

Comparison between aquatic and terrestrial locomotions of the leatherback sea turtle (*Dermochelys coriacea*)

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(With 12 figures in the text)

Kinematic characteristics of the fore- and hindlimb displacements during terrestrial and aquatic locomotions in juvenile marine turtles *Dermochelys coriacea* are compared. Modulations of the spatial displacements of the limbs and durations of the stance and swing phases are analysed in relationship with the constraints of the aquatic and terrestrial environments. The stance and swing phases used for describing the aquatic locomotion are re-evaluated in the light of the spatial displacements of the forelimbs during complete beating cycles.

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Introduction

As in all of the marine turtles, the leatherback turtle, *Dermochelys coriacea* (Vandelli, 1761) uses

swimming for the bulk of locomotion. Only hatchlings at their birth and adult females returning to the beaches for egg-laying use terrestrial locomotor patterns. Actually, few studies have reported the kinematic properties of these locomotor patterns in marine turtles. In 1984, Davenport, Munks & Oxford compared the swimming kinematics and mechanisms in marine (*Chelonia mydas*) and freshwater turtles (i.e. *Kinosternon subrubrum subrubrum*, *Mauremys caspica* and *Trachemys scripta elegans*). To avoid scaling problems, they used only young specimens of green turtles. In 1986, Davenport & Clough described the role of hindlimb displacements during slow swimming behaviour of *Caretta caretta* and, more recently, Davenport (1987) outlined the hydrodynamic properties of the forelimbs in hatchling *D. coriacea*.

In almost all of the cases, studies of swimming have been concentrated on the simultaneous beating of the hypertrophied forelimbs, their hydrodynamics, and the speed of the turtles. As a first approach, this behaviour was compared with bird flight (Carr, 1952). Then, a hydromechanical model was proposed by Blake (1981) using a drag-based mechanism. However, this model cannot be fully applied to marine turtles. Partly for this reason, a lift-based model for forelimb movements was proposed by Davenport *et al.* (1984) and Davenport (1987). However, the foreflippers have a complex movement in space, and are not rigid oars. They combine changes in their orientation with flexibility of their distal parts. Consequently, the cross-sections of the forelimbs, at a particular instant of the cycle of movements, do not have the same shapes, spatial orientations and hydrodynamic properties. In addition, the previous studies have tended to concentrate upon the swimming mechanisms of very young or hatchling sea turtles. For terrestrial locomotion and nest-building, Renous *et al.* (1989) and Renous & Bels (1991) have examined the kinematics of the forelimb in hatchling and small to medium-sized juveniles (snout-vent length: 120 cm).

Precise data for fore- and hindlimb displacements are critical for: (1) comparing the kinematics of the limbs and the body in terrestrial and aquatic environments; and (2) understanding the functioning and the role of the simultaneous paddling of the forelimbs during locomotion on the ground. This paper has two main purposes. First, we describe kinematics of the hindlimbs during terrestrial locomotion for juvenile *D. coriacea* (snout-vent length: 0.25 to 8.80 kg) that is not yet presented. Secondly, we provide a detailed description of the fore- and hindlimb displacements during slow swimming locomotion for the large juvenile (weight: 60 kg; snout-vent length: 120 cm).

Materials and methods

Fourteen juvenile *D. coriacea* weighing 0.25–60.00 kg (snout-vent length: 5–120 cm) were used in this study. They originated from French Guyana, were incubated under artificial conditions, and maintained in a sea water aquarium (Bels, Rimblot-Baly & Lescure, 1988). Briefly, the breeding conditions were as follows: sea water filtered through filter sand/argex at a speed of 6 m/h, a temperature of 25 °C, pH of 8, a salinity of 32 g/l, a photoperiod of 12 h/12 h provided by a double row of fluorescent tubes (True-Lite 65 W), and food based on mussels (*Mytilus edulis*). Particular attention was given to filming a specimen which grew in captivity to 60 kg.

For investigation of swimming, the turtles were filmed by a Beaulieu R 16 camera in their aquarium so that, in the viewfinder, the surface of the front wall of the aquarium and 2 graduated rulers (2 cm graduations) placed against the back wall were visible. Twenty swimming sequences involving between 4 and 20 beats of the turtle's forelimbs were filmed at 25 frames/s. For terrestrial locomotion, several turtles, including those used for films of swimming, were filmed at 25 frames/s, at various stages during growth (0.25, 2.50, 8.80, 11.00 and 60.00 kg) on humid sand, according to the experimental conditions described by Renous & Bels (1991). For terrestrial locomotion, a mirror was placed so that a lateral and a dorsal view of limb displacement was

viewed on each film frame. For analysing the spatial displacements of the limbs during swimming behaviour, it was not possible to use such a mirror. We used lateral and frontal views of limb movements at the same speed.

For facilitating analysis, coloured markers were painted on the edges of the forelimbs, hindlimbs, head and trunk of the animals. In swimming, distances covered relative to a ruler placed in the aquarium was used to calculate the body speed. Frontal and lateral views were then selected and analysed frame-by-frame with an EIKI type NT-1 projector. Each frame was projected on to the frosted glass of a digitizing table (AGMEE, Ulg). The centres of 2 successive points of the table were separated by 0.14 mm. The table was connected to an IBM (AT3) microcomputer. Horizontal and vertical coordinates of the points were recorded frame-by-frame for each digitized point. The data were stored in data files as tables of bipolar (x and y) coordinates for each point. The distances between 2 successive points and angles between 3 successive points were also calculated and stored in the data file. The files were then analysed using a set of computer programs. For comparative purposes, frame 1 in each sequence was arbitrarily chosen to occur at maximal downstroke for swimming, and maximal protraction for terrestrial locomotion.

Results

Terrestrial locomotion

Dermochelys coriacea uses a mode of terrestrial locomotion which does not involve raising of the entire heavy body. A specific repertoire of cyclic and synchronous movement of the fore- and hindlimbs is used. The forelimbs produce essentially the lifting and forward movements of the body as if the turtle was 'walking on crutches' (Renous & Bels, 1991).

Kinematics of the forelimb during terrestrial locomotion

As in all tetrapods (Zug, 1969; Walker, 1979; Alexander, 1984) the forelimbs follow a swing and stance cycle. The swing phase shows two stages: an effective protraction and a repositioning (= 'pause', Renous & Bels, 1991). During the protraction, which represents approximately half of the swing phase duration, the forelimbs are lifted and propelled forwards. The stance phase also involves two stages: a retraction and a repositioning. During retraction, the cutting radial edge of the distal part of the forelimbs digs simultaneously into the sand. The limb lifting lasts for almost 20% of the stance phase and prepares for the next protraction.

Kinematics of the hindlimb during terrestrial locomotion

The swing phase, considered as a classical protraction for all the other turtles (Walker, 1971*a, b*; Zug, 1971), involves two stages in *D. coriacea*: an effective protraction and an immobilization-pulling down (Fig. 1). During protraction, the hindlimb lifts and abducts. As the distal extremity of the toes indicates, the forward and upward amplitudes of the movement are small (around 2 cm for a specimen of 8.8 kg). The longitudinal and vertical speeds, initially reduced, increase (Fig. 2). During the second stage, after protraction, small horizontal oscillations of the limb are observed in 11 sequences out of 36. They reveal a relative instability of the turtle. Its plastron is in contact with the substratum whereas the forelimbs are in the middle or at the end of the swing phase (Renous & Bels, 1991) which corresponds to the repositioning stage, before a new retraction. In general, the hindlimb is first motionless and then moves downwards and slightly backwards. Therefore, its velocity first increases slightly and then reaches a zero value before the beginning of the stance

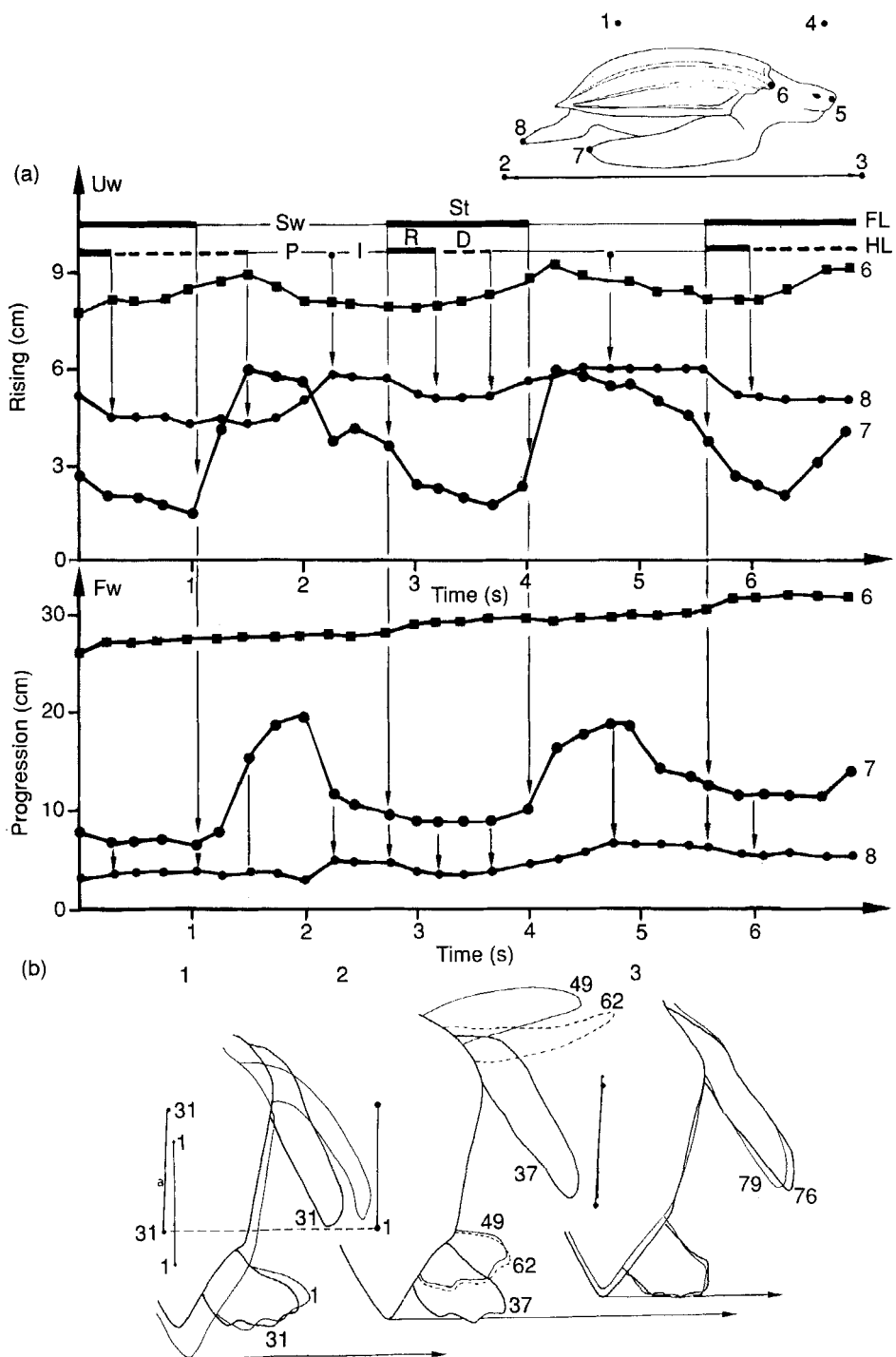


FIG. 1

phase (Fig. 2). This immobilization-pulling down stage represents approximately 40% of the swing duration.

The stance phase, also considered as a classical retraction, shows two main distinct periods: an active retraction and a passive dragging along.

The active retraction begins by contact with the substratum and often coincides with the start of the forelimb retraction. The pushing down can be shown by the print of the paddle in the sand and depression of its distal points (Fig. 1). The latter moves backwards and closer to the medio-ventral line of the body. The longitudinal and vertical speeds increase up to a maximal value at the end of the stage (Fig. 2). During the dragging stage, each hindlimb remains against the sand but it does not pull down. This stage begins when retraction of the forelimbs is between a third and half complete, and the body moves forward. We suggest that the proximal part of the hindlimb is dragged along by the body because its abduction movement continues, and the medial border of the limb moves closer to the medio-ventral axis of the animal. The longitudinal and vertical speeds decrease and the hindlimbs and body speeds are similar in the two directions, at the end of this stage.

Relative movements of the body and the limbs during terrestrial locomotion

The presented data and previous data (Renous & Bels, 1991) pose interesting questions: (1) what relation exists between the forelimbs and the body movements?; (2) what relation exists between the hindlimbs and the body movements?; (3) what is the relationship between the displacements of the two categories of limbs?

The main propulsive effects of the forelimbs in terrestrial propulsion is suggested by kinematic evidences. (1) Whichever points are selected on the body (e.g. anterior limit of the shell or extremity of the snout), the body shows an opposite movement to the simultaneous movement of the forelimbs. (2) The body moves forward during the common forelimb stance phase when the forelimbs are pulling against the substratum and progressively moving closer to the trunk. (3) The maximal forward position of the body corresponds to a cessation of pushing against the sand, and occurs before the small backward movement of the forelimbs which characterizes the end of the stance phase. (4) The maximal upward position of the anterior part of the body occurs before its maximal forward position. (5) The body moves forward and has an opposite movement to the hind limbs during the first period of their stance, the active retraction (Fig. 5).

In contrast, the propulsive effect of the hindlimbs is less evident from the kinematic data because the hind- and forelimb phases occur together (Fig. 3). The body has a great deceleration during the simultaneous stance phase of the two pairs of limbs corresponding to the retraction period of the forelimbs and active retraction of the hindlimbs (Fig. 1; fig. 12 in Renous & Bels, 1991). The body forward velocity decreases because the pushing of the fore- and hindlimbs against the substratum moves gradually backwards. A sudden acceleration, which appears when the elbows contact the

FIG. 1. Progression and rising (cm) of the body and the distal extremity of the ipsilateral fore- and hindlimbs of a juvenile *Dermochelys coriacea* (11 kg) during two limb cycles. (a) Progression (Fw) and rising (Uw) of the body (6), the forelimb (7) and the hindlimb (8). D, dragging; FL, forelimb; HL, hindlimb; I, immobilization-pulling down period; P, protraction; R, active retraction; St, stance; Sw, swing. Vertical arrows indicate the limits of the different phases and stages of the gait. (b) Relative movements of the body and the ipsilateral limbs during a sequence of 79 frames (3-16 s): 1-31, active retraction of the fore- and hindlimbs; 31-37, dragging of the hindlimbs; 37-49, protraction of the two limbs; 49-62, immobilization-pulling down period of the forelimb and repositioning of the forelimb; 62-79 active retraction of the two limbs. Horizontal arrows indicate the stages of the forward progression of the turtle.

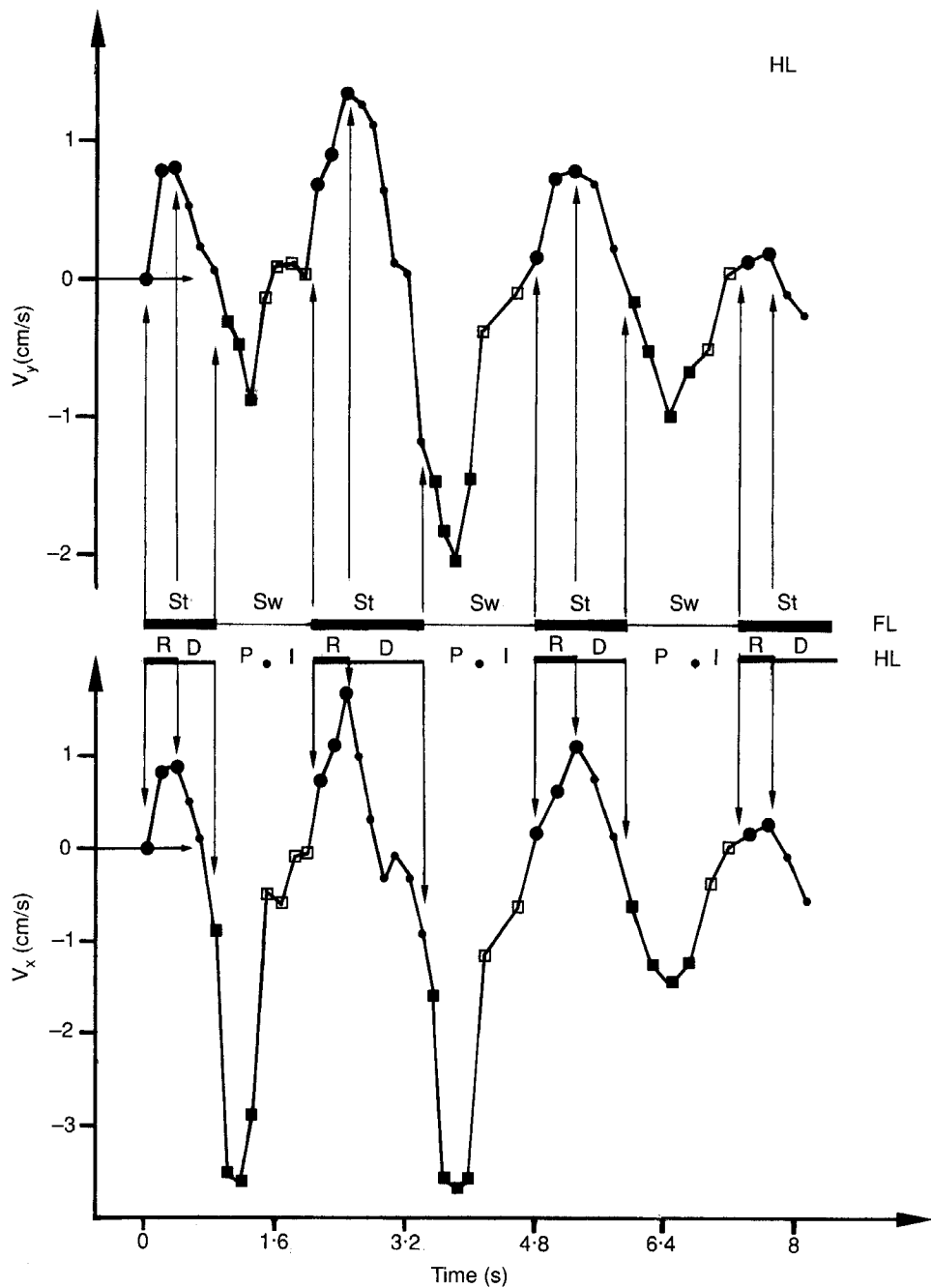


FIG. 2. Variation of the vertical (V_y) and horizontal (V_x) speeds (cm/s) of the distal extremity of the hindlimbs during the terrestrial walk (three successive cycles). D, dragging; FL, forelimb; HL, hindlimb; I, immobilization-pulling down period; P, protraction; R, active retraction; St, stance; Sw, swing. Vertical arrows indicate the limits of the different phases and stages of the gait.

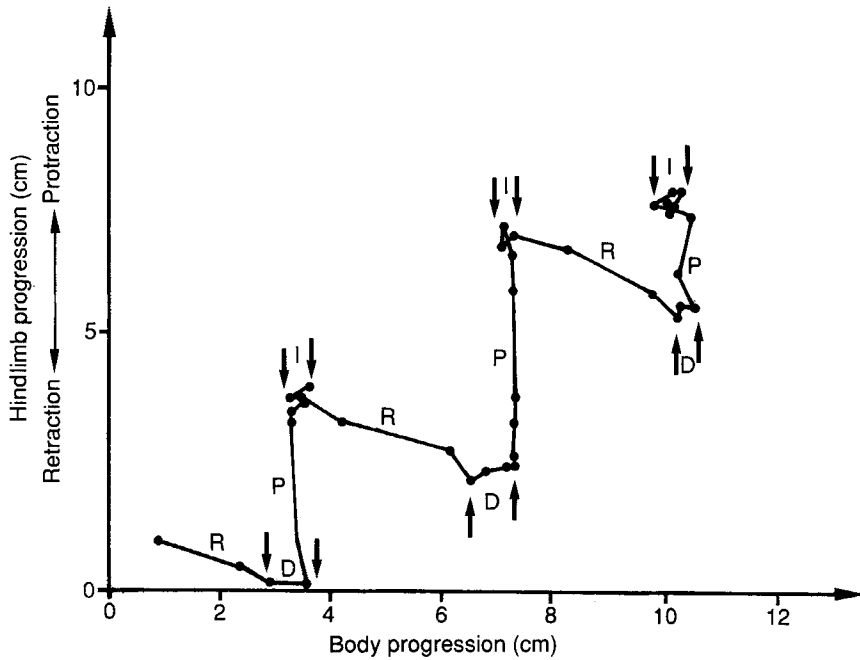


FIG. 3. Relative progression of the body and the hindlimbs during the different phases and sub-phases of the locomotor cycle in the terrestrial walk (three successive cycles) in a juvenile of 11 kg. D, dragging; I, immobilization-pulling down period; P, protraction; R, active retraction; vertical arrows indicate the limits of the different phases and stages of the gait.

ground, produces the effective body rising and buttressing whereas the hindlimbs, resting on the substratum, are dragged down by the body. A constant body speed follows this period of acceleration and characterizes the end of the forelimb stance phase when the head topples over in front of the shoulder articulation, on the crutches formed by the forelimbs. The end of the fall corresponds to the maximal body progression. When the belly touches down, and during the whole period of the simultaneous protraction of the fore- and hindlimbs, the body shows a small backward movement (Renous & Bels, 1991).

Dermochelys coriacea presents a discontinuous progression during terrestrial locomotion. The body displacement begins with vertical rising during the simultaneous retraction of the fore- and hindlimbs. This rising is combined with a forward progression at the end of the forelimb's retraction. The body falls down during the simultaneous swing phase of the two pairs of limbs, before a new rising with a new active simultaneous retraction (Fig. 4). The hindlimbs seem to play an effective role in the body rising. Because the end of the active retraction of the hindlimbs coincides with the pushing of the elbow against the substratum, these limbs may give a complementary mechanical impulse for body rising. The increase in vertical and horizontal speeds of the hindlimbs during the active retraction period may suggest a small pushing action prior to that of the elbows (Fig. 2).

After their complete retraction, the two pairs of limbs have similar angles to the longitudinal axis of the body (Fig. 1). At the beginning of the swing phase, the ipsilateral limbs start from

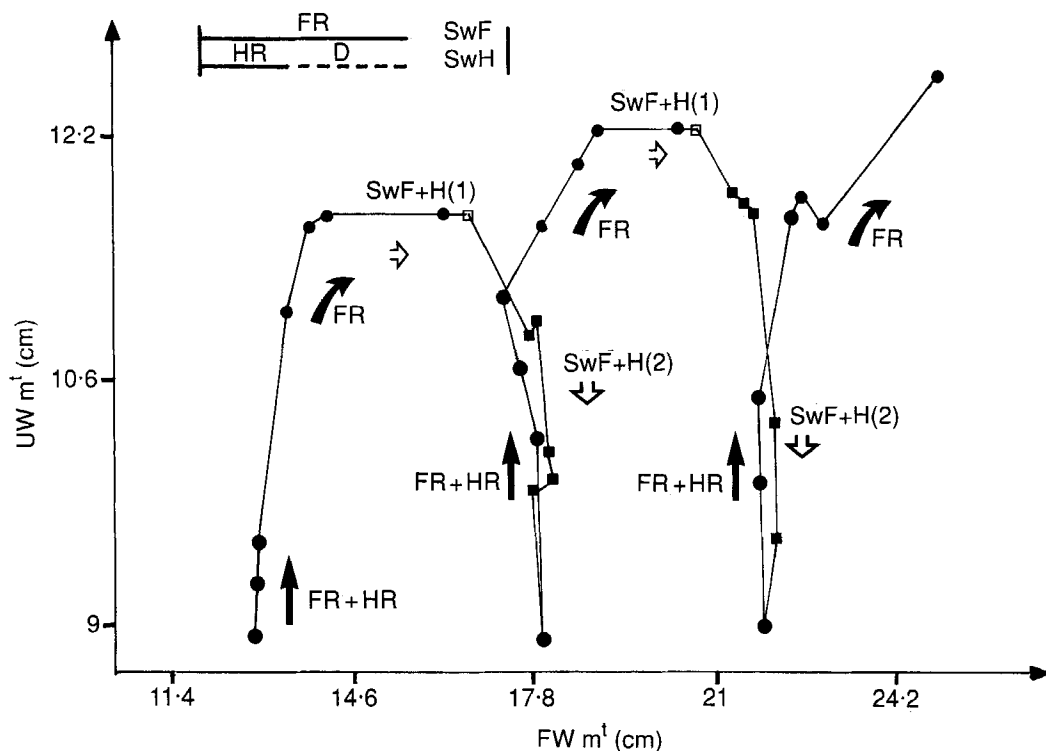


FIG. 4. Displacement of the cranial part of the body (anterior limit of the dorso-lateral hull) of a juvenile of 11 kg in a vertical plane. FR, forelimb retraction; FR + HR, simultaneous retraction of the fore- and hindlimbs; FW m[†], forward movement; HR, hindlimb retraction; SwF and SwH, fore- and hindlimbs' swing; SwF + H (1) and (2), first and second parts of the fore- and hindlimbs' swing; UW m[†], upward movement; D, dragging. The arrows underline the resulting movement.

parallel positions, if we consider two segments limited by their distal extremity and a basal point situated on the medio-dorsal axis of the body (Fig. 5). At the beginning of the swing phase, these segments start from more or less parallel positions. During the swing, the hindlimbs move toward the body whereas the forelimbs move away. The distance between the distal extremities decreases during the forelimb retraction, and increases at the beginning of the common protraction of both limbs, to reach a maximal value with the maximal forward position. The protraction arc of the forelimbs ($65 \pm 10^\circ$, $N = 10$) is at least four times that of the hindlimbs ($15 \pm 4^\circ$, $N = 10$), whereas the retraction arc of the former ($24 \pm 9^\circ$, $N = 10$) is about twice that of the latter ($12 \pm 4^\circ$, $N = 10$). When the turtle speed decreases, the retraction arcs of both pairs of limbs tend to become similar.

In terrestrial tetrapods, the symmetrical displacement results from a diagonal alternate movement of the four limbs (Howell, 1944; Hildebrand, 1966; Sukhanov, 1966). The gaits of freshwater and terrestrial chelonians are basically diagonal (Walker, 1963, 1971a, 1973; Zug, 1971, 1972). They use a slow walk where the body is supported by a stable tripod during 60–80% of the cycle duration (swing + stance) of each limb (Hildebrand, 1966; Jayes & Alexander, 1980). With a rapid walk (Hildebrand, 1966), the duration of the bipedal contacts increases. In the marine turtles, the diagonal coordination disappears because of simultaneous movements of the fore- and hindlimbs. The stance phases of the two pairs of limbs are synchronous (Fig. 1). The beginning of

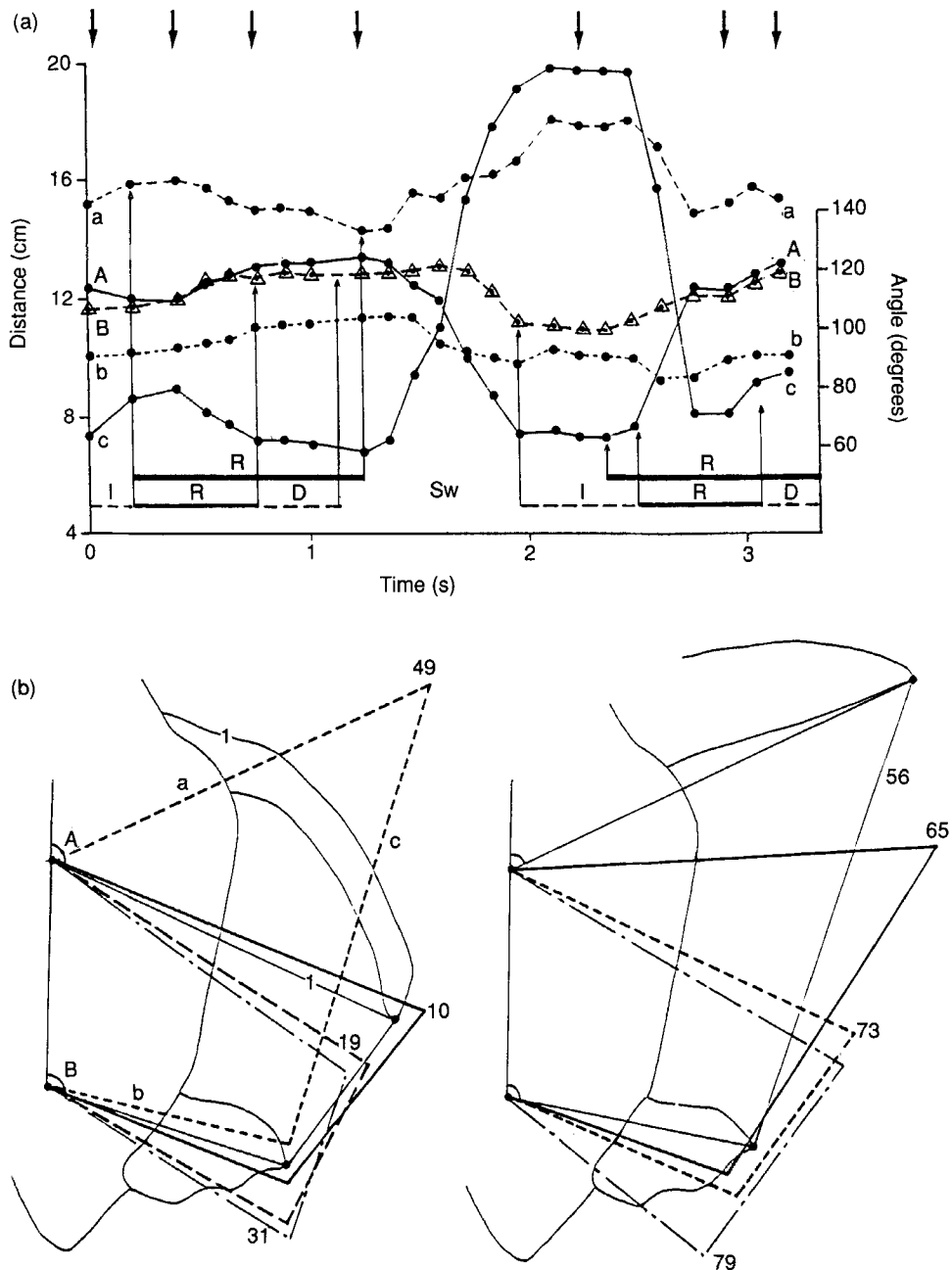


FIG. 5. (a) Length variation of the limb segments and angular variations. (b) Schematization of different frames of the analysed sequence (1–79 frames; 1 frame = 0.04 s). A, Anterior angle between the forelimb segment and the medial body axis; a, forelimb segment limited by the distal extremity of the foreflipper and the medio-dorsal axis of the body; B, anterior angle between the hindlimb segment and the medial body axis; b, hindlimb segment limited by the distal extremity of the hindlimb and the medio-dorsal axis of the body; c, distance between the distal extremity of the two categories of limbs; D, dragging period; I, immobilization-pulling down period; Sw, swing phase; R, retraction of the fore- and hindlimbs.

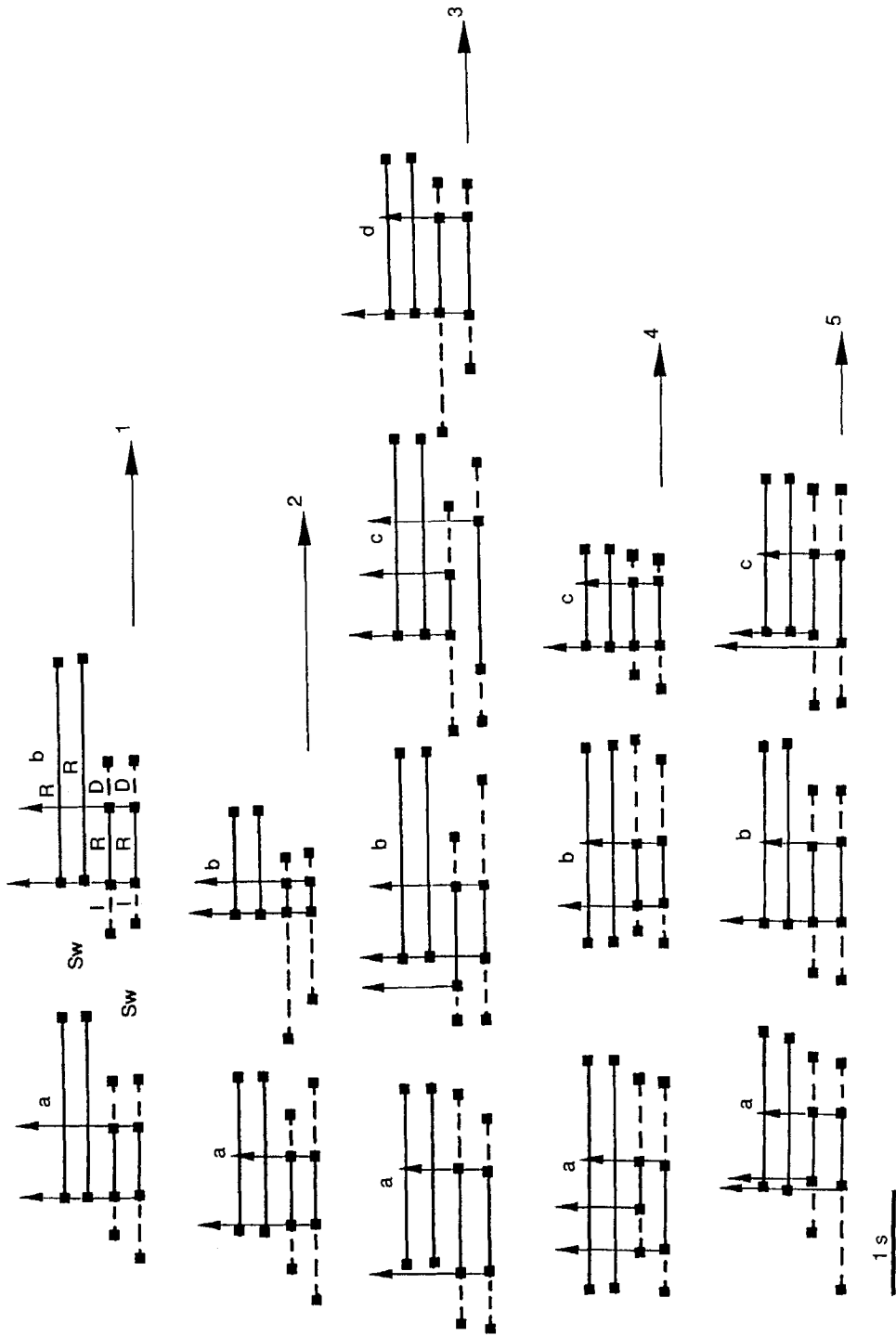


FIG. 6

the forelimbs' retraction and the active hindlimbs' retraction are simultaneous (Figs 3 and 4). This pattern of gait is observed throughout the terrestrial locomotion in hatchlings (Renous, 1988; Renous *et al.*, 1989). It is seen after 3–10 steps in juveniles taken out of the water and put upon the sand, and is also characteristic of the adult females during beach crawls under natural conditions (Fig. 6). Another gait, which shows simultaneous movements of the forelimbs associated with alternate movements of the hindlimbs, is observed in terrestrial locomotion of juveniles put on a smooth substratum, or when first put on sand. Such a pattern during the first steps may be viewed as an adaptation to terrestrial constraints.

Swimming

Under experimental conditions, the juvenile of 60 kg, when it was not frightened, had a very slow progression (order of 5.4 cm/s, range: 4–8 cm/s), slower than the routine swimming reported for hatchlings (Davenport, 1987). According to this author, the swimming essentially results from the synchronous flapping of the forelimbs. Asynchronous forelimb movements were only observed in association with changes of direction, for instance when the animal turns, but never during linear progression (Fig. 7). The juveniles never swam backwards. The hindlimbs have synchronous or asynchronous movements with the foreflippers. During elevation, the forelimbs of the 60-kg juvenile never passed beyond the carapace level.

Kinematics of the foreflipper during swimming

Frontal view: Upstroke phase. The markers evenly located and diametrically opposed on the two edges of the foreflipper (Fig. 8) highlight the limb movement. The maximal lifting and lowering of the tip of the paddle are used to determine the limits of the upstroke and downstroke phases.

At the beginning of the upstroke, all of the points along the two edges follow a similar vertical displacement. However, the anterior edge starts to get ahead of the posterior edge. This results from a combination of two components: elevation of the flipper tip and rotation of the shoulder. The points of the posterior edge reach their highest vertical position at the same time. In contrast, the distal points of the anterior edge reach this value after the proximal points (Fig. 9). The medial part of the foreflipper, parallel to the sagittal plan of the body, becomes frontal at the beginning of the phase. Progressively it becomes more ventral by continuous rotation of the shoulder which turns the lateral surface of the limb upwards.

At the beginning of the upstroke, the projected length of the flipper is maximal. It then decreases with the axial rotation of the shoulder (Fig. 9). During the upstroke, the paddle is twisted and the proximal part of the anterior edge, laterally orientated at first, becomes frontal. The length projection increases when the twisted paddle reaches its maximal lift, and decreases at the end of rotation, when the dorsal surface of the limb faces entirely upwards. The variation in projections of the distances between the opposite points of the two edges also illustrates the winding movement of the paddle (Fig. 9).

The lateral displacements of the points along the two edges of the limb are effected between a

FIG. 6. First successive steps (a–d) of juvenile *Dermochelys coriacea* (0.25 kg) on sand. D, dragging of the hindlimbs; I, immobilization-pulling down period; R, forelimb retraction and active retraction of the hindlimbs; Sw, swing phase. The vertical arrows underline the beginning and the end of the hindlimb retraction.

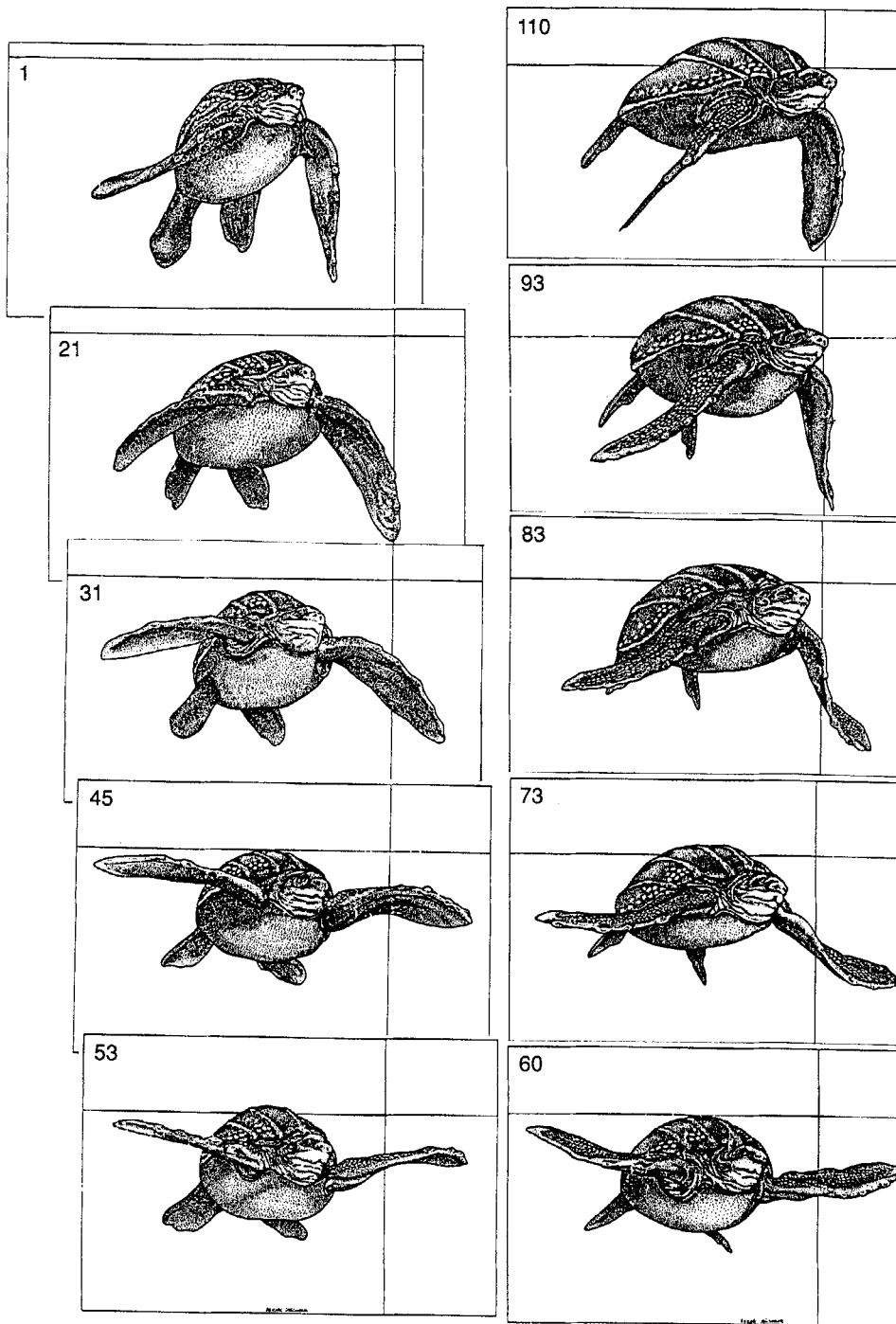


FIG. 7. Frontal and fronto-lateral views of the swimming of a juvenile of 60 kg in an aquarium during an upstroke (1–53) and a downstroke (53–110) of the forelimbs (each frame represents 0.04 s). Two perpendicular rulers underline the vertical and transverse displacements of the body and the limbs.

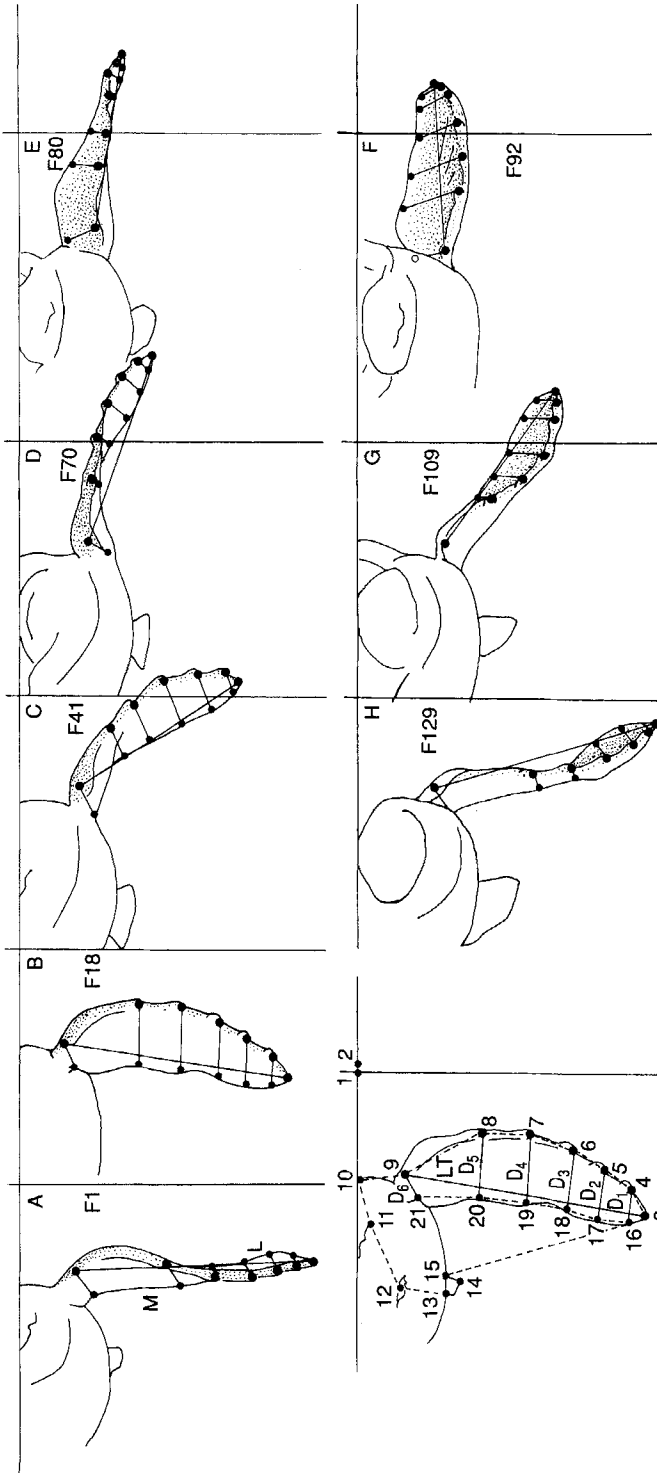


FIG. 8. Two successive movements of slow upstroke (A-E) and downstroke (F-H and A) of a left forelimb, in frontal view (161 frames; 1 frame = 0.02 s). D1-D6, distance between equivalent points of the two edges; F1-F129, frame numbers; L, lateral side; M, medial side of the forelimb delimited by an anterior and a posterior edge; LT, total limb length variation. A schematization of the forelimb indicates the position of the points of reference on the two edges and on the body and the ipsilateral hindlimb.

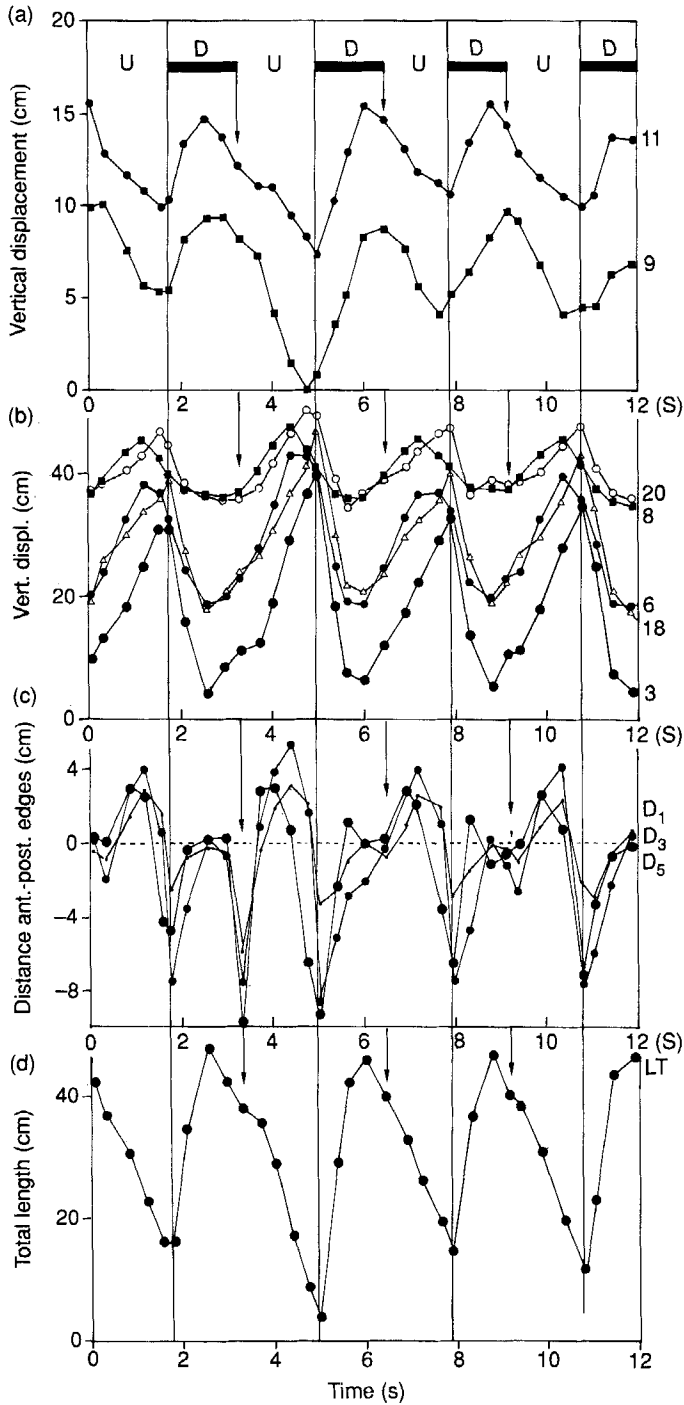


FIG. 9. Graphs of the displacement of points of the forelimb during four cycles of movement. (a) Vertical displacement (cm) of the most proximal point of the limb (9) and a body point (11). (b) Vertical displacement of distal extremity (3) and two opposite points of the anterior (6 and 8) and the posterior (18 and 20) edges of the limb. (c) Variation of the distance between two opposite points of the two edges, D₁ (points 4 and 16), D₃ (points 6 and 18), D₅ (points 8 and 20). (d) Total limb length variation (LT) (between points 3 and 9). D, downstroke; U, upstroke; black rods indicate the downstroke duration; vertical arrows underline the limits between up- and downstrokes.

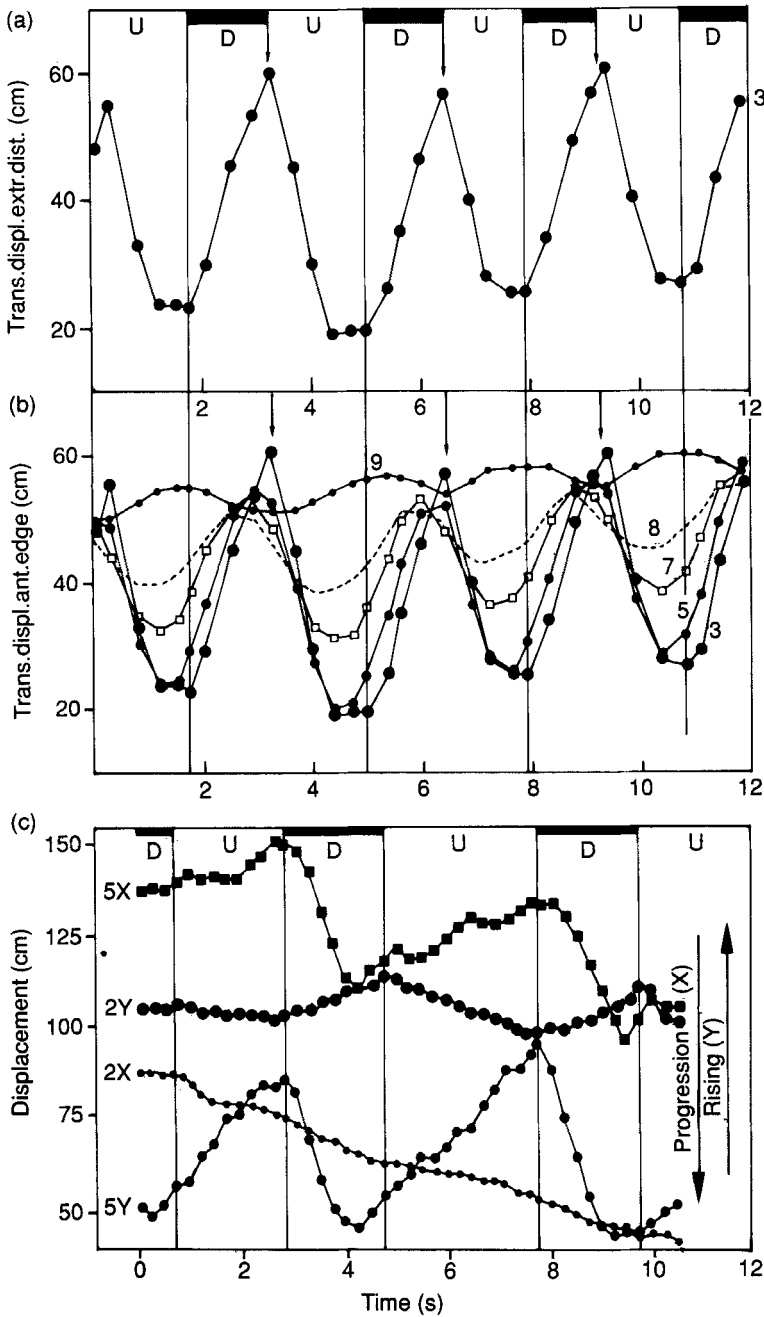


FIG. 10. Transverse, vertical and antero-posterior displacements of the forelimb and the body. (a) Transverse displacement (cm) of the distal extremity of the limb (3), during four successive cycles, in frontal view. (b) Transverse displacement (cm) of points on the anterior edge of the forelimb, between the shoulder and the distal extremity (9, 8, 7, 5 and 3), in frontal view. (c) Forward progression (X) and upward movement (Y) of the body (2), and the distal extremity of the forelimb (5), during three successive cycles, in lateral view. D, downstroke; U, upstroke.

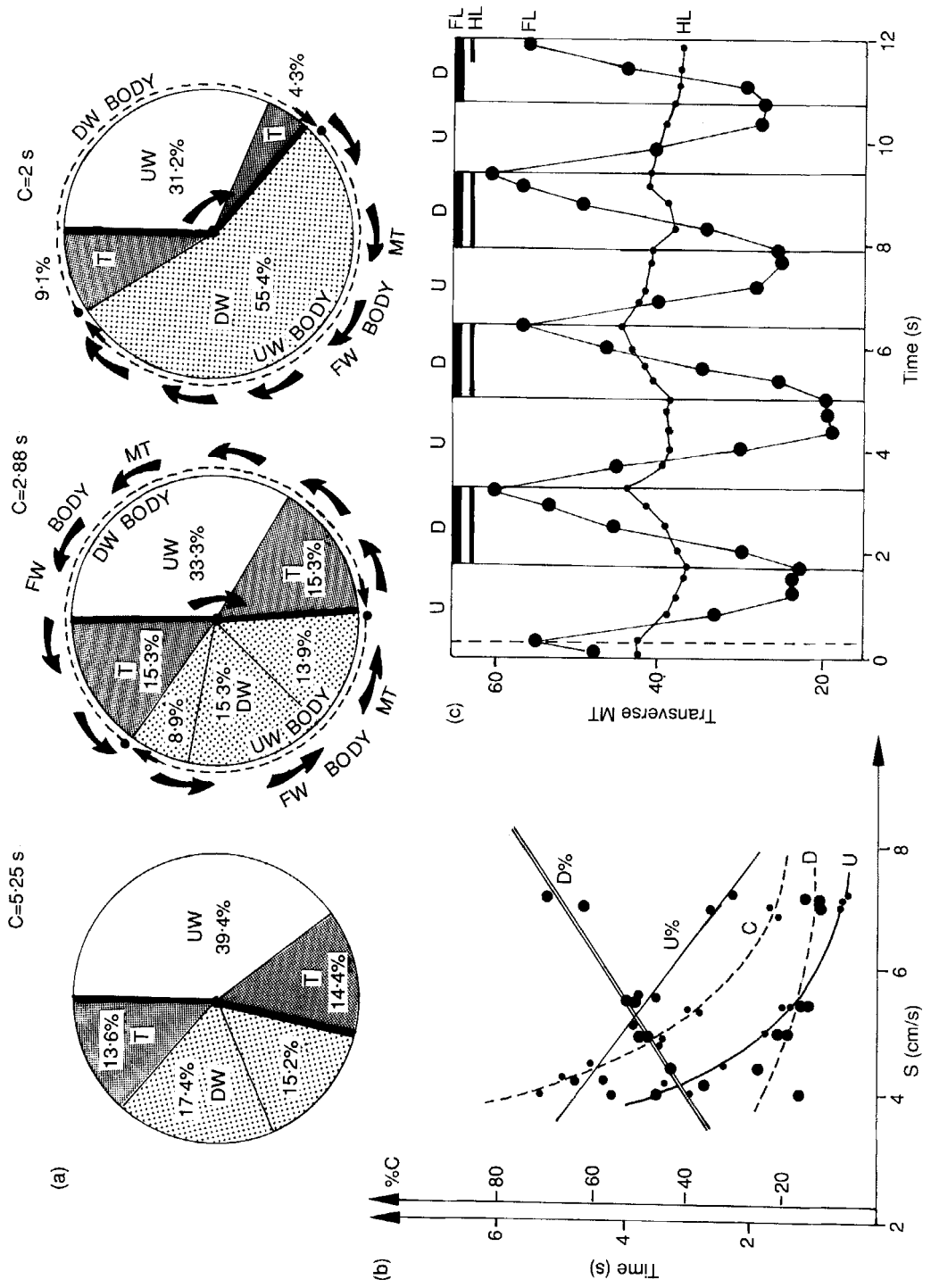


FIG. 11

maximal medial position (nearest position to the body) and a maximal lateral position (furthest position from the body) (Fig. 10a and b). At the beginning of the phase, the foreflipper moves towards the body so that the maximal medial position of its tip is reached after its maximal lower position. In contrast, at the end of upstroke, the tip of the foreflipper reaches its maximal elevation and maximal distance from the body at the same time. The two edges have approximately the same trajectory in the lifting. However, inversion of the value of the points of the two edges suggests a torsion of the limb during the upstroke. The points of the anterior edge are first lower than those of the posterior edge, and then they become higher at the end of the phase. During the upstroke of the forelimbs, the body (extremity of the head, and a mark upon the shoulder) moves downwards.

Frontal view: Downstroke phase. All points of the two flipper edges move downwards. Those of the posterior edge are higher than those of the anterior edge. This suggests a movement without main axial shoulder rotation, at the beginning of the phase. The anterior edge of the foreflipper becomes frontal during the main duration of the phase. The positioning of the lateral surface of the forelimb changes through this phase. From a dorsal orientation at the end of the upstroke, it takes a lateral and posterior position, at the end of the downstroke. Transversally, all points of the two edges and particularly the distal-most, move from lateral to medial orientation. The points of the medial posterior edge are ahead of the anterior edge. This suggests the occurrence of a final axial shoulder rotation which sets the medial surface of the limb forward.

Two axial rotations of the shoulder drive the general displacement of the forelimb. (1) During the upstroke, the first rotation changes the orientation of the two paddle surfaces of the paddle from a lower to an upper position. (2) During the downstroke, a reverse rotation brings the paddle back into its initial orientation.

Lateral view. Observations of the positions of the extremity of the head, and the anterior edge of the forelimb (shoulder, mid, distal points) confirm the vertical movements of the points obtained from the frontal view (Fig. 10c). The body's forward displacement is continuous during the two phases of the limb cycle.

Limits of the two phases in the forelimb cycles

Davenport *et al.* (1984) state 'on the downstroke the blade moves posteriorly, while on the upstroke it moves anteriorly'. Such a definition based on vertical paddle displacement is not sufficient for kinematic analysis of the very slow locomotion (near 5 cm/s) in juveniles. The downstroke of the paddle is a hydrodynamic phase because it generates the thrust. In terrestrial locomotion, it corresponds to the 'contact phase'.

In terrestrial locomotion, the limits of the protraction and retraction phases are very clear. The

FIG. 11. Diagrams of the events during a cycle of forelimb movements, variations of the duration of these events with increasing speed, and synchronous movements of the fore- and hindlimbs. (a) Comparison between the composition of the forelimb cycle of movement, during terrestrial locomotion (cycle of 2 s for a specimen of 8 kg) and during swimming (cycles of 2.88 and 5.25 s for specimen of 60 kg). (b) Relationship between the speed (cm/s) and the duration of the two phases, upstroke (U) and downstroke (D) of the cycle (C) in time (s) or as percentage of the duration of the cycle (%C). (c) Comparison of the transverse displacement of the fore-(FL) and the hind-(HL) limbs. C, cycle; DW, downward movement of the forelimb; DW BODY, downward movement of the body; FW BODY MT, forward body progression; T, forelimb turning; UW, upward movement of the forelimb; UW BODY, upward movement of the body.

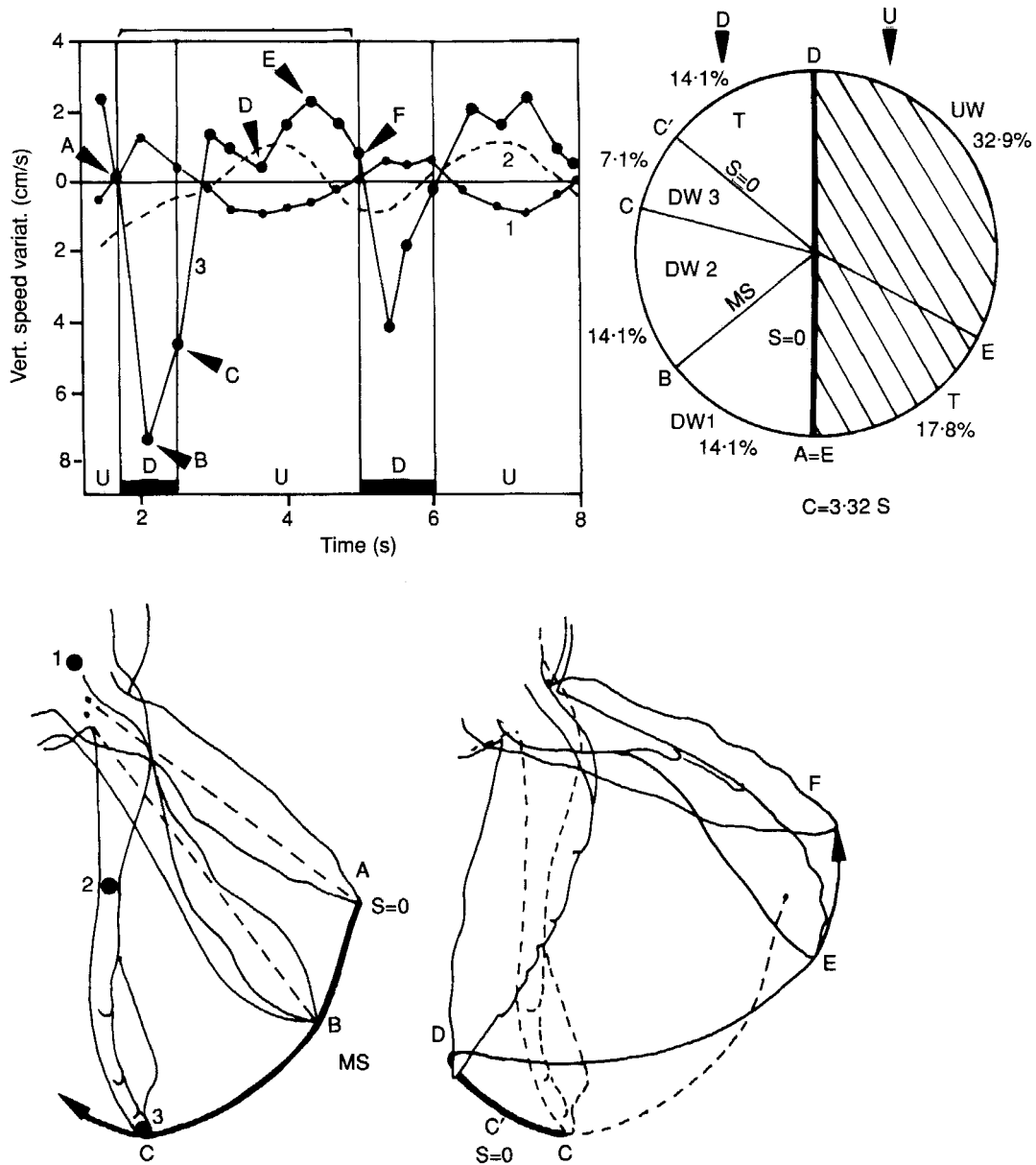


FIG. 12. Speed variation (cm/s) of the forelimb and body vertical displacement, in frontal view (2 cycles). Circular diagram of the first cycle ($c = 3, 32$ s) events concerning the forelimb (percentage of the phases duration) A-F, position of the limb at different stages of the first cycle, during the downstroke (D) and the upstroke (U); A, start of the downstroke when the speed is zero ($S=0$); B, the speed is maximal (MS) after an acceleration phase; C, vertical position of the foreflipper, after a deceleration phase; C', the speed is null; D, maximal adduction and start of the upstroke; DW 1, 2, 3, three phases of the downward movement; E, maximal speed after acceleration phase; F, end of the upstroke and beginning of the downstroke; T, turning; UW, upward movement; 1, body point, near the shoulder; 2, middle of the anterior edge; 3, distal extremity of the limb.

protraction represents a locomotor phase without any contact with the substratum. The distal extremity of the limb lifts up from the substratum, and in a forward movement, contacts it again and digs in. During this phase, the body does not progress forward. The retraction represents the 'contact phase' for all or part of the limb. At the end of this phase, the distal extremity reaches the maximal proximity to the body. With this last contact, the forelimb adopts a position favouring its subsequent lifting. During the retraction, the body is pushed forward. At a body weight of about 8 kg, the speed of a specimen of the leatherback is 35 cm/s (Renous & Bels, 1991). The duration of the paddle cycle of movement ranges between 1.8 and 3.4 seconds. If we consider an average cycle of 2 seconds, the protraction takes 0.72 s (1/3) and the retraction 1.28 s (2/3) (Fig. 11). The ends of protraction and retraction correspond to a limb position change. The paddle velocity reaches zero between the protraction and the retraction and also before the limb position change that ends this last phase (Fig. 12). It is the maximal proximity to the body which limits the two phases of the limb cycle. The limb position change, ending the retraction, must be considered as a part of this phase, because the limb again keeps contact with the substratum. However, the body of the turtle is falling down during this period and throughout protraction, whereas it is lifted during retraction. This body lift corresponds to a vertical progression.

For a swimming velocity, higher than the terrestrial, and shorter than the routine swimming (Davenport, 1987), the forelimb cycle duration ranges between 2.88 cm/s and 5.25 cm/s (for a speed of 5–6 cm/s). Observations of displacement of the limbs from the frontal view reveals an ultimate adduction of the paddle, after the maximal depression of its distal extremity (Fig. 12). This nearness to the sagittal plane of the body results from the axial rotation of the shoulder, prior to the lifting of the limb which is characterized by an opposite rotation and abduction. From the speed variation of the paddle and body points during successive cycles, it may be seen that the speed of the distal extremity reaches zero during maximal lifting and depression (Fig. 12).

If the criteria describing the terrestrial locomotion are used for the downstroke in swimming, divisions of the entire forelimb cycle are similar in terrestrial and aquatic locomotions (Fig. 11). In swimming, the body moves up during the main part of the downstroke, and down during the ultimate adduction period of this phase, and then throughout the entire upstroke (Fig. 9; see also Davenport, 1987). However, the body progresses steadily forward during the two phases and not only during the limb retraction as in terrestrial locomotion. When on a terrestrial substratum, retraction of the forelimb occupies a great part of the entire cycle duration, whereas in the slow pattern of swimming, the upstroke and downstroke have almost similar durations (Figs 11 and 12). Furthermore, the forelimb cycle duration increases, and the upstroke duration represents a higher percentage of this cycle with speed decrease (Fig. 11). In contrast, the duration of retraction of the forelimb in terrestrial locomotion takes a higher percentage of the cycle duration for equal swimming and terrestrial speeds (Figs 11 and 12). Consequently, a fundamental difference between the two modes of locomotion seems to exist because the rhythmic variations in the duration of the forelimb cycle and the body speed are regulated (1) by the upstroke phase in aquatic progression, and (2) by the retraction phase in terrestrial progression. At faster speeds, the duration of the entire cycle decreases in both modes of locomotion; but, in swimming, the duration of the downstroke occupies a lesser percentage of the cycle duration (Fig. 11).

Discussion

Comparison of the spatial displacements of the forelimb in swimming and in terrestrial locomotion

In swimming, the amplitudes of the lateral and forward displacements of the distal extremity of

the paddle are rather constant whatever the medial position reached at the end of the downstroke and the lateral position reached at the end of the upstroke, prior to the maximal lifting (Figs 9 and 10). On the other hand, the amplitude of the vertical displacement of the paddle extremity can change (Fig. 9). In terrestrial locomotion, the amplitude of the vertical displacement seems constant, but the amplitude of the lateral displacement changes with the amplitude of the forward limb progression (Renous & Bels, 1991).

In swimming, the vertical amplitude of the forelimb movement is greater than the lateral amplitude and the forward progression amplitude (Fig. 10). In contrast, in terrestrial locomotion, the last amplitude related to the lateral movement tends to be greater than the vertical amplitude of displacement (Fig. 1).

Vertical amplitude of the limb beat is constant in terrestrial locomotion whereas the lateral amplitude of the limb beat is constant in swimming (Fig. 11; fig. 8 in Renous & Bels, 1991). This difference is in agreement with the duration of the propulsive effect of retraction. During swimming, the duration of the upstroke decreases more significantly than that of the downstroke, as speed increases (Fig. 11). As in other reptiles, there is an opposite situation in terrestrial locomotion. On land, more pronounced reduction of the retraction rather than of protraction occurs with the increasing speed. In swimming, the body progresses steadily throughout the forelimb cycle, whereas forward progression is discontinuous in terrestrial locomotion (Fig. 10). If the swimming gait constitutes the basic pattern for *D. coriacea*, the transitional gaits, which characterize the first steps of terrestrial locomotion and the locomotion on smooth substrata (Renous *et al.*, 1989), can represent a return to diagonal coordination of the limbs, prior to reactivation of the basic pattern.

The hindlimb and the forelimb effects in locomotion

In aquatic and terrestrial environments, the turtle proceeds in a straight line, with perfectly synchronous movements of the two forelimbs (Figs 7 and 11). An asynchrony appears when the animal turns. The duration of the flapping becomes shorter on the side to which the turtle is tacking. During linear progression, the hindlimbs move upward with the foreflippers, but a short time lag may occur (Figs 7, 8, 11). In this case, the maximal lifting of one or both of the hindlimbs coincides with the maximal lifting of the foreflippers. The other hindlimbs anticipate this upward movement (Fig. 6). The maximal depression of the hindlimbs coincides almost with that of the forelimbs. During fast linear forward progression, the fore- and hind limbs start their downstroke at the same time (Fig. 11). However, sometimes, the hindlimbs begin their upstroke a little before the forelimbs (Fig. 6). There is therefore a great similarity between the terrestrial and the aquatic gaits: (1) the stance phase for all the limbs begins simultaneously; and (2) a slight (swimming) or a longer (terrestrial locomotion) time interval occurs between the beginning of the swing phases. The swimming gait pattern probably represents the typical gait pattern for this species (Fig. 7). The terrestrial gait which is derived is modulated by contact between the limbs and the substratum (Renous & Bels, 1991).

Why use simultaneous paddling of the forelimbs during terrestrial locomotion?

By using 'crutches', the body is elevated as a reaction of the forelimb pushing forces against the substratum. Because pushing forces are produced simultaneously by the two forelimbs, their lateral components are opposite and therefore inefficient. Only the vertical and longitudinal

components are effective. During the stance phase, the turtle gains the kinetic energy generated by pushing action of the forelimbs. Because the turtle elevates, this energy is gradually transformed into potential energy, which is then transformed again into kinetic energy during the falling of the body. The hindlimbs are pushing simultaneously with the forelimbs, at least at the beginning of the stance phase (Fig. 1). They may (1) increase the total kinetic energy of the body, and (2) decrease the friction of its ventral surface with the substratum.

From kinematic data, it seems reasonable to suggest that forelimbs are acting largely more powerfully than hindlimbs (see above). In the case of diagonal coordination, pushing of one contralateral fore- and hindlimb should produce a torque by increasing the moment of inertia. This locomotor gait should result in a postural imbalance and decrease of the total kinetic energy. The equilibrium of the body should involve a very large muscular activity of the hindlimbs associated with its extension. The morphological characteristics of the hindlimbs in adapted marine turtles disagree with this hypothesis (i.e. shape, size and possibilities of extension). Thus simultaneous displacements of the forelimb is a kind of energy-saving system appropriate for moving forward such a heavy mass.

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REFERENCES

- Alexander, R. McN. (1984). The gaits of bipedal and quadrupedal animals. *Int. J. Robot Res.* **3**(2): 49–59.
- Bels, V., Rimblot-Baly, F. & Lescure, J. (1988). Croissance et maintien en captivité de la tortue luth *Dermochelys coriacea* (Vandelli, 1761). *Revue fr. Aquariol. Herpetol.* **15**(2): 59–64.
- Blake, R. W. (1981). Mechanics of drag-based mechanisms of propulsion in aquatic vertebrates. *Symp. zool. Soc. Lond.* No. 48: 29–52.
- Carr, A. (1952). *Handbook of turtles of the United States, Canada and Baja California*. New York: Comstock Press.
- Davenport, J. (1987). Locomotion in hatchling leatherback turtles *Dermochelys coriacea*. *J. Zool, Lond.* **212**: 85–101.
- Davenport, J., Munks, S. A. & Oxford, P. J. (1984). A comparison of the swimming of marine and freshwater turtles. *Proc. R. Soc. (B)* **220**: 447–475.
- Davenport, J. & Clough, W. (1986). Swimming and diving in young loggerhead sea turtles (*Caretta caretta* L.). *Copeia* **1986**: 53–57.
- Hildebrand, M. (1966). Analysis of the symmetrical gaits of tetrapods. *Folia biotheor.* No. 6: 9–22.
- Howell, A. B. (1944). *Speed in animals*. Chicago.
- Jayes, A. S. & Alexander, R. McN. (1980). The gaits of chelonians: walking techniques for very low speeds. *J. Zool., Lond.* **191**: 353–378.
- Renous, S. (1988). Retentissement de l'adaptation à la vie pélagique de la tortue luth (*Dermochelys coriacea*) sur sa locomotion terrestre. *Mésogée* **48**: 79–84.
- Renous, S., Lescure, T., Gasc, J. P. & Bels, V. (1989). Intervention des membres dans la locomotion et le creusement du nid chez la tortue luth (*Dermochelys coriacea*) (Vandelli, 1761). *Amphibia-Reptilia* **10**: 355–369.
- Renous, S. & Bels, V. (1991). Etude cinématique de la palette natatoire antérieure de la tortue luth, *Dermochelys coriacea* (Vandelli, 1761), au cours de sa locomotion terrestre. *Can. J. Zool.* **69**: 495–503.
- Sukhanov, V. B. (1966). [General system of terrestrial vertebrate locomotion and progression of the lower vertebrates.] *Inst. Zool. Acad. Sci. U.R.S.S.* [In Russian].
- Walker, W. F., Jr (1963). An analysis of force developed at the feet of turtles in walking. *Am. Zool.* **3**: 488.
- Walker, W. F., Jr (1971a). A structural and functional analysis of walking in the turtle *Chrysemys picta marginata*. *J. Morph.* **134**: 195–214.
- Walker, W. F., Jr (1971b). Swimming in sea turtles of the family Cheloniidae. *Copeia* **1971**: 229–233.

- Walker, W. F., Jr (1973). The locomotor apparatus of testudines. In *Biology of the Reptilia* **4**: 1–100. Gans, C. & Parsons, T. S. (Eds). London & New York: Academic Press.
- Walker, W. F., Jr (1979). Locomotion. In *Turtles. Perspective and research*: 435–454. Harless, M. & Morilock, H. (Eds). New York: J. Wiley & Sons.
- Zug, G. R. (1969). Locomotion and the morphology of the pelvic girdle and hindlimbs of cryptodiran turtles. *Diss. Abstr. Int.* **30B**: 2474–2475.
- Zug, G. R. (1971). Buoyancy, locomotion, morphology of the pelvic girdle and hind limb and systematics of cryptodiran turtles. *Misc. Publ. Am. Zool. Univ. Mich.* No. 142: 1–98.
- Zug, G. R. (1972). A critique of walk pattern analysis of symmetrical quadrupedal gaits. *Anim. Behav.* **20**: 436–438.