Herpetologica, 60(1), 2004, 62–74

MODULATED BUT CONSERVED SEGMENTAL GROWTH OF THE ORIGINAL TAIL IN *CALLISAURUS DRACONOIDES* (PHRYNOSOMATIDAE) AND *CALOTES VERSICOLOR* (AGAMIDAE)

Philip J. Bergmann[1], Amanda M. Hobbs,
Miranda L. Kavalench, and Anthony P. Russell[2]

*Vertebrate Morphology Research Group, Department of Biological Sciences, University of Calgary,
2500 University Dr. N.W., Calgary, Alberta, Canada T2N 1N4*

Abstract: Caudal growth is examined in the phrynosomatid *Callisaurus draconoides ventralis* and the agamid *Calotes versicolor*, both from a segmental point of view and from that of the entire tail. Growth of the entire tail relative to snout–vent length follows negative allometry in the former species and positive allometry in the latter. Despite this result, patterns of segmental growth are differential along the length of the tail in both species and follow a similar pattern in each. In both *C. d. ventralis* and *C. versicolor*, proximal caudal vertebrae grow with positive allometry, followed by an extensive transitional region of approximate isometry, and a distal region of highly negative allometry. The region of positive allometry is more pronounced in *C. versicolor*, resulting in overall positive allometry, whereas the negatively allometric region is highly pronounced in *C. d. ventralis*, resulting in negative allometry of the entire tail. Differential regional growth of the tail is similar to previous findings for the polychrotid *Anolis grahami*, suggesting limited influence of ecological and functional aspects such as caudal autotomy, bipedalism, and arboreality on segmental tail growth. Although rates of growth of the entire tail are highly variable in iguanian lizards, differential patterns of segmental tail growth appear to be conserved and are very similar among the three species.

Key words: *Callisaurus draconoides*; *Calotes versicolor*; Ecomorphology; Growth; Iguania; Morphometrics; Tail; Vertebrae

The Tail of lizards has been extensively studied in relation to functional properties such as autotomy (Baranowitz et al., 1977; Bellairs and Bryant, 1985; Bryant and Bellairs, 1967; Cox, 1969; Meyer et al., 2002), morphology (Barbadillo and Martínez-Solano, 2002; Etheridge, 1967; Mufti and Hafiz, 1972), and its role in locomotion (Arnold, 1994; Russell and Bauer, 1992; Zani, 1996). Studies of ecology and energetics (Dial and Fitzpatrick, 1984; Jaksic and Greene, 1984; Vitt et al., 1977) have also helped to elucidate much about the function of tails in lizards with different morphology and habitat. Growth of the regenerating tail has been documented and modeled (Baranowitz et al., 1977; Cox, 1969), and some studies have examined the absolute or relative growth of the original tail (Garland, 1985; Bates, 1989).

Recently, Bergmann and Russell (2001) explored segmental patterns of growth of the original tail of *Anolis grahami* by integrating data about the growth of individual vertebrae with the pattern of growth of the tail as a single structure. The hypotheses tested were (1) that the tail as a whole grows isometrically with reference to snout–vent length (SVL) and (2) that all vertebrae in the caudal series grow at the same relative rate and, therefore, in direct concordance with SVL. Although the first hypothesis was corroborated, the second was refuted. Bergmann and Russell (2001) uncovered a complex pattern in which the tail as a whole grows isometrically as a result of differential growth of regions of the tail. The proximal region of the tail (including the sacral vertebrae) grew positively allometrically, the intermediate region grew isometrically, and the distal zone grew negatively allometrically. This pattern of growth was hypothesized to be related to the potential imposition of different constraints upon the vertebrae along the caudal series. It was suggested that the proximal vertebrae are encroached upon by non-segmental muscles, the *m. caudofemoralis longus* in both sexes and the *m. retractor penis magnus* in males, involved in hindlimb movement and hemipenial retraction, respectively, and the distalmost vertebrae are the most likely to be lost in an autotomic event.

---

[1] Present Address: Department of Ecology and Evolutionary Biology, 310 Dinwiddie Hall, Tulane University, New Orleans, LA 70118, USA.

[2] Correspondence: e-mail, arussell@ucalgary.ca

The above conclusions led to the formulation of new hypotheses that require further testing. Bergmann and Russell (2001) postulated that examining growth patterns in non-autotomic tails and in tails in which there is much more extensive encroachment of the non-segmental muscles of the tail base (particularly the *m. caudofemoralis longus*) would help to elucidate relationships between differential regional growth of vertebrae and underlying correlative patterns. They also suggested that, in taxa with a more extensive *m. caudofemoralis longus*, the proximal, positively allometric region of the tail would extend further distally in concordance with the extent of that muscle and that in non-autotomic taxa the distal-most vertebrae would not demonstrate marked negative allometry in the growth pattern of these vertebrae because the vertebrae are not in danger of being lost.

Our study tests the above hypotheses in a comparative way by examining patterns of tail growth in two iguanian lizards, the phrynosomatid *Callisaurus draconoides ventralis* and the "agamid" (Frost et al., 2001) *Calotes versicolor*, that exhibit between them, along with the data from *A. grahami*, traits that might influence patterns of tail growth and regional compartmentalization (presence versus absence of caudal autotomy; terrestriality versus arboreality; bipedality versus quadrupedality).

Callisaurus draconoides and *C. versicolor* were chosen for our comparison for a number of reasons. First, as outlined above, the two species exhibit a number of similarities and differences between them that, when supplemented by data available for *A. grahami*, allow several questions to be explored simultaneously. Second, potential covergences between "agamid" and "iguanid" (sensu lato) lizards have often been noted (Cogger, 1994; Gans, 1977; Pianka and Parker, 1972). Third, an extensive series covering a broad range of body lengths was available for each species. Thus, there are interesting admixtures of form, function, and ecology between these species from the two major iguanian radiations that make for potentially informative comparisons.

Callisaurus d. ventralis, like *A. grahami*, possesses the ability to autotomize the tail (Arnold, 1994), with the frequency of autotomy increasing with age (Pianka and Parker, 1972). Unlike *A. grahami*, however, *C. draconoides* is terrestrial, occupying habitat with loose sandy soil (Pianka and Parker, 1972; Smith, 1946). As with *A. grahami*, *C. draconoides* displays pronounced sexual size dimorphism, with the males being the larger sex (Pianka and Parker, 1972). The largest adults of both sexes of *C. draconoides* are a little larger than those of *A. grahami* (Smith et al., 1987).

Callisaurus draconoides is a sit-and-wait predator (Vitt and Ohmart, 1977) that occupies open spaces (Pianka and Parker, 1972) and can attain high speeds, during which the lizard frequently assumes a bipedal posture (Irschick and Jayne, 1999). Bipedal locomotion occurs while running on flat surfaces and inclines (Irschick and Jayne, 1998*a*), and the angle at which the tail is held changes between quadrupedal and bipedal locomotion (Irschick and Jayne, 1998*a*), affecting changes in the location of the center of gravity with respect to the pelvic region (Snyder, 1962). Sprinting may occur over long distances (Zani, 1996) and is likely used in escape responses (Vitt, 1983).

Although bipedal during fast locomotion, the tail of *C. draconoides*, at 57% of total length, is relatively short for lizards that adopt this mode of locomotion (Irschick and Jayne, 1998*a*; Snyder, 1962). In fact, its tail is proportionately shorter than that of *A. grahami*, which accounts for approximately 64% of its total length. Irschick and Jayne (1998*a*) postulated that *C. draconoides* has evolved a relatively long tail (but still short for bipeds) from short-tailed ancestors that are more typical of Phrynosomatidae. Such an event might have implications for patterns of tail growth and regionalization in *C. draconoides*.

As for *A. grahami*, and in contrast to *C. draconoides*, *C. versicolor* is arboreal (Ji et al., 2002; Smith, 1935). During ontogeny, *Calotes* switches to an increasingly more arboreal habitat (Auffenberg and Rehman, 1993), a common trait for this genus (Subba Rao and Rajabai, 1972). Compared to the tail of *C. draconoides*, that of *C. versicolor* is exceptionally long, accounting for between 71% and 75% of the total length of the adult (Ji et al., 2002; Narayanaswamy Iyer, 1943). A relatively long tail is typical of members of the genus *Calotes* (Ota and Hikida, 1991) and of bipeds in general (Snyder, 1962). Bipedalism is practiced by *Calotes* (Manthey and Schuster, 1996; Snyder, 1952, 1962), although less frequently than by

C. draconoides. Running speed for *C. versicolor* has not been measured, but other species within the genus run considerably slower than the highest speed recorded for *C. draconoides* (Subba Rao and Rajabai, 1972) or for other iguanians running bipedally (Irschick and Jayne, 1999). Unlike *C. draconoides* and *A. grahami*, *C. versicolor* cannot autotomize its tail (Arnold, 1984*a*), a primitive state for the Acrodonta (Estes et al., 1988; Frost et al., 2001).

On the basis of our findings for *A. grahami* (Bergmann and Russell, 2001), we formulated the following hypotheses for testing for both *Callisaurus* and *Calotes*: (1) the tail as a whole grows isometrically relative to SVL; (2) a suite of proximal vertebrae, including the sacrals, exhibit positive allometry relative to SVL and to tail growth as a whole; (3) a sequence of intermediate vertebrae exhibit isometric growth relative to SVL and to tail growth as a whole; and (4) a series of distal vertebrae exhibit negative allometry relative to SVL and to tail growth as a whole.

METHODS

Data Collection

The specimens of each species were divided into males, females, and juveniles. For *C. d. ventralis*, males were identified by the presence of well defined, reddish femoral pores, and blue and black lateral stripes on the ventral surface (Smith, 1946). Females lack stripes, and have only barely visible black femoral pores. For *C. versicolor*, males were determined as individuals possessing enlarged spines of the nuchal crest and a swollen tail base (Radder et al., 2001; Smith, 1935). Females lack these enlarged spines and have a more slender tail base. For both species, juveniles were defined as individuals smaller than 55 mm SVL, below which the respective sexual differences were ambiguous. Pianka and Parker (1972) noted that juveniles of *C. draconoides* ranged up to 62 mm SVL, while Radder et al. (2001) defined juveniles of *C. versicolor* as being less than 55 mm SVL.

For each specimen, SVL and total tail length (TTL) were measured three times to the nearest 0.01 mm using Mitutoyo digital calipers; the mean of these measurements was used in statistical analyses. Specimens were then radiographed in a Hewlett-Packard Faxitron radiology unit (model 43805N) with Polaroid® Type 55 black and white positive/negative film. Specimens were placed ventral side down, directly in contact with the packaged film, yielding a 1:1 object to image ratio (Myers, 1998). Radiograph negatives were magnified on a Zeiss microfilm reader, and images were projected onto white paper such that boundaries between adjacent sacral and caudal vertebrae could be marked. These markings, along with a magnification scale, were scanned and imported into Image J (Rashband, 2001), which was calibrated using the "set scale" function. All sacral and caudal vertebrae were measured to the nearest 0.01 mm. In addition, the number of sacral and caudal vertebrae was recorded, as well as the number of the caudal vertebra bearing the first fracture plane in *C. d. ventralis*. Finally, the distalmost insertion of the non-segmental muscles, *m. caudofemoralis longus* and *m. retractor penis magnus* (in males), were dissected on four specimens of *Callisaurus* and six specimens of *Calotes*. These points were marked by using small entomological pins, and the specimens were re-radiographed (Bergmann and Russell, 2001; Blob, 1998), allowing determination of the number of caudal vertebrae bridged by each of these muscles.

Specimen Origin, Selection, and Data Collection

Ontogenetic series were assembled to obtain cross-sectional data from individuals covering the entire spectrum of post-natal development of both species. To minimize spatiotemporal variation, both series were chosen because they included only specimens from a small geographic area that were collected over a relatively short period of time (but see below; Bergmann and Russell, 2001).

An initial ontogenetic series of 63 specimens of *C. d. ventralis* was assembled from specimens borrowed from the Museum of Comparative Zoology (MCZ) at Harvard University (Cambridge, MA) and the Museum of Vertebrate Zoology (MVZ) at the University of California at Berkeley. All these specimens were collected from Organ Pipe Cactus National Monument and Pima County, Arizona. Unfortunately, date of collection could not be controlled as stringently as locality, because the specimens used were collected September

1931–September 1972. These specimens ranged from 31–78 mm SVL, a similar range to that examined by Maisano (2002) in a study of postnatal skeletal ontogeny of this species. Hatchling SVL for *Callisaurus* averages 30 mm, and SVL at sexual maturity averages 69 mm (Tanner and Krogh, 1975), and so the series used herein ranges from hatching to adult size. All specimens examined by us had two sacral vertebrae. The number of caudal vertebrae ranged from 35–40 (mean = 37).

For *C. versicolor*, a cross-sectional ontogenetic series consisting originally of 67 specimens was assembled from material borrowed from the Field Museum of Natural History (FMNH) (Chicago, Illinois). All these specimens were collected between February and November of 1969 from Amphoe Pak Thong Chai, Sakaerat Experimental Station (Nakhon Rachasima Province, Thailand). They ranged from 22–89 mm SVL. All specimens had two sacral vertebrae, and the number of caudal vertebrae ranged from 51–61 (mean = 55). A range in SVL of 25–136 mm (Radder et al., 2001) and a range of 40–52 caudal vertebrae with a mean of 50 (Narayanaswamy Iyer, 1943) in samples of *C. versicolor* from India indicate that there may be significant geographic variation in the upper limit of SVL and in caudal vertebral number in this widespread species. This is further justification for controlling cross-sectional ontogenetic series for spatiotemporal variation.

Principal component analysis (PCA) is appropriate for modeling multivariate growth, but is negatively affected by missing data (Pimentel, 1979). To employ PCA (see below), the data set for each species had to be standardized so that (1) all individuals contributed the same number of vertebrae, and (2) the number of specimens exceeded the number of variables (sacral plus caudal vertebrae) ($n > p$). Specimens for analysis were determined by excluding those specimens that had the fewest caudal vertebrae. Once condition (2) was met, vertebral measurements beyond the 36th caudal vertebra for *C. d. ventralis* and the 53rd for *C. versicolor* were eliminated to meet criterion (1). The final data set for *C. d. ventralis* consisted of 41 individuals with 38 vertebrae represented (2 sacrals and 36 caudals). Of these individuals, 7 were male, 18 female, and 16 juvenile (Appendix I). For *C. versicolor*, the final data set consisted of 59 individuals with 55 vertebrae represented (2 sacrals and 53 caudals). Of those individuals, 27 were male, 12 female, and 20 juvenile (Appendix I).

Statistical Methodology

Data were manipulated using Microsoft Excel XP©, and all statistical analyses were conducted with SYSTAT version 10 (Wilkinson, 2000). All data were $\log_{10}$-transformed prior to analysis to approximate normality and linearity. Log-transformation is of particular importance in studies of growth, because the procedure linearizes the exponential growth equation before linear methods are applied (Jolicoeur, 1963). Assumptions of all analyses (except PCA) were tested using the Kolmogorov-Smirnov test for normality of data or regression residuals, as appropriate, and the F-max test to determine whether data or residuals were homoscedastic.

Prior to analysis, the potential for sexual dimorphism had to be explored to determine whether or not data from both sexes could be pooled. Sexual dimorphism was evaluated in four ways. First, SVL and TTL were compared between sexes using *t*-tests (or Mann-Whitney *U* tests, if assumptions of *t*-tests were violated) to determine whether sexual size dimorphism occurred in the sample of each species. Second, residuals from geometric mean regression (GMR) of TTL on SVL (see below) were compared in the same way to evaluate relative sexual dimorphism (size removed) in TTL. Third, GMR slopes were calculated for males and females independently and then compared using the T_{12} statistic of Clarke (1980) to establish whether the tail as a whole grows at the same rate between sexes. Finally, factor scores from the PCA (see below) were compared between sexes using *t*-tests or Mann-Whitney *U* tests to evaluate differences in vertebral growth and proportion (Adams, 1998; Pimentel, 1979).

Scaling of the entire tail was modeled using GMR. Unlike least squares regression, GMR accounts for error associated with both variables being regressed (Gould, 1966; Ricker, 1984). This property, together with scale independence (Ricker, 1984), makes GMR most appropriate for use in morphometric studies. The GMR slope was tested for isometry using a *t*-test (Ricker, 1984).

Scaling of the vertebral segments was modeled using PCA, as applied previously by Bergmann and Russell (2001). Standard error of allometric loadings was calculated using SYSTAT (Wilkinson, 2000), following the methodology of Jackson (1991). Due to the continuous, linear, and single dimensional nature of the data, the covariance matrix was used to conduct the PCA (Pimentel, 1979). As variable loadings were of primary interest, the R-technique was used (Pimentel, 1979). In addition to measurements of sacral and caudal vertebrae, SVL was included in the PCA (contra Bergmann and Russell, 2001). This procedural modification maximized comparability of our results to those of studies that might not utilize PCA by allowing consideration of segmental tail growth relative to a number of different measures. Since traditional studies tend to relate tail growth to SVL (e.g., Bates, 1989) and the only study (Bergmann and Russell, 2001) on segmental tail growth related growth of caudal vertebrae to that of all vertebrae included in a PCA, there is an apparent gap between the two approaches. By including SVL in a PCA, vertebral growth rates can be indexed to SVL, allowing direct comparison of segmental growth rates to growth of the entire tail and to other studies that may not utilize PCA or examine segmental growth. This relationship is formalized by taking the quotient of allometric loadings of any two variables included in a PCA, which results in the GMR slope relating those two variables (Shea, 1985). Hence, PCA can be used to obtain a GMR slope for any caudal vertebra relative to SVL, allowing comparison of growth of vertebrae to growth of SVL, in addition to a generalized vector of isometry. The PC-1 was tested for isometry (comparison to $p^{-1/2}$ as the theoretical value of isometry) using Anderson's (1963) χ^2 statistic because it is generally interpreted as representing growth or variance associated with size (McKinney and McNamara, 1991; Mosimann, 1970; Pimentel, 1979; Shea, 1985).

The PCA assumes that the data are linear, randomly sampled, and follow a multivariate normal distribution (Pimentel, 1979). The $\log_{10}$-transformation helps to linearize and normalize the data, but these assumptions are not testable in a multivariate context, and the results of testing these assumptions on a bivariate basis cannot be expanded to a multivariate situation (Pimentel, 1979). All three assumptions are generally conservative and are usually met when dealing with $\log_{10}$-transformed data and a well selected sample (Pimentel, 1979).

Results

Analysis of Sexual Dimorphism

Sexual size dimorphism in body size (SVL) occurred in both *C. d. ventralis* (*t*-test: df = 23, $t = 2.285$, $P = 0.032$) and *C. versicolor* (*t*-test: df = 37, $t = 3.148$, $P = 0.003$), with males being larger in both species. These results accord with the findings of Pianka and Parker (1972) for *C. draconoides*, and the qualitative statements of Narayanaswamy Iyer (1943) for *C. versicolor* (but see Radder et al., 2001 for contrary findings). Sexual size dimorphism in tail length was not encountered in *C. d. ventralis* (*t*-test with separate variances: df = 7.1, $t = 1.355$, $P = 0.217$), but was evident in *C. versicolor* (*t*-test: df = 37, $t = 4.301$, $P = 0.000$). In the latter species, males had longer tails than females. Sexual size dimorphism in SVL and vertebral length was revealed when factor scores for PC-1 were compared in both species (*C. d. ventralis*: *t*-test with separate variances: df = 7, $t = 3.428$, $P = 0.011$; *C. versicolor*: *t*-test with separate variances: df = 18.9, $t = 3.898$, $P = 0.001$).

It was necessary to evaluate relative sexual dimorphism (size removed – GMR residuals) because of these differences. Relative sexual dimorphism was found to be absent between the sexes and juveniles for tail length in both *C. d. ventralis* (Kruskal-Wallis test: df = 2, KW = 1.033, $P = 0.596$) and *C. versicolor* (Kruskal-Wallis test: df = 2, KW = 2.760, $P = 0.252$). The GMR slopes for males and females did not differ significantly (*C. d. ventralis*: df = 8.642, $T_{12} = 0.299$, $P = 0.772$; *C. versicolor*: df = 14.272, $T_{12} = 0.488$, $P = 0.633$), indicating that the tail as a whole grows at the same rate relative to SVL for both sexes within each species. Finally, in a multivariate context, relative dimorphism was found to be absent from both species when factor scores for PC-2 were compared between the sexes and between juveniles (*C. d. ventralis*: Kruskal-Wallis test: df = 2, KW = 1.515, P = 0.469; *C. versicolor*: ANOVA: df = 55, F = 0.048, P = 0.953). Based on these findings, pooling of all cases in subsequent analyses was justified.

Scaling of the Entire Tail

With both sexes pooled, the GMR line for *C. d. ventralis* related SVL and TTL through the allometric equation (back-transformed): TTL = 1.300 $(\mathrm{SVL})^{0.978}$ (r^2 = 0.946, $\mathrm{SE}_{\mathrm{coefficient}}$ = 0.047, $\mathrm{SE}_{\mathrm{exponent}}$ = 0.027). The exponent is significantly different from 1 (df = 38, t = –27.924, P = 0.000), indicating that the entire tail of *C. d. ventralis* grows negatively allometrically in relation to SVL.

For *C. versicolor*, the following back-transformed equation described the relationship between SVL and TTL for both sexes: TTL = 2.082 $(\mathrm{SVL})^{1.074}$ (r^2 = 0.951, $\mathrm{SE}_{\mathrm{coefficient}}$ = 0.056, $\mathrm{SE}_{\mathrm{exponent}}$ = 0.031). As for *C. d. ventralis*, the exponent was significantly different from 1 (df = 56, t = 73.165, P = 0.000), but for *C. versicolor* it was greater than 1, indicating positive allometric growth of the entire tail relative to SVL.

Negative allometry of the tail in *Callisaurus* and positive allometry in *Calotes* were then compared to the situation revealed by the individual sacral and caudal vertebrae.

Scaling of the Caudal Vertebrae

The PC-1 is a general component (Pimentel, 1979) and is, therefore, interpreted as representing size-dependent variation, which in an ontogenetic series is a proxy for growth. The PC-2 is a bipolar component (Pimentel, 1979) and is interpreted as representing some size-independent source of variation that is independent of that explained by PC-1. The PC-1 explained the great majority of variance in vertebral lengths for both *C. d. ventralis* (88.4%; eigenvalue 0.547) and *C. versicolor* (84.5%; eigenvalue 0.830). The PC-2 explained much less of the variance: 6.54% (eigenvalue 0.041) for *C. d. ventralis*, and 12.1% (eigenvalue 0.119) for *C. versicolor*. The PC-3 was not interpreted because it accounted for only 1.03% and 1.19% of the variance in caudal vertebral lengths for *C. d. ventralis* and *C. versicolor*, respectively (eigenvalues of 0.006 and 0.012).

For *C. d. ventralis*, PC-1 was significantly different from the theoretical vector of isometry (df = 38, χ^2 = 1751, $P < 0.001$), indicating that the tail does not grow at the same rate along its entire length. Specifically, a proximal region consisting of the sacral vertebrae and the first six caudals demonstrates positive allometry (Fig. 1A). A middle region consisting of the next 21 vertebrae grows isometrically (Fig. 1A). The remaining nine caudal vertebrae at the distal end of the tail grow much slower, with negative allometry (Fig. 1A). When the growth rate of the SVL is compared to the theoretical value of isometry, it grows negatively allometrically (Fig. 1A), resulting in the growth rates of the sacrals and the first 26 caudals being relatively faster than that of SVL, while the remaining (distal) 10 caudal vertebrae grow relatively more slowly. This suggests that the marked negative allometry seen in the distal-most vertebrae is the major contributor to the overall slower growth rate of the tail relative to SVL, as documented by the results of GMR.

Patterns of segmental growth observed for *C. versicolor* were quite similar to those described above for *C. d. ventralis*. The PC-1 was significantly different from the theoretical isometric vector (df = 55, χ^2 = 3073, $P <$ 0.001). As for *C. d. ventralis*, the tail segregated into three regions, in addition to the two markedly negatively allometric sacral vertebrae: a proximal region of positive allometry (9 caudals), an isometric transitional region (28 vertebrae), and a distal negatively allometric region consisting of the remaining 16 vertebrae (Fig. 2A). Of these distal caudal vertebrae, the last three have disproportionately large standard errors and their actual growth rate is ambiguous. When the growth rate of SVL and the sacral vertebrae is considered relative to all of the segments of the tail, they grow markedly negatively allometrically (Fig. 2A). In turn, when vertebral growth is considered relative to SVL, the sacrals grow isometrically, while all caudal vertebrae, except 45–51, grow positively allometrically. Caudals 45–51 grow relatively more slowly than SVL. Clearly, there are differential patterns of growth of vertebrae along the length of the tail for both *C. d. ventralis* and *C. versicolor*, and these patterns are arranged into three distinct regions.

The variance explained by PC-2 was mainly localized in the distal 9 or 10 caudal vertebrae in *C. d. ventralis* and the distal 13 in *C. versicolor*. These loaded highly negatively on

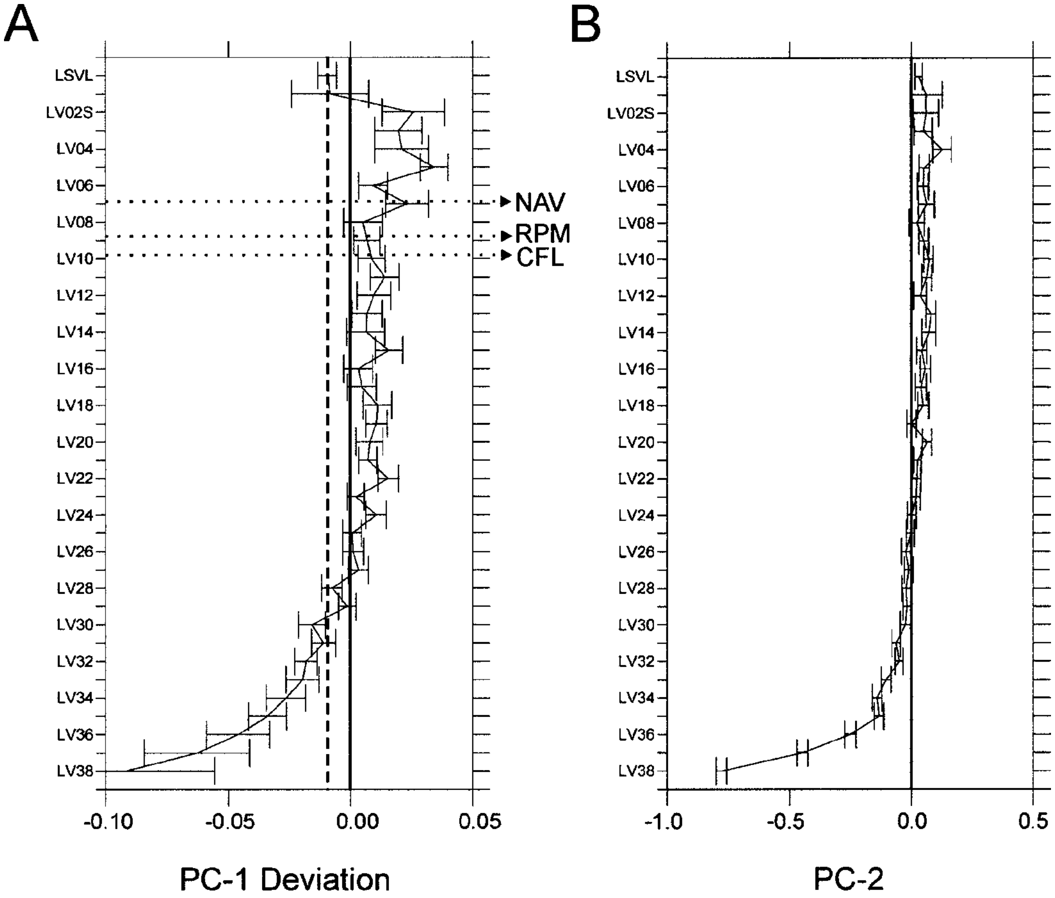

FIG. 1.—Results of principal component analysis (PCA) for *Callisaurus draconoides ventralis.* (A) The deviation of allometric loadings of PC-1 from the theoretical value of isometry ($p^{-1/2}$) for snout–vent length (SVL) and all sacral and caudal vertebrae. Solid vertical line denotes isometry relative to all vertebrae, while dashed vertical line denotes growth of SVL (isometry relative to SVL). Extent of non-autotomic vertebrae (NAV), the *m. caudofemoralis longus* (CFL), and the *m. retractor penis magnus* (RPM) are also marked. (B) Allometric loadings of PC-2 for SVL and all sacral and caudal vertebrae. Solid vertical line represents no loading. In both graphs, allometric loadings are shown for log-transformed SVL (LSVL), sacral vertebrae (LV##S), and caudal vertebrae (LV##). Only every other vertebra is labeled for clarity.

PC-2, whereas all the more proximal vertebrae (including sacrals and SVL) loaded very slightly positively on this component (Fig. 1B for *C. d. ventralis*, Fig. 2B for *C. versicolor*). Although the specific interpretation of the second component is difficult to ascertain, clearly it represents some phenomenon that is most pronounced distally and is increasingly more pronounced as one moves more and more distally along the caudal series.

The robustness of both PCAs with respect to the number of vertebrae included relative to the sample size was evaluated by pairing vertebral lengths and rerunning each PCA (Bergmann and Russell, 2001). This technique reduced the number of variables to fewer than half the sample size. Patterns for PC-1 and PC-2 were identical to those of the unpaired vertebral analyses, with the caveat of reduced resolution resulting from the pairing. These results attest to the robustness of the analyses presented above.

Arnold (1994) reported that *C. d. ventralis* has nine non-autotomic caudal vertebrae and that the *m. caudofemoralis longus* extends to the ninth caudal. Our sample of *C. d. ventralis* compares quite closely, with a mean of 7.04 (range 6–8, $n = 40$) non-autotomic caudal

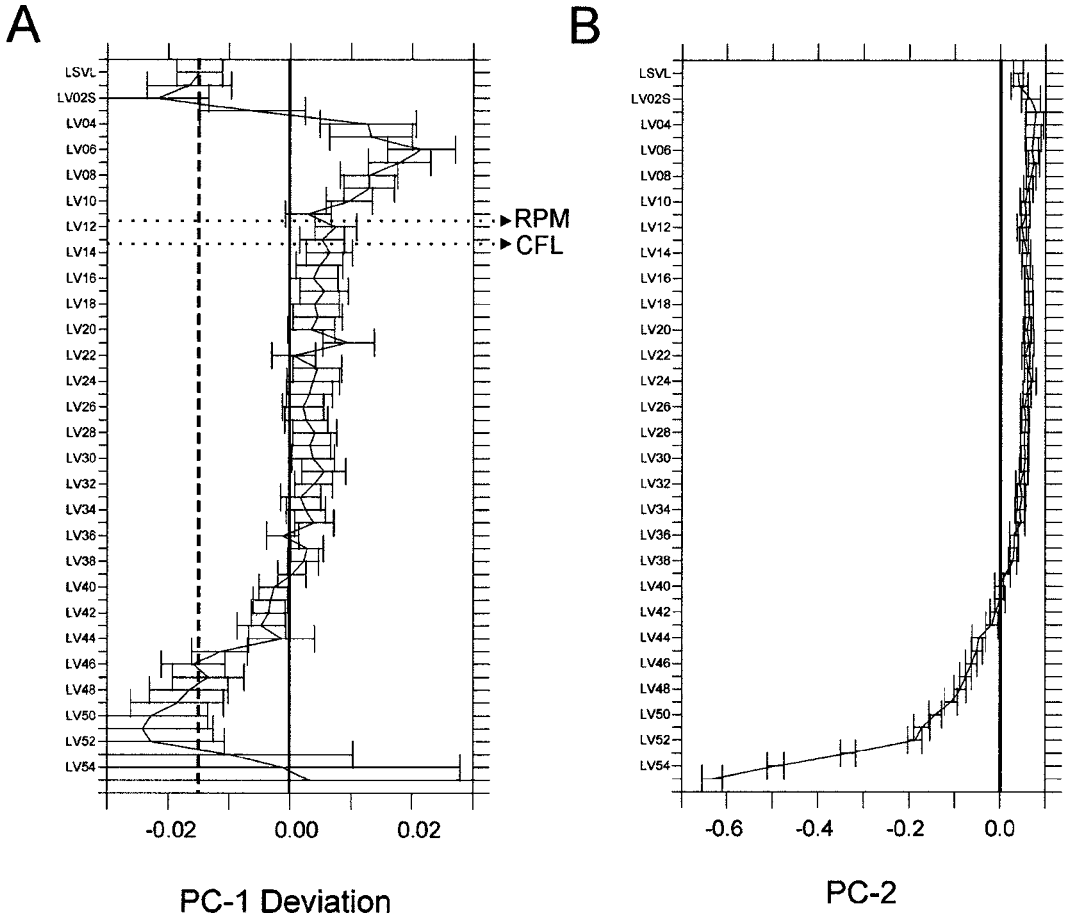

FIG. 2.—Results of principal component analysis (PCA) results for *Calotes versicolor*. (A) The deviation of allometric loadings of PC-1 from the theoretical value of isometry ($p^{-1/2}$) for snout–vent length (SVL) and all sacral and caudal vertebrae. Solid vertical line denotes isometry relative to all vertebrae, while dashed vertical line denotes growth of SVL (isometry relative to SVL). Extent of the *m. caudofemoralis longus* (CFL) and the *m. retractor penis magnus* (RPM) are also marked. (B) Allometric loadings of PC-2 for SVL and all sacral and caudal vertebrae. Solid vertical line represents no loading. In both graphs, allometric loadings are shown for log-transformed SVL (LSVL), sacral vertebrae (LV##S), and caudal vertebrae (LV##). Only every other vertebra is labeled for clarity.

vertebrae. The *m. caudofemoralis longus* and *m. retractor penis magnus* (in males) extend to caudal vertebrae 9.75 (range 9–11, n = 4) and 8.50 (range 8–9, n = 2), respectively. For *C. versicolor* from the Sakaerat Experimental Station, the *m. caudofemoralis longus* extends to the 13.40 caudal vertebra (range 13–14, n = 5). The *m. retractor penis magnus* (in males) extends to caudal vertebra 11.50 (range 11–12, n = 2).

DISCUSSION

Although rates of growth for the complete tail did not differ between the sexes and no relative sexual dimorphism was found for *C. d. ventralis* from Arizona, sexual size dimorphism was evident. Males were larger than females when SVL and caudal vertebrae were considered, which is consistent with the findings of Pianka and Parker (1972) for the same species. In contrast, *C. versicolor* from the Sakaerat Experimental Station, Thailand, displayed sexual size dimorphism not only in SVL (as intimated by Narayanaswamy Iyer, 1943), but also in tail length. Again, males were larger than females in both respects, as reported by other authors (Asana, 1931; Manthey and Schuster, 1996). Sexual size dimorphism was also evident from multivariate statistics when caudal vertebrae were considered. Despite this finding, tails of adult males and females were found to grow at the same rate relative to SVL, and there was no relative sexual dimorphism in tail length, in accord with the findings of Radder et al. (2001), but contrary to those of Ji et al. (2002). Males may simply be considered as hypermorphic females, justifying the pooling of the sexes for analysis. A similar situation (i.e., a lack of relative sexual dimorphism) was found for *A. grahami* (Bergmann and Russell, 2001), facilitating comparison of caudal growth for all three species. Functional comparability of the sexes is further justified, as even significant sexual differences in morphometric shape (= relative dimorphism, which is lacking in our ontogenetic series) need not translate into differences in locomotor performance (Garland, 1985).

Due to their habits (see Introduction), comparison of the two species examined here (*C. d. ventralis* and *C. versicolor*) and their further comparison to *A. grahami* (Bergmann and Russell, 2001) allows for the evaluation of certain functional and ecological correlates with respect to their bearing on tail growth. Since two of these three species are arboreal, two are bipedal, and two possess an autotomic tail, the relationship of these three features to tail growth may be examined. However, it must be noted that there are numerous differences between these three species in addition to their propensity toward autotomy, bipedality, and arboreality. As a result, relationships between growth patterns and these three convenient functional and ecological features can at best be correlative pending further study. Alternate explanations are possible for the patterns of growth observed herein.

From an assessment of these three species, as well as others from the literature, the growth rate of the complete original tail is not conserved among lizards. The tail of *C. d. ventralis* grows in a negatively allometric fashion relative to SVL. In contrast, the tails of *A. grahami* (Bergmann and Russell, 2001) and *Pachydactylus capensis capensis* (Bates, 1989) grow isometrically. The complete original tail of *C. versicolor* (this study) and of *Ctenophorus nuchalis* (Garland, 1985: tail growth relative to body mass) grow in a positively allometric fashion. Positive caudal allometry was also reported for *C. versicolor* from southern China (Ji et al., 2002).

The positive allometry of the tail in *C. versicolor* is not surprising when its cursorial and occasionally bipedal habits are considered in the context of the tail being an important counterbalance (Arnold, 1984*a*; Garland, 1985; Snyder, 1962, 1967). A greater degree of arboreality observed in adults of this species (Smith, 1935; Ji et al., 2002) further corresponds to positive allometry of the tail. A pattern of positive caudal allometry was predicted for bipedal lizards in general by Snyder (1962). However, it is more surprising that the tail of *C. d. ventralis* is not positively allometric, but is in fact negatively so. This species is highly cursorial and bipedal (Irschick and Jayne, 1998*b*), and a longer tail would be predicted to facilitate these habits by acting as a counterbalance (Daniels, 1983; Garland, 1985). For *C. d. ventralis*, however, phylogenetic inertia may well be in operation. This species is a member of Phrynosomatidae, a taxon noted for the possession of short tails (Irschick and Jayne, 1998*a*). Irschick and Jayne (1998*a*) posited that *C. draconoides* has possibly evolved a longer tail from within a clade of short-tailed ancestors (*Uma*, *Holbrookia*, *Cophosaurus*, and *Phrynosoma*). Such a clade was recovered by Reeder and Wiens (1996, their figure 3, node 2; their figure 5, node 2), although tail length was not included in the data matrix that resulted in these phylogenies. Testing of the concept of a short-tailed ancestry of *C. draconoides* must await the mapping of relative tail lengths onto such phylogenies.

The first hypothesis (1) investigated in this study, that the tail of *C. d. venralis* and *C. versicolor* would exhibit isometric growth relative to SVL, is refuted. Caudal growth rate clearly encompasses a broad range among lizards, which suggests that segmental or regional growth patterns may differ between species as well.

Such interspecific differences, however, are not supported, as the tail of both *C. d. ventralis* and *C. versicolor* can be divided into three distinct growth regions, much like that of *A. grahami* (Bergmann and Russell, 2001). Specifically, relative to the theoretical value of isometry ($p^{-1/2}$), a proximal region of positive allometry, a middle region of approximate isometry, and a distal region of negative allometry is identifiable in both species (Figs. 1A, 2A, respectively). Thus, hypotheses (2), (3), and (4) are corroborated. When segmental growth rates are considered relative to SVL, most of the tail of both species grows positively allometrically, while the distalmost nine (*C. d. ventralis*) and eight (*C. versicolor*) caudal vertebrae exhibit negative allometry (Figs. 1A, 2A). The SVL grows much more slowly relative to most caudal segments of *C. versicolor*, but only marginally more slowly in *C. d. ventralis*. This difference is instrumental in explaining whole tail growth patterns in light of the segmental growth rates. As most vertebrae in the tail of *C. versicolor* grow relatively much more quickly than SVL, it is these vertebrae that account for positive allometry of the entire tail relative to SVL. In *C. d. ventralis*, the tail as a whole grows more slowly than SVL because of the distal region, as the more proximal caudal vertebrae grow at a rate only marginally relatively faster than SVL.

A number of structures along the length of the tail has been hypothesized to influence segmental tail growth (Bergmann and Russell, 2001), including the fracture planes in the non-proximal vertebrae, the *m. caudofemoralis longus*, and the *m. retractor penis magnus* (in males), both of which are situated in the base of the tail. *Callisaurus d. ventralis* and *A. grahami* possess fracture planes that facilitate caudal autotomy (Bellairs and Bryant, 1985), but *C. versicolor* lacks these (Arnold, 1984*a*). The *m. caudofemoralis longus* is a major non-segmental muscle that, of the femoral retractor muscles of the caudal group, extends the farthest distally along the tail (Russell and Bauer, 1992). The distalmost point of origin of the *m. caudofemoralis longus* and the proximalmost occurrence of autotomy planes tends to be highly correlated, the former presumably influencing the expression of the latter (Russell and Bauer, 1992; Zani, 1996; but see Arnold, 1994). The *m. retractor penis magnus* is another non-segmental muscle that acts to retract the hemipenes in males and has a single origin on the caudal vertebrae (Arnold, 1984*b*).

In *C. d. ventralis*, autotomy planes begin on the sixth to eighth caudal vertebra, the *m. retractor penis magnus* extends to the eighth or ninth, and the *m. caudofemoralis longus* extends to the ninth to eleventh caudal. The region of positive allometry extends from the sacral vertebrae to the sixth caudal (Fig. 1A) and, hence, is composed of exclusively non-autotomic vertebrae and is completely enveloped by non-segmental muscles in the tail base. In *C. versicolor*, the *m. retractor penis magnus* extends to the eleventh or twelfth, and the *m. caudofemoralis longus* extends to the thirteenth or fourteenth caudal vertebra. The region of positive allometry extends from the first caudal vertebra to the ninth (Fig. 2A). In *A. grahami*, the region of positive allometry extended to only the fourth caudal, which was also not as distally extensive as the first fracture plane, or the distalmost point of origin of the non-segmental muscles (Bergmann and Russell, 2001). Since the region of positive allometry does not extend all the way to the first fracture plane in *C. d. ventralis* and *A. grahami*, or to the terminus of the non-segmental muscles in these two species or *C. versicolor*, we question a causal relationship between this growth region and these structures.

However, morphological differences typically exist between caudal vertebrae, and the transition from non-autotomic to autotomic vertebrae is usually abrupt and quite noticeable (Narayanaswamy Iyer, 1943), spanning only two or three vertebrae (Etheridge, 1967). Proximal non-autotomic caudals tend to be quite short and have markedly developed transverse processes (Etheridge, 1967, his figures 2 and 3; P. J. Bergmann, personal observation). This morphology correlates more closely in all species examined with the region of positive allometry. Also, a noticeable trend in vertebral length along the length of the tail exists: caudal vertebrae are relatively short proximally, lengthen along the length of the tail, and then shorten again distally. This morphological pattern, when superimposed on the hypothesized relationship between the region of positive allometry and vertebrae with greatly pronounced transverse processes, uncovers a provocative paradox: the caudal vertebrae that grow the fastest are also those that are relatively the shortest (with the exception of the terminal vertebrae).

The segmental caudal growth of three species of iguanians has now been compared to patterns of entire tail growth (Bergmann and Russell, 2001; this study). Among these taxa, *A. grahami* and *C. draconoides* are more closely related to one another than either is to the "agamid" *C. versicolor* (Frost and Etheridge, 1989; Frost et al., 2001). In addition, all three species have well documented differences in their habitat, locomotor patterns, and caudal autotomy. Although, to some degree, these functional and ecological differences appear to influence the overall pattern of original tail growth, this is not the case for segmental growth. Instead, patterns of segmental caudal growth appear conserved within these iguanians and may be evolutionarily constrained. However, the species studied to date are nevertheless quite distant phylogenetically, limiting the strength of a phylogenetic hypothesis. In this circumstance, a postulation of evolutionary constraint should be tested by examining caudal segmental growth patterns of other lizard species from within the Iguania and from among the scleroglossans.

The second principal component for *C. d. ventralis* and *C. versicolor* follows an almost identical pattern to that of PC-2 for *A. grahami* (Bergmann and Russell, 2001). Along most of the tail, the magnitude of the allometric loadings for this component is very small, but quickly becomes increasingly negative towards the distal end of the tail (Figs. 1B, 2B). While we assumed that the same phenomenon was shaping PC-2 loadings for all three species, that phenomenon is difficult to identify. However, the Pearson correlation coefficient for PC-2 allometric loadings and PC-1 standard errors for both *C. d. ventralis* and *C. versicolor*, are high ($r > 0.8$) and significant ($P < 0.05$). Although causality cannot be implied, the phenomenon behind PC-2 might not be biological in nature. Instead, this principal component may represent increased error at the distal end of the tail associated with our standardization of vertebral number in the data set.

A major increase in the standard error associated with PC-1 loadings occurs towards the distal end of the tail in both *C. d. ventralis* and *C. versicolor* (Figs. 1A, 2A). Caudal vertebral lengths decrease towards the end of the tail (from unpublished data), and so the increased error in this region may be due to the normalization of caudal vertebral number between specimens in the ontogenetic series (see Materials and Methods). Essentially, the shortest (distalmost) vertebrae are retained in the data set for some individuals, but have been discarded from the data set (and hence the analysis) for others with a more extensive series of caudal vertebrae. These findings call into question the assumption of iterative homology of caudal vertebrae, particularly the terminal ones (Bauer, 1998; Bergmann and Russell, 2001; Haszprunar, 1991; Roth, 1994). Fortunately, this seems to confound patterns of growth of only the most terminal caudal vertebrae retained for analysis.

The findings presented here for segmental original tail growth for *C. d. ventralis* and *C. versicolor* and those presented by Bergmann and Russell (2001) for *A. grahami* are largely congruent. Despite large differences in growth rates of the entire tails, which may reflect functional and ecological differences between species, segmental patterns are very similar for all iguanians examined so far. This conservatism of growth pattern suggests evolutionary constraint and, therefore, might be plesiomorphic for lizards in general.

Acknowledgments.—We thank the staff at the Museum of Comparative Zoology, the Museum of Vertebrate Zoology, and the Field Museum of Natural History for generously loaning the specimens for this study. Dr. M. J. Anguilletta, Jr. and three anonymous reviewers made suggestions that allowed improvement of the manuscript.

LITERATURE CITED

ADAMS, R. A. 1998. Evolutionary implications of developmental and functional integration in bat wings. Journal of Zoology (London) 246:165–174.

ANDERSON, T. W. 1963. Asymptotic theory for principal component analysis. Annals of Mathematics and Statistics 34:122–148.

ARNOLD, E. N. 1984*a*. Evolutionary aspects of tail shedding in lizards and their relatives. Journal of Natural History 18:127–169.

———. 1984*b*. Variation in the cloacal and hemipenial muscles of lizards and its bearing on their relationships. Symposia of the Zoological Society of London 52:47–85.

———. 1994. Investigating the evolutionary effects of one feature on another: does muscle spread suppress caudal autotomy in lizards? Journal of Zoology (London) 232:505–523.

ASANA, J. J. 1931. The natural history of *Calotes versicolor*, the common bloodsucker. Journal of the Bombay Natural History Society 34:1041–1047.

AUFFENBERG, W., AND H. REHMAN. 1993. Studies on Pakistan Reptiles, Part 3: *Calotes versicolor*. Asiatic Herpetological Research 5:14–30.

BARANOWITZ, S. A., S. N. SALTHE, AND P. F. A. MADERSON. 1977. The use of the Gompertz curve in an analysis of the dynamics of lizard tail regeneration. Journal of Theoretical Biology 65:267–279.

Barbadillo, L. J., and I. Martínez-Solano. 2002. Vertebral intercentra in Lacertidae: variation and phylogenetic implications. Copeia 2002:208–212.

Bates, M. F. 1989. Tail-break frequency, tail size and extent of caudal autotomy in the cape thick-toed gecko, *Pachydactylus capensis capensis* (Sauria: Gekkonidae). Navorsinge Van Die Nasionale Museum Blomfontein 6:223–242.

Bauer, A. M. 1998. Morphology of the adhesive tail tips of carphodactyline geckos (Reptilia: Diplodactylidae). Journal of Morphology 235:41–58.

Bellairs, A. d'A., and S. V. Bryant. 1985. Autotomy and regeneration in reptiles. Pp. 301–410. *In* C. Gans and F. Billet (Eds.), Biology of the Reptilia, Vol. 15, Development. B. John Wiley and Sons, New York, New York, U.S.A.

Bergmann, P. J., and A. P. Russell. 2001. Growth of the original tail in *Anolis grahami*: isometry of the whole is a product of regional differences. Journal of Herpetology 35:232–238.

Blob, R. W. 1998. Evaluation of vent position from lizard skeletons for estimation of snout–vent length and body mass. Copeia 1998:792–801.

Bryant, S. V., and A. d'A. Bellairs. 1967. Tail regeneration in the lizards *Anguis fragilis* and *Lacerta dugesii*. Zoological Journal of the Linnean Society 46:297–305.

Clarke, M. R. B. 1980. The reduced major axis of a bivariate sample. Biometrika 67:441–446.

Cogger, H. G. 1994. Reptiles and Amphibians of Australia, 5th ed. Comstock Cornell, Ithaca, New York, U.S.A.

Cox, P. G. 1969. Some aspects of tail regeneration in the lizard, *Anolis carolinensis*. I: A description based on histology and autoradiography. Journal of Experimental Biology 171:127–150.

Daniels, C. B. 1983. Running: an escape strategy enhanced by autotomy. Herpetologica 39:162–165.

Dial, B. E., and L. C. Fitzpatrick. 1984. Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria: Scincidae). Animal Behaviour 32:301–302.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata. Pp. 119–281. *In* R. Estes and G. Pregill (Eds.), Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp. Stanford University Press, Stanford, California, U.S.A.

Etheridge, R. 1967. Lizard caudal vertebrae. Copeia 1967:699–721.

Frost, D. R., and R. Etheridge. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). University of Kansas Museum of Natural History Miscellaneous Publication 81:1–65.

Frost, D. R., R. Etheridge, D. Janies, and T. A. Titus. 2001. Total evidence, sequence alignment, evolution of polychrotid lizards, and a reclassification of the Iguania (Squamata: Iguania). American Museum Novitates 3343:1–38.

Gans, C. 1977. Locomotor responses of *Calotes* to water (Agamidae: Sauria). Journal of the Bombay Natural History Society 74:361–363.

Garland, T., Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. Journal of Zoology Series A 207:425–440.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biological Reviews of the Cambridge Philosophical Society 41:587–640.

Haszprunar, G. 1991. The types of homology and their significance for evolutionary biology and phylogenetics. Journal of Evolutionary Biology 5:13–24.

Irschick, D. J., and B. C. Jayne. 1998*a*. Effects of incline on speed, acceleration, body posture and hindlimb kinematics in two species of lizard *Callisaurus draconoides* and *Uma scoparia*. Journal of Experimental Biology 201:273–287.

———. 1998*b*. A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides*. Physiological and Biochemical Zoology 72:44–56.

———. 1999. Comparative three-dimensional kinematics of the hindlimbs for high-speed bipedal and quadrupedal locomotion of lizards. Journal of Experimental Biology 202:1047–1065.

Jackson, J. E. 1991. A User's Guide to Principal Components. Wiley and Sons, New York, New York, U.S.A.

Jaksic, F. M., and H. W. Greene. 1984. Empirical evidence of non-correlation between tail loss frequency and predation intensity in lizards. Oikos 42:407–411.

Ji, X., Q.-B. Qui, and C. H. Diong. 2002. Sexual dimorphism and female reproductive characteristics in the oriental garden lizard, *Calotes versicolor*, from Hainan, southern China. Journal of Herpetology 36:1–8.

Jolicoeur, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology. Part I: Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

Maisano, J. A. 2002. Postnatal skeletal ontogeny in *Callisaurus draconoides* and *Uta stansburiana* (Iguania: Phrynosomatidae). Journal of Morphology 251:114–139.

Manthey, U., and N. Schuster. 1996. Agamid Lizards. TFH Publications, Neptune City, New Jersey, U.S.A.

McKinney, M. L., and K. J. McNamara. 1991. Heterochrony: the Evolution of Ontogeny. Plenum Press, New York, New York, U.S.A.

Meyer, V., M. R. Preest, and S. M. Lochetto. 2002. Physiology of original and regenerated lizard tails. Herpetologica 58:75–86.

Mosimann, J. E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. Journal of the American Statistical Association 65:930–945.

Mufti, S. A., and R. Hafiz. 1972. Comparative anatomy of the tail in an autotomizing and non-autotomizing lizard. Biologia, Lahore 18:191–199.

Myers, M. F. 1998. Morphometry of the Limb Skeleton of *Anolis garmani*: Practical and Theoretical Implications. M.S. Thesis, University of Calgary, Calgary, Alberta, Canada.

Narayanaswamy Iyer, M. M. 1943. The Habits, External Features and Skeletal System of *Calotes versicolor*. Part I. Half Yearly Journal of Mysore University, New Series, Section B 3:153–170 + 1 plate.

Ota, H., and T. Hikida. 1991. Taxonomic review of the lizards of the genus *Calotes* Cuvier 1817 (Agamidae

Squamata) from Sabah Malaysia. Tropical Zoology 4:179–192.

PIANKA, E. R., AND W. S. PARKER. 1972. Ecology of the iguanid lizard *Callisaurus draconoides*. Copeia 1972:493–508.

PIMENTEL, R. A. 1979. Morphometrics: the Multivariate Analysis of Biological Data. Kendall/Hunt Publishing Co., Dubuque, Iowa, U.S.A.

RADDER, R. S., B. A. SHANBHAG, AND S. K. SAIDAPUR. 2001. Ontogeny of sexual size dimorphism in the tropical garden lizard, *Calotes versicolor* (Daud.). Journal of Herpetology 35:156–160.

RASHBAND, W. 2001. Image J: Processing and Analysis in Java, Version 1.25. Research Sciences Branch, National Institute of Mental Health, Bethesda, Maryland, U.S.A. Available online: http://rsb.info.nih.gov/ij/

REEDER, T. W., AND J. J. WIENS. 1996. Evolution of the lizard family Phrynosomatidae as inferred from diverse types of data. Herpetological Monographs 10:43–84.

RICKER, W. E. 1984. Computation and uses of central trend lines. Canadian Journal of Zoology 62:1897–1905.

ROTH, V. L. 1994. Within and between organisms: Replicators, lineages and homologues. Pp. 301–337. *In* B. K. Hall (Ed.), Homology: the Hierarchical Basis of Modern Biology. Academic Press, San Diego, California, U.S.A.

RUSSELL, A. P., AND A. M. BAUER. 1992. The *m. caudifemoralis longus* and its relationship to caudal autotomy and locomotion in lizards (Reptilia: Sauria). Journal of Zoology (London) 227:127–143.

SHEA, B. T. 1985. Bivariate and multivariate growth allometry: statistical and biological considerations. Journal of Zoology (London) 206:367–390.

SMITH, D. D., P. A. MEDICA, AND S. R. SANBORN. 1987. Ecological comparison of sympatric populations of sand lizards (*Cophosaurus texanus* and *Callisaurus draconoides*). Great Basin Naturalist 47:175–185.

SMITH, H. M. 1946. Handbook of Lizards. Comstock Publishing Associates, Ithaca, New York, U.S.A.

SMITH, M. A. 1935. Fauna of British India, Including Ceylon and Burma, Vol. II. Sauria. Taylor and Francis Ltd., London, U.K.

SNYDER, R. C. 1952. Quadrupedal and bipedal locomotion of lizards. Copeia 1952:64–70.

———. 1962. Adaptations for bipedal locomotion of lizards. American Zoologist 2:191–203.

———. 1967. Adaptive values of bipedalism. American Journal of Physical Anthropology 2:131–134.

SUBBA RAO, M. V., AND B. S. RAJABAI. 1972. Ecological aspects of the agamid lizards *Sitana ponticeriana* and *Calotes nemoricola* in India. Herpetologica 28:285–289.

TANNER, W. W., AND J. E. KROGH. 1975. Ecology of the zebra-tailed lizard *Callisaurus draconoides* at the Nevada test site. Herpetologica 31:302–316.

VITT, L. J. 1983. Tail loss in lizards: the significance of foraging and predator escape modes. Herpetologica 39:151–162.

VITT, L. J., AND R. D. OHMART. 1977. Ecology and reproduction of Lower Colorado River lizards: I. *Callisaurus draconoides* (Iguanidae). Herpetologica 33:214–222.

VITT, L. J., J. D. CONGDON, AND N. A. DICKSON. 1977. Adaptive strategies and energetics of tail autotomy in lizards. Ecology 58:326–337.

WILKINSON, L. 2000. SYSTAT: The System for Statistics. SYSTAT Inc., Chicago, Illinois, U.S.A.

ZANI, P. A. 1996. Patterns of caudal-autotomy evolution in lizards. Journal of Zoology (London) 240:201–220.

Accepted: 11 April 2003
Associate Editor: Michael Angilletta, Jr.

APPENDIX I

Specimens constituting the final samples used in this study. Abbreviations follow Leviton et al. (1985).

Callisaurus draconoides ventralis: MCZ (R-Reptiles): 32101, 32103, 32105–07, 32110, 43977, 62339, 62594, 62598–601, 62604–06, 62610, 62614–19, 62621, 101123–26, 169002. MVZ: 20528, 181162–68, 181170–73.

Calotes versicolor: FMNH: 180496, 180498–500, 180502, 180504, 180509, 180511–12, 180515–16, 180519–20, 180523, 180527–29, 180531, 180533, 180535, 180537, 180539–43, 180545, 180547, 180550, 180552–60, 180562–64, 180566–67, 180572–73, 180579, 180582, 180584, 180586–90, 180593–95, 180597–99.