=0°; C2-1=37°; C3-2=35°; C4-3=26°; C5-4=47°; C6-5=77°; C7-6=70°; C8-7=-92°; D1-C8=-58°). Irrespective the sign, the largest joint angles appear in the most proximal part of the neck, especially in C8-7 and C6-5 (« * » in Fig. 5). Little variation is observed in the joint angles of this final neck configuration between the three specimens.

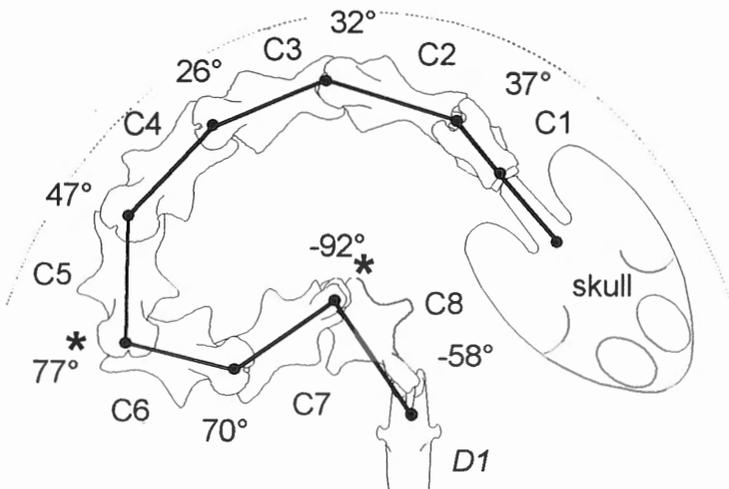


Fig. 5. — *Chelodina longicollis* : Neck configuration with the head completely retracted (e.g. for a right head retraction). C1-C8 : cervical vertebrae. D1 : first dorsal vertebra (fused with the carapace). Asterisks : largest final joint angles. Dotted line represents the outer limits of the carapace.

General considerations of the escape head retraction in Chelodina longicollis

The next description is based on the entire data pool of the analyzed escape head retraction movements in both specimens of *Chelodina* (Chelo #1 and Chelo #2 ; 20 sequences in total). Fig. 6A of Chelo #1 shows the rotation ranges combined for all analyzed sequences. This is done for the left (N=5) and right

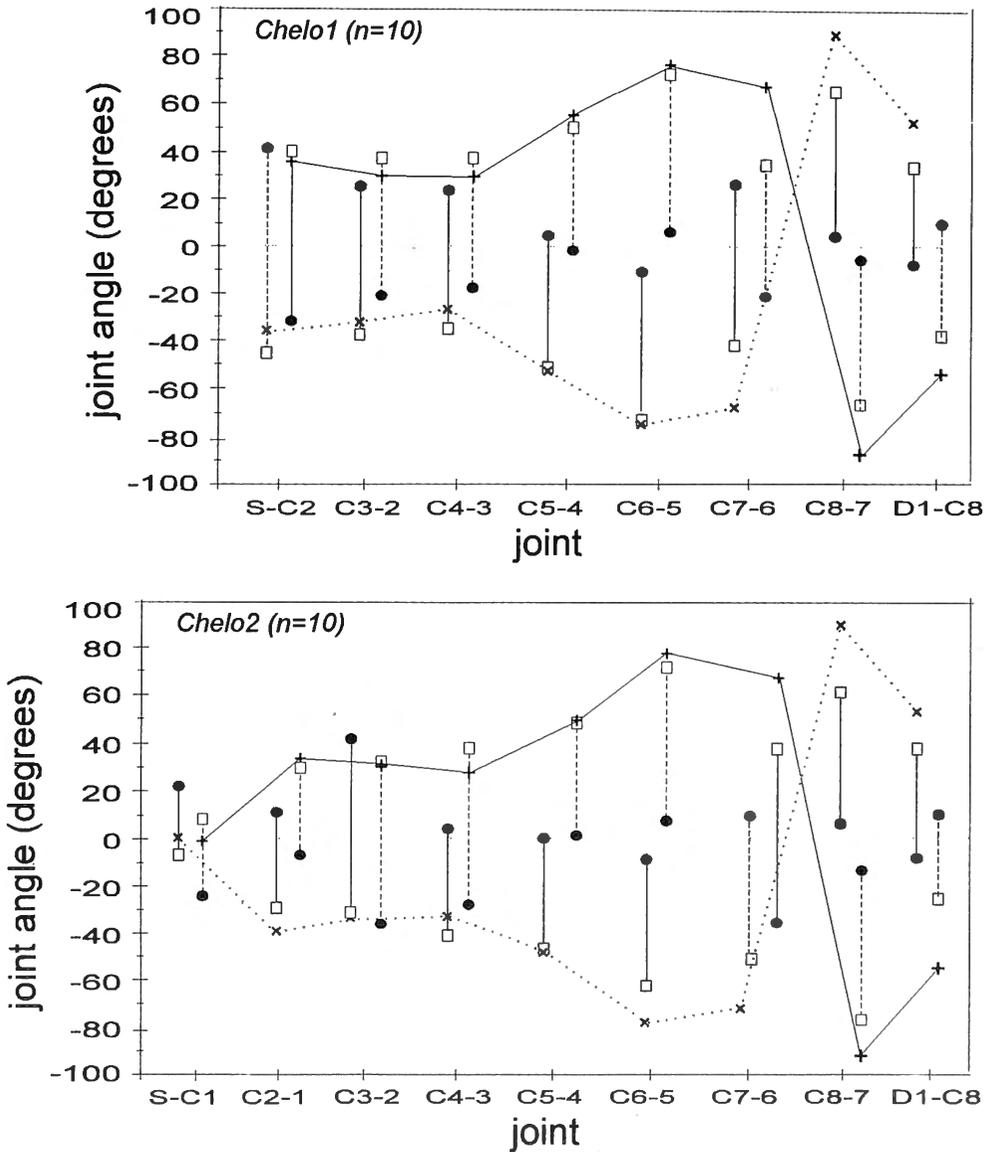


Fig. 6. — *Chelodina longicollis*: Observed ranges of joint rotations during head retraction in Chelo #1 (A) and Chelo #2 (B). Dotted lines: summation of the movement range for 5 ($n=5$) right head retraction movements. Plus signs: joint angles for a complete right head retraction (see also Fig. 5). Solid lines: summation of the movement range for 5 left head retraction movements. Crosses: joint angles for a complete left head retraction. Black dots: starting values. Open squares: final values.

($N=5$) retractions separately. Figure 6B presents the same information for Chelo #2. The patterns for left and right head retractions are clearly mirror images of each other. The more proximal joints attain a larger final joint angle than the more distal joints. The range of motion in the successive joints varies with the configuration of the neck at the beginning of the retraction movement. Nevertheless, some joints show little (C5-4) or no (C6-5 and C8-7) contra-lateral joint excursions. As mentioned earlier, the differences between the observed final joint angles (open boxes in Figs. 6A, 6B) and those at maximal head retraction (« + » and « × » signs in Figs. 6A, 6B) are most conspicuous for the proximal joints (especially C7-6).

Plotted against head position, the joint angles of all the analyzed sequences appear to show similar movement patterns. Superimposing these patterns for all sequences results in the construction of displacement envelopes (Fig. 7), which reveal the range of angular rotations in each joint throughout the escape head retraction (see discussion). The width of an envelope at any specific degree of head retraction expresses the range of angles to which the involved joint is restricted when passing through that particular head-position during retraction. Narrow envelopes thus suggest stereotyped movement patterns, whereas broad envelopes indicate that an animal has considerable kinematical flexibility. Figure 7 shows that envelopes are much narrower for the proximal joints than for the distal ones (*i.e.* freedom increases towards the head). Moreover, for all joints the rotational freedom decreases with increasing retraction (see discussion).

Peak velocities and correlated timing are presented for all analyzed trials in Table 1. Joints S-C1 and C2-1 are not included as they could not be measured for Chelo #1 (see Materials and Methods). The bold figures refer to the observed maxima. The fastest head retraction observed in Chelo #1 was 2.68 m s^{-1} and that for Chelo #2 was 19.66 m s^{-1} (in the table head velocity is expressed in $\% \text{ s}^{-1}$ to facilitate comparisons). Table 1 further shows a tendency towards coinciding timing of the velocity peaks (see also Fig. 6D). The statistical treatment and interpretation is presented in the discussion.

DISCUSSION

Morphologists have investigated and described the cervical system of turtles for about two centuries. The main conclusions were related to the morphological difference between the pleurodiran and cryptodiran neck systems. WILLIAMS (1950) studied the shape of the central articulations between the neck vertebrae in a large number of turtle skeletons. Without taking into account ligamentous connections, zygapophyses and neck musculature this author constructed a diagram representing the two major types of neck movements. He found that joints C6-5 (mostly) and D1-C8 (always) are procoelous in pleurodiran and cryptodiran turtles, and related this to their importance as centres of movement. SCANLON (1982) described the anatomy of the neck of the western painted turtle *Chrysemys picta belli* (Cryptodira) and made predictions concerning patterns of neck movements based upon morphological data and radiographs. This author concluded that predictions about

kinematics of neck movements based on morphological data do not always agree with the observed *in vivo* movements. WEISGRAM and SPLECHTNA (1990) compared the anatomy of the cervical vertebrae in a cryptodiran turtle (*Testudo hermanni*) and in a short necked pleurodiran turtle (*Pelomedusa subrufa*). On the basis of ligamentous preparations and radiographs of these preparations fixed in the retracted position, they determined the maximal range of motility in each joint. Their study suggests that all cervical joints in *Pelomedusa* show the same range of lateral mobility. They conclude that joints C4-3 and C8-7 are the important centres of motion in the neck of *Pelomedusa*. In *Testudo* the cervical joints C3-2 and C8-7 have the largest potential for carrying out movements. Based on these results, WEISGRAM and SPLECHTNA (1990) modified the diagram of WILLIAMS (1950).

Whereas all these studies discuss the functioning of the testudinian neck entirely on the basis of anatomical and static configurational data, WEISGRAM and SPLECHTNA (1992) assessed changes in the neck joints during feeding movements of the Australian side-necked turtle *Chelodina novaeguinae* based on video recordings combined with radiographs. They noted that the three caudal-most cervical joints (D1-C8, C8-7, C7-6) appear to be of major importance. However, no data were presented on head retraction.

Several practical problems are inherent to (ciné-)filming or video-taping neck movements of turtles. The bony shell obscures large parts of the neck, whereas the loose connection between the skin and the underlying parts hampers linkage of the external movements to the precise movements of the neck skeleton. X-ray cinematography allows one to compensate for these problems, although the image can still be blurred (especially in the posterior neck region) due to the presence of the bony shell. The implantation of radio-opaque markers in the neck, as used in the present study, further improves analysis of the intervertebral movements.

Interpretation of the kinematics

Fig. 7 shows the displacement envelopes of the cervical joints in the neck for head retraction movements either to the left or to the right. The narrower the envelope, the less the variation is: the rotations in the involved joint as a function of the degree of head retraction are more stereotyped (see above). An increasing stereotypy from distal to proximal is observed (Fig. 7). This phenomenon can be related to the differentiation of the neck musculature. The proximal vertebrae have highly developed transverse processes (Fig. 2A) which reflect the insertion of the massive muscle bundles of the proximal neck musculature (e.g. m. R.C.C bundles 2, 3, 4; Figs 2D, 2E). This part of the neck is responsible for the largest part of the retraction (Fig. 5). The distal vertebrae receive the insertion of split muscle bundles. Such an increased splitting of the musculature allows smaller, more subtle joint rotations in the distal joints. Therefore, the anterior part of the neck plays an essential role in head orientation (including dorsoventral movements). Fig. 7 also shows that the stereotypy increases for all joints with the degree of head retraction. This means that a small retraction starting from a more or less extended position can be performed in a more versatile way, compared to a retraction over an identical range, but beginning with the neck already partly retracted.

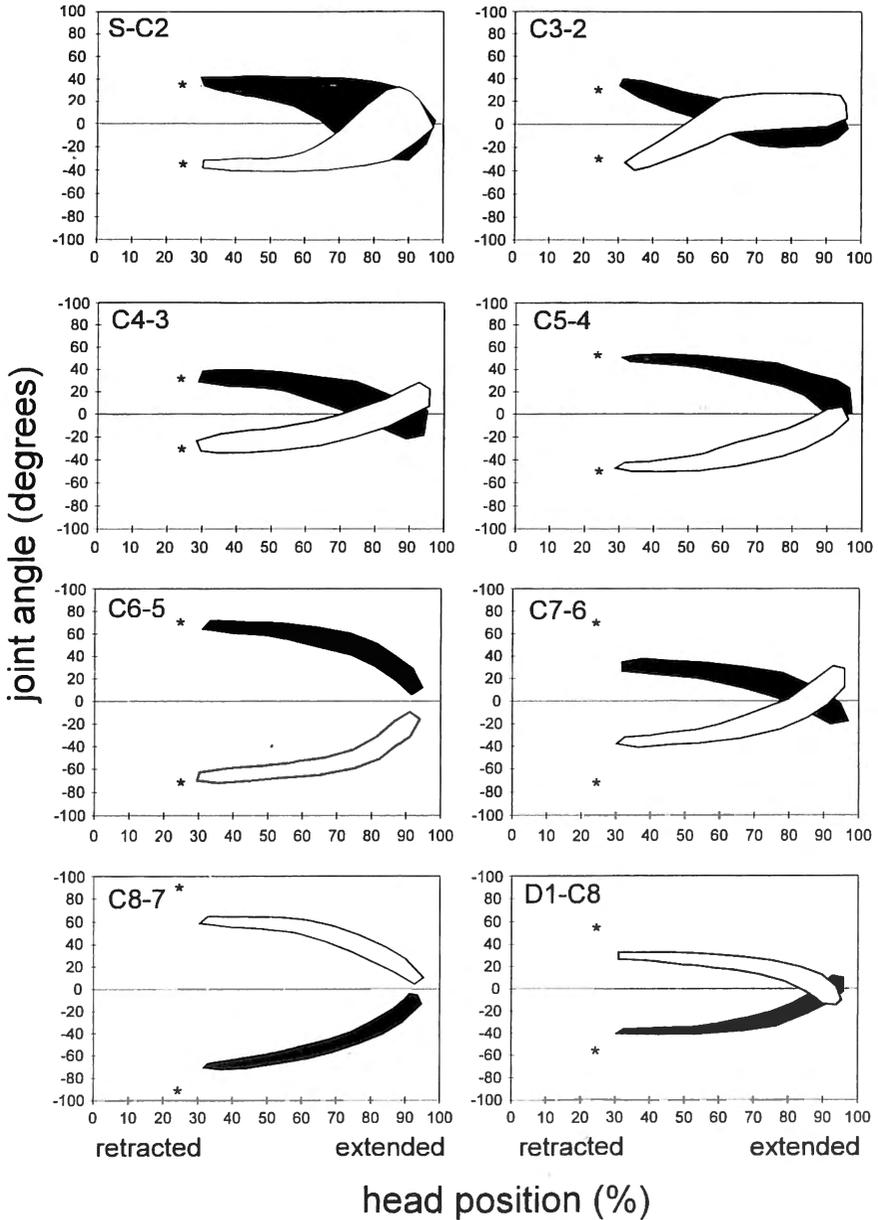


Fig 7. — *Chelodina longicollis*: Displacement envelopes (= changes in joint angle as function of head position) of cervical joint rotations in Chelo #1. Black envelopes: right head retractions (n=5). White envelopes: left head retractions (n=5). Asterisks: final joint angle when the neck is completely retracted.

Besides this stereotypical pattern of changes in joint angle, kinematics of left and right head retraction within each turtle are mirror imaged (Fig. 6). Both facts support the presence of a fixed and simple neuromotor pattern to drive the fast and complete head retraction (for instance in an escape response), because then fast and accurate folding of the neck is assured.

From the kinematic analysis it follows that head retraction never starts from the fully extended neck configuration (e.g. Fig. 3), even when externally the neck appears to be extended. Several joints (C6-5 and C8-7 always, C5-4 often) show initial angles. When the animal is heavily anaesthetized, the neck will be completely extended only if a considerable external force is applied. Initial angles can either be positive or negative, and this is determined by the preceding slow neck movements (head movements from left to right and *vice versa* necessitates such changes). Nevertheless, the symmetrical structure of vertebrae and muscles suggests that the completely extended neck configuration is physiologically feasible.

One could think of a possible damage of the neck musculature due to the insertion of the radio-opaque markers, or of an occasional malformation of the neck. However, identical configurations are observed in both specimens, before as well as after surgery. Therefore, it seems likely to assume that initial angles in an externally extended neck are biologically relevant and coincide with the configuration that minimizes the potential (i.e. elastic) energy in the entire neck system. Energy might be stored in all strained structures crossing the joints (muscles, tendons, joint capsules,...). It has to be noticed, however, that extracapsular ligaments, as described in the avian cervical system (LANDOLT and ZWEERS, 1985) are not present in turtles.

The biological significance of this might be that in this way fast escape head retraction can always be driven by one fixed bilateral symmetrical motor pattern. Due to the presence of initial angles the subsequent angular displacement is determined to a large extent, without necessitating subtle motor control for each individual joint. Retraction starting from a completely extended situation requires a more complex and flexible motor control, and is obviously much more sensitive to erroneous folding of the neck. This can be exemplified by a chain of interconnected rigid links (simulating vertebral elements and head) held in a vertical position, the lower end movably connected to a horizontal rigid support (the body). If this chain is left free, gravity will act on it as a simple, very stereotyped force generator. Starting with all links in line, the manner in which it will fold is indefinite. However, the introduction of a few initial angles between some of the links will reduce the variability of the folding pattern drastically. If initial angles of opposite sign are introduced, the folding pattern will mirror image its counterpart, although the force generator remains unchanged. This hypothesis fits in with the conclusions on stereotyped movements drawn from the displacement envelopes and the configurations of maximal retraction (see above). Based on the morphology of the RCC_1 (its length and the rather ventral and medial course of its tendon in the neck), it is this bundle that powers the fast head retraction. This hypothesis is now being tested by means of electromyography. Preliminary results indeed indicate that left and right RCC_1 muscle bundles show a bilateral synchronous activity during

the fast escape head retraction, independent from the position from which the movement starts (unpublished observations).

Velocity profiles and head retraction

Concerning the timing of joint rotations, three basic types of movement pattern can be proposed. First, the joint rotations could follow a pattern that implies a sequential timing of changes in joint angle from proximal to distal. Secondly, the timing of joint rotations might show a random pattern, but this is difficult to associate with the observed stereotypy. Thirdly, joint rotations can be synchronized, which should nicely integrate with the concept of the fixed motor pattern (see above). To tackle this, the time variables of head retraction and joint rotations (based on peak-velocity; see Table 1) for each trial were statistically analysed using a Friedman Two-way Anova (NORUSIS, 1986). This test reveals a ranking in timing of joint rotations (Chi-Square : 24.9; D.F. : 6; $P=0.0004$; $n=20$; Table 2). However, this time ranking differs from the geometric ranking (*i.e.* position in the neck : no bike chain principle), and only two of the joints (C3-2 and C5-4 : *i.e.* the extremes of the ranking) show a significant difference in timing relative to the head (Wilcoxon Matched-pairs Signed-rank test, Table 2). This means that all cervical joints (except C3-2 and C5-4) and the head tend to peak together. The peak velocity in joint C3-2 occurs significantly later than the peak velocity of the head. This is because, during retraction, the head often remains partly oriented in anterior direction. Only at the very end of the retraction phase, this joint increases its flexion. Peak velocity in C5-4 precedes that of head retraction significantly. This might be related to the insertion morphology of RCC_1 (on all vertebrae in front of this joint; see Fig. 2B).

HEIDWEILLER *et al.* (1992) described the kinematics of cervical movements during upstroke in 1 to 4 week old chickens as a « bike chain » pattern (*i.e.* rotations in neighbouring joints succeed each other in time). This bike chain pattern could be related to movement principles that minimize the rotational forces or maximize the rotation efficiency. These authors also further postulate that the bike chain pattern might also be a consequence of the construction of the cervical column.

A sequential timing of joint rotations from proximal to distal as described in chickens is absent in *Chelodina*. In turtles, such a system might be advantageous when the neck must be withdrawn through a narrow orifice. This bike chain pattern is indeed observed in long necked cryptodiran turtles with an extremely flattened carapace, such as *Trionyx* (unpublished observations). However, in *Chelodina* the outer carapace chamber has a broad slit-like aperture and provides sufficient space for simultaneously rotating joints. The latter may be beneficial when retraction speed must be optimized. One can indeed observe that the head is first withdrawn very fast under the carapace, but that the neck remains partly exposed. Only in a second phase, smaller changes occur, positioning head and neck in their final, maximal retracted configuration. The final positioning involves changes in joint angle mainly in the posterior joints (especially C7-6).

Correlating the peak velocity of head retraction with these of the cervical joints may permit the recognition of important centres of motion in the neck of *Chelodina*. Notice however that linear and angular velocities are related to each other. However, the linear velocity of the head is the result of joint rotations (see VAN INGEN SCHENAU, 1989). Joints showing a significant correlation with the head are believed to be the main effectors of the retraction. Joints which do not correlate are more independent in their speed profiles and probably have primarily a steering function. A canonical analyses was carried out on the peak-velocity data of Table 1. The results are presented in Table 3. Based on an univariate approach high correlations between the head and four specific joints (C4-3, C6-5, C8-7, C9-8) are found. Based on the multivariate approach, the new canonical variable (see standardized canonical coefficients in Table 3) is significantly correlated with the head (Likelihood Ratio : 0.08784 ; $F=17.8$; $DF=7,12$; $P=0.0001$). High correlations are found for only two joints ; C6-5 and C8-7. These are the major bending points in the neck judging their final angles (see Fig. 9), and are precisely the joints which always show an initial angle (see above). The significant correlation found for C4-3 and D1-C8 in the univariate approach indicates that a relationship must be present between D1-C8 and C4-3 and one or more other cervical joints. Table 4 shows the correlation matrix between the different joints (canonical analyses based on peak-velocity data). Joints C9-8 and C4-3 correlate significantly with the two major bending points in the neck C6-5 and C8-7. As expected, there is a high pairwise correlation between these two as well.

The m. retrahens capitis et collicae

The Retrahens muscle complex is one of the most striking muscles in the neck and body of *Chelodina*. The RCC_1 runs from the base of the skull to the last dorsal vertebrae at the level of the pelvic girdle. In other words, the length of the muscle almost equals this of the entire animal. This is because, besides force, contraction speed as well as contraction range are very important for this muscle. Putting more contractile units (sarcomeres) in series increases the speed of the muscle (e.g. Josephson, 1975). Moreover, given a certain shortening distance, the longer the muscle fibres are (= more sarcomeres), the closer to the optimum of the length-tension curve they can maintain while working, thus ensuring a continuously high force output. To avoid non-uniform distribution of the contractile state (= sarcomere length = number of cross bridges) over the length of the fibre, leading to contracting fibre segments extending others, a serial arrangement of shorter muscle fibres, combined to a polysegmental and polyneural innervation would be expected (GANS and DE VREE, 1987). Such an arrangement is indeed found in the short necked cryptodiran turtle *Pseudemys (Trachemys) scripta* (CALLISTER *et al.*, 1992).

TABLE 1

Chelodina longicollis : Absolute values of peak-velocities (upper left value in each cell) and corresponding time from initiating of retraction (lower right value in each cell) for each joint of 20 head retractions. Top half represents 10 head retractions of Chelo #1. Bottom half represents 10 head retractions of Chelo #2).
Bold numbers : maximal peak-velocity observed for each joint in all trials
 (Head in %/s⁻¹, joints in rad.s⁻¹, time in sec.)

	chelo1	chelo1	chelo1	chelo1	chelo1	chelo1	chelo1	chelo1	chelo1	chelo1
HEAD	281 0.18	107 1.06	93 0.62	141 0.68	358 0.22	341 0.22	350 0.70	450 0.82	380 1.02	160 0.20
C3-2	2.58 0.32	2.76 1.06	1.67 0.54	0.56 0.84	1.69 0.26	3.56 0.24	4.01 0.80	4.19 0.80	8.20 1.00	4.36 0.20
C4-3	4.59 0.24	1.29 1.02	1.19 0.40	2.11 0.72	3.75 0.26	4.59 0.16	7.33 0.70	20.93 0.82	17.62 0.94	4.54 0.16
C5-4	6.84 0.16	10.54 1.02	3.70 0.50	1.88 0.68	5.09 0.22	5.02 0.20	6.98 0.68	7.33 0.78	4.71 0.98	2.09 0.16
C6-5	3.73 0.14	0.49 1.06	4.12 0.56	1.92 0.66	5.02 0.20	1.57 0.12	6.98 0.72	8.72 0.78	5.23 0.98	4.01 0.18
C7-6	1.24 0.18	0.51 1.02	2.44 0.82	0.49 0.72	3.73 0.18	5.16 0.12	2.62 0.72	2.97 0.80	1.31 1.02	2.09 0.18
C8-7	3.77 0.18	0.40 1.01	2.60 0.54	1.26 0.64	4.61 0.18	3.11 0.16	6.11 0.70	7.15 0.82	6.98 1.00	3.14 0.22
D1-C8	3.02 0.18	0.52 0.90	1.06 0.60	1.62 0.66	2.08 0.24	1.33 0.16	2.62 0.68	4.01 0.86	3.84 1.08	2.44 0.18
	chelo2	chelo2	chelo2	chelo2	chelo2	chelo2	chelo2	chelo2	chelo2	chelo2
HEAD	470 0.24	458 0.18	591 0.26	305 0.30	190 0.7	230 0.26	280 0.62	510 0.68	580 0.76	70 0.5
C3-2	7.03 0.28	6.84 0.20	9.18 0.30	1.67 0.68	5.58 0.70	3.49 0.30	7.85 0.66	8.90 0.70	4.71 0.76	5.06 0.50
C4-3	9.77 0.22	11.20 0.16	23.64 0.26	3.33 0.26	4.45 0.68	13.61 0.24	10.21 0.60	24.34 0.68	17.27 0.78	5.23 0.48
C5-4	4.10 0.22	2.46 0.16	7.83 0.24	5.16 0.30	6.45 0.72	4.88 0.26	3.49 0.64	6.98 0.64	4.36 0.78	3.84 0.48
C6-5	4.57 0.24	3.72 0.18	13.40 0.24	3.31 0.28	3.84 0.76	5.23 0.24	5.58 0.62	9.07 0.64	11.51 0.76	3.05 0.54
C7-6	0.91 0.22	0.40 0.22	3.16 0.26	0.51 0.28	1.92 0.72	0.87 0.26	3.31 0.62	1.74 0.70	1.92 0.78	1.31 0.48
C8-7	5.44 0.22	5.09 0.18	10.61 0.26	0.72 0.32	3.66 0.72	3.84 0.26	4.88 0.58	8.72 0.70	9.94 0.82	1.74 0.58
D1-C8	3.00 0.24	3.37 0.18	5.02 0.26	1.33 0.32	1.92 0.18	3.49 0.26	2.62 0.62	4.36 0.70	4.01 0.80	2.09 0.56

TABLE 2

Chelodina longicollis : Statistical analysis of the relative time of peak-velocities.
 Middle column : Ranking of the timing of joint rotations
 based on a Friedman Two-way Anova of the time variables. Last column :
 Pairwise comparison of the relative times within trials
 (Wilcoxon matched-pairs signed-ranks tests. P = probabilities for coinciding timing
 of peak-velocity of head retraction and joint rotation)

Joint	mean-ranking (Friedman Anova)	P (Wilcoxon)
C5-4	2.72	0.0061
C6-5	3.22	0.0783
C4-3	3.30	0.3942
C7-6	4.07	0.9547
HEAD	4.20	—
C8-7	4.40	0.9721
C9-8	4.72	0.2489
C3-2	5.55	0.0115

TABLE 3

Chelodina longicollis : Statistical analysis of the peak-velocities. Column A and B :
 Univariate approach. A. correlations between each joint and the head.
 B. correlation between each joint and the new canonical variable.
 Column C. Multivariate approach (taking in to account
 correlations between the joints). Standardized canonical coefficient for each joint
 in the new canonical variable (bold numbers : high correlations)

Joint	Univariate		Multivariate
	R	Correlations between variables and the canonical variable	Standardized canonical coefficients
C3-2	0.584	0.6114	-0.142
C4-3	0.708	0.7407	0.036
C5-4	0.518	0.5424	-0.040
C6-5	0.798	0.8359	-0.580
C7-6	0.245	0.2565	-0.114
C8-7	0.924	0.9678	1.637
C9-8	0.816	0.8547	0.011
	A	B	C

TABLE 4

Chelodina longicollis : Pairwise correlations between peak-velocities of the different cervical joints (bold numbers : $P < 0.001$)

	C3-2	C4-3	C5-4	C6-5	C7-6	C8-7	C9-8
C3-2	1						
C4-3	0.58	1					
C5-4	0.36	0.43	1				
C6-5	0.52	0.77	0.65	1			
C7-6	-0.00	0.29	0.46	0.55	1		
C8-7	0.63	0.78	0.64	0.94	0.42	1	
C9-8	0.60	0.83	0.58	0.82	0.25	0.88	1

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