The Journal of Experimental Biology 204, 3261–3271 (2001)
Printed in Great Britain © The Company of Biologists Limited 2001
JEB3528

Comparative kinematics of the forelimb during swimming in red-eared slider (*Trachemys scripta*) and spiny softshell (*Apalone spinifera*) turtles

Cinnamon M. Pace, Richard W. Blob* and Mark W. Westneat

Department of Zoology, Division of Fishes, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA

*Author for correspondence (e-mail: rblob@fmnh.org)

Accepted 2 July 2001

Summary

Softshell turtles (Family Trionychidae) possess extensive webbing between the digits of the manus, suggesting that the forelimb may serve as an effective thrust generator during aquatic locomotion. However, the hindlimb has previously been viewed as the dominant propulsive organ in swimming freshwater turtles. To evaluate the potential role of the forelimb in thrust production during swimming in freshwater turtles, we compared the forelimb morphology and three-dimensional forelimb kinematics of a highly aquatic trionychid turtle, the spiny softshell *Apalone spinifera*, and a morphologically generalized emydid turtle, the red-eared slider *Trachemys scripta*. Spiny softshells possess nearly twice as much forelimb surface area as sliders for generating drag-based thrust. In addition, although both species use drag-based propulsion, several aspects of forelimb kinematics differ significantly between these species. During the thrust phase of the forelimb cycle, spiny softshells hold the elbow and wrist joints significantly straighter than sliders, thereby further increasing the surface area of the limb that can move water posteriorly and increasing the velocity of the distal portion of the forelimb. These aspects of swimming kinematics in softshells should increase forelimb thrust production and suggest that the forelimbs make more substantial contributions to forward thrust in softshell turtles than in sliders. Spiny softshells also restrict forelimb movements to a much narrower dorsoventral and anteroposterior range than sliders throughout the stroke, thereby helping to minimize limb movements potentially extraneous to forward thrust production. These comparisons demonstrate considerable diversity in the forelimb kinematics of turtles that swim using rowing motions of the limbs and suggest that the evolution of turtle forelimb mechanics produced a variety of contrasting solutions for aquatic specialization.

Key words: locomotion, biomechanics, kinematics, hydrodynamics, swimming, turtle, spiny softshell, *Apalone spinifera*, red-eared slider, *Trachemys scripta.*

Introduction

The locomotor system of turtles is unusual among vertebrates in that the body axis is largely inflexible. Because their dorsal vertebrae are fused to the carapace of a bony shell and, in most species, the tail is highly reduced, turtles rely exclusively on limb movements for propulsion. Many aspects of limb anatomy are strikingly conserved among turtle species, but significant variations in limb morphology are present in species specialized for particular types of locomotion (Walker, 1973). The forelimbs of sea turtles, for instance, are hypertrophied to form elongated flippers that produce lift-based thrust during open-ocean swimming (Walker, 1973; Davenport et al., 1984; Renous and Bels, 1993; Wyneken, 1997). The consequences of this derived limb morphology for sea turtle locomotion have attracted considerable attention (Walker, 1971; Davenport et al., 1984; Renous and Bels, 1993; Wyneken, 1997; Walker and Westneat, 2000). However, the limbs of many turtles specialized for freshwater aquatic habitats also exhibit distinctive morphological features that have received little study in the context of locomotor function.

In freshwater turtles (except *Carettochelys insculpta*, a freshwater species with flipper-shaped forelimbs similar to those of sea turtles), the hindlimb has typically been viewed as the primary propulsive organ during aquatic locomotion (Zug, 1971; Walker, 1973). One factor contributing to this perception is the difference in the amount of webbing between the digits of the fore- and hindfeet. In morphologically generalized emydid turtles (e.g. sliders, cooters) that spend considerable time in both terrestrial and aquatic habitats (Cagle, 1950; Bennett et al., 1970; Gibbons, 1970; Bodie and Semlitsch, 2000), webbing is much more extensive between the toes of the hindfeet than the toes of the forefeet (Walker, 1973). As a result, the hindfoot can form a broad paddle believed to serve as the predominant source of drag-based thrust during swimming (Zug, 1971). However, aquatic specialists such as the softshell turtles (Family Trionychidae) possess extensive

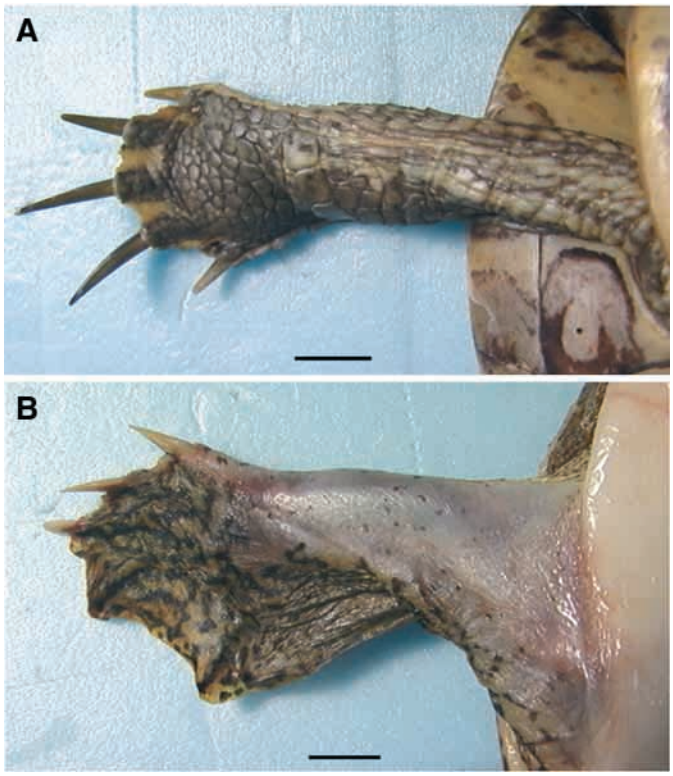

Fig. 1. Ventral views of the right forelimb of *Trachemys scripta*, the red-eared slider (A), and *Apalone spinifera*, the spiny softshell turtle (B). Scale bars, 1 cm.

webbing between the toes of the forefeet and the hindfeet (Webb, 1962) (Fig. 1). This suggests that the forelimbs, as well as the hindlimbs, could form effective paddles for generating drag-based thrust in softshell turtles.

To test for potential differences in the role of the forelimb for aquatic thrust generation among freshwater turtles, we compared the morphology and three-dimensional swimming kinematics of the forelimb in the spiny softshell *Apalone spinifera*, a highly aquatic trionychid, and the red-eared slider *Trachemys scripta*, a morphologically generalized emydid. Through these comparisons, we sought to evaluate whether limb movements, as well as limb morphology, suggested that the forelimb might make substantial contributions to thrust during swimming in some freshwater turtle species. Kinematic data for the forelimbs of swimming freshwater turtles are scant. Davenport et al. (Davenport et al., 1984) illustrate forelimb movements for a few frames of swimming by three freshwater species, but they do not report quantitative measurements of joint angles and did not examine specialized swimmers such as trionychids. It is possible that, despite differences in morphology, freshwater turtles might all move their forelimbs in a similar fashion. If this were the case, then any differences in forelimb thrust production among freshwater turtle species would be due to morphological differences alone. However, because softshell turtles are so highly specialized for aquatic habitats (Webb, 1962; Plummer et al., 1997), it seems likely that kinematic mechanisms, as well as morphological features, might help to enhance forelimb thrust in trionychids. Specifically, because these turtle species use drag-based propulsion (Vogel, 1994; Walker and Westneat, 2000), softshell turtles would be expected to display forelimb kinematics that, relative to sliders, better maximize the surface area of the forelimb perpendicular to the direction of travel during the power stroke. Thus, softshell and slider turtles might be expected to exhibit a number of specific differences in forelimb kinematics, including (i) orientation of the forefoot paddle more nearly perpendicular to the body axis during the power stroke in softshells, (ii) greater forelimb extension during the power stroke in softshells and (iii) greater restriction of forelimb movements to a horizontal plane in softshells to maintain thrust in a forward (rather than vertical) direction. Our kinematic data allow these specific predictions to be tested and, thereby, help to clarify the degree to which limb function, as well as limb shape, contributes to locomotor specialization in turtles.

Materials and methods

Experimental animals

Three *Apalone spinifera* (LeSeur) (carapace length 180±20 mm, mean ± S.D.) and three *Trachemys scripta* (Schoepff) (carapace length 206±14 mm, mean ± S.D.) were collected from Union and Alexander Counties, Illinois, USA (Illinois scientific permit no. A99.0550). The similar sizes of these individuals helped to control for potential effects of body size on locomotor kinematics (Drucker and Jensen, 1997). All animal care and experimental procedures followed Field Museum IACUC guidelines. Animals were housed in plastic tubs (900 mm×600 mm×200 mm) filled with water and fitted with recirculating filters and dry basking areas. Separate tubs were maintained for each species. Water temperature was maintained at 27–28 °C with submerged heaters. A 12 h:12 h light:dark cycle and full-spectrum lighting were provided. Both species were fed earthworms injected with a vitamin/mineral supplement and, in addition, sliders were fed a mixture of lettuce and kale.

Forelimb morphology and limb area

Forelimb segment lengths and surface areas from specimens of *Apalone spinifera* (*N*=3) and *Trachemys scripta* (*N*=6) were measured and compared. The three additional slider specimens had been collected from the same localities noted above and used in other experiments. Forelimbs of dead or anesthetized turtles were extended with the digits spread until foot webbing was unfolded. Forelimb morphometrics, including total limb length and the lengths of each limb segment (shoulder to elbow, elbow to wrist, wrist to longest digit tip), were measured using digital calipers. A digital image of each forelimb specimen was captured in ventral view using a Sony TRV-900 digital video camera and Photoshop 5.5 with PhotoDV firewire digital capture software. The areas of the forelimb paddle (area distal to the wrist) and forelimb shank (area proximal to the wrist) were measured from these digital images using NIH Image

1.62. To normalize measurements and account for differences in the sizes of individuals in interspecific comparisons, each measurement was divided by carapace length (for segment lengths) or (carapace length)^2 (for segment areas). Statistical comparisons of limb morphometrics between species were performed using non-parametric Mann–Whitney *U*-tests.

Kinematic data collection and analysis

Turtles swam in a flow tank and were filmed using digital video (Redlake MotionScope PCI 1000S). Lateral and ventral views were filmed simultaneously at 60 Hz using two digitally synchronized cameras, with the ventral view provided by a mirror placed at 45° under the transparent bottom of the flow tank. Swimming of moderate speed was induced by gently tapping the shell of each animal and by turning on the flow in the tank. The velocities of turtles and flow were calculated from video sequences by measuring the displacements of the swimming turtle and of particles in the water over known times; these velocities were summed to calculate the overall velocity of the turtle for each swimming trial. Locomotor speed was difficult to control in the turtles; in addition, *A. spinifera* typically swims faster than *T. scripta*. Therefore, we examined kinematics over a range of moderate speeds in each species ($0.87\pm0.41\,BL\,s^{-1}$ for *T. scripta*, $3.44\pm0.48\,BL\,s^{-1}$ for *A. spinifera*, where *BL* is body length; means ± S.D.) and evaluated the effects of speed on kinematic variables in each species using least-squares regressions to test for significant correlations between kinematic variables and velocity. It is possible that some kinematic differences between *A. spinifera* and *T. scripta* are related to the different preferred speeds of these species. However, within each species, no significant effects of speed on kinematics were identified in *A. spinifera* and only a few kinematic variables showed correlations with speed in *T. scripta* (see Results). Furthermore, kinematic measurements from *A. spinifera* swimming at unusually slow speeds (i.e. velocities typical of *T. scripta*) would not be useful for clarifying the typical role of the forelimb during aquatic locomotion in this species.

Individuals of both species tended to swim near the bottom of our flow tank, and it is possible that the kinematics of other types of swimming behavior (i.e. mid-stream swimming, diving) might differ from those we report here. However, the behavior we examined is used by each species in nature, because both *A. spinifera* and *T. scripta* live in habitats where near-substratum swimming is frequently required (Cagle, 1950; Plummer et al., 1997). Moreover, examining near-substratum swimming in both species helped us to ensure that the behavior we measured was sufficiently similar for our comparisons between the species to be valid.

Five swimming strokes were analyzed for each individual turtle. To calculate three-dimensional joint coordinates, NIH Image 1.62 and the custom-designed routine QuickImage (Walker, 1998) were used to digitize the positions of shell landmarks and the forelimb joints (including the shoulder, elbow, wrist, metacarpo-phalangeal joint and the tips of the first, third and fifth digits) in lateral and ventral views for every other video frame (producing an effective framing rate of 30 Hz). The shells of the turtles occasionally obscured some joint positions for a few frames in either lateral or ventral view, but never in both views for the same frame. The position of an obscured joint in a specific view was evaluated on the basis of the known measured lengths of the limb segments and on the point of intersection of lines extended in the video frame along the visible portions of the limb segments meeting at the joint. Kinematic variables (three-dimensional joint angles and the angles of limb segments relative to specific planes) were calculated from the three-dimensional coordinate data for each trial using a custom-designed Matlab (Mathworks) program. The program QuickSAND (Walker, 1998) was then used to fit a quintic spline to the kinematic calculations from each trial, smoothing the data and allowing the trials to be normalized to the same duration prior to comparisons among individuals and between species.

The following kinematic variables were calculated throughout each swimming trial: the angle of the humerus relative to both the transverse and horizontal planes, and the angle of the elbow, the angle of the wrist and the orientation of the forefoot relative to the direction of travel. Average kinematic profiles (and standard errors) for each variable through the course of the stroke were calculated for each species using StatView version 4.5 software (Abacus Concepts, 1995). Two-level nested analyses of variance (ANOVAs) were performed using JMP version 3.2.1 software (SAS Institute, Cary, NC, USA) to test for significant differences in kinematic variables between species and among individuals within species. *F*-statistics for the fixed effect (species) were calculated by dividing the species mean square by the mean square for the random effect (individual). The effect of individuals within species was then tested over the residual (Sokal and Rohlf, 1995; Drucker and Jensen, 1997). The use of ANOVAs assumes that values of the variables compared are distributed normally and have equal variances (Sokal and Rohlf, 1995). Shapiro–Wilk *W*-tests for normality (performed using JMP 3.2.1) indicated that kinematic measurements were distributed normally for all variables in *A. spinifera* and for all but one variable (maximum humerus retraction) in *T. scripta*. However, moderate non-normality does not generally affect ANOVAs seriously (Sokal and Rohlf, 1995). Furthermore, the range of values for maximum humerus retraction did not overlap between the species, so our evaluation of differences in this variable between the species was probably unaffected by the violated assumption of normality. F_{max}-tests for equality of variances (Sokal and Rohlf, 1995) indicated that a significant difference was present between the species for the variance of only one variable, the maximum elevation of the humerus. However, only a single measured value of this variable for *T. scripta* overlapped the range of values observed for *A. spinifera*. A Welch ANOVA (performed in JMP 3.2.1), recommended when the assumption of equal variance is invalid (Sokal and Rohlf, 1995), produced the same result for this variable as the standard nested ANOVA. Because the effects on our analyses appear to be

negligible in the few instances when assumptions of either normality or equal variance were invalid, we have reported and discuss only the results of our standard, two-level nested ANOVAs in detail.

Results

Forelimb morphology

T. scripta and *A. spinifera* showed no significant differences in normalized forelimb segment lengths (Table 1). However, the propulsive areas of the limbs differed significantly between these species, with the aquatic specialist *A. spinifera* exhibiting normalized foreleg and forefoot areas that were both nearly twice as great as those found in *T. scripta* (Table 1).

Forelimb kinematics

In both *T. scripta* and *A. spinifera*, the swimming stroke is defined as starting at the beginning of humerus protraction towards the head of the turtle and ending at the start of the next humerus protraction cycle. Thus, the stroke begins with the 'recovery' phase of the locomotor cycle (Fig. 2). The start of the propulsive 'thrust' phase of the locomotor cycle is

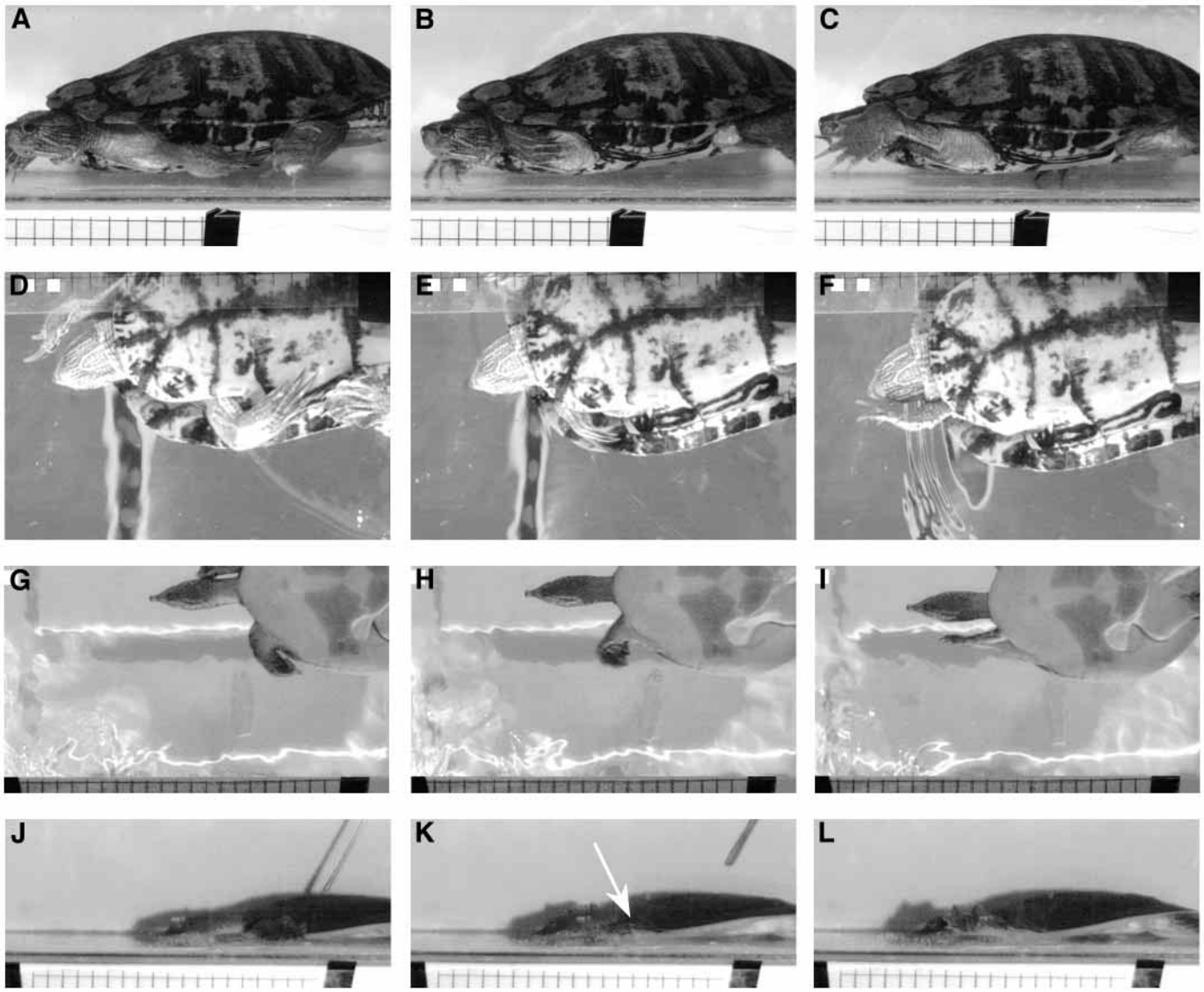

Fig. 2. Frames from video footage of swimming turtles during forelimb protraction (recovery phase). (A–C) *Trachemys scripta*, lateral view. (D–F) *T. scripta*, ventral view. (G–I) *Apalone spinifera*, ventral view. (J–L) *A. spinifera*, lateral view. The grid scale is 1 cm in each frame. Movements of the left forelimb were analyzed; thus, in lateral views, the focal forelimb is the one closest to the viewer, but in ventral views (which were filmed using a mirror) the focal forelimb is the one closest to the bottom of the video frame. Lateral and ventral views for each species are from the same experimental trial. Images in each column depict an approximately equivalent instant in the locomotor cycle: left-hand column (A,D,G,J), early recovery phase; center column (B,E,H,K), mid recovery phase; right-hand column (C,F,I,L), late recovery phase. The white arrow in K points to the forelimb in *A. spinifera*, which is difficult to see in still lateral frames while the forefoot is feathered. Note that video frames illustrated in Fig. 3 depict thrust phase from the same swimming trials, so that sequential viewing of Fig. 2 and Fig. 3 will allow examination of entire kinematic cycles for turtle forelimbs during swimming.

Table 1. *Comparison of morphological variables in* Trachemys scripta *and* Apalone spinifera

Variable	*T. scripta*, *N*=6	*A. spinifera*, *N*=3	*P*
Normalized humerus length	0.170±0.023	0.162±0.011	0.439
Normalized radius/ulna length	0.136±0.008	0.129±0.006	0.121
Normalized forefoot length	0.109±0.003	0.112±0.005	0.606
Normalized foreleg area	0.015±0.002	0.029±0.002	0.020*
Normalized forefoot area	0.013±0.001	0.026±0.001	0.020*

Values are means ± S.D.
*Mann–Whitney *U*-test, $P \leqslant 0.05$.
Limb segment length measurements were normalized by dividing segment lengths by carapace length for each individual.
Area measurements were normalized by dividing foreleg and forefoot areas by (carapace length)^2 for each individual.

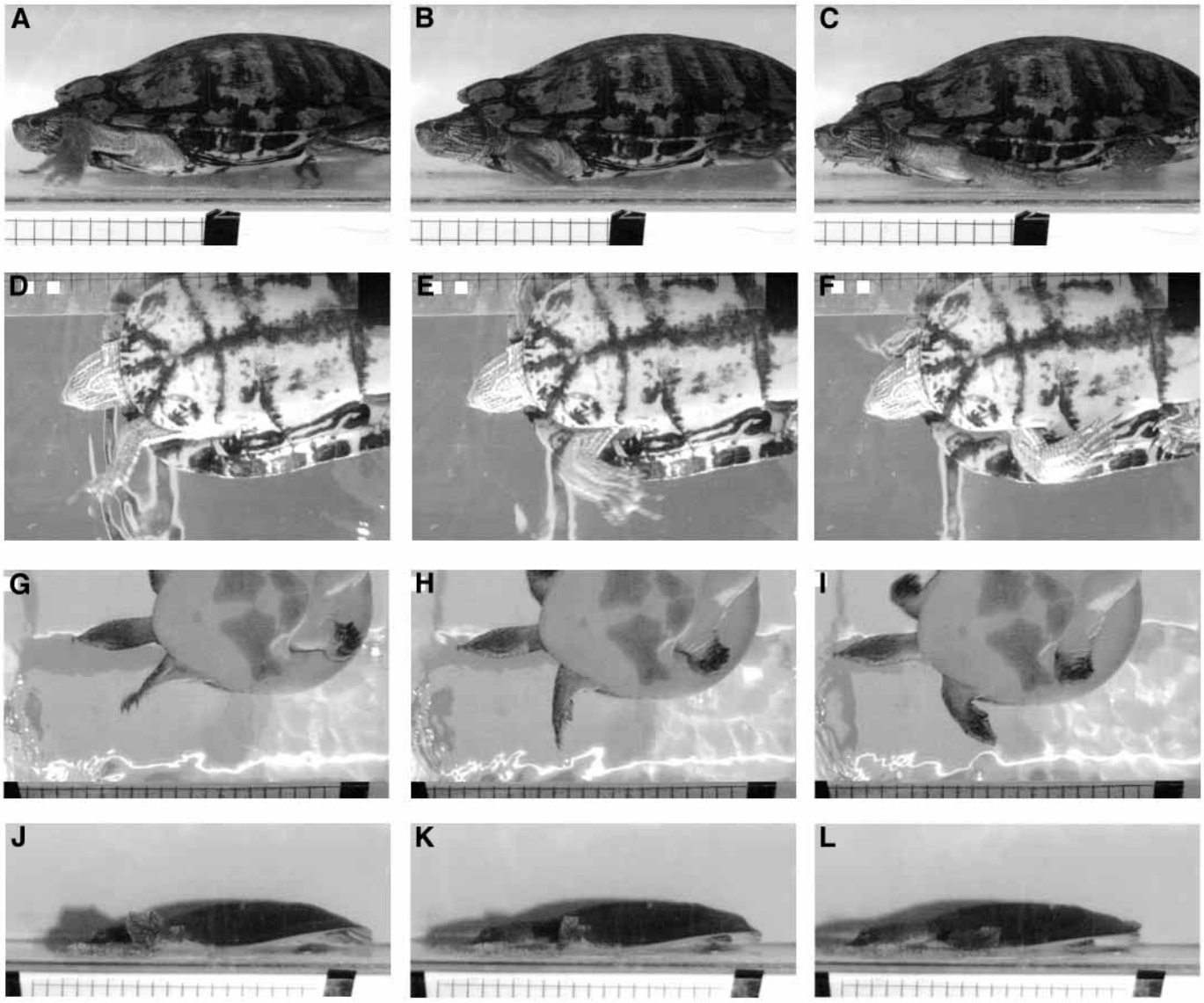

Fig. 3. Frames from video footage of swimming turtles during forelimb retraction (thrust phase). (A–C) *Trachemys scripta*, lateral view. (D–F) *T. scripta*, ventral view. (G–I) *Apalone spinifera*, ventral view. (J–L) *A. spinifera*, lateral view. The grid scale is 1 cm in each frame. As in Fig. 2, in lateral views the focal forelimb is the one closest to the viewer, but in ventral views the focal forelimb is the one closest to the bottom of the video frame. Lateral and ventral views for each species are from the same experimental trial, and the trials illustrated are the same as those illustrated in Fig. 2. As in Fig. 2, images in each column depict an approximately equivalent instant in the locomotor cycle: left-hand column (A,D,G,J), early thrust phase; center column (B,E,H,K), mid thrust phase; right-hand column (C,F,I,L), late thrust phase.

indicated by the beginning of humerus retraction, which occurs after the humerus has achieved its furthest anterior excursion (Fig. 3).

Swimming in Trachemys scripta

In the red-eared slider, protraction comprises the first 34±6 % (mean ± S.D.) of the stroke and retraction occupies the remaining two-thirds of the cycle. During protraction, the humerus is simultaneously elevated and drawn forward until it reaches its greatest elevation (38±9 ° above the horizontal) and anterior position (143±8 ° from the transverse plane) immediately prior to retraction (Fig. 2A–F, Fig. 4A, Fig. 5A; angle ranges are means ± S.D.). The extreme anterior extension of the humerus shifts the flexed elbow (57±5 °; Fig. 6A) medial to the shoulder (Fig. 2F) and above the head (Fig. 2C) in the slider. In addition, the palmar surface of the forefoot is drawn towards the radius and the ulna during protraction so that the wrist reaches a maximum palmarflexion of –39±8 ° by the middle of the recovery phase (Fig. 2E, Fig. 7A). The forefoot of *T. scripta* rotates from a feathered orientation early in protraction to an unfeathered orientation during late protraction (Fig. 8A).

Towards the last third of protraction, the previously flexed elbow extends to a maximum of 114±12 ° (Fig. 2C,F, Fig. 6A). As the elbow extends, and throughout retraction, the humerus is gradually depressed and extended backwards until it is angled below the horizontal (–13±14 °) by the end of the stroke (Fig. 3F, Fig. 5A). Towards the end of retraction, the elbow again flexes, but then re-extends slightly before starting the flexion associated with the recovery phase of the next stroke (Fig. 6A). During the first two-thirds of retraction, the wrist dorsiflexes to a maximum angle of 62±14 °(Fig. 3D–E, Fig. 7A). Then, in the final third of retraction, the wrist angle again closes and the forefoot is drawn into a straight line with the radius and ulna (Fig. 3F, Fig. 7A). The forefoot of *T. spinifera* is nearly perpendicular to the flow of water twice during the stroke, first at the changeover between protraction and retraction and again at the middle of retraction (Fig. 8A). By the end of the thrust phase, the forefoot is positioned so that its dorsal surface faces ventrally, towards the substratum (Fig. 3F).

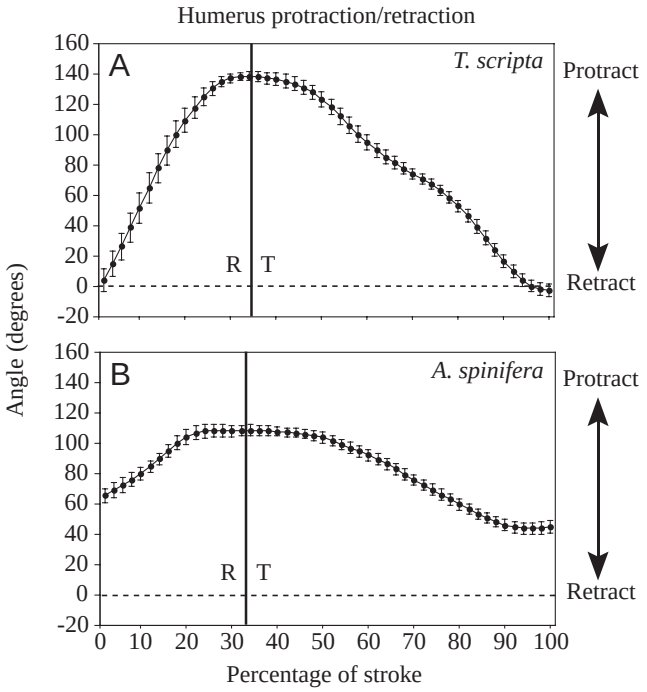

Fig. 4. Mean kinematic profiles of humerus protraction and retraction (i.e. angle from the transverse plane) during turtle swimming. (A) *Trachemys scripta*, (B) *Apalone spinifera*. Each kinematic trial was normalized to the same duration, and values of kinematic angles were interpolated for 100 equally spaced increments through the stroke cycle (Walker, 1998), allowing mean angles and standard errors to be calculated for each 1 % increment through the stroke for each species. Angle values ±1 S.E.M. are plotted for every second increment (every 2 % through the cycle); *N*=15 trials for each species. Angles of 0 ° indicate that the humerus is perpendicular to the anteroposterior midline of the turtle, with negative angles indicating that the distal end of the humerus is directed posteriorly and positive angles indicating that the distal end of the humerus is directed anteriorly. An angle of +90 °, for example, indicates that the distal end of the humerus is directed straight ahead of the turtle. The bold vertical line in each plot demarcates recovery phase (R) from thrust phase (T).

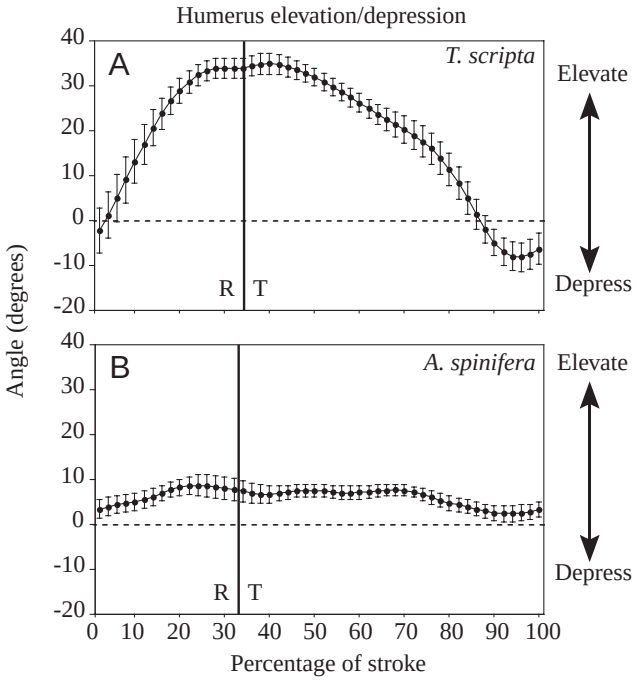

Fig. 5. Mean kinematic profiles of humerus elevation and depression (i.e. angle from the horizontal plane) during turtle swimming. (A) *Trachemys scripta*, (B) *Apalone spinifera*. The format and method of profile calculation are the same as in Fig. 4. Angles of 0 ° indicate a horizontal humerus, while positive angles indicate that the distal end of the humerus is elevated above the proximal end, and negative angles indicate that the distal end of the humerus is depressed below the proximal end. The bold vertical line in each plot demarcates recovery phase (R) from thrust phase (T).

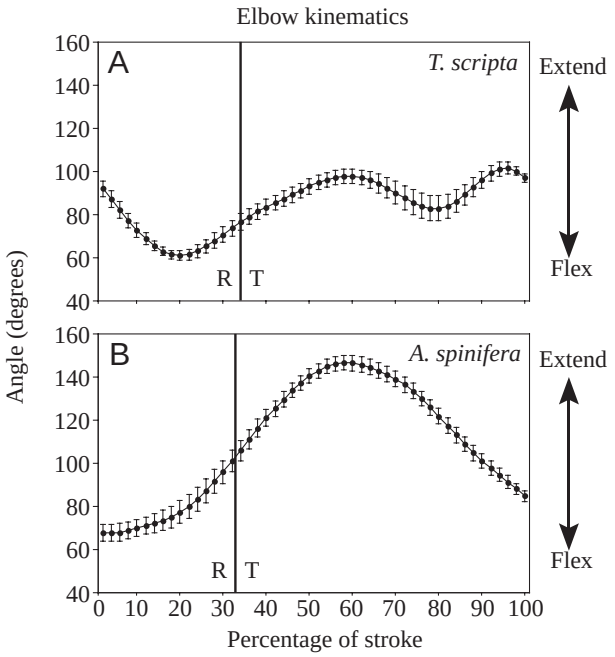

Fig. 6. Mean kinematic profiles of elbow extension and flexion (true angle in three dimensions) during turtle swimming. (A) *Trachemys scripta*, (B) *Apalone spinifera*. The format and method of profile calculation are the same as in Fig. 4. Larger angles indicate greater elbow extension: 180° would indicate a straight elbow joint. The bold vertical line in each plot demarcates recovery phase (R) from thrust phase (T).

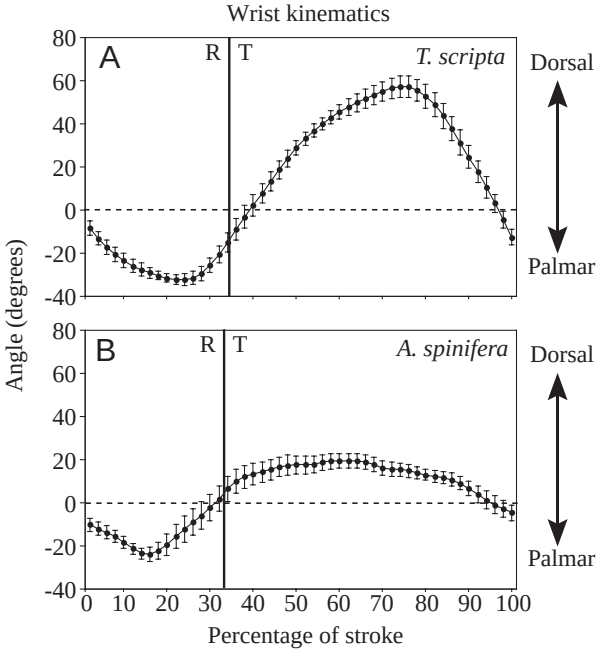

Fig. 7. Mean kinematic profiles of wrist dorsiflexion and palmarflexion (true angle in three dimensions) during turtle swimming. (A) *Trachemys scripta*, (B) *Apalone spinifera*. The format and method of profile calculation are the same as in Fig. 4. Angles of 0° indicate a straight wrist joint, while positive angles indicate dorsiflexion and negative angles indicate palmarflexion. The bold vertical line in each plot demarcates recovery phase (R) from thrust phase (T).

In general, few kinematic variables were affected by changes in swimming velocity in *T. scripta* over the range of speeds examined. In faster swims, sliders tended to elevate the humerus less during protraction (P=0.007), extend the elbow less during retraction (P=0.018) and rotate the forefoot into a higher-drag orientation during protraction (P=0.005). Despite these slight variations, however, the overall forelimb kinematics of *T. scripta* resemble a dog-paddle during swimming. During protraction, the limb is not consistently feathered, while during retraction the limb is pulled diagonally downwards through the water from a raised position.

Swimming in Apalone spinifera

As in the case of sliders, in spiny softshells, humerus protraction accounts for the first 33±6% (mean ± S.D.) of the forelimb stroke, while retraction occupies the remaining two-thirds of the limb cycle. Throughout protraction, the humerus of *A. spinifera* elevates only slightly to a maximum of 14±4° above the horizontal (Fig. 2J–L, Fig. 5B). This occurs while the humerus is extending forward to reach a maximum anterior excursion from the transverse plane of 114±13° (Fig. 2I, Fig. 4B). The elbow flexes to a minimum angle of 62±14° near the start of humerus protraction (Fig. 2G), but gradually extends through the rest of protraction (Fig. 2H,I, Fig. 6B). The wrist palmarflexes through initial protraction in *A. spinifera*, reaching a maximum of −31±10° approximately half-way through the recovery stroke (Fig. 2H, Fig. 7B), but dorsiflexes through the remainder of the recovery phase (Fig. 2I, Fig. 7B). The forefoot remains highly feathered through most of forelimb protraction in spiny softshells, with the span of the forefoot parallel to the flow of water. This orientation reduces the area of foot exposed to the flow of the water as the forelimb is pulled forward in preparation for the thrust phase (Fig. 2J,K, Fig. 8B).

During retraction in *A. spinifera*, the humerus is gradually drawn back and depressed until it extends posteriorly 41±13° from the transverse plane and is depressed −3±8° below the horizontal (Fig. 3G–L, Fig. 4B, Fig. 5B). While the humerus moves posteriorly during retraction, the elbow extends until it is straightened to a maximum of 149±14° approximately midway through the thrust phase (Fig. 3H, Fig. 6B). Wrist motions are variable during the thrust phase in spiny softshells, but tend to dorsiflex to a maximum of 30±13° by mid-retraction (Fig. 7B). Through the first half of the thrust phase, the forefoot of *A. spinifera* shifts from a feathered orientation (parallel with the flow of water) to an orientation nearly perpendicular to the flow of water (Fig. 3J, Fig. 8B). During the last half of the thrust phase, the forefoot rotates back to a feathered orientation with the palmar surface of the forefoot facing ventrally, towards the substratum, by the end of the stroke (Fig. 3I, Fig. 8B). Thus, movements of the forelimbs in spiny softshell turtles resemble oar strokes in which the limb shows little vertical movement.

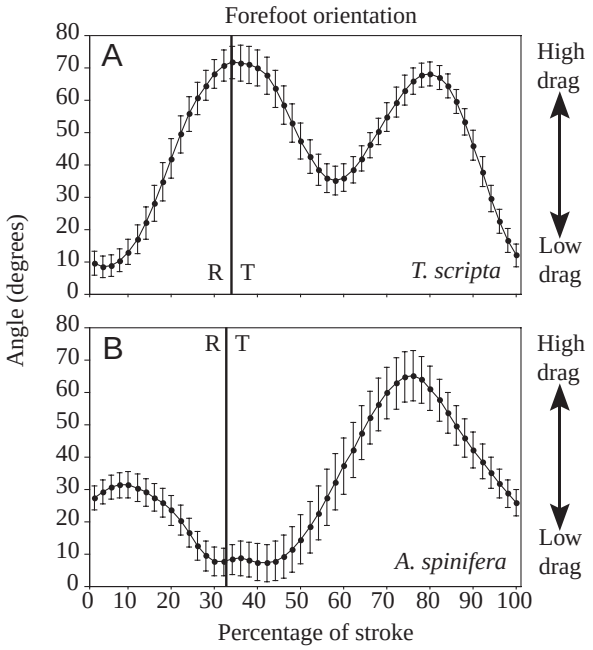

Fig. 8. Mean kinematic profiles of forefoot (paddle) orientation during turtle swimming. (A) *Trachemys scripta*, (B) *Apalone spinifera*. The format and method of profile calculation are the same as in Fig. 4. The angle plotted is the angle between a vector pointing forwards along the anteroposterior midline of the turtle and a vector emerging from the palmar surface of a plane defined by the wrist and the tips of digits 1 and 5 on the turtle manus, transformed by subtracting 90 ° from each value. Thus, a low-drag orientation of the forefoot (perfect feathering) is indicated by an angle of 0 °, whereas a high-drag forefoot orientation, with the palmar surface of the manus facing in the direction opposite to the direction of travel, is indicated by an angle of 90 °. The bold vertical line in each plot demarcates recovery phase (R) from thrust phase (T).

Interspecies comparisons

Two-level nested ANOVAs show that the forelimb kinematics of *T. scripta* and *A. spinifera* exhibit several significant differences even after taking individual effects into account. Although the timing of humerus protraction and retraction are similar in both species, maximum forward protraction is nearly 30 ° greater in *T. scripta* than in *A. spinifera*, and maximum rearward retraction is more than 50 ° greater in *T. scripta*, producing significantly greater anteroposterior excursion of the humerus in *T. scripta* than in *A. spinifera* (Table 2). In addition, dorsoventral elevation and depression of the humerus in *T. scripta* exceeds that in *A. spinifera* by over 30 ° (Table 2). In contrast, *A. spinifera* holds the forelimb much straighter than *T. scripta* during the thrust phase: peak elbow extension is almost 35 ° greater in *A. spinifera*, whereas peak dorsiflexion of the wrist is more than 30 ° greater in *T. scripta* (Table 2). Forefoot orientation also shows significant differences between the species. During protraction, *A. spinifera* shows significantly less rotation of the forefoot paddle away from a feathered orientation than *T. scripta* (Table 2). However, forefoot orientation does not differ significantly between the species through most of the thrust phase.

Discussion

The forelimb makes important contributions to aquatic locomotion in both slider and spiny softshell turtles, but the role of the forelimb differs substantially between the two species. Sliders may generate small amounts of thrust by moving their forelimbs forwards and backwards during swimming; however, the low propulsive surface areas of slider limbs and the orientations of the forelimb during the recovery and power strokes suggest that only low forces could be produced. Our data suggest that sliders use their forelimbs primarily for balance and orientation during aquatic locomotion although, in highly vegetated habitats, the long claws of slider forelimbs could assist in propulsion by facilitating the use of aquatic plants as a substratum. In contrast, in softshells, high forelimb surface areas and the mechanics of both the recovery and power strokes suggest that

Table 2. *Summary of kinematic variables compared between* Trachemys scripta *and* Apalone spinifera, *with* F-*statistics from nested analyses of variance*

			Source of variation	
Variable	*T. scripta*	*A. spinifera*	Between species, d.f.=1	Among individuals, d.f.=4
Maximum humerus protraction (degrees)	143±8	114±13	27.52*	2.29
Maximum humerus retraction (degrees)	–11±16	41±13	48.95*	2.23
Humerus anteroposterior excursion (degrees)	155±16	74±15	119.41**	1.86
Maximum humerus elevation (degrees)	38±9	14±4	27.72*	6.63**
Humerus dorsoventral excursion (degrees)	52±11	17±7	101.32**	1.04
Maximum elbow extension (degrees)	114±12	149±14	30.05*	1.94
Maximum wrist dorsiflexion (degrees)	62±14	30±13	62.66**	0.66
Forefoot excursion during protraction (degrees)	80±18	31±13	45.93*	1.73

Values are means ± S.D.
*$P \leq 0.01$; **$P \leq 0.001$.

the forelimb contributes substantially to forward thrust during swimming. Although propulsion during swimming is drag-based in both softshell and slider turtles, the differences in forelimb kinematics between these species indicate that, even within this locomotor mode, considerable evolutionary diversification in forelimb function has occurred.

Role of the forelimb during swimming in slider and softshell turtles

The shapes of slider and softshell forelimbs differ dramatically, with softshells possessing nearly twice as much forelimb surface area as sliders for generating drag-based thrust. However, kinematic differences between *A. spinifera* and *T. scripta* strongly suggest that forelimb movements, as well as forelimb morphology, contribute to the effective production of forelimb thrust by swimming softshell turtles. Two specific contrasts in forelimb kinematics between the species indicate that the potential surface area of drag-based propulsors is maximized more effectively in spiny softshells than in sliders. Relative to sliders, spiny softshells combine greater elbow extension and lesser wrist flexion to straighten and extend the forelimb more completely during the power stroke (Fig. 3E,H). These movement patterns increase the frontal area of the limb and help to maximize the volume of water that softshell forelimbs can accelerate to generate thrust. A further consequence of increased forelimb extension in softshells is an increase in the velocity of flow over the paddle-like forefoot because it must move a greater arc distance in the same amount of time as more proximal portions of the limb (Blake, 1981a; Blake, 1981b; Webb and Blake, 1985; Webb, 1988). Both species extend the elbow through the first half of the thrust phase, increasing flow velocity over the distal limb, but angular excursion to maximum extension is nearly twice as great in softshells (Fig. 6). Propulsive forces are proportional to the square of flow velocity, so greater forelimb extension in softshells should result in larger propulsive forces than in sliders (Blake, 1981a; Webb and Blake, 1985).

In addition to helping maximize thrust production, the movements of softshell forelimbs also appear to direct thrust in a forward direction more effectively than the movements of slider forelimbs during swimming. Forelimb movements of spiny softshells are restricted to a very narrow dorsoventral range between 14° above and 3° below the horizontal, a pattern that would be expected to help limit dorsal and ventral components of force generated by the limb (Fig. 5; Table 2). In contrast, the slider humerus exhibits peak elevations nearly 40° above the horizontal and moves through a substantial ventral excursion during the powerstroke (Fig. 3, Fig. 5; Table 2). The downward velocity of the forelimb in sliders would be expected to create an upward component of force (e.g. Feldkamp, 1987; Fish, 1996; Walker and Westneat, 1997) that would reduce the forward thrust component generated by the forelimb. However, limited data suggest that sliders are slightly more negatively buoyant than spiny softshells (Zug, 1971). Thus, upward thrust generated by the forelimbs may be necessary to help sliders stay above the substratum while swimming.

Anteroposterior forelimb excursion is also considerably greater in sliders than in softshells and may contribute to differences in forelimb thrust orientation between these species. At the beginning of the power stroke, the slider humerus is directed so that the elbow is medial to the shoulder (Fig. 2F, Fig. 3D, Fig. 4). As a result, for the first part of the power stroke, the humeral segment of the slider forelimb is accelerating water with a slight anterior component, resulting in a posteriorly directed (i.e. backward) reaction force (drag). Similarly, by the end of forelimb retraction, the distal end of the slider humerus is directed posteriorly (Fig. 3F) and, as a result, the proximal forelimb will accelerate water medially (towards the body of the turtle), resulting in a large lateral component to the resultant force. Thus, during both early and late power strokes in sliders, substantial components of the force generated by the forelimbs will not contribute to forward thrust. In contrast, in *A. spinifera*, the humerus is not extended far medial to the shoulder at the start of the power stroke (Fig. 2I, Fig. 4B) and does not retract past an orientation perpendicular to the anteroposterior axis of the turtle (i.e. the direction of travel; Fig. 3I, Fig. 4B). The more restricted range of anteroposterior humeral excursion in the spiny softshell (Fig. 2G–I, Fig. 3G–I, Fig. 4; Table 2) could help maintain effective forward thrust through most of the power stroke.

Although several differences in forelimb swimming kinematics between sliders and spiny softshells suggest that forelimb thrust production is more effective in the softshells, contrasts in movements of the forefoot (i.e. paddle) during the power stroke do not appear likely to be the source of differences in forelimb thrust between these species. For instance, the two species do not differ significantly in the proportion of the power stroke during which the forefoot is positioned in a high-drag orientation (nearly perpendicular to flow). In addition, in both species, peak forefoot orientation is approximately 70° and occurs near mid power stroke (with 90° indicating a high-drag orientation perpendicular to flow) (Fig. 8). However, forefoot kinematics differ significantly between sliders and spiny softshells during the recovery phase of the stroke. Forefoot rotational excursion during recovery is approximately 50° greater in sliders than in softshells (Fig. 8; Table 2). As a result, in sliders, the forefoot is likely to incur high drag that would inhibit forward progression for a substantial portion of limb protraction, whereas in softshells the forefoot is effectively feathered throughout recovery, minimizing resistance to forward swimming. The contrasts in forelimb kinematics between sliders and softshells, therefore, indicate that not only is forelimb thrust production probably enhanced in *A. spinifera* but that drag during stroke recovery is also probably minimized in this turtle species specialized for aquatic locomotion.

Our predictions for differences in forelimb thrust production between swimming softshell and slider turtles, based on the kinematic analyses reported in this study, remain to be tested empirically. Techniques such as digital particle image

velocimetry (DPIV) have recently been applied to evaluate the thrust forces produced by the pectoral fins of fishes during labriform swimming (e.g. Drucker and Lauder, 1999; Drucker and Lauder, 2000). This approach could provide an effective means of quantifying differences in the relative contributions of the forelimb and hindlimb to thrust in swimming turtles. However, in addition to potentially generating a greater proportion of thrust with their forelimbs, highly aquatic softshell turtles might generate a greater total thrust than sliders. Two additional experiments could directly measure the total thrust produced by freely swimming turtles and test this latter hypothesis. First, because turtles possess shells, they present an excellent opportunity for the use of direct force transduction to obtain thrust measurements with minimal interference during normal locomotor behavior. Attachment of animals to a force transducer has enabled accurate estimates of thrust in animals ranging from insects (Dickinson and Götz, 1996) to swimming fishes (Westneat, 1995) and turtles (Davenport et al., 1984), although this technique has not been applied to softshells. Second, tracking the center of mass of an animal through the locomotor cycle is a simple and effective means of documenting changes in velocity and acceleration in aquatic locomotion (Walker and Westneat, 1997). In conjunction with empirical measurements of drag on sliders and softshells, the thrust/drag balance on these species could be estimated accurately and compared.

Another aspect of turtle forelimb function requiring further study is the neuromuscular control of forelimb movements. Our analyses of forelimb kinematics suggest that several specific differences in forelimb muscle activity might be expected between softshell and slider turtles. For example, the wrist is dorsiflexed extensively during thrust phase in sliders, but thrust-phase movements at the wrist are minimal in spiny softshells (Fig. 3E,I, Fig. 7). It is possible that, in softshells, the wrist is actively held straight by contraction of the palmarflexor palmaris longus, but in sliders thrust-phase activity of the palmaris longus is lacking, and wrist dorsiflexion results as a passive consequence of the reaction force of water on the limb during retraction. Alternatively, power-stroke dorsiflexion of the wrist in sliders might be actively controlled by action of the extensor digitorum communis. Electromyographic data from turtle forelimb muscles could test these possibilities.

Diversity and evolution of forelimb function in swimming turtles

Turtle species exhibit a diversity of kinematic patterns in their forelimbs during swimming. The contrast between the flapping forelimb strokes used by swimming marine turtles and the rowing forelimb strokes used by most swimming freshwater turtles has been documented in an extensive range of previous studies (e.g. Walker, 1971; Davenport et al., 1984; Renous and Bels, 1993; Davenport and Pearson, 1994; Wyneken, 1997; Walker and Westneat, 2000). Flapping strokes are characterized by predominantly dorsoventral forelimb movements, whereas rowing strokes are characterized by predominantly anteroposterior forelimb movements combined with rotation of the foot (perpendicular to flow during thrust and feathered during recovery). However, the results of this study demonstrate that turtle species not only exhibit a kinematic dichotomy between forelimb flapping and rowing but also display considerable diversity in their styles of forelimb rowing. In terms of the mechanism employed to generate forelimb thrust, the drag-based system used by sliders, softshells and most other freshwater turtles is clearly distinct from the lift-based system employed by sea turtles (Davenport et al., 1984). Yet, in terms of the motions of limb segments, the substantial elevation and depression of the humerus exhibited by sliders bears a kinematic resemblance to the dorsoventral movements of the humerus in sea turtles that is not evident in the dorsoventrally restricted forelimb movements of the spiny softshell.

Although the use of lift-based mechanisms for generating thrust is widespread among vertebrates that are highly specialized for locomotion in aquatic environments, the persistence of drag-based swimming among aquatic species has been attributed to a variety of factors (Rayner, 1985; Vogel, 1994; Fish, 1996; Walker and Westneat, 2000). Despite the lower energetic efficiency of rowing, drag-based propulsion is frequently observed among secondarily aquatic species and species that retain the ability to travel over land, possibly because rowing requires fewer modifications to a terrestrial locomotor system than flapping (Rayner, 1985; Fish, 1996). Drag-based rowing is also frequently observed among species in which high thrust production is of greater importance than energetic efficiency, such as animals that swim slowly and maneuver extensively (Walker and Westneat, 2000). Although red-eared sliders are known to travel substantial distances over land (Bennett et al., 1970; Gibbons, 1970), spiny softshell turtles are highly specialized for aquatic habitats and very rarely leave the water for extended periods (Webb, 1962; Plummer et al., 1997). Furthermore, the spiny softshell is among the fastest of freshwater turtles. Davenport et al. (Davenport et al., 1984) reported top speeds of $2.3\,BL\,s^{-1}$ for the emydid *Mauremys caspica* and $1.8\,BL\,s^{-1}$ for the kinosternid *Kinosternon subrubrum*, while the top speed measured in this study for *T. scripta* was $1.6\,BL\,s^{-1}$. In contrast, although this study did not attempt explicitly to evaluate the maximum swimming speed of spiny softshell turtles, both the maximum ($4.1\,BL\,s^{-1}$) and mean ($3.4\,BL\,s^{-1}$) swimming velocities measured for *A. spinifera* in this study are substantially greater than those exhibited by other rowing species. Thus, although softshell turtles swim at high velocities and rarely travel over land, they employ forelimb kinematics that are more specialized for rowing than the kinematics of slower, more terrestrial sliders.

The evolution of aquatic specialization in the locomotor function of turtle forelimbs appears to have followed two distinct paths. Among sea turtles and carettochelyids, swimming proficiency is correlated with forelimb hypertrophy and the use of flapping limb kinematics. In contrast, among softshell turtles, swimming proficiency is correlated with

rowing limb kinematics in which the thrust-generating surface area of the limbs is maximized and limb movements extraneous to forward thrust production are minimized. In many respects, although the morphological and behavioral aquatic specializations of softshells are extreme among freshwater turtles, they are not as extreme as those of sea turtles and, thus, the retention of rowing among softshells may not be surprising. For example, softshells probably cannot swim as quickly as sea turtles (e.g. $13\,BL\,s^{-1}$ for *Chelonia mydas*; Davenport et al., 1984) and undoubtedly move over land more frequently than sea turtles. However, it is curious that softshell turtles, with their numerous specializations allowing effective aquatic rowing, form the sister clade to carettochelyids (Shaffer et al., 1997), the only clade of freshwater turtles that employs flapping forelimb kinematics (Rayner, 1985; Ernst and Barbour, 1989; R. W. Blob and J. A. Walker, unpublished data). Furthermore, although emydid turtles such as sliders appear to be morphologically and functionally generalized, the clade composed of softshell turtles and carettochelyids is actually the most basal lineage of cryptodiran turtles (Shaffer et al., 1997), raising the possibility that some apparent morphological or behavioral specializations among softshells could actually represent retentions of ancestral character states. Kinematic analyses of several additional turtle species, particularly pleurodires, kinosternids and chelydrids, will be needed to clarify the pattern of functional evolution in turtle forelimbs. However, the kinematic diversity suggested by this analysis recommends turtle locomotion as a fruitful system for future studies of functional evolution.

We thank N. Espinoza, J. Walker and two anonymous referees for thoughtful reviews of this paper and the Field Museum Biomechanics Group (M. Alfaro, D. Collar, J. Janovetz, L. Rosenberger and B. Wright) for help and advice throughout the course of this study. We also thank J. Walker for help in developing our vector analyses. Support for this research was provided by National Institutes of Health NRSA fellowships (1F32NS10813-01 and 5F32NS10813-02 to R.W.B.) and by a grant from the Office of Naval Research (N000149910184 to M.W.W. and J. Walker).

References

Abacus Concepts (1995). *StatView 4.5*. Berkeley, CA: Abacus Concepts, Inc.

Bennett, D. H., Gibbons, J. W. and Franson, J. C. (1970). Terrestrial activity in aquatic turtles. *Ecology* **51**, 738–740.

Blake, R. W. (1981a). Mechanics of drag-based mechanisms of propulsion in aquatic vertebrates. *Symp. Zool. Soc. Lond.* **48**, 29–52.

Blake, R. W. (1981b). Influence of pectoral fin shape on thrust and drag in labriform locomotion. *J. Zool., Lond.* **194**, 53–66.

Bodie, J. R. and Semlitsch, R. D. (2000). Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. *Oecologia* **122**, 138–146.

Cagle, F. R. (1950). The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). *Ecol. Monogr.* **20**, 31–54.

Davenport, J., Monks, S. A. and Oxford, P. J. (1984). A comparison of the swimming in marine and freshwater turtles. *Proc. R. Soc. Lond. B* **220**, 447–475.

Davenport, J. and Pearson, G. A. (1994). Observations on the swimming of the Pacific Ridley, *Lepidochelys olivacea* (Eschscholtz 1829): comparisons with other sea turtles. *Herpetol. J.* **4**, 60–63.

Dickinson, M.H. and Götz, K. G. (1996). The wake and flight forces of a fruit fly, *Drosophila melanogaster*. *J. Exp. Biol.* **199**, 2085–2104.

Drucker, E. G. and Jensen, J. S. (1997). Kinematic and electromyographic analysis of steady pectoral fin swimming in the surfperches. *J. Exp. Biol.* **200**, 1709–1723.

Drucker, E. G. and Lauder, G. V. (1999). Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J. Exp. Biol.* **202**, 2393–2412.

Drucker, E. G. and Lauder, G. V. (2000). A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. *J. Exp. Biol.* **203**, 2379–2393.

Ernst, C. H. and Barbour, R. W. (1989). *Turtles of the World*. Washington, London: Smithsonian Institution Press.

Feldkamp, S. D. (1987). Foreflipper propulsion in the California sea lion, *Zalophus californianus*. *J. Zool., Lond.* **212**, 43–57.

Fish, F. E. (1996). Transitions from drag-based to lift-based propulsion in mammalian swimming. *Am. Zool.* **36**, 628–641.

Gibbons, J. W. (1970). Terrestrial activity and population dynamics of aquatic turtles. *Am. Midl. Nat.* **83**, 404–414.

Plummer, M. V., Mills, N. E. and Allen, S. L. (1997). Activity, habitat and movement patterns of softshell turtles (*Trionyx spiniferus*) in a small stream. *Chelon. Conserv. Biol.* **2**, 514–520.

Rayner, J. M. V. (1985). Vorticity and propulsion mechanics in swimming and flying vertebrates. In *Principles of Construction in Fossil and Recent Reptiles* (ed. J. Reiß and E. Frey), pp. 89–119. Stuttgart: Universität Stuttgart/Universität Tübingen.

Renous, S. and Bels, V. (1993). Comparison between aquatic and terrestrial locomotions of the leatherback sea turtle (*Dermochelys coriacea*). *J. Zool., Lond.* **230**, 357–378.

Shaffer, H. B., Meylan, P. and McKnight, M. L. (1997). Tests of turtle phylogeny: molecular, morphological and paleontological approaches. *Syst. Biol.* **46**, 235–268.

Sokal, R. R. and Rohlf, F. J. (1995). *Biometry*, third edition. New York: W. H. Freeman & Company.

Vogel, S. (1994). *Life in Moving Fluids.* Princeton, NJ: Princeton University Press.

Walker, J. A. (1998). Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerically different algorithms. *J. Exp. Biol.* **201**, 981–995.

Walker, J. A. and Westneat, M. W. (1997). Labriform propulsion in fishes: kinematics of flapping aquatic flight in the bird wrasse *Gomphosus varius* (Labridae). *J. Exp. Biol.* **200**, 1549–1569.

Walker, J. A. and Westneat, M. W. (2000). Mechanical performance of aquatic rowing and flying. *Proc. R. Soc. Lond. B* **267**, 1875–1881.

Walker, W. F., Jr (1971). 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*, vol. 4, *Morphology D* (ed. C. Gans and T. S. Parsons), pp. 1–100. London: Academic Press.

Webb, P. W. (1988). Simple physical principles and vertebrate aquatic locomotion. *Am. Zool.* **28**, 709–725.

Webb, P. W. and Blake, R. W. (1985). Swimming. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. L. Liem and D. B. Wake), pp. 110–128. Cambridge, MA: The Belknap Press.

Webb, R. G. (1962). North American recent soft-shelled turtles (Family Trionychidae). *Univ. Kansas Publ. Mus. Nat. Hist.* **13**, 431–611.

Westneat, M. W. (1995). Functional morphology of flight in fishes: kinematics, EMG and thrust of labriform locomotion. *Am. Zool.* **35**, 3A.

Wyneken, J. (1997). Sea turtle locomotion: Mechanisms, behavior and energetics. In *The Biology of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 165–198. Boca Raton, FL: CRC Press.

Zug, G. R. (1971). Buoyancy, locomotion, morphology of the pelvic girdle and hind limb and systematics of cryptodiran turtles. *Misc. Publ. Mus. Zool. Univ. Michigan* **142**, 1–98.