

DEVELOPMENT AND EVOLUTION OF BODY FORM AND LIMB REDUCTION IN SQUAMATES: A RESPONSE TO SANGER AND GIBSON-BROWN

JOHN J. WIENS

Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York 11794-5245

E-mail: wiensj@life.bio.sunysb.edu

Received March 8, 2004. Accepted July 7, 2004.

Understanding how major changes in body form arise is an important challenge in evolutionary biology. Squamates offer an exciting model system for addressing this issue (Wiens and Slingluff 2001), because dramatic yet similar changes in body form have occurred in seemingly dozens of independent lineages (Greer 1991; Pough et al. 1998).

Studies of development in selected species (e.g., Cohn and Tickle 1999) and phylogenetic comparative studies of morphology (e.g., Wiens and Slingluff 2001) offer complementary approaches for addressing the evolution of body form. Developmental studies can elucidate the developmental and genetic mechanisms that underlie inferred changes in body form in a limited number of extant species. Comparative studies of morphology actually infer those patterns of evolutionary change, and can do so across a broad range of taxa with dense species-level sampling of extant and fossil taxa. In some cases, comparative morphology may also shed light on developmental mechanisms, because some patterns of morphology (and inferred morphological change) may be inconsistent with some models of development.

The groundbreaking study by Cohn and Tickle (1999; CT hereafter) addressed the developmental mechanisms that are responsible for limb loss and axial patterning in snakes. They went on to suggest a developmental-evolutionary model that involves loss of forelimbs through anterior expansion of Hox gene expression domains. They suggested that “such higher order genetic changes could have accounted for sudden anatomical transformations, rather than gradual changes” (p. 478) in the evolution of snakes.

Wiens and Slingluff (2001; WS hereafter) used a comparative phylogenetic approach to examine the patterns of limb reduction and body form evolution in a family of squamates (Anguillidae). One minor aspect of the WS study was to consider the implications of their findings for the generality of the CT model.

Sanger and Gibson-Brown (2004; SGB hereafter) have published a critique of the WS paper that suggests that WS mischaracterized one part of the model of CT. SGB also provided an extensive and useful review of the relevant developmental literature on this general topic. After reading the SGB paper, I fully agree with them that WS mischaracterized one part of the CT model. However, this is only one of four points made by SGB in their paper. Their other three points are either based on apparent misinterpretations of the WS paper (their points 2 and 3) or have little to do with the WS paper (point 4). Furthermore, although the main point of the SGB paper seemingly is to defend the CT model, SGB fail to discuss other problems with the CT model raised by WS. In this response, I briefly address each of these points in turn (my numbering of points corresponds to theirs), and I discuss

our criticism of the CT paper in light of the comments of SGB.

(1) I agree with SGB that CT did not actually claim that there was a common developmental mechanism linking body elongation and limb reduction, although such a linkage was suggested in the abstract of the CT paper and incorrectly attributed to them by WS and several other authors. Although not mentioned by SGB, it is clear that CT, WS, and SGB all agree that there is no such common mechanism. However, this putative common mechanism was only one aspect of the CT model with which WS disagreed (see below).

(2) SGB stated that WS used presacral vertebral counts “as a measure of body elongation” and implied that these counts were used by WS to address the model of CT (“However, since the model proposed by Cohn and Tickle (1999) deals with. . .”). WS used only morphometric data to address body elongation (i.e., actual body measurements, not vertebral counts). The vertebral counts were used because “previous authors have suggested that elongation in serpentiform squamates is associated with an increase in the number of presacral vertebrae” (WS, p. 2309) and the results suggested that “elongation of the trunk is achieved through an increase in the number of presacral vertebrae” (WS, p. 2313). The presacral vertebral counts were not used by WS to address the model of CT.

SGB also misinterpret WS in their discussion of the two different ecomorphs of limb-reduced squamates. WS pointed out that anguillids—and squamates in general—seem to achieve similar degrees of overall body elongation in two different ways (morphologically); either through elongation of the trunk alone (in burrowers) or through elongation of both the trunk and tail (in surface-dwellers; see also Camp 1923). SGB imply that WS addressed the developmental mechanisms by which these ecomorphs arise, and suggest that WS claimed that they arose through two different developmental processes. WS never made such a claim. Furthermore, SGB claim that “changes in both of these parameters [tail and body length] are the consequences of changes in a single underlying developmental process” but their own statement in their previous sentence suggests that two distinct developmental processes may be involved (i.e., changes in vertebral number as well as changes in the position of the pelvic girdle).

(3) SGB also criticize WS for claiming that the model of CT implies that the pectoral girdle and forelimb elements should be lost at the same time (WS pointed out that they seem to be evolving independently in anguillids). However, SGB acknowledge that “Cohn and Tickle (1999) describe a mechanism that could be responsible for the loss of both pectoral girdle and forelimb bones.” In fact, CT discuss each set of limbs and girdles as if they were a single unit (e.g.,

p. 475). Thus, this criticism seemingly is contradicted both by SGB and CT.

(4) The fourth point of SGB is that different developmental mechanisms may be responsible for forelimb loss and hind limb reduction in squamates. Yet, WS never claimed that the same developmental mechanism was responsible.

A relevant question not discussed by SGB is “to what extent is the criticism of the CT model made by WS still valid?” I argue that much of this criticism remains intact, although one important aspect has now been clarified by SGB. WS rejected the model of CT (at least for anguids) because it seemingly called for (1) linkage of body elongation and limb loss, (2) simultaneous loss of the forelimb and pectoral girdle, and (3) sudden anatomical transformations in the body plan, rather than gradual evolution. As stated above, everyone (i.e., CT, WS, SGB) would agree that the first point is not an issue.

The second point may remain problematic for the CT model. No one would argue that forelimb elements and pectoral girdle elements cannot evolve independently in general, but the CT model suggests that their loss should be simultaneous (see also SGB). Our (WS) limited osteological data for anguids showed that loss of forelimbs is independent of the loss of pectoral girdle elements (i.e., all forelimb elements are absent in taxa in which pectoral girdle elements are retained). Studies of other squamate families with serpentiform taxa also show absence of all forelimb elements in many species in which one or more pectoral girdle elements are retained (e.g., amphisbaenids, dibamids, gymnophthalmids, scincids, pygopodids, trognophids; for a recent review and new data see Kearney 2002).

Similarly, there is abundant evidence that forelimb loss may occur gradually in many groups of squamates, not through “sudden anatomical transformations.” Gradations between fully limbed and limbless forms have been noted in many groups of squamates, such as scincids and gymnophthalmids (e.g., Presch 1975; Lande 1978; Caputo et al. 1995). In these groups, there are species that are fully limbed, fully limbless (at least externally), and with different degrees of limb reduction and digit loss.

The obvious counterargument is that snakes are “special” and therefore that data pertaining to the evolution of limb reduction and body form in other squamates are not relevant to snakes, or vice versa. This argument was made by SGB and was also considered as a possible explanation by WS (i.e., as an alternative to rejecting or revising the CT model). But arguments for such special, taxon-specific developmental processes (e.g., the processes of forelimb loss in snakes being different from those in other squamates) may represent dangerous ground. For example, the CT model is based on com-

paring a relatively advanced snake (a python) to a highly derived nonsquamate (a chicken). The more relevant comparison would have been to compare one or more basal snakes (e.g., a scolecophidian) to limbed squamates that are closely related to snakes. CT implicitly assume that limbed squamates that are closely related to snakes develop like chickens, and that their developmental results are not specific to (for example) birds and pythons. Similarly, many of the arguments of SGB appear to be based on the assumption that developmental results from one group of vertebrates apply universally to others (see SGB points 1, 2, and 3).

This comment is not intended as a critique of evolutionary developmental studies in general or of the CT paper in particular. Instead, I make the general point that studies of *evo-devo* and comparative morphology should strive to be as complementary as possible. For example, evolutionary developmental models should be consistent with the available evidence from comparative morphology; this does not appear to be the case with the CT model, at least as it was originally proposed. Furthermore, we should avoid developmental models that are unique to one group and inconsistent with data from closely related groups, unless these arguments for special cases are well supported and/or applied consistently. SGB have provided a valuable review and clarification of the developmental literature relating to evolution of body form in squamates, but it seems that some clarification of their clarification is required.

LITERATURE CITED

- Camp, C. L. 1923. Classification of the lizards. *Bull. Am. Mus. Nat. Hist.* 48:289–481.
- Caputo, V., B. Lanza, and R. Palmieri. 1995. Body elongation and limb reduction in the genus *Chalcides* Laurenti 1768 (Squamata: Scincidae): a comparative study. *Trop. Zool.* 8:95–152.
- Cohn, M. J., and C. Tickle. 1999. Developmental basis of limblessness and axial patterning in snakes. *Nature* 399:474–479.
- Greer, A. E. 1991. Limb reduction in squamates: identification of the lineages and discussion of the trends. *J. Herpetol.* 25:166–173.
- Kearney, M. 2002. Appendicular skeleton in amphisbaenians (Reptilia: Squamata). *Copeia* 2002:719–738.
- Lande, R. 1978. Evolutionary mechanisms of limb loss in tetrapods. *Evolution* 32:73–92.
- Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 1998. *Herpetology*. Prentice-Hall, Upper Saddle River, NJ.
- Presch, W. 1975. The evolution of limb reduction in the teiid lizard genus *Bachia*. *Bull. So. Calif. Acad. Sci.* 74:113–121.
- Sanger, T. J., and J. J. Gibson-Brown. 2004. A comment on the developmental bases of limb reduction and body elongation in squamates. *Evolution* 58:2103–2106.
- Wiens, J. J., and J. L. Slingsluff. 2001. How lizards turn into snakes: a phylogenetic analysis of body-form evolution in anguid lizards. *Evolution* 55:2303–2318.

Corresponding Editor: R. Harrison