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Dissociation of somatic growth from segmentation drives gigantism in snakes

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Body size is significantly correlated with number of vertebrae (pleomerism) in multiple vertebrate lineages, indicating that change in number of body segments produced during somitogenesis is an important factor in evolutionary change in body size, but the role of segmentation in the evolution of extreme sizes, including gigantism, has not been examined. We explored the relationship between body size and vertebral count in basal snakes that exhibit gigantism. Boids, pythonids and the typhlopid genera, *Typhlops* and *Rhinotyphlops*, possess a positive relationship between body size and vertebral count, confirming the importance of pleomerism; however, giant taxa possessed fewer than expected vertebrae, indicating that a separate process underlies the evolution of gigantism in snakes. The lack of correlation between body size and vertebral number in giant taxa demonstrates dissociation of segment production in early development from somatic growth during maturation, indicating that gigantism is achieved by modifying development at a different stage from that normally selected for changes in body size.

Keywords: gigantism; pleomerism; somitogenesis; dissociation; heterochrony; snakes

1. INTRODUCTION

Extrinsic selective factors influencing the evolution of body size extremes in vertebrates have been heavily studied (Hanken & Wake 1993; Alexander 1998), but the intrinsic developmental mechanisms underlying evolutionary body size change are poorly known. Phyletic body size increases are associated with increased somite numbers (pleomerism) in actinopterygian fish (Lindsey 1975), plethodontid salamanders (Jockusch 1997) and derived colubroid snakes (Lindell 1994), but not in groups whose vertebral column is highly regionalized and functionally constrained like mammals and birds (Wake 1979), in which body size changes are a function of post-embryonic somatic growth. Although pleomerism has been established as a mechanism of body size evolution in snakes, its role in the evolution of gigantism is unknown.

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Gigantism (Gould & McFadden 2004, p. 220) is pronounced in boids, pythonids and typhlopid among snakes (Greene 1997; Murphy & Henderson 1997; Kley 2003). The largest extant snakes consist of the pythonids, *Python molurus*, *Python sebae* (incl. *natalensis*), and *Python reticulatus*, and the boid *Eunectes murinus* (green anaconda), with reliable maximum body lengths between 7 and 9 m (Murphy & Henderson 1997). The typhlopid genera *Typhlops* and *Rhinotyphlops* include some of the smallest snake species (total body length; TBL approx. 10 cm) as well as comparative giants including *Typhlops punctatus*, *Typhlops angolensis*, *Typhlops lineolatus* and *Rhinotyphlops schlegelii*, which achieve body lengths approaching 1 m (Roux-Estève 1974; Kley 2003).

Here, we test developmental mechanisms underlying the evolution of gigantism by examining the relationship between body size and vertebral numbers among the largest and the smallest snakes. If pleomerism is the primary mechanism of body size evolution in snakes, then body size and axial segment counts should covary, but if other mechanisms, such as regulation of somatic growth, are responsible for body size evolution, then size and segment number will be unrelated.

2. MATERIAL AND METHODS

Body size measurements and vertebral counts were collected from examination of museum osteological collections and the literature (see electronic supplementary material). Body size was measured as snout-vent length (SVL) in Boidae (Boinae, Ungaliophiinae and Erycinae; Lawson *et al.* 2004; Burbrink 2005) and Pythonidae, and vertebral counts represent preloacal elements. *Typhlops* and *Rhinotyphlops* possess extremely abbreviated tails representing approximately 1% of TBL (Kley 2003). As a result, TBL approximates SVL in these taxa, and was compared to maximum total number of vertebrae (Roux-Estève 1974). No SVL statistics are published for the largest individuals of *Eunectes* and *Python*, so we estimated those by taking TBL for the largest verifiable published specimens (Murphy & Henderson 1997) and multiplying by the proportion of SVL/TBL derived from data on smaller individuals of *Eunectes notaeus* (Dirksen 2002) and *Python* (Shine *et al.* 1998).

Ventral scale counts correlate with vertebral numbers in most alethinophidian snakes (Alexander & Gans 1966) and are commonly used as proxy data for vertebral counts (Lindell 1994; Shine 2000). We used scale counts where skeletal material and vertebral counts were not available, and used the average of male and female counts for boids and pythonids because sex data were often not available for either specimens or the literature, despite strong dimorphism in vertebral numbers and body lengths for many taxa (e.g. Shine 2000).

We used phylogenetic generalized least squares regression (PGLS; Martins & Hansen 1997) to determine the relationship of body size to vertebral numbers while taking into account the effects of phylogenetic autocorrelation, with body size as the dependent variable regressed onto independent vertebral counts using COMPARE v. 4.6b (Martins 2004). We incorporated phylogenetic topologies derived from molecular and morphological datasets (electronic supplementary material). Resolved branch lengths were set to 1.0. Unresolved polytomies were artificially resolved with branch lengths of 0.001 to satisfy the algorithmic requirements of COMPARE. The small length of unresolved branches is effectively zero as far as the results are concerned (Martins & Hansen 1997).

3. RESULTS

Phylogenetic generalized least squares regression produced a positive and significant correlation in Boidae ($r=0.46$, $p<0.01$), Pythonidae ($r=0.38$, $p=0.03$) and *Typhlops* ($r=0.41$, $p=0.03$; figure 1). *Rhinotyphlops* possessed positive but non-significant correlations (*Rhinotyphlops*: $r=0.31$, $p=0.12$), resulting from extremely low vertebral numbers in the largest taxa. Excluding giants from the regressions increased the positive relationships between vertebral counts and

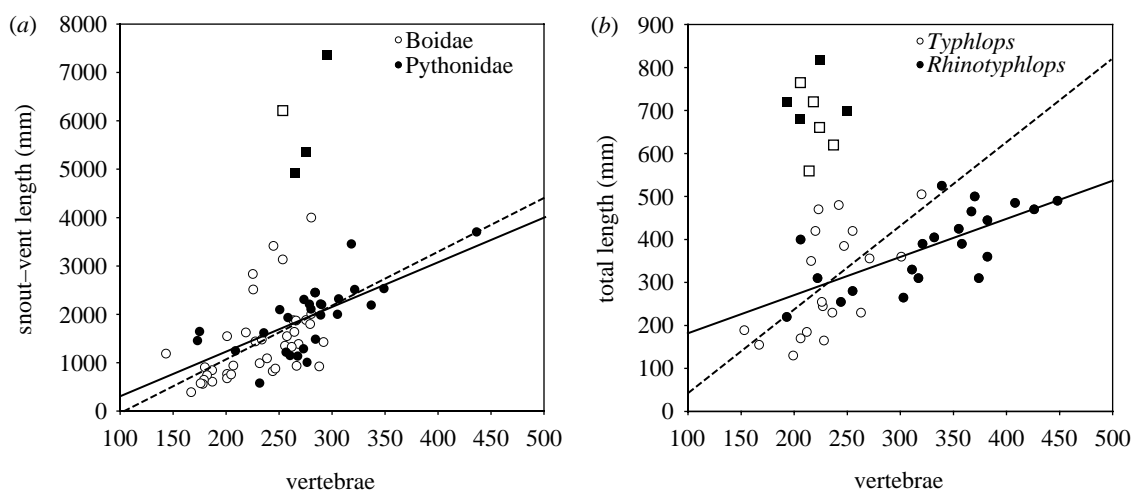


Figure 1. Average vertebral counts plotted against maximum body length for (a) Boidae and Pythonidae and (b) typhloids. Overlain trend lines are PGLS regressions omitting giant taxa. Dashed lines represent (a) Boidae and (b) *Typhlops*. PGLS Regression equations (omitting giant taxa) are: Boidae, $y=11.29x-1202.2$; Pythonidae, $y=9.25x-628.2$; *Typhlops*, $y=1.95x-157.2$; *Rhinotyphlops*, $y=0.89x+89.8$. Squares represent giant taxa.

body size in all clades (Boidae: $r=0.50$, $p<0.01$; Pythonidae: $r=0.71$, $p<0.01$; *Typhlops*: $r=0.63$, $p<0.01$; *Rhinotyphlops*: $r=0.70$, $p<0.01$). The largest species in all four clades have fewer than the expected preloacal vertebrae (figure 1). The largest boids, pythonids and *Typhlops* have vertebral counts near the mean for their respective clades, and the *R. schlegelii* complex possessed among the lowest counts in the genus.

4. DISCUSSION

Results of this study demonstrate pleomerism in basal taxa, indicating that the phenomenon occurs throughout snake phylogeny. Snakes have a greater variability in vertebral numbers than do other amniotes, probably resulting from developmental homogenization of the axial skeleton. In snakes, axial regionalization is reduced by anterior expansion of expression domains for *Hox* genes that code for the dorsal region of the vertebral column, suppressing expression of a distinct cervical region (Cohn & Tickle 1999). As a result, normal constraints on vertebral numbers may be released, allowing for greater variability and providing an additional mechanism for the evolutionary modification of body size (Polly *et al.* 2001).

Correlation between vertebral number and body size does not itself imply causation; however, experiments on early stage embryos have shown that manipulation of body size results in changes in somite size, but not number (Tam 1981). Studies on the relationship between size, growth and vertebral numbers in *Vipera* demonstrated that vertebral counts have direct effects on both overall body size and growth rates (Lindell 1996), and the number of vertebrae in the adult and body size of the embryo in squamates appear to depend on the number of somites that have been produced at the tailbud stage (Raynaud 1994; Richardson *et al.* 1998). The concomitance of segment count and body size at the tailbud stage and in adults suggests that changes in vertebral number in snakes affect body size, but not the converse.

Giant taxa possess relatively low numbers of vertebrae indicating that pleomerism is not the primary mechanism underlying attainment of exceptionally large body size. Pleomerism is a phenomenon associated with segmentation and somitogenesis in the early stages of embryogenesis, but the large size attained by giant snakes must be due to modification of post-somitogenic somatic growth. Normally, in snakes somite number and post-embryonic growth are closely associated, but in giant species these two developmental processes are dissociated (*sensu* Raff 1996).

With the exception of three viperid taxa (Lindell 1994, fig. 11F), dissociation does not appear to play a role in attainment of maximum body sizes in derived colubroid snakes. Colubroids do not achieve the extreme absolute sizes or magnitude of size range in boids and pythonids, but do achieve the sizes and ranges in examined typhloids. The absence of dissociation in the majority of examined derived taxa may represent greater constraint on somatic growth relative to basal snakes.

The dissociation of somite number and somatic growth suggests that gigantism in basal snakes has evolved in an adaptive milieu where selection works on variation associated with growth processes, whereas in other contexts it acts on variation in segment number. In other giant amniotes, large body size can be achieved by either prolonging growth (Erickson & Brochu 1999) or by increasing the rate of growth (Erickson *et al.* 2004). Life-history data for *Python reticulatus* is consistent with the former, as the onset of sexual maturity occurs at a proportionally smaller SVL size than in other snakes (Shine *et al.* 1998) indicating heterochronic extension of somatic growth well into sexual adulthood. Selection on variation in post-embryonic growth duration may represent a more rapid or economic approach to achieving giant body size as opposed to sexual selection and environmental influences on heritable variation in segment number in smaller snakes (Dohm & Garland 1993; Shine 2000). Whatever the

case, giant taxa are exceptional in having evolved through different mechanisms from those driving the body size evolution in most snakes.

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