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**Morphology and Function of the Ophidian Vertebral Column: Implications for the
Paleobiology of Fossil Snakes**

A Dissertation Presented

by

Jacob Alexander McCartney

to

The Graduate School

in Partial Fulfillment of the

Requirements

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Doctor of Philosophy

in

Anatomical Sciences

Stony Brook University

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Abstract of the Dissertation

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Snakes are a speciose, ecologically diverse clade with an evolutionary history spanning the past 100 million years. This diversity makes them an excellent group for study, particularly given their importance in extant faunas. However, the fossil record of snakes is primarily composed of isolated vertebrae, owing to the great number of these elements and loosely articulated nature of the skull. This means that any study of the paleobiology of extinct snakes must rest primarily on vertebrae. The purpose of this dissertation is to add to the current knowledge of snake vertebral ecomorphology, and to begin to extend that understanding to the fossil record.

This is accomplished by two approaches. The first is a pair of studies of the variation within the column of single individuals (intracolumnar variation). The first study is of basal snakes, including the scolecophidian *Afrotyphlops lineolatus*, and three alethinophidians: the boid *Boa constrictor*, the xenopeltid *Xenopeltis unicolor*, and the pythonid *Python molurus*. The second study is of caenophidians (“advanced” snakes), and includes the acrochordid *Acrochordus javanicus*, the colubrine *Pituophis melanoleucus*, the natricine *Nerodia taxispilota*, and the pseudoxyrhophiine *Leioheterodon madagascariensis*. In each snake, a series of 20 measurements was made on each vertebra in the column; two measurements were replaced in the cloacal and caudal regions because of differing morphology resulting in a total of 22 measurements. When plotted against vertebral position, the measurements revealed the pattern of change in morphology throughout the trunk in these snakes. The results show that almost all snakes have a distinct anterior trunk region characterized by tall neural spines and hypapophyses. The results also indicate that some snakes have decreased regionalization of the column. The phylogenetic distribution of this homogenization indicates that multiple lineages have evolved this pattern of intracolumnar variation.

The second part of this dissertation is a study of the relationship between ecology and the number of vertebrae. Vertebral number is correlated with locomotory performance in other animals as well as some snakes. I therefore modeled the evolution of body segment number to see if it is under selection based on several ecological parameters, or if it is essentially a random walk (Brownian motion). The first step was to test for the presence of directional evolution throughout the clade toward higher counts, using BayesTraits to create the models. Directional evolution was not preferred to the null hypothesis of undirected evolution. The second step was to test for selection toward certain optimal body segment numbers based on ecological parameters. Three models of explicit selection using Ornstein-Uhlenbeck processes were explicitly tested, in addition to the null hypothesis of Brownian motion: one model of a single global optimum for all of snakes, a second of two optima, with snakes separated by mode of prey subjugation (constriction vs. nonconstriction), and a third of four optima, with snakes separated by habitat preference (aquatic, arboreal, fossorial, terrestrial). The results strongly support the presence of selection over a random walk; furthermore, there is support for the four-optima model using habitat preference.

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Chapter 1

Introduction

Snakes are among the most distinctive of all tetrapods due to their greatly elongate, limbless body form, which has important consequences for virtually all aspects of their behavior. This body plan differs radically from that of most other squamate reptiles (i.e., “lizards”), which typically retain a far more generalized tetrapodal morphology. Despite the extreme anatomical specializations that they exhibit, snakes have evolved over the course of the last 100+ million years into a highly successful and speciose clade, currently thought to include between 2500 and 3000 species (McDiarmid et al., 1999), which collectively represent approximately 10% of all recognized tetrapod diversity. Moreover, snakes inhabit almost every ecological niche available to them across their nearly worldwide distribution and consequently have evolved great diversity in their locomotory and feeding repertoires.

Given their importance in extant faunas, it is unfortunate that snakes present a distinct problem to the student of paleoherpetology. The nature of their skeletons, being a long series of vertebrae and ribs posterior to a delicate and unfused skull, results in a fossil record that is composed primarily of isolated vertebrae (e.g., Rage, 1984; Holman, 2000). As a result, vertebral morphology is inordinately important in understanding the course of ophidian evolution. In spite of this, snake vertebral morphology is understudied, perhaps because of the complexities of the musculo-skeletal system of these animals (Meckel, 1821; d'Alton, 1834c, b, a; McKay, 1890; Mosauer, 1935; Auffenberg, 1958, 1961, 1966; Gasc, 1967, 1974; Pregill, 1977; Jayne, 1982), the perceived conservatism across taxa, and most importantly the variation in vertebral morphology within a single individual (intracolumnar variation) that has been studied in only a handful of species (Sood, 1948; Hoffstetter, 1960; Hoffstetter and Gayraud, 1964; Gasc, 1967; Hoffstetter and Gasc, 1969; Gasc, 1974; Smith, 1975; Szyndlar, 1984; Hecht and LaDuke, 1988; LaDuke, 1991b, a; Schaal et al., 2005).

However, vertebral morphology has potential to provide insight into the biology of extinct snakes. By virtue of their near or complete limblessness, snakes rely on their vertebral column completely to perform functions that in most other animals are done by the limbs. Locomotion is brought about largely through movements of the vertebral column (except in the case of rectilinear locomotion; Mosauer, 1932b, a; Wiedemann, 1932; Bogert, 1947; Lissmann, 1950); prey is acquired using the trunk to propel the head forward (Greenwald, 1978; Ruben and Geddes, 1983; Kardong and Bels, 1998; Cundall and Greene, 2000; Smith et al., 2002; Alfaro, 2003; Cundall et al., 2007); and prey may be subjugated by use of the trunk in constriction (Ditmars, 1912; Willard, 1977; Greene and Burghardt, 1978). The importance of the trunk in these various behaviors suggests an avenue of study comparing vertebral morphology to various aspects of snake biology, such as locomotion and feeding.

The benefit of such research would be to open up more than 100 million years of evolution to study. The questions surrounding snake evolution have been among the most controversial in the field of vertebrate evolution over the course of the last fifteen years. Chief among these is whether snakes derived from terrestrial or aquatic ancestors. Proponents of the aquatic origin of snakes suggest that a series of elongate marine squamate fossils represent successive outgroups to snakes, and provide an intermediate link in morphology between highly elongate, limbless snakes and fully aquatic, paddle-limbed mosasaurs (e.g., Lee and Caldwell,

2000). There is also evidence in the morphology of the eyes of snakes that suggests to some researchers an aquatic origin of Serpentes (Caprette et al., 2004). However, proponents of a terrestrial origin of snakes point to recent molecular data that suggest snakes are related to primarily terrestrial iguanian and anguimorph lizards (e.g., Townsend et al., 2004; Vidal and Hedges, 2004, 2005; Vidal and Hedges, 2009), and to significant differences in the morphology of the braincase between snakes and mosasaurs (Rieppel and Zaher, 2000), and again to eye anatomy (Walls, 1940).

Another contentious debate surrounds the origin of the feeding mechanism employed by some snakes, allowing them to eat whole prey larger in diameter than their own head. Based on optimization of characters related to feeding on traditional morphological phylogenies, snakes were long interpreted to be plesiomorphically small-object feeders, gradually evolving the kinetic skulls that allowed them to eat considerably larger prey throughout the course of snake evolution (e.g., Gans, 1961; Frazzetta, 1970; Greene, 1983). The evolution of macrophagy under this model is thought to have been facilitated by the development of constriction, which allows snakes to first kill and then eat large and potentially dangerous prey with less risk of trauma (Greene and Burghardt, 1978). The evolution of macrophagy then characterizes, at least in large part, the clade Macrostromata in morphology-based phylogenetic analyses. However, molecular phylogenies find that the macrophagous condition was plesiomorphic for Alethinophidia (Vidal and Hedges, 2002; Lawson et al., 2004; Gower et al., 2005; Vidal et al., 2007a; Wiens et al., 2008; Pyron and Burbrink, 2012; Pyron et al., 2013b), or perhaps even for Serpentes (Vidal and David, 2004). Under this hypothesis of evolution, the key innovation allowing snakes to feed on large prey was the loss of the pectoral girdle that would otherwise prevent the swallowing of extremely large food items (Vidal and Hedges, 2009).

There has also been a recent interest in examining snakes as climatological indicators. As ectothermic organisms, snakes are strongly affected by environmental conditions, particularly with respect to temperature (Huey, 1982). As a result, snakes may be a useful group for examining various aspects of environmental change, including increasing global temperatures and the attendant shifting of habitats. Snake species ranges are already known to have changed following the most recent glaciation (Lawing and Polly, 2011), and climate change is hypothesized to be the reason for the sudden explosion of colubroid snakes in the early Miocene (Savitzky, 1980). Previous workers have noted the tendency for ectotherms to be smaller in cooler environments (Cowles, 1945), and have used the size of fossil snakes to make inferences about the local paleoclimate (Cowles, 1945; Brattstrom, 1967; Head et al., 2009). Relative tail length has also been linked to macrovegetation in extant snakes (Lawing et al., 2012).

This dissertation is a contribution to the study of snake vertebral morphology, and the relationship of that morphology to snake ecology (Ricklefs and Miles, 1994; Wainwright, 1994). There are three parts to this study. The first two parts are a study of intracolumnar variation in both basal snakes and in “advanced snakes” (Caenophidia). This lays the groundwork for future study of snake vertebral morphology, both in a paleontological and neontological context. The last part is a study of the relationship between vertebral number and ecology. Taken together, the studies in this dissertation explore multiple aspects of the vertebral column of snakes and what the morphology can tell of the biology of snakes.

Intracolumnar variation (defined above) has led to difficulties in the study of fossil snakes. Contributing to this difficulty is the fact that snakes are limbless (or nearly so), having lost all vestiges of the pectoral girdle and forelimbs, and with them any clear indication of a neck

beyond the atlas-axis complex. The earliest authors made little attempt to distinguish sub-regions within the ophidian vertebral column, instead referring to just two regions, the precaudal (called presacral by Hoffmann, 1890) and caudal (called postsacral by Hoffmann, 1890) regions (Meckel, 1821; d'Alton, 1836). One notable exception is de Rochebrune (1881) who separated the column into five regions, to which he applied the terms cervical, thoracic, lumbar, pelvic, and caudal. His point of view was generally disregarded on the grounds that the variation was too small and gradual, and furthermore his terminology was suspect, implying homologies with other groups that were difficult to prove (Hoffmann, 1890). More modern authors have taken a somewhat similar approach to further subdividing the column, however. It is now established that snakes have three generally separable vertebral types (Hoffstetter and Gasc, 1969): trunk vertebrae (extending posteriorly beyond the third vertebra), cloacal vertebrae (characterized by lymphapophyses), and caudal vertebrae (typically characterized by haemapophyses and pleurapophyses). Other authors have attempted to further subdivide the vertebral column. Sood (1948) retained de Rochebrune's (1881) divisions of the trunk, including the pelvic region in the caudal region and further splitting the caudals into two groups (Sood, 1941). The most recent detailed treatment of intracolumnar variation in snakes subdivided the trunk vertebrae into anterior trunk, mid-trunk, posterior trunk, and precloacal vertebrae, and provided characters to distinguish them from one another (LaDuke, 1991b). This terminology has become the standard in the field. LaDuke (1991a) was careful to state that his descriptions were restricted to North American colubrids, and perhaps were not applicable to other snakes, but several authors have been successful in applying these characters to other clades (e.g., Scanlon, 1997; Rage et al., 2004; Head, 2005; LaDuke et al., 2010; Smith, 2013).

Quantitative studies of variation within the column of a single snake are uncommon, likely owing the great number of vertebrae involved. Studies began in the 1960s, and were limited to a few taxa (Hoffstetter, 1960; Hoffstetter and Gayrard, 1964; Gasc, 1967; Thireau, 1967b, a). The primary aim of this research was to elucidate phylogenetic relationships, and thus only certain measurements were taken based on perceived phylogenetic importance. The earliest work done with a functional aim was that by Gasc (Gasc, 1967, 1974), in an integrated study of the axial musculoskeletal system. However, as in studies by previous authors, he limited the number of measurements taken, both in terms of metrics and in terms of number of vertebrae measured. Since this time, the study of intracolumnar variation has been undertaken by paleontologists in order to avoid over-splitting the fossil record (Smith, 1975; Szyndlar, 1984; Schaal et al., 2005). Although variation in the axial column is gradual when viewed in a complete column, isolated vertebrae from distant points in the same column have distinct morphology that can be mistaken for the difference between species, something that should be avoided.

Quantifying the intracolumnar variation in a large number of vertebral features across a taxonomically and ecologically broad sample of snakes would be useful to both paleontologists and functional morphologists. It could reveal general regions of potential functional interest, and details of the change in size of functionally important processes providing attachment to trunk flexors and extensors. In addition, it could reveal regional patterns that can be used to sort through isolated fossil vertebrae, and possibly prevent splitting one species into two or more.

In order to quantify the variation in morphology throughout the column of extant snakes, a series of 22 measurements were made throughout the vertebral column in a limited but carefully chosen sample of snakes of disparate body shape, ecology, and phylogeny. Two of

these measurements are represented only in the caudal region, but they replace measurements in the trunk so that a total of 20 measurements could be made on any particular vertebra. Some of these measurements are novel and others have been described by previous authors (Johnson, 1955; Hoffstetter, 1960; Auffenberg, 1963; Hoffstetter and Gasc, 1969; Gasc, 1974; LaDuke, 1991b). For the first study, that of basal snakes, five snakes were included: the typhlopid *Afrotyphlops lineolatus*, the tropidophiid *Tropidophis haetianus*, the boid *Boa constrictor*, the xenopeltid *Xenopeltis unicolor*, and the pythonid *Python molurus*. The second study focused on caenophidians (“advanced snakes”) and included four species: the acrochordid *Acrochordus javanicus*, the colubrids *Pituophis melanoleucus* and *Nerodia taxispilota*, and the pseudoxyrophiine *Leioheterodon madagascariensis*. Of these species, previous quantitative studies of intracolumnar variation exist only for *Boa constrictor* (Schaal et al., 2005) and *Acrochordus javanicus* (Hoffstetter and Gayrard, 1964). These studies are together the first to examine variation in several features across multiple taxa.

Although the ancestry of snakes is poorly understood and controversial (Forstner et al., 1995; Lee, 2000; Lee and Caldwell, 2000; Townsend et al., 2004; Vidal and Hedges, 2004, 2005; Conrad, 2008; Vidal and Hedges, 2009), the vast majority of non-ophidian squamates do not have nearly as many vertebrae as do snakes. Snakes have a wide range in the number of vertebrae making up the column, ranging from just over 100 to more than 500 in the case of the extinct *Archaeophis proavus* (Janensch, 1906; Alexander and Gans, 1966; Lindell, 1994; Lindell, 1996; Shine, 2000). The majority of lizards do not have vertebral counts near this range, particularly in the precloacal region, although some non-snake limbless clades reach the lower end of this range (Hoffstetter and Gasc, 1969).

The pattern of vertebral number evolution in snakes has received increasing attention in recent years. Whereas the earliest authors contented themselves to simply report vertebral counts (e.g., de Rochebrune, 1881), more recent workers have begun to consider evolutionary questions of vertebral number. The broadest study examined pleomerism (i.e., increased vertebral number in longer animals; Lindsey, 1975) in caenophidians, and found that there was indeed evidence for pleomerism both within and among caenophidian clades (Lindell, 1994). Other research indicates that snake vertebral counts may vary by temperature (Klauber, 1941) as they do in fish and salamanders (Peabody and Brodie, 1975; Baumann et al., 2012), although Lindell (1994) did not find evidence to support this.

There are functional considerations for vertebral number as well. Vertebral counts are known to be related to performance in fish (Swain, 1992; Brainerd and Patek, 1998; McDowall, 2003) and lacertid lizards (Van Damme and Vanhooydonck, 2002). Vertebral number and ventral scutes have a one-to-one ratio in most terrestrial snakes (Alexander and Gans, 1966), and studies of ventral counts are correlated with performance in some snakes (Arnold and Bennett, 1988; Kelley et al., 1997; Hampton, 2011). Previous work has shown that constrictors have high vertebral counts, presumably to increase the number of flexion points available to allow formation of tighter coil radii (Jayne, 1982). On the opposite end of the spectrum are fossorial snakes with fewer vertebrae (Marx and Rabb, 1972), presumably to increase stability in the trunk during head-first burrowing (Shine and Wall, 2008). In arboreal snakes, although soft-tissue morphology like longer epaxial muscle tendons (Jayne, 1982) and a lightweight, gracile form may provide extra support during gap-bridging behaviors, it is also possible that vertebral number has an influence. Johnson (1955) found that arboreal snakes had longer and narrower vertebrae than other snakes, suggesting that they may have fewer, longer vertebrae for better

support during cantilevering. Previous work has found that vertebral number is indeed under selective pressure in garter snakes (Arnold, 1988), suggesting that further investigation of vertebral number with relation to ecology may bear interesting results.

In order to study the evolution of snake vertebral number, I constructed an Ornstein-Uhlenbeck model (OU). Ornstein-Uhlenbeck methods model the evolution of traits as if they are under selection (Hansen, 1997). The sample was broken into different ecological groups, and differences in the selected traits were tested for in the context of selection. The fit of such a model was compared with that of a random-walk model of Brownian motion, and the best fitting model chosen (Butler and King, 2004). The OU model has the benefit of also providing estimates of drift and selection, as well as optimal values for the feature of interest within each group. In this study, I compared the Brownian model with OU models of snakes broken into two groups (constrictors and non-constrictors), as well as snakes broken into four groups based on habitat preference (aquatic, arboreal, fossorial, and terrestrial).

Chapter 2

Regional vertebral morphology and intracolumnar variation in basal snakes (Reptilia, Serpentes)

Abstract

The vertebral column of snakes is composed of many serially repetitive elements that differ very gradually throughout the column. This variation is poorly understood and has been an impediment for both paleontologists and functional morphologists. This study investigates the patterns of intracolumnar variation in five basal snakes (one scolecophidian and four basal alethinophidians) by means of a series of 22 measurements taken on all vertebrae throughout the column. Some vertebral features show similar patterns of intracolumnar variation among all taxa sampled, regardless of their ecology or phylogenetic position. These include the absolute vertebral length, which consistently reaches a maximum near the midpoint of the precloacal column. However, relative vertebral length as estimated by the ratio of centrum length to neural arch width, continues to increase throughout the posterior trunk. When compared to the minimum width of the neural arch, the width across the prezygapophyseal accessory processes (the most laterally placed sites of axial muscle attachment) is relatively greatest in the posterior trunk, although this width is less variable relative to centrum width. However, when compared to vertebral length, the width across the prezygapophyseal accessory processes is relatively greatest at about one-third of precloacal vertebral number, except in the phylogenetically and ecologically distinct scolecophidian, in which it is greatest in the anterior and posterior trunk regions. Neural spines and hypapophyses are tallest in the anterior trunk, although both increase in relative height near the cloaca, again except in the scolecophidian sampled. Although these broad patterns are largely shared among the snakes examined in this study, there are numerous deviations that may relate to ecology or phylogeny. The results of this and future such studies will be of use in paleontological research, by aiding in the identification of the relative positions of isolated vertebrae within the column.

Introduction

Limbllessness and extreme body elongation are hallmarks of snake evolution. The evolution of these two features has had a considerable influence on the morphology of the axial skeleton. Snakes achieved such elongation of the trunk predominantly through the addition of vertebrae (rather than through elongation of individual vertebrae), with total vertebral counts ranging from fewer than 150 (multiple taxa; Alexander and Gans, 1966) up to 565 (in the extinct form *Archaeophis*; Janensch, 1906), and possibly even higher based on scale counts in some extant snakes (e.g., Gow, 1977; Hahn and Wallach, 1998) and the 1:1 correspondence between ventral scales and vertebral number in most snakes (Alexander and Gans, 1966). Most of these vertebrae come from the precloacal, or trunk, region of the column, and represent greatly increased numbers relative to those exhibited by most putative snake ancestors. In addition to this increase in vertebral number, the hard- and soft-tissue changes associated with the loss of forelimbs makes it impossible to easily delineate a cervical region that is consistent across all snakes (Pregill, 1977; Cohn and Tickle, 1999; Caldwell, 2000; Cundall and Greene, 2000; Tsuihiji et al., 2006). This makes it difficult to differentiate regions within snake vertebral

columns beyond three broad categories: precloacal, cloacal, and caudal (Hoffstetter and Gasc, 1969).

The relative homogeneity of the vertebral column presents a particular problem in the consideration of the fossil record of snakes, which stretches back over 100 million years (e.g., Gardner and Cifelli, 1999; Rage and Werner, 1999). Although complete body fossils are known (von Meyer, 1860; Haas, 1980; Breithaupt and Duvall, 1986), the vast majority of extinct snake species are known only from isolated vertebral elements (e.g., Rage, 1984). An improved understanding of intracolumnar variation would reduce the chances of designating multiple species on the basis of isolated vertebrae from different regions of a single snake species. In addition, it would help to ensure that studies involving extinct snakes compare vertebrae from similar regions of the vertebral column.

Previous studies of regional variation within the ophidian vertebral column have been primarily qualitative in nature. The earliest workers only differentiated the most obvious regions of the vertebral column, splitting it broadly into precloacal and postcloacal regions, while recognizing the atlas and axis as special (Carus, 1818; Cuvier, 1835; d'Alton, 1836). Subsequent authors have made various attempts to further differentiate the vertebral column into regions, beginning with de Rochebrune (1881), who split the precloacal column into three regions (cervical, thoracic, and lumbar) and the postcloacal column into two (sacral and caudal). However, these subdivisions were not widely recognized by subsequent workers until Sood (1948) reassessed them and largely adopted de Rochebrune's (1881) subdivisions in the trunk. He also recognized three postcloacal regions: anterior, middle, and posterior (Sood, 1941). The definitions of these subregions were later updated by Bullock and Tanner (1966) to accommodate observed differences in the colubrids *Pituophis* and *Thamnophis*, in which they found the middle and posterior caudal regions difficult to distinguish. The most recent assessment of regionality in snakes (LaDuke, 1991a) also focused on North American colubroid snakes, and recognized cervical (atlas and axis), trunk (subdivided into anterior, midtrunk, posterior, and precloacal), cloacal, and postcloacal vertebrae. These divisions have become the standard.

The few previous quantitative investigations of intracolumnar variation in snake vertebrae were primarily aimed at simply describing the morphology, like those of *Acrochordus* (Hoffstetter and Gayrard, 1964) and *Enhydrina* (Thireau, 1967a), or aimed to discern phylogenetic relationships, like those of atractaspids (Thireau, 1967b), boids (Hoffstetter, 1960), colubrids (Szyndlar, 1984), elapids (Smith, 1975), and viperids (Brattstrom, 1964; Szyndlar, 1984; Thireau, 1967b). Because of the relative dearth of quantitative studies, interspecific comparisons have been necessarily limited.

More recent work has shifted the focus away from systematics and toward functional morphology. Gasc (1974) recorded five linear measurements on every tenth vertebra along the length of the column of several species as a means of assessing functional correlates of locomotion. Moon (1999) reported the intracolumnar change in the angles of intervertebral facets, and showed that the zygosphene-zygantrum complex does not eliminate torsion. More recently, Schaal et al. (2005) analyzed a series of measurements made throughout the vertebral column in *Boa constrictor*. These authors took 14 measurements on every vertebra of a single individual in order to determine the way in which these metrics changed throughout the column. They found that vertebral measurements could be split into four types based on the shape of the curves plotting the raw measurements against vertebral number. However, *B. constrictor* was the

only snake so measured, and thus the universality of these patterns remains unknown. Comparison with previously published metrics (Hoffstetter and Gayrard, 1964; Thireau, 1967a, b) shows certain similarities in the way vertebrae vary within the column across taxa. These general similarities are reinforced by examination of the graphs of centrum length and hypapophyseal height in the several snakes for which those data exist (Gasc, 1974; Hoffstetter, 1960).

There is reason to suspect the presence of a functional signal in the vertebral morphology of snakes. As limbless animals, snakes must perform many actions exclusively with their trunks, including locomotion (e.g., Mosauer, 1932a; Gray, 1946; Lissmann, 1950; Gans, 1962; Gans, 1975; Jayne, 1982) and certain aspects of feeding, such as prey acquisition and subjugation (e.g., Greene and Burghardt, 1978; Jayne, 1982; Moon, 2000; Alfaro, 2003; Lourdais et al., 2005; Cundall et al., 2007), especially in the case of constricting snakes. Previous studies have found correlations between axial muscular morphology and feeding and locomotor behavior (Ruben, 1977; Jayne, 1982; Ruben and Geddes, 1983). In addition, vertebral morphology itself was found to correlate with habitat preference (and by extension, locomotion) in the seminal study of vertebral morphology by Johnson (1955). Subsequently, Baszio (2005a) separated arboreal and terrestrial snakes (primarily boids) based on vertebral shape using vertebrae from several points along the column.

A particular problem with comparing previously measured snakes is a lack of measurement standardization. For example, the hypapophysis has been measured both as a vertical depth from the condyle (Smith, 1975; Schaal et al., 2005) as well as an oblique length that more or less follows the long axis of the process (Hoffstetter, 1960; Auffenberg, 1963; Hoffstetter and Gayrard, 1964; Thireau, 1967a, b). In this case, it is likely that the overall pattern of hypapophyseal length is preserved no matter what method is used, but the correspondence between measurements will not be exact. It is particularly problematic in snakes in which the angle of the hypapophysis changes throughout the column; for instance, one can imagine a situation wherein the length of the hypapophysis along its axis does not change, but a changing angle alters the vertical depth of the process.

The purpose of this study is to provide a series of standardized measurements of snake vertebral morphology, and to report these measurements throughout the vertebral column in a phylogenetically, morphologically, and ecologically diverse sample of basal (i.e., non-caenophidian) snakes. For purposes of comparison, one of the snakes included in this study (*Boa constrictor*) was chosen because it has been included in a previous quantitative study of vertebral morphology (Schaal et al., 2005). The results of this study will lay the groundwork for investigation of vertebral morphology in a functional context in both extant and fossil snakes.

Materials and Methods

The species chosen for this study are basal snakes, including one scolecophidian blindsnake and three basal alethinophidians (Fig. 2.1). Scolecophidia is the sister group to Alethinophidia, and *Afrotyphlops lineolatus* is like other members of the clade, a small fossorial snake that specializes on invertebrate prey that it does not constrict (Smith, 1957; Reid and Lott, 1963; Webb and Shine, 1993; Kley and Brainerd, 1999; Kley, 2001). Alethinophidia includes all of the remaining extant snakes. The phylogenetic position of Tropicophiidae is currently controversial (Fig. 2.1); molecular phylogenies find it to be among the most basal

alethinophidians (Wilcox et al., 2002; Lawson et al., 2004; Gower et al., 2005; Wiens et al., 2008; Vidal et al., 2009; Pyron and Burbrink, 2012; Pyron et al., 2013a; Pyron et al., 2013b), but morphological phylogenies find it to be relatively derived (Kluge, 1991; Cundall et al., 1993; Tchernov et al., 2000; Lee and Scanlon, 2002). *Tropidophis haetianus* is a small terrestrial snake, typically found sheltering on the ground, but also found in hanging bromeliads (Stull, 1928; Schwartz, 1975). It is a constrictor that typically feeds on reptilian prey (Stull, 1928; Greene and Burghardt 1978). *Boa constrictor* is a well a known boid, and is in many ways an archetypal snake, being a large-bodied generalist that feeds primarily on relatively large mammals that it kills by constriction (Frazzetta, 1966; Willard, 1977; Greene and Burghardt, 1978; Greene, 1983). The enigmatic snake *Xenopeltis unicolor* belongs to a monotypic family that has a controversial phylogenetic position; some studies find it to be part of a clade with Pythonidae (Lawson et al., 2004; Vidal and David, 2004; Vidal et al., 2007a; Wiens et al., 2008; Pyron and Burbrink, 2012), but other studies find it as more basal, outside of the traditional Booidea (Kluge, 1991; Cundall et al., 1993; Lee and Scanlon, 2002; Gower et al., 2005; Noonan and Chippindale, 2006). It is fossorial and a constrictor, and it primarily feeds on elongate-bodied squamates (e.g., snakes, skinks; Taylor, 1965). It is distinct from the other snakes in this sample in its habit of attacking prey from below rather than head-on (Mertens, 1943). The final snake included in this study, *Python molurus*, is ecologically similar to *B. constrictor*, and shares with that species large body size.

The measurements presented in this study are based on detailed examination of five dried skeletal specimens (Table 2.1; phylogenetic relationships given in Fig. 2.1). Three of these (NJK S-A110-D1, *Afrotyphlops lineolatus*; NJK S-Th09-D1, *Tropidophis haetianus*; NJK S-Xu09-D1, *Xenopeltis unicolor*) were prepared specifically for the purposes of this study from previously frozen intact specimens. Each of these specimens was prepared by disarticulation of the craniovertebral joint and one of the distal caudal intervertebral joints. A length of thin metal wire was then passed through the opened neural canal and tied off at both ends. Finally, the specimens were macerated in water at room temperature for a period of several weeks. This procedure yielded completely cleaned and fully disarticulated skeletal specimens in which the sequential order of the vertebrae was maintained. These specimens are now held in the personal research collection of Nathan J. Kley (NJK). Two additional specimens (YPM R 12323, *Boa constrictor*; YPM R 12545, *Python molurus*) were selected for this study because they were already adequately prepared (i.e., fully cleaned with their vertebral order intact). These two specimens are held at the Yale Peabody Museum of Natural History (YPM). Additional skeletal specimens of these species were examined qualitatively but not measured: *Afrotyphlops lineolatus* (NJK A111-D1; NJK T 9x-1; NJK T 99-2; NJK T1 01-2); *Tropidophis haetianus* (NJK Th06-2; NJK Th06-D3); *Boa constrictor* (NJK NN; YPM R 10580; YPM R 10868); *Xenopeltis unicolor* (NJK Xu A-1); and *Python molurus* (YPM R 11189, YPM R 11233; YPM R 14414).

A series of 20 measurements was made on almost every vertebra throughout the vertebral column of one specimen from each species (Table 2.2; Fig. 2.2). Two of these measurements (hypapophyseal height [HH] and synapophyseal height [SH]) were replaced by alternative metrics (hemapophyseal height [HeH] and trans-pleurapophyseal width [TPW]) in postcloacal vertebrae due to regional differences in vertebral morphology, giving a total of 22 measurements. Note that distal to the anterior trunk hypapophyses are often reduced to a low hemal keel, and the metric HH is continued as a measurement of the height of this keel. In larger specimens, the measurements were made with digital calipers to the nearest 0.1 mm. Smaller specimens were measured from photographs obtained with an Axiocam MRc camera coupled to a Zeiss

Discovery.V12 stereo dissecting microscope using Zeiss AxioVision software (v. 4.4.1.0). This software is integrated with the microscope's control mechanism, allowing accurate measurements based on the focal point of the microscope. Bilateral structures were measured on the left side whenever possible. However, exceptions to this convention were made in cases of damage or pathology. The first and second vertebrae, the atlas and axis, are morphologically quite distinct from succeeding vertebrae. Only the axis bears some features measured on succeeding vertebrae (CNH, CNW, HH, NBL, NH, NTL, TPoW) and thus the atlas was not measured.

Standardized anatomical positions for photography and measurement allow for consistency and repeatability in measurements and therefore facilitate comparisons among specimens (Pearcy and Wijtten, 2010). The positions employed in this study are similar to those used by Gasc (1974). In anterior view, the vertebrae were oriented such that the anterior aperture of the neural canal was completely unobstructed, and the roof and floor of the neural canal were not visible. This left a very thin gap between the postzygapophyseal facets above and the prezygapophyseal facets below. In lateral view, the vertebrae were oriented so that the visible bilateral structures were aligned. Each vertebra was further oriented by ensuring that any particular point on the postzygapophysis was slightly dorsal to the corresponding point on the prezygapophysis. In practice, this was the highest point of each facet, the rest of one facet being obscured by the process on which it sits. Typically, such an arrangement brought the dorsal edge of the neural spine to a horizontal position as well. In dorsal view, the extent to which the neural arch and neural spine overlap the condyle varies between species, and the degree of this overlap was determined by first orienting the vertebra in lateral view. Similarly, in ventral view the dorsal lip of the cotyle and the zygosphene are slightly projecting and therefore visible. The extent of this overhang, as well as the projection of the hypapophysis, vary taxonomically and were determined from the lateral view.

Results

The specimens measured have a range of total vertebral numbers (Table 2.1). *Afrotrophlops lineolatus* has a total of 221 vertebrae, 204 of which are precloacal. The cloacal and caudal regions (often referred to as postcloacal vertebrae) have a total of 17 vertebrae, which is only about 7.7% of the total number of vertebrae. *Tropidophis haetianus* has a similar total number of vertebrae (227), but the precloacal-postcloacal split results in relative more caudal vertebrae, with 183 precloacal and 44 postcloacal (about 19.4% of total vertebral number). *Boa constrictor* has notably more vertebrae with at least 306 (at least the terminal vertebra is not preserved with the specimen), 248 of which are precloacal and 57 of which are postcloacal (about 18.7% of total vertebral number). *Xenopeltis unicolor* has a similar number of vertebrae to *A. lineolatus* and *T. haetianus* with 216, of which 182 are precloacal and 33 are postcloacal (about 15.3% of total vertebral number). *Python molurus* has the most vertebrae in this sample with at least 342 (at least the terminal vertebra is again not preserved), of which 271 are precloacal and 71 are postcloacal (about 20.8% of total vertebral number).

The measurements for each snake sampled in this study are summarized in Figures 2.3–2.7, in which each individual measurement is plotted by its position along the vertebral column (expressed as percent precloacal vertebral number), resulting in species-specific curves for each individual metric. In addition, Table 2.3 provides the relative positions within the column at

which these metrics reach their maxima. All of the snakes sampled show some degree of stochastic variation in these measurements over short vertebral segments, in addition to the broader patterns exhibited over the length of the entire vertebral column. Such local variations are due to a combination of factors, including simple variation and slight measurement error and, in more extreme cases, pathologies or natural asymmetries. However, these minor variations do not obscure the overall patterns that emerge within each measurement for each snake.

In addition to the species-specific curves generated for each individual measurement described above, several ratios were calculated from the data to aid in examining the relative changes in shape of certain aspects of the vertebrae throughout the column. In the past, such ratios have been used for a variety of purposes, including discriminating among fossil taxa and taxa of differing ecologies (e.g., Auffenberg, 1963; Smith, 1975; Van Devender and Mead, 1978; Meylan, 1982; Szyndlar, 1984; Van Devender et al., 1985); such uses have been discouraged for studies of snakes (LaDuke, 1991a), but the ratios are presented here as a means of describing the relationships of certain vertebral features. Note that the length of the prezygapophyseal accessory process, used in the ratio APL/CtW, was calculated by halving the difference between the values of trans-accessory process width and trans-prezygapophyseal width.

Afrotrophops lineolatus. The lone scolecophidian examined, *A. lineolatus* (Fig. 2.3), shows maximal values for all recorded metrics within the anterior 40% of precloacal vertebrae, with the sole exception of centrum length (CL), which peaks at about 49% (Table 2.3). This means that most vertebral features decline in size throughout much of the trunk, but differences in the extent of decline lead to changes in the relative proportions of certain features. Increased amounts of decline in width measurements mean that the vertebrae become relatively narrower and more elongate throughout the trunk (Figs. 2.3C, D, 2.8A). The neural spine is present only as a much-reduced midline tubercle, which in posterior vertebrae projects more strongly posteriorly than dorsally (Fig. 2.3A–C). There are hypapophyses on only the first three vertebrae; distal to this point, the ventral surface of the centrum is smooth and does not project below the ventral edge of the condyle (Fig. 2.3A, B, D). Accordingly, the neural spines were not measured and the hypapophyses were measured only to the third vertebra (Figs. 2.3B, 2.8B, C). The relative width across the zygapophyses is greatest in the anterior trunk and at the cloaca (Fig. 2.8D); the anterior trunk region is also where the prezygapophyseal accessory processes are shortest (Fig. 2.8E). These processes are long (Fig. 2.3A, C, D), and reach their maximum relative length near 20% of precloacal vertebral number.

The tails of blindsnakes are very short, and as a result, most metrics show abrupt declines throughout the cloacal and caudal regions (Fig. 2.3). This includes centrum length (CL; Fig. 2.3D) and neural arch width (NAW; Fig. 2.3C); the ratio between these metrics also declines, indicating the vertebrae become relatively wider in the tail. However, this does not include measurements of articular surfaces. In both pairs of zygapophyses, the articular facets decline in size more slowly than other caudal features (PrFL, PrFW, PoFL, PoFW; Fig. 2.3C, D). This results in relatively large articular surfaces in caudal vertebrae as compared to those in the trunk. The delicate caudal pleurapophyses were damaged in the primary specimen examined, and as such could not be measured. However, qualitative examination of other specimens of *A. lineolatus* with fully intact tails showed a steady decline in the length of these processes.

Tropidophis haetianus. This snake shows parabolic curves of variation in the trunk for most vertebral features (Fig. 2.4). Nearly all recorded vertebral metrics reach their maximum values between about 40–60% of precloacal vertebral number (Table 2.3). The one significant

exception to this generalization is hypapophyseal height (HH), which is greatest at about 3% of precloacal vertebral number. Hypapophyseal height is the most strikingly divergent curve in its overall shape, with local maxima at either end of the precloacal column, so that the hypapophyses are shortest in the mid-trunk region (Fig. 2.4B). Because many vertebral features show the same parabolic pattern of variation throughout the column, some vertebral features show less relative change than in the other snakes examined (Fig. 2.8A, E). The vertebral aspect ratio (centrum length [CL] to neural arch width [NAW]; Fig. 2.8A) remains nearly constant throughout the trunk. Neural spines and hypapophyses are both greatest in their relative heights in the anterior and posterior trunk regions (Fig. 2.8B, C). The hypapophyses persist throughout the trunk (Fig. 2.4A, B, D). The relative width across the prezygapophyses has a peak in the anterior trunk and precloacal regions (Fig. 2.8D). The relative length of the prezygapophyseal accessory processes reaches a maximum at the transition from anterior to mid-trunk regions (Fig. 2.8E).

Vertebral features generally decline in the tail, although some show local maxima in the anterior or mid-tail (Fig. 2.4). The vertebrae abruptly become anteroposteriorly short at the cloaca, but again increase in size to a local maximum in the middle caudal vertebrae (CL, PrPo; Fig. 2.4C, D). The zygosphene shows a distinct increase in size in the cloacal region (TZW; Fig. 2.4A). Neural spines are relatively tall throughout the anterior half of the caudal region (Fig. 2.8B). The hemapophyses are longest in the mid-tail, both relatively and absolutely (Figs. 2.4B, 2.8C).

Boa constrictor. In the trunk of *B. constrictor*, more than half of all recorded vertebral metrics peak within the anterior 40% of precloacal vertebrae (Fig. 2.5; Table 2.3). This includes the widths across both pairs of zygapophyses (TPrW, TPoW) and the neural arch (NAW)—all peaking between 38–40% of precloacal vertebral number—as well as the heights of the neural spines (NH) and hypapophyses (HH), which peak at about 24% and 20%, respectively. Vertebral length shows a parabolic pattern of variation, peaking at about 57% of precloacal vertebral number. The disparity between the anterior peak and more precipitous decline in neural arch width (NAW) and the posterior peak of centrum length (CL) causes the vertebrae to become relatively elongate (higher CL/NAW ratio) throughout most of the mid- and posterior trunk (Fig. 2.8A). Although the absolute height of the neural spines is greatest at about 24% of precloacal vertebral number, their relative height declines throughout the anterior trunk, with a plateau between 10–20% of precloacal vertebral number (Fig. 2.8B). The hypapophyses exhibit a similar decline in their relative height throughout the anterior trunk, also showing a plateau from 10–20% of precloacal vertebral number, before being reduced in the mid-trunk to relatively flat hemal keels (Fig. 2.8C). Hypapophyseal height increases to a local maximum in the precloacal region, such that the precloacal vertebrae redevelop hypapophyses, which are absent in the mid- and posterior trunk (Fig. 2.5A, B, D). The relative width across the prezygapophyses is rather low in the anterior trunk, a pattern also seen in the relative length of the prezygapophyseal accessory processes (Fig. 2.8D, E). Both of these relative width measurements plateau at about 30% of precloacal vertebral number, and remain fairly constant posteriorly to the cloaca.

The postcloacal vertebrae show a mixture of patterns in variation, with some features showing declines throughout the tail and others reaching a local maximum in the anterior caudals. At the cloaca, the centrum length abruptly decreases (CL; Fig. 2.5D) with a concomitant increase in several width measurements including neural arch width (NAW; Fig. 2.5A, C, D). The zygosphene shows an abrupt increase in width in the cloacal region (TZW; Fig. 2.5A). The

neural spines decrease in height at the cloaca, but increase to a local maximum in the anterior part of the tail (NH; Fig. 2.5B). The hypapophyses decline in height in the cloacal vertebrae, and a gap of a single vertebra exists between the last hypapophysis and the first caudal hemapophysis (Fig. 2.5B). The hemapophyses then rapidly reach their maximum length in the anterior caudal region (Fig. 2.5B, 2.8C).

***Xenopeltis unicolor*.** In *X. unicolor*, approximately half of the vertebral metrics recorded reach their maxima in the anterior 40% of precloacal vertebrae (Fig. 2.6; Table 2.3). These include nearly all width measurements, with the exception of condyle width (CnW), which reaches its maximum at approximately 53% of precloacal vertebral number. Vertebral lengths (CL, PrPo), as well as measurements of zygapophyseal facet size (PoFL, PoFW, PrFL, PrFW), reach their maxima between 45–55% of precloacal vertebral number (Fig. 2.6C, D). As a consequence of these differences in the relative anteroposterior positions of vertebral width versus length maxima, overall vertebral shape changes at about 50% of precloacal vertebral number, with vertebral aspect ratio (CL/NAW) increasing markedly (Fig. 2.8A). The neural spines and hypapophyses reach their maximum relative height in the anterior trunk (Fig. 2.8B, C), although the absolute sizes of both processes are quite small (Fig. 2.6A–D). The relative width across the prezygapophyses is greatest in the anterior and posterior trunk regions (Fig. 2.8D). The prezygapophyseal accessory processes increase in relative size throughout the anterior trunk, nearly plateau in the mid-trunk region, and finally increase to their greatest relative length in the posterior trunk (Fig. 2.8E).

The postcloacal regions of *X. unicolor* show less variation in the recorded vertebral metrics than occurs in *B. constrictor*. The most notable changes are decreases in the length measurements centrum length (CL; Fig. 2.6D) and interzygapophyseal distance (PrPo; Fig. 2.6C) and in the width measurements trans-accessory process width (TAPW; Fig. 2.5A), trans-prezygapophyseal width (TPrW; Fig. 2.6A), and trans-postzygapophyseal width (TPoW; Fig. 2.6C). The zygosphene does not show an increase in width at the cloaca (TZW; Fig. 2.6A). Most vertebral features decline in size through the tail; however, the neural spines become somewhat taller and longer anteroposteriorly throughout the anterior part of the tail (Fig. 2.6B). The hemapophyses increase abruptly in length in the anterior caudal vertebrae, and remain long through the middle portion of the tail.

***Python molurus*.** As in *B. constrictor* and *X. unicolor*, approximately half of all vertebral metrics recorded in the trunk of *P. molurus* reach their maxima in the anterior 40% of precloacal vertebrae (Fig. 2.7; Table 2.3), including the heights of both the neural spines (NH, peaking at 19%) and hypapophyses (HH, peaking at 14%), and all width measurements but cotylar and condylar width (CoW and CnW, both peaking at 45%). Vertebral length measurements (CL, PrPo) peak somewhat farther posteriorly at about 49% of precloacal vertebral number. This mismatch of the changes in length and width, as well as a more rapid decline in neural arch width (NAW) as compared to centrum length (CL), results in vertebrae that are relatively longest in the anterior and posterior trunk regions (Fig. 2.8A). The neural spines and hypapophyses are tallest, both relatively and absolutely, in the anterior trunk (Figs. 2.7A, B, 2.8B, C); both processes increase in height near the cloaca, (Fig. 2.7A, B). The relative width across the prezygapophyses is reduced in much of the anterior trunk, but it increases rapidly throughout the region to peak at about 40% of precloacal vertebral number (Fig. 2.8D). No such variation is evident in the prezygapophyseal accessory process, which remains at approximately the same relative length throughout the trunk (Fig. 2.8E).

As in the trunk, the postcloacal patterns of variation in *P. molurus* are broadly similar to those of *B. constrictor*. The vertebral-length metrics centrum length (CL) and interzygapophyseal distance (PrPo) decrease precipitously, as do the widths across both pairs of zygapophyses (TPoW, TPrW; Fig. 2.7A, C, D). The increases in these metrics in the anterior tail are relatively weaker than those shown in the other snakes sampled. The zygosphenes differ from *B. constrictor* and *T. haetianus* in lacking a distinct increase in width in the cloacal region (TZW; Fig. 2.7A). Although the neural spines do not increase in height in the precloacal region, they do become taller, both absolutely and relatively, throughout the cloacal region (NH; Fig. 2.7B, 2.8B). The hemapophyses increase in relative height through the cloacal and anterior caudal regions, reaching their maximum relative size in the mid-caudal region (Fig. 2.8C).

Discussion

The variation measured in *Boa constrictor* in this study compares closely with that reported in Schaal et al. (2005). In that study grouped their measurements into 4 categories based on the patterns of change along the vertebral column. The addition of new taxa in this study blurs the boundaries between these curve types. Instead, it is best to consider curves either as parabolic or as deviating conspicuously from this pattern. A parabolic curve is obtained when a given vertebral metric reaches a maximum value somewhere near the midpoint of the trunk, an expected pattern in an elongate, limbless vertebrate characterized by considerable tapering both anteriorly and posteriorly. As such, the parabolic curve can be considered a “null hypothesis” of sorts, and deviations from this pattern may represent retained ancestral patterns (i.e., those inherited from the quadrupedal ancestors of snakes), or adaptations directly related to vertebral function.

The vertebral metrics that deviate most strongly from displaying a parabolic pattern of intracolumnar variation are the heights of the neural spines (NH) and hypapophyses (HH). This is true of all snakes sampled except the scolecophidian *Afrotrophlops lineolatus*, which effectively lacks these processes. Also deviating from the parabolic pattern are the widths across both pairs of zygapophyses (TPoW, TPrW) and that across the prezygapophyseal accessory processes (TAPW). Each of these bony processes serves as a site of attachment for muscles that participate in generating movements of the trunk.

Afrotrophlops lineolatus. Reduction in the relative sizes of the neural spines and hypapophyses is common among fossorial snakes (see *Xenopeltis unicolor* below), although this is taken to an extreme in scolecophidians (Fig. 2.3A, B). This reduction may be a means of reducing the height of the vertebrae (and thus that of the snakes themselves) in order to facilitate movement through tight burrows. It can be inferred that this reduction negatively impacts the effectiveness of the trunk flexors and extensors that attach to these structures. However, dorsi- and ventroflexion are probably not particularly important in fossorial non-constrictors like scolecophidians.

Throughout the mid-trunk region, other vertebral features follow two broad patterns in *A. lineolatus*: they either show little change or steadily decline in size (Fig. 2.3). Vertebral width measurements tend to decline through the trunk, whereas anteroposterior length measurements remain relatively constant. The confluence of these two patterns means that the relative shape of the vertebrae changes through the column, and specifically that the vertebrae are relatively longer in the posterior half of the column than in the anterior half (Fig. 2.8A). Although this is

generally true in the alethinophidians examined, the change is greatest in the burrowing snakes *A. lineolatus* and *X. unicolor* (see below). The greater strength of this signal in these fossorial snakes may be related to forces incurred during head-first burrowing, with the anterior trunk vertebrae more robust to increase vertebral stability and to better transmit the reaction forces.

The cloacal and caudal regions of this species are so short that there is little room for patterns to emerge. Most vertebral features simply decline throughout these regions, although the articular surfaces do so at a relatively slower rate (i.e., they become relatively large; Fig. 2.3). The great size of the articulations suggests that the tail has function belying its small size. The tip of the tail features an apical spike that is used defensively (e.g., Wall, 1918; Broadley, 1959; Fowlie, 1965), and Hoffstetter and Gasc (1969) suggested that the blunt tail might be used as leverage during burrowing, which is supported by anecdotal observations (e.g., Wall, 1918; Klauber, 1931; Smith, 1943). These behaviors might potentially generate high forces along the tail that could explain the large facets and extra bone, to improve force transmission.

***Tropidophis haetianus*.** In *T. haetianus*, only the heights of the hypapophyses and neural spines deviate notably from the “null hypothesis” of a parabolic pattern of variation. This results in smaller relative changes through the column as compared to those seen in the other snakes sampled in this study (Fig. 2.8A, D, E). The relatively high levels of homogeneity within the vertebral column of *T. haetianus* suggest that most vertebral features are optimized for functions that make use of the entire column, like locomotion, rather than behaviors utilizing only a part of the trunk. However, given the many ecological similarities shared by *T. haetianus* and the other alethinophidians in this study, it is somewhat surprising that the intracolumnar variation exhibited by the former is so distinct. *Tropidophis haetianus* is a constrictor that feeds on relatively large prey (Stull, 1928), and is a terrestrial generalist that is a capable climber, not unlike *Boa constrictor* (Stull, 1928; Schwartz, 1975).

What is consistently shared with the other alethinophidians is the fact that the neural spines and hypapophyses in *T. haetianus* are regionally variable, and are relatively largest in the anterior trunk and immediately anterior to the cloaca (Fig. 2.8B, C). The hypapophyses show this pattern in spite of the fact that tropidophiids like *T. haetianus* retain a deeply projecting hypapophysis throughout the trunk (Malnate, 1972), as opposed to the much reduced, weakly projecting keel in the other snakes examined here.

In the anterior trunk, the neural spines and hypapophyses provide attachments for muscles that are responsible for moving the head during various behaviors, for example climbing or striking at prey. This region also initiates coiling during constriction by a ventral movement (Frazzetta, 1966; Greene and Burghardt, 1978), which presumably makes use of the subvertebral musculature (Mosauer, 1935). The facts that the longest hypapophyses are located in the anterior trunk in all four constrictors in this sample, and that the hypapophyses are so severely reduced in the nonconstrictor, show the potential importance of these processes in improving the mechanical advantage of the subvertebral muscles during the powerful ventroflexion associated with the application of constricting coils.

In *T. haetianus*, the cloacal region features vertebrae that are anteroposteriorly very short, leading to a notable dip in overall aspect ratio (CL/NAW; Fig. 2.8A). This decrease in centrum length is known in almost all snakes in which it has been measured (Hoffstetter, 1960; Hoffstetter and Gayrard, 1964; Thireau, 1967a, b; Smith, 1975; Szyndlar, 1984; Schaal et al., 2005), and furthermore appears to be a general feature of squamates (Hoffstetter and Gasc,

1969). Reduced vertebral length at the base of the tail increases its flexibility by increasing the number of joints available in the cloacal region. Increased muscle mass and flexibility near the base of the tail is important to various caudal movements, including prehensility, caudal luring (unreported in *T. haetianus*, but known in congeners; Neill, 1960), mating behaviors, and defecation.

Boa constrictor. The patterns of intracolumnar variation in *B. constrictor* that were found in this study and by Schaal et al. (2005) are generally similar. When the latter study was published, there was not an extensive comparative sample of measurements from other snakes available, and none from *B. constrictor*. The similarities in intracolumnar variation documented by Schaal et al. (2005) and in this study suggest that the species-specific patterns described herein are reasonably constant; nevertheless, further studies of intraspecific variation will be required to confirm this on a broader basis.

Boa constrictor shares great similarities in its pattern of intracolumnar variation with *Python molurus* (see below), likely a result of shared ancestry and similar natural histories (noted above). In both *B. constrictor* and *Python molurus*, the prezygapophyses and the attendant accessory processes reach maximum lateral projection at approximately one-third of preloacal vertebral number (Fig. 2.5A; TPrW, TAPW). Posterior to this point, they decrease in lateral projection, although the prezygapophyseal accessory processes generally remain at the same relative length until near the cloaca (Fig. 2.8E). This corresponds well with the fact that boid snakes prefer to strike at distances about one-third of body length (although longer strikes will occur; Frazzetta, 1966). The trunk flexors *M. longissimus* and *M. interarticularis superior* originate at this point and extend anteriorly (Mosauer, 1935), and may therefore be important in forming and straightening the coils for strikes; longer accessory processes at this point of the column may improve the mechanical advantage of these muscles.

Boa constrictor also shows some similarities in the pattern of intracolumnar variation with *Tropidophis haetianus*. As noted above, the neural spines and hypapophyses are highest, both absolutely and relatively, in the anterior trunk. Both features also become taller in the preloacal region. Reasons for the strong development of these processes in these regions are likely similar to those mentioned for *T. haetianus*: the anterior trunk is heavily involved in most locomotion and feeding behaviors, and longer processes will allow for larger muscles with potentially improved mechanical advantage.

The patterns of intracolumnar variation observed throughout the cloacal and caudal regions in *B. constrictor* are generally similar to those seen in, and discussed above for, *T. haetianus* (Figs. 2.5, 2.8). One notable difference is the greater relative height of the hemapophyses in the anterior caudal vertebrae, versus the condition in *T. haetianus*, in which the hemapophyses are longest in the mid-tail. The reasons for this are uncertain, and further study of the postloacal regions is necessary.

Xenopeltis unicolor. The intracolumnar variation shown by *X. unicolor* is generally similar to that of both *B. constrictor* and *P. molurus* in spite of the ecological differences between them. However, there are some metrics that are more similar to *A. lineolatus* and are likely related to its semifossorial lifestyle. Vertebral aspect ratio (CL/NAW; Fig. 2.8A), discussed above, shows a similar pattern to that of *A. lineolatus* of dramatic increase in relative length in the posterior part of the trunk, albeit to a lesser degree. Also similar in *X. unicolor* and *A. lineolatus* are the relatively low neural spines and hypapophyses (Figs. 2.6, 2.8B, C), though

the degree of reduction in *X. unicolor* is less than that in *A. lineolatus*. The reduction of the hypapophyses runs counter to the muscular anatomy of the anterior trunk of *X. unicolor*, in which the subvertebral muscle *M. rectus capitis anterior* is distally extensive, presumably to facilitate burrowing (Tsuihiji et al., 2012). The detailed morphology of this muscle has not been described, so this apparent disconnect between myology and osteology remains unexplained.

The accessory processes of *X. unicolor* also show unique intracolumnar variation relative to that seen among the other snakes examined. They are relatively longer than those of the other alethinophidians sampled (again somewhat similar with *A. lineolatus*, although not to the same extent), and furthermore are longest in the posterior trunk, a pattern not seen in any of the other snakes in this study. These relatively long accessory processes may improve the function of the lateral trunk flexors (*M. longissimus*, *M. interarticularis superior*) in the anterior trunk. This may be related to an unusual behavior noted in *X. unicolor*: during forward locomotion, it does not elevate its head, but rather sweeps it side to side to clear a path (Bergman, 1955). Although Bergman (1955) did not specify, this presumably applies when the animal is moving through its typical habitat of loose leaf litter or burrows; in any case, it shows a reliance on lateral movements of the anterior trunk that may be reflected in the morphology of its vertebrae.

Because *X. unicolor* is a semifossorial snake, the tail is under different functional pressures than in the terrestrial alethinophidians, all of which show some degree of prehensility in their tails (Cope, 1886; McDowell, 1975; Emmons and Gentry, 1983). There is no need for prehensility in a fossorial environment, so it might be expected that the tail would show differences from the other three snakes, and perhaps some similarity to the fossorial *A. lineolatus*. However, that is not what occurs; instead, *X. unicolor* shows patterns of variation that are similar to the other alethinophidians (Figs. 2.6, 2.8), possibly indicating a phylogenetic retention.

***Python molurus*.** Most differences between *P. molurus* and *B. constrictor* are simply matters of degrees: for example, the relatively greater height of the hypapophyses and neural spines shown by *B. constrictor* (Fig. 2.8B, C). These similarities may reflect phylogenetic relatedness (see the morphological hypothesis in Fig. 2.1), in addition to the similar functional demands placed on the column by their similar natural history. There is one feature that shows different variation in *Python*, however: the prezygapophyseal accessory processes increase in relative length at about one-third of precloacal vertebral number in *B. constrictor*, whereas they remain at nearly the same relative length throughout the trunk in *P. molurus* (Fig. 2.8E). This may reflect a reduced reliance on the prezygapophyseal accessory process to produce the lateral extension moment of the muscles attached to it, in favor of increasing the size of the entire prezygapophyseal process. Examination of the widths across the prezygapophyses does in fact show a greater relative increase at one-third of precloacal vertebral number in *P. molurus* than in *B. constrictor* (Fig. 2.8D), suggesting that these two species have met similar mechanical demands via slightly different morphological solutions.

Paleontological implications. Previous workers have used ratios of certain vertebral metrics to quantitatively separate fossil taxa in several extinct ophiofaunas containing multiple species of closely related snakes (e.g., Auffenberg, 1963; Smith, 1975; Van Devender and Mead, 1978; Meylan, 1982; Szyndlar, 1984; Van Devender et al., 1985). However, the use of such ratios for this purpose has fallen out of favor. When selecting ratios for their analyses, previous workers chose those ratios that were thought to vary relatively little along the vertebral column, and concentrated on ratios calculated from mid-trunk vertebrae (Auffenberg, 1963). This study

shows that there can be considerable variation throughout even the mid-trunk region of some snakes; more importantly, it shows that closely related species can overlap considerably in the magnitudes of these ratios (Fig. 2.8). These results therefore strongly support the notion that isolated ratios of vertebral metrics should not be used to discriminate between snake taxa, whether they are extant or extinct.

There are many qualitative morphological characters that can be used to assess the intracolumnar position of isolated vertebrae (Auffenberg, 1963; LaDuke, 1991a). In addition, vertebrae can be placed within the column by use of maximum likelihood analysis of shape (Polly and Head, 2004). The addition of the data in this and future such studies can potentially strengthen these approaches by allowing them to be tailored more specifically to appropriate taxonomic or ecological groups. In addition, knowledge of how individual features vary both absolutely and with respect to other components of the vertebrae can help to approximate the position of poorly preserved specimens that are missing the diagnostic features for a particular vertebral region, and that are therefore not conducive to shape analysis.

Conclusions

Intracolumnar variation in vertebral morphology has long been recognized as an important phenomenon in snake biology, particularly with respect to the fossil record (Auffenberg, 1963; Rage, 1984; Szyndlar, 1984; LaDuke, 1991a). This study adds to our understanding of intracolumnar variation by measuring over 20 features on every vertebra throughout the column in five basal snakes. The results show that there are patterns of potential functional significance in the way that vertebral morphology varies, particularly in the relative lengths of processes for muscular attachment, which show reasonably consistent patterns across the alethinophidian taxa examined here. This study also highlights some major differences that exist, particularly between the scolecophidians *Afrotyphlops lineolatus* and the alethinophidians sampled herein, but also within Alethinophidia.

This study also highlights the difficulties associated with identifying isolated vertebrae, particularly if they come from extinct species for which intracolumnar variation is poorly understood or unknown. Overlapping values for certain ratios as well as those for raw measurements makes quantitative separation of taxa difficult, if not impossible. However, when combined with qualitative observations of isolated fossil vertebrae, measurements may help to define or refine vertebral position. As more extant snakes are studied, correlations related to behavior and ecology may become more readily apparent, and aspects of the paleobiology of extinct snakes may become better understood.

Table 2.1. Regional vertebral counts for the snakes examined in this study. *Boa constrictor* and *Python molurus* are lacking at least the terminal vertebra.

Specimen	Species	Trunk (% total)	Cloacal (% total)	Caudal (% total)	Total
NJK S-A110-D1	<i>Afrotyphlops lineolatus</i>	204 (92.3%)	5 (2.3%)	12 (5.4%)	221
NJK S-Th09-D1	<i>Tropidophis haetianus</i>	183 (80.6%)	3 (1.3%)	41 (18.1%)	227
YPM R 12323	<i>Boa constrictor</i>	248 (81.0%)	7 (2.3%)	50+ (16.3%)	306+
NJK S-Xu09-D1	<i>Xenopeltis unicolor</i>	182 (84.3%)	4 (1.9%)	29 (13.4%)	216
YPM R 12545	<i>Python molurus</i>	271 (79.2%)	5 (1.5%)	66+ (19.3%)	342+

Table 2.2. Descriptions of measurements recorded in this study. See also Figure 2.2.

Measurement	Abbreviation	Description
Centrum length	CL	Midline length of centrum from ventral lip of cotyle to posteriormost point on condyle ⁴
Condyle height	CnH	Vertical height of condyle ²
Condyle width	CnW	Maximum width of condyle ⁴
Cotyle height	CtH	Midline height of cotyle ¹
Cotyle width	CtW	Maximum width of cotyle ¹
Hypapophyseal/hemal keel height	HH	By calipers, obtained by subtracting condyle height from vertical height between dorsal edge of condyle and ventral edge of hypapophysis or hemal keel; from photographs, vertical distance between ventral edge of condyle and ventral edge of hypapophysis or hemal keel ²
Hemapophyseal height	HeH	By calipers, obtained by subtracting condyle height from vertical height between dorsal edge of condyle and ventral edge of hemapophysis; from photographs, vertical distance between ventral edge of condyle and ventral edge of hemapophysis ²
Neural arch width	NAW	Minimum width of neural arch ³
Neural spine base length	NBL	Anteroposterior length of neural spine just dorsal to roof of zygantrum ²
Neural spine height	NH	Vertical distance between dorsal edge of zygosphenal facet and dorsal edge of neural spine ²
Neural spine tip length	NTL	Anteroposterior length of neural spine measured along dorsal edge ²
Postzygapophyseal facet length	PoFL	Length of major axis of facet ⁴
Postzygapophyseal facet width	PoFW	Length of minor axis of facet, measured at midpoint of major axis of facet ⁴
Prezygapophyseal facet length	PrFL	Length of major axis of facet ³
Prezygapophyseal facet width	PrFW	Length of minor axis of facet, measured at midpoint of major axis of facet ³
Interzygapophyseal distance	PrPo	Distance between anteriormost edge of prezygapophyseal facet and posteriormost edge of postzygapophyseal facet ³
Synapophyseal height	SH	Distance between dorsal edge of parapophysis and ventral edge of diapophysis, measured along major axis of synapophyseal facet ¹
Trans-accessory process width	TAPW	Maximum width across prezygapophyses (including the accessory processes) ^{1,3}
Trans-postzygapophyseal width	TPoW	Maximum width across postzygapophyseal facets ⁴

Table 2.2 (Continued). Descriptions of measurements recorded in this study. See also Figure 2.2.

Measurement	Abbreviation	Description
Trans-prezygapophyseal width	TPrW	Maximum width across prezygapophyseal facets ³
Trans-pleurapophyseal width	TPW	Maximum width across pleurapophyses of caudal vertebrae ¹
Trans-zygosphenal width	TZW	Maximum distance between dorsal edges of zygosphenal facets ¹

¹Measurement made in anterior view; ²Measurement made in lateral view; ³Measurement made in dorsal view; ⁴Measurement made in ventral view.

Table 2.3. Anteroposterior positions of maxima for the measurements recorded in this study (Fig. 2.3–2.7), expressed as percentages of preloacal vertebral number. For abbreviations of measurements see Figure 2.2 and Table 2.2.

	CL	CnH	CnW	CtH	CtW	HH	NAW	NBL	NH	NTL	PoFL
<i>Afrotyphlops lineolatus</i>	48.5	9.8	19.1	9.8	31.9	1.0	15.2	–	–	–	32.8
<i>Tropidophis haetianus</i>	53.0	50.3	53.0	51.4	44.3	3.3	52.5	57.4	42.1	57.4	37.7
<i>Boa constrictor</i>	56.5	48.8	38.3	47.2	35.5	19.8	40.3	39.9	23.8	29.0	41.9
<i>Xenopeltis unicolor</i>	52.2	37.9	53.3	46.2	34.6	2.7	40.1	–	1.6	75.8	50.5
<i>Python molurus</i>	49.4	39.1	45.4	48.3	45.4	14.0	37.6	32.1	19.2	64.9	37.6

	PoFW	PrFL	PrFW	PrPo	SH	TAPW	TPoW	TPrW	TZW
<i>Afrotyphlops lineolatus</i>	26.0	24.5	20.1	37.7	14.7	22.5	20.1	20.6	2.5
<i>Tropidophis haetianus</i>	53.0	42.6	49.2	55.7	54.1	46.4	48.6	49.2	57.4
<i>Boa constrictor</i>	16.9	35.1	51.2	42.3	49.2	37.5	37.5	37.9	27.4
<i>Xenopeltis unicolor</i>	48.4	46.7	50.0	50	47.8	36.8	36.3	36.8	38.5
<i>Python molurus</i>	49.1	44.3	32.1	48.7	42.8	38.7	39.1	39.5	36.2

Figure 2.1. The phylogenetic relationships of the snakes in this study. The middle columns provide the typical habitat preference and diet for each species, and indicate whether they use constriction as a method of prey subjugation. F, fossorial; T, terrestrial.

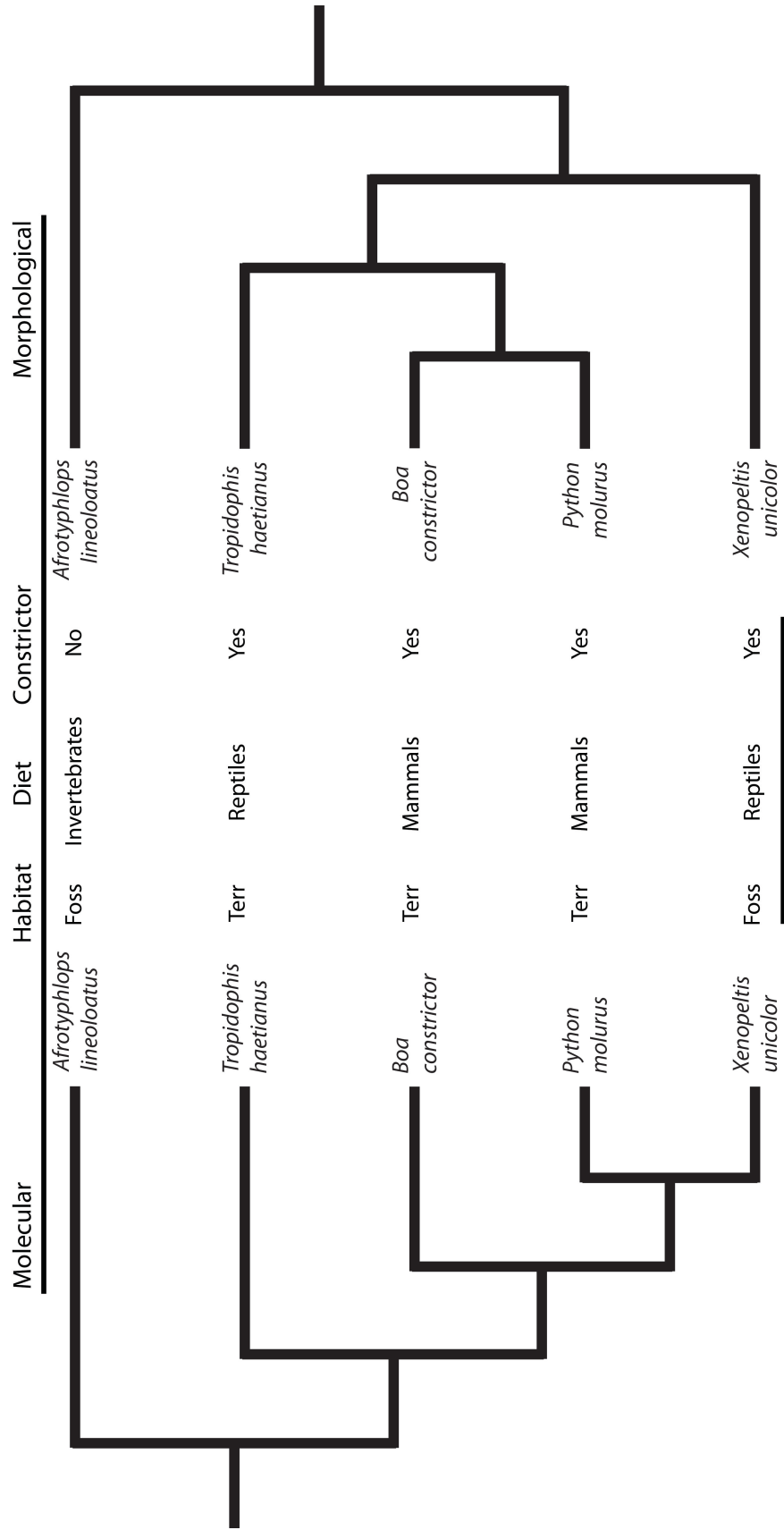
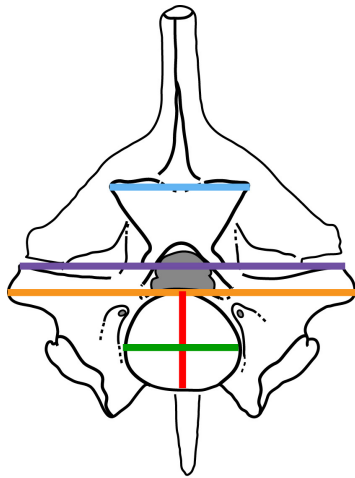
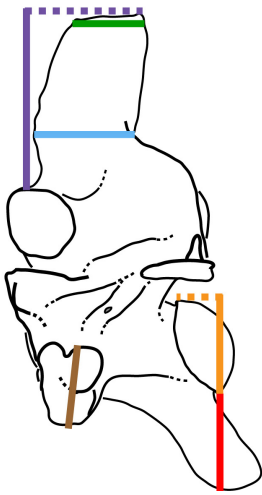
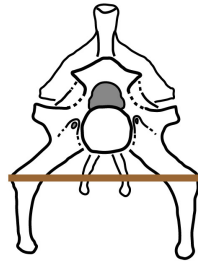


Figure 2.2. The 22 measurements taken in this study, illustrated on standardized anatomical views of representative vertebrae of an adult *Boa constrictor* (YMP R 12323). A. Anterior views of anterior trunk (left) and caudal (right) vertebrae. B. Lateral views of anterior trunk (left) and caudal (right) vertebrae. C. Dorsal view of a mid-trunk vertebra. D. Ventral view of a mid-trunk vertebra. See Table 2.2 for more information. CL, centrum length; CnH, condyle height; CnW, condyle width; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; HeH, hemapophyseal height; NAW, neural arch width; NBL, neural spine base length; NH, neural spine height; NTL, neural spine tip length; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, interzygapophyseal distance; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TPW, trans-pleurapophyseal width; TZW, trans-zygosphenal width.



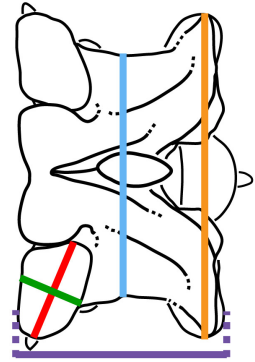
- A
- CtH
 - CtW
 - TAPW
 - TPW
 - TPrW
 - TZW



- B
- CnH
 - HH
 - HeH
 - NBL
 - NH
 - NTL
 - SH



- C
- NAW
 - PrFL
 - PrFW
 - PrPo
 - TPoW



- D
- CL
 - CnW
 - PoFL
 - PoFW

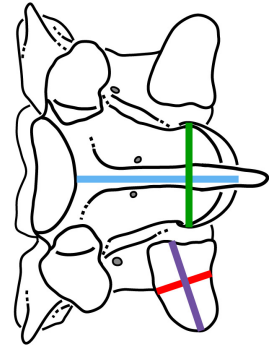
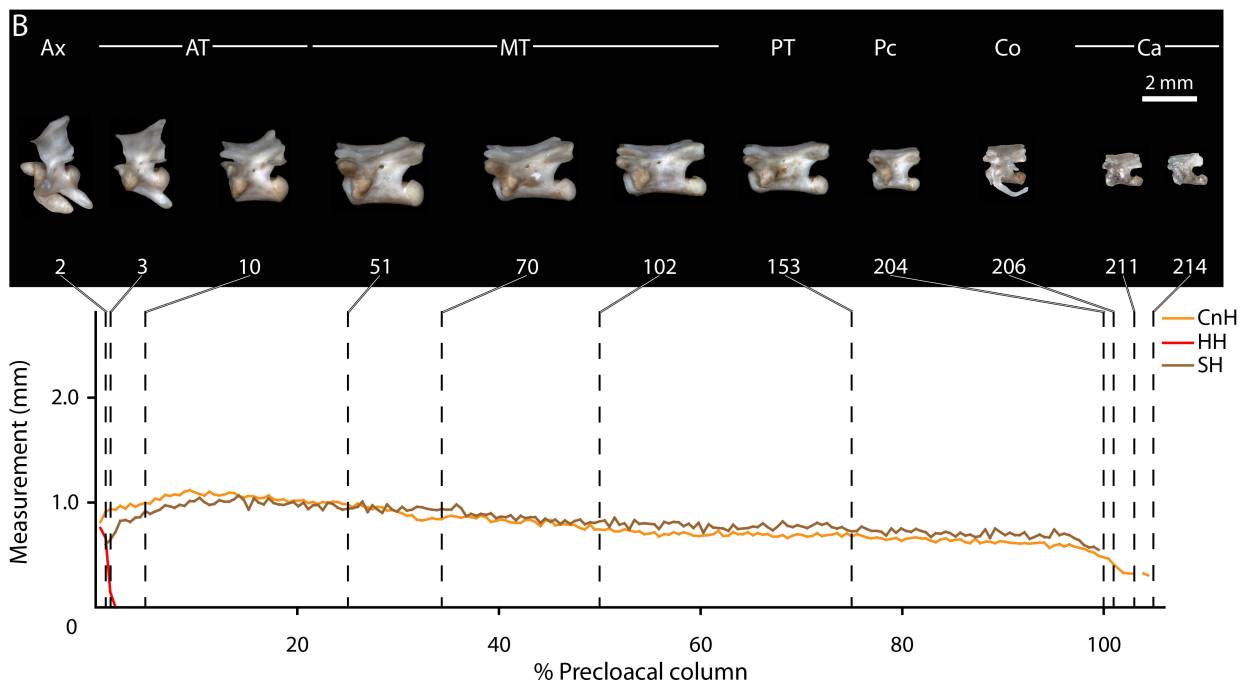
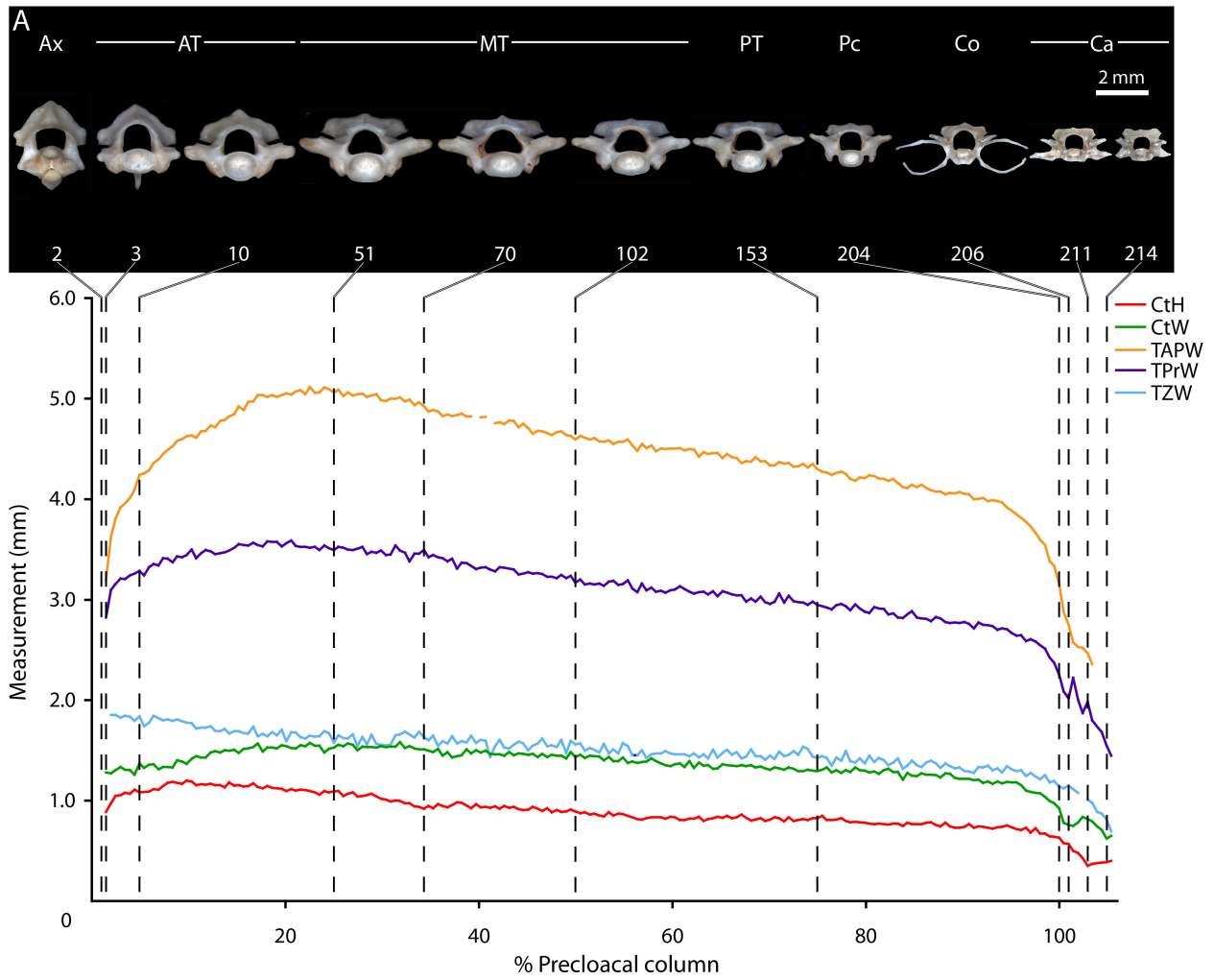


Figure 2.3. Summary of intracolumnar variation in vertebral morphology in *Afrotyphlops lineolatus* (NJK S-A110-D1). Note that the photographed postcloacal vertebrae are taken from a similarly sized specimen (NJK S-A111-D1), but that that measurements were made only on NJK S-A110-D1. Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y-axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x-axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 2.2 and Table 2.2 for additional explanations of the plotted measurements. AT, anterior trunk; Ax, axis; Ca, caudal; CL, centrum length; CnH, condyle height; CnW, condyle width; Co, cloacal; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; MT, mid-trunk; NAW, neural arch width; Pc, precloacal; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, interzygapophyseal distance; PT, posterior trunk; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TZW, trans-zygosphenal width.



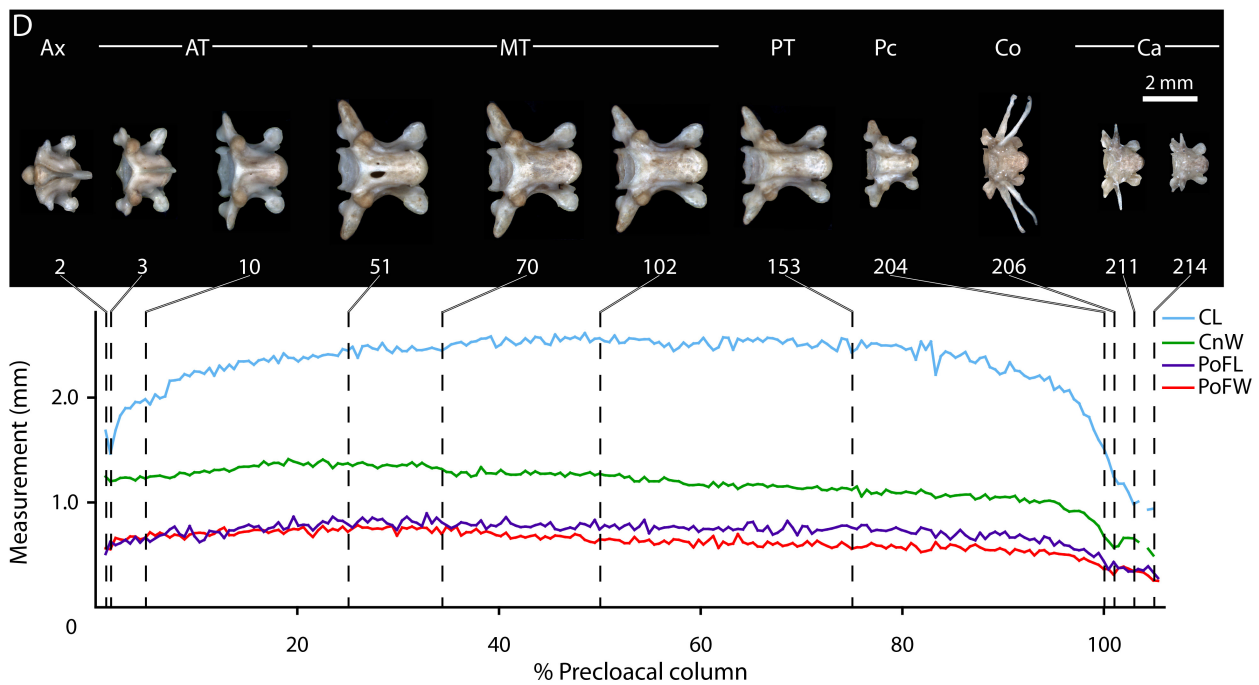
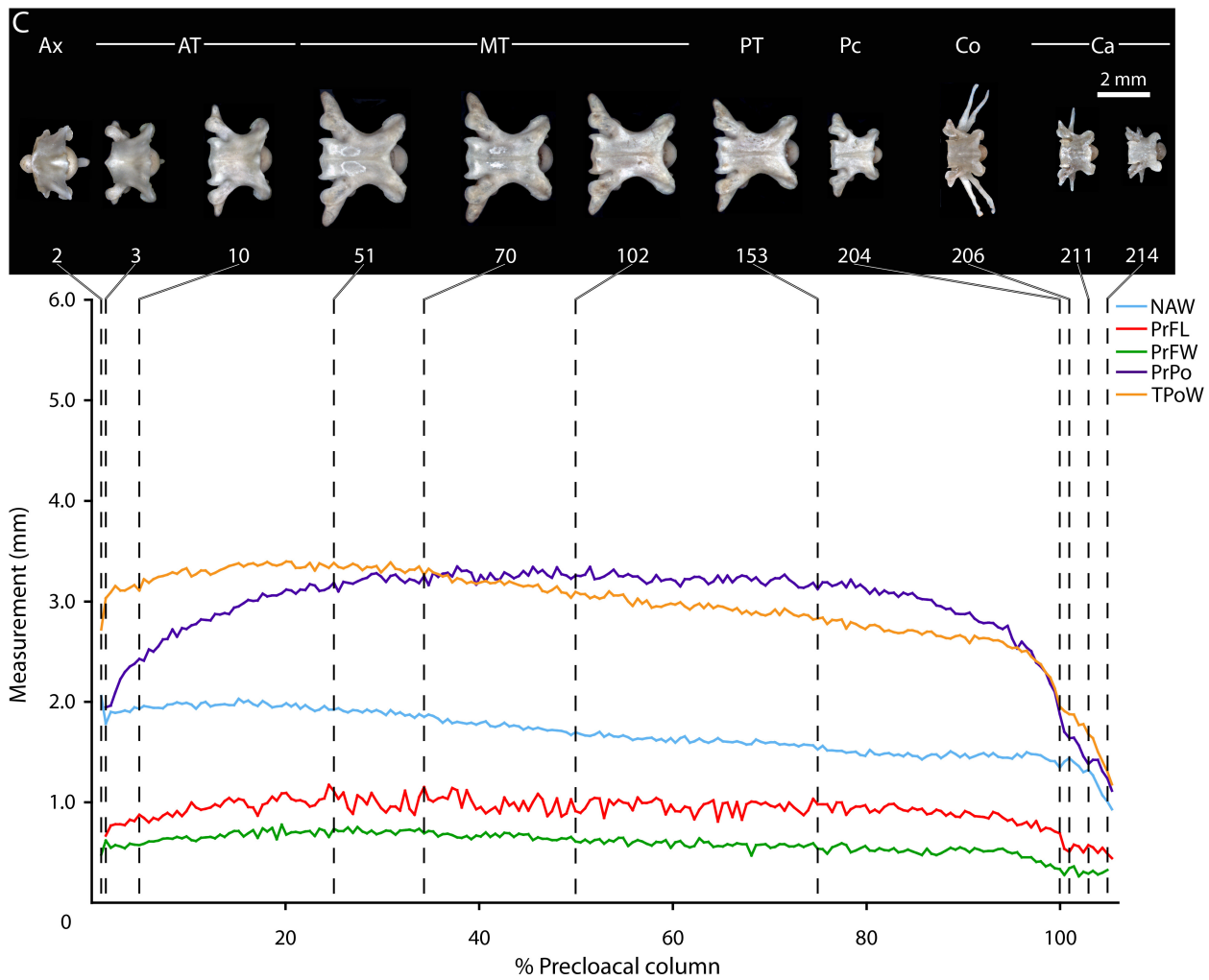
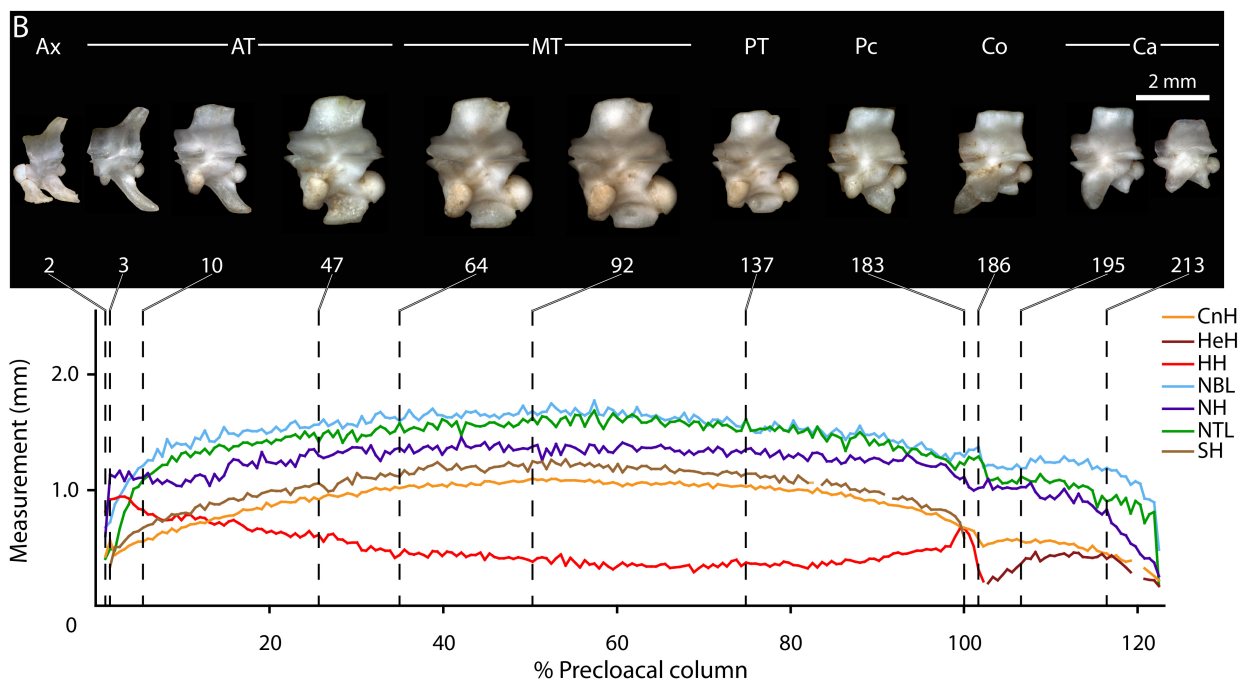
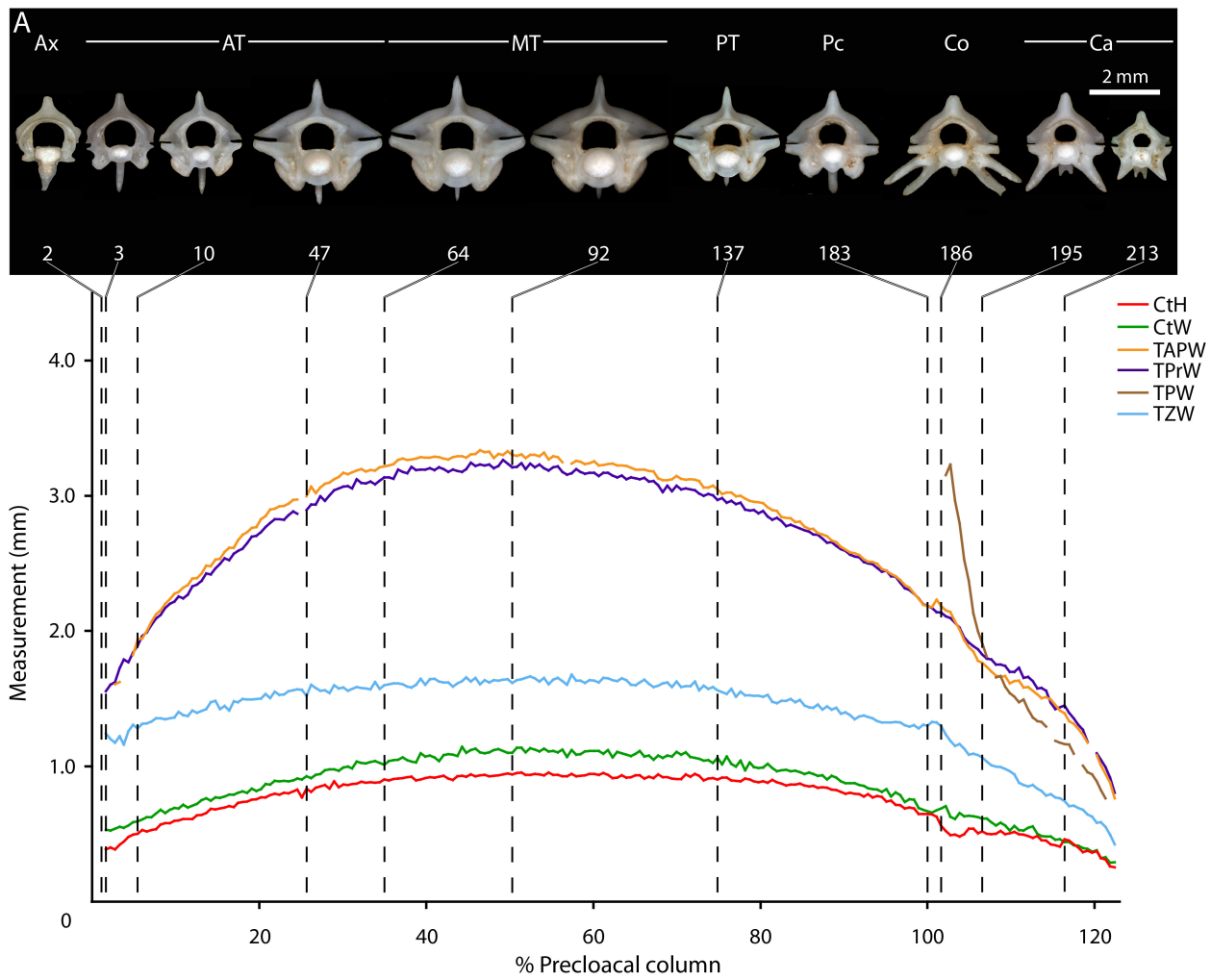


Figure 2.4. Summary of intracolumnar variation in vertebral morphology in *Tropidophis haetianus* (NJK S-Th09-D1). Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y-axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x-axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 2.2 and Table 2.2 for additional explanations of the plotted measurements.

AT, anterior trunk; Ax, axis; Ca, caudal; CL, centrum length; CnH, condyle height; CnW, condyle width; Co, cloacal; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; HeH, hemapophyseal height; MT, mid-trunk; NAW, neural arch width; NBL, neural spine base length; NH, neural spine height; NTL, neural spine tip length; Pc, precloacal; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, interzygapophyseal distance; PT, posterior trunk; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TPW, trans-pleurapophyseal width; TZW, trans-zygosphenal width.



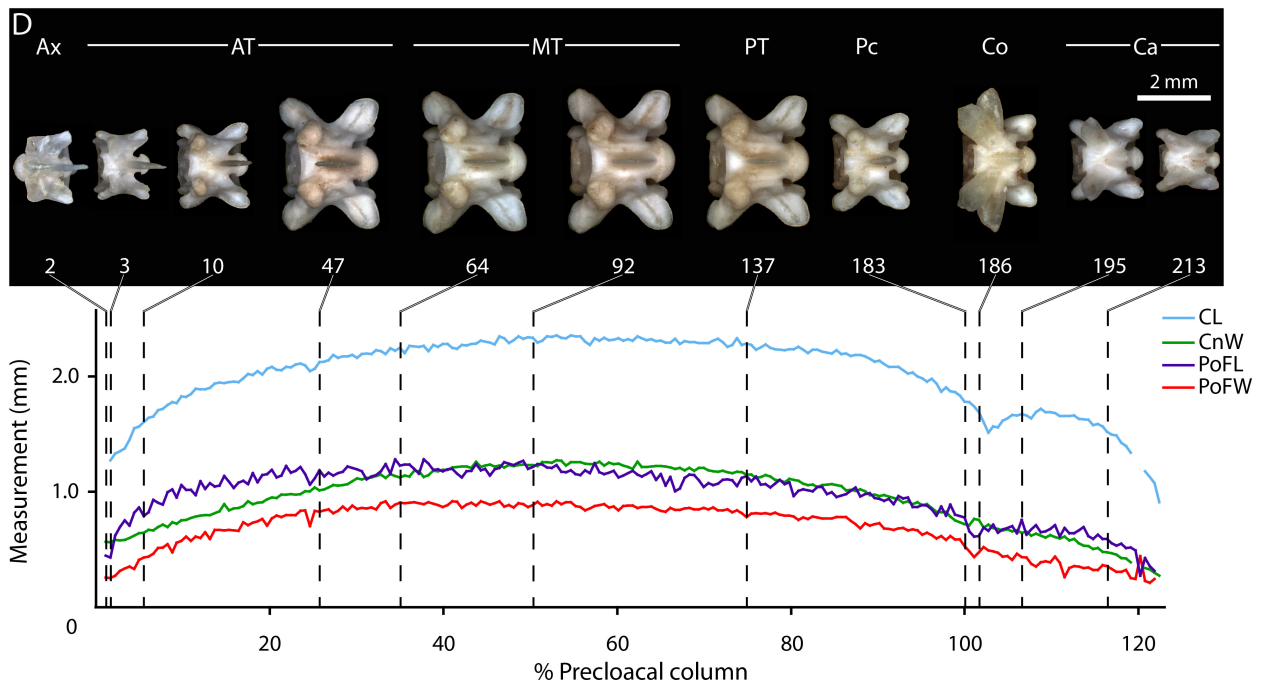
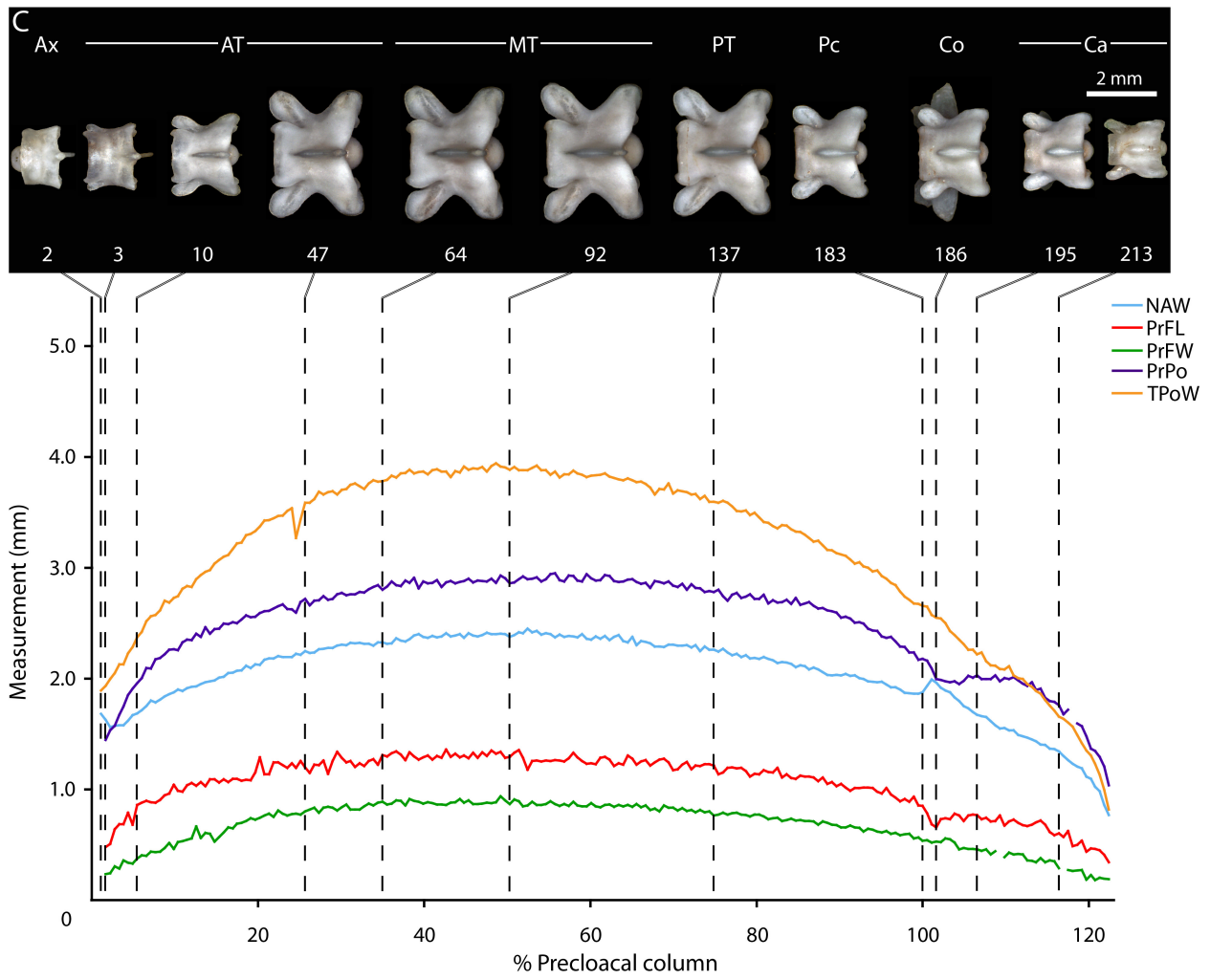
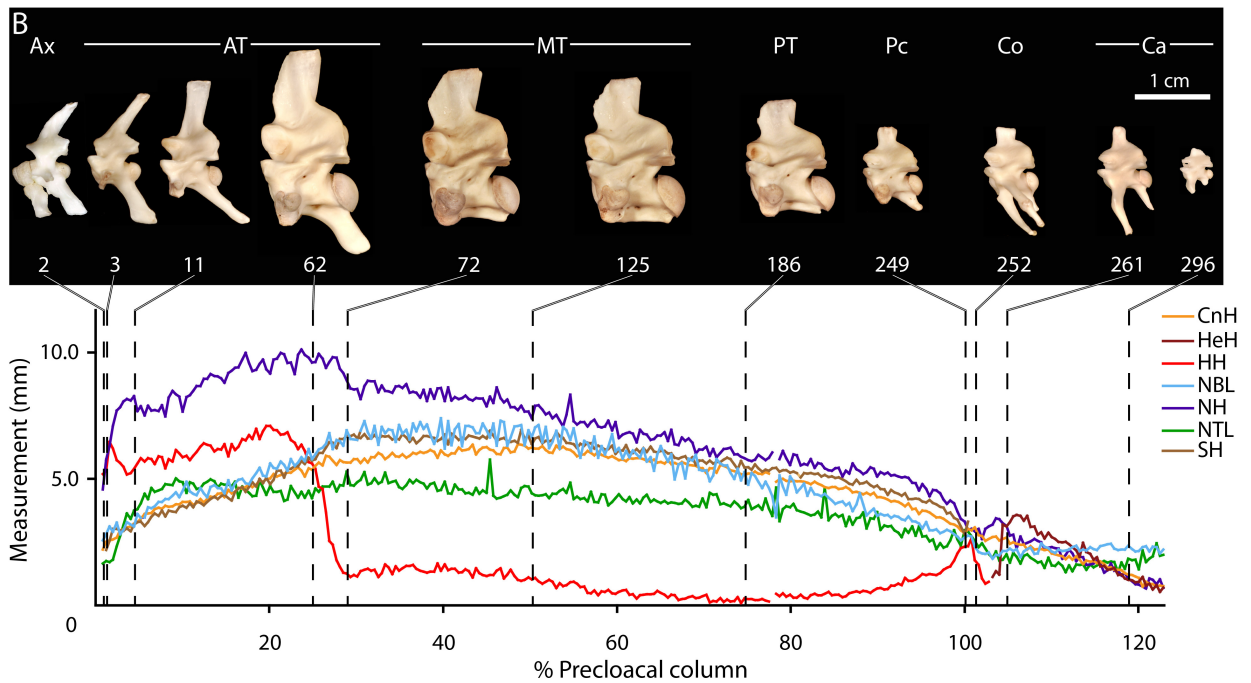
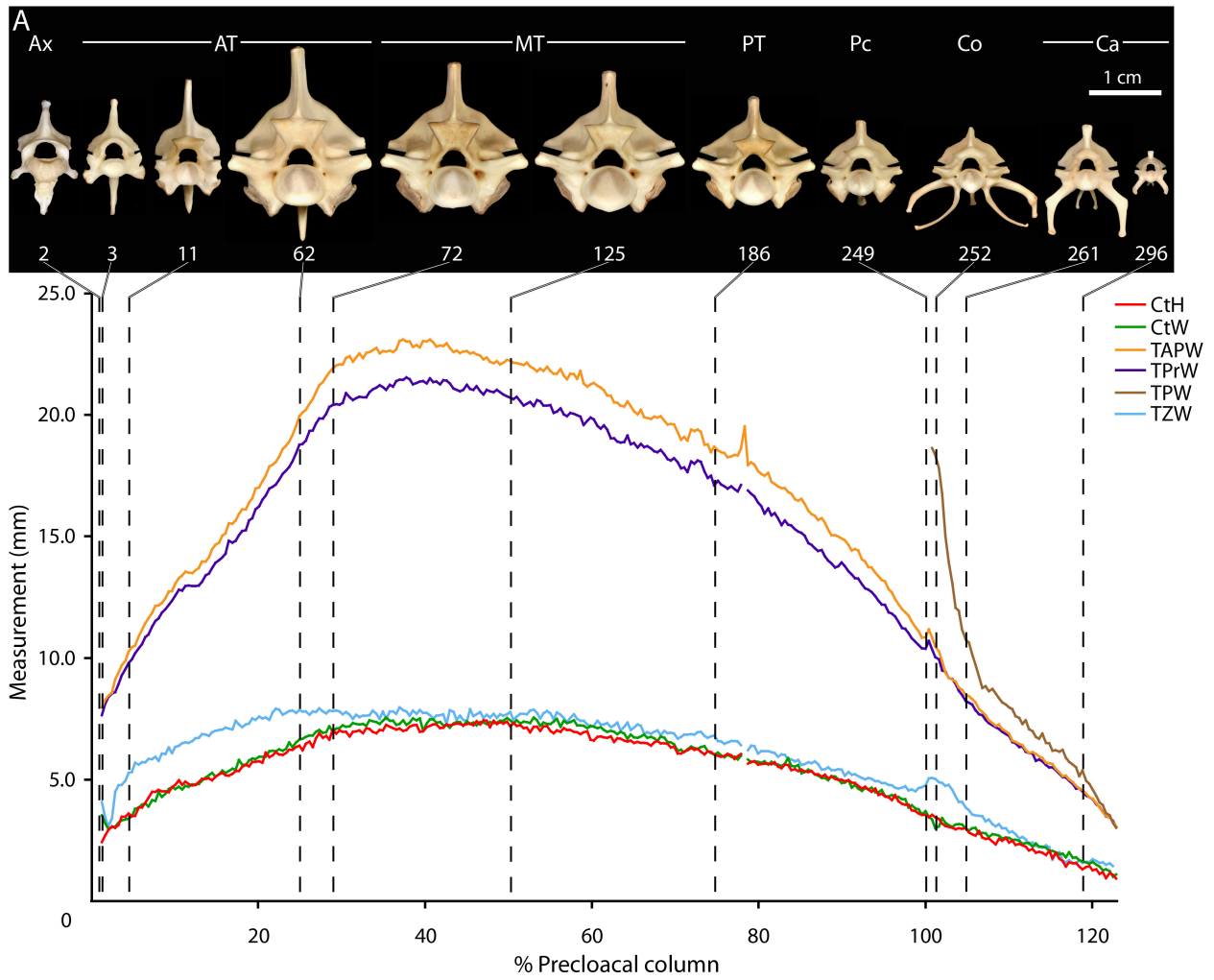


Figure 2.5. Summary of intracolumnar variation in vertebral morphology in *Boa constrictor* (YPM R 12323). Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y-axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x-axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 2.2 and Table 2.2 for additional explanations of the plotted measurements.

AT, anterior trunk; Ax, axis; Ca, caudal; CL, centrum length; CnH, condyle height; CnW, condyle width; Co, cloacal; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; HeH, hemapophyseal height; MT, mid-trunk; NAW, neural arch width; NBL, neural spine base length; NH, neural spine height; NTL, neural spine tip length; Pc, precloacal; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, interzygapophyseal distance; PT, posterior trunk; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TPW, trans-pleurapophyseal width; TZW, trans-zygosphenal width.



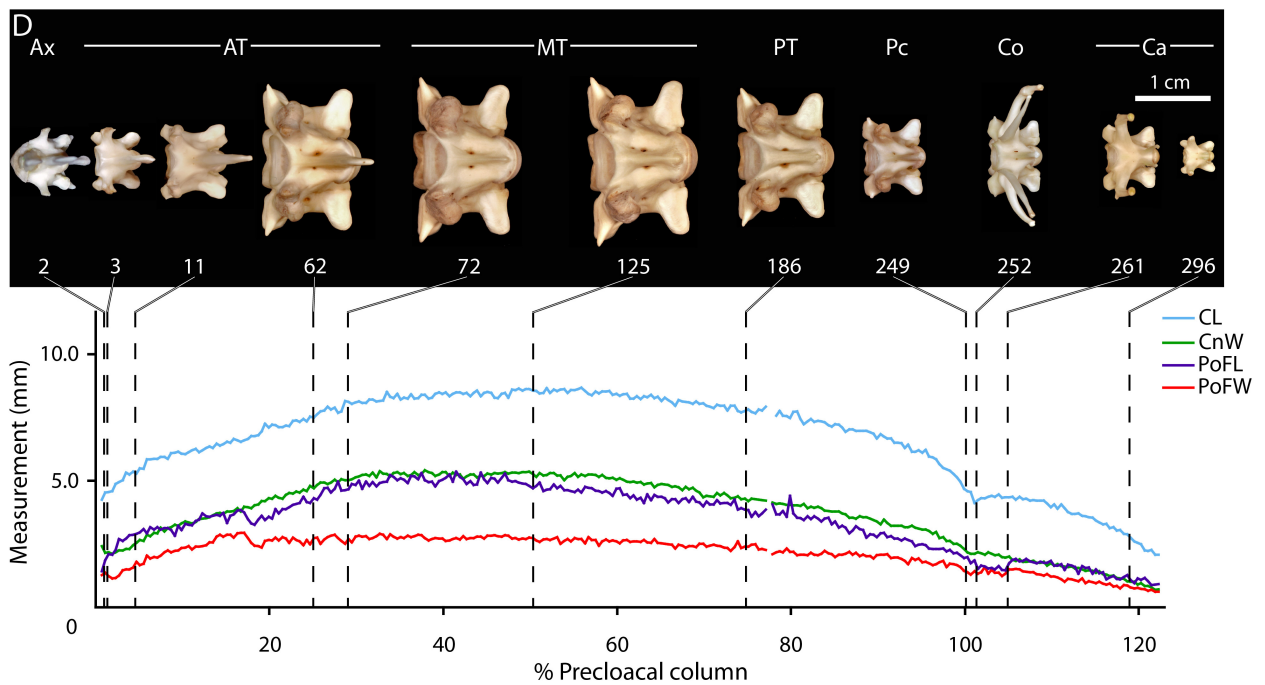
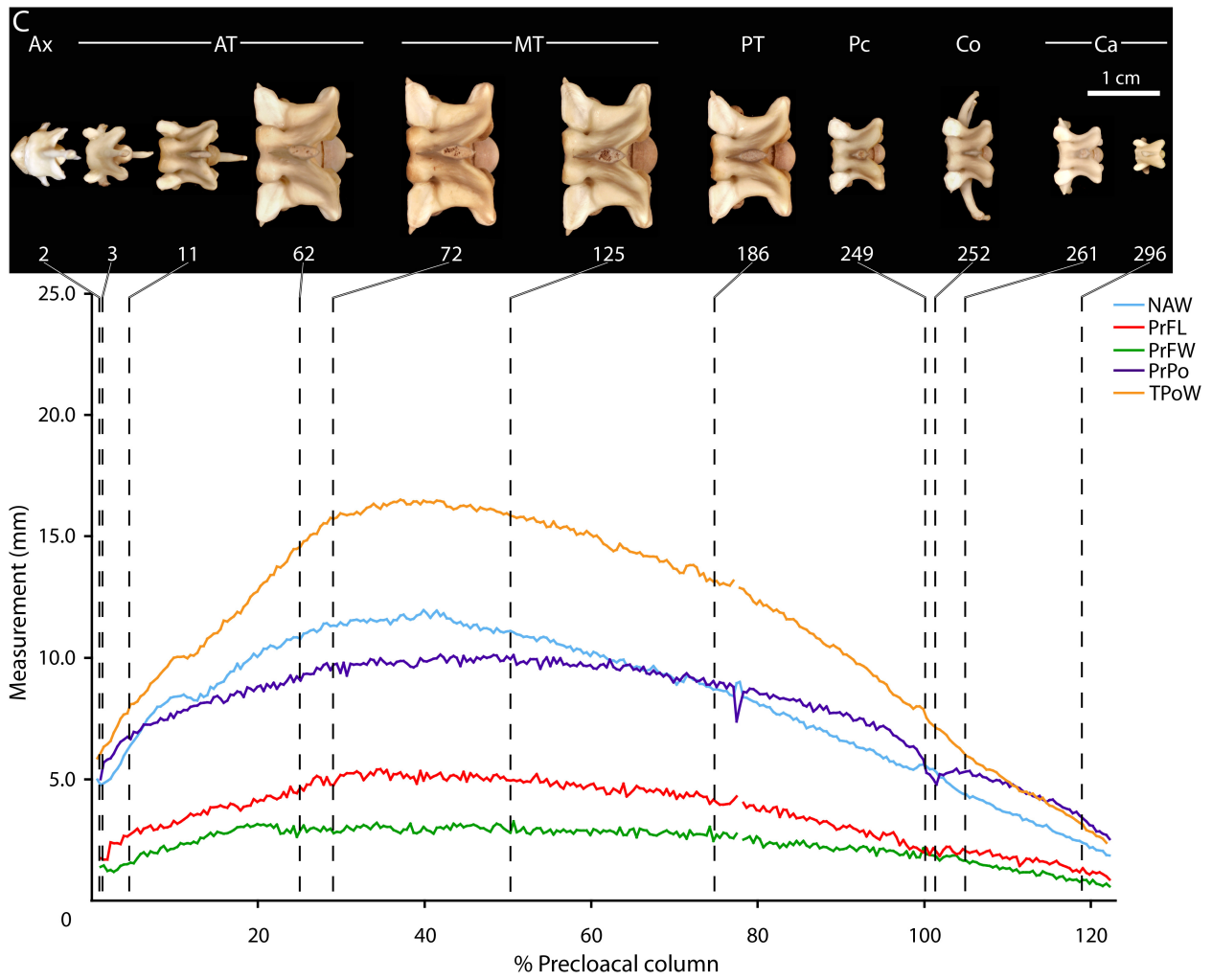
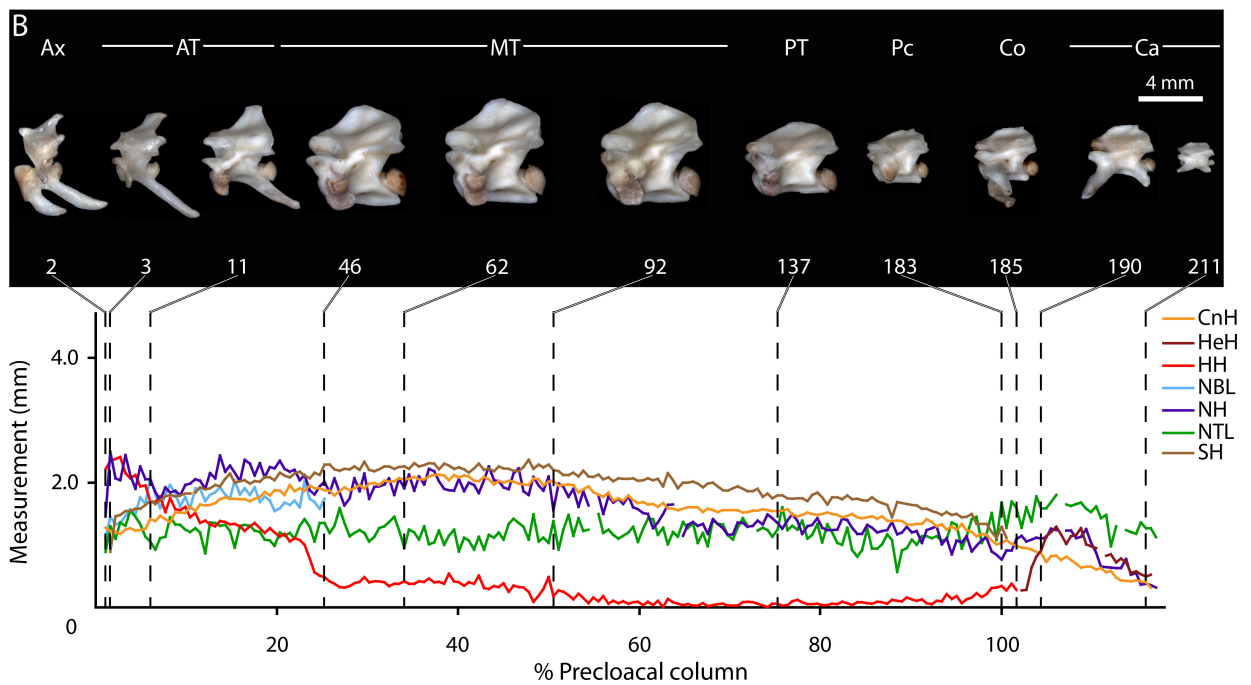
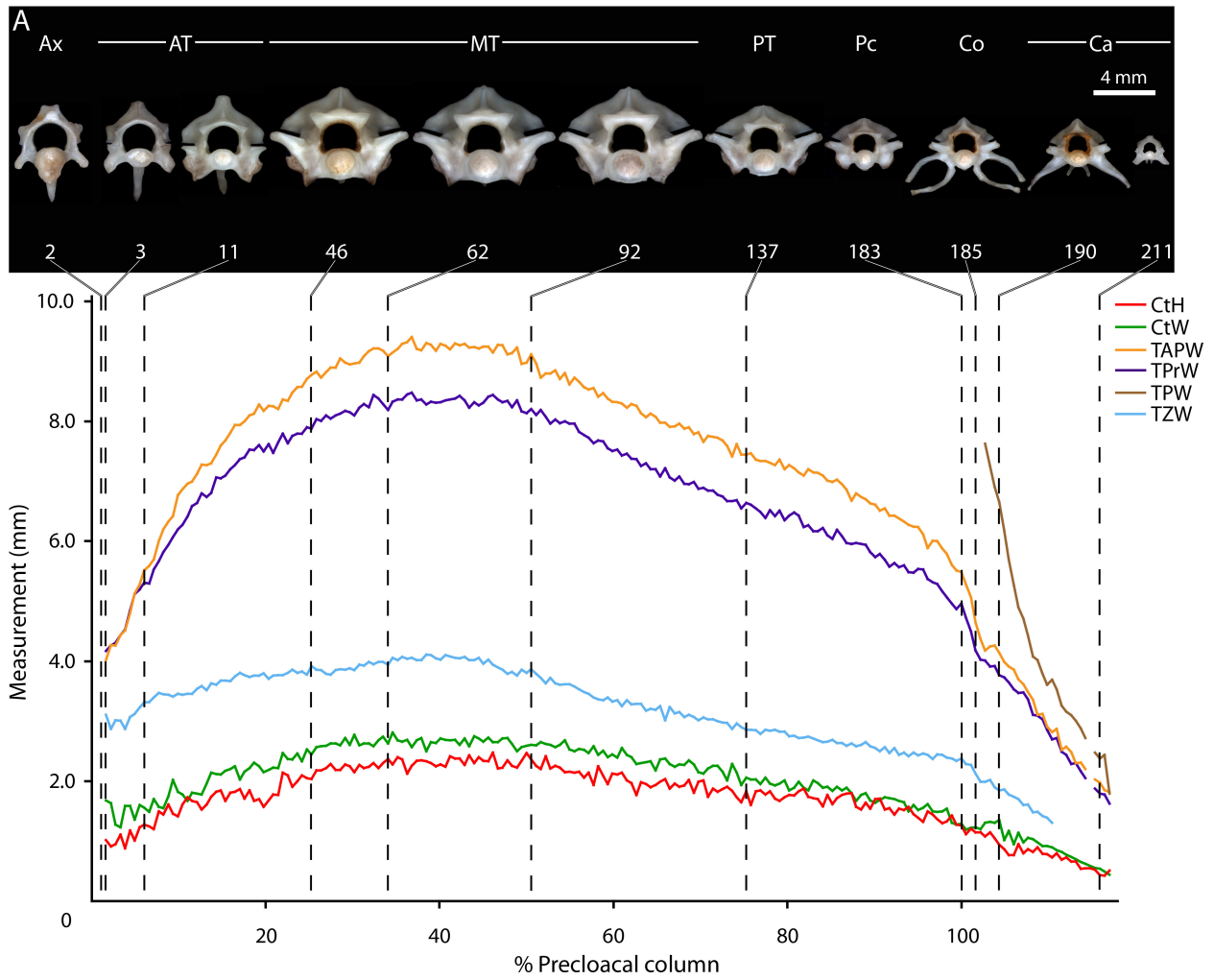


Figure 2.6. Summary of intracolumnar variation in vertebral morphology in *Xenopeltis unicolor* (NJK S-Xu09-D1). Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y-axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x-axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. The height and shape of the neural spines caused the metrics neural spine base length (NBL) and neural spine tip length (NTL) to become effectively indistinguishable beyond approximately 25% of precloacal vertebral number, and thus only tip lengths were recorded posterior to this point. See Figure 2.2 and Table 2.2 for additional explanations of the plotted measurements. AT, anterior trunk; Ax, axis; Ca, caudal; CL, centrum length; CnH, condyle height; CnW, condyle width; Co, cloacal; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; HeH, hemapophyseal height; MT, mid-trunk; NAW, neural arch width; NBL, neural spine base length; NH, neural spine height; NTL, neural spine tip length; Pc, precloacal; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, interzygapophyseal distance; PT, posterior trunk; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TPW, trans-pleurapophyseal width; TZW, trans-zygospheneal width.



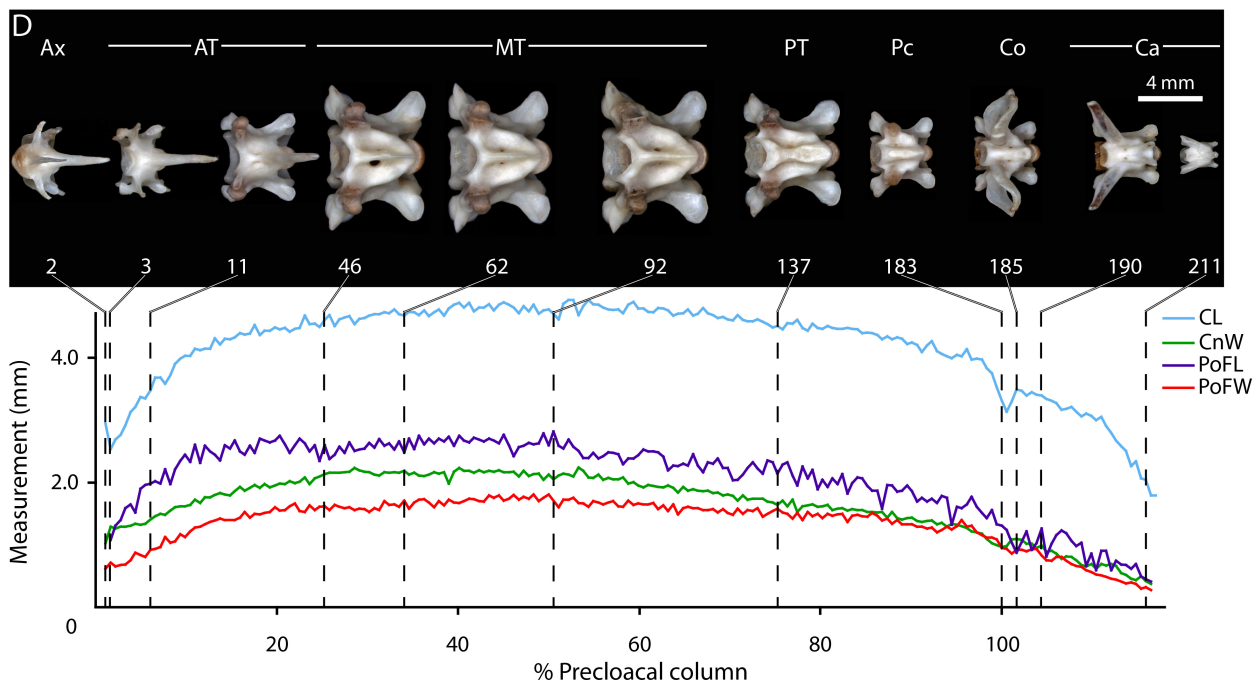
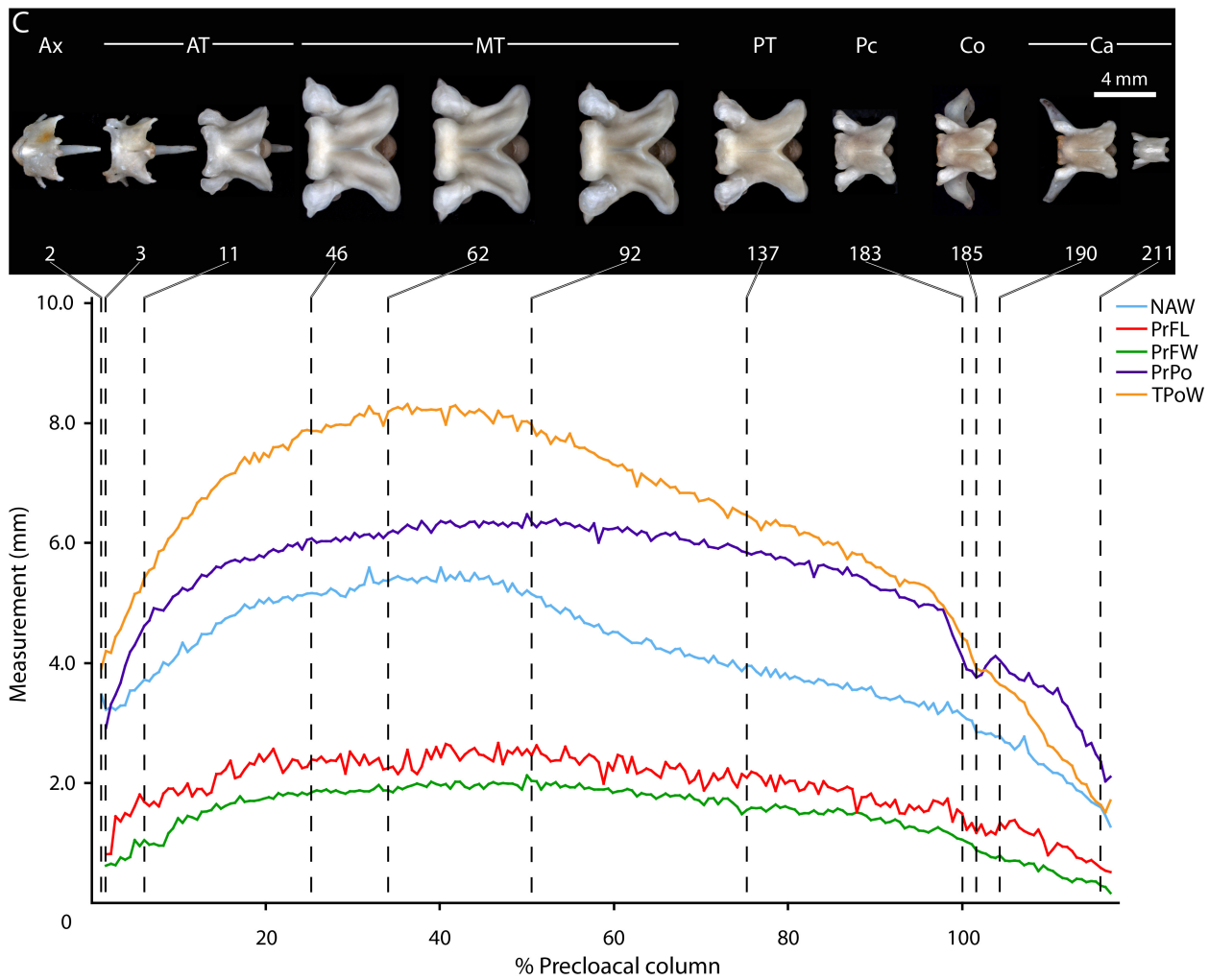
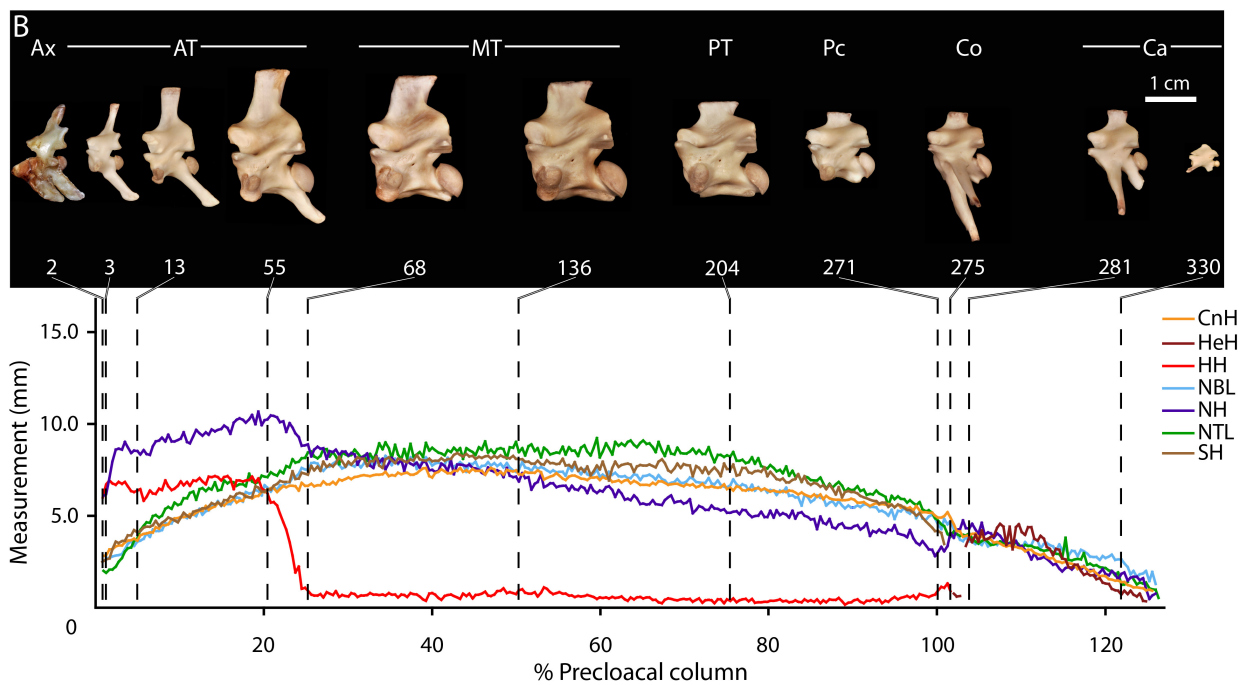
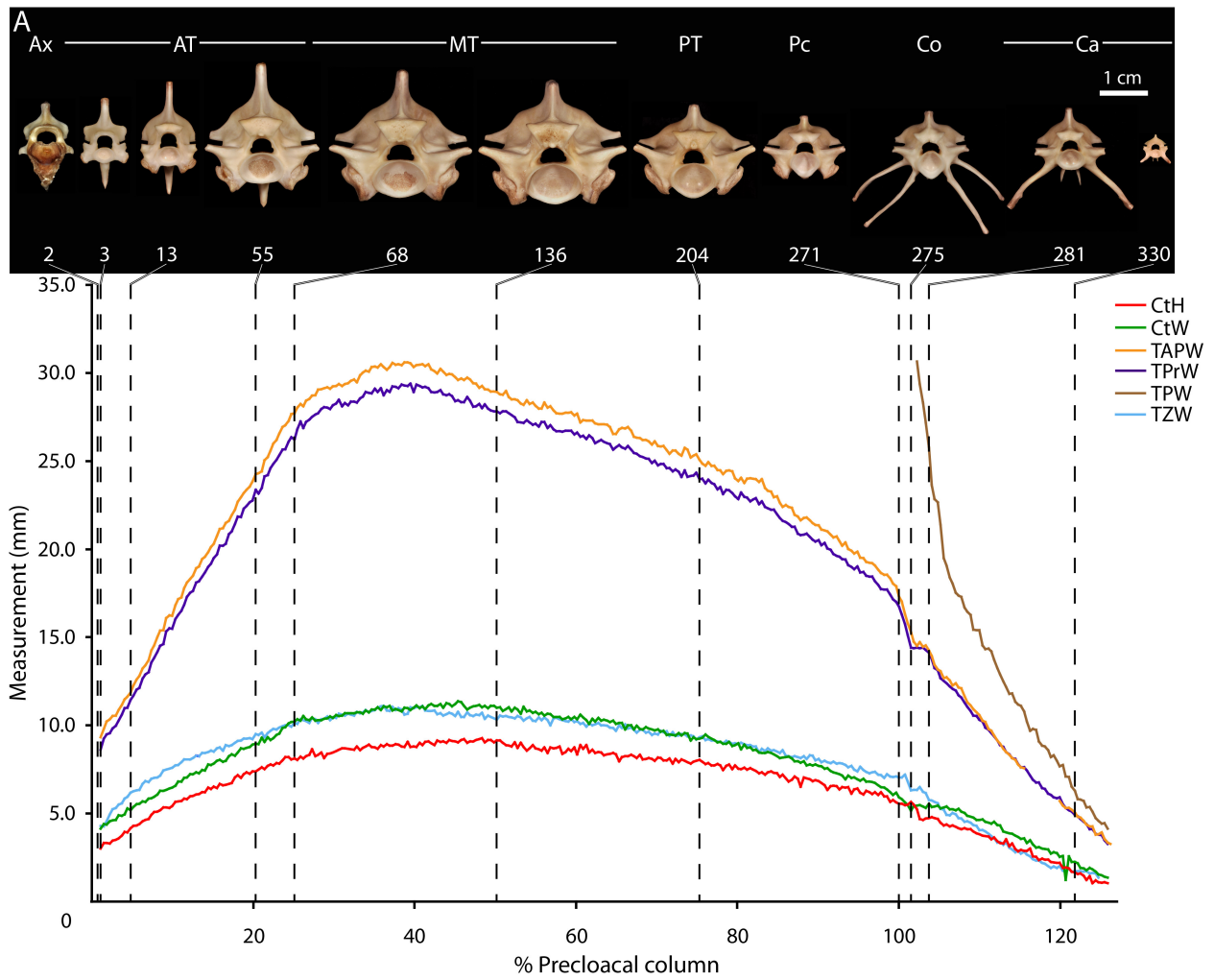


Figure 2.7. Summary of intracolumnar variation in vertebral morphology in *Python molurus* (YPM R 12545). Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y-axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x-axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 2.2 and Table 2.2 for additional explanations of the plotted measurements.

AT, anterior trunk; Ax, axis; Ca, caudal; CL, centrum length; CnH, condyle height; CnW, condyle width; Co, cloacal; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; HeH, hemapophyseal height; MT, mid-trunk; NAW, neural arch width; NBL, neural spine base length; NH, neural spine height; NTL, neural spine tip length; Pc, precloacal; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, interzygapophyseal distance; PT, posterior trunk; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TPW, trans-pleurapophyseal width; TZW, trans-zygosphenal width.



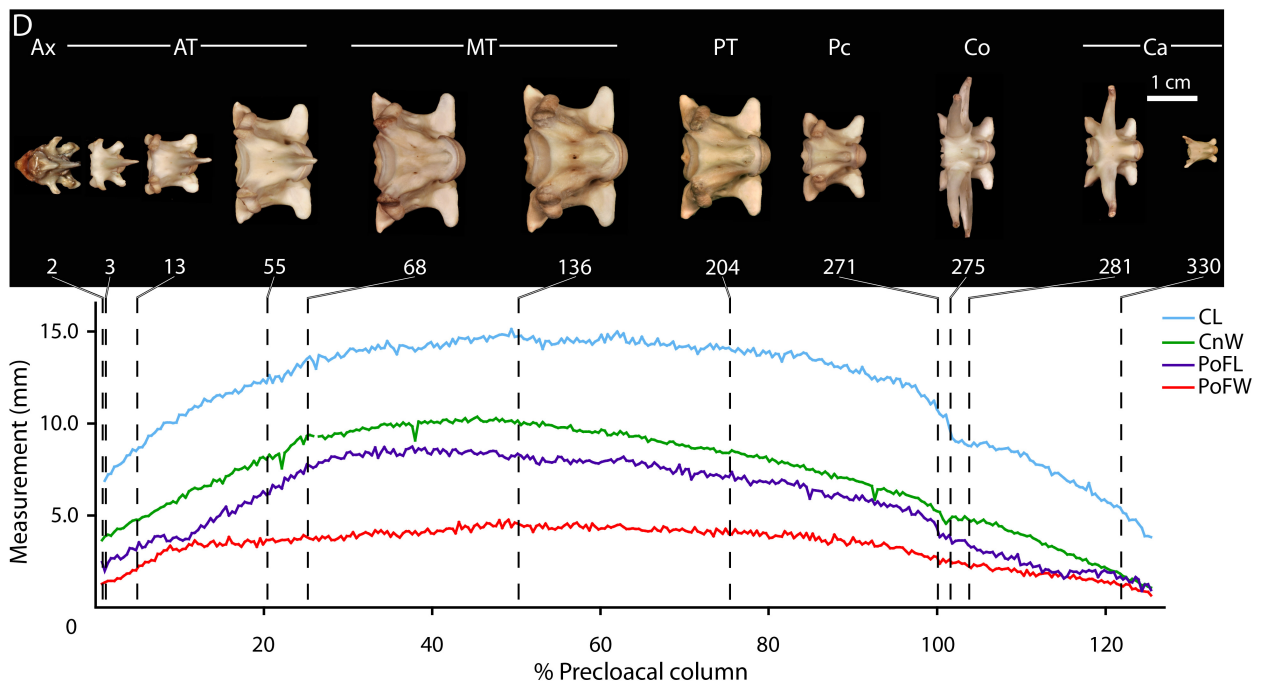
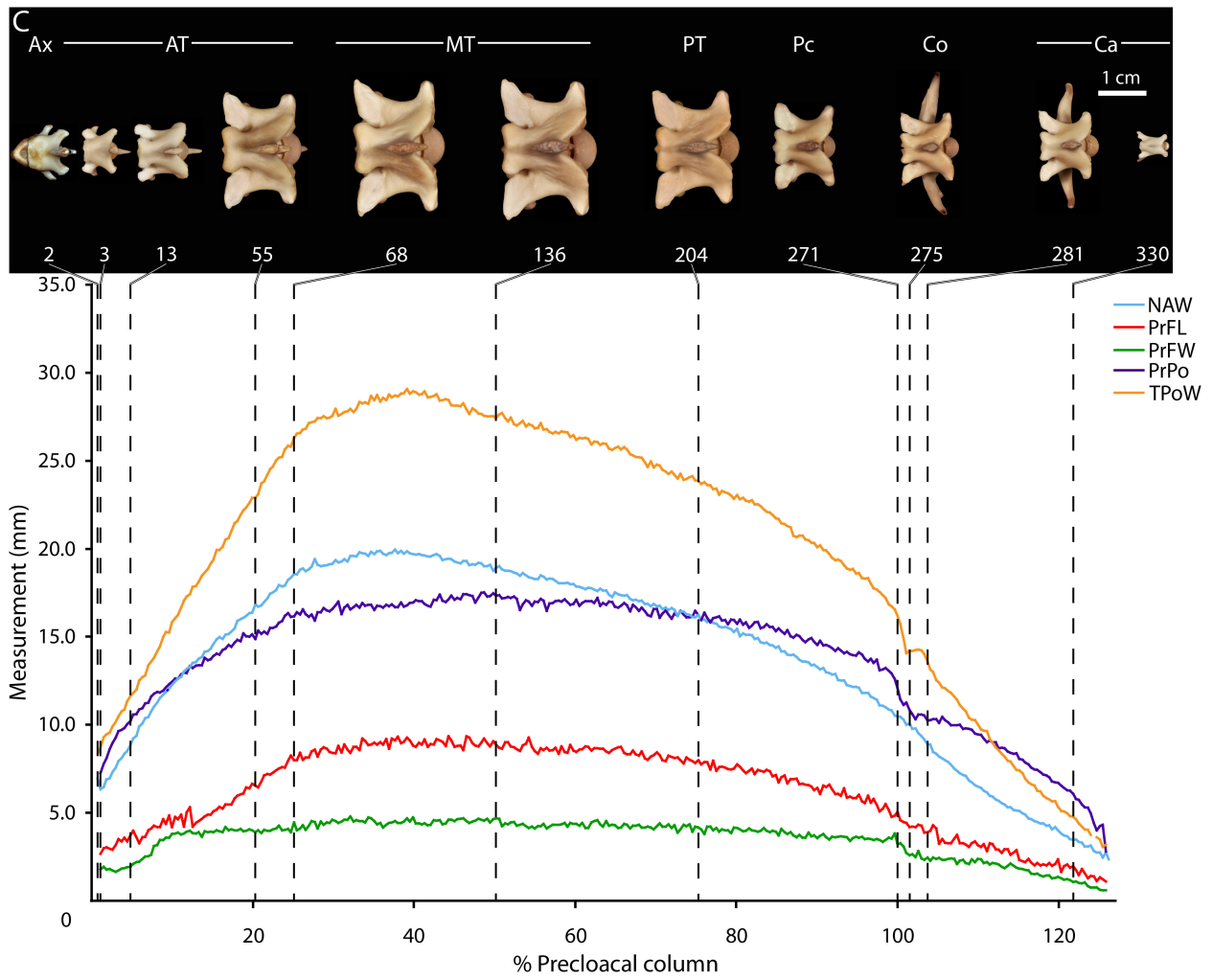
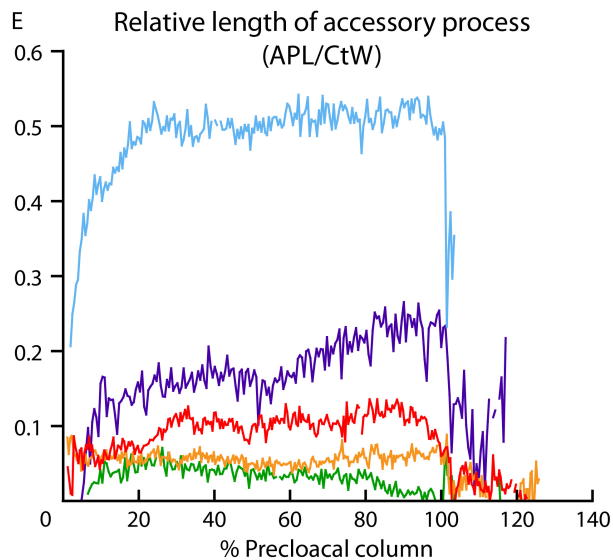
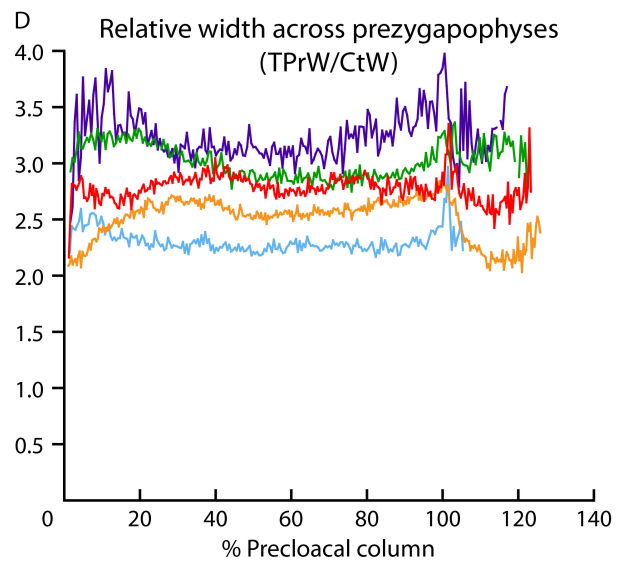
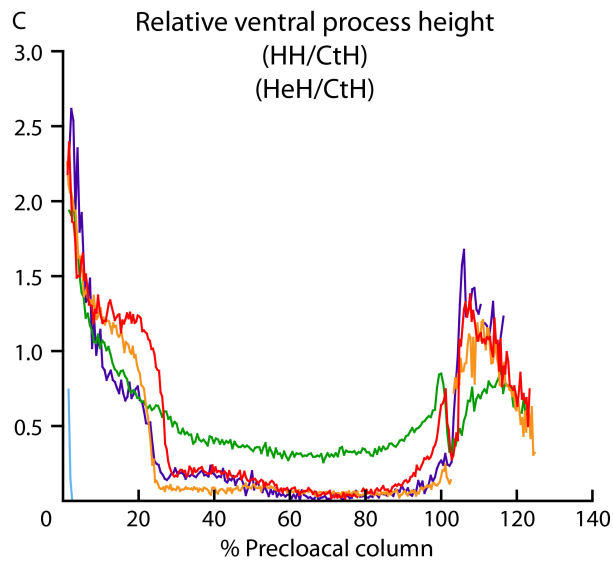
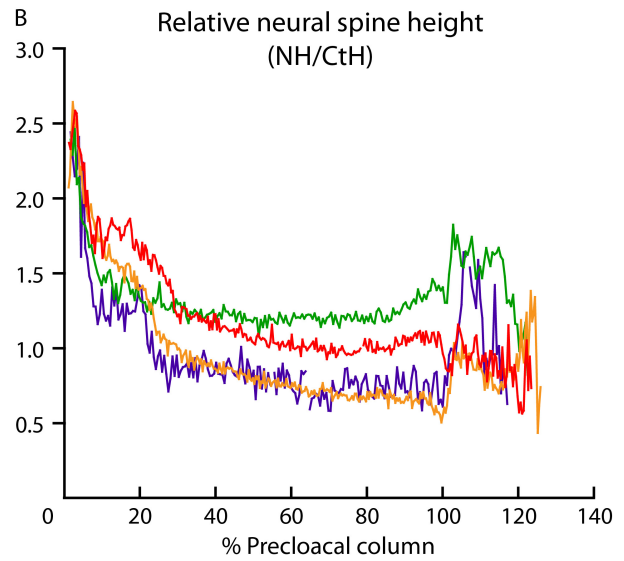
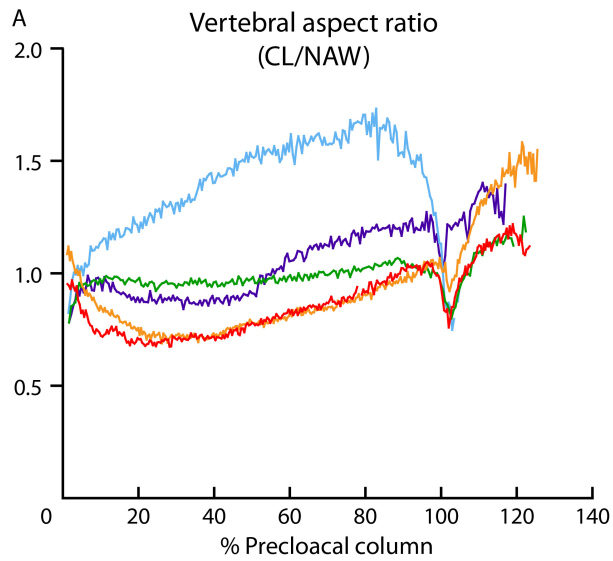


Figure 2.8. Intracolumnar variation in five ratios describing relative vertebral proportions among the snakes sampled in this study. The value of each ratio (y-axis) is plotted against the relative anteroposterior position of the vertebra from which the constituent measurements were taken (x-axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. (A) Overall vertebral aspect ratio, as represented by the ratio of centrum length (CL) to neural arch width (NAW). (B) Relative height of the neural spine, as represented by the ratio of neural spine height (NH) to cotylar height (CtH). (C) Relative height of the ventral process on the centrum, as represented by the ratio of hypapophyseal height/hemal keel (HH) to cotylar height (CtH) in the trunk, and hemapophyseal height (HeH) to cotylar height (CtH) in the postcloacal regions. Postcloacal values are the ratio of hemapophyseal height to cotylar height. (D) Relative width of the prezygapophyses, as represented by the ratio of trans-prezygapophyseal width (TPrW) and cotylar width (CtW). (E) Relative length of the prezygapophyseal accessory processes, as represented by the ratio of accessory process length (APL) to cotylar width (CtW). For definitions of the measurements upon which these ratios are based, see Figure 2.2 and Table 2.2.



- *Afrotyphlops lineolatus*
- *Tropidophis haetianus*
- *Boa constrictor*
- *Xenopeltis unicolor*
- *Python molurus*

Chapter 3

Regional vertebral morphology and intracolumnar variation in advanced snakes (Reptilia, Serpentes, Caenophidia)

Abstract

Snakes have hundreds of morphologically similar vertebrae in their axial columns. The variation within the column of individual snakes is subtle and potentially a confounding factor in studies of paleontology or functional morphology. There have been few investigations of regional morphological variation within the vertebral column of advanced snakes (Caenophidia). This study describes and quantifies intracolumnar variation by means of a series of 22 measurements taken on every vertebra throughout the vertebral column in four caenophidian species. All of the snakes measured show regionalization in neural spine and hypapophyseal heights, which are greatest in the anterior trunk. The pattern of variation in vertebral aspect ratio differs between the species in this study, with *Acrochordus javanicus* and *Nerodia taxispilota* showing patterns seen in booids, and *Pituophis melanoleucus* and *Lieoheterodon madagascariensis* showing little change through the column. In general, *P. melanoleucus* and *L. madagascariensis* show comparatively less regionalization than *A. javanicus* and *N. taxispilota*. The persistence of distinct vertebral regions in the latter two taxa indicates that homogenization of the vertebral column is not universal among advanced snakes, and additional studies of a broader diversity of caenophidians may help to further elucidate the ecomorphological importance of these patterns. It also suggests that homogenous vertebral columns have evolved multiple times in Serpentes. The regionalized nature of the column in these advanced snakes also warrants caution for paleontologists attempting to identify taxa in an extinct assemblage.

Introduction

Caenophidia represents one of the largest extant radiations of snakes, with approximately 2400 species currently recognized (Vidal et al., 2007b). Fossil evidence shows an early appearance of the clade in the Late Cretaceous (Rage and Werner, 1999), but they did not become dominant in snake faunas until the middle of the Cenozoic (Tihen, 1964; Estes, 1970; Szyndlar and Schleich, 1993; Ivanov, 2000, 2001). This diversification and faunal succession appears to have been largely correlated with the evolution of venom-delivery systems. Venom in turn freed the trunk from its functional role in constriction and thus facilitated morphological specialization for rapid, lateral undulatory locomotion (Savitzky, 1980; Kuch et al., 2005). Caenophidians subsequently outcompeted basal snakes, typically ‘sit-and-wait’ ambush predators, in the open habitats created by the expansion of grasslands in the Miocene (Savitzky, 1980). Differences in the functional requirements of caenophidian vertebrae versus those of basal snakes may be reflected in differences in vertebral morphology. Differing functional requirements also may affect the variation in morphology exhibited along an anteroposterior gradient throughout the vertebral column as a whole.

Previous studies have highlighted several aspects of vertebral morphology that have been interpreted as reflecting differences in the natural histories of caenophidians relative to those of basal snakes. Caenophidians appear to have fewer, more elongate vertebrae than basal snakes (Savitzky, 1980). The greater number of vertebrae among the latter, most of which are

constrictors, has been hypothesized to facilitate efficient constriction by reducing the minimum radii of their body coils (Savitzky, 1980; Jayne, 1982; Lindell, 1994). Furthermore, the tendons of the epaxial muscles primarily responsible for powering lateral undulation are longer in caenophidians than in basal snakes, which improves the mechanical advantage of these muscles for producing lateral undulation without greatly increasing mass (Ruben, 1977; Jayne, 1982).

Morphological variation within the vertebral column has been described qualitatively for North American colubrid caenophidians (LaDuke, 1991a). Many of the region-specific features noted in these North American species have been observed subsequently in other snakes from different parts of the world and representing other families within Serpentes (e.g., Head, 2005; LaDuke et al., 2010). However, relatively few quantitative studies of intracolumnar variation in caenophidians have been published. In the first of these, one focusing on the acrochordid *Acrochordus javanicus*, extensive comparisons could not be made with other snakes at the time due to a lack of data (Hoffstetter and Gayrard, 1964). The first comparative study of caenophidian snakes was of two species of viperids, with the aim of differentiating species within that family (Brattstrom, 1964). Subsequent work by Thireau (1967a, b) expanded the collective comparative sample to include an aquatic elapid, two additional viperids, and the atractaspidine *Atractaspis atterima*. These last two studies found numerous differences among the four species studied, with the fossorial *A. atterima* standing out particularly as varying little through the precloacal column, except in measurements of the hypapophyses and neural spines (Thireau, 1967b). However, differences in measurement techniques limit the comparability of data derived from these studies. Since then, limited studies of the variation in a few metrics throughout the column have been expanded to include terrestrial elapids (Smith, 1975) and several European colubrids and viperids (Szyndlar, 1984).

Intracolumnar variation in vertebral morphology is of potential interest to both functional morphologists and paleontologists. Previous work has suggested that behavioral differences are reflected, at least in part, in the morphology of individual vertebrae (Johnson, 1955; Baszio, 2005). Regional differentiation of the vertebral column has also been linked to behavioral differences. Gasc (1974) suggested that caenophidians with a flexible anterior trunk used in rapid, powerful strikes have longer prezygapophyseal accessory processes in that region than those taxa with a more rigid anterior trunk that do not strike. Moon (1999) showed that variation in vertebral morphology allows different degrees of rotation along the column. In addition to these possible functional correlations, the identification of patterns of variation throughout the column of caenophidians, snakes considered to have relatively little variation in the column, may help in the assignment of isolated vertebral fossils to appropriate regions in the column, particularly in cases in which there are multiple taxa in an assemblage.

The purpose of this study is to quantify intracolumnar variation in a sample of four caenophidian snakes. To facilitate comparisons, the measurements made are the same as those reported by McCartney (Chapter 2) for basal (i.e., non-caenophidian) snakes. The snakes sampled in this study come from the family Acrochordidae and three subfamilies of the superfamily Colubroidea (Fig. 3.1). The acrochordid, *Acrochordus javanicus*, has been measured previously (Hoffstetter and Gayrard, 1964), and thus its inclusion in this study is anticipated to shed some light on the degree to which patterns of intracolumnar variation may themselves vary within species.

Materials and Methods

The specimens included in this study are all caenophidian snakes, including one acrochordid and three colubroids (Fig. 3.1). The acrochordid, *Acrochordus javanicus*, is a freshwater aquatic snake that is known to use its coils to hold or constrict fish prey (Dowling, 1960; Greene and Burghardt, 1978; Lillywhite, 1996), although the kinematic details of this behavior are largely unstudied. Acrochordidae is the sister group to all other caenophidians, collectively known as Colubroidea (e.g., Lee and Scanlon, 2002; Kelly et al., 2003; Lawson et al., 2005; Vidal et al., 2007b; Wiens et al., 2008; Pyron et al., 2011; Pyron and Burbrink, 2012; Pyron et al., 2013a). The sample includes two members of the family Colubridae, and one of the family Lamprophiidae. The colubrids include the colubrine *Pituophis melanoleucus*, a terrestrial constrictor that feeds on vertebrates, primarily mammals (Hamilton and Pollack, 1956; de Queiroz, 1984; Diller and Wallace, 1996). The natricine colubrid *Nerodia taxispilota* is a freshwater aquatic piscivore that does not constrict (Hamilton and Pollack, 1956; Camp et al., 1980; Gibbon and Dorcas, 2004). It also has a proclivity toward arboreality (Gibbon and Dorcas, 2004). The last snake included in this study, the pseudoxyrhophiine lamprophiid *Leioheterodon madagascariensis*, is a venomous snake that feeds on vertebrate prey, using constriction for larger food (Conant, 1938; Mori and Randriamahazo, 2002; Cadle, 2003).

The vertebral measurements reported in this study were taken on four specimens, one per species (Table 3.1). One of them (NJK S-Lm09-D1, *Leioheterodon madagascariensis*) was prepared specifically for this study from a previously frozen, fully intact specimen. It was prepared by first disarticulating the craniovertebral joint and the posteriormost intervertebral joint (i.e., that between the last unfused caudal vertebra and the fused terminal caudal vertebrae) and then passing a thin, stiff wire down the length of the neural canal. The specimen was subsequently macerated in water at room temperature for several weeks, which ultimately yielded a completely cleaned skeletal specimen in which vertebral order was fully maintained. This specimen is currently held in the personal research collection of Nathan J. Kley (NJK). The remaining specimens (YPM R 12192, *Acrochordus javanicus*; YPM R 10679, *Pituophis melanoleucus*; YPM R 10601, *Nerodia taxispilota*) were selected for this study because they were already cleanly prepared with their vertebral order maintained. These specimens are held in the collections at the Yale Peabody Museum (YPM). Additional specimen photographed was *Pituophis melanoleucus* (YPM R 16559).

A series of 20 measurements was made on every vertebra throughout the vertebral column (Table 3.2, Fig. 3.2; for additional details, see McCartney, in prep.). Two of these measurements were replaced by alternative metrics in postcloacal vertebrae due to regional differences in morphology, giving a total of 22 measurements. Larger specimens were measured with digital calipers to the nearest 0.1 mm. Smaller specimens were measured from digital photomicrographs captured using an Axiocam MRc camera coupled to a Zeiss Discovery.V12 stereo dissecting microscope. Measurements were made from these photomicrographs using Zeiss Axiovision software (v. 4.4.1.0; Zeiss, 2002–2005) to the nearest 0.1 mm. This software is integrated with the microscope's control mechanism, allowing accurate measurements to be made based on the focal plane of the microscope. Bilateral structures were measured on the left side whenever possible. However, exceptions to this general convention were sometimes made in cases of damaged specimens or those deformed by pathologies. The atlas and axis are morphologically distinct from all succeeding vertebrae and, as such, do not reflect many of the metrics measured elsewhere throughout the column. Only a few metrics (i.e., measurements of

the condyle, neural spine, hypapophysis, and postzygapophyses) were recorded for the axis, and none were recorded for the atlas. Detailed descriptions of the measurements made are given in Table 3.2 and Figure 3.2. Specimens were oriented following the standards described by McCartney (Chapter 2) and, as in that study, a series of ratios was derived from the raw morphometric data to examine changes in the relative sizes of certain features of the vertebrae throughout the column.

Results

Three of the four snakes measured in this study have similar total vertebral numbers (Table 3.1). *Acrochordus javanicus* has a total of 274 vertebrae, of which 193 are precloacal (70.4% of the total number of vertebrae), and 81 cloacal and caudal vertebrae (often referred to as postcloacal vertebrae; 29.6% of the total number of vertebrae). *Pituophis melanoleucus* has a similar total of 273+ vertebrae (at least the terminal vertebra is missing). The number of precloacal vertebrae is 207 (75.8% of the total number of vertebrae), and there are at least 66 postcloacal vertebrae (22.3% of the total number of vertebrae). *Nerodia taxispilota* has the fewest vertebrae, with only 205+ (at least the terminal vertebra is missing). Of these, only 137 are precloacal vertebrae (66.8% of the total number of vertebrae), and at least 68 are postcloacal (33.2% of the total number of vertebrae). *Leioheterodon madagascariensis* has 279 vertebrae, of which 209 are precloacal (74.9% of the total number of vertebrae), and 70 postcloacal (25.1% of the total number of vertebrae).

The data for each snake measured in this study are presented in Figures 3.3–3.6, in which each individual measurement is plotted by its serial position along the vertebral column (expressed as a percentage of total precloacal vertebral number). In addition, Table 3.3 gives the vertebral position at which each metric reaches its maximum value in each snake. All of the snakes show minor stochastic variations in the measurements from vertebra to vertebra, superimposed upon the broader patterns that become clearly visible when these measurements are plotted across the entire length of the vertebral column. This localized, low-amplitude ‘noise’ in the data is attributable to a number of factors, including natural variation and measurement error. These variations are for the most part minor and do not mask broader patterns of regional variation.

***Acrochordus javanicus*.** In the trunk of the acrochordid *A. javanicus* (Fig. 3.3), most vertebral metrics reach their maximal values between 40–60% of precloacal vertebral number, including measurements of both width and length (Table 3.3). The width metrics (NAW, TAPW, TPoW, TPrW; Fig. 3.3A, C) peak near 40% of precloacal vertebral number, whereas vertebral length metrics (CL, PrPo; Fig. 3.3C, D) peak posterior to the midpoint of the column (about 52% and 58%, respectively). This positional differential between width and length maxima, combined with a more rapid decline in vertebral width versus length posterior to these maxima, results in a change in overall vertebral aspect ratio toward relatively longer vertebrae throughout the mid- and posterior trunk regions (Fig. 3.7A). In contrast, the height of the hypapophyses (HH; Fig. 3.3B) reaches its maximum in the anterior trunk, at about 27% of precloacal vertebral number. Neural spine height (NH; Fig. 3.3B) also peaks in the anterior trunk, although at 37% it is close to the region where many width metrics peak. Both features are also relatively highest in the anterior trunk (Fig. 3.7B, C). The relative width across the prezygapophyses (TPrW; Fig. 3.7D) is greatest in the anterior trunk. From about 45% of precloacal vertebral number to about 60%

there is a rapid decline in this metric, but posterior to that point the width is stable. Some of the decline in the relative width across the prezygapophyses that occurs farther posteriorly may be explained by the widening of the cotyles (CtW; Fig. 3.3A) that occurs through the column, and which continues well beyond mid-trunk. The prezygapophyseal accessory processes show the opposite pattern, becoming relatively longer through the anterior and mid-trunk regions (Fig. 3.7E); however, compared to the other snakes examined in this study, these processes remain relatively short throughout the column in *A. javanicus*.

In the postcloacal regions, most vertebral features decrease in size, although some show local maxima in the anterior tail (Fig. 3.3). As is the case for all squamates, the cloacal region in *A. javanicus* is characterized by a rapid decrease in vertebral length as reflected not only in absolute measurements (CL, PrPo; Fig. 3.3C, D), but in relative ones as well (e.g., CL/NAW; Fig. 3.7A). In contrast, the relative heights of the neural spines increase in this region, continuing a trend seen in the posterior trunk (Fig. 3.7B). A similar trend is seen hypapophyseal height throughout the posterior trunk and anterior portion of the cloacal region (Fig. 3.7C); however, the hypapophyses decline rapidly in both absolute and relative size before being replaced by hemapophyses in the tail (Fig. 3.7C). The relative lengths of the accessory processes decline throughout the tail (Fig. 3.7E).

Pituophis melanoleucus. In the trunk of the colubrine *P. melanoleucus* (Fig. 3.4), most vertebral features again reach their maximum sizes between 40–60% of precloacal vertebral number (Table 3.3). Moreover, many vertebral metrics vary in concert across the trunk, such that overall vertebral proportions remain relatively constant throughout much of the precloacal column; vertebral aspect ratio, for instance, remains nearly uniform throughout most of the trunk (CL/NAW; Fig. 3.7A). Only the two metrics neural spine height and hypapophyseal height (NH, HH; Fig. 3.4B) reach their maxima in the anterior trunk, at approximately 23% and 14% of precloacal vertebral number respectively (Table 3.3). The relative height of both processes is greatest in the anterior trunk, with a local maximum in the cloacal region (Fig. 3.7B, C). However, the hypapophyses show a more precipitous decline in relative height, being replaced at about 25% of precloacal vertebral number by low hemal keels that persist throughout the mid- and posterior trunk (Fig. 3.7C). The relative widths across the pre- and postzygapophyses (TPrW, TPoW; Fig. 3.4A, C) show little change throughout the precloacal column (Fig. 3.7D). In contrast, the prezygapophyseal accessory processes increase dramatically in their relative lengths throughout the anterior trunk, peaking at about 40% of precloacal vertebral number (Fig. 3.7E). These processes become relatively shorter through the remainder of the trunk.

Pituophis melanoleucus shows similar patterns in the cloacal and caudal regions to those seen in *A. javanicus*. The most notable differences present in *P. melanoleucus* include an increase in the width of the zygosphenes at the cloaca (TZW; Fig. 3.4A), similar to the condition seen in *Boa constrictor* (see Chapter 2). Also notable in *P. melanoleucus* are the relative lengths of the prezygapophyseal accessory processes (APL; Fig. 3.7E), which are considerably reduced in the tail as compared to those of the trunk.

Nerodia taxispilota. The natricine colubrid *N. taxispilota* (Fig. 3.5) is similar to *A. javanicus* and *P. melanoleucus* in that the majority of recorded vertebral metrics reach their maximal values in the trunk within 40–60% of precloacal vertebral number (Table 3.3). As in *A. javanicus*, a mismatch in the position of the peaks of length measurements and width measurements contributes to a change in the vertebral aspect ratio (CL/NAW; Fig. 3.7A), such that the vertebrae are notably longer than they are wide in the posterior trunk. A notable

difference from *A. javanicus* in this ratio is the extremely elongate vertebrae present in the anterior trunk (Fig. 3.7A), so that only the vertebrae near the transition between anterior and mid-trunk (i.e., between about 25% and 50% of precloacal vertebral number) are nearly equal in length and width. The heights of the neural spines and hypapophyses reach their maxima in the anterior trunk, as in both *A. javanicus* and *P. melanoleucus* (NH, HH; Fig. 3.5B, Table 3.3). The relative heights of both the neural spines and hypapophyses also peak far anteriorly, before declining steadily throughout the anterior trunk (Fig. 3.7B, C). Farther posteriorly, the former decline through the mid-trunk region and then remain nearly constant through the posterior trunk (Fig. 3.7B), whereas the latter remain nearly constant throughout both the mid- and posterior trunk regions (Fig. 3.7C). The widths across the pre- and postzygapophyses (TPrW, TPoW; Fig. 3.5A, C) are greatest at approximately 39% of precloacal vertebral number (Table 3.3). In contrast to the condition seen in *A. javanicus* and *P. melanoleucus*, the relative width across the prezygapophyses is lower in the anterior trunk than in the mid- and posterior trunk (TPrW/CTW; Fig. 3.7D). The prezygapophyseal accessory processes exhibit an abrupt increase and resultant peak in relative length in the anterior trunk region before declining more or less steadily throughout the remainder of the trunk (Fig. 3.7E).

The cloacal and caudal vertebrae of *N. taxispilota* show similar patterns of variation to both *A. javanicus* and *P. melanoleucus* (Fig. 3.7). The most notable feature of the tail of *N. taxispilota* is the number of vertebrae it contains, with almost half as many vertebrae in the tail as in the trunk, considerably more than are present in the other snakes in this sample. Also notable is the sudden decrease in size of the prezygapophyseal accessory processes (Fig. 3.5A; Fig. 3.7E) at the cloaca, to the extent that in middle caudal vertebrae they do not project laterally as far as the prezygapophyseal facets (Fig. 3.5A, 3.7E).

***Leioheterodon madagascariensis*.** The pseudoxyrhophiine lamprophiid *L. madagascariensis* (Fig. 3.6) generally shows parabolic patterns of intracolumnar variation for most vertebral metrics in the trunk, although several measurements peak in the anterior 40% of the column. Among the latter is centrum length (CL; Fig. 3.6D), which peaks at about 38% of precloacal vertebral number (Table 3.3). In contrast, neural arch width (NAW; Fig. 3.6C) peaks farther posteriorly at the approximate mid-point of the column (Table 3.3). This, combined with a greater decrease in neural arch width versus centrum length in the posterior trunk, contributes to a weakly bimodal distribution for the vertebral aspect ratio, though to a lesser degree than that of *N. taxispilota* (CL/NAW; Fig. 3.7A). Both the neural spines and hypapophyses also reach their maximum heights in the anterior trunk, at about 12% and 10% of precloacal vertebral number, respectively (Fig. 3.6B, Table 3.3). The greatest relative heights of both processes are also attained in the anteriormost part of the trunk before steeply declining across the rest of the anterior trunk; throughout the mid- and posterior trunk regions, the relative heights of both processes are comparatively far more uniform (Fig. 3.7B, C). The absolute widths across the zygapophyses reach their maxima at just over 40% of precloacal vertebral number (TPrW, TPoW; Fig. 3.6A, C; Table 3.3). The prezygapophyseal accessory processes show a steep increase in relative length in the anteriormost part of the trunk and an abrupt decrease near the cloaca; between these two points they remain far more uniform in relative size, exhibiting only a slight increase in length throughout the mid- and posterior trunk regions (Fig. 3.7E).

The postcloacal regions generally show similar patterns to the other snakes in this study. The cloacal region is similar to those of the other taxa examined in this study in having relatively anteroposteriorly short vertebrae (CL, PrPo, CL/NAW; Figs. 3.6C, D, 3.7A), with a subsequent

increase in relative vertebral length throughout the tail. A notable difference from the other snakes included in this study is an abrupt increase in the width across the zygapophyses (TPrW, TPoW; Fig. 3.6A, C) in the cloacal region. The tail is also characterized by hemapophyses that are relatively longer in mid-tail vertebrae than are the hypapophyses in the anterior trunk (Fig. 3.7C). The prezygapophyseal accessory processes show similar patterns of decline to those of *A. javanicus* and *P. melanoleucus* (Fig. 3.7E).

Discussion

Schaal et al. (2005) have previously discussed the patterns of intracolumnar variation in *Boa constrictor* as conforming to four general types. However, the addition of new species to the collective dataset blurs the boundaries of these types and, as with basal snakes (see Chapter 2), the curves generated from the measurements in this study are best viewed in light of their conformation to a parabolic pattern (Figs. 3.2–3.6). This is the expected pattern in a column that is composed of a string of vertebrae that tapers at both ends. Such a pattern indicates that a given vertebral feature is largest near the midpoint of the trunk, and smaller at either end. A snake with identical parabolic curves for all vertebral metrics would be proportionally similar throughout the trunk. Deviations from parabolic patterns may be indicative of either functional adaptation or plesiomorphic regionalization (see Chapter 2).

***Acrochordus javanicus*.** Intracolumnar variation in vertebral morphology has been described previously for *A. javanicus* (Hoffstetter and Gayrard, 1964), and measurements common to both that study and this one generally show strong correspondence. A notable difference is the ratio of centrum length to neural arch width (CL/NAW; Fig. 3.3C, D, 3.7A). In both studies, the vertebrae of *A. javanicus* are found to be relatively wide in the anterior trunk (i.e., low CL/NAW values); however, in this study, the relationship between these metrics was found to change such that the vertebrae become longer than wide at the midpoint of precloacal vertebral number, whereas Hoffstetter and Gayrard (1964) found this change to occur in the posterior trunk. The specimens examined in both studies were adult individuals and therefore this difference appears not to be an example of ontogenetic variation, but sexual dimorphism is possibly a factor; the specimen in this study is a female, but the sex of the specimen measured by Hoffstetter and Gayrard (1964) was not known.

Acrochordus javanicus and *Nerodia taxispilota* (below) are similar in showing considerable change to the vertebral aspect ratio throughout the column, although the change is greater in *N. taxispilota* (Fig. 3.7A). Although it is tempting to consider that this is somehow related to the aquatic habits of both species, similar patterns are present in the basal snakes *Boa constrictor*, *Python molurus*, and *Xenopeltis unicolor* (see Chapter 2). The change in vertebral aspect ratio could result in greater flexibility in the anterior part of the column than in the posterior part, depending on soft tissue factors. In the case of *A. javanicus*, increased flexibility in the anterior trunk region would be beneficial to prey capture, achieved by lateral sweeps of the head and tight coils of the body (Dowling, 1960).

Acrochordus javanicus shows an increase in the relative length of the prezygapophyseal accessory processes throughout the trunk, rather than a decrease or maintenance of uniform size (APL; Fig. 3.7E). This pattern also occurs in the unrelated xenopeltid *X. unicolor* (see Chapter 2), but in none of the colubroids included in this sample. Although the reasons for this occurrence in *X. unicolor* are unclear, in *A. javanicus* the lengths of the prezygapophyseal

accessory processes increase as the widths across the prezygapophyses themselves decrease (Fig. 3.7D). The former increase in relative length is therefore likely involved in maintaining adequate mechanical advantage for the lateral flexors (*M. longissimus* and *M. interarticularis inferior*) in the posterior trunk.

In most respects, *A. javanicus* has typical cloacal and caudal morphology, showing a sharp reduction in the relative and absolute lengths of the vertebrae (CL; Fig. 3.3C, D; 3.7A) at the cloaca, as in other snakes (Szyndlar, 1984; Chapter 2). This is in spite of having a tail that appears to be somewhat laterally compressed (Lillywhite, 1996). The caudal neural spines and hemapophyses are relatively lower than those of other caenophidians (Fig. 3.7C), and the pleurapophyses project quite far laterally (Fig. 3.3A), the opposite of what would be expected in a narrow tail.

Pituophis melanoleucus. Variation in the column of *P. melanoleucus* is more similar to that of the basal alethinophidian *Tropidophis haetianus* than to that of *A. javanicus* (see Chapter 2). Both *P. melanoleucus* and *T. haetianus* show generally homogenous vertebral morphology throughout the trunk, with neural spines and hypapophyses showing strong regionalization in both (Fig. 3.4B; Fig. 2.4B). Similar homogenization is present in the vertebral column of *Leioheterodon madagascariensis* as well (see below; Fig. 3.6). Although few other studies of colubroid snakes have measured so many metrics throughout the vertebral column, there is some evidence to suggest that reduced regionalization occurs in some terrestrial colubroids (Thireau, 1967b; Smith, 1975; Szyndlar, 1984).

Based on the intracolumnar variation shown by most lizards (Hoffstetter and Gasc, 1969), the primitive condition for snakes can be inferred to have distinct vertebral regions. If that is the case, then multiple groups have independently homogenized the vertebral column (some Colubridae, Lamprophiidae, Tropidophiidae; see Chapter 2). Alternatively, snake ancestors may have evolved homogenous columns, with subsequent independent re-evolutions of regionalization. Regardless of which evolutionary path is correct, the data available do not support a phylogenetic pattern in homogeneity. Wider study within snakes and putative outgroups is necessary to accurately polarize the patterns of intracolumnar variation.

Postcloacal vertebral variation is mostly similar to that of *A. javanicus*, except in having relatively taller neural spines and deeper hemapophyses, particularly in the mid-caudal vertebrae. The great relative length of the hemapophyses in the middle caudal vertebrae is possibly related to hemipenial musculature or to cloacal musculature, which both attach to the hemapophyses of caudal vertebrae. However, the posterior extent of these muscles is not known in *P. melanoleucus*.

Nerodia taxispilota. The vertebrae of *N. taxispilota* are most elongate in the anterior and posterior trunk (CL/NAW; Fig. 3.7A), reminiscent of the condition documented in the basal alethinophidians *B. constrictor* and *P. molurus* (see Chapter 2). This has the effect of increasing flexibility in the mid-trunk relative to that of the anterior and posterior trunk regions, by increasing the number of flexion points along the trunk in that region. The fact that *B. constrictor* and *P. molurus* share this pattern with the nonconstrictor *N. taxispilota* suggests against it being an adaptation related to constriction. *Nerodia taxispilota* also shares with *B. constrictor* and *P. molurus* relatively narrower width across the zygapophyses in the anterior trunk (TPrW; Fig. 3.7D). The prezygapophyseal accessory processes are also very short in the anterior trunk, although they rapidly become elongate near the transition to the mid-trunk region (APL; Fig.

3.7E). The elongation at this point in the column may be related to the lateral strikes made by *Nerodia* (Alfaro, 2003); the lateral flexors *M. interarticularis superior* and *M. longissimus* that originate at the anterior to mid-trunk transition extend forward into the anterior trunk (Mosauer, 1935; Gasc, 1974), and will therefore be quite effective at producing lateral strikes. However, the short prezygapophyseal accessory processes throughout most of the anterior trunk contradict the hypothesis of Gasc (1974) that shorter processes in the anterior trunk are associated with lower flexibility, as in snakes that are less prone to striking than chasing.

The tail of *N. taxispilota* is not as strongly modified as it is in sea snakes (Hoffstetter and Gasc, 1969), although the neural spines in the proximal tail are relatively tall (NH; Fig. 3.7B). What is notably different from the other snakes in this sample is the relative length of the tail, which contains almost half as many vertebrae as are present in the trunk. Arboreal snakes generally have longer tails than other snakes (Lawing et al., 2012), and thus the arboreal proclivities of *N. taxispilota* (Gibbon and Dorcas, 2004) may explain the relative length of the tail.

***Leioheterodon madagascariensis*.** In spite of its distant phylogenetic relationship, *L. madagascariensis* shows similar patterns to *P. melanoleucus* in having reduced regionalization resulting from largely homogenous vertebral features. The most notable difference in vertebral morphology is the retention of hypapophyses on all precloacal vertebrae in *L. madagascariensis* (HH; Fig. 3.6B). The hypapophyses decline in relative height through the anterior trunk, as is the case in the other snakes in this sample (Fig. 3.7C). However, the hypapophyses remain relatively long throughout the trunk as compared to the other snakes in this study. Many caenophidians retain long hypapophyses in this fashion, including both *A. javanicus* and *N. taxispilota* (see above), but it is unknown what effect this has on the function of the vertebrae. Previous authors have noted the presence of persistent hypapophyses in aquatic snakes (Hoffstetter and Gasc, 1969) and in sidewinding snakes (Gasc, 1974), but many snakes not known to fit these categories retain hypapophyses, including *L. madagascariensis*.

The caudal variation shown by *L. madagascariensis* is similar in some respects to that shown by other snakes, with the vertebrae becoming increasingly elongate, and the prezygapophyseal accessory processes decreasing in length (Fig. 3.7A, E). However, the hemapophyses are notably longer relative to those of other caenophidians, and both the hemapophyses and neural spines remain notably deep and tall until very near the terminal vertebrae. It is possible this is a consequence of sexual dimorphism; this specimen is inferred to be female based on hemapophyseal morphology (Keiser, 1970), but full assessment of dimorphism will require further study.

Paleontological implications. This study has shown that the vertebrae of certain caenophidians are less regionally variable than those of basal snakes (see Chapter 2). This is reflected in large regions of the mid-trunk that show relatively little morphological change, and in the relatively limited change in the relative sizes of some features as revealed by ratios. This fact is of some utility to paleontologists, because it suggests that isolated trunk vertebrae arising from a single species can be easily recognizable as conspecific. Previous work suggests that similar homogeneity occurs in other terrestrial colubroids, although not universally so (Smith, 1975; Szyndlar, 1984). In particular, basal members of the clade, acrochordids and viperids, show greater variation in the column (Brattstrom, 1964; Hoffstetter and Gayrard, 1964; Szyndlar, 1984). Some derived colubrids and elapids also show patterns indicating regional variation (Thireau, 1967a; Smith, 1975). However, the sample sizes involved are all small, owing to the

time-consuming nature of data collection, and thus further work is warranted to investigate the range of variation present in Caenophidia.

Conclusions

This study supplements previous investigations of intracolumnar variation in vertebral morphology among caenophidian snakes (Brattstrom, 1964; Hoffstetter and Gayrard, 1964; Gasc, 1967, 1974; Thireau, 1967a, b; Smith, 1975; Szyndlar, 1984). The snakes examined in this study show intracolumnar variation in some respects similar to that observed in basal snakes (see Chapter 2). Hypapophyses and neural spines are always tallest in the anterior trunk and, in *Acrochordus javanicus* and *Nerodia taxispilota*, the vertebrae increase in width rapidly through the anterior part of the trunk. However, both terrestrial colubrids have less obvious regionalization of the trunk, resulting from greater homogeneity in vertebral morphology, which also occurs in other caenophidians and in the basal snake *Tropidophis* (Smith, 1975; Szyndlar, 1984).

The reduced regionalization shown by some caenophidians means that, throughout much of the trunk, vertebral morphology remains relatively constant. This limits the chances of misidentifying isolated vertebral remains, provided there is not a great amount of interindividual variation. The intracolumnar variation exhibited by the snakes in this study suggests that the evolution of vertebral regionalization in Caenophidia is complex. The two colubrid snakes in this study, *Pituophis melanoleucus* and *N. taxispilota*, show homogenous and regionalized columns, respectively. These disparate patterns within a single clade of advanced snakes suggests that either homogeneity or regionalization had to evolve multiple times, regardless of which condition was basal in snakes. Expanding the current sample of snakes for which intracolumnar variation is known will help to determine the polarity of homogeneity in the column. In addition, the study of patterns of intracolumnar variation within a species is important as well. Comparisons between specimens of *Boa constrictor* measured by Schaal et al. (2005) and McCartney (Chapter 2), specimens of *Acrochordus javanicus* measured by Hoffstetter and Gayrard (1964) and this study, and male and female individuals of *Atractaspis aterrima* measured by Thireau (1967b) suggest that differences in variation do occur in some vertebral features, but that most of these differences are relatively small.

Table 3.1. Regional breakdown of the vertebral column of snakes included in this study.
Pituophis melanoleucus and *Nerodia taxispilota* are lacking at least the terminal vertebra.

Specimen	Species	Trunk (% total)	Cloacal (% total)	Caudal (% total)	Total
YPM R 12192	<i>Acrochordus javanicus</i>	193 (70.4%)	7 (2.6%)	74 (27.0%)	274
YPM R 10679	<i>Pituophis melanoleucus</i>	207 (75.8%)	5 (1.8%)	61+ (22.3%)	273+
YPM R 10601	<i>Nerodia taxispilota</i>	137 (66.8%)	4 (2.0%)	64+ (31.2%)	205+
NJK S-Lm09-D1	<i>Leioheterodon madagascariensis</i>	209 (74.9%)	5 (1.8%)	65 (23.3%)	279

Table 3.2. Descriptions of measurements recorded in this study. See also Figure 3.2.

Measurement	Abbreviation	Description
Centrum length	CL	Midline length of centrum from ventral lip of cotyle to posteriormost point on condyle ⁴
Condyle height	CnH	Vertical height of condyle ²
Condyle width	CnW	Maximum width of condyle ⁴
Cotyle height	CtH	Midline height of cotyle ¹
Cotyle width	CtW	Maximum width of cotyle ¹
Hypapophyseal/hemal keel height	HH	By calipers, obtained by subtracting condyle height from vertical height between dorsal edge of condyle and ventral edge of hypapophysis or hemal keel; from photographs, vertical distance between ventral edge of condyle and ventral edge of hypapophysis or hemal keel ²
Hemapophyseal height	HeH	By calipers, obtained by subtracting condyle height from vertical height between dorsal edge of condyle and ventral edge of hemapophysis; from photographs, vertical distance between ventral edge of condyle and ventral edge of hemapophysis ²
Neural arch width	NAW	Minimum width of neural arch ³
Neural spine base length	NBL	Anteroposterior length of neural spine just dorsal to roof of zygantrum ²
Neural spine height	NH	Vertical distance between dorsal edge of zygosphenal facet and dorsal edge of neural spine ²
Neural spine tip length	NTL	Anteroposterior length of neural spine measured along dorsal edge ²
Postzygapophyseal facet length	PoFL	Length of major axis of facet ⁴
Postzygapophyseal facet width	PoFW	Length of minor axis of facet, measured at midpoint of major axis of facet ⁴
Prezygapophyseal facet length	PrFL	Length of major axis of facet ³
Prezygapophyseal facet width	PrFW	Length of minor axis of facet, measured at midpoint of major axis of facet ³
Interzygapophyseal distance	PrPo	Distance between anteriormost edge of prezygapophyseal facet and posteriormost edge of postzygapophyseal facet ³
Synapophyseal height	SH	Distance between dorsal edge of parapophysis and ventral edge of diapophysis, measured along major axis of synapophyseal facet ¹
Trans-accessory process width	TAPW	Maximum width across prezygapophyses (including the accessory processes) ^{1,3}
Trans-postzygapophyseal width	TPoW	Maximum width across postzygapophyseal facets ⁴

Table 3.2 (Continued). Descriptions of measurements recorded in this study. See also Figure 3.2.

Measurement	Abbreviation	Description
Trans-prezygapophyseal width	TPrW	Maximum width across prezygapophyseal facets ³
Trans-pleurapophyseal width	TPW	Maximum width across pleurapophyses of caudal vertebrae ¹
Trans-zygosphenal width	TZW	Maximum distance between dorsal edges of zygosphenal facets ¹

¹Measurement made in anterior view; ²Measurement made in lateral view; ³Measurement made in dorsal view; ⁴Measurement made in ventral view.

Table 3.3. Anteroposterior positions of maxima for the measurements recorded in this study, expressed as percentages of preloacal vertebral number. For abbreviations of measurements, see Fig. 3.2 and Table 3.2.

	CL	CnH	CnW	CtH	CtW	HH	NAW	NBL	NH	NTL	PoFL
<i>Acrochordus javanicus</i>	51.8	40.9	60.6	44.6	61.1	26.9	42.0	59.6	37.3	59.6	46.1
<i>Pituophis melanoleucus</i>	47.8	51.7	47.3	52.2	51.7	14.0	47.3	57.5	22.7	56.5	45.4
<i>Nerodia taxispilota</i>	56.2	38.7	45.3	38.7	46.0	11.7	46.0	55.5	39.4	55.5	39.4
<i>Leioheterodon madagascariensis</i>	38.3	35.9	42.1	51.2	50.7	10.0	49.3	45.5	12.0	45.5	40.2

	PoFW	PrFL	PrFW	PrPo	SH	TAPW	TPoW	TPrW	TZW
<i>Acrochordus javanicus</i>	56.0	41.5	58.5	58.0	60.6	45.6	42.0	42.5	49.2
<i>Pituophis melanoleucus</i>	42.5	43.0	47.3	51.7	50.2	40.1	46.4	47.3	41.5
<i>Nerodia taxispilota</i>	58.4	37.2	47.4	55.5	38.7	46.7	38.7	39.4	43.8
<i>Leioheterodon madagascariensis</i>	32.1	34.4	34.0	51.2	40.7	42.1	42.1	43.1	51.7

Figure 3.1. The phylogenetic relationships of the snakes in this study, based on Pyron et al. (2011). The columns provide the typical habitat preference and diet for each species, and indicate whether or not each uses constriction as a method of prey subjugation. Aq, aquatic; Terr, terrestrial.

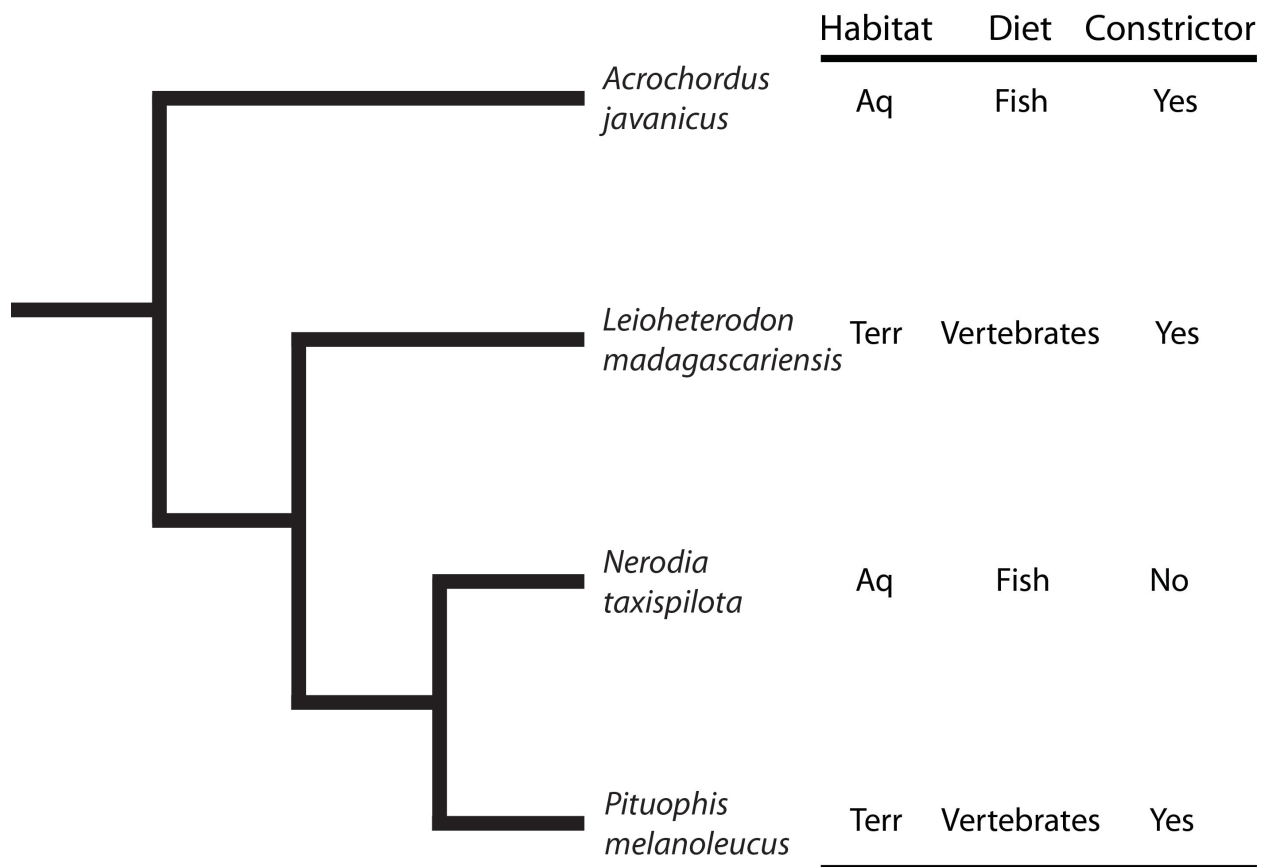


Figure 3.2. The 22 measurements made in this study shown on standardized views of vertebrae of an adult *Leioheterodon madagascariensis* (NJK S-Lm09-D1). A. Anterior views of anterior trunk (left) and caudal (right) vertebrae. B. Lateral views of anterior trunk (left) and caudal (right) vertebrae. C. Dorsal view of a mid-trunk vertebra. D. Ventral view of a mid-trunk vertebra. See Table 3.2 for more information. CL, centrum length; CnH, condyle height; CnW, condyle width; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; HeH, hemapophyseal height; NAW, neural arch width; NBL, neural spine base length; NH, neural spine height; NTL, neural spine tip length; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, length across pre- and postzygapophyses; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TPW, Trans-pleurapophyseal width; TZW, trans-zygosphenal width.

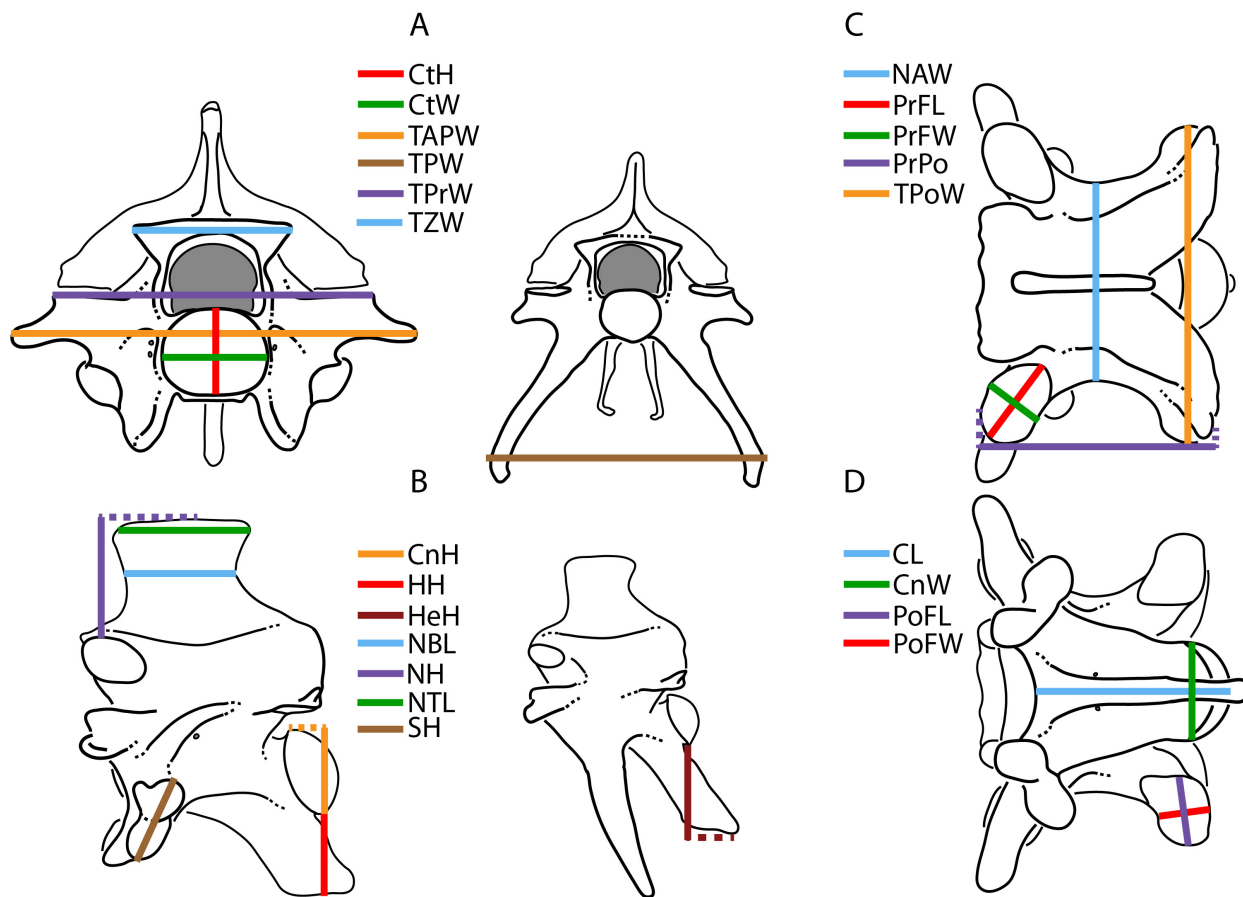
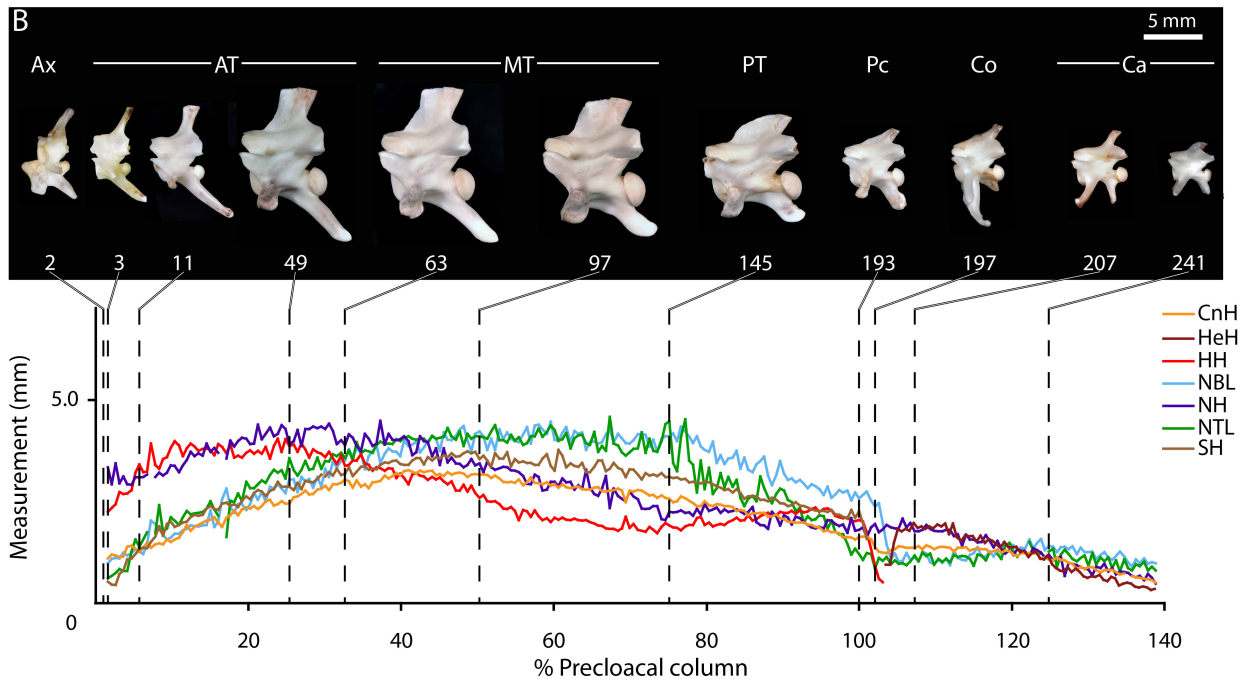
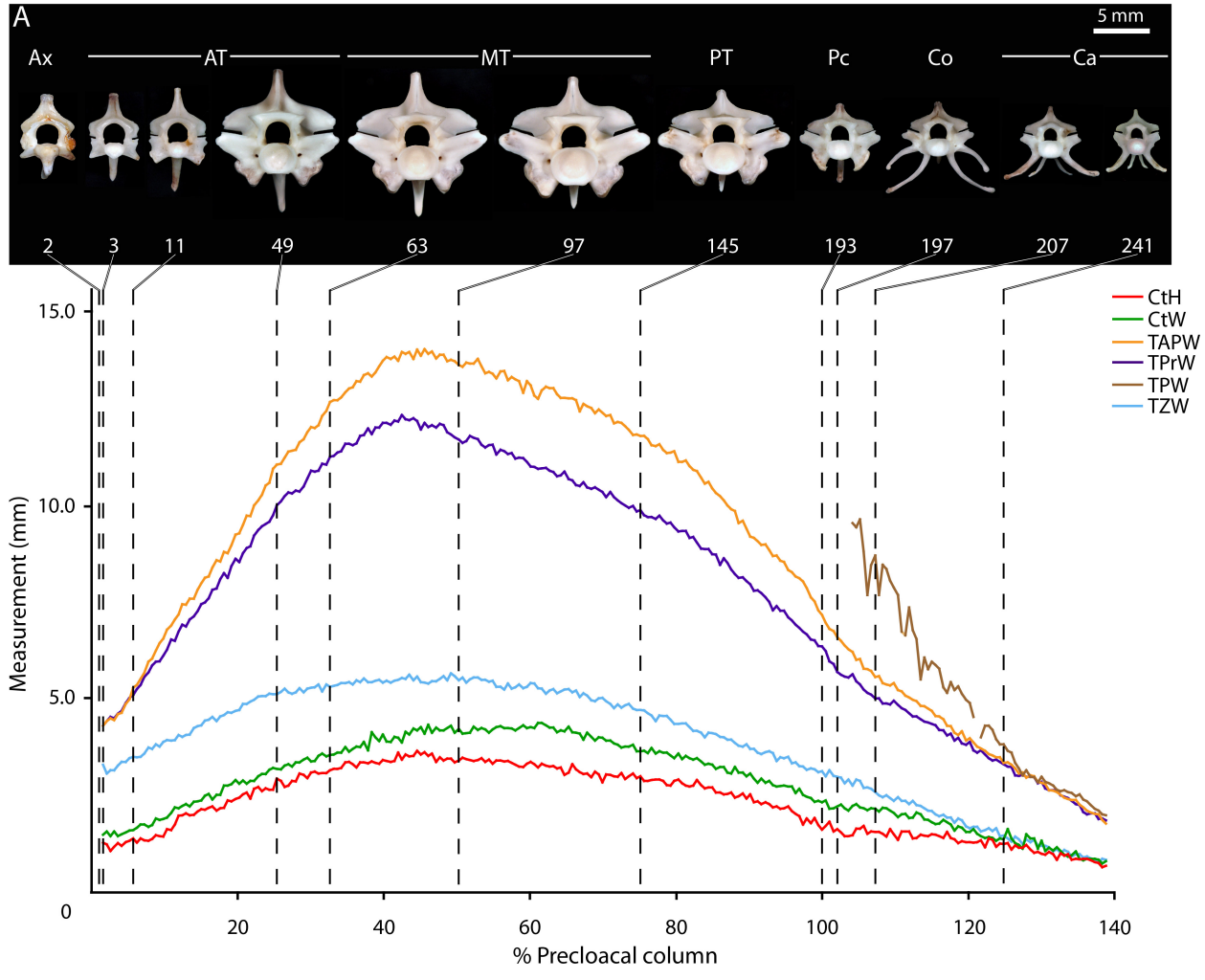


Figure 3.3. Summary of intracolumnar variation in vertebral morphology in *Acrochordus javanicus* (YPM R 12192). Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y -axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x -axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 3.2 and Table 3.2 for additional explanations of the plotted measurements.

AT, anterior trunk; Ax, axis; Ca, caudal; CL, centrum length; CnH, condyle height; CnW, condyle width; Co, cloacal; CtH, cotyle height; CtW, cotyle width; HH, hypapophyseal height; HeH, hemapophyseal height; MT, mid-trunk; NAW, neural arch width; NBL, neural spine base length; NH, neural spine height; NTL, neural spine tip length; Pc, precloacal; PoFL, postzygapophyseal facet length; PoFW, postzygapophyseal facet width; PrFL, prezygapophyseal facet length; PrFW, prezygapophyseal facet width; PrPo, length across pre- and postzygapophyses; PT, posterior trunk; SH, synapophyseal height; TAPW, trans-accessory process width; TPoW, trans-postzygapophyseal width; TPrW, trans-prezygapophyseal width; TPW, trans-pleurapophyseal width; TZW, trans-zygosphenal width.



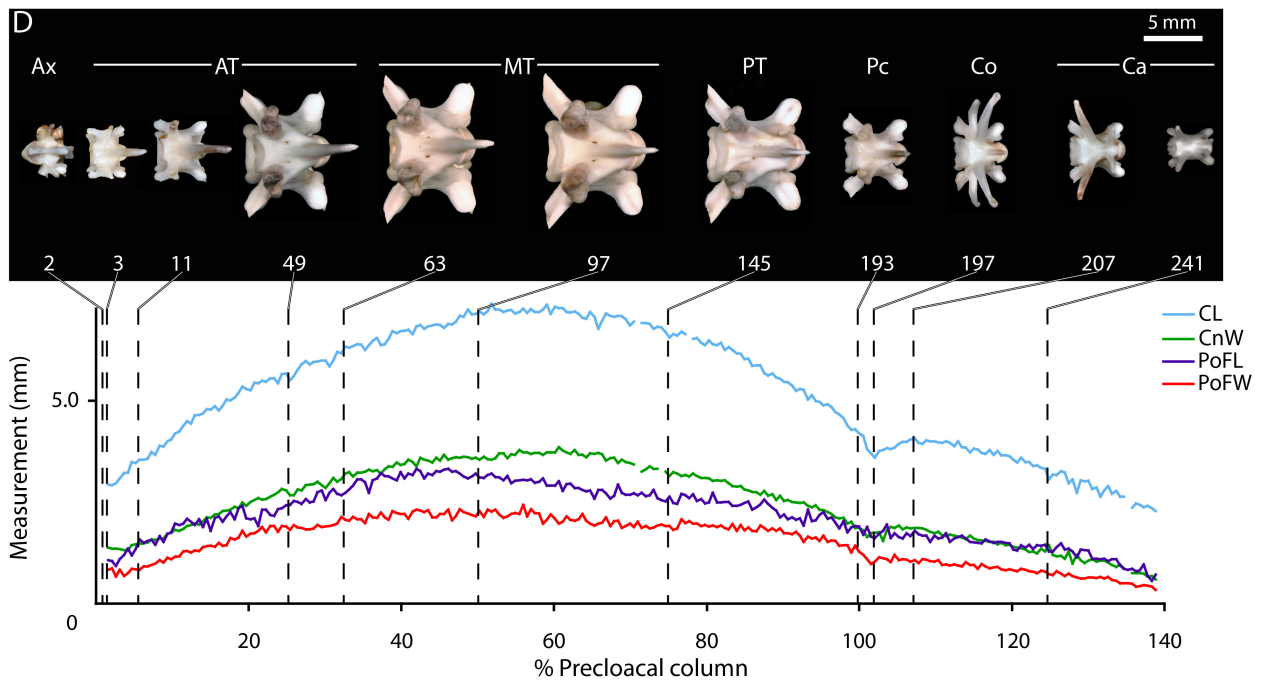
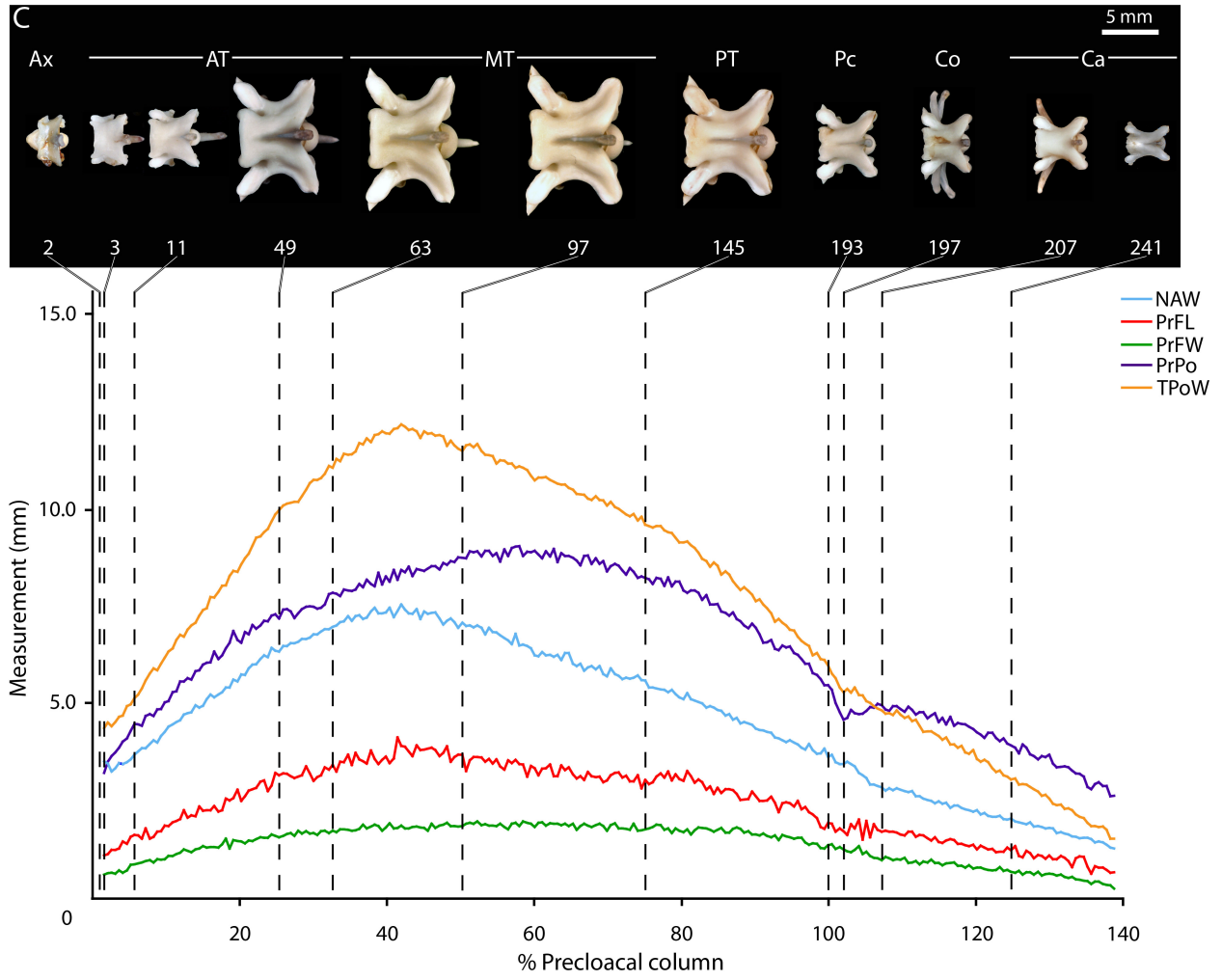
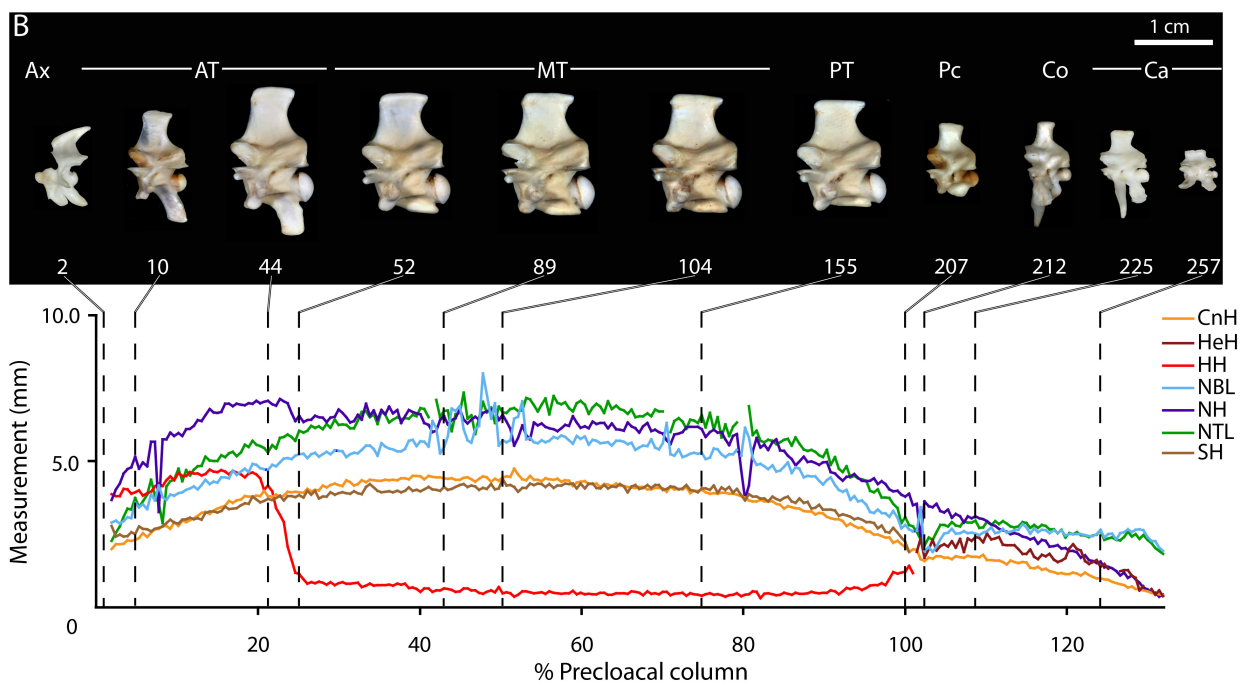
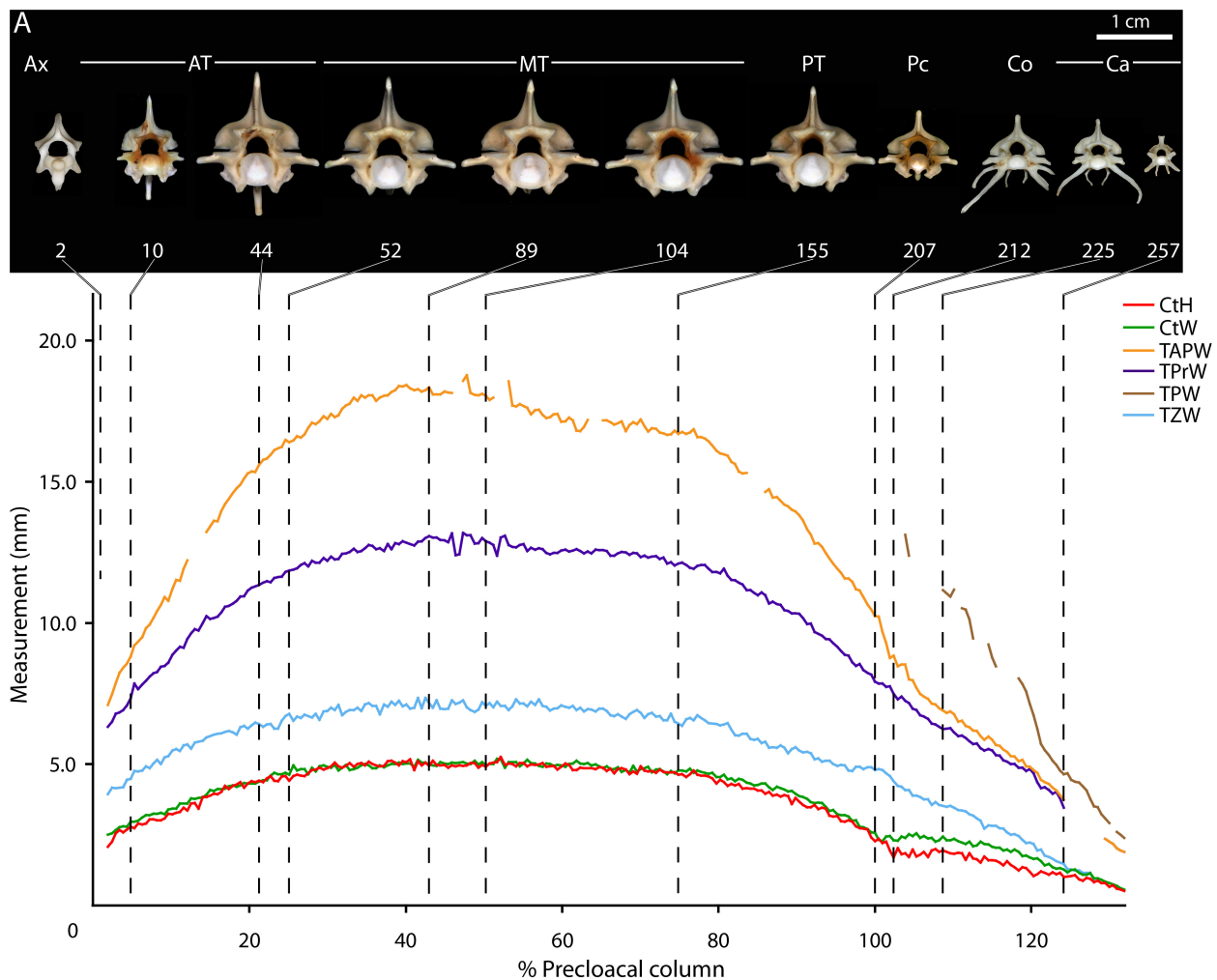


Figure 3.4. Summary of intracolumnar variation in vertebral morphology in *Pituophis melanoleucus* (YPM R 10679). Note that the axis is derived from a similarly sized specimen (YPM R 16559), but that all measurements are of YPM R 10679. Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y -axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x -axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 3.2 and Table 3.2 for additional explanations of the plotted measurements. Abbreviations as in Figure 3.3.



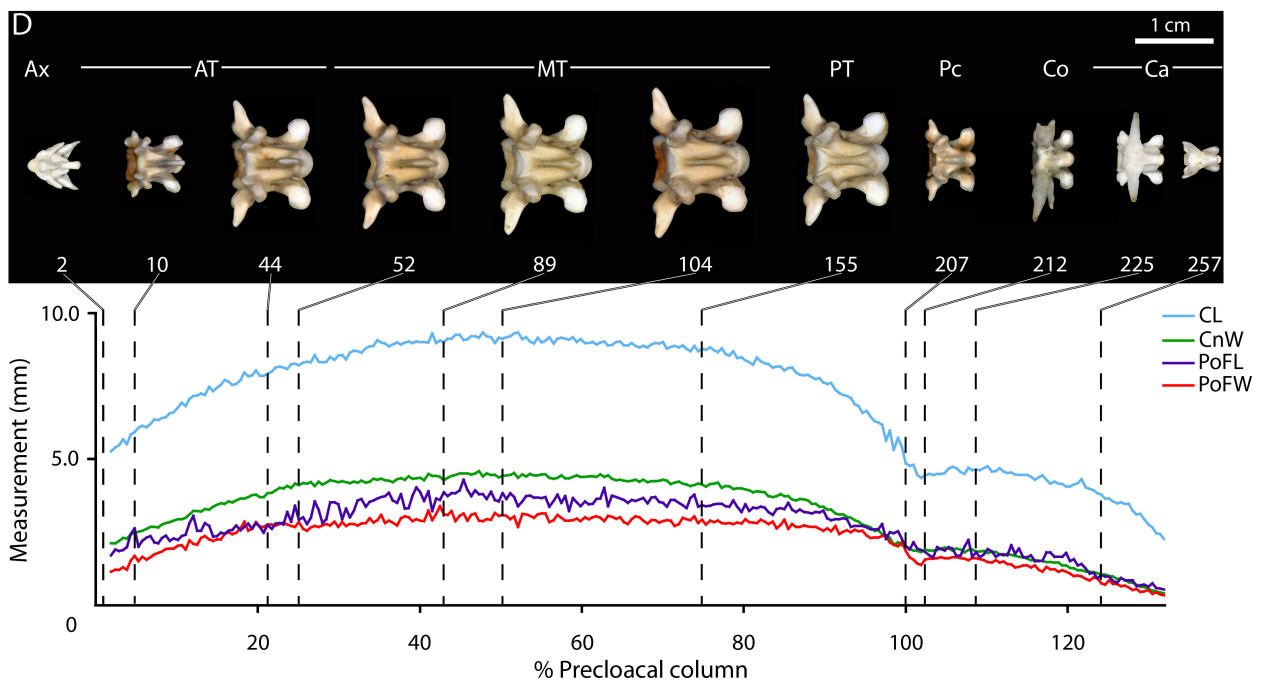
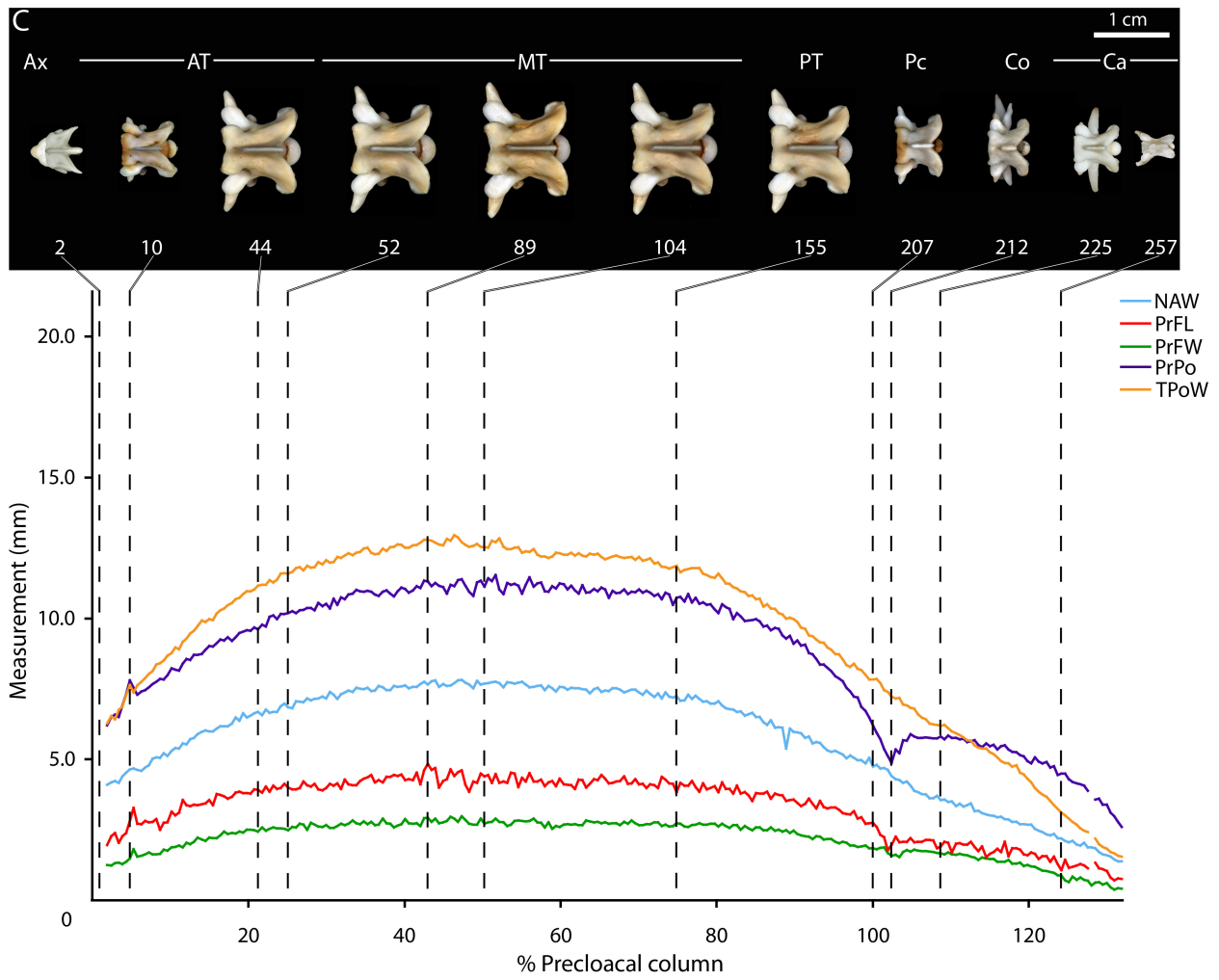
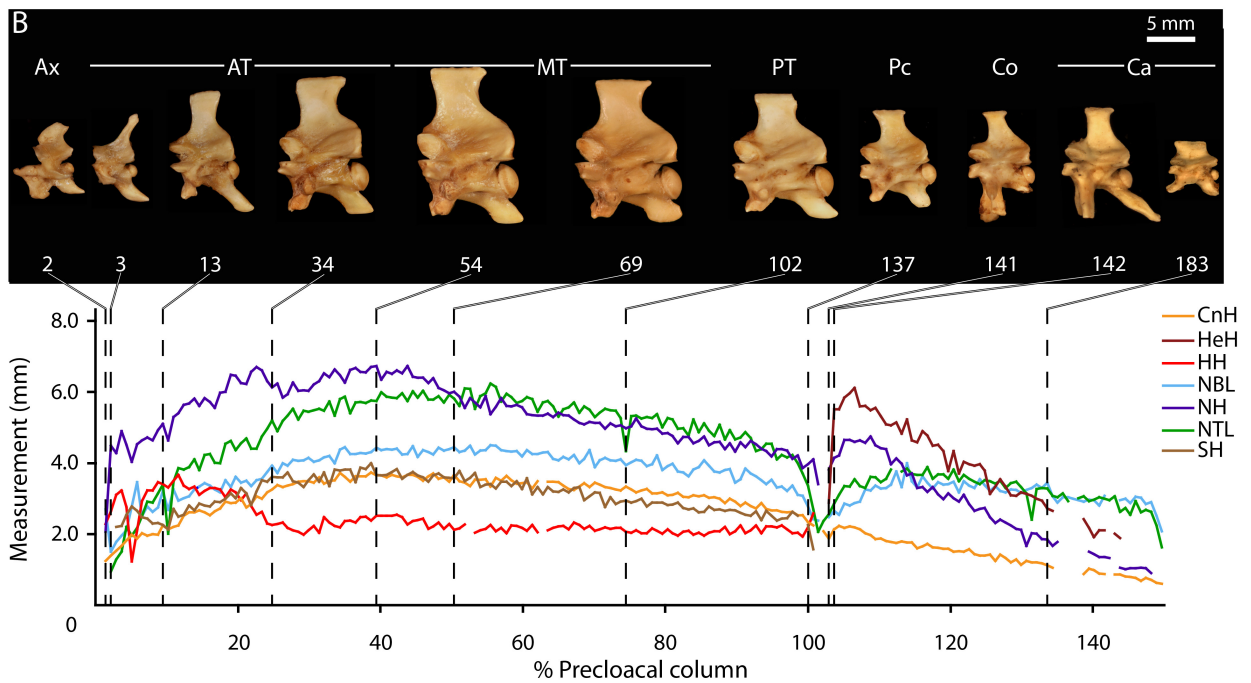
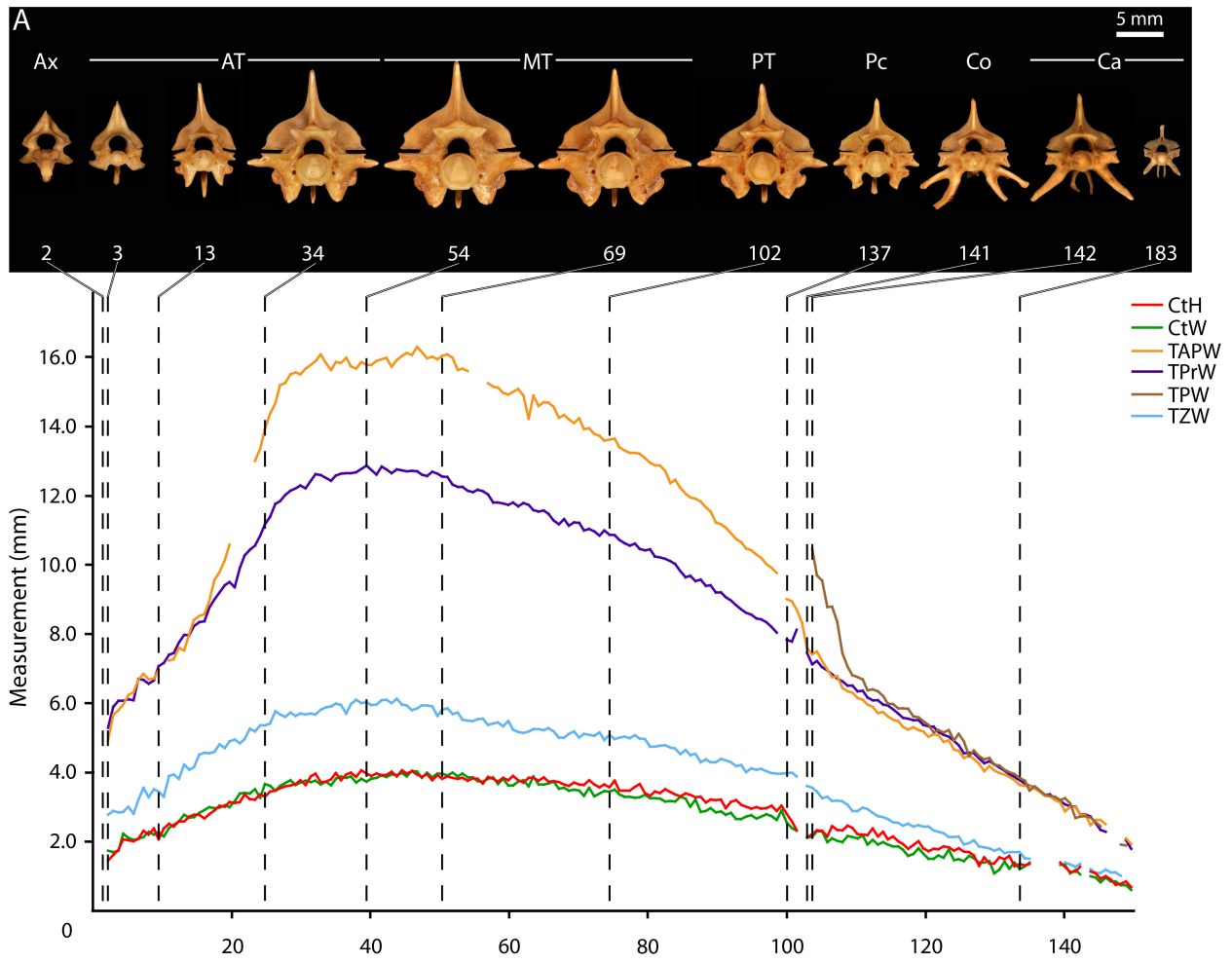


Figure 3.5. Summary of intracolumnar variation in vertebral morphology in *Nerodia taxispilota* (YPM R 10601). Photographs of representative vertebrae from each region of the vertebral column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y -axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x -axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 3.2 and Table 3.2 for additional explanations of the plotted measurements. Abbreviations as in Figure 3.3.



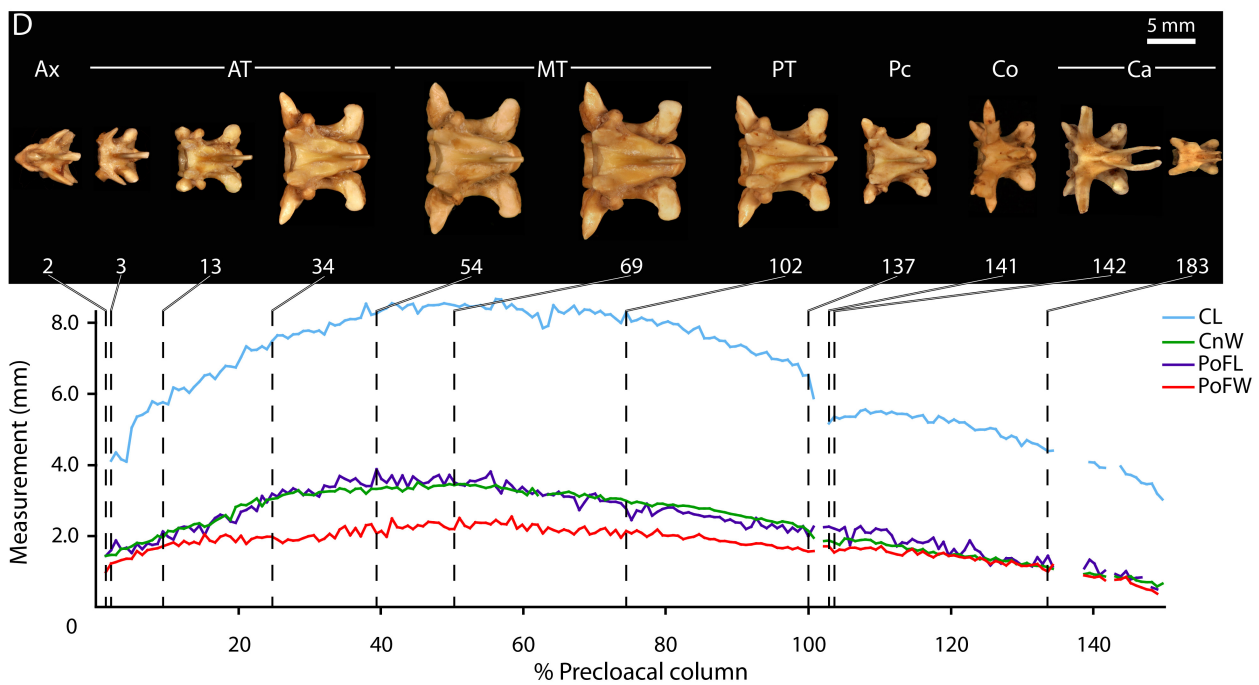
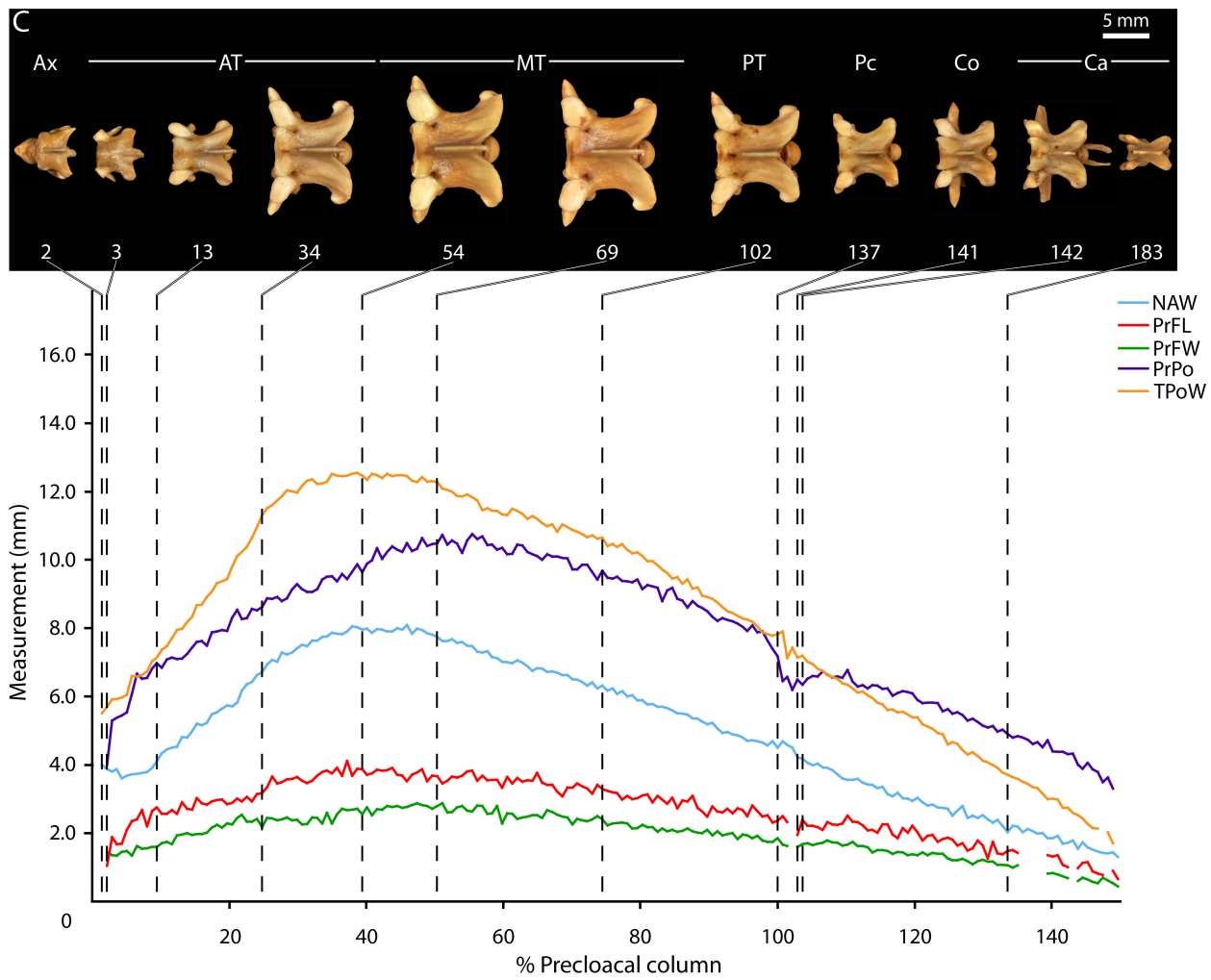
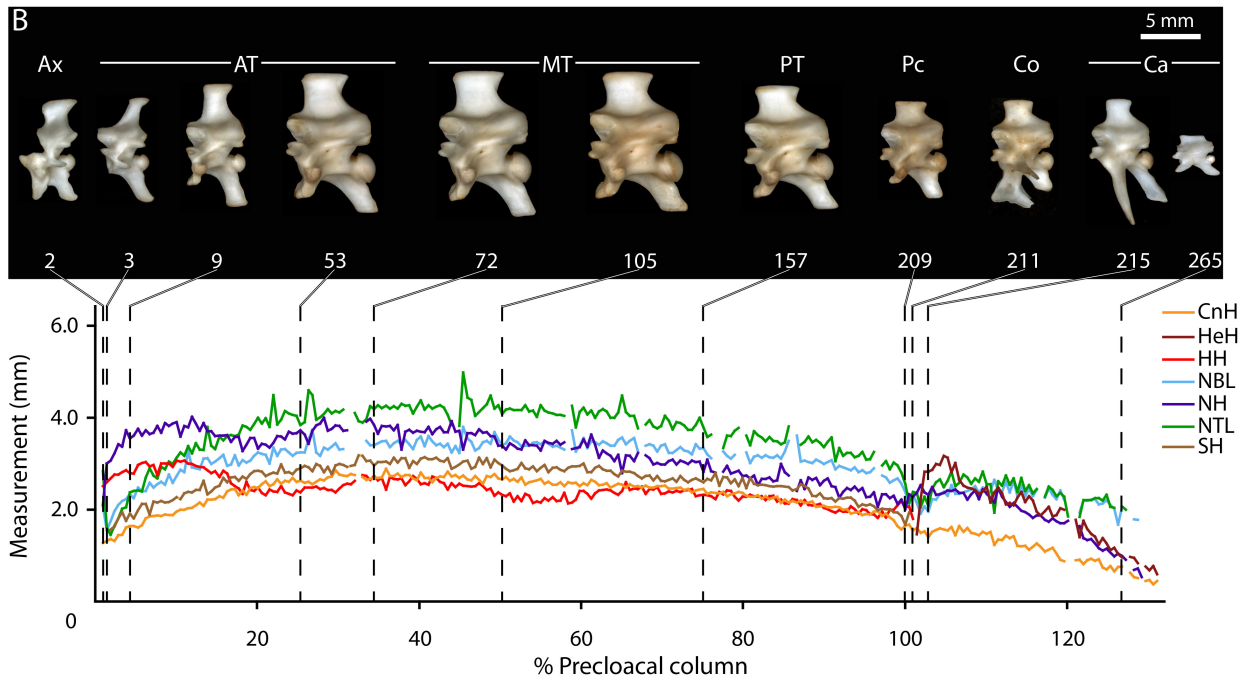
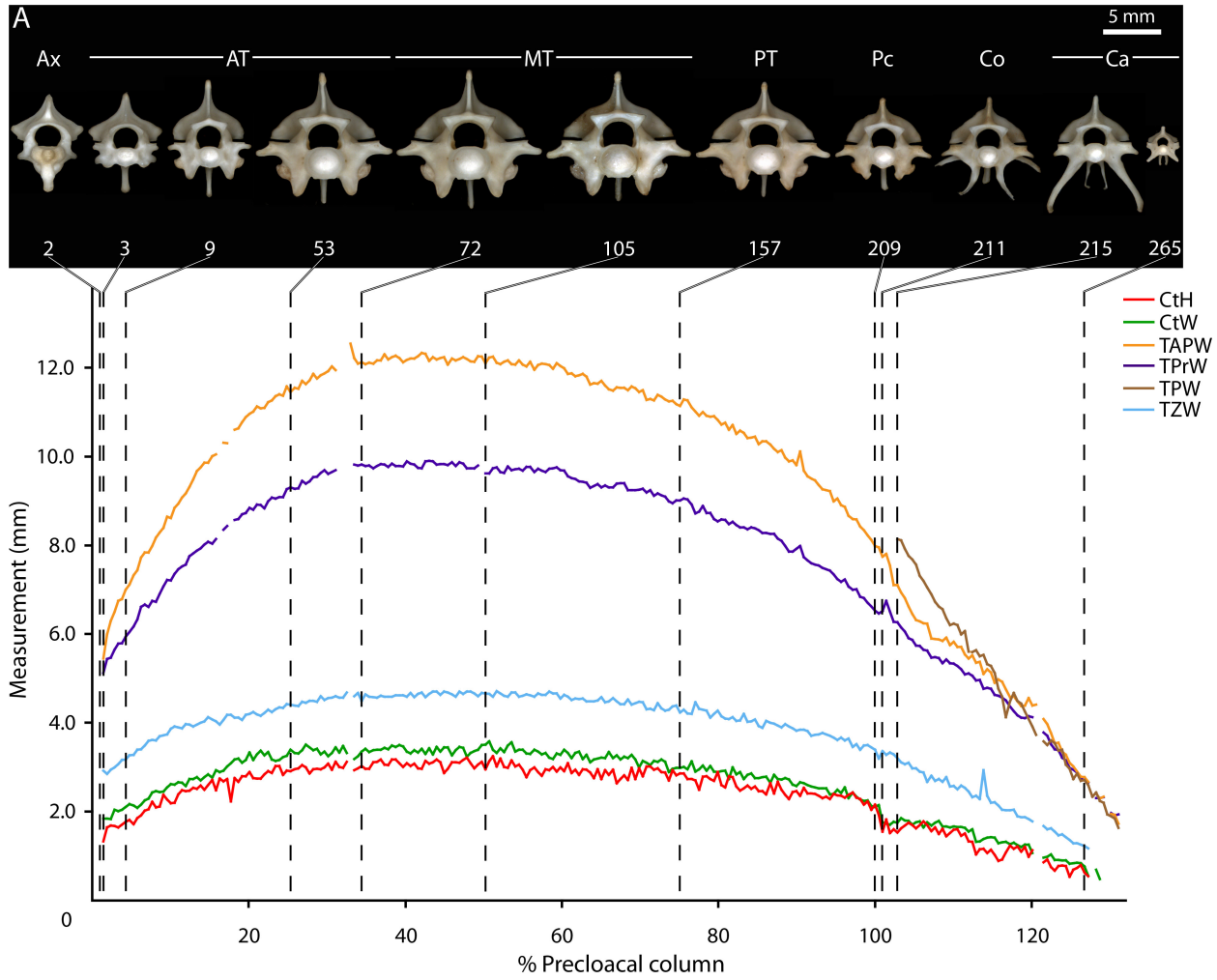


Figure 3.6. Summary of intracolumnar variation in vertebral morphology in *Leioheterodon madagascariensis* (NJK S-Lm09-D1). Photographs of representative vertebrae from each region of the spinal column (above) are shown in anterior (A), left lateral (B), dorsal (C), and ventral (D) views, together with plots of standardized measurements taken throughout the column in each of these views (below). Above and below the photographs of each representative vertebra are its regional classification and absolute numerical identity (as counted from the atlas posteriorly), respectively. In the Cartesian plots, the absolute magnitude of each measurement (y -axis) is plotted against the relative anteroposterior position of the vertebra on which the measurement was taken (x -axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. See Figure 3.2 and Table 3.2 for additional explanations of the plotted measurements. Abbreviations as in Figure 3.3.



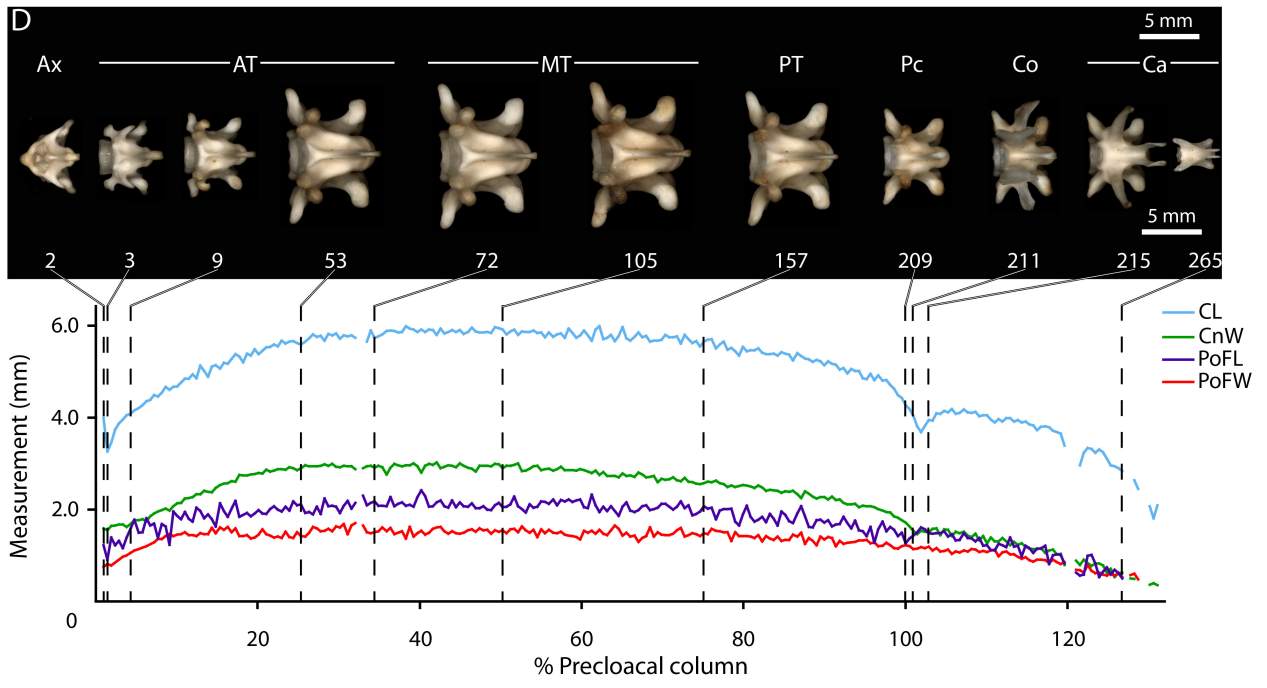
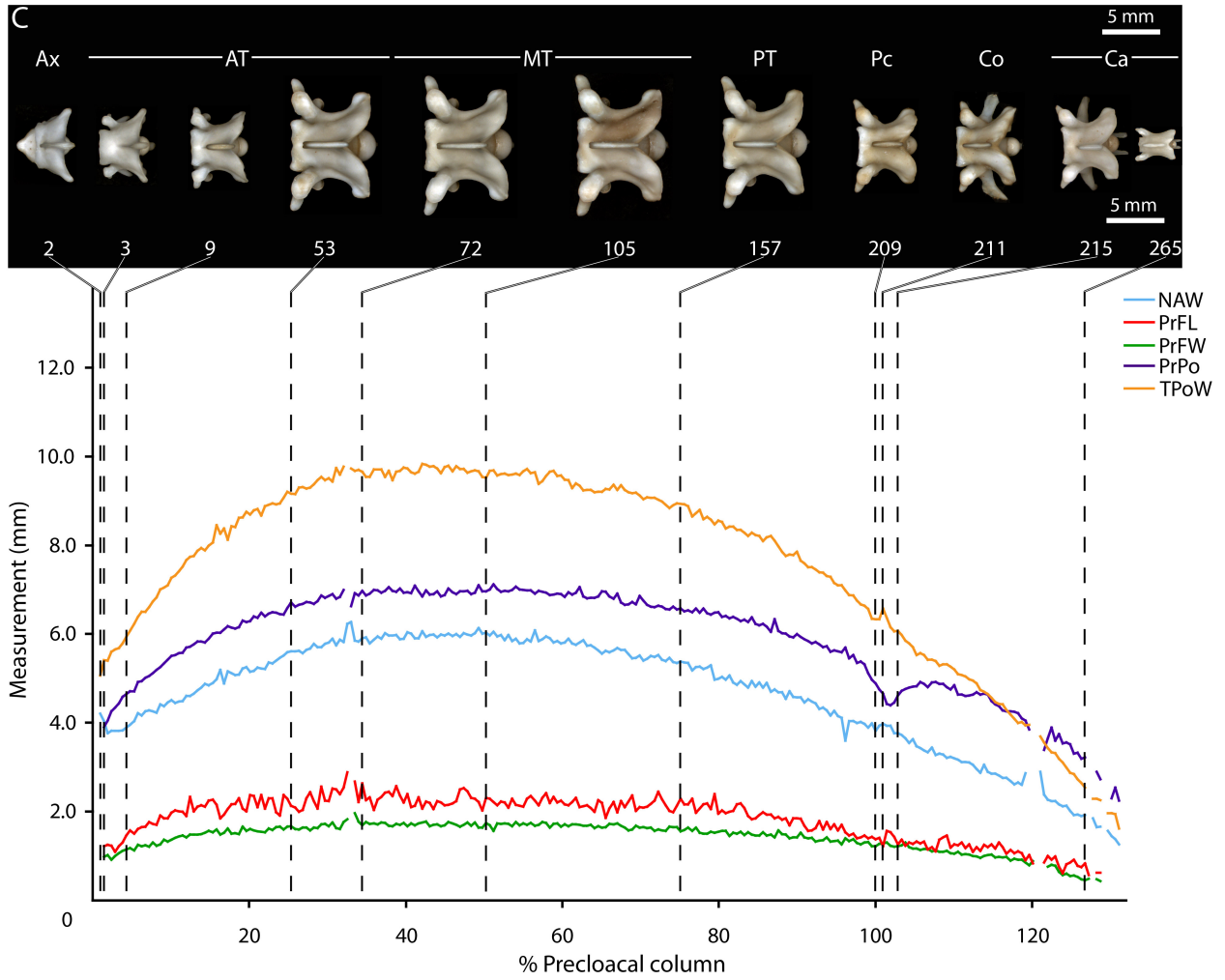
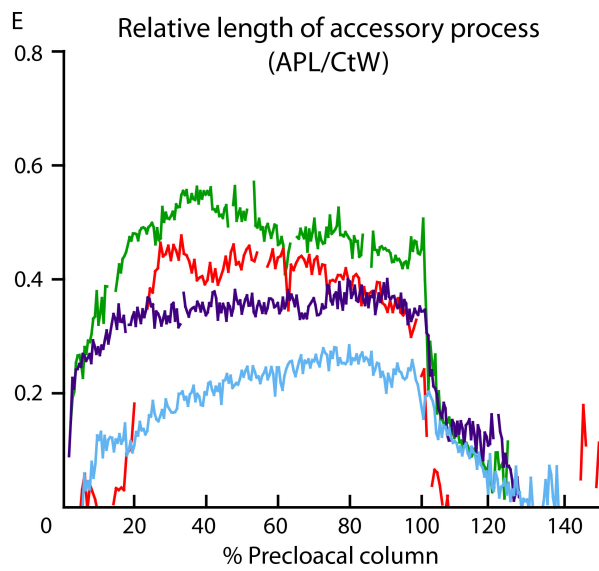
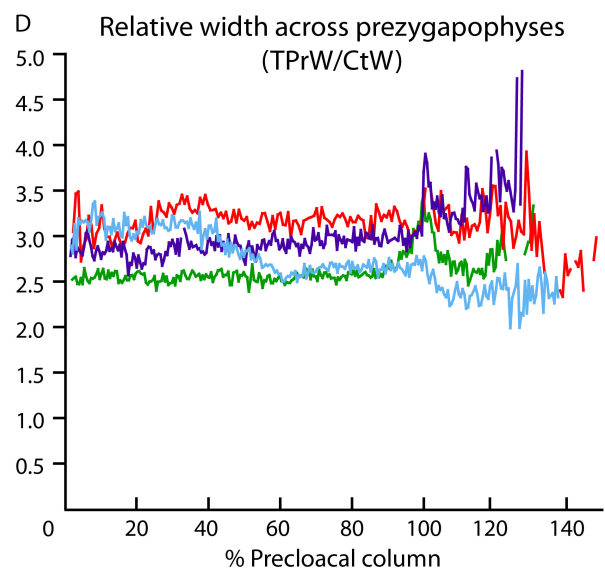
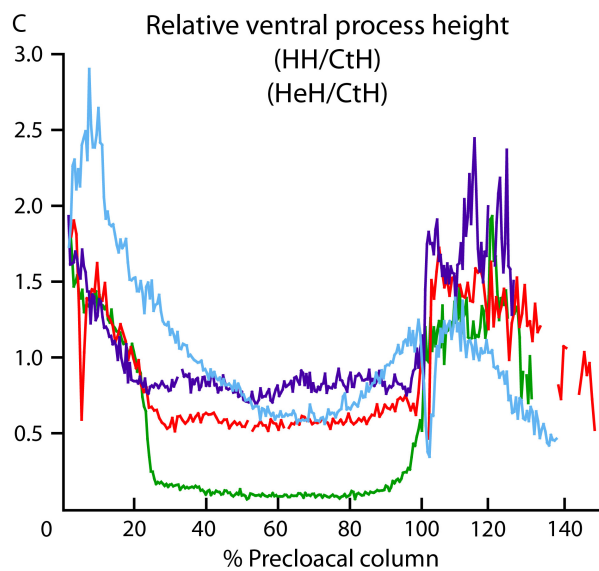
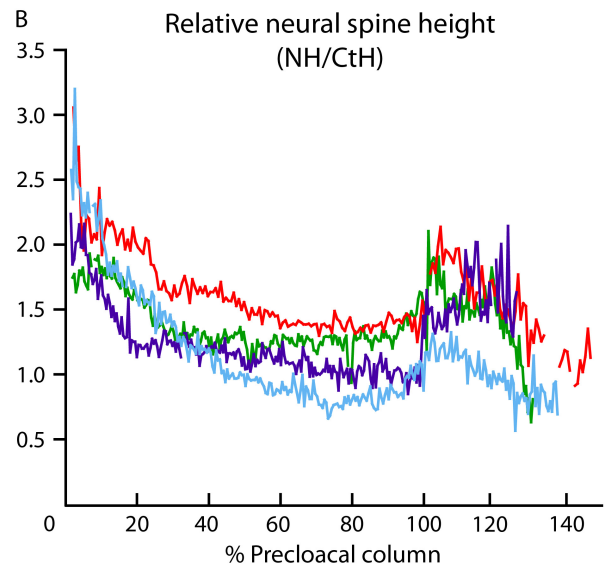
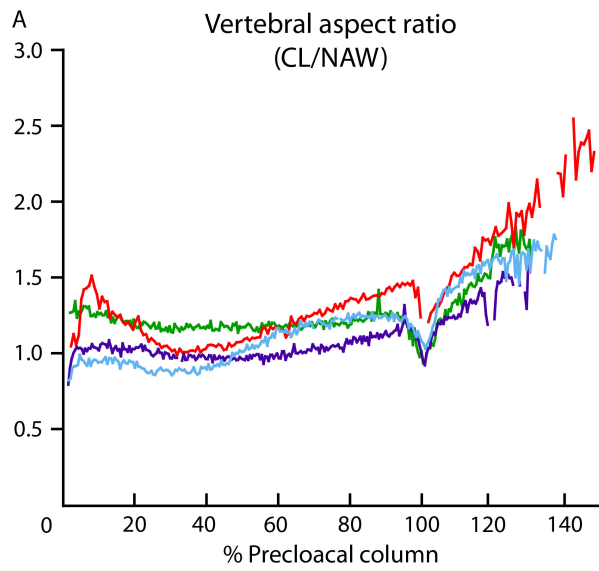


Figure 3.7. Intracolumnar variation in five ratios describing relative vertebral proportions among the snakes sampled in this study. The value of each ratio (y -axis) is plotted against the relative anteroposterior position of the vertebra from which the constituent measurements were taken (x -axis), with the latter expressed as a percentage of the total number of precloacal vertebrae. (A) Overall vertebral aspect ratio, as represented by the ratio of centrum length (CL) to neural arch width (NAW). (B) Relative height of the neural spine, as represented by the ratio of neural spine height (NH) to cotylar height (CtH). (C) Relative height of the ventral process on the centrum, as represented by the ratio of hypapophyseal height/hemal keel (HH) to cotylar height (CtH) in the trunk, and hemapophyseal height (HeH) to cotylar height (CtH) in the postcloacal regions. Postcloacal values are the ratio of hemapophyseal height to cotylar height. (D) Relative width of the prezygapophyses, as represented by the ratio of trans-prezygapophyseal width (TPrW) and cotylar width (CtW). (E) Relative length of the prezygapophyseal accessory processes, as represented by the ratio of accessory process length (APL) to cotylar width (CtW). For definitions of the measurements upon which these ratios are based, see Fig. 3.2 and Table 3.2.



- *Acrochordus javanicus*
- *Pituophis melanoleucus*
- *Nerodia taxispilota*
- *Leioheterodon madagascariensis*

Chapter 4

Habitat ecology as a selective force on snake (Reptilia, Serpentes) body segment number

Abstract

Body segment number is known to affect locomotor performance in many animals, and may therefore be correlated with habitat use. Snakes (Serpentes) are an excellent clade in which to study selection on body segment number because of their great range in vertebral number, large number of species, and wide ecological breadth. This paper examines the evolution of body segment number in snakes by two means: first, data are examined for a directional trend across all of Serpentes; second, the evolution of body segment number is modeled as an Ornstein–Uhlenbeck process, which allows evolutionary models to incorporate selection. This study tests a model of Brownian motion and three selection models: one with selection toward a single global optimum body segment count for all snakes; one with optima corresponding to methods of prey subjugation (constriction or non-constriction); and one with optima corresponding to habitat preference (terrestrial, arboreal, aquatic, semi-aquatic, fossorial, and semi-fossorial). The results indicate that body segment number has not evolved directionally across Serpentes, and that it is under selection; furthermore, selection toward optimal values of body segment number corresponding with habitat preference is the best-fitting model. AICc difference values additionally indicate some support for the model of selection driven by prey subjugation. Optimal vertebral values returned by both model are similar to average values for the groups, indicating that both models are biologically relevant. These results indicate that body segment number is under selection within Serpentes, and that habitat preference is an important driver of that selection.

Introduction

Snakes constitute one of the most successful radiations of tetrapods, with more than 2,500 extant species (McDiarmid et al., 1999). Concomitant with this taxonomic diversity is great ecological diversity, which includes terrestrial generalists as well as arboreal, fossorial, and aquatic specialists (e.g., Greene, 1997). This ecological and phylogenetic diversity comes in spite of the potentially restrictive reduction of limbs. As a result, behaviors that formerly relied on limbs are performed primarily by the trunk. Accordingly, snakes have evolved a suite of behaviors related to feeding and locomotion that involve the trunk, including constriction (e.g., Greene and Burghardt, 1978; Moon, 2000), rapid prey strikes (e.g., Frazzetta, 1966; Cundall and Deufel, 1999), and several locomotory modes useful for moving through different environments and over different substrates (e.g., Mosauer, 1932a; Gans, 1962). In general, several aspects of trunk morphology are known to reflect certain ecological differences between species. There is a relationship between vertebral morphology and habitat preference, which provides an indirect assessment of locomotory mode (Johnson, 1955; Baszio, 2005b, a; Schaal et al., 2005; Lawing et al., 2012). In addition, differences in axial musculature are thought to reflect to some degree differences in feeding behavior and locomotion (Ruben, 1977; Jayne, 1982).

Another aspect of the vertebral column that is of functional importance is vertebral number. It is correlated with habitat use in lacertid lizards (Van Damme and Vanhooydonck, 2002), and the ratio of body to tail vertebrae is related to swimming performance in stickleback fish (Swain, 1992). The number of vertebrae is also positively correlated with the maximum curvature that tetraodontiform fishes are able to form during c-start escape behaviors (Brainerd

and Patek, 1998). Snakes have long been known to exhibit a wide range in total vertebral number within and between different species (e.g., de Rochebrune, 1881; Alexander and Gans, 1966; Lindell, 1994; Shine, 2000), with reported vertebral counts ranging from around 150 (many species; Alexander and Gans, 1966) up to above 550 in the extinct snake *Archaeophis proavus* (see Janensch, 1906). Counts of the ventral and subcaudal scales of the Australian python *Morelia oenpelliensis* exceed 600 (Gow, 1977), and because of the 1:1 correspondence between vertebral number and ventral scale counts in most snakes (including pythonids; Alexander and Gans, 1966), it can be inferred that vertebral counts in this species also exceed 600. Variation in body segment number in snakes (as reflected by either vertebral counts or ventral scale counts) has been linked to aspects of ecology, including increased vertebral number in constricting versus non-constricting snakes (Jayne, 1982; Lindell, 1994), and an inverse relationship between the number of trunk vertebrae and locomotor performance in garter snakes (Kelley et al., 1997). Lindell (1994) found that fossorial snakes have relatively fewer vertebrae for their body length than other snakes, confirming a previous hypothesis of Marx and Rabb (1972). At the opposite end of the spectrum, a recent study of body segment number in viperids found that higher segment densities occur in arboreal vipers, confirming the importance of vertebral density (number of segments per unit body length) to ecology (Hampton, 2011).

The mechanisms controlling vertebral number in snakes are not fully understood. Although there is a strong genetic component (Dohm and Garland, 1993; Richardson et al., 1998; Gomez et al., 2008), it is also influenced by temperature during development (Fox, 1948; Osgood, 1978; Lourdais et al., 2004), and the ratio of trunk to caudal vertebrae is sexually dimorphic in some species (Klauber, 1941; Shine, 2000). Vertebral number also may be geographically variable, depending on habitat (Klauber, 1941) or vary along latitudinal or longitudinal clines (Shea, 1998; Manier, 2004). In addition, there is a positive relationship between maximum body size and vertebral number (Lindell, 1994; Head and Polly, 2007; Hampton, 2011), a pattern known as pleomerism (Lindsey, 1975). Although statistically significant, the relationship between body length and vertebral number is actually weak, with r^2 values typically below 0.50 (Lindell, 1994; Shine, 2000; Head and Polly, 2007; Hampton, 2011). In part, this poor correlation is a result of gigantism in snakes apparently being dissociated from increased body segment number (Head and Polly, 2007). In spite of these potentially complicating factors, it is apparent that vertebral number in some groups is under strong selection (Arnold, 1988; Lindell, 1994; Manier et al., 2007; Hampton, 2011).

However, it is possible that this selection is obscured across Serpentes by a phyletic trend toward increasing vertebral number. Snakes average more vertebrae than any of their putative outgroups. This is true even if snakes belong to a limbless, elongate clade as has been recently suggested (Conrad, 2008; Gauthier et al., 2012). The nearest outgroups within such a clade (amphisbaenian and dibamid lizards) both have at most around 150 vertebrae (Hoffstetter and Gasc, 1969), values that lie at the low end of those seen in snakes (de Rochebrune, 1881; Alexander and Gans, 1966; Lindell, 1994). A phyletic trend may also be evident if the selection snakes experience is directional in nature.

Recent advances have made it possible to model evolution within a clade in an explicitly adaptive context, rather than as random Brownian motion (Butler and King, 2004). Using Ornstein–Uhlenbeck processes, evolutionary models can be generated in which stabilizing selection on a trait results in one or more optimal values for given groups (Hansen, 1997). The Brownian motion and Ornstein–Uhlenbeck selection models can then be directly compared by use of log-likelihood tests and information-criteria scores, so that the best-fitting model can be

chosen (Butler and King, 2004). These methods are well suited for modeling the evolution of body segment number in snakes given the variety of possible evolutionary scenarios driving vertebral number. This study models the evolution of body segment number in snakes, to determine whether it is under selection, random walk, or a phyletic trend toward increased number. First, I test for a phyletic trend in the evolution of vertebral number in snakes. Then, I model the evolution of body segment number as a null hypothesis of Brownian motion lacking any directional selection (i.e., random walk), and three Ornstein–Uhlenbeck models with selection based on the ecological parameters known or thought to influence vertebral number. The selective models are: 1) a single, global optimum vertebral number for all snakes; 2) a two-optima model wherein the snakes are grouped as either constrictors or non-constrictors; and 3) a six-optima model wherein the snakes are grouped by their preferred habitats.

Materials and methods

In all but a small number of clades within Serpentes, there is a 1:1 correspondence between vertebral number and the number of ventral plus subcaudal scales (Ruthven and Thompson, 1913; Alexander and Gans, 1966). Because scale counts are often reported in taxonomic descriptions and faunal surveys, they provide a useful source of data that are equivalent to body segment counts for large numbers of taxa. Therefore, the majority of body segment data used in this study was collected from the literature, supplemented by direct counts on skeletonized specimens (See Appendix 1). However, there are several clades known to deviate from the typical 1:1 correspondence between vertebrae and scales. These include the fossorial typhlopoid and anomalepidid scolecophidians (Alexander and Gans, 1966; List, 1966) as well as the aquatic acrochordids (Alexander and Gans, 1966) and hydrophiine elapids (Voris, 1975). The decoupling between vertebral number and scale number in these snakes may have resulted from relaxation of selective pressures on ventral scutes in these specialists that do not rely primarily on these scales for locomotion as do other snakes (Voris, 1975). In addition to these, some cylindrophids and uropeltids are known for presenting difficulties with accurate scale counts (Gower and Ablett, 2006). Because the correspondence between vertebral counts and ventral scale counts varies within these snakes, scale counts are inappropriate to use as proxies for body segment number. In these cases only vertebral counts were used, either as reported in the literature or from direct counts taken on skeletal specimens specifically for the purposes of this study. Although the combined use of ventral scale counts and vertebral counts in this study may introduce some error, previously reported differences between the two counts are typically on the order of one or two, and do not exceed ten (Ruthven and Thompson, 1913; Alexander and Gans, 1966); given the number of vertebrae involved, such differences are likely to be insignificant. Sexual dimorphism is a possible confounding factor as well, but in many cases the sex of individuals is unreported. Problems related to dimorphism are mitigated by the use of total counts rather than just those from the trunk, because increased trunk counts in females typically come at the expense of caudal segments (Shine, 2000). Because snakes show within species variation in body segment number, in cases with a range of values available the average is used, as in previous studies (Lindell, 1994; Head and Polly, 2007; Hampton, 2011). Ecological data were derived from the literature (See Appendix 1). The data collected included whether the species made use of constriction to subjugate prey or not, as well as habitat preference (arboreal, aquatic, semi-aquatic, fossorial, semi-fossorial, terrestrial generalist). For both characters, the states were codified for entry in a matrix. A total of 232 species was

included, with every family-level clade as well as each colubroid “subfamily” represented in the data set (Fig. 4.1).

Because no published phylogeny includes all of the snakes in this study, no single phylogenetic tree was sufficient for this analysis. Accordingly, a tree was constructed in Mesquite v. 2.75 (Maddison and Maddison, 2009) using multiple published sources (Fig. 4.1). The interfamilial relationships were taken from a recent molecular analysis including at least one species from each family and subfamily of Serpentes, produced by a matrix concatenating several previously published datasets (Pyron and Burbrink, 2012). Intrafamilial relationships were derived from multiple sources, chosen because they were the most recent analyses that included many species and genes (Boidae [Burbrink, 2005]; hydrophiine Elapidae [Lukoschek and Keogh, 2006]; Pythonidae [Rawlings et al., 2008]; Viperidae [Wüster et al., 2008]; Leptotyphlopidae [Adalsteinsson et al., 2009]; Typhlopoidea [Vidal et al., 2010]; Colubroidea [Pyron et al., 2011]). Branch lengths were derived from estimated divergence dates in multiple studies, corroborated by fossils where possible. The divergence times for larger snake clades was derived from Pyron and Burbrink (2012), and intraclade divergences are derived from studies of individual clades (Burbrink et al., 2008; Pyron and Burbrink, 2009; Sanders et al., 2010b; Sanders et al., 2010a; Pyron et al., 2011). These estimates are concordant and in all cases precede the fossil record, as is expected. In cases where divergence estimates do not exist, the time between known divergences was split evenly. Although this may not in all cases exactly represent the radiation of a group, it provides a reasonable hypothesis that is preferable to a lack of branch lengths.

The segment counts were log transformed to meet the assumption of normality required for subsequent statistical analysis. These data were first tested for a phyletic trend using the Continuous algorithm in BayesTraits (Pagel, 1997, 1999). In this analysis, two maximum likelihood models, a random walk and a directional random walk, were compared for fit to the data using a log-likelihood test. Subsequently, the evolution of vertebral number was tested for selection by producing models using the OUCH package v. 2.8-1 (Butler and King, 2004; King and Butler, 2011) in the open-source statistical software R v. 2.14.0 (R Core Team, 2012). Four evolutionary models were tested, and the corrected Akaike Information Criterion (AICc) and the conservative Bayesian Information Criterion (BIC) were used to assess model fit, with lower values indicating the best fit for the data (Akaike, 1974; Hurvich and Tsai, 1989; Butler and King, 2004). The null hypothesis was a Brownian model lacking any selection for a pure random walk of body segment evolution. Three different alternative hypotheses with selection were tested: one with a single, global optimum for all snakes; one with two optima corresponding to constrictors versus non-constrictors; and one model with six optima corresponding to habitat preference. The analyses produced estimates of selection (α) and drift (σ), as well as optimum body segment numbers for each grouping of snakes, allowing comparison with observed values. Optimal values that lie outside the range observed in each group would cast doubt on the appropriateness of the model (Butler and King, 2004).

Results

The results of the BayesTraits analysis do not support a phyletic increase in vertebral number across Serpentes. Both directional and random walk models show identical log-likelihood scores (Table 4.1), resulting in a very high p value. Therefore, the hypothesis that body segment number evolution is directional is rejected in favor of the null hypothesis.

The relative levels of support of the four evolutionary models described above are provided in Table 4.2. Each of the selection-based models fit the data significantly better than the null hypothesis of Brownian motion, as indicated by log-likelihood tests and AICc scores (lower values indicate better fit). Using the likelihood ratio test value (LR), the OU habitat model is strongly preferred over the OU constriction model, the OU global model, and the Brownian Motion model. The two-optima model of selection using constriction (OU constriction) provides a better fit to the data than does the Brownian Motion model, and is a marginally better fit than the global optimum model (OU Global). The six-optima model with snakes grouped according to habitat preference (OU habitat) had the lowest AICc score. The AICc difference values given in Table 4.2 are simply the difference between each AICc score and the minimum score (that of OU habitat), and provide an indication of the support for each model. Values below 2 indicate substantial support, and values above 10 indicate no support. Values in between indicate some degree of support. The AICc difference value for OU constriction is low enough to indicate some support for this model. The AICc difference value for OU global indicates considerably less support. The AICc difference value for the Brownian Motion model indicates effectively no support for that model. An alternative metric for assessing the fit of the models, the Bayesian Information Criterion (BIC), yields different results (Table 4.2). The six-optima OU habitat model is a poorer fit than both the two-optima OU constriction model and the best-fitting OU global model, although it still outperforms the Brownian motion model.

Strengths of selection (α) and drift (σ) estimated by the models are provided in Table 4.3. Strength of selection is greatest in the OU constriction model, followed by the OU habitat model, and selection in the OU global model is lowest. The Brownian motion model by definition features no selection. All of the models provide estimated strengths of drift. The Brownian model reconstructs the lowest strength of drift. Strength of drift is greater in the OU models, but is considerably weaker than the strength of selection, as expected under a selective regime. Both the OU global model and the OU habitat model feature the same drift, and the OU constriction model features the highest drift values.

Each OU model provides the optimal values toward which selection is acting within each group. The optima recovered for each are shown in Table 4.4, along with mean, median, and range values for each group. The OU global model estimates the optimal number of body segments to be 240, as compared to an actual average of 245. The OU constriction model predicts that the optimal number of body segments for constrictors is 286, as compared to the actual mean of 279. Non-constrictors have a lower estimated optimum number of body segments at 272, as compared to the actual mean of 224. The OU habitat model predicts that arboreal snakes have the highest optimal value for body segment count at 351, as compared to the actual mean of 296. Terrestrial snakes have the second highest optimal body segment number at 279, as compared to the actual mean of 252. Aquatic snakes have an estimated optimum of 219 body segments, as compared to the actual mean of 226, and semi-aquatic snakes have a higher optimum of 233 body segments as compared to a mean of 228. Fossorial snakes have an optimal body segment number at 218, as compared to the actual mean of 217, and semi-fossorial snakes have the lowest estimated optimum at only 209 body segments, matching the observed mean of 209.

Discussion

The lack of a phyletic trend toward increased body segment counts across Serpentes is reflected in the wide range of counts within various clades. The range of body segment counts

shown by the basal clade Scolecophidia (184–325; see Table A.1) is comparable to that shown by the derived clade Colubridae (149–371; see Table A.1), and other clades show similarly large ranges. If the outgroup to Serpentes is a clade of typical lizards, the increase in body segment count either occurred so rapidly that it was effectively an instantaneous change, or the elongation occurred outside the crown.

The absence of a trend is also partly a result of selective forces acting on body segment number of snakes. The second analysis of this study found unambiguous support for a selective model of evolution of body segment number, regardless of the test statistic used (Table 4.2). However, the preferred model differs depending on test statistics; both the log-likelihood test and AICc scores indicate stronger support for the OU habitat model, whereas the more conservative BIC indicates support for the simpler OU global model. However, Burnham and Anderson (2002) suggest that the BIC may not be suitable for biological models for a variety of reasons including poor performance at smaller sample sizes, and recommend use of AICc in such cases. However, there is some ambiguity in the AICc scores due to the similar values for OU constriction and OU habitat, with the AIC difference only being 2.87. This indicates that there is support for both models, although it falls outside the range of “substantial support” for OU constriction (AIC difference < 2; Burnham and Anderson, 2002). The preferred model is therefore OU habitat.

One of the benefits of modeling Ornstein–Uhlenbeck processes is that the analysis provides the optimum value favored by selection, allowing comparison with the actual data (Butler and King, 2004). Any predicted optima that fall outside the range of values seen in life throw the model into question as unrealistic. In the present study, all three selective OU models show biologically reasonable values that lie within the range of extant snakes. Furthermore, comparison of the predicted optima to the observed average value for each group reveals generally similar values (Table 4.4), although non-constrictors (OU constriction) and arboreal snakes (OU habitat) show a rather sizeable disparity in values. In both cases, the predicted optimal values are higher than the average values, but the reasons for this are unknown.

A second means of assessing the validity of the model is comparison of the results with previous studies and hypotheses regarding the importance and distribution of body segment number in ecological groups. The OU habitat model shows that fossorial and semi-fossorial snakes have the lowest optimal body segment number among the six ecological groupings. This corresponds well with a study that found low ventral counts occur more frequently in fossorial colubroids (Marx and Rabb, 1972), but it runs counter to the fact that snakes with higher vertebral counts perform better in concertina locomotion (Jayne, 1988), which is commonly used in tunnels. It is possible that the increased stiffness afforded by decreasing the number of vertebrae is important in the generation of adequate forces for head-first burrowing seen in truly fossorial snakes, and that this places greater selective pressure on the column than concertina performance. However, this does not explain low body segment counts and optima recorded for semi-fossorial snakes, which are not generally digging as intensively. Other soft tissue factors, including the diameter of the snake, are also important in affecting the flexibility and performance of snakes in narrow tunnels (Jayne, 1988), and it is possible that fossorial and semi-fossorial snakes differ from other snakes in ways that mitigate the decreased performance resulting from fewer vertebrae.

Lower optimal and observed values in both aquatic and semi-aquatic snakes are possibly related to the need for a particular combination of body stiffness and flexibility in elongate undulatory swimming. There are optimal stiffness levels for swimming performance in elongate

animals (Tytell et al., 2010), and different vertebral numbers can be expected to affect body stiffness. However, Jayne (1985) surprisingly found no difference in swimming kinematics between *Nerodia fasciata* and *Pantherophis obsoletus*, despite the latter having 115 more vertebrae (i.e., lower stiffness). He did find that *P. obsoletus* used more muscle segments and less flexion at each intervertebral joint, effectively decreasing the body stiffness to match that of *N. fasciata*. Therefore, although most if not all snakes are capable of swimming, aquatic snakes with low vertebral counts may already have an optimal stiffness to produce more efficient undulatory waves.

The model predicts that arboreal snakes have the highest body segment counts. This may be related to the potentially wide spread of push points in an arboreal environment. Previous work suggests that more widely spaced push points leads to increased selection for flexibility rather than stiffness, in order to be able to reach enough push points to successfully move (Kelley et al. 1997). Not all arboreal habitats are the same, and some smaller arboreal snakes are likely able to make use of relatively more push points in the environment. In such cases, the need for flexibility may not be as great, and possibly explains in part the lower average count observed for the arboreal group. Better refinement of arboreal behavior and environments may reveal two or more optima within this ecological group.

Conclusions

This study explores the evolution of body segment count in snakes by first testing for a directional trend in body segment number, and then by testing models with selection imposed by feeding and habitat requirements. Three selection OU models were tested against a non-selection Brownian-motion model. There is no support for a phyletic trend toward increasing body segment counts. The favored model of body segment count is OU habitat model, which produced optimal body segment counts for each ecological group that are biologically realistic. The OU habitat model also reconstructs much stronger selection than drift, showing that selection is important in determining body segment number. The drift that does occur may account for the wide ranges in vertebral number seen in each group.

It also highlights the importance of body segment number to elongate animals that must make use of their entire trunk for locomotion. Vertebral number is correlated with habitat and locomotor performance in lizards (Van Damme and Vanhooydonck, 2002) and fishes (Swain, 1992; Brainerd and Patek, 1998) as well as snakes (Lindell, 1994; Kelley *et al.*, 1997; Hampton, 2011), showing the importance of body segment number to locomotion across several groups. Although use of BIC found no support for the two ecology-based models, it still favored a selection-driven model over the simpler Brownian motion model. The tendency for this test statistic to support incorrect models at small sample sizes, combined with the support of the OU habitat model using AICc suggests minimally that habitat is an important component of selection pressures on snake body segment number. Any future models of body segment evolution in snakes should therefore include habitat as an important component of the selection force.

Table 4.1. Model support comparison for test of directional evolution of body segment number.

Model	-2log(likelihood)	df	p
Random Walk	-4.79	3	—
Directional	-4.79	4	1.00

Table 4.2. Model supports for test of selection on body segment number in Serpentes.

Model	AICc	AICc difference	BIC	-2log(likelihood)	LR	df	p
Brownian	-386.02	59.27	-379.18	-390.07	—	2	—
OU global	-440.63	4.66	-430.39	-446.73	56.66	3	< 0.0001
OU constriction	-442.42	2.87	-422.11	-454.79	64.72	6	< 0.0001
OU habitat	-445.29	0	-415.09	-464.11	74.04	8	< 0.0001

Table 4.3. Estimates of selection (α) and drift (σ) for the models of evolution in Serpentes tested in this study.

Model	α	σ
Brownian	-	0.25
OU global	4.28	0.32
OU constriction	5.61	0.34
OU habitat	4.90	0.32

Table 4.4. Estimated optima and observed values for body segment number in the groups of snakes examined in this study. All values rounded to the nearest whole number.

	Global	Constrictor	Non-constrictor	Terrestrial	Fossorial	Semi-fossorial	Arboreal	Aquatic	Semi-aquatic
Estimated	240	286	272	279	218	209	351	219	233
Mean	245	279	224	252	217	209	296	226	228
Range	138–596	155–596	138–390	149–596	152–325	138–305	194–418	165–341	178–311

Figure 4.1. The phylogeny of Serpentes used in the analysis. Select clades are named in the outermost ring; all of the included families and colubroid subfamilies are delineated by alternating grey and white patches. The symbols surrounding the tree indicate habitat preference and the presence or absence of constriction as a mode of prey subjugation. See text for sources.

Chapter 5

Conclusions

Taken together, the studies presented here provide a comprehensive look at the morphology of the ophidian vertebral column, and explore the relationship between the vertebral column and ecology. Provided here for the first time are comparative studies of the morphological variation throughout the vertebral column in individuals (intracolumnar variation) for both basal snakes and caenophidians. These studies will be useful for functional morphologists and paleontologists alike, and provides the basis for further work on the vertebral column by highlighting the types of variation present and the regions of potential functional interest. Building on these studies of variation are two studies of ecomorphology, one of the vertebral column as a whole unit, and the other on the individual parts of that unit, the vertebrae. Vertebral number is an important component of an elongated animal's biology (Kelley et al., 1997; Brainerd and Patek, 1998; Van Damme and Vanhooydonck, 2002; McDowall, 2003; Hampton, 2011), and snakes show variations in vertebral numbers between several different ecological categories. The study here is the first to explicitly test for selection on vertebral number by ecology in an explicitly phylogenetic framework for the whole of Serpentes. Complementing this study of vertebral number is a study of the relationship between vertebral morphology and ecology. In this study, the habitat preference of snakes was predicted based on vertebral metrics using a phylogenetic flexible discriminant analysis, with the aim of using the model to predict habitat preference of extinct snakes.

The basis of any future work on the snake vertebral column must rest on an understanding of intracolumnar variation. Prior to this study, intracolumnar variation had been examined in a handful of taxa scattered across the literature, without any synthesis or comparison across major groups. The results presented here reveal that some vertebral features vary through the column in similar ways across the whole of Serpentes, but that other features are not as constant. The anterior trunk is the most well defined region of the precloacal vertebral column, as might be predicted when considering the functional demands placed on the region immediately posterior to the head. But more interesting is the way that the variation in features differs between taxa, particularly when those taxa are ecologically distinct. Greater homogeneity in the columns of terrestrial colubroid snakes supports the hypothesis that the evolution of venom freed the vertebral column to specialize in locomotion (Savitzky, 1980). Instead of having an anterior trunk that is required to produce strong, rapid strikes and powerful, stereotyped constriction, the whole trunk is primarily used in locomotion. Those colubroids that constrict have apparently re-evolved the behavior, as evidenced by the often haphazard nature of the coils, and the lack of a clear pattern across the clade (Greene and Burghardt, 1978). That said, there are still notable differences in the anterior trunk of colubroids, in the form of tall neural spines and hypapophyses, probably still related to special movements of the head.

Knowledge of intracolumnar variation is also important in paleontological studies. Because vertebrae vary in predictable ways through the column in most snakes (scolecophidians often provide exceptions to the rule), isolated vertebrae can be placed to their appropriate region of the trunk. This can allow an accurate representation of the variation in the column of an extinct snake, although the level of detail will not be as high as in the case of extant snakes where every vertebra can be measured. Differences in the way the column varies between clades

can also be used to potentially identify snakes of uncertain affinities. For example, a particular group of snakes may show a combination of features at specific points of the trunk that do not occur in certain groups. Fossils showing similar combinations at the appropriate points in the column can then be referred to that clade. A taxonomically expanded study of intracolumnar variation will be necessary for this to be fully useful, however.

This research shows the ecomorphological potential of snake vertebral morphology. Vertebral number is linked to ecomorphology, with the results of the study here revealing that vertebral number is under selection. The best fitting model of vertebral number evolution is a four-optimum model, wherein snakes are separated by habitat choice. This model outperformed a Brownian motion random walk model, as well as two other models incorporating selection, one with a single global optimum for all snakes and one with snakes grouped as constrictors or non-constrictors. Each of the selection-based models outperforms the Brownian Motion model. These results show that vertebral number is under selection related to habitat preference.

Major questions of snake evolution remain unresolved, making it a fertile ground for future work. The vertebral column of snakes is understudied, in spite of the great potential for important research into the evolution of snakes. The results of the four studies presented here suggest specific avenues of further investigation, centered on three topics: further inquiry of intracolumnar variation in snakes, refinement of the model of evolution of snake vertebral number, and refinement of the predictive model of habitat preference to increase its utility for paleontology.

This study marks the most in-depth investigation of intracolumnar variation in snakes to date; however, it is by no means definitive, consisting of only a small fraction of the total diversity of snakes. Although it does capture broad ecological and phylogenetic groups of extant snakes, there are smaller clades and ecological specialists that could provide useful information if studied in a similar fashion. Now that the basic patterns exhibited by various features in these disparate groups have been discovered, further study can be accelerated by decreasing the amount of raw measurements. This will in turn allow for more broadly based analyses. The large radiation of caenophidian snakes is of particular interest for further study. This clade is highly speciose and has invaded a wide range of available niches, including fully aquatic sea snakes, prey specialists like egg eaters and slug eaters, and gliding snakes. At the opposite end of the spectrum are the basal snakes like scolecophidians, pipe snakes and shieldtails, which all share subterranean habits; investigations of this portion of the snake tree may provide insights in the evolution of the snake vertebral column, and how it came to be so homogenous when compared to non-snake squamate lizards.

Also of interest are studies of sexual dimorphism and ontogeny. Both of these topics are poorly known with regard to intracolumnar variation, although there is some evidence to suggest there are differences between males and females in the trunk vertebrae (Thireau, 1967a). Vertebral morphology certainly changes during growth, and although no focused study has been performed on the ontogeny of snake vertebral morphology, juvenile snakes have enlarged neural canals, a more gracile build, and different shapes as compared to adult forms. Very little morphometric study of ontogeny has been performed, and what has been done was limited to the viperid *Crotalus adamanteus* (Christman, 1975; Prange and Christman, 1976). Study of both sexual dimorphism and ontogeny is of particular interest to paleontologists, who must attempt to sort isolated vertebrae into species or morphotypes; knowledge of how a particular morphotype might vary between sexes or with age would be helpful in this regard.

The study of the evolution of body segment number in snakes presented a successful model of selection acting on snakes. Although the model can always be altered, such changes must be made cautiously. Increasing complexity of the model will improve the fit of the model, but it will decrease the confidence in the reported parameters (Butler and King, 2004). In addition, the model's parameters cannot exceed the number of data points (i.e., taxa), although in the present case the number of taxa is so high that this is not likely to be an issue. Use of conservative model scores like the Aikake information criterion help to limit the acceptance of an incorrect model.

The complexity of this model could be increased without greatly decreasing its utility, although the success of the results does not indicate it is necessary. Modifications that could potentially be made include adding more historical data. Reconstructing the evolutionary history of the investigated trait can produce a better fitting model (Butler and King, 2004). However, in this case there are difficulties in using that approach. The most basal clade of crown Serpentes (Scoleophidia) will strongly influence the reconstructed habitat preference and vertebral number. However, scoleophidians are highly derived and probably do not reflect the biology of the earliest snakes (Kley, 2001). In addition, the fragmentary nature of the fossil record means that almost no extinct forms can be included in the analysis due to a lack of accurate vertebral counts. This means that the base of Serpentes may be incorrectly reconstructed, which will strongly impact the rest of the tree.

It is clear that a great deal of work remains to be done with snake vertebrae. Research in this area has the potential to provide information not only about the evolutionary history of snakes themselves, but also to provide access to the ecosystems they inhabited. By this means, the historical responses of snake faunas can be studied, and compared to changes that are occurring today. This dissertation provides the basis for such work in the future and provides hypotheses that can be tested further with new studies and techniques.

References

- Adalsteinsson, S. A., W. R. Branch, S. Trape, L. J. Vitt, and S. B. Hedges. 2009. Molecular phylogeny, classification, and biogeography of snakes of the family Leptotyphlopidae (Reptilia, Squamata). *Zootaxa* 2244:1–50.
- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* AC-19:716–723.
- Alencar, L. R. V., M. P. Gaiarsa, and M. Martins. 2013. The evolution of diet and microhabitat use in pseudoboine snakes. *South American Journal of Herpetology* 8:60–66.
- Alexander, A. A., and C. Gans. 1966. The pattern of dermal-vertebral correlation in snakes and amphisbaenians. *Zoologische Mededelingen* 41:171–190.
- Alfaro, M. E. 2003. Sweeping and striking: a kinematic study of the trunk during prey capture in three thamnophiine snakes. *Journal of Experimental Biology* 206:2381–2392.
- Alvarez del Toro, M. 1982. *Los reptiles de Chiapas*. Tuxtla Guitiérrez, Chiapas, Mexico, 248 pp.
- Arnold, S. J. 1988. Quantitative genetics and selection in natural populations: microevolution of vertebral numbers in the garter snake *Thamnophis elegans*; pp. 619–638 in B. S. Weir, E. J. Eisen, M. M. Goodman, and G. Namkoong (eds.), *Proceedings of the Second International Conference on Quantitative Genetics* Sinauer, Sunderland, MA.
- Arnold, S. J., and A. F. Bennett. 1988. Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake (*Thamnophis radix*). *Biological Journal of the Linnean Society* 34:175–190.
- Auffenberg, W. 1949. The racer, *Coluber constrictor stejnegerianus* in Texas. *Herpetologica* 5:53–58.
- Auffenberg, W. 1958. The trunk musculature of *Sanzina* and its bearing on certain aspects of the myological evolution of snakes. *Breviora* 82:1–12.
- Auffenberg, W. 1961. Additional remarks on the evolution of trunk musculature in snakes. *American Midland Naturalist* 65:1–16.
- Auffenberg, W. 1963. The fossil snakes of Florida. *Tulane Studies in Zoology* 10:131–216.
- Auffenberg, W. 1966. The vertebral musculature of *Chersydrus* (Serpentes). *Quarterly Journal of the Florida Academy of Sciences* 29:877–882.

- Auliya, M., P. Mausfeld, A. Schmitz, and W. Böhme. 2002. Review of the reticulated python (*Python reticulatus* Schneider, 1801) with the description of new subspecies from Indonesia. *Naturwissenschaften* 89:201–213.
- Baird, S. F., and C. Girard. 1853. Catalogue of North American reptiles in the museum of the Smithsonian Institution. Part 1. Serpents. Smithsonian Institution, Washington, DC, 172 pp.
- Barbour, T. 1910. Notes on the herpetology of Jamaica. *Bulletin of the Museum of Comparative Zoology at Harvard College* 52:273–301.
- Barbour, T., and F. Carr, Jr. 1940. Notes on *Elaphe* and a new species. *Occasional Papers of the Boston Society of Natural History* 8:337–342.
- Baszio, S. 2005a. Korrelationen der Wirbelmorphologie mit Ökologie, Taxonomie und Allometrie rezenter und fossiler Schlangen. *Courier Forschungsinstitut Senckenberg* 255:185–224.
- Baszio, S. 2005b. Der Indikationswert des Anti-Torsions-Komplexes am Schlangenwirbel für die Lebensweise fossiler Schlangen. *Courier Forschungsinstitut Senckenberg* 255:171–183.
- Baumann, H., J. A. R. Casián, and D. O. Conover. 2012. Contrasting latitudinal variations in vertebral number and sex determination in Pacific versus Atlantic silverside fishes. *Copeia* 2012:341–350.
- Bergman, R. A. M. 1955. The anatomy of *Xenopeltis unicolor*. *Zoologische Mededelingen* 33:209–225.
- Bogert, C. M. 1940. Herpetological results of the Vernay Angola expedition, with notes on African reptiles in other collections. Part I. Snakes, including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History* 77:1–107.
- Bogert, C. M. 1942. Snakes secured by the Snyder East African Expedition in Kenya Colony and Tanganyika Territory. *American Museum Novitates* 1178:1–5.
- Bogert, C. M. 1947. Rectilinear locomotion in snakes. *Copeia* 1947:253–254.
- Brainerd, E. L., and S. N. Patek. 1998. Vertebral column morphology, C-start curvature, and the evolution of mechanical defenses in tetraodontiform fishes. *Copeia* 1998:971–984.
- Branch, W. R. 1993. *A Photographic Guide to Snakes and Other Reptiles of Southern Africa*. Struik Publishers, Cape Town, 144 pp.
- Branch, W. R. 1998. *Field Guide to the Snakes and Other Reptiles of Southern Africa*. Struik, Cape Town, 399 pp.

- Brattstrom, B. H. 1964. Evolution of the pit vipers. Transactions of the San Diego Society of Natural History 13:185–268.
- Brattstrom, B. H. 1967. A succession of Pliocene and Pleistocene snake faunas from the high plains of the United States. Copeia 1967:188–202.
- Breithaupt, B. H., and D. Duvall. 1986. The oldest record of serpent aggregation. Lethaia 19:181–185.
- Broadley, D. G. 1959. The herpetology of southern Rhodesia. Part 1. Snakes. Bulletin of the Museum of Comparative Zoology 120:1–100.
- Bullock, D. J. 1986. The ecology and conservation of reptiles on Round Island and Gunner's Quoin, Mauritius. Biological Conservation 37:135–156.
- Bullock, R. E., and W. W. Tanner. 1966. A comparative osteological study of two species of Colubridae (*Pituophis* and *Thamnophis*). Brigham Young University Science Bulletin, Biological Series 8:1–29.
- Burbrink, F. T. 2005. Inferring the phylogenetic position of *Boa constrictor* among the Boinae. Molecular Phylogenetics and Evolution 34:167–180.
- Burbrink, F. T., F. Fontanella, R. A. Pyron, T. J. Guiher, and C. Jiminez. 2008. Phylogeography across a continent: the evolutionary and demographic history of the North American racer (Serpentes: Colubridae: *Coluber constrictor*). Molecular Phylogenetics and Evolution 47:274–288.
- Burchfield, P. M. 1982. Additions to the natural history of the crotaline snake *Agkistrodon bilineatus taylori*. Journal of Herpetology 16:376–382.
- Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference. Second Edition. Springer-Verlag, New York, 488 pp.
- Butler, M. A., and A. A. King. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. American Naturalist 164:683–695.
- Cadle, J. E. 2003. Colubridae, snakes; pp. 997–1004 in S. M. Goodman and J. P. Benstead (eds.), The Natural History of Madagascar. University of Chicago Press, Chicago.
- Caldwell, M. W. 2000. On the aquatic squamate *Dolichosaurus longicollis* Owen, 1850 (Cenomanian, Upper Cretaceous), and the evolution of elongate necks in squamates. Journal of Vertebrate Paleontology 20:720–735.
- Camp, C. D., W. D. Sprewell, and V. N. Powders. 1980. Feeding habits of *Nerodia taxispilota* with comparative notes on the foods of sympatric congeners in Georgia. Journal of Herpetology 14:301–304.

- Campbell, J. A. 1999. Amphibians and Reptiles of Northern Guatemala, the Yucatán, and Belize. University of Oklahoma Press, Norman, 400 pp.
- Caprette, C. L., M. S. Y. Lee, R. Shine, A. Mokany, and J. F. Downhower. 2004. The origin of snakes (Serpentes) as seen through eye anatomy. *Biological Journal of the Linnean Society* 81:469–482.
- Carpenter, C. C. 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*), the Ribbon Snake (*Thamnophis s. sauritus*), and Butler's Garter snake (*Thamnophis butleri*) in mixed populations. *Ecological Monographs* 22:235–258.
- Carus, C. G. 1818. *Lehrbuch der Zootomie*. Gerhard Fleischer the Younger, Leipzig, 702 pp.
- Chippaux, J.-P. 2006. *Les serpents d'Afrique occidentale et centrale*. 3rd Edition. IRD Éditions, Paris, 311 pp.
- Chirio, L. 2012. Inventaire des reptiles de la région de Sangarédi (Guinée maritime). *Bulletin de la Société herpétologique de France* 144:67–100.
- Christman, S. P. 1975. The status of the extinct rattlesnake, *Crotalus giganteus*. *Copeia* 1975:43–47.
- Cogger, H. G. 1988. *Reptiles and Amphibians of Australia*, Revised Edition. Reed Books, Frenchs Forest, NSW, 688 pp.
- Cohn, M. J., and C. Tickle. 1999. Developmental basis of limblessness and axial patterning in snakes. *Nature* 399:474–479.
- Conant, R. 1938. A note on eggs and young of *Leioheterodon madagascariensis* (Duméril & Bibron). *Zoologica* 23:389–393.
- Conant, R., and J. T. Collins. 1991. *A Field Guide to Reptiles and Amphibians: Eastern and Central North America*, Third Edition, Expanded. Houghton Mifflin, New York, 616 pp.
- Conrad, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* 310:1–182.
- Cope, E. D. 1886. An analytical table of the genera of snakes. *Proceedings of the American Philosophical Society* 23:479–499.
- Corkill, N. L. 1935. Notes on Sudan snakes. A guide to the species represented in the Natural History Museum Khartoum. Sudan Government Museum (Natural History) Publication 3:1–40.
- Cowles, R. B. 1945. Surface-mass ratio, paleoclimate and heat sterility. *American Naturalist* 79:561–567.

- Cundall, D. 1995. Feeding behaviour in *Cylindrophis* and its bearing on the evolution of alethinophidian snakes. *Journal of Zoology*, London 237:353–376.
- Cundall, D., and A. Deufel. 1999. Striking patterns in booid snakes. *Copeia* 1999:868–883.
- Cundall, D., and H. W. Greene. 2000. Feeding in snakes; pp. 293–333 in K. Schwenk (ed.), *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates*. Academic Press, San Diego.
- Cundall, D., V. Wallach, and D. A. Rossman. 1993. The systematic relationships of the snake genus *Anomochilus*. *Zoological Journal of the Linnean Society* 109:275–299.
- Cundall, D., A. Deufel, and F. Irish. 2007. Feeding in boas and pythons: motor recruitment patterns during striking; pp. 169–197 in R. W. Henderson and R. Powell (eds.), *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain, UT.
- Cuvier, G. 1835. *Leçons d'anatomie comparée de Georges Cuvier*. Seconde Édition. 2 Edition. Crochard et Cie., Paris, 587 pp.
- d'Alton, E. 1834a. Beschreibung des Muskelsystems eines *Python bivittatus*. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin* 12:528–542.
- d'Alton, E. 1834b. Beschreibung des Muskelsystems eines *Python bivittatus*. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin* 10:432–450.
- d'Alton, E. 1834c. Beschreibung des Muskelsystems eines *Python bivittatus*. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin* 7:347–364.
- d'Alton, E. 1836. *De Pythonis ac Boarum ossibus commentatio*, Halle, Germany, 38 pp.
- D'Cruze, N. C., and J. A. Sabel. 2005. The reptiles of the southern Mikea Forest, Madagascar. *Herpetological Bulletin* 93:2–8.
- da Cunha, O. R., and F. P. do Nascimento. 1975. Ofídios da Amazônia. VI—*Liotyphops ternetzii* (Boulenger, 1896), ofídio raro e de hábitos subterrâneos, na região leste do Pará (Ophidia, Anomalepididae). *Boletim do Museu Paraense Emílio Goeldi, nova série Zologia* 82:1–8.
- Das, I. 2010. *A Field Guide to the Reptiles of South-East Asia*. New Holland Publishers, London, 376 pp.
- de Queiroz, A. 1984. Effects of prey type on the prey-handling behavior of the bullsnake, *Pituophis melanoleucus*. *Journal of Herpetology* 18:333–336.
- de Queiroz, A., and R. R. Groen. 2001. The inconsistent and inefficient constricting Behavior of Colorado Western terrestrial garter snakes, *Thamnophis elegans*. *Journal of Herpetology* 35:450–460.

- de Rochebrune, A.-T. 1881. Mémoire sur les vertèbres des ophidiens. *Journal de l'Anatomie et de la Physiologie Normales et Pathologiques de l'Homme et des Animaux* 17:185–229.
- de Rooij, N. 1917. The Reptiles of the Indo-Australian Archipelago. II. Ophidia. E. J. Brill, Leiden, 334 pp.
- Degenhardt, W. G., C. V. Painter, and A. H. Price. 1996. *Amphibians and Reptiles of New Mexico*. University of New Mexico Press, Albuquerque, 431 pp.
- Diller, L. V., and R. L. Wallace. 1996. Comparative ecology of two snake species (*Crotalus viridis* and *Pituophis melanoleucus* in southwestern Idaho. *Herpetologica* 52:343–360.
- Ditmars, R. L. 1912. The feeding habits of serpents. *Zoologica* 1:197–238.
- Dohm, M. R., and T. Garland, Jr. 1993. Quantitative genetics of scale counts in the garter snake *Thamnophis sirtalis*. *Copeia* 1993:987–1002.
- Dowling, H. G. 1960. The curious feeding habits of the Java wart snake. *Animal Kingdom* 67:13–15.
- Duellman, W. E. 1958. A monographic study of the colubrid snake genus *Leptodeira*. *Bulletin of the American Museum of Natural History* 114:1–152.
- Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *Miscellaneous Publication of the Kansas Museum of Natural History* 65:1–352.
- Dunn, E. R., and J. R. Bailey. 1939. Snakes from the uplands of the Canal Zone and of Darien. *Bulletin of the Museum of Comparative Zoology* 86:1–22.
- Dunn, E. R., and J. A. Tihen. 1944. The skeletal anatomy of *Liotyphlops albirostris*. *Journal of Morphology* 74:287–295.
- Dunson, W. A., and S. A. Minton. 1978. Diversity, distribution, and ecology of Phillipine marine snakes (Reptilia, Serpentes). *Journal of Herpetology* 12:281–286.
- Emmons, L. H., and A. H. Gentry. 1983. Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *The American Naturalist* 121:513–524.
- Ernst, C., and R. W. Barbour. 1989. *Snakes of Eastern North America*. George Mason University Press, Fairfax, VA, 282 pp.
- Ernst, C. H., and E. M. Ernst. 2011. *Venomous Reptiles of the United States, Canada, and Northern Mexico*. Volume 1. Johns Hopkins University Press, Baltimore, MD, 392 pp.
- Estes, R. 1970. Origin of the Recent North American lower vertebrate fauna: an inquiry into the fossil record. *Forma et Functio* 3:139–163.

- Feldman, C. R., and R. F. Hoyer. 2010. A new species of snake in the genus *Contia* (Squamata: Colubridae) from California and Oregon. *Copeia* 2010:254–267.
- Ferner, J. W., R. M. Brown, R. V. Sison, and R. S. Kennedy. 2000. The amphibians and reptiles of Panay Island, Philippines. *Asiatic Herpetological Research* 9:1–37.
- Forstner, M. R. J., S. K. Davis, and E. Arévalo. 1995. Support for the hypothesis of anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 4:93–102.
- Fowlie, J. A. 1965. The snakes of Arizona: their derivation, speciation, distribution, description, and habits—a study in evolutionary herpeto-zoogeographic phylogenetic ecology. Azul Quinta Press, Fallbrook, CA, 164 pp.
- Fox, W. 1948. Effects of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*. *Copeia* 1948:252–262.
- Frazzetta, T. H. 1966. Studies on morphology and function of skull in Boidae (Serpentes) Part II. Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus*. *Journal of Morphology* 118:217–296.
- Frazzetta, T. H. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward. Part II. Jaw machinery in the earliest snakes. *Forma et Functio* 3:205–221.
- Gans, C. 1961. The feeding mechanism of snakes and its possible evolution. *American Zoologist* 1:217–227.
- Gans, C. 1962. Terrestrial locomotion without limbs. *American Zoologist* 2:167–182.
- Gans, C. 1975. Tetrapod limblessness: evolution and functional corollaries. *American Zoologist* 15:455–467.
- Gardner, J. D., and R. L. Cifelli. 1999. A primitive snake from the Cretaceous of Utah. *Special Papers in Palaeontology* 60:87–100.
- Gardner, S. A., J. R. Mendelson, and G. C. Carpenter. 2003. Diet of the leaf-nosed snakes, *Phyllorhynchus* (Squamata: Colubridae): squamate-egg specialists. *The Southwestern Naturalist* 48:550–556.
- Gasc, J.-P. 1967. Introduction à l'étude de la musculature axiale des squamates serpentiformes. *Mémoires du Muséum National d'Histoire Naturelle. Série A. Zoologie* 48:69–124.
- Gasc, J.-P. 1974. L'interprétation fonctionnelle de l'appareil musculo-squelettique de l'axe vertébral chez les serpents (Reptilia). *Mémoires du Muséum National d'Histoire Naturelle* 83:1–182.

- Gauthier, J. A., M. Kearney, J. A. Maisano, O. Rieppel, and A. D. B. Behlke. 2012. Assembling the squamate tree of life: perspectives from the phenotype and fossil record. *Bulletin of the Peabody Museum of Natural History* 53:3–308.
- Gerald, G. W., M. A. Bailey, and J. N. Holmes. 2006. Habitat utilization of *Pituophis melanoleucus melanoleucus* (Northern Pinesnakes) on Arnold Air Force Base in middle Tennessee. *Southeastern Naturalist* 5:253–264.
- Gibbon, J. W., and M. E. Dorcas. 2004. *North American Watersnakes: A Natural History*. University of Oklahoma, Norman, 438 pp.
- Glass, J. K. 1972. Feeding behavior of the western shovel-nosed snake, *Chionactis occipitalis klauberi*, with special reference to scorpions. *The Southwestern Naturalist* 16:445–447.
- Glaw, F., and M. Vences. 1994. *A Field Guide to the Amphibians and Reptiles of Madagascar, Second Edition*. Vences and Glaw Verlags GbR, Köln, 480 pp.
- Goin, C. J. 1943. The lower vertebrate fauna of the water hyacinth community in northern Florida. *Proceedings of the Florida Academy of Science* 6:143–154.
- Gomez, C., E. M. Özbudak, J. Wunderlich, D. Baumann, J. Lewis, and O. Pourquié. 2008. Control of segment number in vertebrate embryos. *Nature* 454:335–339.
- Gosner, K. L. 1987. Observations on Lesser Antillean pit vipers. *Journal of Herpetology* 21:78–80.
- Gow, G. F. 1977. A new species of *Python* from Arnhem Land. *Australian Zoologist* 19:133–139.
- Gower, D. J., and J. D. Ablett. 2006. Counting ventral scales in Asian anilioid snakes. *Herpetological Journal* 16:259–263.
- Gower, D. J., N. Vidal, J. N. Spinks, and C. J. McCarthy. 2005. The phylogenetic position of Anomochilidae (Reptilia: Serpentes): first evidence from DNA sequences. *Journal of Zoological Systematics and Evolutionary Research* 43:315–320.
- Gray, J. 1946. The mechanism of locomotion in snakes. *Journal of Experimental Biology* 23:101–120.
- Gray, J. E. 1842. Monographic synopsis of the water snakes, or the family of Hydridae; pp. 59–68 in J. E. Gray (ed.), *The Zoological Miscellany*. Treuttel, Wurtz and Co., G. B. Sowerby, W. Wood, London.
- Greene, H. W. 1983. Dietary correlates of the origin and radiation of snakes. *American Zoologist* 23:431–441.

- Greene, H. W. 1997. *Snakes: the Evolution of Mystery in Nature*. University of California Press, Berkeley, 351 pp.
- Greene, H. W., and G. M. Burghardt. 1978. Behavior and phylogeny: constriction in ancient and modern snakes. *Science* 200:74–77.
- Greenwald, O. E. 1978. Kinematics and time relations of prey capture by gopher snakes. *Copeia* 1978:263–268.
- Grismer, L. L., J. L. Grismer, and J. A. McGuire. 2006a. A new species of pitviper of the genus *Popeia* (Squamata: Viperidae) from Pulau Tioman, Pahang, West Malaysia. *Zootaxa* 1305:1–19.
- Grismer, L. L., T. M. Youmans, P. L. Wood, Jr., and J. L. Grismer. 2006b. Checklist of the herpetofauna of the Seribuat Archipelago, West Malaysia with comments on biogeography, natural history, and adaptive types. *The Raffles Bulletin of Zoology* 54:157–180.
- Groombridge, B., and R. Luxmoore. 1991. *Pythons in South-East Asia: A Review of distribution, status and trade in three selected species*. Report to CITES Secretariat, Lausanne, Switzerland.
- Günther, A. 1874. A contribution to the fauna of Savage Island. *Proceedings of the Zoological Society of London*:295–297.
- Haas, G. 1980. Remarks on a new ophiomorph reptile from the lower Cenomanian of Ein Jabrud, Israel; pp. 177–192 in L. L. Jacobs (ed.), *Aspects of Vertebrate History*. Museum of Northern Arizona Press, Flagstaff.
- Hahn, D. E., and V. Wallach. 1998. Comments on the systematics of Old World *Leptotyphlops* (Serpentes: Leptotyphlopidae), with description of a new species. *Hamadryad* 23:50–62.
- Hamilton, W. J., Jr., and J. A. Pollack. 1956. The food of some colubrid snakes from Fort Benning, Georgia. *Ecology* 37:519–526.
- Hampton, P. M. 2011. Ventral and sub-caudal scale counts are associated with macrohabitat use and tail specialization in viperid snakes. *Evolutionary Ecology* 25:531–546.
- Hansen, T. F. 1997. Stabilizing selection and the comparative analysis of adaptation. *Evolution* 51:1341–1351.
- Harvey, M. B., G. R. Fuenmayor, J. R. C. Portilla, and J. V. Rueda-Almonacid. 2008. Systematics of the enigmatic dipsadine snake *Tropidodipsas perijanensis* Alemán (Serpentes: Colubridae) and review of morphological characters of Dipsadini. *Herpetological Monographs* 22:106–132.

- Head, J. J. 2005. Snakes of the Siwalik Group (Miocene of Pakistan): systematics and relationship to environmental change. *Palaeontologia Electronica* 8:1–33.
- Head, J. J., and P. D. Polly. 2007. Dissociation of somatic growth from segmentation drives gigantism in snakes. *Biology Letters* 3:296–298.
- Head, J. J., J. I. Bloch, A. K. Hastings, J. R. Bourque, E. A. Cadena, F. A. Herrera, P. D. Polly, and C. A. Jaramillo. 2009. Giant boid snake from the Palaeocene neotropics reveals hotter past equatorial temperatures. *Nature* 457:715–717.
- Hecht, M. K., and T. C. LaDuke. 1988. Bolyerine vertebral variation: a problem for paleoherpetology. *Acta Zoologica Cracoviensia* 31:605–614.
- Henderson, R. W., and L. G. Hoevers. 1977. The seasonal incidence of snakes at a locality in Northern Belize. *Copeia* 1977:349–355.
- Hensley, M. M. 1950. Results of a herpetological reconnaissance in extreme southwestern Arizona and adjacent Sonora, with a description of a new subspecies of the Sonoran Whipsnake (*Masticophis bilineatus*). *Transactions of the Kansas Academy of Science* 53:270–288.
- Hoffmann, C. K. 1890. III. Schlangen und Entwicklungsgeschichte der Reptilien; pp. 1400–2089, Dr. H.G. Bronn's Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild. Volume 6, Reptilien. C. F. Winter'sche Verlagshandlung, Leipzig.
- Hoffstetter, R. 1960. Sur la classification des boïdés de Madagascar et des Mascareignes. *Bulletin du Muséum National d'Histoire Naturelle* 32:131–138.
- Hoffstetter, R., and Y. Gayraud. 1964. Observations sur l'ostéologie et la classification des Acrochordidae (Serpentes). *Bulletin du Muséum National d'Histoire Naturelle* 36:677–696.
- Hoffstetter, R., and J.-P. Gasc. 1969. Vertebrae and ribs of modern reptiles; pp. 201–310 in C. Gans, A. d. A. Bellairs, and T. S. Parsons (eds.), *Biology of the Reptilia, Volume 1: Morphology A*. Academic Press, London.
- Holman, J. A. 2000. *Fossil Snakes of North America: Origin, Evolution, Distribution, Paleoecology*. Indiana University Press, Bloomington, IN, 357 pp.
- Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles; pp. 25–91 in C. Gans and F. H. Pough (eds.), *Biology of the Reptilia, Volume 12: Physiology C*. Academic Press, New York.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small sample. *Biometrika* 76:297–307.

- Ivanov, M. 2000. Snakes of the lower/middle Miocene transition at Vieux Collonges (Rhône, France), with comments on the colonisation of western Europe by colubroids. *Geodiversitas* 22:559–588.
- Ivanov, M. 2001. Changes in the composition of the European snake fauna during the Early Miocene and at the Early/Middle Miocene transition. *Paläontologische Zeitschrift* 74:563-573.
- Jameson, D. L., and A. G. Flury. 1949. The reptiles and amphibians of the Sierra Vieja Range of southwestern Texas. *Texas Journal of Science* 1:54–77.
- Janensch, W. 1906. Über *Archaeophis proavus* Mass., eine Schlange aus dem Eocän des Monte Bolca. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 19:1–33.
- Jayne, B. C. 1982. Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. *Journal of Morphology* 172:83–96.
- Jayne, B. C. 1985. Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubrid snakes. *Copeia* 1985:195–208.
- Jayne, B. C. 1988. Muscular mechanisms of snake locomotion: an electromyographic study of the sidewinding and concertina modes of *Crotalus cerastes*, *Nerodia fasciata* and *Elaphe obsoleta*. *Journal of Experimental Biology* 140:1–33.
- Johnson, R. G. 1955. The adaptive and phylogenetic significance of vertebral form in snakes. *Evolution* 9:367–388.
- Kardong, K. V., and V. L. Bels. 1998. Rattlesnake strike behavior: kinematics. *Journal of Experimental Biology* 201:837–850.
- Keiser, E. D., Jr. 1970. Sexual dimorphism and ontogenetic variation in the haemapophyses of ophidian postcloacal vertebrae. *Herpetologica* 26:331–334.
- Kelley, K. C., S. J. Arnold, and J. Gladstone. 1997. The effects of substrate and vertebral number on locomotion in the garter snake *Thamnophis elegans*. *Functional Ecology* 11:189–198.
- Kelly, C. M. R., N. P. Barker, and M. H. Villet. 2003. Phylogenetics of advanced snakes (Caenophidia) based on four mitochondrial genes. *Systematic Biology* 52:439–459.
- King, A. A., and M. A. Butler. 2011. ouch: Ornstein-Uhlenbeck models for phylogenetic comparative hypotheses (R package), <http://ouch.r-forge.r-project.org>. 2.8-1.
- Klauber, L. 1941. The correlation between scalation and life zones in San Diego County snakes. *Bulletin of the Zoological Society of San Diego* 17:73–79.

- Klauber, L. M. 1931. Notes on the worm snakes of the southwest, with descriptions of two new subspecies. *Transactions of the San Diego Society of Natural History* 23:333–352.
- Kley, N. J. 2001. Prey transport mechanisms in blindsnakes and the evolution of unilateral feeding systems in snakes. *American Zoologist* 41:1321–1337.
- Kley, N. J. 2003. Blindsnakes (Typhlopidae); pp. 379–385 in *Grzimek's Animal Life Encyclopedia*, 2nd edition, Vol. 7, M. Hutchins, J. B. Murphy, and N. Schlager eds. Gale Group, Farmington Hills, MI.
- Kley, N. J., and E. L. Brainerd. 1999. Feeding by mandibular raking in a snake. *Nature* 402:369–370.
- Kluge, A. G. 1991. Boine snake phylogeny and research cycles. *Miscellaneous Publication of the Museum of Zoology, University of Michigan* 178:1–58.
- Kochva, E. 2002. *Atractaspis* (Serpentes, Atractaspididae) the burrowing asp; a multidisciplinary minireview. *Bulletin of the Natural History Museum of London (Zoology)* 68:91–99.
- Kuch, U., J. Müller, C. Mödden, and D. Mebs. 2005. Snake fangs from the Lower Miocene of Germany: evolutionary stability of perfect weapons. *Naturwissenschaften* 93:84–87.
- LaDuke, T. C. 1991a. Morphometric variability of the precaudal vertebrae of *Thamnophis sirtalis sirtalis* (Serpentes: Colubridae), and implications for interpretation of the fossil record. *Biology*, City University of New York, New York, 235 + i–x pp.
- LaDuke, T. C. 1991b. The fossil snakes of Pit 91, Rancho La Brea, California. *Contributions in Science, Natural History Museum of Los Angeles County* 424:1–28.
- LaDuke, T. C., D. W. Krause, J. D. Scanlon, and N. J. Kley. 2010. A Late Cretaceous (Maastrichtian) snake assemblage from the Maevarano Formation, Mahajanga Basin, Madagascar. *Journal of Vertebrate Paleontology* 30:109–138.
- Lawing, A. M., and P. D. Polly. 2011. Pleistocene climate, phylogeny, and climate envelope models: an integrative approach to better understand species' response to climate change. *PLoS ONE* 6:e28554.
- Lawing, A. M., J. J. Head, and P. D. Polly. 2012. The ecology of morphology: the ecometrics of locomotion and macroenvironment in North American snakes; pp. 117–146 in J. Louys (ed.), *Paleontology in Ecology and Conservation*. Springer-Verlag, Berlin.
- Lawson, R., J. B. Slowinski, and F. T. Burbrink. 2004. A molecular approach to discerning the phylogenetic placement of the enigmatic snake *Xenophidion schaeferi* among the Alethinophidia. *Journal of Zoology, London* 263:285–294.

- Lawson, R., J. B. Slowinski, B. I. Crother, and F. T. Burbrink. 2005. Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 37:581–601.
- Lee, M. S. Y. 2000. Soft anatomy, diffuse homoplasy, and the relationships of lizards and snakes. *Zoologica Scripta* 29:101–130.
- Lee, M. S. Y., and M. W. Caldwell. 2000. *Adriosaurus* and the affinities of mosasaurs, dolichosaurs, and snakes. *Journal of Paleontology* 74:915–937.
- Lee, M. S. Y., and J. D. Scanlon. 2002. Snake phylogeny based on osteology, soft anatomy and ecology. *Biological Reviews* 77:333–401.
- Lillywhite, H. B. 1996. Husbandry of the little file snake, *Acrochordus granulatus*. *Zoo Biology* 15:315–327.
- Lillywhite, H. B., and R. W. Henderson. 1993. Behavioral and functional ecology of arboreal snakes; pp. 1–48 in R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York.
- Lindell, L. E. 1994. The evolution of vertebral number and body size in snakes. *Functional Ecology* 8:708–719.
- Lindell, L. E. 1996. Vertebral number in adders, *Vipera berus*: direct and indirect effects on growth. *Biological Journal of the Linnean Society* 59:69–85.
- Lindsey, C. C. 1975. Pleomerism, the widespread tendency among related fish species for vertebral number to be correlated with maximum body lengths. *Journal of the Fisheries Research Board of Canada* 32:2453–2469.
- Lissmann, H. W. 1950. Rectilinear locomotion in a snake (*Boa occidentalis*). *Journal of Experimental Biology* 26:368–379.
- List, J. C. 1966. Comparative osteology of the snake families Typhlopidae and Leptotyphlopidae. *Illinois Biological Monographs* 36:1–112.
- Lourdais, O., F. Brischoux, and L. Barantin. 2005. How to assess musculature and performance in a constricting snake? A case study in the Colombian rainbow boa (*Epicrates cenchria maurus*). *Journal of Zoology* 265:43–51.
- Lourdais, O., R. Shine, X. Bonnet, M. Guillon, and G. Naulleau. 2004. Climate affects embryonic development in a viviparous snake, *Vipera aspis*. *Oikos* 104:551–560.
- Luiselli, L., G. C. Akani, and D. Capizzi. 1998. Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. *Journal of Zoology, London* 146:125–133.

- Luiselli, L., G. C. Akani, L. Rugiero, and E. Politano. 2005. Relationships between body size, population abundance and niche characteristics in the communities of snakes from three habitats in southern Nigeria. *Journal of Zoology*, London 265:207–213.
- Lukoschek, V., and J. S. Keogh. 2006. Molecular phylogeny of sea snakes reveals a rapidly diverged adaptive radiation. *Biological Journal of the Linnean Society* 89:523–539.
- Maddison, W. P., and D. R. Maddison. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.0, <http://mesquiteproject.org>.
- Madsen, T. 1984. Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden. *Copeia* 1984:707–713.
- Malnate, E. V. 1972. Observations on the vertebral hypapophyses and associated musculature in some snakes, with special reference to the Colubridae. *Zoologische Mededelingen* 47:225–239.
- Manier, M. K. 2004. Geographic variation in the long-nosed snake, *Rhinocheilus lecontei* (Colubridae): beyond the subspecies debate. *Biological Journal of the Linnean Society* 83:65–85.
- Manier, M. K., C. M. Seyler, and S. J. Arnold. 2007. Adaptive divergence within and between ecotypes of the terrestrial garter snake, *Thamnophis elegans*, assessed with FST-QST comparisons. *Journal of Evolutionary Biology* 20:1705–1719.
- Marques, O. A. V., and G. Porto. 1994. Dieta e comportamento alimentar de *Erythrolamprus aesculapii*, uma serpente ofiófaga. *Revista Brasileira de Biologia* 54:253–259.
- Marques, O. A. V., and I. Sazima. 2008. Winding to and fro: constriction in the snake *Anilius scytale*. *Herpetological Bulletin* 103:29–31.
- Martins, M., and M. E. Oliveira. 1998. Natural history of snakes in forests in the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6.
- Marx, H., and G. B. Rabb. 1972. Phyletic analysis of fifty characters of advanced snakes. *Fieldiana* 63:1–321.
- Marx, H., G. B. Rabb, and S. J. Arnold. 1982. *Pythonodipsas* and *Spalerosophis*, colubrid snake genera convergent to the vipers. *Copeia* 1982:553–561.
- McDiarmid, R. W., J. A. Campbell, and T. S. A. Touré. 1999. Snake Species of the World: A Taxonomic and Geographic Reference, Volume 1. The Herpetologists' League, Washington, DC, 511 pp.
- McDowall, R. M. 2003. Variation in vertebral number in galaxiid fishes, how fishes swim and a possible reason for pleomerism. *Reviews in Fish Biology and Fisheries* 13:247–263.

- McDowell, S. B. 1975. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part II. Anilioidea and Pythoninae. *Journal of Herpetology* 9:1–79.
- McKay, W. J. 1890. The osteology and myology of the death adder (*Acanthophis antarctica*). *Proceedings of the Linnean Society of New South Wales* 4:893–986.
- Meckel, J. F. 1821. System der vergleichenden Anatomie. Erster Theil. Allgemeine Anatomie. Rengerschen Buchhandlung, Halle, 474 pp.
- Mehta, R. S. 2003. Prey-handling behavior of hatchling *Elaphe helena* (Colubridae). *Herpetologica* 59:469–474.
- Mertens, R. 1943. Systematische und oekologische Bemerkungen u□ber die Regenbogen-schlange, *Xenopeltis unicolor* Reinwardt. *Der Zoologische Garten, N.F.* 15:213–220.
- Meyers, C. W. 1982. Blunt-headed vine snakes (*Imantodes*) in Panama, including a new species and other revisionary notes. *American Museum Novitates* 2738:1–50.
- Meyers, C. W. 2003. Five new species from Eastern Panama: reviews of Northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates* 3391:1–47.
- Meylan, P. A. 1982. The squamate reptiles of the Inglis IA fauna (Irvingtonian: Citrus County, Florida). *Bulletin of the Florida State Museum, Biological Sciences* 27:1–85.
- Moon, B. R. 1999. Testing an inference of function from structure: snake vertebrae do the twist. *Journal of Morphology* 241:217–225.
- Moon, B. R. 2000. The mechanics and muscular control of constriction in gopher snakes (*Pituophis melanoleucus*) and a king snake (*Lampropeltis getula*). *Journal of Zoology* 252:83–98.
- Mori, A. 1998. Prey-handling behavior of three species of homalopsine snakes: features associated with piscivory and Duvernoy's glands. *Journal of Herpetology* 32:40–50.
- Mori, A., and H. J. A. R. Randriamahazo. 2002. *Leioheterodon madagascariensis* (Madagascar menarana snake). Diet. *Herpetological Review* 33:57.
- Mosauer, W. 1932a. On the locomotion of snakes. *Science* 76:583–585.
- Mosauer, W. 1932b. Über die Ortsbewegung der Schlangen. Eine Kritik und Ergänzung der Arbeit Wiedemann's. *Zoologische Jahrbucher Abteilung für Allgemeine Zoologie und Physiologie der Tiere* 52:191–215.

- Mosauer, W. 1935. The myology of the trunk region of snakes and its significance for ophidian taxonomy and phylogeny. Publications of the University of California at Los Angeles in Biological Sciences 1:81–120.
- Naulleau, G. 1987. Use of Biotelemetry in the study of free-ranging snakes: example of *Elaphe longissima*; pp. 289–292 in J. J. Van Gelder, H. Strijbosch, and P. J. M. Bergers (eds.), Proceedings of the Fourth Ordinary General Meeting, Societas Europaea Herpetologica. Faculty of Sciences, Nijmegen, Nijmegen.
- Neill, W. T. 1960. The caudal lure of various juvenile snakes. Quarterly Journal of the Florida Academy of Sciences 23:173–200.
- Neill, W. T., and E. R. Allen. 1949. A new kingsnake (genus *Lampropeltis*) from Florida. Herpetologica 5:101–106.
- Nitin, W., V. Awsare, S. Karangutkar, V. Wagh, B. Yengal, S. Salvi, and R. Pillai. 2012. Herpetofauna of Maharashtra Nature Park, Mumbai, Maharashtra (India). World Journal of Environmental Biosciences 1:90–99.
- Noonan, B. P., and P. T. Chippindale. 2006. Dispersal and vicariance: The complex evolutionary history of boid snakes. Molecular Phylogenetics and Evolution 40:347–358.
- Norris, K. S., and J. L. Kavanau. 1966. The burrowing of the western shovel-nosed snake, *Chionactis occipitalis* Hallowell, and the undersand environment. Copeia 1966:650–664.
- O'Shea, M. 2007. Boas and Pythons of the World. Princeton University Press, Princeton, 160 pp.
- Osgood, D. W. 1978. Effects of temperature on the development of meristic characters in *Natrix fasciata*. Copeia 1978:33–47.
- Pagel, M. 1997. Inferring evolutionary processes from phylogenies. Zoologica Scripta 26:331–348.
- Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.
- Patterson, J. W., and P. M. C. Davies. 1982. Predatory behavior and temperature relations in the snake *Natrix maura*. Copeia 1982:472–474.
- Peabody, R. B., and E. D. Brodie, Jr. 1975. Effect of temperature, salinity and photoperiod on the number of trunk vertebrae in *Ambystoma maculatum*. Copeia 1975:741–746.
- Pearcy, A., and Z. Wijtten. 2010. Suggestions on photographing crocodile skulls for scientific purposes. Herpetological Review 41:445–447.
- Phelps, T. 2010. Old World Vipers. Edition Chimaira, Frankfurt, 558 pp.

- Pitman, C. R. S. 1935. A guide to the snakes of Uganda. Part II. The Uganda Journal 3:130–148.
- Pitman, C. R. S. 1936. A guide to the snakes of Uganda. Part VI. The Uganda Journal 4.
- Pitman, C. R. S. 1937a. A guide to the snakes of Uganda. Part X. The Uganda Journal 5:93–129.
- Pitman, C. R. S. 1937b. A guide to the snakes of Uganda. Part VIII. The Uganda Journal 4:319–349.
- Pitman, C. R. S. 1937c. A guide to the snakes of Uganda (Part VII). The Uganda Journal 4:220–246.
- Pitman, C. R. S. 1938. A guide to the snakes of Uganda. Part XI. The Uganda Journal 5:160–244.
- Pizzatto, L., S. M. Almeida-Santos, and R. Shine. 2007. Life-history adaptations to arboreality in snakes. *Ecology* 88:359–366.
- Platt, D. R. 1969. Natural history of the hognose snakes, *Heterodon platyrhinos* and *Heterodon nasicus*. University of Kansas Publications Museum of Natural History 18:373–381.
- Polly, P. D., and J. J. Head. 2004. Maximum-likelihood identification of fossils: taxonomic identification of Quaternary marmots (Rodentia, Mammalia) and identification of vertebral position in the pipesnake *Cylindrophis* (Serpentes, Reptilia); pp. 197–221 in A. M. T. Elewa (ed.), *Morphometrics: Applications in Biology and Paleontology*. Springer, New York.
- Pope, C. H. 1961. *The Giant Snakes*. Alfred A. Knopf, New York, 296 pp.
- Prange, H. D., and S. P. Christman. 1976. The allometrics of rattlesnake skeletons. *Copeia* 1976:542–545.
- Pregill, G. K. 1977. Axial myology of the racer *Coluber constrictor*. *Transactions of the San Diego Society of Natural History* 18:185–206.
- Pyron, R. A., and F. T. Burbrink. 2009. Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lampropeltini. *Global Ecology and Biogeography* 18:406–415.
- Pyron, R. A., and F. T. Burbrink. 2012. Extinction, ecological opportunity, and the origins of global snake diversity. *Evolution* 66:163–178.
- Pyron, R. A., F. T. Burbrink, and J. J. Wiens. 2013a. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology* 13:1–53.

- Pyron, R. A., H. K. D. Kandambi, C. R. Hendry, V. Pushpamal, F. T. Burbrink, and R. Somaweera. 2013b. Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. *Molecular Phylogenetics and Evolution* 66:969–978.
- Pyron, R. A., F. T. Burbrink, G. R. Colli, A. Nieto Montes de Oca, L. J. Vitt, C. A. Kuczynski, and J. J. Wiens. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution* 58:329–342.
- R Core Team. 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rabb, G. B., and R. Snedigar. 1960. Notes on feeding behavior of an African egg-eating snake. *Copeia* 1960:59–60.
- Radke, W. R., and J. W. Malcom. 2009. Notes on the ecology of Green Ratsnakes (*Senticolis triaspis*) in Southeastern Arizona. *Herpetological Conservation and Biology* 4:9–13.
- Rage, J.-C. 1984. *Serpentes. Handbuch der Paläoherpetologie*, Vol. 11. Gustav Fischer Verlag, Stuttgart, 80 pp.
- Rage, J.-C., and C. Werner. 1999. Mid-Cretaceous (Cenomanian) snakes from Wadi Abu Hashim, Sudan; the earliest snake assemblage. *Palaeontologia Africana* 35:85–110.
- Rage, J.-C., G. V. R. Prasad, and S. Bajpai. 2004. Additional snakes from the uppermost Cretaceous (Maastrichtian) of India. *Cretaceous Research* 25:425–434.
- Rawlings, L. H., D. L. Rabosky, S. C. Donnellan, and M. N. Hutchinson. 2008. Python phylogenetics: inference from morphology and mitochondrial DNA. *Biological Journal of the Linnean Society* 93:603–619.
- Reid, J. R., and T. E. Lott. 1963. Feeding of *Leptotyphlops dulcis dulcis* (Baird and Girard). *Herpetologica* 19:141–142.
- Richardson, M. K., S. P. Allen, G. M. Wright, A. Raynaud, and J. Hanken. 1998. Somite number and vertebrate evolution. *Development* 125:151–160.
- Ricklefs, R. E., and D. B. Miles. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective; pp. 13–41 in P. C. Wainwright and S. M. Reilly (eds.), *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, Chicago.
- Rieppel, O., and H. Zaher. 2000. The braincases of mosasaurs and *Varanus*, and the relationships of snakes. *Zoological Journal of the Linnean Society* 129:489–514.

- Rivero, J. A. 1998. Los anfibios y reptiles de Puerto Rico. Segunda Edición Revisada. La Editorial, San Juan, PR, 510 pp.
- Robinson, M. D., and D. A. Hughes. 1978. Observations on the natural history of Peringuey's adder, *Bitis peringueyi* (Boulenger) (Reptilia: Viperidae). *Annals of the Transvaal Museum* 31:189–193.
- Rodda, G. H., T. H. Fritts, M. J. McCoid, and E. W. I. Campbell. 1999. An overview of the biology of the brown treesnake (*Boiga irregularis*), a costly introduced pest on Pacific islands; pp. 44–80 in G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka (eds.), *Problem Snake Management: the Habu and the Brown Treesnake*. Cornell University Press, Ithaca, NY.
- Rosén, N. 1905. List of the snakes in the Zoological Museum of Lund and Malmö, with descriptions of new species and a new genus. *Annals and Magazine of Natural History* 15:168–181.
- Ruben, J. A. 1977. Some correlates of cranial and cervical morphology with predatory modes in snakes. *Journal of Morphology* 152:89–99.
- Ruben, J. A., and C. Geddes. 1983. Some morphological correlates of striking in snakes. *Copeia* 1983:221–225.
- Ruthven, A. G., and C. Thompson. 1913. The variations in the number of vertebrae and ventral scutes in two snakes of the genus *Regina*. *The American Naturalist* 47:625–632.
- Sanders, K. L., Mumpuni, and M. S. Y. Lee. 2010a. Uncoupling ecological innovation and speciation in sea snakes (Elapidae, Hydrophiinae, Hydrophiini). *Journal of Evolutionary Biology* 23:2685–2693.
- Sanders, K. L., Mumpuni, A. Hamidy, J. J. Head, and D. J. Gower. 2010b. Phylogeny and divergence times of file snakes (*Acrochordus*): Inferences from morphology, fossils and three molecular loci. *Molecular Phylogenetics and Evolution* 56:857–867.
- Savage, J. M. 2002. *The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas*. University of Chicago Press, Chicago, 934 pp.
- Savitzky, A. H. 1980. The role of venom delivery strategies in snake evolution. *Evolution* 34:1194–1204.
- Savitzky, A. H., and J. T. Collins. 1971. The ground snake *Sonora episcopa episcopa* in Coahuila, Mexico. *Journal of Herpetology* 5:87–88.
- Sawyer, M. W., and J. T. Baccus. 1996. Movement ecology and thermal biology of *Bogertophis subocularis* from Texas (Serpentes: Colubridae). *The Southwestern Naturalist* 41:182–186.

- Sazima, I., and A. S. Abe. 1991. Habits of five Brazilian snakes with coral-snake pattern, including a summary of defensive tactics. *Studies on Neotropical Fauna and Environment* 26:159–164.
- Scali, S., M. Mangiacotti, and A. Bonardi. 2008. Living on the edge: habitat selection of *Hierophis viridiflavus*. *Acta Herpetologica* 3:85–97.
- Scanlon, J. D. 1997. *Nanowana* gen. nov., small madtsoiid snakes from the Miocene of Riversleigh: sympatric species with divergently specialised dentition. *Memoirs of the Queensland Museum* 41:393–412.
- Schaal, S., S. Baszio, and J. Habersetzer. 2005. Differenzierung von Schlangenarten anhand qualitativer und quantitativer Merkmale sowie konventioneller Streckenmaße und Indizes. *Courier Forschungsinstitut Senckenberg* 255:133–169.
- Schätti, B. 1999. *Natrix maura* (Linnaeus 1758) - Vipernatter; pp. 483–503 in W. Böhme (ed.), *Handbuch der reptilien und amphibien Europas*. Band 3/IIA: Schlangen II. Aula-Verlag GmbH, Wiebelsheim.
- Schmidt, A. D. 2002. The herpetofauna of the Langjan Nature Reserve (Limpopo Province, Republic of South Africa) (Amphibia, Reptilia). *Herpetozoa* 15:121–135.
- Schmidt, K. P., and T. F. Smith. 1944. Amphibians and reptiles of the Big Bend region of Texas. *Zoological Series of Field Museum of Natural History* 29:75–96.
- Schmidt, K. P., and D. W. Owens. 1944. Amphibians and reptiles of northern Coahuila, Mexico. *Zoological Series of Field Museum of Natural History* 29:97–115.
- Schmidt, K. P., and F. A. Shannon. 1947. Notes on amphibians and reptiles of Michoacan, Mexico. *Fieldiana Zoology* 31:63–85.
- Schwartz, A. 1975. Variation in the Antillean boid snake *Tropidophis haetianus* Cope. *Journal of Herpetology* 9:303–311.
- Shea, G. M. 1998. Geographic variation in scalation and size of the black whip snakes (Squamata: Elapidae: *Demansia vestigiata* complex): evidence for two broadly sympatric species. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 14:41–61.
- Shine, R. 2000. Vertebral numbers in male and female snakes: the roles of natural, sexual and fecundity selection. *Journal of Evolutionary Biology* 13:455–465.
- Shine, R., and T. Schwaner. 1985. Prey constriction by venomous snakes: a review, and new data on Australian species. *Copeia* 1985:1067–1071.

- Shine, R., and M. Wall. 2008. Interactions between locomotion, feeding, and bodily elongation during the evolution of snakes. *Biological Journal of the Linnean Society* 95:293–304.
- Smith, A. G. 1949. The subspecies of the plains garter snake, *Thamnophis radix*. *Bulletin of the Chicago Academy of Sciences* 8:285–300.
- Smith, H. M. 1938. Additions to the herpetofauna of Mexico. *Copeia* 1938:149–150.
- Smith, H. M. 1957. Curious feeding habit of a blind snake, *Leptotyphlops*. *Herpetologica* 13:102.
- Smith, K. 2013. New constraints on the evolution of the snake clades Ungaliophiinae, Loxocemidae and Colubridae (Serpentes), with comments on the fossil history of erycine boids in North America. *Zoologischer Anzeiger* 252:157–182.
- Smith, M. A. 1943. The Fauna of British India; Ceylon and Burma, Including the Whole of the Indo-Chinese Sub-region. Amphibia and Reptilia. III. Serpentes. Taylor & Francis, London, 583 pp.
- Smith, M. J. 1975. The vertebrae of four Australian elapid snakes (Squamata: Elapidae). *Transactions of the Royal Society of South Australia* 99:71–84.
- Smith, T. L., G. D. E. Povel, and K. V. Kardong. 2002. Predatory strike of the tentacled snake (*Erpeton tentaculatum*). *Journal of Zoology, London* 256:233–242.
- Sood, M. S. 1941. The caudal vertebrae of *Eryx johnii* (Russell). *Proceedings of the Indian Academy of Sciences, Section B* 14:191–195.
- Sood, M. S. 1948. The anatomy of the vertebral column in Serpentes. *Proceedings of the Indian Academy of Sciences, Section B* 28:1–26.
- Spawls, S., and W. R. Branch. 1995. *The Dangerous Snakes of Africa: Natural History, Species Directory, Venoms, Snakebite*. Ralph Curtis Books, Sanibel Island, FL, 192 pp.
- Spawls, S., K. M. Howell, and R. C. Drewes. 2006. *Reptiles and Amphibians of East Africa*. Princeton University Press, Princeton, 240 pp.
- Stebbins, R. C. 2003. *A Field Guide to Western Reptiles and Amphibians*. Houghton Mifflin Harcourt, New York, 533 pp.
- Steen, D. A., J. M. Linehan, and L. L. Smith. 2010. Multiscale habitat selection and refuge use of common kingsnakes, *Lampropeltis getula*, in Southwestern Georgia. *Copeia* 2010:227–231.
- Steward, J. W. 1971. *The Snakes of Europe*. David & Charles Limited, Devon, England, 238 pp.

- Stull, O. G. 1928. A revision of the genus *Tropidophis*. Occasional papers of the Museum of Zoology, University of Michigan 195:1–49.
- Swain, D. P. 1992. The functional basis of natural selection for vertebral traits of larvae in the stickleback *Gasterosteus aculeatus*. *Evolution* 46:987–997.
- Szyndlar, Z. 1984. Fossil snakes from Poland. *Acta Zoologica Cracoviensia* 28:1–156.
- Szyndlar, Z., and H.-H. Schleich. 1993. Description of Miocene snakes from Petersbuch 2 with comments on the Lower and Middle Miocene ophidian faunas of southern Germany. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* 192:1–47.
- Tanner, W. W. 1944. A taxonomic study of the genus *Hypsiglena*. *The Great Basin Naturalist* 5:25–92.
- Taylor, E. H. 1965. The serpents of Thailand and adjacent waters. *University of Kansas Science Bulletin* 45:609–1096.
- Taylor, E. H., and H. M. Smith. 1942. The snake genera *Conopsis* and *Toluca*. *The University of Kansas Science Bulletin* 28:325–363.
- Tchernov, E., O. Rieppel, H. Zaher, M. J. Polcyn, and L. L. Jacobs. 2000. A fossil snake with limbs. *Science* 287:2010–2012.
- Thireau, M. 1967a. Contribution a l'étude de la morphologie caudale, de l'anatomie vertébrale et costale des genres *Atheris*, *Atractaspis* et *Causus* (Vipéridés de l'Ouest Africain). *Bulletin du Muséum National d'Histoire Naturelle* 39:454–470.
- Thireau, M. 1967b. Analyse descriptive et biométrique de la colonne vertébrale du serpent marin *Enhydrina schistosa* Daudin (Hydrophiinés). Caractères vertébraux des hydrophiidés. *Bulletin du Muséum National d'Histoire Naturelle* 39:1044–1056.
- Tihen, J. A. 1964. Tertiary changes in the herpetofaunas of temperate North America. *Senckenbergiana Biologica* 45:265–279.
- Townsend, T. M., A. Larson, E. Louis, and J. R. Macey. 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology* 53:735–757.
- Tsuihiji, T., M. Kearney, and O. Rieppel. 2006. First report of a pectoral girdle muscle in snakes, with comments on the snake cervico-dorsal boundary. *Copeia* 2006:206–215.
- Tsuihiji, T., M. Kearney, and O. Rieppel. 2012. Finding the neck–trunk boundary in snakes: anteroposterior dissociation of myological characteristics in snakes and its implications for their neck and trunk body regionalization. *Journal of Morphology* 273:992–1009.

- Tytell, E. D., C.-Y. Hsu, T. L. Williams, A. H. Cohen, and L. J. Fauci. 2010. Interactions between internal forces, body stiffness, and fluid environment in a neuromechanical model of lamprey swimming. *Proceedings of the National Academy of Sciences* 107:19832–19837.
- Van Damme, R., and B. Vanhooydonck. 2002. Speed versus manoeuvrability: association between vertebral number and habitat structure in lacertid lizards. *Journal of Zoology, London* 258:327–334.
- Van Devender, T. R., and J. I. Mead. 1978. Early Holocene and Late Pleistocene amphibians and reptiles in Sonoran Desert packrat middens. *Copeia* 1978:464–475.
- Van Devender, T. R., A. M. Rea, and M. L. Smith. 1985. The Sangamon interglacial vertebrate fauna from Rancho la Brisca, Sonora, Mexico. *Transactions of the San Diego Society of Natural History* 21:23–55.
- Vidal, N., and S. B. Hedges. 2002. Higher-level relationships of snakes inferred from four nuclear and mitochondrial genes. *Comptes Rendus Biologies* 325:977–985.
- Vidal, N., and S. B. Hedges. 2004. Molecular evidence for a terrestrial origin of snakes. *Biology Letters* 271:S226–S229.
- Vidal, N., and P. David. 2004. New insights into the early history of snakes inferred from two nuclear genes. *Molecular Phylogenetics and Evolution* 31:783–787.
- Vidal, N., and S. B. Hedges. 2005. The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. *Comptes Rendus Biologies* 328:1000–1008.
- Vidal, N., and S. B. Hedges. 2009. The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *Comptes Rendus Biologies* 332:129–139.
- Vidal, N., A.-S. Delmas, and S. B. Hedges. 2007a. The higher-level relationships of alethinophidian snakes inferred from seven nuclear and mitochondrial genes; pp. 27–33 in R. W. Henderson and R. Powell (eds.), *Biology of the Boas and Pythons*. Eagle Mountain Publishing, Eagle Mountain, UT.
- Vidal, N., J.-C. Rage, A. Couloux, and S. B. Hedges. 2009. Snakes (Serpentes); pp. 390–397 in S. B. Hedges and S. Kumar (eds.), *The Timetree of Life*. Oxford University Press, Oxford.
- Vidal, N., A.-S. Delmas, P. David, C. Cruaud, A. Coujoux, and S. B. Hedges. 2007b. The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. *Comptes Rendus Biologies* 330:182–187.

- Vidal, N., J. Marin, M. Morini, S. Donnellan, W. R. Branch, R. Thomas, M. Vences, A. Wynn, C. Cruaud, and S. B. Hedges. 2010. Blindsnake evolutionary tree reveals long history on Gondwana. *Biology Letters* 6:558–561.
- Villiers, A. 1963. *Les Serpents de l'Ouest Africain*. Institut Francais d'Afrique Noir, Dakar, 190 pp.
- von Meyer, H. 1860. *Coluber (Tropidonotus?) atavus* aus der Braunkohle des Siebengebirges. *Palaeontographica* 7:232–240.
- Voris, H. K. 1975. Dermal scale-vertebra relationships in sea snakes (Hydrophiidae). *Copeia* 1975:746–757.
- Wainwright, P. C. 1994. Functional morphology as a tool in ecological research; pp. 42–59 in P. C. Wainwright and S. M. Reilly (eds.), *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, Chicago.
- Wall, F. 1918. A popular treatise on the common Indian snakes. Part XXIV. *Journal of the Bombay Natural History Society* 25:375–382.
- Webb, J. K., and R. Shine. 1993. Pre-size selection, gape limitation and predator vulnerability in Australian blindsnakes (Typhlopidae). *Animal Behaviour* 45:1117–1126.
- Webb, R. G. 1960. Notes on Some Amphibians and Reptiles from Northern Mexico. *Transactions of the Kansas Academy of Science* 63:289–298.
- Wiedemann, E. 1932. Zur Ortsbewegung der Schlangen und Schleichen. *Zoologische Jahrbucher Abteilung fur Allgemeine Zoologie und Physiologie der Tiere* 50:557–596.
- Wiens, J. J., C. A. Kuczynski, S. A. Smith, D. G. Mulcahy, J. W. Sites, T. M. Townsend, and T. W. Reeder. 2008. Branch lengths, support, and congruence: testing the phylogenomic approach with 20 nuclear loci in snakes. *Systematic Biology* 57:420–431.
- Wilcox, T. P., D. J. Zwickl, T. A. Heath, and D. M. Hillis. 2002. Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution* 25:361–371.
- Willard, D. E. 1977. Constricting methods of snakes. *Copeia* 1977:379–382.
- Wright, A. H., and A. A. Wright. 1957. *Handbook of Snakes*, 1105 pp.
- Wüster, W., L. Peppin, C. E. Pook, and D. E. Walker. 2008. A nesting of vipers: Phylogeny and historical biogeography of the Viperidae (Squamata: Serpentes). *Molecular Phylogenetics and Evolution* 49:445–459.

Young, B. A., and M. Morain. 2003. Vertical burrowing in the Saharan sand vipers (*Cerastes*).
Copeia 2003:131–137.

Zeiss, C. 2002-2005. AxioVision 4.4.1.0. Carl Zeiss Vision, Göttingen.

Appendix

The following is the tree utilized in Chapter 3 presented in Newick format.

```
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0000002):5.699999999999999):5.699999999999999):10.259999999999998,(Sanzinia_madaga

scariensis:25.84,(Candoia_aspera:12.92,Candoia_bibroni:12.92):12.92):12.919999999999998):6.2600000000000005,((Lichanura_trivirgata:16.9,Charina_bottae:16.9):16.9,((Eryx_jaculus:11.26,Eryx_jayakari:11.26):11.2500000000000002,(Gongylophis_colubrinus:11.26,Gongylophis_conicus:11.26):11.2500000000000002):11.289999999999996):11.2200000000000006):10.6299999999999995):12.7500000000000007):21.599999999999994):4.0):7.5):33.09,(Liotyphlops_albirostris:57.0,Liotyphlops_ternetzi:57.0):77.59):6.2100000000000008,(((Myriopholis_blanfordi:81.4,(Leptotyphlops_emini:46.8,Leptotyphlops_nigricans:46.8):34.600000000000001):49.8700000000000005,(Rena_maxima:69.1,Epictia_goudotii:69.1):62.1700000000000016):8.129999999999995,((Typhlops_arenarius:62.0,((Typhlops_reticulatus:32.0,((Typhlops_lumbricalis:15.0,Typhlops_rostellatus:15.0):5.0,(Typhlops_richardi:5.0,Typhlops_platycephalus:5.0):15.0):12.0):28.0,((Megatyphlops_schlegelii:21.0,Afrotyphlops_lineolatus:21.0):31.0,Letheobia_unitaeniata:52.0):8.0):2.0):1.0,((Typhlops_luzonensis:48.0,((Ramphotyphlops_polygrammicus:28.0,Austrotyphlops_bituberculatus:28.0):17.0,Ramphotyphlops_braminus:45.0):3.0):9.0,Typhlops_vermicularis:57.0):6.0):76.4):1.40000000000000057):140.8;

Table A.1. Average vertebral number and range of variation for the species included in Chapter 3.

Family	Species	Average No. of Vertebrae	Range of Vertebrae	Specimens Observed	References
Acrochordidae	<i>Acrochordus granulatus</i>	252	249–255		Alexander and Gans, 1966
Acrochordidae	<i>Acrochordus javanicus</i>	264	271–273	YPM R 12192	de Rochebrune, 1881; Polly et al., 2001
Colubridae	<i>Ahaetulla prasina</i>	371	340–402	USNM 297354	de Rochebrune, 1881
Colubridae	<i>Arizona elegans</i>	272	258–282		Schmidt and Owens, 1944; Schmidt and Smith, 1944
Colubridae	<i>Bogertophis subocularis</i>	347	340–356		Schmidt and Owens, 1944; Schmidt and Smith, 1944
Colubridae	<i>Boiga jaspidea</i>	274			de Rochebrune, 1881
Colubridae	<i>Chionactis occipitalis</i>	201	196–205		Stickel, 1943
Colubridae	<i>Coelognathus helena</i>	237			de Rochebrune, 1881
Colubridae	<i>Coluber constrictor stejnegerianus</i>	244	237–251		Webb, 1960
Colubridae	<i>Conopsis nasus</i>	165	158–180		Schmidt and Shannon, 1947
Colubridae	<i>Crotaphopeltis hotamboeia</i>	220	211–232		Bogert, 1940; Gans et al., 1965
Colubridae	<i>Dasypeltis fasciatus</i>	312	308–314		Bogert, 1940
Colubridae	<i>Dasypeltis scabra scabra</i>	295	277–319		Bogert, 1940
Colubridae	<i>Dendrelaphis caudolineatus</i>	285	285		de Rochebrune, 1881
Colubridae	<i>Dipsadoboa duchesnii</i>	310	307–312		Bogert, 1940
Colubridae	<i>Dipsadoboa viridis</i>	320			Bogert, 1940
Colubridae	<i>Dispholidus typus</i>	283	262–323		de Rochebrune, 1881; Bogert, 1942
Colubridae	<i>Drymobius margaritiferus fistulosus</i>	272			Schmidt and Shannon, 1947
Colubridae	<i>Hapsidophrys lineatus</i>	267	265–268		Bogert, 1940
Colubridae	<i>Hapsidophrys smaragdina</i>	308			Bogert, 1940

Colubridae	<i>Hierophis viridiflavus</i>	314		de Rochebrune, 1881
Colubridae	<i>Lampropeltis alterna</i> <i>alterna</i>	282	277–286	Schmidt and Owens, 1944; Wright and Wright, 1957
Colubridae	<i>Lampropeltis alterna</i> <i>blairi</i>	292		Wright and Wright, 1957
Colubridae	<i>Lampropeltis getula goini</i>	269		Neill and Allen, 1949
Colubridae	<i>Lampropeltis triangulum</i> <i>annulata</i>	244		Schmidt and Owens, 1944
Colubridae	<i>Masticophis flagellum</i>	290		Polly et al., 2001
Colubridae	<i>Oxybelis aeneus</i>	349	331–367	de Rochebrune, 1881; Wright and Wright, 1957
Colubridae	<i>Oxybelis fulgidus</i>	348		Polly et al., 2001
Colubridae	<i>Pantherophis</i> <i>alleganiensis</i>	324		Barbour and Carr, 1940
Colubridae	<i>Pantherophis bairdi</i>	338	328–355	Schmidt and Smith, 1944; Webb, 1960
Colubridae	<i>Pantherophis emoryi</i>	279		Jameson and Flury, 1949
Colubridae	<i>Pantherophis guttatus</i>	296	288–306	Schmidt and Owens, 1944; Wright and Wright, 1957
Colubridae	<i>Pantherophis spiloides</i>	319		Barbour and Carr, 1940
Colubridae	<i>Philothamnus irregularis</i>	278	249–306	Bogert, 1940
Colubridae	<i>Philothamnus</i> <i>semivariiegatus</i>	331	321–343	Bogert, 1940
Colubridae	<i>Phyllorhynchus browni</i>	186		Klauber, 1939
Colubridae	<i>Pituophis melanoleucus</i> <i>melanoleucus</i>	274		YPM R 10679
Colubridae	<i>Pituophis melanoleucus</i> <i>mugitus</i>	283	277–288	Wright and Wright, 1957
Colubridae	<i>Pituophis ruthveni</i>	276	273–278	Wright and Wright, 1957
Colubridae	<i>Ptyas mucosa</i>	311		de Rochebrune, 1881
Colubridae	<i>Rhinocheilus lecontei</i> <i>tesselatus</i>	248	246–249	Schmidt and Owens, 1944; Schmidt and Smith, 1944

Colubridae	<i>Salvadora grahamiae</i>	278		Schmidt and Owens, 1944
Colubridae	<i>Senticolis triaspis intermedia</i>	368	354–382	Wright and Wright, 1957; Webb, 1960
Colubridae	<i>Sonora semiannulata</i>	203	191–208	Schmidt and Smith, 1944; Savitzky and Collins, 1971
Colubridae	<i>Spalerosophis diadema</i>	284		de Rochebrune, 1881
Colubridae	<i>Telescopus semiannulatus</i>	294	281–307	Bogert, 1940
Colubridae	<i>Thelotornis kirtlandii</i>	331		Bogert, 1940
Colubridae	<i>Thrasops flavigularis</i>	353	348–359	Bogert, 1940; Alexander and Gans, 1966
Colubridae	<i>Thrasops jacksonii</i>	343	332–354	Alexander and Gans, 1966
Colubridae	<i>Trimorphodon biscutatus</i>	357	348–370	Schmidt and Shannon, 1947
Colubridae	<i>Zamenis longissimus</i>	296		de Rochebrune, 1881
Colubridae	<i>Atractus clarki</i>	207	199–214	Meyers, 2003
Colubridae	<i>Atractus darienensis</i>	184		Meyers, 2003
Colubridae	<i>Contia longicaudae</i>	227		Feldman and Hoyer, 2010
Colubridae	<i>Diadophis punctatus regalis</i>	279	272–283	Schmidt and Smith, 1944; Jameson and Flury, 1949
Colubridae	<i>Dipsas sanctijoannis</i>	262		Harvey et al., 2008
Colubridae	<i>Erythrolamprus aesculapii</i>	271	244–297	de Rochebrune, 1881; Polly et al., 2001
Colubridae	<i>Geophis brachycephalus</i>	162	161–188	Meyers, 2003
Colubridae	<i>Geophis hoffmanni</i>	154	148–160	Meyers, 2003
Colubridae	<i>Heterodon nasicus kennehyi</i>	174	168–179	Schmidt and Owens, 1944
Colubridae	<i>Hypsiglena chlorophaea</i>	242	226–261	Tanner, 1944
Colubridae	<i>Hypsiglena jani</i>	215	201–225	Tanner, 1944
Colubridae	<i>Hypsiglena ochrorhyncha</i>	227	207–256	Tanner, 1944
Colubridae	<i>Hypsiglena slevini</i>	258		Tanner, 1944
Colubridae	<i>Hypsiglena torquata</i>	213	200–247	Tanner, 1944
Colubridae	<i>Imantodes cenchoa</i>	418	375–464	Meyers, 1982
Colubridae	<i>Imantodes gemmistratus</i>	359	351–367	Meyers, 1982

Colubridae	<i>Imantodes inornatus</i>	318	306–334	Meyers, 1982
Colubridae	<i>Leptodeira annulata</i>	255		de Rochebrune, 1881
Colubridae	<i>Leptodeira maculata</i>	239	224–256	Schmidt and Shannon, 1947
Colubridae	<i>Pseudoboa coronata</i>	209		de Rochebrune, 1881
Colubridae	<i>Tretanorhinus nigroluteus</i>	198		Rosén, 1905
Colubridae	<i>Xenodon severus</i>	200	179–221	de Rochebrune, 1881
Colubridae	<i>Grayia ornata</i>	237		Bogert, 1940
Colubridae	<i>Grayia Smythii</i>	248		Bogert, 1940
Colubridae	<i>Natrix maura</i>	252		de Rochebrune, 1881
Colubridae	<i>Natrix natrix</i>	258		de Rochebrune, 1881
Colubridae	<i>Nerodia erythrogaster</i>	215	208–228	Schmidt and Smith, 1944
Colubridae	<i>Nerodia fasciata</i>	203		Osgood, 1978
Colubridae	<i>Nerodia taxispilota</i>	210		YPM R 10601
Colubridae	<i>Regina grahami</i>	238	231–245	Ruthven and Thompson, 1913
Colubridae	<i>Rhabdophis tigrinus</i>	246		de Rochebrune, 1881
Colubridae	<i>Seminatrix pygaea pygaea</i>	173	164–181	Goin, 1943
Colubridae	<i>Storeria dekayi</i>	149		Polly et al., 2001
Colubridae	<i>Storeria storerioides</i>	172	162–183	Schmidt and Shannon, 1947
Colubridae	<i>Thamnophis elegans</i>	224		Baird and Girard, 1853
Colubridae	<i>Thamnophis marcianus</i>	221		Schmidt and Smith, 1944
Colubridae	<i>Thamnophis ordinoides</i>	202		Polly et al., 2001
Colubridae	<i>Thamnophis radix radix</i>	224	216–232	Smith, 1949
Colubridae	<i>Thamnophis sirtalis</i>	257		Carpenter, 1952
Elapidae	<i>Acalyptophis peronii</i>	211	202–220	Voris, 1975
Elapidae	<i>Acanthophis antarcticus</i>	162	154–170	YPM R 013646, USNM 237694
Elapidae	<i>Aipysurus duboisii</i>	196		Voris, 1975
Elapidae	<i>Aipysurus fuscus</i>	214		Voris, 1975
Elapidae	<i>Aipysurus laevis</i>	190		Voris, 1975
Elapidae	<i>Astrotia stokesii</i>	184	180–188	Voris, 1975
Elapidae	<i>Bungarus candidus</i>	223		de Rochebrune, 1881

Elapidae	<i>Bungarus fasciatus</i>	233	230–236	USNM 297453	de Rochebrune, 1881; Smith, 1943
Elapidae	<i>Bungarus multicinctus</i>	348		YPM R 011263	
Elapidae	<i>Chitulia lapemoides</i>	212	204–219		Voris, 1975
Elapidae	<i>Dendroaspis angusticeps</i>	390			Bogert, 1940; Branch, 1998
Elapidae	<i>Dendroaspis viridis</i>	337	327–348	USNM 320709	Bogert, 1942; Polly et al., 2001
Elapidae	<i>Disteira kingii</i>	306			Voris, 1975
Elapidae	<i>Disteira major</i>	212	206–218		Voris, 1975
Elapidae	<i>Elapsoidea guentheri</i>	178			Bogert, 1940
Elapidae	<i>Emyocephalus ijimae</i>	183			Voris, 1975
Elapidae	<i>Hydrophis cyanocinctus</i>	341			de Rochebrune, 1881
Elapidae	<i>Lapemis hardwicki</i>	165	156–173		Alexander and Gans, 1966
Elapidae	<i>Laticauda laticaudata</i>	287	279–299		Alexander and Gans, 1966
Elapidae	<i>Laticauda schistorhynchus</i>	234	225–242		Voris, 1975
Elapidae	<i>Hydrophis elegans</i>	274	261–287	YPM R 13648	Voris, 1975
Elapidae	<i>Leiodelasma spiralis</i>	259			Voris, 1975
Elapidae	<i>Micrurus fulvius</i>	262			Polly et al., 2001
Elapidae	<i>Micrurus tener</i>	256			Schmidt and Owens, 1944
Elapidae	<i>Naja haje</i>	210			de Rochebrune, 1881
Elapidae	<i>Naja nigricollis</i>	263	260–266	USNM 320722	Polly et al., 2001
Elapidae	<i>Parahydrophis mertoni</i>	195			Voris, 1975
Elapidae	<i>Pelamis platura</i>	192			de Rochebrune, 1881
Elapidae	<i>Pseudonaja textilis</i>	266		YPM R 013647	
Homalopsidae	<i>Homalopsis buccata</i>	231			de Rochebrune, 1881
Lamprophiidae	<i>Aparallactus capensis</i>	188			Bogert, 1940
Lamprophiidae	<i>Aparallactus modestus</i>	187			Bogert, 1940
Lamprophiidae	<i>Atractaspis bibroni</i>	272			Bogert, 1940
Lamprophiidae	<i>Buhoma depressiceps</i>	176	173–178		Bogert, 1940
Lamprophiidae	<i>Homonotus modestus</i>	321	315–324		Bogert, 1940
Lamprophiidae	<i>Lamprophis fuliginosus mentalis</i>	257			Bogert, 1940

Lamprophiidae	<i>Lamprophis lineatus</i>	272	252–262	Bogert, 1940
Lamprophiidae	<i>Lamprophis olivaceus</i>	245	234–252	Bogert, 1940
Lamprophiidae	<i>Lamprophis virgatus</i>	259	252–260	Bogert, 1940
Lamprophiidae	<i>Lycophidion capense capense</i>	221	194–235	Bogert, 1940
Lamprophiidae	<i>Mehelya poensis</i>	349	340–357	Bogert, 1940
Lamprophiidae	<i>Hemirhagerrhis nototaenia</i>	243		Bogert, 1940
Lamprophiidae	<i>Malpolon monspessulanus</i>	267	266–267	de Rochebrune, 1881
Lamprophiidae	<i>Psammophis biseriatus</i>	269	247–289	Gans et al., 1965; Bezy and Drewes, 1985
Lamprophiidae	<i>Psammophis lineatus</i>	230		Bogert, 1940
Lamprophiidae	<i>Psammophis schokari</i>	272		de Rochebrune, 1881
Lamprophiidae	<i>Psammophis tanganicus</i>	265	227–313	Bogert, 1940; Bezy and Drewes, 1985
Lamprophiidae	<i>Psammophylax tritaeniatus</i>	238		Alexander and Gans, 1966
Lamprophiidae	<i>Psammophylax variabilis multisquamis</i>	231	224–235	Bogert, 1940
Lamprophiidae	<i>Rhamphiophis rostratus</i>	284	282–286	Bogert, 1940
Lamprophiidae	<i>Pseudaspis cana</i>	264		de Rochebrune, 1881
Lamprophiidae	<i>Duberria lutrix abyssinica</i>	155		Bogert, 1940
Lamprophiidae	<i>Duberria lutrix lutrix</i>	179		Bogert, 1940
Lamprophiidae	<i>Leioheterodon madagascariensis</i>	279		NJK Lm09-D1
Lamprophiidae	<i>Madagascarophis colubrinus</i>	293		Rosén, 1905
Pareatidae	<i>Pareas carinatus</i>	237		Polly et al., 2001
Viperidae	<i>Agkistrodon bilineatus</i>	164	144–183	Schmidt and Owens, 1944
Viperidae	<i>Agkistrodon piscivorus</i>	193	179–209	de Rochebrune, 1881; Campbell and Lamar, 2004

Viperidae	<i>Bothrops lanceolatus</i>	206		de Rochebrune, 1881
Viperidae	<i>Crotalus basiliscus</i>	214		Schmidt and Shannon, 1947
Viperidae	<i>Crotalus durissus</i>	204		Alexander and Gans, 1966
Viperidae	<i>Crotalus horridus</i>	210		de Rochebrune, 1881
Viperidae	<i>Crotalus molossus</i>	212	205–218	Schmidt and Owens, 1944
Viperidae	<i>Lachesis muta</i>	277		Polly et al., 2001
Viperidae	<i>Popeia buniana</i>	245	231–251	Grismer et al., 2006
Viperidae	<i>Sistrurus miliarius</i>	221		de Rochebrune, 1881
Viperidae	<i>Trimeresurus gramineus</i>	198		de Rochebrune, 1881
Viperidae	<i>Vipera aspis</i>	205		de Rochebrune, 1881
Viperidae	<i>Vipera berus</i>	203		de Rochebrune, 1881
Viperidae	<i>Atheris nitschei</i>	194		Bogert, 1940
Viperidae	<i>Bitis arietans</i>	151	145–170	de Rochebrune, 1881
Viperidae	<i>Bitis gabonica</i>	162	159–165	Bogert, 1940
Viperidae	<i>Bitis nasicornis</i>	158	154–161	Bogert, 1940
Viperidae	<i>Bitis peringueyi</i>	159		Bogert, 1940
Viperidae	<i>Causus resimus</i>	165	152–171	Bogert, 1940
Viperidae	<i>Causus rhombeatus</i>	162	148–181	Bogert, 1940
Viperidae	<i>Cerastes vipera</i>	138		de Rochebrune, 1881
Viperidae	<i>Daboia russelli</i>	223		Polly et al., 2001
Viperidae	<i>Echis pyramidum</i>	201	194–207	Bogert, 1940
Boidae	<i>Boa constrictor</i>	297	289–304	YPM R 12323
Boidae	<i>Catabaria reinhardti</i>	255	248–262	NJK Cr07-A
Boidae	<i>Candoia aspera</i>	155	147–165	NJK Ca06-A
Boidae	<i>Candoia bibroni</i>	278	238–301	YPM R 13884
Boidae	<i>Charina bottae</i>	260	259–261	NJK Cb07-A
Boidae	<i>Corallus annulatus</i>	354		Alexander and Gans, 1966
Boidae	<i>Corallus caninus</i>	276		Alexander and Gans, 1966
Boidae	<i>Epicrates cenchria</i>	329		Alexander and Gans, 1966
Boidae	<i>Eryx jaculus</i>	206	193–220	Polly et al., 2001
Boidae	<i>Eryx jayakari</i>	204		de Rochebrune, 1881
				Rieppel, 1978
				NJK Ej08-A

Boidae	<i>Eunectes murinus</i>	311			Polly et al., 2001
Boidae	<i>Eunectes notaeus</i>	303			Alexander and Gans, 1966
Boidae	<i>Gongylophis colubrinus</i>	217	215–219		Alexander and Gans, 1966
Boidae	<i>Gongylophis conicus</i>	208			Alexander and Gans, 1966
Boidae	<i>Lichanura trivirgata</i>	287			Alexander and Gans, 1966
Boidae	<i>Sanzinia madagascariensis</i>	250			Alexander and Gans, 1966
Bolyeridae	<i>Casarea dussumieri</i>	351			Alexander and Gans, 1966
Loxocemidae	<i>Loxocemus bicolor</i>	305	290–328	NJK Lb09-D1	Schmidt and Shannon, 1947
Pythonidae	<i>Antaresia childreani</i>	323		Am06-A	Alexander and Gans, 1966
Pythonidae	<i>Antaresia maculosa</i>	313			Alexander and Gans, 1966
Pythonidae	<i>Aspidites melanocephalus</i>	341			Alexander and Gans, 1966
Pythonidae	<i>Aspidites ramsayi</i>	350			Alexander and Gans, 1966
Pythonidae	<i>Bothrochilus boa</i>	307	302–323	NJK Ar08-1	Alexander and Gans, 1966
Pythonidae	<i>Brogghammerus reticulatus saputrai</i>	427			Auliya et al., 2002
Pythonidae	<i>Leiopython albertisii</i>	342	325–353	YPM R 13799	McDowell, 1975
Pythonidae	<i>Liasis fuscus</i>	358			Alexander and Gans, 1966
Pythonidae	<i>Morelia amethystina</i>	436	424–441		de Rochebrune, 1881
Pythonidae	<i>Morelia oenpelliensis</i>	596	584–608		Gow, 1977
Pythonidae	<i>Morelia viridis</i>	321	306–351		Alexander and Gans, 1966
Pythonidae	<i>Python brongersmai</i>	216		NJK Pb08-1	O’Shea, 2007
Pythonidae	<i>Python curtus</i>	200	194–205	YPM R 13882, YPM R 11405	
Pythonidae	<i>Python molurus</i>	335	327–342	YPM R 12545	Polly et al., 2001
Pythonidae	<i>Python regius</i>	248			Polly et al., 2001
Pythonidae	<i>Python sebae</i>	351	333–370		de Rochebrune, 1881
Xenopeltidae	<i>Xenopeltis unicolor</i>	216	210–220	NJK Xu09-D1	de Rochebrune, 1881; Smith, 1943
Aniliidae	<i>Anilius scytale</i>	251	233–268	NJK Ass08-1	de Rochebrune, 1881
Cylindrophiiidae	<i>Cylindrophis ruffus</i>	201	187–223	NJK Cr09-D1	de Rochebrune, 1881; Smith, 1943
Tropidophiidae	<i>Trachyboa boulengeri</i>	156	155–158		Alexander and Gans, 1966; Dunn and

Tropidophiidae	<i>Tropidophis haetianus</i>	219	213–225	NJK Th06-2, NJK Th09-D1		Alexander and Gans, 1966
Tropidophiidae	<i>Tropidophis melanurus</i>	238	237–239			Alexander and Gans, 1966
Uropeltidae	<i>Melanophidium wynaudense</i>	182				Alexander and Gans, 1966
Uropeltidae	<i>Uropeltis ocellatus</i>	209	205–213			Alexander and Gans, 1966
Uropeltidae	<i>Uropeltis pulneyensis</i>	179	176–182			Alexander and Gans, 1966
Anomalepididae	<i>Liotyphlops albirostris</i>	237	212–260			Dunn and Tihen, 1944
Anomalepididae	<i>Liotyphlops ternetzii</i>	253				Alexander and Gans, 1966
Typhlopidae	<i>Afrotyphlops lineolatus</i>	216		NJK A110-D1		
Typhlopidae	<i>Austrotyphlops bituberculatus</i>	274	232–315			Alexander and Gans, 1966
Typhlopidae	<i>Letheobia unitaeniata</i>	325	315–334			Alexander and Gans, 1966
Typhlopidae	<i>Megatyphlops schlegelii</i>	204	197–211			Alexander and Gans, 1966
Typhlopidae	<i>Ramphotyphlops braminus</i>	186	166–196			de Rochebrune, 1881
Typhlopidae	<i>Ramphotyphlops polygrammicus</i>	209	206–212			Alexander and Gans, 1966
Typhlopidae	<i>Typhlops arenarius</i>	207				Alexander and Gans, 1966
Typhlopidae	<i>Typhlops lumbricalis</i>	184	179–188			de Rochebrune, 1881
Typhlopidae	<i>Typhlops luzonensis</i>	218				Alexander and Gans, 1966
Typhlopidae	<i>Typhlops platycephalus</i>	233				Alexander and Gans, 1966
Typhlopidae	<i>Typhlops reticulatus</i>	152				Alexander and Gans, 1966
Typhlopidae	<i>Typhlops richardi</i>	217				Alexander and Gans, 1966
Typhlopidae	<i>Typhlops rostellatus</i>	193				Alexander and Gans, 1966
Typhlopidae	<i>Typhlops vermicularis</i>	205				Alexander and Gans, 1966
Leptotyphlopidae	<i>Epictia goudotii</i>	250				Alexander and Gans, 1966
Leptotyphlopidae	<i>Rena maxima</i>	219				Alexander and Gans, 1966
Leptotyphlopidae	<i>Leptotyphlops emini</i>	249				Alexander and Gans, 1966
Leptotyphlopidae	<i>Leptotyphlops nigricans</i>	184	141–227			de Rochebrune, 1881

Table A.2. Ecological data for the species included in Chapter 3.

Family	Species	Habitat	Constriction	References
Acrochordidae	<i>Acrochordus granulatus</i>	Aquatic	Yes	Lillywhite, 1996
Acrochordidae	<i>Acrochordus javanicus</i>	Aquatic	Yes	Dowling, 1960
Colubridae	<i>Ahaetulla prasina</i>	Arboreal	No	Lillywhite & Henderson, 1993
Colubridae	<i>Arizona elegans</i>	Terrestrial	Yes	Degenhardt et al., 1996
Colubridae	<i>Bogertophis subocularis</i>	Terrestrial	Yes	Sawyer and Baccus, 1996
Colubridae	<i>Boiga jaspidea</i>	Arboreal	Yes	Rodda et al., 1999
Colubridae	<i>Chionactis occipitalis</i>	Semi-fossorial	No	Norris and Kavanau, 1966; Glass, 1972
Colubridae	<i>Coelognathus helena</i>	Terrestrial	No	Mehta, 2003; Nitin et al., 2012
Colubridae	<i>Coluber constrictor stejnegerianus</i>	Terrestrial	No	Auffenberg, 1949
Colubridae	<i>Conopsis nasus</i>	Semi-fossorial	?	Taylor and Smith, 1942
Colubridae	<i>Crotaphopeltis hotamboeia</i>	Terrestrial	No	Luiselli et al., 2005
Colubridae	<i>Dasyplectis fasciatus</i>	Terrestrial	No	Luiselli et al., 2005
Colubridae	<i>Dasyplectis scabra scabra</i>	Terrestrial	No	Rabb and Snedigar, 1960
Colubridae	<i>Dendrelaphis caudolineatus</i>	Arboreal	?	Grismer et al., 2006b
Colubridae	<i>Dipsadoboa duchesnii</i>	Arboreal	?	Luiselli et al., 2005
Colubridae	<i>Dipsadoboa viridis</i>	Arboreal	?	Branch, 1993
Colubridae	<i>Dispholidus typus</i>	Arboreal	No	Luiselli et al., 2005
Colubridae	<i>Drymobius margaritiferus fistulosus</i>	Terrestrial	No	Henderson & Hoevers, 1977
Colubridae	<i>Hapsidophrys lineatus</i>	Arboreal	?	Luiselli et al., 2005
Colubridae	<i>Hapsidophrys smaragdina</i>	Arboreal	?	Chippaux, 2006
Colubridae	<i>Hierophis viridiflavus</i>	Terrestrial	No	Scali et al., 2008
Colubridae	<i>Lampropeltis alterna alterna</i>	Terrestrial	Yes	Conant and Collins, 1991
Colubridae	<i>Lampropeltis alterna blairi</i>	Terrestrial	Yes	Conant and Collins, 1991
Colubridae	<i>Lampropeltis getula goini</i>	Terrestrial	Yes	Conant and Collins, 1991; Steen et al., 2010
Colubridae	<i>Lampropeltis triangulum annulata</i>	Terrestrial	Yes	Conant and Collins, 1991
Colubridae	<i>Masticophis flagellum</i>	Terrestrial	No	Conant and Collins, 1991
Colubridae	<i>Oxybelis aeneus</i>	Arboreal	No	Campbell, 1999

Colubridae	<i>Oxybelis fulgidus</i>	Arboreal	No	Henderson & Hoevers, 1977
Colubridae	<i>Pantherophis alleghaniensis</i>	Terrestrial	Yes	Conant and Collins, 1991
Colubridae	<i>Pantherophis bairdi</i>	Terrestrial	Yes	Smith, 1938; Conant and Collins, 1991
Colubridae	<i>Pantherophis emoryi</i>	Terrestrial	Yes	Conant and Collins, 1991
Colubridae	<i>Pantherophis guttatus</i>	Terrestrial	Yes	Conant and Collins, 1991
Colubridae	<i>Pantherophis spiloides</i>	Arboreal	Yes	Conant and Collins, 1991
Colubridae	<i>Philothamnus irregularis</i>	Arboreal	?	Chippaux, 2006
Colubridae	<i>Philothamnus semivariatus</i>	Arboreal	Yes	Schmidt, 2002
Colubridae	<i>Phyllorhynchus browni</i>	Semi-fossorial	No	Gardner et al., 2003; Stebbins, 2003
Colubridae	<i>Pituophis melanoleucus melanoleucus</i>	Terrestrial	Yes	de Queiroz, 1984; Gerald et al., 2006
Colubridae	<i>Pituophis melanoleucus mugitus</i>	Terrestrial	Yes	Stebbins, 2003
Colubridae	<i>Pituophis ruthveni</i>	Terrestrial	Yes	Conant and Collins, 1991
Colubridae	<i>Ptyas mucosa</i>	Terrestrial	?	Nitin et al., 2012
Colubridae	<i>Rhinocheilus lecontei</i>	Terrestrial	Yes	Stebbins, 2003
Colubridae	<i>Salvadora grahamiae</i>	Terrestrial	?	Conant and Collins, 1991
Colubridae	<i>Senticolis triaspis intermedia</i>	Terrestrial	Yes	Stebbins, 2003; Radke and Malcom, 2009
Colubridae	<i>Sonora semiannulata</i>	Semi-fossorial	No	Stebbins, 2003
Colubridae	<i>Spalerosophis diadema</i>	Terrestrial	Yes	Marx et al., 1982
Colubridae	<i>Telescopus semiannulatus</i>	Terrestrial	?	Pitman, 1936
Colubridae	<i>Thelotornis kirtlandii</i>	Arboreal	No	Jayne, 1982; Luiselli et al., 2005
Colubridae	<i>Thrasops flavigularis</i>	Arboreal	No	Luiselli et al., 2005
Colubridae	<i>Thrasops jacksonii</i>	Arboreal	No	Chippaux, 2006
Colubridae	<i>Trimorphodon biscutatus</i>	Terrestrial	Yes	Greene and Burghardt, 1978
Colubridae	<i>Zamenis longissimus</i>	Arboreal	Yes	Naulleau, 1987
Colubridae	<i>Atractus clarki</i>	Semi-fossorial	No	Meyers, 2003
Colubridae	<i>Atractus darieniensis</i>	Semi-fossorial	No	Meyers, 2003
Colubridae	<i>Conitia longicauda</i>	Terrestrial	No	Feldman & Hoyer, 2010
Colubridae	<i>Diadophis punctatus regalis</i>	Terrestrial	?	Conant & Collins, 1991
Colubridae	<i>Dipsas sanctijoannis</i>	Arboreal	No	Harvey et al., 2008

Colubridae	<i>Erythrolamprus aesculapii</i>	Terrestrial	No	Sazima and Abe, 1991; Marques and Porto, 1994
Colubridae	<i>Geophis brachycephalus</i>	Semi-fossorial	No	Meyers, 2003
Colubridae	<i>Geophis hoffmanni</i>	Semi-fossorial	No	Meyers, 2003
Colubridae	<i>Heterodon nasicus kennealyi</i>	Terrestrial	No	Platt, 1969
Colubridae	<i>Hypsiglena chlorophaea</i>	Terrestrial	No	Tanner, 1944
Colubridae	<i>Hypsiglena jani</i>	Terrestrial	No	Tanner, 1944
Colubridae	<i>Hypsiglena ochrorhyncha</i>	Terrestrial	No	Tanner, 1944
Colubridae	<i>Hypsiglena slevini</i>	Terrestrial	No	Tanner, 1944
Colubridae	<i>Hypsiglena torquata</i>	Terrestrial	No	Tanner, 1944
Colubridae	<i>Imantodes cenchoa</i>	Arboreal	Yes	Meyers, 1982
Colubridae	<i>Imantodes gemmistratus</i>	Terrestrial	?	Meyers, 1982
Colubridae	<i>Imantodes inornatus</i>	Arboreal	?	Meyers, 1982
Colubridae	<i>Leptodeira annulata</i>	Terrestrial	?	Duellman, 1958
Colubridae	<i>Leptodeira maculata</i>	Terrestrial	?	Duellman, 1958
Colubridae	<i>Pseudoboa coronata</i>	Terrestrial	?	Alencar et al., 2013
Colubridae	<i>Tretanorhinus nigroluteus</i>	Semi-aquatic	No	Henderson & Hoevers, 1977
Colubridae	<i>Xenodon severus</i>	Terrestrial	?	Duellman, 1978
Colubridae	<i>Grayia ornata</i>	Semi-aquatic	?	Chippaux, 2006
Colubridae	<i>Grayia smithii</i>	Semi-aquatic	?	Luiselli et al., 2005
Colubridae	<i>Natrix maura</i>	Semi-aquatic	No	Patterson and Davies, 1982; Schätti, 1999
Colubridae	<i>Natrix natrix</i>	Terrestrial	No	Madsen, 1984
Colubridae	<i>Nerodia erythrogaster</i>	Semi-aquatic	No	Gibbon & Dorcas, 2004
Colubridae	<i>Nerodia fasciata</i>	Semi-aquatic	No	Gibbon & Dorcas, 2004
Colubridae	<i>Nerodia taxipilota</i>	Semi-aquatic	No	Gibbon & Dorcas, 2004
Colubridae	<i>Regina grahami</i>	Semi-aquatic	No	Gibbon and Dorcas, 2004
Colubridae	<i>Rhabdophis tigrinus</i>	Terrestrial	No	Das, 2010
Colubridae	<i>Seminatrix pygaea pygaea</i>	Semi-aquatic	No	Gibbon & Dorcas, 2004
Colubridae	<i>Storeria dekayi</i>	Terrestrial	No	Conant & Collins, 1991
Colubridae	<i>Storeria storerioides</i>	Terrestrial	No	Conant & Collins, 1991

					de Queiroz and Groen, 2001; Stebbins, 2003
Colubridae	<i>Thamnophis elegans elegans</i>	Terrestrial	Yes		
Colubridae	<i>Thamnophis marcianus</i>	Semi-aquatic	No		Stebbins, 2003
Colubridae	<i>Thamnophis ordinoides</i>	Terrestrial	No		Stebbins, 2003
Colubridae	<i>Thamnophis radix radix</i>	Terrestrial	No		Stebbins, 2003
Colubridae	<i>Thamnophis sirtalis</i>	Terrestrial	No		Stebbins, 2003
Elapidae	<i>Acalyptophis peronii</i>	Aquatic	No		Voris, 1975
Elapidae	<i>Acanthophis antarcticus</i>	Terrestrial	No		Cogger, 1988
Elapidae	<i>Aipysurus duboisii</i>	Aquatic	?		Voris, 1975
Elapidae	<i>Aipysurus fuscus</i>	Aquatic	?		Voris, 1975
Elapidae	<i>Aipysurus laevis</i>	Aquatic	Yes		Sine & Schwaner, 1985
Elapidae	<i>Astrotia stokesii</i>	Aquatic	?		Voris, 1975
Elapidae	<i>Bungarus candidus</i>	Terrestrial	?		Das, 2010
Elapidae	<i>Bungarus fasciatus</i>	Terrestrial	No		Smith, 1943
Elapidae	<i>Bungarus multicinctus</i>	Terrestrial	No		Das, 2010
Elapidae	<i>Chitulia lapemoides</i>	Aquatic	?		Smith, 1943
Elapidae	<i>Dendroaspis angusticeps</i>	Arboreal	No		Branch, 1998
Elapidae	<i>Dendroaspis viridis</i>	Arboreal	No		Branch, 1998
Elapidae	<i>Disteira kingii</i>	Aquatic	?		Voris, 1975
Elapidae	<i>Disteira major</i>	Aquatic	?		Voris, 1975
Elapidae	<i>Elapsoidea guentheri</i>	Semi-fossorial	?		Pitman, 1937b
Elapidae	<i>Emydocephalus ijimae</i>	Aquatic	No		Voris, 1975
Elapidae	<i>Hydrophis cyanocinctus</i>	Aquatic	No		Dunson and Minton, 1978
Elapidae	<i>Lapemis hardwicki</i>	Aquatic	No		Smith, 1943
Elapidae	<i>Laticauda laticaudata</i>	Aquatic	No		Smith, 1926
Elapidae	<i>Laticauda schistorhynchus</i>	Aquatic	No		Günther, 1874
Elapidae	<i>Leiodelasma elegans</i>	Aquatic	?		Gray, 1842
Elapidae	<i>Leiodelasma spiralis</i>	Aquatic	?		Smith, 1943
Elapidae	<i>Micrurus fulvius</i>	Semi-fossorial	No		Ernst and Barbour, 1989
Elapidae	<i>Micrurus tener</i>	Semi-fossorial	No		Ernst and Ernst, 2011
Elapidae	<i>Naja haje</i>	Terrestrial	No		Villiers, 1963

Elapidae	<i>Naja nigricollis</i>	Terrestrial	No	Luiselli et al., 2005
Elapidae	<i>Parahydrophis mertoni</i>	Aquatic	?	Voris, 1975
Elapidae	<i>Pelamis platura</i>	Aquatic	No	Smith, 1943
Elapidae	<i>Pseudonaja textilis</i>	Terrestrial	Yes	Shine and Schwaner, 1985
Homalopsidae	<i>Homalopsis buccata</i>	Aquatic	No	Mori, 1998; Das, 2010
Lamprophiidae	<i>Aparallactus capensis</i>	Semi-fossorial	No	Branch, 1993
Lamprophiidae	<i>Aparallactus modestus</i>	Semi-fossorial	?	Luiselli et al., 2005
Lamprophiidae	<i>Atractaspis bibroni</i>	Semi-fossorial	No	Kochva, 2002
Lamprophiidae	<i>Bufo depressiceps</i>	Terrestrial	?	Chippaux, 2006
Lamprophiidae	<i>Homonotus modestus</i>	Terrestrial	Yes	Villiers, 1963
Lamprophiidae	<i>Lamprophis fuliginosus mentalis</i>	Terrestrial	Yes	Luiselli et al., 2005
Lamprophiidae	<i>Lamprophis lineatus</i>	Terrestrial	Yes	Corkill, 1935; Villiers, 1963
Lamprophiidae	<i>Lamprophis olivaceus</i>	Terrestrial	Yes	Chippaux, 2006
Lamprophiidae	<i>Lamprophis virgatus</i>	Terrestrial	Yes	Luiselli et al., 2005
Lamprophiidae	<i>Lycophidion capense capense</i>	Terrestrial	Yes	Branch, 1993
Lamprophiidae	<i>Meheya poensis</i>	Terrestrial	?	Luiselli et al., 2005
Lamprophiidae	<i>Hemirhagerrhis nototaenia</i>	Terrestrial	?	Pitman, 1936
Lamprophiidae	<i>Malpolon monspessulanus</i>	Terrestrial	No	Steward, 1971
Lamprophiidae	<i>Psammophis biseriatus</i>	Arboreal	No	Pitman, 1937a
Lamprophiidae	<i>Psammophis schokari</i>	Terrestrial	No	Villiers, 1963
Lamprophiidae	<i>Psammophis tanganicus</i>	Arboreal	No	Branch, 1993
Lamprophiidae	<i>Psammophylax tritaeniatius</i>	Terrestrial	?	Pitman, 1937a
Lamprophiidae	<i>Psammophylax variabilis multiquamis</i>	Terrestrial	?	Pitman, 1937c
Lamprophiidae	<i>Rhamphiophis rostratus</i>	Semi-fossorial	Yes	Pitman, 1937a
Lamprophiidae	<i>Pseudaspis cana</i>	Terrestrial	Yes	Branch, 1993
Lamprophiidae	<i>Duberria lutrix abyssinica</i>	Terrestrial	No	Branch, 1993
Lamprophiidae	<i>Duberria lutrix lutrix</i>	Terrestrial	No	Branch, 1993
Lamprophiidae	<i>Leioheterodon madagascariensis</i>	Terrestrial	Yes	Mori and Randriamahazo, 2002; Cadle, 2003
Lamprophiidae	<i>Madagascarophis colubrinus</i>	Terrestrial	?	D'Cruze and Sabel, 2005

Pareatidae	<i>Pareas carinatus</i>	Arboreal	No	Das, 2010
Viperidae	<i>Agkistrodon bilineatus</i>	Terrestrial	No	Burchfield, 1982
Viperidae	<i>Agkistrodon piscivorus</i>	Semi-aquatic	No	Campbell & Lamar, 2004
Viperidae	<i>Bothrops lanceolatus</i>	Terrestrial	No	Gosner, 1987
Viperidae	<i>Crotalus basiliscus</i>	Terrestrial	No	Campbell & Lamar, 2004
Viperidae	<i>Crotalus durissus</i>	Terrestrial	No	Henderson & Hoevers, 1977
Viperidae	<i>Crotalus horridus</i>	Terrestrial	No	Ernst & Barbour, 1989
Viperidae	<i>Crotalus molossus</i>	Terrestrial	No	Stebbins, 2003
Viperidae	<i>Lachesis muta</i>	Terrestrial	No	Campbell & Lamar, 2004
Viperidae	<i>Popeia buniata</i>	Arboreal	No	Grismer et al., 2006
Viperidae	<i>Sistrurus miliarius</i>	Terrestrial	No	Ernst & Barbour, 1989
Viperidae	<i>Trimeresurus gramineus</i>	Arboreal	No	Nitin et al., 2012
Viperidae	<i>Vipera aspis</i>	Arboreal	No	Steward, 1971
Viperidae	<i>Vipera berus</i>	Terrestrial	No	Steward, 1971
Viperidae	<i>Atheris nitschei</i>	Arboreal	No	Pitman, 1938
Viperidae	<i>Bitis arietans</i>	Terrestrial	No	Pitman, 1938
Viperidae	<i>Bitis gabonica gabonica</i>	Terrestrial	No	Luiselli et al., 2005
Viperidae	<i>Bitis nasicornis</i>	Terrestrial	No	Luiselli et al., 2005
Viperidae	<i>Bitis peringueyi</i>	Semi-Fossorial	No	Robinson and Hughes, 1978
Viperidae	<i>Causus resimus</i>	Terrestrial	No	Spawls and Branch, 1995
Viperidae	<i>Causus rhombeatus</i>	Terrestrial	No	Pitman, 1937a
Viperidae	<i>Cerastes vipera</i>	Semi-fossorial	No	Young and Morain, 2003
Viperidae	<i>Daboia russelli</i>	Terrestrial	No	Das, 2010
Viperidae	<i>Echis pyramidum</i>	Terrestrial	No	Phelps, 2010
Boidae	<i>Boa constrictor</i>	Terrestrial	Yes	Pizzatto et al., 2007
Boidae	<i>Calabaria reinhardti</i>	Semi-fossorial	Yes	Luiselli et al., 2005
Boidae	<i>Candoia aspera</i>	Terrestrial	Yes	Pizzatto et al., 2007
Boidae	<i>Candoia bibroni</i>	Arboreal	Yes	Pizzatto et al., 2007
Boidae	<i>Charina bottae</i>	Semi-fossorial	Yes	Stebbins, 2003
Boidae	<i>Corallus annulatus</i>	Arboreal	Yes	O'Shea, 2007

Boidae	<i>Corallus caninus</i>	Arboreal	Yes	Pizzatto et al., 2007
Boidae	<i>Epicrates cenchria</i>	Terrestrial	Yes	Pizzatto et al., 2007
Boidae	<i>Eryx jaculus</i>	Semi-fossorial	Yes	Rieppel, 1978
Boidae	<i>Eryx jayakari</i>	Semi-fossorial	Yes	Rieppel, 1978
Boidae	<i>Eunectes murinus</i>	Semi-aquatic	Yes	Pope, 1961
Boidae	<i>Eunectes notaeus</i>	Semi-aquatic	Yes	Pizzatto et al., 2007
Boidae	<i>Gongylophis colubrinus</i>	Semi-fossorial	Yes	Pizzatto et al., 2007
Boidae	<i>Gongylophis conicus</i>	Semi-fossorial	Yes	O'Shea, 2007
Boidae	<i>Lichanura trivirgata</i>	Terrestrial	Yes	Stebbins, 2003
Boidae	<i>Sanzinia madagascariensis</i>	Arboreal	Yes	Pizzatto et al., 2007
Bolyeridae	<i>Casarea dussumieri</i>	Terrestrial	No	Bullock, 1986
Loxocemidae	<i>Loxocemus bicolor</i>	Semi-fossorial	Yes	Schmidt & Shannon, 1947; Alvarez del Toro, 1982
Pythonidae	<i>Antaresia childreui</i>	Terrestrial	Yes	Cogger, 1988
Pythonidae	<i>Antaresia maculosa</i>	Terrestrial	Yes	Pizzatto et al., 2007
Pythonidae	<i>Aspidites melanocephalus</i>	Terrestrial	Yes	Cogger, 1988
Pythonidae	<i>Aspidites ramsayi</i>	Terrestrial	Yes	Pizzatto et al., 2007
Pythonidae	<i>Bothrochilus boa</i>	Terrestrial	Yes	Pizzatto et al., 2007
Pythonidae	<i>Brogghammerus reticulatus saputrai</i>	Terrestrial	Yes	Das, 2010
Pythonidae	<i>Leiopython albertisii</i>	Terrestrial	Yes	Pizzatto et al., 2007
Pythonidae	<i>Liasis fuscus</i>	Terrestrial	Yes	Pizzatto et al., 2007
Pythonidae	<i>Morelia amethystina</i>	Terrestrial	Yes	Cogger, 1988
Pythonidae	<i>Morelia oenpelliensis</i>	Terrestrial	Yes	Gow, 1977
Pythonidae	<i>Morelia viridis</i>	Arboreal	Yes	Pizzatto et al., 2007
Pythonidae	<i>Python brongersmai</i>	Terrestrial	Yes	O'Shea, 2007
Pythonidae	<i>Python curtus</i>	Terrestrial	Yes	Groombridge and Luxmoore, 1991
Pythonidae	<i>Python molurus</i>	Terrestrial	Yes	Pope, 1961
Pythonidae	<i>Python regius</i>	Terrestrial	Yes	Luiselli et al., 1998
Pythonidae	<i>Python sebae</i>	Terrestrial	Yes	Luiselli et al., 2005
Xenopeltidae	<i>Xenopeltis unicolor</i>	Semi-fossorial	Yes	Smith, 1943

Aniliidae	<i>Anilius scytale</i>	Semi-fossorial	Yes	Martins and Oliveira, 1998; Marques and Sazima, 2008
Cylindrophhiidae	<i>Cylindrophis ruffus</i>	Semi-fossorial	Yes	Smith, 1943; Cundall, 1995
Tropidophiidae	<i>Trachyboa boulengeri</i>	Terrestrial	Yes	Dunn and Bailey, 1939
Tropidophiidae	<i>Tropidophis haetianus</i>	Terrestrial	Yes	Stull, 1928
Tropidophiidae	<i>Tropidophis melanurus</i>	Terrestrial	Yes	Stull, 1928
Uropeltidae	<i>Melanophidium wynaudense</i>	Fossorial	No	Smith, 1943
Uropeltidae	<i>Uropeltis ocellatus</i>	Fossorial	No	Smith, 1943
Uropeltidae	<i>Uropeltis pulneyensis</i>	Fossorial	No	Smith, 1943
Anomalepididae	<i>Liotyphlops albirostris</i>	Fossorial	No	Greene, 1997
Anomalepididae	<i>Liotyphlops ternetzii</i>	Fossorial	No	da Cunha and do Nascimento, 1975
Typhlopidae	<i>Afrottyphlops lineolatus</i>	Fossorial	No	Chirio, 2012
Typhlopidae	<i>Austrottyphlops bituberculatus</i>	Fossorial	No	Cogger, 1988
Typhlopidae	<i>Letheobia unitaeniata</i>	Fossorial	No	Spawls et al., 2006
Typhlopidae	<i>Megatyphlops schlegelii</i>	Fossorial	No	Kley, 2003
Typhlopidae	<i>Ramphotyphlops braminus</i>	Fossorial	No	Cogger, 1988
Typhlopidae	<i>Ramphotyphlops polygrammicus</i>	Fossorial	No	Cogger, 1988
Typhlopidae	<i>Typhlops arenarius</i>	Fossorial	No	Glaw and Vences, 1994
Typhlopidae	<i>Typhlops lumbricalis</i>	Fossorial	No	Barbour, 1910
Typhlopidae	<i>Typhlops luzonensis</i>	Fossorial	No	Ferner et al., 2000
Typhlopidae	<i>Typhlops platycephalus</i>	Fossorial	No	Rivero, 1998
Typhlopidae	<i>Typhlops reticulatus</i>	Fossorial	No	Greene, 1997
Typhlopidae	<i>Typhlops richardi</i>	Fossorial	No	Rivero, 1998
Typhlopidae	<i>Typhlops rostellatus</i>	Fossorial	No	Rivero, 1998
Typhlopidae	<i>Typhlops vermicularis</i>	Fossorial	No	Stewart, 1975
Leptotyphlopidae	<i>Epictia goudotii</i>	Fossorial	No	Savage, 2002
Leptotyphlopidae	<i>Rena maxima</i>	Fossorial	No	Greene, 1997
Leptotyphlopidae	<i>Leptotyphlops emini</i>	Fossorial	No	Pitman, 1935
Leptotyphlopidae	<i>Leptotyphlops nigricans</i>	Fossorial	No	Greene, 1997
Leptotyphlopidae	<i>Myriopholis blanfordi</i>	Fossorial	No	Smith, 1943