

# Cope's rule in cryptodiran turtles: do the body sizes of extant species reflect a trend of phyletic size increase?

D. S. MOEN

*Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY, USA*

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Cope's rule;  
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## Abstract

Cope's rule of phyletic size increase is questioned as a general pattern of body size evolution. Most studies of Cope's rule have examined trends in the paleontological record. However, neontological approaches are now possible due to the development of model-based comparative methods, as well as the availability of an abundance of phylogenetic data. I examined whether the phylogenetic distribution of body sizes in extant cryptodiran turtles is consistent with Cope's rule. To do this, I examined body size evolution in each of six major clades of cryptodiran turtles and also across the whole tree of cryptodirans ( $n = 201$  taxa). Extant cryptodiran turtles do not appear to follow Cope's rule, as no clade showed a significant phyletic body size trend. Previous analyses in other extant vertebrates have also found no evidence for phyletic size increase, which is in contrast to the paleontological data that support the rule in a number of extinct vertebrate taxa.

## Introduction

Body size is important in all aspects of an organism's biology (LaBarbera, 1986, 1989; Futuyma, 1998). Consequently, the ecology and evolution of body size has received much scientific attention, including studies of trends in body size evolution (Gould, 1997; Hone & Benton, 2005). The dominant focus has been on the tendency toward size increase in evolution, a phenomenon commonly known as Cope's rule.

The topic of Cope's rule has seen an increase in research intensity within the last 10 years. Though original support for the idea was largely based on anecdotal evidence (Jablonski, 1996), rigorous studies in recent years have supported the pattern in a variety of taxa, including Cenozoic mammals (MacFadden, 1986; Alroy, 1998; Van Valkenburgh *et al.*, 2004) and dinosaurs (Hone *et al.*, 2005) (Table 1). However, other studies have shown that within the same group of organisms, a trend of body size increase exists in some lineages but not others (Alberdi *et al.*, 1995; Jablonski, 1997; Dommergues *et al.*, 2002; Laurin, 2004; Table 1), leading to the conclusion that phyletic size increase is no more

common than other possible patterns of body size evolution (Jablonski, 1997).

Paleontological approaches have traditionally been used to document whether Cope's rule is supported by a given group. This strong emphasis on paleontological approaches to address Cope's rule has resulted in part from two potential limitations of neontological approaches: (1) a lack of adequate neontological tools to study historical evolution using data from extant species and (2) conceptual limitations in the ability of neontological data to demonstrate evolutionary trends. The earliest neontological study of body size evolution relied on an ancestral character reconstruction technique to infer the course of body size evolution (Pianka, 1995; also see Gould & MacFadden, 2004). However, such reconstruction techniques have been shown to be inadequate in the study of evolutionary trends, as they are constrained to reconstruct ancestral nodes at values that are intermediate to values in extant species (Oakley & Cunningham, 2000; Webster & Purvis, 2001). Thus, using parsimony (Swofford & Maddison, 1987; Maddison, 1991) or random-walk maximum likelihood (Schluter *et al.*, 1997) ancestral reconstruction techniques necessarily constrain one to infer that body size has become both smaller and larger than an intermediate ancestral size.

Recently, Pagel (1997, 1999, 2002) described an approach to model character evolution along a phylogeny using generalized least-squares regression (GLS). In

*Correspondence:* Daniel S. Moen, Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY-11794-5245, USA.  
Tel.: +631-632-1886; fax: +631-632-7626;  
e-mail: dmoen@life.bio.sunysb.edu

**Table 1** Review of the evidence for Cope's rule of phyletic size increase.

Taxon*	Cope's rule	Converse to Cope's rule	Increase in range	Decrease in range	Stasis	Time period	Source¶
Stegocephalia‡	1		3			Paleozoic	Laurin, 2004
Vascular plants‡	1					Devonian	Chaloner & Sheerin, 1979
Dinosauria‡	1					Mesozoic	Hone <i>et al.</i> , 2005
Ammonites†	2	4	5	8	2	Jurassic	Dommergues <i>et al.</i> , 2002
Bivalves§	27%	27%	34%	10%	1%	Cretaceous	Jablonski, 1997
Gastropods§	30%	26%	29%	10%	4%	Cretaceous	Jablonski, 1997
Horses‡	2	2	2			Cenezoic	MacFadden, 1986; Alberdi <i>et al.</i> , 1995
Mammals‡	1					Cenezoic	Alroy, 1998
Planktonic foraminifera‡			1			Cenezoic	Arnold <i>et al.</i> , 1995
Freshwater fishes‡		5	4			Extant	Knouft & Page, 2003
Varanid lizards‡		1				Extant	Pianka, 1995; D.S. Moen, unpublished data

Cope's rule is defined here as either (1) a predominance of within-lineage size increase within the entire taxon under study or (2) an increase in body size in both the smallest and largest members of a clade (i.e. a positive shift in the range of sizes, in contrast to an increase only in the size of the largest member of a clade, which would increase the body size range but not shift it to larger sizes). See Jablonski (1996,1997) for a graphical explanation.

\*Values indicate either †number of across-time within-lineage comparisons, ‡number of clades, or §percentage of clades that demonstrated the pattern.

¶Sources represent the most current, comprehensive, and rigorous studies, rather than all studies ever conducted on each group.

the GLS framework, the distribution of phenotypes across a phylogeny can be modelled as either evolving through a random-walk or with a directional bias. In the latter case, one essentially regresses a phenotypic variable (e.g. body size) on the total path length from the root of a clade, while accounting for the nonindependence of shared branch lengths via a variance-covariance matrix. Noncontemporaneous tips are necessary for the analysis, so extinct taxa can be analysed with branch lengths in units of time, extant taxa can be analysed with branch lengths reflecting genetic change, or either can be analysed with unitary branch lengths (see Methods for details; Pagel, 1997, 1999, 2002). The GLS method can therefore be used to detect significant directional trends using the data of extant species, by testing whether a directional model of trait evolution significantly fits the data better than a random-walk model. Additionally, in contrast to random-walk ancestral reconstruction methods, one can estimate trait values at ancestral nodes that are outside the range of their extant descendents, given a strong directional trend (Pagel, 1997, 2002). Thus, using the GLS method reduces the previous limitations of neontological approaches in inferring evolutionary trends.

Conceptually, neontological approaches may be seen as unable to accurately infer evolutionary trends, because data from extant organisms represent only a cross-section of evolutionary time. However, data from extant taxa reflect the results of historical processes, and statistical models (as in the GLS approach above) can estimate how the processes have occurred (Pagel, 1997, 1999). Thus, the result of any processes favouring one

character state over another should be reflected in the phylogenetic distribution of traits among extant taxa. For example, if a trend of body size increase has occurred in a group of organisms, those species whose history is marked by the greatest genetic divergence and/or speciation events since the common ancestor of their clade (as indicated by branch lengths) should also have the largest body sizes.

In addition to overcoming past limitations, the neontological approach has many merits. First, body sizes of extant species are directly measured, not estimated from partial fossils. Although this is not a concern for all paleontological approaches (i.e. studies of invertebrates often include whole-specimen measurements, e.g. Arnold *et al.*, 1995; Jablonski, 1997; Dommergues *et al.*, 2002), it applies to many, particularly studies of plants and vertebrates (e.g. Chaloner & Sheerin, 1979; MacFadden, 1986; Alberdi *et al.*, 1995; Alroy, 1998; Laurin, 2004). Second, the phylogenetic relationships among living species are often more strongly supported and better resolved than those of extinct species, and most authors would agree that a proper analysis of body size evolution, whether paleontological or neontological, requires a robust phylogenetic framework (Pagel, 1997, 1999; Alroy, 2000). Third, recent mechanistic evidence indicates that a trend of phyletic size increase may occur on shorter, more recent time scales than are typically investigated paleontologically. For instance, Kingsolver & Pfennig (2004) conducted an analysis of directional selection on body size in a wide variety of extant taxa, showing that selection on body size is consistently positive, whereas the frequency of positive and negative

selection on other morphological traits was equal. Thus, neontological methods for inferring evolutionary trends are not only possible, but necessary to test the importance of different processes in producing trends (Hone & Benton, 2005).

The first study to use the GLS model to detect trends in body size evolution of extant species was an analysis of body size evolution in North American freshwater fishes. Knouft & Page (2003) examined the relationship between number of cladogenetic events and body size within family-level phylogenies of fishes, finding a significant negative relationship in five of the nine families analysed. Knouft & Page (2003) interpreted their results as reflecting the tendency of clades to be founded by large ancestors inhabiting large bodies of water, while more recent, smaller species were those who had invaded smaller streams and had speciated after becoming isolated in the streams. These results indicate that the idiosyncratic nature of the diversification of a specific group may be more important in producing trends in body size evolution than the general advantages of increased body size (e.g. increased reproductive effort in fishes; Duarte & Alcaraz, 1989; Elgar, 1990).

Despite the interesting results of Knouft & Page (2003), no other studies have used model-based comparative methods to examine trends in body size evolution in other extant organisms. Cryptodiran ('hidden-necked') turtles are an excellent group in which to study patterns of body size evolution because (1) the clade's relatively small size has led to the availability of densely sampled phylogenies and (2) many species show sexual dimorphism in size (Berry & Shine, 1980), which indicates that selection on body size (a putative mechanism driving trends in body size evolution; Kingsolver & Pfennig, 2004) may be important in this group. Cryptodiran turtles are distributed nearly worldwide (except Antarctica), are an ancient group dating to at least 175 mya (Near

*et al.*, 2005), and comprise one of two major clades of turtles (Krenz *et al.*, 2005), with ~210 extant species or roughly 80% of known extant turtle species (Ernst & Barbour, 1989; plus more recent systematic work). Using a GLS approach, I examined whether the patterns of body size evolution in extant cryptodiran turtles are consistent with Cope's rule of phyletic size increase. I tested whether the pattern occurs across the whole tree of cryptodirans and also whether the rule accurately describes body size evolution in each of six smaller clades of cryptodiran turtles.

## Methods

### Data

From literature sources (Table 2), I gathered maximum carapace length (MCL) data as a measure of body size. Although MCL is only one metric of size, I chose it because it is (1) the most widely available measure of turtle body size and (2) less temporally variable than other metrics (e.g. body mass). When MCL was available for multiple subspecies, I assigned the largest of these values to the species. Due to limited data for both sexes, in all species I used the MCL regardless of sex. Because most models of change along a phylogeny assume that data are normally distributed (Freckleton *et al.*, 2002), I ln-transformed all MCL data to reduce the positive skew of the MCL distribution (see Results).

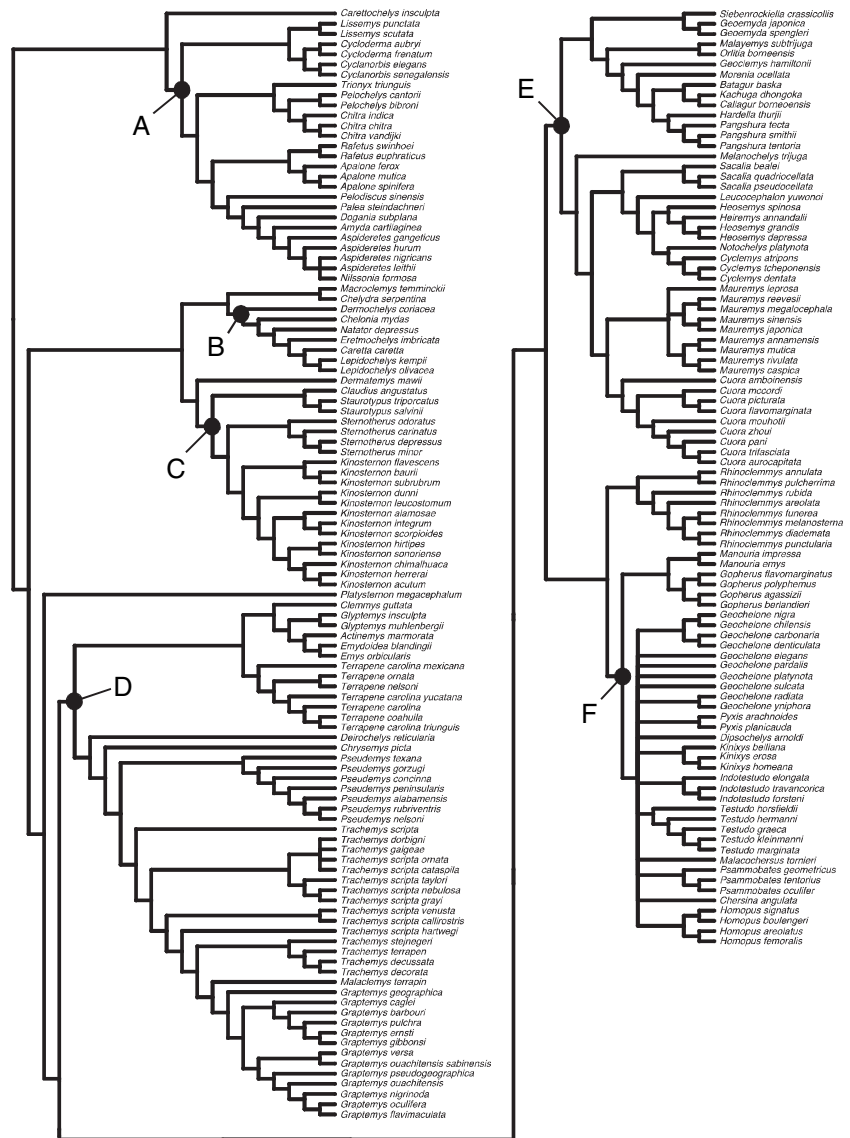
Phylogenetic hypotheses for cryptodiran turtles were obtained from the literature (Table 2, Fig. 1). The entire tree of cryptodiran turtles was pieced together using phylogenies for six clades (see below) nested within the higher-level topology of Krenz *et al.* (2005). For most clades nested within cryptodiran turtles (Emydidae, old World Geoemydidae, Kinosternidae, Trionychidae and Chelonioidae), phylogenies were used as presented in

**Table 2** Literature sources for MCL ‡ and phylogenetic data of cryptodiran turtles used in this analysis.

Clade	MCL data	Phylogenetic data
Trionychidae	Ernst & Barbour, 1989; Ernst <i>et al.</i> , 1994; Pritchard, 2001	Engstrom <i>et al.</i> , 2004
Chelonioidae	Ernst & Barbour, 1989; Ernst <i>et al.</i> , 1994	Dutton <i>et al.</i> , 1996
Old World Geoemydidae	Ernst & Barbour, 1989; J.B. Iverson, personal communication; Iverson & McCord, 1992, 1994, 1997; Lehr <i>et al.</i> , 1998; McCord & Iverson, 1991, 1994; McCord <i>et al.</i> , 1995; Yasukawa <i>et al.</i> , 1992	Spinks <i>et al.</i> , 2004
Testudinidae	Ernst, 1998; Ernst & Barbour, 1989; Ernst & Leuteritz, 1999; Ernst <i>et al.</i> , 1994; Pedrono & Markwell, 2001	Crumly, 1984; Gaffney & Meylan, 1988; Lamb & Lydeard, 1994; Caccone <i>et al.</i> , 1999; Palkovacs <i>et al.</i> , 2002; van der Kuyl <i>et al.</i> , 2002; Fritz <i>et al.</i> , 2005
Emydidae	Ernst & Barbour, 1989; Ernst <i>et al.</i> , 1994; Moll, 1994	Stephens & Wiens, 2003a
Kinosternidae	Berry & Iverson, 2001a,b; Berry <i>et al.</i> , 1997; Ernst & Barbour, 1989; Ernst <i>et al.</i> , 1994; Iverson, 1990, 1991; Iverson <i>et al.</i> , 1998	Iverson, 1998
All cryptodirans*	Pritchard & Trebbau, 1984	Krenz <i>et al.</i> , 2005

\*Includes all of the above data plus the additional data listed here.

‡MCL, maximum carapace length.



**Fig. 1** Complete cryptodiran phylogeny used in this study, which was constructed from the literature (see Table 2). The six major clades analyzed for trends in body size evolution are labelled: A, Trionychidae; B, Chelonioidae; C, Kinosternidae; D, Emydidae; E, Old World Geoemydidae; F, Testudinidae. Note that taxon names follow those names presented in the phylogenetic sources.

their original sources. Maximum-likelihood inferred branch lengths for these phylogenies were obtained from authors (Old World Geoemydidae and Trionychidae) or obtained by downloading sequences from Genbank and optimizing branch lengths on the published topology (Chelonioidae). Maximum-likelihood branch lengths for the Emydidae were not available due to the lack of genetic divergence among many taxa within two genera for the genes sampled in previous studies (Stephens & Wiens, 2003a). Maximum-likelihood branch lengths also were not available for the Kinosternidae due to incongruence between the molecular tree and the combined data tree (the latter was used here; Iverson, 1998).

In cases where published topologies were in conflict, I preferentially used the topologies that (1) had higher statistical support, (2) were based on more data and/or

(3) were based on a greater diversity of data (e.g. morphology, mtDNA, nuclear DNA). In two cases in which phylogenies were very similar in these criteria [*Sternotherus* of Kinosternidae (Iverson, 1998; Walker *et al.*, 1998) and *Cuora* of the Geoemydidae (Parham *et al.*, 2004; Spinks *et al.*, 2004)], I analysed both possible topologies; however, the results were quantitatively similar and qualitatively the same, so I present results only from the preferred topologies (Fig. 1).

The Testudinidae was unique in this analysis in having a largely unresolved phylogeny, with a relatively low amount of available phylogenetic data (compared to other major clades in this study), conflicting morphological and molecular phylogenetic estimates for taxa for which both types of data exist, and inadequate molecular sampling for those taxa whose phylogenetic placement is

most impacted by the conflict. As a result, I took the following approach. First, I included only well-supported relationships or those that are congruent with both morphological and molecular data (Fig. 1). Second, I randomly resolved all polytomies in the entire testudinid tree 100 times in the program *MACCLADE* (Maddison & Maddison, 2000), and then conducted a GLS analysis (see below) on each random resolution. I considered a lack of significant results (at  $\alpha = 0.05$ ) in all 100 random resolutions as a lack of support for a trend in body size evolution. Alternatively, a greater proportion of significant results than expected by chance (i.e.  $>0.05$ ) was considered as possible support for a trend, pending congruence of the significant resolutions with future phylogenetic resolution.

Because I conducted these analyses at the species level, I made modifications to published phylogenies if they included taxa that were suspected hybrids or were subspecies. Suspected hybrid taxa within the phylogeny of Spinks *et al.* (2004) were excluded from this analysis. Subspecies in most published phylogenies were monophyletic within their appropriate species. For these taxa, I pruned all but one subspecies from the phylogeny and averaged branch lengths across subspecies, if applicable (i.e. for the gradual model of character change, see below). However, because the subspecies of two species are not monophyletic in the best estimate of emydid phylogeny (Stephens & Wiens, 2003a), I followed a previous comparative analysis of emydid turtles and considered most Mexican and Caribbean *Trachemys* currently recognized as subspecies, as well as three subspecies of *Terrapene carolina*, as species in this analysis (Stephens & Wiens, 2003b; P.R. Stephens, personal communication; see Fig. 1).

### Phylogenetic signal

An absence of phylogenetic signal would render the modelling of trait evolution along a phylogeny irrelevant. Thus, I first tested whether sufficient evidence exists to reject the presence of phylogenetic signal. To do this, I first estimated the ML value of  $\lambda$ , a metric of phylogenetic signal, using the program *CONTINUOUS* (Freckleton *et al.*, 2002). A value of  $\lambda = 0$  indicates that trait values are approximately distributed randomly across the phylogeny (i.e. similarities among trait values are not consistent with phylogeny). Conversely, a value of  $\lambda = 1$  indicates that the covariances of trait values between species are consistent with the phylogeny and model of trait evolution (e.g. random-walk model). Finally, a value intermediate between zero and one indicates that covariances for a trait are less than what would be expected from phylogeny but greater than trait evolution independent of phylogeny. To test whether further analyses were appropriate, I examined the 95% confidence interval of each ML estimate of  $\lambda$  for each clade. If  $\lambda = 1$  was not within the 95% set, no further analyses

were conducted on the clade. Because the ML estimate of  $\lambda$  is dependent on the model of trait evolution, I conducted separate phylogenetic signal analyses assuming both the random-walk and directional models (see below). However, because the results were nearly identical under both models, only the random-walk results are presented.

### Test for a directional trend in body size evolution

A GLS model was used to investigate possible trends in body size evolution within cryptodirans. Not only can this model incorporate the constant-variance random-walk (Brownian motion) model of character evolution, but it can also accommodate a directional component to continuous trait evolution (Pagel, 1997, 1999, 2002). The directional model can be used to examine the relationship between character values and total path length from the root of the tree. In the case of phyletic size increase, for example, taxa that are farther from the root of the tree would be expected to be larger. The model accounts for the phylogenetic nonindependence of taxa by specifying a variance-covariance matrix based upon the assumed phylogeny.

I tested the fit of the directional model, as compared to the random-walk model, by using a likelihood-ratio test. The likelihood of each model was first computed with the program *CONTINUOUS* (Pagel, 1997, 1999). The likelihood ratio test statistic was calculated as:

$$LR = -2 \ln \frac{H_0}{H_1}, \quad (1)$$

where  $H_0$  represents the likelihood of the null, or random-walk, model and  $H_1$  represents the likelihood of the alternative, or directional, model. When the two models are nested,  $LR$  is expected to be  $\chi^2$  distributed with the degrees of freedom equal to the difference in the number of parameters of the two models (in this case, one; Edwards, 1972). The models compared herein are nested because the directional model is a random-walk model with a directional bias, with the bias specified by the regression parameter  $\beta$  (Pagel, 1997, 1999, 2002). As I recognized significance at  $\alpha = 0.05$ ,  $LR$  in each model test was compared to  $\chi^2_{0.05[1]} = 3.84$  to test whether the directional model significantly fit the data better than the random-walk model.

Because the GLS directional model detects a correlation between a character value and the total path length from the root of a tree, this method cannot be implemented on trees in which the tips are contemporaneous (Pagel, 1997, 1999). For example, the analysis of trends using data from extant taxa cannot use units of time for branch lengths, as the time to the common ancestor of all taxa is the same. Two possible units can be used for branch lengths, depending on the assumed mode of character change.

First, one can assume a speciational (*sensu* Rohlf *et al.*, 1990) model of character evolution, in which almost all character change is assumed to occur at or is at least associated with speciation events (Eldredge & Gould, 1972; Futuyma, 1987). Such an approach involves using a phylogeny with equal branch lengths between all nodes (i.e. all branch lengths are set equal to one). Under this scenario, one effectively examines the relationship between a character value and the number of branching events that have occurred between the terminal taxon and the root (Knouft & Page, 2003). Though Knouft & Page (2003) contend that this model may be suitable in the case of North American freshwater fishes, it is unknown if large changes in body size are generally associated with speciation events and should be modelled as such. Additionally, the branching events may be underestimated: extinct members of a clade, whose placement within a phylogeny would increase the total number of cladogenetic events for some species, are not represented and thus could bias the results in an unpredictable manner (Martins & Garland, 1991; Crisp & Cook, 2005).

Alternatively, one can assume a gradual model of character change, in which evolution is assumed to be primarily anagenetic (Pagel, 1997, 1999). Under this model, branch lengths are represented in units of genetic change (substitutions) along each branch. Note that because all species at the tips of a phylogeny have diverged from their single common ancestor over the same amount of time, these branch lengths cannot be considered as proxies for time. Thus, this model assumes that the amount of genetic change from root to tip (and thus rate of molecular evolution) is a proxy for 'opportunity for [phenotypic] change' (Pagel, 1994, p. 42). Although this assumption of increased molecular evolution potentially leading to increased phenotypic evolution may be intuitively desirable (Pagel, 2002), an association between rates of molecular and morphologi-

cal evolution has received mixed empirical support (Omland, 1997; Bromham *et al.*, 2002). As with the speciational model, the role of gradual change in body size evolution is largely unknown, though it is the most frequently used model of character evolution in phylogenetic comparative analyses. Additionally, this method is less likely to suffer from the bias of extinction mentioned above.

For clades in which I had branch length data in units of genetic change (Old World Geoemydidae, Trionychidae and Chelonioidae), I compared the performance of these two models of character change by analysing the data in both a gradual (genetic branch lengths) and speciational (equal branch lengths) framework (Tables 3 and 4). Because the speciational model assumes that all speciation events are reflected in the phylogeny, additional taxa whose phylogenetic placement has been estimated but for which no genetic branch lengths were available were added to the equal branch length tree in the Trionychidae (three trionychid taxa have only morphological data available; Engstrom *et al.*, 2004). However, in order to compare the gradual and speciational models under trees of equal taxon sampling in the analysis of the Trionychidae, I only analysed the MCL of these added taxa in the complete cryptodiran tree (see below). In the case of the three clades for which I did not have genetic divergence data for the entire phylogeny, I analysed the data only under the speciational model (Tables 3 and 4), following the approach of Knouft & Page (2003). Finally, I tested for the presence of a directional trend in MCL evolution for the entire tree of cryptodirans using the speciational model of character change. Due to the lack of resolution in the Testudinidae, I conducted both a liberal (i.e. most likely to find a directional trend) and conservative (i.e. least likely to find a trend) analysis of all cryptodirans. The liberal analysis included the tortoise topology from the random resolutions that had the highest *LR* and the smallest negative regression coefficient

**Table 3** Results of phylogenetic signal ( $\lambda$ ) analyses.

Clade (common name)	$n\ddagger$	Model of character change	$\lambda$	95% CI
Trionychidae (softshells)	23	Gradual	1.000	0.505–1.000
		Speciational	1.000	0.541–1.000
Chelonioidae (sea turtles)	7	Gradual	0.000	0.000–1.000
		Speciational	0.736	0.000–1.000
Old World Geoemydidae (Old World pond turtles)	45	Gradual	1.000	0.883–1.000
		Speciational	0.920	0.438–1.000
Testudinidae (tortoises)*	39	Speciational	0.816	0.440–1.000
Emydidae (New World pond turtles)	51	Speciational	0.833	0.415–1.000
Kinosternidae (mud turtles and stinkpots)	20	Speciational	1.000	0.367–1.000
All cryptodirans-	201	liberal	0.987	0.903–1.000
		conservative	0.967	0.890–1.000

\*Value of  $\lambda$  represents the mean for the 100 randomly resolved phylogenies, with the 95% CI presented as 47.5% of values above (upper limit) and below (lower limit) the mean of the distribution of random-resolution.

$\ddagger n$  is the number of species analysed within each clade, rather than number of described species in each clade.

**Table 4** Results of GLS analyses for a directional trend of MCL evolution.

Clade (common name)	<i>n</i>	Model of character change	$\alpha \pm SE$	$\beta \pm SE$	ln Likelihood	<i>LR</i> test statistic	<i>P</i> value
Trionychidae (softshells)	23	Gradual	5.358 $\pm$ 0.715	-6.958 $\pm$ 3.769	-10.05	3.388	0.066
		Speciational	3.496 $\pm$ 0.439	0.099 $\pm$ 0.092	-11.44	1.157	0.282
Chelonioidae (sea turtles)	7	Gradual	7.647 $\pm$ 1.245	-14.656 $\pm$ 6.957	-2.99	4.171	0.041
		Speciational	5.577 $\pm$ 0.361	-0.191 $\pm$ 0.160	-3.45	1.480	0.224
Old World Geoemydidae (Old World pond turtles)	45	Gradual	3.452 $\pm$ 0.194	-2.072 $\pm$ 3.972	-11.31	0.250	0.617
		Speciational	3.386 $\pm$ 0.311	-0.018 $\pm$ 0.054	-22.74	0.078	0.781
Testudinidae (tortoises)*	39	Speciational	3.894 $\pm$ 0.342	-0.089 $\pm$ 0.056	-33.91	1.06	
Emydidae (New World pond turtles)	51	Speciational	2.906 $\pm$ 0.213	0.032 $\pm$ 0.034	-8.55	0.880	0.348
Kinosternidae (mud turtles and stinkpots)	20	Speciational	2.822 $\pm$ 0.294	0.020 $\pm$ 0.074	-2.16	-0.001	NA†
All cryptodirans-liberal	201	Speciational	3.868 $\pm$ 0.282	-0.023 $\pm$ 0.027	-117.25	0.704	0.401
		conservative	Speciational	3.745 $\pm$ 0.282	0.006 $\pm$ 0.027	-117.52	0.049

\*Values represent the means for 100 randomly resolved phylogenies, with standard errors derived from the distribution of each statistic among these phylogenies. The *P* value was not presented as a mean because no meaningful interpretation could be made from it.

†This *P* value is undefined, as the *LR* test statistic was negative.

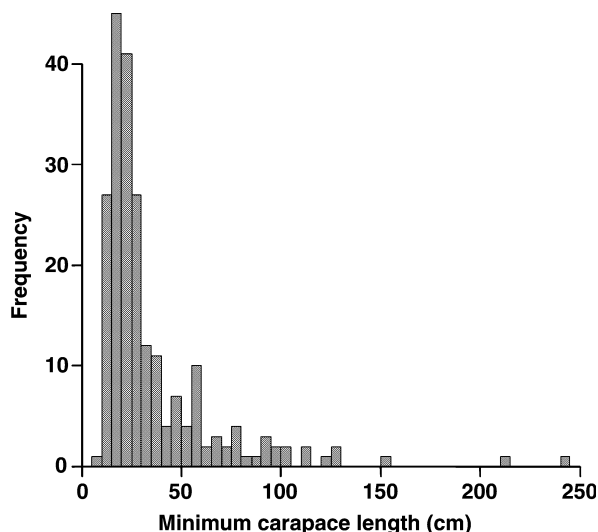
Note: *n* is the number of species within each clade analysed;  $\alpha$  is the maximum-likelihood estimate of the ln-transformed MCL at the root of each tree, as predicted by the directional model, presented with one standard error (SE);  $\beta$  is maximum-likelihood estimate of the ln-transformed regression parameter of the directional model, presented with one SE; and *LR* is as presented in equation (1). MCL, maximum carapace length.

(i.e. the largest absolute value of observed negative coefficients), as the other analyses indicated that the relationship, if any, between MCL and total path length in cryptodiran turtles is negative (see Results). The conservative analysis included the tortoise topology that had the largest positive regression coefficient.

## Results

### Body size

Maximum carapace length obtained from the literature for cryptodiran turtle species ranged from 10 to 244 cm (Fig. 2). Even after ln-transformation, the distribution of



**Fig. 2** Frequency distribution of the raw MCL data for all cryptodiran turtles.

MCL in all cryptodiran turtles was positively skewed ( $g_1 = 0.916$ ;  $t_{216} = 5.545$ ;  $P < 0.0001$ ).

### Phylogenetic signal

Most ML-estimated values of  $\lambda$  for MCL in cryptodiran turtles were close to one (eight of ten, not including the Testudinidae; Table 3). In contrast, the Chelonioidae showed lower values of  $\lambda$  (Table 3). However, the 95% confidence intervals of all clades contained  $\lambda = 1$  (Table 3), indicating that sufficient evidence does not exist to reject the presence of phylogenetic signal in these datasets. Most of the random resolutions of the Testudinidae had high ML-estimated values of  $\lambda$ , and only three of the 100 randomly resolved trees had 95% CIs that excluded one.

### Test for a directional trend in body size evolution

Under either mode of character change, most clades showed no pattern consistent with directional body size evolution (Table 4), except the Chelonioidae under the gradual mode of character change. However, although it was significant at  $\alpha = 0.05$ , a consideration of experiment-wise error rate increases the probability that this result was spurious (per-comparison  $\alpha$  using the Dunn-Sidak method = 0.0047,  $n = 11$  comparisons; Sokal & Rohlf, 1995). Despite the near lack of statistical significance, the gradual models had greater *LR* test statistics than their speciational counterparts in all three of the clades in which the two methods were compared.

In the Testudinidae analysis, only two of 100 random resolutions had a significantly higher likelihood for the directional model, as compared to the random walk. After correcting for the experiment wise error rate, however, none of these results would have been

considered significant even if their respective topology did reflect the true phylogeny (i.e. all  $P$  values were  $>0.0047$ ).

## Discussion

### Cope's rule

Many paleontological studies have documented significant positive directional trends in body size evolution in several vertebrate groups (Alroy, 1998; Laurin, 2004; Hone *et al.*, 2005). My results indicate that MCL evolution in extant cryptodiran turtles is not consistent with Cope's rule of phyletic size increase, a finding that is in concordance with other neontological examinations of body size evolution. Pianka (1995) found that snout-to-vent length evolution in the lizard family Varanidae did not proceed in a consistent direction across the phylogeny of the family. Although Pianka (1995) did not use statistical models of character evolution, a reanalysis of varanids using GLS and a more recent phylogeny (Ast, 2001) indicated that either the converse to Cope's rule (gradual model) or no trend (speciational model) exists (D.S. Moen, unpublished data). Knouft & Page (2003) found a pattern of body size evolution consistent with a trend of phyletic size decrease in five families of North American freshwater fishes, while they found no pattern for four other families. Thus, although very few groups of extant organisms have been examined, no neontological study yet seems to support Cope's rule of phyletic size increase.

One potential source of discordance between this study and most studies of vertebrate fossils is my use of MCL as a metric of size. Paleontological studies often use estimates of body mass, rather than length. However, for a given range of body lengths, the body masses associated with those lengths will demonstrate a much broader range. Therefore, my use of length may be a more conservative approach. Additionally, Silva & Downing (1995) detected patterns in subsets of their mammalian data set only when examining size scales of at least three orders of magnitude. Maximum carapace length in cryptodiran turtles ranges from 10 to 244 cm, a scale of only 1.39 orders of magnitude. Given the reasonably high  $LR$  statistics in two of my analyses, it is possible that analysing body size evolution in terms of mass would produce stronger results, though in the direction of a pattern of phyletic size decrease (as the regression coefficients for these analyses were negative).

To roughly assess this possibility, I conducted an analysis of body mass evolution in cryptodiran turtles using body mass estimates. First, I derived a least-squares regression equation of body mass ( $M_B$ , in  $g$ ) on carapace length ( $C$ , in  $mm$ ) from published cryptodiran data (Iverson *et al.*, 1993). The regression was significant and highly predictive [ $\ln M_B = -7.637 + 2.791(\ln C)$ ;  $F_{1,65} = 3178.19$ ,  $P < 0.0001$ ,  $R^2 = 0.980$ ]. Second, I

used the regression equation to estimate the body mass for each MCL datum in my original data set. Thirdly, I analysed these body mass estimates in the GLS framework exactly as I did for the MCL data, including the entire phylogeny of cryptodirans as well as all six nested clades.

The results for these analyses were qualitatively identical and quantitatively similar to those for MCL (results not shown). Thus, despite the wider range of values in the mass estimates as compared to MCL, it seems that an analysis of body mass in cryptodiran turtles would not show a trend of phyletic size increase or decrease. However, it should be emphasized that this is only a rough approximation of a body mass analysis, because the regression from which masses were estimated was based on data from taxa comprising only about one-third of the MCL dataset.

A previous analysis of body size evolution in early tetrapods and stem-tetrapods (Stegocephali) showed no pattern of phyletic size increase within a large clade, whereas a mid-sized clade nested within this large clade did show a significant pattern of size increase (Laurin, 2004). Furthermore, smaller clades nested within this mid-sized clade did not exhibit the trend (Laurin, 2004). Thus, it is possible that my analysis did not examine body size evolution at the correct scale. However, I examined both a relatively large clade (all cryptodirans,  $n = 201$ ) as well as smaller clades of varying sizes ( $n = 7-51$ ) and found no strong evidence for a trend in body size evolution in any analysis. Certainly, one could examine each sequentially nested clade, but the biological relevance of conducting such an analysis is not clear, especially given that Cope's rule has been primarily interpreted to be a large-scale pattern. Additionally, the power of analyses at levels lower than those I examined may be too low to detect any significant trend. Consequently, the importance of examining body size trends in cryptodiran turtles at other levels than I examined is not apparent.

Of perhaps greater importance is the fundamental difference between examining evolutionary trends from paleontological and neontological perspectives. Studies of phyletic size increase in the fossil record have been aimed at detecting a trend of body size increase over time. In contrast, neontological studies, such as the current study, cannot study trends over time, as all extant clade members have evolved from their common ancestor over the same time period. As a result, this study could only detect whether size increase was correlated with an increased number of speciation events (speciational model) or with increased genetic divergence (gradual model). Both neontological models have some limitations. First, a key assumption of the speciational model is that all speciation events are reflected in the phylogeny. Due to extinctions, this assumption is likely never met in strictly neontological studies. Additionally, lack of knowledge about the phylogenetic placement of some species



may limit the inclusion of all known extant species in an analysis, as is the case for at least two of the clades (Old World Geoemydidae, Kinosternidae) in this study. Second, interpretations from the gradual model results are not easily decoupled from the possible effects of body size (or body-size associated life history variables) on molecular evolution. Because the gradual model examines the relationship between body size and genetic divergence from the root, any pattern of size increase would be in contrast to the generally well-established negative correlation between body size and rate of molecular evolution (Martin & Palumbi, 1993; Mooers & Harvey, 1994; Bromham *et al.*, 1996; Bromham, 2002; but see Slowinski & Arbogast, 1999, for critiques of some of these approaches). Thus, the limitations unique to neontological methods, as well as the types of trends they detect, may influence their ability to reveal trends in body size evolution.

Unfortunately, it is difficult to compare the merits of the two approaches without examining both a fossil group and its extant descendants. No study of trends in body size evolution has yet examined a group's fossil record as well as conducted an analysis on the extant descendants of the same group. Such an analysis would facilitate comparing the approaches by examining potential trends in groups sharing the same underlying natural history, physiology, behaviour, and other aspects of basic biology. An obvious next step for the research of body size trends in turtles would be to examine the group's well-documented fossil record, which could lend insight into the relative merits of the paleontological and neontological approaches.

## Methods of analysis

Previous interspecific analyses of vertebrates have indicated that body size often shows a large amount of phylogenetic signal (Freckleton *et al.*, 2002; Blomberg *et al.*, 2003; Ashton, 2004). My results are congruent with these studies. As the only exception, the Cheloniodea showed both low values of  $\lambda$  and confidence limits that included all possible values of  $\lambda$ . Because this was in contrast to the results of almost all other clades, it may have been an artifact of low sample size ( $n = 7$ ). In an analysis of 102 datasets from 26 clades, Freckleton *et al.* (2002) showed that phylogenies with a low number of taxa were associated with large variances in  $\lambda$ .

The assumption of either a gradual or speciation mode of character change did not seem to greatly affect the outcome of analyses, as no significant pattern was detected in any of the three clades in which analyses of both modes were assumed. However, analyses under the gradual mode seemed to have more power, as they showed consistently higher *LR* statistics than analyses under the speciation mode for the same data sets. This result could be due to one or more of the following

factors: (1) the data actually fit a gradual model better, (2) an effect of body size on molecular evolution strongly influences the gradual model or (3) all speciation events in each clade have not been included, thus violating the key assumption of the speciation model. In regards to the latter factor, nothing is currently known about how speciation models of character evolution perform when this assumption has been violated. Additionally, it is interesting to note that of the three clades in which the two models were tested, the two clades which show a large discrepancy between the two models (Trionychidae and Cheloniodea) are much older (Joyce *et al.*, 2004; Near *et al.*, 2005) and have a richer fossil record (Gaffney & Meylan, 1988) than the group which showed only a minor difference between models, the Old World Geoemydidae. Thus, the speciation analyses of these two older clades would be expected to show the greatest bias of incomplete taxon sampling. However, the sample size of this comparison ( $n = 3$ ) is too small to draw any substantial inference amongst the possible causative factors of the discrepancy between the results of the two models.

Because little is known regarding the predominant mode of body size evolution (but see, for example, Polly, 2001), it seems reasonable to analyse one's data under both modes of character change, if possible. In certain contexts, such as using a composite phylogeny created from piecing together phylogenies from the literature, one is limited to only using the speciation model. Certainly, my results do not indicate that assuming a speciation mode of character change is unreasonable, though it may reduce the power of an analysis.

## Conclusions

Body size evolution in extant cryptodiran turtles does not follow a pattern consistent with Cope's rule of phyletic size increase. This is concordant with other neontological examinations of body size evolution (Pianka, 1995; Knouft & Page, 2003). Though far fewer neontological studies have been conducted, the patterns (or lack thereof) in such data are in contrast to the paleontological trends that gave rise to the formulation of Cope's rule. Certainly, many more studies of body size evolution in extant species, as well as examinations for trends in both extinct and extant taxa of a given group, are necessary to determine whether or not this contrast between extant and extinct lineages is spurious. However, given the available evidence, it is perplexing that a putative microevolutionary mechanism for Cope's rule (selection for large body size) has received recent empirical support (Kingsolver & Pfennig, 2004), yet a pattern consistent with Cope's rule has yet to be observed in extant taxa, those most likely to be influenced by a microevolutionary process (Hone & Benton, 2005).

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