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Tail growth in *Chamaeleo dilepis* (Sauria: Chamaeleonidae): functional implications of segmental patterns

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Abstract

Patterns of growth of caudal vertebrae in the chameleon *Chamaeleo dilepis* were determined using principal component analysis, and compared to growth of the entire tail relative to snout–vent length. Despite significant positive allometry of the whole tail, growth rates of vertebrae differed along the length of the tail. Specifically, there was a proximal region that grew positively allometrically, and an extensive distal portion that grew with negative allometry. Intervening, was a short transitional region of approximate isometry. Positive allometry of the entire tail resulted from the extensive proximal region that grew in this manner. Although the region of positive allometry extended further caudad than the m. caudofemoralis longus, m. retractor penis magnus, and m. ischiocaudalis, its extent correlated more closely with the presence of neural spines (which are used as a proxy for the extent of the m. transversospinalis) and with tail coiling in this species. The positively allometric region housed the non-segmental musculature of the tail and did not bend, and the negatively allometric region identified the portion of the tail that was prehensile.

Key words: growth, morphometrics, tail, vertebrae, Chamaeleonidae, *Chamaeleo dilepis*

INTRODUCTION

Caudal autotomy in lizards has been the focus of many studies (reviewed by Bellairs & Bryant, 1985), with aspects of morphology (Bryant & Bellairs, 1967; Cox, 1969; Baranowitz, 1977; Salthe & Maderson, 1977; Russell & Bauer, 1992; Arnold, 1994) and ecology (Vitt, Congdon & Dickson, 1977; Arnold, 1984; Dial & Fitzpatrick, 1984; Jaksic & Greene, 1984; Zani, 1996) constituting the majority. Growth of the regenerating tail has also been explored (Cox, 1969; Baranowitz *et al*., 1977), but little attention has been paid to the growth of the intact original tail, although its morphology has been documented in a general way in various anatomical descriptions, and in a more specific way in more focused investigations (Etheridge, 1967; Mufti & Hafiz, 1972; Barbadillo & Martínez-Solano, 2002). Growth of the entire original tail has been addressed by some authors (Garland, 1985; Bates, 1989), but only recently (Bergmann & Russell, 2001) have patterns of growth within this segmentally arranged appendage been quantified.

Bergmann & Russell's (2001) study of *Anolis grahami* examined original tail growth by integrating data about segmental units comprising its skeletal axis and exploring how these units collectively relate to the linear growth of the entire tail. These data established a baseline from which to begin comparisons of growth patterns of tails with different functional attributes, where various selective pressures may have produced alternative patterns of overall growth.

In this contribution, the overall and intra-caudal patterns of growth in the chamaeleonid *Chamaeleo dilepis* were examined. Whereas caudal autotomy is plesiomorphic for lizards (Hoffstetter & Gasc, 1969; Arnold, 1984), non-autotomic tails represent a derived condition that has been independently attained on several occasions, including among the chameleons. The absence of autotomy means that the individual vertebrae of the tail are present in all individuals throughout life, contribute to its final form in all individuals, and are permanently involved in the functional roles of the tail. Chameleons are one of the most distinctive clades of lizards, characterized by a huge array of apomorphic features (Estes, de Queiroz & Gauthier, 1988; Frost *et al*., 2001). Among these, the prehensile tail is (along with a vertically compressed body, erect limb posture, enhanced limb, wrist and ankle mobility, and zygodactylous hands and feet) associated with moving on narrow perches (Peterson, 1984; Losos, Walton & Bennett, 1993). This peculiar locomotor mode is associated with obligatory slow progression that is directly related to the physiology, biochemistry, and fibre

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type distribution patterns of the locomotor muscles (Abu-Ghalyun *et al.*, 1988; Abu-Ghalyun, 1990). Such slow progression and associated deliberate acrobatic movements, allow chameleons to negotiate the highly spatially heterogeneous and physically discontinuous habitats that they typically occupy (Bickel & Losos, 2002).

In chameleons in general, the tail is not engaged during normal perch walking, but is used in the execution of acrobatic manoeuvres (Peterson, 1984: plate III), in balancing while straddling perches (Schneiper & Meier, 1989: 18–19, photographs; Martin & Woolfe, 1992: 35, illustration), and in stabilizing the body before ballistic tongue projection in food acquisition (Harkness, 1977: fig. 3). In prehensile activities the distal one-half or so of the tail grasps the surface (illustrations: Schneiper & Meier, 1989: 33 of *C. dilepis*; Martin & Woolfe, 1992: 72, 99), while in normal locomotion it is maintained in a loose or tightly wound coil (illustrations: Schneiper & Meier, 1989: 5, 8, 15, 29; Martin & Woolfe, 1992: pp. 6, 31, 43, 50, 69). Tail mobility is most extensive in the vertical plane (Zippel, Glor & Bertram, 1999), although a limited amount of lateral undulation occurs during steady horizontal locomotion (Peterson, 1984). The highly unusual form and function of the chameleon tail has resulted in its overall anatomy being investigated on several occasions (Mivart, 1870; Mufti and Hafiz, 1972; Renous, 1977; Zippel *et al.*, 1999). Dorsal, lateral and ventral muscle masses extend continuously along the tail from the sacral region to the distal tip, occupying the spaces between the neural spines and zygapophyses, zygapophyses and transverse processes, and transverse processes and ventral midline, respectively (Mivart, 1870). Other, deeper muscle masses occupy the ventral quadrants of the tail and extend back to occupy the first 12 postsacral vertebrae (Mivart, 1870).

These characteristics suggested to us that the patterns of growth observed in the regionally specialized, highly actively functional (Bauer & Russell, 1994) and non-autotomic tails of chameleons may be quite different from those observed in *A. grahami* (Bergmann & Russell, 2001). Although *A. grahami* and *C. dilepis* are both arboreal iguanians (*C. dilepis* was used as an arboreal exemplar by Peterson (1984), although Losos *et al.* (1993) and Bickel & Losos (2002) noted that it is not as exclusively arboreal as some other chameleon taxa), their caudal morphology and function is highly disparate, rendering comparison of patterns of caudal growth between the two species of particular interest. As was done in the previous study of *A. grahami* (Bergmann & Russell, 2001), two null hypotheses were tested regarding the growth of the original tail: (1) the tail as a whole grows isometrically relative to snout–vent length (SVL); (2) all caudal vertebrae grow at the same relative rate and in direct concordance with SVL. Furthermore, in the context of the findings for *A. grahami*, we sought to determine whether the pattern of (3) a positively allometric proximal region of the tail, (4) an extensive middle region of approximate isometry, and (5) a distal negatively allometric region, seen in that taxon are of more general occurrence. These latter possibilities (3–5) are entirely consistent with null hypothesis (1), but present an alternative to null hypothesis (2).

MATERIALS AND METHODS

Specimen origin, selection and data collection

An extensive ontogenetic series of 81 *C. dilepis* was borrowed from the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts. This series was selected because it allowed us to control for spatiotemporal variation by including only specimens from a small geographic area that were collected over a relatively short period of time. Such an approach minimizes the confounding of cross-sectional growth data with variation that may be attributable to time and space (Bergmann & Russell, 2001). All specimens used were collected by Arthur Loveridge in March 1930, and between September 1948 and February 1949, from 4 localities in Tanzania, and 3 localities in neighbouring Malawi.

The specimens were divided into 3 groups: males, females, and juveniles. Males were defined as individuals possessing tarsal spurs (Martin & Woolfe, 1992), hemipenal bulges, and/or having everted hemipenes. Females were determined by the absence of those characters, while juveniles were defined as individuals smaller than 60 mm SVL, below which features of males were not clearly expressed. SVL and total tail length (TTL) were measured 3 times for each specimen to the nearest 0.01 mm using Mitutoyo digital callipers, and the mean of those measurements used in statistical analysis.

Specimens were then radiographed in a Hewlett-Packard Faxitron model 43805N radiology unit on Polaroid® Type 55 black and white positive/negative film, being placed on their right side 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 projected at constant magnification 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, and all sacral and caudal vertebrae were measured to the nearest 0.01 mm. In addition, the number of sacral and caudal vertebrae was counted and recorded. Finally, the distalmost insertion of the non-segmental muscles, m. caudofemoralis longus, m. retractor penis magnus (in males), and m. ischiocaudalis (Mivart, 1870; Renous, 1977) were dissected on 8 specimens. These points were marked using small entomological pins and the specimens were re-radiographed (Blob, 1998; Bergmann & Russell, 2001), allowing determination of the number of caudal vertebrae bridged by each of these muscles (Fig. 1).

Specimens in the ontogenetic series ranged in size from 32 to 161 mm SVL. All specimens had 2 sacral vertebrae, but the number of caudal vertebrae ranged from 47 to 61 (mean = 54). To use principal component analysis (PCA, see below), the dataset had to be standardized so

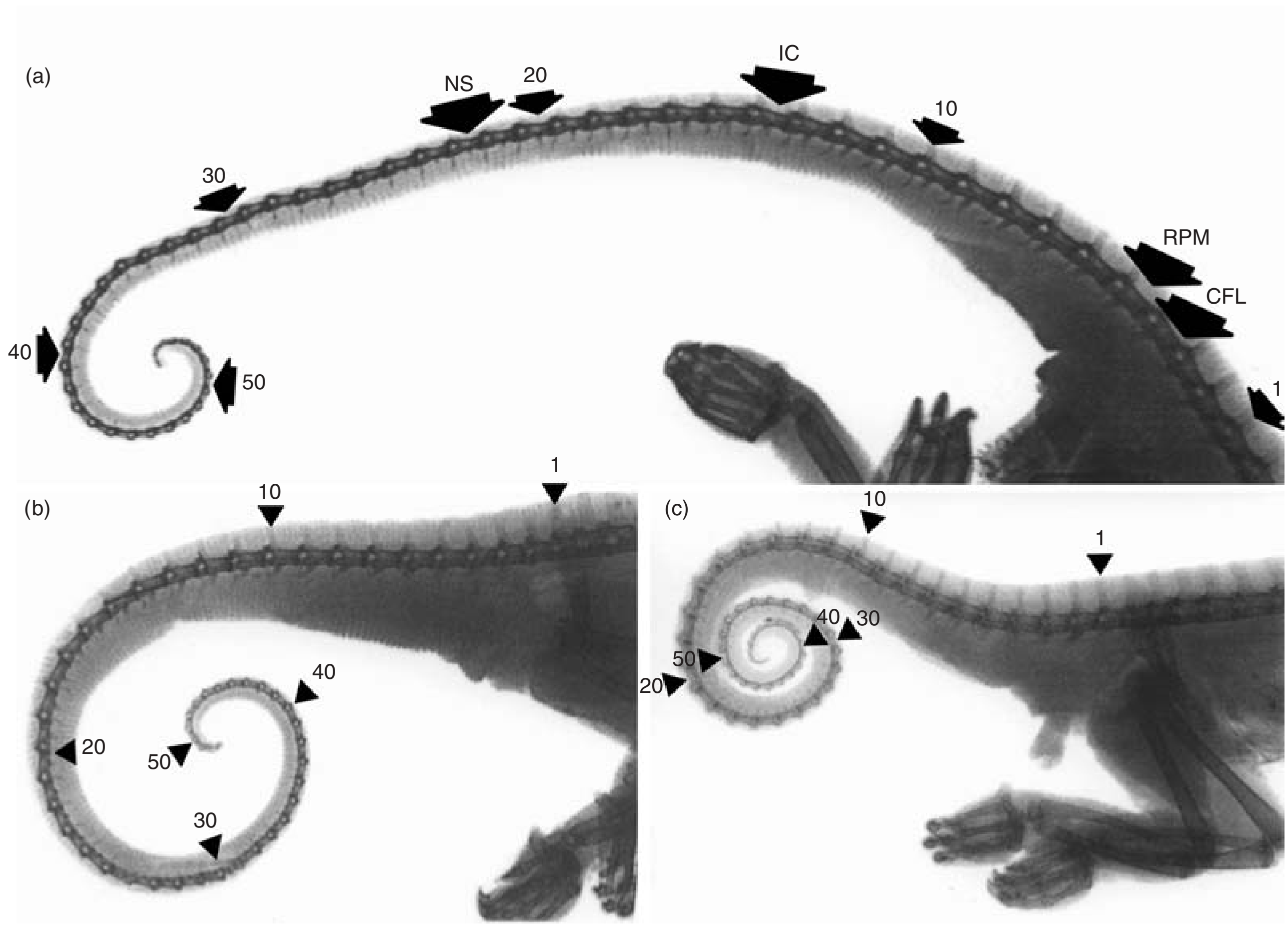

Fig. 1. Form and structure of the tail of *Chamaeleo dilepis*: (a) extended tail of MCZ-R-50611; large arrows, extent of the m. caudofemoralis longus (CFL), m. retractor penis magnus (RPM), m. ischiocaudalis (IC), and neural spines (NS), which are used as a proxy for the extent of the m. transversospinalis; (b) loosely coiled tail of MCZ-R-31099; (c) tightly coiled tail of MCZ-R-50608. Small arrowheads with numbers correspond to caudal vertebral number.

that: (1) all individuals contributed the same number of vertebrae to the dataset; (2) the number of specimens exceeded the number of variables (sacral plus caudal vertebrae) ($n > p$). Specimens for analysis (listed in Appendix) were arrived at by excluding those specimens that had fewer than the optimal number of vertebrae to maximize sample size. Once condition (2) was met, the distalmost vertebrae of individuals with more than the optimal number of vertebrae were eliminated in order to meet criterion (1). The final dataset consisted of 61 individuals with 54 vertebrae represented (2 sacrals and 52 caudals). Of these individuals, 26 were male, 26 female, and 9 juvenile.

Statistical methodology

The dataset was manipulated using Microsoft Excel XP (and all statistical analysis was conducted with SYSTAT version 10 (Wilkinson, 2000). All data were $\log_{10}$ transformed before analysis in order to approximate normality and linearity. Linearity is of particular importance because in studies of growth, the exponential growth equation must be log transformed before linear methods can be used to model it (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.

Before growth analysis, the potential for sexual dimorphism had to be explored to determine whether or not data from different sexes could be pooled into a single overall analysis. Sexual dimorphism was tested for in 4 ways. First, SVL and TTL were compared between sexes using t-tests (or Mann–Whitney U-tests, if assumptions of the t-tests were violated) to determine whether sexual size dimorphism occurred in the sample of *C. dilepis* used. 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. 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 in each sex. 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 (Pimentel, 1979; Adams, 1998).

Scaling of the entire tail was modelled using GMR. Unlike least-squares regression, GMR does not assume that the *x* variable (SVL, in this case) is measured without error (Gould, 1966; Ricker, 1984). This, 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 modelled using PCA, as applied previously by Bergmann & Russell (2001). Standard error of allometric loadings was calculated following the methodology of Jackson (1991) using SYSTAT. 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 sacral and caudal vertebral measurements, SVL was included in the PCA (*contra* Bergmann & Russell, 2001). This maximizes comparability of the analysis to studies that might not utilize PCA and indexes vertebral growth rates to SVL because geometric mean regression slopes relating 2 variables can be derived from principal component loadings of those variables, assuming that they are included in the PCA (Shea, 1985). This approach also allows comparison of vertebral growth rate to growth of SVL, in addition to a generalized vector of isometry. Since the first principal component (PC-1) is generally interpreted as representing growth or variance associated with size (Mosimann, 1970; Pimentel, 1979; Shea, 1985; McKinney & McNamara, 1991), this component was tested for isometry (comparison to p^{-2} as the theoretical value of isometry) using Anderson's (1963) χ^2 statistic.

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 3 assumptions are generally conservative and met when dealing with $\log_{10}$ transformed data and a well-selected sample (Pimentel, 1979).

RESULTS

Analysis of sexual dimorphism

Sexual size dimorphism in *C. dilepis* was not evident in either body size (SVL, *t*-test: d.f. = 50, $t = -1.577$, $P = 0.121$) or tail length (*t*-test: d.f. = 50, $t = -1.134$, $P = 0.262$). Sexual size dimorphism was also tested for in SVL and vertebral length measurements when factor scores for PC-1 were compared, and was also not apparent (*t*-test: d.f. = 50, $t = -0.976$, $P = 0.334$).

In addition to size differences between the sexes, it is prudent to evaluate relative sexual dimorphism (size removed) with residuals from the GMR. Relative differences between males, females and juveniles were not present for tail length (Kruskal–Wallis test: d.f. = 2, KW = 1.577, $P = 0.455$). GMR slopes for males and females were also found to be not significantly different (d.f. = 27.833, $t_{12} = 0.162$, $P = 0.873$), indicating that the tail as a whole grows at the same rate relative to SVL in both sexes. Finally, in a multivariate context, relative dimorphism was absent when factor scores for PC-2 were compared between the sexes and juveniles (Kruskal–Wallis test: d.f. = 2, KW = 3.555, $P = 0.169$). Based on these findings, pooling of all cases in subsequent analyses was justified.

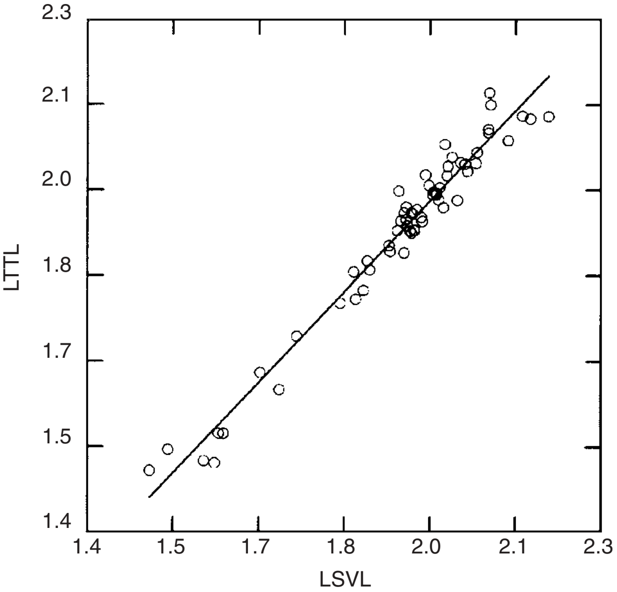

Fig. 2. Log_{10} transformed snout–vent length (LSVL) and total tail length (LTTL) data plotted for *Chamaeleo dilepis*, with the geometric mean regression line characterizing the relationship between the two measures.

Analysis of scaling of the tail and its segments

The GMR line for all cases pooled related SVL and TTL through the allometric equation (back-transformed): $\text{TTL} = 0.659\ (\text{SVL})^{1.081}$ ($r^2 = 0.961$, $\text{SE}_{\text{coefficient}} = 0.053$, $\text{SE}_{\text{exponent}} = 0.027$). The relationship of TTL and SVL, as well as the GMR line are shown in Fig. 2. The exponent is significantly different from 1 (d.f. = 59, $t = 105.497$, $P = 0.000$), indicating that the entire tail of *C. dilepis* grows positively allometrically relative to SVL. This situation was then compared to patterns revealed by the individual sacral and caudal vertebrae.

The first principal component (PC) is a general component (Pimentel, 1979) and is therefore interpreted as representing size-dependent variation, which in an ontogenetic series refers to growth. 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. PC-1 explained most of the variance (93.27%), while PC-2 explained much less

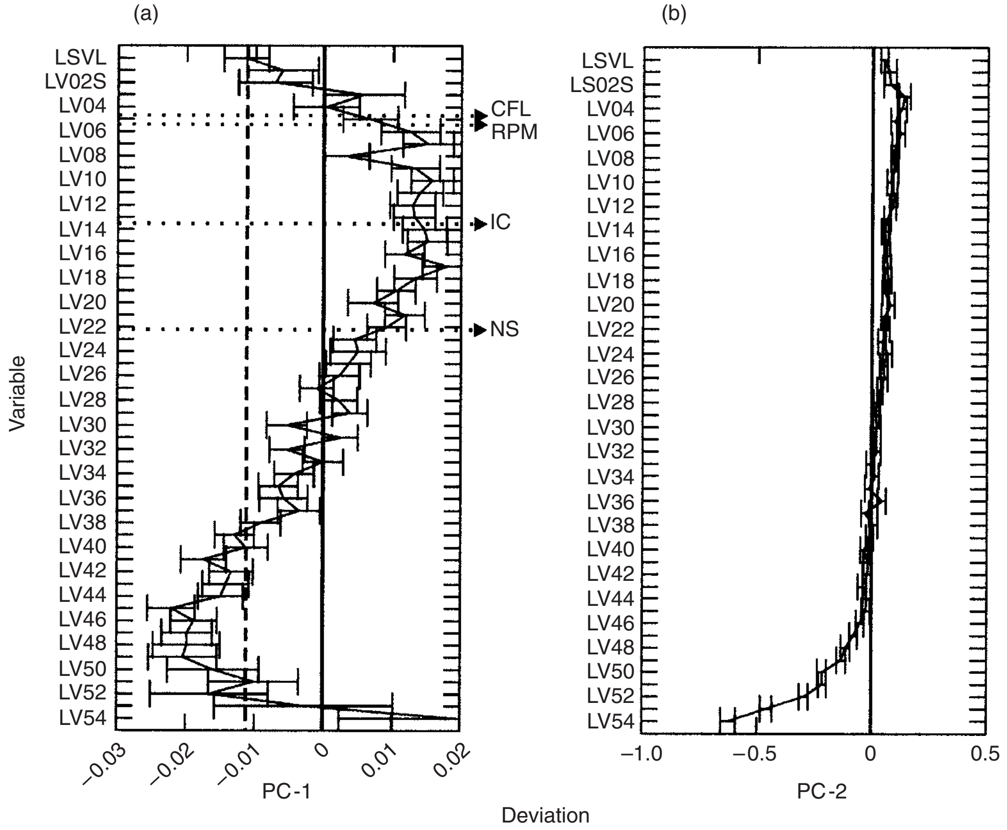

Fig. 3. Allometric loadings and their standard errors from principal component analysis of $\log_{10}$ transformed SVL, sacral vertebral lengths ('S' on the vertical axis), and caudal vertebral lengths of *Chamaeleo dilepis*. (a) Subtraction of the theoretical value of isometry from PC-1 loadings resulting in zero (solid line) representing isometry. Dashed line, growth value for SVL, allowing easy comparison of vertebral growth rates to that of SVL; dotted lines, posterior extent of non-segmental muscles and the neural spines: CFL, m. caudofemoralis longus; RPM, m. retractor penis magnus; IC, m. ischiocaudalis; NS, neural spines. (b) Allomteric loadings for PC-2. Solid line, loading of zero.

(3.63%) (eigenvalues 1.473 and 0.057, respectively). PC-3 was not considered further because it accounted for only 0.60% of the variance in caudal vertebral lengths (eigenvalue of 0.010).

PC-1 was significantly different from the theoretical vector of isometry (d.f. $= 54$, $\chi^2 = 2900$, $P \ll 0.001$), indicating that the tail does not grow at the same rate along its entire length. Specifically, when allometric loadings for this component are examined, a proximal region, consisting of the first 25–27 caudal vertebrae, demonstrates positive allometry (Fig. 3a). The remaining caudals grow much more slowly, displaying negative allometry (Fig. 3a). Of these, the posterior-most pair has a disproportionately large standard error and their growth rate is actually ambiguous. When the growth rate of SVL and the sacral vertebrae is considered relative to all other segments of the tail, all three of these variables reveal negative allometry. There are markedly different patterns of growth of vertebrae along the length of the tail of *C. dilepis*, arranged into two distinct regions.

The variance explained by PC-2 was mainly localized in the distal 11 caudal vertebrae. These loaded highly negatively on PC-2, while all of the more proximal vertebrae (including sacrals and SVL) loaded slightly positively on this component (Fig. 3b). Although the specific interpretation of the second component is difficult to ascertain, it is clear that it represents some effect that is most pronounced distally and increasingly more pronounced sequentially along this series.

In this sample of *C. dilepis*, the m. caudofemoralis longus extended, on average, to caudal vertebra 4.7 (range 4–6, $n = 8$). The m. retractor penis magnus (in males) extended to caudal vertebra 5.1 (range 5–6, $n = 8$). The m. ischiocaudalis extended much further, to a mean of caudal 13.6 (range 12–15, $n = 8$). This accords well with Mivart's (1870) recording of this muscle extending to caudal vertebra 12 in the one example he dissected. Pronounced neural spines are evident as far posteriorly as caudal vertebra 22.2 (mean) (range 21–24, $n = 8$) (Fig. 1).

DISCUSSION

This sample of *C. dilepis* from Malawi and Tanzania was not sexually size dimorphic, as evaluated through the examination of SVL, tail length and PC-1 factor scores. Relative sexual dimorphism, which may be considerably more confounding to pooling both sexes into a single analysis, was evaluated by analysis of GMR residuals for tail length on SVL, and of PC-2 factor scores. Sexual growth dimorphism was also examined by comparison of slopes from male only and female only GMRs. All males and females were comparable, which is unusual for chameleons in general (Martin & Woolfe, 1992), but clearly justifies combined analysis of the sexes in this ontogenetic series. By contrast, only sexual size dimorphism was evident in *A. grahami* (Bergmann & Russell, 2001). Bickel & Losos' (2002) broad overview of morphological variation and its correlates with habitat use in a sample of 56 species of chameleons, did not address potential sexual dimorphism as only two specimens of each species were included.

From a statistical standpoint, the magnitude of growth must be considered in a relative sense. Specifically, caudal growth can be considered in three ways from the analysis presented here. Growth of the entire tail may be considered relative to SVL, as is traditionally done (Garland, 1985; Bates, 1989; Bergmann & Russell, 2001). More rarely, using a multivariate approach, growth of the tail may be considered segmentally and relative to all of the segments of the tail (Bergmann & Russell, 2001). These approaches span a seemingly large gap that prevents their integration into a common approach – the references against which growth is measured differ (SVL *vs* all caudal vertebrae). If, however, caudal vertebral length is compared to SVL, then the segmental growth analysis (multivariate, PCA) is directly comparable to the non-segmental analysis (bivariate, GMR), and to other studies in which the tail is treated as a unitary structure. Fortunately, the quotient of the allometric loadings of two variables gives the GMR slope for the numerator relative to the denominator (Shea, 1985). Hence, the inclusion of SVL in the segmental growth model allows growth of a vertebra to be considered relative to either all variables included in the analysis (Pimentel, 1979), or to SVL. Indeed, growth of any variable can be considered relative to any other variable. The inclusion of SVL in the PCA greatly increases the general utility of this study.

The tail of *C. dilepis* grows faster than the body (SVL). Such positive allometry may simply be owing to the highly active functional nature of the chameleon tail (Vitt *et al*., 1977; Bauer & Russell, 1994), which is used extensively in arboreal locomotion because of its prehensility (see above) (Arnold, 1984; Peterson, 1984; Martin & Woolfe, 1992; Zippel *et al*., 1999). Positive caudal allometry has also been recorded for species that lack prehensility, such as *Ctenophorus nuchalis* (Garland, 1985 – but here tail growth was considered relative to body mass) and *Calotes versicolor* (Ji, Qui & Diong, 2002). The rate of caudal growth may be quite variable in lizards, as the tails of both *A. grahami* (Bergmann & Russell, 2001) and *Pachydactylus c. capensis* (Bates, 1989) have been shown to grow isometrically, rather than positively allometrically. Such findings are suggestive of variable segmental or regional growth patterns of the tail across a variety of species.

However, overall segmental patterns of tail growth in *C. dilepis* are quite similar to those seen in *A. grahami* (Bergmann & Russell, 2001). *Anolis grahami* displays a proximal region of positive allometry, an extensive middle region of approximate isometry, and a distal negatively allometric region, all relative to the theoretical value of isometry ($p^{-0.5}$; Bergmann & Russell, 2001). The situation in *C. dilepis* is essentially a modification of that pattern, in which the transitional middle isometric region is much reduced, from encompassing about three-quarters of vertebral segments in *A. grahami* (Bergmann & Russell, 2001) to less than one-quarter of them in *C. dilepis* (this study, Fig. 3a). When segmental growth rates are considered relative to SVL, the region of positive allometry in *C. dilepis* is greatly expanded and encompasses *c*. two-thirds of the caudal segments, the isometric region is virtually eliminated, and the region of negative allometry is much reduced (Fig. 3a). The standard error associated with the PC-1 allometric loadings of the terminal four vertebrae is much increased compared to the preceding segments, leading to uncertainty as to the actual growth rate of these vertebrae (Fig. 3a). When compared to SVL, the tail grows with pronounced positive allometry, both when considered as a whole and segmentally.

A number of structures along the length of the tail have been hypothesized to influence segmental tail growth (Bergmann & Russell, 2001). Since *C. dilepis* lacks autotomy planes, the potentially influential structures are limited to muscles. Both the m. caudofemoralis longus, and, in males, the m. retractor penis magnus, are situated in the base of the tail. The m. caudofemoralis longus is a major non-segmental locomotor muscle that extends the furthest distally along the tail of any muscles involved in femoral retraction (Russell & Bauer, 1992). However, owing to the slow locomotion exhibited by chameleons, the m. caudofemoralis longus is quite short (Mivart, 1870; Russell & Bauer, 1992), and perhaps of lesser influence on the tail than in other lizards in whom this muscle is more extensive. Owing to the highly derived nature of the locomotor anatomy and behaviour of chameleons, a few additional muscles are of interest. The m. transversospinalis and m. longissimus are epaxial caudal muscles that act to straighten the tail, while the m. ischiocaudalis and m. inferocaudalis are hypaxial muscles that act to curl it (Mivart, 1870; Zippel *et al*., 1999). The mm. caudofemoralis longus, retractor penis magnus, and ischiocaudalis were dissected, and since the m. transversospinalis has multiple origins and insertions on the neural spines (Gasc, 1981) and inserts at each vertebra at both the neural spine and the prezygapophyses (Zippel *et al*., 1999), observable neural spines as revealed on the radiographs were also counted (Fig. 1).

In most lizards the m. caudofemoralis longus, together with the m. retractor penis magnus, among the non-segmental muscles, extend the furthest distally along the tail (Russell & Bauer, 1992). In the ontogenetic series of *C. dilepis* studied here, the m. caudofemoralis longus extends only to the fourth to sixth caudal vertebra, as indicated by Mivart (1870), and the m. retractor penis magnus extends to the fifth or sixth. This accords closely with the situation seen in *C. chameleon*, where the m. caudofemoralis longus extends to the fifth or sixth caudal (Russell & Bauer, 1992), but does not correlate well with any of the growth regions identified here.

Owing to the highly specialized and non-autotomic nature of the chameleon tail (Zippel *et al*., 1999), other muscles, such as the ventral m. ischiocaudalis and the dorsal m. transversospinalis extend further along the tail (Mivart, 1870; Gasc, 1981) than they do in other lizards. In chameleons, these muscles are further candidates for exerting forces (Currey, 1984) and influencing the growth (Kardong, 1998) of the caudal vertebrae. The former muscle mass extends to the 12th–15th caudal in *C. dilepis*, and therefore extends only about halfway along the region of positive allometry (Fig. 3a). However, observable neural spines (Fig. 1), a proxy for the level of encroachment along the tail of the m. transversospinalis, continue to the 21st–24th caudals. This correlates much more closely with the posterior extent of the region of positive allometry (Fig. 3a), so the hypothesis that this region is influenced by the non-segmental muscles of the tail, remains tenable. The notion of such a relationship could only be rejected if the region of positive allometry extended *beyond* all of these muscles.

PC-2 almost exactly reprises the pattern of PC-2 for *A. grahami* (Bergmann & Russell, 2001). Along most of the tail the magnitude of allometric loadings for this component is very small, but quickly increases negatively towards the distal end of the tail (Fig. 3b). Under the assumption that the same phenomenon is influencing PC-2 loadings for both *C. dilepis* and *A. grahami*, it is difficult to identify what this might be. It is noteworthy, however, that the Pearson correlation coefficient for PC-2 allometric loadings and PC-1 standard errors for *C. dilepis*, is high ($r > 0.8$) and significant ($P < 0.05$). Although causality, of course, cannot be implied, it seems that the phenomenon behind PC-2 may not be biological, but may represent differential error associated with the normalization of vertebral number in the dataset.

There is a marked increase in the standard error associated with PC-1 loadings towards the distal end of the tail (Fig. 3a). Caudal vertebral lengths decrease towards the end of the tail (unpubl. data), and so the increased error in this region may be the result of the normalization of caudal vertebral number between specimens in the ontogenetic series (see Materials and Methods). Essentially, the shortest (distalmost) vertebrae are retained in some animals (those with 52 or only a few more caudal vertebrae), while they are discarded from analysis in others with more caudal vertebrae (those individuals approaching the maximum compliment of 61 vertebrae). These findings call into question the assumption of iterative homology of caudal vertebrae (Haszprunar, 1991; Roth, 1994; Bauer, 1998), at least in an operational sense, and variance in pattern will preferentially influence the terminal members of the series. Fortunately, this seems to only minimally confound interpretations of patterns of growth.

In assessing the hypotheses set out for testing, the tail of *C. dilepis*, as a whole, does not grow isometrically relative to SVL, but instead exhibits positive allometric growth (hypothesis 1). This contrasts with the acceptance of this null hypothesis for *A. grahami* (Bergmann & Russell, 2001) and means that integration of patterns of growth of individual vertebrae must produce a pattern of growth of the entire tail that is greater than the rate of growth of SVL. The positive allometry of the tail of *C. dilepis* does not result from combined patterns of individual vertebrae that all grow at the same relative rate (hypothesis 2). Indeed, as in *A. grahami* (Bergmann & Russell, 2001), vertebrae in different regions of the tail exhibit different rates of growth. In general, the predictions made by extrapolating from patterns of vertebral growth in *A. grahami* (Bergmann & Russell, 2001), that there will be a (hypothesis 3) positively allometric proximal zone, (hypothesis 4) an intermediate isometric region, and (hypothesis 5) a distal negatively allometric segment are borne out, albeit with notable modifications. The proximal positively allometric and distal negatively allometric zones in *C. dilepis* are extensive and the intermediate region is greatly truncated, with a rapid transition between the proximal and distal regions (Fig. 3a). The rapid transitional zone approximates the location of the transition between the tail base that is carried straight and the more distal region of the tail that is carried coiled (Fig. 1) while the lizard is in ambulatory progression, straightened when balancing, and curled around supports when undergoing slow acrobatic manoeuvres or stabilizing the body before tongue projection.

The rapid and increasing trend towards negative allometry in the distal portion of the tail can be correlated with the circinate coiling that the distal end of the tail undergoes, and the diminution in size of successive vertebrae permitting tighter and tighter curvature of the coils (Fig. 1c). This trend towards marked negative allometry at the distal end of the tail may have allowed this trait, which is expressed more mildly in *A. grahami* (Bergmann & Russell, 2001), to have become exapted in chameleons in association with tail tip prehensility. On the basis of outgroup comparison (i.e. *Rhampholeon*, Townsend & Larson, 2002), it seems that the distal region of the tail in *Brookesia* has become reduced, permitting the evolution of secondary non-prehensility. *Brookesia* represents a highly conservative clade within the Chamaeleonidae (Bickel & Losos, 2002; Townsend & Larson, 2002) and its members are predominantly terrestrial (Scheiper & Meier, 1989; Martin & Wolfe, 1992). We hypothesize that the absence of prehensility in the tail of *Brookesia* results from a further enhancement of the regional differentiation of relative growth seen in the tail of *C. dilepis*, with the distal, negatively allometric region undergoing significant reduction. The common name for this clade is the stump-tailed chameleons and the external morphology of the tail reveals a thick base and a very rapid and truncated taper to a short distal tip. Estes *et al*. (1988) noted major differences in caudal vertebral structure between *Brookesia* and other chameleons. Comparative observations on caudal vertebral counts and growth patterns will enable testing of the hypothesis that we have articulated.

Bickel & Losos (2002) noted that tail length differs among chameleons that occupy different habitat types (arboreal *vs* terrestrial) and predicted that relative tail length is related to locomotor behaviour when corrected for size. They found that arboreal and terrestrial chameleons differed in relative tail length when *Brookesia* and *Rhampholeon* were included in the dataset, but not when they were excluded. These data indicate that although our findings about patterns of tail growth and segmental growth within the tail may be typical for chameleons with prehensile tails, highly deviant taxa in terms of tail morphology, such as *Brookesia*, may have altered this pattern significantly, as hypothesized above.

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APPENDIX

Specimens constituting the final sample of *Chamaeleo dilepis* used in this study. All specimens from the Museum of Comparative Zoology Reptile collection. The catalogue numbers are: 31087, 31088, 31089, 31090, 31091, 31094, 31095, 31097, 31098, 31099, 31100, 31101, 31102, 31103, 31104, 31105, 31106, 31107, 31108, 31109, 31110, 31113, 31114, 31115, 31116, 31117, 31118, 31119, 31120, 31121, 31122, 31123, 31125, 31127, 31129, 31131, 31133, 31136, 31137, 31139, 50557, 50561, 50562, 50569, 50571, 50575, 50576, 50578, 50580, 50581, 50583, 50587, 50592, 50593, 50608, 50610, 50611, 50612, 50613, 50614, 50616.