Testing an Inference of Function From Structure: Snake Vertebrae Do the Twist

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ABSTRACT   The zygapophyses and zygosphene–zygantrum articulations of snake vertebrae are hypothesized to restrict or eliminate vertebral torsion. This hypothesis is apparently based solely on the inference of function from structure, despite the limitations of such inferences, as well as contradictory observations and measurements. In this study, I observed and measured axial torsion in gopher snakes, *Pituophis melanoleucus*. To examine the structural basis of axial torsion, I measured the vertebral articulation angles along the body and the insertion angles of five epaxial muscles. To examine torsion in a natural behavior, I digitized video images and measured the degree of apparent axial torsion during terrestrial lateral undulation. Finally, I measured the mechanical capacity of the vertebral joints for actual torsion over intervals of 10 vertebrae in fresh, skinned segments of the trunk. Vertebral articulation angles vary up to 30° and are associated with variation in torsional capacity along the trunk. The freely crawling *P. melanoleucus* twisted up to 2.19° per vertebra, which produced substantial overall torsion when added over several vertebrae. The vertebral joints are mechanically capable of torsion up to 2.89° per joint. Therefore, despite the mechanical restriction imposed by the complex articulations, vertebral torsion occurs in snakes and appears to be functionally important in several natural behaviors. Even in cases in which mechanical function appears to be narrowly constrained by morphology, specific functions should not be inferred solely from structural analyses. J. Morphol. 241:217–225, 1999.   © 1999 Wiley-Liss, Inc.

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Understanding the relationship between organismal structure and function is a fundamental goal of morphology and biology in general. In many cases in which the functions of particular structures are not easily (or cannot be) observed, mechanical analyses and modeling have been very productive in supporting functional inferences (e.g., Rudwick, '64; Wainwright et al., '76; Kingsolver and Koehl, '85; Thomason and Russell, '86; Weishampel, '93). Yet in other cases, especially seemingly obvious ones in which function appears to be narrowly constrained by structure, functions are assumed but not directly tested. However, biological structures and their functions generally have complex relationships with one another that rarely, if ever, support specific functional inferences (Gans and Gasc, '92; Lauder, '95). Vertebral torsion in snakes provides a case study in which a reasonable, long-standing functional inference from structure is not supported by experimental testing.

Snakes are unusual among vertebrates in having five points of articulation between adjacent vertebrae (Romer, '56; Hoffstetter and Gasc, '69). Three of these, at each centrum and left and right zygapophysis, represent ancestral features of vertebrates. The two additional articulations, between the left and right zygosphenes and zygantra, are unique to some squamate reptiles and are most highly developed in snakes (Hoffstetter and Gasc, '69). In an early study, Mosauer ('32) observed that the zygapophyses and

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zygosphene–zygantrum articulations oppose one another, and concluded that this architecture makes torsion at the vertebral joints "wholly impossible." Similarly, more recent reviews have assumed that the zygosphene–zygantrum articulations prevent, or at least minimize, vertebral torsion (e.g., Gans, '74; Edwards, '85; Cundall, '87). Nevertheless, this functional inference was based solely on extrapolation from structure.

Gasc ('74, '76) was the first to measure actual torsion of 1–2° between adjacent vertebrae in dried *Python* skeletons, but he argued that torsion would be restricted further in living snakes by the articular cartilages and ligaments. Cundall ('87) stated that this level of torsion is negligible, and therefore presumably functionally unimportant. However, although 1–2° of twisting may be negligible for a single joint, overall torsion can become substantial when added over many vertebrae used in axial bending movements. For example, snakes have 120 to over 350 vertebrae (Hoffstetter and Gasc, '69), and often use 20–100 of these in a single axial bend during locomotion (Jayne, '88a; Moon and Gans, '98).

Several published observations also suggest that vertebral torsion occurs in snakes. For example, axial twisting movements occur during locomotion (Gans and Mendelssohn, '72; Gasc, '74; Moon and Gans, '98), prey capture and feeding (Frazzetta, '66; Greene and Burghardt, '78; Janoo and Gasc, '92), and defense (Fitch, '63). However, the appearance of axial torsion can be produced by three nonexclusive mechanisms: differential abduction of the left and right body walls, which in dorsal view gives the appearance of rotation about the long axis, combined lateral and vertical bending (Gans and Mendelssohn, '72; Gans, '74), and actual torsion at the vertebral joints (Gasc, '74, '76). Therefore, it is important to distinguish between apparent axial torsion, which may involve the multiple mechanisms noted above, and vertebral torsion that occurs at the intervertebral joints.

In a series of studies on the functional morphology of snakes (Moon, '98), I observed axial torsion during terrestrial lateral undulation, prey capture, and constriction in gopher snakes (*Pituophis melanoleucus*). These observations suggested that gopher snakes may indeed be capable of measurable vertebral torsion. Therefore, to test the traditional hypothesis that snake vertebral articulations prevent torsion, I observed and measured the morphological, kinematic, and mechanical bases of the apparent axial torsion. The results document substantial variation in vertebral structure and function along the body, and indicate that even when morphology narrowly constrains mechanical function, inferences of function solely from structural analysis must be tested empirically.

MATERIALS AND METHODS
Specimens

For this study, I used specimens of *Pituophis melanoleucus affinis* (Pma) from southern Arizona, *P. m. deserticola* (Pmd) from Idaho, and *P. m. sayi* (Pms) from Montana. Although *P. melanoleucus* is geographically widespread and variable in external morphology, vertebral morphology was similar among individuals from the different subspecies, so the specimens were combined in the analyses.

Vertebral morphology

To examine the vertebral articulations, I digitized video images of every tenth vertebrae from four skeletons (two Pmd and two Pms) that were cleaned by beetle larvae. I then used Measurement TV (DataCrunch Software) to measure the angles between the left and right articular facets of the zygosphenes and prezygapophyses (Fig. 1).

Epaxial muscle anatomy

The epaxial muscles of snakes are hypothesized to be important axial flexors (Gasc, '74; Ruben, '77; Gasc, '81). Some of these muscles insert at oblique angles and therefore are mechanically suited to producing torsional movements. I measured the insertion angles for five epaxial muscles, the Mm. iliocostalis, longissimus dorsi, multifidis, and both parts of the spinalis-semispinalis (N = 1 Pma). Specifically, I determined the approximate vertical insertion angle of each muscle trigonometrically based on muscle–tendon length and change in height between insertions. The insertion angles also have horizontal components (Gasc, '74, '76) but these were not measured. The epaxial muscular anatomy of snakes has been described in several accounts (Pregill, '77; Gasc, '81; Jayne, '82; Moon and Gans, '98). Therefore, herein I only briefly summarize the gross muscular anatomy of gopher snakes.

A B C

Fig. 1. **A**: Anterior view of vertebra 190 of *Pituophis melanoleucus*. **B**: The articulation angles measured in this study. **C**: The centers of rotation of the centrum (C), pre- and postzygapophysis (P), and zygosphene–zygantrum (Z) articulations.
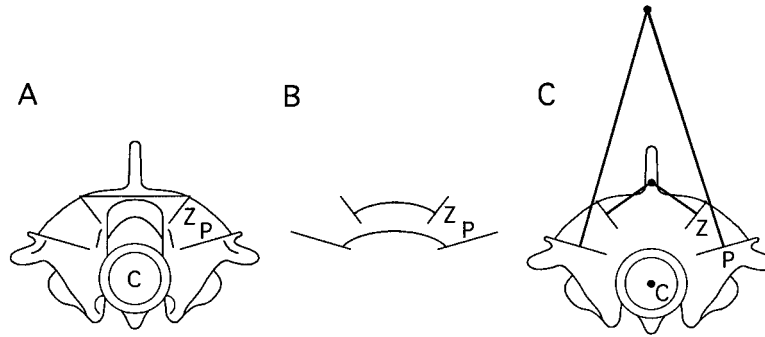
Apparent locomotor torsion

To measure the apparent axial torsion during locomotion, I digitized macro dorsal video images of terrestrial lateral undulation in three gopher snakes (Pma) that were painted with a white stripe along the vertebral midline and a white crossbar at every tenth vertebra. The mid-dorsal skin of most snakes (e.g., Lissmann, '49; Jayne, '88b), including gopher snakes (Pregill, '77), is tightly connected to the neural spines by thick connective tissue that prevents the skin from sliding relative to the vertebral midline. In gopher snakes, the connection of the mid-dorsal skin to the neural spines is so strong that it is difficult to remove the skin from the midline during dissection; in living snakes, the skin cannot be pulled laterally from the vertebral midline by hand or with toothed forceps. Therefore, the painted midline stripe is an acceptable landmark for measuring apparent axial twisting.

The video images recorded the snakes crawling on a smooth, painted plywood board and pushing against a single plastic peg that projected from the center of the board. From these video images, I used Measurement TV to measure the position of the vertebral midline relative to the left and right body walls over lengths of 10 vertebrae in the bend immediately posterior to the point of contact with the peg. Measurements were restricted to the trunk between vertebrae 80 and 130, where the width of the body was uniform. I used a computer spreadsheet to calculate apparent torsion using the relation $T = \arcsin(d/r) * (180/\pi)$, where T = torsion, d = lateral displacement (in dorsal view) of the vertebral midline relative to the body walls over intervals of 10 vertebrae, r = the radius of the snake trunk, and $180/\pi$ converts the value from radians to degrees. I then divided the value by 10 to calculate the torsion per vertebral joint.

Two potential sources or error may complicate these measurements. The calculation of three-dimensional torsion from two-dimensional video images is prone to large error at rotational displacements beyond ca. 30–45° because the amount of lateral displacement per unit of twisting decreases in the two-dimensional dorsal view as rotation increases. Nevertheless, the measurements should be accurate over the limited rotations (up to ca. 20° over 10 vertebrae) exhibited by gopher snakes. In addition, abduction of the ribs and body wall on one side combined with their adduction on the other side would give the appearance in dorsal view of the vertebral midline twisting toward one side in the absence of real twisting. To evaluate the contributions of such movements, as well as of lifting, I made close-up visual observations during all video recordings. Differential movement of the ribs and body wall occurred immediately anterior to the peg, but appeared to be absent from the trunk posterior to the peg, where axial torsion was measured. Therefore, the two-dimensional video measurements provide valid, but preliminary, estimates of axial torsion. I present these data to supplement published observations (see Discussion) indicating that vertebral torsion occurs during natural behaviors. More rigorous three-dimensional methods are needed to make more precise measurements of vertebral torsion in freely moving snakes.

Vertebral capacity for torsion

To measure the capacity of gopher snake vertebrae for actual torsion, I prepared fresh, skinned segments of the body including 20–30 vertebrae from six specimens (four
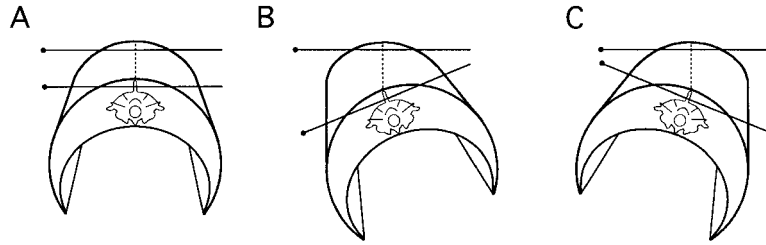
Fig. 2. Method for measuring the capacity for vertebral torsion. **A**: Method of inserting pins horizontally through the dorsal tissues between the neural spines. **B,C**: The section of 10 vertebra was twisted maximally toward the left and then the right without inducing any axial bending. The anterior end of each 10 vertebra section (the end facing into the page, away from the reader) was immobilized in a clamp (not shown). The maximal rotations were digitized and the torsional capacity measured as described in Materials and Methods.

Pmd and two Pma). I clamped each segment at one end, then placed a dissecting pin horizontally through the specimen at the clamped end and at the tenth vertebra from the first pin. I then twisted the free end by hand, digitized video images of maximal left and right rotations (which allowed me to control for differences in starting angle), and measured the angles between the pins at each rotational limit (Fig. 2). The video camera was mounted horizontally and the specimen held horizontally so that its long axis was perpendicular to the video camera. The limits of twisting were clearly detectable and were reached before the movement produced any axial bending. I divided the total rotation by two to calculate the capacity for torsion in one direction, and then divided the value by 10 to calculate the torsion allowed at each vertebral joint. To test for a significant difference in torsion between vertebra 10 and all further posterior vertebrae, I used a one-sample t-test and a significance level of $\alpha = 0.05$

RESULTS
Vertebral morphology

The pre- and postzygapophyses are situated at the upper limit of the centrum and the base of the neural arch. The angle between left and right prezygapophyses in these gopher snakes varies from 154.4–184.8° along the trunk (mean ± SD = 161.14 ± 7.04, N = 4; Fig. 3). In the first 10–20 vertebrae, the zygapophyses are very small and nearly horizontal; because the articular angles are slightly greater than 180 in these vertebrae, the facets face dorsolaterally and the centers of rotation are below the articular facets. The articular facets are most inclined in the midtrunk, then be-

come more horizontal again toward the tail (Fig. 3). Therefore, the zygapophyseal angles of the midtrunk are the most steeply inclined and have centers of rotation well above the vertebrae (Fig. 1).

The zygosphene–zygantrum articulation occurs at the dorsolateral limits of the neural canal, just below the base of the neural spine. The mean angle between left and right zygosphenes varies slightly along the trunk from 63.4–79.7° (mean ± SD = 73.6 ± 3.73, N = 4; Fig. 3). The centers of rotation of these articulations are well above centra along the entire trunk (Fig. 1). As in the zygapophyseal articulations, the inclination of the zygospheneal articular facets is least in the neck and greater posteriorly (Fig. 3). The zygospheneal and zygapophyseal articulations are oriented 45.5–52.6° from one another.
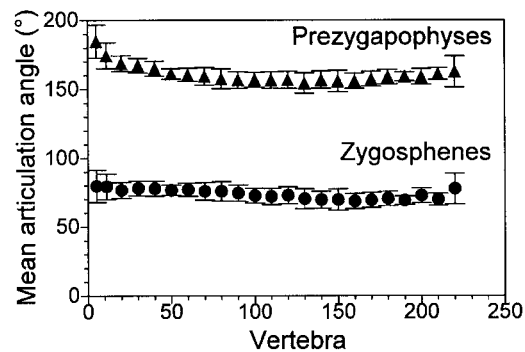

Fig. 3. Mean ± SD angles (N = 4 specimens) between left and right articular facets of the prezygapophyses and zygosphenes along the trunk of *Pituophis melanoleucus*.

Epaxial muscle anatomy

Several of the axial muscles insert on the vertebrae at oblique angles and thus are mechanically suited to producing both lateral bending and torsional movements. All of the angles reported here are for the vertical plane and are relative to the long axis of the vertebral column; positive angles indicate that the muscle–tendon elements are aligned anterodorsal to posteroventral and negative angles indicate anteroventral to posterodorsal alignment. Three of the epaxial muscles interconnect via long tendons to form a complex muscle–tendon chain that spans 22 vertebral joints and has four insertions (Fig. 4). The M. longissimus dorsi originates from the prezygapophyseal process, spans four joints, and has a bifurcating anterior tendon that is continuous ventrally with the M. iliocostalis and dorsally with the M. spinalis-semispinalis. The anteroventral tendon of the M. longissimus dorsi extends anteriorly for four joints at an angle of ca. $-6°$ and is continuous with the M. iliocostalis. The M. iliocostalis spans seven joints, has an anterior tendon that extends five more joints, and inserts on a rib at an angle of ca. $-6°$. The anterodorsal tendon of the M. longissimus dorsi extends four joints anteriorly at an angle of ca. $8°$ and is continuous with the M. spinalis-semispinalis. The two parts of M. spinalis-semispinalis have separate posterior insertions, but share a long anterior tendon and insertion. The spinalis part of the M. spinalis-semispinalis spans three joints and inserts posteriorly by slips onto the lateral surface of the neural spine and the tendon of the M. multifidis; the insertion angle is ca. $-15°$. The fibers of the semispinalis part span four joints. Anteriorly, the long tendon of the M. spinalis-semispinalis spans 10 joints and inserts on the dorsal posterior edge of a neural spine at an angle of ca. $3°$.

Although the M. multifidis gives rise, via its posterior tendon, to a few small slips of the M. spinalis, it is otherwise separate from the epaxial muscle–tendon chain. The M. multifidis arises via a tendon from the posterolateral edge of a neural spine, extends anteroventrally over 2–4 vertebral joints, and inserts at an angle of ca. $-20°$ onto the posterior surface of a postzygapophyseal process.

Apparent locomotor torsion

Gopher snakes moving by lateral undulation at speeds of 0.02 to 0.12 m/s formed lateral bends that encompassed 22–48 vertebrae per half-wavelength. Between vertebrae 80 and 120, the lateral bends showed a mean ($\pm$SD) apparent torsion of $0.64 \pm 0.20°$ per vertebral joint (range $= 0.02$–$2.19°$ per joint, N = 3). The degree of apparent torsion increased when the snakes were moderately restrained, by hand, from free movement.

Close-up visual observations made during the video recordings indicated that lifting of the vertebral column did not occur, which ruled out combined lateral and vertical bending as the source of the apparent torsion. There appeared to be moderate differential abduction of the left and right body walls around the anterior surface of the peg against which the snake pushed. However,
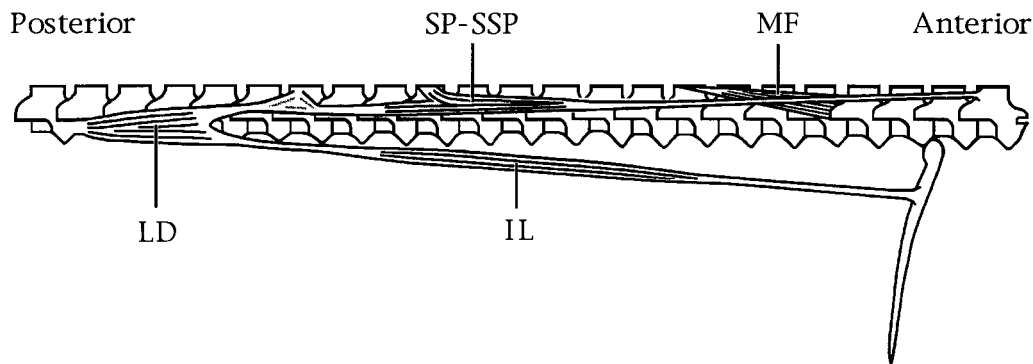

Fig. 4. Epaxial muscular anatomy of the midtrunk of the gopher snake, *Pituophis melanoleucus*. IL = M. iliocostalis, LD = M. longissimus dorsi, MF = M. multifidis, SP-SSP = M. spinalis-semispinalis. The oblique insertions (described in the text) suggest that these muscles can contribute to longitudinal twisting of the vertebral column.

differential rib movements were not apparent in the trunk posterior to the peg, where the apparent torsion was measured. Furthermore, slight twisting of the trunk clearly occurred, and appeared to contribute to postural deformation around the peg.

Vertebral capacity for torsion

The trunk vertebrae allow actual torsion of 1.64–2.89° per vertebral joint (mean ± SD = 1.95 ± 0.29°; Fig. 5). This torsion was reached without inducing any axial bending; however, the amount of torsion could be increased slightly by twisting the trunk segment so far that lateral and vertical bending were forced to occur. The capacity for torsion at vertebra 10 is significantly higher than in a combined sample of the rest of the trunk vertebrae (mean ± SD = 3.03 ± 0.65 vs. 1.93 ± 0.20, t_4 = 10.44, $P < 0.001$; N = 6; Fig. 5). Torsional capacity decreases from the first 10 vertebrae posteriorly to approximately vertebra 20, where it appears to become roughly stable throughout the rest of the trunk.

DISCUSSION
Mechanisms of torsion in natural behaviors

The axial twisting movements observed in many snakes may be produced by combined lateral and vertical bending, without any torsion at the vertebral joints (Gans and Mendelssohn, '72). For example, axial twisting during snail extraction by *Dipsas indica* appears to result largely from combined lateral and vertical bending of the neck (Fig. 1 of Sazima, '89). Snail extraction in *Storeria*

Fig. 5. Mean ± SD values (N = 6 specimens) of vertebral torsion measured in unpreserved, skinned segments of the trunk of *Pituophis melanoleucus*.

dekayi involves cervical twisting of 180–270°, which involves some lateral and vertical bending (Fig. 1 of Rossman and Myer, '90), but also suggests the contribution of vertebral torsion. The sea snake *Fordonia leucobalia* twists the legs off of crabs (Shine, '91), although it is unclear whether the twisting movements involve both lateral and vertical bending movements.

In contrast to movements that involve combined lateral and vertical bending, many twisting movements appear to involve lateral bending with little or no vertical bending; qualitative examples include terrestrial lateral undulation (Gasc et al., '89; Moon and Gans, '98), rolling over and righting during death-feigning in *Heterodon* species (Platt, '69), and the "initial twist" of a constriction coil (Greene and Burghardt, '78). Furthermore, many of the twisting movements exhibited by snakes often involve little or no axial bending. For example, twisting can approach 90° in apparently straight sections of the neck during prey capture in some pythons (Frazzetta, '66) and vipers (Janoo and Gasc, '92). Perhaps the most pronounced and vigorous twisting movements occur in defensive or escape movements in racers (*Coluber constrictor*) and whipsnakes (*Masticophis* species), which can twist their bodies quickly and strongly enough to sever their tails (e.g., Fitch, '63). Similarly, I have observed vigorous twisting in freshly captured *Masticophis bilineatus* while I intentionally held them straight, which suggests that the twisting movements can occur without lateral or vertical bending. All of these descriptions of twisting movements were brief and based on qualitative observations; quantitative studies are clearly needed for better documentation of twisting movements in snakes. Nevertheless, some of these observations, particularly of twisting movements that occur with little or no axial bending, strongly indicate the occurrence of vertebral torsion in natural behaviors.

Although apparent torsion may be produced by several mechanisms, my close-up observations of crawling gopher snakes revealed that at slow to moderate locomotor speeds, lifting of the trunk is negligible, which rules out combined lateral and vertical bending as the source of the apparent torsion. Furthermore, if the axial torsion apparent in dorsal view results solely from differential movement of the body walls, then
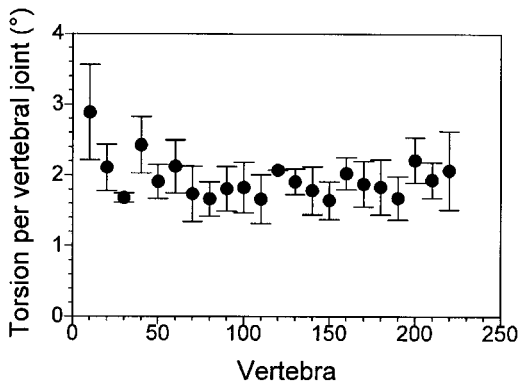
close-up observations should reveal that the vertebral midline does not twist along its axis. Although differential abduction of the left and right body walls appears to occur in parts of some axial bends, actual twisting of the vertebral midline is also visible.

Several of the axial muscles insert on the vertebrae at angles and therefore are mechanically suited to producing torsional movements. However, the forms of the vertebral articulations, particularly the opposing zygospheneal and zygapophyseal articular facets and their noncoincident centers of rotation (Fig. 1), indicate that the articulations do severely restrict torsion at the vertebral joints. Nevertheless, these articulations allow 1.64–2.89° of torsion per vertebral joint, which is sufficient to produce the maximum torsion of 21.9° over the 10 vertebrae that I observed in crawling snakes. This range of torsion in gopher snakes is consistent with the torsion of 1–2° per vertebra recorded by Gasc ('74, '76) in *Python* skeletons. Furthermore, because many kinds of movements in snakes involve large numbers of vertebrae (Gasc, '74; Jayne, '88a; Gasc et al., '89; Moon, '98; Moon and Gans, '98), even this slight torsion per joint can become substantial when added over the many vertebrae used in snake movements.

It is important to note that the measurements reported here for skinned, fresh material indicate the maximal capacity of *Pituophis melanoleucus* vertebrae for torsion, not the degree to which they actually twist in various natural movements. Snakes probably only rarely use their full capacity for vertebral torsion, such as for vigorous antipredator movements.

Anatomical basis of torsion

The largest capacity for torsion occurs in the anteriormost 10–15 vertebrae (Fig. 5), and appears to be related to the very small zygospheneal and zygapophyseal articular facets, and the nearly horizontal orientation of the zygapophyses. This large capacity for torsion in the neck is consistent with published observations of substantial twisting in the neck of snakes during prey capture (Frazzetta, '66; Janoo and Gasc, '92). Posteriorly, the angles of the zygapophyses increase by as much as 30°, concomitant with a lower capacity for torsion than in the first 10 vertebrae.

Longitudinal variation in vertebral morphology

Longitudinal variation in vertebral morphology has been reported in both fossil (Rage and Albino, '89; LaDuke, '91) and living snakes (Johnson, '55; Hoffstetter and Gayrard, '65; Hoffstetter and Gasc, '69; Gasc, '74, '76). However, systematic variation in vertebral articulation angles is not well known. In addition to having potential functional consequences, the substantial variation in zygospheneal and zygapophyseal angles along the trunk suggests that the systematic utility of these characters is less than commonly assumed (e.g., Holman, '95, p. 98). The occurrence of zygapophyseal angles greater than 180° (i.e., laterally oriented facets) only in the first 10 vertebrae calls into question both the inferred longitudinal position of isolated fossil snake vertebrae and the reliability of these angles for identifying fossil taxa. For example, each of the fossil taxa *Russellophis*, *Dolniceophis*, and *Elaphe nebraskensis* is known from a single vertebra that is inferred to be from the midtrunk but has laterally oriented zygapophyses (Rage, '84), which are characteristic only of the 10–15 most anterior vertebrae in gopher snakes. If vertebral morphology in other snakes parallels the longitudinal variation observed in gopher snakes, then it is possible that these fossil vertebrae are from the anterior trunk, and may not represent distinct taxa. Intracolumnar variation in vertebral morphology of the older fossil snake *Dinilysia patagonica* appears to be consistent with that of gopher snakes (Rage and Albino, '89), which gives some support to this conclusion and suggests that intracolumnar variation in articular morphology occurred in ancestral snakes. Clearly, longitudinal variation in snake morphology needs to be accounted for in functional, paleontological, and systematic studies.

Inferring vs. testing function

Biologists have long inferred function from form (Russell, '16). However, biological structures and their functions generally have complex relationships with one another that rarely support specific functional inferences based solely on structural analyses (Gans and Gasc, '92; Lauder, '95). Such complex structure–function relationships occur for several reasons. For example, individual structures usually support multiple functions (e.g., Garland and Huey, '87; Dudley

and Gans, '91; Moon, '98); multiple structures, such as muscles and bones, can be required to control a single function (e.g., Reilly and Lauder, '89; Nishikawa et al., '92; Nishikawa and Gans, '96); functional differences can occur without structural differences (e.g., Kingsolver and Koehl, '85; Sanford and Lauder, '89); and structural differences can occur without functional differences (Lauder and Shaffer, '88). Furthermore, structure–function relationships often vary in different environments (e.g., Lauder and Shaffer, '88; Frolich and Biewener, '92).

Despite these complexities, snake vertebral articulations provide a seemingly clear example in which structure narrowly constrains function. Even qualitative mechanical analyses clearly indicate that the opposing zygapophyses and zygosphene–zygantrum articulations limit the range of torsion that can occur at the vertebral joints of snakes. However, assumptions that vertebral torsion is "wholly impossible" (Mosauer, '32), minimal (Gans, '74), or "negligible" (Cundall, '87) are very specific functional inferences that neglect to consider factors that may mediate the apparent mechanical constraints on vertebral torsion. As noted above, oblique muscle insertions may contribute to torsional movements, and even small amounts of torsion per joint are additive over many vertebrae. Therefore, even apparently obvious cases in which function appears to be narrowly constrained by structure must be tested empirically.

CONCLUSIONS

Many published observations of axial twisting movements in snakes indicate a capacity for vertebral torsion. The gopher snakes examined here clearly have the muscular and mechanical capacity for vertebral torsion and exhibit vertebral torsion in some natural behaviors. Furthermore, variation in the capacity for torsion along the trunk appears to parallel variation in vertebral morphology. Although more direct measurements of torsion are needed to determine the amount of twisting that snakes undergo during natural behaviors, the current experimental results refute the hypotheses that vertebral torsion is impossible or negligible in snakes. Vertebral torsion is restricted by the compound articulations, but it does occur in a variety of natural behaviors and can be substantial when added over the many vertebrae involved in snake movements. These results highlight the importance of empirically testing functional inferences derived solely from structural analyses.

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