Evolution of bite performance in turtles

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Abstract

Among vertebrates, there is often a tight correlation between variation in cranial morphology and diet. Yet, the relationships between morphological characteristics and feeding performance are usually only inferred from biomechanical models. Here, we empirically test whether differences in body dimensions are correlated with bite performance and trophic ecology for a large number of turtle species. A comparative phylogenetic analysis indicates that turtles with carnivorous and durophagous diets are capable of biting harder than species with other diets. This pattern is consistent with the hypothesis that an evolutionary increase in bite performance has allowed certain turtles to consume harder or larger prey. Changes in carapace length tend to be associated with proportional changes in linear head dimensions (no shape change). However, maximum bite force tends to change in proportion to length cubed, rather than length squared, implying that changes in body size are associated with changes in the design of the jaw apparatus. After the effect of body size is accounted for in the analysis, only changes in head height are significantly correlated with changes in bite force. Additionally, our data suggest that the ability to bite hard might trade off with the ability to feed on fast agile prey. Rather than being the direct result of conflicting biomechanical or physiological demands for force and speed, this trade-off may be mediated through the constraints imposed by the need to retract the head into the shell for defensive purposes.

Introduction

It is generally believed that the design of an organism reflects patterns of resource utilization (e.g. Osenberg & Mittelbach, 1989; Perez-Barberia & Gordon, 1999), and that the relations between design and ecology are shaped by the process of natural selection (Losos, 1990; Wainwright, 1991; Irschick et al., 1997). Trophic resource utilization patterns are often linked to differences in design between potential competitors (Kiltie, 1982; Wheelwright, 1985; Dumont, 1999). Simple performance measures such as gape width (enabling animals with larger gapes to eat larger prey; Wheelwright, 1985; Shine,

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1987, 1991; Arnold, 1993) are often correlated with diet. Other potentially important performance measures such as bite force have rarely been measured (but see Herrel et al., 1999, 2001a,b). Improving bite performance may also allow animals to expand their diet (Rieppel & Labhardt, 1979; Pregill, 1984; Wainwright, 1991), or specialize in a largely competitor free niche (Dalrymple, 1979; Freeman, 1979; Greene, 1982).

Despite its putative advantages, an evolutionary increase in bite performance may come at a cost. Biomechanical theory suggests that trade offs are expected between the ability to generate force and speed at both the muscular and musculo-skeletal levels. Whereas parallel-fibred muscle is thought to increase speed, an increase in force is usually achieved by increasing the pennation of a muscle (Gans et al., 1985). Also the biomechanics of force transmission dictate conflicting demands between force and speed. Whereas speed is optimized through long

outlevers, force generation is maximized at short outlever lengths (e.g. Schenk & Wainwright, 2001). This implies that the evolution towards increased bite capacity may come at the expense of jaw closing speed, and potentially also on the ability of an organism to feed on fast elusive prey. Evolutionary trade offs may thus constrain the adaptation of individual traits, and ultimately even the adaptive radiation of a group (e.g. Vanhooydonck *et al.*, 2001; Van Damme *et al.*, 2002).

An increase in bite force can be achieved in many, often mutually nonexclusive, ways. Not only will an increase in overall body or head dimensions increase bite force, also changes in head shape may have an important effect on bite performance. Indeed, evolutionary modifications of the lever arms of a given jaw system could increase bite force considerably. However, modifications of lever arms to optimize force will result in a negative effect on closing speed (Westneat, 1995; Schenk & Wainwright, 2001). Assuming isometry, scaling relationships also dictate that force scales with length to the second power, so an increase in linear skull dimensions such as width and height will have a major effect on bite force (Hill, 1950). Also the intrinsic muscular properties such as total jaw adductor mass (Wainwright, 1996), or muscle architecture (e.g. the degree and angle of pennation, fibre length; Gans *et al.*, 1985; Gans & De Vree, 1987) and even the muscle activation pattern (Gans & De Vree, 1986) can affect bite performance. As it is often hard, or even impossible to measure all these design features simultaneously, the incorporation of *in vivo* measurements of bite perfomance can be a key factor in our understanding of the relations between diet and the design of the feeding apparatus.

Turtles are an interesting group to investigate bite performance in, as they are potentially constrained in the development of their feeding apparatus by the need to fit their heads inbetween the margins of the shell. Whereas terrestrial turtles are thought to be good biters (having short snouts and high skulls; see King, 1996), aquatic turtles (especially pleurodirans) generally have flatter skulls and shells that are thought to reduce the hydro-dynamic drag during locomotion and during the fast head extensions associated with prey capture (Pritchard, 1984; Van Damme & Aerts, 1997). The lack of temporal fenestra and correlated shift of the origin of the jaw adductors posteriad will also likely reduce the mechanical advantage of the jaw closers in turtles. Although cryptodires tend to have fairly high skulls compared with pleurodires, some of the specialized aquatic feeders that rely heavily on suction feeding (e.g., *Apalone*, *Trionyx*; Pritchard, 1984) have flat skulls. Based on biomechanical reasoning, these aquatic turtles are thus not expected to be able to bite hard compared with their terrestrial counterparts, suggesting a potential trade off between biting and the ability to capture elusive prey.

Other genera of aquatic turtles are know to be proficient 'biters' that will use their jaws to crush hard prey, or that will bite in defence. Snapping turtles (*Chelydra serpentina*), for example, are typically omnivorous (eating mostly fish, but also carrion, plants, etc.), but will use their jaws when confronted with predators. Others, such as some of the South American kinosternid turtle species (mud and musk turtles) are known for their tendency to feed on molluscs and even other turtles (Vogt & Guzman, 1988). Obviously, such animals will have to overcome the constraints on head shape, which may have an effect on their ability to feed on elusive prey, and may negatively affect their ability to withdraw the head in the shell.

Here, we test whether an evolutionary increase in bite performance is correlated with an evolutionary change in head dimensions by correlating *in vivo* bite forces with morphometric data for a large sample of turtles. To do so, we test for 28 species of turtles whether coevolutionary patterns of head shape and bite performance exist. Based on biomechanical models, we predict that evolutionary increases in bite force will be correlated with either (1) changes in overall size, (2) changes in overall head size, (3) changes in head shape or (4) changes in the design of the jaw adductors. In addition, we test whether evolutionary relationships between bite performance and trophic ecology can be demonstrated. Based on biomechanical theory, we predict that species specializing on elusive prey (which have flat heads; see Pritchard, 1984) bite less hard than species that eat hard prey.

Materials and methods

Animals

The *C. serpentina* used in this study were trapped in the vicinity of Amherst, Massachusetts (Commonwealth of Massachusetts, Division of Fisheries and Wildlife Scientific Collecting Permit no. 115.00SCRA to A.R) or obtained from commercial dealers. All other species used were obtained from zoos or commercial dealers (see Tables 1 and 2 for a list of species). Our data set includes 28 species representing approximately 70% of the known families of turtles and approximately 25% of all known genera.

Bite forces

We measured *in vivo* bite forces using isometric Kistler force transducers (types 9203, range ±500 N and 9311B, range ±5000 N; Kistler Inc., Winterthur, Switzerland), mounted on purpose-built holders and connected to a Kistler charge amplifier (type 5058A5, Kistler Inc.). Biting causes the upper plate to pivot around the fulcrum, and thus pull is exerted on the transducer. For small animals the set-up as described in Herrel *et al.* (1999, 2001a, b) was used; for larger animals a modified set-up mounted on a 1-m long handle was used. When handling the turtles, they usually assumed a characteristic threat response (opening of the jaws) and tried to bite the

Table 1 Summary of the morphometric and bite force data.

Species	n	Carapace length (mm)	Carapace width (mm)	Mass (g)	Head length (mm)	Head width (mm)	Head height (mm)	Lower jaw length (mm)	Bite force (N)
Amyda cartilaginea	2	185.77 ± 78.53	147.35 ± 61.03	937.40 ± 1043.13	46.62 ± 16.36	32.05 ± 13.11	27.20 ± 14.85	27.67 ± 8.80	210.43 ± 241.55
Apalone ferox	5	111.19 ± 80.45	88.39 ± 57.26	114.11 ± 167.72	29.76 ± 12.36	15.85 ± 5.22	11.90 ± 3.90	18.65 ± 7.61	41.50 ± 64.43
A. spinifera	3	141.41 ± 4.34	121.96 ± 4.09	259.74 ± 23.76	40.47 ± 3.31	21.18 ± 0.98	14.75 ± 0.31	26.42 ± 2.37	12.21 ± 3.42
Callagur borneoensis	2	387.35 ± 62.86	273.05 ± 26.94	10065.00 ± 5812.42	87.05 ± 11.20	52.45 ± 5.39	45.85 ± 6.53	63.64 ± 15.29	146.95 ± 83.00
Chelus fimbriatus	3	140.40 ± 19.77	99.71 ± 15.03	404.70 ± 192.45	38.31 ± 3.17	45.91 ± 5.13	20.61 ± 3.24	31.13 ± 3.72	5.13 ± 1.73
Chelydra serpentina	11	197.30 ± 124.84	167.55 ± 103.54	3940.32 ± 5805.46	65.45 ± 32.15	51.26 ± 30.76	34.80 ± 19.11	46.80 ± 24.64	208.98 ± 226.10
Chinemys reevesii	1	96.66	65.69	137.35	20.47	18.01	13.17	20.07	19.96
Dogania subplana	3	136.34 ± 53.50	108.71 ± 39.25	328.20 ± 352.56	46.48 ± 14.76	30.52 ± 9.54	20.53 ± 7.54	33.18 ± 5.99	37.30 ± 11.27
Elseya novaeguineae	2	158.61 ± 72.68	126.98 ± 54.77	742.69 ± 871.60	40.16 ± 16.42	27.56 ± 11.28	21.39 ± 11.23	27.39 ± 12.63	35.11 ± 36.16
Emydura subglobosa	1	101.38	82.57	118.70	25.52	17.23	13.07	17.73	1.91
Geoemyda spengleri	2	96.01 ± 2.11	68.32 ± 2.60	125.92 ± 11.19	26.07 ± 0.59	15.54 ± 0.30	14.16 ± 1.02	20.05 ± 1.00	11.59 ± 0.21
Heosemys grandis	1	266.70	203.20	2866.00	65.67	42	31.40	35.06	102.35
Kinosternon scorpioides	2	109.70 ± 12.73	73.73 ± 4.39	214.26 ± 68.96	30.81 ± 0.76	22.41 ± 3.38	15.70 ± 1.76	21.83 ± 4.94	38.00 ± 16.77
K. subrubrum	1	88.57	59.34	133.05	32.16	21.40	16.92	21.77	35.21
Macrochelys temminckii	5	139.54 ± 89.18	115.45 ± 68.17	388.21 ± 542.62	57.16 ± 34.13	46.82 ± 27.87	35.80 ± 23.08	47.80 ± 27.30	158.00 ± 176.51
Orlitia borneensis	1	304.80	197.74	3818.00	81.62	47.54	48.19	39.21	117.38
Pelodiscus sinensis	2	140.59 ± 32.00	122.54 ± 31.42	304.50 ± 135.06	40.02 ± 5.29	27.29 ± 3.23	19.47 ± 1.33	34.19 ± 5.37	59.44 ± 28.02
Pelomedusa subrufa	4	114.06 ± 9.49	86.65 ± 6.52	223.53 ± 77.55	30.41 ± 2.28	25.46 ± 2.05	14.86 ± 2.39	22.39 ± 2.67	8.37 ± 2.26
Phrynops nasutus	1	284.00	210.00	1752.00	91.87	75.65	46.25	69.27	432.40
Platemys platycephala	2	136.02 ± 13.38	94.83 ± 9.17	245.48 ± 39.53	32.33 ± 2.16	21.78 ± 1.14	12.40 ± 0.78	18.68 ± 1.48	7.41 ± 0.73
Platysternon megacephalum	6	93.09 ± 3.24	73.78 ± 2.17	136.97 ± 15.10	34.41 ± 1.33	29.54 ± 1.06	21.02 ± 0.34	29.65 ± 2.24	41.58 ± 6.71
Staurotypus salvinii	3	170.96 ± 18.41	111.86 ± 10.68	743.33 ± 211.02	64.32 ± 12.86	44.15 ± 6.91	33.14 ± 5.81	41.80 ± 8.17	251.59 ± 123.40
S. triporcatus	9	122.72 ± 97.35	79.40 ± 44.39	600.34 ± 1200.06	48.43 ± 33.86	30.87 ± 18.95	22.73 ± 12.93	30.24 ± 19.09	139.14 ± 145.70
Sternotherus carinatus	2	122.67 ± 1.39	84.07 ± 1.88	276.45 ± 25.53	40.96 ± 1.75	28.79 ± 0.63	23.24 ± 0.12	28.31 ± 0.59	108.55 ± 56.04
S. odoratus	3	88.71 ± 21.74	64.06 ± 16.32	320.57 ± 250.20	29.44 ± 8.59	20.17 ± 4.03	15.71 ± 2.67	19.44 ± 3.86	30.72 ± 19.20
Terrapene carolina	3	117.74 ± 8.05	91.26 ± 4.77	361.38 ± 114.81	25.76 ± 2.86	18.97 ± 2.11	16.69 ± 1.37	21.89 ± 1.79	24.94 ± 7.62
Testudo horsfieldii	1	112.88	100.15	373.12	19.89	20.19	17.41	21.82	18.20
Trachemys scripta	33	88.77 ± 53.26	74.48 ± 37.06	235.31 ± 411.03	25.20 ± 11.50	16.43 ± 6.88	13.11 ± 5.14	17.78 ± 8.42	14.59 ± 18.76

Species	Classification	References
Elseya novaeguineae	Insectivorous	Pritchard (1979)
Emydura subglobosa	Insectivorous	Pritchard (1979)
Chelus fimbriatus	Piscivorous	Fachin Teran *et al.* (1995)
Phrynops nasutus	Biter (durophagous)	Fachin Teran *et al.* (1995)
Platemys platycephala	Insectivorous	Fretey (1977); Pritchard (1984)
Pelomedusa subrufa	Omnivorous	Branch (1998)
Apalone ferox	Insectivorous	Dalrymple (1977)
A. spinifera	Insectivorous	Babcock (1938); Lagler (1943); Pritchard (1979)
Pelodiscus sinensis	Piscivorous	Pritchard (1979)
Dogania subplana	Biter (carnivorous)	Manthey & Grossmann (1997)
Amyda cartilaginea	Biter (carnivorous)	Manthey & Grossmann (1997)
Chelydra serpentina	Biter (carnivore, omnivore)	Lagler (1943); Budhabhatti & Moll (1990); Alvarez del Toro (1982); Ernst *et al.* (1994)
Macrochelys temminckii	Biter (carnivorous)	Pritchard (1979)
Platysternon megacephalum	Biter (durophagous ⁄ carnivorous)	Pope (1935); Smith (1931); Ernst & Barbour (1989)
Orlitia borneensis	Omnivorous	Pritchard (1979)
Callagur borneoensis	Herbivorous	Manthey & Grossmann (1997)
Chinemys reevesii	Omnivorous	Pritchard (1979)
Heosemys grandis	Herbivorous	Pritchard (1979)
Geoemyda spengleri	Insectivorous	Manthey & Grossmann (1997)
Testudo horsfieldii	Herbivorous	Pritchard (1979)
Trachemys scripta	Omnivorous	Clark & Gibbons (1969)
Terrapene carolina	Insectivorous	Pritchard (1979); Ernst *et al.* (1994)
Kinosternon subrubrum	Biter (durophagous)	Mahmoud (1968)
K. scorpioides	Omnivorous	Vanzolini (1980); Acuna *et al.* (1983); Monge-Najera & Moreva-Brenes (1987)
Sternotherus carinatus	Biter (durophagous)	Mahmoud (1968)
S. odouratus	Biter (durophagous)	Mahmoud (1968); Ernst *et al.* (1994); Lagler (1943)
Staurotypus salvinii	Biter (durophagous)	Pritchard (1979); Alvarez del Toro (1982)
S. triporcatus	Biter (durophagous)	Pritchard (1979); Alvarez del Toro (1982)

person handling them. Less responsive species were stimulated to bite with gentle taps at the sides of their jaws. When the free end of the holder was placed in between the jaws of the animal, prolonged and repeated biting resulted. The place of application of bite forces was standardized by mounting acrylic stops (small animals) or metal shields onto the free end of the holder. Gape angle was standardized by moving the bite plates away from each other for larger animals. Measurements were repeated five times for each animal with an intertrial interval of at least 15 min. The maximal value obtained during such a recording session, was considered to be the maximal bite force for that animal.

Morphometrics

Immediately after the performance trials, the following morphological measurements were taken from each animal: mass, carapace length (CL), carapace width (CW), head length (HL), lower jaw length (LJL), head width (HW) and head height (HH). Head length was measured from the anterior end of the premaxillary to the posterior edge of the parietal crest, lower jaw length from the anterior end of the dentary bone to the posterior edge of the retroarticular process. Head width was measured at the widest part of the skull and includes potential bulging of the jaw muscles, and head height was measured at the highest part of the skull just posterior to the orbita. For small animals, measurements were taken using digital callipers; the largest and more aggressive turtles were filmed in lateral and dorsal views using a digital camera. An object of known size (1 m ruler) was kept in the field of view for scaling purposes. Lateral and dorsal images of the animals were imported in the public domain NIH-image program (version 1.61; developed at the US National Institutes of Health and available on the internet at *http://rsb.info.gov/nih-image/*) and used to estimate head dimensions.

Analysis

As species share a part of their evolutionary history, they cannot be considered statistically independent (Felsenstein, 1985, 1988; Harvey & Pagel, 1991). All analyses were thus performed taking into account the phylogenetic relationships between the species. To do so, a tree was constructed depicting the relationships between the species in our analysis by combining trees from the literature (Fig. 1). This tree should be considered as an estimate of the relationships between species only. As few data are available for the divergence times between species, we set all branch lengths to unity (see Martins & Garland, 1991; Walton, 1993; Irschick *et al.*, 1996; Diaz-Uriarte & Garland, 1998) and inspected diagnostic graphs and statistics in the PDTREE program (Garland

et al., 1999) to verify that these were indeed adequate for all traits. Where branch lengths set to unity were not appropriate they were transformed using Grafen or Pagel transformations (Garland *et al.*, 1999). Species mean values were calculated, and $\log_{10}$ transformed before analysis. Results of univariate tests were corrected for multiple testing using a Bonferroni correction (Hochberg, 1988).

To examine the relationships between head shape and bite force, independent contrasts were calculated using the PDTREE program (Garland *et al.*, 1993). Subsequently, the standardized contrasts of all variables were regressed against the standardized contrast of carapace length (forced through the origin) for all species and residuals were calculated. Next, a multiple regression analysis was used to examine associations among the residual standardized
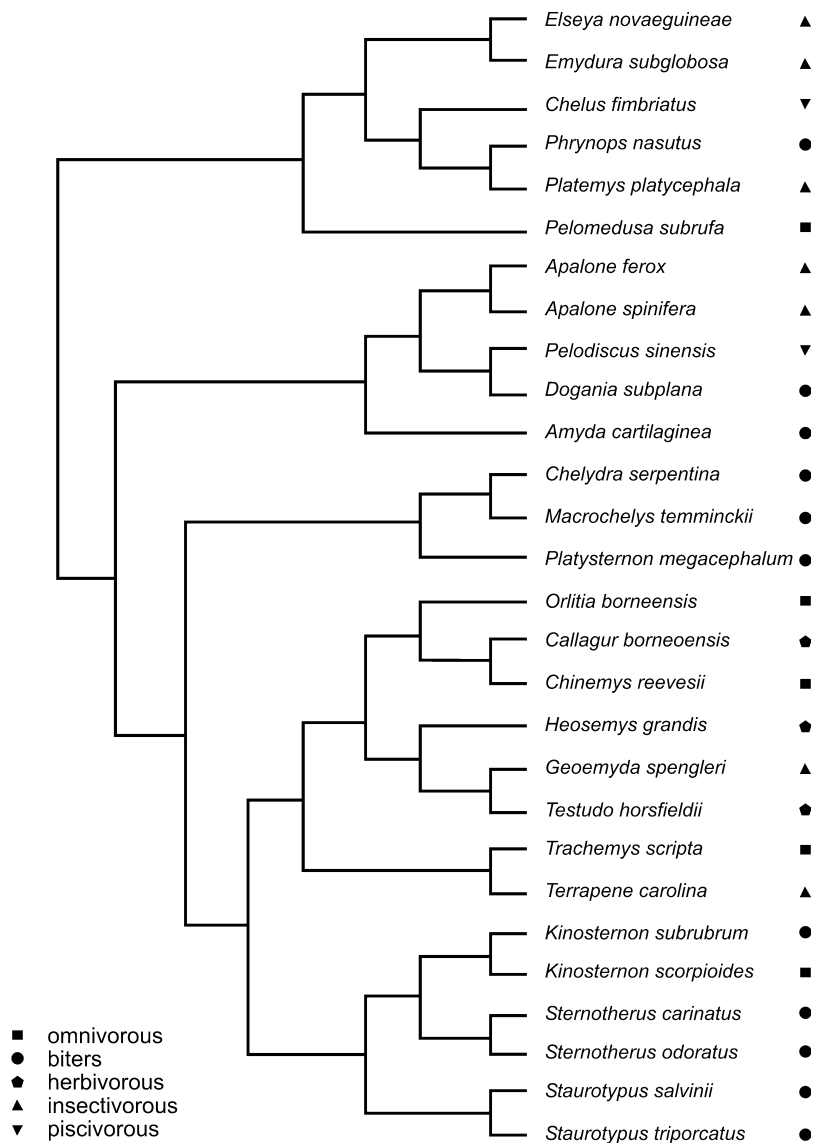

Fig. 1 Phylogeny showing a 'current best estimate' of the relationships between the species used in this paper based on Hirayama (1984) and Sites *et al.* (1984) (Batagurines); Iverson (1998) (Kinosternids); Meylan (1987) (Trionychids); Seddon *et al.* (1997) (Chelids). Interfamilial realtionships based on Shaffer *et al.* (1997). Dietary classification of the species (see Table 2) is indicated by the symbols (squares: omnivores; circles: biters; diamonds: herbivores; triangles: insectivores; inverted triangles: piscivores).

■ omnivorous
● biters
⬟ herbivorous
▲ insectivorous
▼ piscivorous

contrast of bite force and the residual standardized contrasts of the head shape variables (also forced through the origin; see Garland *et al.*, 1992).

To assess scaling relationships across species, the independent standardized contrasts of head length, head width, head height and bite force were regressed against the independent standardized contrasts of carapace length using reduced major axis regression techniques (forced through the origin). The slopes of these regressions were then compared with the theoretically predicted slopes for geometrically growing systems.

To test whether species that differ in trophic ecology also differ in head shape and bite force, simulation analyses were performed (PDSIMUL and PDANOVA programs; Garland *et al.*, 1993). As overall size affects head shape and bite force, we used the residuals of all morphometric variables and bite force ($\log_{10}$ transformed species averages) against carapace length ($\log_{10}$ transformed species averages) as input for the analyses. In the PDSIMUL program the Brownian motion model for evolutionary change was used. We ran 1000 unbounded simulations to create the empirical null distribution against which the *F*-value from the original data could be compared. In the PDANOVA program diet was entered as factor and the residual morphometric and bite force data as independent variables. We considered differences among species mean values significant if the *F*-value was higher than the *F*-95 value of the empirical *F*-distribution.

Animals were assigned to one of five diet categories based on data gathered from the literature (Table 2). Animals were classified as 'biters' if they included considerable amounts of molluscs or other hard food items in their diet (durophagous), or included large vertebrates into their diet (carnivorous). Piscivores were those animals specializing on fish as food items, and typically using suction feeding rather than biting to capture prey. Insectivores were those animals typically eating insects, other small arthropods and invertebrates such as worms. Herbivores were those animals that were reported to eat predominantly plants and omnivores were those species including both plants and insects or small arthropods into their diet (Table 2).

Results

Across the species studied here, average body size varied greatly (e.g. mass varied from just over 100 g to over 10 kg). Accordingly, average head size differed greatly as well (e.g. average head lengths varied from 20 to 90 mm). Average bite forces varied from 5 N to over 400 N for some of the largest species (Table 1). Reduced major axis regression analysis indicated strong correlations between the standardized contrasts of head and body size (Table 3). Interspecific scaling of head and body showed no deviations from geometric similarity (Table 3). Standardized contrasts of bite force, on the other hand, increased positively allometric with the

Table 3 Allometries of morphometric data and bite force against carapace length.

	r	Slope	Confidence limits	
Interspecific scaling (*n* = 28)				
Stand. contrast carapace width	0.98	1.01	0.94	1.09
Stand. contrast body mass	0.94	3.17	2.72	3.62
Stand. contrast head length	0.93	1.09	0.92	1.26
Stand. contrast head width	0.88	1.05	0.85	1.26
Stand. contrast head height	0.90	1.10	0.90	1.29
Stand. contrast lower jaw length	0.85	0.99	0.77	1.20
Stand. contrast bite force	0.75	3.33	2.42	4.24
Scaling of stand. contrast of bite force to standardized contrast of head length	0.77	3.06	2.25	3.86

Reduced major axis regression equations of standardized contrasts of carapace length vs. the standardized contrasts of morphometric and bite force data. Note that in these analysis the regression is forced through the origin causing the intercepts to be 0 by default.

standardized contrast of carapace length (slope 3.3) and head length (slope 3.06) indicating that the evolution of a large body size and of large heads is associated with a disproportionate increase in bite force (Table 3).

A multiple regression analysis (backward) performed on the residual standardized contrasts of the head size variables against the residual standardized contrast of bite force, retained a significant model with the residual contrast of head height as only variable ($r = 0.56$, $F_{1,26} = 11.55$, $P < 0.05$). Evolutionary increases in bite force in turtles thus seem to be associated with an evolutionary increase in head height (Fig. 2).

Simulation analysis indicated significant differences between head shape variables and bite force among dietary categories (all $P < 0.05$ after Bonferroni correction; see Tables 4 and 5). However, species from different dietary groups did not differ in carapace length, residual carapace width and residual body mass (all $P > 0.05$). *Post hoc* tests indicated that biters had a greater residual head length than the other species (Table 5). Additionally, piscivores had significantly longer heads than herbivorous turtles. Head width and lower jaw length were similar in biters and piscivores which both had wider heads and longer lower jaws than species with other diets. Residual head height, on the other hand was largest in biters, and differed significantly from that for all other dietary categories. Biters also had the highest residual bite forces and were biting significantly harder than species from all other dietary categories (piscivores having the lowest relative bite forces; Table 5).

Discussion

Relationships between morphology and bite performance?

Biomechanical theory predicts that an evolutionary increase in bite force can be achieved in several,
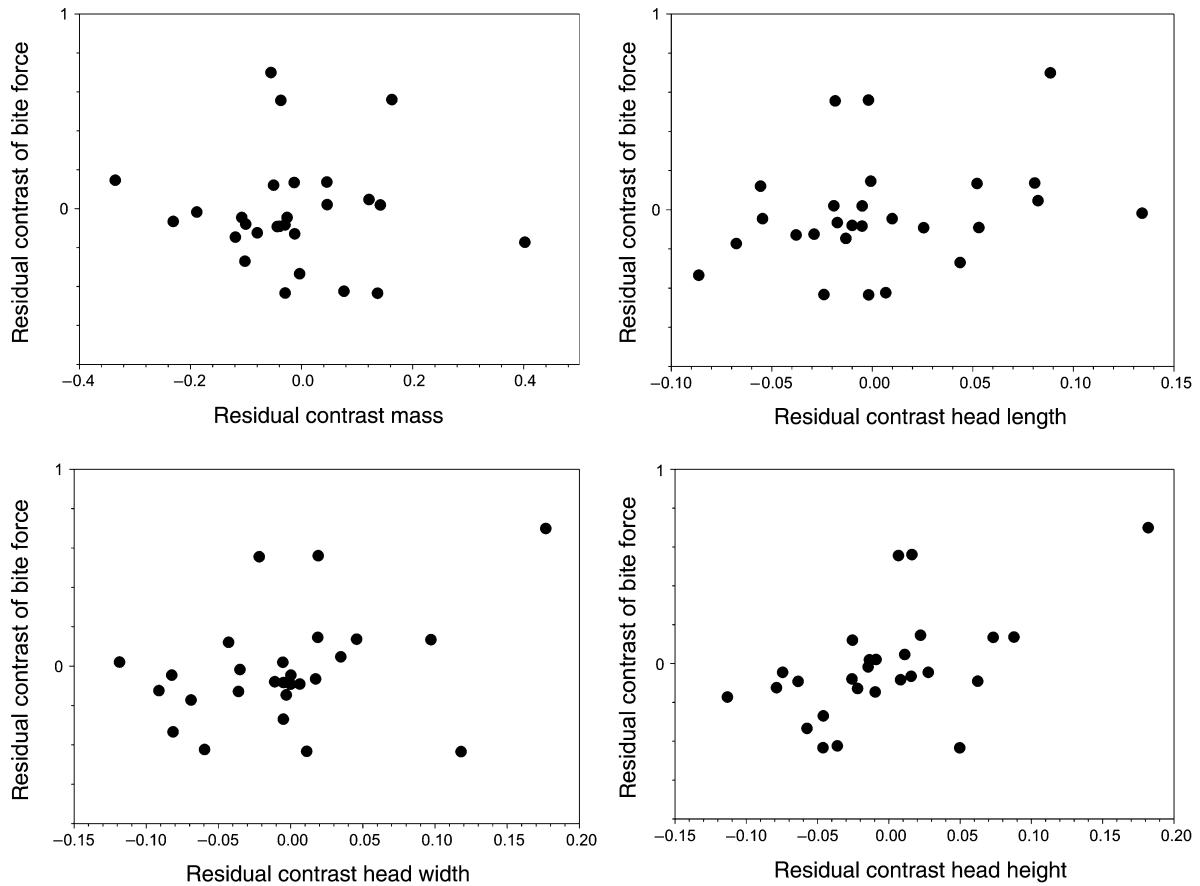
Fig. 2 Results of phylogenetic analysis of the bite force and morphometric data. Except for a significant relation between the standardized residual contrast of head head height and the standardized residual contrast of bite force ($r = 0.56$, $F_{1,26} = 11.55$, $P < 0.05$), no significant correlations between the standardized residual contrasts of body or head measures and the standard residual contrasts of bite force were observed.

Table 4 Interspecific differences in head shape and bite performance for different dietary groups.

Variable	F_{95}	P	F_{phyl}	P_{phyl}
Log_{10} carapace length	1.52	NS	4.61	NS
Residual carapace width	0.89	NS	4.43	NS
Residual body mass	1.60	NS	4.48	NS
Residual head length	12.32	<0.01	4.51	<0.001**
Residual head width	12.77	<0.01	4.29	<0.001**
Residual head height	10.56	<0.01	4.23	<0.001**
Residual lower jaw length	7.10	<0.01	4.04	~0.008*
Residual bite force	8.37	<0.01	3.96	~0.004*

Variables are significantly different if the F_{95} values (traditional ANOVA) are higher than the F_{phyl} values (based on the results of the simulation analysis). *Significant after Bonferroni correction at the $\alpha = 0.05$ level; **significant after sequential Boneferroni correction at the $\alpha = 0.01$ level.

nonmutually exclusive ways. Whereas the simplest way to increase bite force is to simply get bigger, changes in head size, head shape or the design of the jaw apparatus could also result in changes in bite performance. The independent contrast analysis allowed us to account for variation because of relatedness among the species

included in the study, and to determine if changes in size were associated with changes in bite performance. The multiple regression analysis of the residual standardized contrasts regressed against the standardized contrasts of carapace length, allowed us to determine if changes in linear dimensions of the head were correlated with

Variable	Biters	Omnivores	Herbivores	Insectivores	Piscivores
Log_{10} carapace length	2.143	2.103	2.356	2.084	2.148
Residual carapace width	−0.007	−0.022	0.022	0.013	0.019
Residual body mass	0.063	0.020	0.115	−0.130	−0.112
Residual head length	0.084	−0.040	−0.113	−0.052	−0.009
Residual head width	0.092	−0.033	−0.086	−0.111	0.096
Residual head height	0.091	−0.025	−0.045	−0.100	−0.021
Residual lower jaw length	0.077	−0.053	−0.053	−0.078	0.059
Residual bite force	0.418	−0.121	−0.220	−0.368	−0.376

Table 5 Average residual morphometric data and bite forces for the different dietary groups.

Post hoc tests indicated that differences in carapace length, residual carapace width and residual body mass were not different between groups. Biters had significantly longer heads than all other groups. Piscivores also had longer heads than herbivores. Residual head width and residual lower jaw length were similar in biters and piscivores, but larger than for the other groups. Both residual head height and residual bite force were greater in biters compared with all other groups.

changes in bite force independently from changes in body size.

The independent contrast analysis revealed that evolutionary changes in body size are correlated with changes in maximum bite force and implies that changes in body size are correlated with changes in the design of the jaw apparatus. The interspecific scaling analyses showed that evolutionary changes in bite force were linked with changes in body size (as indicated by carapace length) thus supporting the initial prediction that 'just getting bigger' is a potentially important evolutionary strategy to increase bite performance in turtles. However, because all the head measures increased in proportion to one another (i.e. geometric similarity), the changes in bite force associated with the changes in body size are apparently not mediated by changes in head shape. Given that changes in size were not correlated with changes in head shape, and that muscle force is proportional to the physiological cross-sectional area of the muscle, we initially predicted that bite force should change in proportion to carapace length to the second power (Hill, 1950). However, across all contrasts examined, bite force tended to change in proportion to length to the third power (Table 3). Presumably changes in the architecture of the muscle, muscle physiology, or in the biomechanics of the system lie on the basis of this unexpected result. Biomechanical studies examining the structure and function of the jaw adductor muscles in turtles might be especially insightful in elucidating this relationship.

The multiple regression analysis of the residuals of the contrasts (removing the effect of changes in body size) revealed significant variation in head shape that is correlated with changes in bite force. Among the dimensions we measured, only evolutionary changes in head height were significantly correlated with evolutionary changes in bite force. However, only about 50% of the variation in bite force could be explained by differences in head height, indicating that changes in other factors in addition to head shape affect differences in bite force. Whereas larger heads (i.e. wider, higher and longer) likely provide space for more muscle, intrinsic differences in muscle architecture (e.g. degree of pennation, lever arm mechanics) might also affect bite performance (Gans *et al.*, 1985; Gans & De Vree, 1987; Wainwright, 1987; Westneat, 1995). Moreover, our measures of head shape might not have adequately described the space available for muscle, such that simple external head measures might not always be good indicators of the amount of the muscle mass present. Dalrymple (1977), for example, showed that muscle mass increased with a greater slope than predicted relative to basicranial length in *Apalone* (*Trionyx*) *ferox*. The combined results of the two analyses imply that evolutionary increases in bite performance in turtles have been mediated through increases in overall animal size, increases in relative head height and changes in the design of the jaw apparatus.

Ecological relevance of bite performance in turtles

The data from the present study indicate that evolutionary changes in head height are correlated with changes in maximum bite force in turtles. However, one can also ask whether, and how, size-related differences in bite performance have an impact on the ecology of the species considered. As mentioned in the introduction, the ability to bite hard should be relevant in cases where turtles consume hard food items. Turtles consuming molluscs, or those eating large vertebrates or even other turtles (as has been observed for some species of *Staurotypus* and some populations of *Macroclemys*) likely benefit from an increased bite capacity. Prey that would otherwise be too big to eat (large vertebrates), or energetically unfavourable (e.g. molluscs), will then become attractive food sources for which competition is likely to be small. Increased bite performance can thus free turtles from the limitations typically imposed on gape-limited predators (Wheelwright, 1985; Shine, 1987, 1991). The data from this study indicate that animals specializing in hard or

large prey do indeed bite harder for a given body size than more generalized species. An evolutionary shift in trophic niche that results in the inclusion of large or hard prey into the diet of turtles thus seems to be accompanied by an evolutionary increase in bite performance. Moreover, our data show that this increase in relative bite performance is accompanied by an evolutionary increase in head height (relative to carapace length).

Given that an evolutionary increase in bite force is coupled to an evolutionary increase in head height, we suggest that exceptional bite performance may come at the expense of the ability to retract the head into the shell for self defence. Although the exact reason why species with high heads bite harder remains speculative at this point, we suggest that having a higher head likely enables a more perpendicular orientation of the jaw adductors relative to the lower jaw (see Fig. 3). Additionally, higher heads might provide for an enlarged attachment area of the jaw closers. One rather obvious drawback to having relatively tall heads is that species that have them, often cannot fully withdraw their heads into their shells (e.g. *Platysternon* and *Macroclemys*).

In contrast, our analyses suggests that the evolutionary transition to specialization for feeding on fast, elusive prey tends to produce no increase in head height, but does produce an increase in head volume by increasing head width and head length. Thus, suction feeders such as *Chelus* or *Chelodina*, are characterized by heads that are dorsoventrally flattened in shape relative to other turtles.

Previous workers have speculated that the flattened head shape of *Chelus* and *Chelodina* is an adaptation to reduce hydrodynamic drag that allows these species to extend the head–neck system at very high speeds (Pritchard, 1984; Van Damme & Aerts, 1997; Lemell *et al.*, 2002). However, there is no *a priori* reason to believe that selection for hydrodynamic efficiency would produce a flattened head shape. A reduction in drag could evolve by either reducing the frontal area of the head and reducing pressure drag, or by streamlining the head and reducing friction drag. However, for a given head volume, increasing head width at the expense of height would never reduce pressure drag as it will not reduce the area presented to the fluid when the head is moving forward. Only increasing head length, at the expense of either height or width, can reduce drag and increase hydrodynamic efficiency. Thus, the flattened heads of piscivorous turtles do not appear to bestow greater hydrodynamic efficiency than the head shape of other turtles. Indeed, our results suggest that the emergence of piscivory is associated with an *increase* in the frontal area of the head that is produced by increasing head width and that the emergence of piscivory is thus most likely associated with a decrease in the hydrodynamic efficiency of head movements.

The emergence of dorsoventrally flattened heads can be explained by selection for both an increased gape size (for large prey) or buccal volume (for suction feeding) and the simultaneous advantages of being able to retract

Fig. 3 Schematic drawing illustrating how head height might affect bite force in turtles (not to scale). The thick black line represents the line of action of the major jaw closers. Having a higher head can clearly result in a more perpendicular orientation of the jaw adductors (i.e. larger vertical component of the adductor forces, as illustrated for *Emydura* sp.), whereas having an extremely flat head (*Chelus* sp.) will result in a more oblique orientation of the jaw adductors. Drawings based on figures by Gaffney (1977).
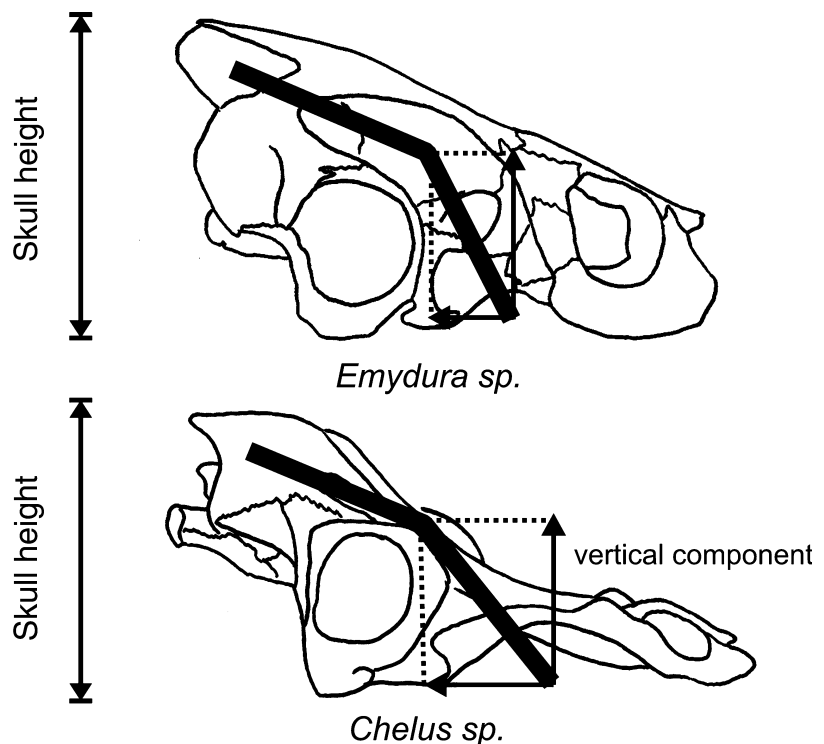
the head between the carapace and plastron. The jaws and hyoid apparatus of a turtle lie almost entirely in the frontal plane of the head and will display little, if any, increase in their range of motion as a result of increasing head height. Thus, gape area can be increased by a combination of increasing gape width or jaw length, neither of which requires an increase in head height. Similarly, buccopharngeal volume (in terms of how much water can be sucked into the mouth and throat during prey capture) will increase proportionally with changes in either head and neck width and length, but change relatively little as a result of changing head and neck height. As underwater feeding on elusive prey is largely determined by the hydrodynamics of fast forward striking and the need to expand the oropharyngeal cavity to generate suction (drawing the prey into the mouth; see Van Damme & Aerts, 1997), jaw closing speed in itself might be of minor importance. Thus, by evolving larger, but flatter heads, piscivorous turtles have increased the important aspects of head size for catching elusive prey, while retaining the ability to retract the head between the carapace and plastron. Whereas our data suggest that the ability to bite hard might trade off with the ability to feed on fast agile prey, rather than being the direct result of conflicting biomechanical or physiological demands for force and speed, this trade-off may be mediated through the constraints imposed by the need to retract the head into the shell for defensive purposes.

Is there a trade-off between suction feeding performance and bite force performance? *Chelus fimbriatus* is an accomplished suction feeder (Lemell *et al.*, 2002) but displays relative poor bite performance. *Chelydra serpentina*, on the other hand, excels in bite performance but seems to be a poor suction feeder, as indicated by limited inertial suction component into its suction mechanism (Lauder & Prendergast, 1992). However, species such as *Pelusios castaneus* seem to combine both performance features, as these turtles can effectively crush large molluscs and are apparently good suction feeders (Lemell & Weisgram, 1997). Clearly, suction performance, bite performance, jaw closing speed and neck extension velocities need to be quantified before conclusive statements about nature of potential trade-offs between bite force and suction efficiency can be made. Species such as *Chelodina*, *Chelus*, *Hydromedusa*, *Deirochelys*, *Chitra* being species specializing on fast moving, mobile prey (Chessman, 1983; Pritchard, 1984; Souza, 1995; Kennett & Tory, 1996; Van Damme & Aerts, 1997), and species such as *Staurotypus*, *Chelydra*, *Phrynops* and *Graptemys* being durophagous specialists or good biters (Lindeman, 2000; this study), might be especially interesting for such an interspecific comparison.

As sample sizes are low for several species used in the interspecific analysis, the results obtained should be verified for larger samples of turtles. However, given the strong evolutionary correlates between morphology, bite performance and trophic ecology we feel that this approach holds great promise for future studies examining ecomorphological patterns of the trophic system in turtles.

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